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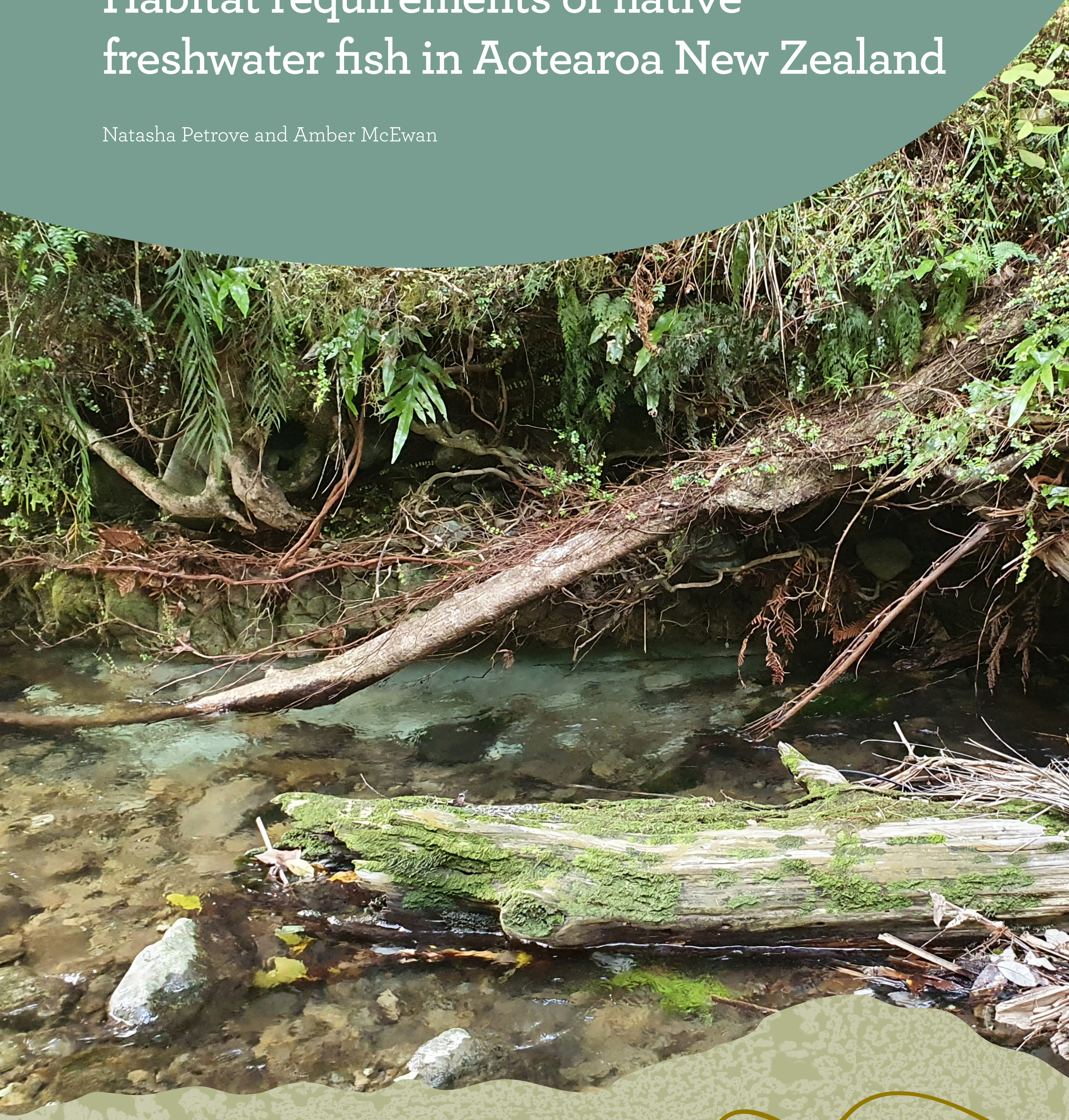
Habitat requirements of native freshwater fish in Aotearoa New Zealand

Natasha Petrove and Amber McEwan



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Cover: Stream habitat in Duncan Bay stream, Tennyson Inlet, Marlborough. *Photo: N. Petrove*

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Abstract

Native freshwater fish in Aotearoa New Zealand are found in waterbodies from the mountains to the sea. They have a wide range of habitat requirements, with some species occupying the same type of habitat throughout their entire life cycle and others living in different habitats at different life stages. The availability of habitat is an important driver of freshwater fish presence and abundance but can be affected by many common instream activities. This report collates information from scientific papers, technical reports, theses, peer-reviewed studies and personal observations to outline the known habitat requirements of 10 native freshwater fish species during their different life stages. These species include tuna / longfin eel (*Anguilla dieffenbachii*), panoko / torrentfish (*Cheimarrichthys fosteri*), giant kōkopu (*Galaxias argenteus*), kōaro (*Galaxias brevipinnis*), dwarf galaxias (*Galaxias divergens*), īnanga (*Galaxias maculatus*), shortjaw kōkopu (*Galaxias postvectis*), piharau / kanakana / lamprey (*Geotria australis*), bluegill bully (*Gobiomorphus hubbsi*) and redfin bully (*Gobiomorphus huttoni*), all of which are river-dwelling species that had a conservation status of Threatened or At Risk – Declining under the 2013 New Zealand Threat Classification System assessment. The review revealed that, in general, the habitat requirements of adult life stages have been best documented, with more limited information being available on larval and juvenile life stages, as well as habitat use during spawning. There are particular knowledge gaps for the larval stages of torrentfish and the galaxias and bully species; the juvenile stages of torrentfish, kōaro, lamprey and bullies; and the spawning habitats of torrentfish and dwarf galaxias, as well as kōaro in lakes.

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1. Introduction

Native freshwater fish in Aotearoa New Zealand are found in waterbodies from the mountains to the sea and have a wide range of habitat requirements. Some species occupy the same type of habitat throughout their entire life cycle, while others live in different habitats at different life stages.

The availability of suitable habitat is an important driver of freshwater fish presence and abundance. In many New Zealand waterways, freshwater fish habitat has been, and continues to be, degraded by common instream activities such as channelisation, drainage and flood control operations. Consequently, fish habitat is often limited or lacks variability and is unlikely to support diverse or abundant fish communities, even when other factors, such as water quality, remain suitable.

The main protection measures for freshwater fish and their habitats often focus on avoiding instream works during the peak migration times of juvenile fish and within īnanga spawning habitats during the spawning season. However, while these restrictions are important for avoiding effects during these critical times, there is an opportunity to better protect native fish by avoiding instream works in key habitats during the times they are most used, as well as enhancing these habitats for the fish communities that are present.

This literature review outlines the known habitat requirements of 10 river-dwelling native freshwater fish species in New Zealand (Table 1). The information has been collated to help those undertaking river management activities or restoration projects to recognise key habitat features for different fish species and life stages that should be maintained and enhanced.

A greater understanding of the habitat requirements of New Zealand's freshwater fish will enable individuals, community groups, agencies, contractors and local councils to better achieve restoration objectives and avoid damaging critical habitats.

Table 1. Freshwater fish species covered in this review.

SCIENTIFIC NAME	COMMON NAME	LIFE HISTORY
Anguilla dieffenbachii	Tuna / longfin eel	Migratory
Cheimarrichthys fosteri	Panoko / torrentfish	Migratory
Galaxias argenteus	Giant kōkopu	Migratory
Galaxias brevipinnis	Kōaro	Migratory
Galaxias divergens	Dwarf galaxias	Non-migratory
Galaxias maculatus	Īnanga	Migratory
Galaxias postvectis	Shortjaw kōkopu	Migratory
Geotria australis	Piharau / kanakana / lamprey	Migratory
Gobiomorphus hubbsi	Bluegill bully	Migratory
Gobiomorphus huttoni	Redfin bully	Migratory

1.1 Scope

This literature review focuses on the key habitat requirements of each of the 10 species during their different life stages. It includes information on the:

- Location of habitat (lowland, high altitude, etc.)
- Riparian characteristics
- Type of habitat (run, riffle, pool, etc.)
- Substrate type
- Instream cover

Other information relating to water quality, biotic interactions and food webs is not covered, except where this directly influences habitat use.

The 10 freshwater fish species covered by this review represent the river-dwelling species that had a conservation status of Threatened or At Risk – Declining under the 2013 New Zealand Threat Classification System assessment (Goodman et al. 2014).[1] Species that primarily inhabit lakes or wetlands and the South Island non-migratory *Galaxias* species (which generally have localised distributions) are not included.

For current distributional information on the species covered by this literature review, refer to NIWA's New Zealand Freshwater Fish Database.

1.2 Methods

This review drew on information that was published in scientific papers, technical reports, theses, peer-reviewed studies and websites from 1840 to 2021, as well as personal observations during the same period. Some sources contained discussion of mātauranga Māori (traditional knowledge) with respect to habitat use, and any terms relating to this have also been included in the habitat descriptions.[2]

Habitat requirements were identified for each freshwater life stage of each species, which generally correspond to the adult, spawning, larval and juvenile life stages. Marine life stages are only covered briefly in this review to provide context for the entire life history of each species.

The key timings for each life stage are provided as a guide. These were obtained from Smith (2014), unless noted otherwise in the relevant section. Note that the timing of habitat use may vary between regions and / or years. The timings provided for juvenile life stages of migratory species are for upstream migration from their larval rearing habitat. Juvenile fish are likely to be utilising habitat more widely than indicated by these timeframes as they mature.

[1] Note that the conservation statuses of freshwater fish were reassessed in 2017, which resulted in redfin bully being reclassified as Not Threatened (Dunn et al. 2018).

[2] The References section includes a list of sources that discuss mātauranga Māori, but we note that this is by no means an exhaustive list of mātauranga on freshwater fish habitat use and acknowledge that there will be much more information available, including mātauranga that may not be in written form.

1.3 Knowledge gaps

This review revealed that the habitat requirements of larval and juvenile life stages are the least documented for most species. In particular, there are knowledge gaps for the:

- Larval stages of torrentfish, giant kōkopu, kōaro, dwarf galaxias, īnanga, shortjaw kōkopu, bluegill bully and redfin bully
- Juvenile stages of torrentfish, kōaro, lamprey (macrophthalmia), bluegill bully and redfin bully

Information on spawning habitat is also limited for most species and tends to be based on only a few observations. There were no records of direct observations of the spawning habitats for torrentfish or dwarf galaxias, or for kōaro in lakes.

Furthermore, this review does not include local knowledge and Mātauranga Māori that might be held on habitats of the species in this review.

2. Tuna / longfin eel (*Anguilla dieffenbachii*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread throughout New Zealand

2.1 Adult stage (year round)

Longfin eels are found in a wide variety of macrohabitats,[3] including wetlands, springs, large rivers, small streams, and high-country and coastal lakes (McDowall 1990; Glova et al. 1998). They are also found in urban streams, especially where riparian vegetation is available (Collier et al. 2009), as well as farm drains and irrigation ditches (Greer et al. 2012). In addition, there is evidence to suggest that some longfin eels never enter fresh water and remain in marine or estuarine environments for their entire lives (Arai et al. 2003).

Longfin eels are exceptional climbers, allowing them to penetrate far inland and to high elevations. However, structures such as hydroelectric dams can be an impediment to their passage, preventing access to inland habitats (McDowall 1990).

Adult longfin eels, particularly larger individuals, tend to have limited home ranges (Chisnall & Kalish 1993). They generally rest under cover during the daytime but sometimes come out to feed (McDowall 1990). Common daytime resting habitats are deep, slow-flowing pools where instream cover is available (Hayes et al. 1989; McDowall 1990; Chisnall & Hicks 1993; Chisnall & Kalish 1993; Glova & Sagar 1994; Chadderton & Allibone 2000; Broad et al. 2002; Jowett & Richardson 2008; Jowett et al. 2009).

Adult longfin eels are also commonly found close to stream edges during the day (Beattie 1994; Glova et al. 1998; Broad et al. 2001), or ki tahaka as it is described in mātauranga Māori (Beattie 1994). They burrow into the stream banks (Polack 1840; Alexander 1863; Colenso 1869; Hamilton 1908; Del Mar 1924; Stack 1935; Hobbs 1948; Pullar 1957) – he rua-tuna in mātauranga Māori (Beattie 1994) – particularly in areas with emergent riparian vegetation such as harakeke / flax (*Phormium tenax*) or where large undercuts and tree roots are present (Hobbs 1948; Burnet 1952; Glova et al. 1998; Jellyman & Glova 1998; Jowett et al. 1998; Glova 1999).

At night, longfin eels move out of cover to feed in more diverse habitats, such as riffles (Chisnall & Kalish 1993; Broad et al. 2002; Jowett & Richardson 2008). However, smaller adults (< 535 mm) are often found in riffles during the day (Glova 1988; McDowall 1990) and pools at night, where they remain close to cover (Broad et al. 2002).

The instream cover used by longfin eels includes aquatic macrophytes (Hobbs 1948; Burnet 1952), submerged wood (Jellyman et al. 2003; Baillie et al. 2013), instream debris (Glova et al. 1998), deep turbid water (Hobbs 1948; Burnet 1952) and large boulders (Jellyman et al. 2003). Habitats that provide daytime cover are considered particularly important for larger individuals (Hobbs 1948; Burnet 1952; Jellyman et al. 2003).

Electrofishing surveys have found adult longfin eels in shallow water – for example, Jowett & Richardson (1995) reported that the optimum depth for longfin eels is < 0.1 m. However, it is likely that resting adult longfin eels prefer deep (> 1 m), slow-flowing water (Burnet 1952; Hayes et al. 1989; Jowett & Richardson 2008), which electrofishing generally fails to sample.

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[3] Where used, the habitat scale classifications applied in this literature review are as per the following example: longfin eels commonly occupy instream debris (microhabitat) in deep pools (mesohabitat) in streams and rivers (macrohabitat).

Longfin eels prefer water with higher concentrations of dissolved oxygen (Jellyman 1977, 1979a) and are less tolerant of low dissolved oxygen levels than shortfin eels (McDowall 1990). During winter, they can be found buried deep in beds of fine sediment (Broad et al. 2001), and during flood conditions, they use inundated stream margins and floodplains to exploit newly available terrestrial food sources (Jellyman 1989).

2.2 Spawning (downstream migration: March–May, with a peak during autumn floods)

During elevated flows, particularly in autumn rainstorms – or 'eel rain' in mātauranga Māori (Best 1925) – migratory longfin eels travel downstream and enter the sea to begin swimming north to their spawning grounds in the Pacific Ocean (McDowall 1990). These grounds are possibly located within the North Fiji Basin, between Vanuatu and Fiji (Jellyman & Bowen 2009).

2.3 Larval (leptocephalus) stage

Longfin eel larvae are pelagic and drift on ocean currents back to New Zealand (McDowall 1990) on a journey that takes around 10 months (Marui et al. 2001). They are present in the ocean throughout most of the year, although their exact location varies.

2.4 Glass eel stage (enter fresh water: July–November, with a peak in August–October)

Longfin glass eels enter estuaries and the lower reaches of rivers from the sea predominantly at night and often during high tides (Jellyman & Lambert 2003). They are attracted to odours that identify freshwater environments (McCleave & Jellyman 2002).

2.5 Juvenile (elver) stage (upstream migration: November–April, with a peak in December–March)

Longfin elvers are commonly found in swift-flowing riffle habitat (Davis et al. 1983; Hayes et al. 1989; McDowall 1990, 2011), where they occupy the spaces between substrate particles (Jellyman 1977). They prefer substrates of coarse gravel and rock (Jellyman 1977, 1979a) but have also been found inhabiting fine substrates (Jellyman et al. 2003). Bank cover (especially undercut banks) and instream debris are important for larger juveniles (Glova et al. 1998).

3. Panoko / torrentfish (*Cheimarrichthys fosteri*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread throughout much of the North and South islands

3.1 Adult stage (year round)

Torrentfish are usually found in rivers and streams with cobble / gravel substrates (McDowall 2000a) and little shading from riparian vegetation but high amounts of native vegetation in the catchment upstream (Leathwick et al. 2008). They are poor climbers and consequently are commonly found at low elevations and close to the coast. However, torrentfish have been recorded at high elevations (usually only short distances (< 100 km) inland in rivers with steep slopes) and at long distances inland (usually in low-gradient streams at lower (< 250 m) elevations) (McDowall 2000a).

Female torrentfish tend to disperse further upstream than males, so the upper reaches of catchments primarily contain females while the lower reaches have a higher abundance of males (Scrimgeour & Eldon 1989; Tana 2009). The females undertake a downstream migration to spawn in the lower reaches of rivers and streams (Warburton 2016).

Torrentfish show a strong preference for riffle / rapid habitats during the day (Best 1929; Mannering 1943; Glova 1988; McDowall 1990; Jowett et al. 2005; Jowett & Richardson 2008; Davey et al. 2011; Warburton 2016) but are found across a more diverse range of habitats at night (Glova et al. 1987; Davey et al. 2011). Within rapids, torrentfish inhabit the spaces between large substrate particles (Hayes et al. 1989; McDowall 1990; Jowett & Richardson 1995; Davey et al. 2011).

Despite this widely recognised preference for fast-water habitats (particularly the steeply sloping downstream ends of riffles and rapids; Davis et al. 1983), torrentfish have also been found in the relatively slow and deep mainstems of the Waipā and Waikato rivers in Waikato (David & Speirs 2010).

Torrentfish have been recorded at depths ranging from 0.1 to 0.35 m (Hayes et al. 1989; McDowall 1990; Jowett & Richardson 1995; Jowett et al. 1996; Davey et al. 2011) and velocities ranging from 0.3 to 1.5 m/s (Glova & Duncan 1985; Hayes et al. 1989; Jowett & Richardson 1995; Jowett et al. 1996, 1998; Davey et al. 2011).

3.2 Spawning (November–May, with a peak in January–April)

Female torrentfish migrate downstream to spawning sites near the sea (Warburton & Closs 2013; Warburton 2016).

Specific torrentfish spawning habitats have not yet been recorded, but torrentfish are thought to lay their eggs among gravel substrates (McDowall 1990) in riffles (Warburton & Closs 2013; Warburton 2016).

3.3 Larval stage (washed downstream: December–June, with a peak in February–May)

Following hatching, torrentfish larvae are washed downstream to the sea (Warburton 2016; Jarvis et al. 2018), where they spend several months (David & Speirs 2010; Warburton 2016) before migrating back into rivers as juveniles. In some situations, torrentfish may spend their larval rearing stage in estuarine environments (Tana 2009). Research by Warburton (2016) indicated that the larvae of this species do not disperse widely when they reach the sea.

3.4 Juvenile stage (upstream migration: March–November, with a peak in March–April)

Juvenile torrentfish occupy benthic habitats as they enter rivers and migrate upstream (McDowall 1994) and have been observed inhabiting the shallows of tidal pools and estuarine river margins (McDowall 2000a). Both male and female juveniles move upstream until they reach maturity; however, at maturity, the males begin to gradually migrate back downstream, while the females continue to move upstream (Warburton 2016).

4. Giant kōkopu (*Galaxias argenteus*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread in lowland areas throughout much of New Zealand

4.1 Adult stage (year round)

Giant kōkopu are found in a variety of macrohabitats, such as gently flowing boggy streams, swamps, lagoons and lakes, but always occur in places with a lot of instream cover (McDowall 1990; Bonnett 2000). They are often found in very small streams (Jowett et al. 1998; Bonnett 2000) but avoid agricultural channels and locations containing trout (David et al. 2002). In Southland and Westland, they have frequently been observed in small streams that are connected to extensive coastal lagoons, swamps and lakes (Bonnett et al. 2002). Giant kōkopu are usually found at low elevations (Baker & Smith 2007) and do not penetrate far inland (Bonnett & Sykes 2002), although some landlocked and higher elevation populations do exist (Bonnett et al. 2002).

Giant kōkopu prefer deep (> 0.5 m), slow-flowing or still water (Bonnett et al. 2002) and have been recorded in waters with velocities of < 0.1 m/s (Bonnett et al. 2002), < 0.15 m/s (Jowett & Richardson 2008) and 0–0.05 m/s at night (David & Closs 2003). During both the day and night, they are almost always observed in deep, open, slow-flowing pools (Bonnett et al. 2002; David 2003; Baker & Smith 2007) – these quiet reaches are referred to as wahi to marino in mātauranga Māori (McDowall 2011). However, they also occasionally use backwaters and runs (Chadderton & Allibone 2000; Baker & Smith 2007).

Giant kōkopu usually remain concealed among cover during the day (Anderson 1942; David & Closs 2003), and the presence of riparian and instream cover is widely recognised as being an important microhabitat requirement for them (Caskey 1997; Jowett et al. 1998; Chadderton & Allibone 2000; Bonnett et al. 2002; David 2002; Baker & Smith 2007). Debris dams and undercut banks are the preferred instream cover (Baker & Smith 2007), but other types of cover are also used, including submerged wood, small debris, and instream and overhanging vegetation (Caskey 1997; Jowett et al. 1998; Bonnett et al. 2002; David 2002; Baker & Smith 2007).

Channel complexity (i.e. the presence of a variety of mesohabitats in a localised area) is also important for giant kōkopu (Bonnett & Sykes 2002; Whitehead et al. 2002; David & Closs 2003), as the adults (particularly smaller, subdominant individuals) have different feeding and resting habitats within their home ranges (Bonnett et al. 2002; David & Stoffels 2003). Larger giant kōkopu tend to be nocturnal and occupy small territories, often in deep, slow-flowing pools, where they do most of their resting and feeding. Smaller individuals are more typically found in shallow, backwater habitats next to areas with high water velocities, travel further for food at night, including to riffle areas, and often forage during the day (David et al. 2002; Whitehead et al. 2002; Hansen & Closs 2005).

In dense populations, giant kōkopu form dominance hierarchies (David & Stoffels 2003). When the food supply is limited, larger individuals spend more time in prime feeding positions in pools and become more aggressive towards subdominant fish, pushing them to spend more time in marginal habitat (Hansen & Closs 2005).

Seasonal variation in habitat use has also been recorded for this species (David & Closs 2003). During winter, giant kōkopu occupy habitats with low velocities, silt substrates and intermediate depths, while in summer they are found in waters with higher flows (up to 0.17 m/s), shallower depths and coarser substrates. They are strictly nocturnal during winter but sometimes use open habitats during the day in summer (David & Closs 2003).

David & Closs (2002) observed giant kōkopu leaving existing territories during floods and then residing in new locations and speculated that some fish may actively use elevated flows to emigrate from small streams.

When resident in lakes, adult giant kōkopu tend to occupy the lake margins (McDowall 1990) and are more commonly observed around vegetated shores than open shores (anecdote reported in Bonnett 2000).

4.2 Spawning (April–August)

Giant kōkopu spawn alongside adult habitat (Reeve et al. 2014). Giant kōkopu spawning sites were first recorded in Bankwood Stream, Hamilton, where the eggs had been laid on low-gradient (< 10°) stream banks among inundated streamside marginal vegetation and leaf litter during elevated flows (Franklin et al. 2015). Giant kōkopu eggs develop out of water and take around 25 days to mature, hatching when they are re-inundated during future high flows (Franklin et al. 2015). It was noted that the Hamilton population experienced spawning failure due to low rainfall as the eggs did not receive a sufficient inundation flow while they remained viable (Franklin et al. 2015).

Ripe male and female giant kōkopu have been captured in lakes (Jellyman 1979b), and there is some speculation that lake-dwelling giant kōkopu on the West Coast spawn in inundated lake margins in response to lake level fluctuations (P. Franklin, NIWA, pers. comm. 9 June 2015). However, it is more likely that lake-dwelling individuals typically spawn in the riparian verges of the inflow streams of the lakes (P. Franklin, pers. comm. 9 June 2015), migrating out of lake environments to do so.

4.3 Larval stage (washed downstream: May–September)

After hatching, giant kōkopu larvae are washed downstream and spend 4–6 months living a pelagic lifestyle in the ocean (McDowall 1990) or in lowland lakes or estuaries (David et al. 2004; Hicks 2012; Hicks et al. 2017).

Larval populations of giant kōkopu are likely to rear in freshwater or estuarine (rather than marine) environments when these are available in the catchment and habitat conditions are suitable, even when there is unimpeded access to and from the sea (David et al. 2004; Hicks et al. 2017). The habitat and rearing requirements for larval giant kōkopu are not currently known (Hicks et al. 2017). However, David et al. (2004) concluded that the rearing of giant kōkopu larvae in freshwater environments may be influenced by river catchment morphology, particularly the presence of still or slow-flowing habitats in the lower reaches of rivers. Ensuring that there is access and connectivity between lowland lakes, rivers and estuaries is likely to be important for the growth and development of giant kōkopu larvae (David et al. 2004).

4.4 Juvenile stage (upstream migration: October–December, with a peak in November)

Juvenile giant kōkopu are found in habitats that have the same characteristics as the preferred habitats of adult giant kōkopu (e.g. low elevation, overhead shade / riparian cover, deep water, low velocity, instream cover) (Bonnett & Sykes 2002; David et al. 2002). However, juvenile giant kōkopu have been observed occupying other microhabitats, including riffles (David et al. 2002) and small, shallow (usually < 0.1 m), faster-flowing backwaters next to riffles (Whitehead et al. 2002), more frequently than adults (which tend to be more closely associated with larger pools) (David et al. 2002; Whitehead et al. 2002).

5. Kōaro (*Galaxias brevipinnis*)

New Zealand status: native

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread throughout New Zealand

Kōaro populations in New Zealand have life histories that are either diadromous (the adults spawn in fresh water, and the larvae drift downstream to the sea and then return to fresh water as juveniles, i.e. sea recruiting) or 'landlocked' (the fish complete their life cycle entirely in fresh water, with the larvae rearing in lakes, i.e. lake recruiting). Lake-recruiting populations may reside in lakes (lake dwelling) or in associated rivers and streams (river dwelling). The habitat requirements for the two different life histories and habitat types are described below.

5.1 Adult stage (year round)

5.1.1 In rivers

River-dwelling adult kōaro are typically found in small streams that are in steep catchments and have moderately stable flows, cobble substrates, and high forest cover in the catchment and along the riparian zones (Leathwick et al. 2008). They are rarely found outside forest environments and, in instances where they are, only occur in streams that have just emerged from forest cover (Main et al. 1985; McDowall 1990; Bell 2001; Eikaas et al. 2005). There have been examples of kōaro populations disappearing after the removal of native bush from stream margins (McDowall 1980). However, in regions such as Otago, adult kōaro can often be found inhabiting small streams and tributaries with riparian tussock / grass / shrub communities (D. Jack, Department of Conservation Te Papa Atawhai, pers. comm. 20 November 2021).

While they are primarily found in small, forested streams, kōaro can also be found in large rivers (such as braided rivers in Canterbury), but usually only occur in small numbers in these habitats (Sagar & Eldon 1983; Main 1988).

Kōaro are exceptional climbers and penetrate far inland, including to high elevations (Woods 1963; Moffat & Davison 1986; McDowall 1990). The highest elevation record for a stream-dwelling kōaro population in the New Zealand Freshwater Fish Database as at 20 July 2023 was 1184 m above sea level.

Kōaro are commonly known as riffle dwellers (McDowall 1990), although they actually utilise a more diverse range of habitats, including pools (Main 1988; Hayes 1996) and backwaters (Chadderton & Allibone 2000). They are also likely to have daily behavioural patterns, utilising different habitats during the day than at night (Chadderton & Allibone 2000). However, kōaro restrict themselves to riffles in the presence of potential predators and / or competitors, including banded kōkopu (*Galaxias fasciatus*) (Main 1988; Chadderton & Allibone 2000), longfin eels (Chadderton & Allibone 2000), shortjaw kōkopu (Bell 2001; McEwan & Joy 2014) and brown trout (*Salmo trutta*) (Main 1988; Chadderton & Allibone 2000; Bell 2001).

Riffles containing kōaro are typically very shallow (5–10 cm deep; Main 1988; McEwan & Joy 2014) with high velocities (> 0.5 m/s; Jowett et al. 1998).

Cobble / boulder substrates are the preferred cover habitats for adult kōaro in rivers (Rowe 1981; Main et al. 1985; Taylor & Main 1987; McDowall 1990; Bell 2001), although kōaro have also been observed using log jams for cover (Bell 2001). Tagging studies have found that kōaro have very small ranges (Kusabs 1989; Bell 2001), often occupying the same riffle corner for extended periods of time (McEwan 2009).

5.1.2 In lakes

Lake-dwelling populations of kōaro are found in numerous locations throughout New Zealand (McDowall 1990), including isolated, high-altitude tarns (McDowall 1988). Adults occupy lakes as well as associated tributary streams and spring habitats. In Lake Rotoaira, Taupō District, kōaro have also been observed utilising underground spring habitat (Fletcher 1919; Rowe et al. 2002).

When occupying lake habitats, adult kōaro are benthic (Michaelis 1982; Rowe 1993b, 1994; McDowall 2011), preferentially occupying rocky habitats (Rowe et al. 2002).

They can be found at great depths – for example, there are records of kōaro at depths of 30 m in Lakes Pukaki and Tekapo in Canterbury (D.K. Rowe unpublished data cited in Rowe et al. 2002), and 50–60 m in Lake Rotoiti / Te Roto kite ā Ihenga i ariki ai Kahu in the Bay of Plenty (Rowe 1993b).

The introduction of trout to lake habitats has seen many lake-dwelling populations of kōaro decline or become locally extinct (Fletcher 1919; Stephens 1983; McDowall 1987, 1990, 2011; Rowe 1993a). Kōaro are more common in turbid rather than clear alpine lakes, possibly because the turbidity helps them to avoid trout predation (Rowe et al. 2009).

5.2 Spawning

5.2.1 Sea-recruiting populations (April–August, with a peak around April–May)

Adult kōaro of sea-recruiting populations spawn alongside adult habitat among inundated gravels on stream banks and margins during elevated flows (O'Connor & Koehn 1998; Allibone & Caskey 2000). Spawning sites observed by O'Connor & Koehn (1998) and Allibone & Caskey (2000) were located adjacent to riffle habitat. Eggs develop out of water on damp surfaces or in places where they are covered by a small amount of water (Allibone & Caskey 2000), and hatch when re-inundated during future high flows (O'Connor & Koehn 1998). Observations of spawning sites in Australia found that the shade and moisture provided by riparian vegetation were critical to egg survival (O'Connor & Koehn 1998).

Kōaro eggs have also recently been found within streams, on the underside of submerged rocks in riffle habitat (Goodman 2018). This indicates flexibility in kōaro spawning, with both instream and marginal habitats being used.

5.2.2 Lake-recruiting populations (November–May, but timing variable and may be related to regional conditions)

Adult kōaro of lake-recruiting populations may be river dwelling or lake dwelling. Little is documented about the spawning of lake-recruiting kōaro, but it is likely that river-dwelling fish spawn in the same types of habitats as sea-recruiting individuals (McDowall 1990; Rowe et al. 2002), i.e. alongside adult habitat (Kusabs 1989; McDowall 1990), among inundated gravels on stream banks and margins during elevated flows (Allibone & Caskey 2000). Augspurger (2017) found that, unlike sea-recruiting populations, the spawning of landlocked kōaro does not coincide with flood events.

Lake-dwelling adult kōaro may either migrate from the lake into tributary streams to spawn (Kusabs 1989; Rowe et al. 2002) or spawn in the lake (Young 2002). Young (2002) found that lake and stream kōaro from Lakes Tarawera and Ōkareka in the Rotorua Lakes District may actually belong to two different sub-populations based on differences in size, growth rate, spawning time and locality, and return to their natal habitats. The life history of landlocked 'stream kōaro' remained similar to that of diadromous sea-recruiting kōaro, with stream fish spawning and hatching in stream habitat, rearing as larvae in the lake, and then returning to tributary streams as juvenile fish. By contrast, 'lake kōaro' most likely spawn in the lake itself, and studies suggest that there is no juvenile migration of lake-spawned fish to tributary streams. There are currently no records of the spawning habitat used by kōaro occupying tarns with no inlet streams.

The timing of spawning is more variable for lake-recruiting populations than for sea-recruiting populations (McDowall 1990; Augspurger 2017) and may be associated with regional conditions (e.g. zooplankton blooms) in lakes (Augspurger 2017). Spawning has been reported in spring (Augspurger 2017), summer (Rowe et al. 2002), autumn (McDowall 1970; Rowe et al. 2002) and early winter (McDowall 1970), and gravid fish were found in two South Island lakes in mid- to late June (Johnson et al. 1976; Meredyth-Young & Pullan 1977). The upstream migration of adult kōaro from lakes to tributary streams to spawn is likely to start from September (Smith 2014). There are also likely to be differences in spawning timing between the North and South islands (Smith 2014).

5.3 Larval stage

5.3.1 Sea-recruiting populations (washed downstream to sea: May–September, with a peak in May–June)

After hatching, kōaro larvae from sea-recruiting populations are washed downstream to sea (McDowall & Suren 1995; Charteris & Ritchie 2002). Kōaro larvae are pelagic and spend 3–6 months in local inshore waters (Hicks 2012) or river plumes (Augspurger 2017), or disperse more widely, including on ocean currents to Australia (McDowall 1990). However, studies by Hicks (2012) and Augspurger (2017) indicated that most kōaro larvae do not disperse far from their natal streams.

5.3.2 Lake-recruiting populations (January–August)

Kōaro larvae of lake-recruiting populations are pelagic (Taylor et al. 2000; Augspurger 2017) and may possibly undertake small movements between stream and lake environments in relation to diel cycles (Rowe et al. 2002). They are found at variable depths that may depend on the season, fish size, water temperature or light levels, and are likely to move up into the littoral (surface) zone when they reach around 30–35 mm in length (Taylor et al. 2000).

Little else is documented on the habitat requirements of kōaro larvae in lakes; however, studies by Hicks et al. (2017) suggested that kōaro are likely to rear in lakes where these habitats are present downstream in the catchment and conditions are suitable, even when there is free access to the sea.

5.4 Juvenile stage (upstream migration: September–November, with a peak in September–October)

5.4.1 In rivers

Juvenile kōaro migrate into rivers from the sea during elevated flows (McDowall 1990). They avoid medium–high levels of suspended sediment (50% avoidance at 70 nephelometric turbidity units (NTU)) (Boubée et al. 1997), warmer streams and streams with a low pH (McDowall 1990). They are attracted to the odours of adult kōaro, so the presence of kōaro pheromones may indicate waterways that contain suitable habitat (Baker & Hicks 2003).

Following river entry, juvenile kōaro have been observed resting for several days in the gravelly shallows of mainstem rivers on the West Coast (McDowall 1990).

Little is documented about juvenile kōaro habitat use. However, Ryder & Keesing (2005) suggested that shallow-edge habitats, such as side braids, provide important habitat for juvenile and small-bodied native fish.

5.4.2 In lakes

Juvenile kōaro can be observed in large numbers in lakes (McDowall 2011), where they congregate in shoals and are limnetic (occupy open surface waters) (Stokell 1955). When they reach around 40–50 mm in length, they are found around lake margins in large shoals. These juveniles then migrate into tributary streams, moving upstream into adult habitats (McDowall 1990), or may remain in the lake (Young 2002). Migration into streams occurs between August and February, with a peak in December (Smith 2014). Larger juveniles can be found on the lake bed, utilising rock crevices and organic debris for cover (Meredyth-Young & Pullan 1977).

6. Dwarf galaxias (*Galaxias divergens*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: North Island – intermittent in the Bay of Plenty and Hauraki Plains, and widespread in the lower North Island south of Hawke's Bay in the east and the Rangitīkei River in the west; South Island – widespread in Marlborough, Nelson and on the West Coast (south to the Hokitika River)

6.1 Adult stage (year round)

Dwarf galaxias are generally found in shallow, cobble-dominated riffle habitats in streams or along the margins of larger rivers, mainly in foothill catchments (McDowall 1990; Jowett & Richardson 2008).

They live in interstitial spaces between substrate particles (McDowall 1990) and burrow deep down into these areas in response to stressors such as reduced water levels (Hartman 1990).

Dwarf galaxias are generally more common in areas with low to moderate flow velocities of 0.15–0.6 m/s (Jowett et al. 1996); however, they have been recorded in relatively deep, slow-flowing, macrophyte-dominated areas with sandy substrates in the Waihou River, Waikato (WRC 2015). They have also been observed occupying pool habitats when preferred habitats become temporarily unavailable (Hay 2009).

Shallow side braids, particularly in large gravel rivers, are important habitats for dwarf galaxias. They provide a more stable environment that is less likely to experience disturbance from flood events, and also act as a refuge from larger, predatory fish such as trout. These habitats also tend to have higher densities of benthic invertebrates – an important food for dwarf galaxias (Hay 2009).

Their small size and non-diadromous life history mean that dwarf galaxias are particularly vulnerable to competition and predation from trout (McIntosh et al. 2010). Dwarf galaxias have a patchy distribution and their populations are often found upstream in areas where trout are not present (McDowall 1990).

6.2 Spawning (September–December)

Dwarf galaxias spawning sites have yet to be documented, although they are likely to be within or near adult habitats (McDowall 2000b). Side braids are likely to be important spawning habitats as they provide refuge from any elevated flows that may occur during the spawning season (Hay 2009).

Observations of eggs laid by dwarf galaxias in aquaria suggest that they may lay their eggs singly or in small groups attached to stones (Hopkins 1971). In the Hinau Stream, Wairarapa, ripe adult fish have been observed from early September to December (Hopkins 1971).

6.3 Larval stage (September–March)

Dwarf galaxias are non-diadromous (McDowall 1990). Larvae are found in the same areas as adults but occupy slow-flowing stream margin, pool and backwater habitats, where they live in small shoals (Hopkins 1971; McDowall 1990, 2000b). Side braid habitats may be particularly important, as these are likely to experience a lower frequency of floods than the main channel, thereby providing a refuge from high flows (Hay 2009).

In the Hinau Stream, Wairarapa, dwarf galaxias larvae were observed from late September to early March (Hopkins 1971).

Little else is documented on the habitat use of dwarf galaxias larvae. However, studies on larvae of other small, stream-dwelling non-migratory galaxiids (alpine galaxias (*Galaxias paucispondylus*) and Canterbury galaxias (*Galaxias vulgaris*)), found that the larvae are only able to tolerate very low flow velocities, being washed away at velocities > 0.1 m/s (Jellyman 2004), and that shallow, marginal refuge habitat was one of the most important factors determining the density of fry (Jellyman 2004). These characteristics are also likely to be important for dwarf galaxias larvae.

6.4 Juvenile stage (in streams year round)

Juvenile dwarf galaxias are found in the same areas as adults but occupy habitats at the margins and edges of streams, where they live in small shoals (McDowall 2000b).

Connections between side braids and the main channel have been suggested to be of high importance to juvenile dwarf galaxias, as they facilitate dispersal (Hay 2009).

Juvenile dwarf galaxias are pelagic in their early life and become more benthic and cryptic when they reach lengths between 25 and 35 mm (age 2–3 months) (Hopkins 1971).

7. Īnanga (*Galaxias maculatus*)

New Zealand status: native

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread in lowland areas throughout New Zealand

7.1 Adult stage (year round)

Adult īnanga are found in slow-flowing lowland rivers, streams, lakes and wetlands. They are poor climbers and do not penetrate far inland (McDowall 1990, 2000b).

Adults of this species prefer slow-flowing water (generally with velocities < 0.18 m/s, with optimum feeding velocities of 0.03–0.07 m/s; Jowett 2002), and are usually found in pools, backwaters and slow runs (McDowall 1990; Sagar 1993). In these habitats, they live in shoals (McDowall 1990) and are pelagic, swimming at a wide range of depths (optimum depths for feeding are > 0.3 m) (Jowett 2002).

Īnanga are capable of negotiating faster velocities for short periods of time, and adults are occasionally found in habitats with swiftly flowing water. In these places, they are found within cover along stream margins and do not shoal (McDowall 1990).

Adult īnanga prefer habitats with marginal vegetation and instream cover (Jowett et al. 2009), especially that provided by aquatic macrophytes, emergent and overhanging vegetation, and debris (Sagar 1993). They avoid environments that are turbid for prolonged periods of time (Rowe et al. 2000).

7.2 Spawning (year round, with a peak in February–May)

Īnanga migrate downstream to spawn in tidally influenced reaches of rivers and estuaries (McDowall 2000b; Hickford & Schiel 2011). Eggs are laid among and adhere to the lower stems and aerial root mats of riparian vegetation that is inundated during high spring tides (Burnet 1965; Benzie 1968; McDowall 1990). Spawning may also occur when water levels are elevated by other factors (e.g. freshes) (Taylor et al. 1992).

Spawning īnanga prefer vegetation that provides a dense, moisture-retentive and humid environment, shading from the sun, and temperature regulation. These conditions provide for optimal egg development (McDowall 1990; Hickford et al. 2010; Hickford & Schiel 2011). Favoured species where eggs are commonly found include:

- Creeping bent (*Agrostis stolonifera*) (Taylor 2002; Hickford & Schiel 2011)
- Yorkshire fog (*Holcus lanatus*) (Taylor & Kelly 2001; Taylor 2002)
- Wīwī / Edgar's rush (*Juncus edgariae*) (Hickford & Schiel 2011)
- Tall fescue (*Lolium arundinaceum*) (Taylor 2002; Hickford & Schiel 2011)
- Raupō / bullrush (*Typha orientalis*) (Taylor & Kelly 2001; Taylor 2002)

Eggs can develop and hatch in fresh water, salt water or a mixture of the two (McDowall 1990). Īnanga have been reported to spawn among instream substrates when lake and river outlets are blocked (biologist observation from Canterbury reported in McDowall 2011), although it is thought that the eggs would be at high risk of predation (McDowall 2011). Eggs have been found near the outlets of Lakes Waihola and Waipori in Otago (Taylor 2002) and on the banks of a small spring-fed stream near the outlet of Lake Ellesmere / Te Waihora in Canterbury (Taylor et al. 1992). There have also been reports of īnanga spawning around the margins of Lake Ellesmere

(Taylor et al. 1992). However, egg mortality is likely to be high if eggs are laid in exposed habitats, e.g. among stones on banks where there is no vegetation present (Hickford et al. 2018). Landlocked, lake-dwelling īnanga may spawn among emergent vegetation (McQueen 2013).

Īnanga spawning can occur year round but peaks in February–May (Orchard 2021). However, observations from īnanga spawning surveys indicate that there is latitudinal variation in the timing of spawning. For example, Taylor (2002) found that īnanga spawning occurred later in the North Island than in the South Island, and Watson et al. (2023) observed latitudinal differences in spawning within a region (Westland). In addition to spatial variation, the exact timing of spawning is also likely to depend on several other factors, such as growth conditions in the previous year.

7.3 Larval stage (hatch and washed downstream: October–August, with a peak in April–July)

Īnanga eggs develop within moist vegetation for around 2–4 weeks and hatch when they are flooded by a future spring tide. The larvae are washed out to sea on the ebbing tide and feed and grow here over the next few months (McDowall 1990; Taylor & Kelly 2001). Landlocked populations of īnanga also exist, with larvae rearing in lakes (Rowe & Graynoth 2002; Hicks 2012; Hicks et al. 2017; David et al. 2019); however, freshwater recruitment is thought to be rare in New Zealand (Hicks et al. 2005; David et al. 2019).

Larvae have been found around coastlines and sometimes far out to sea (e.g. one larva was caught 704 km offshore from New Zealand) (McDowall et al. 1975). However, recent work using otolith microchemistry showed that īnanga larvae commonly stay in inshore environments rather than dispersing long distances offshore (Hicks 2012).

Īnanga larvae are probably planktonic, living at or near the water surface (McDowall 1990).

7.4 Juvenile stage (upstream migration: May–December, with a peak in August–November)

Juvenile īnanga migrate into rivers from their rearing habitat during elevated flows (McDowall 1990).

Feeding rates of juvenile īnanga are significantly reduced by increases in turbidity (Rowe & Dean 1998), and juveniles avoid very high levels of suspended sediment (50% avoidance at > 420 NTU; Boubée et al. 1997). They are also less tolerant of low dissolved oxygen levels than adults (Dean & Richardson 1999).

Shallow edge habitats such as side braids have been suggested as providing important habitat for juvenile īnanga (Ryder & Keesing 2005). Inundated floodplains containing forest or scrub are also likely to be an important source of large zooplankton food items for juveniles (Catlin 2015).

8. Shortjaw kōkopu (*Galaxias postvectis*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): Threatened – Nationally Vulnerable

Distribution: low–moderate elevations throughout the North Island (although the distribution is patchy), upper South Island, West Coast, a few locations on the east coast (e.g. Kaikōura) and Fiordland

8.1 Adult stage (year round)

Adult shortjaw kōkopu are generally found in small, stable, low- to moderate-gradient streams within dense, mature forest that has complete or near-complete canopy cover (Taylor & Main 1987; Taylor 1988; West 1989; McDowall 1990, 1997; Swales & West 1991; McDowall et al. 1996; Bowie & Henderson 2002; Goodman 2002). However, they have also been found in mainstem rivers (Goodman 2002), and one population in Mangatawhiri Reservoir in the Hunua Ranges, Waikato, has been confirmed as being lake recruiting (Smith et al. 2012). Shortjaw kōkopu seem to prefer streams located within podocarp / hardwood forest and are rarely found in beech forest streams (McDowall et al. 1996; McDowall 1997).

Within these macrohabitats, shortjaw kōkopu are strongly associated with large cobble and boulder substrates (McDowall et al. 1996; Bowie & Henderson 2002; Goodman 2002; McEwan 2009; McEwan & Joy 2014) but also use other forms of cover, including instream debris and undercut banks, when large substrates are not available (McDowall et al. 1996; Goodman 2002; Smith et al. 2012).

Shortjaw kōkopu remain concealed among instream cover during the day (Anderson 1942; McEwan & Joy 2014) and move out into pools to feed at night (Anderson 1942; McEwan & Joy 2014).

Pools provide an important habitat component for shortjaw kōkopu. Side pools (embayments) that are adjacent to the main flow, especially those next to riffles or rapids, may be particularly important (New Zealand Freshwater Fish Database records from 1940 to 1995 compiled in McDowall et al. 1996; McEwan & Joy 2014). McEwan & Joy (2014) found that shortjaw kōkopu were strongly associated with these ‘stable’ side pools during both the day and night but only used ‘unstable’ main channel pools (often located at sharp meanders) at night.

Surveys in Jones Creek, Westland, found that shortjaw kōkopu prefer water depths of 0.3–0.4 m and slow velocities of < 0.05 m/s (McDowall et al. 1996). McEwan & Joy (2014) also observed that shortjaw kōkopu in Mangaore Stream, Manawatu, used deeper, swifter-flowing habitats during the day than at night.

8.2 Spawning (April–July, with a peak in May–June)

Shortjaw kōkopu spawn in tightly packed marginal gravels and litter alongside adult habitat during elevated flows (Charteris et al. 2003).

Ripe males were found in March in the lake-recruiting population in Mangatawhiri Reservoir in the Hunua Ranges (Smith et al. 2012).

8.3 Larval stage (washed downstream: May to August, with a peak in June–July)

Shortjaw kōkopu eggs take 3–4 weeks to develop and can remain viable for up to 2 months provided they remain damp. Larvae hatch on elevated flows and are washed downstream to the sea (Charteris et al. 2003) or a lake (Smith et al. 2012).

8.4 Juvenile stage (upstream migration: September–November)

Juvenile shortjaw kōkopu return to rivers from the sea when they are c. 50 mm in length (McDowall et al. 1996). They are found in the same areas as adults, although they tend to occupy shallower, marginal habitats (McEwan 2009). Small shortjaw kōkopu (c. 100 mm in length) have been observed in still pools along the margins of mainstem rivers among cobble / boulder substrates (McDowall et al. 1996).

9. Piharau / kanakana / lamprey (*Geotria australis*)

New Zealand status: native

Conservation status (Dunn et al. 2018): Threatened – Nationally Vulnerable

Distribution: throughout New Zealand

9.1 Adult stage

9.1.1 Marine-phase adults (year round)

Adult lamprey spend several years in the ocean (Glova 1995). They have been known to travel long distances (including to Antarctic waters) in large groups, often swimming near the water surface (Permitin 1966; Potter et al. 1979).

9.1.2 Pre-reproductive adults (enter fresh water: April–November, with a peak in June–September)

Lamprey select rivers based on the presence of pheromones released by conspecific river-dwelling ammocoetes (larvae) (James 2008; Baker et al. 2022) and possibly reproducing adults; however, knowledge about the role of pheromones as a migratory cue remains limited (Baker et al. 2022). Lamprey are likely to enter rivers earlier in the year in the North Island than in the South Island (Maskell 1929; Todd 1992). Once they enter fresh water, pre-reproductive adult lamprey begin migrating upstream to reach suitable spawning habitats (McDowall 1990).

Lamprey move upstream at night and mostly during elevated flows (Maskell 1929; Kelso & Glova 1993) but do not travel during large floods (Jellyman et al. 2002). When the water is turbid, they may move upstream during the day as well as at night (Maskell 1929). Lamprey tend to remain close to river margins and avoid the main flow (Makereti 1986). They prefer to move when the water temperature is between 12 and 14.5°C, when rain is falling, when there is extensive cloud cover and / or during the dark phase of the moon (Potter et al. 1983).

During the day, upstream migrating lamprey shelter among instream cover, including:

- Large cobble complexes and boulders that are c. 25 cm in diameter (Kelso & Glova 1993; McDowall 2000b)
- Holes and crevices (Todd 1992)
- Instream and bankside debris (Kelso & Glova 1993; Jellyman et al. 2002)

However, while they show a strong need for instream cover, migrating lamprey may simply select the best cover available between periods of movement that occur at night (Jellyman et al. 2002).

Lamprey spend up to 16 months in fresh water before spawning (Jellyman et al. 2002; Baker et al. 2017). Maturing lamprey are predominantly found within small boulder substrates in run and riffle habitats (Baker et al. 2017).

9.2 Spawning (spring – early summer)

Lamprey spawning has only been formally observed in the Okuti River catchment on Banks Peninsula (Baker et al. 2017), but observations of pre-spawning adults provide further supporting information about their spawning habitat.

Lamprey spawn in cavities under large instream boulders, where there is good water flow and hard surfaces for egg laying (Baker et al. 2017, 2022). The eggs adhere to each other and the underside of the boulder in a cluster. After spawning, the male and female remain in the nest, with the male appearing to guard and groom the eggs and possibly assisting with hatching (Baker et al. 2017).

Of the six nest sites located by Baker et al. (2017), two were within backwaters adjacent to riffle habitat and four were among boulder clusters within shallow riffles.

Spawning may occur long distances inland (e.g. pre-spawning adults have been found more than 200 km from the sea) and often takes place in small, forested streams (Maskell 1929; McDowall 1990). Adult lamprey are very good climbers (McDowall 1990) but are unable to pass some dams (Jellyman & Robertson 1997), so access to some potential spawning habitat may be restricted.

9.3 Larval (ammocoete) stage (year round)

Lamprey ammocoetes begin to hatch after approximately 6 weeks and remain in clusters within the nest for 2–3 weeks, where they adhere to the undersides of the boulders (Baker et al. 2017).

Ammocoetes are usually found in slow-flowing muddy backwaters (McDowall 1990), river and stream margins (Maskell 1929), and shallow runs with overhead shade (Jellyman & Glova 2002) but have also been found in water races (Maskell 1929). Within these habitats, ammocoetes remain buried during the day (commonly at depths of 3–9 cm) and then partially emerge at night to filter feed (Maskell 1929).

Ammocoetes prefer low flow velocities (Jowett & Richardson 2008) – for example, Jowett et al. (1996) reported preferences for water velocities of < 0.15 m/s, while Jellyman & Glova (2002) noted values of < 0.05 m/s. They also prefer deep (Kelso & Todd 1993) and fine substrates (Maskell 1929; Kelso & Todd 1993; McDowall 2000b; Jowett & Richardson 2008) that are < 1 mm in size (Jellyman & Glova 2002), including small pockets of deposited sediment downstream of boulders, logs and other obstructions to flow. They may also occupy fine and coarse gravel habitats provided that these are not hard packed and contain spaces for the ammocoetes to burrow into (Baker et al. 2022).

Ammocoetes tend to move downstream as they grow, with upstream sites predominantly containing smaller individuals and sites further downstream generally having ammocoetes of a greater size and size range (Kelso & Todd 1993). Kelso & Todd (1993) typically found metamorphosing larvae in downstream reaches within habitats that had coarser substrates and higher water velocities. This size segregation could be active or passive and may be related to flood events (James 2008).

Ammocoetes live in rivers for c. 3.5 years before metamorphosing into macrophthalmia (Todd & Kelso 1993).

9.4 Juvenile (macrophthalmia) stage (metamorphosis: begins around January; downstream migration: July–August)

Lamprey metamorphose from the eyeless form of an ammocoete to a form with the morphology of a miniature adult (macrophthalmia) and then migrate downstream and out to sea (McDowall 1990). This migration takes place at night during increased river flows (Potter et al. 1980).

Metamorphosis begins around January, and migration takes place in July–August (Potter & Hilliard 1986; Empson & Meredith 1987).

Little is known regarding the habitat preferences of macrophthalmia, but they have been observed in riffles during normal flows (A. Perrie, Greater Wellington Regional Council, pers. comm. 12 May 2015), as well as swimming in the middle of the river at night (Empson & Meredith 1987).

10. Bluegill bully (*Gobiomorphus hubbsi*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): At Risk – Declining

Distribution: widespread throughout much of New Zealand

10.1 Adult stage (year round)

Adult bluegill bullies are found in gravelly streams and rivers, including large, open mainstem rivers (Atkinson & Joy 2009). They are usually found in the low–mid reaches (McDowall 1990), although some have been found up to 70 km inland (Davis et al. 1983). Within these habitats, bluegill bullies occupy interstitial spaces (Glova & Duncan 1985) among coarse gravel and cobble substrates (Hayes et al. 1989; McDowall 1990; Jowett & Richardson 1995; Davey et al. 2011) in riffles and fast runs (Glova & Duncan 1985; McDowall 1990; Jowett et al. 2005).

Davey et al. (2011) found that while bluegill bullies are generally restricted to shallow riffle habitats with coarser substrates during the day, they show broader habitat use patterns at night, including occupying runs.

Adult bluegill bullies have been recorded as preferring velocities ranging from 0.3 to 1 m/s (Davis et al. 1983; Glova & Duncan 1985; Hayes et al. 1989; Jowett & Richardson 1995; Jowett et al. 1996, 1998; Davey et al. 2011). They have also been recorded at a range of depths between 0.2 and 0.33 m (Davis et al. 1983; Glova & Duncan 1985; Hayes et al. 1989; Jowett & Richardson 1995; Jowett et al. 1996; Davey et al. 2011).

Jowett et al. (1996) reported that bluegill bullies are more likely to occur in waterways within native forest than those in exotic forest.

10.2 Spawning (August–February)

Bluegill bullies spawn on the underside of flat, unembedded rocks and cobbles in shallow, broken water (Jarvis 2015; Jarvis et al. 2018). Jarvis et al. (2018) found that spawning in the Waianakarua River in Otago occurred predominantly in the lower reaches (< 2–5 km from the sea).

The males of other bully species clear silt from the nest surface before the females spawn and then remain to guard the nest until the eggs hatch, fanning the eggs to keep them oxygenated and free of silt (McDowall 1990). Jarvis et al. (2018) also observed this behaviour in bluegill bully, with males defending spawning sites that may each contain the eggs of multiple females. It is likely that there is strong competition between males for preferred spawning sites.

Cues for hatching are unknown but hatching may occur in response to bed disturbance during elevated flows or may perhaps be stimulated by the male parent (Jarvis 2015). Little else is documented about bluegill bully spawning.

10.3 Larval stage (washed downstream: September–March)

After hatching, bluegill bully larvae are washed downstream to the sea (McDowall 1990; Jarvis 2015; Jarvis et al. 2018). Larval drift has been observed to peak just after sunset, with the majority occurring between sunset and midnight and only a small amount taking place during the day (Jarvis 2015; Jarvis & Closs 2015). An experiment on larval survival across salinity levels by Jarvis et al. (2018) indicated that areas of intermediate salinity (e.g. estuaries and river mouths) may be important for bluegill bully larval survival.

In the sea, bluegill bully larvae are pelagic (Jarvis 2015). Bluegill bully larvae recruiting into different rivers were found to have unique larval trace element signatures (Warburton et al. 2018), indicating that fish from different rivers are likely to have reared in different marine environments and that bluegill bully larvae may be able to remain within the freshwater plumes of rivers during their marine growth stage (Warburton et al. 2018).

There are no known lake-recruiting populations of bluegill bully. However, work using otolith microchemistry has shown that redfin bullies, which were previously considered to be strictly diadromous, also rear in lakes, and that those larvae that do rear in the sea are likely to do so in restricted inshore areas, rather than dispersing widely (Hicks 2012). Bluegill bully larvae also appear to have limited dispersal (Warburton et al. 2018). Therefore, it is possible that bluegill bullies might also be able to rear in freshwater environments (where suitable habitat is available) and that an oceanic stage may not be an obligate requirement for larval rearing (Jarvis 2015).

10.4 Juvenile stage (upstream migration: November–March)

Juvenile bluegill bullies migrate into rivers from their larval rearing habitats and are generally found in the lower reaches of the mainstems of large rivers (McDowall 1990). Bluegill bullies may use conspecific odours and natural stream odours to detect streams with suitable habitat (Atkinson & Joy 2008), or they may remain associated with the river plumes during their larval growth, recruiting back into these rivers as juveniles (Warburton et al. 2018).

11. Redfin bully (*Gobiomorphus huttoni*)

New Zealand status: endemic

Conservation status (Dunn et al. 2018): Not Threatened

Distribution: widespread throughout much of New Zealand

11.1 Adult stage (year round)

Adult redfin bullies are generally found in stable rivers and streams with moderately to swiftly flowing water (McDowall 1990). They avoid gravelly, unstable rivers and enriched, weedy streams (McDowall 1990), and are uncommon in turbid rivers, likely due to high concentrations of settled solids reducing their food supply and benthic habitat (Rowe et al. 2000; Jowett & Boustead 2001).

Within these macrohabitats, redfin bullies are strongly associated with large cobble and boulder substrates (McDowall 1964; Hayes et al. 1989; Jowett & Richardson 1995; McEwan & Joy 2013; Moore 2014), with McDowall (1964) specifying that they are most abundant among loosely aggregated boulders at the heads of riffles. Redfin bullies are often found in pools and may selectively occupy areas based on their habitat structure, particularly substrate type (Moore 2014). The abundance of invertebrate prey species may also be a potential driver of habitat selection (Moore 2014).

Redfin bullies seek cover within cobble / boulder interstices during the day (McDowall 1990; Jowett & Richardson 1995; McEwan & Joy 2013) and then emerge from cover at night to feed, foraging in cobble areas (Moore 2014), as well as other habitat types (McEwan & Joy 2013). During the day, McEwan & Joy (2013) recorded adult redfin bullies primarily occupying areas with large substrates and lots of interstitial refuges, while at night they were distributed across virtually all available habitats. Smaller adults are more likely to be found in shallower edge habitats (McEwan 2009).

Male redfin bullies commonly establish territories, occupying and defending specific areas of substrate, particularly during the breeding season (McDowall 1965, 1990). Moore (2014) found that male redfin bullies tend to occupy patches with deeper water, slower velocities and larger substrate sizes.

11.2 Spawning (August–November)

Redfin bullies usually spawn within slower-flowing, shallow areas of their adult habitat. Nest sites are typically located towards the ends of pools, where flows are sufficiently high to minimise the deposition of silt (McDowall 1965).

Spawning occurs on flat surfaces on the undersides of rocks that have a flow of water beneath them. Where the availability of suitable rocks is low (e.g. in slow-flowing, silty streams), redfin bully nests have been observed on other solid objects, including planks, logs, bottles and tyres (McDowall 1965).

It is likely that a male redfin bully prepares its nest territory by clearing silt from the lower surface of the rocks within the nest site. Female redfin bullies lay their eggs on the underside of selected rocks, with the male following to fertilise the eggs (McDowall 1965). The male then guards the nest (McDowall 1965, 1990) for 2–4 weeks until hatching occurs, which may be stimulated by floods (McDowall 1990).

11.3 Larval stage (washed downstream: September–February)

After hatching, redfin bully larvae are washed downstream. The larvae are pelagic and inhabit marine environments where they either disperse widely (McDowall 1990) or remain in local inshore areas (Hicks 2012). They are also able to rear in lakes (e.g. Lakes Moeraki and Paringa on the West Coast) (Hicks 2012; Hicks et al. 2017).

11.4 Juvenile stage (upstream migration: November–March)

Juvenile redfin bullies migrate into rivers and streams from their rearing habitats (McDowall 1990).

Juveniles and small adults are more often seen on sandy gravel shallows at stream margins (McDowall 1990; McEwan 2009), suggesting that they are either less dependent on cover or are outcompeted by larger individuals.

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13.11 Redfin bully

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13.12 Mātauranga Māori

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[Describes the use of an utu piharau (lamprey) weir to catch lamprey migrating upstream, including mātauranga relating to movements upstream]

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[Discusses mātauranga and the importance of freshwater fish in relation to Māori culture]

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[Includes a brief description of traditional eeling and 'mud hole' habitats occupied by eels in Blueskin Bay, Otago]

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[Discusses Māori lamprey fisheries, including mātauranga relating to instream habitats used by lamprey]