

## 6 Whitebait

**Family:** Galaxiidae

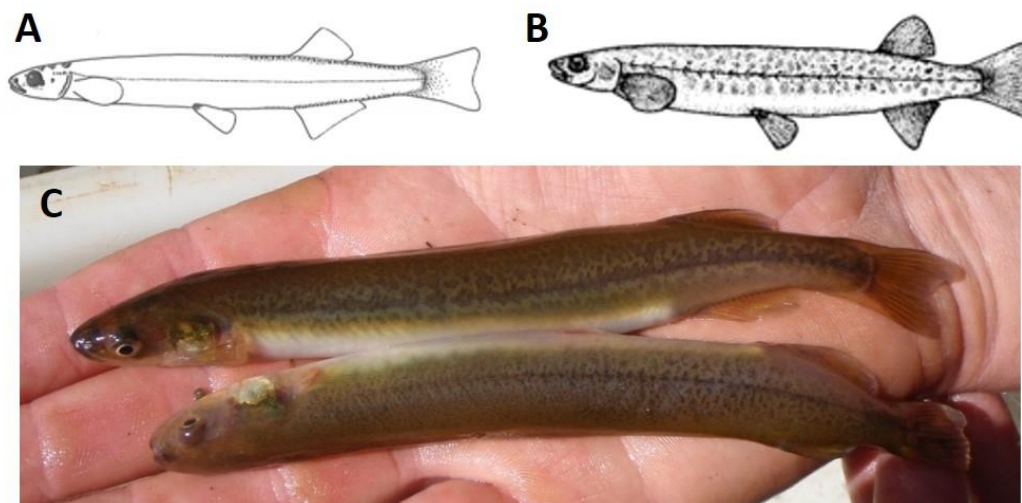
**Species:** *Galaxias maculatus*, *Galaxias postvectis*, *Galaxias brevipinnis*, *Galaxias argenteus*, *Galaxias fasciatus*

The whitebait catch is made up of five separate fish species belonging to the family Galaxiidae. This ancient group of fishes is found throughout the cool-temperate regions of the Southern Hemisphere incorporating eight genera and about 50 species (McDowall 2006). Galaxiids are characterised as small (usually 40–150 mm, but up to 500 mm in some species) tubular fishes with no scales and only a single dorsal fin. The skin is thick and leathery and there is a strong spotted pattern in some species that is said to “resemble the Milky Way galaxy”, hence the family name Galaxiidae (McDowall 1990). Galaxiids are rich in terms of the number of species that there are in Australasia (McDowall 1970, McDowall & Frankenberg 1981, McDowall 1990), with Aotearoa-NZ containing the greatest species diversity (about 35 species and two genera) (Waters et al. 2001, Waters & Wallis 2001, McDowall 2006).

In this section, we briefly introduce each of the five whitebait species that are the focus of this report, before going into more detail about their respective life cycles (Section 6.2), distribution (Section 6.2), and pressures on populations (Section 6.6).

### Īnanga (*Galaxias maculatus*)

Adult Īnanga (Figure 43) are the smallest of the five species, rarely getting bigger than 110 mm in length. Their silvery belly and forked tail make them easy to tell apart from the other galaxiids, except for their close relative the dune lake galaxias (also called dwarf galaxias, *G. divergens*). Īnanga is the most abundant whitebait species, probably comprising at least 90% of the total national catch (McDowall 1990). Although Īnanga migrate well upstream in some rivers, this species is normally considered as a “lowland species” as they favour gently flowing and still waters such as estuaries, lowland streams, lagoons and backwaters (McDowall 1990). Land-locked populations of Īnanga are found largely in the North Island (McDowall 1990).



**Figure 1:** (A) Juvenile Īnanga; (B) Adult Īnanga; and (C) Adult Īnanga caught from the Taumārere River, April 2008. (Diagrams: Bob McDowall; Photo: Bruce Davison).

### Shortjaw kōkopu (*Galaxias postvectis*)

Shortjaw kōkopu (Figure 44) have an undercut jaw, with the lower jaw being shorter than the upper jaw. Another distinguishing feature of shortjaw kōkopu is the distinctive dark blotch on each side of their body just behind the gills. Shortjaw kōkopu are endemic to Aotearoa-NZ and do not occur on Stewart or Chatham Island. Although they make their way well inland in many catchments, they appear to be restricted to streams with native forest vegetation.

Even though it is widespread, the shortjaw kōkopu is probably the rarest of the whitebait galaxiids as it is unusual to capture more than a few fish at a given site. It is usually found in streams with large boulders in pools and is sometimes difficult to catch using conventional sampling methods. Because this fish has been so rarely encountered, little is known about its life history. In the Taranaki region spent (i.e., recently finished spawning) fish were first recorded in May by Allibone and Caskey (2000), while Charteris et al. (2003) found spawning occurred in June. In 2008, the first land-locked population was discovered in a reservoir within the Hunua ranges (Baker et al. 2008).

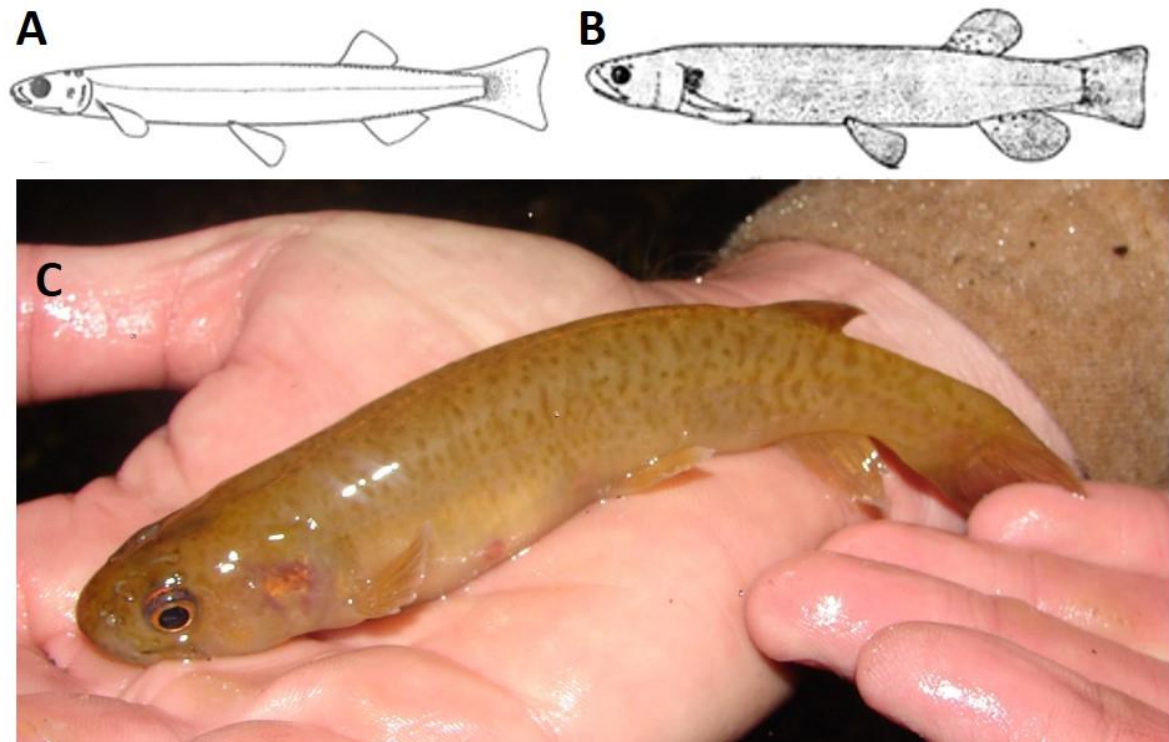


**Figure 2:** Shortjaw kōkopu caught from the Waikirikiri Stream, November 2008. (Photo: Bruce Davison).

### Kōaro (*Galaxias brevipinnis*)

The kōaro is unlikely to be confused with the other diadromous whitebait species because of its shape. It is more elongate and slender shaped, almost like a tube (Figure 45). The sides and back are covered in a variable pattern of light patches and bands. Kōaro have the ability to make their way well inland and climb to high elevations in many river systems, and thus have a more widespread distribution than the other whitebait species. In addition to the mainland, they are also found on Chatham and Stewart Island, in Australia, and on the sub-Antarctic Auckland and Campbell Island. Rocky, tumbling streams are the preferred habitat of kōaro, and they are almost always found in streams with native bush catchments except for tributaries of upland lakes that may be above the bush line. To date the oldest age observed by West (1989) was 8+ years at 208 mm total length.

Although kōaro comprise part of the whitebait catch, they also form land-locked populations in lakes. Populations of land-locked kōaro are sustained by fish that complete their life cycle in fresh water and are found in many man-made and natural lakes. For example, kōaro populations occur in the catchments of many of the Te Arawa Lakes, Taupō-nui-a-Tia, Rotoaira, Manapōuri, Tekapō, Pukaki (Figure 46), and Wanaka. Lake kōaro populations were decimated by predation from introduced trout and are now much lower than in pre-European time, or have become extinct, e.g., Lakes Rotoehu and Rotomā (Rowe & Kusabs 2007).



**Figure 3:** (A) Juvenile kōaro; (B) Adult kōaro; and (C) Adult kōaro caught from Te Hirau Stream, Lake Tarawera. (Diagrams: Bob McDowall; Photo: Shane Grayling).

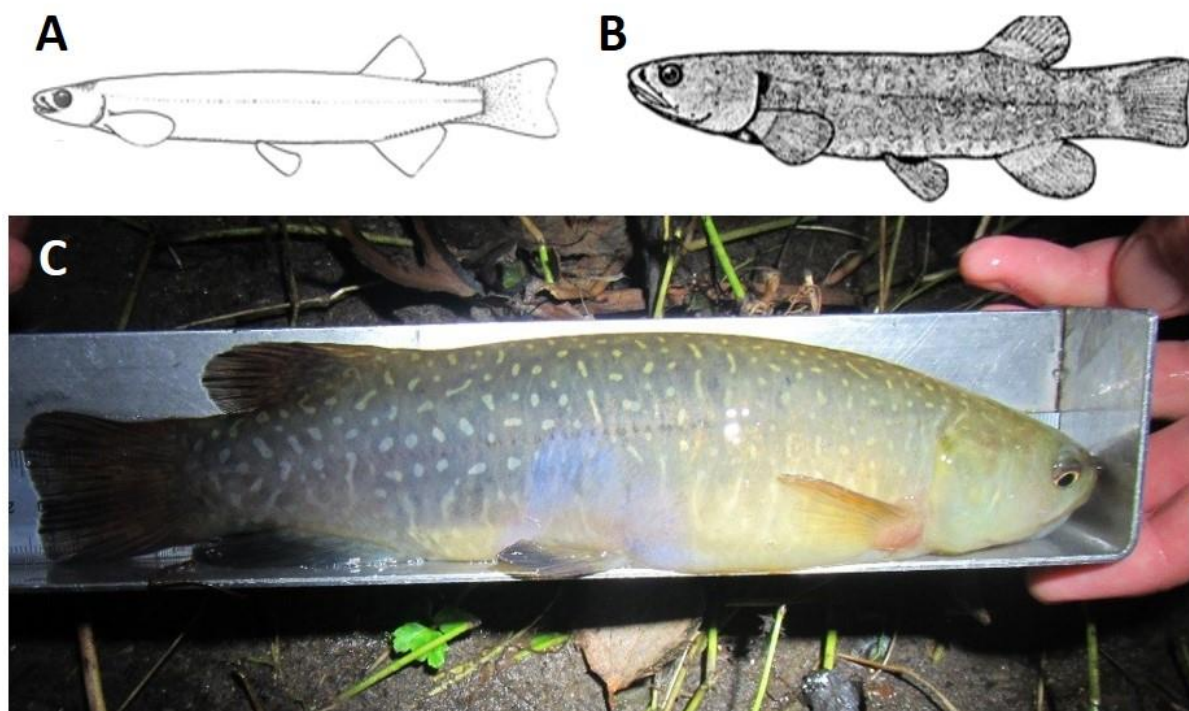


**Figure 4:** Adult kōaro from Lake Pukaki, Waitaki River catchment. In this lake adult kōaro are pure white in colour, tinged with pink, due to the glacial silt present in the water and their habit of living in deep waters where the light does not penetrate (see Rowe 1999 and Graynoth 2011 for more information). (Photo: Dave Rowe).

#### Giant kōkopu (*Galaxias argenteus*)

As its name implies, the giant kōkopu (Figure 47) is the largest member of the Galaxiidae family. The golden spots and other shapes on the bodies of larger fish are very distinctive, although small specimens may be difficult to tell apart from banded kōkopu. Specimens of over 450 mm in length have been reported, although fish in the 200–300 mm range are far more common. To date the oldest age observed by West (1989) was a 7+ year old female (231 mm total length).

Giant kōkopu are uncommon in the whitebait catch and usually run late in the season. Giant kōkopu are primarily a coastal species and do not usually penetrate inland very far. They are endemic to Aotearoa-NZ and are also found on the major offshore islands. Like banded kōkopu and kōaro, they can establish land-locked populations. In streams, they prefer the slow flowing waters that occur in lowland runs and pools. They are also usually associated with some form of instream cover like overhanging vegetation, undercut banks, logs, or debris clusters. It is thought that they lurk quietly in this cover awaiting their prey, which ranges from kōura to terrestrial insects such as spiders and cicadas.



**Figure 5:** (A) Juvenile giant kōkopu; (B) Adult giant kōkopu; and (C) Adult giant kōkopu caught from Bankwood Stream, Hamilton. (Diagrams: Bob McDowall; Photo: Eimear Egan).

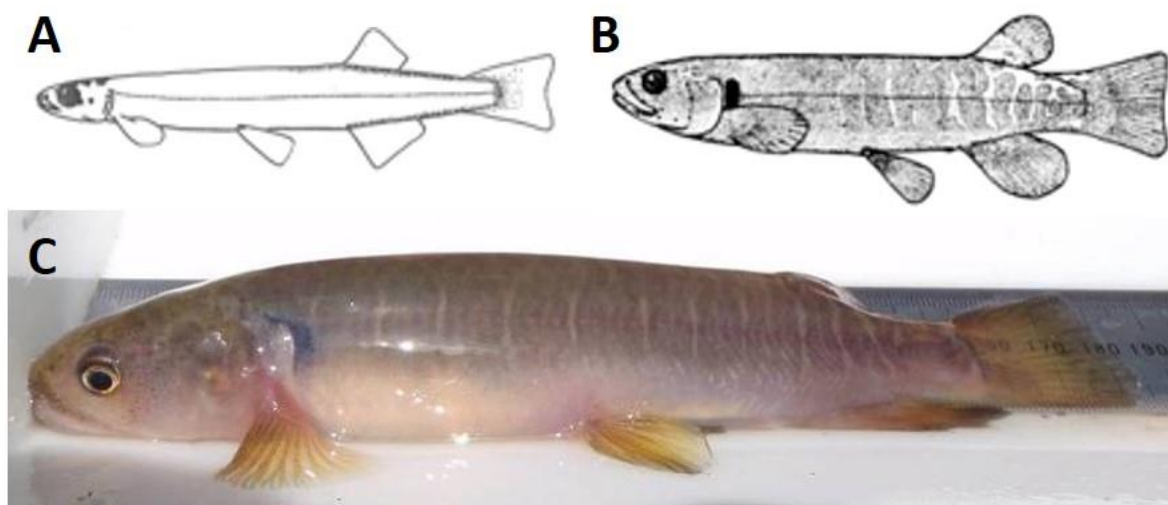
### Banded kōkopu (*Galaxias fasciatus*)

Banded kōkopu (Figure 48) are generally the smallest of the five whitebait species when they are small have an overall golden colour. The juveniles are very good climbers and will often try and escape from buckets by clinging to and wriggling up the sides. Adult banded kōkopu can be distinguished from the other galaxiid species by the presence of the thin, pale, vertical bands along the sides and over the back of the fish. These bands begin to develop quite early, but similar bands also appear on juvenile giant kōkopu, and it is easy to confuse young fish of these species. Banded kōkopu commonly grow to over 200 mm.

Adult banded kōkopu usually live in the pools of small tributaries where there is virtually a complete overhead canopy of vegetation. This vegetation does not have to be native bush, however, and banded kōkopu happily live in urban streams and streams under exotic pine plantations so long as overhead shade is present. They only occur in pools where there is instream cover such as an undercut banks, large rocks or wood debris. They depend on terrestrial insects for a large proportion of their diet and can detect the small ripples made by moths and flies that become stuck on the water surface of the pool.

Although the juveniles are good climbers, banded kōkopu do not penetrate very far inland and are primarily a coastal species. They are also found on Chatham and Stewart Island. Banded kōkopu are rare along the east coast of the North Island south of East Cape and down the east coast of the South

Island, but common elsewhere. This distribution is probably a result of intensive land development and the sensitivity of the juveniles to suspended sediments. Rivers containing glacial flour or eroding sedimentary catchments are not attractive to the whitebait of this species.



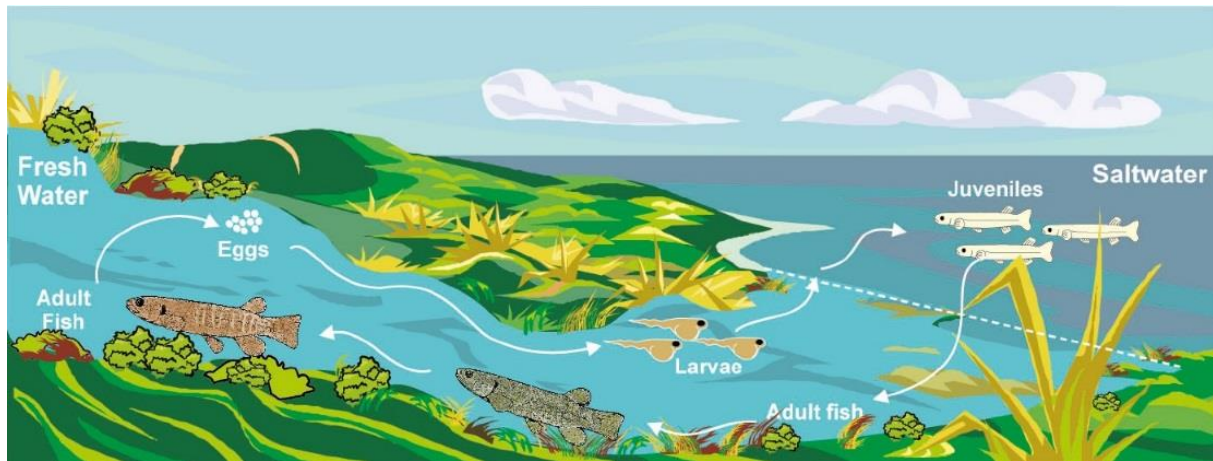
**Figure 6: (A) Juvenile banded kōkopu; (B) Adult banded kōkopu; and (C) Adult banded kōkopu caught from the Kaikou River, November 2008.** (Diagrams: Bob McDowall; Photo: Bruce Davison).

## 6.1 Life Cycle

Whitebait are diadromous as their life cycle is completed in marine and freshwater environments. Amphidromy is the specific type of diadromous migration that Galaxiids display which typically involves downstream larval transport, dispersal and development in the marine environment followed by inward migration of post-larvae (whitebait) to freshwater where most feeding and growth occurs (McDowall 1998). The life cycle and migrations of amphidromous species, of which there are at least 250 worldwide, are not well known (McDowall 2007). Studies of amphidromous species like whitebait are challenging because of the extensive larval period in the sea which often means larvae cannot be located or identified (Hickford & Schiel 2003).

Although the five Galaxiid species are largely considered diadromous, recent research shows there is considerable flexibility in their migration patterns and life histories. The chemistry of Galaxiid ear-bones (called otoliths) has been used to discern whether individuals completed their life in marine, estuarine or freshwater environments (also see Section 6.5.4). In Aotearoa-NZ, freshwater larval development has been documented for *īnanga* from coastal populations with downstream access to the sea and upstream access to lakes (Hicks 2012). Other studies have shown that *īnanga* larval development occurs exclusively in the marine environment; *īnanga* whitebait migrate directly from the sea to freshwater, spending little time in estuaries (Hicks et al. 2005). Evidence for freshwater larval development as opposed to marine larval development is also known for giant kōkopu (David et al. 2004), *kōaro* (Hicks 2012) and banded kōkopu (Tana & Hicks 2012).

Among the five-whitebait species, the spawning ecology/behaviours of *īnanga* are the most widely understood (Figure 49); however, research on the other species is being progressed (see following sections). For diadromous populations of *īnanga*, mature adults (50–125 mm in length) move downstream to their spawning sites (McDowall 1968), while land-locked populations move upstream to spawn (Pollard 1972). For *īnanga* that are diadromous, spawning occurs on riparian vegetation where the salt water wedge penetrates freshwaters at high tides (McDowall 1988). Spawning is linked to lunar and tidal cycles with most spawning occurring on spring-tide events. Cues like day length and seasonal changes in temperature are important for the onset of sexual maturity and spawning in *īnanga* (Barbee et al. 2011).



**Figure 7:** Diagram showing the life stages and habitats used by diadromous populations of īnanga. (Source: NIWA).

Īnanga spawn over an extensive period, from January in the south through to July in the north, with peripheral spawning also found outside of these ‘peak’ spawning times (Mitchell 1991, Taylor 2002, Hicks et al. 2013). The eggs are typically deposited 10–15 cm above the highwater mark, take 2–4 weeks to develop and require humid conditions for successful development (Hickford & Schiel 2011). Analysis of the hatch-dates of īnanga whitebait, as well as mature adults, confirms their extensive spawning period even though eggs are rarely observed year-round (Egan 2017).

Using gonad histological analysis, Stevens et al. (2016) showed that some īnanga can survive spawning but most die. Size at sexual maturity, body condition and gonad weight tend to decline throughout the spawning season (McDowall 1968, Barbee et al. 2011). These patterns might be related to multiple spawning events or that the reproductive dynamics of fish that are mature later in the year differ to those that mature earlier. Generally, larger females produce more eggs but there is considerable variation in egg production among individuals. For example, up to six-fold differences in egg production were found among females that were 80 mm in length (McDowall 1968).

Larval hatching is triggered by re-inundation of the eggs on the next tidal cycle, usually 3–4 weeks later. It is thought that larval hatching also occurs on flood flows although this has never been demonstrated (Rowe & Kelly 2009). Īnanga eggs can survive for up to 6 weeks in the vegetation but their viability declines with longer egg development times (Benzie 1968). Newly hatched larvae, on average 7 mm length, drift downstream to the marine environment. There are few observations of īnanga in this environment so little is known of their larval ecology.

Īnanga whitebait migrate to freshwaters during late-winter through spring, but can be observed in lower abundances throughout the year (McDowall et al. 1994). The average size at migration is 51 mm but this ranges from 36 mm to 60 mm throughout Aotearoa-NZ. They are on average 124 days old at inward migration but this can vary widely (60–187 days). Īnanga change into the adult form in the lower reaches of rivers, while adult growth and development occurs further upstream (McDowall 1968). They are an annual species with few individuals surviving to their second year (Egan 2017). Less is known about the life cycle of land-locked īnanga populations in Aotearoa-NZ. In Australia, land-locked populations spawn in littoral (lake shore) vegetation, larvae rear in the limnetic zone (lake surface waters away from shore) and adults live for up to four years (Chapman et al. 2006).

**Shortjaw kōkopu** spawn along bank margins during elevated flows (Charteris et al. 2003), but can be quite variable in the selection of their spawning sites/habitats. Spawning sites for shortjaw kōkopu have been shown to include a mixture of small vegetation, gravel and woody debris (Charteris et al. 2003).

In stream populations, **kōaro** spawning occurs during autumn/winter. Downstream drift of kōaro larvae was observed in May by Charteris et al. (2003) for Taranaki streams, but kōaro larvae have also been observed in March in South Island streams (McDowall & Suren 1995). Examination of hatch date distributions of returning kōaro whitebait to South Island rivers observed a spawning season of May through to July (McDowall et al. 1994). Kōaro deposit their eggs amongst marginal gravels and litter during periods of elevated stream flow (Allibone & Caskey 2000). The larvae hatch typically 3–4 weeks later if the eggs are re-inundated during high flow events. The hatched larvae (about 7–8 mm long) go to sea to feed and grow for about 17–20 weeks, then as whitebait (c. 45–50 mm long) migrate upstream in early spring (McDowall 1990). Lake populations of kōaro have a life history pattern similar to that of sea-going stocks, although the spawning season may vary (McDowall 1990).

Little is known about **giant kōkopu** spawning habits with the most information to date coming from studies on a single population in the Waikato region (Franklin et al. 2015). It is thought that giant kōkopu adults migrate to a common spawning site and lay their eggs in bankside vegetation (Figure 50). Currently, the known spawning vegetation is mostly *Tradescantia fluminensis* (wandering willie), an invasive perennial herb; but it is highly likely that giant kōkopu use other species of native and exotic grasses for spawning (Franklin et al. 2015). Spawning occurs during elevated flows following rainfall events and is not triggered by cues related to tidal cycles. Spawning has only been recorded from two sites in Aotearoa-NZ, an urban stream in Hamilton and at Awaawaroa Wetland on Waiheke Island. Spawning is known to occur from late April to late June (Franklin et al. 2015).

Similar to shortjaw kōkopu, **banded kōkopu** spawn along bankside margins during elevated flows (Charteris et al. 2003), but can be quite variable in the selection of their spawning sites/habitats. Spawning sites for banded kōkopu have been shown to include a mixture of small vegetation, gravel and woody debris (Charteris et al. 2003).



**Figure 8: Giant kōkopu spawning site, Bankwood Stream, Hamilton.** (Left) The pink tape marks the location of the only monitored spawning site of giant kōkopu in Aotearoa-NZ. Giant kōkopu eggs are mostly found on *Tradescantia fluminensis* (wandering willie) which is the most dominant bankside vegetation in this stream; (Right). A spawning aggregation of giant kōkopu. Spawning was witnessed for the first time by NIWA

scientists in June 2017. Giant kōkopu spawned on rising and receding water levels following a significant rain event. The pink tape marks the location of eggs from a previous spawning event. (Photos: Eimear Egan).

### How many eggs does it take to make a whitebait fritter?

Franklin (2014) draws on our current knowledge of the īnanga life cycle and the gauntlet negotiated by these fish (i.e., survival rates) to estimate how many whitebait eggs might be needed to eventually end up on our plates as fritters. He estimates that:

*“An average sized adult female īnanga will lay around 2–3,000 eggs (McDowall 1984). Studies have shown that on average, only about 11% of eggs survive to hatch (Hickford et al. 2010). Once the eggs hatch and the larvae make it to sea, survival is very low. No data are available specifically for īnanga, but mortality of larval fish in the marine environment has been estimated to be more than 98% (Zeldis et al. 2005). On returning to freshwater, investigations have shown that around 30% of whitebait may be caught in the whitebait fishery (Baker and Smith 2014). An unknown number of these remaining fish then survive to adulthood and successfully spawn (let’s assume 50%, but it has been suggested this is more likely to be less than 20%). If we assume a cup of whitebait (about 500 fish) is used to make a whitebait fritter, we can work out that it actually takes close to 650,000 eggs to make one whitebait fritter!”*

## 6.2 Distribution

Generally, most of the whitebait species are found close to the ocean, except for kōaro which can penetrate large distances inland (Figures 51–53). **Īnanga** are almost exclusively found within close proximity of the coast, particularly in the South Island but are largely absent from Fiordland (Figure 51).

**Shortjaw kōkopu** show specific distributions in the South and North Island. In the South Island, shortjaw kōkopu are only regularly found along the West Coast and along the top of the South Island. There are a few observations north of Kaikōura, but the remaining east coast of the South Island has no observations of this species. There are also a few observations of shortjaw kōkopu around the mouth of the Waiau River in Murihiku. The Waitakere ranges and Taranaki are the two areas in the North Island with the most observations of shortjaw kōkopu. There are a few intermittent records of this species at large distances inland around Whanganui National Park, Hamilton and Whakatāne (Figure 51). Yungnickel (2017) has identified shortjaw kōkopu whitebait from the Whakatāne River (Bay of Plenty), Rangitikei River (Manawatū-Whanganui), Orowaiti and Buller Rivers (Buller) and Waimea Creek (Westland) using genetic methods.

**Kōaro** are found across a wide variety of habitats and at high distances inland because of their climbing ability (McDowall 1990). Kōaro can climb vertical structures allowing them to reach high altitudes and account for most of the highest fish observations in the NZFFD. Kōaro also form land-locked populations (McDowall 1990), which are included in Figure 52 because it is not possible to separate diadromous from non-diadromous stock within the NZFFD. Most of the kōaro observations in the South Island have been recorded along the Southern Alps mountain ranges and the West Coast. Most of the observations of kōaro in the North Island are located along the Waitakere ranges and Taranaki (Figure 52).

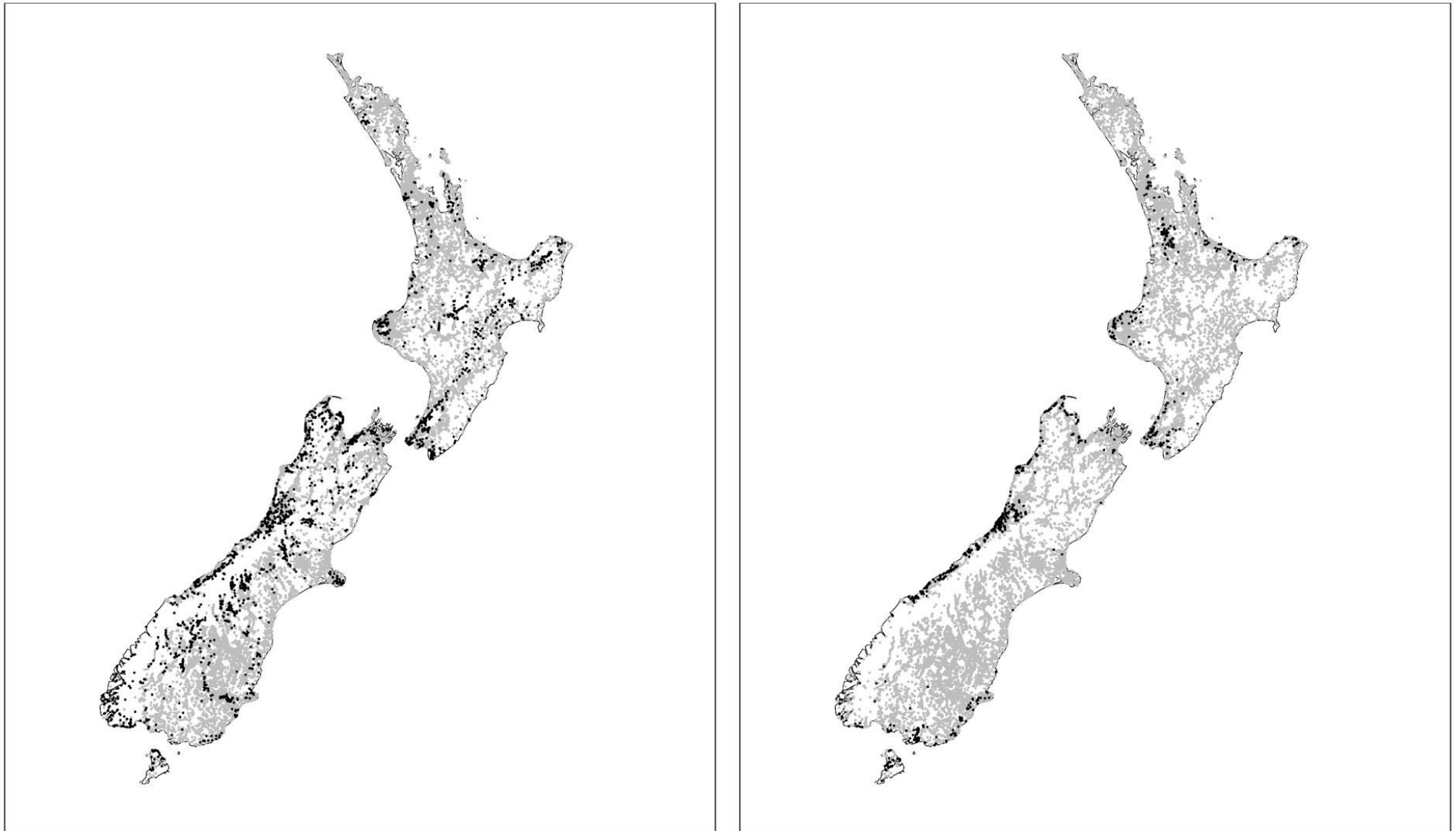
**Giant kōkopu** (Figure 52) are a coastal species that appears to have a patchy distribution across Aotearoa-NZ. In the South Island, they are predominantly absent around Fiordland and along the East Coast (with the exception a couple of small streams), apart from the South Otago Region. The most records in the South Island have come from the West Coast region. The most records in the North Island have been recorded from around Wellington, Taranaki and the Waikato. There are also a few records from around South Auckland and Tauranga, but the remaining areas in the North Island have very few records of giant kōkopu.



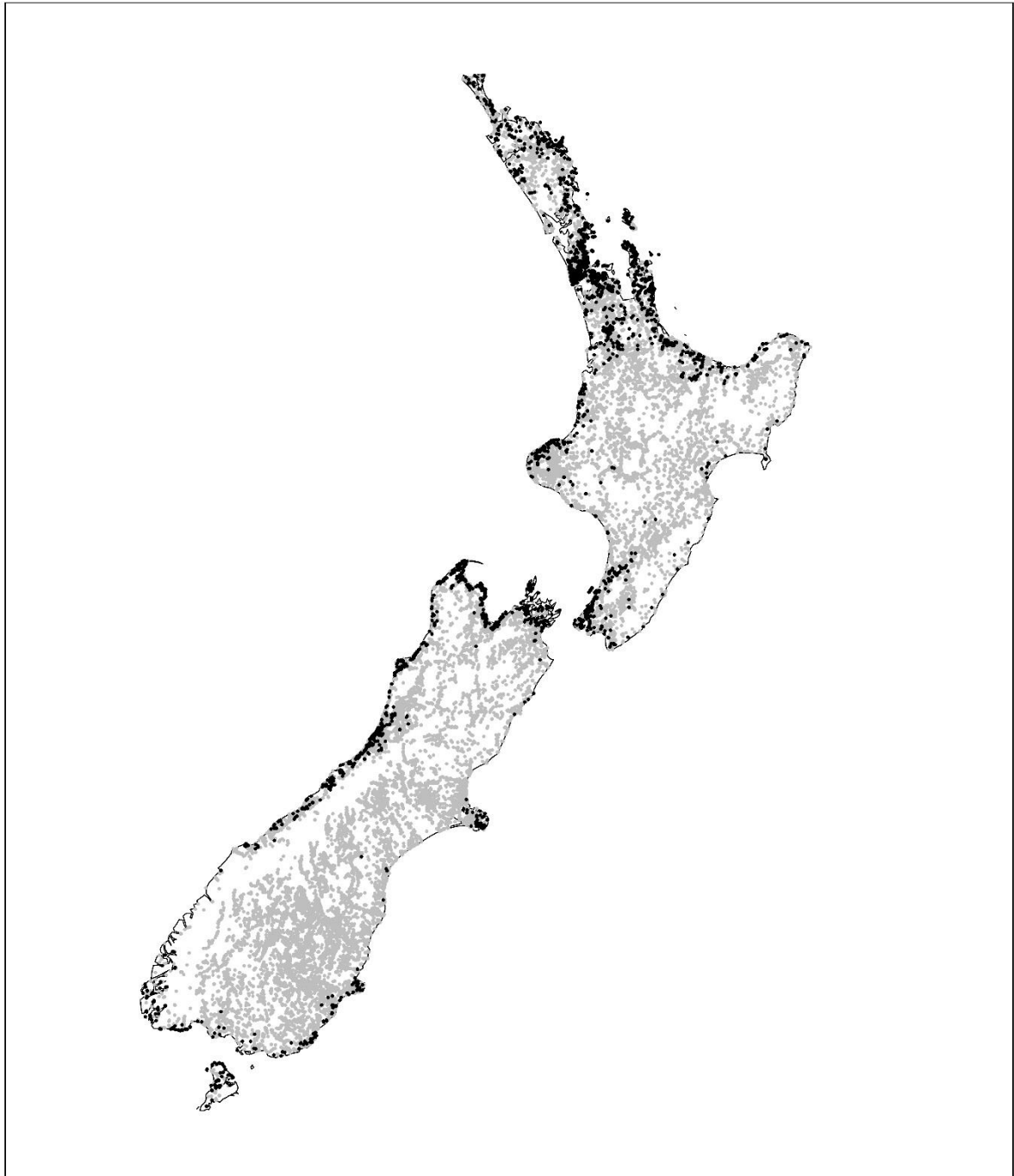
**Banded kōkopu** have a very coastally restricted distribution, similar to īnanga, but not as widely spread throughout the country (Figure 53). Like giant kōkopu in the South Island (Figure 52), banded kōkopu are absent from North and South Canterbury, but are present around Banks Peninsula. They are commonly found South of Dunedin and along Westcoast of the South Island. In the North Island, banded kōkopu are commonly found north of Wellington and on the North Taranaki Coast. This species is also commonly found around Auckland and between Whakatāne and the Coromandel (Figure 53).



**Figure 9: Locations of NZFFD records where (Left) inanga and (Right) shortjaw kōkopu are present (black circles) and absent (grey circles).**



**Figure 10:** Locations of NZFFD records where (Left) kōaro and (Right) giant kōkopu are present (black circles) and absent (grey circles).



**Figure 11:** Locations of NZFFD records where banded kōkōpu are present (black circles) and absent (grey circles).

## 6.3 State and Trends in Abundance

### 6.3.1 Method Recap

To account for some of the limitations in the NZFFD data, Crow et al. (2016) drew on several statistical approaches to address some of the biases that come with using this dataset. To identify if the ‘probability of capture’ for a taonga freshwater species through time appears to be increasing (getting better), decreasing (getting worse) or staying the same, Crow et al. (2016) completed simple linear regression<sup>1</sup> calculations (how does X relate to Y?) using two different techniques.

The first technique was the Sen Slope Estimator (SSE), while the second technique was a weighted version of the SSE. The weighted SSE (called WSSE hereafter) assigns a weighting value based on the size of the confidence intervals<sup>2</sup> (CI). In the WSSE, pairs of years that collectively have small CIs are weighted more heavily than pairs of years that collectively have large CIs because we were more confident in these probability of capture values.

Both WSSE and SSE results are presented in this report because, together, they help us understand whether or not we can be confident in the analysis and detect a trend over time (either increasing or decreasing) – or if we cannot detect a trend.

### 6.3.2 Kōaro Results

Kōaro was the only galaxiid species able to be assessed by Crow et al. (2016) using NZFFD records. While the SSE trend over the 1977–2015 period was indeterminate, the WSSE showed a decreasing trend. Weighted SSE results show that the probability of capture was decreasing at a median ( $\pm 95\%$  CI) rate of 0.05 ( $\pm 0.02$ ) %/year. In summary, the two trend analyses over the full-time series available (1977–2015) were not in agreement and did not show a strong trend in either direction; however, between 1995–2015 both analyses showed a decreasing trend (Figure 54) (Crow et al. 2016).

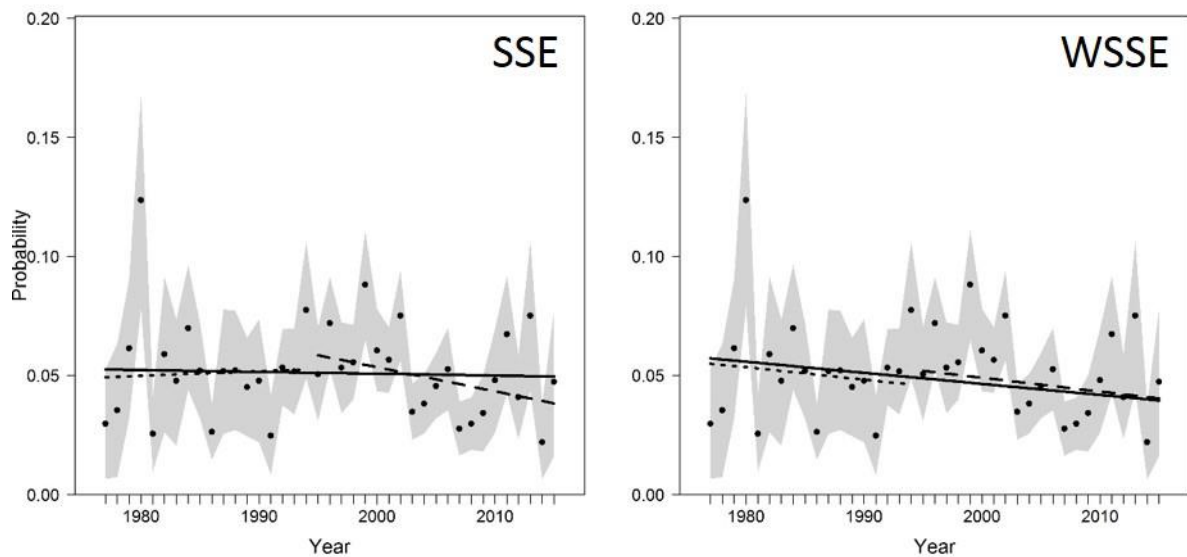
### 6.3.3 Lower Waikato River

In a review of the whitebait fishery in the lower Waikato River, Baker and James (2010) compared the annual catch estimated from commercial buyers records between 1930 and 1990 (Figure 55). Although there was some evidence of a decline between 1950 and 1980, more recent data suggest that the fishery has improved. However, these figures are highly variable and are considered to be of limited value for assessing the status of the fishery because annual purchases of whitebait will reflect fluctuations in demand and supply, as well as annual variations in the catch. Baker and James (2010) concluded that an historic decline in the fishery has probably occurred, although the magnitude and timing of this change is unknown. Baker and James (2010) concluded that a decline in whitebait has probably occurred in the Waikato River, as supported by knowledge of habitat decline in the Waikato River catchment (e.g., NIWA 2010), and anecdotal information of whitebait fishery decline from around Aotearoa-NZ (e.g., Hayes 1931, McDowall 1984).

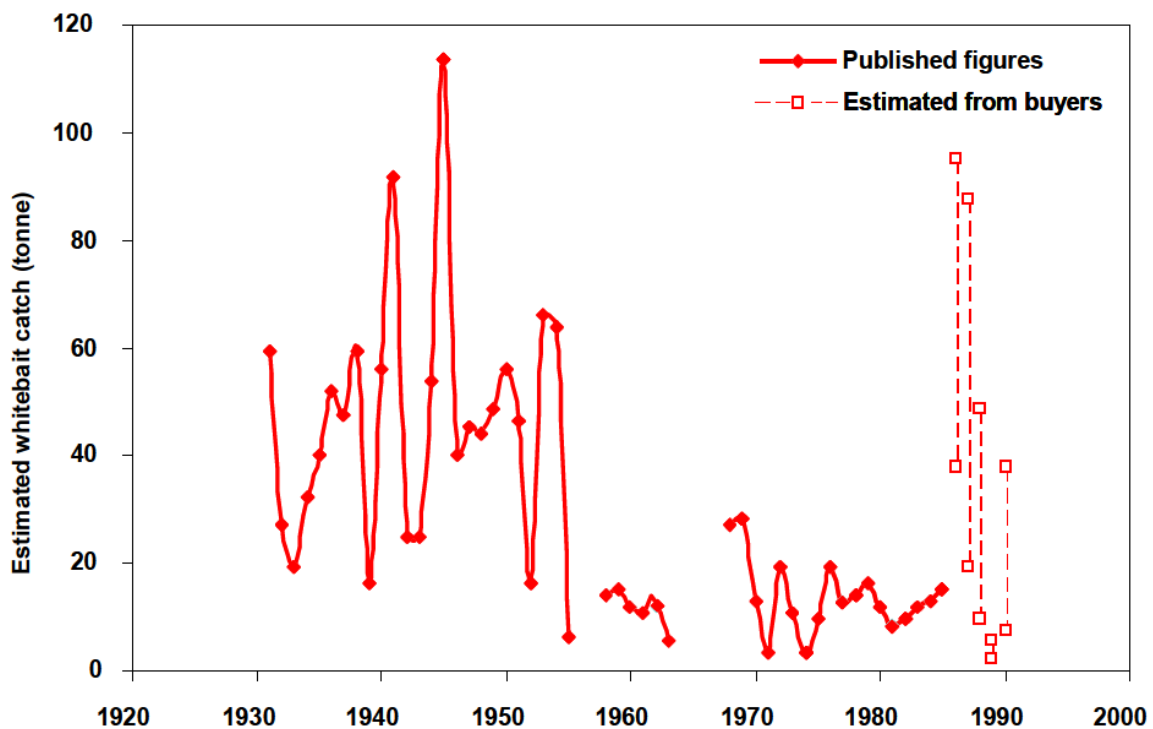
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<sup>1</sup> Simple linear regression is a statistical method that allows us to summarise and study relationships between two continuous (quantitative) variables.

<sup>2</sup> A confidence interval is a range of values we are fairly sure our true value lies within.



**Figure 12: Change in the probability of kōaro capture associated with year for the NZFFD.** Plots show the characteristic probability of capture for each year (black circles) and 95% CI (grey shaded area). SSE (left) and WSSE (right) are shown for 1977–2015 (solid black line), 1977–1994 (dotted black line) and 1995–2015 (dashed black line) (Source: Crow et al. 2016).



**Figure 13: Estimated annual total catch of whitebait from the Waikato River (galaxiids plus smelt) based on: (1) Catch records from Marine Department records (1931–1973); (2) Records from an Auckland canning factory (1958–1963); and (3) Commercial buyers records (1975–1990).** (Source: Baker & James 2010).

## 6.4 Threat Rankings

The latest New Zealand Threat Classification System assessment has classified īnanga, kōaro and giant kōkopu as ‘At Risk – Declining’. Shortjaw kōkopu are classified as ‘Threatened – Nationally Vulnerable’ with 5,000–20,000 mature individuals, and a predicted population decline of 30–70%; and banded kōkopu are listed as ‘Not Threatened’ (Goodman et al. 2014) (Table 9).

In 2014 īnanga and kōaro were assessed by IUCN as being of ‘Least Concern’. The panel recognised that īnanga remains widespread and abundant throughout its current range, but it acknowledged that this species has suffered from extensive habitat loss and deterioration throughout parts of its range which is likely to have had historical impacts on the Aotearoa-NZ population (David et al. 2014a). The panel noted that there is no information available on the global population trend of this species. The natural distribution of kōaro was recognised by the panel as fragmented throughout its range (probably due to habitat loss and degradation); however, it was noted that this species can penetrate well inland in many river systems and therefore have a more widespread distribution than the other large galaxiid species (David et al. 2014b) (Table 9).

The IUCN assessment panel have ranked shortjaw kōkopu as ‘Endangered’ (West et al. 2014a) as this species is sparsely distributed and is only known from a few sites in many areas. It is only found in specific habitats and is sometimes not found in neighbouring habitats, even though they appear very similar (West et al. 2014a). West et al. (2014b) ranked giant kōkopu as ‘Vulnerable’. Although specific data on the rates of giant kōkopu population decline are unavailable, the panel assumed on the basis of past, existing and continuing human pressures that the population has experienced at least a 25% decline over the past 20 years. Furthermore, it is possible that large, old fecund specimens could be sustaining populations in the face of habitat loss and drain clearing mortalities and a 10–20 year lag may be weakening the current observations of a decline (West et al. 2014b). Banded kōkopu have been rated as being of ‘Least Concern’ because this species is widespread and locally abundant throughout its range and the population is considered relatively stable (West et al. 2014c) (Table 9).

**Table 1: Threat rankings for Aotearoa-NZ whitebait species according to the New Zealand Threat Classification System and IUCN.** (see Section 2.3 for more information about these assessment methods).

Common name	Species	DOC Ranking	IUCN Ranking
Īnanga	<i>Galaxias maculatus</i>	At Risk–Declining	Least Concern (Population trend unknown) <sup>3</sup>
Shortjaw kōkopu	<i>Galaxias postvectis</i>	Threatened–Nationally Vulnerable	Endangered (Population decreasing) <sup>4</sup>
Kōaro	<i>Galaxias brevipinnis</i>	At Risk–Declining	Least Concern (Population trend unknown) <sup>5</sup>
Giant kōkopu	<i>Galaxias argenteus</i>	At Risk–Declining	Vulnerable (Populations decreasing) <sup>6</sup>
Banded kōkopu	<i>Galaxias fasciatus</i>	Not Threatened	Least Concern (Population trend stable) <sup>7</sup>

## 6.5 Pressures on Populations

Several pressures on whitebait populations have been identified (Figure 56), many of them are common to other freshwater taonga species. For example, the pressures outlined in Section 3.5.1–3.5.3 also apply to whitebait populations and will not be repeated below. Generally, most of the pressures operating on whitebait/galaxiids are poorly understood and do not have large amounts of supporting evidence for their effects. Potential pressures are, however, discussed below in relation to the limited information that is available.

### 6.5.1 Loss of Habitat

Habitat loss is likely to be the largest pressure on all whitebait species, but direct evidence for the impact of this pressure on whitebait populations is lacking. Historically, whitebait habitat is likely to

<sup>3</sup> <http://www.iucnredlist.org/details/197279/0>

<sup>4</sup> <http://www.iucnredlist.org/details/8813/0>

<sup>5</sup> <http://www.iucnredlist.org/details/197277/0>

<sup>6</sup> <http://www.iucnredlist.org/details/8817/0>

<sup>7</sup> <http://www.iucnredlist.org/details/197278/0>

have been reduced nationwide by swamp and wetland drainage. Wetland areas are important spawning habitat for some whitebait, but these areas have been reduced by an estimated 90% in Aotearoa-NZ (Hansforth 2011). These areas are particularly important for the dominant whitebait species (īnanga), which spawns on river/stream banks and wetlands among vegetation inundated by spring high tides. Aotearoa-NZ's loss of wetlands means that most īnanga spawning is now likely to occur along river margins only.

Because shortjaw, giant and banded kōkopu are found in areas with lots of overhead cover, the extensive deforestation in Aotearoa-NZ is considered the biggest threat to these species. The amount of forest coverage is estimated to have been reduced from 85% to just 28% (Taylor & Smith 1997), which has undoubtedly influenced habitat availability of the kōkopu species.

## 6.6 Land and Infrastructure Management

Whitebait spawning habitat along river margins may also suffer from stock grazing and any flood control works. It has also been shown that egg densities and survival are reduced by 75% and 25%, respectively, if spawning grasses are disturbed (e.g., cut) several months prior to the spawning season (Hickford & Schiel 2014). In larger river systems, the removal of riparian vegetation and the installation of hard-structures for flooding and erosion control have reduced the availability of īnanga spawning habitat. This effectively creates “sink” populations whereby īnanga cannot access sufficient spawning habitat, diminishing the reproductive output of a given river and likely fragmenting population connectivity (Hickford & Schiel 2011). The specific spawning habitats of kōaro and the kōkopu species are not well known. As such, alteration of riparian margins or instream habitat has unknown consequences for these species (Franklin et al. 2015). Furthermore, īnanga and giant kōkopu repeatedly use the same spawning sites (spawning site fidelity) meaning that compromised spawning habitat can impact on reproductive output and egg survival over the course of an entire spawning season and multiple years (Franklin et al. 2015) resulting in localised depletions.

Increased suspended sediment associated with land use intensification and urban development is also likely to have impacted on whitebait abundance. Increased suspended sediment is thought to be a major contributor to the current global decline in freshwater fish biodiversity (Maitland 1995, Hazelton & Grossman 2009), which has also been shown to impact on Aotearoa-NZ fishes (Rowe & Dean 1998). Rowe and Dean (1998) found that feeding rates of banded kōkopu and īnanga decreased with increasing turbidity, suggesting that increased suspended sediment may reduce growth rates. In addition to reduced feeding ability, whitebait have also been shown to avoid high suspended sediment (Boubée et al. 1997).



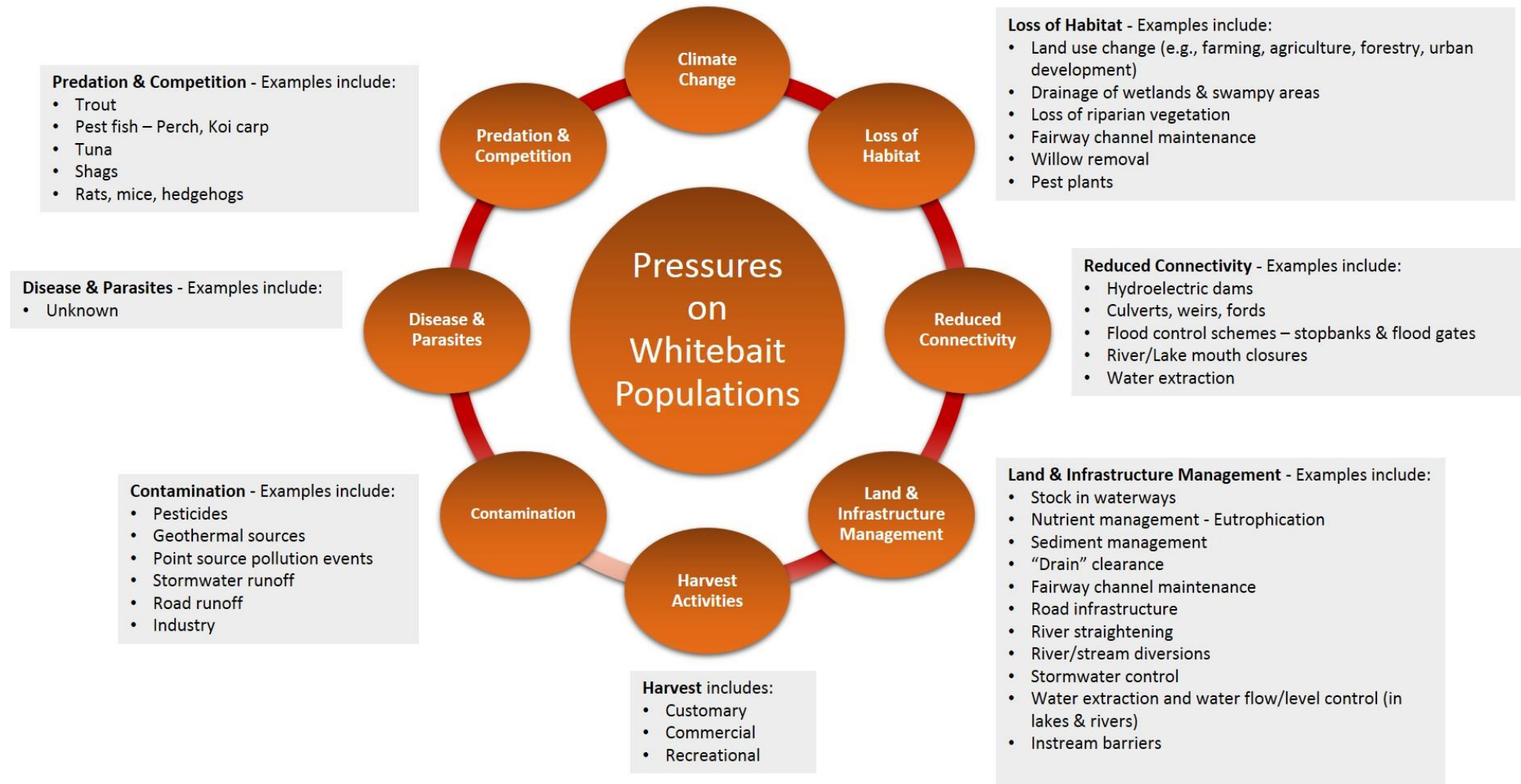


Figure 14: Examples of some of the pressures on Aotearoa-NZ whitebait populations.

There are few published studies in Aotearoa-NZ that have attempted to quantify or document the effects of mechanical or chemical drain cleaning on mortality of freshwater fish. Greer (2014) demonstrated that native fish abundance was reduced by 52% after mechanical excavation of macrophytes, but species diversity was not affected. Although partial macrophyte removal was still found to reduce fish abundance significantly, this technique might prevent large individuals of this species from leaving targeted waterways. In another study, Allibone and Dare (2015) found that giant kōkopu numbers declined from 18 fish to only 1, one year after drain clearance activities.

Modifications to the hydrological regime of rivers can impact negatively on populations of migratory Galaxiids at various stages of their life cycle. For example, flood flows stimulate the inward migrations of whitebait to rivers (McDowall 1995) with the largest runs often occurring after flood events. Low flows and less frequent flooding events may therefore delay or even limit the ability of whitebait to migrate in to freshwaters. The rate of upstream migration to the adult habitat, at least for īnanga, is influenced by stream flows among other factors such as water clarity (Allibone et al. 1999) and temperature.

Reduced flows can also affect spawning and egg survival for whitebait. Franklin et al. (2015) found that because of low winter rainfall in 2013, sufficient flows to re-inundate giant kōkopu eggs and stimulate larval hatching did not occur. Although the eggs remained alive for up to ten weeks in riparian vegetation, their viability decreased and high egg mortality rates ensued (Franklin et al. 2015). For non-diadromous populations of whitebait, higher flows are needed to stimulate upstream migration for spawning (Chapman et al. 2006). Low flows may affect land-locked populations by restricting upstream movement for spawning. In catchments with high demands for water resources, management of flow variability is important for spawning success of kōkopu species (Charteris et al. 2003, Franklin et al. 2015) and is likely similar for kōaro.

Following hatching, amphidromous larvae are considered largely passive because of their small size and poorly developed sensory abilities (McDowall 2009). As such, their initial dispersal is dictated by hydrology and other abiotic conditions. For diadromous populations, the downstream transport of larvae may be affected by variation in flows (Charteris et al. 2003). Conversely, given the recent observations that kōaro larvae in lakes display strong signals to flows (J. Augspurger, pers. comm.), larval dispersal and thereby population connectivity is likely influenced by flows, but at present this is not well understood.

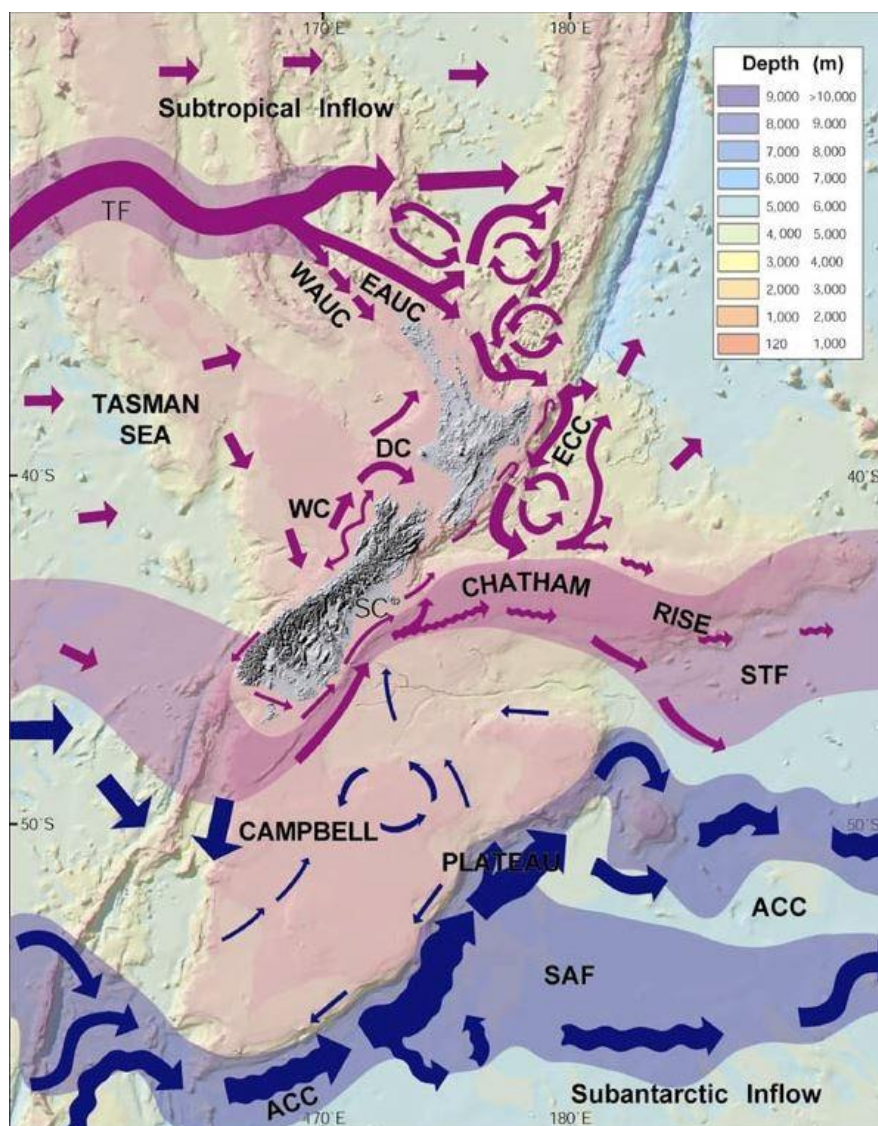
### 6.6.1 Predation and Exotic Species

The exotic species present in Aotearoa-NZ compete and predate on whitebait. Most of the predation pressure placed on whitebait by exotic species is likely to come from brown trout (McIntosh et al. 2010). Predation is likely to be especially high when sea-run/estuarine-living trout are present because these salmonids live in the lowland areas that most of the whitebait species occupy. Predation may be particularly high around the southern coasts of Aotearoa-NZ where ambient temperatures are lower and brown trout may be more anadromous (McDowall 1990). Glova (2003) presented evidence, from behavioural studies in a small stream simulator, that the number of īnanga declined when they shared the stream habitats with brown trout (255–390 mm long), and also that the galaxiids shifted their microhabitat with trout present. Presumably, this resulted in the galaxiids occupying less favourable microhabitats for drift feeding on invertebrates. Predation may also occur from rainbow trout and perch, but there is limited information on the direct effects of these exotic species.

### 6.6.2 Oceanic Conditions

Aotearoa-NZs oceanography is dynamic, with distinct temperature and productivity gradients associated with latitude, strong seasonal variation in abiotic conditions and complex ocean current

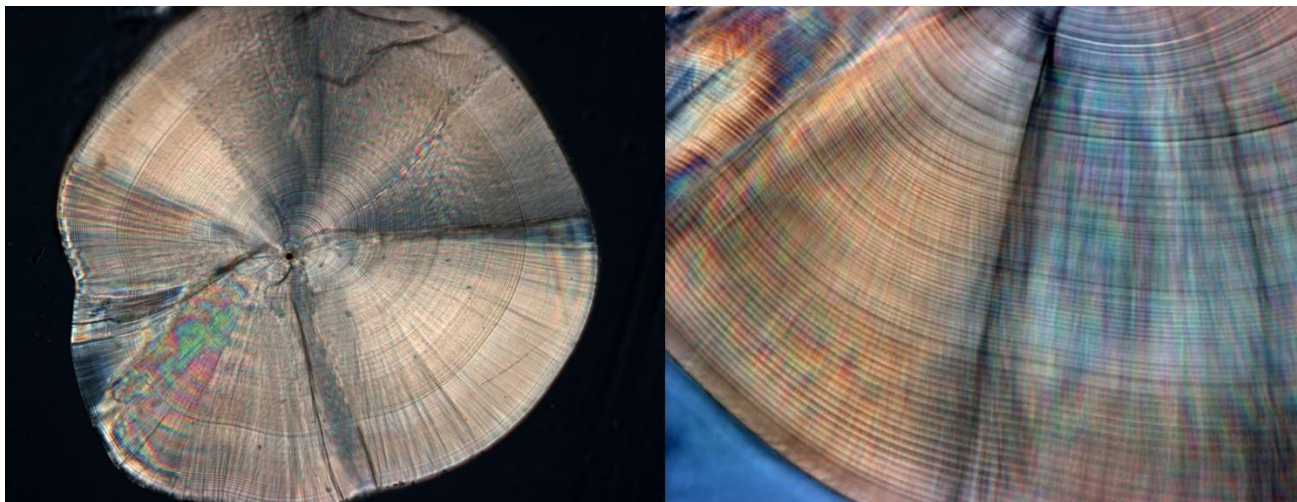
systems (Murphy et al. 2001, Stevens & Chiswell 2006, Chiswell et al. 2015) (see Figure 57). The extensive distribution and protracted spawning time, observed for some of the diadromous Galaxiids, means larvae undoubtedly encounter a wide range of environmental conditions during their marine life phase. The effects of oceanic conditions on the larval ecology of Galaxiids is mostly unknown, largely because larvae are rarely captured *in situ*.



**Figure 15: Ocean currents around Aotearoa-NZ.** Three major water masses coming in from the west influence Aotearoa-NZ ocean currents: the Tasman Front (TF), the Subtropical Front (STF), and the Sub Antarctic Front (SAF). The Tasman and Subtropical fronts are relatively warm surface currents. The Sub Antarctic Front is cooler and is associated with the cold Antarctic Circumpolar Current (ACC) that hugs the deep ocean floor to the east of the Campbell Plateau and Chatham Rise. (Source: Stevens & Chiswell 2006).

Within and across years, variation in the abundance of returning whitebait is likely to be impacted on by oceanic conditions (Rowe & Kelly 2009) and is not solely influenced by processes occurring in the adult or spawning habitats (Hickford & Schiel 2013). Despite difficulties associated with understanding the marine larval phase, Egan (2017) took an alternative approach and reconstructed the larval growth phase of *inanga* whitebait upon inward migration using their otoliths (Figure 58). Comparisons of *inanga* growth histories within and among four regions (Canterbury, Buller, Golden Bay and Bay of Plenty) as well as among larval hatching times were done to examine geographical

and temporal variation in marine growth. Results showed that īnanga whitebait in the Bay of Plenty were faster growing, migrate at a significantly younger age (95 days) and smaller mean size (36.5 mm) compared to īnanga in Canterbury that were slower growing, older at inward migration (mean age of 144 days) and larger (50.5 mm in length). There was little difference in marine growth rates, age or size at migration for īnanga in Buller and Golden Bay regions. These regional differences, and in some instances similarities, suggest that sea surface temperatures and productivity gradients are key environmental drivers of marine larval growth rate variation across Aotearoa-NZ.



**Figure 16:** The otolith or ear-bone of an īnanga, viewed under a high-powered microscope. The dark lines are the rings that are deposited every day of its life. The number of rings are used to estimate īnanga age, while distances between each ring are used to examine growth rates. (Photos: Eimear Egan).

Egan (2017) showed there is a growth rate threshold for migration that is determined during 40–60 days of marine larval life. īnanga with higher growth rates during this phase attained higher growth rates for the remainder of their life at sea and migrated at a younger age compared to slower growing larvae during this phase. Temperature is widely known to affect dispersal via its effects on growth and stage durations in fish (O'Connor et al. 2007) and is an important factor constraining īnanga growth rates, regulating larval dispersal duration with important ramifications for the connectivity of populations.

Furthermore, Egan (2017) found that the marine growth histories of īnanga vary with larval hatching times. īnanga larvae hatched in the winter months grew faster during larval life and returned to freshwaters at a younger age than īnanga hatched during autumn across Aotearoa-NZ. Uncoupling between spawning/larval hatching and favourable oceanic conditions for growth and survival may result in high larval mortalities at sea of specific larval cohorts. This may partly explain some of the temporal variation seen in abundances of whitebait throughout the migration season. The larval-juvenile life stage of most freshwater fishes is the most susceptible phase to mortality, with more than 90 % of the juveniles dying (e.g., Hayes 1988). Identifying the sources of mortality for whitebait and the role oceanic conditions plays in regulating larval mortality is difficult. In addition, it is uncertain if mortality rates differ among species. Because of life-history differences among the whitebait species (e.g. larval size at hatch, yolk sac size, fecundity), it is plausible that larval-juvenile mortality rates differ accordingly but this is unresolved.

Climate change and associated changes to sea surface temperature and circulation patterns have been implicated in the decline of īnanga in south-west Australia (Barbee et al. 2011) but this is currently unknown for Galaxiids in Aotearoa-NZ. The implications of increasing sea levels on īnanga spawning habitat availability is currently being studied (Shane Orchard, University of Canterbury). It is important to recognise that much of what is known about the marine larval life of migratory

Galaxiids, and relationships with ocean conditions is specific to īnanga. Species-specific studies are needed to understand if and how oceanic conditions impact on kōaro and kōkopu species. The application of new techniques like otoliths analyses alongside dispersal modelling will help address some of these knowledge gaps.

### 6.6.3 Harvest

Īnanga are the most abundant species in the whitebait catch, and kōaro are the second most abundant. Kōaro are usually the first species to run up the rivers after floods and are often referred to as “run bait” by fisherman because they are the first sign that a run of whitebait may be coming. Kōaro can be the most abundant species at certain times of the year in some West Coast rivers where habitat is ideal from this species (McDowall 1990). Banded and giant kōkopu run later in the season, with banded kōkopu often being referred to as golden bait because of their amber colour. Because of the later running of these species they are likely to be less susceptible to fishing pressures. Little is known about the timing of shortjaw kōkopu whitebait because they are can't be easily distinguished from the other whitebait species. Non-whitebait species are accidentally caught by whitebaiters and are mostly regarded as “by-catch”. These species include smelt, freshwater shrimp, glass eels, adult eels, juvenile and adult bullies, yellow-eyed mullet and lamprey (Yungnickel 2017).

Despite whitebait supporting substantial commercial, recreational and customary fisheries, there is a very limited amount of information available on the extent or potential impacts of these harvests. The limited information available suggests that fishing pressure in large rivers can potentially reduce recruitment of whitebait. For example, a study on the Mōkau River used dye-stained whitebait to determine how many whitebait escaped past anglers' nets (Baker & Smith 2014). Baker and Smith (2014) found that fisherman captured between 3 and 27% of the tagged fish in the mainstem of the Mōkau River. Other studies on the Awakino River showed capture rates of up to 44% (Allibone et al. 1999), and the Operau River had catch rates between 6% and 23%. Overall, these results showed that whitebaiters can catch up to 45% of the run. A parallel study showed that only about 20% of the whitebait that escaped, survived to reach adulthood (Allibone et al. 1999). The differences in catch rates between the mainstem and the tributary site suggest that smaller streams are likely to have high catch rates. This is possibly because whitebait have a smaller area to evade capture in these small streams.

The limited data available on fishery catches makes it difficult to quantify the impact of harvests on the whitebait population. McDowall (1990) previously suggested that the whitebait population has almost certainly declined since human settlement, but this is likely to be have driven by multiple interacting effects such as those mentioned previously. When it comes to only quantifying the effect of harvest alone on the whitebait population, there is no data other than that outlined above. However, we do know that fast-growing annual species are especially susceptible to over-exploitation and precise knowledge of their stock structure is imperative for sustainable fishery management (Aguera & Brophy 2011).

## 6.7 Management

### 6.7.1 Stock Structure

In Aotearoa-NZ rivers, whitebait fisheries are typically based on the juvenile, upstream migrant phase of five galaxiid species (includes īnanga, kōaro, giant kōkopu, banded kōkopu, shortjaw kōkopu) and smelt <sup>e.g.,<sup>8</sup></sup>. A stock is defined as a “semi-discrete group of fish with definable genotypic, phenotypic and demographic attributes” (Begg et al. 1999). The whitebait fishery is currently

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<sup>8</sup> <https://www.mpi.govt.nz/food-safety/community-food/whitebait/>

managed as a single stock, despite these species having diverse distributions, habitat requirements and widely different life history traits (e.g., egg size, size and age at sexual maturity, fecundity, spawning times and migration patterns). Management as a single stock assumes that the five Galaxiid species show similar genetic, phenotypic and demographics characteristics throughout Aotearoa-NZ. It further assumes, for a given species (e.g., īnanga), that these characteristics are similar in the context of current fishery management practices. The existence of sub-populations and/or separate stocks has long been recognised as one of the priorities for the management of the whitebait fishery (McDowall 1999). However, a general lack of basic information on the biology and ecology of whitebait has made studies of stock structure difficult.

Genetic methods were used by Waters et al. (2000) to investigate the genetic structure of īnanga whitebait from five sites from the Cascade River in Westland to the Bay of Islands in Te Tai Tokerau. No genetic differences were found among these areas suggesting that īnanga larvae are widely dispersed with considerable population exchange during their marine life (Waters et al. 2000) and little evidence for different stocks. No genetic studies have been completed for the kōkopu species or kōaro, however, on-going research by Jane Goodman (University of Otago) is addressing some of these knowledge gaps.

It has long been speculated that there are multiple stocks of īnanga in Aotearoa-NZ based on “phenotypic” (physical characteristics) rather than “genotypic” (heritable genetic identity) features. In 1980, McDowall and Eldon suggested that sub-population structures of īnanga exist based on regional variation in whitebait size at inward migration (McDowall & Eldon 1980). Regional differences in age at inward migration further show spatial differences in early life history traits (McDowall et al. 1994, Rowe & Kelly 2009) giving more evidence for stock structure. McDowall (2003) showed that īnanga whitebait in the North Island have fewer vertebrae than those in the South Island, which might be indicative of larvae having resided in thermally distinct water masses, and thereby relatively discrete stocks. Hickford and Schiel (2016) showed that less than 3% of īnanga returned to their natal stream, which suggests there are significant levels of mixing between river systems and less evidence for river-specific stocks. Despite this mixing, there is evidence for discrete larval pools based on regional variation in otolith-chemical signatures between the west and east coasts of the South Island. This suggests that larval dispersal between these areas is limited (Hickford & Schiel 2016).

Further evidence for different īnanga stocks comes from analysis of otolith morphology and growth rates by Egan (2017). Although the exact origins of inward migrating īnanga are unknown, significant spatial differences in growth rates during the first ten days of life show there is a clear separation between īnanga in the Bay of Plenty and South Island populations. Morphological analyses further show separation between the Bay of Plenty and Buller/Golden Bay regions. Egan (2017) suggested that oceanography (see Figure 57) and environmental conditions play an important role in the spatial structuring of populations among these regions. Although īnanga whitebait in Canterbury showed significantly different growth patterns to those in the Bay of Plenty, no morphological differences were detected between these regions. Egan (2017) suggested there may be extensive mixing of īnanga populations along the east coast of Aotearoa-NZ. Larval dispersal and mixing along the east coast was found for torrentfish, another amphidromous species (Warburton 2015). However, extensive mixing of īnanga along this coastline is speculative and was not resolved in the Egan (2017) study.

Greater spatial coverage is needed to ascertain if more stocks exist along with a better integration of multiple techniques like genetic and otolith analyses. Studies of the stock structure of kōaro and kōkopu species have not been done. However, there is preliminary evidence for spatial differences in size and age at migration that show similar patterns to īnanga (McDowall et al. 1994, Yungnickel

2017). Resolving the stock structure of kōaro and kōkopu species is important to ensure the sustainability of the whitebait fishery, especially considering kōaro and banded kōkopu comprise up to 25% of the whitebait catch in some parts of Aotearoa-NZ (Yungnickel 2017).

### 6.7.2 Agencies Involved in Management

The whitebait fishery has been described as “a highly dispersed activity, lightly regulated, and very lightly enforced” (McDowall 1991). Multiple agencies are involved in the management of the fishery and the processing of whitebait for human consumption. Rules around catching whitebait are set by DOC, while MPI’s role is to ensure that any processed whitebait is safe for human consumption<sup>9</sup>.

Limitations/restrictions are in place on equipment and fishing season, but no restrictions have been made on catch size (e.g., weight of fish). There are **two different regulations** for fishing seasons: (1) From 15 August to 30 November for all areas except the West Coast of the South Island (and the Chatham Islands); and (2) From 1<sup>st</sup> December to the last day in February for the West Coast of the South Island. The season for the West Coast also places limits on the upstream limit where fishing can occur (limit is marked by “upper pegs” in the river banks) and by not allowing fishing in the hours of darkness.

At present, information on the number of fishers, catches, distribution and sales from this extensive customary and recreational fishery that occurs across the country is lacking. In the lower Waikato River alone Morris et al. (2013) recently identified 869 whitebait stands, 31% of which also had a small to large “bach” associated with the stand.

Whitebait is the only fish species in Aotearoa-NZ that can be sold by recreational fishers, and can reach prices as high as \$130 a kilogram e.g., 10&11. Wild-caught whitebait has been sold commercially from various locations around the country since early European settlement, with the first canning factory established on the Waikato River in 1887. Wild-caught whitebait is being sourced for the commercial market from places like the West Coast (e.g., Cascade Whitebait), South Westland (Curly Tree’s Whitebait), and “rivers of the east and west coast of the North Island”<sup>12</sup> (Hawkes Bay Seafoods).

There is little known about escapement before, after or during the fishing seasons. The lack of data on escapement and fishery catch means that there has never been any ability to relate catches to populations, estimate the impact of fishing on the stocks, or to monitor any of the fundamental aspects required for effective fishery management. The regulatory focus on equipment and fishing behaviour has been done to limit enforcement costs. It is more costly exercise to enforce/set and monitor quotas and/or daily limits on all rivers, than it is to set fixed limitations on the equipment and how it is used. Because the whitebait fishery includes some vulnerable and declining species, DOC have a challenge to manage the contrasting values between the fishery and the preservation of our native biodiversity.

Compliance for whitebait stands and associated structures are the responsibility of regional councils, under the Resource Management Act 1991, and in the case of the Waikato River, the **Waikato-Tainui Raupatu Claims (Waikato River) Settlement Act 2010** which recognises the traditional activity of fishing for whitebait, including the use of traditional whitebait stands (Morris et al. 2013, Mahuta et al. 2016). Other legislation and regulations of relevance to whitebait stands and

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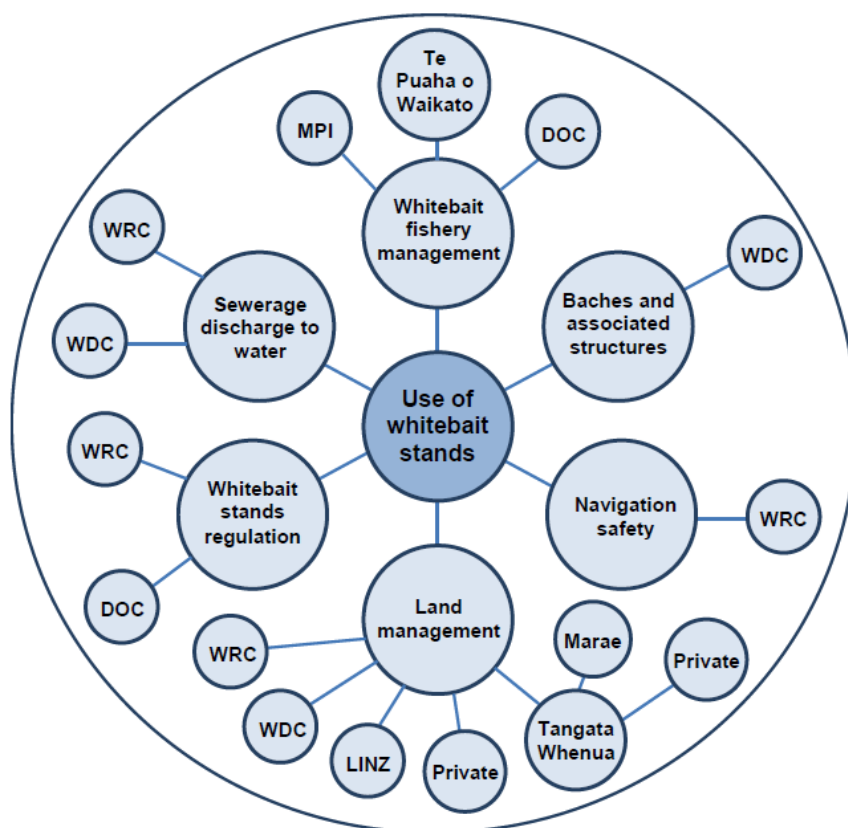
<sup>9</sup> <https://www.mpi.govt.nz/food-safety/community-food/whitebait/>

<sup>10</sup> <http://www.stuff.co.nz/national/11021/Whitebait-snapped-up-at-130-a-kg>

<sup>11</sup> [http://www.nzherald.co.nz/nz/news/article.cfm?c\\_id=1&objectid=3594881](http://www.nzherald.co.nz/nz/news/article.cfm?c_id=1&objectid=3594881)

<sup>12</sup> <https://www.hawkesbayseafoods.co.nz/category/113396>

associated structures includes the Building Act 2004, the Navigation Safety Bylaw 2009 (for the Waikato River), Land Act 1948 and Public Works Act 1981 (Morris et al. 2013) (Figure 59).



**Figure 17:** Some of the agencies involved in the management of the lower Waikato River whitebait fishery. Where WRC = Waikato Regional Council; WDC = Waikato District Council; LINZ = Land Information New Zealand. (Source: Morris et al. 2013).

All five whitebait species are presently managed by DOC, and with the exception of *īnanga*, are included in DOC's, **large galaxiid recovery plan** 2003–2013 (DOC 2005), which outlined a number of options for recovery. This document is expected to be updated in the very near future. Giant and shortjaw *kōkopu* are listed as two of the 150 priority threatened species listed in DOC's draft **Threatened Species Strategy** (see Section 11.2).

Because *kōaro* can form land-locked populations, parts of this species range occur in protected areas where fishing is prohibited or does not occur. Historical land status changes have occurred with the creation of **three faunistic reserves** (Lake Chalice, Lake Christabel and Lake Rotopounamu), specifically to preserve lake-locked populations of *kōaro* (DOC 2005). This species is also covered within the 2009 Action Plan for South Australian Freshwater Fishes and it also occurs in several conservation reserves in South Australia.

A **national *īnanga* spawning database** is presently being revived by the University of Canterbury in collaboration with NIWA, DOC, Aquatic Ecology Ltd, local councils and community groups (<https://inangaconservation.wordpress.com/inanga-spawning-sites-seasketch/>). The database aims to collate all existing information on *īnanga* spawning and assemble these data into one place in a consistent and accessible format. The database is open access and anyone can contribute data. The database contains information on the spatial locations of spawning observations along with associated environmental information for the site.



A **New Zealand Fish Passage Advisory Group**<sup>13</sup> convened by DOC has been established to develop, communicate, promote, and advocate for improved technical guidance and policy to support fish passage and connectivity of our waterways.

## 6.8 Aquaculture

Several individuals, organisations and partnerships are also involved in developing whitebait aquaculture. The late Charlie Mitchell developed an interconnected system of coastal ponds to spawn and rear whitebait, in a style akin to “ranching”. Mahurangi Technical Institute have recently developed the technology to “close the life cycle” and breed whitebait in captivity and are now partnering with others to develop commercial whitebait farms and provide this product for market (e.g., Manāki Premium New Zealand Whitebait<sup>14</sup>) (Figure 60).



**Figure 18:** Example of the whitebait products available via Manāki Premium New Zealand Whitebait. (Source: <https://twitter.com/whitebaitnz/status/763165387877789696>).

<sup>13</sup> <http://www.doc.govt.nz/nature/habitats/freshwater/fish-passage-management/advisory-group/>

<sup>14</sup> E.g., <https://www.stuff.co.nz/business/farming/aquaculture/96142508/new-zealands-only-whitebait-farm-looks-to-protect-species-under-strain>