

SHORT COMMUNICATION OPEN ACCESS

Swimming Under the Radar: Trout-Free Kōaro Populations in Aotearoa Lakes and Tarns Are Rare, Understudied, and Disappearing

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ABSTRACT

Over the last 150 years, most large, easily accessible lakes and tarns in Aotearoa (New Zealand) have experienced trout introductions or incursions, leaving few salmonid-free reference lakes. Using database information and field surveys, we characterized lake, pond/tarn, and wetland systems found throughout Aotearoa that support populations of kōaro (*Galaxias brevipinnis*) known or putatively believed to be trout-free. These systems require more research because our existing knowledge is outdated, patchy, and largely unacknowledged, while their kōaro populations may be increasingly vulnerable. Although persisting trout-free kōaro populations tend to be found in small, isolated, and difficult to access lakes, at least 10% and potentially up to 22% of known trout-free kōaro populations may have already been lost in the last 20 years. The causes of these losses are varied and highlight the sensitivity of the remaining populations, which are likely genetically isolated and evolutionarily significant. Historic and modern threats to these remaining kōaro populations include incursions of introduced fishes and worsening climate impacts. Lakes supporting isolated kōaro populations hold substantial conservation value, require more consistent monitoring to prevent additional losses of irreplaceable populations, and need targeted conservation of this important taonga (treasured species) consistent with the diversity they contribute to Aotearoa's broader freshwater biodiversity.

1 | Introduction

Freshwater ecosystems worldwide are heavily invaded by non-native organisms (Havel et al. 2015; Gallardo et al. 2016). The consequences of lake introductions are wide-ranging, including community homogenization (Muthukrishnan and Larkin 2020), food-web disruption (Wainright et al. 2021), and ecosystem collapse (Reynolds and Aldridge 2021). As invasions continue, uninvaded systems have become rarer but offer “reference” for comparison with invaded systems (Correa and Hendry 2012), are highly valued by indigenous peoples, and hold unique biodiversity.

Prior to European arrival in Aotearoa (New Zealand; henceforth Aotearoa), native kōaro (*Galaxias brevipinnis*) were likely present in many inland lakes (Stokell 1955; McDowall 1990; Rowe and Schallenberg 2004). Isolated kōaro populations are derived from diadromous populations that facultatively ceased migrating, fish “stuck” inland by geological processes (deglaciation, landslides, drying), or mahinga kai (food sources) introductions by Māori (Rowe and Schallenberg 2004). The life history plasticity of kōaro (Hicks et al. 2020; Augspurger et al. 2021) likely contributed to this adaptability to both flowing and nonflowing systems (Figure 1). Once established, kōaro likely became

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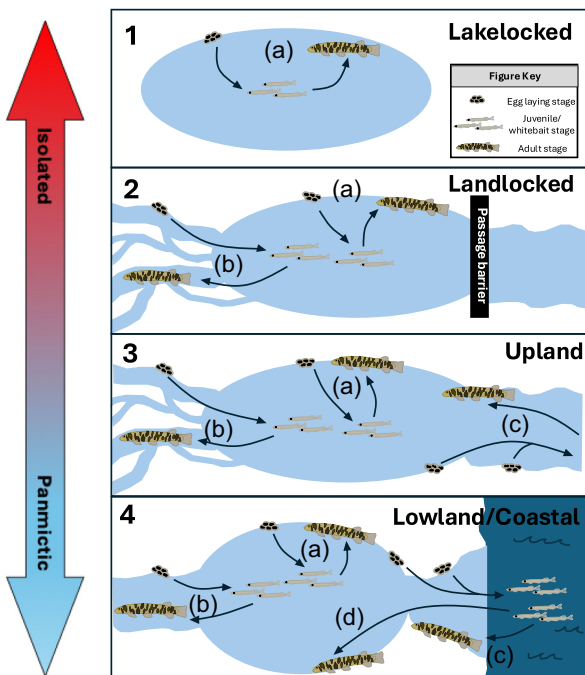


FIGURE 1 | Conceptual diagram of potential kōaro life history strategies and habitat use across different freshwater systems of Aotearoa with varying degrees of population isolation. (1) In the most isolated lake-locked systems with no inflows or outflows, kōaro use lake habitat in both juvenile and adult life stages (a). (2) In landlocked systems with both river and lake habitat, but with downstream access blocked by barriers of either natural (e.g., landslip) or manmade (e.g., hydroelectric dam) origin, kōaro can either (a) spend their entire life cycle in lake habitat or (b) use lake habitat as juveniles and river habitat as adults. (3) In upland systems with both river and lake habitat and direct but geographically distanced access to the sea, kōaro can either (a) spend their entire life cycle in lake habitat, (b) use lake habitat as juveniles and river habitat as adults. Some emergent fry (c) may also be flushed further downstream to lowland systems and return to use upland habitat (either lake or stream) as adults. (4) In panmictic lowland and coastal systems, kōaro can (a) spend their entire life cycle in lake habitat, (b) use lake habitat as juveniles and river habitat as adults, (c) flush out to sea as fry and later use river habitat as adults, or (d) flush out to sea as fry and later use lake habitat as adults. Actual kōaro life history strategies and habitat usage may not reflect the full spectrum of potential strategies depicted here, depending upon habitat availability, competition with other native species, impacts of introduced species, and other factors.

abundant in littoral and pelagic lake habitats (Rowe et al. 2002; McDowall 2011).

Introduced salmonids (trout) have fundamentally altered kōaro persistence (Rowe 1993), size (Fletcher 1919; Hobbs 1948), and ecosystem roles (Hayes 1995) in many lakes following both legal and illegal introductions for sport (McDowall 1994) and spread through sea-run populations. Impacts on lake kōaro include competition with adults, predation on juveniles, reductions in density, and habitat-use changes (Rowe et al. 2002; Rowe et al. 2003).

Isolated lakes that are free of introduced species are the “last ark,” revealing how Aotearoa lake ecosystems functioned historically and how lake and kōaro ecology change over time. Further, these lakes are the few remaining examples where the abundance of this taonga (treasure) could be sufficient to support mahinga kai.

Many inland kōaro populations, for example, were likely placed by Māori tūpuna (ancestors) as mahinga kai (McDowall 2011). Consequently, the persistence of these populations is whakapapa, a direct connection to the landscape across generations.

To date, there has not been a nationwide assessment of trout-free populations of kōaro in lakes. Information about these populations is confined to opportunistic and historic database records, and the current condition of many of these populations is unknown or outdated. Here, we use these database records combined with in-person site visits to evaluate the status and characteristics of presumed trout-free kōaro lakes in Aotearoa, and highlight the vulnerability and conservation value of these lakes to help ensure the continued persistence of these taonga.

2 | Methods

Sites with putative trout-free kōaro populations were identified by searching the New Zealand Freshwater Fish Database (NZFFD; Richardson 1989; accessed 13 Dec 2023 and 19 March 2025) and consulting local experts. We selected systems using sequential filters: first, we selected all observations from nonstream systems and then observations of kōaro. From there, we removed any systems which also contained at least one NZFFD trout observation. To account for patchy database records (especially trout records), sites were also removed if additional evidence, such as listing on fishing blogs, indicated trout presence. The resulting list provided a set of putatively trout-free lakes to study (Table 1).

A subset (26%) of these lakes was subsequently visited in 2024 to evaluate kōaro population status (Table 2) as part of a wider study. Site selection was influenced by existing mana whenua relationships, sampling permits, and ethics agreements held by the research team. Sites were surveyed with ~7 traps (Gee minnow traps, fyke nets) per site and visual observations (e.g., trout jumping or cruising). Kōaro population status was updated (e.g., confirmed extant, no kōaro observed, etc.), and lakes where no kōaro were observed were resampled 2–3 more times to further assess absences.

Time (in years) since the last kōaro NZFFD observation for each system was calculated, and lake characteristics such as depth, area, and distance to the nearest road were incorporated (if known) or calculated (LINZ Data Service). Calculations, filtering of database records, and data visualization were performed in R (version 4.4.3), and maps were generated using the *nzffdr* package (Lee and Young 2021). Kōaro populations were categorized as either “lake-locked,” “landlocked,” “upland,” or “lowland”, according to kōaro movement likelihood and sea access (Figure 1). Lake-locked kōaro populations are limited exclusively to isolated lake habitat, while landlocked populations can access both lake and river habitat above a passage barrier. The other two lake types both have upstream and downstream river connections for adult and juvenile kōaro and some degree of sea access for migrating juveniles, but upland lakes are farther from the sea compared to lowland lakes.

3 | Results

3.1 | Database Analyses

Of over 170,000 NZFFD observations (as of March 2025), only 10.3% were from lakes, ponds/tarns, or wetlands (hereafter,

TABLE 1 | Characteristics of presumably trout-free, kōaro-containing lakes in Aotearoa New Zealand, sourced from NZFFD, expert knowledge, and LINZ Data Service.

Region	Kōaro population status	Years since last NZFFD survey	Year of most recent kōaro NZFFD record	Number of kōaro observed at last NZFFD record	Presumed trout-free status	Lake type	Max. depth, m	Lake area, Ha	Lake elevation, m	Distance to nearest road, km
Bay of Plenty	NKO - S	0	1954	1	Y	Landlocked	—	52	330	0.1
Hawkes' Bay	PE	20	2004	38	Y	Landlocked	—	2.4	960	5.6
	PE	20	2017	87	Y	Landlocked	—	13.1	670	0.3
Nelson/Tasman	PE	22	2002	—	N	Upland	—	1.4	1260	12.9
	PE	26	1998	1	Y	Landlocked	—	28.9	1325	2.49
Marlborough	PE	52	1972	17	Y	Landlocked	—	5.6	1340	2
	PE	21	2003	2	Y	Upland	—	0.6	1300	12.2
	PE	2	2023	444	Y	Upland	—	13.7	1200	10
	PE	23	2001	—	Y	Upland	—	8.7	1008	0.5
	CE	0	2004	193	Y	Landlocked	36	42	744	2
West Coast	PE	12	2012	204	N	Upland	—	1.1	1040	0.7
	PE	12	2001	—	N	Upland	—	25.7	1030	0.4
	PE	18	2007	14	N	Upland	—	258	650	3.9
Canterbury	PE	21	2003	3	Y	Landlocked	—	15.4	970	5.4
	PE	30	1994	—	Y	Lowland/Coastal	24.2	34.9	405	5.2
Canterbury	PE	2	2022	12	Y	Lakelocked	1.5	1.2	760	0.1
	NKO - T	0	2024	42	Y	Lakelocked	1.5	3	678	0.3
Canterbury	PE	16	2008	2	N	Upland	—	1.7	693	1.2
	CE	0	2005	5	Y	Lakelocked	2.4	7.1	815	0.08
Canterbury	NKO - U	0	2005	1	Y	Lakelocked	1.7	6.4	795	0.2
	CE at nonviable numbers	0	2020	6	Y	Landlocked	2	0.4	650	1
Canterbury	NKO - S	0	—	—	Y	Landlocked	6	10	661	5.6
	CE	0	—	—	Y	Landlocked	5	1.5	1177	3.2
Canterbury	PE	44	1980	—	Y	Upland	—	25	590	0.3
	PE	36	1988	1	Y	Lakelocked	10	4	420	0.04
Canterbury	PE	19	2005	49	Y	Lakelocked	—	0.5	890	0.1

(Continues)

TABLE 1 | (Continued)

Region	Kōaro population status	Years since last NZFFD survey	Year of most recent kōaro NZFFD record	Number of kōaro observed at last NZFFD record	Presumed trout-free status	Lake type	Max. depth, m	Lake area, Ha	Lake elevation, m	Distance to nearest road, km
Southland	PE	47	1977	—	Y	Lakelocked	—	0.6	600	0.2
	PE	13	2011	110	Y	Landlocked	—	1.6	627	20.1
	PE	43	1981	—	Y	Upland	—	81.4	695	2.5
	PE	22	2002	—	Y	Upland	37	47.4	486	36.4
	PE	20	2004	2	Y	Upland	—	207	570	30.2
	CE	0	2021	3	Y	Landlocked	9.8	13.3	694	1.6
	PE	46	1974	—	Y	Lakelocked	—	11	205	0.2
	PE	43	1981	1	Y	Lakelocked	—	26.7	23	63.3

Abbreviations for kōaro population status: CE, confirmed extant; PE, presumed extant; NKO - T, no kōaro observed, likely extirpated due to trout incursion; NKO - U, no kōaro observed due to unknown causes; NKO - S, no kōaro observed, likely due to smelt incursion. Trout-free status indicates whether a given lake is likely free of trout (Trout free, Y) or is likely to contain or is confirmed to contain trout (Trout free, N); lakes presumed to contain trout are grayed out and excluded from analysis. Lakes that were visited during field surveys are denoted in bold type. Lake type categories follow the system described in Figure 1. Individual lake names are redacted here but are available upon request to the authors. Lake area, elevation, and distance to nearest road were calculated using data sourced from the LINZ Data Service licensed for reuse under CC BY 4.0.

“lakes;” $n = 18,003$). Approximately 1,406 lake systems had some kind of fish survey, and of those, only 81 had kōaro observations (Figure 2). Those 81 systems accounted for 150 kōaro observations and only 3.2% of kōaro observations nationwide; the remaining 96.8% came from stream/river systems. Less than half of the 81 lakes with kōaro observations were initially identified as putatively trout-free ($n = 34$; Figure 2), and five lakes were excluded for likely trout presence (final trout-free lake count: $n = 29$). The majority of putatively trout-free kōaro lakes were lakelocked or landlocked ($n = 9$ and $n = 11$, respectively; Table 1), and trout-containing lakes outnumbered trout-free lakes in all categories except lakelocked (Figure 3). The 29 kōaro lakes were typically small, elevated, and isolated (Table 1); average [\pm SD]: maximum lake depth, 11.4m [\pm 13.3m; $n = 12$]; area, 22.9 ha [\pm 40.3ha]; elevation, 744 m [\pm 326m]; and distance to nearest road, 7.3 km [\pm 14.0km]. Even factoring in the nine sites surveyed within the past 2 years for this study, the average age of the most recent kōaro record for these trout-free lakes was 19.0 years \pm 17.7 years SD (Figure 4; Table 1). Thus, these populations are not monitored regularly.

3.2 | Site Visits

From the field visits, five of the nine visited lakes were confirmed to have kōaro present (Figure 5), although at one site, only one individual was detected in 24 traps across three site visits, so is likely at extremely low density or on the verge of extirpation. Two visited lakes appear to have experienced kōaro population declines or losses: one site with kōaro observed in early 2024 experienced an adult trout incursion, likely in late 2023 or early 2024, after which no kōaro have since been observed; while the other had not been sampled in 19 years and possible reasons for kōaro decline are unclear (Table 1). Both systems were resampled at least two times, yielding zero kōaro. The final two systems experienced historic introductions of common smelt (*Retropinna retropinna*) and also yielded no kōaro (Table 1), corroborating records for these lakes (NZFFD; Rowe and Taumoepeau 2004). Kōaro extirpation following smelt invasion has been observed before in other Aotearoa lakes and likely results from the combined impacts of two mechanisms: smelt predation on kōaro larvae, and interspecific competition between smelt and adult kōaro for food resources (Rowe 1993; Kelly and McDowall 2004; Ward et al. 2005; Stewart et al. 2024). Overall, the status of this subsample of ‘trout-free’ kōaro lakes was concerning.

4 | Discussion

We assessed the state of trout-free kōaro populations in Aotearoa lakes finding the number of trout-free kōaro populations is decreasing and populations are confined to small, shallow, inland lakes almost exclusively on Te Waipounamu (the South Island). The isolation of these systems may have largely precluded nonnative species from invading these sites, also explaining why lentic systems with unimpeded connections to the sea are underrepresented in this dataset. We found that most trout-free kōaro lakes are lakelocked or landlocked; upland and lowland lakes are less likely to be trout-free because of their riverine connections to other invaded freshwater systems and the ability of sea-run salmonids to migrate between these systems. Road access likely also influences trout-free status: trout-free lakes were on average 7.3 km away

TABLE 2 | Results of field survey visits (abbreviations follow conventions used in Table 1).

Region	Kōaro population status	Updated trout-free status following surveys	Max. depth, m	Lake area, Ha	Gee minnow traps, fyke nets deployed (successive surveys are additional rows)	Kōaro catch, (average per trap)	Other fish species catch, (average per trap)
Bay of Plenty	NKO - S	Y	—	52	0,4	0	Common smelt 132 (33) <i>Arguilla</i> spp. 1 (0.25)
Marlborough	CE	Y	36	42	8,1	207 (23.0)	—
Canterbury	NKO - T	N (formerly Y)	1.5	3	4, 0	42 (7.0)	—
					8, 0	0	Rainbow trout (visual obs.) 2
					7, 1	0	
	CE	Y	2.4	7.1	6, 1	57 (8.1)	<i>Gobiomorphus</i> spp. 70 (10.0)
					6, 0	8 (1.3)	<i>Gobiomorphus</i> spp. 74 (12.3)
					6, 0	71 (11.8)	<i>Gobiomorphus</i> spp. 19 (3.2)
	NKO - U	Y	1.7	6.4	6, 1	14 (2.3)	<i>Gobiomorphus</i> spp. 20 (3.3)
					5, 0	0	—
					4, 0	0	—
					4, 0	0	—
	CE at nonviable numbers	Y	2	0.4	8, 0	0	—
					8, 0	0	—
	NKO - S	Y	6	10	8, 0	1 (0.1)	—
					7, 1	0	<i>Gobiomorphus</i> spp. 94 (11.8)
	CE	Y	5	1.5	8, 1	18 (2.0)	Common smelt 6 (0.8)
					8, 1	49 (5.4)	—
Southland	CE	Y	9.8	13.3	8, 1	250 (27.8)	—

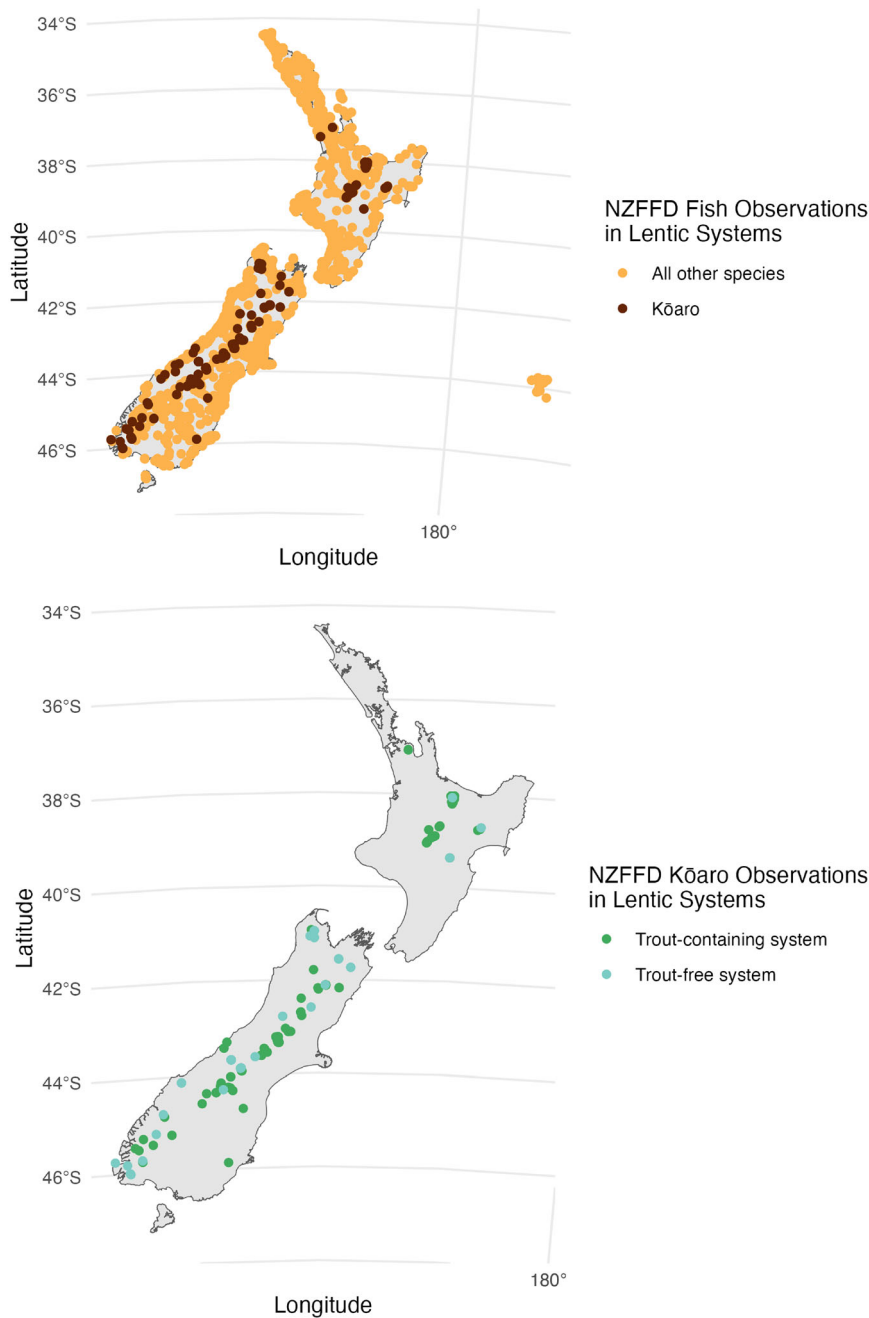


FIGURE 2 | All lentic kōaro observations recorded in the NZ Freshwater Fish Database (NZFFD; upper panel, dark points) highlighted among all lentic fish observations in the NZFFD (upper panel, light points), and all NZFFD observations of kōaro in lentic systems categorized by whether the system is trout-free (lower panel, dark fill) or trout-containing (lower panel, light fill).

from the nearest road, whereas the average trout-containing lake was within 1 km of the nearest road. Despite the putative isolation of some lake systems, introductions or invasions can occur at any time, as demonstrated by introductions of smelt to Lake Rotopounamu in the 1980s (Rowe 1993), smelt to Lake Marion in the 1940s or earlier (NZFFD), trout and smelt to Lake Rotokawau (date unknown), trout to Lake Christabel in the 1980s (P. Gerbeaux, *pers. comm.*), and trout to one field site in 2024 (Table 2). Invasions at all but one lake resulted in kōaro extirpation, highlighting their vulnerability despite their isolation.

Of the nine sites we surveyed, we corroborated that no kōaro were observed at two lakes that experienced historic smelt introductions, we observed no kōaro at two lakes where kōaro were

previously observed, and we found that one population has such low densities it is likely nonviable. These findings underline the perilous state of isolated kōaro lakes. The two (and potentially, soon to be three) likely extirpations first documented here were discovered by chance; the current kōaro population status may be uncertain in many other trout-free kōaro lakes because they have not been surveyed in decades. Extrapolating our survey suggests that up to 22% of these populations could already be lost. Our study relied on existing, public database records which are not comprehensive enough to establish the current extent of trout-free lake kōaro populations in Aotearoa. Yet, this is also the best available resource, and substantially more records are available for streams than lakes. Unstudied kōaro populations likely exist

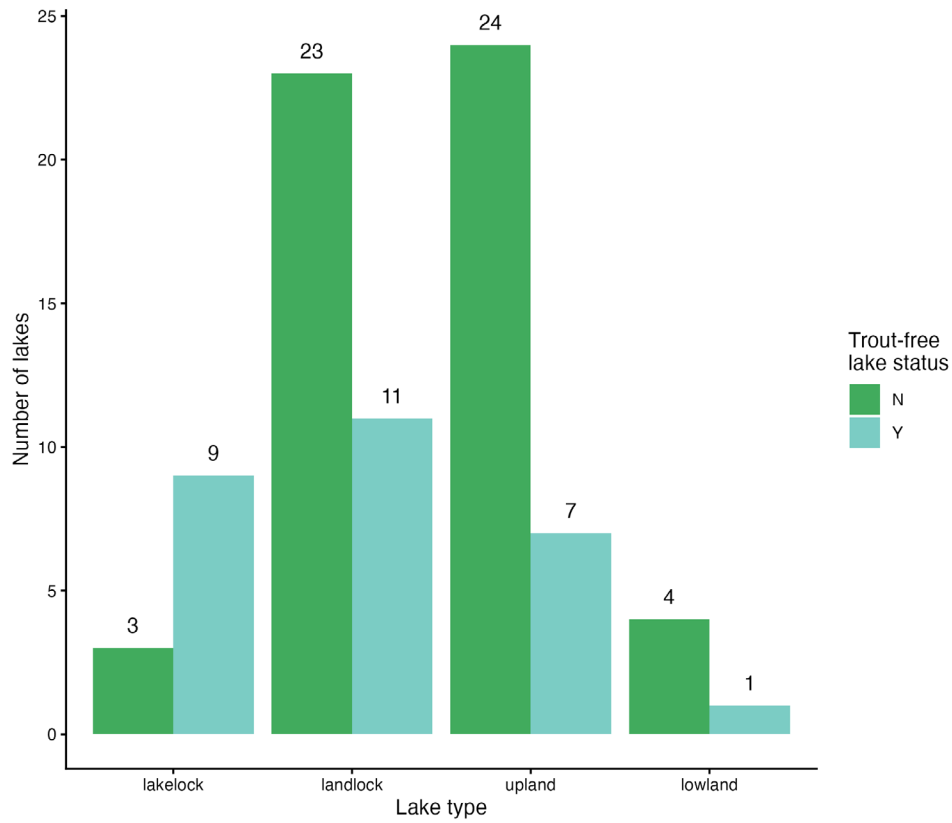


FIGURE 3 | Lakes with kōaro observations (numbers) grouped by lake type and trout presence/absence (colours; N, no; Y, yes). Trout free lake status is N if trout are believed to be (or are confirmed to be) present in the lake; status is Y if the lake is believed to be free of trout. Lake type is defined in the context of fish passage, described in Figure 1.

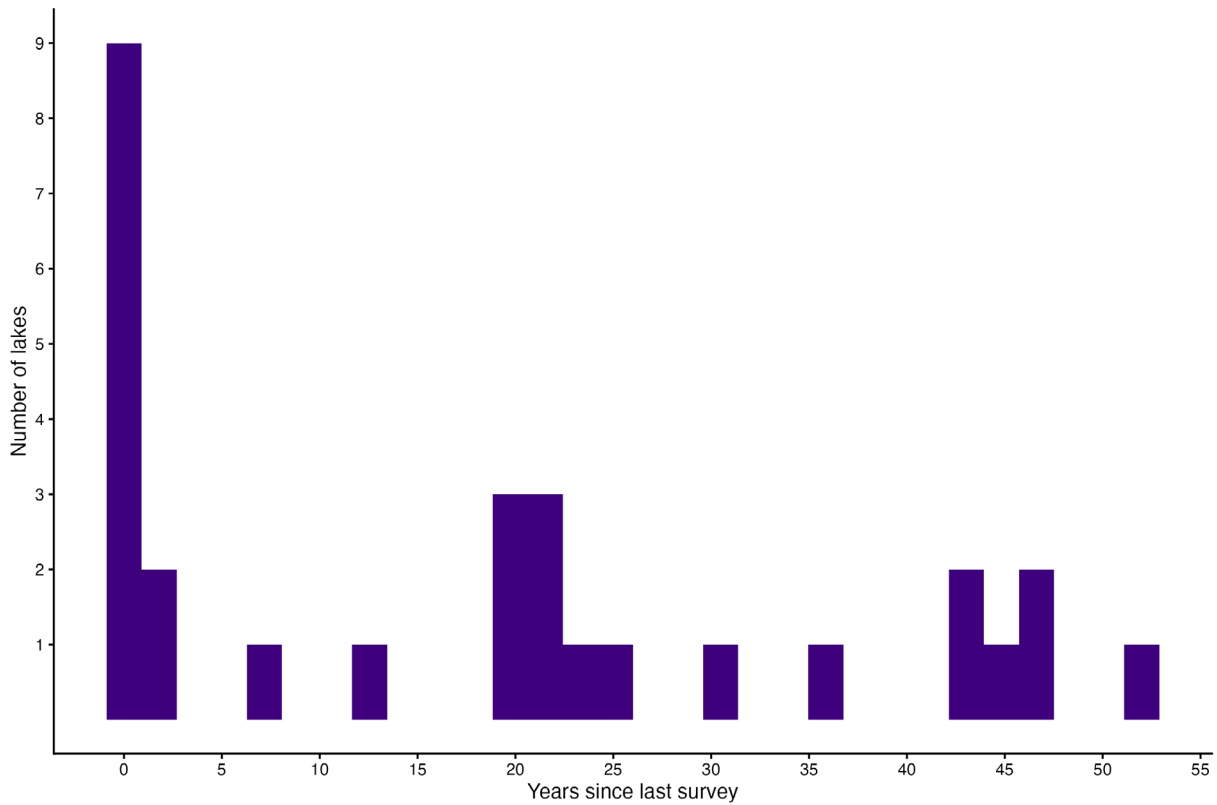


FIGURE 4 | Number of years since putatively trout-free, kōaro-containing lake systems were last surveyed for fish populations (NZFFD observations). More than half of putatively trout-free lakes have not been surveyed in nineteen years or more.

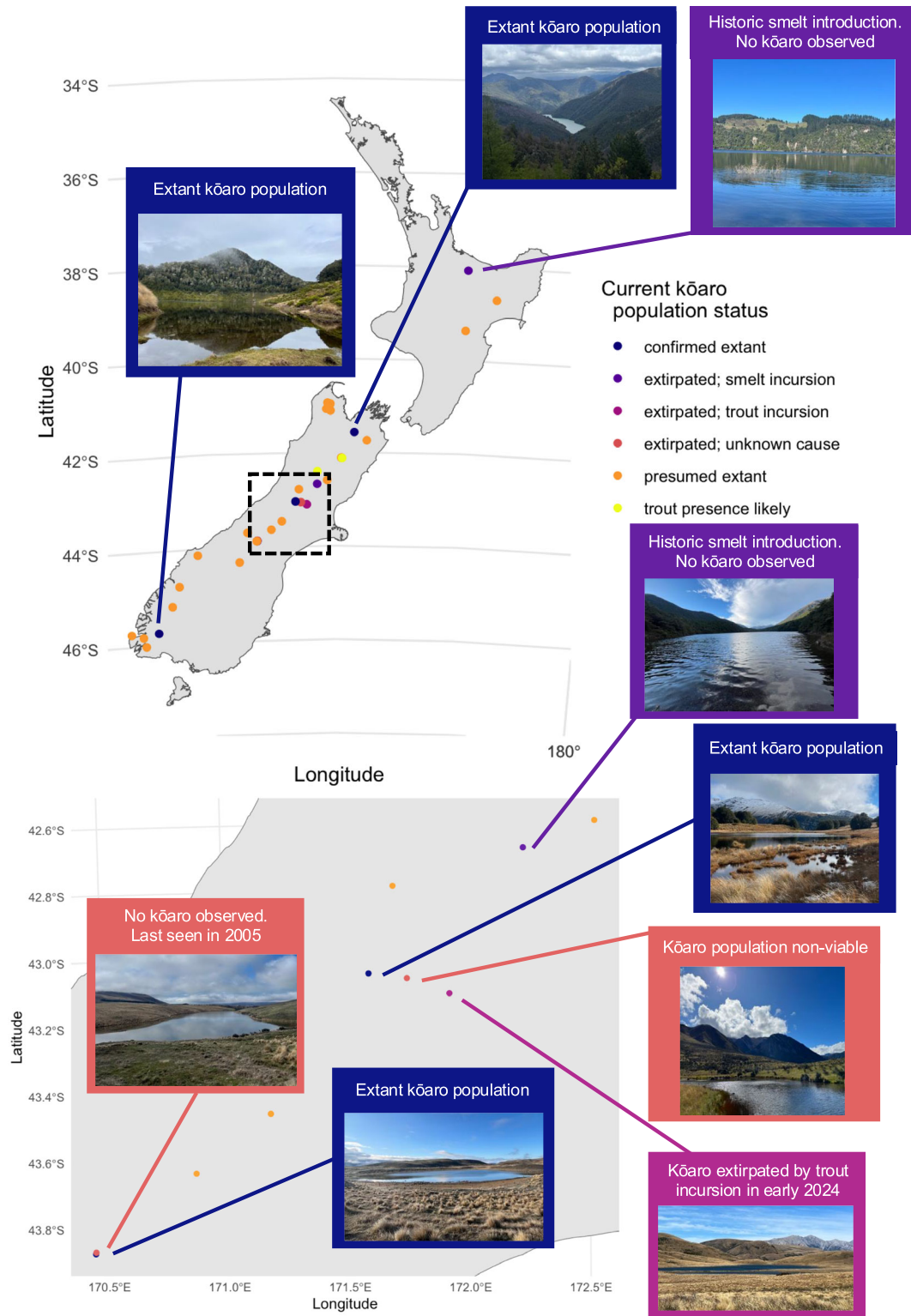


FIGURE 5 | Status (colors) after site visits to nationwide (upper panel), presumed trout-free lake systems with kōaro observations, and an inset focusing on Canterbury region sites (lower panel). Pictures illustrate each visited lake. Four populations were confirmed to be extant (blue), two were corroborated as extirpated by common smelt (purple), one was potentially extirpated by trout incursion (pink), and two were potentially extirpated (or soon to be extirpated) due to unknown causes (coral). Remaining systems were not surveyed but are presumed to still contain populations of kōaro (orange), though trout are likely present at two of these sites (yellow). The inset panel of Canterbury region lakes indicates that even systems in close geographical proximity can have different risks of kōaro population loss.

in remote lakes but remain undetected to date. Challenges notwithstanding, surveying remote lakes for kōaro is urgent because they may be especially vulnerable to changing climates and

further invasions; we risk losing them before they are documented. Further, we acknowledge that proving a negative (in this case, that kōaro are completely absent from lakes where we failed

to detect them) is statistically improbable and that our sampling effort cannot rule out that perhaps kōaro continue to persist at some lakes at very low densities that are challenging to detect. However, our observations also raise important questions about how much sampling effort is needed to accurately document declines or extirpations of native fish in lake ecosystems, especially in systems that have only been sporadically monitored over decades with opportunistic data records that may reflect limited sampling efforts.

Isolated kōaro populations are vulnerable for several reasons, and this vulnerability may be exacerbated because invasions are not closely monitored and Māori are separated from their fisheries in these systems. The small size and variable hydrology of these lakes risks elevated water temperatures and low oxygen levels during heat waves and droughts (Woolway et al. 2021; Shinohara et al. 2023), making them vulnerable to drastic changes in community composition and food web structure (Bertani et al. 2016). Small populations may be more vulnerable to disease outbreaks and more affected by invasions (De Castro and Bolker 2005; Jamieson et al. 2008). Climate change will worsen these threats, and more isolated kōaro populations could be silently lost.

Trout-free systems present the closest available analog to how Aotearoa lakes functioned prior to European arrival, with kōaro likely the main pelagic fish in lakes (Rowe and Schallenberg 2004; Ingram and Bennington 2018). That so few trout-free kōaro lakes exist could suggest that inland establishments and landlocking of kōaro were uncommon, but it is more likely that extensive trout introductions altered systems before they were documented. Trout-free reference lakes are a valuable comparison to evaluate how introduced species and anthropogenic impacts alter lake ecosystems. Unlike panmictic, amphidromous kōaro populations, many of these lakelocked and landlocked kōaro have been isolated for long periods, may have evolutionary value for their unique contributions to Aotearoa fish biodiversity, and could reveal new lineages (Jense et al. 2024). The habitat differences between, for example, a lakelocked population and a diadromous population are substantial, and kōaro could have developed unique traits necessary for surviving solely in lake habitat.

Urgent conservation actions for securing trout-free kōaro include: classifying isolated kōaro lakes as a threatened ecosystem type; monitoring and detecting populations in peril; safeguarding systems from threats; and codesigning specific conservation guidelines for isolated kōaro with mana whenua that acknowledges their cultural roles. Kōaro are primarily managed within the context of coastal, diadromous whitebait, lacking specific management plans for landlocked or lakelocked kōaro. Since isolated kōaro have inherently different conservation needs from migratory populations with fish passage access, landlocked and lakelocked systems would benefit from classification as a threatened ecosystem type. Additionally, regular, consistent monitoring will help track vulnerable populations and inform surveillance during high-risk periods (e.g., hot and dry summers). Frequent monitoring could more quickly identify incidents, such as trout invasions or unexpected population declines due to disease, and provide more robust data to justify rapid interventions like the removal of an invasive organism, treating poor environmental conditions in situ, or even relocating a population into temporary captivity before collapse.

The persistence of these kōaro also depends on their continued isolation from invaders; preventing introductions increases the security of these populations but relies on goodwill. Information campaigns, signage, and the installation of didymo detergent kits in areas with populations of significance could help prevent accidental pest incursions and discourage intentional fish introductions (Boon et al. 2008; Gates et al. 2009; Vagias et al. 2014; Azevedo-Santos et al. 2015; Rahel and Smith 2018; Gill et al. 2020). Additionally, since lakes close to roads or invaded waterways are more vulnerable to invasion, and since 16 of the 29 known trout-free kōaro lakes are positioned at or within 2 km of the nearest road, these sites may require greater monitoring or public engagement than more isolated lakes. In general, public awareness of the diversity of kōaro and value beyond their familiar role as whitebait could promote their stewardship.

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Data Availability Statement

The data that support the findings of this study are openly available on Figshare at <https://doi.org/10.6084/m9.figshare.31664125>.

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