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ORIGINAL PAPER

Invasive catfish linked to the decline of freshwater crayfish in two Aotearoa New Zealand lakes

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Abstract The introduction of invasive species can have profound impacts on ecosystems, especially where endemic species have evolved in isolation. However, determining the influence of invasive species on native biota can be difficult because long-term data are lacking. Our study examines the impact of invasive brown bullhead catfish (*Ameiurus nebulosus*) on native kōura (freshwater crayfish, *Paranephrops planifrons*) populations in two North Island, Aotearoa New Zealand lakes (Rotoiti and Rotorua). The invaded lakes were compared with two control lakes (Ōkāreka and Rotokākahi) where catfish are absent using a quasi-BACI (Before-After, Control-Impact) design. Long-term monitoring data in the invaded lakes (2005–2024) show significant declines in kōura abundances and biomass with changes in size structure after catfish establishment. In contrast, kōura populations in control lakes showed no significant changes in abundance or biomass in 2009 compared to 2021. Environmental variables (water quality, dissolved oxygen, and invasive macrophytes) showed minimal change in the same period. Netting data showed catfish abundances increased as kōura numbers fell, supporting the conclusion that catfish predation—rather than broader environmental degradation—is the main driver of kōura decline. The impact of catfish on kōura has severe cultural ramifications, to the extent that customary Māori fisheries are no longer viable in Lake Rotoiti. Restoration of kōura populations will require catfish control, habitat enhancement, and ongoing monitoring to prevent further spread of invasive species. More broadly, integrated invasive species management and habitat restoration are crucial to protect culturally and ecologically significant native species in Aotearoa New Zealand's freshwater ecosystems.

Tuhinga Whakarāpopoto Ki te kuhu mai tētahi momo koiora kia tū mātotoru ka kino rawa pea mō te taiao, te iwi me te ōhanga anō hoki inarā kua tupu motuhake ai ngā momo Māori pēnei i ngā taiao pānekeneke i Aotearoa nei. Hoi anō he āhua uaua te kite i te kaha whakawaeawe o te momo rāwaho i te korenga o ngā raraunga titiro whāroa. Ko tēnei mātainga e āta titiro ana ki te kawekawe o ngā ika-

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poti kīrehe (*Amerius nebulosus*) ki ngā kōura Māori (*Paranephrops planifrons*) i roto i ētahi roto moana e rua i Te-Ika-ā-Mauī, Aotearoa (Ko Te Rotoiti me Rotorua). Nā te tauira ō BACI (Before-After, Control Impact) I whakatairitehia ngā moana i whakaekea e te ikapoti ki ētahi moana e rua anō kāre he ikapoti ā rāua (ko Ōkareka me Rotokākahi). Nō te roa o te mātai ki ngā moana i whakaeketia e te ikapoti (2005–2024) ka kitea te kaha heke o te rahi me te maha o ngā kōura. He mea whakatairite kē te tataunga kōura i Ōkāreka me Rotokākahi i mau tonu ki aua nama i waenga i ngā tau 2009–2021. I taua wā tonu kāre i tino rerekē ngā āhuatanga taiao pēnei i te pai o te wai, te memehatanga o te hāora me ngā rimurimu kīrearea. Nā te whakakao mātaihanga ka kitea te piki o te ikapoti i a te kōura e heke ana. He tohu tērā e mea ana nā te kai a te ikapoti i ngā kōura taiohi kē i mimiti ai te kōura, ehara nā ngā kino i te taiao. Inā rā te kino o te ikapoti mō ngā mahinga kai a te iwi kāre he take o te rama kōura me te mahi tau kōura tonu i ēnei rā. Mā te patu i te ikapota, mā te whakatika i te wāhi noho me te āta tiaki i te taiao kia kaua e kuhu mai he kīrearea anō, e rauorahia mai ai te kōura. Kia kotahi hoki te mahi karo i ngā kararehe me ngā rākau kīrearea me te whakarauora i te taiao hai tiaki i ngā ika māori kai ngā taiao wai māori o Aotearoa.

Keywords Non-native species · Long-term ecological data · *Ameiurus nebulosus* · *Paranephrops planifrons* · Mātauranga Māori · Traditional ecological knowledge

Introduction

Invasive species are one of the main threats to biodiversity (Clavero and García-Berthou 2005). Invasions are directly responsible for ecological impacts in natural ecosystems, as well as economic damage to fisheries, aquaculture, infrastructure, and human health (Haubrock et al. 2022). In freshwater ecosystems, ecological impacts due to invasive fish include declines in native fish populations and species extinctions (Bernery et al. 2022), which can cause profound changes in food webs and further drive trends toward biotic homogenization (Su et al. 2021).

While invasive species pose a global threat to ecosystems and are the subject of extensive scientific research, long-term assessments of their effects on native species are still relatively uncommon (Pergl et al. 2020; Haubrock et al. 2025). This is primarily due to the limited access to long-term data needed to evaluate these impacts alongside other environmental drivers (Grarock et al. 2014; Su et al. 2021). Robust approaches to detecting the effects of invasive species on native species are demanding. They require the collection of standardized data on the abundance of native biota before and after the establishment of the invasive species, in multiple invaded areas and multiple control areas where the invasive species is not established (Blossey 1999; Underwood 1994). As an archipelago with a long history of geographical isolation, Aotearoa (=New Zealand, Aotearoa hereafter) has been impacted by a wide range of invasive species, making it ideally placed to illustrate the many challenges that invasions present worldwide (Hulme 2020).

Freshwater ecosystems in Aotearoa are subject to multiple stressors (Burdon et al. 2013), including invasions by non-native species. Various ecological impacts due to invasive non-native fish have been reported, including declines and extinctions of native fish species (McDowall 1990). Non-native species now represent more than 25% of the freshwater fish diversity found in Aotearoa, leading to it being described as a global invasion hotspot (Leprieur et al. 2008). Twenty-one species of non-native freshwater fish have established populations in Aotearoa; some are highly valued, but many pose a threat to freshwater biodiversity (DOC 2003). The brown bullhead catfish (*Ameiurus nebulosus* Lesueur, 1819, hereafter bullhead catfish) has spread from its native range in North America to several other continents, including Europe, Asia and South America (Froese and Pauly 2025). It was introduced to Aotearoa in 1877, making it the only ictalurid found in an archipelago with no native species of catfish (McDowall 1990).

Globally, non-native bullhead catfish have been reported as having adverse effects on freshwater ecosystems (Froese and Pauly 2025) and have been associated with reductions in native biodiversity. Catfish can reduce water quality and increase nutrient status through the resuspension of sediments and excretion (Cline et al. 1994). Further, their omnivorous diet means that they can prey on a wide variety of native species, including fish, freshwater crayfish and other macroinvertebrates, (Scott and Crossman 1973; McDowall 1990). Invading catfish

may impact the demography of crayfish populations by reducing abundances and altering size distributions. Crayfish–fish interactions are primarily structured by crayfish body size, which strongly modulates vulnerability to fish predation (Butler and Stein 1985). Larger crayfish experience reduced predation risk, influencing both encounter outcomes and behavioral responses in size-dependent ways consistent with ecological theory (Stein and Magnuson 1976; Werner and Gilliam 1984).

Aotearoa has two endemic species of freshwater crayfish that are commonly known by the indigenous Māori word 'kōura'. The northern kōura, *Paranephrops planifrons* White, 1842 occurs in the North Island and the West Coast of the South Island, and the southern kōura, *P. zealandicus* (White, 1847) occurs in the east and south of the South Island (McDowall 2011). Catfish predation of Aotearoa's kōura offers further insights into how insular faunas respond to non-native predators, with expected negative effects due to each species' nocturnal behaviour and overlapping habitat use. At the national level, the impacts of this invasive predator is of great interest due to the cultural and ecological importance of kōura (Hiroa 1921; Kusabs and Quinn 2009; Kusabs et al. 2015a). Kōura support limited recreational fisheries throughout Aotearoa (McDowall 2011), but important customary fisheries in the central North Island including the Rotorua Te Arawa lakes (Arawa lakes hereafter) and Lake Taupō, where kōura are abundant (Kusabs and Quinn 2009). They are a 'keystone' species, reflecting overall freshwater ecosystem health (Collier et al. 1997).

In Aotearoa's Lake Taupō, bullhead catfish commonly consume kōura (particularly juveniles) and are considered a more effective predator of kōura than introduced rainbow trout (*Oncorhynchus mykiss*; Barnes and Hicks 2003). Kōura were found in the guts of 15% of small (50–149 mm fork length; FL) and 64% of large bullhead catfish (> 250 mm) caught in rocky areas (Barnes and Hicks 2003). Predation on kōura is likely to be even more severe in shallow and mesotrophic lakes, as kōura are unable to find refuge from catfish as they do in deep, oligotrophic lakes (Dedual 2002; Kusabs and Taiaroa 2015). In addition to directly feeding on kōura, bullhead catfish may compete with crayfish for shelter and food resources (Barnes 1996), and can initiate anti-predator responses, ultimately affecting feeding and growth (Nyström 2002).

Bullhead catfish have continued to spread throughout Aotearoa. In 2016 and 2018, respectively, catfish were officially recorded in two Arawa lakes, Lakes Rotoiti and Rotorua (Fig. 1), where they are now well established. There is evidence the invasion began earlier in 2009, and has raised grave concerns because the Arawa lakes have traditionally supported substantial populations of kōura, considered a taonga ('treasured') species for Te Arawa iwi (tribes) living in the region (Hiroa 1921; Kusabs and Quinn 2009). The invasion occurred during long-term monitoring of kōura populations in the lakes using the tau kōura method, a customary Māori technique for capturing freshwater crayfish (Kusabs and Quinn 2009). This invasion provides a rare opportunity to examine the effects of a non-native catfish on an endemic freshwater crayfish species. Our study explores the relationship between invasive catfish and native kōura populations whilst accounting for changes in environmental conditions. We assessed ecological impacts using long-term data of kōura abundances and sizes from four Arawa lakes. We hypothesised that catfish invasion leads to reduced kōura abundance and biomass and alters population size structure (a relative increase in larger crayfish) when compared to uninvaded lakes.

Materials and methods

Study area

The Arawa lakes are in the Bay of Plenty region of Aotearoa's North Island (Fig. 1). The indigenous Te Arawa people are the hunga tiaki (custodial guardians) of the lakes. The Arawa lakes comprise of 12 major lakes (Fig. 1) which are generally monomictic.

The two invaded lakes are Lakes Rotoiti and Rotorua. Lake Rotoiti (38.03724° S, 176.42795° E) is a deep, warm, monomictic, mesotrophic lake (von Westernhagen et al. 2010; Table 1). It consists of a shallow western basin (max. depth 25 m) and a deeper eastern basin (max. depth 128 m). For nine months of the year, the lake is stratified and mixes once in late autumn, resulting in extensive deoxygenation of the bottom waters (Kusabs and Quinn 2009). Lake Rotoiti's water quality has declined significantly

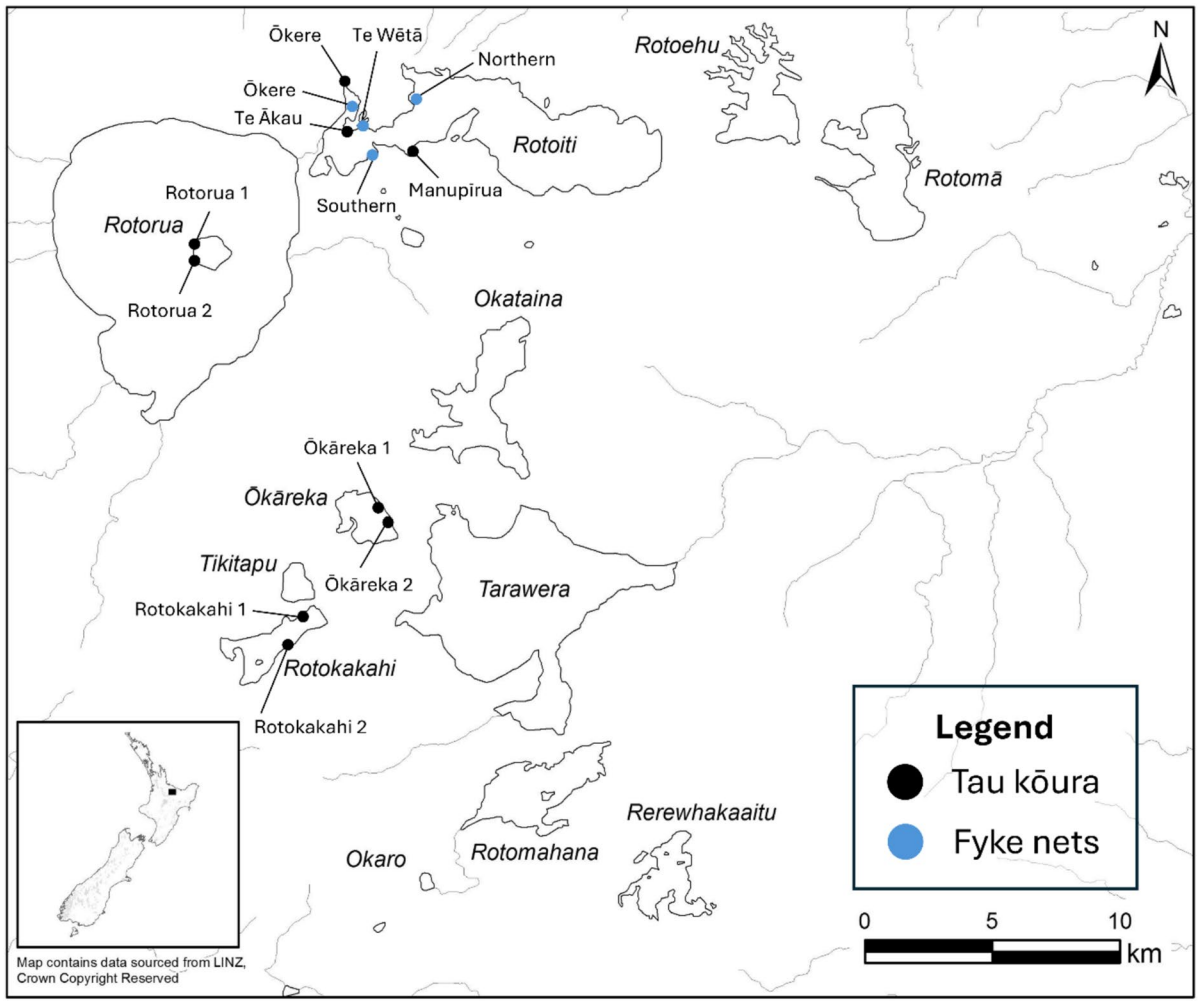

Fig. 1 Map of the Arawa Lakes in the Bay of Plenty region, Aotearoa New Zealand showing the sampling locations for kōura (*Paranephrops planifrons*) and bullhead catfish (*Ameiurus nebulosus*). The kōura monitoring programme used the tau kōura method to sample crayfish in lakes (Kusabs and Quinn 2009). The catfish monitoring programme used fine mesh fyke nets; both catfish and kōura were caught using this method

(1960–2000) due to nutrient-rich inflows from Lake Rotorua via the Ōhau Channel (von Westernhagen et al. 2010). To restore the lake, an inflow diversion wall was completed in 2008, redirecting these nutrient-laden waters to the Kaituna River outlet (Hamilton et al. 2012). Lake Rotorua (38.08333° S, 176.26700° E) is a large, shallow (mean depth 11 m), polymictic lake classified as eutrophic (LAWA 2025; Table 1).

The two control lakes, Ōkāreka (38.17056° S, 176.35597° E) and Rotokākahi (38.21517° S, 176.32064° E), are both medium-sized, mesotrophic lakes (Table 1). They were selected as control lakes because they share comparable nutrient status, stratification patterns, and extended periods of deoxygenation with Lake Rotoiti, but have not been invaded by bullhead catfish. Both lakes also have surface outlets, which, as in Lakes Rotoiti and Rotorua, results in minimal variation in water levels.

Kōura and fish species

Northern kōura is the only crayfish species present in the Arawa lakes. Rainbow trout (*Oncorhynchus mykiss* Richardson, 1836), common smelt (*Retropinna retropinna* Richardson, 1848) and

Table 1 Morphometry and limnological characteristics of the four study lakes in the Arawa Lakes district, North Island, Aotearoa New Zealand

Invasion	Lake	Trophic state	Mixing regime	Mean depth (m)	Max depth (m)	Lake area (ha)	Catchment agriculture (%)	Dominant invasive macrophytes	Sediment deposition (mm/year)
Impact	Rotoiti	Mesotrophic	Monomictic	32	124	3460	23.9	*Ceratophyllum demersum*	1.7
	Rotorua	Eutrophic	Polymictic	11	45	8079	51.8	*Egeria densa*/*Lagarosiphon major*	3.0
Control	Ōkāreka	Mesotrophic	Monomictic	20	34	324	55.8	*L. major*	1.4
	Rotokākahi	Mesotrophic	Monomictic	18	32	452	26.3	*Elodea canadensis*	1.0

Data sourced from LAWA (2025) except net sediment deposition rates for the period 1995 – 2006 from Trolle et al. (2008) and dominant invasive macrophytes from Burton (2017)

common bullies (*Gobiomorphus cotidianus* McDowall, 1975) dominate fish assemblages. Brown trout (*Salmo trutta* Linnaeus, 1758) are common in Lake Rotorua and present in low numbers in Lake Rotoiti. Tuna (eels, *Anguilla australis* Richardson, 1841 and *A. dieffenbachii* Gray, 1842) are present in all four lakes but are rare as juveniles cannot naturally access the lakes from the sea (Martin et al. 2007).

Catfish are only known to be present in lakes Rotoiti and Rotorua. The presence of bullhead catfish in Lake Rotoiti was first documented in January 2009, following the discovery of a dead individual at Ōkawa Bay (Blair and Hicks 2009). However, the first confirmed detection of live individuals occurred in March 2016 at Te Wētā Bay, where a weed-harvesting contractor observed two live catfish and caught onel (Francis 2019). Subsequent sampling in April and July 2016 resulted in the capture of catfish across a broad range of size classes, including 390 juveniles measuring < 100 mm fork length (FL). Age-distribution data from netting of live individuals between August and December 2018 indicated that estimated birth dates of catfish in Lake Rotoiti extended back to May 2008 (Table A1 & Fig. A1, Supporting Information). This data suggests that the species was present in the lake several years prior to the official confirmation in 2016, consistent with the discovery of a dead individual in 2009. Catfish were officially confirmed in Lake Rotorua in December 2018, likely entering via the Ōhau Channel connecting the two lakes (Grayling 2017).

Environmental data

The Trophic Level Index (TLI) is an indicator of lake trophic status in Aotearoa lakes and is derived from the following four water quality parameters: Secchi depth, chlorophyll a, total phosphorus and total nitrogen concentrations (Burns et al. 1997). Mean annual TLI data for all four lakes (1995–2023) was obtained from the Bay of Plenty Regional Council (BOPRC; Scholes 2024). Monthly dissolved oxygen (mg/L) profiles for three lakes (Rotoiti, Rotorua, Ōkāreka) were recorded by BOPRC (Scholes 2024) between 2005 and 2021 using a CTD (Seabird 19Plus or 19PlusV2, WA, USA). Lake Submerged Plant Indicators (LakeSPI) data used for ecological monitoring of Aotearoa lakes was obtained for the four Arawa lakes (1988–2021) from Earth Science NZ (lakespi.niwa.co.nz; Burton 2017). Mean net sedimentation rates in the four study lakes are reported to range between 1.0 and 3.0 mm per year (Trolle et al. 2008; Table 1).

Kōura sampling sites and timing

Kōura sampling was conducted between 2005 and 2024, with the majority of sampling occasions undertaken in Lake Rotoiti (Table 2). Three sites were sampled in Lake Rotoiti: Manupīrua in the eastern basin,

Table 2 Kōura sampling information for the four Arawa lakes studied from 2005 to 2024

Invasion	Lake	Season (month) and year sampled	Source	Surveys (*n*)	Whakaweku depth range (m)
Impact	Rotoiti	Summer 2005 Summer (February, December), Winter, Spring, 2006 Summer, Autumn, Winter, Spring 2009 Summer, Autumn, Winter, Spring 2010 to 2022 Summer, Spring 2023 Spring 2024	Kusabs (2024a)	64	10–25
	Rotorua	Summer, Autumn, Winter, Spring 2009 Summer 2010, Summer 2011, Winter 2016 Autumn, Winter, Spring 2017 Summer, Autumn, Winter, Spring 2018, 2019, 2020, 2021, 2022, 2023, 2024	Kusabs et al. (2015b), Kusabs (2024b)	37	4–17
Control	Ōkāreka	Autumn, Winter, Spring 2009 Spring 2019; Autumn, Winter 2020	Kusabs et al. (2015b) Kusabs (2020)	6	7–22
	Rotokākahi	Autumn, Winter, Spring 2009 Spring 2020; Autumn, Winter 2021	Kusabs et al. (2015b), Kusabs (2021)	6	9–23

Depths for whakaweku (bracken fern bundles used to trap crayfish) at Lake Rotoiti were for Te Ākau and Manupīrua sites only; Ōkere was not included due to its proximity to the outlet

Te Ākau Point in the western basin, and the Ōkere Arm (a lake outlet where water from lakes Rotoiti and Rotorua flow towards the Kaituna River) (Fig. 1). The Ōkere Arm represents a shallow environment (maximum depth 7 m) with a kōura population dominated by smaller individuals relative to the other two sites (Kusabs et al. 2015b). Manupīrua is deeper (maximum depth of 25 m), whereas Te Ākau Point extends to 16 m.

Two sites were sampled in each of lakes Rotorua, Ōkāreka, and Rotokākahi. As sites within each lake shared similar depth and substrate characteristics, data for each respective lake were combined for key analyses (Fig. 1; Table 2). Locations and sites descriptions are provided in Kusabs et al. (2015b).

Kōura monitoring

Kōura were sampled using the tau kōura, a traditional method used by Te Arawa and Ngāti Tūwharetoa (Māori tribes) to catch kōura in the Central North Island lakes, Aotearoa (Kusabs and Quinn 2009). This method involves placing whakaweku (bundles of bracken fern, *Pteridium esculentum*, G. Forst.) on the lakebed for kōura to colonise; the whakaweku are typically left for three months then retrieved into a boat and kōura collected. Tau kōura were set at two locations in each lake except for Lake Rotoiti, where an additional site was added in the Ōkere Arm (Fig. 1). Tau kōura were deployed in depths ranging from 4 to 34 m on the dominant substrate type present in each of the lakes. Depths were measured using electronic fish finders (Furuno LCD sounder LS6000, Furuno Electric Co. Ltd. Nishinomiya, Japan; Lowrance HDS-7, Lowrance Electronics, Norway).

Orbital-carapace length (OCL) of individual kōura was measured using vernier callipers (±0.5 mm). All kōura were returned close to the place of capture after processing. Using the author's data (Fig. A2, Supporting Information), a power regression equation (Eq. 1) was used to estimate kōura wet weight: (1):

$$W(g) = 0.0005\ L^{3.0765} \quad (1)$$

where W is wet weight (g) and L is the OCL (mm). Catch per unit effort (CPUE) was defined as the number of kōura per whakaweku and biomass per unit effort (BPUE) as estimated wet weight (g) of kōura per whakaweku.

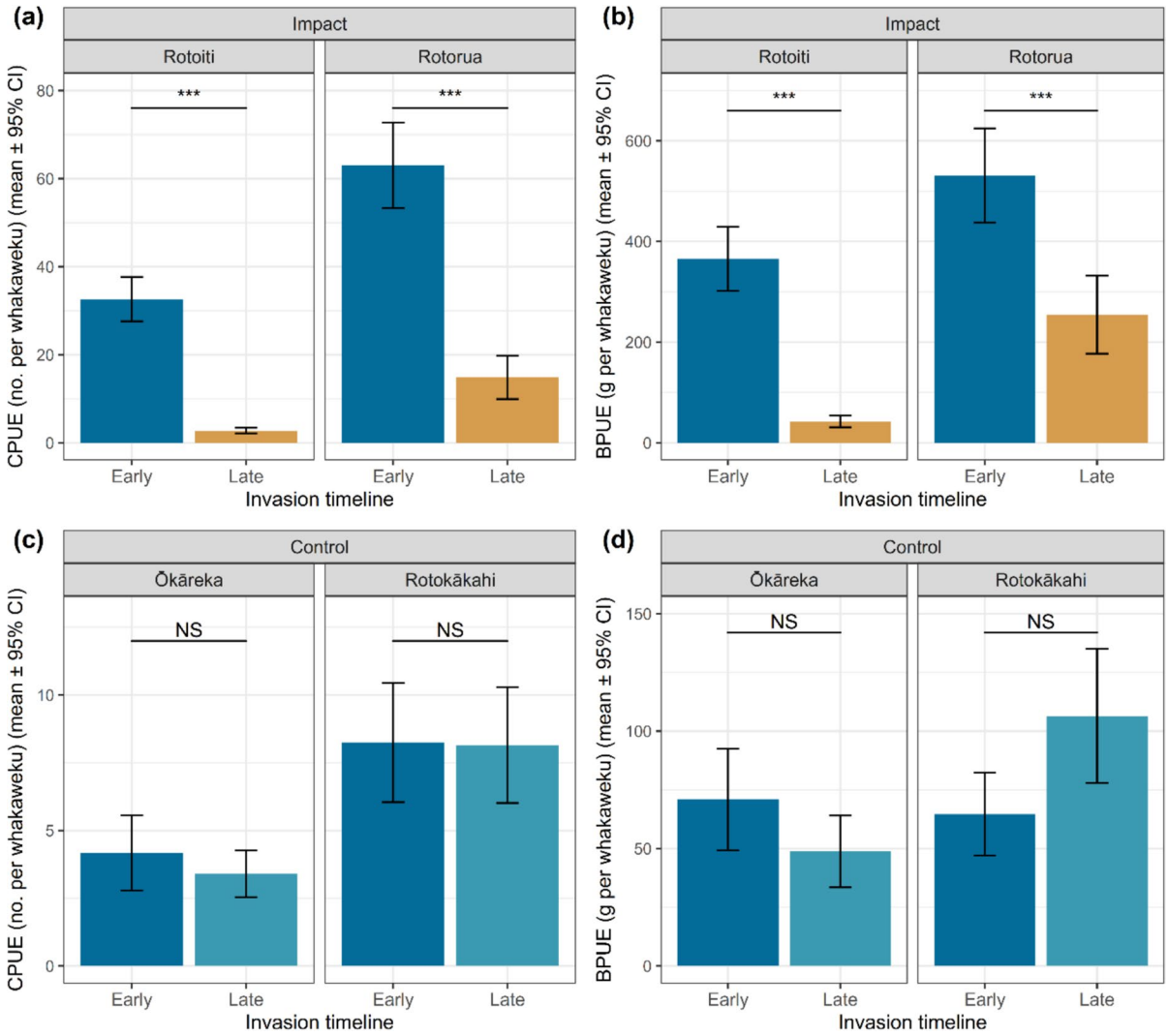

Fig. 2 Changes in mean catch per unit effort (CPUE) at **a** impacted and **c** control lakes; and changes in estimated mean biomass per unit effort (BPUE) at **b** impacted and **d** control lakes before and after the invasion of brown bullhead catfish in Lakes Rotoiti and Rotorua. Kōura were caught using the tau kōura method (Kusabs and Quinn 2009) where whakaweku (bracken fern bundles) are used to trap crayfish. The comparisons used a quasi-BACI (Before-After, Control-Impact) design with two time periods "early" and "late" in the invasion of catfish to both impacted lakes. All "Early" data was collected in 2009. "Late" data was collected in 2021 except for Lake Ōkāreka which was sampled in 2020. Error bars represent the 95% confidence interval (CI). ***$p < 0.001$; NS, not significant

Catfish monitoring

Since March 2016, the Bay of Plenty Regional Council has monitored bullhead catfish populations in Lake Rotoiti. Although a range of netting methods have been used (Francis 2019), our study focuses on catch data obtained from unbaited, fine-meshed fyke nets with a choked entry. Forty fyke nets were set in shallow water (< 7 m deep) for 24 h on any given night of sampling, and four key sites around the lake were sampled monthly between 2017 and 2021 to assess community dynamics and spatio-temporal "lag effects" (Crooks 2005) in the catfish invasion.

Counts were made of all fish species present. Catfish were removed, but kōura and other fish

species were returned to the lake. From August 2018 onwards, catfish lengths were measured.

Data analysis

To test the hypothesised impact of catfish on kōura populations using the tau kōura catch data, we used a quasi-BACI (Before-After, Control-Impact) monitoring design. Due to the uncertainty in the catfish invasion timeline, our "Before" sampling likely captures kōura population dynamics during the early stages of the invasion and thus cannot be regarded as "Before" sampling in the traditional BACI sense. For this reason, we have used the term "Early" for data collected in 2009 because it reflects kōura populations at the time of the first catfish detection in Lake Rotoiti (i.e., early in the invasion). The second period ("Late") used data collected in 2021 except for Lake Ōkāreka where the data was collected in 2020, thus indicating "After" data in a traditional BACI sense by representing a later stage of the invasion when catfish were established in both impacted lakes. Our design also does not conform to optimal BACI sampling with multiple years to compare impacted and control sites, but it does allow for comparisons across multiple seasons within years (autumn, winter, spring) at the two impacted and two control sites. We used linear mixed effects (LME) and Generalised Linear Mixed Models (GLMM) to test changes in the four lakes over time using random effects (Season nested in Year and Site nested in Lake). The GLMM testing CPUE assumed a negative binomial distribution. We square-root transformed BPUE and log-transformed size (OCL).

We used available monitoring data (TLI, dissolved oxygen concentration, and LakesSPI) to assess changes in environmental conditions before and after the establishment of catfish in impacted lakes relative to the control lakes. Changes in annual TLI data for five years before (2005–2009) and five years after (2017–2021) were tested for each of the four lakes using a general linear model (GLM). Monthly dissolved oxygen concentrations and monthly minimums at three depth levels (0–10, 10–20, 20–30 m) for 5 years before (2005–2009) and five years after (2017–2021) catfish establishment were tested using a Bayesian LME with random effects for Sampling Location nested in Lake and Month sampled nested in Year. We focused on dissolved oxygen concentrations for five months (January-May) spanning late summer and autumn when the Arawa lakes are most likely to stratify. Dissolved oxygen data was $\log(x+1)$-transformed. LakesSPI data (LakeSPI, Invasive impacts, Native condition %) collected before (1988–2009) and after (2011–2021) were tested using a GLMM assuming a binomial distribution with Year surveyed as a random effect.

We used Generalised Additive Models (GAMs) to investigate temporal trends in kōura catch data (mean CPUE, BPUE, and OCL) from Lakes Rotoiti and Rotorua collected using the tau kōura method. Each GAM was fitted for a single site on Lake Rotoiti. The two sites on Lake Rotorua were pooled. The GAMs were fitted with the "gam" function in the "mgcv" R package assuming a Tweedie distribution. We also plotted size-frequency data for kōura from the two impacted lakes (Rotoiti and Rotorua) and the two control lakes (Rotokākahi and Ōkāreka) at the two points in time. Size-frequency data was pooled across seasons since patterns were conserved throughout the year.

We analysed the three Lake Rotoiti sites independently owing to their distinct depth profiles and kōura population characteristics. We fitted GAMs for CPUE, BPUE and mean size data through time. We also compared these three indicators in 2009 and 2021 using LME and GLMMs with the effects of Site, Time, and their interaction and blocking interaction term for Season and Year. The GLMM testing CPUE data assumed a negative binomial distribution. BPUE was was square-root-transformed, and size (OCL) log-transformed.

We selected four sites in the Lake Rotoiti catfish monitoring data that had nearly continuous monthly netting between the beginning of 2017 and end of 2021. This data accounted for over 55% of the monitoring data available for Lake Rotoiti, equivalent to 8646 nets per night. Monthly sampling data for kōura and catfish CPUE were averaged and temporal trends investigated using GAMs as described above. We fitted GAMs for both $\log(x+1)$ transformed and untransformed data but chose to use the transformed data in our visualisations to aid interpretability. We also plotted $\log(x+1)$-transformed mean monthly kōura and catfish CPUE against each other for each site and calculated Pearson correlation coefficients to test the hypothesis that catfish abundances are negatively correlated with kōura abundances.

We also compared kōura and catfish CPUE data in 2017 (as catfish were spreading in Lake Rotoiti) with the CPUE data in 2021, when catfish were well established in the western half of Lake Rotoiti. We used GLMMs assuming a negative binomial distribution to test changes in kōura and catfish CPUE between year (2017 and 2021), Site (Te Wētā, Ōkere, Northern and Southern shorelines), and their interaction. The random effect was day of capture. We also calculated the ratio of kōura to catfish caught from the individual net data (i.e., kōura abundances divided by catfish abundances). Where no catfish were recorded, we assigned the kōura catch data to avoid infinite values. Kōura to catfish ratios were tested using the same mixed model structure described above assuming a binomial distribution.

Data analysis and visualization were performed using R (R Core Team 2024). We use the R packages "glmmTMB" and "lme4" to fit mixed models. In all LME and GLMMs, we identified post-hoc differences using a least-squares means approach with multiplicity adjustments (Tukey's HSD) obtained from the R package 'lsmeans'. We used the performance R package to confirm our models were not affected by overdispersion.

For more details on methods used, see Supporting Information, Appendix A.

Results

Environmental variables

Water quality (Trophic Level Index) significantly improved in lakes Rotoiti, Rotorua and Rotokākahi and also showed improvement in Lake Ōkāreka over the study period (Table 3). Dissolved oxygen concentrations (at 10–20 m) for the months January–May significantly decreased in three lakes after 2009 (Table 3). There was no significant change in the monthly minimum dissolved oxygen concentrations in the impacted lakes after catfish establishment, although it did decrease in Lake Ōkāreka (Table 3). The LakeSPI data shows macrophyte communities have remained relatively stable within the lakes over time. Native condition significantly improved in Rotorua and worsened in Rotokākahi (Table 3). Rotokākahi also recorded a significant increase in invasive macrophyte impacts, leading to an overall decline in LakeSPI (Table 3).

Tau kōura catch data

Abundances (catch per unit effort, CPUE) and estimated mean biomass (biomass per unit effort, BPUE) of kōura have exhibited significant declines in lakes where catfish are present (Fig. 2). By contrast, kōura populations in the control lakes, Ōkāreka and Rotokākahi, showed no significant change in abundances or estimated mean biomass in the surveys conducted over a decade after catfish were first reported in Lake Rotoiti (Fig. 2). In contrast, changes in mean size (OCL mm) were equivocal in response to catfish presence, with mean size not changing in Lake Rotoiti but significantly increasing in Lake Rotorua ($p < 0.001$; Fig. B1.a, Supporting Information). Similarly, control lakes showed significantly increased sizes in Rotokākahi ($p < 0.001$) but no change in Ōkāreka (Fig. B1.b, Supporting Information). Size histograms show differences in size-abundance relationships in the lakes where catfish have invaded compared to the control lakes (Fig. 3).

Lake Rotoiti

Kōura abundances and estimated BPUE declined significantly at all three Lake Rotoiti sites between 2009 and 2024 ($p < 0.001$; Fig. 4a, b). Mean kōura size has increased significantly over time at Ōkere and Te Ākau ($p < 0.001$), but the temporal pattern at Manupīrua is less obvious (Fig. 4c).

Between 2009 and 2021, mean kōura CPUE decreased by 85% at Manupīrua (from 32.6 to 2.8), 94% at Te Ākau (from 21.7 to 1.4), and 95% at Ōkere (from 45.2 to 2.4). Similarly, mean BPUE declined by 88% at both Manupīrua (from 365.6 to 42.6 g) and Te Ākau (from 436.0 to 52.0 g), and by 89% at Ōkere (from 172.0 to 19.4 g). These changes were all highly significant (Fig. 5a, b).

Mean kōura size differed at two Rotoiti sites between 2009 and 2021. At Ōkēre**,** mean OCL increased by 23.4%, rising from 17.5 mm in 2009 to 21.6 mm in 2021 ($p < 0.001$; Fig. 5c). At Te Ākau, mean OCL increased by 18.5%, from 30.9 mm in 2009 to 36.6 mm in 2021 ($p < 0.001$; Fig. 5c). Manupīrua exhibited a 13.3% decline, from 27.8 mm in 2009 to 24.1 mm in 2021 ($p < 0.001$; Fig. 5c).

Table 3 Environmental change over time in the four Arawa lakes

Response	Predictor	Unit	Invasion	Lake	Early	Late	*p*-value	% change
Water quality	TLI	unitless	Impact	Rotoiti	4.02 ± 0.08	3.75 ± 0.17	**0.035**	−6.8
				Rotorua	4.73 ± 0.41	4.30 ± 0.14	**0.004**	−9.2
			Control	Ōkāreka	3.27 ± 0.24	3.20 ± 0.05	0.431	−2.4
				Rotokākahi	4.09 ± 0.11	3.58 ± 0.13	**< 0.001**	−12.5
	DO	mg/L	Impact	Rotoiti	7.47 ± 1.92	6.44 ± 1.98	**0.010**	−13.7
				Rotorua	7.86 ± 2.02	7.04 ± 1.66	**0.027**	−8.3
			Control	Ōkāreka	7.27 ± 2.11	5.30 ± 2.70	**< 0.001**	−27.1
				Rotokākahi	–	–	–	–
	Min. DO	mg/L	Impact	Rotoiti	6.35 ± 2.34	5.12 ± 2.27	0.055	−19.4
				Rotorua	6.85 ± 2.70	6.14 ± 2.24	0.471	−10.4
			Control	Ōkāreka	5.31 ± 2.13	2.34 ± 2.11	**< 0.001**	−55.9
				Rotokākahi	–	–	–	–
Habitat	LakeSPI	%	Impact	Rotoiti	21.7 ± 4.0	19.9 ± 0.9	0.593	−8.3
				Rotorua	22.0 ± 3.0	24.6 ± 3.0	0.163	11.7
			Control	Ōkāreka	47.1 ± 21.1	43.1 ± 9.3	0.702	−8.5
				Rotokākahi	38.0 ± 12.5	28.6 ± 1.9	**0.020**	−24.6
	Invasive	%	Impact	Rotoiti	87.2 ± 3.4	91.4 ± 1.7	0.191	4.7
				Rotorua	77.4 ± 8.3	80.0 ± 1.7	0.571	3.4
			Control	Ōkāreka	57.3 ± 32.4	59.3 ± 17.1	0.853	3.4
				Rotokākahi	66.7 ± 12.5	77.0 ± 1.9	**0.005**	15.6
	Native	%	Impact	Rotoiti	26.0 ± 6.7	26.7 ± 2.7	0.732	2.6
				Rotorua	20.4 ± 2.2	26.8 ± 4.7	**0.023**	31.3
			Control	Ōkāreka	51.2 ± 13.4	47.4 ± 7.2	0.667	−7.4
				Rotokākahi	40.9 ± 17.7	24.0 ± 3.7	**< 0.001**	−41.3

Mean (± standard deviation) Trophic Lake Index (TLI) scores, dissolved oxygen (DO) concentrations (10–20 m) including monthly minimums, and Lake Submerged Plant Indicators (LakeSPI, invasive impacts, and native condition %) are provided before and after establishment of catfish in impacted lakes. Dissolved oxygen was not monitored in Rotokākahi. A lower TLI score indicates improved lake ecosystem health. The comparisons used a quasi-BACI (Before-After, Control-Impact) design with two time periods "early" and "late" in the invasion of catfish to both impacted lakes. *P*-values in bold indicate statistically significant differences (α=0.05)

Length-frequency analysis of kōura catch data shows that the decline at Ōkere was due to a reduction in the numbers of small-sized kōura (< 22 mm OCL) recorded (Fig. B2, Supporting Information). Medium-sized kōura (22–32 mm OCL) were disproportionately reduced at Te Ākau (Fig. B2, Supporting Information), although most size classes declined. In contrast, small-sized kōura (< 22 mm OCL) were relatively more abundant at the deepest Lake Rotoiti site, Manupīrua (Fig. B2, Supporting Information), helping to explain the decrease in mean size between 2009 and 2021 (Fig. 5). Kōura at this site were generally absent at > 23 m depth on most autumn sampling occasions due to hypolimnion deoxygenation.

Lake Rotorua

Monitoring data for 2009 to 2024 shows that there have been significant declines in kōura mean CPUE and estimated mean BPUE in Lake Rotorua ($p < 0.001$; Fig. 6a, b). Mean kōura size has increased over the same period, although there are indications that this trend has peaked (Fig. 6c).

Between 2009 and 2021, mean annual CPUE declined by 76.4%, from 63.0 kōura per whakaweku in 2009 to 14.9 kōura per whakaweku in 2021 ($p < 0.001$). Mean BPUE declined by 52.1%, from 531.1 g kōura per whakaweku in 2009 to 254.4 g kōura per whakaweku in 2021 ($p < 0.001$).

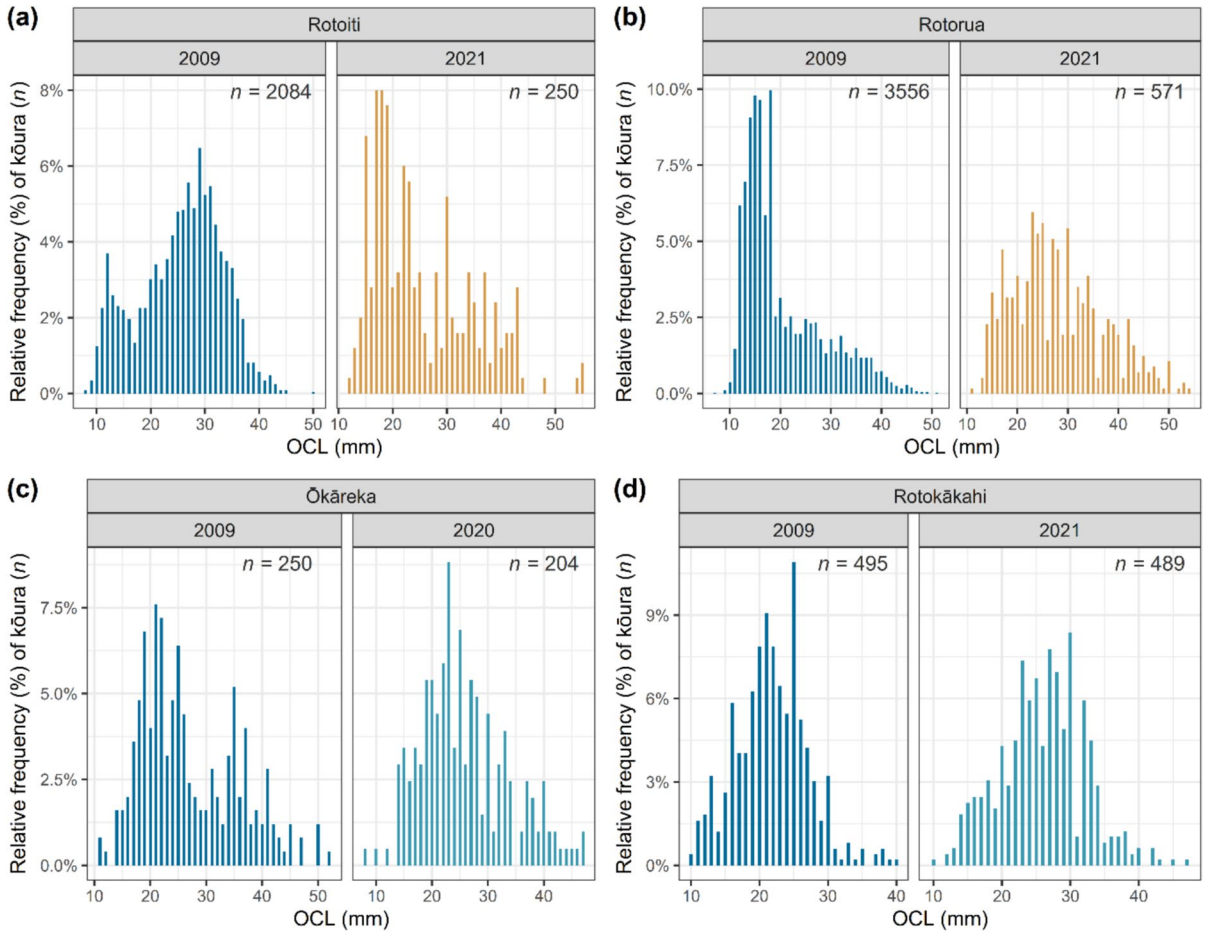

Fig. 3 Annual length-relative frequency distributions of kōura in four Arawa Lakes at two points in time: **a** Lake Rotoiti (2009, 2021), **b** Lake Rotorua (2009, 2021), **c** Lake Rotokākahi (2009, 2021), and **d** Lake Ōkāreka (2009, 2020). Kōura were caught using the tau kōura method (Kusabs and Quinn 2009). OCL, orbital carapace length. Yellow bars indicate kōura length-frequency distributions following the invasion of brown bullhead catfish in Lakes Rotoiti and Rotorua

Mean kōura size increased significantly by 36.98%, from 20.39 mm in 2009 to 27.93 mm in 2021 ($p < 0.001$, Fig. B1.a, Supporting Information). Length–frequency distributions indicate that this is due to a decline in the abundance of small size classes (10–18 mm OCL) recorded in 2021 (Fig. 3b). Whakaweku were set at depths from 3 to 12.5 m in Lake Rotorua, so catches were not affected by prolonged periods of deoxygenation.

Lake Ōkāreka

Kōura abundances per whakaweku in Ōkāreka varied from 4.2 in 2009 to 3.4 in 2020, although this difference was not significant. Mean BPUE ranged from 70.9 g in 2009 to 48.8 g in 2020. Kōura ranged in size from 8 to 47 mm OCL in 2020 compared to 11 to 52 mm OCL in 2009 (Fig. 3c). Kōura mean size was not significantly different in 2020 than in 2009, with a mean size of 26.9 mm recorded in 2020 compared to 25.7 mm in 2009 (Fig. B1.b, Supporting Information). No kōura were collected below 20 m on 6 November 2009 and 22 m on 8 November 2019.

Lake Rotokākahi

Kōura abundances per whakaweku in Rotokākahi did not differ significantly between 2009 (8.3) and 2021 (8.2) (Fig. 2c). By contrast, mean BPUE increased by 64.5%, from 64.7 g in 2009 to 106.4 g in 2021,

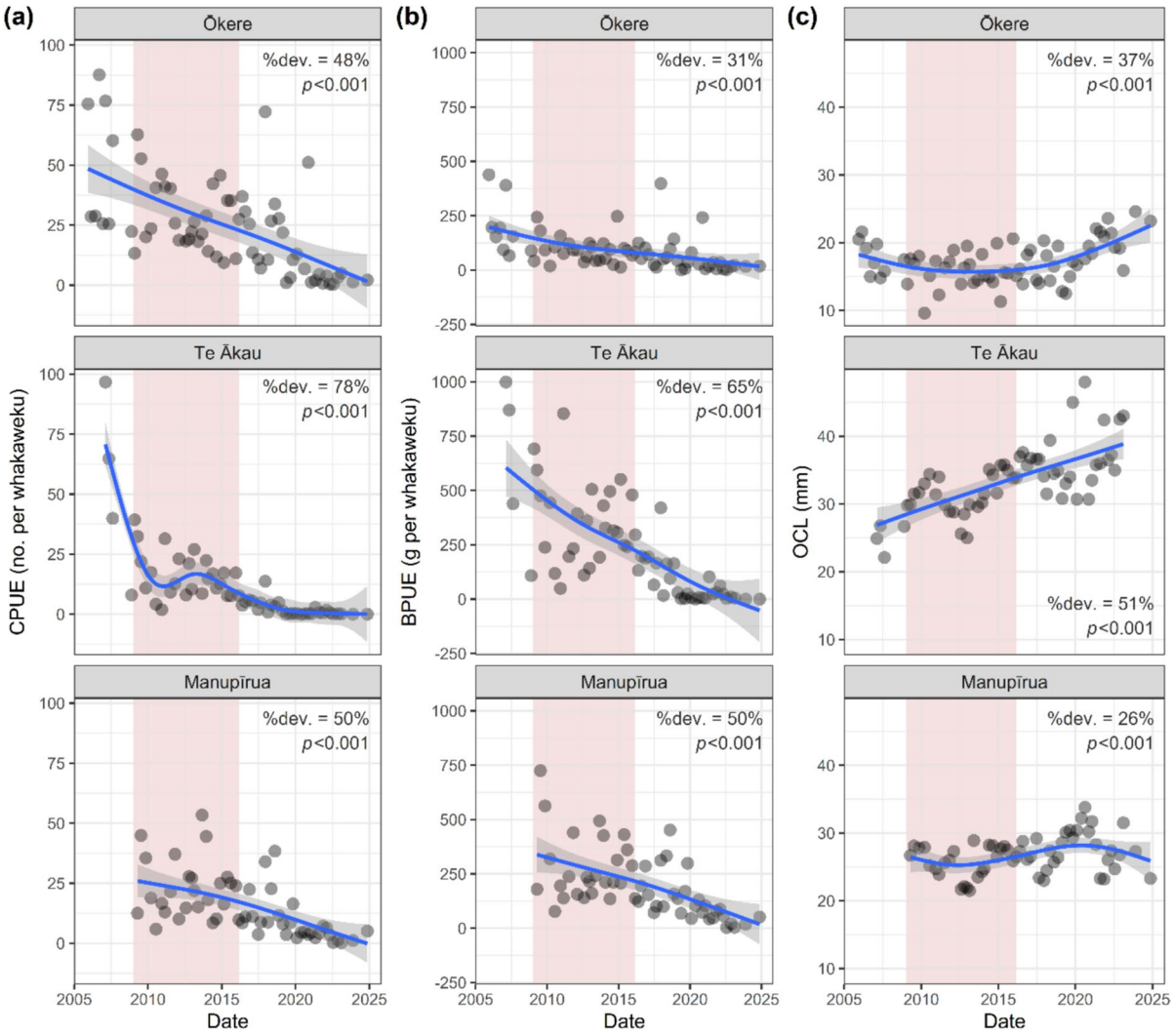

Fig. 4 Temporal patterns in **a** mean catch per unit effort (CPUE), **b** estimated mean biomass per unit effort (BPUE), and **c** mean orbital carapace length of kōura at three sites in Lake Rotoiti (Ōkere, Te Ākau and Manupīrua) over time (2005–2024). Kōura were caught using the tau kōura method (Kusabs and Quinn 2009) comprised of whakaweku (bracken fern bundles). The red band ranges between the date of the first reported observation (January 2009) of a bullhead catfish in Lake Rotoiti (Blair and Hicks 2009) and the first confirmed capture of live catfish in the lake (March 2016). Lines are fitted with generalised additive models. Grey ribbons indicate the 95% confidence intervals

although this difference was not statistically significant (Fig. 2d). Kōura size ranged from 10 to 47 mm OCL in 2021, compared to 10–40 mm OCL in 2009 (Fig. 3d). Mean size was significantly higher in 2021 than in 2009, increasing from 21.8 mm in 2009 to 26.0 mm in 2021, representing an 18% increase ($p < 0.001$, Fig. B1.b, Supporting Information). No kōura were recorded at depths greater than 14.6 m in May 2009 or 17.5 m on 14 May 2021 due to deoxygenation of the hypolimnion.

Fyke net catch data

Mean CPUE of bullhead catfish at four locations in Lake Rotoiti all increased between 2017 and 2022 ($p < 0.001$, Fig. 7a). There were marked fluctuations in catfish abundances, despite the overall trend for increased CPUE. In contrast, mean CPUE of kōura at the same sites all declined over time ($p < 0.001$, Fig. 7b). In general, catfish CPUE was negatively correlated with kōura CPUE (Fig. 7c). Significant

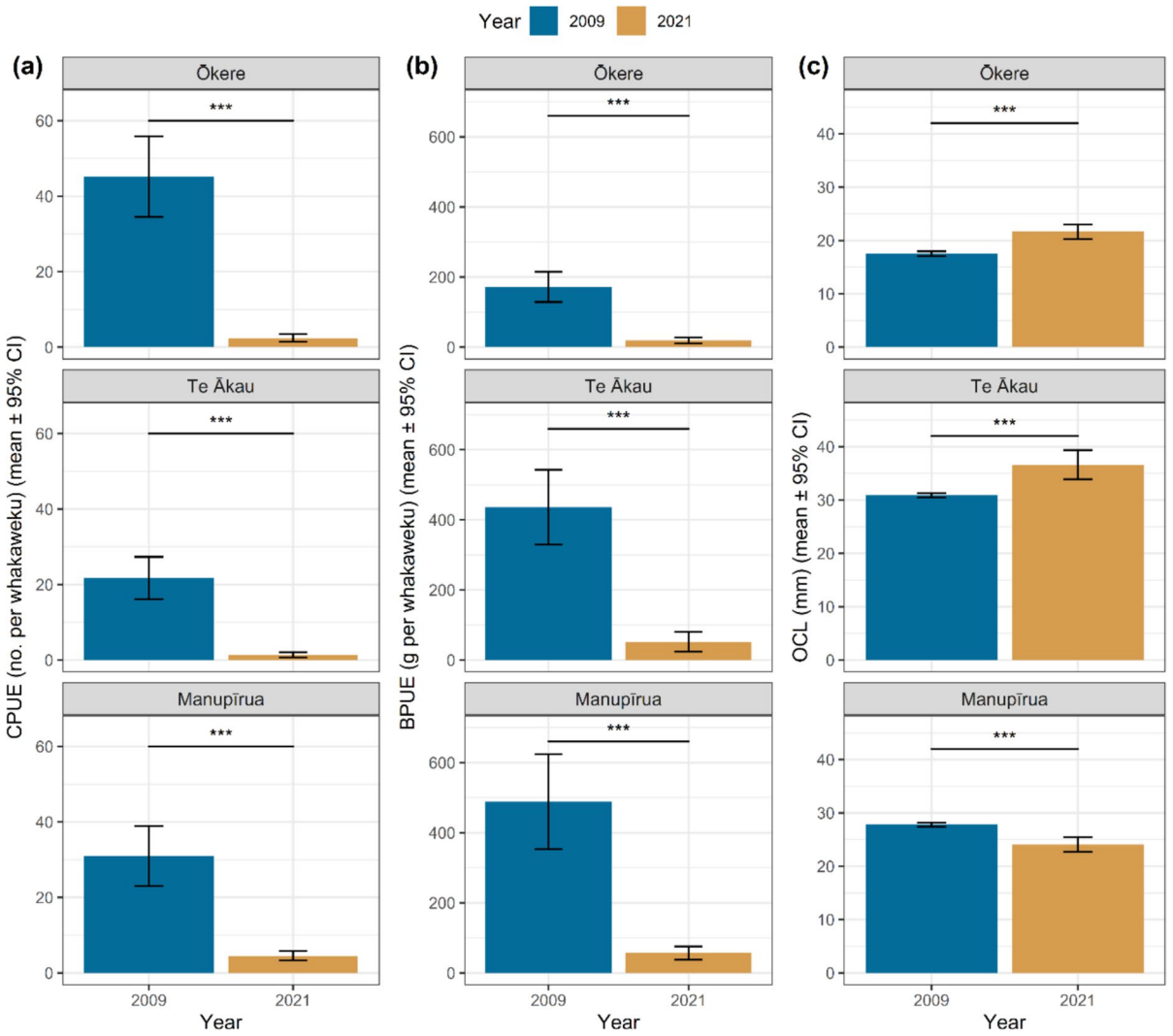

Fig. 5 Changes in **a** mean catch per unit effort (CPUE), **b** estimated mean biomass per unit effort (BPUE), and **c** mean orbital carapace (OCL) length of kōura at three sites in Lake Rotoiti (Ōkere, Te Ākau and Manupīrua) between 2009 and 2021. Kōura were caught using the tau kōura method (Kusabs et al. 2009) comprised of whakaweku (bracken fern bundles). Error bars represent the 95% confidence interval (CI). ***$p < 0.001$

negative correlations were recorded at three sites (Te Wētā, Northern and Southern shores). Only Ōkere failed to record a significant correlation, despite there being evidence of a shift in abundances of the two species (Fig. 7c).

We also compared the CPUE for both species in 2017 at the beginning of the monitoring and in 2021, when the catfish was becoming well established in the lake. Catfish CPUE increased significantly at all four sites in Lake Rotoiti (Fig. 8a). The greatest increase was recorded at the Southern Shorelines site, where mean CPUE increased from 0.02 catfish net^{-1} night^{-1} to 6.33 catfish net^{-1} night^{-1}, a 418-fold increase. This large increase was despite the Southern Shorelines having the lowest catfish CPUE of the four sites in 2021. The highest mean catfish CPUE in 2021 (15.5 catfish net^{-1} night^{-1}) was recorded at the Te Wētā Bay site, but the relatively modest 7-fold increase indicated that this species was already becoming well established at this site in 2017.

In contrast, kōura CPUE significantly decreased at all four sites in the same period (Fig. 8b). The largest

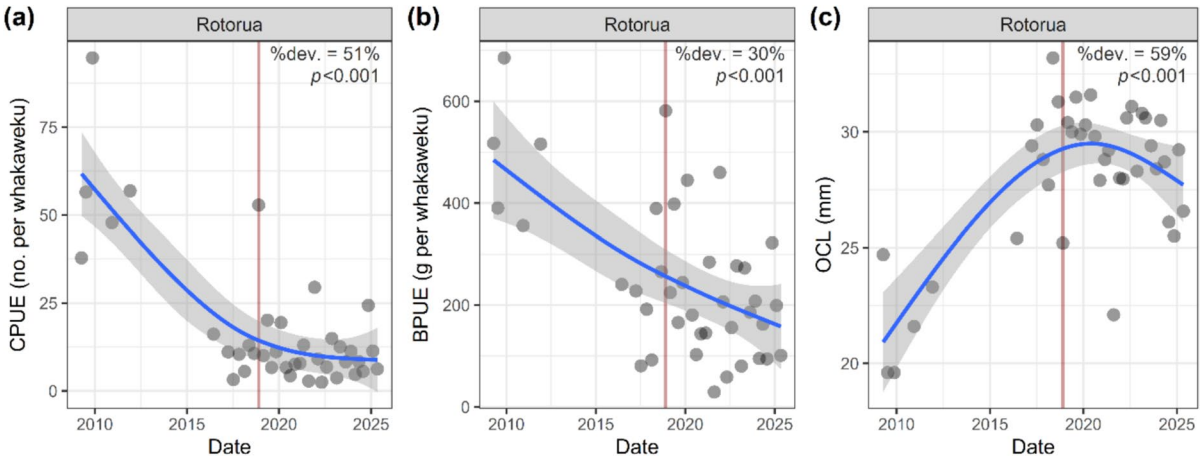

Fig. 6 Patterns of **a** mean catch per unit effort (CPUE), **b** mean estimated biomass per unit effort (BPUE), and **c** mean orbital carapace length (OCL) of kōura captured on tau kōura (composed of 10–20 whakaweku at two sites; data combined for both sites) deployed in Lake Rotorua from 14 April 2009, 2010, 2011, 2016 to 7 May 2025. Only single surveys were carried out in 2010 and 2011 (both in December). The red line indicates the date of the first confirmed record of bullhead catfish in Lake Rotorua. Lines are fitted with generalised additive models. Grey ribbons indicate the 95% confidence intervals

decrease (89%) was recorded at the Te Wētā Bay sites, although both northern and southern shoreline sites recorded decreases of 84%, and Ōkere had a decrease of 70%. These changes led to large reductions in the number of kōura caught relative to the number of catfish caught, with significant decreases in the kōura to catfish ratio at all four monitoring sites (Fig. 8c).

For additional results including tables of statistical tests, see Supporting Information, Appendix B.

Discussion

Kōura abundances and estimated biomass have declined significantly in Lakes Rotoiti and Rotorua over the last decade, and we conclude that bullhead catfish, a well-known predator of kōura, are primarily responsible. In nearby Lake Taupō, Barnes (1996) found that kōura comprised 64% of food items in the diet of large bullhead catfish (250–349 mm FL). Supporting our assertion that bullhead catfish are responsible for the decline in kōura, our results show no significant changes to kōura populations over the same period in Lakes Ōkāreka and Rotokākahi where bullhead catfish are absent. Other studies have identified the presence of predatory fish, physicochemical conditions, food supply, and refuge availability as important factors affecting freshwater crayfish (Lodge and Hill 1994; Kershner and Lodge 1995; Usio and Townsend 2000; Nyström et al. 2006; Kusabs et al. 2015b).

Predatory fish

Past studies show that fish are the most important predator of freshwater crayfish in terms of affecting abundance, behaviour and growth (Nyström 2002). Field data show a negative correlation between predatory fish and crayfish abundance in lakes and streams (e.g., Stein and Magnuson 1976; Lodge and Hill 1994; Englund 1999). A notable example is the relationship between eels and the noble crayfish, *Astacus astacus* (Linnaeus, 1758), in Swedish lakes (where large eel populations correspond to low crayfish numbers), whereas lakes with fewer eels have larger crayfish populations (Svardson 1972, 1974 in Nyström 2002). In Aotearoa, the relatively high abundances of kōura in the Arawa Lakes have been attributed to the low densities of eels (tuna) (Hiroa 1921; Kusabs et al. 2015b). Eels are known predators of kōura in Aotearoa (Cairns 1942; Burnet 1952). For example, Hicks (1997) reported that kōura were the second most frequent prey items of shortfin eels in North Island forested streams.

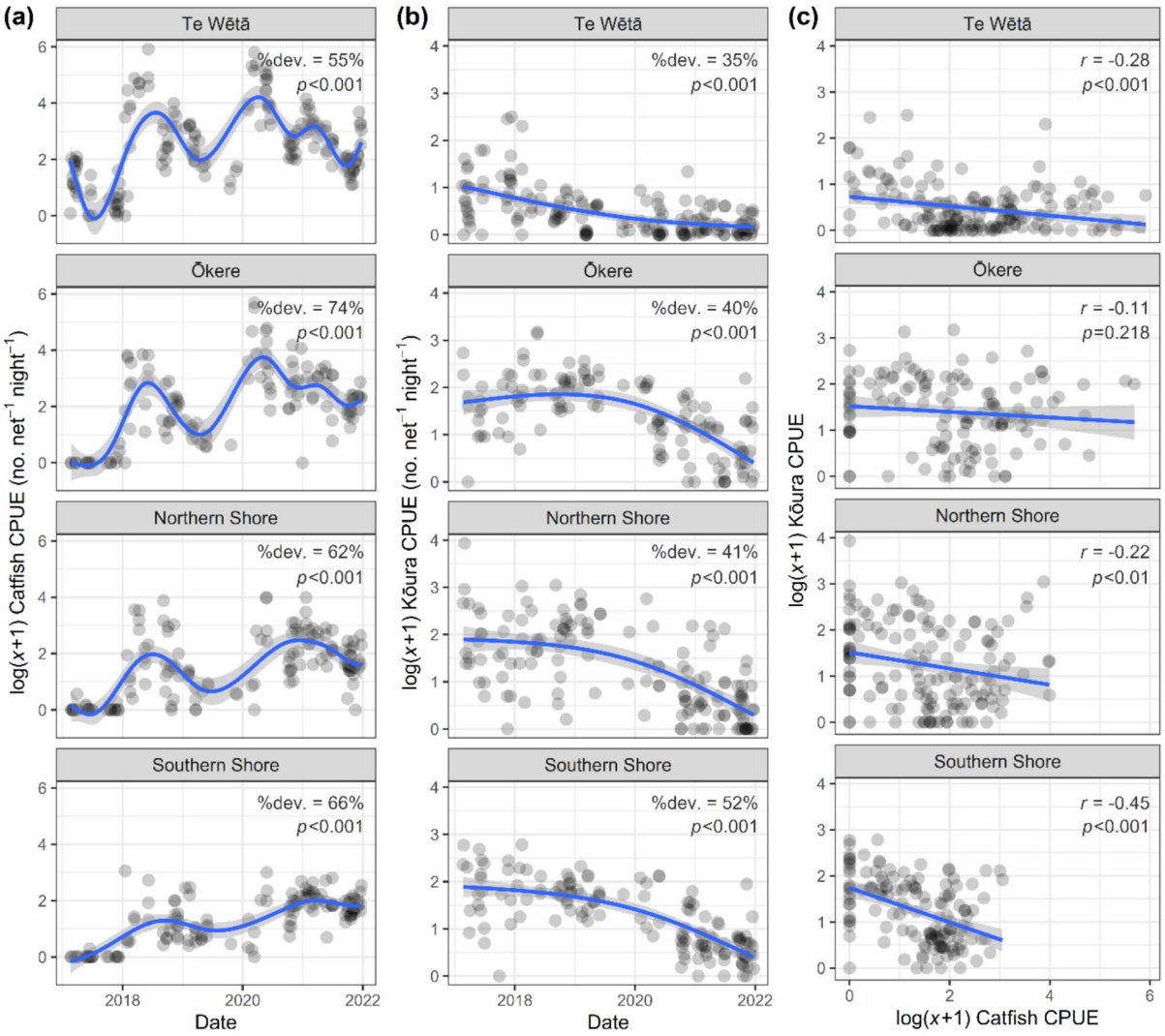

Fig. 7 Patterns in **a** mean catch per unit effort (CPUE) of brown bullhead catfish and **b** kōura at four sites in Lake Rotoiti (Te Wētā, Ōkere, Northern and Southern Shores) over time (2017–2022); and **c** the relationship between catfish and kōura CPUE at each site. Catfish and kōura were caught using fyke nets. CPUE is log($x+1$) transformed. Lines in (**a**, **b**) are fitted with generalised additive models; lines in (**c**) are linear regressions. Grey ribbons indicate the 95% confidence intervals

Kusabs et al. (2015b) hypothesised that the introduction of predatory fish such as eels (*Anguilla* spp.), bullhead catfish and perch (*Perca fluviatilis* Linnaeus, 1758), all efficient predators of kōura, could adversely affect kōura populations in the Arawa lakes. Our data supports this hypothesis. Bullhead catfish can tolerate a wide variety of environmental conditions (Scott and Crossman 1973) and, unlike catadromous eels, are able to establish self-sustaining resident populations in lakes and rivers. Bullhead catfish, like eels, are mainly nocturnal, bottom feeding predators hunting by smell and vibration rather than sight. Keast (1985) found that adult bullhead catfish in their native range increasingly feed on decapod crustaceans with age, leading the author to speculate that they are specialized crayfish feeders as adults. In Aotearoa, bullhead catfish are known to prey predominantly on invertebrates, including larval insects and molluscs (Patchell 1977; McDowall 1990; Barnes and Hicks 2003). Catfish increasingly feed on kōura at lengths > 150 mm FL (Barnes and Hicks 2003) and are thought to be partially responsible for the decline or absence of

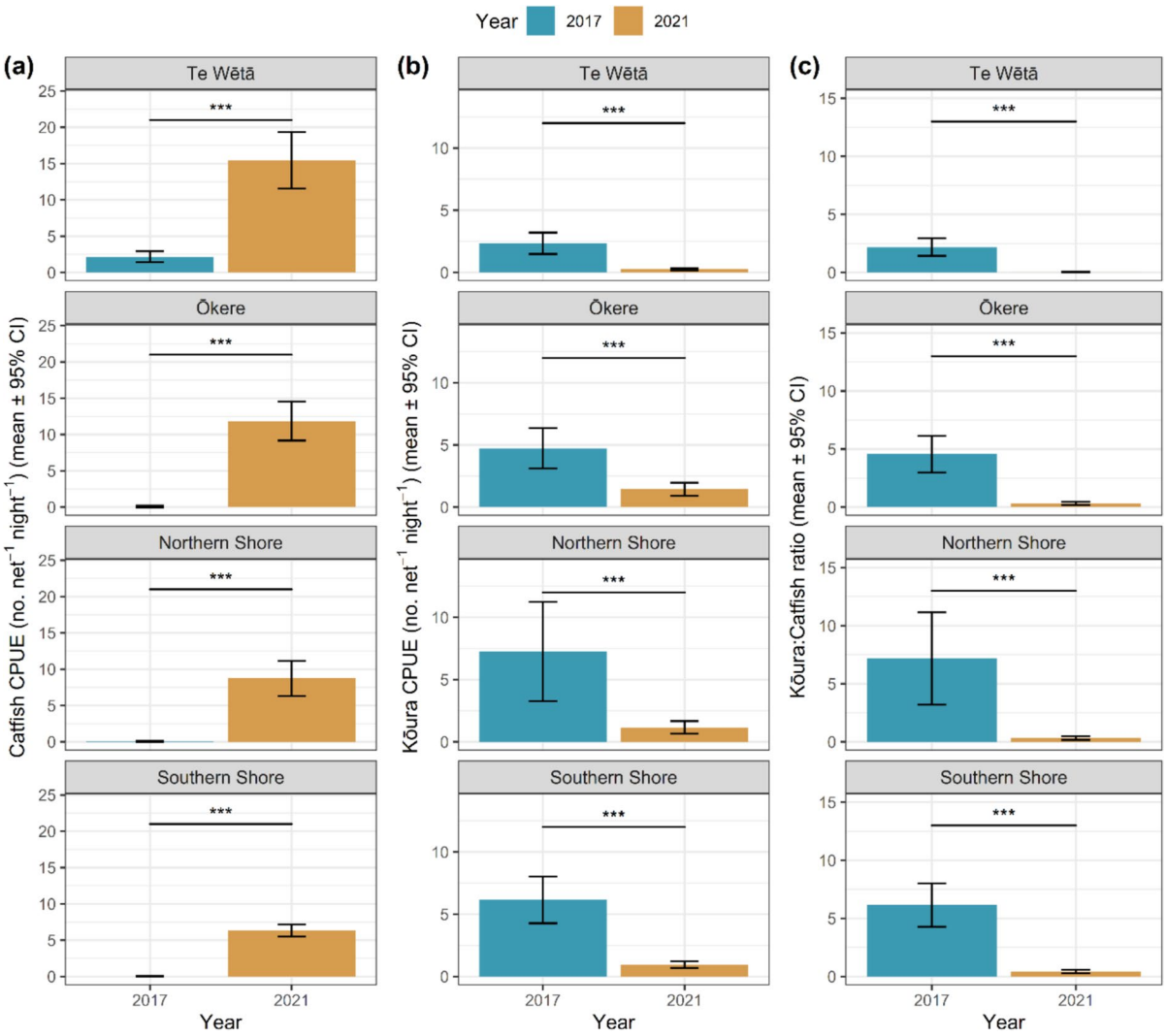

Fig. 8 Changes in mean catch per unit effort (CPUE) of **a** bullhead catfish, **b** kōura, and **c** the ratio of kōura to catfish caught at four sites in Lake Rotoiti (Te Wētā, Ōkere, Northern and Southern Shores) between 2017 and 2021. Catfish and kōura were caught using fyke nets. Error bars represent the 95% confidence interval (CI). ***$p < 0.001$, **$p < 0.01$

kōura when in high densities in North Island hydrolakes (Clearwater et al. 2014). Catfish may also exert indirect effects on kōura by reducing activity rates and competing for shelter and food resources, thus leading to fitness consequences and altered population demographics (Adams 2007; Wood and Moore 2020; Musil et al. 2023; MacNeil et al. 2025).

To the best of our knowledge, there are no published studies on the effects of introduced bullhead catfish on freshwater crayfish outside of Aotearoa. Studies do, however, show other non-native catfish species consuming freshwater crayfish. The invasive flathead catfish (*Pylodictis olivaris*) (Rafinesque, 1818) in Lake Mitchell, South Dakota, USA, was found to primarily consume crayfish (*Faxonius* spp.) (Lucchesi et al. 2017). Similarly, the invasive channel catfish (*Ictalurus punctatus*) (Rafinesque, 1818) was found to consume large numbers of crayfish in the Neuse River, North Carolina, USA, accounting for 25% of catfish diet (Baumann and Kwak 2011).

Our analyses indicate that kōura population declines have been influenced by the establishment of bullhead catfish. Using netting data, we found that kōura abundances were negatively correlated with

catfish abundances in the Lake Rotoiti littoral zone. Between 2017 and 2021, kōura abundances decreased at four sites on Lake Rotoiti whilst catfish abundances increased by several orders of magnitude. Dietary analysis of catfish in Lake Rotoiti showed that kōura were consumed mainly by large catfish (> 240 mm FL) indicating that predation by catfish was at least partially responsible for the decline in kōura abundance (Francis 2019).

Our results also indicate that in lakes Rotoiti and Rotorua, where bullhead catfish are present, recruitment of juvenile kōura appears markedly constrained compared with catfish-free lakes Ōkāreka and Rotokākahi. This hypothesis is supported by significant increases in mean kōura size (OCL) across all sites in lakes Rotoiti and Rotorua. Length-frequency analyses show that juvenile size classes < 15 mm OCL were disproportionately affected, with pronounced reductions at Ōkere Arm, Te Ākau, and in Lake Rotorua.

"Lag effects"

Lag effects in invasion ecology refer to the period between when a species is introduced to a new region and when it becomes invasive and begins to spread rapidly (Crooks 2005). A well-known example is the introduction of Nile perch (*Lates niloticus*) to Lake Victoria, where the species remained a minor component of the fish fauna for nearly two decades before undergoing a series of population explosions in the eastern, northern, and southern regions of the lake during the early 1980s (Kaufman 1992). The trigger for these irruptions remains unknown, and it is notable that the species persisted at low densities for an extended period prior to the population increase and resulting impacts on native biodiversity (Kaufman 1992).

Prior to the confirmed presence of catfish in Lake Rotoiti, the Bay of Plenty Regional Council (BOPRC) received several reports of suspected occurrences, including in 1995 and 2003 (Blair and Hicks 2009). We used 2009 as a marker in the Lake Rotoiti invasion timeline, when a large catfish (450–500 mm FL) was recovered dead from the lake (Blair and Hicks 2009). Despite these reports, surveillance efforts failed to verify catfish presence and official confirmation of the incursion only occurred in March 2016, when a live catfish was caught in Te Wētā Bay (BOPRC 2018). Two weeks later, an incursion response was initiated, and within a one-year period (2016–2017), a total of 3,272 catfish were captured, with > 98% of the catch occurring in Te Wētā Bay (Francis 2019). Te Wētā Bay lies approximately 0.6 km from the Te Ākau site on the same shoreline, and it is therefore unsurprising that kōura abundance declined earlier at Te Ākau than at the Ōkere and Manupīrua sites, which are located farther away at ~ 2.5 km from Te Wētā Bay.

The observed declines in kōura abundance and increases in mean size were detected prior to the official incursion of bullhead catfish to Lake Rotoiti in 2016 and Lake Rotorua in 2018. The combined pattern of reduced kōura abundance and changes in size structure appears to be a reliable indicator of catfish presence. Whilst our case-study further highlights the need for long-term monitoring, it also shows that crayfish population metrics have the potential to act as early warning signals of invasive predator establishment when lag effects make early detection of the species difficult.

Habitat quality

Assessing the impact of invasive species on native species can be complicated by environmental factors, such as habitat degradation. However, environmental conditions influencing kōura populations—such as water quality (TLI), dissolved oxygen, and aquatic vegetation—have remained relatively stable across the four lakes. Water quality has improved in the lakes. There has been minimal change to the lakebed sediments, a key determinant of kōura abundance (Kusabs et al. 2015b), due to the following reasons: (a) all whakaweku were located outside macrophyte beds (the aphotic/limnetic zone), and (b) no significant physical disturbance that would alter lakebed sediments (e.g., eruptions) has occurred in any lake since 2009. The construction of the Ōhau diversion wall on Lake Rotoiti is unlikely to have substantially affected kōura populations given the distances of study sites (Ōkere 1 km, Te Ākau 0.5 km, Manupīrua 4 km). Similar kōura declines and increases in OCLs in Lake Rotorua suggest that the trends seen in Rotoiti are unrelated to the wall.

Habitat compression

The importance of habitat for species abundances means that understanding the impacts of introduced species needs to also consider habitat variation (Garrock et al. 2014). Hypolimnetic deoxygenation is a key factor affecting kōura and catfish interactions in Aotearoa lakes, as prolonged low oxygen reduces available kōura habitat and increases predation risk. Lake trophic status and morphology indirectly influence kōura distribution through hypolimnetic deoxygenation (Kusabs et al. 2015b). Kōura are excluded from deoxygenated hypolimnia (< 5 mg/L DO) in lakes Ōkāreka, Rotoiti and Rotokākahi in the autumn during stratification, and periodic stratification events also cause intermittent low oxygen in Lake Rotorua (Burger et al. 2008; Trolle et al. 2011; Kusabs and Butterworth 2011).

Devcich (1979) reported strong correlations between kōura presence and DO in Lake Rotoiti, with abundance declining below 5 mg/L and kōura absent below 1.2 mg/L. In late summer and autumn, DO falls below 5 mg/L at depths of 24 m in the main (eastern) basin and 15 m at Te Ākau in the smaller western basin, forcing kōura into shallower, oxygenated depths where catfish are active. Catfish generally swim within the top 10 m, occasionally to 17 m (Dedual 2002), overlapping with kōura migrations into the littoral zone (< 10 m) for feeding and the release of juveniles (Devcich 1979). In lakes Rotomā and Tarawera, however, juvenile kōura < 5 mm OCL have been found at depths > 30 m suggesting that kōura in deep, oligotrophic lakes may be able to complete their lifecycles at depths outside the range of catfish (Kusabs 2023). In Lake Taupō, kōura abundance, biomass, and size remain comparable to catfish-free lakes despite catfish being present since the 1980s (Barnes and Hicks 2003; Dedual 2002), because habitat overlap is limited. Catfish occupy littoral and macrophyte zones, while kōura prefer rocky sites and deeper areas outside of the macrophyte beds (Kusabs and Taiaroa 2015). In contrast, Lake Rotoiti's hypolimnion remains anoxic for ~ 6 months (Pearson et al. 2010), and this habitat compression forces kōura to occupy the same zone as catfish for extended periods of time.

Reduced kōura abundance has also been linked to exotic macrophyte cover, which can restrict movement, alter food availability, and modify sediment conditions (Kusabs et al. 2015b). The littoral zone of Lake Rotoiti is dominated by dense stands of introduced macrophytes. Past studies show invasive macrophytes excluding crayfish from shallow zones and sharply reducing populations (Skurdal and Qvenild 1989; Ramberg-Pihl et al. 2018). In contrast, bullhead catfish benefit from dense macrophyte beds, which provide daytime cover, feeding habitat, and spawning sites (Dedual 2002; Barnes and Hicks 2003).

Customary kōura fishery

Lake Rotoiti used to support the most popular kōura fishery in the Arawa Lakes and arguably throughout Aotearoa. Kōura declines have caused this fishery to collapse, and the practice of traditional methods such as tau kōura and rama kōura (hand capture at night) have mostly ceased. For example, kōura are no longer served at local marae (communal spaces) where people of the Ngāti Pikiao iwi congregate (T. Grant, cultural practitioner, Tāheke Marae, pers. obs.). Preventing the spread of catfish and other invasive species to remaining kōura lakes, particularly Rotomā, Ōkataina, and Tarawera, is critical. Restoring kōura in Lake Rotoiti will require habitat enhancement, catfish control, and improved water quality to mitigate hypolimnetic deoxygenation. While climate warming is expected to intensify stratification (Hamilton et al. 2012), short- and medium-term actions such as catfish harvesting, weed management, and artificial reef construction can help rebuild kōura populations.

Bullhead catfish in Lake Taupō spawn in shallow, sheltered bays (e.g., Motuoapa Bay) from September to December. Targeted harvesting during this period could increase the efficacy of control measures (Dedual 2002). In Lake Rotoiti, harvesting should focus on shallow habitats, including the Ōkere Arm, Okawa Bay, Te Wētā Bay, and selected eastern bays. Controlling exotic macrophytes in these bays would reduce catfish spawning and juvenile habitat while improving kōura habitat.

Habitat complexity enhances crayfish survival by providing refuge from predation (Stein and Magnuson 1976; Lodge and Hill 1994). Kōura abundances increase with sediment size in the Arawa lakes (Kusabs et al. 2015b), yet fine sediments dominate the substrate. Artificial reefs—rocky structures mimicking natural habitat—have successfully boosted crayfish populations in Lake Krøderen, a large Norwegian lake (Johnsen and Taugbøl 2008) and are currently

being trialled in Lakes Rotoiti and Rotorua to enhance kōura abundance and harvest potential.

Conclusions

Kōura abundance and estimated biomass have declined significantly in lakes Rotoiti and Rotorua where bullhead catfish are now well established. In lakes Ōkāreka and Rotokākahi, where catfish are absent, the abundance and biomass of kōura populations have remained stable. Disentangling the respective roles of invasions and other anthropogenic stressors in causing major ecological impacts is a key challenge to invasion ecology. In our example, environmental variables (water quality, invasive macrophyte cover, and lakebed sediment composition) have remained relatively stable over the study period in both lakes. Several initiatives are being investigated to restore the kōura fishery, and these include improving water quality, harvesting catfish, aquatic weed management, and constructing artificial reefs for kōura.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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