

Article

Abundance of larval native and nonnative fishes in floodplain habitats of the lower Waikato River, New Zealand

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Abstract

The floodplains of many large rivers worldwide are important spawning and nursery habitats for multiple fish species. We investigated the potential importance of different floodplain habitats for fish larvae. Samples were collected from 14 sites along the Waikato River, northern New Zealand, from September to October 2010. Larval fishes were identified using traditional morphological identification and DNA analyses. Our results revealed high densities of invasive koi carp and goldfish larvae in flooded terrestrial habitats compared to other habitat types. Species richness was highest in the wetland habitat. Redundancy analysis revealed that koi carp and goldfish abundances were strongly positively correlated with chlorophyll *a* concentrations and zooplankton densities. Floodplain habitats seem to be important habitat for larvae of both native and introduced fish species in the lower Waikato River. Because introduced larval fish out-numbered native fishes in floodplain habitats managers should consider implementing measures that at key times provide controlled access to floodplain habitats for native species and also limit access of introduced fishes.

Key words: common carp, fish larvae, floodplain, flood pulse, introduced fish

Introduction

Flooding is an essential ecological interaction between low-gradient rivers and floodplain habitats (Junk et al. 1989). Floodplains are considered one of the most diverse and productive ecosystems on Earth (Tockner and Stanford 2002) and are often important in the life cycles of riverine biota (Ward et al. 1999). Natural floodplain habitats are frequently modified by building flood control structures, erecting hydropower dams, and altering land-use practices (Nilsson et al. 2005); these activities that alter floodplain inundation patterns can also change conditions for the recruitment of larval fishes (Humphries and Lake 2000) and may benefit invasive species (Gehrke and Harris 2001, Górski et al. 2012a).

The flood pulse concept suggests that annual flooding, defined by the hydrological and geomorphic conditions of the catchment, is the primary force driving the high biological productivity of river–floodplain systems (Junk et al. 1989) where temporary seasonal inundation can

result in heightened productivity, diversity, and biomass (Petts 1996, Thomaz et al. 2007). Many fish species migrate and spawn during spring floods when primary production is at its highest (Górski et al. 2010), resulting in enhanced larval recruitment (Poizat and Corivelli 1997, Baber et al. 2002, King et al. 2003, Sommer et al. 2004). In New Zealand, native fishes such as eels (*Anguilla australis* and *Anguilla dieffenbachii*), īnanga (*Galaxias maculatus*), and common bullies (*Gobiomorphus cotidianus*), similarly use floodplain habitats during their inundation (Chisnall 1989, Górski et al. 2012b).

Invasive fishes are considered a serious threat to New Zealand's freshwater ecosystems. They alter the turbidity of waterbodies (Zambrano and Hinojosa 1999, Bajer and Sorensen 2010), cause dramatic shifts in invertebrate community composition (Kloskowski 2011), reduce native macrophyte abundance (Zambrano and Hinojosa 1999), increase nutrient concentrations (Chumchal et al. 2005), and compete with native fishes for food resources (David and Speirs 2010). High densities of cyprinid fishes

such as common carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*) are notorious for altering freshwater ecosystems through the mobilisation of fine sediments that cause clear, shallow lakes to become turbid (Richardson et al. 1995, Miller and Crowl 2006, Bajer et al. 2009, Kloskowski 2011). The lower section of New Zealand's longest river, the Waikato River, is now home to a number of invasive fish species, including an ornamental variety of common carp (hereafter referred to as koi carp), goldfish, and gambusia (*Gambusia affinis*), any or all of which could potentially use floodplain habitats as spawning sites.

Floodplains are increasingly valued for their roles in flood protection and for enhancement of riverine ecological function (Galat et al. 1998, Middleton 2002, Siziba et al. 2011), but use of floodplain habitats by fish larvae during seasonal flooding remains unstudied in New Zealand rivers. Thus, there is a need to determine whether and how access to floodplain habitats influences larval fish abundance, and to delineate both the intended and unintended consequences of restoring floodplain connectivity. Consequently, the aim of this study was to investigate the use of different floodplain habitats by larval fishes in the lower Waikato River (New Zealand). We assessed the abundances of larval fishes of both native and nonnative species in various types of floodplain habitats and tested for their association with various environmental variables to examine the importance of floodplain habitats for larvae of fish species under consideration. Based on the flood pulse concept, our primary hypothesis was that the numbers of fish larvae in temporarily inundated floodplain habitats would be greater than those in permanent aquatic riverine habitats because of the higher temperatures and potentially higher food availability in temporarily inundated habitats.

Study site

The Waikato River drains a catchment area of 14,443 km² and has a mean annual discharge of approximately 450 m³ s⁻¹ at its mouth (Brown 2010). The river is fed mostly by rainfall and groundwater and is characterised by low flows in the austral summer and autumn and high flows (floodplain inundation) in winter and spring. The lower section of the river has been highly constrained since flood protection measures began in the 1950s and 1960s (Chapman 1996).

Despite significant anthropogenic alteration, the lower Waikato River remains linked to a variety of complex habitats (Fig. 1), with wetlands (Whangamarino, Opuatia), riverine lakes (i.e., Whangape, Waahi, and Waikare), and floodplains being important to the native biota and for

migrating fishes (Górski et al. 2012b). Before European arrival, the lower Waikato River's floodplain measured 364 km²; however, only 172 km² currently remain. Swamps and peat bogs connected to the Waikato River have shrunk by 92% from pre-European time (2026 km²) to the present (155 km²; Collier et al. 2010).

The native fish community of the Waikato River system consists of 19 species, with smelt (*Retropinna retropinna*), grey mullet (*Mugil cephalus*), common bully, and eels (*A. australis* and *A. dieffenbachii*) being the most abundant (David and Speirs 2010). In addition, 12 fish species have been introduced, and at present, koi carp and goldfish are the abundant invasive species in the lower river (Collier et al. 2010).

Methods

Data collection

Larval fishes were collected approximately weekly using hoop nets (45 cm diameter opening, 1 mm mesh) at 12 sites along the lower Waikato River (Fig. 1) during the austral spring (expected spawning season for multiple fish species; McDowall 2000) from 17 September 2010 to 25 October 2010. Some sites dried out during the sampling period, such that 41 total samples were ultimately collected (3–5 per site). Each sample site was categorised as one of 5 habitat types, based on the physical characteristics of the site:

1. "flooded terrestrial" habitats were inundated floodplain areas, 175–250 m from the main river channel, approximately 0.4–0.7 m deep, and had no flow;
2. "lake outflow" habitats occurred approximately 150 m upstream from confluences with the main river channel, where we sampled in areas with moderate to no flow and depths of 0.3–0.7 m;
3. "tributary" habitats occurred 150–300 m upstream of confluences with the river main channel, and we sampled at depths 0.4–1.0 m where there were moderate to low flows, and partial in-stream cover was provided by aquatic vegetation or willow (*Salix* spp.) roots;
4. "wetland" habitats comprised portions of peat-swamp complexes and occurred approximately 200 m from the main river channel in areas with low or no water flow and dense vegetation cover where water depths were 0.4–0.7 m; and
5. "main channel" habitat occurred on the main channel, downstream from other sampling sites, and we sampled where flows were moderate to high and partial in-stream cover was provided by aquatic vegetation or willow roots.

On each sampling occasion, the hoop net was dragged along the surface of, on average, 3 transect lines for approximately 5 m (depending on the characteristics of the site), moving at a constant speed of approximately 0.5 m s^{-1} . The collected larval fishes were preserved in bottles with 70% ethanol and then sorted and identified in the laboratory under a Nikon SMZ-645 stereo microscope (Nikon Instruments Inc., Melville, NY, USA) at $8\times$ (larger specimens) or $25\times$ (small specimens) magnification. All specimens were identified to species based on their morphology and pigmentation (Koblitskaya 1981, Laurila and Holopainen 1990, McDowall 2000). Larvae were distinguished from juveniles by the lack of developed scales, fins, and eyes, and their semitransparent body pigmentation.

To confirm accuracy of identification, DNA samples from each of 5 larval fish from each of the most abundant species (koi carp, goldfish, common bully) were analysed for their mitochondrial cytochrome c oxidase subunit I

(COI-5P) gene sequences (Hogg and Hebert 2004). This sequence is widely used to distinguish between species because of its high mutation rate. The results of DNA analyses were compared with known DNA sequences available in BOLD database (<http://www.barcodinglife.org>) for koi carp, goldfish, and common bully. All sampled DNA were identical to previously reported DNA sequences and correlated with the morphological identification.

Daily water level and water temperature data at Rangiriri ($37^{\circ}26'0''\text{S}$; $175^{\circ}10'0''\text{E}$; Fig. 1) were obtained from the Waikato Regional Council, Hamilton, New Zealand. Water quality and zooplankton samples were collected on each fish sampling occasion. Water temperature ($^{\circ}\text{C}$) and dissolved oxygen (% saturation) were also measured at each site, at a depth 0.2 m below water surface using a handheld YSI model 55 dissolved oxygen meter and a YSI 30 temperature meter, respectively (Yellow Springs Instruments, Ohio, USA).

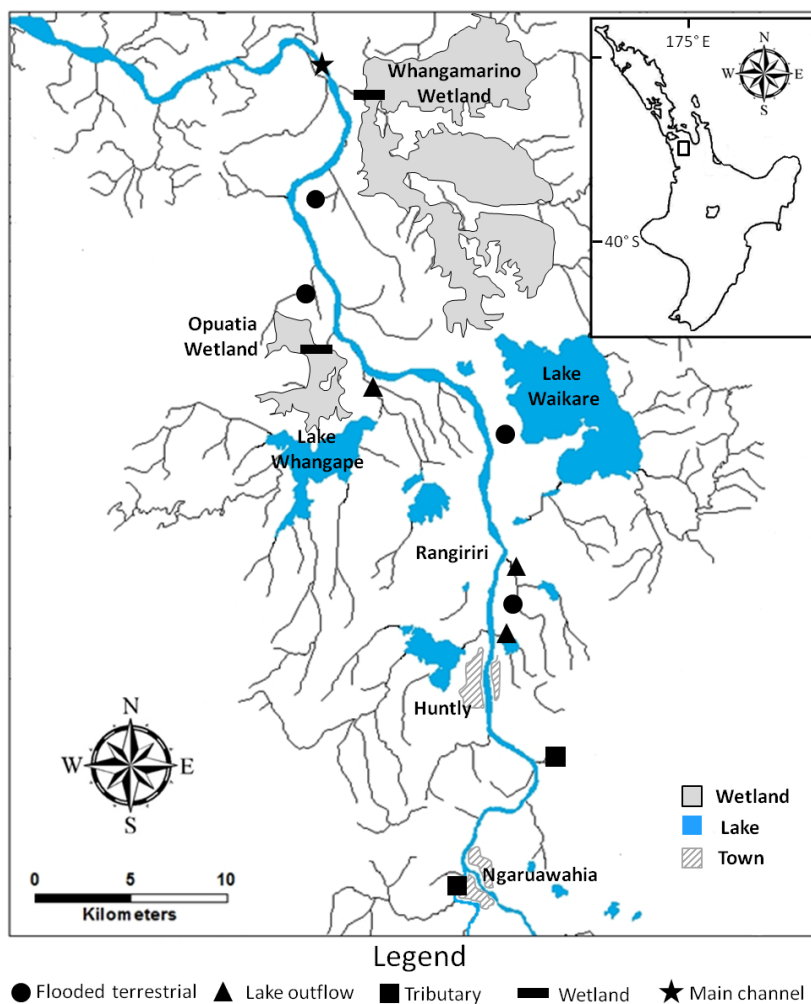


Fig. 1. Map of the Lower Waikato River showing sampling locations and location of the lower Waikato River in the North Island of New Zealand.

Chlorophyll *a* samples were collected by filtering 60 mL of water through a 0.45 μm filter and were quantified following a standard fluorometric determination protocol (Hauer and Lamberti 1996). Zooplankton samples were collected by filtering 40 L of water through a 45 μm net and were preserved in 70% ethanol. In the laboratory, zooplankton samples were drained through a 40 μm mesh strainer and then rinsed with tap water. The sample was then placed in a tray of water, and a 5 mL auto-pipette was used to deposit a subsample of known volume onto a sorting plate. Individual zooplanktoners were counted and identified to species using an Olympus SZ60 compound microscope (Olympus Corporation Inc., Shinjuku-ku, Tokyo, Japan).

Data analysis

Given that the hoop net aperture was of constant size, catch per unit effort (CPUE) was calculated for each sample as number of larval fishes caught per distance sampled (fish m^{-1}). These data were compared among the habitat types using a nonparametric Kruskal-Wallis test because their nonnormality violated ANOVA assumptions. In addition, relative abundance (%) of each fish species was calculated by dividing fish species from each habitat by the total larvae fish caught (excluding gambusia). The mean zooplankton density (ind L^{-1}) from each habitat was calculated along with the relative abundance (%) by dividing each zooplankton taxa by the total density caught in each habitat. We tested for differences in water quality among the habitat types using one-way analyses of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) tests. The dissolved oxygen values required \log_{10} transformation to meet the normality assumption of ANOVA.

Redundancy analysis (RDA; Ter Braak and Van Tongeren 1995) was performed to examine the relationship among the larval fish species CPUEs and the measures of water quality (chlorophyll *a* concentrations, water temperature, and dissolved oxygen saturation) and zooplankton density (densities for each of the major taxa: Cladocera, Copepoda, and Rotifera). Because juvenile and adult gambusia were in high abundance in some sample sites, and their potential to negatively impact native fishes is substantial (Ling and Willis 2005), their densities were also included in this analysis. Global Monte Carlo permutation tests (1000 permutations) were performed to determine the statistical significance of the explanatory variables at $\alpha = 0.05$. Fish abundance data were square-root transformed prior to analysis to improve the normality of the data.

Results

Flooding and temperature

Water levels and water temperature from June 2010 to June 2011 varied seasonally (Fig. 2). Water levels rapidly increased in spring from 7.3 m (1 Aug 2010) to 10.03 m (21 Sep 2010), inundating the floodplains. Our sampling took place from 17 September 2010 to 25 October 2010 during the spring flood.

Fish abundance

Samples from flooded terrestrial habitats produced the highest mean CPUEs (15.4 fish m^{-1}), followed by wetlands (3.4 fish m^{-1} ; Fig. 3 top). The larval fish CPUEs differed significantly among habitat types (Fig. 3 top; $P < 0.005$). Post hoc testing revealed that larval fish CPUEs from

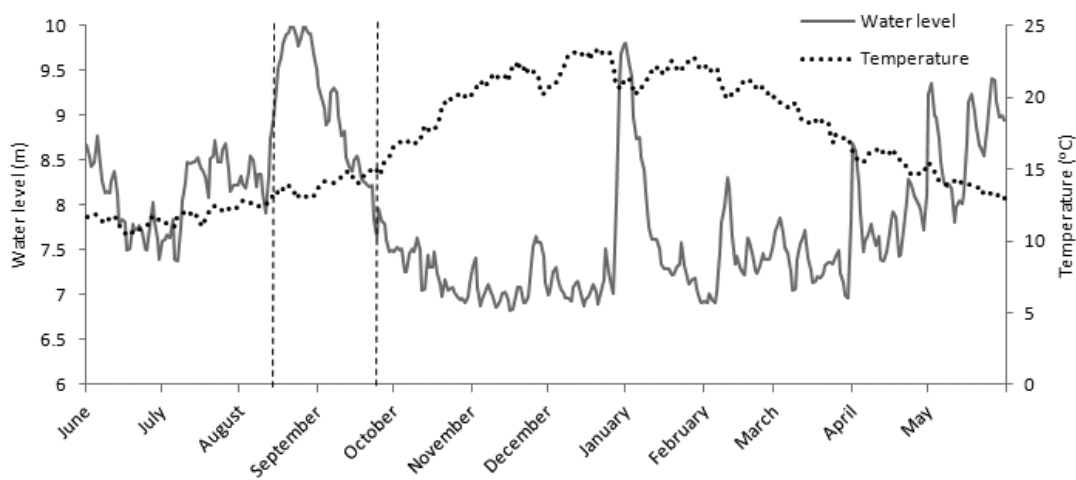


Fig. 2. Daily water level and water temperature at Rangiriri from 27 June 2010 to 26 June 2011. The dashed vertical lines indicate the period for sampling larval fish.

Table 1. Total number of larval invasive and native fishes caught in different habitat types. (*) indicates juvenile and adult *G. affinis* caught during sampling.

Scientific name	Common name	Habitat type				
		Flooded terrestrial	Lake outflow	Main channel	Tributary	Wetland
Invasive						
<i>Cyprinus carpio</i> (Linnaeus, 1758)	Koi carp	683	23	0	3	20
<i>Carassius auratus</i> (Linnaeus, 1758)	Goldfish	130	27	0	0	36
<i>Gambusia affinis</i> (Baird & Girard, 1853)*	Gambusia	0	14	1	53	273
Native						
<i>Gobiomorphus cotidianus</i> (McDowall, 1975)	Common bully	3	48	1	1	43
<i>Neochanna diversus</i> (Stokell, 1949)	Black mudfish	0	0	0	0	2
<i>Anguilla australis</i> (Richardson, 1841)	Shortfin eel	0	0	0	0	1

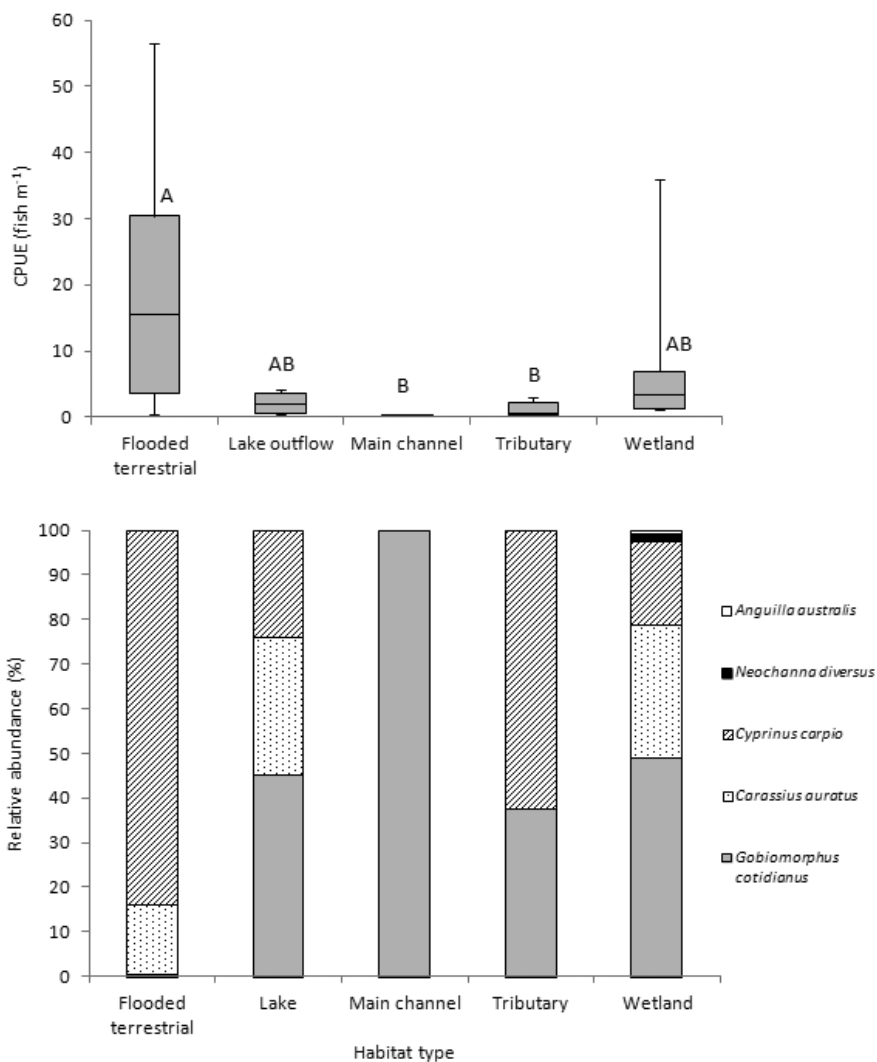


Fig. 3. Average larval fish catch per unit effort (CPUE) for each habitat type (top). Box represents standard deviation, line within the box represents the mean, and whiskers represent the range for each variable. Letters above the boxes indicate significant differences. Relative abundance (%) of the average larval fish CPUE for each species in each sampled habitat type (bottom).

Table 2. Average (SD) temperature, dissolved oxygen saturation, and chlorophyll *a* concentration for each habitat type sampled weekly from 17 September 2010 to 25 October 2010 (*n* = number of samples collected). Letters next to mean values indicate significant differences based on Tukey's honest significant difference test.

Habitat type	Temperature (°C)	Dissolved oxygen (%)	Chlorophyll <i>a</i> (mg/m ³)
Flooded terrestrial (<i>n</i> = 8)	15.2 (1.33)	65.05 (33.20) AB	19.84 (33.56) A
Lake outflow (<i>n</i> = 9)	16.11 (2.04)	82.1 (24.72) A	31.66 (18.79) B
Main channel (<i>n</i> = 5)	14.7 (0.43)	76.86 (6.55) AB	9.96 (5.19) A
Tributary (<i>n</i> = 8)	14.82 (1.20)	59.4 (21.95) AB	3.83 (4.11) AB
Wetland (<i>n</i> = 11)	15.66 (0.99)	35.7 (18.75) B	11.35 (7.25) A

Table 3. Redundancy analysis (axes 1–2) of the water quality (temperature, dissolved oxygen), chlorophyll *a*, and zooplankton density values relative to the larval fishes abundance measures.

P-value*	F-ratio	Eigenvalues	
		1	2
0.002	5.28	0.29 (28.9)	0.11 (39.5)

* Based on 1000 permutations (test of significance of the first canonical axis vs. all canonical axes).

flooded terrestrial habitats were significantly higher than for main channel ($P < 0.005$) and tributary ($P < 0.05$) sites (Fig. 3 top). Species richness for larval fish was highest in wetland habitats (5 species; Fig. 3 bottom).

Invasive fishes including koi carp, goldfish, and gambusia dominated the samples taken from every habitat type except the main channel (Table 1). The abundance of koi carp larvae was significantly higher in flooded terrestrial habitats (Fig. 3; mean CPUE = 56.6 fish m⁻¹) than in the remaining habitat types. Similarly, goldfish densities were also highest in flooded terrestrial habitats. No gambusia were recorded in the floodplain terrestrial habitat; however, adults and juveniles were abundant in wetland habitats and tributary sites (Table 1). The numbers of fish larvae belonging to native species were comparatively low in all habitat types but were greatest in the wetlands and lake outflows (Table 1).

Water quality and zooplankton

Water temperatures were similar among habitat types (Table 2). Dissolved oxygen saturation levels were significantly lower in wetland habitats (35.7%) compared to lake outflows (82.1%; Table 2 and 3). Chlorophyll *a* concentrations differed significantly among the sampled habitats, being highest in lake outflows and lowest in flooded terrestrial habitats and tributaries (Table 2).

The average zooplankton densities (Fig. 4 top) were highest in flooded terrestrial (13.4 ind L⁻¹) and wetland (7.7 ind L⁻¹) habitats and lowest in the main channel

(1.4 ind L⁻¹). The highest percentage of Cladocera (72%) occurred in flooded terrestrial habitats (Fig. 4 bottom). Rotifers were most abundant in the lake outflows (51%), whereas copepods generally occurred at low densities, comprising 15% of the samples overall. Copepods were well represented in main channel, tributary, and wetland habitat samples, however, ranging from 40 to 45% of samples (Fig. 4 bottom).

Environmental associations

RDA revealed that water quality variables (temperature, dissolved oxygen, chlorophyll *a*) and zooplankton densities accounted for 41.7% of the variation in fish larvae CPUEs on the first 3 axes (Fig. 5; Table 3). The ordination revealed that heightened koi carp and goldfish densities were strongly associated with elevated Cladocera densities and higher chlorophyll *a* concentrations. Gambusia densities were negatively associated with dissolved oxygen saturation levels (Fig. 5).

Discussion

High densities of larval fishes occurred in conjunction with annual flooding in the lower Waikato River; however, not all species responded in the same fashion as previous studies have shown in Australia (King et al. 2003, Beesley et al. 2012), Europe (Górski et al. 2011), and North America (Baber et al. 2002, Barko et al. 2006). Wetlands yielded the greatest diversities of larval fishes, potentially due to their more stable hydrology relative to the inundated terrestrial habitat. Low CPUE of fish larvae in some habitats may have been due to low sampling efficiency, and differences in sampling efficiency among habitats may have influenced assessment of interhabitat differences in relative abundance within and among species. Because sampling effort was similar in each habitat, it is unlikely that observed differences are solely due to sampling protocol; therefore, we considered the patterns observed to be useful indicators of larval fish–floodplain habitat associations in the lower Waikato River.

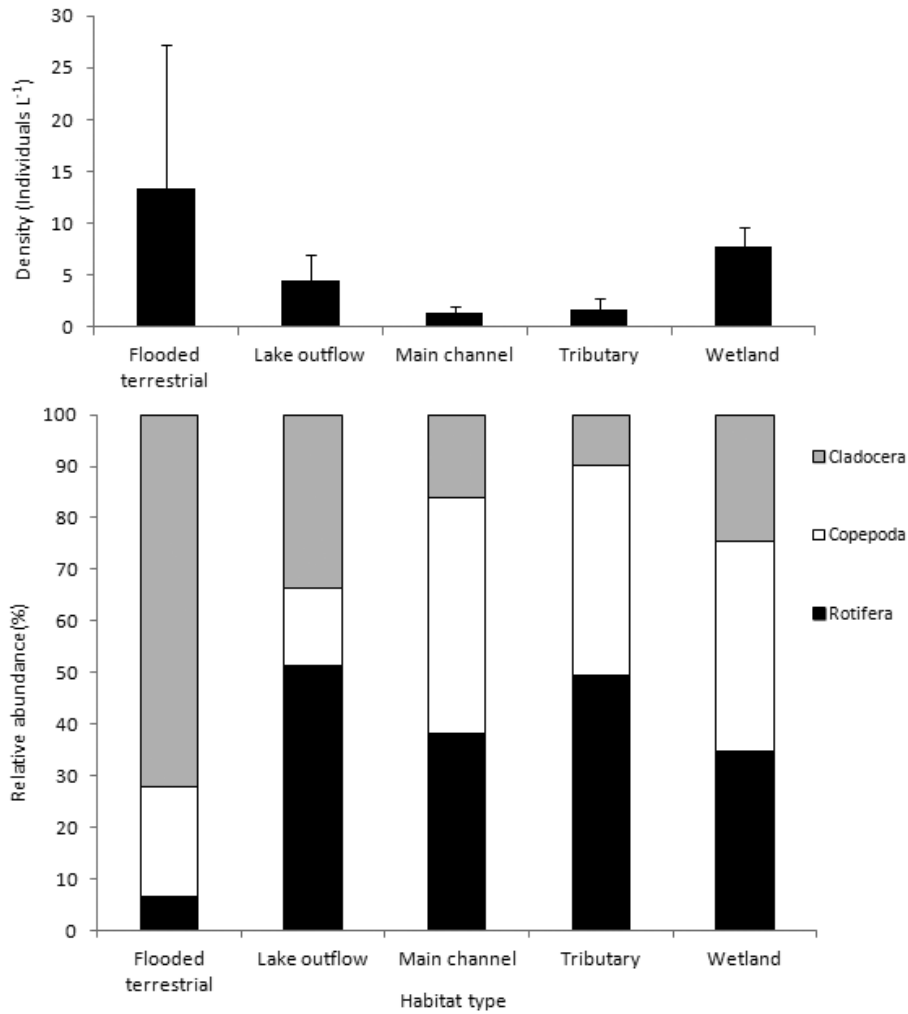


Fig. 4. Mean total zooplankton densities (\pm standard deviation) for each habitat type (top). Relative abundance (%) of zooplankton taxa in each sampled habitat type (bottom).

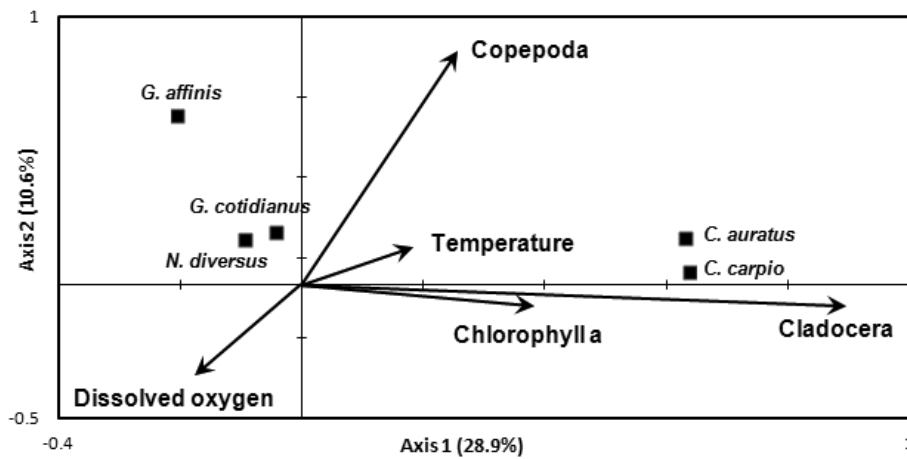


Fig. 5. Redundancy analysis of larval fish species' CPUEs related to water quality and zooplankton variables, shown as percentage variation (%). The closer the size and direction of the vectors for each fish species and variable, the stronger the association between them.

Larval fish in different riverine habitats

Our greatest catches of larval common bully occurred in lake outflows, wetland, and main channel habitats. Flooded terrestrial habitats produced low numbers of common bully larvae, suggesting that more permanent waterbodies constitute the dominant nursery habitat of this species. In addition, common bully spawn mostly in summer (McDowall 2000) when flooded habitats are not available; they also have superior feeding abilities in turbid waters (Rowe 1999) and can tolerate hypoxia (Landman et al. 2005). Consequently, the turbid and productive lower Waikato riverine lakes and wetlands may also offer suitable nursery areas for common bully. Larval black mudfish (*Neochanna diversus*), a wetland specialist species (McDowall 2000), were caught only in wetland habitats. They usually spawn in late autumn (O'Brien and Dunn 2007), which explains their low abundance in our samples.

Invasive koi carp were abundant in flooded terrestrial habitats. Studies in the Murray River (Stuart and Jones 2006) and the Ovens River (King et al. 2003) of Australia have shown that carp larvae occur in high abundance following flood peaks. As Nannini et al. (2012) found in the Illinois River, we likewise recorded low numbers of carp larvae at the lake outflow; in contrast to Nannini et al. (2012), we did not find carp larvae in the main channel, even though carp numbers in the adjacent floodplain habitats were high. Carp use flooded habitats for spawning and feeding (Barko et al. 2006). Their diets consist primarily of zooplankton (McCrimmon 1968), and therefore successful recruitment of koi carp in flooded terrestrial habitats might be related to the high abundance of food organisms in these habitats. Guerden et al. (1999) suggested that larval carp are able to tolerate starvation, however, and experimental studies are needed to assess the degree to which food abundance influences larval carp recruitment.

The abundance of spawning adults could also be important in shaping the abundance of carp larvae in these flooded habitats. Telemetry studies of New Zealand koi carp show that large numbers of adult fish move from the river mainstem to riverine lakes, wetlands, and flooded terrestrial habitats for spawning and feeding (Daniel 2009, Daniel et al. 2011). Parental stock numbers often do not correlate directly with larval abundance in cyprinid fish (Mooij 1996), however, potentially because predation may also be an important determinant of larval fish abundance. Several studies have suggested that predation and competition play stronger roles in regulating populations in permanent waters as wetlands and riverine lakes (Corti et al. 1996, Hicks et al. 2010), whereas floodplains may provide temporary shelter and areas of suitable habitat for the development of larval fishes.

Potential role of food sources in influencing larval fish abundance

We recorded higher concentrations of chlorophyll *a* in lake outflows compared to tributary and main channel habitats, likely because their lotic nature does not support high phytoplankton densities. Although high phytoplankton abundances can in turn support high densities of zooplankton (Lampert et al. 1986), we did not find this reflected in our results. This is perhaps due to a potential time lag in the response of zooplankton to elevated abundance of phytoplankton (Lampert et al. 1986), which would not be detected in our dataset because we measured all variables simultaneously. Instead, high zooplankton densities were followed by high larval fish abundances, with the flooded terrestrial habitats yielding the highest values. This finding suggests that prey densities may shape larval fish abundance in floodplain habitats because more lentic floodplain habitats of many large river systems accommodate high numbers of zooplankton, and succession of zooplankton biomass is largely determined by the floodplain hydrologic regime (Baranyi et al. 2002, Górski et al. 2013). High inputs of inorganic and organic materials, along with increased temperatures during seasonal inundation, can result in high productivity and thus a high biomass of zooplankton and larval fishes in floodplains of large rivers (Baranyi et al. 2002, Górski et al. 2013). We found a strong association between larval koi carp and goldfish abundances and Cladocera densities. High zooplankton densities could have contributed to the selection of inundated terrestrial habitat as spawning sites by these species (Stuart and Jones 2006).

Conclusions

The success of floodplain restoration efforts necessitates an understanding of how floodplain physical environments influence fish recruitment and species population dynamics (Buijse et al. 2002, Tockner and Stanford 2002). Our results indicate that inundated floodplain habitats of the lower Waikato River support both native and nonnative fish larvae, with densities of nonnative substantially higher. Consequently, floodplain reconnection strategies in the lower Waikato and other large river systems that accommodate introduced fish species need to consider how to facilitate access to preferred floodplain habitats by native fishes during seasonal inundation, while at the same time minimizing the access of nonnative species (Ribeiro et al. 2012). Controlling the movement of nonnative fish into floodplain inlets could be achieved, for example, through flow bottlenecks with barriers or exclusion nets that would allow movement of native fish (of which the majority are small bodied) and limit access

of larger adult carps (Daniel 2009, Hillyard et al. 2010). Our findings are based on a limited number of samples collected in a single year, however, and further studies are needed to better establish how larval abundance and species specific recruitment success are linked among riverine habitats and how to prevent nonnative fish species from disproportionately benefitting from floodplain reconnection efforts.

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