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## RESEARCH ARTICLE

# Biological plasticity of non-native European perch (*Perca fluviatilis*) populations and the implications for management in northern New Zealand

A Sabetian<sup>a\*</sup>, EDL Trip<sup>b</sup>, P Wheeler<sup>a</sup>, L Sands<sup>a</sup>, S Wakefield<sup>a</sup>, V Visconti<sup>a</sup> and F Banda<sup>a</sup>

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Size and age structure, longevity, growth, and reproductive activity of European perch (*Perca fluviatilis*) were studied at Lake Wainamu in March 2012 and 2013 as part of an introduced species eradication programme. Size and age structure of *P. fluviatilis* were dominated by smaller and younger individuals, while maximum age was estimated at 6 and 5 years for both years, respectively. Initial growth by the end of first year was faster when compared with selected studies in Europe, but size-at-equivalent age thereafter was smaller at Lake Wainamu. Oocyte atresia, asynchronous gonad development and vitellogenic oocytes were prevalent in ovaries at time of sampling in later summer, which warrant further investigation of *P. fluviatilis* as an iteroparous spring-spawning species in northern New Zealand. Our findings imply that the population dynamics of *P. fluviatilis* are highly plastic and may be influenced by local biogeographical factors. This has strong implications for the management of *P. fluviatilis* in New Zealand freshwater systems.

**Keywords:** redfin perch; reproductive activity; growth; age; introduced species

## Introduction

Introduced species have the potential to disrupt and out-compete native species through competition for food resources, habitat and via direct predation. These impacts can be exacerbated for native species that have evolved without natural predators (Townsend 1996). New Zealand's lack of dominant freshwater piscivores has meant that the introduction of the European perch (*Perca fluviatilis*), commonly known as the redfin perch, can have a significant impact on endemic New Zealand fishes (Ludgate & Closs 2003) that have essentially evolved without pressure from dominant predators. Additionally, the increasing abundance of *P. fluviatilis* has contributed to a decline in water clarity in some New Zealand lakes through a top-down disruption in the food web (Rowe 2007). This is thought to reflect the predation impact of

young *P. fluviatilis* on zooplankton and of older *P. fluviatilis* on planktivorous fishes which feed on zooplankton, thereby directly and indirectly affecting organisms that can keep a lid on planktonic algal blooms. Jeppesen et al. (1997) report that the top-down effect of these changes may be greatest in shallow lakes.

*Perca fluviatilis* was introduced to the South Island of New Zealand in 1868 for the purpose of sport fishing (McDowall 1990), but failed to become established as a popular angling fish such as trout or salmon. They have since been translocated north by the public into lakes and slow-flowing rivers. Although highly regarded as an important food-fish species in Europe, *P. fluviatilis* is not widely consumed in New Zealand. It is listed as a sport fish in the First Schedule of the Freshwater Fisheries Regulations 1983. *Perca fluviatilis* is managed as an acclimatised sport fish by regional

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councils, Department of Conservation, and Fish & Game New Zealand, where efforts are focused on containment (Dean 2003). In the Auckland region an agreement was reached between the former Auckland Regional Council (now Auckland Council) and Fish & Game New Zealand to allow their control and removal from 11 high conservation value (HCV) water bodies and their catchments, as specified in the Auckland Regional Pest Management Strategy (Auckland Regional Council 2007). In these 11 water bodies, *P. fluviatilis* are designated as a pest species, whereas throughout the rest of the Auckland region they are still classified as a sport fish and require a licence to fish for from Fish & Game New Zealand. One of these HCV water bodies is Lake Wainamu (36°53'22"S, 174°28'07"E) where an exotic fish removal programme was established in 2004 by the former Auckland Regional Council in order to investigate the link between introduced fish populations and the decreasing water clarity that had been observed over previous years (Rowe & Smith 2001).

The widespread distribution of *P. fluviatilis* in the North Island appears to suggest that they have the ability to tolerate relatively warmer climatic conditions compared to the South Island or, indeed, their native Europe. The ecological manifestations of adapting to warmer waters have yet to be fully assessed for *P. fluviatilis* in northern New Zealand. Morgan et al. (2002) discuss the possibility that the latitudinal range of *P. fluviatilis* in Western Australia (c. 32–35°S) compared to its native range in the Northern Hemisphere (c. 41–70°N), in conjunction with warmer climate, increased food supply and limited competition, can lead to higher growth rates and earlier age at maturity. The implications of such population characteristics are important from management and conservation perspectives and need to be examined in detail.

Information on an invaders' life history characteristics form the basis for understanding their ecology and can help elucidate the theory of invasion biology (Townsend 1996) at the individual, population, community and ecosystem levels (Townsend 2003). This study aims to contribute to the body of knowledge on *P. fluviatilis* population dynamics in New Zealand. The specific

objectives were to establish size and age structure, longevity and growth, sex ratio and reproductive activity of *P. fluviatilis* in Lake Wainamu. Much of what is known about the population dynamics of *P. fluviatilis* in New Zealand is sourced from Jellyman (1980). However, Jellyman's study was conducted on Lake Pounui (41°20'41"S, 175°6'46"E) on the southern reaches of the North Island, which, given the plasticity of *P. fluviatilis* life history traits with latitude (Heibo et al. 2005), could display characteristics that are different to *P. fluviatilis* in Lake Wainamu, some 800 km to the north. The possibility of *P. fluviatilis* exhibiting plastic life-history traits across different spatial and latitudinal gradients provides a strong basis for this study, and our findings may highlight characteristics that have allowed *P. fluviatilis* to become dominant piscivores in New Zealand's unique ecological settings.

## Materials and methods

### Study location

Sampling was undertaken at Lake Wainamu, a small dune lake west of Auckland, New Zealand. Thompson (1979) found that *P. fluviatilis* were not present in Lake Wainamu in the late 1970s, which indicates that they must have been released into the lake sometime thereafter.

### Sampling

The exotic fish removal programme is conducted by Auckland Council's Freshwater Research, Investigations and Monitoring Unit (FRIMU) in March of each year. We collected samples from this group from their 2012 and 2013 expeditions. The exercise involves setting 48 gill-nets of three different sizes (14, 25, 43 mm stretched mesh) perpendicular to the shoreline in the littoral margins of the lake and clearing these three times daily. Mesh selectivity is determined by FRIMU based on size class frequency data from previous years. A total of 648 and 2745 specimens were caught in 2012 and 2013, respectively, the majority of which were between 160 mm and 180 mm in standard length (SL). From those, 110 (2012) and

145 (2013) *P. fluviatilis* were selected, representing a selection from the most abundant size class (160–180 mm) and everything else that was caught. The selection of 14 mm mesh gill-net prohibited the acquisition of very small specimens (< 100 mm SL) which are best caught using fyke nets (e.g. Ludgate & Closs 2003). Furthermore, the lack of larger specimens (> 400 mm SL) is also due to the success of netting in previous years. As a result, the lack of very small and very large specimens renders the population sample in this study as size-class biased. Specimens were weighed (total weight, in g) and measured for SL (in mm). Sagittal otoliths were removed, cleaned and stored dry for estimation of age, and gonads were dissected out and preserved in a formalin-based fixative for histological analysis.

### Age estimation

Age estimates were based on sectioned sagittal otoliths following established methods for estimation of age in fish (Campana 2001). Transverse sections were examined under a dissecting microscope with transmitted light, and the number of opaque zones was enumerated. The age of each fish at the time of capture (20–25 March) was calculated, assuming a birth date of 1 September (Jellyman 1980). Specimens with no discernable opaque zone were allocated a mean age of 0.6 years (i.e. 7 months), while those with visible zones had 0.6 years added to their estimated annual age. The annual periodicity of opaque and translucent zone formation in *P. fluviatilis* has previously been validated through marginal increment analysis using whole otoliths (Morgan et al. 2002)

### Growth

The relationship between size and age of *P. fluviatilis* was modelled for males and females and for both years sampled, using Francis' reparameterised von Bertalanffy growth function (rVBGF; Francis 1988) (e.g. Moulton et al. 1992; Welsford & Lyle 2005; Trip et al. 2008; Claisse et al. 2009; Ruttenberg et al. 2011). The rVBGF describes growth in the same way as the

standard von Bertalanffy growth function (VBGF), but has the advantage of providing parameter estimates that express expected mean body size at three arbitrary ages of tau, omega and nu, thereby generating biologically relevant information that can be directly compared across populations or sexes. Tau and nu are two arbitrary ages, and age omega is the mean of tau and nu. Tau, omega and nu were 1, 3 and 5 years, as ages 1 to 5 were well represented in the dataset and covered the growth of *P. fluviatilis* across their lifespan. rVBGF parameters were thus expected mean size-at-ages 1, 3 and 5 years (i.e. parameters L1, L3 and L5, respectively). Growth functions were fitted by minimising the negative log of the likelihood assuming a normal distribution of the residuals (Haddon 2001).

Size-at-age data were also fitted with a standard VBGF (Kimura 1980), with parameters  $t_0$  (hypothetical age at length zero),  $K$  (curvature coefficient), and  $L_\infty$  (mean asymptotic size), so as to allow comparison of growth parameters with that reported in other demographic studies of *P. fluviatilis*.

Few individuals were present in the very small size classes, a characteristic that can lead to substantial errors in growth model parameter estimates such as underestimation of the rate of growth in the early parts of the lifespan and overestimation of mean adult size achieved (Berumen 2005). In order to take this into account, the growth functions used were fitted by constraining size-at-age zero to mean size-at-hatching. Mean size-at-hatching was calculated from 20 newly hatched captive individuals and was 6.8 mm ( $\pm$  0.2 SEM) in total length. Our size-at-hatching is in general agreement with Le Cren's (1958) estimate of 6 mm.

Likelihood ratio tests (LRT) were used to compare growth between the two years sampled, and between males and females for both 2012 and 2013 (Kimura 1980; Cerrato 1990). The null hypothesis of no difference in growth between groups was rejected at alpha = 0.05, with  $q$  (degrees of freedom) being the number of parameters being constrained (e.g.  $q = 3$  for coincident curves).

The relationship between length and total weight was also analysed. This relationship is best described as ( $W = a \times L^b$ ) (Rickter 1973), where  $W$  is the total weight (g),  $L$  is the standard length (mm), exponent  $a$  is the y-intercept or the initial growth coefficient and exponent  $b$  is the slope or the growth coefficient. Growth is isometric for most fish species, where  $b$  is close to 3.0, with  $< 3.0$  indicating negative allometric growth and  $> 3.0$  positive allometric growth.

### Reproductive analysis

Whole gonads were weighed to the nearest 0.001 g before histological analysis. In order to test for development differences along the length of the gonad, three sections of c. 3–4 mm in thickness were dissected from the proximal (P), medial (M) and distal (D) regions. This was performed for a subsample of randomly selected individuals ( $n = 25\%$  of each population). Our justification for doing this was two-fold; first, gonadal anomalies have been previously identified in *P. fluviatilis* (Sandström et al. 1997), and, second, Jellyman (1976) had identified a functional hermaphrodite *P. fluviatilis* from Lake Pounui. As we found no differences in gonad development across the length

of the gonad, a medial section only was taken from the remaining 75% of samples. The structure of *P. fluviatilis* gonads is characterised by immature males and females having two gonadal lobes whereas, when females mature, the two lobes fuse together to form one gonadal sac with males retaining two separate gonadal lobes. This is an unusual characteristic that is uncommon in fin fishes. Tissue sections were processed for histology. All sections were stained using Mayers' haematoxylin and Young's eosin–erythrosin.

For each specimen, the gender, developmental stage (stage of oocyte and sperm growth) and reproductive activity were recorded. Stages of gonad development were assessed from the latest stage of non-atretic oocyte or sperm growth present (Grier 1981; West 1990). Reproductive activity was assessed as one of two categories: 1. reproductively active ('developing', 'spawning' or 'spent'), which included fish that showed signs of gonad maturation in preparation for spawning; and 2. reproductively inactive, which included fish that were either immature or mature resting (Table 1). Criteria used in the diagnosis of gender, reproductive activity and developmental stages were modified from Treasurer & Holiday (1981), and are summarised in Table 1. Female gonads which

**Table 1** Histological features used in the diagnosis of *Perca fluviatilis* male and female reproductive activity.

Sexual identity	Latest most abundant stage present	Reproductive activity	Gonad developmental stage
Female	Peri-nucleolar oocytes	Inactive	Inactive (immature or resting)
	Cortical alveoli oocytes	Active	Mature developing
	Vitellogenic oocytes	Active	Mature developing
	Hydrated oocytes	Active	Mature spawning
	Peri-nucleolar and cortical alveoli oocytes, and degenerating vitellogenic or hydrated oocytes present in the lumen	Active	Mature spent
	Atretic oocytes with no post-ovulatory follicles and hydrated oocytes	Active	Atretic
Male	Spermatogonia, or both spermatogonia and spermatocytes present	Inactive	Inactive (immature or resting)
	Spermatids	Active	Mature developing
	Spermatozoa	Active	Mature spawning

**Table 2** Parameter values of best-fit models for *Perca fluviatilis* at Lake Wainamu in 2012 and 2013. Parameters presented are growth parameters of the reparameterised and standard von Bertalanffy growth functions (rVBGF and VBGF, respectively), showing sex-specific and overall growth trajectories for both years, length–weight relationship fitted with a power curve ( $W = a \times L^b$ ), otolith weight–age relationship fitted with a linear regression, and sex ratio.

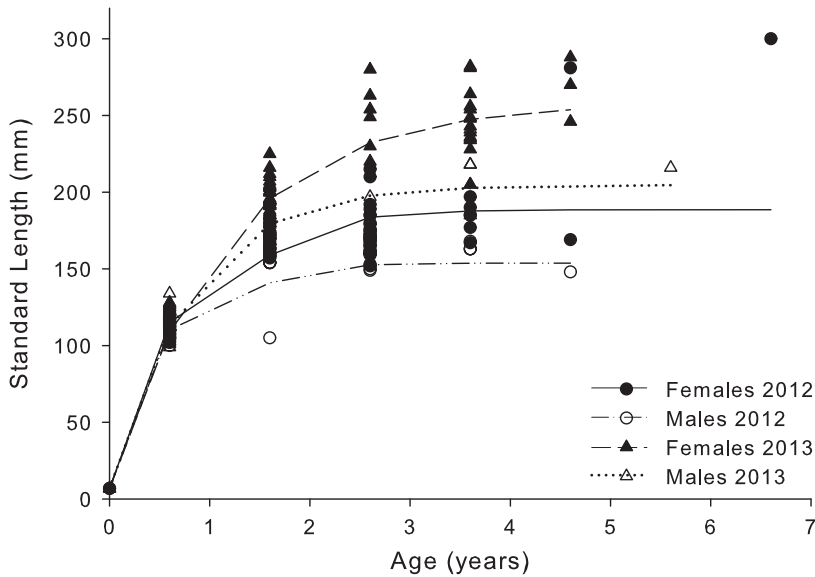
Function	Parameters	2012	2013
rVBGF	L1	141.0 (mm)	151.3 (mm)
	L3	177.0 (mm)	230.5 (mm)
	L5	178.7 (mm)	242.7 (mm)
rVBGF (male)	L1	135.4 (mm)	150.0 (mm)
	L3	158.0 (mm)	200.5 (mm)
	L5	158.5 (mm)	204.4 (mm)
rVBGF (female)	L1	142.9 (mm)	153.1 (mm)
	L3	184.3 (mm)	239.9 (mm)
	L5	186.7 (mm)	255.1 (mm)
VBGF	$L_\infty$	178.8 (mm)	245.0 (mm)
	$K$	1.88	0.93
	$t_0$	-0.02	-0.03
VBGF (male)	$L_\infty$	159.0 (mm)	202.8 (mm)
	$K$	1.88	1.36
	$t_0$	-0.02	-0.0004
VBGF (female)	$L_\infty$	186.0 (mm)	256.7 (mm)
	$K$	1.48	0.91
	$t_0$	-0.00	-0.0004
Length–weight relationship	$n$	110	145
	$b$	2.9987	3.2915
	$R^2$	0.98	0.99
Otolith–weight–age relationship	$R^2$	0.7663	0.8125
Sex ratio	(F:M)	1.75:1	1.4:1

displayed atretic oocytes were grouped into a separated category ('atretic'). Given that oocyte atresia has previously been observed in freshwater fishes including *P. fluviatilis* subjected to higher temperatures (Sandström et al. 1997; Luksiene et al. 2000), we were mindful of not associating atresia alone as sole evidence of spawning. This is because, in the case of spawning, atresia is often associated with other evidence such as post-ovulatory follicles and hydrated oocytes, which were not observed together in any of our samples. Other anomalies such as asynchronous gonad development have also been observed in freshwater fish species (Luksiene et al. 2000). Gonads with oocytes in at least two different stages of development were categorised as 'asynchronous'.

## Results

### Growth and life span

Age was estimated from sectioned sagittal otoliths of 110 and 145 *P. fluviatilis* captured in 2012 and 2013, respectively. There was a strong relationship between otolith weight and age for both years (Table 2), validating the assumption of otolith growth with age. Longevity was estimated at 6+ and 5+ years for 2012 and 2013, respectively. The relationship between size and age of *P. fluviatilis* across both 2012 and 2013 population samples was asymptotic, with very rapid somatic growth in the first year of their lifespan before reaching an asymptote. However, this is affected by the size biased nature of our population samples. There



**Figure 1** Sex-specific growth trajectories of male and female *Perca fluviatilis* at Lake Wainamu in 2012 and 2013. Growth curves shown are reparameterised von Bertalanffy growth functions (rVBGF).

were differences in growth trajectories between both years and between sexes (Fig. 1). The growth trajectory of *P. fluviatilis* (both overall and sex-specific) was significantly different between the 2012 and 2013 populations, with rVBGF parameters suggesting differences in expected mean size-at-ages 1, 3 and 5 years between the two years sampled (LRTs, Table 3). Individuals sampled in 2013 achieved significantly larger mean size at ages 1, 3 and 5 years. In both 2012 and 2013, females achieved larger sizes than males at the ages of 3 and 5 years. Standard VBGF parameters (Table 2) also indicated that, in 2013, *P. fluviatilis* reached a higher mean asymptotic size ( $L_{\infty} = 245.0$  mm SL), while sex-partitioned data confirmed that females reach higher asymptotic size over males.

*Perca fluviatilis* in Lake Wainamu exhibited a strong relationship between length (L) and weight (W) (Fig. 2). *Perca fluviatilis* in 2012 exhibited isometric L–W growth ( $b = 2.9987$ ) while in 2013 this relationship was positively allometric ( $b = 3.2915$ ) (Table 2), indicating that individuals were heavier at equivalent lengths.

### Length and age distribution

Keeping in mind the inherent size bias of the sampling procedure, length and age class mode of *P. fluviatilis* from Lake Wainamu were found to be 160–179 mm and 0.6 year in 2012, and 180–199 mm and 1.6 years in 2013 (Fig. 3). The age and size distribution trends between the two years differed, with 2013 being dominated by younger and larger at equivalent-age individuals. Furthermore, the 2013 population is also represented by specimens in the larger (> 220 mm) size groups, while the same groups are absent in 2012, apart from two individuals above 280 mm SL.

### Reproductive biology

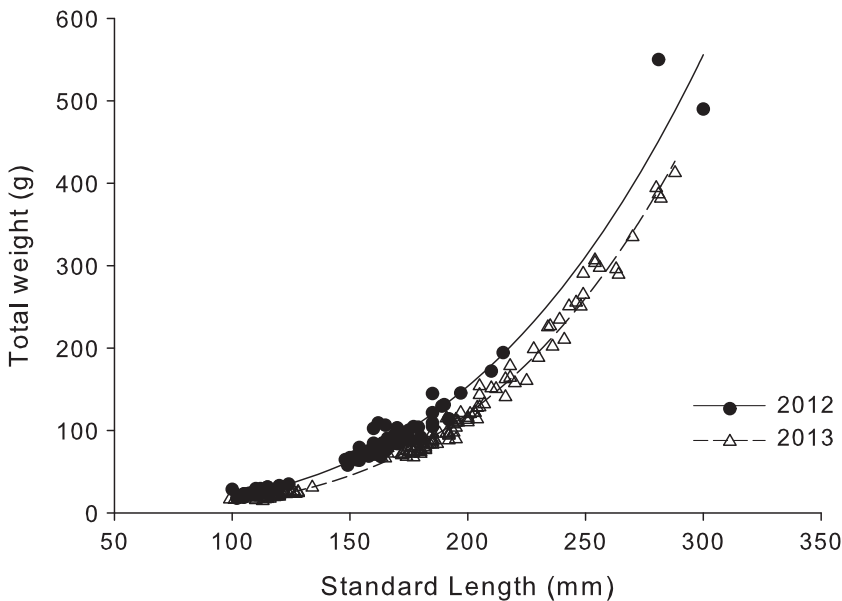
Samples for both years were female dominated with sex ratio of 1.75:1 and 1.4:1 for 2012 and 2013, respectively. There were more inactive (immature or resting) and less active *P. fluviatilis* in 2013 than in 2012. Inactive males (Fig. 4A) accounted for 83% of the total male population in 2012, compared to 97% in 2013, while inactive females (Fig. 4B) only made up 21% and 26% for



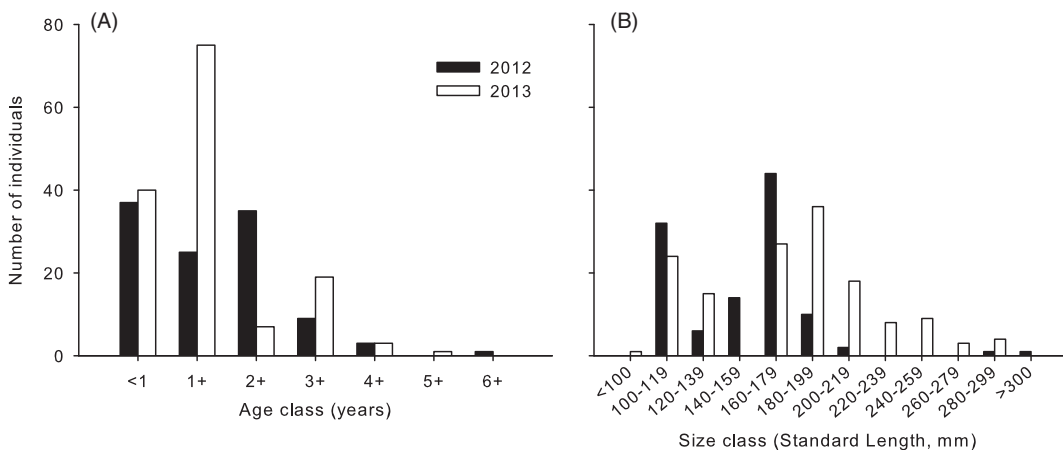
**Table 3** Likelihood ratio tests comparing reparameterised von Bertalanffy growth functions fitted to *Perca fluviatilis* at Lake Wainamu between years sampled (2012 vs 2013), between males and females sampled in 2012 (Males vs Females 2012), and between males and females sampled in 2013 (Males vs Females 2013).

	Base case	Coincident curves	= L1	= L3	= L5
2012 vs 2013 ( $N = 257$ )					
RSS <sub>ω</sub>	85303.7	158838.2	88470.1	151671.1	137738.0
$\chi^2$	–	159.8	9.37	147.9	123.1
d.f.	–	3	1	1	1
$P$	–	< 0.001	< 0.01	< 0.001	< 0.001
Males vs Females 2012 ( $N = 112$ )					
RSS <sub>ω</sub>	34932.9	42314.6	35578.6	41996.7	41545.7
$\chi^2$	–	21.5	2.1	20.6	19.4
d.f.	–	3	1	1	1
$P$	–	< 0.001	0.152	< 0.001	< 0.001
Males vs Females 2013 ( $N = 147$ )					
RSS <sub>ω</sub>	28774.3	42989.1	28968.6	42116.0	39908.6
$\chi^2$	–	59.0	0.99	56.0	48.1
d.f.	–	3	1	1	1
$P$	–	< 0.001	0.320	< 0.001	< 0.001

Base case represents the hypothesis of separate curves, coincident curves represents the hypothesis of a single curve, and = L1, = L3 and = L5 the hypotheses that the growth curves differ in the parameter of interest. RSS<sub>ω</sub> is total residual sum of squares, and  $N$  is total number of samples for the two groups combined. Significant results are shown at  $P < 0.05$ .



**Figure 2** Weight-at-length of *Perca fluviatilis* at Lake Wainamu in 2012 and 2013. Regression lines fitted are power curves for each year (parameters are presented in Table 2).



**Figure 3** A, age and B, size distributions of *Perca fluviatilis* at Lake Wainamu in 2012 and 2013.

their respective populations for 2012 and 2013, respectively (Fig. 5). There were less developing males (Fig. 4C) and females (Fig. 4D) in 2013 than in 2012, with males declining from 18% to 3%, while developing females declined from 73% in 2012 to 50% in 2013. Reproductively active and inactive males and females occurred across all age and size classes.

Female gonads showing signs of atresia accounted for 6% and 24% of samples in 2012 and 2013, respectively (Fig. 4E). Gonads exhibiting signs of asynchronous development (Fig. 4F) accounted for 27% and 33% of samples in 2012 and 2013, respectively.

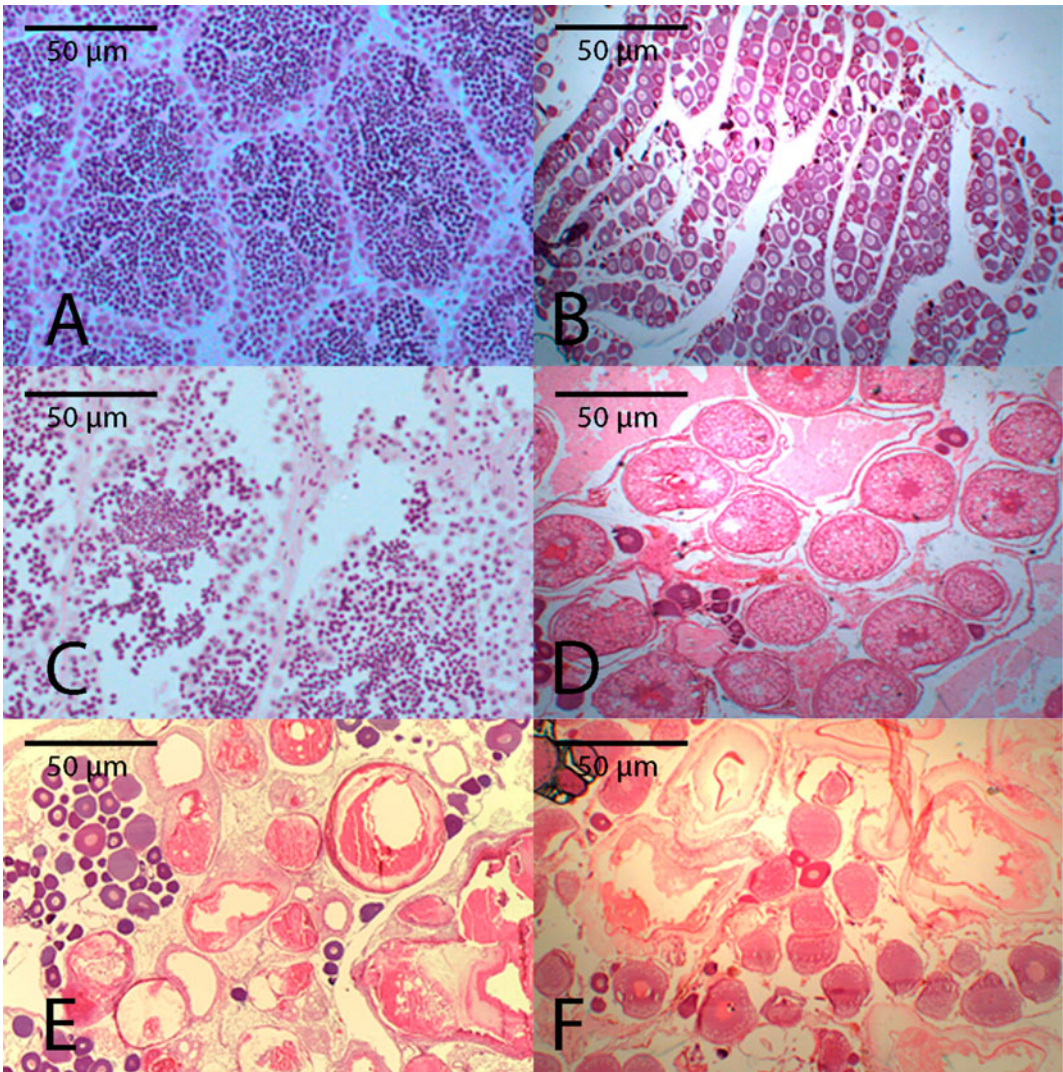
## Discussion

This study has established three important life-history parameters for *P. fluviatilis* in Lake Wainamu which can impact on management measures of this species: 1. rapid early growth; 2. early onset of sexual maturation; and 3. the possibility of an extended spawning season. These findings, in the context of *P. fluviatilis* population dynamics at Lake Wainamu, point to a situation where fast early growth and reproduction may be creating conditions where population turnover is occurring more rapidly than the effort to eradicate them through a one-off annual netting effort. Since 2004 approximately

20,000 fish have been removed, with 80% of the total catch being *P. fluviatilis*. However, Lake Wainamu's eradication programme appears to have had limited success, with *P. fluviatilis* numbers going through a boom and bust cycle: 2013 ( $n = 2745$ ), 2012 ( $n = 648$ ), 2011 ( $n = 457$ ), 2010 ( $n = 3598$ ), 2009 ( $n = 521$ ), 2008 ( $n = 762$ ), 2007 ( $n = 305$ ), 2006 ( $n = 2221$ ), 2005 ( $n = 2725$ ) and 2004 ( $n = 1945$ ) (Graham Surrey, Auckland Council, pers. comm.)

Detailed life-history information are critical if we are to discuss whether this lack of apparent success in the eradication programme is related to the inevitable escapees from annual netting. If so, their rapid growth and early sexual maturation are contributing sufficiently to regeneration of a population that has little or no competition from other species. Life-history traits such as natural lower mortality have been proposed as possible reasons why brown trout (*Salmo trutta*) enjoy high biomass in New Zealand rivers (Townsend 2003). Whatever the reason, the findings of this study warrant further detailed investigation of *P. fluviatilis* population dynamics in New Zealand.

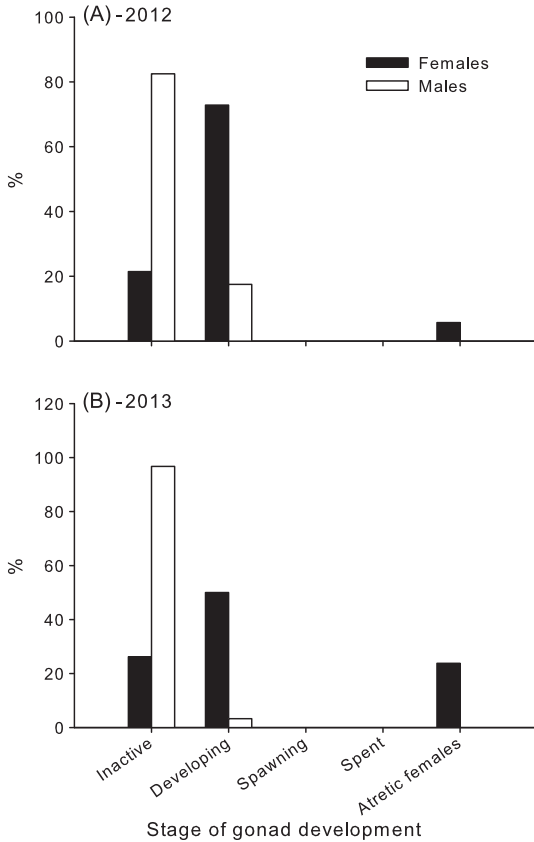
*Perca fluviatilis* at Lake Wainamu grew very fast over the first year of their life. This indicates that rapid early growth is extremely important to this species, a characteristic that may reflect the impact of cannibalism on the very early stages of



**Figure 4** Photographs of transverse histological sections of male and female gonads of *Perca fluviatilis* at Lake Wainamu. **A**, Inactive testis containing spermatogonia and spermatocytes; **B**, inactive ovary containing peri-nucleolar stage oocytes; **C**, developing testis containing a congregation of spermatids; **D**, developing ovary containing vitellogenic oocytes; **E**, atretic ovary containing atretic vitellogenic oocytes; **F**, asynchronous ovary containing peri-nucleolar and early vitellogenic (cortical alveoli) oocytes, as well as degenerating hydrated oocytes.

their lifespan (Claessen et al. 2000; Ludgate & Closs 2003; Byström et al. 2012). Comparisons of early growth rates for both 2012 and 2013 with studies in the Northern Hemisphere (e.g. Le Cren 1992; Sandström et al. 1995; Linlökken & Holst Seeland 1996; Heibo & Vøllestad 2002; Ceccuzzi

et al. 2011) indicate that *P. fluviatilis* in Lake Wainamu grow relatively faster and attain a larger size by age 1 compared with their Northern Hemisphere counterparts. However, Northern Hemisphere *P. fluviatilis* appear to attain sizes that are larger at equivalent age thereafter. Our data



**Figure 5** Frequency distributions of male and female gonad activity of *Perca fluviatilis* at the time of sampling (March) at Lake Wainamu in **A**, 2012 and **B**, 2013. Male and female gonad activity was established using gonad histology from the latest stage of sperm and oocyte development, respectively.

for the larger size classes is likely to be skewed towards smaller *P. fluviatilis* by the eradication programme, which presumably has removed many big *P. fluviatilis* to date. Comparisons with Southern Hemisphere studies indicate that our expected size at age 1 (see rVBGF values Table 2) are generally similar to those reported by Jellyman (1980) (male at age 1 = 154 mm FL, female at age 1 = 164 mm FL), and higher than those reported by Morgan et al. (2002) (male at age 1 = 102 mm TL, female at age 1 = 104 mm TL). It must be noted that we use standard length for our size measurement, compared to fork length (FL) and total

length (TL) used by Jellyman and Morgan et al., respectively.

The notion that *P. fluviatilis* grow faster in warmer waters has been proposed in both anthropogenically-induced (Sandström et al. 1995) and natural conditions (Le Cren 1958, 1992). Our data show that *P. fluviatilis* exhibit varying growth rates, with the 2013 population showing faster somatic growth than in 2012. Faster growth in 2013 coincided with a hotter and dryer than average preceding summer in the upper part of the North Island (NIWA 2013). This was reflected in significantly warmer surface water temperatures during the summer period at Lake Wainamu ( $P < 0.05$ ), with a near 3 °C difference between mean monthly temperature in 2012 ( $19.76 \pm 0.01$  °C SEM) and 2013 ( $22.24 \pm 0.02$  °C SEM) at the time of sampling. Le Cren (1992) attributes fluctuations in growth from year to year to differences in summer water temperatures, where warmer conditions result in higher number of YOY (young-of-the-year) cohort, which in turn become an additional food source for older, cannibalistic *P. fluviatilis*. And cannibalism is not restricted to older fish as intercohort cannibalism has been observed in YOY *P. fluviatilis* (Persson et al. 2000). Here, the hypothesis of ‘increased food consumption’ appears to be supported by the positive allometric growth ( $b = 3.29$ ) of *P. fluviatilis* in 2013, indicating more girth per unit size. However, whether in Lake Wainamu increased growth in 2013 can be attributed to increased cannibalism cannot be answered as no diet analysis was conducted.

Another possibility is that, in 2013, pelagic zooplankton may have been more accessible to younger planktivorous *P. fluviatilis* within a reduced lake volume, allowing for faster early growth. Although we do not have access to depth data, Lake Wainamu was visibly shallower in 2013 compared to 2012. This is supported by rainfall records which show that the Auckland region only received 50% of expected summer rainfall in 2013 while experiencing warmer than average temperatures (NIWA 2013). Jeppesen et al. (1997) discuss the possibility that reduced lake levels lead to increased fish predation pressure on zooplankton, as the efficacy of zooplankton predation-avoidance

through vertical migration is reduced in these conditions. While it cannot be ascertained that a similar phenomenon was driving the faster growth rates found in Lake Wainamu in 2013, these results clearly identify a knowledge gap which will need to be addressed if we are to better understand the population dynamics of this species.

Warmer temperatures have also been linked with asynchronous egg cell development, extended spawning season, oocyte atresia during vitellogenesis, and early onset of sexual maturation in *P. fluviatilis* and other freshwater fish species (Luksiene et al. 2000). In *P. fluviatilis* oocyte atresia and asynchronous gonad development are considered anomalies. For example, *P. fluviatilis* normally display group-synchronous gonadal development that culminates in a well-defined spawning season (Treasurer & Holliday 1981). In this study, histological analysis of *P. fluviatilis* gonads from Lake Wainamu appears to suggest that oocyte atresia and asynchronous egg cell development occurred in significant proportions of the population each year. In synchronous teleost fishes, gametogenesis is gradational where a single cohort of gametes goes through successive stages of development from immature to mature (Munro & Lam 1993). In contrast, asynchronous gonads display oocytes at various stages of development and occur in serial-spawning species (McMillan 2007). Approximately a third of female *P. fluviatilis* from Lake Wainamu displayed asynchronous structure in both years, with oocytes in different stages of development. This finding must be treated with caution as only detailed comparative analysis of *P. fluviatilis* reproductive history across spatial scales can be elucidated, whether its gonad development has been modified since its introduction to New Zealand, or whether this is an anomaly restricted to Lake Wainamu and its local environmental conditions.

As with Luksiene et al. (2000), we also suspect that oocyte atresia and asynchronicity are likely to be temperature induced. As discussed above, summer temperature from Lake Wainamu was significantly warmer in 2013 than in 2012. The warmer temperatures in 2013 coincided with a 4-fold increase in the numbers of oocytes undergoing

atresia in *P. fluviatilis*. The presence of vitellogenic oocytes ('developing' females category) at the time of sampling during late summer could indicate that our understanding of *P. fluviatilis* as a spring-spawning species in New Zealand may not be accurate. This finding warrants a full investigation of *P. fluviatilis* reproductive biology spanning its complete reproductive cycle over 12 months, the results of which may have strong implications for eradication programmes (especially in Lake Wainamu for the present case study) that need information on the regenerative capacity (e.g. mortality, spawning season, fecundity, size and age at sexual maturity, growth rates) of targeted species. In a broader sense, however, our results provide circumstantial evidence that *P. fluviatilis* reproductive parameters may have changed after 146 years of acclimatisation to New Zealand's warmer climate. We can no longer take at face value that *P. fluviatilis*, which have now existed for over a century in reproductively isolated populations in New Zealand lakes, possess the same spawning season, reproductive strategies, or even genetic makeup as their European parental lineage. Phylogenetic analysis will be an important line of enquiry that could shed light on some of these questions.

*Perca fluviatilis* is dominant both in number and biomass in nutrient-rich New Zealand lakes (Jeppesen et al. 2000). Although the underlying reasons for this dominance are yet to be fully examined at various ecosystem levels, population dynamics information can lay the foundation for the discussion of invasion biology. This study has identified some interesting growth and reproductive parameters of *P. fluviatilis* which may have broader management and conservation implications, thus demonstrating the need for further research.

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