New Zealand Journal of Marine and Freshwater Research, 2006, Vol. 40: 571–583
0028–8330/06/4004–0571

Age composition, growth, and reproduction of koi carp (*Cyprinus carpio*) in the lower Waikato region, New Zealand

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Abstract A total of 566 koi carp (*Cyprinus carpio*) from the lower Waikato region were aged from scales and opercular bones, and growth was modelled with the von Bertalanffy growth function. There was no difference in growth rate between male and female carp. Growth of koi carp between zero and 3 years of age was lower than that of common carp in Europe and Australia. However, after 5 years of age the growth of koi carp was higher than that of common carp in Europe, but still below that of carp in Australia. Males rarely lived in excess of 8 years, whereas females lived to 12 years. Mean total fecundity calculated from 44 running-ripe females was 299 000 oocytes (±195 600 SD) (range 29 800–771 000). Relative fecundity ranged from 19 300 to 216 000 oocytes kg^{-1} total body weight, with a mean of 97 200 (±35 000 SD) oocytes kg^{-1}. Feral koi carp in the Waikato are capable of multiple spawnings within their lifetimes. Within a spawning season, Waikato populations of feral koi carp contained females that spawned once, and females that had the potential to have spawned repeatedly. Female gonadosomatic index (GSI) varied with season and was negatively related to water temperature.

M05058; Online publication date 26 October 2006
Received 1 September 2005; accepted 17 January 2006

Keywords common carp; koi; age; growth; invasive species; maturity; fecundity

INTRODUCTION

Common carp (*Cyprinus carpio* L.) are generally considered to be one of the most ecologically detrimental of all freshwater invasive fish species (Crivelli 1983; Zambrano et al. 2001; Davidson 2002; Dean 2003; Koehn 2003). Their ability to reach high biomass and their feeding behaviour have been implicated in causing major environmental degradation in many freshwater ecosystems (Crivelli 1983; Roberts et al. 1995; Zambrano et al. 1999; Barton et al. 2000; Zambrano et al. 2001).

Koi carp appear to be an ornamental variant of the east Asian common carp that were taken to Japan from China and bred for coloration and scale patterns (Axelrod 1973). These fish were recognised as a threat to New Zealand's aquatic ecosystems in the 1970s (Pullan & Little 1979), but feral populations of koi carp did not cause significant concern until self-sustaining populations were discovered in the Waikato River system in 1983 (Pullan 1986). At this stage, a multi-agency programme was set up to monitor the spread of koi carp; however, this work was never carried out (McDowall 1996).

Despite the recognition of their threat to New Zealand's lakes and rivers (Hanchet 1990), little research has been conducted into the biology of feral koi carp in New Zealand, and the spread of koi carp continues despite the establishment of a containment zone and the eradication of a few highly limited populations (Chadderton et al. 2003; Dean 2003). There are now extensive populations of koi carp in the lower Waikato River, its lakes and tributaries, with koi carp well established in the Waikato River from Port Waikato to the Karapiro Dam upstream of Cambridge, and in the Waipa River to upstream of Otorohanga (National Institute of Water and Atmospheric Research Limited, New Zealand Freshwater Fish Database). The Auckland region also has extensive populations of koi carp and

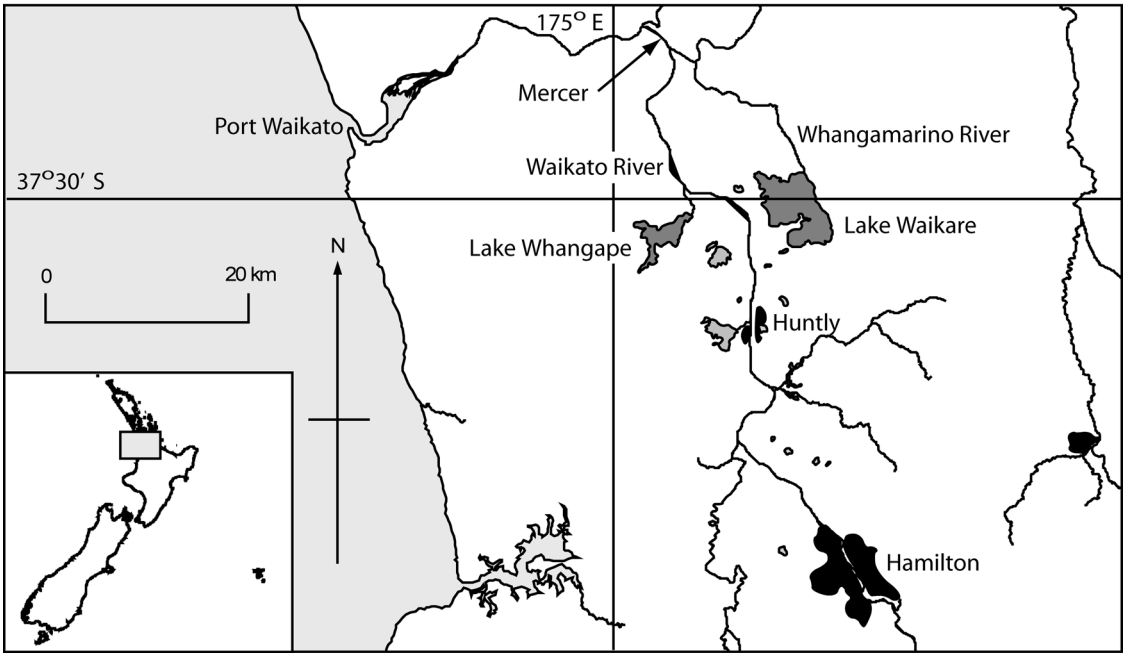

Fig. 1 Lower Waikato region, New Zealand, including koi carp (*Cyprinus carpio*) sampling areas of the Waikato River, Whangamarino River, Lake Waikare and Lake Whangape.

they are also patchily distributed in other parts of the North Island (NIWA, New Zealand Freshwater Fish Database). The detection of two koi populations in the Nelson-Marlborough region in 2000 (Chadderton et al. 2003) is of particular concern as feral koi have previously been absent from the South Island and can only have arrived there through deliberate introduction.

From research on carp populations around the world it appears that growth rates for carp in temperate latitudes are very variable. After their first year fish size can vary from 105 to 190 mm fork length (FL), reaching 195 to 300 mm FL in their second year. At 7 to 11 years of age fish may reach 500 mm FL (McCrimmon 1968; Crivelli 1981; Prochelle & Campos 1985; Fernández-Delgado 1990; Vilizzi & Walker 1999a,b).

Age at which maturity is reached is also variable, ranging from 1 to 5 years for both males and females (Crivelli 1981; Prochelle & Campos 1985; Fernández-Delgado 1990; Vilizzi & Walker 1999a). Water temperature and sexual maturity are correlated (Fernández-Delgado 1990), and latitude therefore plays an important role in the rate of carp development. Carp can mature at 3 months of age (90 to140 mm FL) in tropical waters, whereas it may take up to 5 years (355 to 430 mm F.L) for carp to reach maturity in northern Europe or North America (Fernández-Delgado 1990). Males appear to mature earlier than females, and under natural conditions carp rarely live longer than 15 years (McCrimmon 1968; Vilizzi & Walker 1999a).

The determination of fecundity and the length of spawning period are fundamental to understanding a fish species' biology (Sivakumaran et al. 2003). Accurate estimates of fecundity increase the efficiency of stock management and improve predictions of offspring production (Crim & Glebe 1990). Such measures are important in estimating the potential of invasive species for spread and ecosystem impacts (Arthington & Mitchell 1986; Hutchison & Armstrong 1993). Carp are a highly fecund species; a ripe 5 kg female may produce 1 000 000 mature oocytes (Prochelle & Campos 1985; Sivakumaran et al. 2003). Typically, relative fecundity ranges from 100 000 to 300 000 oocytes kg^{-1} total body weight (Hanchet 1990).

If effective management measures are to be implemented in New Zealand, an understanding of the population biology of koi carp is necessary. Because of factors such as latitude and temperature on growth and development, and because koi carp

are genetically different to other feral common carp populations worldwide (e.g., Murakaeva et al. 2003), overseas research findings could have limited applicability to New Zealand populations. The main objective of this study was to provide an assessment of the age structure, growth, and reproduction of koi carp.

MATERIALS AND METHODS

Bimonthly (every 2 months) samples of up to 20 koi carp per site were taken from the Whangamarino River, lower Waikato River, Lake Whangape, and Lake Waikare (Fig. 1) from November 2002 to November 2003. Koi carp were collected using a variety of methods including fyke netting (10 mm mesh, set overnight), gill netting (30 m × 2 m, mesh 100 mm), trammel netting (50 m × 2 m, inner mesh 100 mm, outer mesh 300 mm), and boat electrofishing (operational parameters were 50–500 V DC and 2–8 A pulsed at 60 Hz). After retrieval, fish were immediately placed in a 300 mg litre^{-1} benzocaine solution until dead. They were then transported to the laboratory and stored at 4°C overnight before processing. Samples were also obtained from the annual New Zealand Bowhunters Association competitions in early November of 2002 and 2003 and were processed on site at Lake Waahi. Fork length (± 1 mm), total body weight (± 1 g) and gonad weight (± 0.1 g) were recorded from all euthanased fish. Fish were also sexed and female maturity determined by macroscopic examination of gonads.

Ageing and growth

The development of age-at-length regressions enables calculations of growth rates, which reflect environmental and habitat conditions affecting fish populations. Growth can be a useful measure for evaluating habitat suitability, prey availability or the influence of management activities on a target species (DeVries & Frie 1996).

Both scales and opercular bones were used to estimate koi carp age. These structures were selected as they were the easiest to prepare and the use of two structures would provide greater accuracy. Only samples where both the opercular bones and scales were available for ageing were selected for determining the growth parameters. Both left and right opercular bones were excised and soaked in hot 10% potassium hydroxide for 24 h to remove excess flesh. They were then rinsed in fresh water and any remaining flesh was manually removed. Following cleaning they were left to dry for 6 to 7 days in a ventilated room. Between five and ten scales were removed from the left anterior side of each fish just above the lateral line as per Vilizzi & Walker (1999a). The scales were placed into warm 10% potassium hydroxide solution and soaked for c. 3 h. They were then rinsed and wiped clean to remove any flesh and mucilage. Non-regenerated scales were then mounted between two glass microscope slides and dried for 6 to 7 days. Replacement scales, i.e., those showing opaque areas without annuli were excluded from analysis.

Opercular bones and mounted scales were interpreted using an Olympus stereo microscope model SZ60 (10–20×) under transmitted light. For the scales, an annulus was taken as a transition between two uninterrupted zones of closely- and widely-spaced circuli (daily growth rings), with a growth check as an essential criterion. An opercular bone annulus was taken as a sharp transition between a translucent and an opaque zone. The concave surface of the opercular bone provided the best surface for interpretation (Vilizzi & Walker 1999a). Three months after initial interpretation, estimated ages from both scales and opercular bones for each fish were reconciled. If the initial estimated ages matched, then that age was taken as the final estimated age. If the estimated ages did not match, both structures were reinterpreted. Once a consistent age between both structures was achieved, the estimated age was taken as final. During interpretations, no prior knowledge of date of capture, length or weight of the fish was known by the interpreter.

Age validation

Between September 2002 and February 2005 a total of 1300 adult carp (>180 mm FL) were dart-tagged along the lower Waikato River from Hamilton to Mercer (Fig. 1). A scale was removed from the tag insertion point and a 100 mm plastic dart tag (Hallprint, Type PD series) was inserted into the epaxial musculature and locked between pterygiophores spines using a needle applicator on the left side of the fish.

Validation of ages was achieved by comparing annuli of scales from 10 recaptured fish from the Waikato River. Between 6 and 10 scales were removed from the left anterior side of the fish at initial capture and assessed, these were then compared with the ages of 6 and 10 scales removed from the right side of the recaptured fish. Scales were aged by three independent assessors with no prior knowledge of

date of capture, fish length or weight. Tagged and recaptured fish were at liberty for between 244 and 743 days (mean 487 days).

Once the estimated ages were finalised, summary statistics for each age class were calculated. These data were then used to calculate growth, using the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty (1-e^{-K(t-t_0)})$$

where L_t is the length at age t, L_∞ is the theoretical maximum (or asymptotic) length that the species would reach if it lived indefinitely, K is a growth coefficient which is a measure of the rate at which maximum size is reached, and t_0 is the theoretical age at zero length (Ricker 1975). The VBGF curve was fitted to the data using the maximum obtainable length obtained from a Ford-Walford plot (DeVries & Frie 1996). The VBGF was used because Vilizzi & Walker (1999a) found it provided a more realistic representation of growth than polynomial functions.

Reproduction

All gonad material from both males and females was removed, weighed (± 0.1 g) and the gonadosomatic index (GSI) subsequently calculated according to Crim & Glebe (1990). Female gonads were macroscopically staged using the definitions of Fouché et al. (1985). For example, a stage III (early developing) ovary is opaque and reddish with blood vessels, and eggs are visible to the eye as whitish and granular. A stage IV (developing late), ovary is reddish and opaque with eggs clearly discernable. Stage V (gravid) eggs are completely round and only appear translucent a few days before spawning, and the ovary fills most of the ventral body cavity. Spawning was designated as stage VI; the roe is extruded with slight pressure to the abdomen and the eggs are translucent.

Small samples (10 to 20 g) of gonad material were taken from several sections of each ovary of all mature (stage III to stage VI) female koi carp and preserved in 10% formalin. After fixing, a subsample (1–2.5 g) was taken and spread out over a black 10 cm × 10 cm plastic tray and covered with 0.5 cm of water. The subsamples were then photographed using a Nikon D1X digital camera. After calibrating the image size, the mean diameter of each individual oocyte and total number of oocytes were automatically assessed using Image Pro plus version 4.5.1.22 for Windows (Media Cybernetics, Inc., Silver Spring, MD, United States).

Hydrated and yolked oocytes were distinguished from atretic oocytes by differences in colour, shape and transparency. Yolked oocytes possessed yellow granules and were round in shape, whereas atretic oocytes were opaque and irregular in shape (Sivakumaran et al. 2003). Atretic oocytes or ovarian tissue were manually removed from the oocyte count. The sample was then filtered using Whatman 41 ashless filter paper and weighed to ±0.0001 g with a Denver Instrument M-310 laboratory balance.

A subsample of 155 ovaries was analysed and instantaneous fecundity and mean oocyte diameter were calculated. Oocyte analyses were not conducted on fish sampled from the Bowhunters competition in 2003 as samples had already been obtained for a November sampling period the previous year. Instantaneous fecundity was calculated as the total number of yolked oocytes per mature female at each sampling period. TF was determined from the standing stock of advanced oocytes (yolked oocytes and hydrated oocytes) at the beginning of the spawning season in September (n = 44) as this was when fecundity would be highest (Sivakumaran et al. 2003). TF was calculated by dividing the number of oocytes in the sample by the weight of the sample. This figure was then multiplied by the total weight of the ovaries to obtain the total number of oocytes. TF was then divided by total body weight, resulting in a relative fecundity value (Sivakumaran et al. 2003).

Statistical analysis

All statistical tests were carried out using Minitab™ 13.30 statistical software (Minitab Inc., State College, PA, United States). All statistical tests were considered significant at the $\alpha < 0.05$ level.

Regression analyses were performed between TF, mean oocyte diameter (MOD), FL, total body weight, and age. Where significant relationships existed with MOD either linear, exponential or power regressions were fitted to describe the relationship. The best fitting regression was identified from the adjusted coefficient of determination statistic (r^2). Also, differences between bimonthly MOD were tested using one-way analysis of variance (ANOVA) followed by Tukey's pairwise comparisons (Zar 1996).

Differences in growth rate between sexes were tested using ANOVA (Zar 1996). Direct comparisons between male and female mean length-at-age were tested using Student's t test. Owing to the skewed distribution of the age data, the non-parametric Mood median test was used to determine differences in male and female ages (Zar 1996). Where assumptions of normality and homogeneity of variance were met and sample sizes allowed, one-way ANOVA was

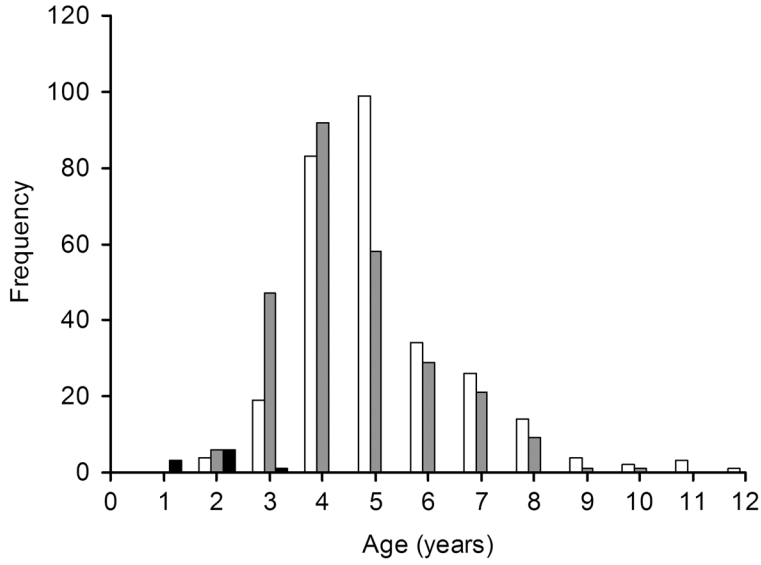

Fig. 2 Age-frequency of 290 female, 264 male, and 12 immature koi carp (*Cyprinus carpio*) from the lower Waikato region, New Zealand. Open columns, females; grey columns, males; black columns, immature fish.

used to test differences in length-at-age (Zar 1996) between the Waikato River, Lake Waikare, Lake Whangape, and Whangamarino River populations.

Linear regression analyses were conducted between mean bimonthly water temperatures for the Waikato River at Huntly, Lake Waikare outlet, and the Whangamarino River (data supplied by Environment Waikato) and mean bimonthly GSI of both male and female koi carp.

RESULTS

Age composition and growth

Validation of annuli from tagged and recaptured fish resulted in 80% conformity between observed and expected annuli, with annuli assumed to form in late winter (i.e., August) (Table 1). Where conformity was not attained, the difference between observed and expected annuli resulted in the underestimation of age by 1 year for each fish by all three assessors.

A total of 566 carp were aged during this study. Initial interpretations resulted in a 45% agreement between structures, and 99.6% conformity was achieved after the second interpretation 3 months later, with only two instances where conformity between scales and opercular bone estimated ages could not be achieved.

Samples were dominated by 4- and 5-year-old fish, with relatively few fish in excess of 8 years (Fig. 2). There were few males in excess of 7 years of age and only two greater than 8 years of age. The mean age of all males and females was significantly different at 4.6 and 5.2 years, respectively (Mood median test; $\chi^2 = 15.8$; d.f. = 1; $P < 0.001$; male $n = 264$, female $n = 290$). There were also significant differences in fish age between locations (Mood median test $\chi^2 = 11.2$; d.f. = 3; $P < 0.01$) with Lake Waikare and the Whangamarino River (4 years) having lower median ages than the Waikato River and Lake Whangape (5 years).

Males and females exhibited similar mean length-at-age values until 6 years of age when female mean length was significantly greater than male mean length (Student's t test; $t = 2.26$; d.f. = 61; $P < 0.05$; male $n = 29$, female $n = 34$). After 6 years of age, mean female length continued to exceed male mean length for the remaining age groups, but these differences were either not statistically significant or there were insufficient samples to perform statistical tests. Mean FL ranged from 107 mm for 1-year-old fish to 700 mm for one 12-year-old female (Table 2). There were no significant differences in growth rates between males and females (Student's t test; $t = 0.4$; d.f. = 1; $P = 0.7$). The VBGF parameters for the combined age-at-length data were $L_\infty = 675$ mm, $K = 0.21$, and $t_0 = 0.15$ year.

Growth of the combined Waikato koi carp populations (Fig. 3) was slower than growth of common carp for populations from Australia (Vilizzi

Table 1 Expected and observed growth checks based on assumed check formation in August, which were used in age validation of tagged and recaptured koi carp (*Cyprinus carpio*) from the lower Waikato River, New Zealand.

	Initial capture		Recapture						
Date	Age (years)	Fork length (mm)	Date	Age (years)	Fork length (mm)	Days at liberty	Length increase (mm)	Growth (mm/day)	Expected checks	Observed checks
19 May 2004	3	349	5 Nov 2005	5	410	535	61	0.114	2	2
15 Dec 2004	4	437	16 Aug 2005	5	456	244	19	0.078	1	1
19 May 2004	4	440	25 Jul 2005	5	450	432	10	0.023	1	1
26 May 2004	6	447	14 Dec 2005	8	458	567	11	0.019	2	2
19 May 2004	4	459	16 Aug 2005	5	466	454	7	0.015	2	1
15 Dec 2004	7	464	14 Nov 2005	8	474	334	10	0.030	1	1
23 Jan 2004	5	478	16 Aug 2005	7	484	571	6	0.011	2	2
19 May 2004	6	491	5 Nov 2005	8	535	514	44	0.086	2	2
19 May 2004	6	540	16 Aug 2005	7	547	454	7	0.015	2	1
24 Oct 2004	7	543	5 Nov 2005	9	541	743	–2	–0.003	2	2

& Walker 1999a), but was initially similar to common carp from France (Crivelli 1981), Spain (Fernández-Delgado 1990), and Chile (Prochelle & Campos 1985). At older ages, growth of Waikato koi carp approached that of carp in Australia, and exceeded common carp growth in Europe and Chile.

Reproduction

A total of 674 koi carp were sexed, including 317 mature females and 317 mature males. Immature fish consisted of 10 males, 30 females, and a further 12 fish were indeterminate. Males were typically mature at 2 years of age and females at 3 years of age.

Total fecundity, relative fecundity and mean oocyte diameters were determined from 44 mature females captured in September 2003. Total oocyte numbers varied between 29 800 and 771 000 with a mean of 299 000 (±195 600 SD) oocytes. Relative fecundity varied between 19 300 and 215 700 oocytes kg^{-1} total body weight, with a mean of 97 200 (±35 000 SD) oocytes kg^{-1} total body weight.

There was no significant relationship between relative fecundity and maternal size or age (maternal size $F = 1.79$, d.f. = 1, $P = 0.18$; age $F = 2.54$, d.f. = 1, $P = 0.11$). However, significant regression relationships were found between TF and FL ($TF = 12534e^{0.0062\ FL\ (mm)}$, $P < 0.001$, $r^2 = 0.648$), total body weight ($TF = 175.79$ total body weight $(g)^{0.9153}$, $P < 0.001$, $r^2 = 0.682$), and age ($TF = 13117\ age^{1.663}$, $P < 0.001$, $r^2 = 0.569$).

Mean yolked oocyte diameter (MYOD) was greatest in September and least in January and ranged between 0.30 and 1.85 mm. There were significant

Table 2 Mean length-at-age of koi carp (*Cyprinus carpio*) in the lower Waikato region, New Zealand.

Age		Fork length (mm)			
(years)	*n*	Mean	SEM	Min.	Max.
1	3	107.3	5.9	100	119
2	16	205.7	8.6	150	270
3	67	305.1	5.2	204	368
4	175	375.7	2.7	279	442
5	158	418.3	3.3	300	494
6	63	475.7	5.1	400	552
7	49	514.8	7.1	419	602
8	23	575.4	6.4	518	629
9	5	568.8	17.2	519	610
10	3	604.3	34.4	560	672
11	3	637.0	16.9	610	668
12	1	700.0	–	–	–

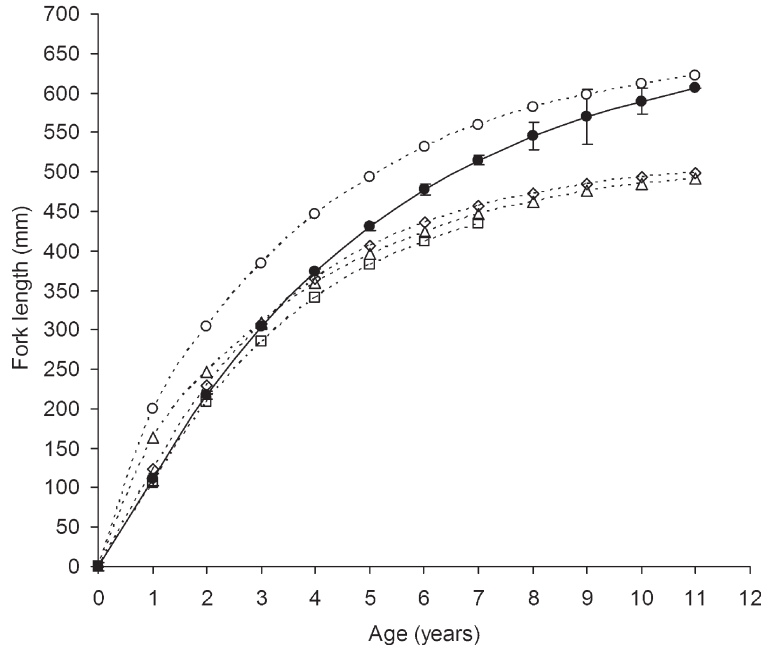

Fig. 3 von Bertalanffy growth curves of koi carp (*Cyprinus carpio*) for combined Waikato, New Zealand, populations (filled circles; ±SEM) and for populations from Australia (open circles, Vilizzi & Walker 1999a), France (open triangles, Crivelli 1981), Spain (open squares, Fernández-Delgado 1990), and Chile (open diamonds, Prochelle & Campos 1985).

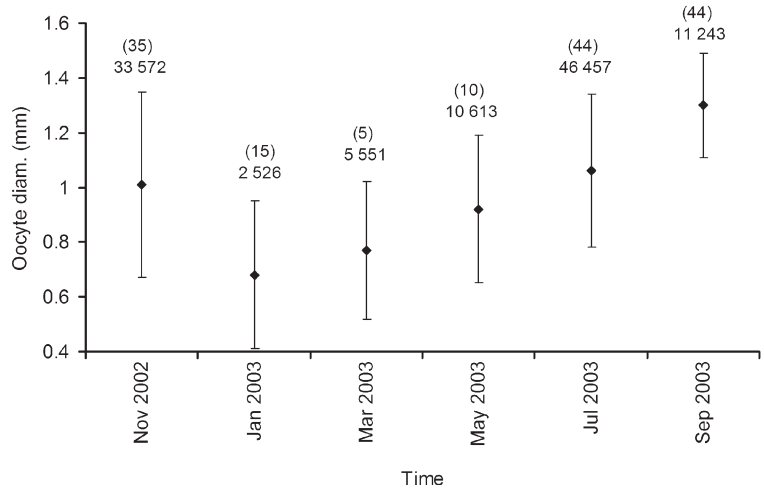

Fig. 4 Mean yolked oocyte diameter (±1 SD) of koi carp (*Cyprinus carpio*) over time. Sample numbers of measured oocytes are given above each value with numbers of fish sampled in parentheses.

increases in MYOD between each sampling period from January 2003 to September 2003 (ANOVA, $F = 3.69$, d.f. = 5, $P < 0.05$). There was also a significant decrease in MYOD between November 2002 and January 2003 (Fig. 4). Mean oocyte diameter for ripe ovaries in September was 1.16 mm.

Both unimodal and polymodal size distributions of oocytes were observed throughout the year (Fig. 5). Individual female oocyte size distributions were most synchronous in September and least synchronous in the November 2002 and January 2003 sampling periods. However, both unimodal and bimodal distributions were still observed in September 2003 (Fig. 6). A wide distribution in oocyte diameters was present in all sampling periods as were mature yolked oocytes.

Gonadosomatic index (GSI) for 317 males and 317 females from November 2002 to November 2003 changed seasonally, with female GSI at a minimum in January 2003 rising to a peak in

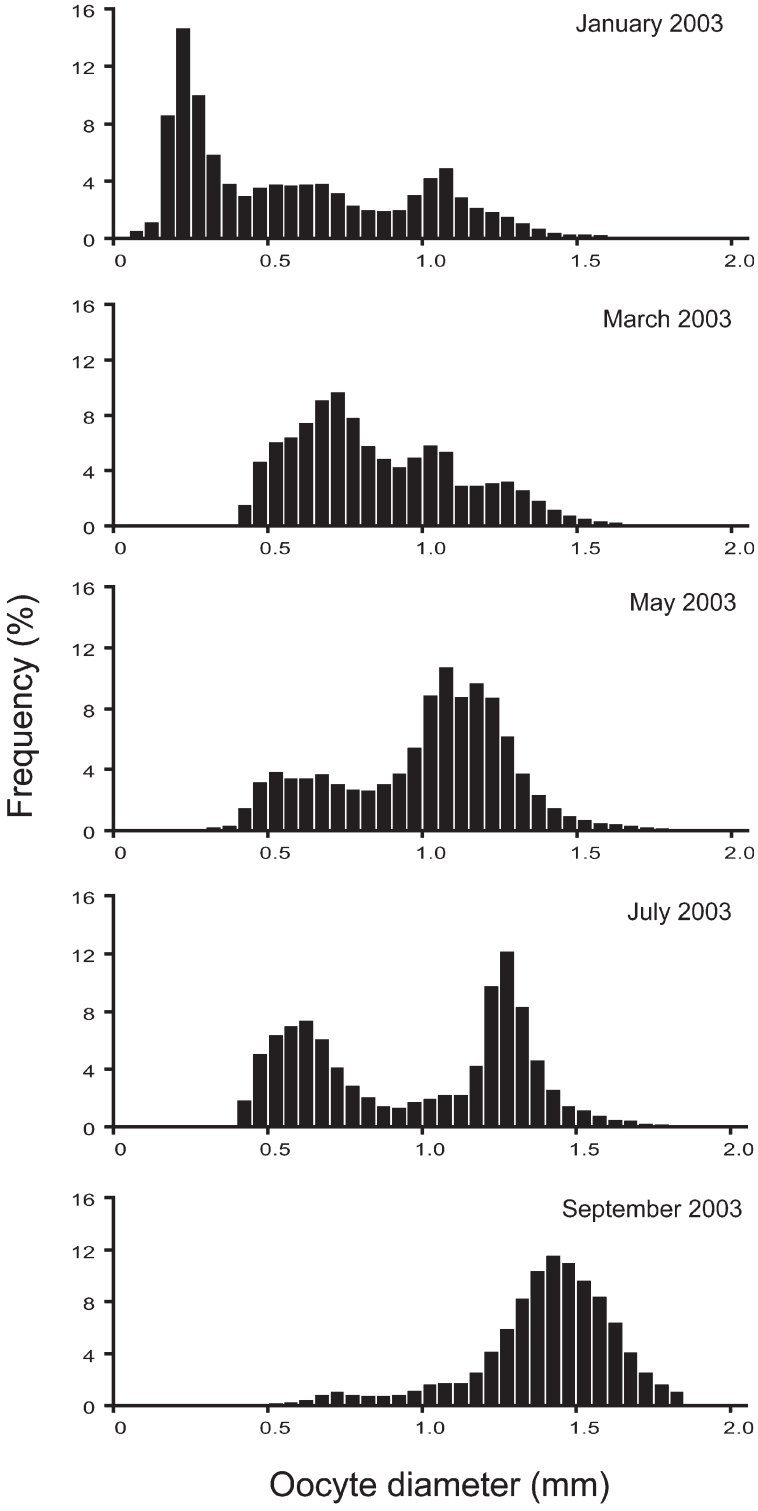

Fig. 5 Changes in oocyte diameter percentage occurrence over time throughout the year of koi carp (*Cyprinus carpio*) from the lower Waikato region, New Zealand.

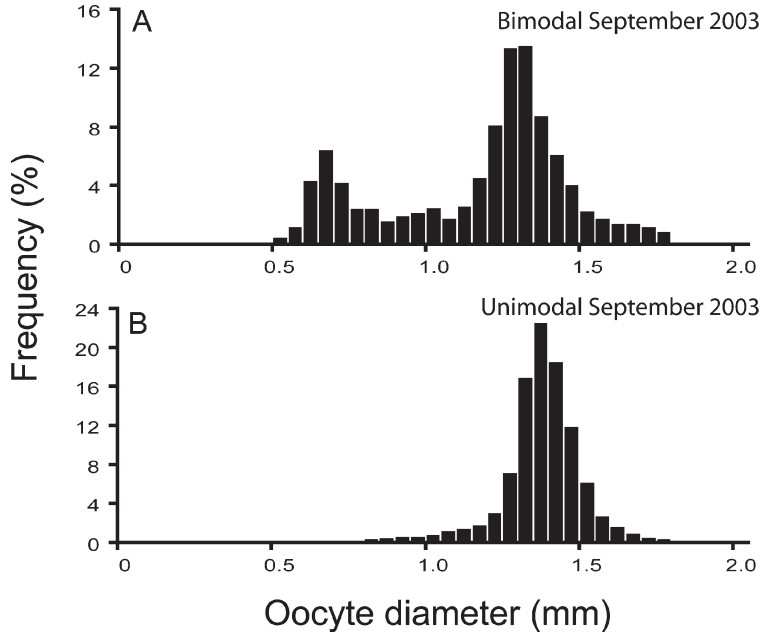

Fig. 6 Examples of **A**, bimodal and **B**, unimodal frequency distributions for oocyte diameter (n = 1225 and 1429) from individual koi carp (*Cyrpinus carpio*) sampled during September 2003 at the beginning of the spawning season in the lower Waikato region, New Zealand.

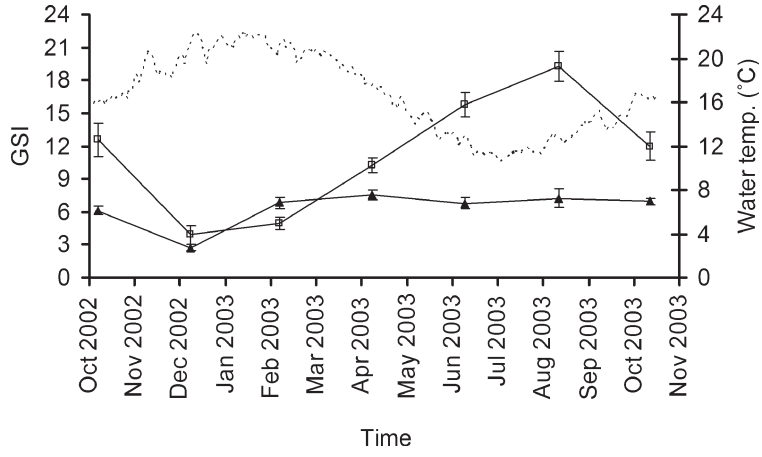

Fig. 7 Mean gonadosomatic indices (GSI; ±SEM) of koi carp (*Cyprinus carpio*) across all sites over time, males (filled triangles) and females (open squares). Daily mean water temperatures in the lower Waikato River, New Zealand, during the sampling period are also displayed (dashed line).

September 2003 when the first spawning activity of the season was observed (Fig. 7). Male GSI did not show the same degree of seasonal variation as female GSI. Both male and female GSI reached a minimum in January 2003. Regression analysis indicated a significant negative relationship between female GSI and water temperature (F = 17.21, d.f. = 1, $P < 0.01$); there was no significant relationship between male GSI and water temperature (F = 2.12, d.f. = 1, P = 0.205). There was a high degree of variability in the stage of female gonad maturity between November 2002 and May 2003. During this period, ovarian developmental stages from III to V were observed in females of approximately the same size. This variability decreased from July 2003 as female ovarian development became more synchronous. By September 2003, most females were at stage V, but by November 2003 variability had returned, with stages of ovarian development once again ranging from stage III to stage V. Ovaries at stage VI (spawning) were only observed in four fish in September 2003.

DISCUSSION

Age composition and growth

Growth rates for New Zealand koi carp fall within the range reported for populations of common carp elsewhere. Hanchet's (1990) statement of rapid carp growth of 165–280 mm FL in 190 days is therefore not supported. Koi exhibited similar growth rates during their first and second years, but higher growth rates from about 6 years of age compared with common carp in France (Crivelli 1981), Spain (Fernández-Delgado 1990), and Chile (Prochelle & Campos 1985). However, Australian common carp have much higher growth rates from zero to 5 years of age compared with carp from Europe, Chile, and New Zealand (Vilizzi & Walker 1999a), although Australian and New Zealand carp reach comparable maximum size of c. 600 mm FL by age 12. Growth rate may be strongly temperature-dependent and, by inference, latitudinally dependent, although carp growth may also be depressed by increasing salinity (Wang et al. 1997). Differences in growth rate between New Zealand koi carp and other feral carp populations may also be attributable to genetic variances.

McCrimmon's (1968) conclusion that wild carp rarely attained ages in excess of 20 years is supported by the finding that no koi older than 12 years of age were collected. Vilizzi & Walker (1999a) found relatively few common carp older than 12 years from the lower Murray River, Australia, although Brown et al. (2005) found a significant number of 12–20-year-old carp in the mid-Murray River and associated Barmah Forest Wetlands.

Male koi carp appear to rarely live longer than 8 years. No explanation can be provided for this age limit other than that large numbers of male koi have been observed dead soon after spawning (G. W. Tempero pers. obs.), and it is possible that the frenetic activity of spawning may lead to fatal exhaustion of some males.

Relatively few fish were aged at zero to 2 years owing to the inherent bias against small fish when using 100 mm trammel nets. The size range of captured fish increased with the inclusion of boat electrofishing, but fish smaller than 150 mm FL were still difficult to obtain. Therefore, further investigation into the growth of young-of-the-year fish would improve estimations of koi growth in the Waikato Region.

As we did not overestimate age, pseudoannuli from tagging or spawning appear to be absent or

Table 3 Age at maturity, oocyte diameter, and fecundity of common carp and koi carp (*Cyprinus carpio*).

Country	Latitude	Variant	Stock type	Age at maturity		Oocyte diam. (mm)	Fecundity		Source
				Males	Females		Oocytes female^{-1}	Oocytes kg^{-1}	
Canada	50°N	Common	Wild	3–4 years	4–5 years		36 000–2 208 000		McCrimmon (1968)
Central Europe	47°N	Common	Wild	3–4 years	3–4 years				Sterba (1962)
Kazakhstan (2002)	45°N	Common	Wild			1.2	375 000		Vila-Gispert & Moreno-Amich
France	43°N	Common	Wild	3 years	3 years		215 097		Crivelli (1981)
Spain (2002)	42°N	Common	Wild	2 years	2 years	1.5–2.0	221 683		Vila-Gispert & Moreno-Amich
United States	40°N	Common	Wild	2 years	2 years				McCrimmon (1968)
Turkey	40°N	Common	Wild	2 years	2 years				Karatas (2000)
Spain	37°N	Common	Wild	2 years	2 years	0.8–1.5	1 633–190 778		Fernández-Delgado (1990)
Egypt	29°N	Mirror	Farmed		1 year	1.2–1.35		123 000	Bishai et al. (1974)
India	25°N	Common	Farmed		1 year	1.0–1.5		9 927–104 884	Dobriyal et al. (1990)
India	20°N	Common	Farmed	6 months	8 months			155 900	Parmeswaran et al. (1972)
Australia	35°S	Common	Wild			0.4–1.6	120 000–1 540 000	163 000	Sivakumaran et al. (2003)
New Zealand	37°S	Koi	Wild	2 years	3 years	1.2	299 000	97 200	This study
Chile	39°S	Scale & mirror	Wild	3 years	3 years	1.4	up to 917 000	120 000	Prochelle & Campos (1985)

rare. Underestimation of annuli from tagged and recaptured fish may have been owing to incomplete formation of the growth check, as the fish in which these occurred were recaptured in early August. Therefore, future studies involving ageing of samples from koi collected at this time of year should be treated with caution.

Reproduction

The spawning period for common carp is typically when water temperature is between 18 and 28°C (McCrimmon 1968), although spawning has been observed at water temperatures as low as 15°C (Stuart & Jones 2002). In northern New Zealand, this means spawning could extend for up to 8 months from September through to April given favourable conditions. Spawning activity that was observed in September 2003 occurred at 16.5°C and viable larvae were collected from the same area one week later (G. W. Tempero pers. obs.). Spawning was observed from September 2002 to January 2003 and from September 2003 to November 2003 when observations ceased. The presence of eggs and newly hatched larvae confirmed spawning activity (G. W. Tempero pers. obs.). In Australia, spawning periods of this length have been observed by Sivakumaran et al. (2003) and Smith & Walker (2003). Common carp are able to adapt their reproductive strategies to take advantage of local environmental conditions. At high latitudes where water temperatures required for spawning only occur for a limited time, carp may spawn only once over a 2–4-month period (McCrimmon 1968). In comparison, Guha & Mukherjee (1991) reported two clear reproductive cycles per year in common carp from west Bengal. This difference in findings is directly related to latitude. The optimum interval between consecutive ovulations is 2000 degree-days, with a minimum period of 1600 degree-days (Linhart et al. 1995).

Age at maturity in common carp is related to latitude and sex; males often mature before females, and fish mature earlier at low latitudes compared with higher latitudes (Table 3). In pond culture in India, males matured at 6 months of age and females at 8 months (Parmeswaran et al. 1972), whereas in the wild in Canada, males matured at age 3–4 years (356 mm FL), and females at age 4–5 (432 mm FL; McCrimmon 1968). Koi carp from the Waikato region matured at 2 years for males and 3 years for females. The number of degree-days to maturity is generally c. 10 000 for males and c. 15 000 for females (Horvath 1985).

The fecundity of feral koi carp in New Zealand (mean 299 000 oocytes per fish or 97 200 oocytes kg^{-1} total body weight) was less than that of carp elsewhere in the world (Table 3). Common carp in Victoria, Australia, had high fecundity (120 000 to 1 540 000 oocytes per fish or 163 000 eggs kg^{-1} total body weight; Sivakumaran et al. 2003).

The diameter of mature oocytes appears to be relatively variable (0.4–2.0 mm), but includes the mean mature oocyte diameter for koi carp from the Waikato region (1.2 mm). The presence of both unimodal and polymodal distributions of yolked oocyte diameters indicates that multiple and single spawning females are present in the population. Oocyte development appears to be synchronous early in the spawning season and gradually becomes more asynchronous as the season progresses. This lack of synchronicity also occurred in carp in India, Poland, and Australia (Parmeswaran et al. 1972; Bieniarz et al. 1979; Sivakumaran et al. 2003). From observations made on whole ovaries and individual oocyte diameters it appears that the spawning period for the 2002–03 season was limited. Owing to dry conditions over the late summer and autumn (G. W. Tempero pers. obs.), it is unlikely that any spawning activity occurred between January and August 2003.

Female GSI exhibited an inverse relationship to water temperature similar to carp in Chile (Prochelle & Campos 1985). During the winter (June to early September), when water temperatures were at their lowest, female GSI increased substantially as oocytes matured in preparation for spawning during the spring and early summer. The subsequent release of gametes over the spring and early summer caused a decrease in GSI in both males and females. Regeneration of gonad tissue took place from January to March. Mature reproductive products were observed in both males and females in the post-December period indicating that spawning was possible given favourable conditions. Water temperatures were within the known preferred spawning temperature range during this time, so it is probable that falling water levels (G. W. Tempero pers. obs.) precluded spawning, as common carp are known to prefer spawning over recently flooded areas (Balon 1995). Photoperiod is an important regulator of spawning (Sivakumaran et al. 2003), but appears to be secondary to temperature (Davies & Hanyu 1986).

Management implications

Removing large, mature koi carp by selective netting may fail as a population control method, and is likely to induce compensatory recruitment and growth so that the overall number of eggs produced may not be

reduced. We base this conclusion on our finding that though larger females produce more eggs, the lack of relationship between relative fecundity and age suggests that increased growth rates will maintain the quantity of eggs produced. Nevertheless, older and larger females produce larger eggs which may contribute larger, more viable larvae than smaller females. Models simulating control strategies for feral carp populations should take into account the relationships between maternal size, age, and egg quality owing to their potential to affect recruitment (Sivakumaran et al. 2003).

The long spawning period and multiple spawning characteristics of koi carp in New Zealand may restrict the effectiveness of management strategies aimed at limiting spawning opportunities by environmental manipulation, such as water draw-downs as used by Shields (1958), or the targeted fishing of pre-spawning aggregations.

ACKNOWLEDGMENTS

This work would not have been possible without the support of Alan Metcalfe and the New Zealand Bowhunters Association. We also thank Barry O'Brien for assistance with the photography of numerous oocyte samples, the Department of Conservation for the use of their trammel nets, and the Waikato branch of the Royal New Zealand Forest and Bird Society and Environment Waikato for their generous financial support and provision of water temperature data. Finally, we thank the three anonymous reviewers of this paper for their time and helpful recommendations.

REFERENCES

Arthington AH, Mitchell DS 1986. Ecology of biological invasions: an Australian perspective. Groves RH, Burdon JJ ed. Canberra, Australian Academy of Science. Pp. 34–53.

Axelrod HR 1973. Koi of the world: Japanese colored carp. Neptune City, TFH Publications. 239 p.

Balon EK 1995. Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. Aquaculture 129: 3–48.

Barton DR, Kelton N, Eedy RI 2000. The effects of carp (*Cyprinus carpio*) on sediment export from a small urban impoundment. Journal of Aquatic Ecosystem Stress and Recovery 8: 155–159.

Bieniarz K, Epler P, Thuy L, Kogut E 1979. Changes in the ovaries of adult carp. Aquaculture 17: 45–68.

Bishai HM, Ishak MM, Labib W 1974. Fecundity of the mirror carp *Cyprinus carpio* at the serow fish farm (Egypt). Aquaculture 4: 257–265.

Brown P, Sivakumaran KP, Stoessel D, Giles A 2005. Population biology of carp (*Cyprinus carpio* L.) in the mid-Murray River and Barmah Forest Wetlands, Australia. Marine and Freshwater Research 56: 1151–1164.

Chadderton L, Kelleher S, Brow A, Shaw T, Studholme B, Barrier R 2003. Testing the efficacy of rotenone as a piscicide for New Zealand pest fish species. In: Managing invasive freshwater fish in New Zealand. Proceedings of a workshop hosted by Department of Conservation, 10–12 May 2001, Hamilton. Pp. 113–130.

Crim LW, Glebe BD 1990. Reproduction. In: Schreck CB, Moyle PB ed. Methods for fish biology. Maryland, American Fisheries Society. Pp. 529–547.

Crivelli AJ 1981. The biology of the common carp, *Cyprinus carpio*, in the Camargue, southern France. Journal of Fish Biology 18: 271–290.

Crivelli AJ 1983. The destruction of aquatic vegetation by carp. A comparison between southern France and the United States. Hydrobiologia 106: 37–41.

Davidson S 2002. Carp crusades. Ecos 112: 8–12.

Davies PR, Hanyu I 1986. Effect of temperature and photoperiod on the sexual maturation and spawning of the common carp: I. Under conditions of high temperature. Aquaculture 51: 277–288.

Dean T 2003. Invasive freshwater fish in New Zealand; DOC's present and future management. In: Managing invasive freshwater fish in New Zealand. Proceedings of a workshop hosted by Department of Conservation, 10–12 May 2001, Hamilton. Pp. 1–8.

DeVries DR, Frie RV 1996. Determination of age and growth. In: Murphy BR, Willis DW ed. Fisheries Techniques. 2nd ed. Maryland, American Fisheries Society. Pp. 483–508.

Dobriyal AK, Bahuguna AK, Kotnala CB, Kumar N, Singh HR 1990. A case study on the reproductive capacity of common carp (*Cyprinus carpio*) from India. Acta Societatis Zoologicae Bohemicae 54: 91–96.

Fernandez-Delgado C 1990. Life history patterns of the common carp, *Cyprinus carpio*, in the estuary of the Guadalquivir River in south-west Spain. Hydrobiologia 206: 19–28.

Fouché CH, Vermaak JF, van Vuren JHJ, Schoonbee HJ 1985. The female reproductive cycle of the European common carp, *Cyprinus carpio*, at a Transvaal fish farm: gonadal morphometric development. South African Journal of Zoology 20: 172–176.

Guha D, Mukherjee D 1991. Seasonal cyclical changes in the gonadal activity of common carp, *Cyprinus carpio*. Indian Journal of Fisheries 38: 218–223.

Hanchet S 1990. The effects of koi carp on New Zealand's aquatic ecosystems. New Zealand Freshwater Fisheries Report No. 117. Freshwater Fisheries Centre, MAF Fisheries, Rotorua. Pp. 1–41.

Horvath L 1985. Egg development in the common carp. In: Muir J, Roberts R ed. Recent Advances in Aquaculture. London and Sydney, Croom Helm. Baluyut 2: 31–77.

Hutchison MJ, Armstrong PH 1993. The invasion of a south-western Australian river system by *Perca fluviatilis*—history and probable causes. Global Ecology and Biogeography Letters 3: 77–89.

Karatas M 2000. Investigations on the reproduction properties of the common carp (*Cyprinus carpio*) population in Kazova Lake, Tokat, Turkey. Turkish Journal of Veterinary and Animal Sciences 24: 261–265.

Koehn J 2003. Rationale, results and management implications of recent carp research in Australia. In: Managing invasive freshwater fish in New Zealand. Proceedings of a workshop hosted by Department of Conservation, 10–12 May 2001, Hamilton. Pp. 11–18.

Linhart O, Kudo S, Billard R, Slechta V, Mikodina EV 1995. Morphology, composition and fertilization of carp eggs: a review. Aquaculture 129: 75–93.

McCrimmon HR 1968. Carp in Canada. Fisheries Research Board of Canada Bulletin 165: 1–89.

McDowall RM 1996. A brief history of carp in New Zealand. In: Roberts J, Tilzey R ed. Controlling carp: exploring the options for Australia. Proceedings of a workshop, 22–24 October 1996, Albury. 129 p.

Murakaeva A, Kohlman K, Kersten P, Kamilov B, Khabibullin D 2003. Genetic characterization of wild and domesticated common carp (*Cyprinus carpio* L.) populations from Uzbekistan. Aquaculture 218: 153–166.

Parmeswaran S, Alikunhi KH, Sukumaran KK 1972. Observations on the maturation, fecundity and breeding of common carp, *Cyprinus carpio*. Indian Journal of Fisheries 19: 110–124.

Prochelle O, Campos H 1985. The biology of the introduced carp *Cyprinus carpio*, in the River Cayumapu, Valdivia, Chile. Studies on Neotropical Fauna and Environment 20: 65–82.

Pullan S 1986. Monitoring programme planned for koi in the Waikato. Freshwater Catch 29: 15–17.

Pullan S, Little R 1979. Native and exotic fishes: koi carp a beautiful menace. Freshwater Catch 4: 9.

Ricker WE 1975. Computation and interpretation of biological statistics in fish populations. Bulletin of Fisheries Research Board of Canada 191. 382 p.

Roberts J, Chick A, Oswald L, Thompson P 1995. Effect of carp, *Cyprinus carpio*, an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. Marine and Freshwater Research 46: 1171–1180.

Shields JT 1958. Experimental control of carp reproduction through water draw-downs in Fort Randall Reservoir, South Dakota. American Fisheries Society 1958: 22–33.

Sivakumaran KP, Brown P, Stoessel D, Giles A 2003. Maturation and reproductive biology of female wild carp, *Cyprinus carpio*, in Victoria, Australia. Environmental Biology of Fishes 68: 321–332.

Smith BB, Walker KF 2003. Spawning dynamics of carp (*Cyprinus carpio*) in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. In: Australian Society of Fish Biology Annual Conference Handbook. Wellington, New Zealand. P. 106.

Sterba G 1962. Freshwater fishes of the world. London, Vista Books. Pp. 240–241.

Stuart I, Jones M 2002. Ecology and management of common carp in the Barmah-Millewa Forest. Final report of the point source management of carp project to Agriculture Fisheries and Forestry Australia. Victoria, Arthur Rylah Institute. 214 p.

Vila-Gispert A, Moreno-Amich R 2002. Life-history patterns of 25 species from European freshwater fish communities. Environmental Biology of Fishes 65: 387–400.

Vilizzi L, Walker KD 1999a. Age and growth of the common carp, *Cyprinus carpio*, in the River Murray, Australia: validation, consistency of age interpretation, and growth models. Environmental Biology of Fishes 54: 77–106.

Vilizzi L, Walker KD 1999b. The onset of the juvenile period in carp, *Cyprinus carpio*: a literature survey. Environmental Biology of Fishes 56: 93–102.

Wang JQ, Lui HL, Po HY, Fan LN 1997. Influence of salinity on food consumption, growth and energy conversion efficiency of common carp (*Cyprinus carpio*) fingerlings. Aquaculture 148: 115–124.

Zambrano L, Perrow MR, Macias-Garcia C, Aguirre-Hidalgo V 1999. Impact of introduced carp (*Cyprinus carpio*) in subtropical shallow ponds in Central Mexico. Journal of Aquatic Ecosystem Stress and Recovery 6: 281–288.

Zambrano L, Scheffer M, Martinez-Ramos M 2001. Catastrophic response of lakes to benthivorous fish introduction. Oikos 94: 344–350.

Zar JH 1996. Biostatistical analysis. 3rd ed. New Jersey, Prentice Hall. 718 p.