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Life history traits of an equatorial common carp *Cyprinus carpio* population in relation to thermal influences on invasive populations

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ABSTRACT

Marginal increment ratio analysis of scales collected from the exploited common carp *Cyprinus carpio* (Linnaeus, 1758) population of Lake Naivasha between June 2008 and November 2009 revealed they were valid for ageing purposes, with an annual growth check formed. Individuals were fast growing and only present to the age of 4 years. Growth was sexually dimorphic (females being faster growing) and the temporal pattern in the gonadosomatic index suggested reproduction was asynchronous and occurred throughout the sampling period. A meta-analysis of traits of carp from across their range revealed that temperature was a major determinant of their growth parameters (L_∞ and the K of the von Bertalanffy growth model). Populations in more seasonal climates (as described by increased differences between the minimum and maximum monthly mean temperature in a year) were slower growing but had increased potential for attaining larger sizes. This helped explain the expression of their traits in Lake Naivasha where the mean monthly temperatures of between 20 and 23 °C were aseasonal. The life history traits of carp in Lake Naivasha provided their population with resilience to fishery exploitation with increased catches being independent of fishing effort. The influence of temperature on this globally invasive fish is in line with the findings for other invasive fishes and provides insights into their invasion patterns and processes.

1. Introduction

Some introduced fishes can have the capacity to develop invasive populations and cause ecological harm in the environment (Cucherousset and Olden, 2011). Although the proportion of introduced freshwater fishes that subsequently develop invasive populations is relatively low (Gozlan, 2008), these fishes raise considerable ecological concern due to their potential for causing detrimental impacts arising from, for example, increased interspecific competition and disruptions of ecosystem functioning (Gozlan et al., 2010a,b; Britton et al., 2010a). As introduced fishes are inherently difficult to manage in the environment once they have established invasive populations (Britton et al., 2010b), then predicting those fishes that have a high probability of developing invasive populations is important (Copp et al., 2009). Spatial analyses of life history traits of invasive fishes, such as those performed on data collated from across their extended range, may be used to assist invasion predictions as they can reveal the environmental conditions under which the species may thrive, for example their optimum thermal conditions. The association of expression of life-history traits with environmental parameters have thus been used to explain invasion patterns and processes (e.g., Benejam et al., 2009) and identify regions vulnerable to invasion by certain species (Cucherousset et al., 2009).

The common carp *Cyprinus carpio* (Linnaeus, 1758) has been introduced into numerous countries around the world (Lever, 1996) and is one of only eight fish on the IUCN list of the World's worst 100 invaders (Lowe et al., 2000). This is through a combination of their potential to be invasive and their ecological impacts. Their invasive potential arises from their life history traits that facilitate the colonisation of new waters, for example their capability for fast growth, early maturity and high fecundity (Sivakumaran et al., 2003; Smith and Walker, 2004; Britton et al., 2007). Ecological impacts arising from their invasions relate to their function as a bioengineering species that impacts water quality such as losses of submerged vegetation and increased turbidity (Koehn, 2004;

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Zambrano et al., 2006; Matsuzaki et al., 2007, 2009). Invasive populations have been reported from relatively warm countries such as Australia (Koehn, 2004), Mexico (Zambrano et al., 2006) and parts of the USA (Weber and Brown, 2009) but not in temperate countries such as England (Britton et al., 2010c). This suggests there may be a strong relationship between the ability of carp to develop invasive populations and the ambient climatic conditions of the area concerned.

In this study, we investigate the relationship between invasive carp populations and climatic variables by studying their population trends and life history traits in the equatorial Lake Naivasha, Kenya. The thermal conditions in the lake are aseasonal, with daily water temperatures ranging between 20 and 32 °C, with a daily mean of 20–23 °C (Britton et al., 2010a). Carp were accidentally introduced in 1998/99 following their presence in a fish farm in the catchment that subsequently flooded, with escapee fish ending in the lake (Hickley et al., 2002; Hickley et al., 2004). These founders established a population that were being heavily exploited in the lake's commercial fishery only six years later (Britton et al., 2007). An initial study suggested their growth was fast and reproductive traits such as length at maturity enabled spawning relatively early in life (Britton et al., 2007). However, these outputs were based on data collected over a limited time period (one sample per year over a four year period) that prevented validation of the ageing method and the identification of temporal trends in reproductive traits and behaviours (e.g., annual peaks in spawning activity). Consequently, in this study, data were collected regularly over a 17-month period (June 2008–December 2009) to enable determination of: (i) the current status of the *C. carpio* population in Lake Naivasha; (ii) the validity of using their scales for ageing; (iii) their somatic growth parameters in association with their reproductive traits; and (iv) how these traits compare with data collected from populations elsewhere in their invasive range. Consequently, the study initially focuses on the Lake Naivasha carp population before comparing their outputs in a review of published data from across their invasive range. We test the hypothesis that the equatorial *C. carpio* population in Lake Naivasha will be very fast growing and reproduce early in life compared with populations from more seasonal and temperate climates due to the influence of temperature on their life history traits.

2. Materials and methods

2.1. Lake Naivasha, its commercial fishery and fish sample collection

Lake Naivasha is a shallow, freshwater lake in Kenya's Rift Valley located 190 km south of the equator (0°45′S, 36°21′E) at an elevation of 1890 m above sea level. Its area fluctuates according to water levels, but is approximately 100–150 km^2 and up to 6 m deep (further details available in Oyugi et al., 2011). To identify the population trends in the *C. carpio* since their introduction and through to the conclusion of this study, data were used from the lake's commercial gillnet fishery that has a legal fish landing size of 180 mm. Commercial gill nets of minimum mesh size 5 in. are usually set from the surface and fished continuously on a 24 h cycle, with the fish removed from the nets in the early morning. All the fish captured from the lake are individually weighed at landing beaches on a daily basis, with the fishery data then released by the Naivasha Fisheries Department that allow calculation of the catch indices total annual *C. carpio* catch and catch per unit effort (CPUE), calculated as total catch of carp in that year (t)/total fishing effort in that year (the sum of the number of operating boats per month within each year). Note that due to low catches (carp had yet to be captured in the lake), the fishery was closed between January 2001 and June 2002 to allow population recovery of the exploited tilapiines (Hickley et al., 2002; Hickley et al., 2004). The lengths of fish exploited in the fishery were demonstrated by sub-samples of carp measured in September 2005 (Britton et al., 2007) and in June 2008.

To analyse life history traits, samples of *C. carpio* were collected monthly between July 2008 and September 2009 using gangs of multi-mesh gillnets that were set in the major lake habitats (for example, rocky shore, littoral zone, and open water). The nets comprised of three panels of 7 gill nets each of varying bar mesh size (38, 51, 64, 76, 88, 102, 127 mm). On lifting the nets, fish were removed, sorted by species, measured (fork and total length; L_F, L_T, nearest mm), weighed (nearest 0.1 g) and up to 6 scales removed from the antero-medial region of the body immediately above the lateral line. In the laboratory, the fish were dissected to enable sex determination and where mature female fish were identified their ovaries were removed and weighed (nearest 0.01 g).

2.2. Analysis of reproductive traits

The reproductive traits of *C. carpio* were analysed for sex ratio, age and length at maturity, absolute fecundity (F, ripe female fish only) and the temporal trend in reproductive effort over a 12 month cycle. For an individual fish, absolute fecundity was determined from a total egg count (vitellogenetic oocytes) of a weighed subsample of a weighed ovary and then multiplied up to represent the total egg number of that ovary. Age at maturity was calculated from the percentage of mature fish in each age class (following the ageing analysis) using the formula of DeMaster (1978). Length at maturity was determined using a modification of this formula, with 50 mm length intervals in place of age classes (Trippel and Harvey, 1987); a fish was classed as mature when developed testes or ovaries could be identified in the body cavity. Reproductive effort was assessed by the gonadosomatic index (GSI) of the female fish, calculated as gonad weight/(body weight − gonad weight) × 100.

2.3. Analysis of scales, and age and growth data, in Lake Naivasha

To assess the validity of the scales for ageing, the frequency and timing of check formation on the scales was determined through analysis of 158 samples taken randomly from the collection. These were assigned 'blind' reference numbers so that the primary reader had no prior knowledge of the month in which the scales were collected. To ensure precision in the process, a quality control process was used that utilized a secondary reader, with 50% of the scales read independently and also used blind numbering. Following agreement between both readers on their interpretation of the growth checks on the scales, the following measurements were taken from one scale per fish: total scale radius (S_R), distance from the focus to the last formed check (L_A) and distance to the second-last formed check (L_{A-1}). On completion of the scale reading, the data were sorted from their reference numbers back into their monthly samples and then subjected to marginal increment ratio analysis (MIRA; Haas and Recksiek, 1995; Vilizzi and Walker, 1999), where the MIRA calculation of the marginal increment ratio (MIR) was determined by MIR = $[(S_R - L_A)/(L_A - L_{A-1})] \times 100$. When only one check was observed, the denominator was the distance from the scale focus to the check (Vilizzi and Walker, 1999). Fish with no growth check present were not used in the analysis.

Assuming that using scales for ageing *C. carpio* was validated then scale ageing was applied to all scales collected in the survey and then from the scales collected during previous studies (*cf.* Britton et al., 2007). The scales were analysed and checks counted to enable calculation of their growth data. This was completed using the von Bertalanffy growth model of the form $L_t = L_\infty(1 - \exp^{-Kt})$ where L_t was the actual length of each fish at observed age

t, L_∞ was the asymptotic length and K was the growth coefficient. The model was fitted using a non-linear minimization of the negative log-likelihood of the form $-\ln = n \ln \sigma + n/2$, where $\sigma = \sqrt{(\sum (L_i - L'_i)^2/n}$ and L_i, L'_i and n are the respective observed and predicted lengths-at-age, and the number of data points.

2.4. Analysis of growth and temperature of *C. carpio* in its distributional range

The final analytical step was to compare the life history traits of *C. carpio* in Lake Naivasha with data from elsewhere in their range. The data were collated from a review of published studies; as these were limited for reproductive traits then focus was given solely to growth parameters taken from 29 populations. To identify the role of climatic conditions, climatic data were sourced from weather stations in their locality (National Climatic Data Center, 2009) for each population. The temperature metric used for testing in the growth review had to reflect the range of climatic types within the data (equatorial, continental, temperate, Mediterranean). Consequently, the metric developed calculated the difference between the mean maximum monthly temperature and the mean minimum monthly temperature over a 12-month period and has been termed the 'Annual temperature range'. This metric was effective as it was able to describe the populations that, for example, experienced temperate, seasonal conditions (large difference between the maximum and minimum temperature) and those that experienced aseasonal conditions (low difference between the maximum and minimum temperature). The relationship between the temperature metric and growth parameters was then tested using linear and non-linear methods.

All statistics were completed in SPSS v.14.0; where parametric tests have been used, the data were initially tested for normality.

3. Results

3.1. Status of *C. carpio* in Lake Naivasha

The first appearance of *C. carpio* in the commercial fishery was during 2002 and since then catches have generally increased on an annual basis, with the highest total catch achieved in 2009 (approximately 677 t were captured; Fig. 1). Catch per unit effort also increased annually to 2009, with the relationship between fishing effort and catch not significant ($R^2 = 0.11$, $F_{1,6} = 0.75$, $P > 0.05$; Fig. 1). Fork lengths of carp captured in the fishery in 2005 and 2008 were between 224 and 694 mm, with the majority of fish captured of lengths 300–400 mm (Fig. 1). Captured fish were significantly larger in 2005 than 2008 (Mann Whitney U test: mean rank 385 and 287 mm respectively, $Z = -6.54$, $P < 0.01$; Fig. 1).

3.2. *C. carpio* reproductive traits in Lake Naivasha

In the samples collected during 2008 and 2009, a total of 916 mature fish were sampled with an overall sex ratio of 1 M: 1.01 F which was not significantly different from 1:1 ($\chi^2 = 0.04$, $P > 0.05$). Although there was no significant difference in the lengths of female and male fish (Mann Whitney U test: mean rank 465 and 452 mm respectively, $Z = -0.74$, $P < 0.05$), females dominated the larger sizes. This was demonstrated by fish at lengths above 400 mm comprising 68% female and 32% male, with this significantly different from 1:1 ($\chi^2 = 4.45$, $P < 0.04$).

The length at 50% maturity of males was 340 mm and females 420 mm (L_T) (Fig. 1). The GSI of ripe female fish reached 40.4%, although the mean GSI of females across the sample was 2.5 ± 4.4%. As there was a positive and significant relationship between fish length and GSI ($R^2 = 0.15$, $F_{1,465} = 82.15$, $P < 0.01$), ANCOVA was used

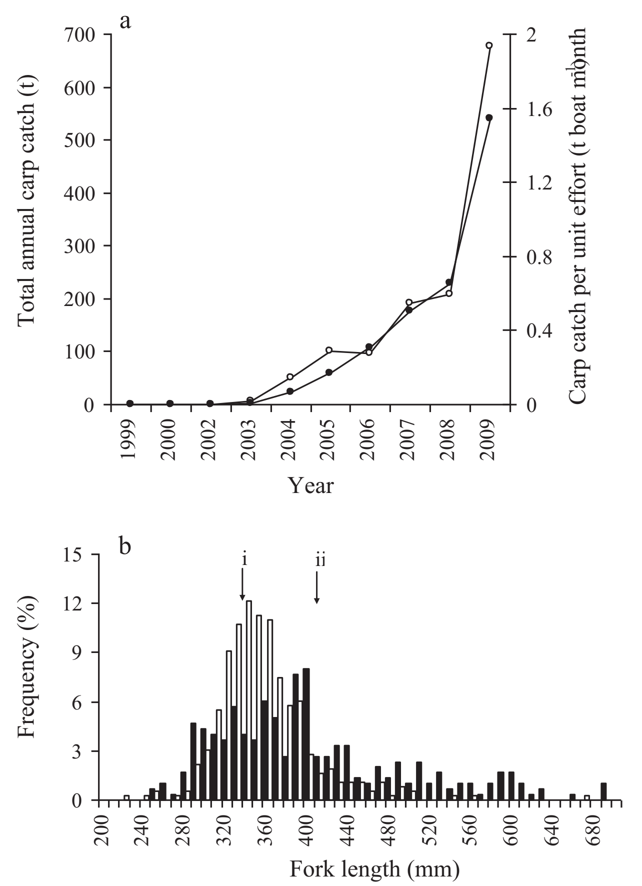

Fig. 1. (a) Total annual catch (•) and catch per unit effort (○) of carp in the Lake Naivasha fishery, 1999–2009; (b) length frequency of carp in the Lake Naivasha fishery in September 2005 (■, $n = 412$) and June 2008 (□, $n = 399$); i, length at 50% maturity of males; ii, length at 50% maturity of females.

to test the mean differences in GSI between months where fish length was controlled in the model. The mean adjusted GSI values by month revealed reproduction throughout the year, albeit with temporal variation as shown by a peak between March and May 2009 (Fig. 2). However, pairwise comparisons with Bonferroni adjustments for multiple comparisons revealed the differences between all combinations of months were not significant ($P > 0.05$). Mean absolute fecundity was 106,765 ± 18,209 vitelloge-

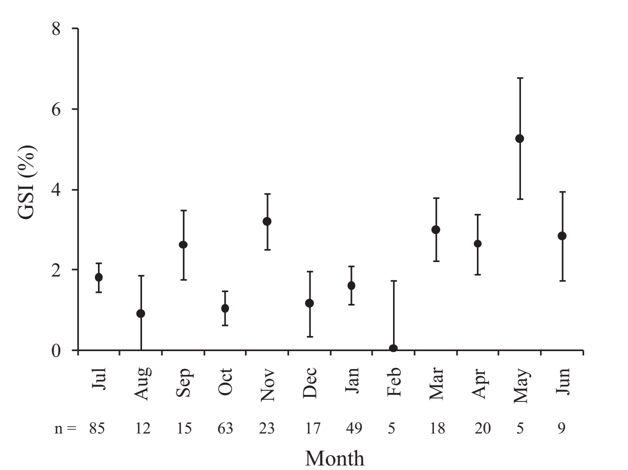

Fig. 2. Mean gonadosomatic index by month (±SE; means adjusted for the effect of fish length) of female *Cyprinus carpio* in Lake Naivasha between July 2008 and June 2009.

Table 1
Tukeys post hoc test in ANOVAs showing the mean differences (±SE) and their significance in mean monthly marginal increment ratios of scales of *Cyprinus carpio* in Lake Naivasha collected between December 2008 and September 2009.

Month		Mean difference ± SE	P
December 2008 (n = 18)	January 2009 (n = 14)	−4.1 ± 4.6	>0.05
	February 2009 (n = 13)	−8.1 ± 4.6	>0.05
	March 2009 (n = 14)	−17.6 ± 4.5	<0.01
	April 2009 (n = 15)	−15.2 ± 4.5	<0.05
	May 2009 (n = 15)	−17.5 ± 4.6	<0.01
	June 2009 (n = 12)	−18.0 ± 4.3	<0.01
	July 2009 (n = 13)	−19.5 ± 4.4	<0.01
	August 2009 (n = 10)	−36.5 ± 5.0	<0.001
	September 2009 (n = 10)	−34.3 ± 6.6	<0.001
	October 2009 (n = 12)	−36.5 ± 5.8	<0.001
	November 2009 (n = 12)	−37.9 ± 12.3	<0.001

netic oocytes (range 2670–475,175) and was significantly related to individual fish length (R^2 = 0.62, $F_{1,33}$ = 515.16, P < 0.01; F (per 10,000 eggs) = 0.0847L_T − 26.656).

3.3. Scale check formation and growth parameters of C. carpio in Lake Naivasha

Analysis of scales collected between June 2008 and November 2009 revealed that growth check formation was apparent. Marginal increment analysis revealed that there were significant temporal differences (measured as monthly means) in the marginal increment ratios over the period (Table 1; Fig. 3; ANOVA $F_{10,146}$ = 11.96; P < 0.01); suggesting that check formation commenced in November and peaked in December (Fig. 3). Furthermore, using December 2008 as the month for the baseline, the mean values for subsequent months suggested check formation was annual (Table 1). Correspondingly, these data suggest consistent annual check formation on scales making them valid for ageing purposes. Testing mean GSI by month with mean monthly marginal increment ratios revealed a significant relationship between the metrics (Figs. 2 and 3; R^2 = 0.57; $F_{1,5}$ = 6.81, P < 0.05), with check formation coinciding with a period of low reproductive effort.

The maximum number of annual growth checks on the scales was 4 for females and 3 for males. Plotting observed age against fork length at capture suggested that growth rates differ between sexes (Fig. 4). Therefore, von Bertalanffy growth parameters were calculated for all data combined and then for males and females separately. Values of L_∞ and K respectively were 767 mm and 0.53 (sexes combined), 618 mm and 0.68 for males, and 755 mm and 0.75 for females.

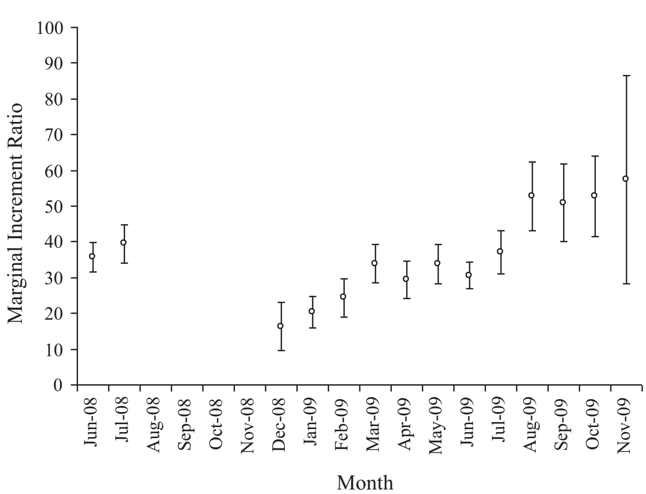

Fig. 3. Mean marginal increment ratio by month for *Cyprinus carpio* in Lake Naivasha, June 2008 to September 2009. See Table 1 for sample size per month.

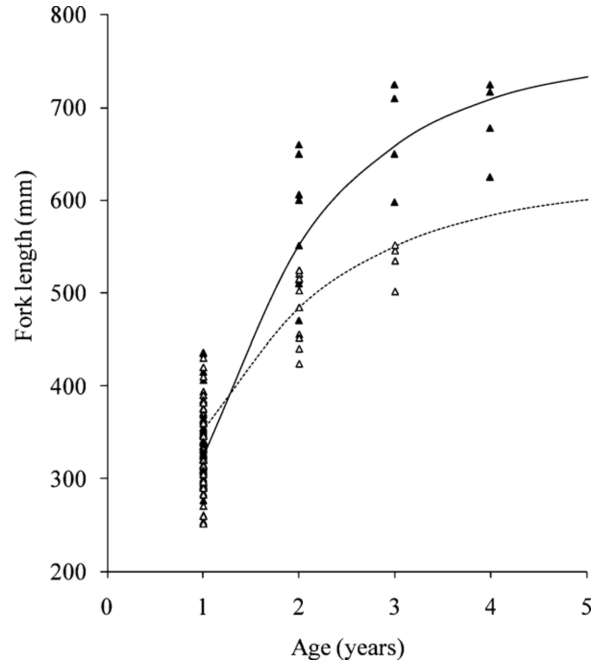

Fig. 4. Observed length at age of female (▲) and male (△) carp in Lake Naivasha with von Bertalanffy growth curves (solid line: female; dashed line: male).

3.4. Influence of temperature on growth of C. carpio in its invasive range

The 29 *C. carpio* populations for which growth data were available were from across their invasive range, including Australia, France, Turkey and the USA, and covering a latitudinal range of 36°S–40°N. The relationship between L_∞ and K for these populations was linear and significant, with increased L_∞ as K decreased (R^2 = 0.32, $F_{1,28}$ = 7.35, P < 0.02; Fig. 5). Although the value of L_∞ for the Lake Naivasha population was within the range recorded elsewhere, their K values were higher, suggesting much faster growth towards L_∞ than recorded elsewhere (Fig. 5). The carp populations experienced a range of thermal conditions, with the difference between the minimum and maximum mean monthly temperature (annual temperature range) ranging between approximately 3 and 45 °C (Fig. 5). A significant positive and non-linear relationship between L_∞ and annual temperature range was observed (R^2 = 0.78, $F_{2,27}$ = 16.60, P < 0.01; Fig. 5). The relationship between annual temperature range and the K was linear, with significant decreases as the temperature range increased (R^2 = 0.25, $F_{1,28}$ = 7.70, P = 0.01; Fig. 5).

4. Discussion

Marginal increment ratio analysis validated annual growth check formation on the scales of carp in Lake Naivasha and subsequent growth analyses revealed that their population grew very fast towards their L_∞ when compared with other populations in their range. This is also consistent with an initial study on this population (Britton et al., 2007). The climatic data for Lake Naivasha revealed thermal conditions were aseasonal as they experienced a relatively low annual range in monthly temperatures, certainly compared with elsewhere in their range. In conjunction with the lake's mean water temperatures only fluctuating between 20 and

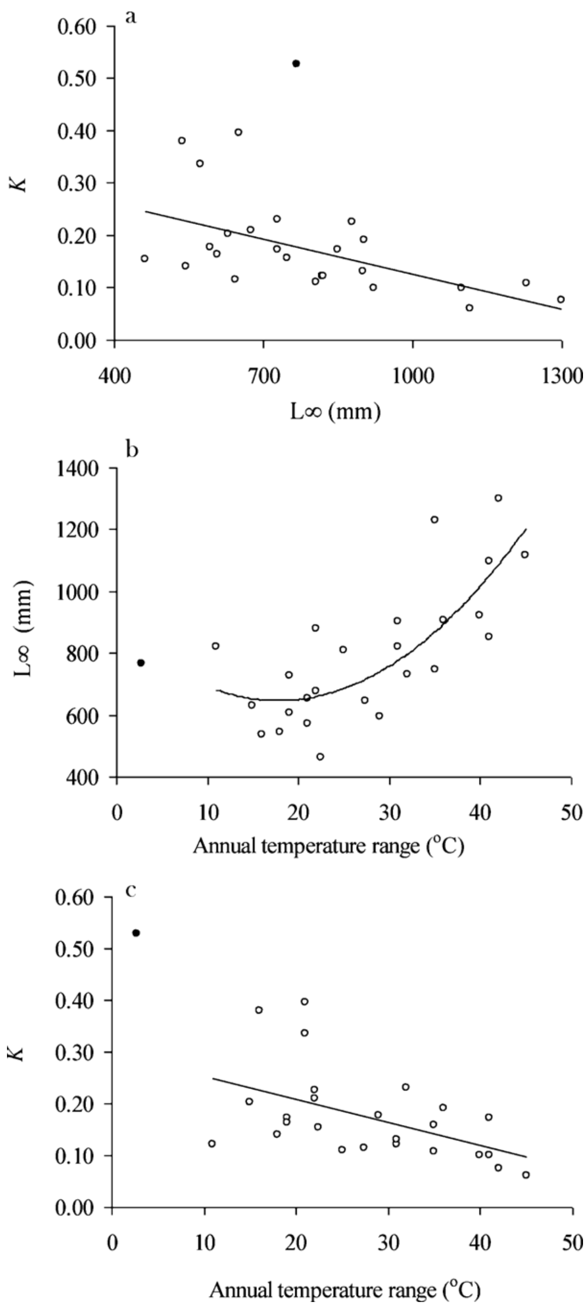

Fig. 5. (a) Relationship of L_∞ and the K of the von Bertalanffy growth model for populations of *Cyprinus carpio*; (b) relationship of the annual temperature range experienced by populations with their L_∞; (c) relationship of the annual temperature range experienced by populations with their K; where ○, their invasive range and •, Lake Naivasha.
(Data sources: Erdem, 1988; Cengizler and Erdem, 1989; Erdem et al., 1992; Ahmet and Süleyman, 2000; Ozyurt and Avsar, 2001; Vila-Gispert and Moreno-Amich, 2003; Sivakumaran et al., 2003; Treer et al., 2003; Brown and Walker, 2004; Pinto et al., 2005; Tempero et al., 2006; Karatas et al., 2007; Jackson et al., 2008; Frose and Pauly, 2010).

23 °C, this was likely to have facilitated their unusually fast growth. By comparison, even in countries where carp are highly invasive such as Australia, their growth and reproductive season rarely extends beyond seven months a year (Koehn, 2004; Smith and Walker, 2004). Thus, the hypothesis that *C. carpio* in Lake Naivasha will grow very fast compared with populations from more seasonal and temperate climates was validated.

The relationship between abiotic variables, such as temperature, and the expression of life history traits of invasive fish across their range has been used to explain patterns in the invasion success of some fishes. In the absence of temperature data, many studies have used latitude as a surrogate of temperature and have revealed that faster growth, earlier reproduction and increased reproductive investment tends to occur in populations at lower latitudes (i.e., warmer temperatures) (Vondracek et al., 1988; Copp et al., 2004; Copp and Fox, 2007). For instance, latitude has been used to explain why populations of the North American pumpkinseed *Lepomis gibbosus* are highly invasive in Southern Europe but not in Northern Europe (Cucherousset et al., 2009). The mosquitofish *Gambusia holbrooki* revealed significant shifts in their reproductive traits in Spain and France that occurred over a latitudinal gradient of only 5°N (Benejam et al., 2009). Across this latitude, the maximum mean difference in temperature between the populations was approximately 2.8 °C. In this study, to account for the large latitudinal range of the populations and the differences in climatic conditions (continental, temperate, equatorial, Mediterranean) then the seasonal difference in temperature was used as the temperature metric. It was successful in revealing changes in the growth patterns of *C. carpio* in relation to temperature where climates with more pronounced differences in their annual temperature range had populations that were relatively slow growing but with the potential for fish to obtain increased lengths. Notwithstanding, the relationships between life history traits of invasive fishes and temperature/temperature surrogates should also acknowledge the likelihood of complex trade-offs between somatic growth, reproduction and multiple environmental factors that will include mean summer temperatures (in additional to contrasts between seasons) and also issues relating to lake productivity (e.g., Johnston and Leggett, 2002; Power et al., 2005; Benejam et al., 2009).

The expression of the life history traits of *C. carpio* enabled their population to support a commercial fishery where catches have increased year-on-year since the fish first appeared in the fishery in 2002. Catch per unit effort revealed the increased catches were independent of fishing effort. Thus, the traits of the carp appear to have provided their population with resilience to the exploitation through providing rapid growth to maturity and the opportunity for early life reproduction prior to their capture. The high exploitation of the carp was also suggested by the absence of fish over the age of 4 years, despite carp being capable of considerably longer life spans (Koehn, 2004). The gonadosomatic index of female *C. carpio* suggested their reproduction was asynchronous and occurred throughout the year. This is supported by studies completed elsewhere that suggest female gonad development is continuous when the photoperiod is above 10 or 12 h, with oocyte maturation and ovulation constant when temperatures are above 16 °C (Crivelli, 1981; Guha and Mukherjee, 1991; Smith and Walker, 2004). Both criteria are satisfied in Lake Naivasha. Indeed, Alikunhi (1966) suggested that in tropical systems, carp will behave as perennial spawners where females may release up to five batches of eggs per year which is advantageous in fish whose life span is compromised as at Lake Naivasha. The life history trait expressions of carp in the lake has therefore provided resilience to exploitation and has enabled the fishery to successfully utilize the population in a manner that, so far, has not resulted in catches being regulated by fishing effort.

In summary, the *C. carpio* population in Lake Naivasha has been successful in establishing a highly abundant population that supports a local fishery. This is assisted by the expression of their life history traits that provide fast growth and spawning throughout the year. This life history trait expression appeared to be facilitated by the warm and aseasonal conditions of the region, with populations elsewhere in their range more constrained through seasonal changes in temperature. These outputs suggest that in optimal conditions, *C. carpio* can be a highly successful invasive fish that, at Lake Naivasha at least, can also provide some benefits through fishery exploitation but, on the evidence from case studies around the world, may also invoke significant ecological impacts.

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