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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 $\text{MIR} = [(S_R - L_A)/(L_A - L_{A-1})] \times 100$. 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