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From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006

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Following the accidental introduction of the carp *Cyprinus carpio* into Lake Naivasha during 1999, a sustainable population became rapidly established and in early 2004 became the principal species exploited in the commercial fishery. Over 9000 kg of carp were harvested from the lake between October 2005 and 2006, when fish were captured between fork lengths (L_F) 200 and 800 mm (>8 kg). Diet of carp <100 mm L_F was dominated by zooplankton, >100 mm L_F there was a shift to benthic macro-invertebrates, with these carp feeding principally upon food resources previously unexploited by the fish community. Contrary to predictions and despite the increasing carp abundance, there has been macrophyte regeneration in littoral areas since 2004. There have been substantial increases in areal cover, with coverage in 2006 at levels not observed since the late 1980s, and significant increases in species richness. Possible reasons for this, and the significance of this carp introduction, are discussed.

Key words: *Cyprinus carpio*; invasion; macrophyte; *Procambarus clarkii*.

INTRODUCTION

The carp *Cyprinus carpio* L. is a species that has been extensively translocated around the world and is generally considered an exotic pest (Sivakumaran *et al.*, 2003). Their introduction into new waters often results in dramatic ecological disruptions at the community and ecosystem levels (Titus *et al.*, 2004), which are related to their vigorous benthic foraging that, for example, disturbs sediment and disrupts aquatic vegetation (Williams *et al.*, 2002; Parkos *et al.*, 2003). Adverse impacts have been recorded across the world, including North

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America (Crivelli, 1983; Crowder & Painter, 1991), India (Nandeesha *et al.*, 1989) and Australia (Koehn, 2004).

Lake Naivasha is a shallow, freshwater lake in Kenya's Rift Valley located 190 km south of the equator at an elevation of 1890 m a.s.l. (Fig. 1). It is *c.* 150 km^2 in area, 3–6 m deep, and water temperatures rarely fall below 20° C (Hickley *et al.*, 2002). Although it became a Ramsar site in 1995 (Wetlands International, 2003), considerable pressures remain on its ecosystem, with habitat degradation and major fluctuations in water level resulting from climatic factors, anthropogenic activities and the adverse impacts of alien species introductions (Harper & Mavuti, 2004). An example of the degraded habitat is the substantial loss of macrophytes and increased turbidity that has occurred since the 1970s, when transparency was still in excess of 1 m and the aquatic flora was dominated by the floating-leaved lilies and submerged water plants described by Beadle (1932). The floating-leaved lilies have since disappeared, the submerged flora fluctuates between periods of absence and recovery, and there has been an associated increase in turbidity (Harper, 1992; Harper *et al.*, 1995; Harper & Mavuti, 2004). This fluctuation in macrophyte density is associated with the cyclic abundance of the exotic crayfish *Procambarus clarkii* Girard that graze upon them (Harper *et al.*, 2002; Smart *et al.*, 2002). Exotic crayfish species have been shown to heavily modify aquatic foodwebs (Lodge *et al.*, 1998) and following their successful introduction in 1970, Lake Naivasha proved no exception (Harper *et al.*, 2002).

Lake Naivasha has a long history of species introductions, with examples of alien fishes, mammals, plants and invertebrates introduced since the 1920s (Harper *et al.*, 1990; Harper & Mavuti, 2004). Alien fish species that have successfully established populations and have been exploited commercially since 1959 are the largemouth bass *Micropterus salmoides* (Lacépède), and the tilapia species *Tilapia zillii* (Gervais) and *Oreochromis leucostictus* (Trewavas) (Hickley & Harper, 2002; Hickley *et al.*, 2002). The commercial fishery has experienced

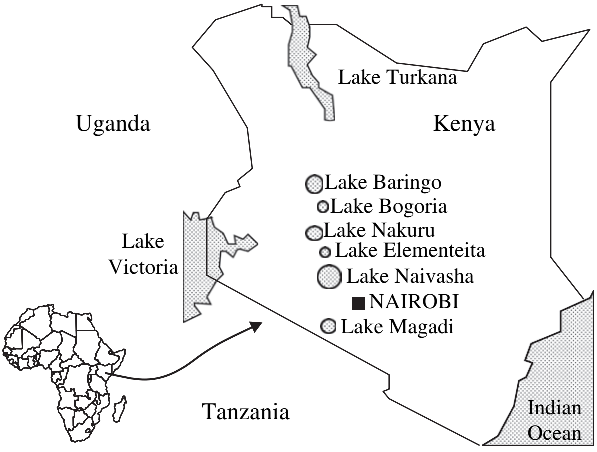

FIG. 1. Location of Kenya in Africa, and Lake Naivasha in Kenya and its relation to other Rift Valley Lakes. Areas of water are shaded.

considerable temporal fluctuations in fish catches since its inception, and despite regulation and periods of closure, there has been a general decline in the catch of all species since the mid 1980s (Hickley *et al.*, 2002; Britton *et al.*, 2006). The most recent alien fish introduction occurred in 1999 when *C. carpio* juveniles escaped during a flood at an on-line aquaculture site in the catchment and were washed into the lake (Hickley *et al.*, 2004*a*). The first report of carp in the lake occurred in March 2001 and they appeared in commercial fishery catches the following year (Hickley *et al.*, 2004*a*).

Carp are a species that exhibit early sexual maturity, rapid growth and wide environmental tolerances (Koehn, 2004). As these are attributes that provide introduced fishes with considerable potential for invasion success, it was predicted that a sustainable population would rapidly develop in Lake Naivasha (Hickley *et al.*, 2004*a*). Given the reported adverse impacts of carp on aquatic ecosystems (Titus *et al.*, 2004), then the extirpation of the remaining submerged plant community of the lake was also predicted, removing any opportunities for subsequent regeneration during periods of low crayfish abundance (Hickley *et al.*, 2004*a*). Using these predictions as testable hypotheses, this paper studies aspects of the establishment, biology and ecology of the carp population in Lake Naivasha, and assesses their initial impacts.

MATERIALS AND METHODS

To investigate the establishment and biology of *C. carpio* in Lake Naivasha, samples of fish were collected between 2002 and 2006 using two principal methods. Fish of *c.* <200 mm (fork length, L_F) were sampled annually using gangs of multi-meshed gillnets of mesh-size 8·5–50 mm. Samples were taken in July 2002 and 2003, September 2004 and October 2005 and 2006. Each sampling period lasted for 12 days during which nets were set daily at first light at locations covering the major habitat types (for example, rocky shore and open water) and lifted after *c.* 5 h fishing. Following their removal from the net, fish were identified, measured (L_F, nearest mm) and weighed (nearest g). From each fish, six to 10 scales were removed from the antero-medial region of the body immediately above the lateral line, an area in which normal scales are usually found in carp (Vilizzi & Walker, 1999); otoliths were also extracted and intestines removed for gut contents analyses. Fish of *c.* >200 mm L_F were sampled using the commercial gillnet fishery where regulations stipulated a minimum mesh-size of 102 mm (4 inches) to be used. The catch statistics for the fishery were available from the Naivasha District Fishery Office and these revealed the amount of fishes, by species, being caught each month. During each annual sampling period described above, samples of carp >250 mm L_F were also collected at the fish landing beaches where daily catches were recorded by the District Fishery Office. Individual catches were counted, fish measured (L_F, nearest mm), and samples taken and treated similarly to the samples collected in the multi-mesh gillnets. To maximize scale collection, scales were also collected from fish caught in the commercial fishery between March 2005 and October 2006 by a representative of the District Fishery Office, although collection was not possible at certain times due to, for example, a mandatory closed season. Scales were removed from the same area of the body as those collected in the annual samples.

The relative abundance of each species sampled in the multi-mesh gillnets was calculated using a catch per unit effort index (CPUE), using the method of Hickley *et al.* (2002). Individuals were sexed according to immature, male and female from macroscopic examination of gonads; reproductive stage was assigned to one of the categories of Smith & Walker (2004). The L_F at 50% maturity (L_{FM}) was determined by Trippel & Harvey (1987). The sex ratio was expressed as the relative proportion of mature female:

male fish. The gonado-somatic index (I_G) was calculated from $I_G = M_G (M_T - M_G)^{-1}$, where M_G is gonad mass and somatic mass was total mass (M_T) minus M_G. The fecundity (F) of individual females was determined gravimetrically, with the number of ripe oocytes determined in a weighed sub-sample of the ovary. The relationship between F and L_F was described by the logarithmic transformation of the power curve $\ln F = \ln a + b \ln L_F$, where a and b are coefficients (Bagenal & Braum, 1978). The F at L_F estimates were then available from $F = aL_F^b$. During determination of individual fecundity, the diameters of 30 ripened eggs were measured and the mean taken. Subsequent examination of scales on a projecting microscope revealed check formation occurred, so the frequency and timing of formation was determined using marginal increment ratio analysis (MIRA; Haas & Recksiek, 1995; Vilizzi & Walker, 1999). The MIRA calculation of the marginal increment ratio (R_{MI}) on scales was calculated using: $R_{MI} = (S_R - L_A)(L_A - L_{A-1})^{-1}$, where S_R = total scale radius, L_A = distance from focus to last formed check and L_{A-1} = distance to the second-last formed check. When only one check was observed, the denominator was the distance from the scale focus to the check (Vilizzi & Walker, 1999).

The scale data were supplemented by otolith microstructure examination. The formation of daily growth increments in carp otoliths has been validated by a number of authors (Vilizzi, 1998*a*; Smith & Walker, 2003); under a light microscope, these appear as paired, concentric, translucent (light) and opaque (dark bands), representing the growth for 1 day (Campana & Neilson, 1985; Vilizzi, 1998*a*). After Vilizzi (1998*a*), only lapilli otoliths were used, with preparation involving grinding (using 9 and 12 μm aluminium oxide micro-finishing film) and polishing (using 3 μm aluminium oxide micro-finishing film). Using a compound microscope (×100 to ×400), the number of daily increments was determined. Validation of the number of daily increments for each fish was provided by analysis of both lapilli otoliths (Campana & Jones, 1992); number was expressed as the mean increment count. This analysis was only completed on fish between 49 mm L_F (the smallest carp sampled) and 150 mm L_F; above this length, differences in incremental counts between otoliths of the same fish began to increase and often exceeded 10% of the mean. To supplement data on the number of daily increments at captured L_F, backcalculated L_F were determined using otolith measurements in the body-proportional equation (Francis, 1990). For each fish, both otoliths were measured to the same number of daily increments and the corresponding L_F backcalculated; outputs for each fish were mean backcalculated L_F at a specific daily increment number.

The diet and feeding habits of *C. carpio* were determined using gut contents analyses. Contents of the digestive tract were stripped into a Petri dish and examined using a dissecting microscope. Taxa were identified, counted and the total number of each food item in all the guts recorded to enable percentage composition to be calculated. Direct counting of small food items, such as microcrustaceans, was impractical, so sub-sampling was undertaken (Khan, 2003). A known volume of the suspension was transferred to a counting cell, with the number of items per taxa counted under a microscope and total number estimated by multiplying numbers in the sub-sample by sample volume. Percentage composition was used to provide an indication of the proportion of each food type in the diet for which a number could be determined. Frequency of occurrence for each dietary item was expressed as the number of guts in which the item was recorded divided by the total number of guts examined.

To complement the stomach contents analyses and provide a longer-term perspective of assimilated diet, stable isotope analysis was completed on relevant samples, including *C. carpio* of >180 mm L_F, collected in September 2003. Preparation of particulate organic matter (<250 μum) and zooplankton samples involved filtering onto precombusted filters. Chironomids, oligochaetes and *Anisops* sp. were individually picked and >50 individuals amalgamated for each analysis; tail muscle was excised from *P. clarkii*, and dorsal muscle collected from carp. All samples were dried at 60° C and pulverized. Sediments, plant debris and hippopotamus-mediated organic matter were prepared as given by Grey & Harper (2002). For carbon and nitrogen stable isotope analyses, samples were weighed (0·7–6·0 mg dependent upon nitrogen composition) into tin-cups prior to combustion in a Eurovector elemental analyser coupled to a Micromass Isoprime continuous flow isotope ratio mass spectrometer. Isotope ratios were given using the δ notation expressed as ‰. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite (for carbon) and atmospheric N_2 (for nitrogen). Repeat analyses of internal standards resulted in typical precision of ±0·1‰ for carbon and ±0·3‰ for nitrogen. All samples were analysed at the Max Planck Institute for Limnology, Plön, Germany.

To monitor the macrophyte community of the lake, submerged macrophytes were sampled in July 2003 in areas adjacent to the multi-mesh gillnets. In 2004, the GPS co-ordinates of 22 sites positioned at the intersections of a 2 km grid covering the area of the lake were sampled for submerged plants using at least three replicate 10 m grapnel trawls. Each site was revisited in August 2005 and August 2006 and plants sampled using the same method. The plants present in each sample were identified to species. For analysis purposes, the 22 sites were combined into five areas (north, west, east, south and central) and mean species richness and 95% CL calculated for each area. Estimation of the approximate lake area with macrophyte growth, areal cover, between 2004 and 2006 was calculated primarily from data collated from the 22 sampling sites as described above. To provide greater spatial lake coverage, these data were supplemented with up to 10 *c.* 100 m and 1000 m linear plant trawls in each year and presence and absence data from spot samples. For the 2006 output, validation was provided by study of aerial photographs of the southern and western shores. The presence and absence and areal coverage of the macrophyte beds were visible on these photographs that were taken from a light aircraft flying at 100 m above the lake. The final figures, expressed as areal cover ha^{-1}, were compared with historical data available from Gouder de Beauregard *et al.* (1998) and Hickley & Harper (2002).

Due to the historical relationship between crayfish and macrophyte abundance, the crayfish population was also studied. Adult abundance was assessed between 1999 and 2006 using a series of crayfish traps baited with dead fishes (*T. zillii* and *O. leucostictus*) and set close to the multi-mesh gillnets for between 1 and 2 h. On lifting the traps, all crayfish were removed, counted and carapace length measured to the nearest mm. Abundance was measured using catch per effort (number of crayfish per trap per h). Juvenile crayfish samples were assessed using the method of Harper *et al.* (2002).

To test temporal relationships between the data-sets, cross correlation and principal components analyses (PCA) were completed using SPSS v.14.0. Cross correlation analysis was used first to identify the presence of time lags between data with high cross correlation factors, so that lagged data could then be used in PCA, if necessary.

RESULTS

The commercial fishery of Lake Naivasha has historically been the subject of considerable fluctuations in catch rates, particularly of *O. leucostictus* (Fig. 2). In recent years, catches of *M. salmoides* in both the commercial fishery and the annual samples have decreased markedly and remain at extremely low levels (Fig. 2). Although the first recording of *C. carpio* in the fishery was in March 2002, they initially remained only a minor component of total catch compared with both tilapia species. At the start of 2004, however, there was a marked shift in catches from tilapia to *C. carpio* and since this time, catches have generally comprised >90% carp (Fig. 2). Between October 2005 and March 2006, the total mass of carp landed was 5511 kg, equivalent to *c.* 370 kg ha^{-1}. The principal size range of exploited carp was *c.* 300–450 mm L_F, although fish were measured between 195 and 725 mm L_F (8 kg), with anecdotal reports of fish up to 800 mm L_F landed (Fig. 2). In the multi-mesh gillnets, CPUE of *C. carpio* increased with each sampling year (Fig. 2). Unlike the commercial fishery, however, they were not the dominant species in catches; between 2002 and

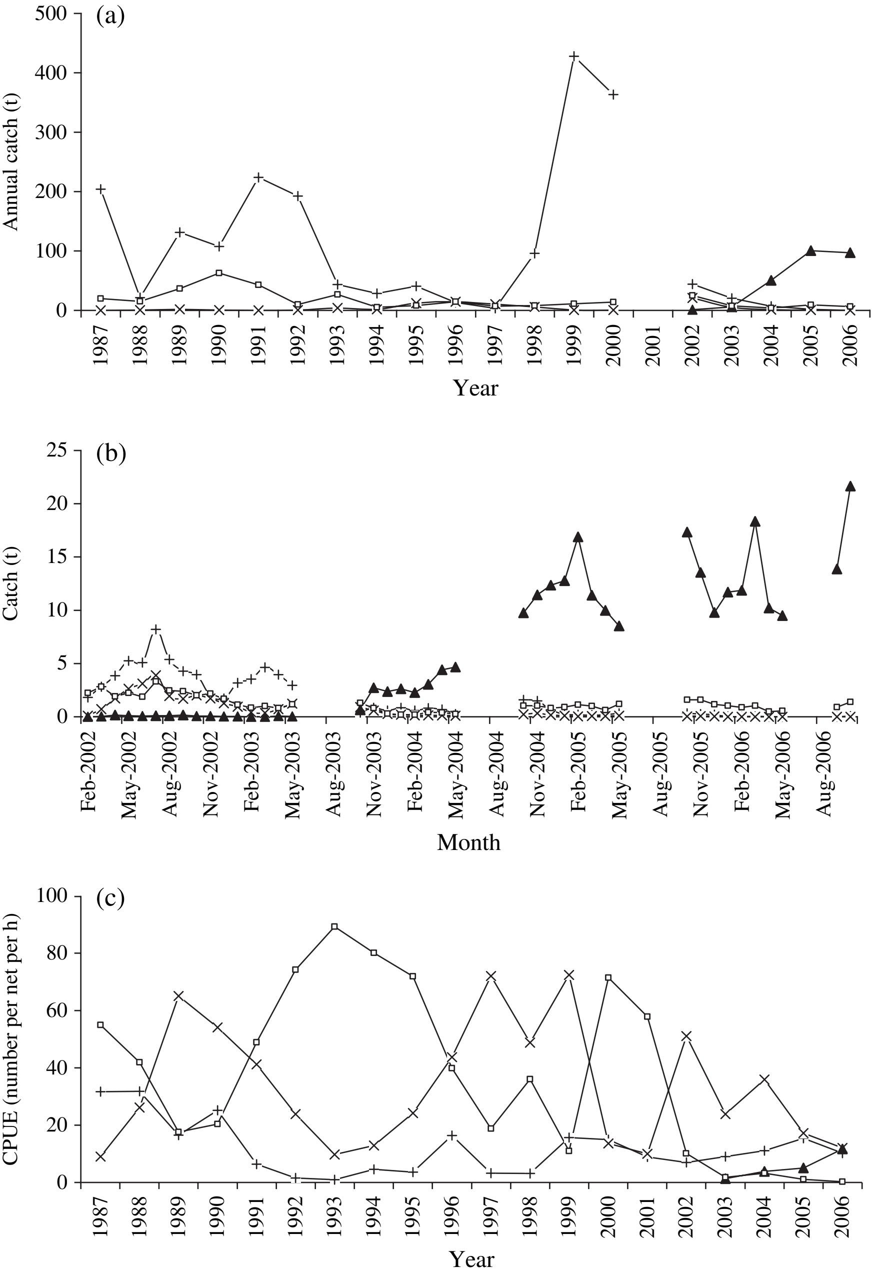

FIG. 2. Composition of catches in Lake Naivasha of *Tilapia zillii* (×), *Oreochromis leucostictus* (+), *Micropterus salmoides* (□) and *Cyprinus carpio* (▲). (a) Annual catches in the commercial fishery, 1987 to 2006, (b) catch per month in the commercial fishery, February 2002 to October 2006, and (c) catch per unit effort of catches using multi-mesh gillnets, 1987 to 2006.

2005, CPUE of *O. leucostictus* and *T. zillii* was considerably higher than *C. carpio*, and similar in 2006 (Fig. 2). The principal size range of carp in these samples was 50–150 mm L_F (Fig. 3).

Despite the collection of scales from a consistent area of the body, check formation was only observed on scales from 52% of the sampled carp >220 mm L_F (Fig. 4), with no checks present on scales from fish below this size. Of the remaining fish >220 mm L_F, some had no apparent scale checks (even in fish >600 mm L_F) and others had patterns that could not be consistently interpreted (*e.g.* there was considerable variation between scales taken from the same fish). The reasons for this inconsistency were not apparent. They were not related to the month of sampling or L_F but do suggest that use of scales may be unreliable in providing robust age data for these fish. Notwithstanding, in fish whose scales revealed consistent check formation, the number of checks generally increased with L_F, with up to four checks present on scales of carp

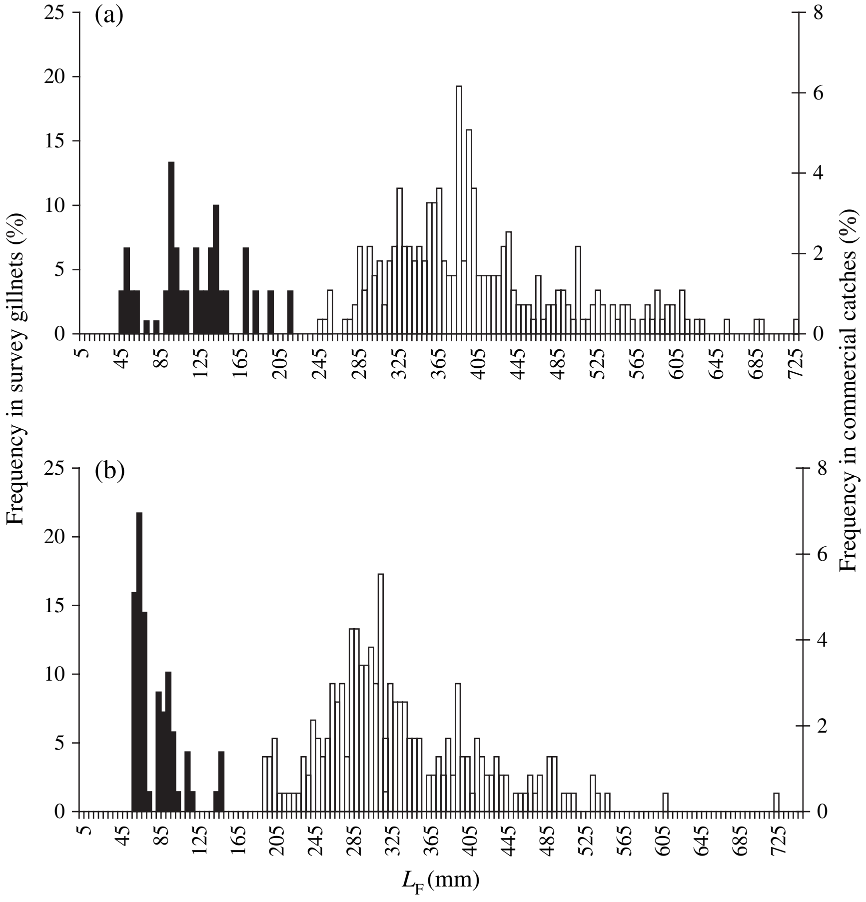

FIG. 3. Fork length (L_F) frequency of *Cyprinus carpio* in multi-mesh gillnets (■) and the commercial fishery (□) in October (a) 2005 ($n = 76$, $n = 249$, respectively) and (b) 2006 ($n = 101$, $n = 248$, respectively).

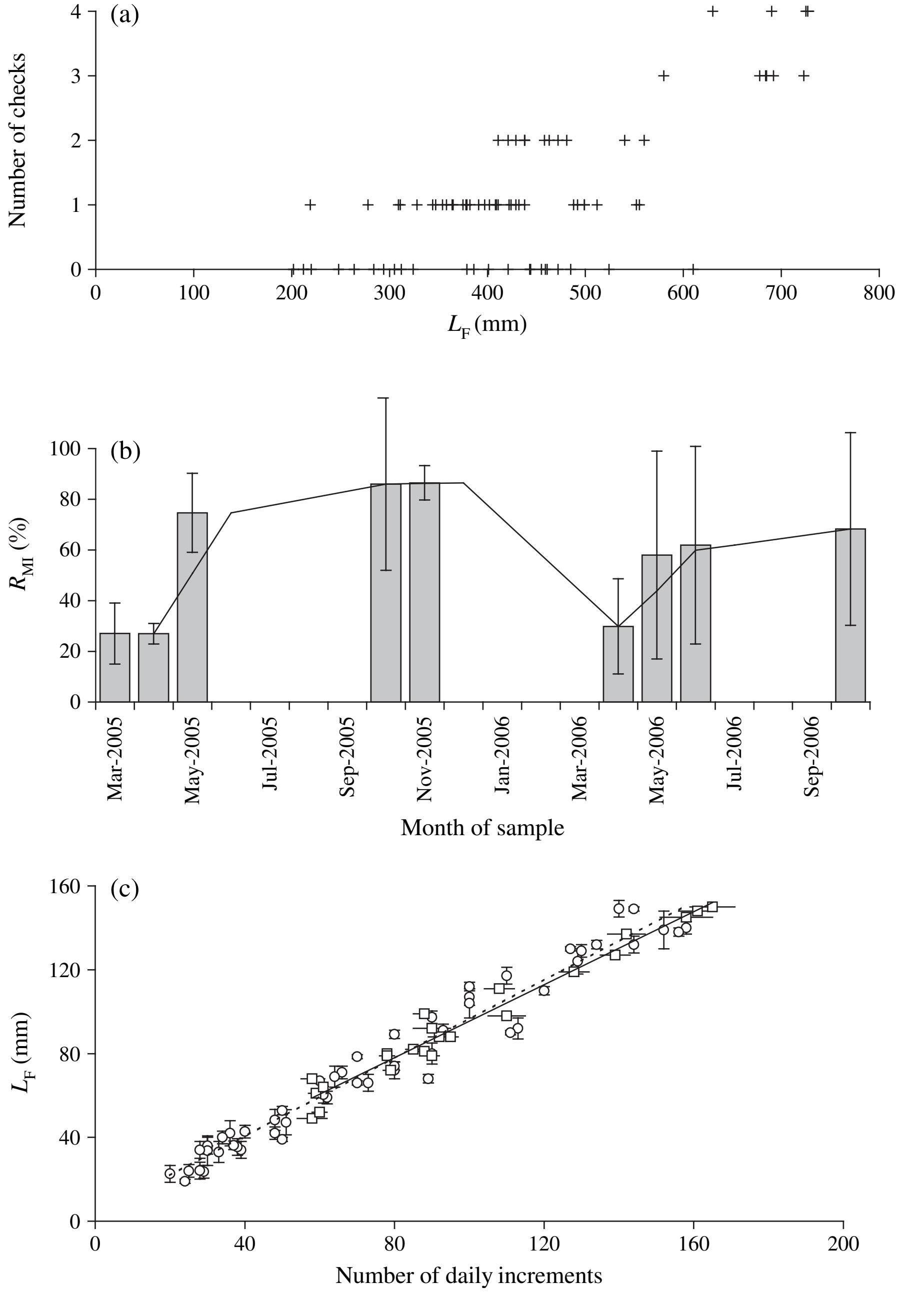

FIG. 4. (a) Number of checks observed on scales of *Cyprinus carpio* by fork length (L_F) (+; $n = 100$). (b) Mean ± S.E. monthly values of the marginal increment ratio (R_{MI}), expressed as a percentage of the previous increment, in scales of *C. carpio* collected from Lake Naivasha. The line denotes the moving average (2 point). (c) Number of daily growth increments by L_F on lapilli otoliths of *C. carpio* from Lake Naivasha [□ = daily mean ± S.D. increment number at sampled L_F; the curve (···) was fitted by $y = 0{\cdot}882x + 7{\cdot}014$ ($r^2 = 0{\cdot}96$, $P < 0{\cdot}001$); ○ = backcalculated mean ± S.D. L_F at daily increment number; the curve (——) was fitted by $y = 0{\cdot}934x + 3{\cdot}235$ ($r^2 = 0{\cdot}96$, $P < 0{\cdot}001$)] .

>620 mm L_F (Fig. 4). Regarding time of check formation, the trend of low marginal increment ratios in April 2005 and 2006, with higher ratios between and after, suggested check formation was annual and occurred in the period between high (November) and low (April) ratios (Fig. 4). Otolith microstructure examination revealed the growth of juvenile carp was linear across the L_F range analysed (Fig. 4).

Males matured at smaller sizes (254 mm L_{FM}) than females (363 mm L_{FM}) and sex ratios (F:M) revealed a male-dominated population (1:2·7), although females were the dominant sex at L_F >450 mm and no males were recorded >578 mm. Given the annual sampling regime, the actual length of the spawning season could not be ascertained. Samples taken in October 2005 and 2006, however, revealed mature females present at all reproductive stages, with varying I_G (0·04–0·39) and mean egg diameters (0·05–2·1 mm). The F and L_F relationship of female carp was described by $F = 00029L_F^{2{\cdot}97}(n = 52,\ r^2 = 0{\cdot}81,\ P < 0{\cdot}001)$.

The diet of carp revealed an ontogenetic shift from zooplankton to benthic macro-invertebrate food resources. Diet of carp <100 mm L_F was based mainly on zooplankton (Cladocera and Copepoda). With increasing L_F, diet comprised greater proportions of oligochaete and chironomid larvae, although zooplankton was present in the guts of carp in all size classes (Table I). Although larger carp >200 mm L_F utilized a broad food assemblage, a relatively small number of items comprised >80% of items ingested (Table I). Algae, detritus and plant material were present in the diet of carp over all size ranges examined, but their contribution could not be quantified numerically. Carp >112 mm L_F were also found to take small crayfish and fishes, although these remained a comparatively minor item numerically. Stable isotope analyses revealed basal resources to be isotopically distinct, with a relatively ^{13}C-depleted planktonic food 'chain' compared to a more ^{13}C-enriched benthic food 'chain', especially when C4 terrestrial grass-derived hippopotamus faecal matter is considered (Fig. 5). There was considerable isotopic variability in crayfish reflecting their omnivorous potential; this was not related to body size. Carp and crayfish mean δ^{13}C was similar but carp exhibited the highest δ^{15}N values of all analysed components in the food web. Carp isotopic variability could not be attributed to individual size as all fish used in the analysis were between 180 and 270 mm L_F.

Macrophytes were virtually absent from the lake in July 2003, and completely absent in August 2004 (Table II). Contrary to predictions, however, regeneration was observed in 2005 and 2006. In August 2005, seedlings carpeted much of the shallow, eastern part of the lake, and some of the southern shore, although areal cover was only 400 ha. By 2006, submerged water plants had re-colonized much of the littoral, with significant increases in species richness in four of the five sampling areas. Five submerged species previously recorded in the lake were now present in the eastern area (Table II). Elsewhere in the lake, particularly in central and western areas, water depth was most likely limiting plant re-colonization. In 2006, areal cover had increased to *c.* 2030 ha, the highest recorded coverage in Lake Naivasha since the late 1980s, when it was recorded at 2600 ha in 1988 and 2300 ha in 1989 (Gouder de Beauregard *et al.*, 1998; Hickley & Harper, 2002). Between 1990 and 2005, coverage never exceeded 900 ha.

TABLE I. (a) Items and their numerical composition (%) in the diet of *Cyprinus carpio* in Lake Naivasha and (b) frequency of occurrence of all dietary items

	L_F range (mm)				
	51–100	101–150	151–200	201–250	>251
n	15	10	10	10	10
Item					
(a)					
Zooplankton	75	36	18	14	12
Corixids	1	3	6	4	5
Chironomid larvae and pupae	10	29	44	53	49
Oligochaetes	5	15	21	23	21
Seeds	8	7	0	0	1
Fishes	0	3	4	2	5
Procambarus clarkii	0	5	7	4	7
Other	1	2	0	0	0
(b)					
Zooplankton	100	100	60	50	60
Corixids	7	20	20	30	30
Chironomid larvae and pupae	53	90	100	100	100
Oligochaetes	13	70	80	90	90
Plant debris	13	20	30	40	30
Detritus	86	70	90	80	60
Seeds	79	60	0	0	20
Algae	72	80	40	0	20
Fishes	0	30	50	40	60
Procambarus clarkii	0	20	60	30	70

L_F, fork length; *n*, number of fish examined in that L_F range.

Sampling of crayfish using quadrats in marginal vegetation generally sampled juvenile crayfish, with traps catching adults in more open water habitats (Fig. 6). Both methods revealed a peak in population abundance in the late 1990s that coincided with the formation of dense mats of the invasive water hyacinth *Eichhornia crassipes* that afforded excellent refuge, even during periods of low macrophyte abundance, and enabled a population 'boom' (Fig. 6; Harper *et al.*, 2002). The subsequent breakdown of the *E. crassipes* mats, in combination with the disappearance of submerged macrophytes in the early 2000s, resulted in a crayfish population 'crash'. Despite the considerable macrophyte regeneration and sustained low abundance of *M. salmoides*, by October 2006 there had not been any sign of an associated recovery in the crayfish population.

The first step in testing relationships between these time series data was the use of cross correlation analysis; as this revealed that the highest cross correlation factors (>0·80) were principally encountered at zero lag time, data were used in this manner in principal components analysis. This revealed the time series of carp abundance indices were significantly correlated with areal cover and macrophyte species richness ($P < 0·01$), and with no other tested variable (Table III and Fig. 7).

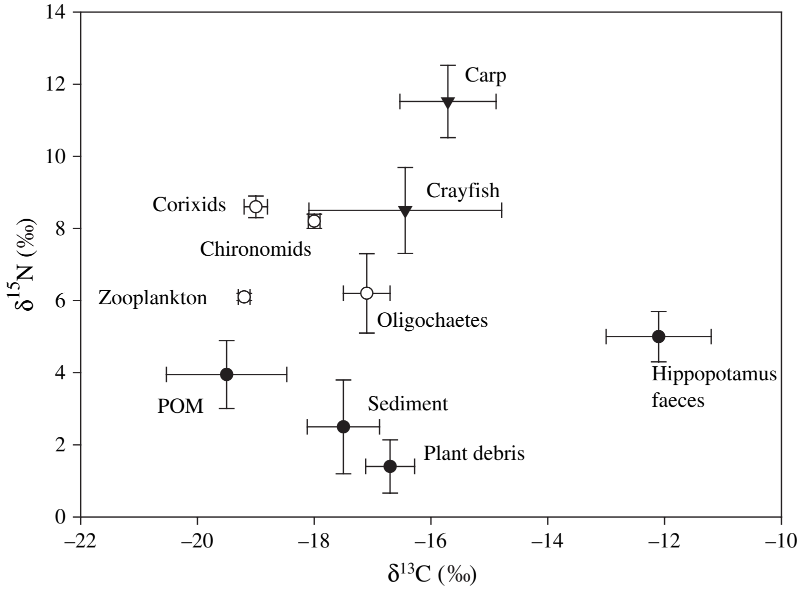

FIG. 5. Stable isotope analysis output showing mean ± S.D. values for all items [●, based resources (POM, particulate organic matter); ○, invertebrates; ▼, carp and crayfish].

DISCUSSION

The hypotheses being tested were following carp introduction into Lake Naivasha, a sustainable population would establish and prevent any subsequent regeneration of macrophytes, irrespective of fluctuations in *P. clarkii* grazing pressure. That a sustainable carp population established quickly is beyond question and their population had a very positive impact on the catches in the commercial fishery. Only after 5 years post-introduction, they became the principal exploited species following >40 years of *O. leucostictus* dominance (Britton *et al.*, 2006). Yet, despite carp establishment, and contrary to expectation, macrophyte regeneration also occurred, with areal cover in 2006 at levels not observed in Lake Naivasha since the late 1980s. Therefore, the direct and indirect effects of benthic foraging by carp had, to date, been insufficient in preventing macrophyte regeneration.

The ability of carp to establish a sustainable population in Lake Naivasha was enhanced by the prevailing conditions of the lake; it is shallow (<7 m), warm (>20° C) and highly productive (Hickley *et al.*, 2004*a*, *b*), conditions ideally suited for carp invasion success (Koehn, 2004). The population appeared to comprise individuals that were fast growing, matured at lengths often achieved at an early age and were highly fecund; female carp >600 mm were capable of spawning >500 000 eggs. Similar traits have been observed in invasive carp populations around the world (Parameswaran *et al.*, 1972; Sivakumaran *et al.*, 2003; Smith & Walker, 2004), although variation in traits such as length at maturity is apparent (Brown *et al.*, 2005). It is, however, recommended that the outputs of the carp ageing are treated cautiously, particularly due to the

TABLE II. Areal cover and mean ± 95% CL species richness (mean number of species per area) of submerged macrophytes in five areas of Lake Naivasha

	North (n = 3)	West (n = 4)	Central (n = 6)	East (n = 5)	South (n = 4)
2004 areal cover = 0 ha					
Plant species richness	0	0	0	0	0
2005 areal cover = 400 ha					
Plant species richness	0	0	0	0·33 ± 0·05	0·25 ± 0·06
Plant list				*N. horrida* *P. octandrus* *P. pectinatus*	*N. horrida* *P. octandrus* *P. pectinatus*
2006 areal cover = 2030 ha					
Plant species richness	1·33 ± 0·44	0·50 ± 0·08	0	2·20 ± 0·54	0·50 ± 0·08
Plant list	*N. horrida* *P. octandrus*	*N. horrida* *P. schweinfurthii*		*N. horrida* *N. hyalina* *P. octandrus* *P. pectinatus* *P. schweinfurthii*	*N. horrida*

n, number of sampling sites in each area; *N. horrida*, *Najas horrida* A. Br. ex Magnus; *N. hylina*, *Nitella hyalina* (DC) Ag.; *P. octandrus*, *Potamogeton octandrus* Poir.; *P. pectinatus*, *Potamogeton pectinatus* L.; *P. schweinfurthii*, *Potamogeton schweinfurthii* A. Benn.

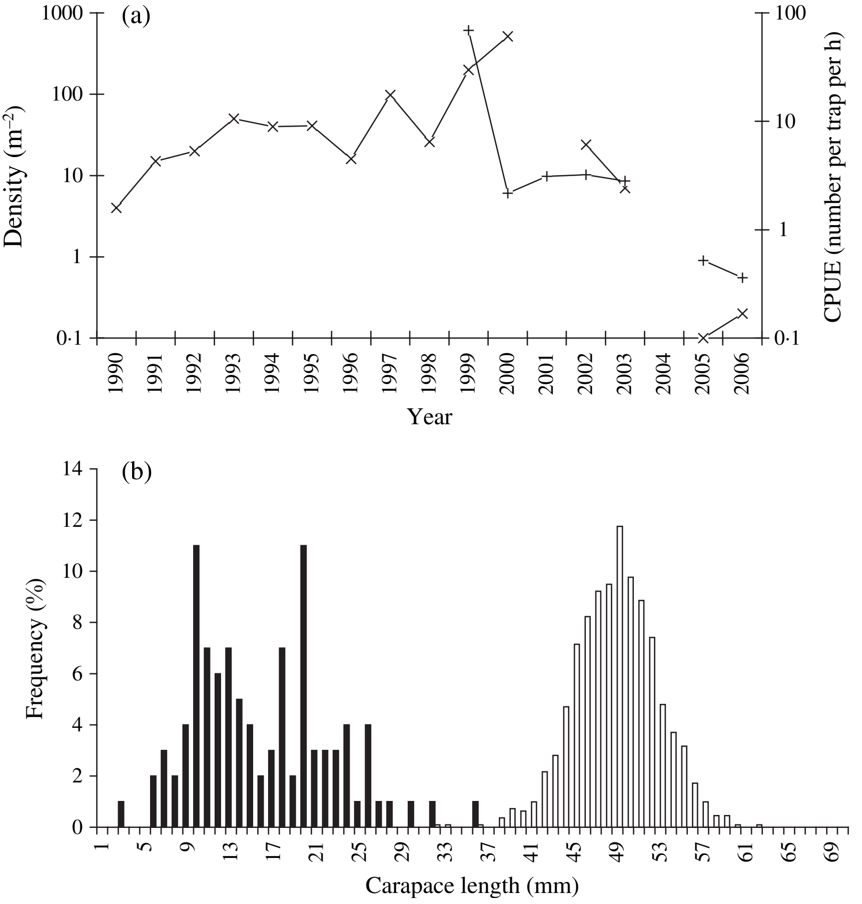

FIG. 6. (a) Mean density of crayfish sampled in quadrats (×) and traps (+), 1990 to 2006 (note use of logarithmic scale). (b) Length frequency of *Procambus clarkii* sampled by [quadrats (■; $n = 100$), and traps (□; $n = 152$)] in July 2003.

inconsistency of check formation apparent in scales of individual fish. Similar age determination problems have been observed in other studied carp populations that demonstrated variable growth rates and protracted spawning seasons (Vilizzi & Walker, 1999).

As a result of sampling intensively only once per year, the length of carp spawning season in Lake Naivasha could not be observed directly. The combination of I_G data of female carp collected in October 2005 and 2006, modes in the length frequency of carp <150 mm and the daily growth increment data, however, suggests the adoption of asynchronous spawning over an extended period. This is a common trait of *C. carpio*; for example, in Australia, Smith & Walker (2004) revealed a carp spawning season lasting 7 months during which individual female carp spawned up to three discrete batches of eggs. Female gonad development was continuous, but required a photoperiod of >10 h and water temperature >16° C for oocyte maturation and ovulation (Smith & Walker, 2004). Similar temperatures have been required in European

TABLE III. Correlation matrix representing relationships between carp, crayfish, macrophytes and lake level, 1999 to 2006

	1	2	3	4	5	6	7	8	9
1		0·88**	0·76**	0·72*	−0·37	−0·49	−0·45	−0·50	−0·76*
2	0·88**		0·97**	0·96**	−0·35	−0·46	−0·43	−0·55	−0·68
3	0·76**	0·97**		0·99**	−0·28	−0·36	−0·34	−0·46	−0·55
4	0·72*	0·96**	0·99**		−0·26	−0·34	−0·32	−0·45	−0·53
5	−0·37	−0·35	−0·28	−0·26		0·19	−0·08	−0·05	0·88**
6	−0·49	−0·46	−0·36	−0·34	0·19		0·66	0·13	0·44
7	−0·45	−0·43	−0·34	−0·32	−0·08	0·66		0·23	0·23
8	−0·50	−0·55	−0·46	−0·45	−0·05	0·13	0·23		0·19
9	−0·76*	−0·68	−0·55	−0·53	0·88**	0·44	0·23	0·19	

1, annual catch of carp in the commercial fishery; 2, catch per unit of carp in the survey gillnets; 3, areal cover; 4, macrophyte species richness; 5, mean density of crayfish (traps); 6, mean density of crayfish (quadrat); 7, catch per unit of largemouth bass in the survey gillnets; 8, annual catch of largemouth bass in the commercial fishery; 9, mean annual lake level.

*$P < 0·05$; **$P < 0·01$.

populations, but with a 12 h photoperiod (Crivelli, 1981; Horvath, 1985; Guha & Mukherjee, 1991). Furthermore, in tropical fresh waters, carp may behave as perennial spawners, with females capable of releasing four or five discrete batches of eggs per year (Alikunhi, 1966). As water temperatures are permanently >20° C in Lake Naivasha and the region experiences a day length of *c.* 12 h, this also supports the assertion that carp are asynchronous spawning over an extended period in the lake.

Before the carp introduction, the fish fauna of Lake Naivasha comprised only five species and dietary analyses had revealed that various food resources, particularly in the benthos, were under-utilized and would provide a vacant niche for an introduced benthic feeding species (Muchiri *et al.*, 1994; Hickley *et al.*, 2002). Although the subsequent introduction of carp was accidental, stomach contents and stable isotope analyses revealed benthic food resources are now being exploited. Whilst carp <100 mm mainly fed upon microcrustaceans, the proportion of dietary chironomids and oligochaetes increased with body length >100 mm. Microcrustaceans are known to be a major dietary component of invasive small carp (Vilizzi, 1998*b*; García-Berthou, 2001; Khan, 2003), and benthic macro-invertebrates become increasingly important in carp diet with increased body lengths (Chapman & Fernando, 1994; García-Berthou, 2001; Khan, 2003). Active selection of chironomids by carp has also been observed (Lammens & Hoogenboezem, 1991). Plant matter rarely comprises a large portion of carp diet; when both plant and animal matter are abundant, animal items are preferred (Eder & Carlson, 1977). In this study, although only present as relatively minor food items, fishes and crayfish were present in the diet, with carp as small as 112 mm containing remains of small tilapia. Certainly, the elevated δ^{15}N values of carp relative to crayfish by *c.* 3‰ suggest an element of predation by carp. The comparable δ^{13}C values of carp and crayfish also point to exploitation of similar carbon sources, *i.e.* oligochaetes

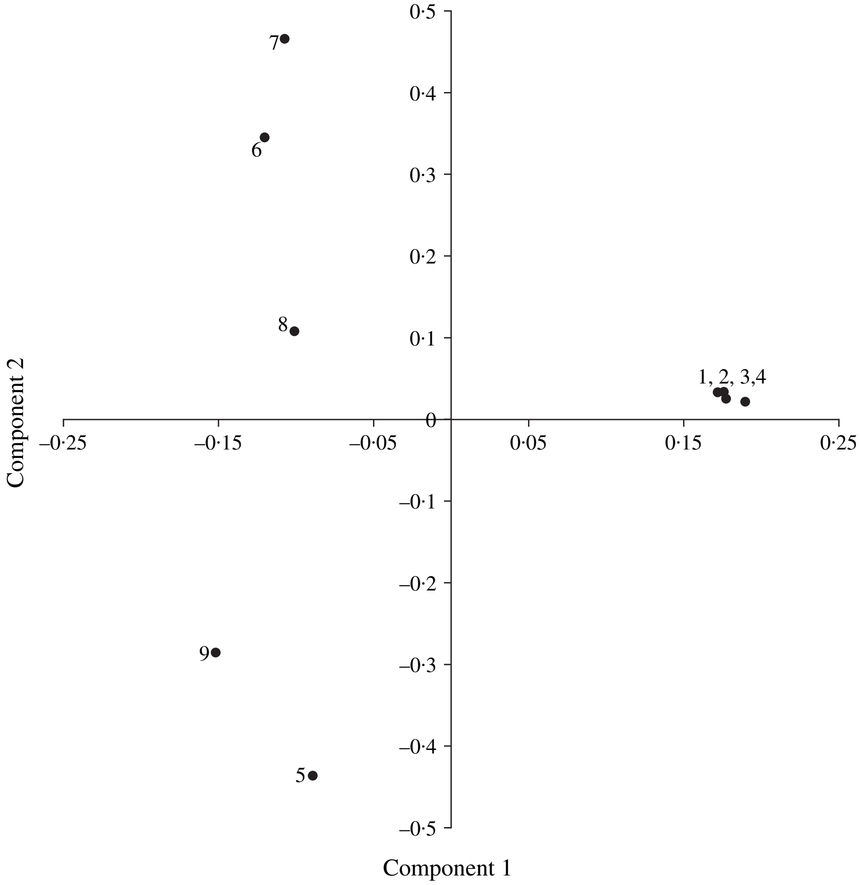

FIG. 7. Principal components analysis output for Lake Naivasha (see Table III).

and chironomids. As a result of both digestion and the powerful pharyngeal teeth of carp (García-Berthou, 2001), the size of the depredated fishes and crayfish could not be reconstructed, although the optimum size of items in carp diet has been shown to be 0·2–0·4 of mouth size (Hasan & MacIntosh, 1992). Thus, any depredated crayfish were likely to be juveniles, although adult crayfish have been shown to be vulnerable to carp predation during ecdysis (Hinojosa-Garro & Zambrano, 2004).

Benthic feeding by invasive carp usually results in adverse impacts upon the invaded ecosystem, with declines in submerged vegetation and the re-suspension of sediments attributed to their vigorous benthic foraging (Lougheed *et al.*, 1998; Titus *et al.*, 2004). Both direct (consumption) and indirect effects (mechanical damage, uprooting) have been observed (Kerfoot & Sih, 1987; Parkos *et al.*, 2003; Hinojosa-Garro & Zambrano, 2004; Lougheed *et al.*, 2004). In experimental enclosures, the abundance of *Potamogeton pectinatus*, a species found in Lake Naivasha, increased when carp were excluded, with associated increases in total stem length of up to 90% (Miller & Crowl, 2006). Williams *et al.* (2002) reported adverse impacts on macrophytes when carp biomass was

>200 kg ha^{-1}, with Parkos *et al.* (2003) reporting carp biomass >470 kg ha^{-1} had a greater impact on turbidty and suspended solids than at 174 kg ha^{-1}. As carp >100 mm were principally benthic foragers in Lake Naivasha (Table I), then similar impacts on macrophytes may have been expected, and had been hypothesized (Hickley *et al.*, 2004*a*). The regeneration of macrophytes in 2005 and 2006 and their significant correlation with indices of increasing carp abundance was, therefore, contrary to prediction.

The ecological mechanisms that enabled macrophyte regeneration to occur in conjunction with the establishment and subsequent fishery dominance of carp are, however, unclear. Hickley *et al.* (2004*b*) stated that submerged plants are 'decimated' by crayfish when largemouth bass predation is not sufficient to control their density. As there has been a sustained period of extremely low bass catches in the commercial fishery, but no significant crayfish population increase (by October 2006), an alternative mechanism may now be constraining the crayfish population and so allowing macrophyte regeneration. A study in shallow ponds in Mexico revealed crayfish (*Cambarellus montezumae*) abundance was reduced when carp density was high, attributed to direct predation, removal of refuge and crayfish behaviour modification (Hinojosa-Garro & Zambrano, 2004). Crayfish avoided carp, moved significantly faster in their presence and sought carp-free habitats, so losing the potential benefits of macrophyte cover (Hinojosa-Garro & Zambrano, 2004). Notwithstanding, the relationships between the fluctuating aquatic flora and fauna of Lake Naivasha are evidently more complex, making it difficult to definitively ascertain the mechanisms involved.

In summary, the introduction of *C. carpio* into Lake Naivasha has resulted in the establishment of a sustainable population that now dominates catches in the commercial fishery. Far from being an exotic pest, their population actually provides a viable and profitable species for exploitation in a period when the catch returns of the other exploited species have declined markedly. To date, adverse ecological impacts of their introduction have been less apparent, and their establishment and subsequent dominance in the commercial fishery has been coincident with significant macrophyte regeneration. It is likely, however, that it is too early in the invasion of Lake Naivasha by *C. carpio* to assess fully their ecological impact. Subsequent adverse impacts may become apparent if their population continues to increase. Notwithstanding the benefits that carp introduction has produced, their status is, arguably, a damning statement of the extent of environmental and fishery decline that has occurred in Lake Naivasha since the 1970s. It is recommended that this alien introduction is not viewed as a panacea for other declining fisheries in degraded Kenyan lakes. Rather, it should act as a further warning of the threat posed by carp to fisheries currently based upon indigenous and naturalized species.

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