Management Implications of the Response of Two Tilapiine Cichlids to Long-Term Changes in Lake Level, Allodiversity and Exploitation in an Equatorial Lake

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Abstract The tilapiine cichlids *Oreochromis leucostictus* and *Tilapia zillii* were introduced into Lake Naivasha, Kenya, in 1956. Previous studies on data collected to 1987 revealed they were persistent following establishment, despite environmental variability and exploitation. Recent data, however, suggest this persistence is under threat as data indicate some significant declines in aspects of their abundance since 1999. The influence of changes in lake level, allodiversity and fishing effort on this decline was tested and showed that a decline in lake level was a significant causal factor. The recent change in allodiversity, with the establishment and dominance of *Cyprinus carpio* in the fishery, was not significant on the catch per unit effort of *O. leucostictus* but was on *T. zillii*. Since 1999, catches of tilapiines in the fishery have been independent of fishing effort, contrary to between 1975 and 1987, suggesting their management through application of fishery models may no longer be applicable. As it was anthropogenic-mediated lake level changes that were mainly responsible for their decline, then lake management should focus on sustainable water utilization that maximizes lake levels in accordance with the basin-wide water balance.

Keywords *Oreochromis leucostictus* · *Tilapia zillii* · Catch per unit effort · Fishery catch · Environmental change

INTRODUCTION

Tilapiine cichlids are a highly successful group of fishes in African freshwaters as they can maintain population sustainability even during adverse environmental conditions (Duponchelle and Panfili 1998; Beveridge and McAndrew 2000; Duponchelle et al. 2000). This is due to factors such

as plasticity in the expression of their life-history traits, for example, in their somatic growth and length at sexual maturity (Lowe-McConnell 1982; Kolding 1993; Coward and Bromage 1999; Beveridge and McAndrew 2000). Peaks in growth and reproductive traits often correspond with periods of flooding that increase resource availability, suggesting a strong association between environment change and fish population response (Fryer and Iles 1972; Wootton 1984; Duponchelle et al. 2000).

In Lake Naivasha, Kenya, *Tilapia zillii* (Gervais) and *Oreochromis leucostictus* (Trewavas) were introduced in 1956 where they led to a commercial gillnet fishery being developed (Siddiqui 1977; Muchiri et al. 1994; Hickley and Harper 2002). Initial studies in the early 1970s were conducted during a period when environmental and ecological change in the lake was primarily limited to the fish introductions (e.g. Siddiqui 1977). In that period, the lake was described as having clear waters and an extensive papyrus fringe with dense growth of submerged macrophytes within lagoons and low allochthonous nutrient input (Siddiqui 1977). Water levels were relatively natural and primarily dependent upon catchment rainfall (Becht and Harper 2002). Since then, however, increased water abstraction from the catchment, changes in allodiversity (such as introduction of the crayfish *Procambarus clarkii* Girard) and substantial increases in human population density have resulted in the almost total loss of lagoons, and the macrophytes and fringing papyrus. High water turbidity also results from frequent algal blooms caused by increased eutrophication (Kitaka et al. 2002; Harper and Mavuti 2004; Britton et al. 2007). Becht and Harper (2002) used a hydrological model based on lake level and rainfall data to show that water abstraction for agriculture, geothermal electricity production and export for domestic water supply to Nakuru has become excessive over the last 30 years

(Harper and Mavuti 2004). Consequently, the level of the lake has become increasingly disconnected with rainfall patterns and has decreased by up to 4 m as a result (Becht and Harper 2002).

A study conducted between 1975 and 1988 on the two introduced tilapiine fishes in the lake suggested that their populations were persistent in the face of environmental variability and relatively heavy fishing pressure (Muchiri et al. 1995). It was concluded that this was due to factors, such as their detritus-based diet, acting as buffers against these pressures, with water level changes primarily an issue affecting reproduction, not feeding (Muchiri et al. 1995). Subsequent work has suggested that for their fishery to be improved, the marginal fringe of papyrus (*Cyperus papyrus*) requires protection to reduce eutrophication (Hickley et al. 2004) and revealed that the lake's fishery catches are now dominated by the invasive common carp *Cyprinus carpio* L. rather than *O. leucostictus* (Britton et al. 2007; Hickley et al. 2008). Consequently, the aim of this study was to use these studies as a base-line in order to identify the subsequent responses of the tilapiine populations to the continued environmental and ecological changes in the lake through completion of the following objectives: (i) quantify the extent of lake level change between 1970 and 2008 as a proxy for environmental change; (ii) quantify the temporal relationships in the relative abundance of the two tilapia species over this period and (iii) determine the influence of lake level change, fishing effort and recent changes in allodiversity on these temporal relationships. Completion of these objectives then enabled identification of whether previously suggested management methods remain appropriate today.

MATERIALS AND METHODS

Lake Naivasha is located in the Rift Valley of Kenya at 0°45'S and 36°21'E and is at approximately 1,890 m above sea level (m.a.s.l.). It is a relatively shallow lake (maximum depth of the main lake is up to 8 m) with a surface area that varies between 100 and 160 km². It is fresh (EC of 300–450 µS/s) due to underground seepage and permanent freshwater input (Becht and Harper 2002; Harper and Mavuti 2004). The data available for this study were collated from a range of sources and this meant there were some inconsistencies in providing complete time series of data across the entire study period (1975–2008). These inconsistencies are explained within each of the following sub-sections.

Environmental Change

Despite the considerable environmental change has been evident in the lake Naivasha in recent years due to

increased human activities (Harper and Mavuti 2004), data records for many of the associated environmental variables were incomplete and collected in an inconsistent manner. An exception was the collection of a time series of monthly lake level data collected between 1970 and 2008 that were used here as a proxy for the environmental change. To identify the patterns in this time series of lake level change, a Loess smoothing procedure was used. Loess is based on a local regression technique in which i least squares regressions are fitted for neighbourhoods centred on a predictor value x_i , where data are weighted as an increasing function of their proximity to x_i . The smoothing parameter determines the neighbourhood size used with values used between 0.5 and 1.0 to identify the general patterns of change in the time series (Lappalainen et al. 2008). Here, values of 0.5 (50% of points to fit the line), 0.75 (75%) and 0.95 (95%) were used so that the major periods of lake level change could be identified between 1970 and 2008. Mean annual lake levels were used subsequently to test the effect of environmental change on the population metrics recorded in the tilapiine fishes.

Tilapiine Population Data

Data on the tilapiine populations were available from two sources; the lake's commercial gillnet fishery that has a legal fish landing size of 18 cm and from annual surveys of multi-mesh gillnets that target fish of below these lengths. These enabled calculation of the metric catch per unit effort (CPUE), which was used as a metric representing the relative abundance of these fishes in the lake (for fish <18 cm and >18 cm according to the method).

The commercial gillnet fishery commenced on the lake in 1959 and was initially based upon *O. leucostictus*, *T. zillii* and largemouth bass *Micropterus salmoides* (Lacépède). However, following their introduction in 1999, *C. carpio* now comprise >90% of all catches (Britton et al. 2007). The commercial gill nets are usually set from the surface and fished on a 24 h cycle, with the fish removed from the nets in the early morning. Catches of fish in the commercial fishery landings were available from 1975 to 2008, although some annual catch totals were missing (1977, 1978 and 1980–1984) and prior to 1985 catches were expressed only as total catch rather than split by species. Notwithstanding, the primary species exploited in this period was *O. leucostictus* and comprised >90% of the catch in most years (Muchiri et al. 1995). Data on annual fishing effort were, however, only available for between 1975 and 1987 (Muchiri et al. 1995) and between 1999 and 2008 (from the Naivasha Fisheries Department). Consequently, the majority of data used from the commercial fishery concentrated on providing analysis between the periods 1975 and 1987 and between 1999 and 2008 as this

allowed focus on the metric CPUE, calculated as total catch of tilapiines in that year (kg)/total fishing effort in that year (the sum of the number of operating boats per month within each year).

The multi-meshed gill net (mesh size 8.5–50 mm) annual surveys only commenced in 1987 but were then completed every year to 2008. Sampling was completed once per year (generally in July) with each sampling period lasting for 12 days when nets were set daily at first light at locations covering the major habitat types (rocky shore, aquatic macrophytes and open water). Unlike the commercial gill nets, these surveys were not completed on a diurnal basis; instead fishing was generally for between 4 and 6 h and provided data collected using a consistent methodology and effort over a 21-year period. Following lifting of the nets, fish were removed, identified, measured (total length L_T , nearest mm) and weighed (nearest g). Their relative abundance by species was calculated using a CPUE index, following the method of Hickley et al. (2002).

Influence of Lake Level, Fishing Effort and Allodiversity on Tilapiine Population Metrics

Initial analyses identified the relationship between annual catches in the commercial fishery and mean annual lake level at time t and time t_{+1} . This time step was tested as a change in lake level in a given year may not impact catches in the commercial fishery until the following year as the fish may not enter the exploitable size range (>18 cm) until then. As annual fishing effort fluctuated considerably over time then subsequent analyses focused on catch, fishing effort and CPUE. These data were tested to determine the relationships of: (i) tilapiine catch and effort in the commercial fishery in the periods 1975–1987 and 1999–2008; (ii) tilapiine CPUE and lake level at time t and t_{+1} in the periods 1975–1987 and 1999–2008 and (iii) changes in allodiversity with introduction of *C. carpio* and the CPUE of each tilapiine species since 2002 (the initial appearance of *C. carpio* in the commercial fishery).

The respective roles of lake level, fishing effort and the recent change in allodiversity (*C. carpio*) on the annual catch of tilapiines were tested using multiple regression analysis. This had to use total catch values rather than CPUE as the latter metric was already adjusted for the effect of fishing effort in its calculation. Tilapiine catch (the dependent variable) was tested against fishing effort (expressed as the total number of boats operating per year), lake level (mean annual water level) and allodiversity (*C. carpio* catch) (all as independent variables). The effects of the independent variables on catch were compared using their standardized beta coefficients (β) and their significance; the variable with the largest β value made the

strongest singular contribution to explaining the dependent variable when the other model variables were controlled. As effort data were not available for the fishery between 1989 and 1998, two separate periods had to be used; 1975–1987 and 1998–2008. When multiple regression was used to test the influence of effort and lake level on tilapiine catch between 1999 and 2008 (to enable comparison with the output using data from 1975 to 1987), the value for total catch omitted the catch of *C. carpio* due to its sudden appearance in 2002 and subsequent increases (Britton et al. 2007). All statistics were completed in SPSS v.14.0 with $\alpha = 0.05$.

RESULTS

Lake Level

There was an overall decline in lake level between 1970 and 2008, from a peak in June 1981 of 1889.7 m.a.s.l. to a low of 1885.6 m.a.s.l. in May 2006 (Fig. 1). Use of Loess smoothed lines confirmed this overall decline. Where 50 and 75% of points were used to fit the smoothed line, these suggested that there were two breaks in the lake level trends; one occurring in 1983 that initiated a period of substantial lake level decline and then in 1990 when this decline became less severe, although it still continued (Fig. 1). Thus, the smoothed lines suggest three periods of lake level in the time series: 1970–1983 where although some fluctuation was evident in lake level there was no overall decline; between 1983 and 1990 where despite brief periods of inundation, the lake level declined substantially; and 1990 to the present where despite fluctuations, the lake level has continued to fall (Fig. 1).

Tilapiine Catches in the Commercial Fishery

Temporal fluctuations have been a feature of the catches of both tilapiine fishes in the lake since fishery records began, but both show a general temporal decline and show that catches in recent years are below their long-term mean annual catch (Fig. 2). Catches of *O. leucostictus* peaked at 1,293,254 kg in 1979 and reduced to 94 kg in 2007; catches of *T. zillii* peaked at 21,278 kg in 1976 and reduced to 21 kg in 2006 (Fig. 2). Catches of *O. leucostictus* were significantly associated with lake level over the period, with higher catch rates obtained from periods of higher lake level (Fig. 2). The most significant relationship between annual mean lake level at time t with *O. leucostictus* total catch was at a time step of t_{+1} , with regression analyses revealing the relationship was non-linear and best described by polynomial regression ($R^2 = 0.91$; $F_{1,25} = 62.2$; $P < 0.001$). In contrast to *O. leucostictus*, the effect of the annual mean

Fig. 1 Temporal relationship of the level of Lake Naivasha (measured as metres above sea level, recorded monthly) between 1970 and the present, where the *solid line* represents the Loess smoothed line and where **a** shows the Loess smoothed line where 50% of points fit the line, **b** shows the Loess smoothed line where 75% of points fit the line and **c** shows the Loess smoothed line where 95% of points fit the line. Mean lake level over the entire period was 1887.5 ± 1.1 m.a.s.l

Fig. 2 **a** Annual catch (kg) of *O. leucostictus* (filled circle) and *C. carpio* (open circle) in relation to mean annual lake level (times) between 1975 and 2008 in the commercial gill net fishery of Lake Naivasha; **b** annual catch (kg) of *T. zillii* (filled circle) and *C. carpio* (open circle) in relation to lake level (times) between 1975 and 2008 in the commercial gill net fishery of Lake Naivasha. The *dashed horizontal line* on both graphs denotes the mean catch of *O. leucostictus* (**a**) and *T. zillii* (**b**) over the study period

lake level on the annual catch of *T. zillii* was not significant at any time step ($R^2 < 0.17$; $P > 0.05$ in all cases). Although insightful, the applicability of using total catch data is limited as it does not account for variation in fishing effort and it was apparent there were considerable fluctuations in annual fishing effort in both study periods (1975–1987 and 1999–2008; Fig. 3). Consequently, CPUE was calculated and used in subsequent tests.

Factors Affecting Tilapiine CPUE of the Commercial Fishery

In the period 1975–1987, there was a significant relationship between annual effort and annual tilapiine catch (linear regression: $R^2 = 0.43$, $F_{1,12} = 7.58$, $P < 0.02$, Fig. 3) but not between tilapiine CPUE and annual mean lake level at time t and t_{+1} (linear regression; time t : $R^2 = 0.03$,

Fig. 3 *Top* Relationship of annual catch of *Oreochromis leucostictus* and total annual fishing effort in Lake Naivasha between 1975 and 1987 (open circle) and between 1999 and 2008 (filled circle); the solid line is the significant linear relationship of the variables between 1974 and 1988. *Bottom* Relationship of mean annual lake level and total annual catch of *Oreochromis leucostictus* at time t_{+1} in Lake Naivasha between 1975 and 1987 (open circle) and between 1999 and 2008 (filled circle); the dashed line is the significant relationship described by polynomial regression of the variables between 1999 and 2008. Refer to text for results of the statistical tests

$F_{1,12} = 0.36$, $P > 0.05$; time t_{+1} : $R^2 = 0.02$, $F_{1,12} = 0.24$, $P > 0.05$, Fig. 3). In contrast, between 1999 and 2008, the relationship between fishing effort and total tilapiine catch was not significant (linear regression: $R^2 = 0.43$, $F_{1,7} = 0.04$, $P > 0.05$, Fig. 3) but was between annual mean lake level and tilapiine catch per unit at both time steps and was best described by polynomial regression linear regression (time t : $R^2 = 0.81$, $F_{1,7} = 9.1$, $P < 0.05$; time t_{+1} : $R^2 = 0.91$; $F_{1,7} = 21.6$, $P < 0.01$, Fig. 3). The relationship between CPUE of *C. carpio* and the CPUE of the tilapiines was best described by a power curve where increases in *C. carpio* CPUE were related to CPUE reductions in the tilapiines (Fig. 4). This relationship between *C. carpio* and *T. zillii* was significant ($R^2 = 0.86$, $F_{1,6} = 35.97$, $P < 0.001$; Fig. 4) but was not significant between *C. carpio* and *O. leucostictus* ($R^2 = 0.36$, $F_{1,6} = 3.38$, $P > 0.05$; Fig. 4).

Fig. 4 Relationship between the CPUE of *Cyprinus carpio* with CPUE of *Oreochromis leucostictus* (filled triangle) and *Tilapia zillii* (open triangle) in Lake Naivasha between 2003 and 2009. The solid line describes the power regression relationship for *O. leucostictus* and dashed line the power regression relationship for *T. zillii*

Multiple regression revealed fishing effort explained most of the catch variation between 1975 and 1988, with the effect of lake level not significant (Table 1). Between 1999 and 2008, lake level explained most of the annual catch variation and was the only significant variable in the model (Table 1). Thus, whereas catches between 1975 and 1988 were a function of fishing effort, this was no longer the case between 1999 and 2008 when tilapiine catches were solely a function of lake level.

Factors Affecting Tilapiine CPUE of the Multi-mesh Gillnets

In the period 1987–2008, the CPUE of both tilapiine fishes in the multi-mesh gill nets fluctuated between years, with levels recorded since 2001 generally depressed from levels recorded before then (Fig. 5). This recent decrease in their catch rates reflects the trends observed in the commercial fishery and, indeed, the relationship between CPUE of *O. leucostictus* in the multi-mesh gill nets, and the commercial fishery at time t and time t_{+1} was significant and best described by polynomial regression (t : $R^2 = 0.85$, $F_{1,7} = 7.9$, $P < 0.05$; time t_{+1} : $R^2 = 0.88$, $F_{1,6} = 8.2$, $P < 0.05$, Fig. 6). This was also the case for *T. zillii* at time t ($R^2 = 0.94$, $F_{1,7} = 10.1$, $P < 0.05$, Fig. 6) but not at time t_{+1} ($R^2 = 0.32$, $F_{1,6} = 1.45$, $P > 0.05$, Fig. 6). Given the effect of lake level on catch per unit of the tilapiines in the commercial fishery between 1999 and 2008 (Fig. 3), CPUE of the multi-mesh gillnets was tested against lake level in the same period (Fig. 7). This revealed that the effect of lake level on CPUE at time t was significant for both

Table 1 Output of multiple regression analysis on the influence of fishing effort (f), lake level (at a time-step of minus 1 year, H_{t-1}) and common carp CPUE (W_c) on the annual catch of tilapiine fishes in

Lake Naivasha in the two time periods where fishing effort data were available, 1975–1987 and 1999–2008

Variable	β (standardised)	p
Period: 1975–1987		
Regression equation: $W_T = -14413993 + 296.4f + 76402.4H_{t-1}$, significance of model: $R^2 = 0.55$; $F_{2,12} = 7.25$, $P < 0.01$		
Fishing effort	0.51	0.03
Lake level	0.41	0.07
Common carp	n/a	
Period: 1999–2008		
Regression equation: $W_T = -331083371 + 17.8f + 175531.9H_{t-1}$, significance of model: $R^2 = 0.92$; $F_{3,5} = 18.49$, $P < 0.01$		
Fishing effort	0.11	0.55
Lake level	1.10	0.03
Common carp	0.17	0.74

Fig. 5 **a** CPUE of *Oreochromis leucostictus* in the multi-mesh gill nets between 1987 and 2008; **b** CPUE of *Tilapia zillii* in the multi-mesh gill nets between 1987 and 2008. On both graphs, the annual values of CPUE is expressed as its difference from the mean CPUE over the entire period

species (*O. leucostictus*: $R^2 = 0.51$, $F_{1,8} = 8.46$, $P < 0.02$; *T. zillii*: $R^2 = 0.44$, $F_{1,8} = 6.40$, $P < 0.04$; Fig. 7) but not for CPUE at time t_{+1} (*O. leucostictus*: $R^2 = 0.17$,

$F_{1,8} = 1.48$, $P > 0.05$; *T. zillii*: $R^2 = 0.23$, $F_{1,8} = 2.06$, $P > 0.05$; Fig. 7).

DISCUSSION

Changes in the water level of Lake Naivasha between 1970 and 2008 have declined substantially with analysis revealing three distinct periods of lake level, ranging from a period of relative stability prior to 1983 to two distinct periods of decline since then. The change in the water level of the lake has been a significant influence on the two CPUE indices (relative abundance) of both tilapiine fishes since at least 1999. Years of high water events following inundation resulted in significantly increased relative abundance of fish <18 cm in the same year and >18 cm in the same and following year. Significantly, this decline in lake level has resulted in catches in the commercial fishery no longer being a function of fishing effort; i.e. today, no matter what fishing effort is applied, tilapiine catches are unlikely to increase unless it happens to be coincident with a period of water inundation. The effect of the recent change in allodiversity, the introduction and rapid establishment of *C. carpio*, was not a significant influence on *O. leucostictus* relative abundance, but was for *T. zillii*. It should be noted, however, that the testing of these data was reliant on limited data (2002–2008) and so the low number of degrees of freedom may have impacted the significance of the output for *O. leucostictus*. Although the causal mechanism of *C. carpio* impacting tilapiines remains unclear, it may be that benthic foraging of *C. carpio* interferes with some aspects of tilapiine behaviour, such as their reproduction and foraging (Britton et al. 2007). However, this requires further testing and remains speculative. In combination, the outputs of this study suggest that: (i) the receding water levels of the lake that are

Fig. 6 Relationship of CPUE of *Oreochromis leucostictus* (a, b) and *Tilapia zillii* (c, d) in the multi-mesh gill nets at time t and CPUE in the commercial fishery at time t (a, c) and t_{+1} (b, d). Solid lines denote the significant relationship between the variables according to polynomial regression

associated with human activities in the catchment, such as high levels of abstraction (Becht and Harper 2002), have had a direct, measureable and detrimental effect on the tilapiine populations and their fishery catches since at least 1999 and (ii) fishery management models, such as maximum sustainable yield, that are based on fishing effort and catch, and as calculated by Muchiri et al. (1995) for the Lake Naivasha tilapiine fishery, may no longer be valid for the lake in its current state. Indeed, the fish dominating the fishery today, *C. carpio*, is a species well suited to foraging in highly degraded, freshwater habitats (Koehn 2004; Britton et al. 2007).

Lake level was able to explain much of the recent variation in the relative population abundance of the tilapiines, but it does not explain the underlying ecological and biological mechanisms involved. In studies where the inundation of the margins of African lakes by flood waters has occurred, the combination of decaying submerged terrestrial vegetation and the increased fluvial input of nutrients has resulted in increased production of detritus, phytoplankton, periphyton and zooplankton (Weyl 2007), with phytoplankton production also enhanced by the decreased turbidity (Guenther and Bozelli 2004). In response to the inundation and increased food resources, production of the tilapia species increases (McKaye et al. 1995; Bwanika et al. 2004; Njiru et al. 2004; Peterson et al. 2004, 2005; Britton et al. 2009). Increased growth rate and recruitment success following flood events have also been generally observed in cichlid populations (Dudley 1975,

1979; De Silva 1985; Weyl 2007) and appears evident in Lake Naivasha (Britton and Harper 2008). Indeed, lake inundation is generally considered as a beneficial process that increases fish production in the capture fisheries of many African lake that are reliant on tilapia stocks (Jul-Larsen et al. 2003; Kolding and van Zweiten 2006; Britton et al. 2009). Thus, the ecological mechanisms that were associated with increased water level and the subsequently increased fish catches in Lake Naivasha were likely to be associated with the increased nutrient inputs and food availability that resulted from the inundation of lake margins. This was likely to have enabled the fishes to increase their growth rates and reproductive fitness, resulting in enhanced juvenile survival, recruitment and production.

The difficulty of explaining the mechanisms involved in the population dynamics and changing abundances of the tilapiine fishes highlights the problematic issues associated with measuring long-term, temporal ecological changes in large equatorial lakes in the developing world such as Lake Naivasha. The non-seasonal aspects to the growth and reproduction of the fishes (e.g. Britton et al. 2007; Britton and Harper 2008) make it difficult to use these particular metrics as an indicator of change, particularly over the time periods used in this study (1970–2008). Consequently, the metrics of fishery catch statistics and CPUE from research gill nets remain the most collected and easily interpretable metrics on these fishes. Thus, it is recommended these should continue to be adopted as indicators of tilapiine population status in Lake Naivasha in relation to the

Fig. 7 **a** Relationship of CPUE of *Oreochromis leucostictus* at time t (filled circle) and time $t+1$ (open circle) against the difference between the annual lake level and the mean lake level between 1999 and 2008. **b** Relationship of CPUE of *Tilapia zillii* at time t (filled circle) and time $t+1$ (open circle) against the difference between the annual lake level and the mean lake level between 1999 and 2008. The solid lines on both graphs show the significant relationship described by linear regression for time t only. Refer to text for test results

changing environmental conditions still being encountered. Similarly, if continued long-term monitoring of the status of Lake Naivasha is to be continued, then the metrics of lake level and fishery catch statistics (catch and fishing effort of tilapiine fishes and *C. carpio*) represent data that are efficient and simple to collect, and build upon large, existing data sets. Indeed, lake level could then be used as an indicator of environmental change in accordance with fishery catches of *O. leucostictus* being used as an indicator of ecological change, enabling more in-depth study of other metrics when resources allow.

To promote the restoration of the Lake Naivasha fishery, Hickley et al. (2004) suggested an ecohydrological approach (Zalewski et al. 1997; Harper and Mavuti 2004), commencing with protection and recovery of the lake's natural fringe of papyrus to reduce eutrophication, facilitate the transition to a clear water state and promote macrophyte growth. However, given the profound

influence of lake level on the relative abundance indices of the tilapiine fishes, for the restoration of their fishery we argue that enhancing lake levels would have a greater positive effect and would then augment papyrus regeneration anyway. Whilst the tilapiine populations have been subject to natural variations in water levels since their introduction, increased human activities in the catchment has decreased the relative amount of water reaching the lake in the recent years thereby increasing the influence of low rains on lake level (Becht and Harper 2002). The reduction of water recharge into the lake is exacerbated by heavy abstraction from the lake itself to support horticulture and geothermal energy generation (Harper and Mavuti 2004; Hickley et al. 2004; Britton et al. 2010). Thus, improved water management schemes that aim to maximize the proportion of river water reaching the lake, such as increased regulation of abstraction and irrigation, would increase and consequently help maintain lake levels and provide considerable ecological benefits for the tilapiine fishes. Steps towards this goal have been undertaken, with schemes developed under the new (2002) Water Act by the Lake Naivasha Water Resource Users Association (LaNaWRUA) to regulate water abstraction and implement a catchment management plan that seeks the sustainable use of water. However, this has yet to prevent further reductions in lake level as abstraction limits are still more voluntary than regulatory and so consequently, the ability of the tilapiine populations and their fishery to persist in the face of continued environmental change appears uncertain.

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