# Fish condition in introduced tilapias of Ugandan crater lakes in relation to deforestation and fishing pressure 

Jackson Efitre • Lauren J. Chapman • Debra J. Murie

Received: 22 June 2007 / Accepted: 2 February 2009
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#### Abstract

This study identifies environmental predictors of the condition of two introduced tilapia species (Oreochromis leucostictus and Tilapia zillii) that are known to have divergent trophic niches (planktivore and herbivore, respectively) in 17 crater lakes in western Uganda. We asked whether fish condition differs among lakes characterized by differences in fishing pressure and catchment deforestation; and we related relative condition factor to gradients of environmental variation across lakes. Lakes characterized by severe catchment deforestation tended to be lakes with high fishing pressure, so it was difficult to


[^0]explore independent and interactive effects. However, mean relative condition factor was higher in populations with high fishing pressure compared to populations with low fishing pressure for both $O$. leucostictus and T. zillii. The condition of $O$. leucostictus populations was higher in lakes with severely deforested catchments; but mean relative condition factor of $T$. zillii did not differ between deforestation categories. Principal components analysis (PCA) was used to describe the major environmental gradients of variation among the lakes; and PCA factor scores were regressed against relative fish condition. The association between fish condition and environmental gradients was stronger for O. leucostictus than for T. zillii. For O. leucostictus, fish condition was related to $\mathrm{PC1}$ ( $43 \%$ of the variance) and factors that loaded most heavily included Chl-a, water transparency, lake area and depth, suggesting higher condition in lakes characterized by higher primary productivity and smaller size. For T. zillii, PC3 (11\%) was the only axis related to fish condition; and factors that loaded most heavily included lake area (positive), and conductivity and total nitrogen (negative). Some of the larger lakes are characterized by higher availability of macrophytes that may positively affect the food base for $T$. zillii.

Keywords Human disturbance • Fishing pressure • Environmental predictors • Primary productivity Oreochromis leucostictus • Tilapia zillii • East Africa • Length-weight relationships

## Introduction

Fish condition, defined as the robustness or wellbeing of an individual fish (Le Cren 1951; Bulow et al. 1981; Blackwell et al. 2000), is an essential component of fishery biology used to assess the general health of populations (Gulland 1983; Sparre et al. 1989). Condition can vary dramatically both within and among populations; and it is therefore critical to identify environmental predictors of this variation to optimize fishery production. Two types of condition indices are generally used by fisheries scientists as surrogates of fish health and growth (Wootton 1990; Pauly 1993; Petrakis and Stergiou 1995; Binohlan and Pauly 1998). The first are somatic indices such as calorific and proximate (e.g., lipid content) indices (Brown and Murphy 1991), and liver-, fat-, and gonado-somatic indices (Adams et al. 1982). The second group are length-weight based indices such as Fulton's condition factor (Le Cren 1951; Ricker 1975), relative condition factor (Le Cren 1951), and relative weight (Wege and Anderson 1978). Length-weight based condition indices are the most frequently applied because the data are relatively easy, efficient, and cost-effective to collect. Length-weight relationships have thus been used extensively in fisheries biology to convert growth-in-length to growth-in-weight equations for use in stock assessments (Oscoz et al. 2005) and to provide an index of condition (Le Cren 1951; Bolger and Connolly 1989).

Relationships between fish condition and population structure, fecundity, life history adaptations, environmental conditions, and/or management actions have been studied for a variety of fish species in temperate regions (e.g., Brown and Murphy 1991; Blackwell et al. 2000). Studies in tropical fisheries are far less prevalent, but there is a growing body of literature on the condition of tilapiine fishes in the larger tropical freshwater lakes and reservoirs that suggest great variation in tilapia condition within and among systems (Welcomme 1970; Fryer and Iles 1972; Siddique 1977; Lowe-McConnell 1982). Given the ecological and commercial importance of tilapiine fishes in tropical fresh waters and in aquaculture systems, an understanding of environmental predictors of tilapia condition is becoming increasingly important. In particular, we need to more fully explore the impact of harvest on tilapia
condition that may be regulated through densitydependent processes, as well as effects of other anthropogenic drivers. Comparative study of tilapia condition across gradients of anthropogenic disturbance (e.g., fishing pressure, catchment deforestation) and other environmental factors offers the opportunity to identify significant predictors of fish condition.

In western Uganda, three tilapia species, Oreochromis niloticus, Oreochromis leucostictus, and Tilapia zillii, were introduced into a large number (approx. 89) of volcanic crater lakes in the 1940s, and subsequent years, to increase available protein to the local communities. Currently, many of these lakes seem to be producing "stunted" tilapia populations, causes of which remain unknown but may reflect resource limitations associated with the crater lake environment and/or low mortality leading to high levels of intraspecific competition. There is great variation in fishing pressure among the lakes from almost no fishing, to individual based hook-and-line fishing, to small-scale commercial gillnet fisheries run by communities around these lakes. In addition, many of the crater lakes lie outside protected areas and are increasingly threatened with deforestation of the crater rims due to the rapidly expanding human populations. However, information on the effects of anthropogenic disturbances and fishing pressure on the biology of tilapiine species in these lakes is non-existent, challenging the development of effective management goals for fish in these very abundant lakes. The aim of the present study was to explore the effects of anthropogenic factors (e.g., deforestation and fishing) on the condition of two introduced species ( $O$. leucostictus and T. zillii) in 17 crater lakes in western Uganda with varying extent of catchment deforestation and fishing pressure. We selected two tilapia species that are widely introduced in these lakes and have divergent trophic niches as adults (planktivore and herbivore, respectively), because we anticipated that they might respond differently to the anthropogenic disturbances. We ask whether fish condition differs significantly among lakes characterized by differences in fishing pressure and catchment deforestation; and we relate relative condition factor to gradients of environmental variation across lakes for each species.

## Methods and materials

Study area
The study was conducted in the Kasenda cluster of crater lakes of western Uganda ( $0^{\circ} 23^{\prime}-0^{\circ} 33^{\prime} \mathrm{N}, 30^{\circ}$ $\left.10^{\prime}-30^{\circ} 20^{\prime} \mathrm{E}\right)$ at an altitude of 925 m to 1520 m (Melack 1976; Fig. 1). Most of the Kasenda cluster of crater lakes are small, and the 17 lakes used in this study had surface areas ranging from 2 ha (Lake Nyanswiga) to 50 ha (Lake Ntanda), maximum depth ( $z_{\mathrm{m}}$ ) ranging from 5 m (Lake Kifuruka) to 259 m (Lake Ntanda), and mean depth ranging from 2.9 m (Lake Kifuruka) to 59.7 m (Lake Rukwanzi). In addition, the lakes also differ in their level of fishing pressure and the extent of deforestation of their catchments. Owing to their volcanic origin, most of the lakes have steep sides, with little littoral vegetation except a few shallow lakes or shallower parts of the deep lakes that have a
diversity of aquatic macrophytes such as Nymphaea spp., Ceratophyllum spp., and Potamogeton spp. (Kizito et al. 1993). Rainfall is bimodal, with two wet seasons from March-May and SeptemberNovember, with 1702 mm of total rainfall received annually (1990-2005). Between 1990 and 2004, the mean daily minimum temperature was $14.9^{\circ} \mathrm{C}$, and the mean daily maximum temperature was $20.2^{\circ} \mathrm{C}$. Baseline environmental data existed for a large number of the crater lakes (Kizito et al. 1993; Chapman and Chapman unpublished data). The lakes were therefore selected to cover a large range of areas with varying levels and types of anthropogenic disturbance, and to represent as broad an environmental gradient as possible. However, lakes with severe catchment deforestation were often characterized by high fishing pressure, probably due to accessibility, so we were unable to cross all levels of catchment deforestation with all levels of fishing.

Fig. 1 Location of the Kasenda cluster of crater lakes in western Uganda ( $0^{\circ} 23^{\prime}-0^{\circ} 33^{\prime} \mathrm{N}, 30^{\circ} 10^{\prime}-30^{\circ}$ $20^{\prime} \mathrm{E}$ ) where Oreochromis leucostictus and Tilapia zillii were sampled along with environmental variables from July 2004 to July 2005


## Environmental data

Environmental parameters were measured simultaneously with fish collections and they showed the same tendencies obtained in other works performed previously, confirming their adequacy to relate with biological data. The physical and chemical characteristics determined in each lake included: lake area, maximum depth, mean depth, vertical profiles of dissolved oxygen (DO) concentration and water temperature, pH , conductivity (corrected to $25^{\circ} \mathrm{C}$ ), water transparency, chlorophyll a (Chl-a) concentration, total phosphorus (TP), and total nitrogen (TN). Water temperature and dissolved oxygen concentration were determined in situ with a YSI oxygen/ temperature meter. Conductivity and pH were measured using a YSI conductivity meter and an OAKTON pH Testr 1, respectively. Water transparency was estimated with a $20-\mathrm{cm}$ Secchi disk. Chlorophyll a was determined using a spectrophotometric technique. Total phosphorus and total nitrogen were determined using standard limnological techniques following APHA (1988). Measurement of all the environmental parameters was done concurrently with sampling of the fish populations in each lake.

Fishing and deforestation characterization

Lakes were grouped into three categories of fishing pressure ("low", "medium", and "high") based on the average number of fishermen observed during a 6-day sampling period in each lake, and presence or absence of gillnets in a lake. The lakes with "low" fishing effort either had no fishing pressure or a small number $(<20)$ of hook-and-line fishermen. Lakes with "medium" fishing had a large number (30-45) of hook-andline fishermen and occasionally gillnets. The lakes with "high" fishing pressure had an established gillnet fishery. Large predatory fish species are absent in most of the lakes except Lake Kasenda where the catfish Clarias gariepinus was recently introduced. In addition, Pomeroy and Seavy (2003), in a recent survey of the crater lakes, found low populations of waterfowl (including fish-eating birds, mean number per lake=14). We therefore assumed that fishing is the main source of predation in these lakes and that mortality caused by the fish-eating birds may be minimal. Fishing pressure at each lake was determined at the time of sampling the fish population in
each lake. Though the lakes were sampled at different times of the year (over 1-year period), there were no significant changes in fishing pressure in each lake during the entire sampling period. We also grouped the lakes using a modification of the deforestation categories developed by Pomeroy and Seavy (2003), where minimal deforestation has $50-100 \%$ of the lake area still forested, moderate deforestation has $25-49 \%$ forested, severe deforestation has only small forest patches or scattered trees left ( $<25 \%$ forested), and complete deforestation has no forest trees along the crater rim. Due to the low number of lakes in some categories, the minimal and moderate ("moderate") and severe and complete ("severe") deforestation categories were combined for the statistical analyses.

Fish sample collection
A sample of 2116 O. leucostictus and 2697 T. zillii were included in the calculation of relative condition factor. The fish were collected between July 2004 and July 2005 from 17 crater lakes. Each lake was sampled once over a 5-6 day period. Significant effort was made to sample fish in different size classes by using the following fishing gears: 1) two experimental monofilament gillnets $(60-\mathrm{m}$ long and $1.0-\mathrm{m}$ deep) with stretched mesh sizes of 25.4 mm , $50.8 \mathrm{~mm}, 76.2 \mathrm{~mm}$, and 101.6 mm ; 2) gillnets used by artisanal fishermen (1800-m long) comprised of mesh sizes $25.4 \mathrm{~mm}, 50.8 \mathrm{~mm}, 63.5 \mathrm{~mm}$, and 76.2 mm ; and 3) 20 metal minnow traps ( $450-\mathrm{mm}$ long and $7-\mathrm{mm}$ square wire mesh). The fishing gears were set between 14:00-16:00 hr and pulled the following morning between 08:00-10:00 hr. To obtain samples representative of fish populations in each lake, fishing gears were set in all major habitats, including open water, at the edge of shoreline vegetation, and on rocky shores. Individual fish were measured to the nearest 1 mm for both total (TL) and standard (SL) length, and weighed to the nearest 0.1 g for both total weight (WT) and weight with the gonads removed (DW).

Calculation of relative condition $\left(\mathrm{K}_{\mathrm{n}}\right)$

To facilitate comparisons among lakes and for the development of predictive models of fish condition, we calculated the relative condition factor of fish,
which is the ratio of observed individual fish weight to expected weight of an individual of a given length, using the formula: $\mathrm{K}_{\mathrm{n}}=\mathrm{W}_{\mathrm{i}} / \mathrm{aL}_{\mathrm{i}}^{\mathrm{b}}$ (Le Cren 1951); where $W_{i}$ is observed individual fish weight, $L_{i}$ is observed individual fish total length, and a and b are species-specific constants. These regression constants were obtained from the regional length-weight relationship ( $\mathrm{W}=\mathrm{aL}^{\mathrm{b}}$ ) derived by pooling data for all lakes for each species separately. Length and weight data were log-transformed and the resulting linear relationships fitted by least square regression using weight as the dependent variable. To minimize error arising from seasonal fluctuations in body weight due to reproduction, we used fish weight devoid of gonads for calculating relative condition factor. It should be noted that in these lakes we have found all gonad stages present throughout the year; although there may be a modest peak in reproduction in the rainy seasons. However, we attempted to sample during both the wet and dry season for each fishing/ deforestation category to minimize any potential bias driven by season.

A minimum of 30 individuals per lake was considered acceptable for computing the relative condition factor, but sample size (n) varied from 49 fish (Lake Marusi) to 317 fish (Lake Mwamba) for O. leucostictus; and from 63 fish (Lake Wakenzi) to 341 (Lake Mwegenywa) for T. zillii. To compare relative condition factor across lakes within each species, we excluded very small fish; this resulted in only a small percentage ( $8 \%$ ) of fish being removed from the analyses. We excluded fish less than 80 mm TL for O. leucostictus and less than 68 mm for Tilapia zillii. This provided good overlap in size across populations within each species. For $O$. leucostictus, fish between $80-340 \mathrm{~mm}$ TL were included in the inter-lake analyses, and a size range of $68-287 \mathrm{~mm}$ TL was used in the analysis of $T$. zillii relative condition. Not all lakes contained both species, and relative condition factor was determined in 13 lakes for $O$. leucostictus and 13 lakes for T. zillii.

Statistical analyses
ANCOVA was used to detect an overall difference in the adjusted mean body mass of the two tilapia species based on the bilogarithmic weight-length regressions. The mean relative condition of fish in each lake was computed to explore relationships
between environmental variables and fish condition. One-way ANOVA was used to test for differences in mean relative condition of each fish species in lakes exposed to different fishing pressures (high, medium, and low) and different levels of catchment deforestation (moderate versus severe). We were unable to run a two-way ANOVA because of missing categories of deforestation-fishing pressure combinations. The Scheffé post-hoc test was used for multiple comparisons.

To detect important environmental correlates of fish condition, principal components analysis (PCA) was used to describe the major environmental gradients of variation among the lakes. Only principal components (PCs) with Eigenvalues greater than 1 were retained for interpretation. The factor scores in PCA were saved and used as independent variables in a linear regression analysis for relative fish condition. We also used the PCA factor scores to plot the relationship between fish condition and PCA scores for axes that were significant predictors of fish condition; categorization by deforestation category and fishing pressure on the plots was used to infer relative importance of these stressors. Since the lakes were sampled at different times of the year, correlation analysis was used to test for relationships between rainfall (representing wet and dry seasons) and relative condition of $O$. leucostictus and $T$. zillii across the different lakes. Analyses were performed with Fishery Analysis and Simulation Tools software (FAST version 2.0) and SPSS for Windows (version 12.0).

## Results

Length-weight relationships and relative condition
The size of the two tilapia species captured ranged from $37-340 \mathrm{~mm}$ TL and 7-612 g DW for $O$. leucostictus (Table 1) and $60-287 \mathrm{~mm}$ TL and $5-418 \mathrm{~g}$ DW for T. zillii (Table 2). The regional relationship between mass and length for each species, derived by pooling data across all lakes for each species, was significant (both species, $p<0.001$, Fig. 2a, b). The length-weight allometry between the two species was also significantly different (ANCOVA, intercepts; $F=513.4$, $p<0.0001$ ), with $T$. zillii being on average heavier at a given length than $O$. leucostictus.

Table 1 Lake catchment deforestation levels, fishing pressure, range in total length and degonaded weight, and length-weight regressions ( $\mathrm{W}=\mathrm{aL}^{\mathrm{b}}$ ) for Oreochromis leucostictus from 13 crater

| Lake | Deforestation | Fishing <br> pressure | Sample <br> size $(\mathrm{n})$ | Mean <br> total length <br> $(\mathrm{mm})$ | Range in <br> total length <br> $(\mathrm{mm})$ | Range in <br> degonaded <br> weight $(\mathrm{g})$ | Log $_{10} \mathrm{a}$ | b | $\mathrm{r}^{2}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Wankenzi | Severe | High | 181 | 143 | $113-172$ | $27-86$ | -3.59 | 2.5 | 0.90 |
| Mwamba | Severe | High | 317 | 149 | $106-177(46-177)$ | $22-88(2-88)$ | -3.82 | 2.6 | 0.88 |
| Kanyango | Severe | High | 278 | 142 | $91-210(65-210)$ | $13-160(5-160)$ | -3.88 | 2.6 | 0.85 |
| Lugembe | Severe | High | 285 | 143 | $89-205$ | $12-163$ | -3.98 | 2.6 | 0.87 |
| Murigarime | Severe | High | 114 | 140 | $80-340(70-340)$ | $8-612(5-612)$ | -4.81 | 3.0 | 0.98 |
| Lyantonde | Severe | Medium | 157 | 148 | $87-188$ | $13-115$ | -3.54 | 2.5 | 0.90 |
| Marusi | Severe | Medium | 49 | 155 | $80-275(78-275)$ | $8-399(7-399)$ | -4.52 | 2.8 | 0.97 |
| Wandakara | Severe | Medium | 115 | 143 | $118-238$ | $28-230$ | -4.65 | 2.9 | 0.90 |
| Nyinabulitwa | Moderate | Medium | 171 | 154 | $93-340(37-340)$ | $13-420(5-420)$ | -4.52 | 2.9 | 0.93 |
| Nkuruba | Moderate | Low | 126 | 161 | $102-262$ | $18-281$ | -3.72 | 2.5 | 0.90 |
| Ntanda | Moderate | Low | 99 | 144 | $85-160(47-160)$ | $7-63(5-63)$ | -3.89 | 2.6 | 0.92 |
| Kerere | Moderate | Low | 94 | 137 | $80-235(62-235)$ | $7-207(4-207)$ | -4.58 | 2.9 | 0.97 |
| Kasenda | Moderate | Low | 130 | 162 | $80-290$ | $7-411$ | -4.65 | 3.0 | 0.97 |

The reported sample size, mean, and range represent the fish used in the condition analyses. The bracketed range includes some small fish that were captured in a few of the lakes to improve overlap in size ranges across lakes, but not included in our condition analyses

Table 2 Lake catchment deforestation levels, fishing pressure, range in total length and degonaded weight, and length-weight regressions $\left(\mathrm{W}=\mathrm{aL}^{\mathrm{b}}\right)$ for Tilapia zillii populations from 13 crater
lakes in western Uganda, where $\mathrm{b}=$ slope of regression and $\log _{10} \mathrm{a}=$ intercept of regression

| Lake | Deforestation | Fishing <br> pressure | Sample <br> size (n) | Mean <br> total length <br> $(\mathrm{mm})$ | Range in <br> total length <br> $(\mathrm{mm})$ | Range in <br> degonaded <br> weight $(\mathrm{g})$ | Log $_{10}$ a | b | $\mathrm{r}^{2}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Kanyango | Severe | High | 160 | 124 | $78-197$ | $9-134$ | -4.87 | 2.8 | 0.95 |
| Lugembe | Severe | High | 206 | 149 | $77-265$ | $8-300$ | -4.33 | 2.8 | 0.98 |
| Wankenzi | Severe | High | 63 | 124 | $73-253$ | $7-297$ | -4.45 | 2.9 | 0.97 |
| Kifuruka | Severe | High | 265 | 137 | $69-243$ | $5-278$ | -4.66 | 3.0 | 0.97 |
| Lyantonde | Severe | Medium | 234 | 129 | $68-211$ | $5-163$ | -4.72 | 3.0 | 0.98 |
| Wandakara | Severe | Medium | 187 | 122 | $73-234$ | $7-226$ | -4.80 | 3.0 | 0.99 |
| Mwegenywa | Severe | Medium | 341 | 140 | $71-233(66-233)$ | $6-235(4-235)$ | -4.99 | 3.1 | 0.97 |
| Rukwanzi | Severe | Low | 144 | 147 | $75-287$ | $7-418$ | -4.78 | 3.0 | 0.99 |
| Nyinabulitwa | Moderate | Medium | 234 | 125 | $70-272$ | $6-353$ | -4.98 | 3.1 | 0.99 |
| Nyanswiga | Moderate | Low | 273 | 148 | $68-270(60-270)$ | $6-290(6-90)$ | -4.33 | 2.8 | 0.99 |
| Nkuruba | Moderate | Low | 193 | 131 | $68-176$ | $6-384$ | -4.71 | 3.0 | 0.99 |
| Kasenda | Moderate | Low | 112 | 120 | $75-204$ | $7-151$ | -4.98 | 3.0 | 0.98 |
| Ntanda | Moderate | Low | 285 | 130 | $76-222(63-222)$ | $8-180(6-180)$ | -4.98 | 3.1 | 0.98 |

The reported sample size, mean, and range represent the fish used in the condition analyses. The bracketed range includes some small fish that were captured in a few of the lakes to improve overlap in size ranges across lakes, but not included in our condition analyses


Fig. 2 Regional relationships between degonaded weight (g) and total length (mm) for Oreochromis leucostictus (a) and for Tilapia zillii (b) derived by pooling data from 13 crater lakes in western Uganda

Fishing pressure, catchment deforestation, and condition factor

Mean relative condition varied among lakes with different fishing pressure for both species ( $O$. leucostictus: $\mathrm{F}_{2,13}=5.05, p=0.031 ;$ T. zillii: $\mathrm{F}_{2,13}=6.138, p=$ 0.018). Oreochromis leucostictus in lakes with high fishing pressure had a higher relative condition compared to lakes with low and medium fishing pressure (Scheffé: $p<0.05$, Fig. 3), which did not differ significantly from each other (Scheffé: medium versus low, $p=0.80$ ). Tilapia zillii in lakes with high fishing pressure also had a higher relative condition compared to lakes with low fishing pressure, but did not differ from lakes with medium fishing pressure (Scheffé: high versus low, $p=0.02$; Fig. 3).

Mean condition of $O$. leucostictus also differed between lakes with moderately and severely deforested catchments ( $\mathrm{F}_{1,13}=4.74, p=0.05$ ), with fish exhibiting a higher condition than average in lakes with severely deforested catchments and conversely a lower condition than average in lakes with moderately


Fig. 3 Mean relative condition of Oreochromis leucostictus and Tilapia zillii in crater lakes of western Uganda exposed to high, medium, and low fishing pressure. Vertical bars represent $\pm 1$ standard error. Different letters above the fishing pressure categories indicate a significant difference at $p \leq 0.05$
deforested catchments (Fig. 4). However, mean relative condition of $T$. zillii did not differ between lakes with severely and moderately deforested catchments ( $\mathrm{F}_{1,13}=2.45, p=0.15$; Fig. 4).

Environmental characters and relative condition factor
For lakes with populations of Oreochromis leucostictus, PCA yielded three principle components with Eigenvalues greater than 1 that explained $80.6 \%$ of the variance in the environmental data. Variable loadings of the first three principle components are given in Table 3a. The first three PCA axes accounted for $42.9 \%, 23.3 \%$, and $14.4 \%$ of the variance, respectively. Relative condition of $O$. leucostictus


Fig. 4 Mean relative condition of Oreochromis leucostictus and Tilapia zillii in crater lakes of western Uganda exposed to moderate and severe catchment deforestation levels. Vertical bars represent $\pm 1$ standard error. Different letters above the deforestation levels indicate a significant difference at $p \leq 0.05$

Table 3 Results of principal component analysis (PCA) describing the major environmental gradients of variation in lakes harboring (a) Oreochromis leucosticus and (b) Tilapia zillii

| Variable (Log 10) | Component |  |  |  |  |
| :--- | ---: | ---: | ---: | :---: | :---: |
|  | 2 |  |  |  | 3 |
|  |  |  |  |  |  |
| a) Oreochromis leucostictus lakes |  |  |  |  |  |
| Chlorophyll a | $\mathbf{0 . 8 9 9}$ | 0.259 | 0.125 |  |  |
| Water transparency (Secchi depth) | $\mathbf{- 0 . 8 1 9}$ | -0.493 | -0.058 |  |  |
| Dissolved oxygen | 0.301 | $\mathbf{0 . 8 2 1}$ | 0.156 |  |  |
| pH | 0.066 | 0.193 | $\mathbf{0 . 8 8 7}$ |  |  |
| Conductivity | $\mathbf{0 . 5 9 2}$ | 0.378 | -0.367 |  |  |
| Total phosphorus | 0.389 | $\mathbf{- 0 . 7 2 6}$ | 0.488 |  |  |
| Total nitrogen | $\mathbf{0 . 6 7 3}$ | -0.367 | -0.045 |  |  |
| Lake area | $\mathbf{- 0 . 7 6 6}$ | 0.413 | 0.299 |  |  |
| Maximum depth | $\mathbf{- 0 . 8 6 4}$ | 0.317 | -0.025 |  |  |
| Total variance explained (\%) | 42.914 | 23.310 | 14.382 |  |  |
| b) Tilapia zillii lakes |  |  |  |  |  |
| Chlorophyll a | $\mathbf{0 . 8 6 5}$ | 0.282 | 0.360 |  |  |
| Water transparency (Secchi depth) | $-\mathbf{0 . 8 8 9}$ | -0.290 | -0.267 |  |  |
| Dissolved oxygen | 0.154 | $\mathbf{0 . 8 5 3}$ | 0.242 |  |  |
| pH | -0.007 | $\mathbf{0 . 8 9 0}$ | -0.178 |  |  |
| Conductivity | $\mathbf{0 . 5 8 4}$ | 0.239 | -0.466 |  |  |
| Total phosphorus | $\mathbf{0 . 6 2 6}$ | -0.584 | 0.370 |  |  |
| Total nitrogen | $\mathbf{0 . 6 0 2}$ | 0.268 | -0.451 |  |  |
| Lake area | $\mathbf{- 0 . 5 9 4}$ | 0.480 | 0.456 |  |  |
| Maximum depth | $\mathbf{- 0 . 7 3 9}$ | 0.375 | 0.005 |  |  |
| Total variance explained (\%) | 39.523 | 28.036 | 11.746 |  |  |

Highest loadings for each environmental variable are highlighted in bold
was significantly correlated with PC1 $(r=0.573, p=$ 0.041 ), but not with PC2 or PC3 ( $p>0.19$ ). Factors that loaded most heavily on PC 1 included Chl-a ( 0.899 ), water transparency ( -0.819 ), and maximum depth ( -0.864 , Table 3 ). When relative condition was regressed against PC1 with deforestation and fishing categories indicated on the plots, there is a pattern that emerges supporting the ANOVA results, with the highest condition in lakes with severe catchment deforestation and high fishing pressure (Fig. 5a, b).

For lakes with populations of T. zillii, PCA yielded three principle components with Eigenvalues greater than 1 that explained $79.3 \%$ of the variance in the environmental data. The first three PC axes accounted for $39.5 \%, 28.0 \%$, and $11.7 \%$ of the variance, respectively (Table 3b). However, only PC3 was
significantly correlated with the relative condition of T. zillii ( $r=0.615, p=0.025$ ), suggesting that the suite of variables considered explained only a small proportion of variance in T. zillii condition. Factors that loaded most heavily on PC3 included conductivity ( -0.466 ), lake area ( 0.456 ), and total nitrogen ( -0.451 , Table $3 b$ ). When relative condition was regressed against PC3 with deforestation and fishing categories indicated on the plots, there was a weak qualitative pattern that emerged supporting the ANOVA results, with the highest condition in lakes with severe deforestation (a less clear pattern) and high fishing pressure (Fig. 6a, b).

We found no relationship across lakes between mean relative condition and rainfall ( $r=-0.041, p=$ $0.89, n=13$ for $O$. leucostictus; $r=0.017, p=0.96, n=$ 13 for T. zillii). In addition, a one-way ANOVA indicated no differences in the mean rainfall for the sampling periods of lakes with high, medium, and low fishing pressure for both $O$. leucostictus $(\mathrm{F}=0.11$, $p=0.89$; mean $\pm$ SE: high $=37.3 \pm 13.7 \mathrm{~mm}$; medium= $30.4 \pm 27.5 \mathrm{~mm}$; low $=31.8 \pm 15.2 \mathrm{~mm}$ ) and T. zillii ( $F=0.34, p=0.72$; mean $\pm$ SE: high $=42.2 \pm 20.8 \mathrm{~mm}$; medium $=42.0 \pm 38.9 \mathrm{~mm}$; low $=56.4 \pm 29.7 \mathrm{~mm}$ ). Thus, although we cannot eliminate the possibility of seasonal effects on condition, these data suggest that seasonality was not a major source of bias.

## Discussion

The introduction of the tilapia species into crater lakes of western Uganda was motivated by the need to facilitate increased protein supplies for local villagers; thus the size, condition, and density of the fish is of significance. In a few crater lakes, $O$. leucostictus seemed to reach a size comparable to some larger systems, though in many of the lakes the maximum size was much smaller. In our study, the largest $O$. leucostictus were a 340 mm TL male in Lake Nyinabulitwa and a 340 mm TL female from Lake Murigarime. This is greater than the maximum size of 300 mm TL for male and 280 mm TL for female $O$. leucostictus reported for the open waters of Lake Victoria (Welcomme 1967). In Lake Naivasha, Kenya, O. leucostictus was reported to reach a maximum size of 310 mm TL for males and 280 mm TL for females (Siddique 1977). For $O$. leucostictus collected in our study, the overall value of the regression coefficient $b$ for the weight-length

Fig. 5 Relationship between total relative condition of Oreochromis leucostictus and PC1 of environmental variables for 13 crater lakes with varying levels of (a) catchment deforestation (moderate and severe) and (b) fishing pressure (low, medium, and high). PC1 explained $43 \%$ of the variance in the independent variables


regression was 2.81 for fish between 80 mm and 340 mm TL. This is lower than earlier studies of this species in Lake Naivasha ( $b=2.90$, Siddique 1977; $b=$ 3.06, Britton and Harper 2006). The largest T. zillii individual caught in this study was a 287 mm TL male from Lake Rukwanzi, and the value of the regression coefficient $b$ for the weight-length regression was 2.99 for fish between 68 mm and 287 mm TL. This is higher than the length-weight regression coefficients for T. zillii populations in Lake Zwai in Ethiopia (2.98 for fish between $55-320 \mathrm{~mm}$ TL, Negassa and Getahun 2003), but lower than for some West African lakes where this species has also been introduced (3.2 for fish between 70-150 mm TL, Teugels and Thys
van den Audenaerde 1991) and Lake Naivasha (3.2 for fish between $37-210 \mathrm{~mm}$ TL, Britton and Harper 2006). Thus, T. zillii and $O$. leucostictus in the crater lakes of western Uganda are reaching relatively large size in some lakes; however, the condition of the fish seems lower relative to some other systems into which they have been introduced.

Fish condition is known to vary seasonally depending on changes in gonadal development, food availability, and other environmental factors (Pope and Willis 1996). As such, it would be best to compare condition of fish populations sampled at the same time of the year. In this study, the populations were sampled during different seasons

Fig. 6 Relationship between total relative condition of Tilapia zillii and PC3 of environmental variables for 13 crater lakes with varying levels of (a) catchment deforestation (moderate and severe) and (b) fishing pressure (low, medium, and high). Note that PC3 explained only $12 \%$ of the variance in the independent variables


of the year, and we therefore did not include gonad weight in our estimates of condition. In addition, both $O$. leucostictus and $T$. zillii are known to spawn throughout the year with slight variation in intensity of breeding (Welcomme 1967; Siddique 1977). In a study of $O$. leucostictus in Lake Naivasha, Siddique (1977) found all stages of gonad maturation all year round and did not note any seasonal fluctuation in relative condition, which he attributed to a constant proportion of fish with gonads in different stages of development. In the present study, we also observed both male and female fish of both species at various stages of gonad development during the different seasons. Although seasonal changes in condition may occur, we found no evidence for a relationship between mean relative fish condition and rainfall across lakes. In addition, for each species, the mean rainfall was similar across categories of fishing pressure. Thus, we believe that bias in our study associated with seasonal variation is likely minimal.

Quantification of fish condition for both tilapia species in the crater lakes region suggests that fishing pressure may be an important driver of condition directly through the reduction of intraspecific competition, or because fishing pressure is often correlated with high levels of land conversion that increase nutrient input. The effects of fishing on life history traits are well documented, especially for major commercial fish stocks (e.g. Ricker 1981; Grift et al. 2002; Olsen et al. 2004, 2005). It is often assumed that fishing-induced reductions in population density of target stock lead to increased yield because of reduction in intraspecific competition that releases populations from density-dependence resulting in faster growth and earlier maturation (Jennings and Kaiser 1998; Hall 1999; Law 2000; Rochet et al. 2000). A reduction in intraspecific competition is also likely to foster better fish condition. In a study of largemouth bass, Micropterus salmoides, both the growth and condition of largemouth bass in small water bodies was found to be affected by densitydependence (Wege and Anderson 1978; Schindler et al. 1997). In our study of Ugandan crater lakes, mean relative condition of the $O$. leucostictus and $T$. zillii species differed among lakes characterized by different fishing pressures; however, the effect was stronger for O. leucostictus.

It is difficult to separate the effects of deforestation and fishing pressure on the condition factor of $O$. leucostictus and $T$. zillii because often lakes with
higher levels of accessibility are characterized by both high fishing pressure and high levels of land conversion; in addition, our sample size of 13 lakes per species limits the power of our statistical resolution. Thus, we were not able to directly test for the interaction of these two anthropogenic stressors; however, there was evidence to suggest that fishing pressure was more strongly related to condition in $T$. zillii. We found no difference in the mean relative condition factor of $T$. zillii between lakes with severe and moderate catchment deforestation; however, lakes characterized by high fishing pressure harboured populations with higher condition than lakes with very low fishing pressure. To detect other environmental correlates of fish condition, principal components analysis was used to describe the major environmental gradients of variation, and PCA factor scores were regressed against relative fish condition. The association between fish condition and environmental gradients was stronger for $O$. leucostictus than T. zillii. For O. leucostictus fish condition was related to PC1 (43\% of the variance), and factors that loaded most heavily included Chl-a (positive loading), water transparency, lake area and maximum depth (negative loading). This suggests higher relative fish condition in lakes characterized by higher productivity and smaller size. For T. zillii, PC3 (11\%) was the only PC axis related to fish condition; and factors that loaded most heavily included lake area (positive loading), and conductivity and total nitrogen (negative loading). From PC - fish condition plots, we can infer the importance of deforestation and fishing pressure in explaining variation in fish condition across lakes. Results of the PCA analyses were consistent with the ANOVA analyses. For $O$. leucostictus relative condition was highest in lakes characterized by severe deforestation, high fishing pressure and higher PC1 scores. For T. zillii, the trend was less evident; condition was generally higher in lakes with high fishing pressure and high PC3 scores, but the trend with deforestation was less evident.

The diet of $O$. leucostictus has been observed to consist predominantly of phytoplankton (Trewavas 1983). In the present study, the differences in condition of $O$. leucostictus among lakes with high fishing pressure and the lakes with low to medium fishing pressure may reflect a greater availability of phytoplankton in response to reduction in population density caused by fishing. In addition, high levels of
land conversion and associated nutrient loading may have contributed to a richer food base. For the phytoplanktivorous $O$. leucostictus, water transparency (Secchi depth) and Chl-a loaded heavily on PC1 that positively correlated with fish condition. In these crater lakes water transparency is highly correlated with Chl-a (an index of phytoplankton abundance) and is also characteristic of lakes with severely deforested catchments (Efitre 2007). One possible scenario is that the lakes experiencing severe deforestation, increased erosion and nutrient loading have accelerated primary productivity that may enhance the food base for the phytoplanktivorous $O$. leucostictus; while higher fishing pressure may reduce intraspecific competition for the richer food base.

Tilapia zillii is characteristically a macrophyte feeder (Buddington 1979), but may also feed on macrobenthos (Greenwood 1966). In the crater lakes, in general, macrophytes are quite rare, but if they do occur, it is often in shallow lakes or large lakes with a better developed littoral zone. Although the relationship between the relative condition of $T$. zillii and gradients of environmental variation were weak, lake area loaded positively on PC3, the axis most strongly related to fish condition. Macrophytes should be more of a limited resource than phytoplankton, which should cause $T$. zillii to respond strongly to reductions in population density through fishing. However, our results suggest otherwise. One possibility is the fact that $T$. zillii is more adaptable in its diet. In the smaller crater lakes with little or no macrophyte flora, T. zillii may have broadened its dietary niche to include food items other than macrophytes, hence the weak relationship between condition and lake area. A qualitative assessment of the diet of T. zillii in a small crater lake Nkuruba (3 ha.) found that detritus (plant materials) constituted the greatest percentage ( $>50 \%$ ) of its diet. However, phytoplankton, fish scales, gastropods (Sphaerium sp.), and benthic invertebrates (Chironomidae larvae) were also present in T. zillii stomachs (Efitre 2007).

Measures of fish condition are generally intended to be indicators of tissue energy reserves and may characterize components of the environment in which the fish lives (e.g., habitat, prey availability, and competition) (Vila-Gispert et al. 2000; Vila-Gispert and Moreno-Amich 2001). In this way, indices of fish condition are of value to fisheries managers who must assess population status, the impact of management
actions, and anthropogenic influences on the resource they are managing (Brown and Murphy 1991); although information on condition alone is not sufficient to manage a fishery or assess the status of a fish population. In this study, we have quantified relative condition of two tilapiine species across a suite of lakes that vary markedly in environmental parameters including deforestation level and fishing pressure. Results from the present study suggest that fishing pressure may be an important regulator of fish condition for both $O$. leucostictus and T. zillii. Crater lakes with heavy fishing pressure also had severely deforested catchments, and this may have increased nutrient loading and primary productivity providing a richer food base for $O$. leucostictus. It should be noted that deforestation of the crater rims of many of the crater lakes is relatively recent (Chapman et al. 2005); it is unclear whether continued nutrient loading will result in hypereutrophication that may ultimately negatively affect fish production (Crisman et al. 2003). Cultural eutrophication in Crater Lake Saka (not included in our study) that has occurred over several decades has resulted in a hypereutrophied system with high levels of algal toxins (Crisman et al. 2001; Chapman and Phlips, unpublished data). There may be an optimal level of land conversion and/or reforestation that could maintain water quality and maximize $O$. leucostictus condition.

Acknowledgements We thank Kibale Fish and Monkey Projects in Uganda for the infrastructure and other logistical support during field data collection. We are also grateful to James Kyomuhendo (Abwooki), James Magaro (Apuuli) and John "the fisherman", for their invaluable field assistance. Financial support for the field sampling was provided by the International Foundation for Science (IFS), Sweden, and Rufford Small Grant to Jackson Efitre, as well as support from the Wildlife Conservation Society and NSERC (Canada) to Lauren J. Chapman, for which we are grateful.

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[^0]:    J. Efitre

    Department of Zoology, Makerere University, P.O. Box 7062, Kampala, Uganda
    L. J. Chapman

    Department of Biology, McGill University, 1205 Avenue Docteur Penfield,
    Montreal, QC H3A 1B1, Canada
    J. Efitre $(\square) \cdot$ D. J. Murie

    Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA
    e-mail: jefitre@zoology.mak.ac.ug
    L. J. Chapman

    Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA

