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

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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 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 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

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Introduction

Fish condition, defined as the robustness or well-being 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 density-dependent 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°23′–0°33′N, 30°10′–30°20′E) 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_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 September-November, with 1702 mm of total rainfall received annually (1990–2005). Between 1990 and 2004, the mean daily minimum temperature was 14.9°C, and the mean daily maximum temperature was 20.2°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.

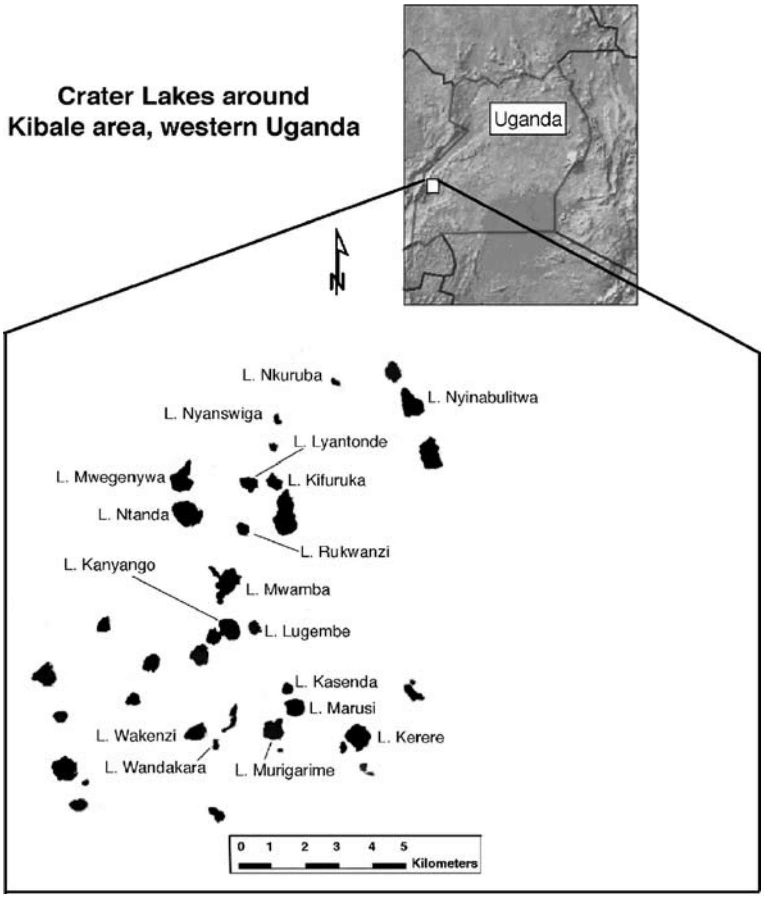

Fig. 1 Location of the Kasenda cluster of crater lakes in western Uganda (0°23′–0°33′N, 30°10′–30°20′E) where *Oreochromis leucostictus* and *Tilapia zillii* were sampled along with environmental variables from July 2004 to July 2005

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°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 an YSI oxygen/temperature meter. Conductivity and pH were measured using an YSI conductivity meter and an OAKTON pH Testr 1, respectively. Water transparency was estimated with a 20-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-and-line 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-m long and 1.0-m deep) with stretched mesh sizes of 25.4 mm, 50.8 mm, 76.2 mm, and 101.6 mm; 2) gillnets used by artisanal fishermen (1800-m long) comprised of mesh sizes 25.4 mm, 50.8 mm, 63.5 mm, and 76.2 mm; and 3) 20 metal minnow traps (450-mm long and 7-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 (K_n)

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: $K_n = W_i / aL_i^b$ (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 ($W=aL^b$) 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 mm TL were included in the inter-lake analyses, and a size range of 68–287 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 mm TL and 7–612 g DW for *O. leucostictus* (Table 1) and 60–287 mm TL and 5–418 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 ($W=aL^b$) for *Oreochromis leucostictus* from 13 crater Lakes in western Uganda, where b=slope of regression and $\log_{10}a$=intercept of regression

Lake	Deforestation	Fishing pressure	Sample size (n)	Mean total length (mm)	Range in total length (mm)	Range in degonaded weight (g)	Log_{10} a	b	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 ($W=aL^b$) for *Tilapia zillii* populations from 13 crater Lakes in western Uganda, where b=slope of regression and $\log_{10}a$=intercept of regression

Lake	Deforestation	Fishing pressure	Sample size (n)	Mean total length (mm)	Range in total length (mm)	Range in degonaded weight (g)	Log_{10} a	b	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

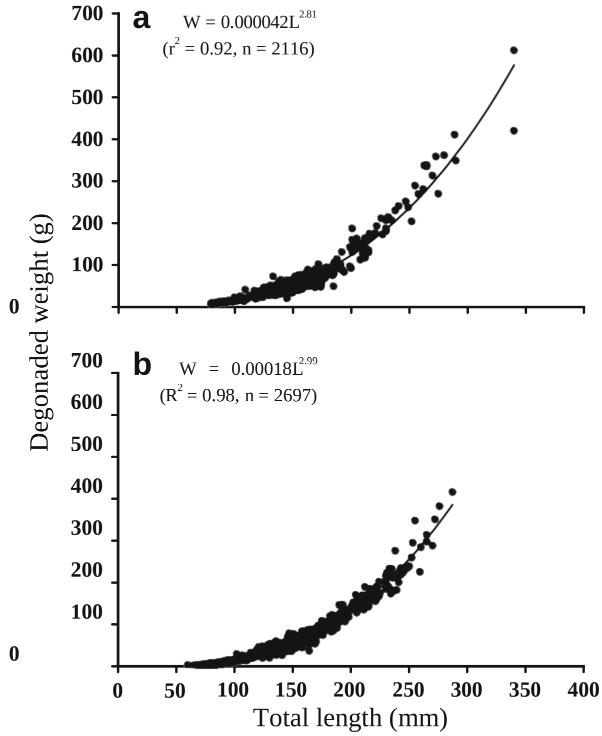

Fig. 2 Regional relationships between degonaded weight (g) and total length (mm) for *Oreochromis leucostictus* (a) and for *Tilapia zillii* (b) derived by pooling data from 13 crater lakes in western Uganda

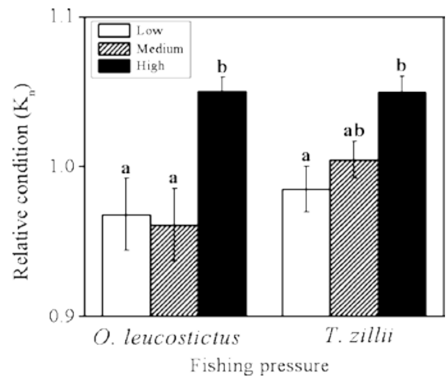

Fig. 3 Mean relative condition of *Oreochromis leucostictus* and *Tilapia zillii* in crater lakes of western Uganda exposed to high, medium, and low fishing pressure. Vertical bars represent ±1 standard error. Different letters above the fishing pressure categories indicate a significant difference at $p \leq 0.05$

Fishing pressure, catchment deforestation, and condition factor

Mean relative condition varied among lakes with different fishing pressure for both species (*O. leucostictus*: $F_{2,13}$=5.05, p=0.031; *T. zillii*: $F_{2,13}$=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 ($F_{1,13}$ = 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 deforested catchments (Fig. 4). However, mean relative condition of *T. zillii* did not differ between lakes with severely and moderately deforested catchments ($F_{1,13}$=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*

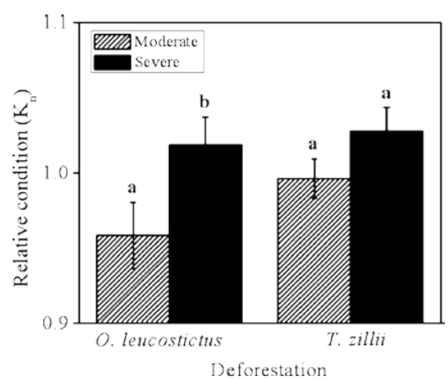

Fig. 4 Mean relative condition of *Oreochromis leucostictus* and *Tilapia zillii* in crater lakes of western Uganda exposed to moderate and severe catchment deforestation levels. Vertical bars represent ±1 standard error. Different letters above the deforestation levels indicate a significant difference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

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

Variable (Log 10)	Component		
	1	2	3
a) Oreochromis leucostictus lakes			
Chlorophyll a	*08.99*	*0.259*	*0.125*
Water transparency (Secchi depth)	-0.819	-0.493	-0.058
Dissolved oxygen	0.301	0.821	0.156
pH	0.066	0.193	0.887
Conductivity	0.592	0.378	-0.367
Total phosphorus	0.389	-0.726	0.488
Total nitrogen	0.673	-0.367	-0.045
Lake area	-0.766	0.413	0.299
Maximum depth	-0.864	0.317	-0.025
Total variance explained (%)	42.914	23.310	14.382
b) Tilapia zillii lakes			
Chlorophyll a	0.865	0.282	0.360
Water transparency (Secchi depth)	-0.889	-0.290	-0.267
Dissolved oxygen	0.154	0.853	0.242
pH	-0.007	0.890	-0.178
Conductivity	0.584	0.239	-0.466
Total phosphorus	0.626	-0.584	0.370
Total nitrogen	0.602	0.268	-0.451
Lake area	-0.594	0.480	0.456
Maximum depth	-0.739	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 PC1 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 3b). 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* (F =0.11, p=0.89; mean ± SE: high=37.3±13.7 mm; medium= 30.4 ± 27.5 mm; low = 31.8 ± 15.2 mm) and *T. zillii* (F =0.34, p = 0.72; mean ± SE: high = 42.2 ± 20.8 mm; medium = 42.0 ± 38.9 mm; low = 56.4 ± 29.7 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

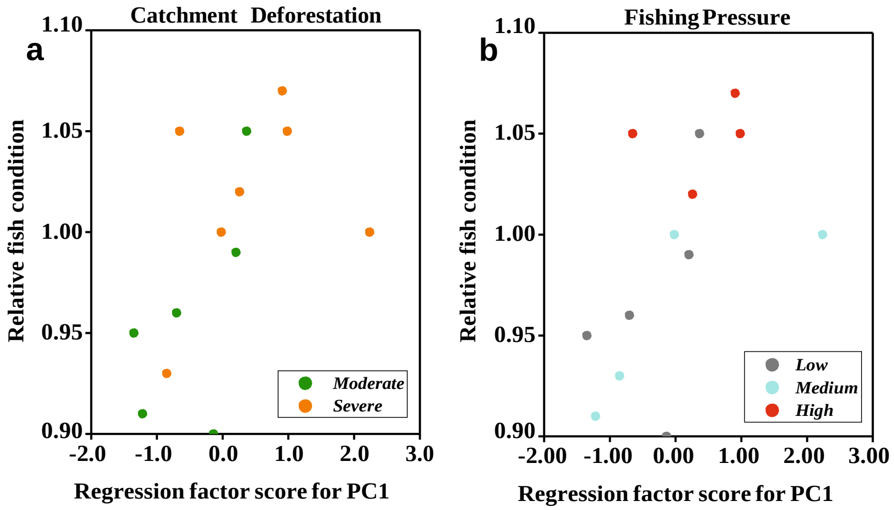

Fig. 5 Relationship between total relative condition of *Oreochromis leucostictus* and PC1 of environmental variables for 13 crater lakes with varying levels of (a) catchment deforestation (moderate and severe) and (b) fishing pressure (low, medium, and high). PC1 explained 43% of the variance in the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

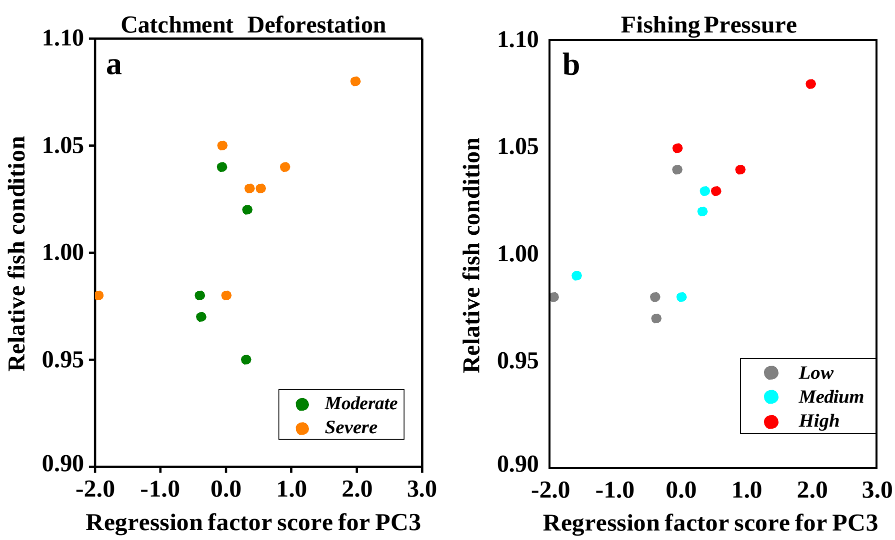

Fig. 6 Relationship between total relative condition of *Tilapia zillii* and PC3 of environmental variables for 13 crater lakes with varying levels of (a) catchment deforestation (moderate and severe) and (b) fishing pressure (low, medium, and high). Note that PC3 explained only 12% of the variance in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

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References

Adams SM, McLean RB, Parrotta JA (1982) Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Trans Am Fish Soc 111:549–558, doi: 10.1577/1548-8659(1982)111<549: EPILBU>2.0.CO; 2

American Public Health Association (1988) Standard methods for the examination of water and wastewater, 17th edn., Washington, D.C.

Binohlan C, Pauly D (1998) The length-weight table. In: Froese R, Pauly D (eds) Fishbase 1998: concepts, design and data sources. ICLARM, Manila, pp 121–123

Blackwell BG, Brown ML, Willis DW (2000) Relative weight (W_r) status and current use in fisheries assessment and management. Rev Fish Sci 8:1–44, doi: 10.1080/10641260091129161

Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement of fish condition. J Fish Biol 34:171–182, doi: 10.1111/j.1095-8649.1989.tb03300.x

Britton JR, Harper DM (2006) Length-weight relationships of fish species in the freshwater Rift Valley lakes of Kenya. J Appl Ichthyology 22:334–336, doi: 10.1111/j.1439-0426.2006.00769.x

Brown ML, Murphy BR (1991) Relationship of relative weight (Wr) to proximate composition of juvenile striped bass and hybrid striped bass. Trans Am Fish Soc 120:509–518, doi: 10.1577/1548-8659(1991)120<0509:RORWTP>2.3. CO; 2

Buddington RK (1979) Digestion of an aquatic macrophyte by *Tilapia zillii*. J Fish Biol 15:449–456, doi: 10.1111/j.1095- 8649.1979.tb03628.x

Bulow FL, Zeman ME, Winningham JR, Hudson WF (1981) Seasonal variation in RNA-DNA ratios and indicators of feeding, reproduction, energy storage and condition in a population of bluegill, *Lepomis macrochirus* (Rafinesque 1819). J Fish Biol 18:237–244, doi: 10.1111/j.1095-8649.1981. tb03766.x

Chapman CA, Struhsaker TT, Lambert JE (2005) Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. Int J Primatol 26:539–555, doi: 10.1007/s10764-005-4365-z

Crisman TL, Chapman LJ, Chapman CA, Printer J (2001) Cultural eutrophication of a Ugandan highland crater lake: A twenty-five year comparison of limnological parameters. Verh Int Verein Limnol 17:272–282

Crisman TL, Chapman LJ, Chapman CA (2003) Incorporating wetlands and their ecotones in the conservation and management of freshwater ecosystems of Africa. In: Crisman TL, Chapman LJ, Chapman CA, Kaufman LS (eds) Conservation, Ecology, and Management of African Freshwaters. University Press of Florida, Gainesville, pp 210–228

Efitre J (2007) Life history variation in tilapia populations within the crater lakes of western Uganda: the role of size-selective predation. Ph.D. Thesis. University of Florida, Gainesville, p 189

Fryer G, Iles TD (1972) The Cichlid Fishes of the Great Lakes of Africa. Oliver and Boyd, London, p 641

Greenwood PH (1966) The Fishes of Uganda. The Uganda Society, Kampala

Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U (2002) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar Ecol Prog Ser 257:247–257, doi: 10.3354/meps257247

Gulland JA (1983) Fish stock assessment: a manual of basic methods. FAO/Wiley Series, Food and Agriculture Organization, Rome

Hall SJ (1999) The Effects of Fishing on Marine Ecosystems and Communities. Blackwell, Oxford, p 274

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201–352, doi: 10.1016/S0065-2881(08)60212-6

Kizito YS, Nauwerck L, Chapman LJ, Koste W (1993) A limnological survey of some western Uganda crater lakes. Limnologica 23:335–347

Law R (2000) Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57:659–669, doi: 10.1006/jmsc.2000.0731

Le Cren ED (1951) The length-weight relationship and seasonal cycle in gonad weight and condition in Perch (*Perca fluviatilis*). J Anim Ecol 20:201–219, doi: 10.2307/1540

Lowe-McConnell RH (1982) Tilapias in fish communities. In: Pullin RSV, Lowe-McConnell RH (eds) The Biology and Culture of Tilapias. ICLARM Conference Proceedings 7, Manila, pp 83–113

Melack JM (1976) Limnology and dynamics of phytoplankton in Equatorial African lakes. Ph.D. Thesis. Duke University, Durham, p 453

Negassa A, Getahun A (2003) Breeding Season, length-weight relationship and condition factor of introduced fish, *Tilapia zillii* Gervais 1948 (Pisces: Cichlidae) in Lake Zwai, Ethiopia. SINET Ethiop J Sci 26:115–122

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935, doi: 10.1038/nature02430

Olsen E, Lilly GR, Heino M, Morgan MJ, Brattey J, Dieckmann U (2005) Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 62:811–823, doi: 10.1139/f05-065

Oscoz J, Campos F, Escala MC (2005) Weight-length relationships of some fish species of the Iberian Peninsula. J Appl Ichthyology 21:73–74, doi:10.1111/j.1439-0426.2004.00587.x

Pauly D (1993) Fishbyte section. Editorial. Naga. ICLARM Q 16:26

Petrakis G, Stergiou KI (1995) Weight-length relationships for 33 fish species in Greek waters. Fish Res 21:465–469, doi: 10.1016/0165-7836(94)00294-7

Pomeroy DE, Seavy NE (2003) Survey of Great Crested Grebes *Podicepus cristatus* and other water birds on the Kasenda cluster of crater lakes in western Uganda. J East Afr Nat Hist 92:49–62, doi: 10.2982/0012-8317(2003)92 [49: SOGCGP] 2.0.CO; 2

Pope KL, Willis DW (1996) Seasonal influences on freshwater fisheries sampling data. Rev Fish Sci 4:57–73, doi: 10.1080/10641269609388578

Ricker WE (1975) *Computation and Interpretation of the Biological Statistics of Fish Populations*. Bulletin of the Fisheries Research Board of Canada Number 191, Department of the Environment, Fisheries and Marine Services, Ottawa

Ricker WE (1981) Changes in average size and average age of Pacific Salmon. Can J Fish Aquat Sci 38:1636–1656, doi: 10.1139/f81-213

Rochet MJ, Cornillon PA, Sabatier R, Pontier D (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. Oikos 91:255–270, doi: 10.1034/j.1600-0706.2000.910206.x

Schindler DE, Hoggson JR, Kitchell JF (1997) Density-dependent changes in foraging specialization of largemouth bass. Oecologia 110:592–600, doi: 10.1007/ s004420050200

Siddique AD (1977) Reproductive biology, length-weight relationship and relative condition of *Tilapia leucostica* (Trewavas) in Lake Navaisha Kenya. J Fish Biol 10:251–260, doi: 10.1111/j.1095-8649.1977.tb05130.x

Sparre P, Ursin E, Venema SC (1989) Introduction to tropical fish stock assessment, Part 1. Manual. FAO Fisheries Technical Paper. No. 306.1, Rome

Teugels GG, Thys van den Audenaerde DFE (1991) Tilapia. In: Daget J, Gosse JP, Teugels GG, Thys van den Audenaerde DFE (eds) Check-list of the freshwater fishes of Africa (CLOFFA). ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris, Vol. 4

Trewavas E (1983) Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum of Natural History, London, p 583

Vila-Gispert A, Moreno-Amich R (2001) Mass-length relationship of Mediterranean barbel as an indicator of environmental status in south-west European stream ecosystems. J Fish Biol 59:824–832, doi: 10.1111/j.1095-8649.2001.tb00153.x

Vila-Gispert A, Zamora L, Moreno-Amich R (2000) Use of the condition of Mediterranean barbel (*Barbus meridionalis*) to assess habitat quality in stream ecosystems. Arch Hydrobiol 148:135–145

Wege GJ, Anderson RO (1978) Relative weight (W_r): a new index of condition for largemouth bass. In: Novinger GD & Dillard GJ (eds) New Approaches to the Management of Small Impoundments. Bethesda, pp 79–91

Welcomme RL (1967) Observations on the biology of the introduced species of *Tilapia* in the Lake Victoria. Rev Zool Bot Afr 76:249–279

Welcomme RL (1970) Studies on the effects of abnormally high water levels on the ecology of fish in certain shallow regions of L. Victoria. J Zool 160:405–436

Wootton RJ (1990) Ecology of Teleost Fishes. Chapman & Hall, New York