

1 **The Nile perch invasion in Lake Victoria: cause or consequence of**  
2 **the haplochromine decline?**

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## 27 **Abstract**

28 We review alternative hypotheses and associated mechanisms to explain Lake Victoria's Nile  
29 perch takeover and concurrent reduction in haplochromines through a (re)analysis of long term  
30 climate, limnological and stock observations in comparison with size-spectrum model predictions of  
31 co-existence, extinction and demographic change. The empirical observations are in agreement with  
32 the outcomes of the model containing two interacting species with life-histories matching Nile perch  
33 and a generalized haplochromine. The dynamic interactions may have depended on size related  
34 differences in early juvenile mortality: mouth-brooding haplochromines escape predation mortality  
35 in early life stages, unlike Nile perch that have miniscule planktonic eggs and larvae. In our model  
36 predation on the latter by planktivorous haplochromine fry act as a stabilizing factor for co-existence,  
37 but external mortality on the haplochromines would disrupt this balance in favor of Nile perch. To  
38 explain the observed switch, mortality on haplochromines would need to be much higher than the  
39 fishing mortality that can be realistically re-constructed from observations. Abrupt concomitant  
40 changes in algal and zooplankton composition, decreased water column transparency, and  
41 widespread hypoxia from increased eutrophication most likely caused haplochromine biomass  
42 decline. We hypothesize that the shift to Nile perch was a consequence of an externally caused,  
43 climate triggered, decrease in haplochromine biomass and associated recruitment failure rather than  
44 a direct cause of the introduction.

## 45 **Keywords**

46 Lakes, Eutrophication, Predator-prey interaction, Invasive species, Climate change

47

48 **Introduction**

49 Invasions of non-native species into ecosystems become increasingly common through  
50 anthropogenic activities, facilitated by climate change (Cheung et al. 2009). For most invasions little  
51 is known about interactions with the resident community until the invader is well established  
52 (García-Berthou 2007). One of the best known cases, the Nile perch (*Lates niloticus*) introduction and  
53 subsequent profound community changes in Lake Victoria (Barel et al. 1985; Goudswaard et al. 2008;  
54 Witte et al. 1992) (Figure 1), has been studied since 1969 together with the resident assemblage of  
55 haplochromine cichlids. It thus provides a unique possibility to test hypotheses on the nature of the  
56 interactions between the invader, resident communities and system drivers of community change.  
57 We review some of these hypotheses and mechanisms through a (re)analysis of existing long term  
58 observations on limnological changes and stock developments before, during and after the switch  
59 from a cichlid dominated to a perch dominated assemblage and we compare these observations with  
60 dynamic size-based model predictions of co-existence, extinction and demographic change in Nile  
61 perch and haplochromine populations.

62 Between 1954 and the early 1960s small numbers of Nile perch, a large piscivorous predator,  
63 were introduced on several occasions in the Ugandan and Kenyan parts of the lake with the aims of  
64 creating a recreational fishery and to convert the large biomass of the indigenous small bony  
65 haplochromine cichlids into a less productive but more valuable commodity (Anderson 1961; Fryer  
66 1960; Pringle 2005; Welcomme 1988). Nile perch spread rapidly across the Lake and by October  
67 1961 was reported in Mwanza, Tanzania, over 300 km from the sites of introduction. However, it  
68 remained scarce for the next 20 years. By 1972-1975 it was caught all over the lake as large adults  
69 (Kudhongania and Cordone 1974b; Pringle 2005), in coarse-meshed, 5-7 inch gillnets (Scully 1976a,  
70 b) but in negligible quantities (Marten 1979). During this period, haplochromines dominated in terms  
71 of fisheries and biomass, which increased and then decreased well before a sudden switch to Nile  
72 perch dominance in the early 1980s and concomitant disappearance of several hundred species of

73 haplochromines (Kolding et al. 2008). Top down (fishing) and bottom up (eutrophication)  
74 mechanisms have been proposed as switch-inducing catalyzers (Goudswaard et al. 2008; Hecky 1993;  
75 Kolding et al. 2008; Seehausen et al. 2003). Importantly, it was only after the Nile perch upsurge that  
76 large numbers of recruits < 15 cm appeared in the lake (Goudswaard et al. 2008), leading to a major  
77 change in the size-structure of the Nile perch population. Since then a large and economically  
78 important Nile perch fishery developed with landings fluctuating around a long term annual average  
79 of 240,000 ton (Kolding et al. 2013). Later, from the late 1990s, a reappearance of a small number of  
80 haplochromine species (Balirwa et al. 2003; Downing et al. 2014; Seehausen et al. 1997b) has  
81 resulted in a renewed fishery with reported catches of around 100,000 ton, two to five times larger  
82 than before the collapse (Kolding et al. 2013).

83         A long time lag from introduction to dominance by an invader is a common feature of  
84 invasions (Boggs et al. 2006; Sakai et al. 2001). For Lake Victoria two general hypotheses have been  
85 proposed to explain this time lag: (1) a trophic cascade resulting from top down control of  
86 haplochromines through Nile perch predation and (2) recruitment depensation. Downing et al.  
87 (2013) showed that simple logistic population growth would be sufficient to explain the timing and  
88 speed of the Nile perch invasion as a trophic cascade. A further refinement of this hypothesis is the  
89 particular observed spatial sequence of the haplochromine collapse starting from the north by a  
90 wave of migrating Nile perch dispersing over the Lake (Goudswaard et al. 2008). Downing et al.  
91 (2013) argue that, although depensatory mechanisms could play a role locally, on a whole-lake scale  
92 no depensation would be needed to explain the initial slow expansion of Nile perch. On the other  
93 hand, using a consumer-resource model, van de Wolfshaar et al. (2014) found that co-existence of  
94 Nile perch with a generalized haplochromine was possible. In fact in other African lakes  
95 haplochromine communities do co-exist with large *Lates* species including Nile perch.

96         The depensatory hypotheses focus on the community size structure where Nile perch  
97 recruitment is limited through predation and/or competition between juvenile Nile perch and

98 haplochromines. Under these hypotheses, external factors are needed to break an initial co-  
99 existence. A range of contending explanatory hypotheses focusses on the nature of the depensatory  
100 restriction on Nile perch recruitment (hereinafter referred to as the haplochromine filter) through  
101 competition or predation and the associated disturbance required to release it (Goudswaard et al.  
102 2008; Kolding et al. 2008; van de Wolfshaar et al. 2014; Walters and Kitchell 2001). The  
103 haplochromine filter breaks if there is a recruitment failure or a decreased biomass of adult  
104 piscivorous haplochromine predating on early life stages of Nile perch (Witte et al. 2007) a  
105 mechanism also proposed for other aquatic systems (Persson et al. 2007).

106 Mechanisms suggested for catalysing the switch through external mortalities on all or  
107 piscivorous haplochromines include top-down stress from fishing on haplochromines (Goudswaard et  
108 al. 2008), and/or bottom-up stress caused by eutrophication leading to structural trophic and  
109 biophysical changes in the lake (Hecky 1993; Kolding et al. 2008; Seehausen et al. 1997a). These  
110 include changes in phytoplankton and zooplankton communities changing food availability and  
111 quality at the base of the haplochromine food web (Hecky et al. 2010; Kling et al. 2001), changes in  
112 light attenuation affecting visibility and feeding efficiency of haplochromines (Seehausen et al.  
113 1997a) and changes in extent and duration of hypoxia and anoxia during stratification (Verschuren et  
114 al. 2002).

115 Here we will review these hypotheses and present a refinement of the mechanism for  
116 recruitment depensation, where the switch from haplochromines to Nile perch depends on size-  
117 related differences in early juvenile predation mortality. Haplochromines, being maternal mouth  
118 brooders, protect their offspring from predation mortality in their early life stages whereas Nile  
119 perch with miniscule planktonic eggs and larvae (Hopson 1969) do not (Figure 2). The comparatively  
120 large haplochromine fry are nearly all initially planktivores, irrespective of the highly diverse adult  
121 feeding specializations. Thus, a decline in overall haplochromine biomass would release Nile perch  
122 from early high mortality on the planktonic egg and larval stage. This would induce a subsequent

123 switch, but the cause would be an externally driven decrease in haplochromines, and not a trophic  
124 cascade induced by Nile perch predation. We test the likelihood of this hypothesis using a dynamic  
125 size-spectrum model of two interacting species, comprising a resident species with a haplochromine-  
126 like life history and an introduced species with a Nile-perch-like life history. We will examine the  
127 different alternative suggestions for the catalyzing decrease in haplochromine biomass that occurred  
128 prior to the switch. Lastly we will discuss the consequences of the proposed mechanisms in the light  
129 of the observed renewal of the haplochromine biomass and the eutrophication status of the Lake.

## 130 **Methods**

131 Critical in distinguishing between various hypotheses is the observed temporal sequence of changes  
132 in the fish community as well as the variables that potentially affect these changes through (1)  
133 eutrophication-related processes using time series of climate, water chemistry and primary and  
134 secondary production; and (2) fishing, through quantitative changes in abundance, biomass and size  
135 structure of haplochromines and Nile perch.

### 136 *Climate and limnology*

137 A set of indicators describing developments in eutrophication in relation to climate and changes in  
138 lower trophic levels as potential drivers of haplochromine collapse is given in Table 1. Methods of  
139 reconstruction of climate time series and limnological variables are described in Appendix A. All  
140 indicators are presented as standardised anomalies through  $(\text{value} - \text{mean})/(\text{standard deviation})$ .

### 141 *Fisheries and fish data*

142 All observations on Nile perch size and abundances as well as haplochromine abundances are  
143 obtained from experimental trawl surveys which began on the lake in 1969 (Kudhongania and  
144 Cordone 1974b) and have since been conducted on a fairly frequent basis. The reconstruction and  
145 consolidation of these data sets is described in Kolding et al. (2005, 2008) and extended with  
146 experimental surveys conducted up till 2011. A short summary is given in Appendix B. Experimental

147 catch data for the Kenyan part of the lake, including the Winam Gulf (aka Kavirondo or Nyanza Gulf)  
148 exist, but only published aggregates of Nile perch and haplochromine biomass estimates were  
149 available to us (Goudswaard et al. 2008; Muller and Benda 1981). Acoustic survey estimates of Nile  
150 perch biomass, used for validation of trawl surveys, were taken from Everson et al. (2013) and  
151 EAF/LVFO (2013). Catch estimates by species category from the three countries were compiled by  
152 the LVFO (Kolding et al. 2005) and an updated time series of annual catches was published in Kolding  
153 et al. (2013). Data on sizes of haplochromine fry were collected in the laboratory of the Swiss Federal  
154 Institute for Aquatic Science and Technology (Eawag) (Appendix C) and were used to parameterise  
155 the model.

156 Length  $L$  of Nile perch was converted to weight  $W$  by the Beyer (1987) algorithm with  
157  $a=0.011 \text{ g/cm}^b$  and  $b=3.044$ . Here we define mature adults as  $\geq 70$  cm (Mkumbo and Marshall 2014;  
158 Witte and Winter 1995), sub-adults as  $< 70$  cm and  $\geq 15$ cm, and recruits as  $< 15$  cm standard length.  
159 Juvenile (immature) Nile perch are defined as  $<70$  cm standard length.

160 Spatially defined catch rates from the experimental fishery were corrected for trawl duration  
161 to a standard haul of 60 minutes using total biomass (kg) of all species (see Appendix E for details).  
162 Weights are continuous and log-normally distributed. We used a hurdle model to make use of the  
163 information contained in zero catches and thus obtain three time series of indicators related to  
164 changes in Nile perch population: the catch probability, or encounter rate ( $P_c$ ); the catch rate of  
165 positive catches or patch density ( $\text{CPUE}_{po}$ ); and the relative biomass or catch rate adjusted for the  
166 encounter rate ( $\text{CPUE}_{ad} = P_c \times \text{CPUE}_{po}$ ). The encounter rate can be interpreted in terms of dispersion  
167 and establishment of the species over the lake. The positive catch rates ( $\text{CPUE}_{po}$ , kg/hr) are an  
168 estimate of the density in a swept area of a 60 minute haul, thus representing the patch density,  
169 which is the average density of Nile perch when encountered in a standardized trawl swept area of  
170 6.8 ha. The catch rates adjusted by the probability of catch  $\text{CPUE}_{ad}$  (kg/hr) represent the overall  
171 average relative density (see Appendix D for details). To confront the empirical results with the size-

172 based model results two relative density ratios were examined: the juvenile Nile perch: adult Nile  
173 perch (J/A) and the haplochromine: Nile perch (H/N) biomass ratio (See Appendix D for details).

174 To test the hypothesis that the external haplochromine mortality prior to the switch was  
175 caused by fishing alone, we estimated the biomass decline and the decline in haplochromine  
176 productive capacity of the Tanzanian part of the lake between 1969 and 1982. We assume that  
177 fishing was confined to <30 m depth (11500 km<sup>2</sup>) representing 35% of the Tanzanian area of the lake.  
178 This depth range was estimated to contain 45% of the demersal fish biomass (mostly  
179 haplochromines) (Cordone and Kudhongania 1971, Kudhongania and Cordone 1974a). Demersal  
180 biomass estimates were calculated from average catch rates (kg/hr). For the Mwanza Gulf, Witte at  
181 al. (2012) estimated the demersal haplochromine biomass at 36% of the total haplochromine  
182 biomass in the water column, which we assume is representative of other parts of the lake.  
183 Reported catches from Tanzania (Kolding et al. 2005) were used to calculate annual harvest rates as  
184  $H = C/B$ , where C is catch (ton/yr) and B is biomass (ton) and fishing mortality,  $F = -\ln(1-H) / \text{yr}$  (Haddon  
185 2011) . To estimate the exploitation ratio ( $E = C/P$ ), where P is production (ton/yr), a conservative P/B  
186 ratio of 1.4 /yr was used (Moreau 1995) (See Appendix D). To induce the switch in the size-spectrum  
187 model the haplochromine model population was subjected to an additional mortality F which was  
188 converted to an equivalent estimate of the total catch required to attain this mortality by  $C = B \cdot (1 - e^{-F})$   
189 (Haddon 2011).

#### 190 *Size-based model*

191 To examine the depensation hypotheses we use the size-spectrum model of Law et al. (2014)  
192 (see Appendix E for model equations), parameterized to represent the introduced Nile perch and a  
193 resident species with a haplochromine-like life history. The model is not intended to capture the  
194 dynamics of the haplochromine assemblage in Lake Victoria with its extremely diverse range of  
195 feeding behaviours and habitat specialisations (Greenwood 1974; Seehausen 1996; Witte and van



196 Oijen 1990). Instead, we use a simplified model to investigate the possible outcomes when a resident  
197 and an introduced species interact.

198 A size-spectrum model is an appropriate tool to study depensation because it incorporates  
199 important size-dependencies between prey mortality, predator growth and recruitment, allowing  
200 predation to change as fish grow (Andersen and Beyer 2006; Benoît and Rochet 2004; Law et al.  
201 2014). It can generate explicit predictions of population abundance and size-structure, which can be  
202 compared with empirical patterns. Stage-based processes emerge naturally from size-based  
203 processes, and thus are present in the much simpler size-structure. Another advantage is that the  
204 type of "control" that different size classes in the two populations exert on other size classes is an  
205 emergent feature of the model. Predator-prey interactions are assumed to be determined by relative  
206 body sizes only, thus predators are indifferent to the species identity of potential prey and target  
207 prey in a size range around a specified predator-prey body mass ratio. So, haplochromines of all sizes  
208 feed on other haplochromines, Nile perch and plankton provided they are the right size. Lastly, the  
209 number of parameters required is lower than other approaches, such as consumer-resource models  
210 (van de Wolfshaar et al. 2014) and physiologically structured models (Persson et al. 2007), and  
211 reliable estimates for these parameters are provided by general allometric rules.

212 The size-spectrum model has, at its core, a bookkeeping of biomass flow from prey to predator and  
213 from parent to offspring (Datta et al. 2010). Predators assimilate a fixed proportion of 20% of  
214 ingested prey biomass. Of the assimilated mass, a proportion  $\epsilon$  is allocated to somatic growth and  
215 the remaining proportion  $1-\epsilon$  to reproduction. The proportion  $\epsilon$  is a decreasing function of predator  
216 size  $w$ , so that small individuals allocate all assimilated mass to somatic growth, while larger  
217 individuals allocate increased proportions to reproduction. The size at which the function  $\epsilon(w)$  equals  
218 zero corresponds to the asymptotic size  $w_\infty$  for that species. In addition to the two interacting  
219 species, there is a resource (plankton) spectrum consisting of objects up to a maximum of 0.02 g in  
220 size. The resource productivity (i.e. its turnover rate) is assumed to operate on a faster timescale

221 than fish productivity, allowing us to make the simplifying assumption that the resource spectrum is  
222 fixed, though the availability of the resource to a given fish species can be modified through an  
223 interaction coefficient  $\theta$  (see Appendix E). The model is non-spatial and assumes that the community  
224 is well mixed. To examine, conceptually, the effects of dispersal of Nile perch from a single part of  
225 the lake we devised a two patch model with dispersal where modelled populations each  
226 independently have the same governing dynamics as in the size-spectrum model, and with net  
227 migration between them.

228 To represent the life-history of a generalized haplochromine species, we set the egg size at 0.01 g,  
229 the mass at 50% maturity at 6 g and the asymptotic mass at 30 g. This corresponds to a species that  
230 is planktivorous in its early life stages, switching gradually to piscivory in adulthood. To incorporate  
231 the mouth-brooding behavior of haplochromines, we assume that individuals of this species smaller  
232 than 0.05 g (Appendix C) are protected from predation by mouth brooding, but feed and grow  
233 normally. To represent Nile perch, we estimated the egg size as 0.001 g (corresponding with the 1.2  
234 mm diameter of the egg, Hopson 1969), the size at 50% maturity as 4.4 kg and the asymptotic size as  
235 60 kg. The mean predator-prey body mass ratio (PPMR) for the haplochromine-like species was  
236 estimated at 150 and for Nile perch as 300. Table 2 shows all parameters and values used in the size-  
237 spectrum model.

238 The size-based model is used to address four specific questions: (1) is stable co-existence  
239 possible; if so is it likely that (2) fishing alone (3) predation or (4) limnological changes weakened  
240 depensation enough to initiate the Nile perch upsurge. Furthermore the impact of the Nile perch  
241 fishery starting at the switch is examined by applying a fishing mortality  $F=0.5$  to Nile perch  $>40\text{cm}$ .

## 242 **Results**

### 243 **Empirical observations**

244 *Limnological changes in Lake Victoria 1920 to 2000*

245 Relatively rapid changes observed in sediment cores (Hecky et al. 2010) along with a shift in  
246 meteorological conditions imply that a rapid change to a more eutrophic condition occurred abruptly  
247 just prior to and during the Nile perch upsurge. Eutrophication in Lake Victoria as a result of land-  
248 based processes has progressed over the last century (Hecky et al. 2010, Figure 3). The phosphorous  
249 (P) loading has increased in nearshore regions since the 1940s in synchrony with human population  
250 growth with ensuing deforestation, agriculture and urbanisation (Kolding et al. 2008; Verschuren et  
251 al. 2002). In offshore regions, a rapid change after the early 1980s (Figure 3B) was a result of  
252 changing oxygen conditions in the lake (Hecky et al. 2010). A steady decline in oxygen concentrations  
253 has been observed offshore starting around 1960 and between the late 1970s and early 1980s  
254 waters below 40 m suffered prolonged anoxia (Hecky et al. 1994; Verschuren et al. 2002). Based on  
255 time series of meteorological data, we infer that the change was caused by increased stratification  
256 caused by prolonged low wind stress starting around 1975 and exacerbated by an El Niño event in  
257 1983 (Kolding et al. 2008; MacIntyre 2013; MacIntyre et al. 2014) (Figure 3A). Those conditions set  
258 the stage for limited vertical mixing, causing a larger anoxic volume in the deeper waters and a  
259 substantial increase in the availability of P liberated from internal sedimentary sources. Upon mixing  
260 in the water column, this additional internal loading resulted in enhanced phytoplankton bloom  
261 conditions (Cózar et al. 2012) .

262 The primary productivity record shows stable values from 1920 until 1940 and then a steady  
263 increase since 1940 up to the late 1980s in offshore sediments (Figure 3C). The nearshore primary  
264 production was variable until 1975, when a substantial increase in  $\delta^{13}\text{C}$  took place. By 1985 both  
265 nearshore and offshore  $\delta^{13}\text{C}$  stabilized or were still increasing at levels approximately 3 ‰ higher  
266 than in the 1940s. Productivity in Lake Victoria is nitrogen deficient (Talling 1966): much of the  
267 increased productivity was probably accomplished by N-fixing cyanobacteria. As TP concentrations  
268 rose rapidly in sediments after 1980, N concentrations did not keep pace and N:P ratios steadily  
269 decreased until 1982 when it suddenly dropped precipitously as P increased (Figure 3D). The decline  
270 in the N:P ratio caused a concomitant shift in algal community composition from diatom and

271 chlorophyte dominance the 1960s to cyanobacteria (Kling et al. 2001) around the time of the Nile  
272 perch surge, exacerbated probably by the increased anoxia in deeper waters of the lake. Anoxia  
273 would favour increased denitrification which maintained N deficiency in the lake.

274 Increased diatom microfossils (Hecky 1993) indicate that increased diatom productivity  
275 initially preceded the changes in P loading (Figure 3D). In addition to the subsequent shift to  
276 cyanobacteria, a shift to smaller diatom species that were more efficient in growing on low dissolved  
277 Si concentrations occurred as increased productivity depleted silica in the lake (Hecky 1993,  
278 Verschuren et al. 2002). This is consistent with the stratigraphic record that shows a drop in  
279 *Aulacoseira* spp. valve concentrations indicating a shift from the large heavily silicified *Aulacoseira* to  
280 the smaller species from 1977 (nearshore) and 1982 (offshore) onwards (Kling et al. 2001;  
281 Verschuren et al. 2002), just prior to and during the start of Nile perch takeover. Quiescent winds,  
282 waters with lowered temperatures, limited mixing and anoxic conditions in the decade after 1975  
283 can explain the rapid loss of the heavy, fast sinking *Aulacoseira* that was most abundant in deeper  
284 waters (Stager et al. 2009).

285 Zooplankton communities were equally affected by eutrophication. Starting prior to the Nile  
286 perch takeover, nearshore *Cladocera* fossils (primarily *Bosminidae*) slowly decreased till 1985,  
287 followed by a sharp decrease. This decline was already well underway before the disappearance of  
288 demersal zooplanktivorous haplochromines that were replaced by the pelagic zooplanktivorous  
289 *Rastrineobola* (in Tanzania from 1984 onwards) and small (<5 cm) Nile perch. The combined  
290 biomasses of these two zooplankton eaters were lower than the zooplanktivorous haplochromine  
291 biomasses prior to the shift (Wanink et al. 2002). The decline in small cladocerans inshore may be a  
292 result of the change to filamentous and colonial cyanobacteria (Kling et al. 2001; Wanink et al. 2002).  
293 It may also be a result of changing inshore oxygen conditions permitting *Chaoborus*, a hypoxia  
294 tolerant zooplanktivorous insect, to become more abundant inshore, as indicated by their increased  
295 remains in sediment cores (Bridgeman 2001). In summary, the limno-chemical changes and changes

296 at the low trophic levels were as dramatic and profound as the haplochromine collapse, and were all  
297 well underway prior to the shift to Nile perch (Figure 3E,F).

#### 298 *Changes in densities of Nile perch and haplochromines*

299 From 1969 onwards in Tanzania Nile perch were present in trawl surveys with stable average  
300 densities of around 1 kg/hr between 1974 and 1979. By 1983, overall densities had increased tenfold  
301 followed by another order of magnitude jump in 1984 (Figure 4). The rate of increase then slowed  
302 down until relative densities reached an average of around 120 kg/hr (CV=32%) over the next  
303 decade. In Uganda, Nile perch density was 200 times that in Tanzania in 1969/71 and still 20 times  
304 higher in 1981 to 1983. Original data no longer exist for the period between 1971 and 1981, but in  
305 1981 experimental catch rates were twice as high as in 1971. After 1982 densities started increasing  
306 from around 10 kg/hr to a long-term average of around 70 kg/hr (CV=35%) over the next two  
307 decades.

308 Meanwhile, the haplochromine biomass increased both in Uganda and Tanzania during the  
309 early 1970s. In Uganda, haplochromine biomass doubled between 1971 and 1984, after which it  
310 decreased. In Tanzania, haplochromine biomass peaked at 1900 kg/hr around 1974 and then  
311 decreased to 600 kg/hr in 1982, just before the start of the switch in Tanzania in 1983 (Goudswaard  
312 et al. 2008). From 1983 until the collapse in 1985, haplochromine biomass fluctuated between 314  
313 and 785 kg/hr (Figure 4). The lowest average biomass levels were 0.7 kg/hr in Tanzania (1988) and  
314 0.01 kg/hr in Uganda (1993). Since then, haplochromine biomasses increased to between 100 and  
315 250 kg/hr.

#### 316 *Changes in size structure of Nile perch*

317 From the early 1960s until the upsurge, Nile perch had self-sustaining populations all over  
318 the Lake consisting mainly of adults ( $\geq 70$  cm) and with only very low numbers of the smallest juvenile  
319 specimens, the recruits ( $< 15$  cm) (Figure 5). Between 1969 and 1975, median sizes of the few Nile

320 perch caught in experimental surveys were 99 cm (range 43-106 cm, N=5) and 95 cm (34-158cm,  
321 N=53) in Tanzania and Uganda respectively. The average size decreased between 1979 and early  
322 1985, but large numbers of Nile perch recruits only appeared in Tanzania in the second half of 1985  
323 and in Uganda perhaps as late as 1989. Since then, large numbers of Nile perch recruits have been  
324 present in all experimental trawl hauls irrespective of depth and location, with highest abundances in  
325 shallow inshore waters (Tumwebaze et al. 2002). This suggests that the early scarcity of Nile perch  
326 recruits was not a sampling artifact. Early reports of Nile perch catches refer to large mesh sizes only  
327 (Marten 1979; Scully 1976a, b), although small-meshed gillnets were used to catch haplochromines  
328 and would have caught Nile perch recruits if present (Cornelissen et al. 2015; Marten 1979). The  
329 immense recruitment potential of Nile perch therefore appeared very late during the Nile perch  
330 invasion. The rapid timing of the burst of recruits is clearly shown in the Tanzanian data set (Figure  
331 6A): while between September 1984 to July 1985, no fish <6 g was caught, small recruits suddenly  
332 appeared between July and December 1985. In the course of a year, the Nile perch size spectrum  
333 developed from a highly right-skewed distribution to a flat, Sheldon-type distribution after the  
334 appearance of sub-adult Nile perch of around 30 – 40 cm (Figure 6A, arrow) between January and  
335 April 1985. This appearance cannot be explained by local population growth based on the available  
336 Nile perch adult biomass in the Mwanza Gulf. The flat distribution stabilizes over the following 15  
337 years examined here. Similar developments in Nile perch size structure were seen in the Emin Pasha  
338 Gulf to the West of the Mwanza Gulf, while in the Kagera area recruitment was fully developed by  
339 1985, before the Mwanza gulf (Goudswaard et al. 2008).

#### 340 *Nile perch spatial distribution: dispersion and patch density*

341 Two processes need to be distinguished in the observations on the biomass increase of Nile  
342 perch since its introduction: dispersion over the lake, described by the encounter rates ( $P_c$ ), and  
343 density increase, described by the patch density ( $CPUE_{po}$ ). The changes of Nile perch encounter rates  
344 and patch densities over depth and time are well described by the thin-plate spline regression model,

345 which is significant for all time-series examined (see Appendix D). However, there is a large variability  
346 in spatial distribution of Nile perch as the model explains only 10% to 40% of the deviance in  
347 encounter rate. Patch densities are equally variable as only 8% to 31% of the deviance is explained by  
348 depth and time. Both results highlight the large variability in experimental catches and the spatial  
349 heterogeneity in Nile perch abundances (Cornelissen et al. 2015; Taabu-Munyaho et al. 2013; Taabu-  
350 Munyaho et al. 2014).

351           Following 1970, Nile perch encountered in experimental trawl hauls changed in terms of  
352 their size, from large adults to small recruits, in their depth distribution, from shallow to deep, and in  
353 their location, from northern parts of the lake to southern parts (Figure 7A,B,C). By 1969, in the  
354 shallow Ugandan part of the lake, adults ( $\geq 70$  cm) were encountered already in 10% of the hauls,  
355 increasing to 35-40% in recent years. In Tanzania adult encounters started from low levels to 12-25%  
356 of the hauls at the start of the upsurge in 1983, peaked around 1990 and since decreased to levels  
357 comparable with Uganda. Sub-adult (between  $\geq 15$  and  $<70$  cm) encounter rates were very low prior  
358 to the start of the Nile perch boom, but increased rapidly to 90-95% of the hauls in Tanzanian  
359 shallow waters around the end of the 1980s, while in Uganda the sub-adult population development  
360 started later and peaked 5-7 years later. The upsurge in Nile perch recruits was more pronounced,  
361 more rapid and occurred later than the increase in adults and sub-adults. The start of the  
362 recruitment burst was both less concentrated in time and possibly later in Uganda compared to  
363 Tanzania. Loss of raw data in the crucial period between 1984 and 1988 may have obscured the  
364 precise timing, but no recruits were found by experimental fishing in 1984 while they were present in  
365 virtually all hauls from 1988 onwards. In both countries Nile perch encounter rates of all sizes were  
366 highest at 20 m depth and lowest at 45 m depth. Expansion into deeper waters is still ongoing for all  
367 size categories (Figure 7A,B,C).

368           Adult Nile perch was well established prior to the surge where it occurred: patch densities  
369 ( $CPUE_{p0}$ ) in Uganda remained remarkably stable before and after the switch where it hovered

370 between 4-8 kg/ha in 1969 and 7-10 kg/ha in 2011 (Figure 7D). In Tanzania adult patch density  
371 increased at all depths from 1969 onwards by around a factor 2-3 to around 8 kg/ha till the end of  
372 the 1990s, similar to Uganda. Sub-adult patch densities increased with different speeds in the two  
373 countries and depths but were around 14-16 kg/ha by 2011. Patch densities of recruits in shallow  
374 waters increased rapidly after 1985 but leveled off around 1995 in Uganda. The same level was  
375 reached in Tanzania 10 years later following a plateau between 1987 and 2000. In deeper waters  
376 recruitment levels still continue to increase but always around 4x higher in Tanzania than in Uganda.  
377 Surprisingly, in Tanzania patch biomass added over all sizes increased only by a factor 1.5 - 2 between  
378 1975 and 1988. Since then it increased and leveled off at a factor 2.4-2.6 depending on depth  
379 between 2000 and 2011. In Uganda total patch biomass continues to increase (at least until 2011)  
380 without any signs of leveling off to a factor 1.4 -1.8 of the 1975 level.

381           The adult relative biomass ( $CPUE_{ad}$ ) highlights the different developments in the north and  
382 south. In Uganda the estimated adult biomass was initially 2.5 to 10 times higher than in Tanzania,  
383 increased by a factor 4-5 until it stabilized around 1983 with some fluctuations after the switch; in  
384 contrast adult relative biomass in Tanzania increased with a factor 50-100 until the early 1990-ies  
385 after which it stabilized or decreased to similar levels as in Uganda. In both areas and at all depths  
386 both sub-adult and recruit relative biomass continued to increase to level off in shallow waters only  
387 in recent years. In 2011 the total relative biomass over all sizes was still increasing in both the  
388 Ugandan and Tanzanian parts of the lake.

### 389 **Results of the size-spectrum model**

390           In the single-species size-spectrum model, a haplochromine-like species can successfully  
391 establish from a low density with only the resource spectrum as an initial food supply. In contrast,  
392 when run as a single-species model, Nile perch on its own cannot establish from low introduced  
393 densities. Instead, it requires a “trophic ladder” (Hartvig et al. 2011), i.e. a smaller resident species to  
394 provide a food source to allow juvenile Nile perch to grow to adulthood. In the two-species model,



395 the introduction of a small population of large (between 4.4 kg and 12 kg) adult Nile perch to an  
396 established resident haplochromine population leads to an initial expansion of the Nile perch  
397 population (Figure 8), after which the system settles down to co-existence. During co-existence, the  
398 haplochromine biomass is reduced to approximately 60% of the pre-invasion level and larger sized  
399 haplochromines (>18 g) almost disappear from the distribution (98% decline). The total biomass of  
400 the resident species is around 3 times the Nile perch biomass, which is dominated by adults ( $\geq 70$  cm)  
401 with relatively few juveniles (<70 cm) and a juvenile to adult biomass ratio of 0.2.

402 To induce a switch from stable co-existence, an increased external mortality rate of 5 /yr was  
403 applied to the adult (>6 gr) haplochromines. This caused a rapid decline and eventual collapse of the  
404 haplochromines and a simultaneous increase in juvenile Nile perch over the following 8-10 years  
405 (Figure 8, 6B). During this period, the adult Nile perch biomass remains relatively unchanged, but the  
406 juvenile to adult biomass ratio increases from 0.2 to 2.4. The predicted speed of the switch depends  
407 on the external mortality rate applied to the haplochromines: the higher the external mortality rate,  
408 the faster the switch. At a mortality rate of 5 /yr, the duration of the switch is around 10 years.  
409 However, the minimum additional mortality rate on the adult haplochromines needed to cause the  
410 switch is around 4 /yr, while an overall mortality of 1 /yr is sufficient if all size classes of the  
411 haplochromines are affected rather than just fish of >6g. Applying a fishing mortality of  $F=0.5$  /yr to  
412 Nile perch > 40cm, starting simultaneously with the external mortality on haplochromines reduces  
413 the density of adult Nile perch, but otherwise doesn't have a major impact: the switch still takes  
414 place and almost as rapidly. However, we stress the point that the haplochromine 'collapse' is not an  
415 alternative stable state: removing the additional mortality before the haplochromine goes extinct  
416 results in a return to co-existence. So, the coexistence state is stable and the Nile perch only state is  
417 unstable. This means that, in a single patch, the Nile perch can never drive the haplochromines to  
418 complete collapse on its own. Adding dispersal between patches to the model does not change this  
419 prediction because dispersal can never stabilize the unstable Nile-perch only equilibrium (Appendix  
420 D). It is possible that dispersal could destabilize the coexistence state. This could lead to periodic

421 solutions (similar to a predator-prey cycle), asymmetric solutions (e.g. large Nile perch population  
422 and small haplochromine population in one patch and vice versa the next) or more complex  
423 dynamics. However, without external mortality, it cannot lead to extirpation of the haplochromines  
424 in either patch.

#### 425 **Confronting the size-spectrum model with the data**

##### 426 *Size-spectrum model prediction 1: development of Nile perch and haplochromine biomass*

427 The size-spectrum model results broadly match with the survey observations during the late  
428 1970s and early/mid 1980s, when the haplochromine collapse was accompanied by a rapid increase  
429 in numbers of juvenile Nile perch. Both in Tanzania and Uganda, there were few observations of  
430 juveniles prior to 1982 – hence the ratio is close to 0 (Figure 9A). After 1982, the juvenile to adult  
431 biomass ratios ranged on average from 0.3 to 8 in 2011. The model ratio predictions on co-existence  
432 and Nile perch only states imply that in Tanzania the system became unstable between 1975/8 (20-  
433 45 m depth) and 1982 (5 m), and switched to an, on average, Nile perch only state in 1983 (20 m),  
434 1985 (45 m) and 2000 (5 m) (Figure 9A). Correspondingly, in the Mwanza Gulf, the recruitment burst  
435 was observed in 1985 (Figure 6A,B). In Uganda the system became unstable around 1982 (5 m depth)  
436 and 1986 (>20 m), and the predicted ratio of juvenile to adult ratio of the Nile perch only state was  
437 reached on average in 1991, three years after the observed recruitment burst (Figure 9B). The  
438 observed duration of the development from co-existence to Nile-perch only was 7-10 (45-20 m), to  
439 20 years (5 m) in Tanzania and between 7 (5-20 m) to 35 years (45 m) in Uganda (Figure 9A). The  
440 observed switch in much of the lake's waters therefore was faster than or as fast as predicted by the  
441 size-spectrum model using an external haplochromine adult mortality rate of 5 /yr. This suggests that  
442 in reality adult mortality rates of haplochromines would have been higher, or that mortality occurred  
443 over a wider size range of haplochromines simultaneously.

444 During co-existence in the size-spectrum model, total Nile perch biomass is about  $0.22 \text{ g/m}^3$   
445 and the haplochromine biomass is  $0.67 \text{ g/m}^3$  corresponding to a haplochromine: Nile perch (H/L)

446 biomass ratio of about 3. The observed pre-switch H/L ratio was around 10 in Uganda and around  
447 200 in Tanzania. In the Winam Gulf (Kenya), pre-switch H/L ratios were measured at 34 and 10  
448 (Figure 9B). H/L ratios decreased in all countries and the predicted co-existence ratios were passed  
449 around 1979 (Kenya), 1983 (Uganda) and 1985 (Tanzania), coinciding with the appearance of Nile  
450 perch recruits <15 cm in Kenya and Tanzania. Haplochromines nearly vanished shortly after the  
451 switch, but started increasing again from the early 1990s onwards (Figure 4). Presently, in waters less  
452 than 20 m depth in Tanzania, the H/L ratio is back up to around 3 (Figure 9B).

453 *Size-spectrum model prediction 2: did fishing disturb co-existence?*

454 Fishing on haplochromines took place all over the lake in the 1970s (Marten 1979). Between 1969  
455 and 1985, Tanzanian catch and biomass estimates result in back-calculated fishing mortalities of 0.04  
456 – 0.31 /yr (Table 3), much lower than the 4 /yr required to induce the switch in the model. The  
457 average exploitation (C/P) ratio was 0.09, indicating that on average less than 10% of the annual  
458 demersal production was fished. These estimates do not take into account the 63% pelagic fraction  
459 of the haplochromine biomass (Witte et al. 2012), nor the unfished haplochromine biomass deeper  
460 than 30 m. Between 1974 and 1982, the observed haplochromine demersal biomass decreased by  
461 150,000 ton, which corresponds to a decrease of 61% of the productive capacity. Even if catch was  
462 underestimated, exploitation rates would need to be at least 5 times higher than reported to explain  
463 the observed decrease in demersal biomass.

464 According to Goudswaard (2008), the Nile perch upsurge started in the Winam Gulf, a 1400 km<sup>2</sup>  
465 enclosed Gulf comprising 20% of the Kenyan area of the lake, followed by a migrating wave of sub-  
466 adult Nile perch that spread anti-clockwise around the lake and subsequently triggered switches as  
467 the wave hit new areas. This domino effect was thought to have been activated by a local decline in  
468 haplochromine biomass caused by fishing in the Winam Gulf (Goudswaard, 2008). Reported catches  
469 from Winam Gulf result in estimated fishing mortality rates of 0.15 - 0.46 /yr and exploitation (C/P)  
470 ratios of 0.20 - 0.26, much higher than in Tanzania, but still considerably lower than what is required

471 to induce the switch in the model. In 1979 Nile perch recruitment had started (Goudswaard et al.  
472 2008) and the H/L ratio had dropped to 1.3, well below the co-existence level predicted by the model  
473 (Figure 9B). Between 1977 and 1979 a decrease of 10 kg/ha in demersal haplochromine biomass was  
474 observed (Table 3). To produce this decrease by fishing alone would have required a catch twice as  
475 high as the reported total catch of 3000 ton annually over the two years. Likewise a fishing mortality  
476 of 4 /yr needed to induce a switch, would require a catch of 7300 ton/yr, around 2.7 times higher  
477 than the reported total haplochromine catch. Fishing pressure was relatively high and thus may have  
478 speeded up the observed haplochromine decline in the Winam Gulf, and it is indeed the first area in  
479 the lake where the Nile perch switch was observed. But fishing mortality alone was, according to our  
480 model, probably not high enough to produce the observed rapid local haplochromine biomass  
481 decrease needed to instigate the switch.

482 *Size-spectrum model prediction 3: did Nile perch predation disturb co-existence?*

483 Neither can the decrease in haplochromine biomass be attributed to an increase in Nile perch  
484 biomass. In Tanzania the strongest decrease in haplochromine biomass was between 1976 and 1979  
485 when Nile perch stocks were still very low (Figure 4, 7). Then the demersal relative biomass of  
486 haplochromines fluctuated around 550 kg/hr (CV=33%), just before the next rapid decrease when the  
487 Nile perch took over in 1985. By comparison, in Uganda, the haplochromine biomass initially  
488 increased after 1970 despite the much higher abundance of Nile perch over the whole pre-surge  
489 period. The decline started in 1981, and stocks collapsed after 1983. In the Winam gulf the 1977 Nile  
490 perch biomass estimate was 2.8 kg/ha (Muller and Benda 1981) largely consisting of adults. Given a  
491 consumption ratio  $Q/B=2.41$  /yr (Moreau 1995), the Nile perch would consume around 950 ton/yr  
492 corresponding to 6% of the total demersal and pelagic production of haplochromines, insufficient to  
493 produce a collapse.

494 *Size-spectrum model prediction 4: did eutrophication disturb co-existence?*

495 While primary productivity doubled since 1962, algal biomass increased 4-10 fold (Hecky et al.  
496 2010) and eutrophication also changed the size spectrum of phyto- and zooplankton (Jackson 2004;  
497 Yasindi and Taylor 2003) as well as water turbidity. Thus the available food resources to juvenile  
498 haplochromines and Nile perch may have changed. We modelled such a change by reducing the  
499 plankton abundance available to fish. Reducing the overall plankton resource in the size-spectrum  
500 model reduces the initial food supply equally for small haplochromines and Nile perch. This causes a  
501 drop in biomass for both, but, although the drop is larger for haplochromines, it will not instigate a  
502 Nile perch boom or a haplochromine collapse. If, however, the plankton availability is reduced for  
503 haplochromines, but maintained for Nile perch, then the switch does occur similar to the results  
504 shown (Figure 7). Thus, a reduction in those plankton resources available to haplochromines without  
505 a reduction in plankton resources available to Nile perch is a potential alternative mechanism to  
506 cause a switch.

## 507 Discussion

508 Two alternative hypotheses and associated mechanisms have been suggested to explain the  
509 demise of the haplochromines and takeover of the Lake Victoria fish assemblage by Nile perch: a  
510 trophic cascade instigated by Nile perch predation on haplochromines and released recruitment  
511 depensation. Before we discuss these hypotheses, we give a brief summary of the more remarkable  
512 features that have emerged from the observed trends in long term data series and the confrontation  
513 of model predictions with these observations: (1) the initial rapid lake wide expansion of large adult  
514 Nile perch from a small number of introduced sub-adults without any measureable amounts of  
515 recruits; (2) the two decades of relatively stable co-existence between adult Nile perch and  
516 haplochromines, which we suggest can be a result of intraguild, size-dependent, predation (Van de  
517 Wolfshaar et al. 2006); (3) the high level of external mortality of haplochromines that the size-  
518 spectrum model requires to induce a switch to a Nile perch dominated state; (4) the good  
519 correspondence between the predictions of the size-spectrum model with external mortality of

520 haplochromines and the observed development in the demographic structure of the Nile perch  
521 stock; (5) the spatial developments of the Nile perch population in the lake, with continued  
522 expansion into the deep offshore waters, as well as continued increase in relative biomass, both  
523 indicating that the colonization of Lake Victoria by Nile perch is still not complete; and (6) the gradual  
524 recent return of the haplochromines to densities at predicted co-existence levels.

525         The most straightforward explanation of the Nile perch invasion is a simple trophic cascade  
526 (Downing et al. 2013). However, this hypothesis does not really fit with the observed demographic  
527 size structure and the sequence of biomass developments in both Nile perch and haplochromines.  
528 Between 1969 and 1980, the years where logistic growth was supposed to be in a log-linear phase,  
529 the observed Nile perch growth rates at different depths were in the range 0.29-0.37/yr in Tanzania  
530 and 0.15-0.18 /yr in Uganda, thus much lower than 0.73 /yr used in the logistic growth model (Figure  
531 10B). In addition, Nile perch was fished almost immediately after its introduction putting constraints  
532 on the logistic growth (Figure 10A). The development in Nile perch catches may suggest an  
533 underlying logistic process in biomass development but is as dependent on a starting fishery. Early  
534 catch reports may not be reliable, but imply very high harvest rates ( $H=C/B$ ) prior to 1975 (Figure  
535 10A). Lastly, under steady-state conditions, the observed resurgence of haplochromines does not  
536 conform to the mechanism behind logistic growth; Nile perch has not changed its prey preferences,  
537 its population is still increasing and by 2011 may even not have reached its carrying capacity (Figure  
538 4,7). Thus several empirical observations contradict the hypothesis of a simple trophic cascade. Our  
539 analysis largely supports Goudswaard et al.'s (2008) description of the chronology and initiation of  
540 the Nile perch switch in Lake Victoria. But there are few data to support the hypothesis that a wave  
541 of sub-adult Nile perch originating in Kenya was sufficient to induce a cascading domino effect. The  
542 size-spectrum model predicts that, in a well-mixed lake, coexistence of Nile perch and a  
543 haplochromine-like species is stable. Conversely, the Nile-perch only state is unstable to the  
544 introduction of a small population of haplochromines. Including spatial heterogeneity and dispersal  
545 in the model would not change this key result. In particular, if the Nile perch density increased in a

546 localised part of the lake for some reason, dispersal would eventually cause this area to revert to  
547 coexistence, rather than to propagate the switch to adjacent areas of the lake. Hence, the switch in  
548 the Winam Gulf (Kenya) would likely have remained a local affair were it not for the decrease in  
549 stocks over most of the lake areas in the years prior to the lake-wide switch, still with low Nile perch  
550 densities and no recruitment. Given the similar larval feeding habits of Nile perch and  
551 haplochromines, but strikingly different early life history strategies, and absence of Nile perch  
552 recruitment until after the surge, it is reasonable to assume that predator-prey interactions may have  
553 been reciprocated and that depensation may have prevented a simple or locally induced cascade.

554           Although the two-species size-spectrum model gives a very simplified picture of the complex  
555 assemblage of haplochromines in Lake Victoria and their diverse range of adult feeding and habitat  
556 niches, it nevertheless suggests that stable co-existence was possible for the two first decades after  
557 introduction. During coexistence in our model, haplochromines had a depensatory effect on the Nile  
558 perch population, via strong predation on its miniscule and unprotected egg and fry stages, which  
559 would explain the empirically observed absence of juveniles. Co-existence through haplochromine  
560 predation on Nile perch was proposed by Walters and Kitchell (2001) and predicted from a  
561 consumer-resource model by van de Wolfshaar et al. (2014), who used a “foraging arena” approach  
562 to predator consumption. They assumed that at decreasing haplochromine densities, the more  
563 sheltered, and harder to catch species, e.g. rock cichlids, were the ones remaining. However,  
564 empirical data show that co-existence was not just between rock-dwelling species inaccessible to  
565 open water Nile perch, but existed in all habitats. For instance, during a 1995-96 acoustic survey in  
566 the Ugandan part of the lake, 84% of the pelagic fish biomass was haplochromines (Tumwebaze  
567 1997). Based on our analysis, we propose that co-existence depends on size-related differences in  
568 early juvenile feeding and survival caused by mouth brooding of the haplochromines. This is another  
569 “foraging arena” but one that does not require a spatial separation of haplochromines with different  
570 vulnerabilities to predation: the functional response emerges directly from size-based predation  
571 processes and the behavior of haplochromines. Only when the haplochromines are subjected to

572 additional external mortality, our model suggests, the control on the introduced Nile perch is  
573 gradually lost with subsequent cascading collapse of the resident species and the appearance of Nile  
574 perch recruits.

575 Expansion of Nile perch still takes place (Figure 7), but the observed gradual lake-wide  
576 population growth pattern of Nile perch is not predicted by the size-spectrum model as it has no  
577 spatial dimension and hence contains no information on dispersal processes. But co-existence takes  
578 place at the patch level: the observed developments in Nile perch patch densities and recruitment  
579 are reflected in the results of the size spectrum-model, indicating that co-existence between Nile  
580 perch and haplochromines is possible. Patch densities of adult Nile perch in Uganda were stable  
581 before and after the switch as predicted (Figure 7D). In Tanzania Nile perch arrived at least 7 years  
582 after the first introduction. Twenty years later, by the time of the switch, it had on average not yet  
583 reached the predicted co-existence levels. This implies that the development towards coexistence is  
584 slower than the 8-10 years suggested by the model. Modelled total Nile perch biomass increased by  
585 a factor 1.9 (with fishing) to 2.6 (without) from pre-switch levels, which is close to the observed total  
586 patch biomass increase since 1975 in Tanzania and Uganda (factor 2.4-2.6 and 1.4–1.8 respectively).  
587 The model stabilizes within 10-13 years after the external mortality on haplochromines and between  
588 15-20 years after the recruitment burst of 1985 as observed in Tanzania (Figure 8).

589 Species diversity aspects are ignored in the present analysis. The size-spectrum model  
590 collapses the formerly 500+ species rich haplochromine assemblage consisting of many stenotopic  
591 species with differing ecologies, into one generalized resident species with maximum size and large  
592 protected fry as main traits (Table 2). Loss of diversity, in particular the early loss of large piscivorous  
593 haplochromines (Witte et al. 1992), could have played a facilitating role in the Nile perch invasion.  
594 Nevertheless, haplochromine diversity is not needed in our model. Fry of most haplochromines start  
595 feeding on zooplankton and most of the trophic niche specialization emerges only later during  
596 ontogeny. Our model result then would imply that it is the total biomass of adult haplochromines



597 that determines co-existence. The size spectrum model also predicts a loss of 98% of the largest  
598 haplochromines over 18 g during the first 10 years of co-existence. Hence, size specific predation,  
599 and possibly competition with Nile perch could result in loss of predatory haplochromine species  
600 diversity already during the stable co-existence phase. This may explain the observed early demise of  
601 many large piscivores among the cichlids (Witte et al. 1992). We cannot exclude the hypothesis that  
602 a decline in larger piscivorous haplochromines (Witte et al. 2007), rather than total haplochromine  
603 biomass, was sufficient to initiate the Nile perch upsurge. But then it remains to be explained why  
604 the burst took place 3-5 years after the observed decline of the large piscivores in all areas where  
605 adult Nile perch was present prior to the boom. No spatial effect of the haplochromine filter can be  
606 expected here as Nile perch recruits are encountered all over the lake - though more so in shallow  
607 waters - and many small adult sized piscivorous Haplochromine species existed as well just prior to  
608 the Nile perch recruitment burst.

609 External reduction of the haplochromines needed for disrupting co-existence in the model  
610 was larger than can be reasonably explained by fishing mortality alone. If so, then fishing on  
611 haplochromines was at most a proximate cause exacerbating the negative effects on already  
612 declining haplochromine stocks, but not sufficient on its own. Additional mortality may likely be  
613 sought in the changes associated with long term eutrophication, as first proposed by Hecky (1993).  
614 Our model suggests that a reduction in resource availability specific to haplochromines, but not  
615 affecting Nile perch is a potential alternative mechanism to increased haplochromine mortality. The  
616 concomitant fundamentally transformed zooplankton and phytoplankton assemblages altering the  
617 trophic base for the haplochromine assemblage, as well as increased hypoxia and decreased visibility  
618 for successful mating and feeding have been proposed as agents (Hecky et al. 1994; Hecky et al. 2010;  
619 Seehausen et al. 1997a; Seehausen et al. 2003). Theory predicts that loss of visibility impairs feeding  
620 efficiency of specialized predators, and predator populations would become less productive and/or  
621 less specialized (Seehausen et al. 2003). Both of these effects have been documented for Lake  
622 Victoria by Witte et al. (2013), who concluded that reduced water transparency had a negative

623 impact on species coexistence through effects on both reproduction and feeding behaviour. After  
624 1969, the Winam Gulf experienced a severe decline in transparency because of mineral turbidity  
625 from soil erosion which lead to an approximately 50% reduction in Secchi Disc transparency and a  
626 nearly proportional decline in primary productivity (Gikuma-Njuru et al. 2013) . From 1975, a decade  
627 of prolonged low windstress (Figure 3A) caused lake-wide shallower stratification (MacIntyre 2013)  
628 with ensuing blooms of cyanobacteria, resulting in increased anoxic volume, a decrease in large  
629 diatoms (Hecky et al. 2010) and a rapid decline in visibility in the mixed layer. Haplochromines were  
630 thus likely affected both by reduced visibility and reduced accessibility to plankton resources. The  
631 rapid decline in visibility in the mixed layer (Hecky et al. 2010; Mugidde 1993; Silsbe et al. 2006)  
632 coincided with the rapid decrease in haplochromine biomass as observed in Tanzania. Whether  
633 lowered visibility would affect Nile perch recruits similarly may be irrelevant as the decrease resulted  
634 in the release of the huge recruitment potential of Nile perch and sheer numbers would have  
635 resulted in the recruitment burst anyway. Moreover, unlike haplochromines, Nile perch eyes are  
636 equipped with a tapetum lucidum (Seehausen et al. 2003). In closely related Barramundi (Lates  
637 calcarifer) this structure develops already 10 days after hatching (size app. 5.6 mm) allowing feeding  
638 under low light conditions (Yahaya et al. 2011). The ontogeny of the tapetum lucidum in Nile perch is  
639 not known, but if similar, it may lead to a competitive predatory advantage over like sized juvenile  
640 haplochromines.

641           Another aspect of eutrophication is the overall increased productivity of the lake (Kolding et  
642 al. 2008). Immediately after the surge of Nile perch a large fishery developed; catches rapidly  
643 increased and have been fluctuating around 240000 ton since 1987. Under steady state conditions  
644 the biomass would have been stable or decreasing. However, up until the end of the time series  
645 (2011) Nile perch biomass has continued to increase at all depths, but particularly in deeper waters.  
646 This indicates that primary and secondary productivity may have increased to sustain the catches  
647 (Kolding et al. 2008). But it also indicates that deeper waters have become more habitable for Nile  
648 perch, suggesting that effects of deoxygenation following stratification may now be less severe than

649 during the switch phase. This is supported by a resumed wind stress and mixing since around 1990  
650 (Figure 3A) (Cózar et al. 2012; MacIntyre 2013). Since 1998 no ENSO events have occurred to induce  
651 strong stratification, resulting in more benign oxygen conditions as well as increased visibility  
652 (Cornelissen et al. 2014; MacIntyre et al. 2014; Marshall et al. 2013).

653         The haplochromine stocks have also gradually increased again since the early 1990s and the  
654 haplochromine to Nile perch biomass ratio of 2011 is close to the predicted level of renewed co-  
655 existence (Figure 9B). In addition, if the proposed mechanism of depensation through a  
656 haplochromine fry predation filter is indeed operating, then a reversal to cichlid domination again is  
657 possible. If so, then both previous observations and our model predict a strongly reduced Nile perch  
658 recruitment, and a strong decrease in the adult stock that would severely affect the lucrative Nile  
659 perch fishery. However, while pre-biomass ratios have almost restored, neither juvenile:adult Nile  
660 perch ratios nor recruitment levels of Nile perch have decreased, and the predicted consequences of  
661 the reversal have not – yet? – occurred. The current haplochromine species assemblage also has  
662 little resemblance to the pre-switch stage, as it consists primarily of demersal and pelagic taxa that  
663 used to feed on detritus and zooplankton before their near-extirpation but some of which now feed  
664 on a mixed diet with benthic macro invertebrates (Downing et al. 2014). None of the pelagic and  
665 bathypelagic piscivore species shows any sign of recovering, except a pelagic species, now in a dwarf  
666 form that may not feed on fish but probably on zooplankton (Seehausen pers. obs.). Given that the  
667 new haplochromine assemblage appears better adapted to the effects of eutrophication (Witte et al.  
668 2013, Witte et al. 2008) as well as to Nile perch predation, a stable co-existence between  
669 haplochromines and, perhaps, a reduced Nile perch stock may become likely. Haplochromines and  
670 *Lates* species coexist in other African Great Lakes as well, and so the Nile perch outburst in Lake  
671 Victoria, possibly a consequence of the haplochromine demise, was perhaps an anomaly.  
672 Nevertheless, eutrophication of the lake has continued unabated and the precarious climate  
673 conditions of low windstress and decreased mixing that likely contributed to the fundamental change

674 in the in 1980s may again return. Lake Victoria has, during the last century, gone through dramatic,  
675 unprecedented and unexpected changes and may yet surprise us again.

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## 689 **References**

- 690 Andersen, K.H., and Beyer, J.E. 2006. Asymptotic Size Determines Species Abundance in the Marine  
691 Size Spectrum. *The American Naturalist* **168**(1): 54-61.
- 692 Anderson, A.M. 1961. Further observations concerning the proposed introduction of Nile perch into  
693 Lake Victoria. *East African Agricultural and Forestry Journal* **26**: 195 - 201.
- 694 Balirwa, J.S., Chapman, C.A., Chapman, L.J., Cowx, I.G., Geheb, K.I.M., Kaufman, L.E.S., Lowe-  
695 McConnell, R.H., Seehausen, O.L.E., Wanink, J.H., Welcomme, R.L., and Witte, F. 2003. Biodiversity

- 696 and Fishery Sustainability in the Lake Victoria Basin: An Unexpected Marriage? *BioScience* **53**(8): 703-  
697 716.
- 698 Barel, C.D.N., Dorit, R., Greenwood, P.H., Fryer, G., Hughes, N., Jackson, P.B.N., Kawanabe, H., Lowe-  
699 McConnell, R.H., Nagoshi, M., Ribbink, A.J., Trewavas, E., Witte, F., and Yamaoka, K. 1985.  
700 Destruction of fisheries in Africa's lakes. *Nature* **315**(6014): 19.
- 701 Benoît, E., and Rochet, M.-J. 2004. A continuous model of biomass size spectra governed by  
702 predation and the effects of fishing on them. *J. Theor. Biol.* **226**(1): 9-21.
- 703 Bergstrand, E., and Cordone, A.J. 1971. Exploratory bottom trawling in Lake Victoria. *African Journal*  
704 *of Tropical Hydrobiology and Fisheries (Kenya)* **1**(1): 13 - 23.
- 705 Beyer, J.E. 1987. On length-weight relationships. Part I: Computing the mean weight of the fish in a  
706 given length class. *Fishbyte* **April** 11 - 13.
- 707 Boggs, C.L., Holdren, C.E., Kulahci, I.G., Bonebrake, T.C., Inouye, B.D., Fay, J.P., McMillan, A.N.N.,  
708 Williams, E.H., and Ehrlich, P.R. 2006. Delayed population explosion of an introduced butterfly. *J.*  
709 *Anim. Ecol.* **75**(2): 466-475.
- 710 Bridgeman, T.B. 2001. The ecology and paleolimnology of food web changes in Lake Victoria, East  
711 Africa, University of Michigan, Ann Arbor MI, USA.
- 712 Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting  
713 global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**(3): 235-251.
- 714 Cordone, A.J., and Kudhongania, A. 1971. Observations on the influences of codend mesh size on  
715 bottom trawl catches in Lake Victoria, with emphasis on the *Haplochromis* population pages. *African*  
716 *Journal of Tropical Hydrobiology and Fisheries* **1**(2): 1 - 19.

- 717 Cornelissen, I.J.M., Silsbe, G.M., Verreth, J.A.J., van Donk, E., and Nagelkerke, L.A.J. 2014. Dynamics  
 718 and limitations of phytoplankton biomass along a gradient in Mwanza Gulf, southern Lake Victoria  
 719 (Tanzania). *Freshwater Biology* **59**(1): 127-141.
- 720 Cornelissen, I.J.M., van Zwieten, P.A.M., Peter, H.K., and Nagelkerke, L.A.J. 2015. Nile perch  
 721 distribution in south-east Lake Victoria is more strongly driven by abiotic factors, than by prey  
 722 densities. *Hydrobiologia* **755**(1): 239-255.
- 723 Cózar, A., Bruno, M., Bergamino, N., Úbeda, B., Bracchini, L., Dattilo, A.M., and Loiselle, S.A. 2012.  
 724 Basin-Scale Control on the Phytoplankton Biomass in Lake Victoria, Africa. *PLoS ONE* **7**(1): e29962.
- 725 Datta, S., Delius, G., and Law, R. 2010. A Jump-Growth Model for Predator–Prey Dynamics: Derivation  
 726 and Application to Marine Ecosystems. *Bull. Math. Biol.* **72**(6): 1361-1382.
- 727 Downing, A., Galic, N., Goudswaard, K., van Nes, E., Scheffer, M., Witte, F., and Mooij, W.M. 2013.  
 728 Was Lates Late? A Null Model for the Nile Perch Boom in Lake Victoria. . *PLoS ONE* **8**(10): e76847.
- 729 Downing, A.S., van Nes, E.H., Balirwa, J.S., Beuving, J., Bwathondi, P.O.J., Chapman, L.J., Cornelissen,  
 730 I.J.M., Cowx, I.G., Goudswaard, K.P.C., Hecky, R.E., Janse, J.H., Janssen, A.B.G., Kaufman, L., Kische-  
 731 Machumu, M.A., Kolding, J., Ligtvoet, W., Mbabazi, D., Medard, M., Mkumbo, O.C., Mlaponi, E.,  
 732 Munyaho, A.T., Nagelkerke, L.A.J., Ogutu-Ohwayo, R., Ojwang, W.O., Peter, H.K., Schindler, D.E.,  
 733 Seehausen, O., Sharpe, D., Silsbe, G.M., Sitoki, L., Tumwebaze, R., Tweddle, D., van de Wolfshaar, K.E.,  
 734 van Dijk, H., van Donk, E., van Rijssel, J.C., van Zwieten, P.A.M., Wanink, J., Witte, F., and Mooij, W.M.  
 735 2014. Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's  
 736 ecosystem services. *Ecology and Society* **19**(4 C7 - 31).
- 737 Duponchelle, F., Ribbink, A.J., and (eds.). 2000. Fish Ecology Report. Lake Malawi/Nyasa/Niassa  
 738 Biodiversity Conservation Project. SADC/GEF (Southern African Development Community, Gaborone,  
 739 Botswana / Global Environmental Facility, Washington, D.C.).

- 740 EAF/LVFO. 2013. Revised Nile Perch fishery management plan (NPFMP2) for Lake Victoria: years  
741 2014 - 2019. SOFRECO, ACP Fish II programme, East African Community.
- 742 Everson, I., Taabu-Munyaho, A., and Kayanda, R. 2013. Acoustic estimates of commercial fish species  
743 in Lake Victoria: Moving towards ecosystem-based fisheries management. *Fish. Res.* **139**: 65 - 75.
- 744 Fryer, G. 1960. Concerning the proposed Introduction of Nile perch into Lake Victoria. *East African*  
745 *Agricultural Journal* **25**: 267-270.
- 746 García-Berthou, E. 2007. The characteristics of invasive fishes: what has been learned so far? *J. Fish*  
747 *Biol.* **71**: 33-55.
- 748 Gikuma-Njuru, P., Guildford, S.J., Hecky, R.E., and Kling, H.J. 2013. Strong spatial differentiation of N  
749 and P deficiency, primary productivity and community composition between Nyanza Gulf and Lake  
750 Victoria (Kenya, East Africa) and the implications for nutrient management. *Freshwater Biology*  
751 **58**(11): 2237-2252.
- 752 Goudswaard, P.C. 2006. Causes and effects of the Lake Victoria ecological revolution. PhD, Faculty of  
753 Mathematics and Natural Sciences and those of Medicine, Leiden University, Leiden.
- 754 Goudswaard, P.C., Witte, F., and Katunzi, E.F.B. 2008. The invasion of an introduced predator, Nile  
755 perch (*Lates niloticus* L.) in Lake Victoria (East Africa): chronology and causes. *Env. Biol. Fish.* **81**: 127 -  
756 139.
- 757 Goudswaard, P.C., Witte, F., and Wanink, J.H. 2006. The shrimp *Caridina nilotica* in Lake Victoria (East  
758 Africa), before and after the Nile perch increase. *Hydrobiologia* **563**: 31 - 34.
- 759 Greenwood, P.H. 1974. Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a  
760 species flock. John Wright and Sons Ltd., Stonebridge Press, Bristol, UK.

- 761 Haddon, M. 2011. Modelling and quantitative methods in fisheries. CRC Press, Taylor & Frances  
762 Group, Boca Raton, US.
- 763 Hartvig, M., Andersen, K.H., and Beyer, J.E. 2011. Food web framework for size-structured  
764 populations. *J. Theor. Biol.* **272**: 113 - 122.
- 765 Hecky, R.E. 1993. The eutrophication of Lake Victoria. *Verhandlungen des Internat. Verein. Limnol.* **25**:  
766 39 - 48.
- 767 Hecky, R.E., Bugenyi, F.W.B., Ochumba, P., Talling, J.F., Mugidde, R., Gophen, M., and Kaufman, L.  
768 1994. Deoxygenation of the Deep Water of Lake Victoria, East Africa. *Limnol. Oceanogr.* **39**(6): 1476.
- 769 Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., and Kling, G.W. 2010. Multiple stressors cause  
770 rapid ecosystem change in Lake Victoria. *Freshwater Biology* **55**: 19-42.
- 771 Hopson, A.J. 1969. A description of the pelagic embryos and larval stages of *Lates niloticus* (L.)  
772 (*Pisces* : *Centropomidae*) from Lake Chad, with a review of early development in lower percoid fishes.  
773 *Zoological Journal of the Linnean Society* **48**(1): 117-134.
- 774 Jackson, V.S. 2004. The production and fate of picoplankton and protozoa in the pelagic food web of  
775 Napoleon Gulf, Lake Victoria, East Africa, University of Waterloo, Waterloo, Ontario, Canada.
- 776 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G.,  
777 Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C.,  
778 Wang, J., Leetmaa, A., Reynolds, R., Jenne, R., and Joseph, D. 1996. The NCEP/NCAR 40-year  
779 reanalysis project. *Bull. Am. Met. Soc.* **77**: 437 - 471.
- 780 Kanamitsu, M., Ebisuzaki, W., Woollen, J., Yang, S.-K., Hnilo, J.J., Fiorino, M., and Potter, G.L. 2002.  
781 NCEP-DEO AMIP-II Reanalysis (R-2). *Bulletin of the Atmospheric and Meteorological Society* **83**(1631  
782 - 1643).



- 783 Kling, H.J., Mugidde, R., and Hecky, R.E. 2001. Recent changes in the phytoplankton community of  
784 Lake Victoria in response to eutrophication. *In* Great Lakes of the World: food webs, health and  
785 integrity. *Edited by* M. Munawar and R.E. Hecky. Backhuys, Leiden, the Netherlands. pp. 47 - 66.
- 786 Kolding, J., Medard, M., Mkumbo, O., and van Zwieten, P.A.M. 2013. Status, trends and management  
787 of the Lake Victoria Fisheries. *In* Inland fisheries evolution and management - case studies from four  
788 continents. *Edited by* R.L. Welcomme, J. Valbo-Jorgensen and A.S. Halls. Food and Agriculture  
789 Organisation of the UN, Rome, Italy.
- 790 Kolding, J., van Zwieten, P.A.M., Manyala, J., Okedi, J., Mgaya, Y.D., and Orach-Meza, F. 2005. Lake  
791 Victoria Environmental Management Program (LVEMP): Regional Synthesis Report on Fisheries  
792 Research and Management. States, trends and processes. Final report prepared for LVEMP National  
793 Secretariat. Lake Victoria Environmental Management Program, Entebbe, Uganda.
- 794 Kolding, J., van Zwieten, P.A.M., Mkumbo, O., Silsbe, G., and Hecky, R.E. 2008. Are the Lake Victoria  
795 Fisheries Threatened by Exploitation or Eutrophication? Towards an Ecosystem-based Approach to  
796 Management. *In* The Ecosystem Approach to Fisheries. *Edited by* G. Bianchi and H.R. Skjoldal. CAB  
797 International, Rome. pp. 309 - 354
- 798 Kudhongania, A.W., and Cordone, A.J. 1974a. Batho-spatial distribution pattern and biomass  
799 estimate of the major demersal fishes in Lake Victoria. *African Journal of Tropical Hydrobiology and*  
800 *Fisheries* **3**: 15 - 31.
- 801 Kudhongania, A.W., and Cordone, A.J. 1974b. Past trends, present stock and possible future state of  
802 the fisheries of the Tanzanian part of Lake Victoria. *African Journal of Tropical Hydrobiology and*  
803 *Fisheries* **3**: 167 - 181.
- 804 Law, R., Plank, M.J., and Kolding, J. 2014. Balanced exploitation and coexistence of interacting, size-  
805 structured, fish species. *Fish and Fisheries*.

- 806 MacIntyre, S. 2013. Climatic variability, mixing dynamics, and ecological consequences in the African  
807 great lakes. *In* Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for  
808 Ecosystems and Societies, First Edition. *Edited by* C.R. Goldman, M. Kumagai and R.D. Robarts. John  
809 Wiley & Sons Ltd. pp. 311 - 336.
- 810 MacIntyre, S., Romero, J.R., Silsbe, G.M., and Emery, B.M. 2014. Stratification and horizontal  
811 exchange in Lake Victoria, East Africa. *Limnology and Oceanography* [Limnol Oceanogr] **59**(5): 34.
- 812 Marshall, B.E., Ezekiel, C.N., Gichuki, J., Mkumbo, O.C., Sitoki, L., and Wanda, F. 2013. Has climate  
813 change disrupted stratification patterns in Lake Victoria, East Africa? *African Journal of Aquatic  
814 Science* **38**(3): 249-253.
- 815 Marten, G.G. 1979. Impact of Fishing on the Inshore Fishery of lake Victoria (East Africa). *J. Fish. Res.  
816 Bd Can.* **36**: 891 - 900.
- 817 Mkumbo, O.C., and Marshall, B.E. 2014. The Nile perch fishery of Lake Victoria: current status and  
818 management challenges. *Fish. Manage. Ecol.*: n/a-n/a.
- 819 Moreau, J. 1995. Analysis of species change in Lake Victoria using ECOPATH, a multispecies trophic  
820 model. *In* The Impact of Species Changes in African lakes. *Edited by* T.J. Pitcher and P.J. Hart.  
821 Chapman and Hall, London. pp. 137 - 161.
- 822 Mugidde, R. 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria  
823 (Uganda). *Verhandlungen des Internat. Verein. Limnol.* **25**: 846-849.
- 824 Muller, R.G., and Benda, R.S. 1981. Comparison of bottom trawl stock densities in the inner  
825 Kavirondo Gulf of Lake Victoria. *J. Fish Biol.* **19**: 399 - 401.
- 826 Okaronon, J.O. 1999. The fish stocks of Lake Victoria. *In* Report on third Fisheries Data Working  
827 Group (FIDAWOG) workshop held at the Triangle Hotel, Jinja, 29 March to 1 April 1999. *Edited by*

- 828 D.a.C. Tweddle, I.G. Fisheries Data Working Group of the Lake Victoria Fisheries Research Project,  
829 Jinja, Uganda. pp. 30-37.
- 830 Persson, L., Amundsen, P.-A., de Roos, A.M., Klemetsen, A., Knudsen, R., and Primicerio, R. 2007.  
831 Culling prey promotes predator recovery - alternative stable states in a whole lake experiment.  
832 *Science* **316**: 1743 - 1746.
- 833 Pringle, R.M. 2005. The origins of the Nile perch in Lake Victoria. *BioScience* **55**(9): 780 - 787.
- 834 Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J.,  
835 Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., and Weller, S.G.  
836 2001. The Population Biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**(1): 305-332.
- 837 Scully, R.J. 1976a. The importance of Furu (the haplochromine " species flock" ) in Lake Victoria's gill  
838 net fishery. Part I of a completion report on the passive gear fishery in the Tanzania waters of Lake  
839 Victoria. East African Freshwater Fisheries Research Organsiation (E.A.F.F.R.O.), Mwanza, Tanzania.
- 840 Scully, R.J. 1976b. Species composition estimates of commercial and experimental gillnet catches  
841 from the Tanzania waters of Lake Victoria (October 1973 - january 1975). Part II of a completion  
842 report on the passive gear fishery in the Tanzania waters of Lake Victoria. East African Freshwater  
843 Fisheries Research Organsiation (E.A.F.F.R.O.), Mwanza, Tanzania.
- 844 Seehausen, O. 1996. Lake Victoria rock cichlids: taxonomy, ecology and distribution. *Verduyn cichlids*.
- 845 Seehausen, O., Alphen, J.J.M.v., and Witte, F. 1997a. Cichlid fish diversity threatened by  
846 eutrophication that curbs sexual selection. *Science* **277**: 1808-1811.
- 847 Seehausen, O., van Alphen, J.J.M., and Witte, F. 2003. Implications of eutrophication for fish vision,  
848 behavioral ecology and species coexistence. *In Conservation, Ecology, and Management of African*

- 849 Fresh Waters. *Edited by* T.L. Crisman, L.J. Chapman, C.A. Chapman and L.S. Kaufman. University Press  
850 of Florida, Gainesville, FL, USA.
- 851 Seehausen, O., Witte, F., Katunzi, E.F., Smits, J., and Bouton, N. 1997b. Patterns of the Remnant  
852 Cichlid Fauna in Southern Lake Victoria. *Conservation Biology* **11**(4): 890-904.
- 853 Silsbe, G.M., Hecky, R.E., Guildford, S.J., and Mugidde, R. 2006. Variability of chlorophyll a and  
854 photosynthetic parameters in a nutrient-saturated tropical great lake. *Limnol. Oceanogr.* **51**(5): 2052.
- 855 Stager, J.C., Hecky, R., Grzesik, D., Cumming, B., and Kling, H. 2009. Diatom evidence for the timing  
856 and causes of eutrophication in Lake Victoria, East Africa. *Hydrobiologia* **636**(1): 463-478.
- 857 Taabu-Munyaho, A., Kayanda, R.J., Everson, I., Grabowski, T.B., and Marteinsdóttir, G. 2013.  
858 Distribution and exploitation of Nile perch *Lates niloticus* in relation to stratification in Lake Victoria,  
859 East Africa. *Journal of Great Lakes Research* **39**(3): 466-475.
- 860 Taabu-Munyaho, A., Nyamweya, C.S., Sitoki, L., Kayanda, R., Everson, I., and Marteinsdóttir, G. 2014.  
861 Spatial and temporal variation in the distribution and density of pelagic fish species in Lake Victoria,  
862 East Africa. *Aquatic Ecosystem Health & Management* **17**(1): 52-61.
- 863 Talling, J.F. 1966. The annual cycles of stratification and phytoplankton growth in Lake Victoria (East  
864 Africa). *International Revue gesamten Hydrobiologie* **50**: 1 - 32.
- 865 Tsehaye, I., Machiels, M.A.M., and Nagelkerke, L.A.J. 2007. Rapid shifts in catch composition in the  
866 artisanal Red Sea reef fisheries of Eritrea. *Fish. Res.* **86**(1): 58-68.
- 867 Tumwebaze, R. 1997. Application of hydroacoustics in fish stock assessment of Lake Victoria. MPhil  
868 thesis, University of Bergen, Bergen, Norway.

- 869 Tumwebaze, R., Getabu, A., Bayona, MacLennan, D., and Cowx, I.G. 2002. Fisheries of Lake Victoria:  
870 an underwater perspective. *In* Management and Ecology of Lake and Reservoir Fisheries. *Edited by*  
871 I.G. Cowx. Fishing News Books, Blackwell Science, Oxford, UK. pp. 70-83.
- 872 van de Wolfshaar, K., HilleRisLambers, R., Goudswaard, K.C., Rijnsdorp, A., and Scheffer, M. 2014.  
873 Nile perch (*Lates niloticus*, L.) and cichlids (*Haplochromis* spp.) in Lake Victoria: could prey mortality  
874 promote invasion of its predator? *Theor Ecol* **7**(3): 253-261.
- 875 Van de Wolfshaar, K.E., de Roos, A.M., and Persson, L. 2006. Size-dependent interactions inhibit  
876 coexistence in intraguild predation systems with life-history omnivory. *The American Naturalist* **168**:  
877 62 - 75.
- 878 Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., and  
879 Hecky, R.E. 2002. History and timing of human impact on Lake Victoria, East Africa. *Proceedings of*  
880 *the Royal Society London B: Biological Sciences* **269**: 289-294.
- 881 Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and  
882 recruitment: implications for the theory of fishing *Can. J. Fish. Aquat. Sci.* **58**(1): 39-50.
- 883 Wanink, J. 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake  
884 Victoria. *Hydrobiologia* **407**(0): 183-189.
- 885 Wanink, J.H., Katunzi, E.F.B., Goudswaard, K.P.C., Witte, F., and van Densen, W.L.T. 2002. The shift to  
886 smaller zooplankton in Lake Victoria cannot be attributed to the 'sardine' *Rastrineobola argentea*  
887 (*Cyprinidae*). *Aquat. Living Resour.* **15**(1): 37-43.
- 888 Wanyala, B., and Marten, G. 1974. Survey of the Lake Victoria Fishery in Kenya. ANNUAL REPORT  
889 1974. East African Freshwater Fisheries Research Organization, Jinja, Uganda.

- 890 Welcomme, R.L. 1988. International introductions of inland aquatic species. FAO Fisheries Technical  
891 Paper. FAO, Rome, Italy.
- 892 Weyl, O.L.F., Booth, A.J., Mwakiyongo, K.R., and Mandere, D.S. 2005. Management  
893 recommendations for *Copadichromis chrysonotus* (Pisces: Cichlidae) in Lake Malombe, Malawi,  
894 based on per-recruit analysis. *Fish. Res.* **71**(2): 165-173.
- 895 Witte, F., Goldschmidt, T., Wanink, J.H., Oijen, M.J.P.v., Goudswaard, P.C., Witte-Maas, E.L.M., and  
896 Bouton, N. 1992. The destruction of an endemic species flock: quantitative data on the decline of the  
897 haplochromine cichlids of Lake Victoria. *Env. Biol. Fish.* **34**: 1-28.
- 898 Witte, F., Seehausen, O., Wanink, J., Kische-Machumu, M., Rensing, M., and Goldschmidt, T. 2013.  
899 Cichlid species diversity in naturally and anthropogenically turbid habitats of Lake Victoria, East Africa.  
900 *Aquatic Sciences* **75**(2): 169-183.
- 901 Witte, F., Silsbe, G.M., Hecky, R.E., Goudswaard, P.C., Guildford, S.J., Kische-Machumu, M.A., and  
902 Wanink, J.H. 2012. Did the loss of phytoplanktivorous fish contribute to algal blooms in the Mwanza  
903 Gulf of Lake Victoria? *Hydrobiologia* **679**(1): 283-296.
- 904 Witte, F., and van Oijen, M.J.P. 1990. Taxonomy, ecology and fishery of Lake Victoria haplochromine  
905 trophic groups. *Zoologische Verhandelingen* **262**: 1-47.
- 906 Witte, F., Wanink, J.H., Kische-Machumu, M., Mkumbo, O.C., Goudswaard, P.C., and Seehausen, O.  
907 2007. Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake  
908 Victoria. *Aquatic Ecosystem Health & Management* **10**(4): 416 - 433.
- 909 Witte, F., Welten, M., Heemskerk, M., van der Stap, I., Ham, L., Rutjes, H., and Wanink, J. 2008. Major  
910 morphological changes in a Lake Victoria cichlid fish within two decades. *Biological Journal of the*  
911 *Linnean Society* **94**(1): 41 - 52.

- 912 Witte, F., and Winter, W.d. 1995. Appendix II. Biology of the major fish species of Lake Victoria. *In*  
913 Fish stocks and fisheries of Lake Victoria. A handbook for field observations. *Edited by* F. Witte and  
914 W.L.T.V. Densen. Samara Publishing Limited, Dyfed, Great Britain. pp. 301-320.
- 915 Yahaya, S., Lim, L.-S., Shaleh, S.R.M., Mukai, Y., Anraku, K., and Kawamura, G. 2011. Ontogenetic eye  
916 development and related behavioural changes in larvae and juveniles of barramundi *Lates calcarifer*  
917 (Bloch). *Marine and Freshwater Behaviour and Physiology* **44**(6): 339-348.
- 918 Yasindi, A.W., and Taylor, W.D. 2003. Abundance, Biomass and Estimated Production of Planktonic  
919 Ciliates in Lakes Victoria and Malawi. *Aquatic Ecosystem Health & Management* **6**(3): 289 - 297.
- 920
- 921

- 1 **Table 1.** Indicators describing drivers of structural trophic and biophysical changes in the lake co-occurring with haplochromine collapse and the Nile perch
- 2 increase, and sources of data and methodologies in constructing time-series.

Driver	Relation to hypothesis on eutrophication driven haplochromine collapse	Indicator	Showing	Data and methods
Climate	A climate related event before, and during the switch caused strengthened stratification, lake wide deep water anoxic conditions and speeded up eutrophication	Windspeed (m/s)	Windstress induces conditions for stratification	1948 – 2000 National Centers for Environmental Prediction and National Center for Atmospheric Research Reanalysis 1 (Kalnay et al. 1996). See also appendix A.
		Humidity (%)	Supporting evidence: higher humidity and lower temperature are associated with lower windstress	
		Temperature (°C),		
		El Niño event	Strengthened stratification during El Niño years	
Eutrophication	Nutrient enrichment changes nitrogen, phosphorus and silica balance of the lake and with that size-structure and composition of primary producers, overall primary productivity and visibility.	Human population	Increase human activities a.o. in agriculture and associated pasture burning, deforestation is related to nutrient enrichment.	(Verschuren et al. 2002)
		Total phosphorus (TP, mg/g)	Eutrophication record can be related to the timing and magnitude of phosphorus (TP) enrichment.	(Hecky et al. 2010)
Primary production and producers	Productivity, size structure and composition of phytoplankton community changes the amount and quality of the resource spectrum as well as visibility of haplochromine food resources.	$\delta^{13}\text{C}$ (‰)	Carbon isotopic ( $\delta^{13}\text{C}$ ) composition of sedimentary organic matter is an indicator of phytoplankton production	(Hecky et al. 2010)
		N:P ratio	Productivity is Nitrogen (N) limited (Talling 1966) - hence N:P ratios indicate changes in Nitrogen fixation and a shift in from diatoms and chlorophytes to nitrogen fixating cyanobacteria that cause phytoplankton blooms and limits visibility.	(Hecky et al. 2010)
		Aulacoseira valves	The shift in the diatom community to smaller thinly silicified species as a result of silica depletion is represented here by the density changes in large <i>Aulacoseira</i> species.	(Hecky 1993, Hecky et al. 2010, Kling et al. 2001, Verschuren et al. 2002)
Secondary producers	Changes in zooplankton size structure and community and the zooplanktivorous community limits availability of zooplankton to juvenile and zooplanktivorous haplochromines.	Cladocerans	Shifts in the zooplankton community with a decline in small bodied cladocerans, primarily <i>Bosmina</i> , and an increase in zooplanktivorous lake flies are compared with the timing and appearance of the pelagic zooplanktivorous <i>Rastrineobola argentea</i> that, together with small Nile perch, replaced the demersal (zooplanktivorous) haplochromines	(Bridgeman 2001)
Tertiary producers		<i>Rastrineobola argentea</i>		(Wanink 1999, Wanink et al. 2002)



3 **Table 2.** Parameter values for the size-spectrum model.

Parameter	Haplochromines	Nile perch	Units	Comments
<i>Fish life history</i>				
$w_0 e^{x_0}$	0.01	0.001	g	Mass of fish egg
$w_0 e^{x_l}$	0.05	0.001	g	Minimum size subject to predation
$w_0 e^{x_m}$	6	4400	g	Mass at 50 % maturity
$w_0 e^{x_\infty}$	30	60000	g	Asymptotic mass
$\rho$	0.2	0.2	-	Exponent for reproduction function
$\rho_m$	10	10	-	Measures width of transition from immaturity to maturity
<i>Dynamic size spectrum</i>				
$K$	0.2	0.2	-	Food conversion efficiency
$\alpha$	0.8	0.8	-	Search rate scaling exponent
$A$	750	750	$\text{m}^3 \text{yr}^{-1} \text{g}^{-\alpha}$	Feeding rate constant
$\beta$	5	5.72	-	Natural log of mean predator-prey mass ratio
$\sigma$	2	2.2	-	Measure of diet breadth
$\mu_{i,0}$	0.1	0.1	$\text{yr}^{-1}$	Intrinsic (non-predation) mortality rate at size $w_0$
$\xi_i$	-0.2	-0.2	-	Exponent for intrinsic (non-predation) mortality rate
<i>Fixed plankton size spectrum</i>				
$w_0 e^{x_{p,\max}}$	0.02		g	Maximum body mass of plankton
$u_{0,p}$	100		$\text{m}^{-3}$	Plankton density at 0.001 g
$\gamma$	2		-	Exponent of plankton spectrum

4

5

- 6 **Table 3.** Haplochromine catch, biomass, catch over biomass (C/B) and catch over production (C/P) over selected years prior to the Nile perch switch.
- 7 F=fishing mortality= $-\ln(1-C/B)$ . Catch estimates from (Kolding et al. 2013, Kolding et al. 2005) except where indicated. Nile perch Q/B=2.41 /yr and
- 8 haplochromine P/B=1/4 /yr (Moreau 1995). CV=Coefficient of Variation.

Area	Year	Catch (ton/yr) (CV%)	Biomass haplochromines (<30m depth)		C/B (F) (/yr)	C/P (/yr)	Biomass Nile perch (kg/ha) (ton)	Nile perch consumption/ Haplochromine Production (/yr)	Assumptions
			demersal kg/ha	total ton (CV%)					
Tanzania	1974	16624	361	416000	0.04 (0.04)	0.03			1)Haplochromine biomass excluding biomass at depth $\geq 30$ m and pelagic haplochromines, 62% of total biomass (Witte et al. 2012)
	1980	20765	67	77000	0.27 (0.31)	0.17			
	1974 – 1980	22000 (30%)		180000 (50%)	0.14 (0.15)	0.09			
Kenya (Winam gulf)	1969/70***	2700, 3800*	35.8	13200	0.20 (0.23)	0.14			1)1500 out of 2000 vessels were used in haplo fishery* 2)50% total Kenya haplo biomass was from the Winam gulf 3) 50% Kenyan haplo catch was from Winam gulf* 3) Biomass includes pelagic haplochromines, 62% of total biomass
	1975	2300	32.7	12055	0.19 (0.21)	0.14			
	1977***	2700	28.4	10500	0.26 (0.30)	0.18	2.8 (400)	0.06	
	1979****	3000*	18.4	6700	0.49 (0.67)	0.49	14.4 (2000)	0.51	

- 9 \*(Marten 1979, Wanyala and Marten 1974), \*\*(Kudhongania and Cordone 1974), \*\*\* (Muller and Benda 1981), \*\*\*\*(Goudswaard et al. 2008)

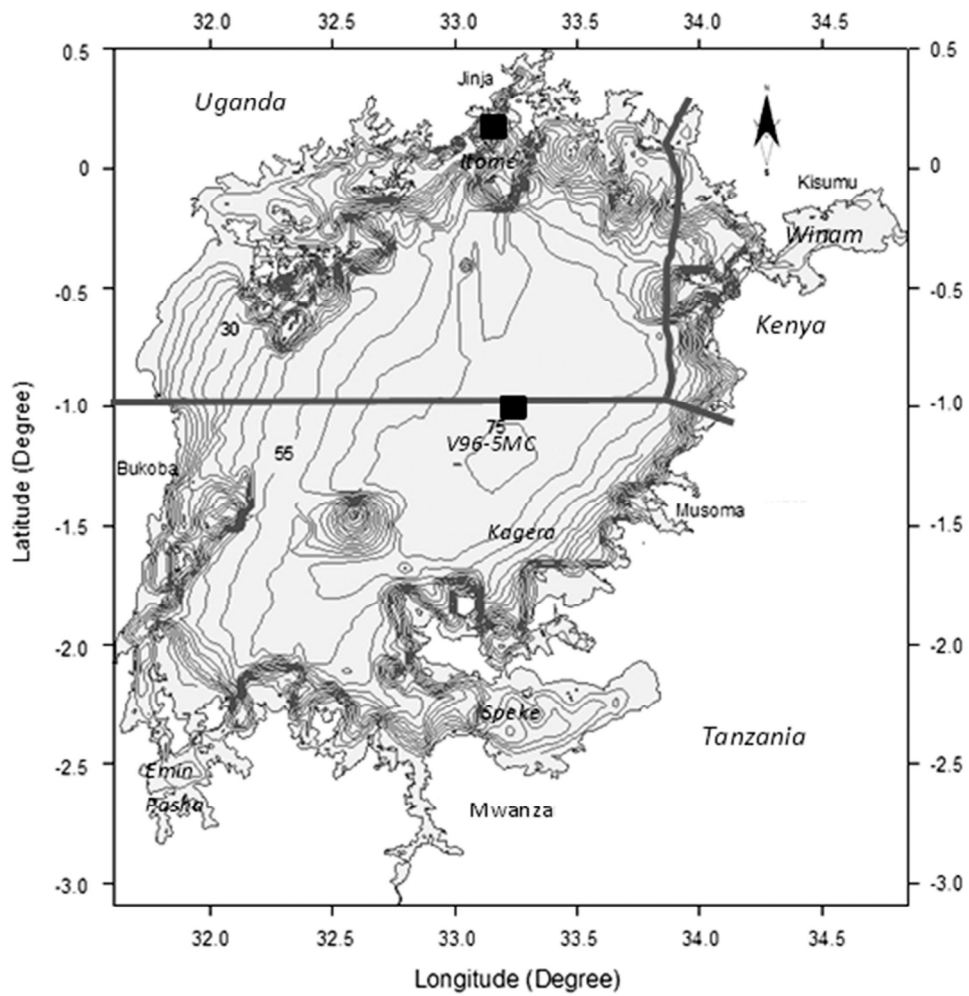


Figure 1. Map of Lake Victoria showing depth contours and main areas of the lake as discussed in the text. Black squares are the locations of two sediment cores Itome and V96-5MC (Hecky et al. 2010). 100x101mm (300 x 300 DPI)

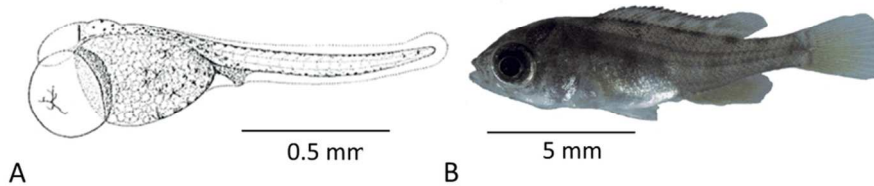


Figure 2. Comparison of sizes of (a) freeswimming Nile perch fry, 1.9 mm (Hopson 1969), and (b) a haplochromine larvae, *Paralabidochromis chilotes*, photographed the first day that the mother was no longer collecting the larvae into the buccal cavity upon stimulated disturbance. Note the prominence of the eye.

See Appendix B.

88x30mm (300 x 300 DPI)

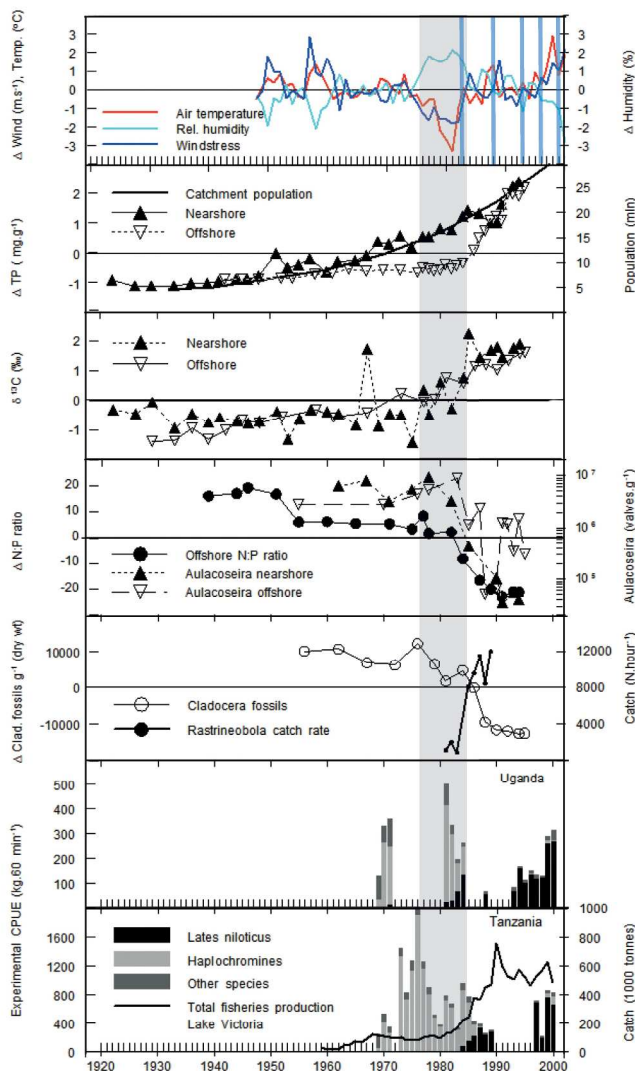


Figure 3 a: Standardised anomalies ((value-mean)/stdev) of over-lake air temperature ( $^{\circ}\text{C}$ ) (mean=19.6 sd=0.26), wind speed (m/s) (mean= 2.33, sd=0.20) and humidity (%) (mean= 88.0, sd=2.42) over the period 1948-2000 (Kalnay et al. 1996). Blue bands: El Niño years

3b: Catchment population (mln); Standardised anomalies of total phosphorus (TP) (mg/g) inshore Itome core (mean = 1.26, stdev = 0.20, N=38); TP offshore core V96-5MC (mean = 1.19 stdev = 0.74 N = 30) (Hecky et al. 2010).

3c: Standardised anomalies in stable isotopic carbon signatures of sedimentary organic matter.  $\delta^{13}\text{C}$  ( $\text{‰}$ ) inshore Itome core (mean= -20.80, stdev = 1.09 N= 38); offshore V96-5MC core (mean= -21.56, stdev = 0.35, N= 22) (Hecky et al. 2010).

3d: Anomalies in offshore N:P ratio (mean= 37.4, N= 18); Aulacoseira concentrations in sediment cores (valves/g dry weight) (nearshore N = 11; offshore N=14) (Hecky et al. 2010).

3e: Anomalies in cladoceran fossils (number/g dry weight) (mean = 14327, N= 14) in a core taken from Grant Bay (Uganda) (Bridgeman 2001); Rastrineobola catch rates (N/hour) (Wanink 1999).

3f, 3g: Catch rates (kg/hr) of *Lates niloticus*, Haplochromines and other species from experimental trawl surveys conducted in Tanzania and Uganda (see text and Kolding et al. (2008)). Total fisheries production Lake Victoria from Kolding et al. (2013).

Δ in front of a legend indicates (standardised) anomalies around the mean.  
306x455mm (300 x 300 DPI)

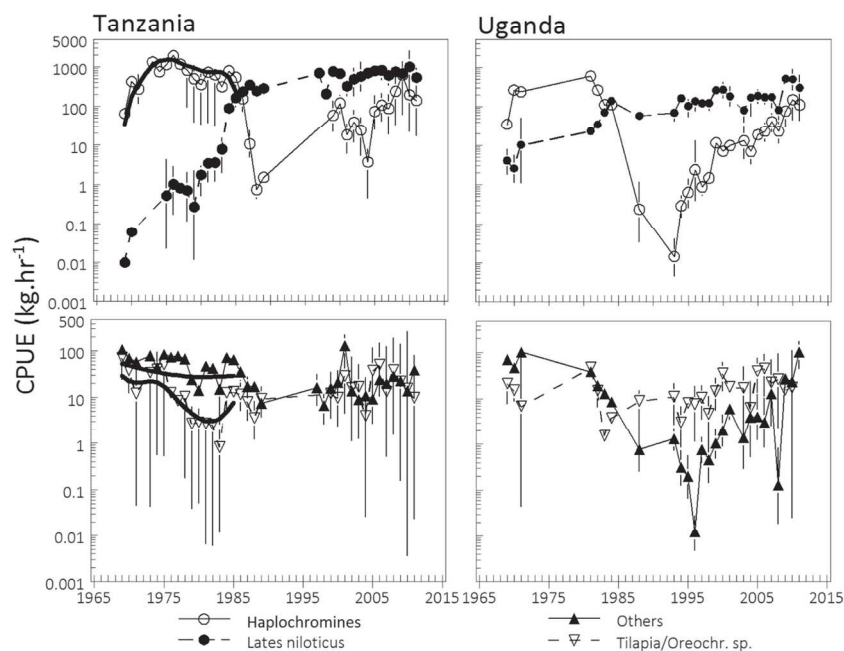


Figure 4. Standardized geometric mean catch per unit effort (CPUE, kg/hr) in experimental trawl surveys in Uganda and Tanzania for all stations less than 40 m depth for *Lates niloticus*, haplochromines, tilapiines and other species between 1969 and 2011. Experimental trawlers do not catch *Rastrineobola* or *Caridina*, which are not included in "others". Vertical grey areas represent the start of the Nile perch boom in Kenya (1979) and Tanzania (1982) according to Goudswaard et al. (2006). Thick black curve is a spline regression on the developments in haplochromine, tilapiine and other species relative biomass in Tanzania: overall, between 1974 and 1985 and prior to the Nile perch upsurge in 1985, the haplochromine decrease was 9.6% per year.

139x112mm (300 x 300 DPI)

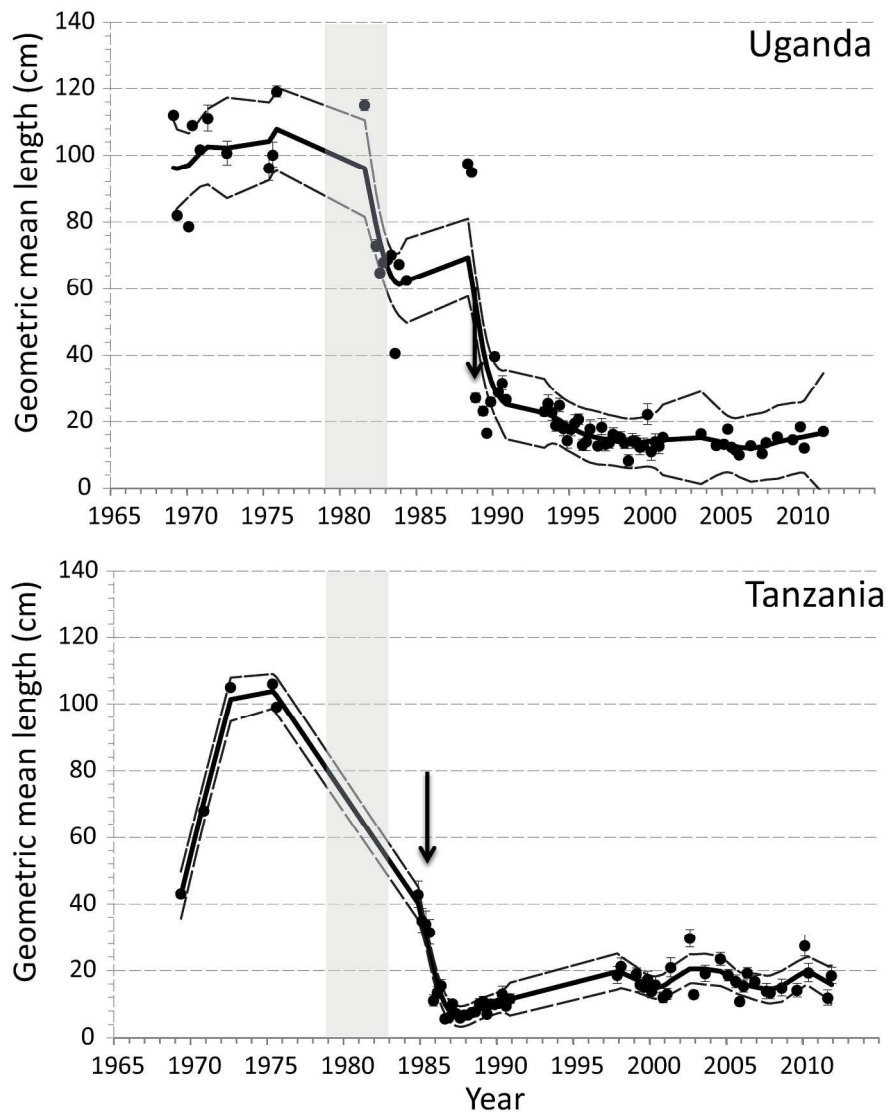


Figure 5. Left: Geometric mean length of Nile perch and 95% confidence intervals by quarter and year in the catches of the experimental trawl surveys. Vertical grey bar: start of the upsurge defined as catch rates  $>45$  kg/hr Nile perch (Goudswaard et al. 2008) in respectively Kenya and Uganda (top) and Kenya and Tanzania (bottom). Arrow: first recording in the experimental surveys of the burst in numbers of recruits  $<15$  cm.  
212x278mm (300 x 300 DPI)



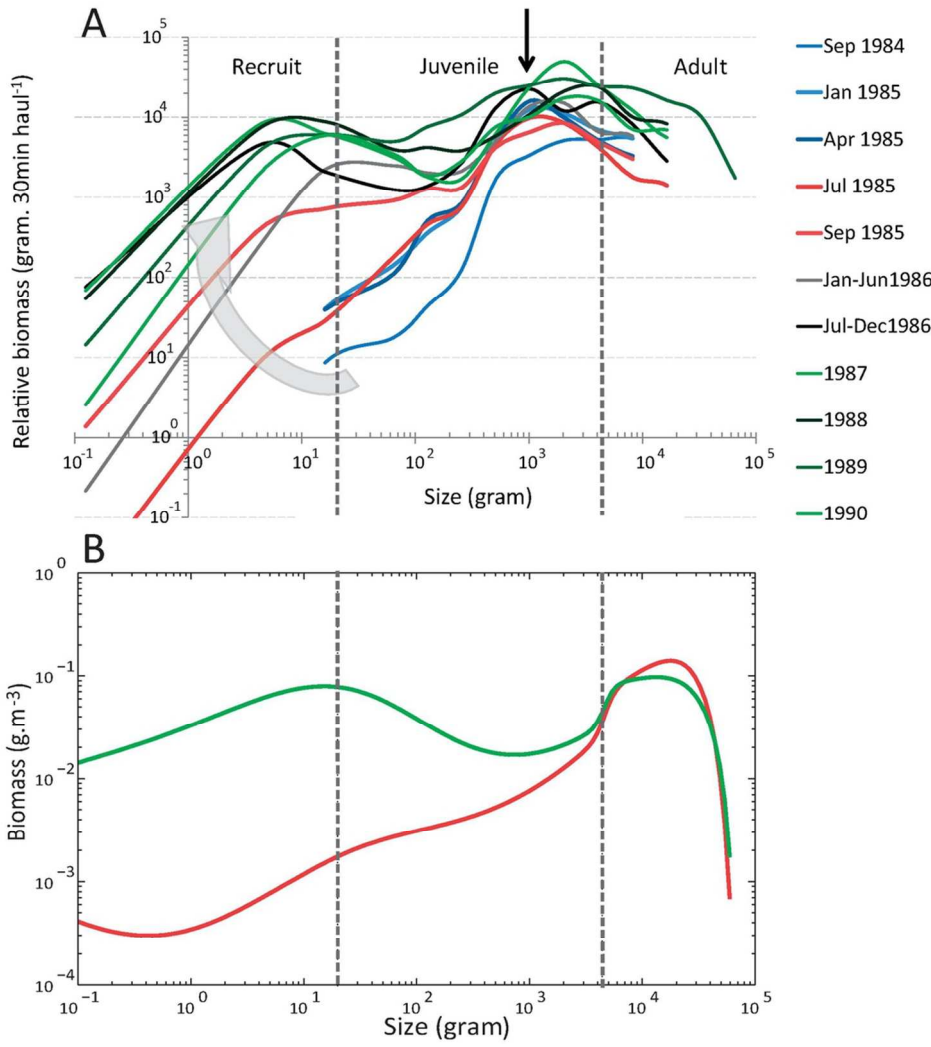


Figure 6. Top: Development of the observed relative biomass-size distribution of Nile perch in the Mwanza Gulf between September 1984 and December 1990 in experimental trawl surveys. The recruitment burst started between July 1985 and December 1985. Prior to that the Nile perch population consisted predominantly of specimen >500 gr. Bottom: two-species size-spectrum model results of the size distribution of Nile perch prior to the switch in co-existence with haplochromines (red line) and post-switch after the extirpation of haplochromines (green line).  
99x106mm (300 x 300 DPI)

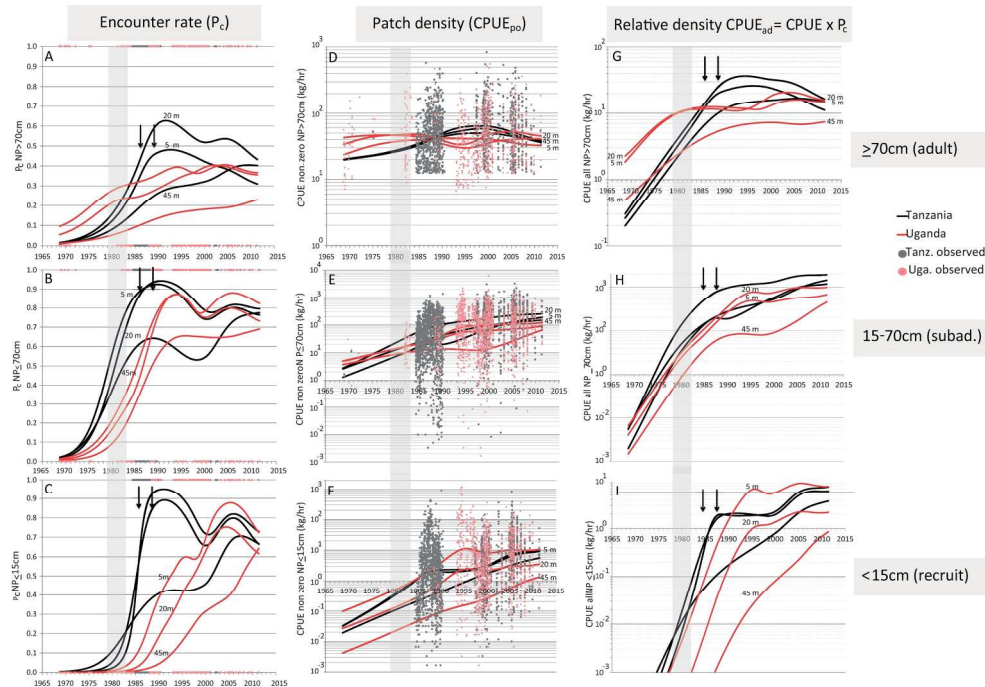


Figure 7. Development in encounter rate ( $P_c$ ), patch density ( $CPUE_{ad}$ , kg/hr) and relative density ( $CPUE_{ad}$ , kg/hr) of adult (>70 cm), subadult (>15cm - < 70 cm) and recruits (<15cm) of Nile perch in trawl surveys in Tanzania and Uganda at 5, 20 and 45 m depth. Grey and red dots: observed zero and non-zero catches and positive catch rates. Grey bar represent the start of the Nile perch boom in Kenya (1979) and Tanzania (1982); left arrows: start of recruitment in Tanzania (Mwanza Gulf); right arrows: first observed recruitment in Uganda. Vertical indication of depth sequence is the same for both Ugandan and Tanzanian series in a graph at the point it is indicated.

197x134mm (300 x 300 DPI)

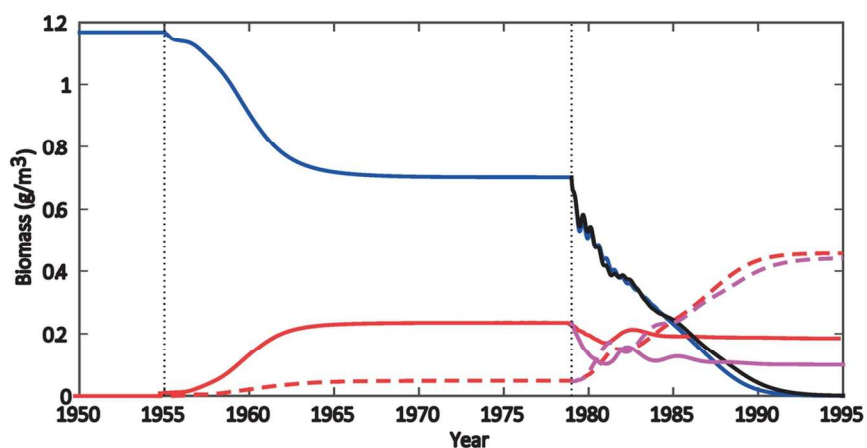


Figure 8. Size-spectrum model time series of the total haplochromine biomass (blue, black), the adult (>70 cm) Nile perch biomass (solid red, purple) and the juvenile (< 70 cm) Nile perch biomass (dashed red, purple). A small population of large, adult Nile perch was introduced to the model in 1955 and an additional mortality rate of 5 /yr was applied to adult haplochromines from 1979 onwards. The black and purple lines indicate an additional fishing mortality of 0.5 /yr on Nile perch >40cm simultaneous with the additional haplochromine mortality.

113x82mm (300 x 300 DPI)

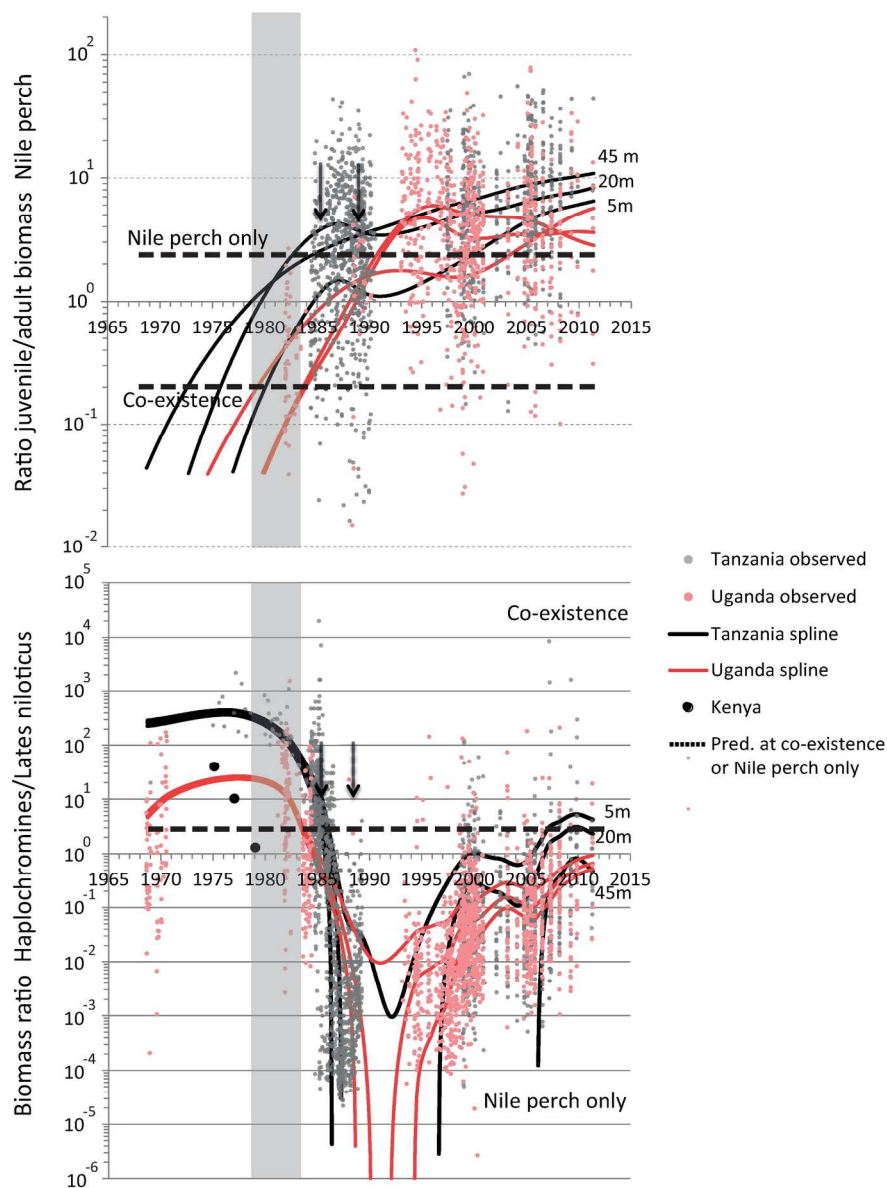


Figure 9. A. Ratio adult (>70cm) to juvenile (< 70cm) Nile perch in experimental trawl surveys. Curves are thin plate spline predictions from a general additive model at 5, 20 and 45m depth. Grey bar and arrows as in previous figures. Horizontal lines are the ratios at co-existence (pre-switch) and after extirpation of haplochromines (post switch) predicted by the size-spectrum model

B. Relative biomass ratio of haplochromines:Lates niloticus (CPUE) in experimental trawl surveys. Curves are thin plate spline predictions from a general additive model at 5, 20 and 45m depth. Grey bar and arrows as in previous figures. Dotted horizontal line is biomass ratio at coexistence predicted by the size spectrum model.

180x225mm (300 x 300 DPI)

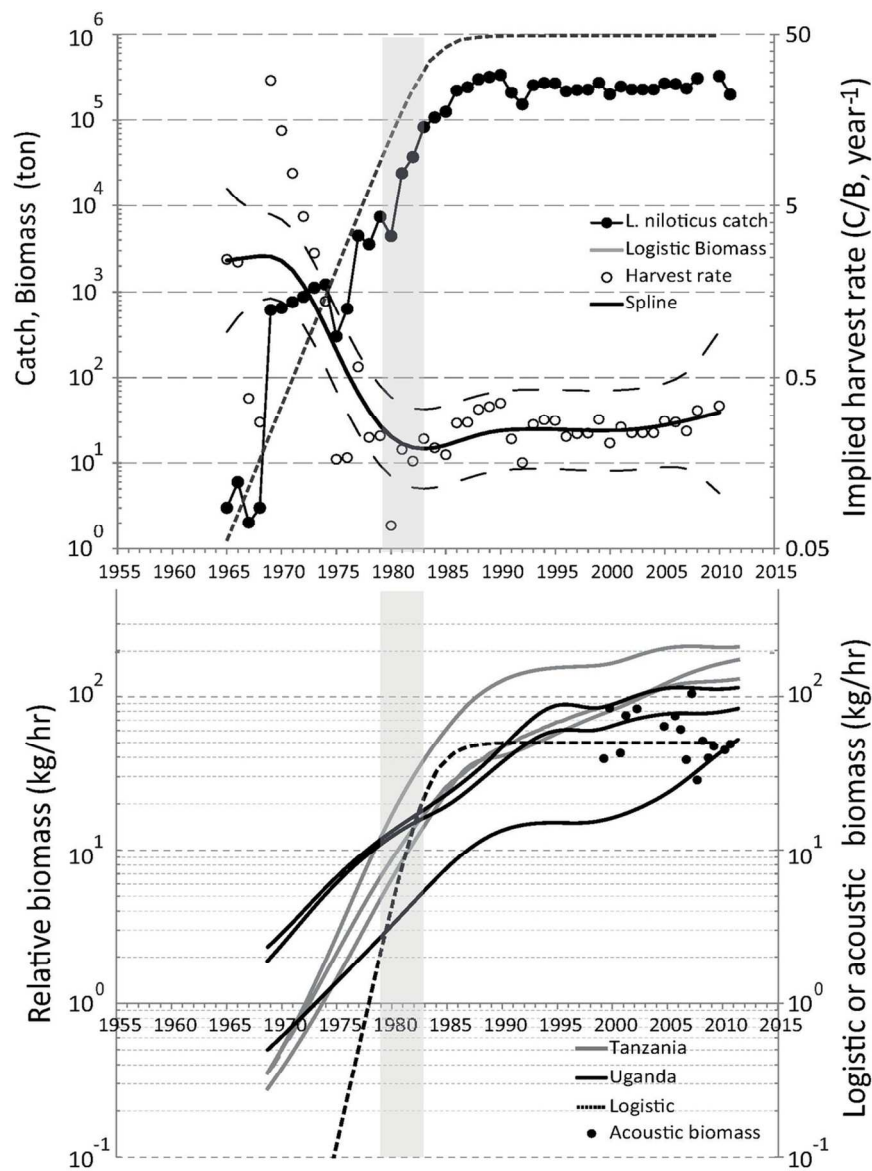


Figure 10. Comparison of the development in Nile perch biomass according to a logistic growth model with an inoculation of 400gr,  $r=0.73$  /yr and  $K=963200$  ton (Downing et al. 2013) with the development in reported catch (top) and relative biomass CPUE ad (bottom) of Nile perch. Top: includes implied harvest rate ( $H=C/B$ ) from the modelled biomass. Bottom: development in relative biomass in Tanzania (broken line) and Uganda (full line) at 5, 20 and 45m depth, as well as absolute biomass estimates from acoustic surveys (black dots) (Everson et al 2013, EAF/LVFO, 2013). Relative, logistic and acoustic biomass are scaled to a swept area of a standard 60 minute trawl haul (3.5 knots, 24.5 m head-rope, 2m net depth) amounting to a swept volume of  $112300\text{m}^3$  (proportional to  $4.3 \cdot 10^{-8}$  times the volume of Lake Victoria), indicating that acoustic and experimental relative biomass estimates are in the same order of magnitude.

98x129mm (300 x 300 DPI)

## 1 APPENDIX A. Climate and limnological data

2 Time series of windstress, temperature and relative humidity were taken from NCEP  
3 Reanalysis 1 (Kalnay et al. 1996) Gaussian Grid point 1 with Lat = -0.9524 S and Lon 31.8750 E. Data  
4 are available every six hours; annual averages were calculated in Matlab using the function binaver  
5 (Kanamitsu et al. 2002). MacIntyre et al. (2014) indicated that temperature changes computed using  
6 surface energy budgets with Reanalysis I data were similar to temperature changes in the lake  
7 whereas those from Reanalysis 2 data were inaccurate. Uncertainty exists as to the cause of the low  
8 winds and air temperatures and high relative humidity from the late 1970s until the early 1980s.  
9 They may result from inaccuracies in melding the pre-satellite modelled data with that including  
10 satellite data. However, measured rainfall data from all the meteorological stations in the Lake  
11 Victoria basin support the inference of El Nino-like conditions in the late 1970s (Chris Funk and Pete  
12 Peterson, personal communication).

13

14 Radiometrically dated sediment records of total phosphorous (TP, mg/g), total N (mg/g),  
15 stable isotopic carbon signatures of as well as *Aulacoseira* concentrations (valves/g dry weight) are  
16 constructed from two sediment cores taken nearshore at Itome (Napoleon Gulf, Uganda, position:  
17 00°13 N, 33° 14'E) and offshore in Tanzania in the deepest part of the lake west off its center (V96-  
18 5MC) (position: 01° 13.9' S, 33° 11.8' E). The two cores (see Hecky et al. (2010) for a full discussion)  
19 enable direct comparison of changes in magnitude and timing of significant limnological changes in  
20 shallower waters with changes in offshore areas. Cladoceran fossils (number/g dry weight) are taken  
21 from in a core taken from Grant Bay (Uganda) (Bridgeman 2001). The sedimentary organic N:P molar  
22 ratios are calculated from the TN and TP measured from the cores described.

23

## 24 **APPENDIX B. Experimental trawl surveys on Lake Victoria**

25 Trawl survey data from Uganda and Tanzania, representing independent replicates from the  
26 same lake, were made available through Lake Victoria Fisheries organization (LVFO) and individual  
27 researchers in Uganda and Tanzania. Data from lake-wide surveys with the RV-Ibis conducted from  
28 1969 to 1971 were digitized from the original sources recovered at the library of NAFIRRI in Jinja,  
29 Uganda. In Uganda the extant data from experimental trawl surveys covered the period from 1981-  
30 1984, 1988 and from 1993-2005 (except 2002) by RV Ibis. Available trawl catches in Tanzania covered  
31 the periods 1971-1983 (MS Mdiria) compiled by PC Goudswaard and the HEST surveys from 1984-  
32 1990 (RV Kiboko). Both sets focused on the Mwanza Gulf: information on sampling procedures and  
33 sites can be found in Goudswaard (2006). From 1997 onwards the surveys, covering the Tanzanian  
34 sector and from 2005 onwards also in Uganda, were carried out with the RV Explorer. RV Ibis and RV  
35 Mdiria both used trawl nets with headropes of respectively 24 and 25m long with codend mesh sizes  
36 of 20-25mm, fished with a speed of 3.5 knots. With an effective horizontal opening of the trawl off  
37 33.3% of the head rope length this results in a swept area of 5.3 ha/hr. RV Kiboko used a trawl with a  
38 headrope of 18.5m and a 20mm codend with a trawling speed of 3-4knots resulting in a swept area  
39 of 3.3-4.5 ha/hr (Bergstrand and Cordone 1971, Goudswaard et al. 2006, Okaronon 1999). From 2005  
40 onwards the RV Explorer was run under Standard Operating Procedures (SOPs) developed by LVFO  
41 for the collection of data on catch rates and length frequencies through bottom trawling, acoustic  
42 surveys, and the environment. The 250-HP, 16.5 m long RV Explorer was equipped with a trawl net of  
43 24.5m head rope and a cod end of 25mm mesh size. Towing speed was 3.0 knots, resulting in a swept  
44 area of 4.5 ha/hr. Shallow areas, less than 4m depth, were not covered due to the vessel draught  
45 while rough habitats and rocky substratum were also not sampled.

46 Catches were recorded by haul and by species category in weight (kg). Haplochromines  
47 generally were recorded as one single category; all other species were recorded at least by genus but  
48 mostly at the species level. Length-frequencies (nearest cm standard length) were recorded for Nile

49 perch in all surveys. In early surveys with the RV Ibis the total weight per length-category was  
50 recorded as well, but these data were excluded from this analysis. For each haul, duration, location  
51 (by name and later also by latitude and longitude) and depth were recorded. For the RV Mdiria no  
52 information on depth and location were recorded but the vessel operated in the Mwanza Gulf.  
53 Potential sources of bias in using these survey data are discussed in Kolding et al. (2008).



54 **APPENDIX C. Haplochromine fry size**

55 Haplochromine fry of several species kept and bred in the laboratory of the Swiss Federal  
56 Institute for Aquatic Science and Technology (Eawag), were photographed to obtain an average and  
57 range of fry sizes. Photographing was done within two days of termination of maternal brood care in  
58 a petri dish on top of a cm grid. Sizes were converted to weight using a length weight relation for  
59 guppies (*Poecilia reticulata*) with  $a = 0.02 \text{ (g/cm}^3\text{)}$  and  $b = 3.049$  (Kolding unpublished data). The  
60 estimated weights were used to validate the parameter values used in the size-spectrum model  
61 (Table C1).

62

63 **Table C1.** Larval size and weight of a range of haplochromine cichlids measured the first day that the  
 64 mother was no longer collecting larvae into the buccal cavity upon stimulated disturbance. Days post  
 65 first release captures the variation in the duration of mouth brood care after first release. Number in  
 66 brackets indicates different individuals of the same species. N = number of fry measured sd =  
 67 standard deviation.

Species	Habitat, trophic group, current status	Days post first release	N	Size (sd) mm	Weight (sd) gr
<b>Pundamilia pundamilia Senga</b>	Rocky inshore, insectivore abundant	5-6	10	11.8 (0.85)	0.033 (0.007)
<b>Pundamilia nyererei Python</b>	Rocky inshore, zooplanktivore abundant	4	9	11.7 (0.30)	0.032 (0.002)
<b>Pundamilia nyererei Kissenda</b>	Rocky inshore, zooplanktivore abundant	3	11	11.0 (0.32)	0.027 (0.002)
<b>Pundamilia nyererei x P. pundamilia</b>	Rocky inshore, zooplanktivore, insectivore	8	12	12.8 (0.50)	0.043 (0.005)
<b>Neochromis omnicaeruleus Makobe</b>	Rocky inshore, algal scraper abundant	8	8	13.3 (0.98)	0.048 (0.011)
<b>Neochromis sp. (unicuspid)</b>	Rocky inshore, algal scraper, abundant	1	12	11.5 (0.26)	0.026 (0.002)
<b>Yssichromis pyrrocephalus</b>	Pelagic offshore, zooplanktivore, recovered	3	12	11.4 (0.51)	0.030 (0.004)
<b>Haplochromis tanaos</b>	Pelagic inshore, zooplanktivore, recovered	3	7	14.2 (0.39)	0.059 (0.005)
<b>Lipochromis melanopterus</b>	Inshore, paedophage, survived	6	7	14.4 (0.37)	0.061 (0.005)
<b>Paralabidochromis rockkribensis (1)</b>	Rocky inshore, insectivore abundant	4	8	13.2 (0.38)	0.046 (0.004)
<b>Paralabidochromis rockkribensis (2)</b>		4	9	13.4 (0.60)	0.049 (0.007)
<b>Paralabidochromis chilotes Makobe (1)</b>	Rocky inshore, insectivore abundant	10	14	14.6 (0.51)	0.063 (0.006)
<b>Paralabidochromis chilotes Makobe (2)</b>		9	13	13.9 (0.80)	0.055 (0.009)
<b>Astatotilapia tweddlei (1)</b>	Riverine,	6	5	10.0 (0.13)	0.020 (0.001)
<b>A. tweddlei (2)</b>	Generalist, Lake Chilwa	8	6	10.7 (0.34)	0.025 (0.002)
<b>A. calliptera</b>	Riverine generalist, Lake Malawi	2-3	10	11.8 (0.21)	0.033 (0.002)
<b>A. burtoni</b>	Riverine, generalist Lake Tanganyika	7	10	13.7 (0.61)	0.053 (0.007)
<b>A. sp. Lake Challa</b>	Riverine generalist, Lake Challa	6-7	11	10.9 (0.45)	0.026 (0.003)
<b>Average lake</b>					0.044
<b>Average riverine</b>					0.031

68

69 **APPENDIX D. Experimental survey data standardisation and time series analysis**

70 Catch rates from the experimental fishery in biomass (kg) by species were corrected for trawl  
71 duration to a standard haul of 60 minutes using total biomass of all species

$$72 \quad 1) \quad CPUE_{ix}^s = CPUE_i \left( \frac{\bar{f}}{f_{ix}} \right)^\beta$$

73 Where  $CPUE_{ix}^s$  is the standardised CPUE for the  $i$ -th fishing trip of vessel  $x$  ( $\text{kg.haul}^{-1}$ ) and  $\bar{f}$  is the  
74 common trawl duration of 60minutes;  $\bar{f}/f_i$  represents the reciprocal of the standardised trip and  $\beta =$   
75  $\beta_1 + \beta_2$  is the coefficient for this effort measure from the following separate slopes model (Tsehaye et  
76 al. 2007)

$$77 \quad 2) \quad E(\text{Log}_{10}(CPUE_{ix})) = \alpha + vessel_{ix} + \beta_1 \cdot \text{Log}_{10}(duration_i) + \beta_2 vessel_{ix} \cdot \text{log}_{10}(duration_i) + \varepsilon_{ix} \text{ iid} \sim$$

$$78 \quad N(0, \sigma^2).$$

79 No significant effect of vessel was detected for total Nile perch weight in the catch. Weights  
80 calculated from length frequencies were standardized to a 60 minute trawl haul duration with  $\beta =$   
81 0.73.

82 *Time series analysis: hurdle model:*

83 For each haul a new variable was constructed with a probability of catch ( $P_c$ ) or encounter  
84 rate equal to 0 for no catch and 1 for a positive catch (weight > 0) as well as a variable containing  
85 positive catch weights. Zero catches are assumed to be structural, related to below detection limits  
86 or non-presence of fish; the probability of false zeroes as a result of observation or sampling errors is  
87 assumed to be low and constant over the observation period.

88 Developments of  $P_c$  and  $CPUE_{po}$ , the positive trawl catches or patch density, over time and  
89 depth were examined with maximum likelihood methods through a Generalized Additive Model  
90 (GAM) with a thin plate regression spline (TPS),

91 3)  $E(Y_i | date, depth) = \beta_0 + s(date, depth) + \varepsilon_i \text{ iid} \sim N(0, \sigma^2).$

92 Where estimates  $E(Y)$  with  $Y = P_c$  or  $\log_{10}(CPUE_{po})$  are obtained for adults, sub-adults and  
 93 recruits sampled at a date and depth, and  $S(x_1, x_2)$  is the nonparametric thin plate smoothing  
 94 function for the independent variables  $x_1 = \text{date}$  and  $x_2 = \text{depth}$ . The model was implemented  
 95 specifying a binomial and Gaussian distribution respectively for  $P_c$  and  $\log_{10}(CPUE_{po})$  with their  
 96 canonical link functions. The value of the smoothing parameter selected by generalized cross  
 97 validation (GCV) led to jagged over-parameterised curves utilising a high number of degrees of  
 98 freedom that obscured the general pattern in developments. As the calculation of the thin plate  
 99 spline smoother was computationally intensive, a GAM model estimating separate splines and linear  
 100 regressors for depth and date was used to estimate the appropriate allowable degrees of freedom  
 101 (df) for the smoothing parameter. After obtaining a satisfactory regression spline with limited change  
 102 in the deviance of the final estimate, the sum of the two df's for depth and date then were used in  
 103 the thin plate spline estimate. Analyses were done separately for Uganda and Tanzania. To examine  
 104 developments at different depths estimates of Nile perch encounter rates and catch rates were  
 105 calculated for 5m, 20m and 45m. Developments in  $CPUE_{ad}$  were obtained by multiplying the model  
 106 results for  $P_c$  and  $CPUE_{po}$ .

107 A thin plate spline regression was also used to examine the developments over time and  
 108 depth of two abundance ratios: the juvenile Nile perch: adult Nile perch (J/A) and the Haplochromine:  
 109 Nile perch (H/N) biomass ratio. To obtain normality and homoscedasticity in the residuals and take  
 110 account of 0 values in the trawls, the J/A ratio was transformed as  $(Y+10^{-4})^{0.2}$ . The H/A ratio was  
 111 transformed as  $(Y+10^{-7})^{0.44}$ . Powers of the transformation were estimated through a search over  
 112 parameter values of  $\lambda$  of the BoxCox-transformation minimizing the Akaike Information Criterion  
 113 (AIC) and the Schwartz's Bayesian Criterion (SBC). Values predicted by the size-spectrum model of  
 114 both abundance ratio's at the Nile perch switch were compared with the observed values at the  
 115 moment in time that recruitment of <15cm Nile perch commenced. All statistical models were

116 implemented using SAS/STAT® software Version 8 of the SAS system for Windows using the GLM,  
117 GENMOD and GAM procedures. Model results are in Table D1.

118 *P/B Estimates*

119 A conservative P/B estimate of 1.4 /yr was used in the calculations of haplochromine  
120 productivity. P/B estimates for Lake Victoria haplochromine cichlids are scant, but this value is in the  
121 lower part of the range of fished haplochromines from Lake Malawi that had an average P/B=3.1 /yr  
122 (N=22, CV=30%, max=4.7 /yr, min=1.6 /yr) (Duponchelle et al. 2000) and from Lake Malombe,  
123 average P/B=1.6 /yr (N=5, CV=46%, min=0.56 /yr, max=2.7 /yr) (Weyl et al. 2005).

124 **Table D1.** Results GAM analysis  $P_c$  and CPUE of adult ( $\geq 70\text{cm}$ ), sub-adult ( $< 70\text{cm}$ ,  $\geq 15\text{cm}$ ) and recruits  
 125 ( $< 15\text{cm}$ ) of Nile perch and the ratios juvenile/adult Nile perch CPUE and haplochromines/Nile perch  
 126 CPUE. Nobs = Number of observations used in the analysis, DF= final degrees of freedom used in the  
 127 thin plate spline regression. Intercepts all significant at  $Pr>|t|<0.05$ , ns is non-significant. Explained  
 128 deviance is the ratio of the residual deviance of the final estimate of the model and the total  
 129 estimated deviance of the null model  $E(Y)=\text{intercept}$ .

Distribution	Country	Model	Intercept	Lambda	GCV	NObs	DF	$\chi^2$	$Pr>\chi^2$	Explained deviance (%)
Link		$E(Y)=s(\text{depth},\text{date})$								
Binomial Logit	Tanzania	Adult $P_c$	-0.26	$4.96 \cdot 10^{-5}$	0.90	2396	12	321.2	<0.001	11.5
		Sub-adult $P_c$	1.24	$4.07 \cdot 10^{-5}$	0.82	2396	12	574	<0.002	9.5
		Recruit $P_c$	0.64	$1.20 \cdot 10^{-5}$	0.80	2396	20	698	<0.001	18.7
	Uganda	Adult $P_c$	-0.77	$3.72 \cdot 10^{-5}$	0.94	2018	12	197.2	<0.001	39.9
		Sub-adult $P_c$	0.86	$2.76 \cdot 10^{-5}$	0.84	2019	12	617	<0.001	30.4
		Recruit $P_c$	0.32	$6.57 \cdot 10^{-6}$	0.66	2018	20	341	<0.001	38.9
Gaussian Lognormal	Tanzania	Adult CPUE	4.24	$1.82 \cdot 10^{-4}$	0.12	1090	12	10.4	<0.001	8.5
		Sub-adult CPUE	4.33	$2.02 \cdot 10^{-4}$	0.54	1770	12	95.8	<0.002	8
		Recruit CPUE	2.96	$1.88 \cdot 10^{-4}$	0.69	1563	12	35.9	<0.001	31.1
	Uganda	Adult CPUE	4.16	$1.70 \cdot 10^{-4}$	0.14	676	12	5.87	<0.001	9.2
		Sub-adult CPUE	4.32	$1.65 \cdot 10^{-4}$	0.56	1226	12	13.6	<0.001	23.0
		Recruit CPUE	3.04	$1.23 \cdot 10^{-4}$	0.76	984	12	19	<0.001	12.9
Gaussian	Tanzania	(Haplo:Lates CPUE ratio) <sup>0.2</sup>	ns	8.17.6	7.1	1888	12	1245.9	<0.001	33.0
Normal	Uganda	(Haplo:Lates CPUE ratio) <sup>0.2</sup>	0.51	944.1	1.14	1444	12	1089.7	<0.001	35.0
	Tanzania	(Sub-adult:Adult CPUE ratio) <sup>0.4</sup>	1.28	$7.18 \cdot 10^{-5}$	0.08	1090	18	568.6	<0.001	30.5
	Uganda	(Sub-adult:Adult CPUE ratio) <sup>0.4</sup>	1.19	$6.4 \cdot 10^{-5}$	0.11	676	18	835.1	<0.001	51.3

130

131

132 **APPENDIX E. Size spectrum model equations and two-patch model with dispersal**

$\frac{\partial u_i}{\partial t} = -\frac{\partial}{\partial x}(\varepsilon_i g_i u_i) + \frac{b_i R_i e^{-x}}{2} - (\mu_i + \mu_{n,i} + \mu_{e,i}) u_i$	Rate of change of density $u_i(x)$ of species I and body size $w_0 e^x$
$g_i(x) = A_i K e^{(\alpha_i - 1)x} \sum_j \theta_{ij} \int e^{x'} s_i(e^{x-x'}) u_j(x') v_j(x') dx'$	Mass-specific food assimilation rate
$\mu_i(x) = v_i(x) \sum_j A_j \theta_{ji} \int e^{\alpha_j x'} s_j(e^{x'-x}) u_j(x') dx'$	Predation mortality rate
$\mu_{n,i}(x) = \frac{\mu_{0,i} \exp(-\xi(x - x_{i,0})) g_i(x_{i,0})}{g_i(x)}$	Intrinsic non-predation mortality rate
$R_i = \int (1 - \varepsilon_i(x)) g_i(x) u_i(x) dx$	Reproduction rate of species i
$1 - \varepsilon_i(x) = \left(1 + \exp(-\rho_{i,m}(x - x_{i,m}))\right)^{-1} \exp(\rho_i(x - x_{i,\infty}))$	Proportion of assimilated biomass used for reproduction
$s_i(e^r) = \begin{cases} C \exp\left(-\frac{(r - \beta_i)^2}{2\sigma_i^2}\right), & r > 0 \\ 0, & r \leq 0 \end{cases}$	Feeding kernel as a function of log predator:prey body mass ratio $r$
$\theta = \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix}$	$\theta_{ij}$ is the preference of species I for prey of species j
$b_i(x) = \delta(x - x_{i,0})$	Distribution of egg sizes for species i
$v_i(x) = H(x - x_{i,l})$	Vulnerability to predation
$u_0(x) = \begin{cases} u_{0,0} e^{(1-\gamma)x}, & x \leq x_{0,\max} \\ 0, & x > x_{0,\max} \end{cases}$	Abundance of plankton of body size $w_0 e^x$

133

134 The external mortality function  $\mu_{e,i}(x)$  is used to apply size- and species-dependent mortalities due  
 135 to external factors, such as fishing or habitat degradation.  $H(x)$  is the Heaviside function (equal to 0  
 136 if  $x < 0$  and equal to 1 if  $x > 0$ ) and  $\delta(x)$  is the Dirac delta function (equal to 0 if  $x \neq 0$  and with the  
 137 property  $\int \delta(x) dx = 1$ ).

138 **Two-patch model with dispersal**

139

140 In a single patch, the dynamics of  $n$  species size spectra,  $\mathbf{u}(x) = (u_1(x), \dots, u_n(x))$ , can be written  
 141 compactly in terms of a nonlinear operator  $N$ :

$$\frac{\partial \mathbf{u}}{\partial t} = N(\mathbf{u}).$$

142 Suppose  $\mathbf{u} = \mathbf{u}^*$  is an equilibrium of the single-patch model, i.e.  $N(\mathbf{u}^*) = 0$ . The stability of  $\mathbf{u}^*$  is  
 143 determined by the eigenvalues of the linearization  $L$  of the operator  $N$  about  $\mathbf{u}^*$ . An eigenvalue  $\lambda$  of  
 144  $L$  satisfies

$$L\mathbf{v} = \lambda\mathbf{v}$$

145 for some function  $\mathbf{v}(x)$ . The equilibrium is stable if  $\text{Re}(\lambda) < 0$  for all eigenvalues  $\lambda$ .

146 Now suppose the system is separated into two distinct patches, with size spectra  $\mathbf{u}_1$  and  $\mathbf{u}_2$   
 147 respectively. If the dynamics within the two patches are the same and the patches are coupled by  
 148 passive dispersal, then the dynamics are described by

$$\begin{aligned}\frac{\partial \mathbf{u}_1}{\partial t} &= N(\mathbf{u}_1) + c_1 D(x)(\mathbf{u}_2 - \mathbf{u}_1), \\ \frac{\partial \mathbf{u}_2}{\partial t} &= N(\mathbf{u}_2) + c_2 D(x)(\mathbf{u}_1 - \mathbf{u}_2),\end{aligned}$$

149 where  $c_i > 0$  is a constant inversely proportional to the volume of patch  $i$  and  $D(x)$  is a diagonal  
 150 matrix such that  $d_{ii}(x) \geq 0$  is the inter-patch dispersal rate for a individuals of species  $i$  and size  $x$ .

151 Clearly the single-patch equilibrium  $\mathbf{u}_1 = \mathbf{u}_2 = \mathbf{u}^*$  is also an equilibrium of the two-patch model. The  
 152 stability of this equilibrium is determined by the eigenvalues  $\mu$  of the linearization of the two-patch  
 153 model. These eigenvalues satisfy

$$\begin{aligned}L\mathbf{v}_1 + c_1 D(\mathbf{v}_2 - \mathbf{v}_1) &= \mu\mathbf{v}_1, \\ L\mathbf{v}_2 + c_2 D(\mathbf{v}_1 - \mathbf{v}_2) &= \mu\mathbf{v}_2,\end{aligned}$$

154 for some pair of functions  $(\mathbf{v}_1(x), \mathbf{v}_2(x))$ . Clearly, setting  $\mathbf{v}_1 = \mathbf{v}_2 = \mathbf{v}$  and  $\mu = \lambda$  satisfies these  
 155 equations. So if  $\lambda$  is an eigenvalue of the single-patch equilibrium, it is also an eigenvalue of the  
 156 corresponding two-patch equilibrium. This shows that if the single-patch equilibrium is unstable then  
 157 the corresponding two-patch equilibrium must also be unstable.

158 Also, setting  $\mathbf{v}_2 = -c_2/c_1\mathbf{v}_1$  gives

$$L\mathbf{v}_1 - (c_1 + c_2)D\mathbf{v}_1 = \mu\mathbf{v}_1,$$



159 Hence, the remaining eigenvalues of the two-patch equilibrium are the eigenvalues of the linear  
 160 operator  $M$ , defined by

$$M\mathbf{v} = L\mathbf{v} - (c_1 + c_2)D\mathbf{v}.$$

161 If the rate of dispersal is the same for all size classes and all species then  $D = dI$  where  $d > 0$  is the  
 162 constant rate of dispersal and  $I$  is the identity. Hence,

$$M = L - (c_1 + c_2)dI,$$

163 and the eigenvalues of  $M$  are  $\mu = \lambda - (c_1 + c_2)d$  and so  $\text{Re}(\mu) < \text{Re}(\lambda)$ .

164 If dispersal is species- and/or size-dependent, but is relatively weak (small  $D(x)$ ), the eigenvalues of  
 165  $M$  will be close to the eigenvalues of  $L$ . If dispersal is strong (large  $D(x)$ ), the eigenvalues of  $M$  will all  
 166 have negative real part.

167 In any of these three cases (i. weak dispersal limit, ii. strong dispersal limit, or iii. equal dispersal for  
 168 all species and sizes), the two-patch equilibrium will have the same stability as the corresponding  
 169 single-patch equilibrium. For intermediate dispersal, it is possible that the leading eigenvalue of  $M$   
 170 will have positive real part, even though the leading eigenvalue of  $L$  has negative real part. In other  
 171 words, the right rate of dispersal between patches could destabilize an equilibrium that is stable in  
 172 the single-patch model.

173 For the Nile perch – haplochromine model in the absence of additional external mortality on  
 174 haplochromines, the coexistence state is stable and the Nile perch only state is unstable. This means  
 175 that, in a single patch, the Nile perch can never drive the haplochromines to complete collapse.  
 176 Adding dispersal between patches to the model does not change this prediction because, as shown  
 177 above, dispersal can never stabilize the unstable Nile-perch only equilibrium. It is possible that  
 178 dispersal could destabilize the coexistence state. This could lead to periodic solutions (similar to a  
 179 predator-prey cycle), asymmetric solutions (e.g. large Nile perch population and small haplochromine

180 population in patch 1 and vice versa in patch 2) or more complex dynamics. However, it cannot lead  
181 to extirpation of the haplochromines in either patch.

182 **References to Appendices**

- 183 Bergstrand, E., and Cordone, A.J. 1971. Exploratory bottom trawling in Lake Victoria. African Journal of Tropical  
184 Hydrobiology and Fisheries (Kenya) **1**(1): 13 - 23.
- 185 Bridgeman, T.B. 2001. The ecology and paleolimnology of food web changes in Lake Victoria, East Africa,  
186 University of Michigan, Ann Arbor MI, USA.
- 187 Duponchelle, F., Ribbink, A.J., and (eds.). 2000. Fish Ecology Report. Lake Malawi/Nyasa/Niassa Biodiversity  
188 Conservation Project. SADC/GEF (Southern African Development Community, Gaborone, Botswana / Global  
189 Environmental Facility, Washington, D.C.).
- 190 Goudswaard, P.C. 2006. Causes and effects of the Lake Victoria ecological revolution. PhD, Faculty of  
191 Mathematics and Natural Sciences and those of Medicine, Leiden University, Leiden.
- 192 Goudswaard, P.C., Witte, F., and Wanink, J.H. 2006. The shrimp *Caridina nilotica* in Lake Victoria (East Africa),  
193 before and after the Nile perch increase. Hydrobiologia **563**: 31 - 34.
- 194 Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., and Kling, G.W. 2010. Multiple stressors cause rapid  
195 ecosystem change in Lake Victoria. Freshwater Biology **55**: 19-42.
- 196 Kalnay, E., Kanamitsu, M., R.Kistler, Collins, W., D.Deaven, Gandin, L., Iredell, M., Saha, S., White, G., Woollen,  
197 J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Leetmaa,  
198 A., Reynolds, R., Jenne, R., and D.Joseph. 1996. The NCEP/NCAR 40-year reanalysis project. Bull. Am. Met. Soc.  
199 **77**: 437 - 471.
- 200 Kanamitsu, M., Ebisuzaki, W., Woollen, J., Yang, S.-K., Hnilo, J.J., Fiorino, M., and Potter, G.L. 2002. NCEP-DEO  
201 AMIP-II Reanalysis (R-2). Bulletin of the Atmospheric and Meteorological Society **83**(1631 - 1643).
- 202 Kolding, J., Zwieten, P.A.M.v., Mkumbo, O., Silsbe, G., and Hecky, R.E. 2008. Are the Lake Victoria Fisheries  
203 Threatened by Exploitation or Eutrophication? Towards an Ecosystem-based Approach to Management. *In* The  
204 Ecosystem Approach to Fisheries. Edited by G. Bianchi and H.R. Skjoldal. CAB International, Rome. pp. 309 -  
205 354
- 206 MacIntyre, S., Romero, J.R., Silsbe, G.M., and Emery, B.M. 2014. Stratification and horizontal exchange in Lake  
207 Victoria, East Africa. Limnology and Oceanography [Limnol Oceanogr] **59**(5): 34.
- 208 Okaronon, J.O. 1999. The fish stocks of Lake Victoria. *In* Report on third Fisheries Data Working Group  
209 (FIDAWOG) workshop held at the Triangle Hotel, Jinja, 29 March to 1 April 1999. Edited by D.a.C. Tweddle, I.G.  
210 Fisheries Data Working Group of the Lake Victoria Fisheries Research Project, Jinja, Uganda. pp. 30-37.
- 211 Tsehaye, I., Machiels, M.A.M., and Nagelkerke, L.A.J. 2007. Rapid shifts in catch composition in the artisanal  
212 Red Sea reef fisheries of Eritrea. Fish. Res. **86**(1): 58-68.
- 213 Weyl, O.L.F., Booth, A.J., Mwakiyongo, K.R., and Mandere, D.S. 2005. Management recommendations for  
214 Copadichromis chrysonotus (Pisces: Cichlidae) in Lake Malombe, Malawi, based on per-recruit analysis. Fish.  
215 Res. **71**(2): 165-173.

216