Modeling trophic interactions in Lake Kivu: What roles do exotics play?

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Abstract:

An Ecopath model of the southern part of Lake Kivu, a deep African equatorial lake was constructed to quantitatively describe the possible impact of fish introductions in this ecosystem. This study is considered as an initial step in summarizing ecological and biological information, under a coherent framework, on this ecosystem. Fourteen compartments were considered. As a phytoplankton-based food web, it is observed that key food sources are not fully utilized as transfer efficiencies per trophic levels (TL) varies between 4.5 and 9.4%. Zooplankton plays a major role in transferring organic matter from TL1 to higher TLs due to the abundance of zooplanktivores. Shifts in food preferences and distribution of some of the fish functional groups were observed as a response to competition. The majority of fish biomass concentration is in TL3 (55%). The fishery is concentrated at TL3 and can, therefore, be consider as "immature", sensu Odum. The direct and indirect effects of predation between system components (i.e. fish, invertebrates, phytoplankton and detritus) are quantitatively described and the possible influence and role in the ecosystem's functioning of introduced fish species are discussed.

Keywords: Food web structure; Transfer efficiency; Invasion; Exotic fishes; Lake Kivu

Introduction

Introduction of alien species in aquatic ecosystems is stimulated by increasing demand for food to sustain increasing human population and poverty, enhance fish stocks, generate economic benefits, as biomanipulation stratagem and sustain recreational fisheries (Welcomme, 1988 Welcomme, R.L., 1988. International Transfers of Inland Fish Species. FAO Fisheries Technical Papers 294, 318 pp.[Welcomme, 1988], [Pitcher and Hart, 1995], [Irz et al., 2004] and [Saltveit, 2006]). However, this strategy is often unacceptable as it leads to detrimental impacts on ecology of wild stocks that frails ecosystem structure ([Wilcove et al., 1998], [Lodge et al., 1998], [Allen and Humble, 2002], [Kolar and Lodge, 2002], [Sax and Gaines,

25   2003; Gurevitch and Padilla, 2004; Didham *et al.*, 2005; Arim *et al.*, 2006), fisheries economy

26   (Mack *et al.*, 2000; Pimentel *et al.*, 2001) and recreation (Winfield and Durie, 2004).

27

28   Widespread introductions of non indigenous species have been categorized as a major

29   cause of natural species extinction compared to habitat fragmentation (MacDonald *et al.*, 1989;

30   Lodge *et al.*, 1998; Davis and Thompson, 2000; Allen and Humble, 2002; Sax and Gaines, 2003;

31   Gurevitch and Padilla, 2004; Didham *et al.*, 2005; Arim *et al.*, 2006) in both terrestrial

32   (Rejmánek and Richardson, 1996; McCann, 2000; Smith *et al.*, 2000; Allen and Humble, 2002;

33   Guo *et al.*, 2006; Lovett *et al.*, 2006) and aquatic systems (Mills *et al.*, 1993; Pitcher and Hart,

34   1995; Puth and Post, 2005; Latini and Petrere Jr., 2004; Dudgeon *et al.*, 2006). Although in the

35   latter, biological invasions have been recognized as a persisting problem compared to pathologic

36   crisis in terrestrial ecosystems (Dudegeon *et al.*, 2006).

37

38   Questions on success of exotics and the damaging impacts to native stocks at the

39   ecosystem level have fascinated many ecologists, such as Crawley (1987), Naeem *et al.* (2000)

40   and Kennedy *et al.* (2002). Ecological systems are extremely complex networks, consisting of

41   many biological species that interact in many different ways, such as mutualism, competition,

42   parasitism and feeding relationships. The latter can cause invasions, extirpations, and population

43   fluctuations of a species to dramatically affect other species within a variety of natural habitats

44   (Pimentel *et al.*, 2001; Winfield and Durie, 2004). According to Hobbs (1989), successful

45   invasion in natural communities depend on species dispersal, establishment and survival with the

46   number of species per area established by immigration-extinction equilibrium. Success of exotics

47   also depends on tolerance and broad ecological demands, ability to adapt to habitat and

48   environmental conditions and *r*-selected life histories (Craig, 1992; Murichi *et al.*, 1995).

49

50   Cases where introduction of exotics have been reported beneficial are rare in both

51   terrestrial (Schutzenhofer and Valone, 2006) and aquatic ecosystems (Gottlieb and

52   Schweighofer, 1996). Elevated biodiversity has been observed to increase resistance from

53   invasions in terrestrial and aquatic systems by creating insurance through functional redundancy

54   (Simberloff and Von Holle, 1999; Sax and Brown, 2000; Naeem *et al.*, 2000; Kennedy *et al.*,

55   2002; Raffaelli *et al.*, 2002; Stachowicz *et al.*, 2002).

56

57   The importance of considering a trophic network approach is that it can elucidate feeding

58   relationships which occur between species in an ecological community and determine functional

59   roles of species groups in the ecosystem (Yodzis and Winemiller, 1999). Indeed, numerous

60   evidences suggest that food web structures are susceptible to a wide array of human activities,

61   including species introductions or invasions (Vander Zanden *et al.*, 1999), habitat alteration

62   (Wootton *et al.*, 1996), and global environmental warming (Petchey *et al.*, 1999).

63

64   Quantitative trophic analyses at the ecosystem level were carried out in some African

65   Lakes where exotic species were introduced (Moreau, 1995; Moreau *et al.*, 1993; 2001;

66   Villaneuva and Moreau, 2001). A similar approach has been carried out in other African lakes,

67   i.e. Lake Victoria (Moreau, 1995; Villanueva and Moreau 2001), Lake Naivasha (Mavuti *et al.*,

68   1996; Moreau *et al.*, 2001) or Lake Kariba (Moreau, 1997), to determine the state of biologic

69   community alterations following fish introductions. As effects of fish introductions and its

70   exploitation on the community and ecosystem level are still unknown in Lake Kivu. The aim of

71   the present contribution is to study the food web structure, species interactions, role of exotics in

72   the ecosystem and compare these to observations in other tropical lakes where fish introductions

73   occurred. Understanding trophic links is crucial in predicting future impact of species invasion in

74   natural food web structure and functioning.

75

76   **Material and Methods**

77   *Study site*

78

79   Lake Kivu (Fig.1) has a surface area of 2 370 km² of which 1370 km² is a part of the

80   Congolese territory. An international aquatic system situated along the Congo-Rwanda border at

81   an altitude of 1 463 m. It is located between 1°30' and 2°30' latitude south and between 28°50'

82   and 29°23' longitude east. It is a deep (maximum depth 490 m) equatorial lake with an average

83   water depth of about 240 m. The littoral area stretches not further than 50 m away from the

84   lake's extensive (1200 km) shoreline (Van den Bossche and Bernascek, 1990; Verheyen *et al.*,

85   2003). It is a meromictic lake with deep relict hypolimnion where beneath lies a vast methane

86   gas reserves (Coulter *et al.*, 1984; Snoeks, 1994). Permanent water stratification is observed:

87   anoxic below 60 m while the deeper part of the lake is methane saturated (Coulter *et al.*, 1984;

88   Van den Bossche and Bernascek, 1990; Isumbisho et al., 2006; Sarmento et al., 2006). Annual

89   precipitation in the region is about 1 300 mm, relatively higher along the occidental than the

90   oriental side of the lake, which experiences virtually no variations in water level. The average

91   surface water temperature is about 24°C (Snoeks, 1994).

92

93   Several lakes of the East African Rift Valley are characterized by a deep pelagic zone

94   which is colonized by abundant native small pelagic fish (Coulter *et al.*, 1984; Lowe-McConnell,

95   1993). A well documented exception among these lakes is Lake Kivu. Compared to other lakes

96   of the Rift Valley the fish diversity is relatively poor with only 26 endemic species belonging to

97   the Cichlidae, Clariidae, Cyprinidae and Clupeidae families (Hanek *et al.*, 1991; Snoeks, 1994).

98   The Cichlids are the most represented with 17 endemic haplochromines (De Vos *et al.*, 2001).

99

100   Exotic fishes were introduced to increase biodiversity and productivity of the lake

101   (Welcomme, 1988). Fish stocking in Lake Kivu dates back in the 1950s where two cichlids,

102   *Oreochromis macrochir* (Boulenger) and *Tilapia rendalli* (Boulenger), were introduced due to

103   the renowned ecological plasticity of these species (Chapman *et al.*, 2003; De Vos *et al.*, 2001).

104   Two endemic sardines of Lake Tanganyika, *Limnothrisssa miodon* (Boulenger) and *Stolothrissa*

105   *tanganyicae* (Regan), were then simultaneously introduced in 1959 (Van den Bossche and

106   Bernascek, 1990; Spliethoff *et al.*, 1983) to occupy the pelagic zone (90%). *S. tanganyicae*,

107   however, was not able to adapt to the local conditions in the lake (Hauser *et al.*, 1995).

108

109   The Lake Kivu fishery is predominantly artisanal (Van den Bossche and Bernacsek,

110   1990; Hanek *et al*., 1991; de Iongh *et al.*, 1995) which is similar to other East African Lakes

111   (Pitcher and Hart, 1995; Preikshot *et al.*, 1998). In terms of the fishing activity, fishery in the site

112   considered is the most important in the Congolese sector (Hanek *et al.*, 1991). Annual production

113   is generally observed higher in the Rwandese sector where fishing activities are more active and

114   developed. At the zone considered in this study annual production in 1990 represented 20% of

115   overall production (Hanek *et al*., 1991; Marshall and Mubamba, 1993). Fishermen operate with

116   various fishing gears depending on season, investment level, fishing areas and species targeted.

117   A specific fishery, trimaran, uses light attraction and liftnet and selectively targets *L. miodon* and

118   planktivore haplochromines (Van den Bossche and Bernacsek, 1990; Hanek *et al.*, 1991; de

119   Iongh *et al*., 1995; Kaningini *et al.*, 1999). Beach seines capture mainly the benthopelagic

120   haplochromines, but have been observed to accidentally catch other species such as *L. miodon*.

121   Gillnets capture mainly tilapias although smaller mesh-sized (10 mm) nets are employed to trap

122   *L. miodon* and some haplochromines. Longlines target mainly Clarias species (Hanek et al.,

123   1991).

124

125   The lake is an international area shared by Rwanda (East) and RD Congo (ex-Zaire,

126   West). For this study, we considered the Bukavu basin of the Congolese sector (Fig. 1) which is

127   approximately 140 km², as this zone is better documented in terms of biological community

128   ecology and fisheries compared to the Rwandese sector. This zone also represents an important

129   socio-economic aspect (Hanek *et al.*, 1991). It should be noted that parameters integrated in the

130   model were mainly estimated using data collected in this area.

131

132   ***Theoretical Approach***

133

134   We used the Ecopath model (Christensen and Pauly, 1993; Christensen *et al.*, 2005) to

135   construct a steady-state description of the Bukavu Bay. The model has already been used for

136   quantifications of food webs in different ecosystems to study the impact of fisheries for

137   management purposes (Pauly *et al.*, 2003; Christensen and Walters, 2004b). It comprises a set of

138   simultaneous linear equations, one for each group under consideration, where the production of

139   the group is equal to the sum of all predation, non-predatory losses and export:

140

141    $$B_i \cdot \frac{P}{B_i} = \sum_{j=1}^{n} B_j \cdot \frac{Q}{B_j} \, DC_{ji} + B_i \cdot \frac{P}{B_i} (1\text{-}EE_i) + EX_i \qquad (1)$$

142

143   where B_i is the biomass of group i (in t km^{-2} fresh weight); P/B_i is the annual production/biomass

144   ratio of i equal to the total mortality coefficient (Z) in steady-state conditions (Allen, 1971); EE_i

145   is the ecotrophic efficiency representing the part of the total production consumed by predators

146   or captured in the fishery or exported; B_j is the biomass of the predator group j; Q/B_j is the annual

147   food consumption per unit biomass of the predatory group j; DC_{ji}, is the proportion of the group i

148   in the diet of its predator group j; EX_i, is the export or catch in fishery of group i, that is assumed

149   to be exploited in the fishery (Christensen *et al.*, 2005).

150

151   In addition to balancing the model, Ecopath can be used to compute parameters and

152   indices corresponding to the food web characteristics. Some parameters that can be estimated

153   using the software are as follows:

154

155   a.) The group-specific omnivory index *OI* is computed as the variance of the *TLs* of each

156   predator's prey groups (Christensen and Pauly, 1993) while the system omnivory index *(SOI)* is

157   computed as the average omnivory index of all consumers weighted by the logarithm of each

158   consumer's food intake *Q* (Christensen *et al.*, 2005). It indicates the allocation of predator170

159   prey interactions linking each *TL* (Christensen and Walters, 2004a). Both *OI* and *SOI* indices

160   vary from 0 to 1, where a value close to 0 indicates high predatory specialization (feeding on one

161   trophic level only) and 1 indicates a maximum feeding versatility on several trophic levels.

162

163   b.) The connectance index (*CI*) is the ratio between the number of actual definite trophic

164   associations among all the groups and the theoretical possible number of connections, $(N-1)^2$ for

165   *N* groups, including consumption of detritus (Christensen and Walters, 2004a; Christensen *et al.*,

166   2005). This index is correlated with the maturity e.g. the level of evolution of the ecosystem, as

167   defined by Odum (1969), of the ecosystem because the food chain structure changes from linear

168   to web-like as a system matures (Odum, 1971).

169

170 c.) Niche overlap is measured by using a symmetrical index derived from the one proposed by

171 Pianka (1973) based on competition coefficients of the Lotka-Volterra equation (Volterra, 1931)

172 and derived from the Jaccard similarity index (Harris, 1968). It is used to describe mainly the

173 trophic aspect of niche partitioning. An index value close to 0 indicates that two groups have a

174 low resemblance in terms of food consumed and vise versa for a value close to 1 (Christensen *et*

175 *al.*, 2005).

176

177 d.) Trophic aggregation per discrete *TL*, *sensu* Lindeman (1942), is based on an approach

178 suggested by Ulanowicz (1995). This routine facilitates calculation of flows per *TL* based on diet

179 compositions by reversing the routine for calculation of fractional trophic levels quoted above.

180 More particularly, the transfer efficiencies between the successive discrete trophic levels are

181 calculated as the ratio between the sum of the exports plus the flow that is transferred from one

182 trophic level to the next, and the throughput at this trophic level (Christensen *et al.*, 2005).

183

184 e.) The gross efficiency of the fishery (GE_F) is computed as the ratio between the total catch and

185 the total primary production in the system. The value will be higher for systems with a fishery

186 harvesting fish belonging mainly to low *TLs* than for systems whose fisheries concentrate on

187 high *TLs*. Therefore, this index may increase with fisheries 'development' as defined by Pauly *et*

188 *al.* (1998).

189

190 ***Model construction***

191

192   The model was constructed using data collected from 2002 and 2003. These are

193   complemented by additional published works by Ulyel (1991), Snoeks (1994) and Kaningini *et*

194   *al.* (1999). For simplification purposes, species with similar ecological characteristics (i.e.

195   metabolism, diets and predators) were pooled together following the indications of Yodzis and

196   Winemiller (1999). In such a case, the biological characteristics of the most abundant species

197   were considered. A total of 14 groups were considered in this study and the ecological grouping

198   of biological assemblages is the following one.

199

200   *Detritus*: A standing stock of 165t.km^{-2} (fresh weight, fw) was calculated using the

201   empirical equation of Pauly *et al.* (1993) based on an annual primary production estimated in the

202   system (see below) and a euphotic zone of 32 m. It is an input required to run the model

203   (Christensen and Pauly, 1993).

204

205   *Phytoplankton and primary production:* The dominant groups are diatoms (*Nitzschia* spp

206   and *Fragilaria* spp) and cryptophytes (*Chroomonas* spp and *Rhodomonas* spp). Chlorophyll-*a*

207   concentration showed clear seasonal variations and increases during the dry season, after deep

208   mixing in the basin of Bukavu (Ishumbisho *et al.*, 2006; Sarmento *et al.*, 2006). The average

209   Chlorophyll-*a* content is 1.53 mg m^{-3} for the area considered. It can be extrapolated over 60 m as

210   suggested by Isumbisho *et al.* (2006) and the resulting fresh biomass (32.1 t km^{-2} fw) was used as

211   an input in the model. The annual primary production was measured at 273 g C.m^{-2} by Sarmento

212   *et al.* (2006) and concords with annual range values (240 – 379 gC.m^{-2}) indicated earlier by

213   Jannasch (1975), Van den Bossche and Bernacsek (1990) and Descy and Fourniret (1991). A

214   similar value was estimated using the Photosynthesis simulator of Capblanc and Dauta (1999).

215   Assuming 1 g C is equal to 10 g fw (Sarvala *et al.*, 1999). A *P/B* ratio of 85 yr^{-1} was used as an

216   input in the model.

217

218   *Zooplankton and secondary production:* The zooplanktonic community is dominated by

219 copepods (*Thermocyclops*) and, to a lesser extent, cladocerans (*Diaphanosoma*) though seasonal

220 density variations can be observed (Isumbisho *et al.*, 2006). The average *B* is 5.64 t.km^{-2}

221 estimated from Isumbisho *et al.* (2006) and an annual *P/B* value of 30 yr^{-1} was used (Sarvala *et*

222 *al.*, 1999; Irvine and Waya, 1999). *Q/B* value of 180 yr^{-1} was adopted from Sarvala *et al.* (1999).

223

224   *Benthic fauna:* Only limited information was available for this group. This includes

225 benthic deposit feeders such as the nematodes, ostracods, insects, bivalve mollusks, gastropods

226 and other benthic organisms which develop only along the littoral zone due to the relative

227 steepness of the lake. A *P/B* value of 4.5 yr^{-1} (Payne, 1986; Mavuti *et al.*, 1996) was adopted and

228 *Q/B* of 45.0 yr^{-1} was assumed from a gross efficiency (*GE* or *P/Q*) value of 0.1 (Christensen and

229 Pauly, 1993). An input value of 0.900 for *EE* was used to estimate the biomass based on intense

230 predation noted from higher *TL* consumers.

231

232   *Fish groups:* When possible the *B/P* ratio was estimated from recently collected length

233 frequency distributions by using the FiSAT software (Gayanilo *et al.*, 2002). In a first step, this

234 software was used to estimate the growth parameters of the von Bertalanffy growth function i.e.,

235 the asymptotic length (L_∞) and the growth coefficient (*K*) which are needed for *P/B* computation

236 by reference to the length converted catch curve method. Otherwise, the predictive models of de

237 Merona (1983) or Fröese and Binohlan (2000) were employed to estimate these demographical

238 parameters. Natural mortality, *M*, was computed using the predictive formula of Pauly (1980).

239 The demographical data of the fish populations considered here are summarized on Table 1.

240

241   The food consumption per unit of biomass (Q/B) has been estimated in a few cases using

242   Maxims (Jarre *et al.*, 1991), a software model based on the method of Pauly (1986) which allows

243   the computation of Q/B from an estimate of the daily food consumption of individual fish of a

244   particular size. Otherwise, Q/B was calculated using the multiple regression formula of

245   Palomares and Pauly (1998).

246

247   For most fish groups, local field data on diet composition were available. Additional

248   information was taken from Snoeks (1994) and Ulyel *et al.* (1991).

249

250   The biomass (B) of each fish group was estimated assuming equilibrium conditions, such

251   that:

252           $B = Y/F$ (3)

253   where Y is yield in t.km^{-2}.yr^{-1} and F is the coefficient of fishing mortality. F is the difference

254   between total and natural mortalities: $F = Z - M$, assuming that Z is equal to P/B as indicated by

255   Allen (1971).

256

257   Due to habitat preferences of the species under investigation, the littoral area which is

258   about 10% of the total surface of the lake (based on depth and bathymetry) was separated from

259   the pelagic zone. The biomass of each compartment was calculated according to habitat area. For

260   littoral groups, the biomass per km² as computed as an average for the whole lake was, then,

261   multiplied by 10 in order to express the concentration of this group in the littoral area.

262

263   Catch data and the proportion of each group in the total catch were obtained from various

264   sources (i.e., Van den Bossche and Bernacsek, 1990) including unpublished data (J-C. Micha,

265 FUNDP; B. Kaningini and M. Isumbisho, UERHA pers. comm.) recently collected as a part of

266 an on-going Belgium Project for development of a gillnet fisheries in the lake.

267

268 The following groups were considered

269

270 **1°)** *Clarias* **spp**: This group includes *Clarias gariepinus* (Burchell) and *C. liocephalus*

271 (Boulenger) which is quite rare in the lake and has been observed only in open waters. *C.*

272 *gariepinus* has been considered as the key species for this group due to its predominance and

273 well-studied ecological characteristics (B. Kaningini, UERAH, pers. comm.). Ulyel (1991)

274 considered this species as a benthic polyphage, feeding on insects, crustaceans and fishes.

275

276 **2°)** *Raiamas moorei***:** This species, formerly known as *Barilius moorei* (Boulenger), is the only

277 cyprinid inhabiting most areas of the lake. It feeds mainly on small bottom mollusks and insects,

278 as well as on small cichlids and clupeids. *EE* was set at 0.50 as this group is rarely targeted by

279 fishermen and seems to be exposed to a limited predation by *Clarias* spp and *Haplochromis*

280 *vittatus* (Boulenger).

281

282 **3°)** *Haplochromis* **spp:** A list of 17 species was proposed and observed by Snoeks (1994). For

283 the purpose of the present study, these species have been re-grouped based on their feeding

284 ecology (Snoeks, 1994; Ulyel *et al.*, 1991; Fourniret *et al.*, 1992; Kaningini *et al.*, 1999; Fröese

285 and Pauly, 2006) into three groups:

286   • *H. vittatus*, a piscivore species which inhabits both the near shore and open waters.

287   • Benthos-feeding haplochromines are mostly *H. gracilior* (Boulenger), *H. graueri*

288   (Boulenger), *H. astatodon* (Regan), *H. nigroides* (Pellegrin) and *H. paucidens*

289   (Regan). They inhabit the littoral areas and feed mainly on small mollusks,

290   nematodes, insects and their larvae. The biological characteristics of *H. graueri*

291   were *c*onsidered since this is the most abundant among the benthophages.

292   • Plankton-feeding haplochromines are dominated by *H. kamiranzovu* (Snoeks) which

293   was considered as the key species for this group.

294   Diet compositions of haplochromine groups were adapted from Ulyel *et al.* (1991) and

295   Fourniret *et al.* (1992).

296

297   ***4•) Limnothrissa miodon*:** This pelagic fish feeds mainly on zooplankton (Copepods) during its

298   juvenile stage and may consume insects and small-sized fishes (de Iongh *et al.*, 1983; Kaningini,

299   1995; Isumbisho *et al.*, 2004). According to Pearce (1995), it is capable of adapting its diet

300   preferences according to the local conditions (i.e., food availability), as this species is not

301   specialized with regards to its preys. Demographic studies have been carried out by de Iongh *et*

302   *al.* (1995) and Kaningini (1995). According to de Iongh *et al.* (1995), three length classes can be

303   identified for this species based on condition factor changes. For this study, however, only two

304   length classes were considered based on the length at first maturity (50% of the gonads

305   maturing) to separate the pelagic adults (>8.0 cm total length) from the sub littoral juveniles (<

306   8.0 cm total length). This repartition takes into account the difference of their spatial distribution

307   (Spliethoff *et al.*, 1983; Lambœuf, 1991), spawning-related migrations (Marshall, 1991) and

308   ontogenetic diet variations (de Iongh *et al.*, 1983). Several studies on feeding patterns have also

309   indicated occurrence of cannibalism (Spliethoff *et al.*, 1983; Isumbisho *et al.*, 2004).

310

311   It should be noted that the adults have a low *P/B* ratio (1.75 yr^{-1}) compared to juveniles

312   (6.69 yr^{-1}), a feature which was already noted when juveniles and adults are separated in an

313   Ecopath model such as for *Lates niloticus* (Linnaeus) in Lake Victoria (Villanueva and Moreau,

314   2001). It is due to higher exploitation and predation on the latter, which are also integrated into

315   the adult pool. As juveniles sardines prey mainly on zooplankton and small benthos, their *Q/B*

316   values measured using MAXIMS are also higher (35.8 yr^{-1}) than those of adults (19.20 yr^{-1})

317   which feed on zooplankton but also on small fish. In addition, small fish consume much more

318   food relatively to their size than larger ones (Pauly and Palomares, 1987).

319

320   *5•) Barbus* **spp** inhabit near-shore area. This group includes *Barbus kerstenii* (Peters), *B*

321   *pellegrini* (Poll), *B. pleurogramma* (Boulenger) and *B. altianalis* (Boulenger). This group feeds

322   basically on microphytes, insects and other benthic organisms, and on small littoral fishes (Ulyel,

323   1991; Kaningini *et al.*, 1999; Fröese and Pauly, 2006). This group is one of the least consumed

324   and exploited and least predated upon in the lake; *EE* was, therefore, admitted to be 0.50.

325

326   *6•) Oreochromis niloticus eduardianus* (Boulenger) is an endemic, microphage fish inhabiting

327   the littoral areas. It is the most abundant, native cichlid species in the lake due to its high

328   fecundity (Trewavas, 1983).

329

330   **7°) Other Tilapiine fish** include two introduced cichlid species, *O. macrochir* and *T. rendalli)*,

331   with the latter being more abundant possibly due to its efficient reproduction and feeding

332   plasticity (Trewavas, 1983). In its original environment, *T. rendalli* is, however, regarded as a

333   macrophyte-feeding species (Fröese and Pauly, 2006). Both inhabit the littoral areas of the lake

334   and feed on macrophytoplankton and other organic material (Ulyel, 1991; Kaningini *et al.*,

335   1999).

336

337   **Results**

338

339   The basic input for each group and the parameters computed by the model are presented

340   in Table 2 and 4, while the relative diet compositions are given in Table 3 whereas Figure 2

341   summarizes the main flows within this ecosystem. Total estimated fish biomass is low, 3.705

342   t.km^{-2}, compared to other African inland waters (Christensen and Pauly, 1993). The resulting

343   biomass for benthos looks low (3.676 t.km^{-2}) for the whole lake, though concentration along the

344   littoral zones yields 36.76 t.km^{-2}. This is in agreement with the importance of this group in the

345   diets of several fish groups. A high abundance of zoobenthic organisms has already been noted

346   in shallow areas of Lake George (Moreau *et al.*, 1993) or Lake Ihéma (Mavuti *et al.*, 1996).

347

348   Highest *TLs* were estimated for *Clarias* spp, *R. moorei* and *H. vittatus* (*TL* >3.3) due to

349   their carnivorous feeding ecology (Table 3). Most groups belonging to *TL*3 and more are

350   predatory carnivores.

351

352   *Ecotrophic efficiencies*

353   A low *EE* value of 0.079 has been calculated for the detritus as most of it sinks to the

354   bottom in the deepest parts of the lake. Phytoplankton has a higher *EE* of 0.633, indicating that

355   this group is the base food source in the lake even if it seems that it is not fully utilized by

356   organisms of higher *TLs*, at least in this area of the lake. This may be attributed to the limited

357   quantity of fish basically consuming this group. A high value of *EE* is noted as well for

358   zooplankton (0.764). Carnivorous zooplankton (Copepods) partly feed on the herbivorous

359   zooplankton (mainly Cladocerans and Rotifers), as noted in the feeding matrix (Table 2)

360   although they consume also phytoplankton. Ecotrophic efficiencies of fish groups are variable.

361   For the two groups of Tilapiine fish, *EE* is quite low (*EE* = 0.479 and 0.233), suggesting a very

362   limited exploitation and predation in the lake. The maximum *EE* value (0.917) is recorded for *L.*

363   *miodon* juveniles, as we expected because these fish are exploited and predated.

364

365   ***The gross efficiencies***

366   The *P/Q* ratios (Table 4) are low for *R. moorei* and adult *L. miodon*. This might be due to

367   the low density of their prey, particularly the zooplankton, and the necessity for these fish to use

368   more energy for hunting their prey, which are available only at low densities. It should be noted

369   that the density of zooplankton per volume basis is very low: 0.0914 g.m^{-3} fresh weight

370   (Isumbisho *et al.*, 2006). The low *P/Q* ratios obtained for the 2 groups of Tilapiine fish (0.040

371   and 0.045) are in agreement with the low quality of their preferred preys which are principally

372   phytoplankton and decaying organic material. A high *P/Q* ratio is estimated for zoophagous

373   haplochromines (0.202) due to their carnivorous feeding habits. The maximum value (0.220) was

374   obtained for the juveniles *L. miodon* and this is in relationship with their small size. This value is

375   higher than for adults, which is in agreement with the basis of the method of computation of *Q/B*

376   implemented by Pauly and Palomares (1987). Ichthyophagous fishes (*Clarias* spp and *H.*

377   *vittatus)* have surprisingly low *P/Q* values. It might come from the scarcity of their possible prey

378   in terms of biomass per volume unit.

379

380   ***Omnivory indices and diet overlap***

381   The omnivory index (*OI*) of each group is presented in table 4. In general, high *OI* values

382   are observed in high *TLs*, which indicate more complexity in this part of the food web. Highest

383   *OI* are observed for three predators: *Clarias* spp*, Barbus* spp and *H. vittatus* (0.282, 0.349 and

384   0.339, respectively), and is related to their large feeding spectrum and distribution in the lake.

385   These observations concord with the indication of Lindeman (1942) that prey tend to be more

386   specialized than their predators.

387

388   Adults of *L. miodon* have a lower *OI* (0.153), than their juveniles (0.218) due to the

389   latter's feeding flexibility (Isumbisho *et al.*, 2004). Accordingly, our results indicate that, in

390   habitats where it is already acclimated, *L. miodon* adjusts its trophic behavior to the availability

391   of aquatic macro invertebrates. This has already been noted by Marshall (1995), Kaningini

392   (1995) and recently by Isumbisho *et al.* (2004). Compared to *H. vittatus*, Haplochromines groups

393   4 and 5 have a lower *OI* (0.155 and 0.179, respectively)*,* which suggests a higher specialization.

394

395   *OI* of *O. niloticus* is zero as this fish consumes only preys from the first trophic level,

396   mainly phytoplankton (Table 3). Preference for phytoplankton of this species has been observed

397   in other tropical lakes (Tadesse, 1999; Lu *et al.*, 2006). Other Tilapiines, on the other hand, have

398   a higher *OI* due to their trophic plasticity, particularly for *T. rendalli*, that enables dietary shifts

399   from plant or detrital material to animal material (Ulyel 1991; Kaningini *et al.*, 1999).

400

401   High values of individual *OI* for groups sharing the same type of food can be associated

402   with estimates of niche overlaps. *L. miodon* juveniles (group 7) have a low overlap as predator or

403   prey for most groups, except for the adults (group 6) which show high overlap in prey (Fig. 3).

404   Groups 9 (*O. niloticus*) and 10 (Other Tilapiines) show the highest overlap which suggests high

405   competition for similar resources. Groups 2 (*R. moorei*) and 7 have the lowest overlap which

406   expresses divergent preferences in terms of resources consumed (Fig. 3).

407

408   The *SOI* for the southern part of Lake Kivu is low, 0.150 with a connectance index (*CI*)

409   of 0.396 (Table 4). This *CI* value is slightly higher than the theoretical value (0.317) computed

410   using the regression model of Christensen and Pauly (1993). Both values can imply that most

411   functional groups exhibit a certain degree of diet specialization. This indicates as well the co-

412   existence of weak and strong interactions observed among groups as expressed by the various *EE*

413   values (Table 2). According to Quince *et al.* (2002), this is common in food webs of especially

414   competitive communities which might be the case here. Moreover, McCann (2000) indicated that

415   recurrent food-web structures, with omnivory and apparent competition, can enhance ecosystem

416   stability if the distribution of consumer–resource interaction strengths is skewed towards weak

417   interaction strengths and McCann referred to as the "weak-interaction effect" which contributes

418   to community-level stability.

419

420   ***Biomass flux and transfer efficiency***

421   Trophic aggregation revealed that transfer efficiency from *TL*1 (phytoplankton and

422   detritus groups combined) to higher *TLs* is about 8.4%. This indicates that this resource may not

423   be fully exploited due to the presence of herbivores in the littoral area, which makes up only 10%

424   of the lake, leading to increased unconsumed nutrient accumulation (Table 5). The average

425   transfer efficiency is at any *TL* is less than 10% (Table 5). This is higher than that observed in

426   other ecosystems such as Lake Navaisha (Moreau *et al.*, 2001). Most of the fish biomass and

427   ecological production take place at *TL*3 or more, as summarized in table 5.

428

429   The ecosystem is phytoplankton-based as 61% of the total flow originating from *TL*1

430   comes from primary producers while only 39% originates from detritus (Table 5), a feature of

431   relevance in a deep-water body (Christensen and Pauly, 1993). Most primary production is

432   consumed by zooplankton and juveniles *L. miodon*. Detritus is consumed only by benthic fauna

433   (group 11) and, to a certain degree, by some fish groups: *Barbus* spp., *O. niloticus* and other

434   Tilapiines (Table 3). The elevated proportion of primary production flowing back to detritus

435   (about 65 % of the total) is the result of increasing algal biomass surplus unconsumed, especially

436   in the open waters of the lake.

437

438   A high ratio between production and respiration (3.92) is noted. Most likely, a limited

439   quantity of organic matter is imported by inflowing rivers. An important part of the production of

440   several groups is not utilized (*EE* is low) and is therefore lost as incorporated into the sediments

441   on the bottom of the lake which has a deep anoxic hypolimnion. This might explain this

442   unusually high value of the production/respiration value.

443

444   Fish productivity is linked to primary production by many intermediate trophic links. The

445   primary production required (PPR) in order to support the fishery is 15.2% of the total primary

446   production (Table 6) which is low compared to an average value suggested by Pauly and

447   Christensen (1995) for tropical lakes and rivers (23.6 %). When expressed relative to the total

448   flow from *TL*1, the *PPR* (primary production required) used in Ecopath corresponds to the

449   ecological footprint (*EF*). For the catch the expression is $EF = PPR/PP*C$ where *PP* is the total

450   flow from *TL*1, and *C* the catch, will give the size of the area in km², assuming the unit is,

451   needed to sustain a catch of 1 ton for the given resource. As a consequence, a low ecological

452   footprint (Folke and Kautsky, 1996) of the fishery (0.04 km²) is observed, similar to those

453   observed by Villanueva *et al.* (2006) in two West African lagoons.

454

455   The GE_F is quite low (0.0015) compared to what was observed for Lake George (Moreau

456   *et al.*, 1993), Lake Ihéma (Mavuti *et al.*, 1996) and Lake Victoria (Villanueva and Moreau, 2001)

457   or other tropical inland water bodies (Christensen and Pauly, 1993). The mean *TL* of the fishery

458   is 2.9 (Table 6) as it targets mostly *L. miodon*.

459

460   ***Model predictions of the effects of environment changes***

461

462   The mixed trophic impact (*MTI*) routine of Ecopath (Ulanowicz and Puccia, 1990) shows

463   the direct and indirect influences of abundance variations of any species group on all other

464   groups considered (Fig. 4). An initial condition that should be considered for this routine is that

465   diet composition of each functional group does not change, despite possible variations in

466   abundance of their various preys. An increased abundance of fish groups of high *TLs* (about 3 or

467   more) would have various levels of negative impacts on other groups. This is particularly the

468   case for *Clarias* spp (group 1) and *L. miodon*. An increasing abundance of non fish groups would

469   generate a positive impact on most groups including fish groups. The impact of zooplankton

470   biomass variations would be less important compared to the phytoplankton group. The extent of

471   bottom-up control is elevated, as an increase in abundance of phytoplankton would have a strong

472   positive effect on all higher *TLs* (Fig. 4), especially on the herbivores (groups 5, 9, 10 and 12).

473

474   A top-down trophic cascade effect (Pace *et al.*, 1999; Persson, 1999) on phytoplankton

475   biomass is also observed in the *MTI* simulation (Fig. 4). The primary productivity is increased

476   due to the increase in planktivorous fish (*TL*3) that regulates herbivores, which in turn prey on

477   phytoplankton. Hence, this may lead to a build-up of nonutilized phytoplankton. This was also

478   experimentally observed by Lynch and Shapiro (1981).

479

480   Figure 5 shows the susceptibility of some fish to human exploitation than others. Fishing

481   gears employed capture a specific species in the lake (Hanek *et al.*, 1991). An increase of 10% in

482   the fishing effort shows a substantial increase in catch of target species, i.e. *Clarias* spp.,

483   *Haplochromines*, adult and juvenile *L. miodon*. Positive impacts on groups at lower *TLs* is a

484   consequence of lower predation pressure when stock of fish predators decline due to increased

485   fishing. An increasing fishing effort with beach seine and longline would have a slight negative

486   impact on zooplankton. Both gears do not target *L. miodon* juveniles which are the principal

487   predator of this group.

488

489   **Discussion**

490

491   Successful colonization of *L. miodon* in Lake Kivu has been attributed to the absence of

492   other pelagic planktivores (de Iongh *et al.*, 1995; Marshall, 1995; Munyandorero and Mwape,

493   2003) and low diversity of native species (Johannesson and Lambœuf, 1989). These combined

494   with the relative stability of environmental factors suitable for its growth, provided opportunities

495   for successful colonization of this sardine (Marshall, 1991; 1995) and other Cichlids.

496   Acclimatization of stocked species has been also observed in other African lakes such as Lakes

497   Kyoga (Ogutu-Ohwayo, 1990), Kariba (Karenge and Kolding, 1995), Navaisha (Muchiri *et al.*,

498   1995; Moreau *et al.*, 2001), Nabugabo (Chapman *et al.* 1996) and Tana (de Graaf *et al.*, 2000) as

499   well as in other ecosystems in the world (Vitousek *et al.*, 1997; Wilcove *et al.*, 1998; Latini and

500   Petrere Jr., 2004). Environmental condition modifications have already been cited as a major

501   factor in enhancing long-term success and dominance of exotics species in several ecosystems

502   (Muchiri *et al.*, 1995; Smith *et al.*, 2000; Dudgeon *et al.*, 2006).

503

504   The ability of *L. miodon* to coexist with other zooplanktivores may be essentially due to

505   spatial heterogeneity, thus, an absence of co-adapted competitors. Competition between similar

506   functional groups may also alleviate indirect effects of predators on ecosystem processes and

507   exhibits functional redundancy in ecosystems (Lawton and Brown, 1993; Loreau *et al.*, 2001;

508   Raffaelli *et al.*, 2002; Stachowicz *et al.,* 2002). Similar observations in other ecosystems were

509   made in Lake Kariba (Karenge and Kolding, 1995), Parakrama Samudra reservoir (Moreau *et*

510   *al.*, 2001) and in the Great Lakes (Mills *et al.*, 1993). Coexistence seems possible based on a

511   competitive exclusion principle (Richards *et al.*, 2000) by limiting competition through space

512   budgeting (Isumbisho *et al.*, 2003) between or within-guild species. Some haplochromines

513   inhabit mostly the inshore zone while *L. miodon* occupies essentially the open waters. The

514   significance of spatial heterogeneity in favoring increase of species abundance has also been

515   observed by Le Pape *et al.* (2003) in the Bay of Biscay.

516

517   Similar to *L. miodon,* naturalized tilapias still remain at limited levels without major

518   impacts on the indigenous Nile Tilapia. Coexistence of both endemic and alien tilapias may be

519   due to niche partitioning aside from the broad tolerance of tilapias against environmental

520   changes (Murichi *et al.*, 1995; Iwama *et al.*, 1997; Khallaf *et al.*, 2003). In Lake Kivu, these

521   tilapias inhabit essentially the shallow waters (>10 m deep). The endemic *O. niloticus*

522   *eduardianus*, however, is abundant in rocky bottoms while introduced Tilapiine fishes (*O.*

523   *macrochir* and, especially, *T. rendalli*) colonize better the muddy littoral zones (Trewavas,

524   1983). Spatial segregation limits competition for food and nursery sites similarly observed in

525   Lakes Victoria and Kyoga (Twongo, 1995). *O. niloticus* and *O. macrochir* are both microphages

526   which may explain the elevated prey-predator overlap (Fig. 3). Resistance of *O. niloticus*

527   *eduardianus* may be mediated by its opportunistic behavior despite dietary overlap with *O.*

528   *macrochir*. Broadening of diet spectrum can increase a species tolerance to stress (Murichi *et al.*,

529   1995; Sax and Brown, 2000; Wanink and Witte, 2000; Villanueva *et al.*, 2006). Dietary shifts of

530   *O. niloticus* are similarly observed in Lake Victoria (Njiru *et al.*, 2004).

531

532   This, however, may not apply to other species of lower environmental tolerance in the

533   lake. Low omnivory indices were observed for some groups, indicating a less diversified diet.

534   This is not the case for the sub-littoral inhabiting cichlids which contribute to the efficient

535   utilization of some resources, i.e. here the primary producers. Despite the low contribution of the

536   detritus group, it is still utilized as a buffering agent in case of resource limitation. Similar

537   observations were indicated by in Lake Navaisha (Munichi *et al.*, 1995; Mavuti *et al.*, 1996) and

538   in some West African lagoons (Villanueva *et al.*, 2006).

539

540   Both the predation-based regulation of the lower *TLs* and the resource-based regulation of

541   the upper *TLs* are present in the ecosystem studied. The strength of both bottom-up and top-down

542   controls determine system diversity though their relative importance and intensity which are

543   based on the structure and functioning of groups among *TLs* (Herendeen, 2004). Differences in

544   migration patterns and food availability may influence predation rates of predators, such as *C.*

545   *gariepinus*, *H. vittatus* and *L. miodon* (Isumbisho *et al.*, 2004). This is similar to observations of

546   Bruton (1979) and Huddart (1994) in other African lakes.

547

548   The *MTI* analysis (Fig. 4), nonetheless, demonstrated the importance of bottom-up forces

549   through the strong potential influence of any phytoplankton abundance variation on the whole

550   food web. In ecological theory, bottom-up forces would dominate the ecosystem process (Platts

551   and Ulanowicz, 1985; Dyer and Letourneau, 2003). According to Proulx *et al.* (1996),

552   production can also be modified through algal community structure modification as a function of

553   variations in size distribution (Perin *et al.*, 1996) or through predation-mediated modifications in

554   plankton community structures (Hansson and Carpenter, 1993; Dyer and Letourneau, 2003).

555

556   Isumbisho *et al.* (2004) observed variations on zooplankton community abundance and

557   distribution which is mainly due to predation by *L. miodon* juveniles and partly, in relation, to

558   fishery practices. Predation-related variations within functional groups may lead to

559   compensatory population increases by less vulnerable species in response to predation on

560   vulnerable species (Steiner, 2001). Predation and competition affect aquatic communities

561   indirectly by causing behavioral changes in prey species (Nyström *et al.*, 2001; Steiner, 2001).

562   Predation is an important part of ecosystem functioning though an increase in aggressive

563   invaders or top predators can equally multiply effects of feeding interactions and contribute to

564   reorganization of ecosystem structure indirectly (Fulton *et al.*, 2003; Didham *et al.*, 2005).

565   Changes in zooplankton community structure have also been observed in Lake Donghu (China)

566   by Yang *et al.* (2005) as a consequence of increased predation pressure of zooplanktivores. In

567   Lake Victoria such phenomenon is attributed to eutrophication (Wanink *et al.,* 2002).

568

569   The introduction of *L. miodon* and tilapias in the lake has surely improved energy transfer

570   efficiencies in the lake, especially in the pelagic zone. Significant changes in functional roles at

571   individual (i.e., changes in behavior and habitat use) and population (i.e. change in the

572   abundance and distribution) levels were observed in the lake. Species change has also

573   contributed to an entirely new configuration of the fisheries (Van den Bossche and Bernacsek,

574   1990; Preikshot *et al.*, 1998). Compared to other ecopath-modeled deep lakes in Africa (see

575   Villanueva and Moreau, 2001), however, there are many functional groups in Lake Kivu with

576   low *EE* values which imply that lower *TLs* are not saturated and predator abundance variations

577   can create vacant niches leaving unexploited resources in lower *TLs*. Functional consequences of

578   low biodiversity and species specific traits (i.e., size, trophic role, rarity, distribution and degree

579   of specialization) or combined effects of both may explain inefficiencies of energy transfers in

580   this lake. Lower energy transfer efficiencies in high *TLs* have been observed in other poorly

581   diverse systems (Loreau *et al.*, 2001; Raffaelli *et al.*, 2002; Stachowicz *et al.*, 2002).

582

583   Fish stocking is an important aspect of fishery management but comes with considerable

584   risks. Invasive species can redefine an ecosystem by converting diverse communities into mono

585   specific ones as introduced species often become invasive and may lead to native species

586   extinctions (McKinney and Lockwood, 1999; Simberloff, 2000; Lodge, 2001; Rosenzweig,

587   2001; Davis and Thompson, 2000; de Graaf *et al.*, 2000; Mack *et al.*, 2000; Pimentel *et al.*, 2001;

588   Dudgeon *et al.* 2006). In African freshwater systems, an ominous example is the loss of

589   biodiversity in Lake Victoria following the Nile perch introduction (Kudhongania and

590   Chitamwebwa, 1995; Pitcher and Hart, 1995; Preikshot *et al.*, 1998). Biodiversity in Lake Kivu,

591   however, is low and fish were stocked to boost up the lake's biodiversity and productivity.

592

593   The role of biodiversity has been hypothesized as insurance to ecosystem functioning in

594   case of modifications (Loreau *et al.*, 2001). Biodiversity after introduction is affected in two

595   manners either by global homogenization of regional biota or by affecting native species

596   functions (Levine *et al.* 2003; Didham *et al.*, 2005; Korniss and Caraco, 2005; Puth and Post,

597   2005; Olden and Rooney, 2006). Predators and resources manipulations can cause direct changes

598   of diversity at one *TL*, which in turn, affect diversity of other *TLs*. Indirect biodiversity effects of

599 varying resources and consumers, on the other hand, are supposed to be stronger in aquatic

600 ecosystems compared to terrestrial systems and detritus based food webs (Dyer and Letourneau,

601 2003). Intraspecific food resource limitation had been observed on adults of *L. miodon* which

602 had evolved from a mere pelagic planktivore to a piscivore, preying on its juveniles (Lowe-

603 McConnell, 1993). The sequestration of space and nutrients by adults may limit resources that

604 eventually provoked such cannibalistic behavior similar to observations of Mandima (1999) on

605 *L. miodon* in Lake Kariba and by Bundy and Pitcher (1995) on Nile Perch in Lake Victoria.

606

607   In Lake Kivu, however, fish introductions showed no detrimental changes at both the

608 biodiversity and ecological levels of the fish community (Marshall, 1995; Ogutu-Ohwayo *et al.*,

609 1997). It can be suggested that, under non-limiting food conditions, *L. miodon* which is

610 occupying mainly the open waters of the lake do not have a particular deleterious effects on other

611 indigenous species, i.e. provoking mass extinction of the latter. It actually represents the lake's

612 most important stock in terms of biomass and production (Hanek *et al.*, 1991). It has also

613 stimulated the commercial fishery with an estimated potential annual yield of 55 kg.ha^{-1} in the

614 early 90s (Johannesson and Lambœuf, 1989; van den Bossche and Bernacsek, 1990; Hanek *et*

615 *al.*, 1991). At present, introduced fish species in this lake comprise 85% of the catch (B.

616 Kaningini, UERHA, pers. data). A similar phenomenon observed in Lake Kariba (Coulter *et al.*,

617 1984; Marshall and Mubamba, 1993). Despite the increasing intensity of the fishing activity on

618 exotics, they seem resilient to human exploitation. Tilapias are known to be highly resilient to

619 intensive fisheries due to their unspecialized ecological flexibility.

620

621   Based on the classification of colonizers discussed by Davis and Thompson (2000), *L.*

622 *miodon* is a type 2 colonizer due to its eventual key role function in the ecosystem (Spliethoff *et*

623   *al.*, 1983; Isumbisho *et al.*, 2006), especially in the fisheries (van den Bossche and Bernacsek,

624   1990; Marshall and Mabamba, 1993). In most cases, exotic fishes stocked have evolved

625   pervasive in other lakes not only in Africa (Mills *et al.*, 1993; Ogutu-Ohwayo *et al.* 1997; de

626   Graaf *et al.*, 2000) but worldwide (Villanueva and Moreau, 2001; Dudgeon *et al.*, 2006). Once

627   the biodiversity is altered, the ecosystem is transformed into new configurations often

628   detrimental to human welfare (Ruesink *et al.*, 1995; McCann *et al.*, 2001; Pimentel *et al.*, 2005;

629   Dudgeon *et al.*, 2006; Lovett *et al.*, 2006). In Lake Victoria, for example, the Nile Tilapia has

630   evolved as a "keystone species" though its introduction led to the alteration of ecosystem

631   function, biotic interactions and biotic homogenization (Moreau, 1995; Bundy and Pitcher, 1995,

632   Villanueva and Moreau 2001).

633

634   **Conclusion**

635

636   For this study, we have tried to quantify the impact of invasive species on ecosystem

637   process and functioning. Based on this study, energy fluxes from primary producers in this

638   ecosystem are largely phytoplankton-based because of the importance of zooplankton and

639   abundance of zooplankton consumers. The fragility of the ecosystem to environmental changes

640   lies, therefore, in the production of the zooplankton group (*TL* 2), which evidently links the

641   transfer of primary production to higher *TLs*, and in the paucity of species diversity. The existing

642   competitions for food among some groups can be limited mostly by the specialization of some of

643   them to narrow spatial distributions.

644

645   Broad-scale or ecosystem-level approach is recognized as crucial in describing and

646   understanding the trophic structure in Lake Kivu and the importance of the introduced species. It

647　is a requirement to elucidate and, eventually, predict possible impact of exotic species on natural

648　food webs. Fish introductions in Lake Kivu is interesting in the sense that the introduction of

649　exotic species have increased energy flux transfers between *TLs* for what may have been initially

650　a 'dead zone' before the sardine colonization. Exotics play key role functions in the ecosystem

651　(Spliethoff *et al.*, 1983; Isumbisho *et al.*, 2006), especially in the fisheries (van den Bossche and

652　Bernacsek, 1990; Marshall and Mabamba, 1993). It is possibly one of the rare occasions where

653　introduction of exotics can be acknowledged as positive in terms stimulating commercial

654　fisheries (Johannensson and Lambœuf, 1989; van den Bossche and Bernacsek, 1990; Hanek *et*

655　*al.*, 1991) and improving fish biodiversity with minor consequences on trophic structure and

656　functioning.

657

658　**Acknowledgements**

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667　**References**

668

669　Allen, K.R. 1971. Relation between production and biomass. Journal of the Fisheries

670　Research Board of Canada, *28*: 1573-1581.

671

672 Allen, E.A. and Humble, L.M. 2002. Nonindigenous species introductions: A threat to Canada's

673 forests and forest economy. Canadian Journal of Plant Pathology, 24:103-10.

674

675 Arim, M., Abades, S.R., Neill, P.E., Lima, M. and Marquet, P.A. 2006. Spread dynamics of

676 invasive species. Proceedings of the National Academy of Sciences, 103(2): 374-378.

677

678 Bruton, M.N. 1979. The role of diel inshore movements by *Clarias gariepinus* (Pisces:

679 Clariidae) for the capture of fish prey. Transactions of the Zoological Society of London, 35:

680 115-138.

681

682 Bundy, A. and Pitcher, T.J. 1995. An analysis of species changes in Lake Victoria: did the Nile

683 perch act alone?, pp. 111-135. *In*: T. Pitcher and P.J.B.Hart (Eds.), The impact of Species

684 Changes in African Lakes. Fish and Fisheries Series, 18, Chapman and Hall, London.

685

686 CapBlanc, J. and Dauta, A. 1999. Photosynthesis simulator ver 2.1. Université Paul Sabatier and

687 C.N.R.S., Toulouse.

688

689 Chapman, L.J., Chapman, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L. and Keiter, A.E.

690 1996. Refugia for endangered species from an introduced predator in Lake Nabugabo,

691 Uganda. Conservation Biology, 10: 554-561.

692

693 Christensen, V. and Pauly, D. (Eds.) 1993. Trophic Models of Aquatic Ecosystems. ICLARM

694 Conference Proceedings, 26: 390 pp.

695

696 Christensen, V. 1995. Ecosystem maturity - towards quantification. Ecological Modelling, 77:

697 3-32.

698

699 Christensen, V. and Walters, C. 2004a. Ecopath with Ecosim: methods, capabilities and

700 limitations. Ecological Modelling, 172: 109-139.

701

702 Christensen, V. and Walters, C. 2004b. Trade-offs in ecosystem-scale optimization of fisheries

703 management policies. Bulletin of Marine Science, 74 (3): 549-562.

704

705 Christensen, V., Walters, C. and Pauly, D. 2005. Ecopath with Ecosim: a User's Guide. Fisheries

706 Centre Research Reports, 12 (4): 154 pp.

707

708 Coulter, G.W., Allanson, B.R., Bruton, M.N., Greenwood, P.H., Hart, R.C., Jackson, P.B.N. and

709 Ribbink, A.J. 1984. Unique qualities and special problems of the African Great Lakes.

710 Environmental Biology of Fishes, 17(3): 161-183.

711

712 Craig, J.F. 1992. Human-induced changes in the composition of fish communities in the African

713 Great Lakes. Review in Fish Biology and Fisheries, 2: 93-124.

714

715 Crawley, M.J. 1987. What makes a community invasible?, pp. 429-453 *In*: A.J. Gray, M.J.

716 Crawley and P.J. Edwards (Eds.), Colonization, Succession and Stability. Blackwell Scientific

717 Publications, Oxford.

718

719   Davis, M.A. and Thompson, K. 2000. Eight ways to be a colonizer, two ways to be an invader: a

720   proposed nomenclature scheme for invasion ecology. Bulletin of the Ecological Society of

721   America, 81: 226–230.

722

723   de Graaf, M., Dejen, E., Sibbing, F.A. and Osse, J.W.M. 2000b. *Barbus tanapelagius*, a new

724   species from Lake Tana (Ethiopia): its morphology and ecology. Environmental Biology of

725   Fishes, 59: 1–9.

726

727   de Iongh, H.H., Splithoff, P.C. and Frank, V.G. 1983. Feeding habits of the clupeid *Limnothrissa*

728   *miodon* (Boulenger) in Lake Kivu. Hydrobiologia, 102: 113-122.

729

730   de Iongh, H.H., Spliethoff, P.C. and Roest, F. 1995. The impact of an introduction of sardine into

731   Lake Kivu, pp. 278-297. *In*: T. Pitcher and P.J.B. Hart (Eds.), The impact of Species Changes in

732   African Lakes. Fish and Fisheries Series 18, Chapman and Hall, London.

733

734   De Merona, B. 1983. Modèle de croissance des poissons d'eau douce d'Afrique. Revue

735   d'Hydrobiologie Tropicale, 19 : 1-12.

736

737   Descy, J.-P. and Fourniret, Y. 1991. Quelques données récentes sur la production planctonique

738   du lac Kivu (Rwanda), pp.147-149. *In* P. Vernet (Ed.), Hommage à F.A. FOREL, Proceedings of

739   the 3rd CILEF, Morges, Switzerland.

740

741   De Vos, L., Snoeks, J. and Thys van den Audenaerde, D.K. 2001. An annotated checklist of the

742   fishes of Rwanda (East-central Africa) with historical data on introductions of commercially

743   important species. Journal of East African Natural History, 90: 41-68.

744

745   Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. and Gemmell, N.J. 2005. Are

746   invasive species the drivers of ecological change? Trends in Ecology and Evolution, 20 (9):

747   470-474.

748

749   Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C.,

750   Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L. and Sullivan, C.A. 2006.

751   Freshwater biodiversity: importance, threats, status and conservation challenges. Biology

752   Review, 81: 163-182.

753

754   Dyer, L.A. and Letourneau, D. 2003. Top-down and bottom-up diversity cascades in detrital vs.

755   living food webs. Ecology Letters, 6: 60-68.

756

757   Folke, C. and Kautsky, N. 1996. The ecological footprint concept for sustainable seafood

758   production. Proceedings of the International Conference on "Ecosystem Management for

759   Sustainable Marine Fisheries" 19-23 February 1996. Monterey, California.

760

761   Fourniret, Y., Plisnier, P.D. and Micha, J.-C. 1992. Régime alimentaire de quatre espèces du

762   genre *Haplochromis* (Téléostéi, Cichlidae) du lac Ihéma (Rwanda) Annales de Limnologie, 28

763   (1): 57-69.

764

765   Fröese, R. and Binohlan, C. 2000. Empirical relationships to estimate asymptotic length, length

766   at first maturity and yield at maximum yield per recruitment in fishes, with a simple method to

767   evaluate length frequency data. Journal of Fish Biology, 56: 758-773.

768

769   Fröese, R. and Pauly, D. (Eds.) 2006. Fishbase. http://www.fishbase.org.

770

771   Fulton, E.A., Smith, A.D.M. and Johnson, C.R. 2003. Mortality and predation in ecosystem

772   models: is it important how these are expressed? Ecological Modelling, 169: 157-178.

773

774   Gayanilo, F.C. Jr., Sparre, P. and Pauly. D. (Eds.) 2002. The FAO-ICLARM Stock Assessment

775   Tools II (FiSAT II Ver. 1.0) FAO http://www.fao.org/fi/statist/fisoft/fisat/.

776

777   Gottlieb, S.J. and Schweighofer, M.E. 1996. Oysters and the Chesapeake Bay Ecosystem: A case

778   for exotic species introduction to improve environmental quality? Estuaries, 19 (3): 639-650.

779

780   Guo, Q., Qian, H., Ricklefs, R.E. and Xi, W. 2006. Distributions of exotic plants in eastern Asia

781   and North America. Ecology Letters, 9 (7): 827-834.

782

783   Gurevitch, J. and Padilla, D.K. 2004. Are invasive species a major cause of extinctions? Trends

784   in Ecology and Evolution, 19 (9): 470-474.

785

786   Hanek, G., Leendertse, K. and Farhani, B. 1991. Socio-Economic Investigations of Lake Kivu

787   Fisheries. UNDP/FAO Regional Project for Inland Fisheries Planning (IFIP), RAF/87/099-

788   TD/23/91 (En): 55 p.

789

790   Hansson, L. and Carpenter, S.R. 1993. Relative importance of nutrient availability and food

791   chain size for community composition in phytoplankton. Oïkos, 67: 257-263.

792

793   Harris, Z. 1968. Mathematical Structures of Language, Wiley, New York. Var. pag.

794

795   Hauser, L., Carvalho, G.R. and Pitcher, T.J. 1995. Morphological and genetic differentiation of

796   the African clupeid *Limnothrissa miodon* 34 years after its introduction to Lake Kivu. Journal of

797   Fish Biology, 47: 127-144.

798

799   Herendeen, R.A. 2004. Bottom-up and top-down effects in food chains depend on functional

800   dependence: an explicit framework. Ecological Modelling, 171: 21–33.

801

802   Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions, pp. 389-405. *In*: J.

803   Drake, F. di Castri, R. Groves, F. Kruger, H. Mooney, M. Rejmanek and M. Williamsom (Eds.),

804   Ecological invasions: A global perspective. Wiley, Chichester.

805

806   Huddart, R. 1994. Aspects of biology of the Lake Tanganyika sardine, *Limnothrissa miodon*

807   (Boulenger) in Lake Kariba. African Journal of Tropical Hydrobiology and Fisheries, 5: 31-

808   44.

809

810   Irvine, K. and Waya, R. 1999. Spatial and temporal patterns of zooplankton standing biomass

811   and production in Lake Malawi. Hydrobiologia, 407: 191-205.

812

813   Irz, P., Argillier, C. and Proteau, J.-P. 2004. Contribution of native and non-native species to fish

814   communities in French reservoirs. Fisheries Management and Ecology, 11: 165-172.

815

816   Isumbisho, P., Kaningini, B., Descy, J-P. and Baras, E. 2004. Seasonal and diel variations in the

817   diet of the young stages of *Limnothrissa miodon* in Lake Kivu, Eastern Africa. Journal of

818   Tropical Ecology, 20: 1-11.

819

820   Isumbisho, P., Sarmento, H., Kaningini, B., Micha, J.-C. and Descy, J.P. 2006. Zooplankton of

821   Lake Kivu, East Africa: half a century after the Tanganyika sardine introduction. Journal of

822   Plankton Research, 28: 971-989.

823

824   Iwama, G.K., Takemura, A. and Takano, K. 1997. Oxygen consumption rates of tilapia in

825   freshwater, sea water and hypersaline sea water. Journal of Fish Biology, 51 (5): 886-894.

826

827   Jannasch, A.W. 1975. Methane oxidation in Lake Kivu (Central Africa). Limnology and

828   Oceanography, 20: 860-864.

829

830   Jarre, A., Palomares, M.L.D., Soriano, M., Sambilay, V. and Pauly, D. 1991. Some new

831   analytical and comparative methods for estimating the food consumption of fish. ICES Journal of

832   Marine Science, 193: 99-108.

833

834   Johannensson, K. and Lambœuf, M. 1989. Estimation acoustique de l'abondance de stock

835   d'Isambaza (*Limnothrissa miodon*) du lac Kivu, par une méthode basée sur le comptage des

836   échos de poissons, Gisenyi. RWA/87/012/TRAM/13, 64 pp.

837

838 Kaningini, B. 1995. Étude de la croissance, de la reproduction et de l'exploitation de

839 *Limnothrissa miodon* au lac Kivu, bassin de Bukavu (Zaïre). Thèse de doctorat, FUNDP,

840 Presses Universitaires de Namur, Belgium, 211p.

841

842 Kaningini, B., Micha, J.-C., Vandenhaute, J., Platteau, J.-P., Watongoka, H., Merlard, C.,

843 Wilondja, M.K. and Isumbisho, P. 1999. Pêche du Sambaza au filet maillant dans le lac Kivu.

844 Rapport final du Projet ONG/219/92/Zaïre. Presses Universitaires de Namur, Belgium.

845

846 Karenge, L. and Kolding, J. 1995. Inshore fish population and species changes in Lake Kariba,

847 Zimbabwe, pp. 245-275. *In* T. Pitcher and P.J.B. Hart (Eds.), The impact of Species Changes

848 in African Lakes. Fish and Fisheries Series 18 Chapman and Hall, London.

849

850 Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. and Reich P. 2002.

851 Biodiversity as a barrier to ecological invasion. Nature, 417: 636-638.

852

853 Khallaf, E.A., Galal, M. and Authman, M. 2003. The biology of *Oreochromis niloticus* in a

854 polluted canal. Ecotoxicology, 12: 405-416.

855

856 Kolar, C.S. and Lodge, D.M. 2002. Ecological predictions and risk assessment for alien fishes in

857 North America. Science, 298:1233–1236.

858

859 Korniss, G. and Caraco, T. 2005. Spatial dynamics of invasion: The geometry of introduced

860 species. Journal of Theoretical Biology, 233: 137-150.

861

862   Kudhongania, A.W. and Chitamwebwa, D.B.R. 1995. Impact of environmental changes, species

863   introductions and ecological interactions on the fish stocks of Lake Victoria, pp. 19-32. *In*: T.

864   Pitcher and P.J.B. Hart (Eds.), The impact of Species Changes in African Lakes. Fish and

865   Fisheries Series 18, Chapman and Hall, London.

866

867   Lambœuf, M. 1991. Abondance et répartition du *Limnothrissa miodon* du lac Kivu, résultat des

868   prospections acoustiques d'avril 1989 à juin 1991. DOC/TR No. RWA/87/012/DOC/TR/46

869   (Fr) FAO, 41 p.

870

871   Latini, A.O. and Petrere Jr., M. 2004. Reduction of a native fish fauna by alien species: an

872   example from Brazilian freshwater tropical lakes. Fisheries Management and Ecology, 11: 71-

873   79.

874

875   Lawton, J.H. and Brown, V.K. 1993. Redundancy in ecosystems, pp. 255-270. *In*: E.D. Schulze

876   and H.A. Mooney (Eds.), Biodiversity and ecosystem functions. Springer-Verlag.

877

878   Le Pape, O., Chauvet, F., Mahévas, S., Lazure, L., Guérault, G. and Désaunay, Y. 2003.

879   Quantitative description of habitat suitability for the juvenile common sole *(Solea solea* L.) and

880   contribution of different habitats to the adult population in the Bay of Biscay (France). Journal

881   of Sea Resources, 50: 139–149

882

883   Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. and Lavorel, S. 2003.

884   Mechanisms underlying the impact of exotic plant invasions. Philosophical Transactions of the

885   Royal Society of London, 270: 775–781.

886

887 Lindman, R.L. 1942.The trophic dynamic aspect of ecology. Ecology, *23*: 399-418.

888

889 Lodge, D.M. 2001. Lakes, pp. 277–313. *In:* F.S. Chapin III, O.E. Sala and E. Huber-Sannwald

890 (Eds.), Global biodiversity in a changing environment: scenarios for the 21st century. Springer-

891 Verlag, New York.

892

893 Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Brönmark, C., Garvey, J.E. and

894 Klosiewski, S.P. 1998. Predicting impact of freshwater exotic species on native biodiversity:

895 challenges in spatial scaling. Australian Journal of Ecology, 23: 53–67

896

897 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U.,

898 Huston, M.A., Raffaelli, D., Schmidt, B., Tilman, D. and Wardle, D.A. 2001. Biodiversity and

899 Ecosystem Functioning: Current Knowledge and Future Challenges. Science, 294: 804-808.

900

901 Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C. and Fitzhugh, R.D. 2006. Forest

902 ecosystem responses to exotic pests and pathogens in eastern North America. BioScience,

903 56 (5): 395-405

904

905 Lowe-McConnell, R.H. 1993. Fish Faunas of the African Great Lakes: Origins, Diversity, and

906 Vulnerability. Conservation Biology, 7 (3): 634-643.

907

908 Lu, K., Jin, C., Dong, S., Gu, B. and Bowen, S.H. 2006. Feeding and control of blue-green algal

909 blooms by tilapia (*Oreochromis niloticus*). Hydrobiologia, 568: 111-120.

910

911   Lynch, M. and Shapiro, J. 1981. Predation, enrichment and phytoplankton community structure.

912   Limnology and Oceanography, 26: 86-102.

913

914   MacDonald, I.A., Loope, L.L., Usher, M.B. and Hamann, O. 1989. Wildlife conservation and the

915   invasion of nature reserves by introduced species: a global perspective, pp. 215-255. *In*: J.A.

916   Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmdnek and M. Williamson

917   (Eds.), Biological invasions: A global perspective. John Wiley and Sons, Chichester.

918

919   Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. 2000.

920   Biotic invasions: Causes, epidemiology, global consequences, and control. Issues in Ecology, 5.

921

922   Mandima, J.J. 1999. Spatial and temporal variations in the food of the sardine *Limnothrissa*

923   *miodon* (Boulenger 1906) in Lake Kariba, Zimbabwe. Hydrobiologia, 407: 175-182.

924

925   Marshall, B.E. 1991. Seasonal and annual variations in the abundance of the clupeid

926   *Limnothrissa miodon* in Lake Kivu. Journal of Fish Biology, 39: 641-648.

927

928   Marshall, B.E. 1995. Why is *Limnothrissa miodon* such a successful introduced species and is

929   there anywhere else we should put it?, pp. 527-545. *In*: T.J. Pitcher & P.J.B. Hart (Eds.), The

930   impact of species changes in African Lakes. Fish and Fisheries Series 18, Chapman and Hall,

931   London.

932

933 Marshall, B.E. and Mubamba R. (Eds.) 1993. Biology, stock assessment and exploitation of

934 small pelagic fish species in the African Great Lakes Region. CIFA Occasional Paper 19, FAO,

935 Rome, 270 p.

936

937 Mavuti, K., Moreau, J., Munyandorero, J. and Pisnier, D. 1996. Analysis of trophic relationships

938 in two shallow equatorial lakes: Lake Naivasha (Kenya) and Lake Ihéma (Rwanda) using a

939 multispecifies trophic model. Hydrobiologia, 321: 89-100.

940

941 McCann, J. 2000. The diversity stability debate. Nature, 405: 228-233.

942

943 McKinney, M.L. and Lockwood, J.L., 1999. Biotic homogenization: A few winners replacing

944 many losers in the next mass extinction. Trends in Ecology and Evolution, 14: 450-453.

945

946 Mills, E.L., Leach, J.H., Carlton, J.T. and Secor, C.L. 1993. Exotic species in the Great Lakes:

947 A history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research,

948 19(1): 1-54.

949

950 Moreau, J. 1995. Analysis of species changes in Lake Victoria using ECOPATH, a

951 multispecies trophic model, pp. 137-162. *In* T.J. Pitcher and P.J.B. Hart (Eds.), The impact of

952 species changes in African Lakes. Chapman Hall, London.

953

954 Moreau, J., Arrignon, J. and Jubb, R.A. 1988. Les introductions d'espèces étrangères dans

955 les eaux continentales africaines, pp. 395-426. *In*: C. Lévêque, M.N. Bruton and G.W.

956   Ssentongo (Eds.), Biologie et écologie des poissons d'eau douce africains. Coll. Travaux Doc.

957   216, ORSTOM, Paris.

958

959   Moreau, J., Christensen, V. and Pauly, D. 1993. A trophic ecosystem model of Lake

960   George, Uganda, pp. 124-129. *In* V.Christensen and D. Pauly (Eds.), Trophic models of

961   aquatic ecosystems. ICLARM Conference Proceedings 26, ICLARM, Manila, Philippines.

962

963   Moreau, J., Mavuti, K. and Daufresne, T. 2001. A synoptic Ecopath model of biomass flows

964   during two different static ecological situations in Lake Nakuru (Kenya). Hydrobiologia, 458:

965   63-74.

966

967   Moreau, J., Villanueva, M.C., Amarasinghe, U.S and Schiemer, F. 2001. Trophic relationships

968   and possible evolution under various fisheries management strategies in Sri Lankan reservoir, pp.

969   201-214. *In*. S.S. De Silva and P. Lynch (Eds.), Fisheries management and Aquaculture in

970   Southeast Asian Lakes and Reservoirs. ACIAR Publications 98, Canberra, Australia.

971

972   Munyandero, J. and Mwape, L. 2003. Some records of Lake Tanganyika Clupeid and Latid fish

973   species, pp. 132-155. *In* M.L.D. Palomares, B. Samb, T. Diouf, J.M. Vakily and D. Pauly

974   (Eds.), Fish biodiversity: local studies as basis for global interferences. ACP-EU Fisheries

975   Research Report 14, Brussels.

976

977   Murichi, S.M., Hart, P.J.B. and Harper, D. 1995. The persistence of the two introduced species in

978   Lake Navaisha, Kenya, in face of environmental variability and fishing pressure, pp. 229-319. *In*

979   T. Pitcher ad P.J.B. Hart (Eds.), The impact of species changes in African Lakes. Fish and

980   Fisheries Series 18, Chapman and Hall, London.

981

982   Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. and Gale, S. 2000. Plant

983   diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oïkos, 91:

984   97-108.

985

986   Njiru, M., Okeyo-Owuor, J.B., Muchiri, M. and Cowx, I.G. 2004. Shifts in the food of the Nile

987   tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya African Journal of Ecology, 42: 163-

988   170.

989

990   Nyström, P., Svensson, O., Lardner, B., Broenmark, C. and Graneli, W. 2001. The influence of

991   multiple introduced predators on a littoral pond community. Ecology, 82 (4): 1023-1039.

992

993   Odum, E.P. 1969. The strategy of ecosystem development. Science, 104: 262-270.

994

995   Odum, E.P. 1971. Fundamentals of ecology. W.B. Saunders Co, Philadelphia, 574 pp.

996

997   Odum, W.E. and Heald, E.J. 1975. The detritus-based food web of an estuarine mangrove

998   community, pp. 265-286. *In:* L.E. Cronin (Ed.), Estuarine research Vol. 1. Academic Press,

999   New York.

1000

1001   Ogutu-Ohwayo, R. 1990. The decline of the native fishes of Lake Victoria and Kyoga (East

1002   Africa) and the impact of introduced species, especially Nile Perch, *Lates niloticus,* and Nile

1003   tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes, 27: 81-96.

1004

1005   Ogutu-Ohwayo, R., Hecky, R.E., Cohen, A.S. and Kaufman, L. 1997. Human impacts on the

1006   African Great Lakes. Environmental Biology of Fishes, 50: 117–131.

1007

1008   Olden, J.D. and Rooney, T.P. 2006. On defining and quantifying biotic homogenization. Global

1009   Ecology and Biogeography, 15: 113-120.

1010

1011   Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F. 1999. Trophic cascades revealed in

1012   diverse ecosystems. Trends in Ecology and Evolution, 14: 483–488.

1013

1014   Palomares, M.L. and Pauly, D. 1998. Predicting food consumption of fish populations as

1015   functions of mortality, food type, morphometrics, temperature and salinity. Marine and

1016   Freshwater Research, 49: 447-453.

1017

1018   Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and

1019   mean environmental temperature in 175 fish stocks. Journal of the International Council for

1020   the Exploitation of the Sea, 39(3): 175-192.

1021

1022   Pauly, D. 1986. A simple method for estimating the food consumption of fish population from

1023   growth data and food conversion experiments. Fisheries Bulletin, 84: 827-840.

1024

1025   Pauly, D. and Palomares, M.L. 1987. Shrimp consumption by fishes 992 in Kuwait waters, a

1026   methodology, preliminary results and their implication for management and research. Kuwait

1027   Bulletin of Marine Sciences, 8: 101-125.

1028

1029   Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries.

1030   Nature, 374: 255-257.

1031

1032   Pauly, D., Christensen, V., Dalsgaard, J., Fröese, R. and Torres, F.C. Jr. 1998. Fishing down

1033   marine food webs. Science, 279: 860-863.

1034

1035   Pauly, D, Palomares, M.D. and Vakily, M. 2003. Trophic models of Northwest African marine

1036   ecosystems. *In* D. Pauly, M.D. Palomares and M. Vakily (Eds.), Marine Fisheries,

1037   Ecosystems and Societies in West Africa: Half a century of change, SIAP/EP/DT/03 24-28

1038   June 2002 Dakar, Senegal.

1039

1040   Pauly, D., Soriano-Bartz, M. and Palomares, M.L. 1993. Improved construction,

1041   parameterization and interpretation of steady-state ecosystem models, pp. 1-13. *In* V.

1042   Christensen and D. Pauly (Eds.), Trophic models of aquatic ecosystems. ICLARM Conference

1043   Proceedings 26, ICLARM, Manila.

1044

1045   Payne, I.A. 1986. The ecology of tropical lakes and rivers. Wiley & Sons, New York, 301 p.

1046

1047   Pearce, M.J. 1995. Effects of exploitation on the pelagic fish community in the south of Lake

1048   Tanganyika, pp. 425-441. *In:* T.J. Pitcher and P.J.B. Hart (Eds.), The impact of species

1049   changes in African Lakes. Fish and Fisheries Series 18 Chapman and Hall, London.

1050

1051 Perin, S., Pick, F.R., Lean, D.R.S. and Mazumder, A. 1996. Effects of planktivorous fish and

1052 nutrient additions in primary production of shallow versus deep (stratified) lake enclosures.

1053 Canadian Journal of Fisheries and Aquatic Sciences, 53: 1125-1132.

1054

1055 Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the

1056 end of the road. Oïkos, 85: 385–397.

1057

1058 Petchey, O.L., McPhearson, P.T., Casey, T.M. and Morin P.J. 1999. Environmental warming

1059 alters food-web structure and ecosystem function. Nature, 402: 69-72.

1060

1061 Pianka, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and

1062 Systematics, 4: 53-74.

1063

1064 Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E.,

1065 Russel, L., Zern, J., Aquino, T. and Tsomondo, T. 2001. Economic and environmental threats of

1066 alien plant, animal, and microbe invasions. Agriculture, Ecosystems, and Environment, 84:1-

1067 20.

1068

1069 Pitcher, T.J. and Hart, P.J.B. (Eds.). 1995. The impact of species changes in African Lakes.

1070 Kluwer Academic, Dordrecht, The Netherlands, 640 p.

1071

1072 Platts, T. and Ulanowicz, R.E. (Eds.) 1985. Ecosystem theory for biological oceanography.

1073 Canadian Bulletin of Fisheries and AquaticSciences, 213: 260 p.

1074

1075   Preikshot, D., Nsiku, E., Pitcher, T. and Pauly, D. 1998. An interdisciplinary evaluation of the

1076   status and health of African lake fisheries using a rapid appraisal. Journal of Fish Biology, 53

1077   (supplement A): 381-393.

1078

1079   Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B. and Lean, D.R.S. 1996. Effects of

1080   nutrients and planktivorous fish on phytoplankton community structure versus deep (stratified)

1081   aquatic systems. Ecology, 77: 1556-1572.

1082

1083   Puth, L.M. and Post, D.M. 2005. Studying invasion: Have we missed the boat? Ecology Letters,

1084   8: 715-21

1085

1086   Quince, C., Higgs, P.G. and McKane, A.J. 2002. Food web structure and the evolution of

1087   ecological communities, pp. 281–298. *In* M. Lässig and A. Valleriani (Eds.), Biology

1088   Evolution and Statistical Physics. Springer, Berlin.

1089

1090   Raffaelli, D., van der Putten, W.H., Persson, L., Wardle, D.A., Petchey, O.L., Koricheva, J., van

1091   der Heijden, M., Mikola, J. and Kennedy, T. 2002. Multi-trophic dynamics and ecosystem

1092   processes, pp. 147-154. *In* M. Loreau, S. Naeem and P. Inchausti (Eds.), Biodiversity and

1093   ecosystem functioning: Synthesis and perspectives. Oxford University Press, Oxford.

1094

1095   Rejmánek, M.D. and Richardson, M. 1996. What attributes make some plant species more

1096   invasive? Ecology, 77: 1655-1661.

1097

1098   Richards, S.A., Nisbet, R.M., Wilson, W.G. and Possingham, H.P. 2000. Grazers and diggers:

1099   exploitation competition and coexistence among foragers with different feeding strategies on a

1100   single resource. The American Naturalist, 155: 266-279.

1101

1102   Rosenzweig, M.L. 2001. The four questions: what does the introduction of exotic species do to

1103   diversity? Evolutionary Ecology Research 3: 361-367.

1104

1105   Ruesink, J.L., Parker, I.M., Groom, M.J. and Kareiva, P.M. 1995. Reducing the risks of

1106   non indigenous species introductions. BioScience, 45 (7): 465-467.

1107

1108   Saltveit, S.J. 2006. The effects of stocking Atlantic salmon, *Salmo salar*, in a Norwegian

1109   regulated river. Fisheries Management and Ecology, 13: 197-205.

1110

1111   Sarmento, H., Isumbisho, P. and Descy, J.P. 2006. Phytoplankton ecology of Lake Kivu (Eastern

1112   Africa). Journal of Plankton Research, 28: 815-8829.

1113

1114   Sarvala, J., Salonen, K., Järvinen, M., Aro, E., Huttula, T., Kotilainen, P., Kurki, H., Langenberg,

1115   V., Mannini, P., Peltonen, A., Plisnier, P.D., Vourinen, I., Möslä, H. and Lindqvist, O. 1999.

1116   Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. Hydrobiologia,

1117   407: 149-173.

1118

1119   Sax, D.F. and Brown, J.H. 2000. The paradox of invasion. Global Ecology and Biogeography,

1120   9: 363-371.

1121

1122   Sax, D.F. and Gaines, S.D. 2003. Species diversity: from global decreases to local increases.

1123   Trends in Ecology and Evolution, 18 (11): 561-566.

1124

1125   Schutzenhofer, M.R. and Valone, T.J. 2006 Positive and negative effects of exotic *Erodium*

1126   *cicutarium* on an arid ecosystem. Biological Conservation, 132: 376-381.

1127

1128   Simberloff, D., Von Holle, B. 1999. Positive interactions of non-indigenous species: invasional

1129   meltdown? Biological Invasions, 1: 21-32.

1130

1131   Smith, S.D., Huwman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S.,

1132   Fenstermakerk, L.K., Seeman, J.R. and Nowak, R.S. 2000. Elevated CO_2 increases productivity

1133   and invasive species success in an arid ecosystem. Nature, 408: 79-82.

1134

1135   Snoeks, J. 1994. The Haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa): A

1136   taxonomic revision with notes on their ecology. Annales de Sciences Zoologiques, 270: 221-

1137   1102.

1138

1139   Snoeks, J., De Vos, L., Coenen, E. and Thys van den Audenaerde, D.T. 1990. Description de

1140   deux nouvelles espèces d'*Haplochromis* (Teleostei, Cichlidae) du Lac Kivu, Rwanda. Cybium,

1141   14(1): 63-76.

1142

1143   Spliethoff, P.C., De Iongh, H.H. and Frank, V.G. 1983. Success of the introduction of the

1144   freshwater clupeid *Limnothrissa miodon* (Boulenger) in Lake Kivu. Fisheries Management,

1145   14: 17-31.

1146

1147   Stachowicz, J.J., Fried, H., Whitlatch, R.B. and Osman, R.W. 2002. Biodiversity, invasion

1148   resistance and marine ecosystem function: reconciling pattern and process. Ecology, 83: 2575-

1149   2590.

1150

1151   Steiner, C.F. 2001. The effects of prey heterogeneity and consumer identity on the limitation

1152   of trophic-level biomass. Ecology, 82: 2495-2506.

1153

1154   Tadesse, Z. 1999. The nutritional status and digestibility of *Oreochromis niloticus* L. diet in Lake

1155   Langeno Ethiopia. Hydrobiologia, 416: 97-106.

1156

1157   Trewavas, E. 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakila*.

1158   British Museum (Natural History), 654 p.

1159

1160   Twongo, T. 1995. Impact of fish species introductions on the tilapias of Lake Victoria and

1161   Kyoga, pp. 45-57. *In*: T.J. Pitcher and P.J.B. Hart (Eds.), The impact of species changes in

1162   African Lakes. Fish and Fisheries Series, 18 Chapman and Hall, London.

1163

1164   Ulanowicz, R.E. 1995. The part-whole relation in ecosystems, pp.549-560. *In*: B.C.

1165   Patten and S.E. Jørgensen (Eds.), Complex ecology. Prentice-Hall, Englewood Cliffs, New

1166   Jersey.

1167

1168   Ulanowicz, R.E. and Puccia, C.J. 1990. The mixed trophic impact routine. Coenose, 5: 7-16

1169

1170   Ulyel, A.P. 1991. Écologie alimentaire des Haplochromis spp. (Telepstei: Cichlidae) du Lac

1171   Kivu en Afrique Centrale. Thèse de Doctorat, Katholieke Universiteit Leuven, Département

1172   de Biologie, Écologie et de l'Aquaculture, 271 p.

1173

1174   Ulyel, A.P., Ollevier, F., Ceusters, R. and Thys van den Audenaerde, D.T. 1991. Food and

1175   feeding habits of *Haplochromis* (Teleostei: Cichlidae) from Lake Kivu (Central Africa) II. Daily

1176   feeding periodicity and dietary changes of some *Haplochromis* species under natural conditions.

1177   Belgian Journal of Zoology, 121 (2): 93-112.

1178

1179   Van den Bossche, J.P. and Bernacsek, G.M. 1990. Source book for the inland fishery resources

1180   of Africa: Volume 1, CIFA Technical Paper No.18.1, FAO, Rome, 240 pp.

1181

1182   Van der Zanden, M.J., Casselman, J.M. and Rasmussen, J.B. 1999. Stable isotope evidence for

1183   the food web consequences of species invasions in lakes. Nature, 401: 464–467.

1184

1185   Verheyen, E., Salzburger, W., Snoeks, J. and Meyer, A. 2003. Origin of the superflock of cichlid

1186   fishes from Lake Victoria, East Africa. Science, 300: 325-328.

1187

1188   Villanueva, M.C., Lalèyè, P., Albaret, J.-J., Laë, R., Tito de Morais, L. and Moreau, J. 2006.

1189   Comparative analysis of trophic structure and interactions of two tropical lagoons. Ecological

1190   Modelling, 197: 461-477.

1191

1192   Villanueva, M.C. and Moreau, J. 2001. Recent trends of evolution in Lake Victoria fisheries as

1193   assessed by Ecopath 4 (with Ecosim) software, pp. 96-110. *In*: I.G. Cowx (Ed.), Lake and

1194   Reservoirs Fisheries Management. The University of Hull Publication, United Kingdom.

1195

1196   Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. and Westbrooks, R. 1997.

1197   Introduced species: A significant component of human-caused global change. New Zealand

1198   Journal of Ecology, 21(1): 1-16.

1199

1200   Volterra, V. 1931. Variations and fluctuations of the number of individuals in animal species

1201   living together, 409-448 pp. *In*: R.N. Chapman (Ed.), Animal Ecology. McGraw-Hill, New York

1202   and London.

1203

1204   Wanink, J.H. and Witte, F. 2000. The use of perturbation as a natural experiment: effects of

1205   predator introduction on the community structure of zooplanktivorous fish in Lake Victoria.

1206   Advances in Ecological Research, 31: 553-570.

1207

1208   Wanink, J.H., Katunzi, E.F.B., Goudswaard, K.P.C., Witte, F. and van Densen, W.L.T. 2002.

1209   The shift to smaller zooplankton in Lake Victoria cannot be attributed to the 'sardine'

1210   *Rastrineobola argenta* (Cyprinidae). Aquatic Living Resources, 15: 37-43.

1211

1212   Welcomme, R.L. 1988. International transfers of inland fish species. FAO Fisheries Technical

1213   Papers 294, 318 p.

1214

1215   Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. and Losos, E. 1998. Quantifying threats to

1216   imperilled species in the United States. Bioscience, 48: 607-615.

1217

1218   Winfield, I.J. and Durie, N.C. 2004. Fish introductions and their management in the English

1219   Lake District. Fisheries Management and Ecology, 11: 195-201.

1220

1221   Wootton, J.T., Power, M.E., Paine, R.T. and Pfister, C.A. 1996. Effects of productivity,

1222   consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal

1223   community. Proceedings of the National Academy of Sciences, 93: 13855–13858.

1224

1225   Yang, Y.F., Huang, X.F., Liu, J.K. and Jiao, N.Z. 2005. Effects of fish stocking on the

1226   zooplankton community structure in a shallow lake in China. Fisheries Management and

1227   Ecology, 12: 81-89.

1228

1229   Yodzis, P. and Winemiller, K.O. 1999. In search of operational trophospecies in a tropical

1230   aquatic food web. Oïkos, 87: 327-340.

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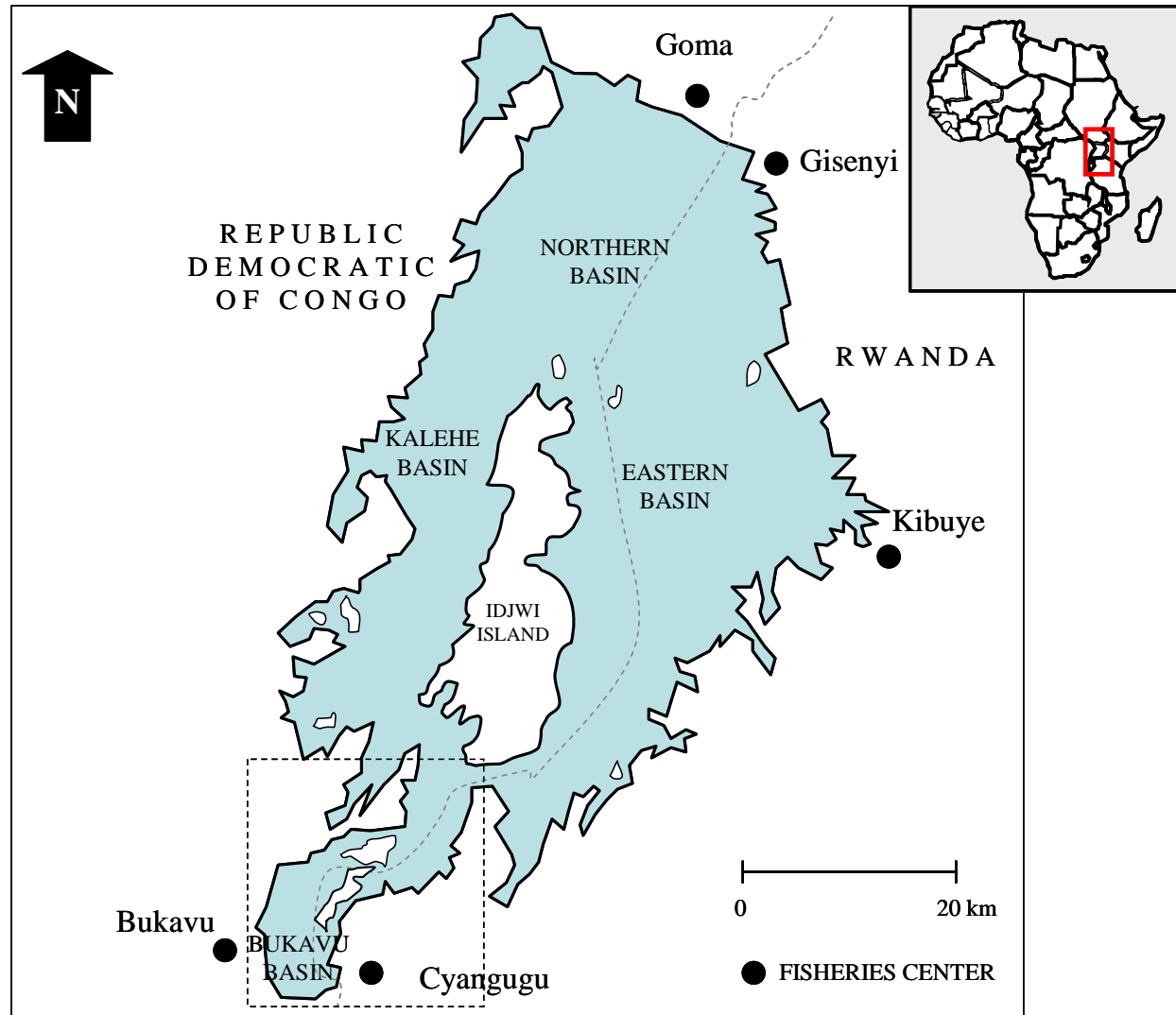
Figure 1

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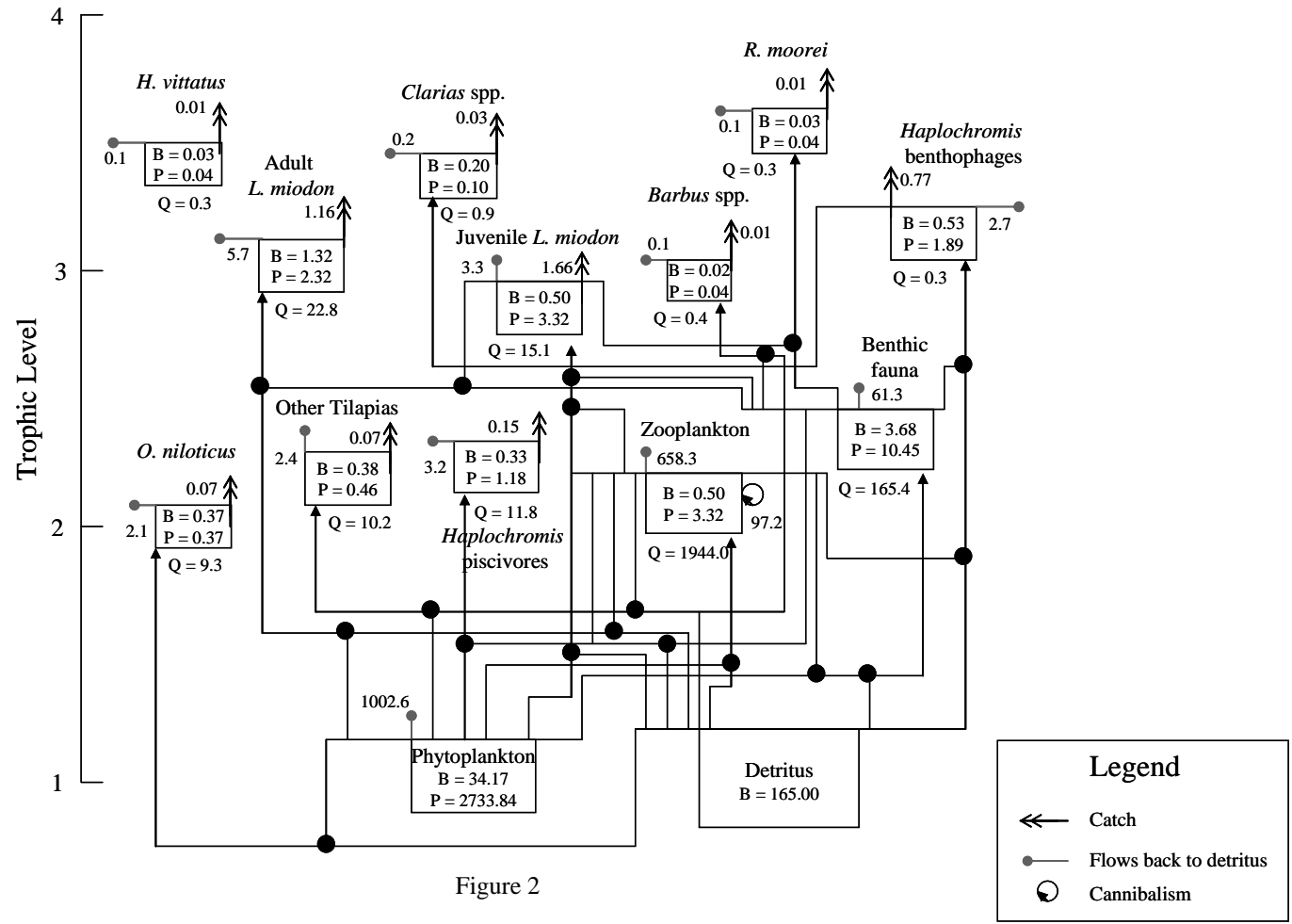
Figure 2

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Figure 3

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Legend

1 *Clarias* spp
2 *R. moorei*
3 *H. vittatus*
4 *Haplochromis* benthophages
5 *Haplochromis* planktivores
6 Adult *L. miodon*
7 Juvenile *L. miodon*
8 *Barbus* spp
9 *O. niloticus*
10 Other Tilapiines
11 Benthic fauna
12 Zooplankton

■ Impacting group □ Impacted group
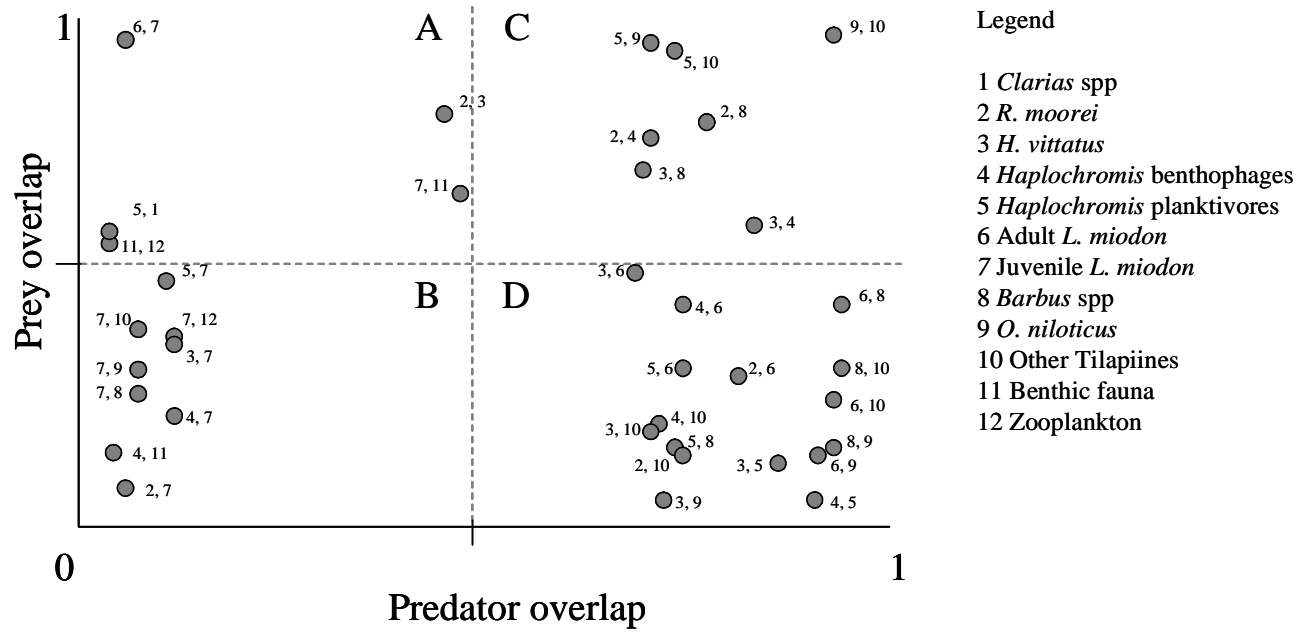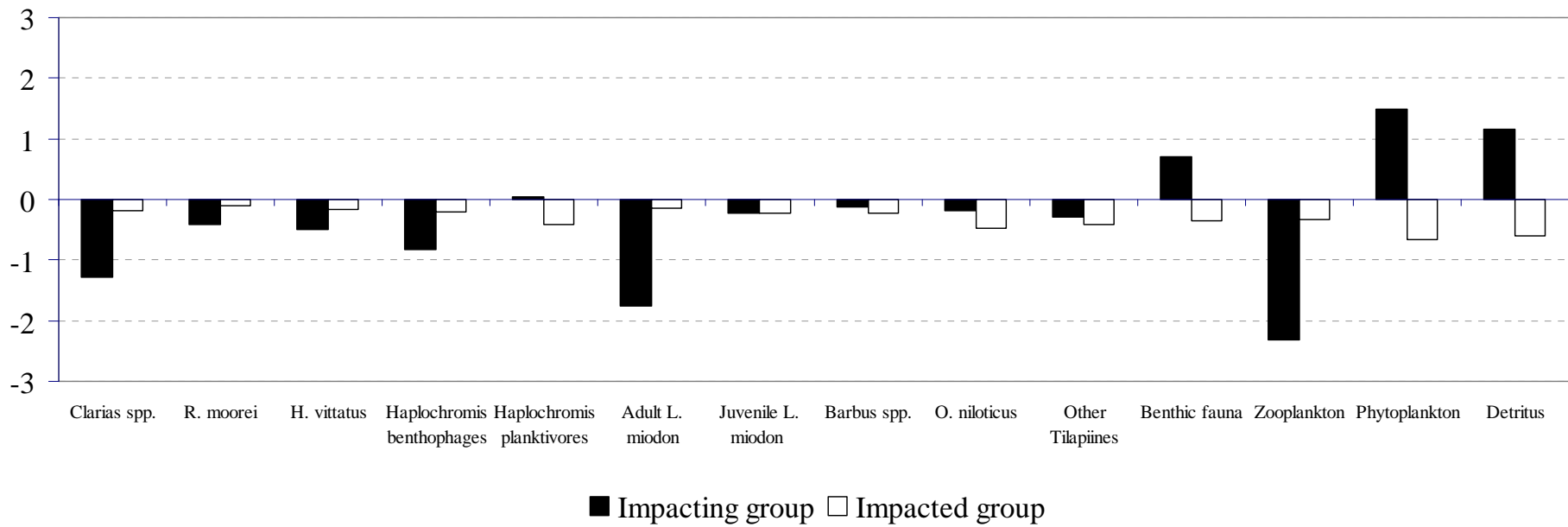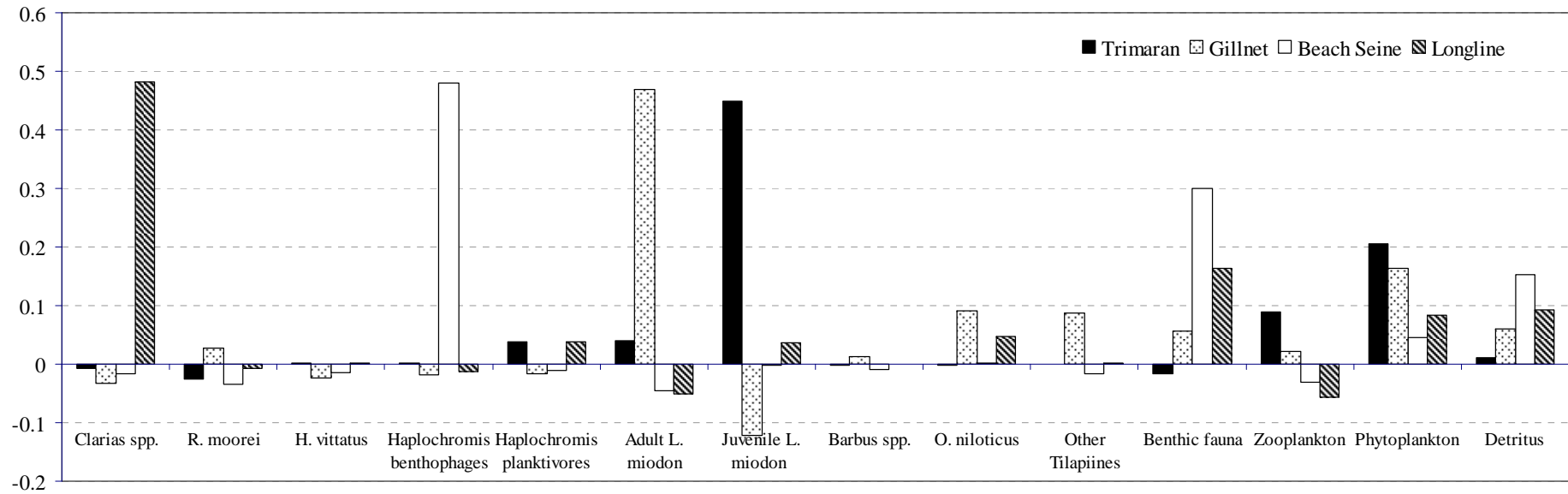
Figure 4

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Figure 5

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Table 1. Growth parameters for fish populations as incorporated in the model.

Species	L_∞ (TL cm)	K (yr^{-1})	Z (yr^{-1})	M (yr^{-1})
Clarias gariepinus	102.8 [a]	0.165 [a]	0.500 [a]	0.363 [c]
Raiamas moorii	23.0 [b]	0.680 [b]	1.640 [b]	1.389 [c]
Haplochromis vittatus	32.5 [b]	0.550 [b]	1.450 [b]	1.100 [c]
Haplochromis graueri	17.2 [b]	1.085 [b]	3.550 [b]	2.049 [c]
Haplochromis nigroides	10.7 [b]	1.682 [b]	3.580 [b]	3.115 [c]
Adult *Limnothrissa miodon*	18.0 [b]	1.100 [b]	1.750 [b]	2.147 [c]
Juvenile *Limnothrissa miodon*	15.0 [b]	1.100 [b]	6.690 [b]	2.040 [c]
Barbus kerstenii	11.7 [a]	1.330 [a]	2.786 [b]	2.601 [c]
Oreochromis niloticus eduardianus	38.7 [a]	0.550 [a]	1.008 [a]	0.806 [c]
Oreochromis macrochir	28.3 [a]	0.653 [a]	1.200 [a]	1.007 [c]

[a] Estimated based on models of de Merona (1984) and Fröese and Binohlan (2000) based on observed maximum total length
[b] Computed using the FiSAT software (Gayanilo *et al.*, 2002);
[c] Calculated using the predictive formula of Pauly (1980).

Table 2. Input values and calculated parameters (in **bold**) for the Ecopath model of the Congolese sector of Lake Kivu. TL is the trophic level, HA is the habitat area (%), B_{HA} is the biomass calculated for the habitat area (t.km^{-2}), B is the total biomass (t.km^{-2}), P/B is the production rate (yr^{-1}), Q/B the annual foof consumption per unit biomass (yr^{-1}), Y the total catch (t.km^{-2} yr^{-1}).and EE is the ecotrophic efficiency .

Group name	TL	HA	B_{HA}	B	P/B	Q/B	Y [d]	EE
Clarias spp	**3.36**	1.0	**0.204**	0.204[a]	0.50[c]	4.30[e]	0.028	**0.275**
Raiamas moorei	**3.56**	1.0	**0.025**	**0.025**	1.64[c]	21.03[f]	0.010	0.500[d]
Haplochromis vittatus	**3.42**	1.0	**0.029**	0.029[a]	1.45[c]	10.04[e]	0.010	**0.797**
Haplochromis benthivores	**3.15**	0.1	**5.320**	0.532[a]	3.55[c]	17.56[e]	0.773	**0.544**
Haplochromis planktivores	**2.20**	1.0	**0.329**	0.329[a]	3.58[c]	35.80[e]	0.153	**0.279**
L. miodon adults	**3.04**	1.0	**1.324**	1.324[b]	1.75[c]	17.20[f]	1.159	**0.511**
L.miodon juveniles	**2.80**	1.0	**0.496**	0.496[b]	6.69[c]	30.36[f]	1.659	**0.917**
Barbus spp	**2.98**	0.1	**0.156**	**0.016**	2.79[c]	27.86[e]	0.010	0.500[d]
O. niloticus eduardianus	**2.00**	0.1	**3.670**	0.367[a]	1.01[c]	25.39[e]	0.075	**0.479**
Other Tilapiine fish	**2.18**	0.1	**3.830**	0.383[a]	1.20[c]	26.74[e]	0.074	**0.233**
Benthic fauna	**2.32**	0.1	**36.757**	3.676	4.50[d]	45.00[d]		0.900[d]
Zooplankton	**2.05**	1.0	**10.800**	10.800	26.00[d]	180.00[d]		**0.626**
Phytoplankton		1.0	**34.173**	34.173	80.00[d]	-		**0.633**
Detritus		1.0	**165.00**	165.00[d]	-	-		**0.151**

[a] Biomass (B) was estimated when possible directly from the ratio between catch (Y) and annual fishing mortality as computed in Ecopath ($B = Y/F$);
[b] Based on echo sound data by Lambœuf (1991). Biomass of adults are higher (1.324 t.km^{-2}) than those of their juveniles (0.496 t.km^{-2}) due to the demographical structure of the population.
[c] P/B of functional group is assumed equal to the total mortality estimated (*cf.* Table 1);
[d] Sources indicated in text;
[e] Estimated using the predictive model of Palomares and Pauly (1998);
[f] Estimated using the MAXIMS software (Jarre *et al.*, 1991).

Table 3. Diet composition (%) of the groups considered in the Ecopath model of the Lake Kivu Congolese sector.

	Group name	1 [a]	2 [b]	3 [c]	4 [d]	5 [e]	6 [b]	7 [f]	8 [g]	9 [h]	10 [i]	11 [j]	12 [k]
1	*Clarias* spp												
2	*Raiamas moorei*	0.005		0.020									
3	*Haplochromis vittatus*	0.015	0.02										
4	Haplochromis benthivores	0.120	0.15	0.200					0.03				
5	Haplochromis planktivores	0.090	0.10	0.080					0.05				
6	*L. miodon* adult	0.020		0.025									
7	*L.miodon* juvenile	0.100	0.25	0.100			0.05						
8	*Barbus* spp	0.010		0.010									
9	*O. niloticus eduardianus*	0.100		0.050									
10	Other Tilapiine fish	0.030		0.025									
11	Benthic fauna	0.400	0.46	0.270	0.78	0.03	0.20	0.05	0.57		0.10		
12	Zooplankton	0.040	0.01	0.150	0.12	0.15	0.65	0.70	0.10		0.05	0.30	0.05
13	Phytoplankton	0.020	0.01	0.020	0.01	0.8	0.09	0.23	0.05	0.80	0.65	0.30	0.85
14	Detritus	0.050		0.050	0.09	0.02	0.01	0.02	0.20	0.20	0.20	0.40	0.10

a. Diet composition based on indications of Mavuti *et al*. (1996) and from Fröese and Pauly (2006);
b. From Kaningini *et al.* (1999);
c. Ulyel (1991) and Kaningini *et al.* (1999);
d. Considered diet composition of *Haplochromis graueri* (Ulyel, 1991);
e. Considered diet composition of *Haplochromis kamiranzovu* (Ulyel, 1991);
f. Kaningini *et al.* (1999) and Roest (1999);
g. M. Isumbisho (UERAH, unpublished data);
h. From Trawavas (1983) and B Kaningini (UERAH, pers.   omm..);
i. Considered diet composition of *O. macrochir* from Fröese and Pauly (2006);
j. Based on indications of Christensen and Pauly (1993);
Table 52.   From Christensen and Pauly (1993) and Sarvala *et al*. (2003).

Table 4. Ecological characteristics of the groups considered in the model. *P/Q* is the production/consumption ratio, FtD is the flow to detritus (t $km^{-2}yr^{-1}$), *NE* is the net efficiency and *OI* is the omnivory index.

Group name	*P/Q*	*FtD*	*NE*	*OI*
Clarias spp	0.116	0.249	0.145	0.282
Raiamas moorei	0.078	0.124	0.097	0.150
Haplochromis vittatus	0.144	0.067	0.181	0.339
Haplochromis benthivores	0.202	2.730	0.253	0.155
Haplochromis planktivores	0.100	3.205	0.125	0.179
L. miodon adult	0.102	5.688	0.127	0.153
L.miodon juvenile	0.220	3.286	0.275	0.218
Barbus spp	0.100	0.108	0.125	0.349
O. niloticus eduardianus	0.040	2.057	0.050	0.000
Autres Tilapiine fish	0.045	2.401	0.056	0.195
Benthic fauna	0.100	51.277	0.143	0.233
Zooplankton	0.144	688.307	0.206	0.053
Phytoplankton	-	1002.627	-	0.000
Detritus	-	0.000	-	0.298

Table 5. The trophic structure of the Lake Kivu ecosystem (Congolese sector) as estimated by the Ecopath software.

Trophic level (TL)	Catch (t km^{-2} yr^{-1})	(%) per TL	Biomass (t km^{-2})	% per TL	Transfer efficiency (%)
V	0.0031	0.08	0.012	0.32	4.60
IV	0.3405	8.62	0.365	9.86	7.60
III	2.7310	69.12	2.034	54.93	9.40
II	0.8767	22.19	1.292	34.89	4.50

Proportion of total flow originating from detritus:	0.31	
Transfer efficiencies: 1) From primary producers:	6.80 %	
2) From detritus:	7.10 %	
Total:	6.90 %	

Table 6. Summary statistics of Lake Kivu.

Parameter	Value	Units
Sum of all consumption	2190.04	t.km^{-2}.yr^{-1}
Sum of all exports	1499.85	t.km^{-2}.yr^{-1}
Sum of all respiratory flows	1233.99	t.km^{-2}.yr^{-1}
Sum of all flows into detritus	1762.12	t.km^{-2}.yr^{-1}
Total system throughput	6686.00	t.km^{-2}.yr^{-1}
Sum of all production	3040.00	t.km^{-2}.yr^{-1}
Mean trophic level of the catch	2.90	
Gross efficiency (catch/net p.p.)	0.001445	
Input total net primary production	2733.84	t.km^{-2}.yr^{-1}
Calculated total net primary production	2733.84	t.km^{-2}.yr^{-1}
Total primary production/total respiration	2.21	
Net system production	1499.85	t.km^{-2}.yr^{-1}
Total primary production/total biomass	52.22	
Total biomass/total throughput	0.008	
Total biomass (excluding detritus)	52.35	t.km^{-2}
Total catch	3.95	t.km^{-2}.yr^{-1}
Connectance Index (*CI*)	0.396	
System Omnivory Index (*SOI*)	0.148	