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Ecosystem models of Lake Victoria (East Africa): exploring the sensitivity of ecosystem effects of fishing to model choice

Short title: Ecosystem simulation models and sensitivity to fishing pressure

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22 **Abstract**

23 Ecosystem simulation models are valuable tools for strengthening and promoting
24 ecosystem-based fisheries management (EBFM). However, utility of these models in
25 practical fisheries management is often undermined by lack of simple means to test the
26 effect of uncertainty on model outputs. Recently, the use of multiple ecosystem models has
27 been recommended as an ‘insurance’ against effects of uncertainty that comes with
28 modelling complex systems. The assumption is that if models with different structure and
29 formulation give consistent results, then, policy prescriptions are robust (i.e. less sensitive to
30 model choice). However, information on the behaviour of trends from structurally-distinct
31 ecosystem models with respect to changes in fishing conditions is limited, especially for
32 freshwater systems. In this study, we compared outputs of two ecosystem models, Ecopath
33 with Ecosim (EwE) and Atlantis, for Lake Victoria under different fishing pressure scenarios.
34 We compared model behaviour at the ecosystem level, and also at a level of functional
35 groups. At functional group level, we determined two questions: what is the change in the
36 targeted group, and what are the consequent effects in other parts of the system? Overall
37 results suggest that different model formulations can provide similar qualitative predictions
38 (direction of change), especially for targeted groups with similar trophic interactions and
39 adequate data for parameterization and calibration. However, considerable variations in
40 predictions (where models predict opposite trends) may also occur due to inconsistencies in
41 the strength of the aggregate multispecies interactions between species and models, and
42 not necessarily due to model detail and complexity. Therefore, with more information and
43 data, especially on diet, and comparable representation of feeding interactions across

44 models, ecosystem models with distinct structure and formulation can give consistent policy
45 evaluations for most biological groups.

46

47 **Introduction**

48 **Ecosystem modelling for ecosystem-based fisheries management**

49 **(EBMF)**

50 In the recent years, calls for the implementation of ecosystem-based fisheries
51 management (EBFM) have increased [1], despite the slow progress towards its adoption [2,
52 3]. The slow adoption of EBFM has largely been due to divergences in the interpretation
53 among professionals [4, 5]. The advantages of EBFM are clearly understood. For example, it
54 considers how fishing impacts entire ecosystem and fisheries through both direct and
55 indirect mechanisms when formulating fisheries management strategies and actions [5].

56 Ecosystem simulation models can be used to evaluate ecosystem properties and
57 provide information on the potential effects that changes in EBFM practices would have on
58 the ecosystems [6]. Within the last two decades, ecosystem models have become popular
59 tools for influencing and strengthening EBFM [7]. However, ecosystem models differ in detail
60 of their biological processes and how they are represented, projection length and solution
61 time steps [8]. This variation in model detail and assumptions introduces varying levels of
62 uncertainty that often undermine utility of end-to-end models in practical fisheries
63 management [9].

64 The high levels of uncertainty inherent in some ecosystem models means that no
65 ecosystem model is perfect for all purposes under the EBFM framework [10]. This is
66 exacerbated by the subjective nature of the modelling process as parameter estimation

67 within the models is not possible. Although these models are constructed based on the
68 knowledge of the system (i.e. to minimize process uncertainty), and also utilizing the best
69 available data, these are not adequate safeguards to uncertainty that comes with modelling
70 complex systems. In ecosystem models with intermediate complexity such as Ecopath with
71 Ecosim (EwE), Monte Carlo algorithm is applied to examine the sensitivity of simulation
72 results to the initial input parameters [11]. However, for complex end-to-end ecosystem
73 models, such as Atlantis with thousands of parameters, full-scale sensitivity analysis is not
74 feasible.

75

76 **The use of multiple ecosystem models**

77 To limit on the effect of model uncertainty on policy recommendations, the use of
78 multiple and complementary ecosystem models to provide input for management is strongly
79 recommended [12, 13]. However, this requires a clear understanding of the level of
80 robustness of results from different model formulations. Robustness here is considered to
81 refer to consistency of performance across alternative model formulation, model
82 uncertainty, and levels of perturbation intensity [14].

83 Multi-species models are multi-dimensional, and comparing them is generally a
84 complex task. Consequently, recent investigations have focused on simpler approaches to
85 understand how ecosystem impacts of fishing are sensitive to model choice using a range of
86 indicators [15–19]. At the broadest level, these studies have found considerable coherence
87 in general predictions (i.e. direction of change) across models but still with major differences
88 observed for the multi-species effects. Whereas the general causes of discrepancies have
89 been identified, including model structure and differences in representation of diets, some
90 variations are ecosystem-specific [19].

91 The structural and functional differences between the multi-species models are huge.
92 For example, EwE is a whole ecosystem biomass model, which is not spatially resolved unless
93 coupled with Ecospace, where predation is regulated by explicit diet parameters and
94 foraging vulnerability [11]. On the other hand, Atlantis is a whole ecosystem, age- and size-
95 structured population model that is resolved in three dimensions with user-defined
96 polygonal model zones and multiple depth layers [20, 21]. Predation in Atlantis is regulated
97 by a diet preference matrix, but the actual resulting diet is subject to mouth-gape limitations
98 and prey availability. The two modelling approaches have no systematic variation in
99 assumptions; yet, they are designed almost to achieve the same ultimate goal: evaluation of
100 system-level trade-offs of alternative management strategies. Determining whether the
101 different model formulations predict similar outcomes in response to changes in fishing
102 conditions is important in the EBFM context. Even where models predict different outcomes,
103 such comparisons are useful in highlighting areas where different assumptions may lead to
104 varying predictions, which can be used to improve the models.

105

106 **Ecosystem models of Lake Victoria (East Africa)**

107 Considerable attempts have been made towards constructing ecosystem models for
108 Lake Victoria to understand ecosystem dynamics (structure and functioning) as well as
109 ecosystem-level effects of alternative fishery policies. Emphasis has been put on use of EwE
110 and Atlantis modelling frameworks because of their popularity across the African Great
111 Lakes [22], and generally across the globe [10, 23].

112 EwE and Atlantis models of Lake Victoria have been constructed to answer specific
113 questions that are common to both models: food web structure and function and ecosystem
114 effects of fishing [22]. However, to improve our confidence in results from these models,

115 there is need for systematic analysis of sensitivity of ecosystem impacts of fishing to model
116 structure and formulation.

117 In this paper, we compared the behaviour of EwE and Atlantis model simulations of
118 the Lake Victoria ecosystem. We compared model behaviour at the ecosystem level, and
119 also at a level of functional groups. The work described here is not intended to recommend
120 one model over another. Rather, the main objective is to investigate how ecosystem effects
121 of fishing are sensitive to model choice, and which ecosystem indicators are most sensitive
122 to model uncertainty and complexity. Because the outputs of complex ecosystem models
123 such as the Atlantis are huge, to ease comparisons, we aggregated the results and
124 concentrated on comparing the behaviour of ecosystem indicators. For biomass-based
125 indicators, results from Atlantis were aggregated to show trends through time, with no
126 spatial and age-structure considerations.

127

128 **Materials and Methods**

129 **Study area**

130 Lake Victoria, located in East Africa (Fig 1), is the most productive freshwater lake in
131 the world, with annual fish landings of about one million tonnes, and the second largest in
132 terms of size (with a surface area of about 68,800 km²). The fishery currently employs more
133 than one million people directly in fishing and other value-chain related activities; when
134 their dependents are included, Lake Victoria supports local livelihoods of about four million
135 people [24].

136

137 **Fig 1. Location of Lake Victoria (East Africa) within Africa.**

138

139 The present-day Lake Victoria fishery represents a massive transformation from the
140 traditional and highly species-diverse fishery (i.e. before 1960s), known for its 500+ species
141 of haplochromines, to a less species-diverse but highly productive and lucrative fishery
142 dominated by introduced species especially Nile perch (*Lates niloticus*). An elaborate
143 account of changes that have occurred, and how the fishery has persisted amidst multiple
144 stressors e.g. species introductions, fishing, habitat degradation, eutrophication, and climate
145 variability and change can be found in published literature [25—27].

146

147 **Modelling frameworks**

148 **Ecopath with Ecosim (EwE)**

149 The EwE modelling suite has been widely documented [11]. Briefly, EwE has an
150 ecosystem trophic mass balance routine (Ecopath), where an ecosystem is partitioned into
151 functional groups based on ecological roles and feeding interactions. Biomass flows in an
152 ecosystem are regulated by gains (consumption, production, and immigration) and losses
153 (mortality and emigration), through predator-prey relationships. For each functional group,
154 the net difference between gains and losses is equal to the instantaneous rate of biomass
155 change, which is parameterized with Biomass Accumulation. Key model parameters include
156 biomass per unit of habitat area, production rate per unit of biomass, consumption rate per
157 unit of biomass of predator, and ecotrophic efficiency (EE, the proportion of production that
158 is utilized in the system). The model uses the input data along with algorithms and a routine
159 for matrix inversion to estimate one missing basic parameter for each functional group,
160 usually the EE. The Trophic level (TL) of each functional group is calculated on the basis of

161 average annual predation by aggregating diet data. Primary producers and detritus are
162 assigned a TL of 1, and the TL of consumer groups is calculated as the biomass-weighted
163 average TL of its prey +1.

164 The time dynamic routine of EwE, Ecosim, uses Ecopath parameters to provide
165 predictions of biomass and catch rates of each group as affected directly by fishing,
166 predation, and change in food availability, and indirectly by fishing or predation on other
167 groups in the system. Predation is governed by the concept of foraging arena, where species
168 are divided into vulnerable and non-vulnerable components, such that the overall feeding
169 rate is somehow limited by prey density. Calibration is achieved by adjusting diet and
170 vulnerabilities until satisfactory fits are achieved.

171

172 **Atlantis**

173 The Atlantis modelling framework has also been described elsewhere [20, 21].
174 Briefly, Atlantis is a deterministic, spatially resolved tool that is based on dynamically
175 coupled biophysical and fisheries sub models (consumption, biological production, waste
176 production, reproduction, habitat dependency, age structure, mortality, decomposition, and
177 microbial cycles). Biophysical and biological processes are modelled in interconnected cells
178 representing major features of the physical environment. The spatial domain is resolved in
179 three dimensions using irregular polygons defined by the modeller to represent
180 biogeographic features. Exchange of biomass occurs between polygons according to
181 seasonal migration and foraging behaviour, while water fluxes (which control advection of
182 nutrients and plankton), heat, and salinity flux across boundaries are represented by a
183 coupled hydrodynamic model.

184 Functional groups, as with EwE, are determined based on ecological roles,
185 ontogenetic behaviour and feeding interactions, except that vertebrates in Atlantis are
186 represented as age-structured groups and lower trophic groups as biomass pools. The flow
187 of energy is tracked as nitrogen, which in all vertebrate groups is partitioned into structural
188 and reserve nitrogen. Structural nitrogen determines growth, while reserve nitrogen (whose
189 amount varies depending on the food intake) is used for reproduction. The model simulates
190 dynamic feeding interactions, with all functional feeding responses based on a modified
191 Holling type II response. Trophic levels of model groups are computed on the same basis as
192 in EwE.

193

194 **Operating models**

195 In this study, we used the EwE and Atlantis models constructed for Lake Victoria as
196 operating models. The models were constructed with an ultimate goal of exploring the
197 ecosystem impacts of fishing, making it possible to compare the model behaviour under
198 various fishing pressure scenarios. Fig 2 shows a summarized representation of the major
199 features for the two models used in this study. The two models are similar in spatial extent
200 (3.05°S to 0.55°N and 31.5° to 34.88°E), covering the area of approximately 68,800 km², and
201 were constructed to represent the ecosystem of Lake Victoria during the period when most
202 of non-native species had just been introduced i.e. 1958 for Atlantis and 1960 for EwE. The
203 calibration approach in two models differs substantially, but the period is comparable.

204

205 **Fig 2. Schematic diagram showing the major features of EwE and Atlantis models for Lake**
206 **Victoria used in this study.**

207

208 The detailed EwE model used in this study (including set up, parameterization, and
 209 calibration) can be found at <https://doi.org/10.6084/m9.figshare.7306820.v2>. The model
 210 comprises 25 groups, including fish eating birds, the Nile crocodile, 15 fish groups (either as
 211 individual fish species or several species grouped together based on similarity in life history,
 212 habitat or diet), three invertebrate groups, two producer groups, and a detrital group (Table
 213 1). Haplochromines, which is a group of major ecological importance (forage group), are
 214 modelled in one group, differing from Atlantis where haplochromines are modelled in three
 215 groups (Table 1). Nile perch, another group of focus in the fishing scenarios (see below), is
 216 also modelled as a single group, despite the species' dietary preferences related to size [29].
 217 Although Nile perch is also modelled as one in Atlantis model, it is divided into 10 age classes
 218 [31]; and therefore, the juvenile and adult individuals can have different diet and spatial
 219 distribution. In EwE, this is only modelled implicitly by including all possible prey for juvenile
 220 and adult Nile perch in the same diet matrix.

221

222 **Table 1. Functional groups used in the Lake Victoria EwE and Atlantis models.**

Common name	EwE	Atlantis	Species included
Birds	Yes	Yes	Fish-eating birds
Crocodiles	Yes	Yes	<i>Crocodylus niloticus</i>
Nile perch	Yes	Yes	<i>Lates niloticus</i>
North African catfish	Yes	Yes	<i>Clarias gariepinus</i>
Semutundu	Yes	Yes	<i>Bagrus docmak</i>
Marbled lungfish	Yes	Yes	<i>Protopterus aethiopicus</i>
Squeakers	Yes	Yes	<i>Synodontis victoriae, S. afrofisheri</i>
Snout fishes	Yes	Yes	Predominantly <i>Momyrus kanume</i>
Silver catfish	Yes	Yes	<i>Schilbe intermedius</i>
Rippon barbel	Yes	Yes	<i>Labeobarbus altianalis</i>

Small barbs	Yes	Yes	<i>Enteromius</i> spp.
Robbers	Yes	Yes	<i>Brycinus jacksoni</i> , <i>B. sadleri</i>
Ningu	Yes	Yes	<i>Labeo victorianus</i>
Haplochromines	Aggregated	Three groups	Phytoplanktivorous, Benthivorous, Piscivorous
Silver cyprinid	Yes	Yes	<i>Rastrineobola argentea</i>
Nile tilapia	Yes	Yes	<i>Oreochromis niloticus</i>
Other tilapias	Yes	Yes	<i>O. esculentus</i> and <i>O. variabilis</i>
Freshwater shrimp	Yes	Yes	<i>Caridina nilotica</i>
Insects and molluscs	Aggregated	Five groups	Macroinvertebrates, Benthic filter feeder, Shallow filter feeder, Deep filter feeder Microphytobenthos
Zooplankton	Aggregated	Two groups	Microzooplankton, Mesozooplankton,
Phytoplankton	Aggregated	Four groups	Macroalgae, Large phytoplankton, Dinoflagellates, Pico-phytoplankton
Macrophytes	Yes	No	
Bacteria	No	Two groups	Pelagic and sediment bacteria
Detritus	Aggregated	Two groups	Labile and refractory detritus

223

224 The Atlantis model used in this study has been described in detail elsewhere [31, 32].

225 A complete set up of this model was retrieved from

226 <https://doi.org/10.6084/m9.figshare.4036077.v1>. The model has 12 unique spatial regions,

227 each region with 1-3 depth layers depending on the total depth, and a total of 34 of

228 biological groups (i.e. 17 fish groups, fish eating birds, Nile crocodile, nine invertebrate and

229 six primary producer groups). The 19 vertebrate groups are modelled as age-structured

230 components, while the remaining 15 lower trophic groups are modelled as biomass pools.

231 Except for haplochromines, which are separated into three groups in Atlantis (Table
232 1), the choice of functional grouping at the vertebrate level for the two models is the same,
233 although representation of diet is quite different (Fig 3). For the invertebrate and producer
234 groups, the choice of functional groups differ substantially across models. Atlantis model has
235 nine invertebrates groups and six producer groups compared to three invertebrate and two
236 producer groups in the EwE model (Table 1). The detrital group in the Atlantis model is also
237 divided into refractory and labile detritus. Therefore, our analysis focuses on groups that are
238 comparable across models (Fig 3), excluding fish eating birds and crocodiles. For
239 haplochromines, results for the three groups from Atlantis are aggregated and presented as
240 one group.

241

242 **Fig 3. Schematic representation of predation interactions in EwE and Atlantis models of**
243 **the Lake Victoria ecosystem.** Model groups shown here are only for fish species, which are
244 fairly represented in both models, to ease comparisons. Note that arrows move towards the
245 predators and arrow thickness is consistent with the contribution of prey to the predator's
246 diet. Thick and black arrows indicate that the prey species makes up more than 30% of the
247 predator's diet, while thin arrows indicate that the prey species makes up less than 5% of
248 the predator's diet.

249

250 **Fishing scenarios**

251 We focused on Nile perch and haplochromines in our fishing scenarios because of
252 their greatest economic and ecological importance in the Lake Victoria ecosystem [33]. In
253 addition, these groups are the most studied on the lake; we assume their representation in
254 both models is fairly grounded in data, and their projections are less affected by data

255 uncertainty compared to lesser-studied species. The fishing mortality for the last year of
256 each historical model run (2015) was taken as the baseline fishing pressure. In the first and
257 second scenarios, we reduced and increased, respectively, Nile perch fishing pressure by
258 40% from the baseline level. For the third scenario, we halted fishing of haplochromines (the
259 major prey for Nile perch, see Fig 3). We also included the status quo scenario, where we
260 maintained fishing pressure for all functional groups at the baseline level (i.e. as of 2015).
261 We included the status quo scenario because the ecosystem would be expected to change
262 under any level of fishing, and therefore the final results of the status quo scenario may not
263 necessarily be the same as baseline values. For each scenario, biomass and catch for the
264 individual species/groups were projected for 20 years into the future, and results are
265 presented at the end of the projection period relative to the baseline (2015) values.

266

267 **Ecosystem indicators for comparison**

268 Ecosystem indicators spanning a wide range of processes and biological groups have
269 been used in several studies to detect a range of impacts from fishing [14]. To compare the
270 changes that occur at a species/group level in response to fishing pressure scenarios, we
271 looked at biomass of individual groups for each model but focused only on fish groups as
272 they were represented in both models. We calculated Pearson correlation coefficient (r) for
273 every functional group to examine the consistency of trends from both models under each
274 fishing scenario. Our focus was on the direction of change in relative projections; so our
275 subsequent interpretation of we use the term “consistency” to refer to any positive value of
276 r and “inconsistency” to refer to negative values r .

277 Community-level indicators, on the other hand, are useful for detecting ecosystem-
278 level changes [14]. These include relative abundance of key functional groups (e.g. piscivores

279 and planktivores), mean TL in community and catch. Aggregating model groups into feeding
280 guilds of fish species with broadly similar diets i.e. piscivores and planktivores is important
281 because these feeding guilds are expected to respond to fishing pressure more predictably
282 than individual species [28]. For instance, relative biomasses of piscivores and planktivores
283 can indicate a change in the trophic structure of the system, as can shift in TL of the catch.
284 Functional groups in the piscivore guild included Nile perch, North African catfish,
285 Semutundu, Silver catfish, and piscivorous haplochromines (TL>3.0). The planktivore guild
286 included groups such as Silver cyprinid, Nile tilapia, other tilapia, Robbers, Ningu, Small
287 barbs, phytoplanktivorous/Benthivorous haplochromines. Since the haplochromines in EWE
288 are not segregated, we used relative abundance of Lake Victoria's haplochromine trophic
289 guilds [34] to assign biomass to each group.

290 We calculated Mean TL in community ($MTL_{biomass}$) as the average TL of the model
291 groups, weighted by their biomass according to equation 1

$$292 \quad MTL_{biomass} = \sum_i TL_i \times \frac{B_i}{B} \quad (1)$$

293 where TL_i and B_i are the trophic level and biomass of model group i , and B is the total
294 biomass of all the fish groups (see Table 1). We only considered fish groups to avoid the
295 influence of lower trophic planktonic groups (zooplankton and phytoplankton) that have
296 comparatively greater biomasses. We preferred this approach because all the planktonic
297 groups are not represented in all the models; therefore, focusing only on fish groups keeps
298 the analysis comparable. Besides, the biomasses of planktonic groups can vary greatly with
299 environmental effects, and such fluctuations may not be relevant to fisheries management.

300 We also calculated mean TL in catch (MTL_{catch}) using the same approach as with
301 $MTL_{biomass}$, but using the biomass of catch for each model group rather than stock biomass
302 i.e. as the mean TL of all landed fish, weighted by the biomass of catch (equation 2).

$$303 \quad MTL_{catch} = \sum_i TL_i \times \frac{B_{Ci}}{B_C} \quad (2)$$

304 where B_{Ci} is the biomass of catch of model group i . This indicator is important as it can signal
305 to the depletion of high-trophic-level species i.e. ‘fishing down the food web’ [30].

306

307 **Results**

308 **Biomasses of individual model groups**

309 Fig 4 shows correlation values representing the change of trend of relative biomass
310 of functional groups under different fishing pressure scenarios. Qualitative similarities
311 (change in the same direction) between the two models are shown by functional groups with
312 positive correlation values. Overall, the response to shifts in fishing pressure scenarios for
313 individual functional groups was diverse across models, depending on the fishing pressure
314 scenario in question. Projections with similar trends were observed for targeted groups and
315 their prey/predator (depending on the strength of the feeding interaction), but large
316 discrepancies were also observed especially for the indirect effects of the fishing pressure
317 scenarios on non-target ‘distant’ groups. Only two groups (Nile perch and Nile tilapia)
318 showed similar biomass trajectories (consistent trends) simultaneously in all the four
319 scenarios.

320

321 **Fig 4. Correlation between the relative biomasses of species/groups projected by the two**
322 **models under four different fishing scenarios.** Haplos stands for haplochromines, M.

323 lungfish is Marbled lungfish, and N.A. catfish is North African catfish.

324

325 The scenario of increasing Nile perch fishing pressure by 40% from baseline showed
326 the highest level of consistency in biomass projections among functional groups (i.e. 11 out
327 of the 14 model groups showed similar trends across models). The three groups whose
328 trends differed were Robbers, Semutundu and snout fishes, where relative biomass
329 increased in EwE but decreased in Atlantis. However, when Nile perch fishing pressure was
330 instead reduced by 40% from the baseline, the number of groups with similar trends across
331 models reduced to nine, although Robbers, Semutundu and snout fishes showed similar
332 trends under this scenario. Only six groups (Nile perch, haplochromines, North African
333 catfish, Nile tilapia, Ningu, and squeakers) showed similar direction of change across models
334 under the two contrasting Nile perch fishing pressure scenarios.

335 The scenario of halting haplochromine fishing yielded the least number of groups
336 with similar direction of change in biomass (i.e. six out of the 14 model groups).
337 Unexpectedly, the response of haplochromines was also inconsistent, although the response
338 of its major predator, Nile perch, was consistent under this scenario. The response of
339 individual model groups under this fishing scenario was quintessentially similar to the status
340 quo scenario. With the exception other tilapias, where Atlantis and EwE predicted an
341 increase and decrease, respectively, the rest of the groups (Marbled lungfish, North African
342 catfish, Ningu, Silver cyprinid, small barbs) decreased in Atlantis but increased in EwE.

343 Fig 5 shows change in predicted biomass by the two models under fishing pressure
344 scenarios at the end of the simulation, relative to baseline. All outcomes of fishing pressure

345 scenarios are compared at the end of 20 years, where values of zero indicate no change in
346 biomass (relative to baseline levels). Qualitative agreements between models are shown by
347 predictions in the same direction, indicated by bars on the same side of the zero line (either
348 positive or negative sign). Quantitative agreements between models are shown by
349 predictions with similar magnitude, indicated by bars with the same height. Generally,
350 qualitative agreements were higher for the target groups (e.g. Nile perch, Nile tilapia,
351 haplochromines, Silver cyprinid, Semutundu, and snoutfishes) than the non-target groups,
352 although the magnitude of predictions differed substantially. Except for the scenario where
353 Nile perch fishing was increased by 40% from baseline, Atlantis was generally more
354 responsive to shifts in fishing pressure than EwE.

355

356 **Fig 5. Relative change in biomass of functional groups at the end of forecasting period as**
357 **predicted by Atlantis and EwE models.**

358

359 Under the scenario of increasing Nile perch fishing pressure, Nile perch decreased
360 both in EwE and Atlantis; however, the magnitude of the decrease was six times higher in
361 EwE than Atlantis. As expected, the major prey for Nile perch (haplochromines) increased in
362 both models, although Atlantis was more responsive than EwE. The response in other
363 groups, except for Ningu and other tilapias, was highly variable, with EwE predicting an
364 increase in biomass of most groups and Atlantis predicting a decrease.

365 Under the scenario of decreasing Nile perch fishing pressure, Nile perch increased
366 while haplochromines decreased in both models, although the magnitude of decrease for
367 haplochromines was higher (47%) in Atlantis than EwE (20%). For the rest of the groups,
368 apart from Marbled lungfish and other tilapias, whose biomasses respectively increased and

369 decreased in EwE and Atlantis (by at least 3%), the biomasses of other groups decreased in
370 both models.

371 In the two other scenarios (maintaining status quo and halting haplochromine
372 fishing), the predicted biomasses at the end of the simulation were highly variable across
373 models, except for Nile perch, whose biomass increased, and three other groups
374 (Snoutfishes, Semutundu, and Robbers) whose biomasses decreased consistently across
375 models. Under these two scenarios, the responsiveness of the two models to shifts in fishing
376 pressure was clearly higher in Atlantis than EwE.

377

378 **Ecosystem-level indicators**

379 Fig 6 shows the proportional change in system-level indicators across the models
380 under at the end each fishing pressure scenario. All indicators are shown as relative change
381 from 2015 to 20135 for each scenario, where zero indicates no difference. Overall,
382 ecosystem-level indicators were more consistent across models compared to the individual
383 biomass-based indicators.

384

385 **Fig 6. Relative change in system-level indicators in EwE and Atlantis under the four**
386 **different fishing pressure scenarios.** pisciv:planktiv stands for piscivorous to planktivorous
387 ratio, MTL_{biomass} and MTL_{catch} are mean trophic level in community and catch, respectively. ;

388

389 The biomass of piscivore guild relative to planktivore guild increased across models,
390 except for the scenario of increasing Nile perch fishing, where Atlantis predicted a massive
391 increase and EwE predicted a decrease. However, overall fish biomass decreased
392 consistently across models.

393 MTL_{biomass} showed consistent direction of change across the models except under the
394 scenario of halting haplochromine fishing, where the indicator value increased in Atlantis
395 and decreased in EwE. MTL_{biomass} increased with the reduction Nile perch fishing and
396 maintaining status quo, but decreased with an increase in Nile perch fishing. Similarly,
397 MTL_{catch} was consistent across models, except the scenario of increasing Nile perch fishing
398 pressure where Atlantis predicted an increase and EwE predicted a decrease. For the
399 remaining scenarios, MTL_{catch} increased either by halting haplochromine fishing or
400 maintaining status quo, but decreased by reducing Nile perch fishing pressure.

401

402 **Discussion**

403 **Biomass of individual model groups**

404 Ecosystem models are predominantly used to gain understanding of ecosystem-level
405 processes and (in most cases) to indicate qualitative trends associated with changes in
406 fishing (or some other form of forcing) conditions. Studies exploring consistency of
407 ecosystem effects of fishing across models that have already taken place indicate that
408 consistent general predictions (in terms of direction of change) can emerge from different
409 model formulations, although considerable variations may occur in detailed model results
410 especially for multispecies effects [14—19]. This is consistent with our general findings from
411 this study. Our results suggest that the direction of change in biomass predictions is driven
412 by trophic interactions, while the magnitude of change in predicted biomass depends on
413 both the processes included in the model (model detail and complexity) as well as the
414 strengths of feeding interactions.

415 The choice of biological groupings and representation of diets can greatly influence
416 the level of connectivity between groups. This in turn has an effect on the projected
417 magnitude of one species' biomass or catch affected by other species' fishing mortality. In
418 our study, the effect of feeding interactions is illustrated by the two Nile perch fishing
419 scenarios. Fig. 3 shows that the greatest proportion of Nile perch diet in both models is
420 contributed by haplochromines. Reducing fishing pressure on Nile perch causes an expected
421 increase in the abundance of Nile perch, which subsequently causes a decline in their
422 preferred prey (haplochromines). The reverse is true as well owing to high fishing pressure
423 and predation release on Nile perch and haplochromines, respectively. Although Nile perch
424 feeds on other fishes such as Mabbled lungfish, Ningu, North African catfish, other tilapias,
425 Robbers, Semutundu and squeakers, which all showed wide discrepancies in predicted
426 biomass across models; these are weak feeding interactions, where each group contributes
427 less than 3% in Nile perch diet. However, one striking feature about these groups (Mabbled
428 lungfish, Ningu, North African catfish, other tilapias, Robbers, Semutundu and squeakers) is
429 that they are all benthic-pelagic, largely feeding on invertebrates (not shown in Fig. 3) at the
430 bottom sediment. Given that these groups don't constitute a significant prey at the top of
431 the food chain, changes in their abundance are governed by abundance of the lower TL
432 invertebrate groups, whose grouping differs considerably across models (Table 1). Atlantis
433 has nine invertebrate groups, while EwE has only three, with different feeding connections
434 to high TL dependant groups. The discrepancies in biomass trend for these groups that
435 depend on invertebrate prey can therefore be attributed to the differences in choice of
436 functional groups at the bottom of the food chain, and not necessarily differences in model
437 processes. This is especially true considering that Atlantis predicts a uniform decline in these
438 groups under every fishing scenario.

439 Whereas the direction of change in model forecasts is largely governed by feeding
440 interactions, model sensitivity to perturbation and the resulting magnitude of change in
441 individual group biomasses seem to be driven both by the modelled processes and strength
442 of the feeding dependencies. Studies that have previously compared Atlantis and EwE have
443 found Atlantis to be less sensitive to changes in fishing pressure compared to EwE [16—18,
444 35, 36]. The authors have attributed the lower responsiveness of Atlantis to flexibility in
445 feeding and incorporation of age structure and reproductive behaviour, which can delay the
446 reproductive response of the population. In Atlantis predation is regulated by a diet
447 preference matrix, although the actual resulting diet a function of mouth-gape and prey
448 availability, while predation in EwE is regulated by a fixed diet matrix and foraging
449 vulnerability. Fig 3 shows Atlantis model of Lake Victoria with more feeding linkages
450 amongst compartments than EwE. This feeding flexibility in the Atlantis model, in addition to
451 the ‘delaying’ model processes, were expected to dampen the sensitivity of predators to
452 shifts in abundance of prey and result into lower responsiveness of Atlantis than EwE.
453 However, this only occurred for Nile perch under the scenario where Nile perch fishing
454 pressure was reduced; the magnitude of change for Nile perch in Atlantis was lower than in
455 EwE (Fig. 5). For the rest of the groups, Atlantis was largely more sensitive to fishing than
456 EwE, despite incorporating the delaying features of age structure and reproductive
457 behaviour as well as allowing for diet flexibility. In this case, the strengths of diet
458 dependencies likely outweighed the delaying system features.

459

460 **Ecosystem-level indicators**

461 The shifts in biomass-weighted TL in community and catch, especially for the two
462 contrasting Nile perch scenarios, were all consistent with expectation. Nile perch is a

463 voracious predator at the top of the food chain; intensifying exploitation of this group
464 decrease the average TL of the community, and the reverse occurs when Nile perch
465 increases following a reduction in fishing. However, the sensitivity of the indicator is very
466 low, which is caused by the large biomass of Silver cyprinid (a high-biomass pelagic
467 zooplanktivore) that dampens the change in MTL_{biomass} .

468 Under the 'fishing down' the food web hypothesis [30], TL of catch is expected to
469 decline in response to fishing due to the preferential depletion of high-trophic-level species.
470 In EwE, the direction of change of this indicator with respect to increased exploitation of Nile
471 perch (top predator) was consistent with the 'fishing down' hypothesis. In Atlantis, however,
472 TL of catch increased with increasing fishing pressure on Nile perch. Whereas this seems
473 counter-intuitive, it is not entirely surprising because the increase in catches of the predator
474 in the short-term can increase TL of the catch, which seems to be the case with the scenario
475 of increasing exploitation on Nile perch.

476 By examining the feeding guilds, we expected to observe a fishing-driven decline in
477 the piscivore guild under the scenario of increased fishing pressure on Nile perch. In turn, we
478 expected this to cause an increase in the planktivore guild, which are major prey for the
479 piscivore guild. Whereas results of EwE were consistent with this expectation, Atlantis
480 predicted the opposite. The piscivorous to planktivorous ratio increased (substantially) in
481 Atlantis even under heavy exploitation of Nile perch. This can be attributed to the rapid
482 decline in Silver cyprinid, a dominant pelagic planktivore, possibly due to competition with
483 haplochromines following predation release from intensively fished Nile perch. The rapid
484 decline of Silver cyprinid cancels out any effect of small decline in Nile perch because when
485 this indicator is calculated without the Silver cyprinid under the same scenario, the results
486 are consistent with the above expectation.

487

488 **Conclusions**

489 The overall model structure and formulation can provide similar qualitative
490 predictions (direction of change), especially for groups with similar trophic interactions,
491 although considerable variations may arise due to the differences in the strength of the
492 aggregate multispecies interactions between species and models. Whereas qualitative
493 model results depend on feeding interactions, model sensitivity to perturbation and the
494 resulting magnitude of change in individual group biomasses are driven both by modelled
495 processes and strength of the feeding dependencies. Availability of data for model
496 parameterization and calibration also plays a role in the consistency of results across models.
497 For example, Nile perch, Nile tilapia, and haplochromines (whose qualitative trends across
498 models were all consistent in the scenarios tested) have been widely studied and
499 documented, given their ecological and economic importance. The attention given to these
500 species means that they are less likely to be affected by data uncertainty compared to
501 lesser-studied species. Therefore, with more information and data, and comparable
502 representation of trophic interactions across models, ecosystem models with distinct
503 structure and formulation can easily give consistent policy evaluations for most of biological
504 groups.

505 In the Lake Victoria Atlantis model, the strengths of diet dependencies exert bigger
506 influence on model outcomes than any of the 'delaying' ecosystem features, such as age-
507 and size structure or reproductive behaviour, which are common to Atlantis models. This is
508 in regard to the higher sensitivity of Atlantis model to fishing pressure scenarios than EwE.
509 Therefore, confidence in results from multiple models can be greatly enhanced by improving

510 the accuracy of diet data through rigorous diet studies, especially for the less studied groups,
511 and accurate definition of biological groups across models.

512 Ecosystem-level indicators are less sensitive to model choice compared to biomass of
513 individual model groups; therefore, the actual ecosystem impacts of fishing from changes in
514 these aggregated indicators needs to be interpreted with caution. This is true especially
515 where the magnitude of change in indicator is small, as seen in this study, which could arise
516 from opposite trends in several biological groups cancelling each other. Biomass information
517 at the species level is still important for interpreting dynamics in ecosystem response to
518 fishing. Even where models seem to give diverging results, this evaluation provides an
519 account of possible changes from reference state and points to areas where different model
520 considerations may lead to varying predictions, which can be used to improve the models.

521

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525

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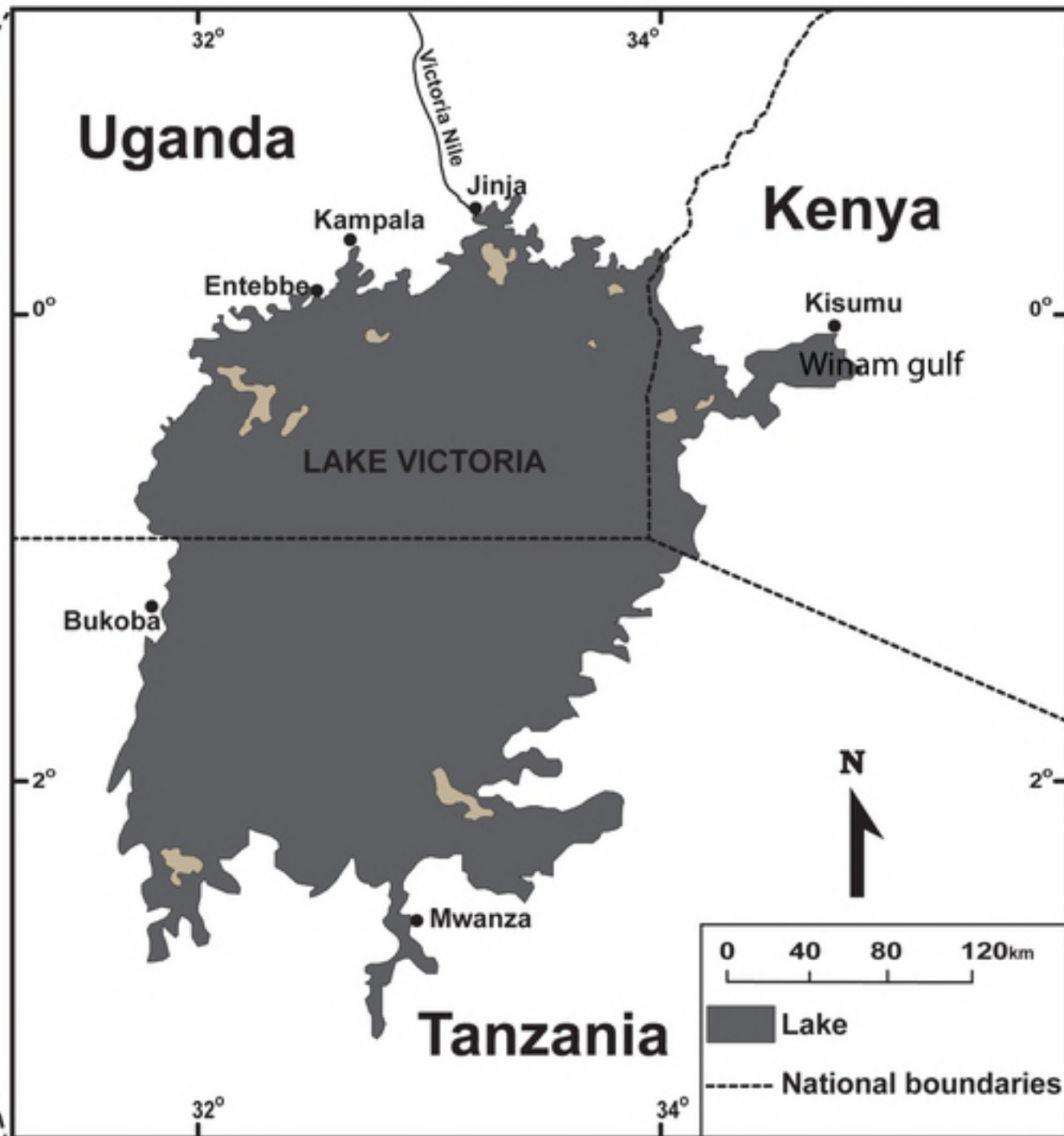
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Ecopath

- Biomass model
- Reference year 1960
- Fixed diet matrix
- Zero dimensions

Calibration

- Foraging vulnerability
- Catch time series forcing

Ecopath with Ecosim

- Hindcasting biomass and catch: 1960-2015

Forward simulation: 20 years
2015 fishing pressure as baseline

Atlantis

- Age and size-structured population model
- Reference year 1958
- Diet preference matrix
- Three dimensions, polygonal model zones, multiple depth layers

Calibration

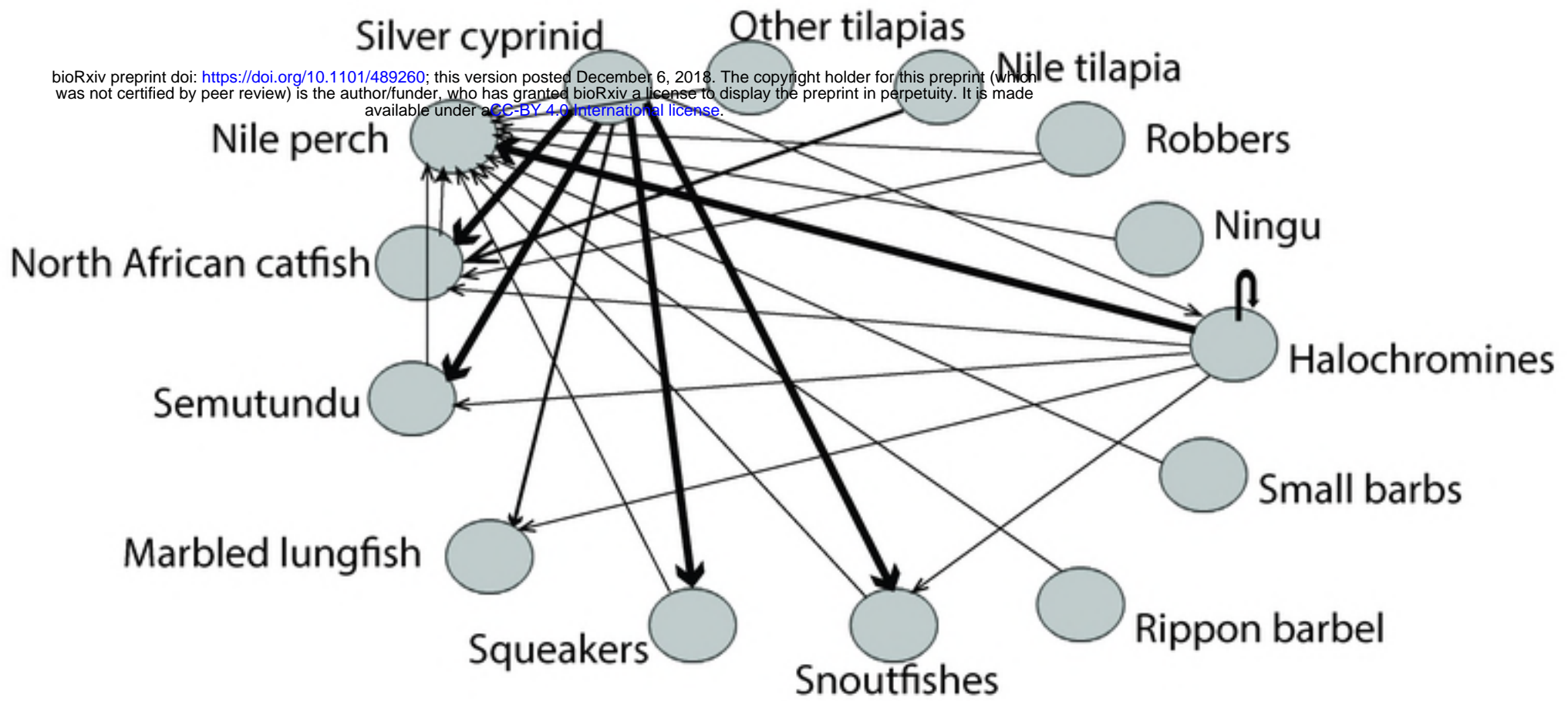
- Tracking age and weight at age of fish groups
- Catch time series fitting

Atlantis

- Hindcasting biomass and catch: 1958-2015

Forward simulation: 20 years
2015 fishing pressure as baseline

EWE



Atlantis

