



Operational, environmental, and resource productivity factors driving spatial distribution of gillnet and longline fishers targeting Nile-perch (*Lates niloticus*), Lake Victoria

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1 **Operational, environmental, and resource productivity factors driving spatial**
2 **distribution of gillnet and longline fishers targeting Nile-perch (*Lates niloticus*), Lake**
3 **Victoria.**

4

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13 **Abstract**

14 Operational and environmental factors limited available resource space of gillnet and longline
15 fishers targeting Nile perch in the Speke gulf and open lake of southern Lake Victoria and drove
16 their encounter rates with patches of fish resulting in gear specific distributional patterns.
17 Catch-rate patterns were similar by region and gear: large (>50cm) Nile-perch densities
18 increased over distance from homeport and deeper in the water column while small Nile perch
19 (<50cm) densities decreased. Effects of season, (setting) depth and region were present but
20 small and obscured by high variation in daily catch-rates and individual fisher strategies. Both
21 fisheries distributed themselves over the size-productivity spectrum of Nile perch but reacted

22 differently to patterns in size distribution of Nile perch: gillnetters focused more on numbers of
23 productive juveniles between 30-60cm at on average 5km distance (59min travel time) from
24 homeport and longliners on larger sized 40-80cm Nile perch deeper in the water column at
25 7km (108min). Sampled fishers likely were representative of most of the Nile perch fisheries.
26 If so, this means that fishing pressure is mainly exerted on nearshore lake areas, and more
27 lightly fished offshore areas then may act as a refuge for adult Nile perch. Total catch-rates by
28 gear were generally equalized over the resource space, increasing slightly with distance from
29 homeport, according to ideal free distribution predictions. Nile perch fishers on Lake Victoria
30 appear to distribute themselves according to the underlying productivity distribution of the
31 resource within the constraints of their available resource space.

32 **Keywords**

33 Effort allocation; resource space; Ideal Free Distribution; size-productivity spectrum; patch
34 density; encounter rate.

35

36 Introduction

37 The distribution of fishers over a resource is determined by operational and observational
38 constraints of individual operations as well as environmental factors and resource productivity
39 features. In small-scale fisheries, characterized by limited investment in assets such as
40 vessels, gears and other technology, the resource space over which fishers can allocate their
41 effort is bounded. The type of propulsion used, gear setting demands, and on-board
42 preservation all limit their action radius. Fishers furthermore generally prefer fishing close to
43 their homeports (Salas and Gaertner 2004) as operational costs (time, money) are minimized.
44 Seasonal weather patterns, associated stratification and other environmental patterns affect
45 encounter rates with patches of fish and thus co-determine the effort allocation options of
46 fishers. Nevertheless, it can be expected that over the long run, and averaged over their
47 resource space, fishers will distribute themselves over the available resources within that
48 space such that catch-rates reflect the underlying dynamics in the distribution of the resource.
49 This is a prediction of the Ideal Free Distribution (IFD) theory that describes how predators
50 distribute themselves over a prey resource, where the number of predators at a given location
51 is proportional to the rate at which prey are produced at that location, while all individual
52 predators obtain the same prey intake rate (Kacelnik et al. 1992). IFD theory has been used to
53 predict that effort will be distributed spatially over a fished resource in such a way that catch
54 per unit of effort is equalized over all locations (Gillis et al. 1993, Gillis and van der Lee 2012).
55 Concentration of fishing effort in a resource space creates crowding, local competition and,
56 potentially, interference competition and induce redistribution of effort over larger spaces within
57 the operational constraints of small-scale fishers (Gillis 2003, Gillis et al. 1993, Poos and
58 Rijnsdorp 2007) resulting in such equalising of catch-rates.

59 The IFD argument can be extended to the selection of sizes of the available resource in
60 relation to their productivity. When unconstrained by strong preferences of sizes and species

61 or externally imposed size-regulations, individual fishers' attempts to optimize their CPUE
62 implies that fishing effort will be distributed in proportion to the productivity of the resource
63 (Plank et al. 2017), leading to the emergence of balanced harvesting (Garcia et al. 2012, Garcia
64 et al. 2016). Such distribution over the size spectrum over the resource has been observed in
65 small scale freshwater fisheries in Africa (Kolding et al. 2015, Kolding et al. 2016, Kolding and
66 Zwieten 2011). A shift to target smaller sizes of a resource with increased effort both within
67 populations of species and in a multispecies fishery is a well-known and common phenomenon
68 in small-scale fisheries (van Zwieten et al. 2003, Welcomme 1999). This shift is also an
69 outcome of harvesting over a size-spectrum leading to balanced harvesting described by Plank
70 et. al (2017) as smaller sized fish generally are also more productive. This result implies that
71 under unconstrained conditions the spatial allocation of effort will reflect the distribution of the
72 productivity of a resource, meaning that, within their resource space, fishers can be expected
73 to fish at locations where renewal rates are highest. It follows that, in the long run and averaged
74 over their available resource space, signals from fishing outcomes will lead fishers to distribute
75 themselves according to the underlying productivity distribution of the resource.

76 We focus on Nile perch from southern Lake Victoria targeted by small-scale gillnet and
77 longline fishers. Nile perch is one of the commercially targeted species in Lake Victoria
78 contributing on average 240,000 ton per year or up to 30% of the total landings (Mkumbo and
79 Marshall 2015). After introduction, the species initially dominated in shallower waters, but over
80 time the abundance of larger fish in deeper waters appeared to be increasing and Nile perch
81 is now found at all depths (Goudswaard et al. 2008, van Zwieten et al. 2016). Adult Nile perch
82 (≥ 54 cm male; ≥ 76 cm female, Hughes (1992), Mkumbo (2007)) are distributed over all habitats
83 while juveniles are more dominant in shallower coastal waters (Katunzi et al. 2006). Nile perch
84 densities change seasonally in relation to stratification patterns: during the stratified season
85 (November to March) densities increase in upper water layers, while during the windy mixing

86 season (June to October) higher densities are encountered in deeper water (Taabu-Munyaho
87 et al. 2013).

88 The main gears targeting Nile perch are gillnets and longlines operated from wooden
89 vessels of 5-11m. These vessels are propelled by paddles (60%), small outboard engines
90 (32%) and by sail (8%) (Anonymous 2015, 2017). Fishing in Lake Victoria takes place from
91 many landing sites along the shore. Most fishing operations are day trips, with limited use of
92 ice, further limiting the potential action radius of a fishing trip. Nile perch fisheries are regulated
93 through a minimum mesh (6 inches, 152 mm stretched mesh) and a recommended hook-size
94 (<10), next to a minimum landing size. However, enforcement of these regulations is weak
95 (Medard Ntara 2015). While the primary market for Nile perch are the fish factories that are
96 only allowed to buy Nile perch of ≥ 50 cm total length, a large regional market for smoked
97 juvenile Nile perch exists (Medard Ntara 2015).

98 Probabilities of catching large Nile perch are expected to be higher further from the shore
99 (Schofield and Chapman 1999). As numbers of fishers have increased (Mkumbo and Marshall
100 2015), they increasingly compete over the same nearshore resources suggesting that, as a
101 result of this competition and according to IFD predictions, distribution of effort will be extended
102 to deeper waters further from the shore. This also will depend on the productivity and spatial
103 patterns of the different size-classes of Nile perch. As productivity of Nile perch decreases with
104 size, spatial separation of size classes should lead to spatially differentiated production
105 patterns (Natugonza et al. 2016).

106 Given the size-selectivity characteristics of their gears, fishers using longlines or gillnets
107 are expected to target different size classes of the Nile perch stock that are in part spatially
108 separated (Chitamwebwa et al. 2009, Msuku et al. 2011). A further differentiation in spatial
109 allocation may be on setting depths of different gears. While Nile perch is found all over the
110 water column highest densities are found in the upper 20m of water in nearshore shallow

111 regions while in coastal and deep waters distribution is more even or bimodal with a deep water
112 peak at 30-40m depth (Cornelissen et al. 2015, Taabu-Munyaho et al. 2013). Reported
113 distributional patterns over the water column are derived from aggregated lake wide acoustic
114 observations, a scale much larger than the individual scales of operation of Nile perch fishers.
115 Such generalized patterns will be obscured for an individual fisher when variability in encounter
116 rates of patches of fish is high due to locality, seasonal environmental effects and species-
117 specific distributional characteristics (van Densen 2001).

118 The focus of this paper is to better understand how fisher effort is allocated spatially and
119 temporally resulting from fishing operational factors as well as fish presence, fish density and
120 environmental factors. Operational factors limit the resource space of fishers and drive the
121 encounter rates with fish densities leading to a specific distribution of the fishery over a
122 resource which are expected to follow IFD predictions on effort distribution over its size-
123 productivity spectrum. We will examine (1) the distributional patterns of longline and gillnet
124 fishers targeting Nile perch in Lake Victoria in two contrasting regions (gulf and open lake
125 region); (2) the operational and environmental factors driving encounter rates and observed
126 patch densities of different size classes of Nile perch; (3) compare the relative biomass
127 estimates of Nile perch with what is known about the patterns in spatial distribution of different
128 size classes of Nile perch; and (4) discuss the resulting variability in spatial distribution and
129 catch rate patterns of the two fisheries in the light of the IFD predictions on distribution over
130 the size-productivity spectrum of a resource. Effort allocations studies (Hilborn and Ledbetter
131 1985) in small-scale and artisanal fisheries in the tropical marine realm are scarce (Pet-Soede
132 et al. 2001, van Oostenbrugge et al. 2001) and to our knowledge are non-existent for tropical
133 freshwater systems.

134

135

136 **Materials and methods**

137 *Study Area*

138 Lake Victoria is the largest freshwater fishery in the world with close to 1 million ton of
139 fish harvested annually (Kolding et al. 2013). This study was conducted in the southern part of
140 the lake in the territorial waters of Tanzania where around 49% of the fishers are found
141 (Anonymous 2015, 2017). Four landing sites in two regions were selected based on their
142 locations along the shallower Speke gulf and the deeper open lake area, and on our knowledge
143 of the fishery gained in discussion with staff of the Tanzanian Fisheries Research Institute and
144 scientists who have worked in the region. The sites were likely to be representative of other
145 landing sites in southern Lake Victoria: Kayenze and Muluseni were located along the Speke
146 gulf (gulf region) and Muhula and Kome-Mchangani were facing the open lake (open lake
147 region) (Fig. 1; Table 1). The gulf region ranges down to 40m depth but is for the most part
148 <25m deep; the open lake region is characterized by steep descending slopes down to 57m
149 depth. As fishers operate from both shores of the gulf, fishing areas were more likely to overlap
150 compared to the open lake fisheries. While the number of fishers per km shore line may be the
151 same, fishing pressure per unit area was expected to be higher in the gulf region. Of the villages
152 chosen, Kayenze is more developed in terms of landing facilities and is accessible by an all-
153 weather road. However, fishers in all four villages had daily access to traders and weighing
154 scales, and all had fisheries officers responsible for enumeration and levy collection. All four
155 villages had substantial longline and gillnets fisheries.

156 In the southern part of Lake Victoria three seasons are distinguished, during which the
157 lake experience winds of different strength. During the long rains from February-May, there is
158 less or no wind resulting in stratification of the lake and the build-up of deep water hypoxia and
159 anoxia that affects the available habitat for hypoxia-intolerant species like Nile perch (Schofield

160 and Chapman 2000). During the dry period from June-August the lake experiences strong
161 winds that mix up the lake water (Mugidde et al. 2005, Njiru et al. 2011). The short rains from
162 October-January is a transition period from the dry (mixed) to the wet (stratified) season. The
163 pronounced impact of the seasonal wind regime on the mixing of the lake waters are likely to
164 influence size and density distributions of Nile perch.

165 *Logbooks*

166 Ten gillnet fishers and nine longline fishers targeting Nile perch and operating from four
167 fishing locations were trained to record in logbooks their daily operations and resulting catches
168 using their own fishing gear in logbooks as well as in the use of a handheld GPS device (Table
169 1). Training was done in a series of interactive sessions where an initial logbook was tested by
170 fishers in the field and, after discussion with them, adjusted to a final version (Ticheler et al.
171 1998) (Appendix 1). Fishers were selected based on experience in Nile perch fishing, type of
172 gear used, landing site, and willingness to participate in the research project. The selected
173 fishers were representative of the majority of the fishers on the lake in that they (1) targeted
174 Nile perch as over half number of fishers (116,000 = 52%) on lake Victoria do (Anonymous
175 2017); (2) used either gillnets or longlines, where almost 100% of longlines and 85% of the
176 gillnets used in the lake are reported to target Nile perch. In 2010, 84% of the hooks used in
177 longlining were small hooks with sizes >10 (that is numbers 11, 12 and 13), while 90% of the
178 meshes used were within the range of 4-8 inches (101–203 mm stretched mesh) (Fig. 2). Lastly
179 (3), the selected fishers used so called “Sesse boats”, planked vessels that are either propelled
180 by paddle and sail (67% of the in total 77000 vessels used on the lake) or with outboard engines
181 of 9.9hp or 15hp (34%) (Anonymous 2015, 2017).

182 Furthermore, to examine representativeness of the selected fishers, we interviewed 49
183 gillnet fishers and 58 longline fishers from Buhama (Kome-Mchangani), Kayenze , Muhula and

184 Muluseni on gear use, effort allocation (travel time, fishing time, seasonality, fishing grounds),
185 catch, average cost of fishing and reasoning behind location choices in time and space. In
186 addition, in each village two focus group discussions were held, one for longline and one for
187 gillnet fishers attended by a minimum of 7 fishers each, to verify insights obtained through the
188 individual interviews and the training of fishermen using logbooks.

189 The logbooks distributed to the fishers focused on catch characteristics and operational
190 factors. The total catch per trip in number of fish and weight (kg) was recorded in two size
191 categories of Nile perch, $<50\text{cm}$ (small Nile perch) and $\geq 50\text{cm}$ (large Nile perch) together with
192 the catch in number and weight for other species. For each category, it was noted whether the
193 catch was sold or consumed. With regard to operational factors fishers recorded their mode of
194 propulsion; travel time from the homeport to the fishing location and back; soak-time (start and
195 end time); fishing location by name and GPS coordinate; setting depth of the gear; depth of
196 location; gillnet fishers recorded the number and size of gillnets (length by depth) used by
197 mesh-size; longline fishers recorded the hook-size, number of hooks and type of bait. Lastly,
198 reasons for not going out fishing on a day were reported. Fishers recorded data daily and
199 logbooks were collected from them monthly for data entry and quality checking. A post-hoc
200 check on the quality of the data was carried out by examining the frequency distributions of the
201 catch records that are expected to be close to log-normal. As it cannot be expected that fishers
202 are able to deliberately record approximately log-normal distributed data when noting catches
203 on a day-to-day basis, substantial deviations from log-normality are strong evidence for
204 inventing data (Ticheler et al. 1998). We gave fishers monthly feedback on their performance
205 and a fee if they had performed well. All fishers used their own gears. Each set of gillnets used
206 were recorded by their mesh-size. Sizes of gear were recorded by measuring the length and
207 depth of gillnet panels of different mesh-sizes, and a surface area per each panel (m^2) was

208 calculated. For longlines the sizes and number of hooks used were recorded each day in the
209 logbook.

210 Data were collected for 10 months from October 2010 to July 2011, capturing the main
211 periods in lake stratification. Months were categorized based on the rain pattern, with October
212 2010 to January 2011 as short rain season, February to April 2011 as long rain season and
213 May to July 2011 as dry season.

214

215 ***Data treatment and statistical analysis.***

216 *Data exploration*

217 Data exploration was carried out according to Zuur et al. (2010), in particular by plotting
218 the different response and explanatory variables to detect outliers and examine collinearity
219 between explanatory variables, determine the statistical distribution of the data as well as
220 checking for zero catches (166 – 171)s.

221 *Representativeness of logbook fishers*

222 Representativeness of the selected logbook fishers was analysed by comparing their
223 daily reports of travel time, as a proxy for distance travelled and spatial effort allocation, with
224 those of 107 gillnet and longline fishers who in interviews reported the travel time of their last
225 two fishing operations. Travel time for each of the two groups separately was then examined
226 in a MANOVA with propulsion type and gear-type as explanatory factors and outcomes
227 compared.

228 *Finding an unbiased catch rate and standardization*

229 Standardization of observed daily total catch-rates per trip was done by adjusting for
230 sizes of gillnet and numbers of hooks, hook-size, bait type, and soak-time of both gear-types.

231 Total observed catch-rates were the sum of the weights and numbers of the size categories
 232 small and large Nile perch: there were no zero daily total catches of Nile perch. For longlines
 233 a multiple regression analysis of the observed catch-rates was carried out with bait and hook-
 234 size, the number of hooks and soak-time – the time the hooks were in the water – as
 235 explanatory variables:

$$236 \log_{10}(CPUE_{ijk}^{obs}) = a + \beta_1 \log_{10}(N_i) + \beta_2 \log_{10}(S_i) + b_j + h_k + (b * h)_{jk} + \epsilon_{ijk} \quad (1)$$

$$237 \epsilon_{ijk} \sim \text{iid}(N(0, \sigma^2),$$

238 where, $CPUE_{ijk}^{obs}$ = observed CPUE in number of fish or weight (kg) on the i -th fishing trip, which
 239 is classified by the bait type j and the hook-size k used on that trip, and where N_i , number of
 240 hooks and S_i , soak-time, are the continuous predictor variables for that trip. The model
 241 coefficients to be estimated are the intercept a , the slopes β_z , for the continuous variables and
 242 the effects of the levels of the categorical variables bait type (b_i) and hook-size (h_k) and their
 243 interaction. The errors are assumed independent and normally distributed with average 0 and
 244 variance σ^2 . Two categories of hook-sizes were defined: small (13) and large (11 and 12). Bait
 245 had four categories (haplochromines, dagaa, *Clarias* and *Synodontis*). Model (1) had “small
 246 hooks (13)” and “*Synodontis*” as baselines.

247 For gillnets, we examined whether there was a consistent use of specific mesh-sizes
 248 at different lake depths, setting depths or by region. Although mesh-size would be an important
 249 predictor of fish size caught, it was not possible to associate mesh-sizes with size categories
 250 of fish, as these were not reported in relation to the mesh-sizes in which they were caught.
 251 Therefore, we used the total surface area of the nets used per day - the sum of the surface
 252 area of each mesh-size used on a trip - to standardise catch rates. Then for gillnets a multiple

253 regression analysis of the observed catch-rates was carried out with soak-time and the surface
 254 area of the gillnet as explanatory variables.

$$255 \log_{10}(CPUE_i^{obs}) = a + \beta_1 \log_{10}(N_i) + \beta_2 \log_{10}(S_i) + \epsilon_i \quad (2)$$

$$256 \epsilon_i \sim \text{iid}(N(0, \sigma^2))$$

257 where, N_i , size of net, and S_i , soak-time are the continuous predictor variables used by a fisher
 258 on the i -th fishing trip. Other symbols as previous. A standardized daily catch rate $CPUE^{st}$ was
 259 subsequently calculated with appropriate corrections for bait-type and hook-size in case of
 260 longlines (Tsehaye 2007) as:

$$261 \quad CPUE_i^{st} = \left(CPUE_i^{obs} \left(\frac{\bar{N}}{N_i} \right)^{\beta_2} \left(\frac{\bar{S}}{S_i} \right)^{\beta_1} \right) * 10^{-(b_j + h_k + (bh)_{jk})_i} \quad (2)$$

262 where, $CPUE_i^{st}$ = standardized catch rate on the i -th trip in weight (kg) or number of fish per
 263 standard trip duration and gear size, $CPUE_i^{obs}$ = observed catch rate in weight or number of fish
 264 on the i -th trip, \bar{N} = median net size or average number of hooks and \bar{S} = average soak-time
 265 over all fishers and days fished by gear-type, and where the term $(b_j + h_k + (bh)_{jk})_i$ adjust for
 266 the effects of bait-type (b_j) hooksize (h_k) and the interaction between bait-type and hooksize.
 267 Other symbols are as previous.

268 While there were no trips with no catch of Nile perch, the two size categories reported
 269 in the logbooks were not always caught together on each trip. Therefore, zero daily catches
 270 had to be accounted for when analyzing catch-rates by size-category. When catch-rates need
 271 to be log-transformed to obtain approximate normality in model residuals, often a low number
 272 is added to remove the zeroes (see e.g. (Deroba and Bence 2009)). However, because zero
 273 daily catches contain information on the encountered presence of Nile perch we opted to retain
 274 them and use a hurdle model to examine factors that determine the relative densities as
 275 encounter rate (P_c) times patch density ($CPUE_{st}$). The encounter rate (P_c) was defined as the

276 probability of catch per trip of small or large Nile perch, and was determined by analyzing the
 277 presence/absence of a catch through a binary logistic model; patch density ($CPUE_{st}$) was
 278 defined as the weight (kg) or number of the positive catch per trip and was examined by
 279 analyzing the positive catch-rates. A multiplication of the two yielded the catch-rates ($CPUE_{ad}$
 280 $= P_c \times CPUE_{st}$) (kg/trip).

281

282 *Encounter rates: factors determining the probability of catch*

283 Here and in the next section we present the general full model that includes effects for
 284 all categorical and continuous variables and their interactions. As will be described we adopted
 285 a model selection process that evaluated alternative models that included only a subset of the
 286 effects. The occurrence of a positive catch of Nile perch is modeled as coming from a binomial
 287 distribution with probability of a positive catch of Nile perch P_c . We analyzed the observed
 288 positive occurrences using a generalized linear mixed modelling approach with a logit-link
 289 function:

$$290 \log\left(\frac{P_c}{1-P_c}\right)_{ijk} = \mu + \sum_{l=1}^z \gamma(B_{ijkl}) + \sum_{m=1}^n \beta_m X_{imjk} + \text{two-way interactions} + \varepsilon_i \quad (3)$$

$$291 \varepsilon_i \sim \text{iid}(N(0, \sigma_a^2))$$

292 where i represents fisher or the combination of fisher and fish size category, j is trip, k is size
 293 category, μ is intercept, B_{ijkl} is the value of the l -th categorical variable for category i , trip j and
 294 size k , $\gamma(B_{ijkl})$ is the coefficient for that categorical variable, β_m is the coefficient of the m -th
 295 continuous variable, X_{mjk} is the value of the of the m -th continuous variable for trip j , and size
 296 k . The number of categorical and continuous variables included in the model are z and n
 297 respectively. Continuous X variables for both gillnets and longlines are distance from homeport
 298 to fishing location (km) and setting depth (m). Categorical variables are region (gulf, open lake),
 299 season (dry, long, short) and Nile perch size categories (<50cm, \geq 50cm). To take account of

300 longline characteristics, the continuous variables \log_{10} (hook number), \log_{10} (soak-time) and the
301 categorical variables bait (*Clarias*, haplochromines, dagaa, *Synodontis*) and hook-size (large,
302 small) were added to the longline model. For the gillnet model these were \log_{10} (net size) and
303 \log_{10} (soak-time). Only two-way interactions between all the variables were examined. The error
304 ε_i is assumed independent and normally distributed with average zero and variance σ_a^2 .

305 Fisher or the interaction between fisher \times size was modelled as a random effect (random
306 intercept), as clustering of sampled data can be expected due to differences in fishers skills
307 and operational characteristics not accounted for by the fixed effect model. As fishers appeared
308 to make different choices in use of meshes or hook-sizes this led to the examination of the
309 interaction between fisher \times size as random effect. Final model choice was based on several
310 criteria: the most likely model was obtained by backward selection of variables in a full random
311 intercept model with all fixed effects (variables and their two way-interactions) by minimizing
312 the Akaike Information Criterion (AIC). The size of the decrease in AIC also was used to
313 compare a random intercept model with no fixed effects to an intercept only model. The
314 significance of the final mixed model was compared to a random intercept model with no fixed
315 effects through a Likelihood Ratio Test (deviance test). Model fit was further examined through
316 the dispersion parameter (χ^2/df). To overcome overdispersion different random intercepts
317 including bait and size of hooks were tested always with fisher or fisher \times size included. For the
318 final model we used the interaction between fisher \times size of Nile perch as random intercept as
319 this led to a dispersion parameter close to 1. The contribution of the random effect to the total
320 variability in P_c was tested by examining the Intraclass Correlation Coefficient (ICC) calculated
321 as $ICC = \theta / (\theta + 3.29)$ where θ = estimate of the covariance parameter (random intercept)
322 (O'Connell et al. 2008). The significance of the estimate of the covariance parameter was
323 tested using a Wald Z test.

324 Odds ratio's – i.e. the ratio between the odds $p_1/(1-p_1)$ of encountering Nile perch at
 325 one set of factors against the odds $p_2/(1-p_2)$ of encountering Nile perch at a contrasting set,
 326 were calculated to make broad comparisons over factors season, region, size and bait. To do
 327 so the continuous variables distance and setting depth were fixed at respectively 5 km, 4 m
 328 depth and 20 km, 15 m depth for gillnets and for median net size. For longlines distance and
 329 setting-depth were fixed at 7 km, 4 m depth and 20 km, 15 m depth respectively, average
 330 number of hooks and *Synodontis* as bait.

331 *Patch densities: factors determining positive standardized catch-rates*

332 The standardized positive catch rates of Nile perch ($CPUE^{st}$) are log-normally
 333 distributed and are modeled after log-transformation as coming from Gaussian distribution. We
 334 analyzed the observed positive catch rates using a generalized linear mixed modelling
 335 approach with an identity link function:

336
$$\log_{10}(CPUE_{ijk}^{st}) = \mu + \sum_{l=1}^z \gamma(B_{ijkl}) + \sum_{m=1}^n \beta_m X_{mijk} + \text{two-way interactions} + \varepsilon_i \quad (5)$$

337
$$\varepsilon_i \sim \text{iid}(N(0, \sigma_a^2))$$

338 where, $CPUE_{ijk}^{st}$ is the standardized positive catch rate of fisher i by size category k on the j -th
 339 fishing day in weight (kg) or number of fish. Other effects are defined as for equation 4 above,
 340 excluding the effects of bait type, soak-time, number of hooks, hook-size and net size as these
 341 are accounted for in the standardisation step (model 3). Fisher was included as a random
 342 effect. The choice of the random effect was examined by the AIC criterion by comparing an
 343 intercept only model with a fixed effect model with no random effects included. A range of
 344 models was examined through backward selection of the full model based on the AIC criterion,
 345 and significance tested on the restricted log-likelihood ratio. The contribution of the random
 346 effect to the total variability in the probability of catching Nile perch was tested by examining
 347 the Intraclass Correlation Coefficient (ICC) calculated as $ICC = \theta / (\theta + \theta_{res})$ where θ = estimate

348 of the covariance parameter (intercept) and θ_{res} the residual variability. The significance of the
349 estimate of the covariance intercept parameter was tested using a Wald Z test. As individual
350 fishers can be expected to return to sites with successful catches auto-correlation can be
351 expected to violate the assumption of independence. However, it is less likely that daily catches
352 between fishers are correlated, reducing the impact of auto-correlation when modelling over
353 all data. We checked for the existence of such correlation between fishers in daily catches over
354 successive days which was not the case.

355 *Relative densities and individual average size of Nile perch in the catch*

356 Relative densities were calculated by multiplying the probability of catch and the
357 positive standardized catch-rates as ($CPUE_{ad} = P_c \times CPUE_{st}$) in weight and numbers of fish.
358 We provide some sense of the length of fish in the catch by calculating the length of a fish from
359 this average weight. By necessity, our equation for length given weight (in gram) is the inverse
360 function $L=(W/0.0042)^{(1/3.26)}$ based on a regression of log-length on log-weight with parameters
361 taken from the W-L relation for Nile perch (Kayanda 2012). This is reasonable given the
362 typically tight relationship between weight and length. To determine the average size of Nile
363 perch targeted by fishers using the two gears we divided the $CPUE_{ad}(\text{weight})/CPUE_{ad}(\text{number})$
364 and examined the results graphically over the relevant explanatory variables.

365 All statistical models were carried out using SAS/STAT software version 9.2 of the SAS
366 system for Windows using the GLM and GLIMMIX procedures.

367

368 **Results**

369 *Descriptive results*

370 Out of the 19 trained fishers who participated in this study, four fishers (2 gillnet and 2
371 longline) gave incomplete data and were dropped from the analysis. The remaining 15 fishers
372 were consistent in writing day to day operations and catch data, including GPS positions. The
373 consolidated database had a total of 3100 fishing trips (1703 gillnet;1397 longline) and 253
374 days of no fishing (141 gillnet;112 longline) (Table 1). Both gears predominantly caught Nile
375 perch: a total of 748 non-Nile perch catches were found (720 gillnet; 28 longline) representing
376 respectively 11% and 0.16% of the total catch weight. Bycatch consisted in terms of weight of
377 0.01% *Alestes*, 7.3% *Tilapia*, 0.8% *Mormyrus*, 1.0% *Bagrus*, 0.7% *Protopterus*, 0.3% *Clarias*
378 spp and 0.1% *Synodontis* spp in gillnets, and 0.15% *Bagrus*, <0.01% *Tilapia* and <0.01%
379 *Haplochromines* in longlines. These data were not further considered. No-fishing days
380 occurred because of operational (gear was stolen, boat burst, gear repair and no bait),
381 environmental (heavy rain, strong winds), personal (illness, resting and holidays, village
382 meetings, elections and travel) and economical (no fish) reasons.

383 The average (sd) total gillnet size used was 15000 (12000) m² (median 12000 m²) with
384 panels of mesh-sizes ranging from 4" to 8". Longlines were equipped with 800 (130) hooks,
385 with hook-sizes 11, 12 and 13. Individual fishers often changed nets and lines between trips
386 resulting in different total net sizes and hook numbers as well as mesh-sizes and hook-sizes
387 per trip. In the gulf area mesh-sizes from 4-7" were used in about equal proportion (~18%) of
388 the time while 8" mesh-sizes were used in around 8% of the trips; in the open lake area 61%
389 of mesh-sizes used were 5" and 6", while mesh-sizes 4", 5", 7.5" and 8" were used in about
390 equal proportion (app. 10%) of the trips (Fig. 3, top).

391 Small hook-sizes (13) were dominant in both regions, but more so in the open lake
392 region, while the largest hook-size (11) only was used in the gulf region. All mesh-sizes and
393 hook-sizes were used at all distances from the homeport. Larger meshes and hook-sizes
394 tended to be used further offshore and small mesh-sizes in both regions and small hook-sizes

395 in the gulf region were used more often nearshore up to approximately 5 km (Fig. 3, bottom).
396 In the open lake area on average smaller hook-sizes were used compared to the gulf with no
397 trend in hook-size over distance from the homeport. In subsequent catch-rate analyses hook-
398 sizes were categorised as small (13) and large (11 and 12), as these groups differed
399 significantly in total catch weight ($F_{1,1312} = 44.67$, $P < 0.001$, $r^2 = 0.03$). Soak-time for gillnets
400 ranged from 4-15 hr with an average (sd) of 10 (2) hr and longline 2-13 hr with an average of
401 6 (1) hr.

402 *Standardisation of observed catch-rates*

403 Haplochromines, Dagaa, *Synodontis*, and *Clarias* were the main bait types used in
404 longline fishing. The operational factors bait type, hook-size and their interaction all had a
405 significant effect on the observed catch-rates both for weight ($F_{1312,7} = 28.8$, $p < 0.001$, $r^2 = 0.13$)
406 and number ($F_{1312,7} = 40.0$, $P < 0.001$, $r^2 = 0.17$). Bait types *Clarias* and *Synodontis* had a higher
407 CPUE in terms of weight both for small and large hook-sizes compared to Haplochromines and
408 Dagaa, while Haplochromines and to a lesser extent *Clarias* on average caught larger numbers
409 of Nile perch. Average Nile perch sizes caught for all bait-types except *Synodontis* ranged
410 between 0.7 kg (dagaa, large hook-size) to 2.3 kg (*Clarias*, large hook-size) with an average
411 of 1.5 kg over these bait types. *Synodontis* bait resulted in an average individual fish size of 3
412 kg and 8.8 kg for small and large hook-sizes respectively (Fig. 4).

413 The operational factors net size, number of hooks and soak-time all had a significant
414 effect on the size of the catch per trip expressed in weight of fish. Net size and hook-number
415 did not have a significant effect on observed catch per trip in number; only soak-time was
416 significant (Table 2). For both weight and number of Nile perch catch per trip for gillnets were
417 standardized to the median size of a net of 12000 m² and a soak-time of 10 hr; for longlines

418 catch per trip in weight was standardized to 800 hooks and a soak-time of 6 hr according to
419 model (3) with parameter estimates as in Table 2.

420 Average daily standardized catch-rates of Nile perch ranged between 17-32 kg.day⁻¹ and
421 15-25 fish for gillnets; and 34-40 kg.day⁻¹ (10-18 fish.day⁻¹) for longlines. Variation in
422 standardized daily catch-rates in gillnets and longlines was high on average, both in weight
423 (CV=68% and 72% respectively) and number (CV=67% and 83%) (Table 1). Gillnet fishers
424 caught less large (≥ 50 cm) Nile perch (median=10 trip⁻¹) compared to longlines (23 trip⁻¹) and
425 around the same number of small Nile perch (10 trip⁻¹). The weight of small Nile perch caught
426 was higher for gillnets (10 kg.trip⁻¹) than for longlines (7 kg.trip⁻¹). In contrast, the weight of
427 large Nile perch caught by longlines (23 kg.trip⁻¹) was larger than those caught by gillnets (10
428 kg.trip⁻¹) (Table 3), suggesting that long-liners focus more on larger sizes of Nile perch than
429 gillnetters.

430 *Resource space*

431 The resource space of gillnet and longline fishers overlapped but on average gillnet fishers
432 fished closer to the shore than longline fishers while both appeared to fish over the same range.
433 The distance travelled daily from a homeport to a fishing location for gillnets ranged between
434 0.1-39.3 km and was on average (sd) 5 (5.6) km; longlines travelled within a range of 0.2-37.9
435 km with an average (sd) of 7 (5) km (Fig. 1). These calculations included gillnet fishers who
436 temporarily took residence in other areas in the lake and thus appeared to extend their
437 resource space to other areas. However, within those new locations, distances travelled to
438 fishing grounds from the new port fell within the same ranges of their original locations. Fishing
439 operations of fishers who normally operated from the sites around the Speke gulf but who
440 temporarily moved to open lake sites were, in subsequent analyses, considered as open lake
441 operations. Gillnet fishers with engines travelled 6 km (5%-95% range 1.7-21.4 km, N=864)

442 compared to gillnet fishers with paddles 2 km (5%-95% range 0.23-10.5 km, N=945). One of
443 the longline fishers with an engine who was dropped from further analyses travelled on average
444 5 km (2.3-10.9 km, N=17), suggesting a large overlap in resource space between propulsion
445 types in this fishery.

446 The travelling time to cover these distances, recorded daily by the fishers participating in
447 the logbook survey, appeared to be highly comparable to those of a group of 107 longline and
448 gillnet fishers, interviewed on their fishing activities, suggesting that the participating fishers
449 are representative for a large proportion of southern Lake Victoria fishers. The geometric
450 average, logbook recorded travelling time for gillnet fishers was 59 minutes (5%-95% range:
451 24-121 min). Average travelling time between gillnet fishers ranged between 36–83 min
452 indicating different fishing strategies, though within fisher variation was high ($F_{7,1637}=66.13$,
453 $p<0.001$, $r^2=0.22$). Longliners needed on average 108 min (51-188) to reach their fishing
454 grounds: average between fisher variation was much lower (77-120 min), but with only 16% of
455 the variation explained again with large within fisher variation ($F_{6,1289}=41.02$, $p<0.001$, $r^2=0.16$).
456 Fishers with engines travelled significantly shorter, 46 min (5%-95% range: 20-103 min), than
457 fishers with paddles and sails who used 70 min (30-135 min) to reach their fishing ground.
458 However, only 14% of the variation in travel time was explained by propulsion type
459 ($F_{1,1643}=259.51$, $p<0.001$, $r^2=0.14$). By comparison the interviewed group of fishers, who
460 reported their travelling time of their last two fishing days, travelled 75 min (90% range: 20-
461 180). Of this group, longliners travelled significantly longer (93 min) than gillnetters (57 min),
462 while no significant difference was found between fishers using engines (68 min) and paddles
463 and sail (90 min) ($F_{2,211}=14.99$, $p<0.001$, $r^2=0.12$; Type III error $p=0.11$ for type of propulsion
464 and $p<0.001$ for type of gear).

465 The group of interviewed fishers also were highly comparable to the group of logbook
466 fishers in that they used the same boat-types (Sesse), engines, mesh-sizes of gillnets - 94%

467 of which were of sizes between 5-7 inch (127-178 mm) - and longline hook-sizes - 96%
468 between hook-size 11 and 13 - numbers of hooks (average (sd): 700 (256)) and bait types. As
469 none of the remaining longline fishers in the logbook survey had engines, propulsion was not
470 further used explicitly as an explanatory factor, but as fisher was included as random effect in
471 the models explaining encounter rates and patch densities this operational factor was
472 accounted for indirectly.

473 Distance travelled, and the environmental factor location depth were highly collinear. A
474 regression of $\log_{10}(\text{depth})$ for gillnet over region, season with $\log_{10}(\text{distance})$ as co-variate was
475 significant ($F_{4,1769} = 1130$, $p < 0.001$, $r^2 = 0.59$). Gillnet fishers fished in deeper waters in the open
476 lake region compared to the gulf region irrespective of distance. Seasonality explained a mere
477 $< 1\%$ of the variation in location depth, where fishers were fishing in slightly deeper waters
478 during the transitional short rain season. For gillnet fishers from the open lake region the most
479 common location depth at 5 km from the shore was 25 m (max. 48 m depth at 40 km) while
480 their colleagues in the gulf were fishing at 13 m depth (max. 25 m depth at around halfway the
481 gulf). Compared to fishers in the open lake region who headed more towards open waters
482 gillnet fishers from the gulf were fishing more often parallel to the shore at a distance from their
483 homeport (Fig. 1). For longlines the relationship was also significant though less clear as
484 distance explained less variation in depth of location while the difference between regions was
485 not as pronounced as with gillnets ($F_{1318,6} = 55.7$, $p < 0.001$, $r^2 = 0.20$). The most common fishing
486 depth around the average of 7 km from the homeport for longline fishers from the open lake
487 region was approximately 21 m while their colleagues in the gulf were fishing at 17 m depth.
488 Longline fishers were fishing at slightly deeper waters and hence further from the shore during
489 the windy, dry, season but this accounted for 1.5% of the variation. In the remainder of the
490 analyses, only distance travelled will be considered and used as a proxy for the environmental

491 factor location depth. Setting depth of the two gear-types had limited overlap. Longlines were
492 set about twice as deep (1-24 m; average (sd)=11 (5) m) as gillnets (1-15 m; 5 (3) m).

493 *Random effects: clustering by fisher and size of Nile perch*

494 Before discussing the full models for encounter rate and patch density we first discuss
495 the choice of random effects for these models, as these give insights in the operational
496 strategies of individual fishers. Clustering by fisher×size interaction for models examining
497 encounter rates (model 4) lead to a substantial reduction in AIC compared to the null model
498 (intercept only) and accounted for gillnets and longlines respectively 34% and 44% of the
499 variability (ICC, covariance parameter estimate: $p < 0.01$) in the log-odds of catching Nile perch
500 (Table 4). In the final model, that included size and interactions of size with other variables as
501 fixed-effects, the amount of variation explained by the random effect as expressed by the ICC
502 was reduced to 16% and 23% ($p < 0.05$), suggesting that a large amount of variability was taken
503 up by size of Nile perch as fixed effect. The fisher×size interaction can be understood not just
504 as variation in skills and operational strategies in location choice of fishers but also because of
505 differences in choice of mesh-sizes and hook-numbers. An in-depth examination of this
506 random effect in the final model showed that for gillnet fishers most variation was found in the
507 odds of catching small Nile perch that varied between 0.3 and 3, while those of large Nile perch
508 varied between 0.7 and 6. However, in all cases but two the odds were not significantly different
509 from 1. The two exceptions were fishers who both had significantly lower odds (0.3) of catching
510 small Nile perch, indicating that they predominantly used larger mesh-sizes or fished further
511 from the shore where large Nile perch predominate, as will be shown below. Similar differences
512 in operational characteristics and apparent choice of hook-sizes were found for longlines. For
513 longlines most variability between fishers again was found in the odds of catching small Nile
514 perch. The odds ranged between 0.2 and 3, while the odds of catching large Nile perched

515 ranged between 0.9 to 6 and were, with three exceptions, not significantly different from 1. The
516 exceptions were a fisher with odds 6 and 0.3 respectively for catching large and small Nile
517 perch and another fisher with low odds (0.2) for catching small Nile perch. Choice of bait or
518 hook-size most likely were not causes of variation as these were accounted for as fixed effect.
519 We checked this by including hook-size and bait as random effects. Co-variance parameter
520 estimates were non-significant when including hook-size ($\theta=0.05$, $Z(2)=0.89$, $p=0.19$) or bait
521 as a random effect, the latter both on its own ($\theta=0.44$, $Z(4)=1.36$ $P=0.09$) or in addition to the
522 random effect fisher \times size ($\theta=0.71$, $Z(18)=1.28$, $p=0.10$). As number of hooks, net size and
523 soak-time were all accounted for as fixed effects, all other fixed effects related to the size
524 category of Nile perch and interactions with size category in encounter rates therefore now can
525 be considered as characteristics of the environment and of gear-Nile perch interactions and
526 thus are most likely not caused by specific differences in skills and operational characteristics
527 of fishers.

528 For patch densities (model 5), we included a random effect for fisher, which led to a
529 reduction in AIC compared to the null model. But the effect accounted for only 2% to 7% of
530 variability in patch density expressed as ICC in all models examined, non-significant in both
531 longline weight and number models and just significant ($p<0.05$) in the two gillnet models. The
532 amount of variation or significance levels did not change in the final model, indicating that the
533 fisher effect was fully accounted for. Although ICC estimates indicated that fisher as random
534 effect could be removed for the longline models it was kept in to make comparisons between
535 models fully compatible.

536 *Encounter rates: fixed effects determining the probability of catch*

537 The final random intercept models examining encounter rates (model 4) included as
538 fixed effects environmental (distance as proxy for depth, setting depth, region, season),
539 operational (distance as proxy for travelling time, soak-time, hook-size, bait, number of hooks

540 and size of nets) factors, Nile perch characteristics (size) and their two-way interactions. These
541 were significantly different from the random intercept model only (Gillnets $\chi_{diff}^2 = 151.8$,
542 $p < 0.001$; Longlines $\chi_{diff}^2 = 225.1$, $p < 0.001$). Both final models were only slightly over-dispersed.
543 During the backward selection procedure many interactions between main effects were
544 removed as well as the main effects soak-time and hook-size and their interaction. The effect
545 of soak-time and hook-size thus was only apparent in the catch densities and not in not the
546 probability of catching Nile perch. Bait-type was retained in the model and apparently overrode
547 the effect of hook-size (Table 4). All further analysis in this section refers to table 4.

548 Net size and number of hooks had small but significant effects on Pc in gillnets and
549 longlines respectively. Pc increased from 97% to almost 100% with an increase in number of
550 hooks from 100 to 1000. In gillnets it increased from 95% to close to 100% for large Nile perch,
551 while for small Nile perch decreased slightly from 99% to 98% with an increase in net area
552 from 100 to 10000 m².

553 Bait effects with their interactions were all significant but were dominated by the main
554 size effect for longlines, where large Nile perch ($Pc = 0.73$) was 76 times more likely to be
555 caught than small Nile perch ($Pc = 0.01$). Taking all effects into account the four bait-types had
556 similar or higher Pc for large Nile perch (*Synodontis*, $Pc = 0.73$; Dagaa, 0.73; *Clarias*, 0.76-1;
557 and haplochromines, 0.97-1). For some bait-types Pc increased with increasing distance.
558 However, confidence intervals for all estimates are large (Table 4): odds ratio estimates
559 comparing the various bait types with each other at 7 km distance and at 7 and 20 km distance
560 confirmed these differences but were invariably not significantly different from unity highlighting
561 the high variability around the estimates (Fig. 7). The analyses of the remaining factors all are
562 with bait-type *Synodontis* as baseline.

563 The size category of Nile perch was the most dominant effect for both gears, but with
564 opposite main effects: for gillnets it was 45 times more likely to catch a small Nile perch ($P_c =$
565 0.997) than a large Nile perch ($P_c = 0.73$), while for longlines it was over 200 times more likely
566 to catch a large Nile perch ($P_c=0.73$) compared to small Nile perch ($P_c<0.01$). Spatial
567 environmental factors distance, setting depth and region all contributed to a lowering of AIC
568 but signals were less clear than size.

569 Spatial environmental effects in relation to size changing these overall size effects were
570 prominent in gillnets and to a lesser extent in longlines. For gillnets size, distance and
571 interaction effects of size with region, distance and setting depth and of distance with region
572 were highly significant (Table 4). Overall odds for catching Nile perch increased with distance
573 by 1%, but these were offset by a range of interaction effects that resulted in a different pattern
574 for the open lake region compared to the gulf region. For small Nile perch a regional effect led
575 to an overall 2% lower probability of catch in the open lake region, but this difference was only
576 observed at close distances to the homeport: the most dominant effect was the 17% decrease
577 in odds per km distance for small Nile perch in the open lake that was offset by a 17% increase
578 in odds over distance in the gulf. These effects led to a major difference between regions.
579 Whereas in the gulf the P_c for small Nile perch increased from around $P_c = 0.8-0.9$ to close to
580 $P_c = 1$ at further distances from the homeport, in the open lake region $P_c = 0.8-0.96$ in the first
581 10 km from the homeport decreased rapidly to almost zero at larger distances (Fig. 5). Spatial
582 effects in relation to size for longlines were dominated by the difference in odds of catching
583 large and small Nile perch, already discussed, the 37% overall lower probability of catch of Nile
584 perch in the gulf to the open lake, and an interaction effect of size with setting depth. The 5%
585 decrease in odds with distance affected both small and large Nile perch, leading to much
586 lowered encounter rates at larger distances for small Nile perch, comparable to gillnets in the
587 open lake region (Fig.6).

588 With every meter increase in setting depth of gillnets, the odds of catching small Nile
589 perch increased by 4% and of large Nile perch by 11%, leading to a slight effect of increased
590 probabilities of catch for both size classes (Fig. 5). For longlines setting depth did not affect the
591 P_c for large Nile perch, but the odds of catching small Nile perch per meter increased 9% with
592 every meter setting depth. However, here the odds for setting depth and its interaction with
593 size were not significantly different from 1 indicating that for longlines the signal of setting-
594 depth for size of Nile perch was slight (Fig. 6).

595 Overall the spatial environmental effects lead to contrasting effects for gillnets and
596 longlines: while the odds of catching Nile perch was lower in the gulf than the open lake the
597 opposite was the case for gillnets. Longlines had overall lower odds of catching small Nile
598 perch than gillnets, whereas for gillnets the odds of catching the two sizes was not significantly
599 different from 1. For both gears the most conspicuous effect were the higher odds of catching
600 large Nile perch at larger distances from homeport (Fig. 7).

601 Seasonal effects were not prominent and were unrelated to distance, setting depth or
602 size of Nile perch for both gears. Only overall effects and differences between regions were
603 observed. In general, for both gears and areas slightly elevated catch probabilities were
604 encountered during the transition period between stratified and mixed season (Fig. 7).
605 However, in the gulf region P_c was elevated during the stratified season and not significantly
606 different from the transitional season. In the open lake again highest P_c 's were found during
607 the transitional season, followed by the stratified and mixed seasons that were not significantly
608 different (Fig. 5, 6; Table 4).

609 *Patch density: fixed effects determining positive catch-rates*

610 The final random intercept models examining patch densities (model 5) included as
611 fixed effects the same environmental and operational factors as the previous model. After

612 parameter selection based on minimising AIC three of the four models of patch densities by
613 weight and number were significant at $p < 0.001$ based on a restricted log likelihood deviance
614 test of the nested null and full models. The model for patch density expressed in numbers for
615 longlines had the lowest decrease in AIC and the deviance test was non-significant ($\chi^2_{34} = 46.3$,
616 $p = 0.08$), suggesting that an intercept only with random fisher effect model would be the most
617 parsimonious. We decided to keep the parameter estimates of fixed main effects and their
618 interactions after backward selection, their confidence intervals and significance levels (Table
619 5).

620 Size of Nile perch again was the dominant effect in all models. The main differences
621 between the two gears was found when including region and interactions with size. Gillnets
622 caught patches of small Nile perch between around $13.5 \text{ kg.trip}^{-1}$ in both open lake and gulf
623 region and respectively 12 and 14 fish.trip^{-1} , so with individual sizes around 1 kg. Longlines
624 caught between 12 kg.trip^{-1} (gulf) and 14 kg.trip^{-1} (open lake) of small Nile perch but in lower
625 numbers (7–6 fish.trip^{-1}), so with individual sizes of around 2 kg. Gillnet densities for large Nile
626 perch are between 4.6 kg.trip^{-1} (2 fish) in the open lake and 7.1 kg.trip^{-1} (5 fish) in the gulf, for
627 longlines the values are respectively 18 kg.trip^{-1} (3 fish) and 21 kg.trip^{-1} (3 fish). These numbers
628 indicate that longlines overall target fish that are 2-3 times larger in weight than gillnets and
629 that overall patch densities in the two regions are comparable, if slightly higher in the gulf.

630 Besides region, the spatial factors distance from the homeport, setting depth and
631 interactions of these with size and region, when present, were all significant resulting in
632 increased patch densities and size of large Nile perch a slight decrease in patch densities for
633 small Nile perch with increasing distance. Overall weight and number of large Nile perch in the
634 open lake increased with increasing distance for both gillnets and longlines with respectively 3
635 kg.trip^{-1} (1.5 fish) and 2.4 kg.trip^{-1} (1 fish) per 10 km. The increase was lower in the gulf region
636 for both gears with 1.3 kg.trip^{-1} (0.6 fish) per 10 km. Patch densities of small Nile perch in the

637 open lake region increased with increasing distance with 1.4 kg.trip^{-1} (0.9 fish) per 10 km, but
638 decreased slightly with distance from homeport for gillnets in the open lake and for longlines
639 in both regions by respectively 0.3 kg.trip^{-1} (0.1 fish) and 4 kg.trip^{-1} (0.1 fish) per 10 km. Patch
640 densities for large Nile perch slightly increased in weight and number with deeper net and line
641 sets with respectively 1.9 kg.trip^{-1} (0 fish) and 0.5 kg.trip^{-1} (0.9 fish) per 10 m setting depth.
642 Small Nile perch patch densities for gillnets decreased by 1.1 kg.trip^{-1} (1.5 fish) every 10m
643 depth indicating an increase in individual sizes for gillnets and a slight decrease for longlines.

644 Seasonal effects in patch densities suggested generally slightly lowered patch densities
645 during the dry mixed season compared to the long-rain stratified and short rain transitional
646 seasons but were not significant (Figure 4, 5). Interactions of seasons with size appeared in
647 all models with generally a slight increase in weight and decrease in numbers for the dry and
648 rainy season compared to the short-rain, transitional season. Interactions of season with
649 region, setting depth and distance were present in different models with very different effects
650 partially cancelling out each other.

651 In summary, patch densities showed similar patterns over distance for both gears and
652 regions except for gillnets in the open lake region. Over 20 km, the distance over which around
653 90% of the longline and gillnet operations of all fishers take place, small Nile perch patch
654 densities decreased by 20-46% in weight and 7-38% in number. In absolute terms this
655 represents a decrease in patch density over 20 km between $3\text{--}6 \text{ kg.trip}^{-1}$ and $1\text{--}3 \text{ fish.trip}^{-1}$.
656 For large Nile perch patch densities increased between 26–50% in weight and 4–19% in
657 number. In absolute terms this represents an increase over 20 km of between $4\text{--}6 \text{ kg.trip}^{-1}$ and
658 $0.1\text{--}1 \text{ fish trip}^{-1}$. The exception was for gillnets in the open lake region, where both large and
659 small fish patch densities increased over 20 km in both weight and number, respectively by
660 58% weight (32% number) for small fish, and 58% (128%) for large fish. This represented an
661 increase in patch density for small and large Nile perch respectively of 8 kg.trip^{-1} (4 fish.trip^{-1})

662 and 6 kg.trip⁻¹ (91 fish.trip⁻¹). In general, over 20 km distance the change in average individual
663 weight of small Nile perch in the gulf and open lake regions was between -250 and 220 gram,
664 while individual weight for large Nile perch increased in all cases between 380 and 1410 gram.
665 In other words, at further distances patch densities of small fish were less numerous but
666 individuals were smaller in the gulf and larger in the open lake area, while the patch densities
667 of large Nile perch remained the same or increased somewhat, but individual fish were larger.

668 *Factors determining relative biomass and density*

669 Overall the relative biomass ($CPUE_{st} * Pc$, kg.trip⁻¹) for both longlines (Fig. 6) and gillnets
670 (Fig. 5) had similar patterns in the gulf and open lake regions and at different depths whereby
671 large Nile perch $CPUE_{st}$ increased over distance from the homeport while small Nile perch
672 decreased rapidly after 10-15km distance, more prominent so with gillnets. The exception was
673 gillnets in the gulf region for which relative biomass for small Nile perch remained the same or
674 decreased slightly.

675 Size effects dominated spatial patterns of relative biomass and density of catch for both
676 gears and regions (Fig. 5 and 6). Large Nile perch $CPUE_{ad}$ increased in both gears and regions.
677 For longlines, over the first 20 km from homeport, this led to an average increase in catch rate
678 from 19 kg.trip⁻¹ to 24 kg.trip⁻¹ in the gulf and from 16 to 21 kg.trip⁻¹ in the open lake, where in
679 all cases around 4 fish.trip⁻¹ were caught. The average weight (length) of large Nile perch thus
680 ranged between 4.5 kg (71 cm) to 5.7 kg (76 cm). Gillnets on average caught less large Nile
681 perch in weight and more in number. Over the first 20 km this amounted to an increase from
682 9.2 kg.trip⁻¹ (6 fish) to 15.4 kg.trip⁻¹ (9 fish) in the gulf. A more dramatic increase was observed
683 in the open lake from 6.2 kg.trip⁻¹ (3 fish) to 21.3 kg.trip⁻¹ (11 fish). Large Nile perch in gillnets
684 thus was smaller than caught by longlines: the average weight (length) ranged between 1.6
685 kg.trip⁻¹ (52 cm) and 2.1 kg.trip⁻¹ (56 cm). Small Nile perch $CPUE_{ad}$ in all cases decreased. In

686 longlines this amounted to a decrease in catch rates in the gulf over 20 km from 1 kg.trip⁻¹ (1
687 fish) to 0.3 kg.trip⁻¹ (0.2 fish) gulf and in the open lake region from 3.4 kg.trip⁻¹ (2 fish) to 1.2
688 kg.trip⁻¹ (1 fish). This led to an average individual weight (length) range between 1.5kg.trip⁻¹
689 (50cm) to 1.6 kg.trip⁻¹ (52cm). In gillnets small Nile perch catch rates in the gulf decreased from
690 5.7 kg.trip⁻¹ (7fish) to 4.9 kg.trip⁻¹ (6 fish) and in the open lake from 9.3 kg.trip⁻¹ (9 fish) to 4.2
691 kg.trip⁻¹ (5 fish). The average individual weight thus was 0.8kg (41cm) to 0.9kg (46cm), again
692 smaller than caught by longlines.

693 Setting depth had a pronounced effect for large Nile perch on relative biomass and
694 density. In gillnets comparing 4 m and 15 m setting depth over 20 km distance resulted in an
695 increase between 2.5–5 kg.trip⁻¹ (5-8 fish) in the gulf and 1–8 kg.trip⁻¹ (4-10 fish) in the open
696 lake. Small Nile perch decreased in catch rate with increasing setting depth between 1-2 kg.trip⁻¹
697 ¹ and 1-2 fish, with limited seasonal effects. Differences were even more limited for longline
698 catch-rates that over the first 20km from homeport showed an increase of 0.8 kg.trip⁻¹ (0.5 fish)
699 to 0 kg.trip⁻¹ in the gulf and 2 kg.trip⁻¹ (1fish) to 0 kg.trip⁻¹ in the open lake. Catch rates in weight
700 of small Nile perch did not change with increased setting depth in weight for large fish, and
701 only slightly increased in number.

702 Seasonal effects suggested slightly elevated catch rates during the short rain,
703 transitional, and long-rain stratified season, with a stronger effect for gillnets and for smaller
704 Nile perch in weight and number. However, confidence intervals around CPUE estimates over
705 distance for different seasons and setting depth overlapped and estimates were non-significant
706 from each other over the whole range examined. While the slopes were significant, the width
707 of the confidence intervals also implied that the observed changes were detectable only over
708 large distances, except for small Nile perch densities that showed a clear overall decrease
709 over distance.

710 *Long-term large-scale relative biomass changes: IFD predictions.*

711 Over the period sampled total relative biomass summed over the size categories and
712 averaged over depth and season for each of the two fisheries increased over distance.
713 Nearshore relative biomass for the two gears ranged between 15-20 kg.trip⁻¹ and over the first
714 20 km distance from the homeport, covering 90% of all fishing operations, increased to
715 between 20-25 kg.trip⁻¹. At larger distances, expected catch rates increased to around 25-28
716 kg.trip⁻¹ except for gillnets in the open lake region that showed a larger increase (Fig. 8). Catch
717 rate in numbers of fish were even more stable, for gillnets in the first 20 km increasing from 13
718 to 15 fish.trip⁻¹ and for longlines hovering between 4-5 fish.trip⁻¹. Thus, also average size
719 differences over distance were small and increased with distance from homeport by between
720 0.1-0.3 kg for gillnets and 0.7-0.8 kg for longlines. Overall average Nile perch sizes for gillnets
721 are 47-52cm and for longlines between 66-75 cm. Except for gillnets in the open lake at large
722 distances from the homeport, total relative biomass estimates over distance thus were highly
723 similar between the gulf and open lake regions and the two gears.

724 **Discussion**

725 The resource space of Nile perch fishers was determined by the travel distance which
726 for both gears ranged up to 39 km and was centered around 3.5 km (gillnets) to 6.2 km
727 (longlines) from the homeport (Fig.1). Distances travelled, and location depths were highly
728 collinear meaning that travelling further also meant fishing in deeper waters, while fishers
729 mostly moved away from the shore. The exception were gillnet fishers in the gulf region, who
730 travelled more alongshore. While resource spaces of longline and gillnet fishers overlapped,
731 especially when gillnet fishers used outboard engines, there was limited interference between
732 the two gears as gillnets were set overnight and longlines during the day. Furthermore,
733 longlines generally were set twice as deep than gillnets. Finally, the two gears targeted on

734 average different size classes of Nile perch, with gillnets targeting overall smaller Nile perch
735 than longlines.

736 Over the resource space up to around 15-20 km where 90% of all fishing activities took
737 place, average total CPUE in weight increased slightly and in numbers was relatively stable
738 over all locations and seasons. Fishers generally did not venture much further and location
739 choice appeared not to be strongly driven by expected higher catch-rates away from the shore.
740 This suggests that large daily variability in catch rates and the limited strength in other signals
741 of fish distributional patterns that fishers received from the environment obscured the relatively
742 small increase in total catch rates over distance. Other than the clear spatial patterns in size
743 classes of Nile perch related to distance from the shore and depth, signals from the
744 environment had limited informational value for location choice. Environmental effects from
745 region, season, setting depth of gears were present but small and were largely obscured by
746 the high variation in encounter rates, patch densities and resulting catch rates, as well as
747 random effects from different fisher strategies.

748 The high individual variability and the limited strength of environmental signals from the
749 resource imply that fishers have a limited capacity to direct effort in space within this resource
750 space (van Densen 2001, van Oostenbrugge et al. 2002). Their distribution over the resource
751 may be to a large extent driven by operational constraints including costs as available time and
752 money (Salas and Gaertner 2004). However, clear patterns in Nile perch size distribution
753 existed to which the two gears reacted differently. We will first review these patterns and then
754 discuss the resulting allocation effects in relation to the IFD predictions.

755 Of the environmental signals examined, size of Nile perch explained most variability in
756 encounter rates and patch densities, both as main effect and in interactions with other
757 environmental and operational effects. Encounter rates of small Nile perch decreased rapidly

758 towards deeper waters, as has been described earlier (Katunzi et al. 2006, Taabu-Munyaho et
759 al. 2013). In contrast, encounter rates with large Nile perch for both gear types and in both
760 regions were always high and increased with increasing distance from the shore. Patch
761 densities of Nile perch were hardly explained by any of the main effects except size, indicating
762 that local variations in Nile perch densities within the area covered by a gear were not strongly
763 driven by environmental or operational factors. For gillnetters in the Speke gulf region,
764 encounter rates with small and large Nile perch remained high and even increased with
765 distance from homeport, while patch densities remained the same or increased. This was most
766 likely a result of their more along-shore choice in fishing locations and these fishers thus
767 remained in areas with high encounter probabilities and overall stable catch rates of small Nile
768 perch. Their increase in total catch rates over distance came mostly from large Nile perch,
769 suggesting also that at further distances from homeport along the shore these fishers had less
770 competition with other fishers targeting large Nile perch.

771 We expected larger Nile perch to be caught more in deeper, less heavily fished open
772 lake areas (van Zwieten et al. 2016). Catch rates indeed did increase with increasing distance
773 for both gears and especially for gillnetters in the open lake region. However, catch-rates of
774 large Nile perch in nearshore areas up to 20 km did not differ much between regions, though
775 the average size of Nile perch increased with distance. Possibly, this indicates that fishing
776 pressure on larger sizes was more evenly spread over the resource spaces of the Nile perch
777 fisheries, or that the gulf with its higher fishing pressure, is more productive than the open lake
778 area.

779 Seasonal effects driving Nile perch densities equally had limited informational value for
780 daily fishing decisions. Generally, somewhat elevated Nile perch densities were present during
781 the transitional, short-rain and the stratified, long rain season. Increased densities of Nile perch
782 higher in the water column during the stratified seasons have been observed in acoustic

783 surveys and in seasonally aggregated catch-rates based on catch assessment surveys
784 (Taabu-Munyaho et al. 2013), but also in that case the effect was not strong. This indicates
785 that either the upward movement and resulting change in densities during stratification and in
786 the transitional period during which turnover and mixing of waters takes place was not very
787 strong; or that, in our case, the stratification during the period of our research was not very
788 strong (Cornelissen et al. 2015). Furthermore, no clear evidence for changes in setting-depths
789 or location was found over the seasons indicating that individual fishers do not seem to change
790 their fishing behavior strongly in reaction to the effects of stratification on Nile perch, and that
791 effects may only visible when aggregated over large numbers of fishers.

792 The weak seasonal signal indicates that there is no clear inshore spawning movement
793 of Nile perch (Mkumbo 2002), while there is also no evidence for inshore nursery areas of
794 targeted juvenile fish from 30 cm onwards. Both types of movement would increase patch
795 densities during specific seasons in areas close to the shore, which was not the case. Though
796 Nile perch is known to have higher densities of small juveniles of <30 cm close to the shore
797 (Katunzi et al. 2006, Nyboer and Chapman 2013), speculations about specific “spawning
798 grounds” and “nursery areas” (Ligtvoet and Mkumbo 1989) do not seem warranted, at least
799 not for the areas covered in this study. The highly variable encounter rates and patch densities
800 for both gears indicated that Nile perch was highly dispersed over space and did not appear in
801 large groups that could be specifically targeted, as was also suggested by hydro-acoustic
802 surveys (Goudswaard et al. 2004). Nile perch >30 cm, the lower size limit caught by fishers in
803 this study, is a non-schooling solitary fish (Goudswaard et al. 2004). The high variation in patch
804 densities and limited explanatory value of seasonal and spatial factors confirms the highly
805 heterogeneous distribution of Nile perch found by Cornelissen et al. (2015).

806 The different patterns in encounter rates and patch densities of sizes of Nile perch for
807 the two gears highlight different operational strategies resulting from their specific catch

808 characteristics. Gillnets retain fish passively over a surface area while longlines attract
809 individual fish to bait on a hook (Bjordal 2002). Mesh-sizes set by individual gillnet fishers
810 ranged between 4 and 8 inches (101 – 203 mm stretched mesh), targeting Nile perch of 40 cm
811 and 70 cm modal lengths (Msuku et al. 2011). Actual mesh sizes used varied almost daily, but
812 nets set always included a range of small and large meshes. Except very close to the shore
813 where smaller mesh sizes were used, on average mesh sizes did not differ much over the
814 distance from the home-port and by setting depth indicating that fishers always targeted Nile
815 perch over this size range. Moreover, next to targeting a large size range, 11% of the catch
816 weight consisted of several other species. This range of sizes and species caught in gillnets
817 amounts to a bet-hedging fishing strategy: by increasing the portfolio of fish over sizes and
818 species in the catch variability in daily fishing outcomes decrease (Schindler et al. 2015, van
819 Densen 2001).

820 In contrast, while the range of Nile perch sizes caught in our study by the different hook-
821 sizes 11-13 does not differ much with the reported modal lengths of 59-62 cm selected by
822 these hook-sizes (Msuku et al. 2011), their reported range in sizes caught of approximately
823 20-100 cm is high (Chitamwebwa et al. 2009). Chitamwebwa (2009) highlights that the choice
824 of bait has an important effect on Nile perch sizes, and shows the opportunistic character of
825 Nile perch choices in size of food relative to its own size. With hook-sizes 10-12 *Clarias* bait
826 caught Nile perch with a dome shape peaking at 60 cm but with a range of approximately 20-
827 100 cm, whereas haplochromine bait caught the same size range but skewed with a peak at
828 40 cm. Most likely the condition and size of bait also may have impacts on the catch success
829 (Kumar et al. 2015, Sistiaga et al. 2018), in our case possibly explaining the differences and
830 high variability in catch probability of the different bait types observed. That large Nile perch is
831 caught by the relatively small hooks dominant in the fishery may be explained by the function
832 of bait. Hook-size had no significant effect in encounter rates with Nile perch, while there was

833 a strong interaction between hook-size and bait type. Bait type thus to a large extent
834 determines the catch characteristic of longlines as different bait types attract different species
835 and sizes (Wraith et al. 2013) regardless of hook-size. Furthermore, larger fish have larger
836 feeding ranges and thus may be more successful in competing for bait (Løkkeborg and Bjordal
837 1992). We do not have the information to further investigate these effects on daily outcomes,
838 but for longlines bet-hedging then shifts to the choice of bait-type in combination with small
839 hook-sizes and remaining relatively close to the shore. By doing so longline fishers still can
840 target large Nile perch using the attraction characteristics of the bait while also making use of
841 the smaller, more productive, size classes encountered closer to the shore.

842 While effort allocation was more driven by encounter rates than by patch densities,
843 daily patterns in encounters with patches of fish gave rise to an aggregated relative biomass
844 that relates to the underlying biomass targeted by the two fisheries. Patterns in relative catch-
845 rates were similar for the two gears and between regions and in general, coincided with what
846 is known about the distributional patterns of Nile perch. Large, adult Nile perch occupies all
847 open water habitats in the lake (Schofield and Chapman 2000) and increases further offshore,
848 is more common in deeper waters, and moves higher in the water column during the stratified
849 season (Taabu-Munyaho et al. 2014), though the latter effect was small. As was the case for
850 large Nile perch, smaller juvenile Nile perch were found at all depths in the lake but with higher
851 densities in nearshore shallow waters (Katunzi et al., 2006), possibly since they are more
852 tolerant to hypoxia (Robb and Abrahams 2003) a condition found in shallow or nearshore
853 habitats (Cornelissen et al. 2014).

854 Clear patterns of Nile perch size-distributions thus exist directing fishers decisions in
855 location choice. Although fishers are constrained by their daily movements from a single
856 homeport and limited action radius due to time constraints and propulsion methods, violating
857 the IFD assumption of free movement, overall catch-rates within gears and over gears showed

858 only a limited increase over distance. Thus fishers largely appear to follow the prediction of
859 IFD theory of distribution over space such that resource outcomes are equalized (Gillis et al.
860 1993, Gillis and van der Lee 2012). As a consequence of the IFD theory, patterns in effort
861 allocation are predicted to follow the underlying size/productivity-spectrum of Nile perch (Plank
862 et al. 2017), which implies that spatial allocation of effort aggregated over all fishers and time
863 will reflect the underlying productivity distribution of a resource. Other than size, Nile perch
864 densities are only to a limited extent explained by other spatial and temporal environmental
865 signals factors indicating that these only have limited value in driving location choice of fishers.
866 Thus, fishers can then be expected to distribute themselves over the resource where renewal
867 rates are highest, if revenues per kg of fish do not differ much between sizes. Natugonza et al.
868 (2016) estimated the P/B ratio of juvenile Nile perch, in their study defined as <40 cm, at 3.5
869 year⁻¹, while adult Nile perch (>40 cm) had a P/B=0.92 year⁻¹. Productivity of 30-50 cm juvenile
870 Nile perch, the main target in the fishery, thus is high, and this size range is found within the
871 10 km distance from the shore in which most fishing takes place.

872 As Natugonza et al. (2016) showed, current exploitation patterns in Lake Victoria are
873 skewed to the least productive higher trophic level categories including large Nile perch, with
874 significantly less fishing occurring at the most productive lower trophic level categories
875 including small Nile perch. While enforcement up till recently¹ has been weak, mesh size
876 regulations still appear to form a constraint on the use of smaller mesh-sizes, as attested by
877 the distribution of mesh-sizes over the open lake peaking at 6 inches (152mm) (Fig. 2). The
878 decreasing mesh-size and hook-size frequencies respectively from 6 inches (152mm) and size

¹ “Lake Victoria Anti-Illegal Fishing Initiative Gets 4bn/ - Allocation”, Tanzania Daily News 8 March 2018.
<http://allafrica.com/stories/201803080398.html>. “Magufuli amplifies war on illegal fishing gears” 15 March 2018
<https://allafrica.com/stories/201803130320.html>. Kenya, Tanzania, and Uganda pledged to contribute 600,000 US
dollars to curb illegal fishing of the Nile perch.

879 >10 onwards suggests that Lake Victoria's fishing patterns were distributed proportionally to
880 the productivity spectrum of the resources. Overall fishing pressure was higher in the enclosed
881 gulf compared to the open lake region (Anonymous 2017). Our starting point in contrasting
882 open lake and gulf regions that this would lead to lower catch-rates and higher competition
883 over resources while fishers would distribute over a larger resource space was not observed
884 in this study. Despite the higher fishing pressure, catch-rates in gulf and open lake regions
885 were highly similar and fishing strategies and resulting fishing patterns may currently be
886 optimised in a trade-off between operational costs and expected outcomes at locations where
887 renewal rates of Nile perch are high. If the fishers of our study indeed are representative of the
888 Nile perch fishery around the lake, as we suggest they are, this would mean that currently a
889 large part of the open lake and even the middle part of the gulf's surface and deeper waters
890 are only lightly fished and thus could serve as refuge for less productive large Nile perch.
891 Current gear regulations, if enforced, force gillnet and longline fishers to focus on the lower
892 productive adult Nile perch stock further from the shore and deeper in the water column.
893 Without concurrent effort regulations to reduce the number of fishers this may be
894 counterproductive and lead to overfishing of the large Nile perch size classes.

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Table 1: Daily mean standardized catches of Nile perch in kilogram and number and coefficient of variation (CV) by individual fisher. G1-G8 = gillnet fisher, L1-L7 = longline fisher; E = engine; P = paddle/sail.

Village, coordinates	Gear, Fisher	Propulsion (Nobs)	Fishing days (N)	No fishing	Mean (kg)	CV (kg)	Mean (N)	CV (N)
Kayenze (Gulf) 02° 23.335' S 33° 4.730' E	G1	E	271	14	17	59	16	66
	G2	E	205	13	22	48	22	49
	G3	E	275	7	28	87	23	76
	L1	P	177	9	38	68	13	83
	L2	P	239	5	37	78	10	76
Muluseni (Gulf) 02° 8.265' S 33° 11.054' S	G4	E	188	4	19	70	24	70
	G5	E (189), P	217	51	21	86	18	81
	G6	E (79), P	198	6	32	77	21	79
Muhula (Open lake) 02° 4.993' S 32° 57.44' E	L3	P	239	11	40	93	17	115
	L4	P	272	1	37	81	12	111
	G7	E (105), P	227	0	28	43	22	45
Buhama (Open lake) 2° 16.652' E 33° 32.172' S	G8	E (102), P	122	46	25	76	15	71
	L5	P	107	30	37	49	18	54
	L6	P	151	0	34	68	17	77
	L7	P	212	56	35	55	13	68
Total	15		3100	253				

Table 2: Parameter estimates for hook-size, bait, net-size, hook-number and soak-time used for the standardization of observed catch rates (kg.trip⁻¹ and N.trip⁻¹). Hook-size was standardized to “small hooks (13)”; bait was standardized to “*Synodontis*”. A trip is defined as 6hr duration with 800 hooks for longlines and 10hr with 12000m² of net for gillnets. *** p<0.001, ** p<0.01, * p<0.05, ns= non-significant. N=Number, Df=Degrees of freedom, F = F-statistic, r²= coefficient of determination, Hs=Hook size.

Gear type	Nile perch	Net size	Soak time	Bait	Hook	Bait*Hs	N	Df	F	r ²
		/N hooks (β ₁)	(β ₂)	size						
Gillnet	Weight	0.095 ^{***}	-0.623 ^{***}	-	-	-	1793	2	100.4	0.10
	Number	-0.018 ^{ns}	-0.432 ^{***}	-	-	-	1793	2	10.3	0.01
Longline	Weight	0.467 ^{***}	0.347 ^{**}	***	***	***	1313	9	25.7	0.15
	Number	0.200 ^{ns}	0.657 ^{***}	***	*	***	1313	9	34.6	0.19

Table 3: Average (mean), median, standard deviations (SD) and coefficient of variation (CV) of standardized positive catch rates CPUE for small (<50 cm) and large (>50cm) Nile perch with gillnet and longlines gears in $\text{kg}\cdot\text{trip}^{-1}$ and $\text{number}\cdot\text{trip}^{-1}$. The median trip duration and effort for longlines is 6hrs with 800 hooks and for gillnet is 10hrs with 12000m² of net. N_{pos} = number of positive catches. Total number of observations exclude zero catches Gillnets $N=3406$; Longlines $N=2636$.

	CPUE _{stand}	Gear	Size	Prob	N_{pos}	Mean	CV	Median
$N\cdot\text{trip}^{-1}$	Gillnet	<50	0.92	1593	11	78	10	
		≥ 50	0.91	1567	13	112	10	
	Longline	<50	0.64	845	14	97	10	
		≥ 50	0.95	1264	30	84	23	
$\text{kg}\cdot\text{trip}^{-1}$	Gillnet	<50			14	77	10	
		≥ 50			7	110	10	
	Longline	<50			10	95	7	
		≥ 50			8	110	5	

Table 4. Parameter estimates of fixed effects, random effects and model diagnostics of encounter rates (probability of positive catch (Pc)) for gillnet and longline Nile perch fishers Wald test: Wald Z test covariance parameter: ** p<0.01, * p<0.05, §=Likelihood ratio (deviance) test: p<0.001. Bold numbers indicate significant parameter estimates.

Model		Gillnet encounter rate				Longline encounter rate			
Effect		Estimate	Confidence interval		p	Estimate	Confidence interval		p
Fixed effects			lower	upper			lower	upper	
	Intercept	-3.8	-7.9	0.29	0.066	0.99	-4.38	6.37	0.693
	Log ₁₀ (Net area)								
	Log ₁₀ (N-hooks)								
Bait ¹	Clarias	1.5	0.51	2.5	0.003	1.75	0.14	3.37	0.033
	Dagaa					-2.31	-3.88	-0.74	0.004
	Haplochr.					-3.28	-4.78	-1.77	<0.001
	Haplochr.					-2.13	-3.46	-0.79	0.002
Distance	Dis	0.01	-0.06	0.09	0.731	-0.05	-0.08	-0.01	0.016
Setting Depth	SD	0.12	-0.02	0.26	0.097	0	-0.07	0.08	0.984
Season ²	Dry	-1.3	-2	-0.6	<0.001	-0.03	-0.53	0.47	0.910
	Long	-1.22	-1.82	-0.62	<0.001	-0.91	-1.26	-0.55	<0.001
Size ³	<50	9.61	3.52	15.7	0.005	-5.63	-7.67	-3.58	<0.001
Region ⁴	Gulf	0.36	-1.13	1.84	0.638	-1.5	-2.83	-0.18	0.026
Interactions	NA(<50)	-1.92	-3.35	-0.49	0.008				
	Dis(<50)	-0.19	-0.29	-0.09	<0.001				
	Dis*Gulf	0.19	0.1	0.28	<0.001				
	SD(<50)	-0.08	-0.25	0.09	0.339	0.09	0.01	0.17	0.036
	Gulf*<50	-1.74	-3.74	0.26	0.089				
	Gulf*Dry	0.39	-0.43	1.21	0.346	-0.89	-1.69	-0.09	0.030
	Gulf*Lon	1.29	0.57	2.01	0.001	0.74	0.07	1.42	0.032
	Dis(Cla)					0.15	0.03	0.27	0.017
	Dis(Dag)					0.15	-0.03	0.32	0.095
	Dis(Hap)					0	-0.06	0.06	0.984
	Cla*<50					2.5	1.06	3.94	0.001
	Dag*<50					5.41	4.02	6.8	<0.001
	Hap*<50					3.15	1.89	4.41	<0.001
Random effects		Null model	Random intercept	Final Model		Null model	Random intercept	Final model	
Fisher*Size	N		16	16			14	14	
	ICC		0.34**	0.16*			0.44**	0.23*	
Diagnostics									
AIC		2004.3	1711.2	1587.4		2639.6	1933.7	1689.5	
-2LL		2002.3	1707.2	1555.4§		2637.6	1929.7	1647.5§	
Observation	N	3406	3406	3366		2636	2636	2610	
Dispersion	χ ² /df	1.0	0.9	1.1		1.0	1.0	1.1	

Base levels intercept: ¹ Bait: *Synodontis*, ² Season: short rain, ³ Size: >50, ⁴Region: Lake

Table 5. Parameter estimates of fixed effects, random effects and model diagnostics of patch density (positive catch) in weight and number for gillnet and longline Nile perch fishers Wald Z test for covariance parameter: * = $p < 0.05$, ns=not-significant. Residual Log-likelihood ratio: § = $p < 0.001$. Bold numbers indicate significant parameter estimates.

Model	Effect	Gillnet Patch density (Weight)				Longline Patch density (Weight)				Gillnet Patch density (Number)				Longline Patch density (Number)			
		Est	Confidence interval		p	Est	Confidence interval		p	Est	Confidence interval		p	Est	Confidence interval		p
Fixed effects			lower	upper			lower	upper			lower	upper			lower	Upper	
	Intercept	0.66	0.48	0.83	<0.001	1.25	1.17	1.33	<0.001	0.34	0.18	0.49	0.002	0.49	0.34	0.64	<0.001
	Distance Dis	0.03	0.02	0.03	<0.001	0.01	0.00	0.01	0.009	0.03	0.02	0.04	<0.001	0.01	0.01	0.02	<0.001
	Setting depth SD	0.02	0.01	0.02	<0.001					0.02	0.01	0.02	<0.001	0.01	0.00	0.01	0.008
	Region ¹ Gulf	0.19	0.04	0.35	0.013	0.07	0.00	0.15	0.051	0.34	0.21	0.47	<0.001	0.03	-0.13	0.19	0.717
	Season ² Dry	0.03	-0.06	0.12	0.492	0.00	-0.06	0.06	0.909	-0.03	-0.12	0.06	0.452	0.25	0.10	0.40	0.001
	Long	0.05	-0.01	0.12	0.123	0.01	-0.04	0.06	0.754	0.00	-0.06	0.07	0.925	0.06	-0.05	0.17	0.292
	Size ³ <50	0.47	0.38	0.55	<0.001	-0.11	-0.19	-0.03	0.007	0.75	0.66	0.83	<0.001	0.34	0.25	0.42	<0.001
	Interactions Dis(Gulf)	-0.02	-0.02	-0.01	<0.001					-0.02	-0.03	-0.01	<0.001				
	Dis(<50)	-0.02	-0.02	-0.01	<0.001	-0.02	-0.02	-0.01	<0.001	-0.01	-0.02	-0.01	<0.001	-0.02	-0.02	-0.01	<0.001
	Dis(Dry)													-0.03	-0.04	-0.01	0.003
	Dis(Lon)													-0.01	-0.02	0.00	0.014
	SD(<50)	-0.03	-0.04	-0.02	<0.001					-0.03	-0.04	-0.02	<0.001				
	SD(Dry)													-0.01	-0.01	0.00	0.197
	SD(Lon)													0.01	0.00	0.01	0.089
	Dry*<50	0.00	-0.07	0.07	0.966	-0.20	-0.29	-0.10	<0.001	0.07	0.00	0.14	0.041	-0.14	-0.23	-0.04	0.005
	Lon*<50	0.05	0.00	0.10	0.062	-0.17	-0.25	-0.09	<0.001	0.09	0.03	0.14	0.002	-0.17	-0.24	-0.09	<0.001
	Gulf*<50	-0.33	-0.39	-0.27	<0.001	-0.15	-0.23	-0.07	<0.001	-0.31	-0.37	-0.25	<0.001	-0.09	-0.17	-0.01	0.028
	Gulf*Dry	-0.12	-0.20	-0.03	0.009					-0.19	-0.28	-0.10	<0.001				
	Gulf*Lon	0.00	-0.06	0.07	0.975					-0.03	-0.09	0.04	0.449				

<i>Random effects</i>		<i>Null model</i>	<i>Random intercept</i>	<i>Final model</i>	<i>Null model</i>	<i>Random intercept</i>	<i>Final model</i>	<i>Null model</i>	<i>Random intercept</i>	<i>Final model</i>	<i>Null model</i>	<i>Random intercept</i>	<i>Final model</i>
Fisher	N		8	8		7	7		8	8		7	7
	ICC		0.07*	0.07*		0.02 ^{ns}	0.01 ^{ns}		0.04*	0.04*		0.04 ^{ns}	0.05 ^{ns}
<i>Diagnostics</i>													
AIC		2290.6	2094.9	1823.5	2535.8	2521.2	2135.4	3010.5	2908.2	2044.8	2242.1	2196.0	2149.7
-2ResLL		2286.6	2090.9	1819.5 [§]	2531.8	2517.2	2131.4 [§]	3006.5	2904.2	2040.8 [§]	2238.1	2192.0	2145.7 ^{ns}
Observation	N	3112	3112	3081	2109	2109	2088	3112	3112	3081	2096	2096	2075

Base levels intercept ¹ Season: short rain ² Size: >50 ³ Region: open lake

Figure 1: Map of the southern part of Lake Victoria with landing sites (large grey dots A-Kome-Mchangani, B- Kayenze, C- Muhula and D- Muluseni) and fishing locations (small black dots) included in this study and frequency of fishing events per km distance from homeport covered by gillnet fishers (above) and longline fishers (below). N=number of observations; Min, Max=minimum and maximum observed distance (km); SD=standard deviation (km).

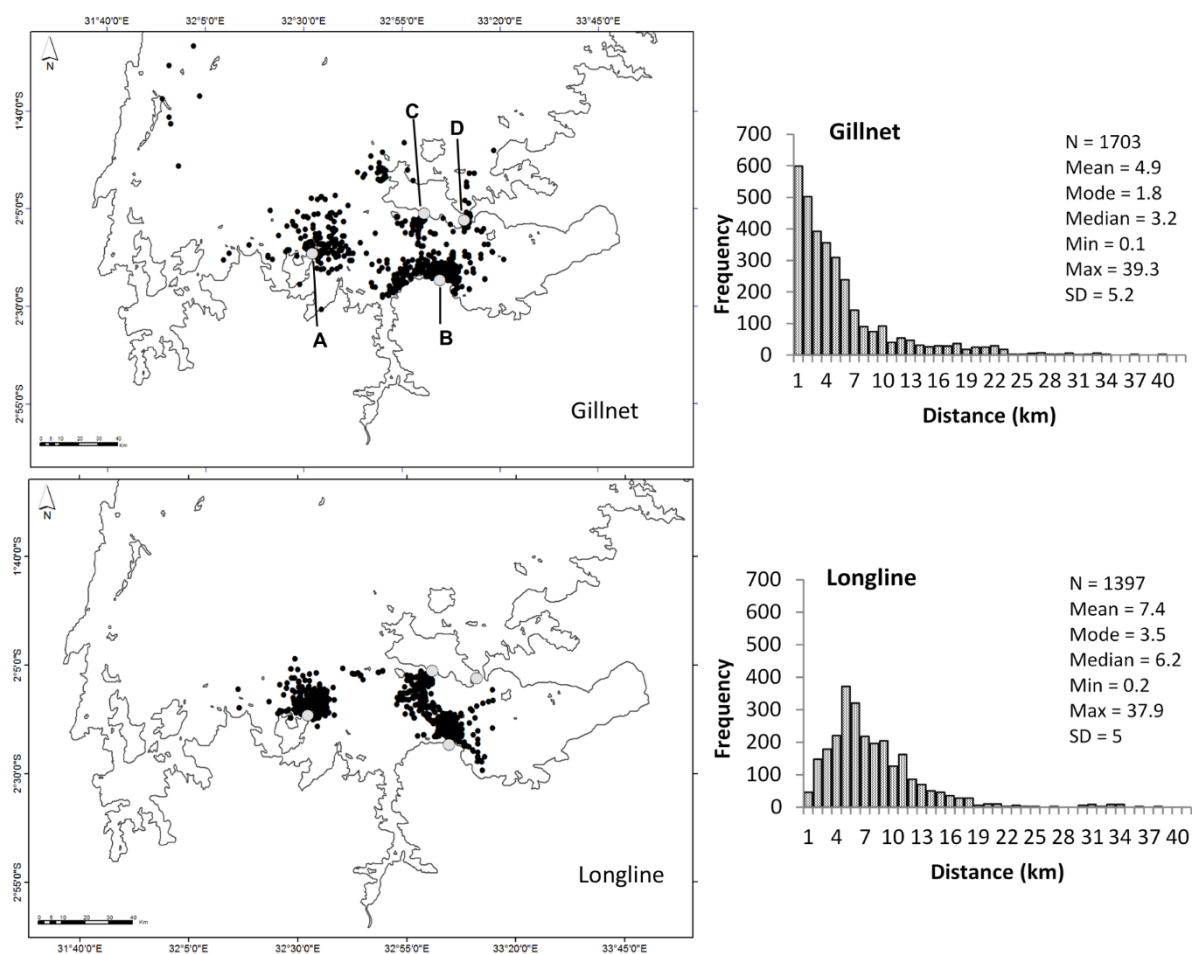


Figure 2: Proportion by year of total number of gillnets by mesh-size and longline hooks by hook-size in Lake Victoria based on frame surveys held between 2010 and 2016 (Anonymous 2017).

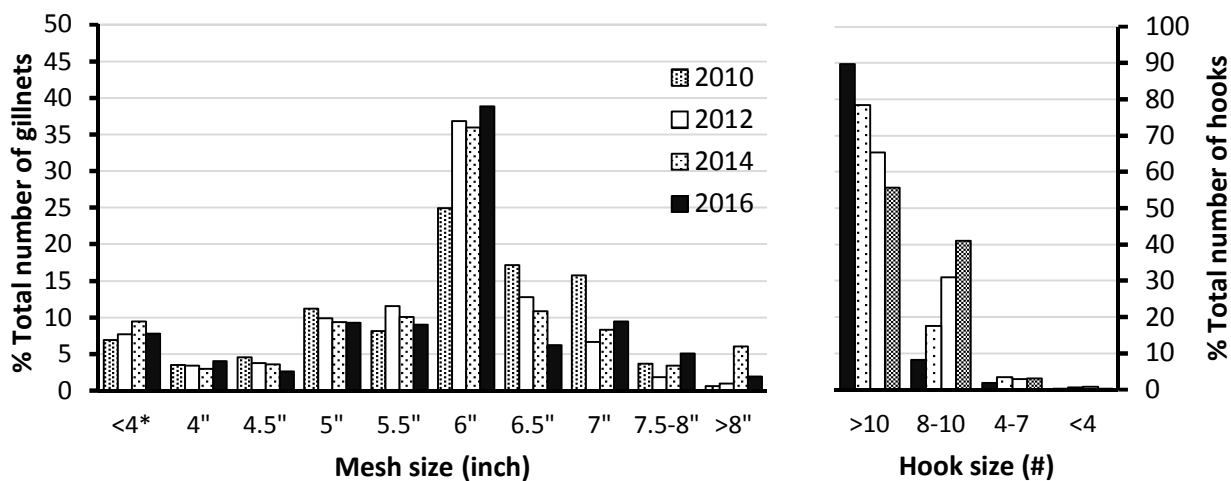


Figure 3: Top: % Frequency distribution of mesh- and hook-sizes used by gillnet and longline fishers in the gulf and open lake region ($N_{\text{meshsize Gulf}}=5404$, $N_{\text{meshsize lake}}=928$, $N_{\text{hooksize Gulf}}=2075$, $N_{\text{hooksize Lake}}=754$). Bottom: Mesh- and hook-size in relation to distance from the homeport, indicating the geometric mean distance (± 2 standard deviations) (circles and error bars) and the average mesh and hook size over distance (lines) by region. Letters indicate significantly different groups of mean distances of mesh size or hook size use based on a Bonferroni corrected multiple comparisons test. Dotted lines are confidence intervals.

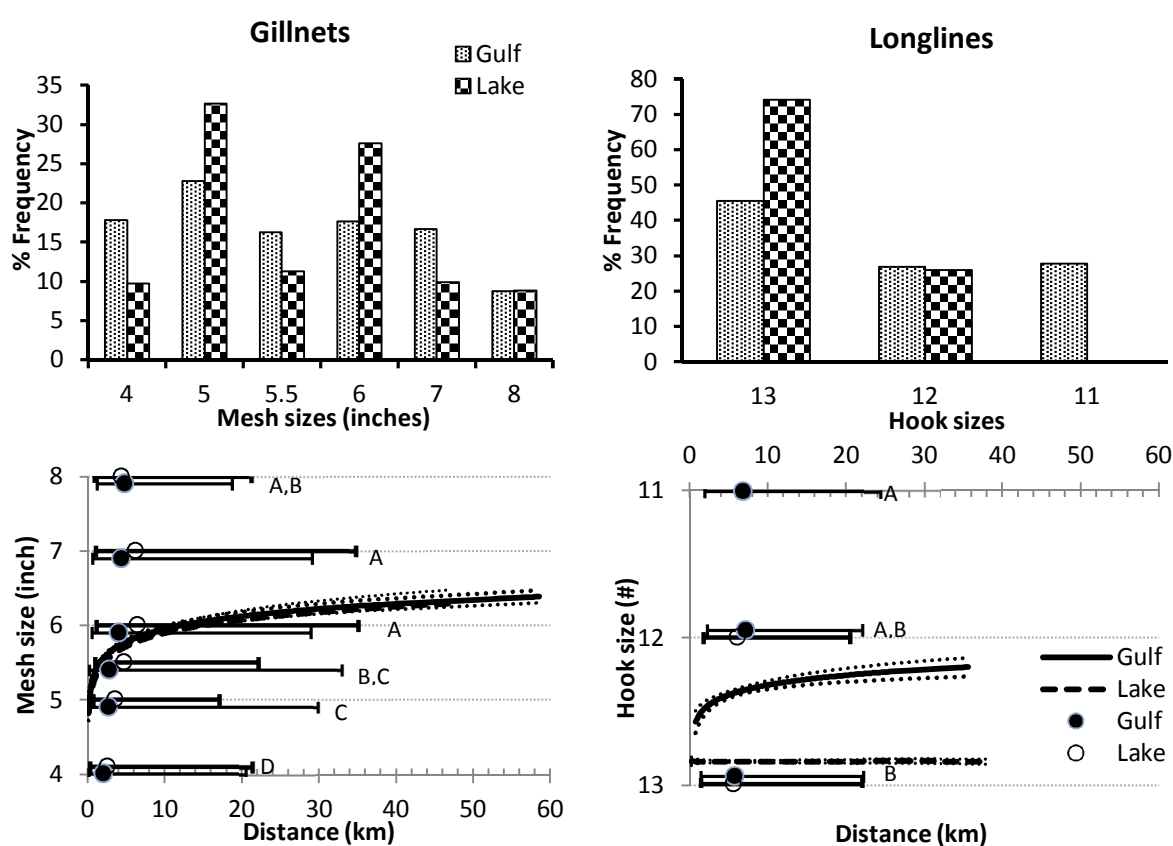


Figure 4: Mean CPUE_{standardised} in weight (left) and number (right) of Nile perch by bait types *Clarias* spp. (N=310), *Rastrineobola argentea* (Dagaa) (N=97), Haplochromines (Haplo) (N=456) and *Synodontis afrofishery* (Synod) (N=455) and hooksize (large= 11, 12) and small (13). Letters indicate significantly different groups of mean CPUE_{observed} based on a Bonferroni corrected multiple comparisons test.

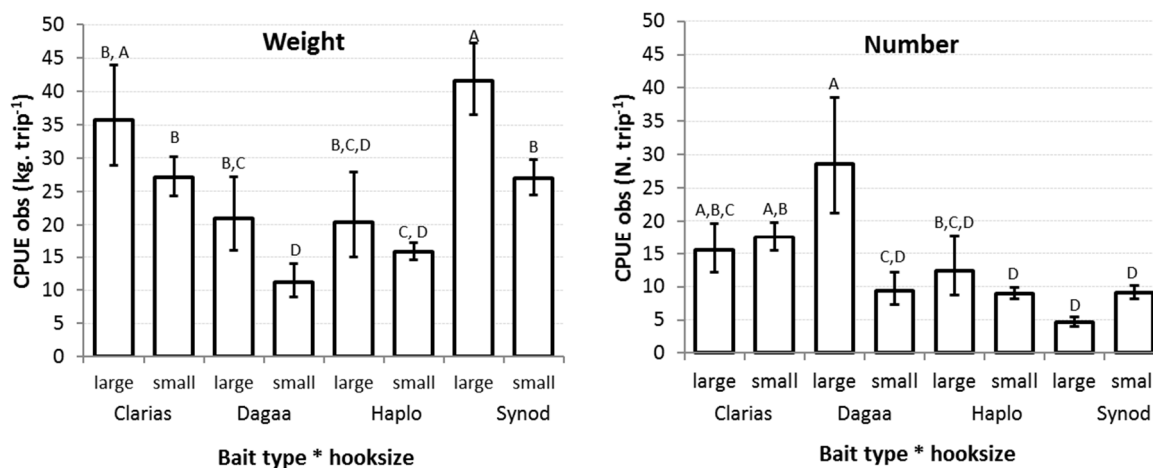


Figure 5: Gillnet fishing encounter rate (P_c calculated at 12000m^2 gillnet and 10hr setting time), patch density ($\text{CPUE}_{\text{non-zero}}$, $\text{kg} \cdot 12000\text{m}^{-2} \cdot 10\text{hr}^{-1}$), and relative density ($\text{CPUE}_{\text{non-zero}} \times P_c$, $\text{kg} \cdot 12000\text{m}^{-2} \cdot 10\text{hr}^{-1}$) by Nile perch size group ($<50, \geq 50\text{cm}$) with distance from the homeport at gear setting depths 4m and 15m in the open lake region (top two rows) and gulf region (bottom two rows). Dotted lines are 95% confidence limits. L= long rain/stratified season, D= dry/mixing season.

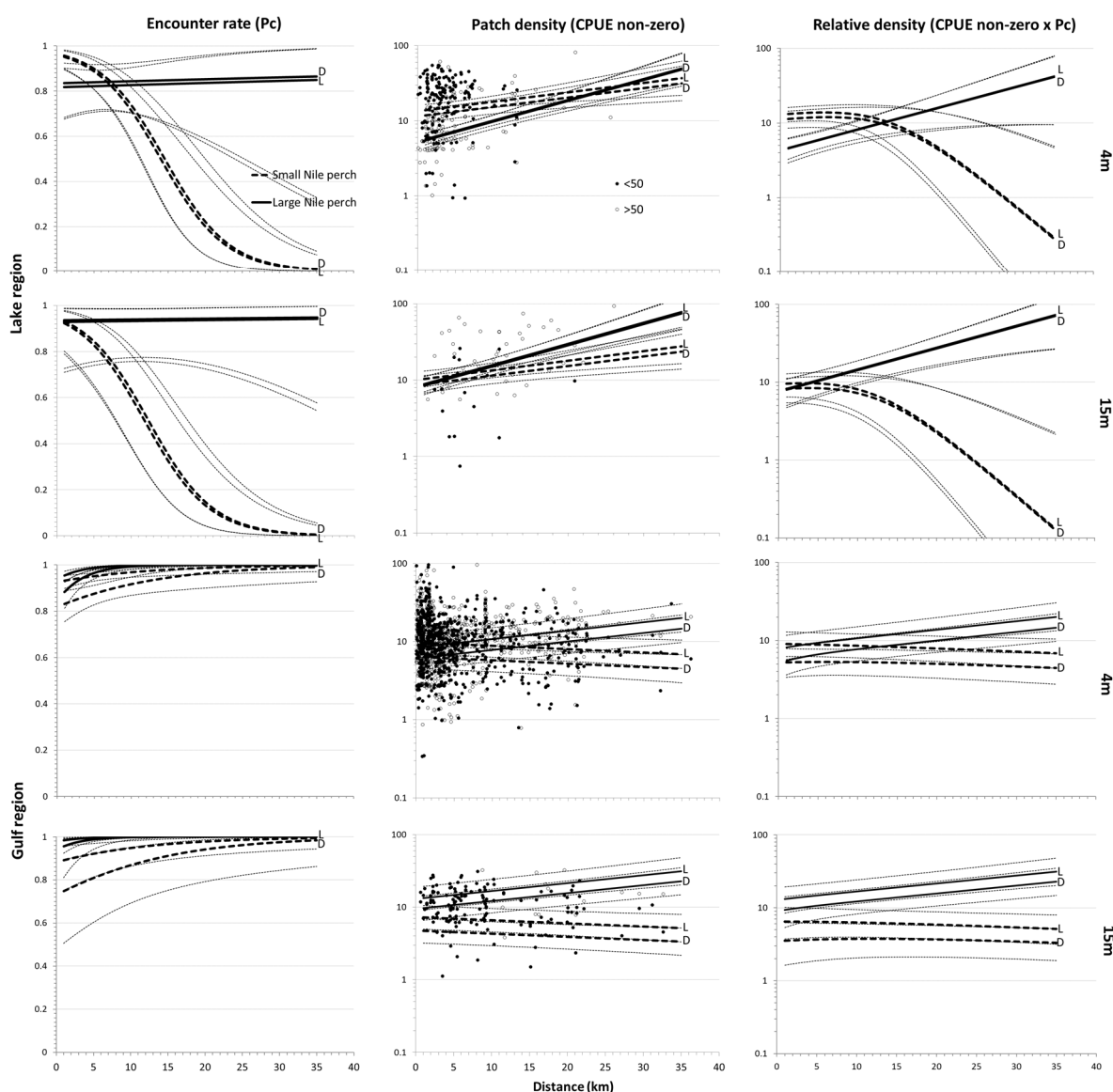


Figure 6: Longline fishing encounter rate (P_c calculated at 800 hooks and 6hr setting time), patch density ($CPUE_{non-zero}$, $kg \cdot 800hooks^{-1} \cdot 6hr^{-1}$), and relative density ($CPUE_{non-zero} \times P_c$, $kg \cdot 800hooks^{-1} \cdot 6hr^{-1}$) by Nile perch size group (<50, >50cm) all with *Synodontis* spp. as bait and hook size small (13) with distance from homeport at gear setting depths 4m and 15m in the open lake region (top two rows) and gulf region (bottom two rows). Dotted lines are 95% confidence limits. L = long rain/stratified season, D= dry/mixing season.

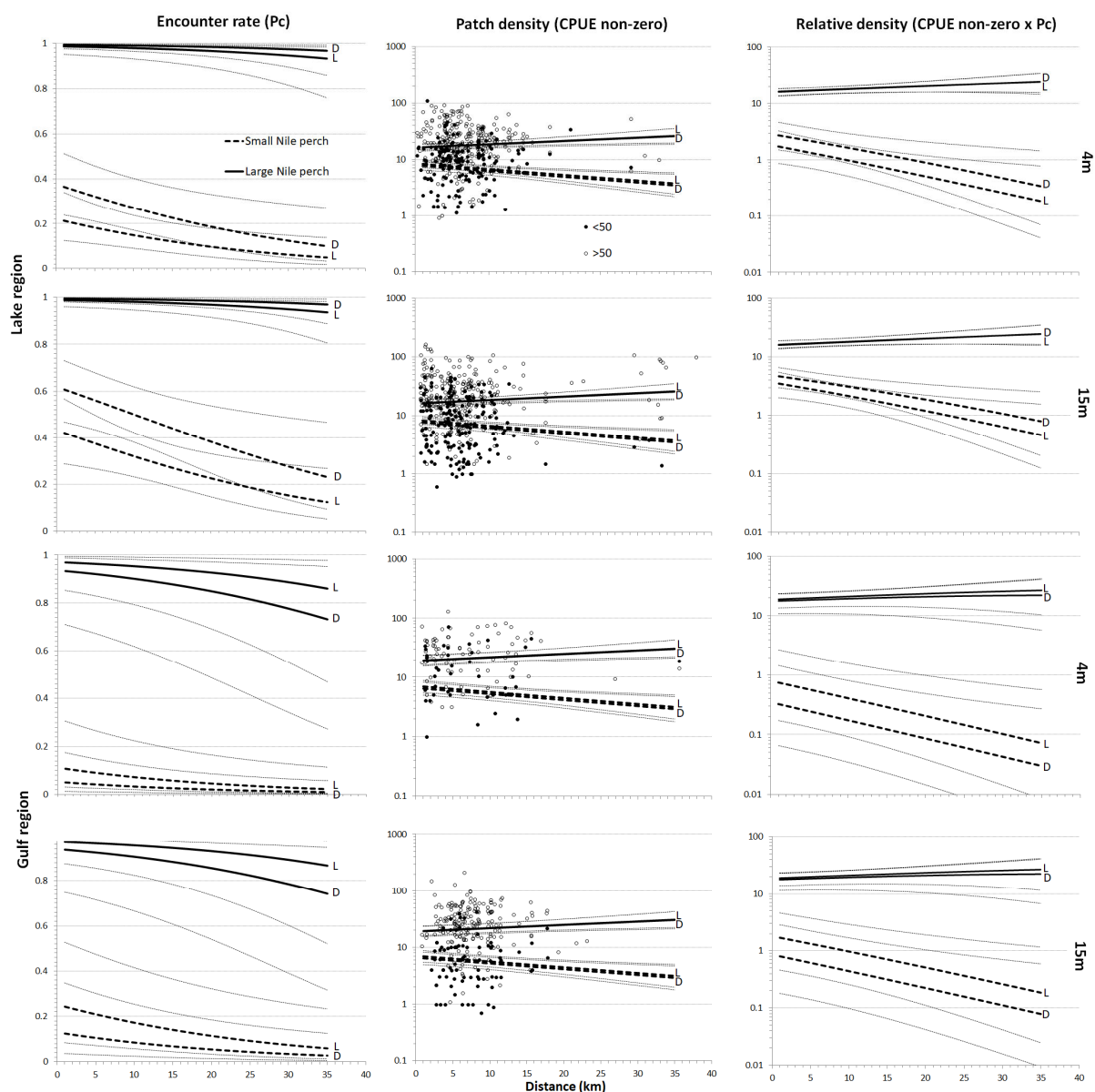


Figure 7: Odds ratios (Log₁₀(odds ratio)) of encounter rates (probabilities of catch) of Nile perch related to region (lake, gulf) season (long, short, dry), size (small Nile perch <50 cm, Large Nile perch ≥50cm), distance (DI, km) and setting depth (SD, m) of gillnets and longlines. Odds of encounter rates are calculated for or compared with the probability of catch at the average distance from the homeport that a gear type is employed (gillnets 5km, longlines=7m) and a setting depth of 4m. Odds ratios are calculated for a gillnet of 1200 m² and 10 hours soak time and for longlines with 800 hooks and soak time 6 hours with *Synodontis* as bait and hook size small. Arrow: odds ratio >999.9

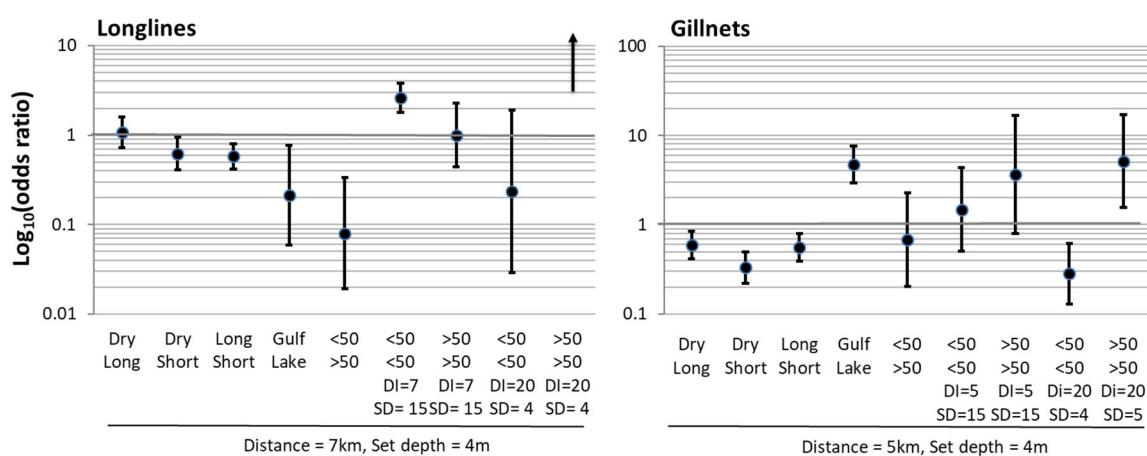


Figure 8: Expected CPUE (kg.trip⁻¹ (left)), number.trip⁻¹ (right)) of Nile perch over the water column summed over large (≥ 50 cm) and small (<50 cm) Nile perch and averaged over 4 and 15m setting depth and the three seasons for longline and gillnet fishers in the Gulf and Lake regions. Horizontal bars: 90% of the trip observations were within the range of distances from the homeport indicated for gillnets (GN, dark gray) and longlines (LL, light gray).

