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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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Abstract

Operational and environmental factors limited available resource space of gillnet and longline fishers targeting Nile perch in the Speke gulf and open lake of southern Lake Victoria and drove their encounter rates with patches of fish resulting in gear specific distributional patterns. Catch-rate patterns were similar by region and gear: large (>50cm) Nile-perch densities increased over distance from homeport and deeper in the water column while small Nile perch (<50cm) densities decreased. Effects of season, (setting) depth and region were present but small and obscured by high variation in daily catch-rates and individual fisher strategies. Both fisheries distributed themselves over the size-productivity spectrum of Nile perch but reacted differently to patterns in size distribution of Nile perch: gillnetters focused more on numbers of productive juveniles between 30-60cm at on average 5km distance (59min travel time) from homeport and longliners on larger sized 40-80cm Nile perch deeper in the water column at 7km (108min). Sampled fishers likely were representative of most of the Nile perch fisheries. If so, this means that fishing pressure is mainly exerted on nearshore lake areas, and more lightly fished offshore areas then may act as a refuge for adult Nile perch. Total catch-rates by gear were generally equalized over the resource space, increasing slightly with distance from homeport, according to ideal free distribution predictions. Nile perch fishers on Lake Victoria appear to distribute themselves according to the underlying productivity distribution of the resource within the constraints of their available resource space.

Keywords

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

Introduction

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

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

We focus on Nile perch from southern Lake Victoria targeted by small-scale gillnet and longline fishers. Nile perch is one of the commercially targeted species in Lake Victoria contributing on average 240,000 ton per year or up to 30% of the total landings (Mkumbo and Marshall 2015). After introduction, the species initially dominated in shallower waters, but over time the abundance of larger fish in deeper waters appeared to be increasing and Nile perch is now found at all depths (Goudswaard et al. 2008, van Zwieten et al. 2016). Adult Nile perch (≥54cm male; ≥76cm female, Hughes (1992), Mkumbo (2007)) are distributed over all habitats while juveniles are more dominant in shallower coastal waters (Katunzi et al. 2006). Nile perch densities change seasonally in relation to stratification patterns: during the stratified season (November to March) densities increase in upper water layers, while during the windy mixing season (June to October) higher densities are encountered in deeper water (Taabu-Munyaho et al. 2013).

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

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

Given the size-selectivity characteristics of their gears, fishers using longlines or gillnets are expected to target different size classes of the Nile perch stock that are in part spatially separated (Chitamwebwa et al. 2009, Msuku et al. 2011). A further differentiation in spatial allocation may be on setting depths of different gears. While Nile perch is found all over the water column highest densities are found in the upper 20m of water in nearshore shallow regions while in coastal and deep waters distribution is more even or bimodal with a deep water peak at 30-40m depth (Cornelissen et al. 2015, Taabu-Munyaho et al. 2013). Reported distributional patterns over the water column are derived from aggregated lake wide acoustic observations, a scale much larger than the individual scales of operation of Nile perch fishers. Such generalized patterns will be obscured for an individual fisher when variability in encounter rates of patches of fish is high due to locality, seasonal environmental effects and species-specific distributional characteristics (van Densen 2001).

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

Materials and methods

Study Area

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

In the southern part of Lake Victoria three seasons are distinguished, during which the lake experience winds of different strength. During the long rains from February-May, there is less or no wind resulting in stratification of the lake and the build-up of deep water hypoxia and anoxia that affects the available habitat for hypoxia-intolerant species like Nile perch (Schofield and Chapman 2000). During the dry period from June-August the lake experiences strong winds that mix up the lake water (Mugidde et al. 2005, Njiru et al. 2011). The short rains from October-January is a transition period from the dry (mixed) to the wet (stratified) season. The pronounced impact of the seasonal wind regime on the mixing of the lake waters are likely to influence size and density distributions of Nile perch.

Logbooks

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

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

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

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

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

Data treatment and statistical analysis.

Data exploration

Data exploration was carried out according to Zuur et al. (2010), in particular by plotting the different response and explanatory variables to detect outliers and examine collinearity between explanatory variables, determine the statistical distribution of the data as well as checking for zero catche166 – 171)s.

Representativeness of logbook fishers

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

Finding an unbiased catch rate and standardization

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

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

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

ε_{ijk}~ iid(N($0, \sigma^2$)),

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

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

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

ε_i~ iid(N($0, \sigma^2$))

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

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

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

While there were no trips with no catch of Nile perch, the two size categories reported in the logbooks were not always caught together on each trip. Therefore, zero daily catches had to be accounted for when analyzing catch-rates by size-category. When catch-rates need to be log-transformed to obtain approximate normality in model residuals, often a low number is added to remove the zeroes (see e.g. (Deroba and Bence 2009)). However, because zero daily catches contain information on the encountered presence of Nile perch we opted to retain them and use a hurdle model to examine factors that determine the relative densities as encounter rate (P_c) times patch density ($CPUE_{st}$). The encounter rate (P_c) was defined as the probability of catch per trip of small or large Nile perch, and was determined by analyzing the presence/absence of a catch through a binary logistic model; patch density (*$CPUE_{st}$*) was defined as the weight (kg) or number of the positive catch per trip and was examined by analyzing the positive catch-rates. A multiplication of the two yielded the catch-rates ($CPUE_{ad} = P_c \times CPUE_{st}$) (kg/trip).

Encounter rates: factors determining the probability of catch

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

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

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

where *i* represents fisher or the combination of fisher and fish size category, *j* is trip, *k* is size category, μ is intercept, B_{ijkl} is the value of the *l*-th categorical variable for category *i*, trip *j* and size *k*, $\gamma(B_{ijkl})$ is the coefficient for that categorical variable, $\beta_{m,}$ is the coefficient of the *m*-th continuous variable, X_{mjk} is the value of the of the *m*-th continuous variable for trip *j*, and size *k*,. The number of categorical and continuous variables included in the model are *z* and *n* respectively. Continuous *X* variables for both gillnets and longlines are distance from homeport to fishing location (km) and setting depth (m). Categorical variables are region (gulf, open lake), season (dry, long, short) and Nile perch size categories (<50cm, ≥50cm). To take account of longline characteristics, the continuous variables $\log_{10}$(hook number), $\log_{10}$(soak-time) and the categorical variables bait (*Clarias*, haplochromines, dagaa, *Synodontis)* and hook-size (large, small) were added to the longline model. For the gillnet model these were $\log_{10}$(net size) and $\log_{10}$(soak-time). Only two-way interactions between all the variables were examined. The error ε_i is assumed independent and normally distributed with average zero and variance $\sigma_a{}^2$.

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

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

Patch densities: factors determining positive standardized catch-rates

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

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

$\varepsilon_i \sim iid(N(0, \sigma_a^2)$

where, $CPUE_{ijk}^{st}$ is the standardized positive catch rate of fisher *i* by size category *k* on the *j*-th fishing day in weight (kg) or number of fish. Other effects are defined as for equation 4 above, excluding the effects of bait type, soak-time, number of hooks, hook-size and net size as these are accounted for in the standardisation step (model 3). Fisher was included as a random effect. The choice of the random effect was examined by the AIC criterion by comparing an intercept only model with a fixed effect model with no random effects included. A range of models was examined through backward selection of the full model based on the AIC criterion, and significance tested on the restricted log-likelihood ratio. The contribution of the random effect to the total variability in the probability of catching Nile perch was tested by examining the Intraclass Correlation Coefficient (ICC) calculated as ICC= $\theta/(\theta+ \theta_{res})$ where θ = estimate of the covariance parameter (intercept) and θ_{res} the residual variability. The significance of the estimate of the covariance intercept parameter was tested using a Wald Z test. As individual fishers can be expected to return to sites with successful catches auto-correlation can be expected to violate the assumption of independence. However, it is less likely that daily catches between fishers are correlated, reducing the impact of auto-correlation when modelling over all data. We checked for the existence of such correlation between fishers in daily catches over successive days which was not the case.

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

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

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

Results

Descriptive results

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

The average (sd) total gillnet size used was 15000 (12000) m^2 (median 12000 m^2) with panels of mesh-sizes ranging from 4″ to 8″. Longlines were equipped with 800 (130) hooks, with hook-sizes 11, 12 and 13. Individual fishers often changed nets and lines between trips resulting in different total net sizes and hook numbers as well as mesh-sizes and hook-sizes per trip. In the gulf area mesh-sizes from 4-7″ were used in about equal proportion (~18%) of the time while 8” mesh-sizes were used in around 8% of the trips; in the open lake area 61% of mesh-sizes used were 5″ and 6″, while mesh-sizes 4″, 5″, 7.5″ and 8″ were used in about equal proportion (app. 10%) of the trips (Fig. 3, top).

Small hook-sizes (13) were dominant in both regions, but more so in the open lake region, while the largest hook-size (11) only was used in the gulf region. All mesh-sizes and hook-sizes were used at all distances from the homeport. Larger meshes and hook-sizes tended to be used further offshore and small mesh-sizes in both regions and small hook-sizes in the gulf region were used more often nearshore up to approximately 5 km (Fig. 3, bottom). In the open lake area on average smaller hook-sizes were used compared to the gulf with no trend in hook-size over distance from the homeport. In subsequent catch-rate analyses hook-sizes were categorised as small (13) and large (11 and 12), as these groups differed significantly in total catch weight ($F_{1,1312}$ = 44.67, P<0.001, r^2 = 0.03). Soak-time for gillnets ranged from 4-15 hr with an average (sd) of 10 (2) hr and longline 2-13 hr with an average of 6 (1) hr.

Standardisation of observed catch-rates

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

The operational factors net size, number of hooks and soak-time all had a significant effect on the size of the catch per trip expressed in weight of fish. Net size and hook-number did not have a significant effect on observed catch per trip in number; only soak-time was significant (Table 2). For both weight and number of Nile perch catch per trip for gillnets were standardized to the median size of a net of 12000 m^2 and a soak-time of 10 hr; for longlines catch per trip in weight was standardized to 800 hooks and a soak-time of 6 hr according to model (3) with parameter estimates as in Table 2.

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

Resource space

The resource space of gillnet and longline fishers overlapped but on average gillnet fishers fished closer to the shore than longline fishers while both appeared to fish over the same range. The distance travelled daily from a homeport to a fishing location for gillnets ranged between 0.1-39.3 km and was on average (sd) 5 (5.6) km; longlines travelled within a range of 0.2-37.9 km with an average (sd) of 7 (5) km (Fig. 1). These calculations included gillnet fishers who temporarily took residence in other areas in the lake and thus appeared to extend their resource space to other areas. However, within those new locations, distances travelled to fishing grounds from the new port fell within the same ranges of their original locations. Fishing operations of fishers who normally operated from the sites around the Speke gulf but who temporarily moved to open lake sites were, in subsequent analyses, considered as open lake operations. Gillnet fishers with engines travelled 6 km (5%-95% range 1.7-21.4 km, N=864) compared to gillnet fishers with paddles 2 km (5%-95% range 0.23-10.5 km, N=945). One of the longline fishers with an engine who was dropped from further analyses travelled on average 5 km (2.3-10.9 km, N=17), suggesting a large overlap in resource space between propulsion types in this fishery.

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

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

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

Distance travelled, and the environmental factor location depth were highly collinear. A regression of $\log_{10}$(depth) for gillnet over region, season with $\log_{10}$(distance) as co-variate was significant ($F_{4,1769} = 1130$, $p<0.001$, $r^2 = 0.59$). Gillnet fishers fished in deeper waters in the open lake region compared to the gulf region irrespective of distance. Seasonality explained a mere <1% of the variation in location depth, where fishers were fishing in slightly deeper waters during the transitional short rain season. For gillnet fishers from the open lake region the most common location depth at 5 km from the shore was 25 m (max. 48 m depth at 40 km) while their colleagues in the gulf were fishing at 13 m depth (max. 25 m depth at around halfway the gulf). Compared to fishers in the open lake region who headed more towards open waters gillnet fishers from the gulf were fishing more often parallel to the shore at a distance from their homeport (Fig. 1). For longlines the relationship was also significant though less clear as distance explained less variation in depth of location while the difference between regions was not as pronounced as with gillnets ($F_{1318,6} = 55.7$, $p<0.001$, $r^2 = 0.20$). The most common fishing depth around the average of 7 km from the homeport for longline fishers from the open lake region was approximately 21 m while their colleagues in the gulf were fishing at 17 m depth. Longline fishers were fishing at slightly deeper waters and hence further from the shore during the windy, dry, season but this accounted for 1.5% of the variation. In the remainder of the analyses, only distance travelled will be considered and used as a proxy for the environmental factor location depth. Setting depth of the two gear-types had limited overlap. Longlines were set about twice as deep (1-24 m; average (sd)=11 (5) m) as gillnets (1-15 m; 5 (3) m).

Random effects: clustering by fisher and size of Nile perch

Before discussing the full models for encounter rate and patch density we first discuss the choice of random effects for these models, as these give insights in the operational strategies of individual fishers. Clustering by fisher×size interaction for models examining encounter rates (model 4) lead to a substantial reduction in AIC compared to the null model (intercept only) and accounted for gillnets and longlines respectively 34% and 44% of the variability (ICC, covariance parameter estimate: $p<0.01$) in the log-odds of catching Nile perch (Table 4). In the final model, that included size and interactions of size with other variables as fixed-effects, the amount of variation explained by the random effect as expressed by the ICC was reduced to 16% and 23% ($p<0.05$), suggesting that a large amount of variability was taken up by size of Nile perch as fixed effect. The fisher×size interaction can be understood not just as variation in skills and operational strategies in location choice of fishers but also because of differences in choice of mesh-sizes and hook-numbers. An in-depth examination of this random effect in the final model showed that for gillnet fishers most variation was found in the odds of catching small Nile perch that varied between 0.3 and 3, while those of large Nile perch varied between 0.7 and 6. However, in all cases but two the odds were not significantly different from 1. The two exceptions were fishers who both had significantly lower odds (0.3) of catching small Nile perch, indicating that they predominantly used larger mesh-sizes or fished further from the shore where large Nile perch predominate, as will be shown below. Similar differences in operational characteristics and apparent choice of hook-sizes were found for longlines. For longlines most variability between fishers again was found in the odds of catching small Nile perch. The odds ranged between 0.2 and 3, while the odds of catching large Nile perched ranged between 0.9 to 6 and were, with three exceptions, not significantly different from 1. The exceptions were a fisher with odds 6 and 0.3 respectively for catching large and small Nile perch and another fisher with low odds (0.2) for catching small Nile perch. Choice of bait or hook-size most likely were not causes of variation as these were accounted for as fixed effect. We checked this by including hook-size and bait as random effects. Co-variance parameter estimates were non-significant when including hook-size ($\theta=0.05$, $Z(2)=0.89$, $p=0.19$) or bait 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 random effect fisher×size ($\theta=0.71$, $Z(18)=1.28$, $p=0.10$). As number of hooks, net size and soak-time were all accounted for as fixed effects, all other fixed effects related to the size category of Nile perch and interactions with size category in encounter rates therefore now can be considered as characteristics of the environment and of gear-Nile perch interactions and thus are most likely not caused by specific differences in skills and operational characteristics of fishers.

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

Encounter rates: fixed effects determining the probability of catch

The final random intercept models examining encounter rates (model 4) included as fixed effects environmental (distance as proxy for depth, setting depth, region, season), operational (distance as proxy for travelling time, soak-time, hook-size, bait, number of hooks and size of nets) factors, Nile perch characteristics (size) and their two-way interactions. These were significantly different from the random intercept model only (Gillnets χ_{diff}^2 = 151.8, p<0.001; Longlines χ_{diff}^2 = 225.1, p<0.001). Both final models were only slightly over-dispersed. During the backward selection procedure many interactions between main effects were removed as well as the main effects soak-time and hook-size and their interaction. The effect of soak-time and hook-size thus was only apparent in the catch densities and not in not the probability of catching Nile perch. Bait-type was retained in the model and apparently overrode the effect of hook-size (Table 4). All further analysis in this section refers to table 4.

Net size and number of hooks had small but significant effects on *Pc* in gillnets and longlines respectively. Pc increased from 97% to almost 100% with an increase in number of hooks from 100 to 1000. In gillnets it increased from 95% to close to 100% for large Nile perch, while for small Nile perch decreased slightly from 99% to 98% with an increase in net area from 100 to 10000 m^2.

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

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

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

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

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

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

Patch density: fixed effects determining positive catch-rates

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

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

Besides region, the spatial factors distance from the homeport, setting depth and interactions of these with size and region, when present, were all significant resulting in increased patch densities and size of large Nile perch a slight decrease in patch densities for small Nile perch with increasing distance. Overall weight and number of large Nile perch in the open lake increased with increasing distance for both gillnets and longlines with respectively 3 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 for both gears with 1.3 kg.trip^{-1} (0.6 fish) per 10 km. Patch densities of small Nile perch in the open lake region increased with increasing distance with 1.4 kg.trip^{-1} (0.9 fish) per 10 km, but decreased slightly with distance from homeport for gillnets in the open lake and for longlines 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 densities for large Nile perch slightly increased in weight and number with deeper net and line sets with respectively 1.9 kg.trip^{-1} (0 fish) and 0.5 kg.trip^{-1} (0.9 fish) per 10 m setting depth. Small Nile perch patch densities for gillnets decreased by 1.1 kg.trip^{-1} (1.5 fish) every 10m depth indicating an increase in individual sizes for gillnets and a slight decrease for longlines.

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

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

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

Factors determining relative biomass and density

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

Size effects dominated spatial patterns of relative biomass and density of catch for both gears and regions (Fig. 5 and 6). Large Nile perch $CPUE_{ad}$ increased in both gears and regions. For longlines, over the first 20 km from homeport, this led to an average increase in catch rate 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 all cases around 4 fish.trip^{-1} were caught. The average weight (length) of large Nile perch thus ranged between 4.5 kg (71 cm) to 5.7 kg (76 cm). Gillnets on average caught less large Nile perch in weight and more in number. Over the first 20 km this amounted to an increase from 9.2 kg.trip^{-1} (6 fish) to 15.4 kg.trip^{-1} (9 fish) in the gulf. A more dramatic increase was observed 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 thus was smaller than caught by longlines: the average weight (length) ranged between1.6 kg.trip^{-1} (52 cm) and 2.1 kg.trip^{-1} (56 cm). Small Nile perch $CPUE_{ad}$ in all cases decreased. In longlines this amounted to a decrease in catch rates in the gulf over 20 km from 1 kg.trip^{-1} (1 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 kg.trip^{-1} (1 fish). This led to an average individual weight (length) range between 1.5kg.trip^{-1} (50cm) to 1.6 kg.trip^{-1} (52cm). In gillnets small Nile perch catch rates in the gulf decreased from 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 kg.trip^{-1} (5 fish). The average individual weight thus was 0.8kg (41cm) to 0.9kg (46cm), again smaller than caught by longlines.

Setting depth had a pronounced effect for large Nile perch on relative biomass and density. In gillnets comparing 4 m and 15 m setting depth over 20 km distance resulted in an 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 lake. Small Nile perch decreased in catch rate with increasing setting depth between 1-2 kg.trip^{-1} and 1-2 fish, with limited seasonal effects. Differences were even more limited for longline catch-rates that over the first 20km from homeport showed an increase of 0.8 kg.trip^{-1} (0.5 fish) 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 of small Nile perch did not change with increased setting depth in weight for large fish, and only slightly increased in number.

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

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

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

Discussion

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

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

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

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

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

Seasonal effects driving Nile perch densities equally had limited informational value for daily fishing decisions. Generally, somewhat elevated Nile perch densities were present during the transitional, short-rain and the stratified, long rain season. Increased densities of Nile perch higher in the water column during the stratified seasons have been observed in acoustic surveys and in seasonally aggregated catch-rates based on catch assessment surveys (Taabu-Munyaho et al. 2013), but also in that case the effect was not strong. This indicates that either the upward movement and resulting change in densities during stratification and in the transitional period during which turnover and mixing of waters takes place was not very strong; or that, in our case, the stratification during the period of our research was not very strong (Cornelissen et al. 2015). Furthermore, no clear evidence for changes in setting-depths or location was found over the seasons indicating that individual fishers do not seem to change their fishing behavior strongly in reaction to the effects of stratification on Nile perch, and that effects may only visible when aggregated over large numbers of fishers.

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

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

In contrast, while the range of Nile perch sizes caught in our study by the different hook-sizes 11-13 does not differ much with the reported modal lengths of 59-62 cm selected by these hook-sizes (Msuku et al. 2011), their reported range in sizes caught of approximately 20-100 cm is high (Chitamwebwa et al. 2009). Chitamwebwa (2009) highlights that the choice of bait has an important effect on Nile perch sizes, and shows the opportunistic character of Nile perch choices in size of food relative to its own size. With hook-sizes 10-12 *Clarias* bait caught Nile perch with a dome shape peaking at 60 cm but with a range of approximately 20-100 cm, whereas haplochromine bait caught the same size range but skewed with a peak at 40 cm. Most likely the condition and size of bait also may have impacts on the catch success (Kumar et al. 2015, Sistiaga et al. 2018), in our case possibly explaining the differences and high variability in catch probability of the different bait types observed. That large Nile perch is caught by the relatively small hooks dominant in the fishery may be explained by the function of bait. Hook-size had no significant effect in encounter rates with Nile perch, while there was a strong interaction between hook-size and bait type. Bait type thus to a large extent determines the catch characteristic of longlines as different bait types attract different species and sizes (Wraith et al. 2013) regardless of hook-size. Furthermore, larger fish have larger feeding ranges and thus may be more successful in competing for bait (Løkkeborg and Bjordal 1992). We do not have the information to further investigate these effects on daily outcomes, but for longlines bet-hedging then shifts to the choice of bait-type in combination with small hook-sizes and remaining relatively close to the shore. By doing so longline fishers still can target large Nile perch using the attraction characteristics of the bait while also making use of the smaller, more productive, size classes encountered closer to the shore.

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

Clear patterns of Nile perch size-distributions thus exist directing fishers decisions in location choice. Although fishers are constrained by their daily movements from a single homeport and limited action radius due to time constraints and propulsion methods, violating the IFD assumption of free movement, overall catch-rates within gears and over gears showed only a limited increase over distance. Thus fishers largely appear to follow the prediction of IFD theory of distribution over space such that resource outcomes are equalized (Gillis et al. 1993, Gillis and van der Lee 2012). As a consequence of the IFD theory, patterns in effort allocation are predicted to follow the underlying size/productivity-spectrum of Nile perch (Plank et al. 2017), which implies that spatial allocation of effort aggregated over all fishers and time will reflect the underlying productivity distribution of a resource. Other than size, Nile perch densities are only to a limited extent explained by other spatial and temporal environmental signals factors indicating that these only have limited value in driving location choice of fishers. Thus, fishers can then be expected to distribute themselves over the resource where renewal rates are highest, if revenues per kg of fish do not differ much between sizes. Natugonza et al. (2016) estimated the P/B ratio of juvenile Nile perch, in their study defined as <40 cm, at 3.5 $year^{-1}$, while adult Nile perch (>40 cm) had a P/B=0.92 $year^{-1}$. Productivity of 30-50 cm juvenile Nile perch, the main target in the fishery, thus is high, and this size range is found within the 10 km distance from the shore in which most fishing takes place.

As Natugonza et al. (2016) showed, current exploitation patterns in Lake Victoria are skewed to the least productive higher trophic level categories including large Nile perch, with significantly less fishing occurring at the most productive lower trophic level categories including small Nile perch. While enforcement up till recently[1] has been weak, mesh size regulations still appear to form a constraint on the use of smaller mesh-sizes, as attested by the distribution of mesh-sizes over the open lake peaking at 6 inches (152mm) (Fig. 2). The 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.

>10 onwards suggests that Lake Victoria's fishing patterns were distributed proportionally to the productivity spectrum of the resources. Overall fishing pressure was higher in the enclosed gulf compared to the open lake region (Anonymous 2017). Our starting point in contrasting open lake and gulf regions that this would lead to lower catch-rates and higher competition over resources while fishers would distribute over a larger resource space was not observed in this study. Despite the higher fishing pressure, catch-rates in gulf and open lake regions were highly similar and fishing strategies and resulting fishing patterns may currently be optimised in a trade-off between operational costs and expected outcomes at locations where renewal rates of Nile perch are high. If the fishers of our study indeed are representative of the Nile perch fishery around the lake, as we suggest they are, this would mean that currently a large part of the open lake and even the middle part of the gulf's surface and deeper waters are only lightly fished and thus could serve as refuge for less productive large Nile perch. Current gear regulations, if enforced, force gillnet and longline fishers to focus on the lower productive adult Nile perch stock further from the shore and deeper in the water column. Without concurrent effort regulations to reduce the number of fishers this may be 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)	G1	E	271	14	17	59	16	66
02° 23.335' S	G2	E	205	13	22	48	22	49
33° 4.730' E	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)	G4	E	188	4	19	70	24	70
02° 8.265' S	G5	E (189), P	217	51	21	86	18	81
33° 11.054' S	G6	E (79), P	198	6	32	77	21	79
Muhula (Open lake)	L3	P	239	11	40	93	17	115
	L4	P	272	1	37	81	12	111
02° 4.993'S								
32° 57.44 E	G7	E (105), P	227	0	28	43	22	45
Buhama (Open lake)	G8	E (102), P	122	46	25	76	15	71
	L5	P	107	30	37	49	18	54
2° 16.652' E	L6	P	151	0	34	68	17	77
33° 32.172' S	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 12000m^2 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, r^2= coefficient of determination, Hs=Hook size.

Gear type	Nile perch	*Net size /N hooks (β₁)*	Soak time (β₂)	Bait	Hook size	Bait*Hs	N	Df model	F	r^2
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 kg.trip^{-1} and number.trip^{-1}. The median trip duration and effort for longlines is 6hrs with 800 hooks and for gillnet is 10hrs with 12000m^2 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.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
kg.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)	NA, NH	1.5	0.51	2.5	**0.003**	1.75	0.14	3.37	**0.033**
Bait[1]	*Clarias*					-2.31	-3.88	-0.74	**0.004**
	Dagaa					-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	$\chi 2/df$	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, [4]Region: 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		**Gillnet Patch density (Weight)**				**Longline Patch density (Weight)**				**Gillnet Patch density (Number)**				**Longline Patch density (Number)**			
	Effect	*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				

Random effects		*Null model*	*Random intercept.*	*Final model*	*Null model*	*Random intercept.*	*Final model*	*Null model*	*Random intercept*	*Final model*	*Null model*	*Random intercept.*	*Final model*
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}
Diagnostics													
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	$1819.5^{\S}$	2531.8	2517.2	$2131.4^{\S}$	3006.5	2904.2	$2040.8^{\S}$	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).

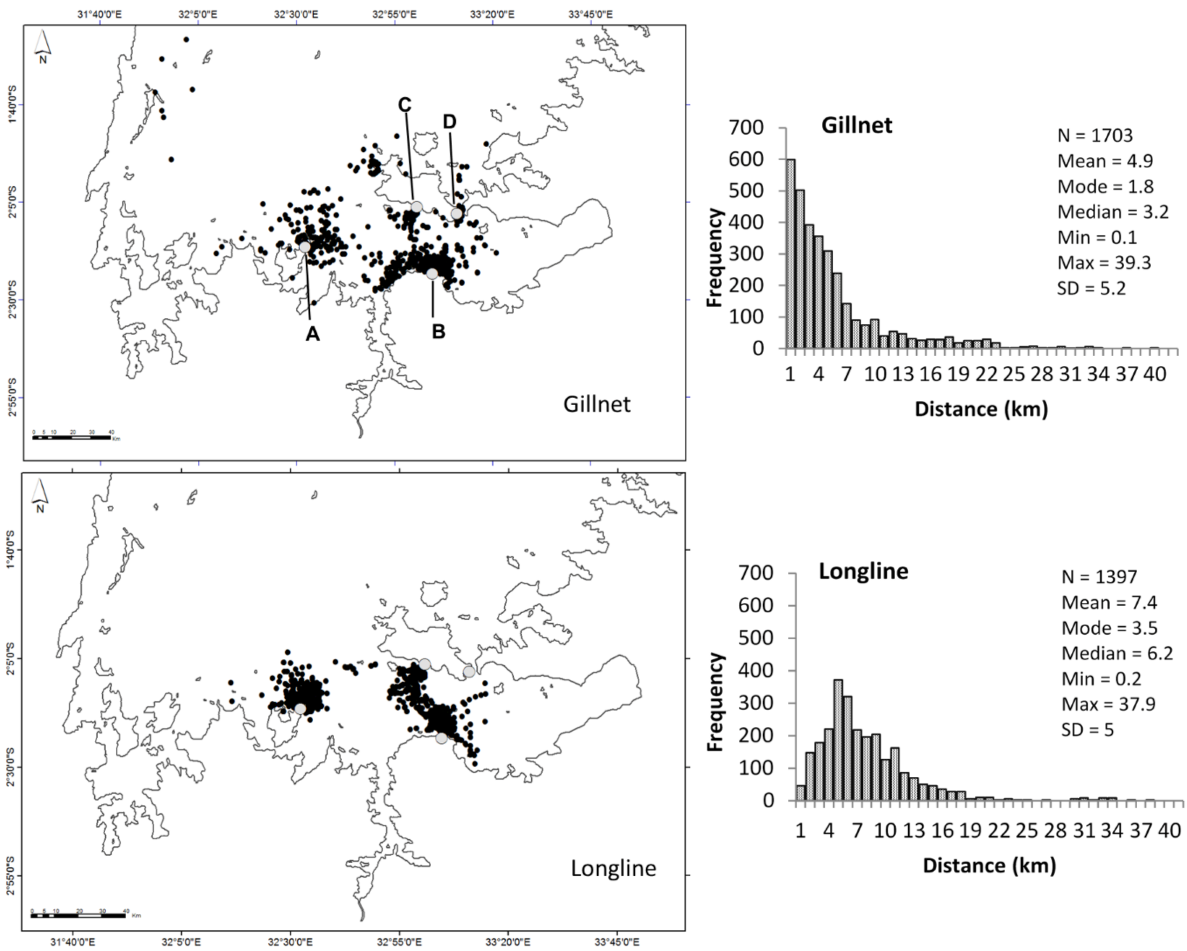

Figure 2: Proportion by year of total number of gillnets by mesh-size and longline hooks by hook-size in Lake Victoria based on frame surveys held between 2010 and 2016 (Anonymous 2017).

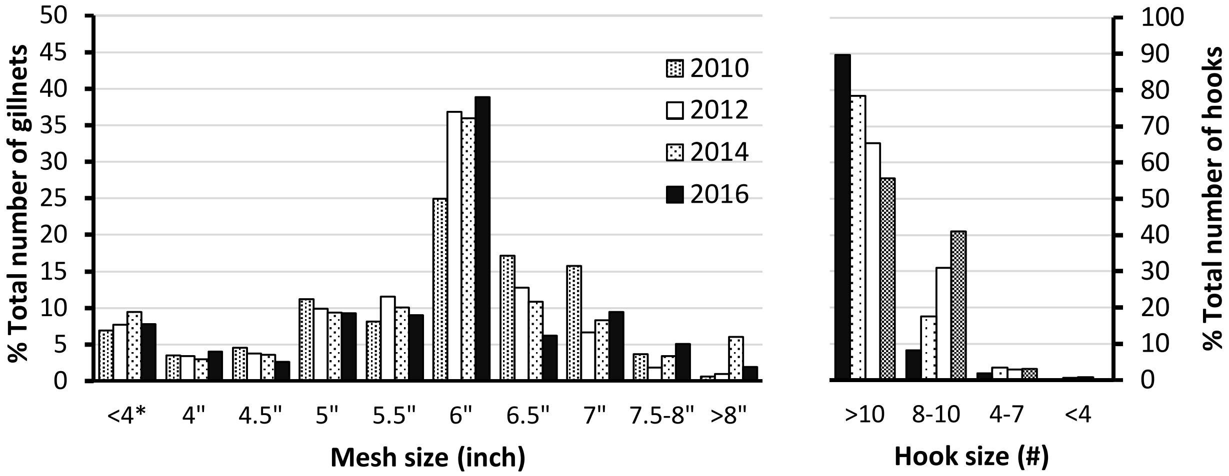

Figure 3: Top: % Frequency distribution of mesh- and hook-sizes used by gillnet and longline fishers in the gulf and open lake region ($N_{meshsize\ Gulf}$ =5404, $N_{meshsize\ lake}$ =928, $N_{hooksize\ Gulf}$ =2075, $N_{hooksize\ Lake}$=754). Bottom: Mesh- and hook-size in relation to distance from 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.

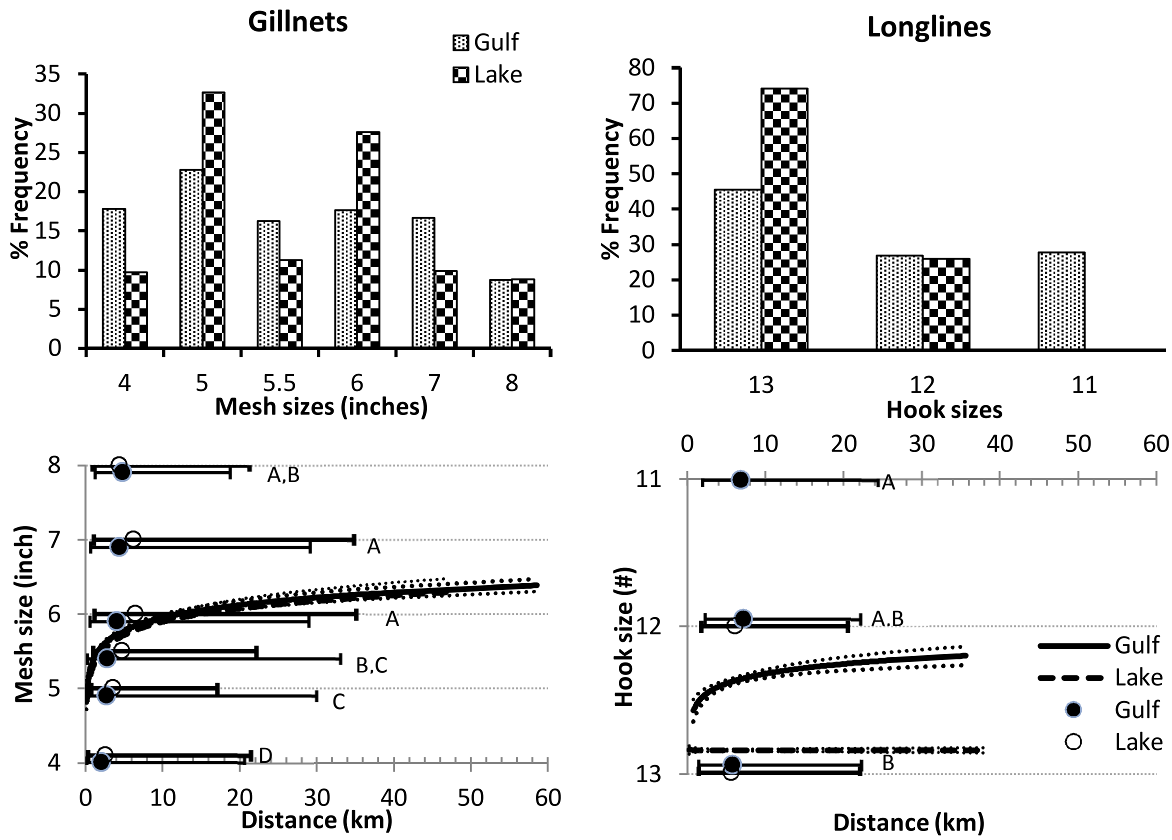

Figure 4: Mean $CPUE_{stdardised}$ in weight (left) and number (right) of Nile perch by bait types *Clarias* spp. (N=310), *Rastrineobola argentea* (Dagaa) (N=97), Haplochromines (Haplo) (N=456) and *Synodontis afrofishery* (Synod) (N=455) and hooksize (large= 11, 12) and small (13). Letters indicate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

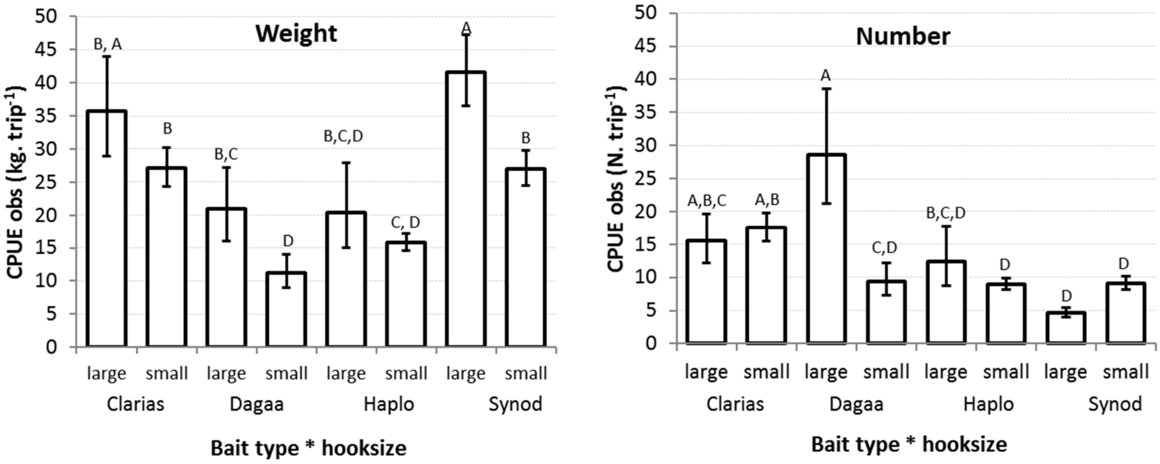

Figure 5: Gillnet fishing encounter rate (P_c calculated at 12000m^2 gillnet and10hr setting time), patch density ($CPUE_{non-zero}$, kg·12000m^{-2}.10hr^{-1}), and relative density ($CPUE_{non-zero}$ x P_c, kg·12000m^{-2}.10hr^{-1}) by Nile perch size group (<50, ≥50cm) with distance from the homeport 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.

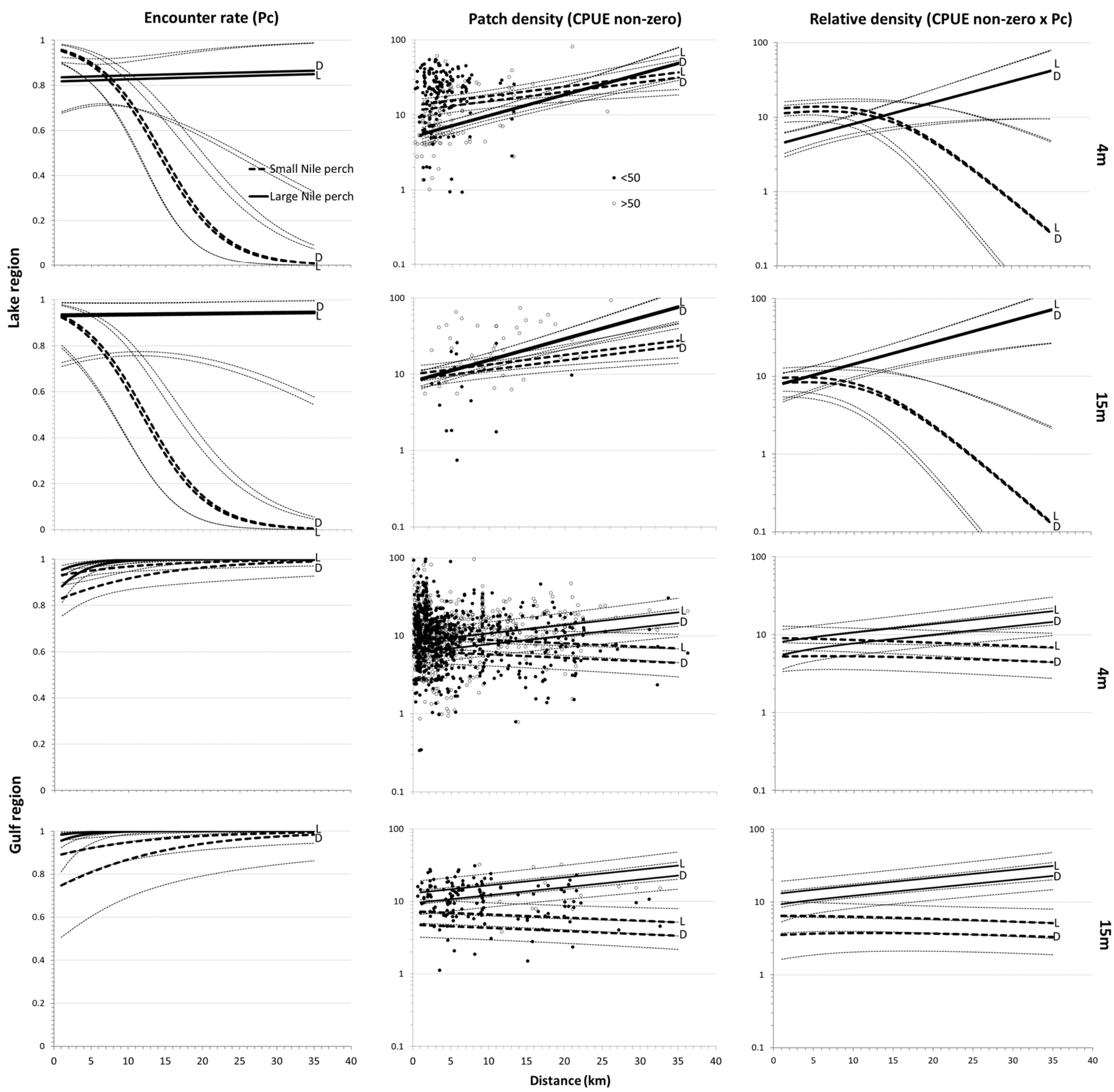

Figure 6: Longline fishing encounter rate (P_c calculated at 800 hooks and 6hr setting time), patch density ($CPUE_{non\text{-}zero}$, kg·800hooks^{-1}.6hr^{-1}), and relative density ($CPUE_{non\text{-}zero}$ x P_c, kg·800hooks^{-1}.6hr^{-1}) by Nile perch size group (<50, >50cm) all with *Synodontis* 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.

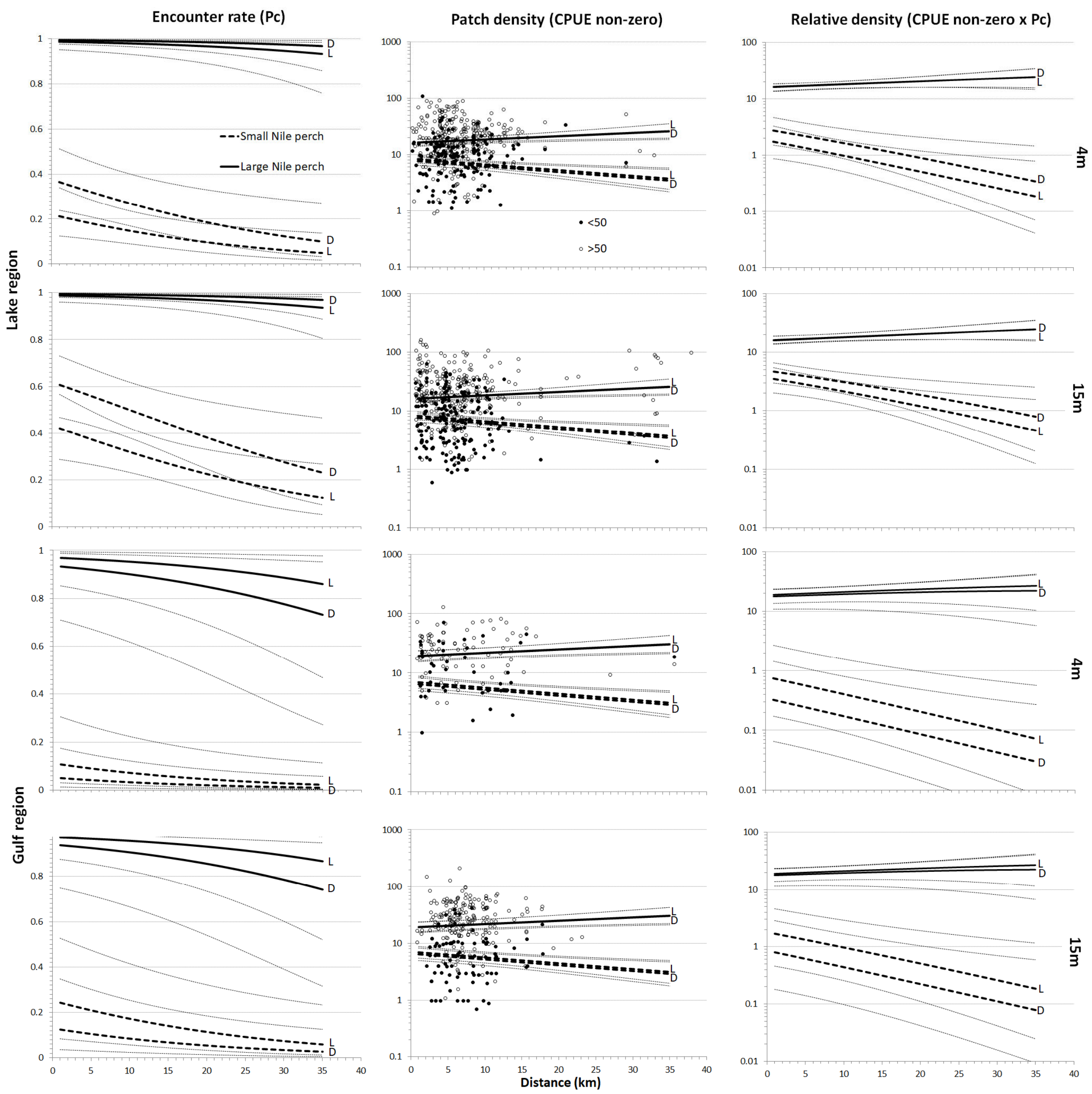

Figure 7: Odds ratios (Log10(odds ratio)) of encounter rates (probabilities of catch) of Nile perch related to region (lake, gulf) season (long, short, dry), size (small Nile perch <50 cm, Large Nile perch ≥50cm), distance (DI, km) and setting depth (SD, m) of gillnets and longlines. Odds of encounter 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 m[2] 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

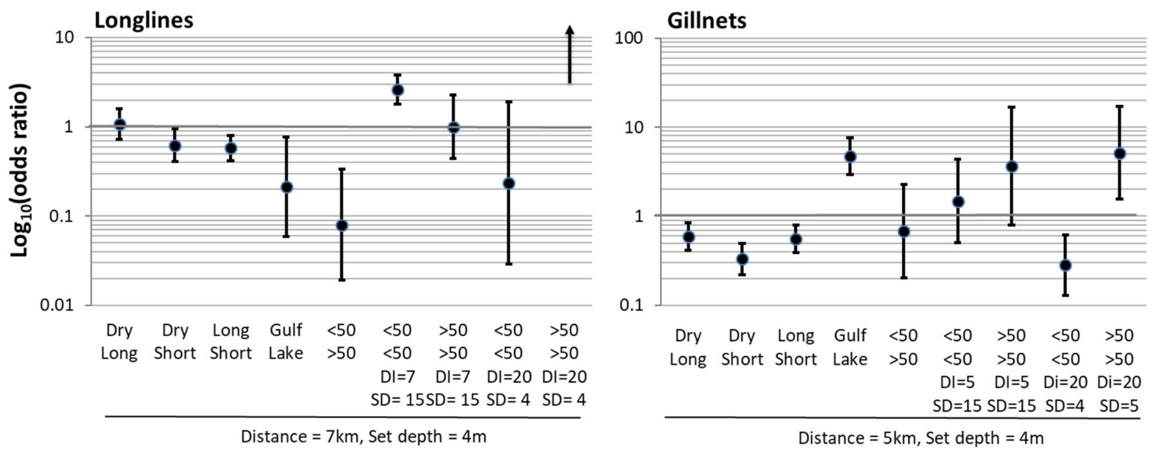

Figure 8: Expected CPUE (kg.trip^{-1} (left)), number.trip^{-1} (right)) of Nile perch over the water column summed over large (≥50 cm) and small (<50 cm) Nile perch and averaged over 4 and 15m setting depth and the three seasons for longline and gillnet fishers in the Gulf and Lake regions. Horizontal 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).