



Canadian Journal of Fisheries and Aquatic Sciences  
Journal canadien des sciences halieutiques et aquatiques

# Maximizing fisheries yields while maintaining community structure

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0098.R2
Manuscript Type:	Article
Date Submitted by the Author:	31-Aug-2015
Complete List of Authors:	Kolding, Jeppe; University of Bergen, Department of Biology Jacobsen, Nis S; DTU Aqua, Andersen, Ken; Technical University of Denmark, National Institute of Aquatic Resources van Zwieten, Paul; Wageningen University, Aquaculture and Fisheries Group
Keyword:	SMALL-SCALE FISHERIES < General, MANAGEMENT < General, MODELS < General, Selectivity, Balanced harvesting

SCHOLARONE™  
Manuscripts

## Maximizing fisheries yields while maintaining community structure

Jeppe Kolding<sup>1,2</sup>, Nis Sand Jacobsen<sup>3</sup>, Ken H. Andersen<sup>3</sup>, Paul A.M. van Zwieten<sup>4</sup>

<sup>1</sup>Department of Biology, University of Bergen, PO Box 7800, N-5020 Bergen, Norway

<sup>2</sup>Hjort Centre for Marine Ecosystem Dynamics, 5817 Bergen, Norway

<sup>3</sup>Centre for Ocean Life, DTU AQUA, Jægersborg Allé 1, 2920 Charlottenlund, Denmark

<sup>4</sup>Aquaculture and Fisheries Group, Wageningen University, PO Box 338, 6700AH Wageningen, The Netherlands

Draft

## Abstract

Under the Ecosystem Approach to Fisheries an optimal fishing pattern is one that gives the highest possible yield while causing the least structural impact on the community. Unregulated, open access African inland fisheries have been observed to sustain high catches by harvesting a broad spectrum of species and sizes, often in conflict with current management regulations in terms of mesh and gear regulations. Using a size and trait-based model we explore whether such exploitation patterns are commensurable with the Ecosystem Approach to Fisheries, by comparing the impacts on size spectrum slope and yield with the different size limit regimes employed in the Zambian and Zimbabwean side of man-made Lake Kariba. Long-term multispecies data under fished and unfished conditions are used to compare and validate the model results. Both model and observations show that the highest yields and low structural impact on the ecosystem are obtained by targeting small individuals in the community. These results call for a re-evaluation of the size based management regulations that are ubiquitous in most fisheries.

Keywords: Small-scale fisheries, Fisheries management, Models, Selectivity, Balanced harvesting

## Introduction

Size selectivity is deeply rooted in fisheries theory and it has been a long standing policy in fisheries management to protect the juveniles and target the adults (Caddy 1999; Kolding and van Zwieten 2011). These regulations are justified by the results of the traditional yield-per-recruit models (Beverton and Holt 1957) that are widely used for simulations to optimize relative yields as a function of entry-age and fishing pressure in single species assessments. The notion of growth-overfishing by harvesting juvenile fish is a result of these models and has become a universally accepted truism for promoting targeting adults only. That so-called non-selective fisheries or indiscriminate fisheries are destructive and depleting stocks is so paradigmatic that it usually does not warrant any verification. Yet, there is increasing evidence that the selective removal of adult fish causes adverse consequences, and does not achieve the global official goal of maximizing sustainable yields (UNCLOS 1982; WSSD 2002) but instead causes destabilizing changes in the structure of exploited populations and communities (Pope 1991; Anderson et al. 2008; Hsieh et al. 2010; Zhou et al. 2010; Garcia et al. 2012; Law et al. 2012, 2014).

But maximizing yields is not the only global goal for fisheries management. The main objective of the internationally agreed Convention of Biological Diversity (CBD 1992) is to develop strategies for the conservation and sustainable use of biological diversity in an equitable way, and the so-called “Ecosystem Approach” is the primary framework for reaching these objectives (UNEP 2000). A priority target of the ecosystem approach is to maintain ecosystem services while conserving the ecosystem structure and functioning (Malawi principle 5). The rationale is that ecosystem function and resilience depends on a dynamic relationship within species, between species and their abiotic environment, so that the conservation of these interactions and processes is of greater significance for the long-term maintenance of biological diversity than simple protection of species (UNEP/CBD/COP 1998). Thus one of the cardinal questions in the use of renewable biological resources for an expanding human

population is how we maximize food production, while making least structural and functional disturbance to ecosystems.

To mitigate many of the adverse ecological effects of selective fishing, while supporting sustainable fisheries it has been suggested to adopt a balanced harvesting strategy that distributes moderate fishing pressure across the widest possible range of species, stocks, and sizes of an ecosystem, in proportion to their natural productivity (Garcia et al. 2012). Such a strategy would prescribe a higher fishing mortality on small fast growing individuals and species than on larger slow growing individuals. While there are several studies that theoretically support this strategy (Law et al. 2012, 2013, 2014; Jacobsen et al. 2014), there are few empirical examples to serve as evidence. One exception is the fishing pattern observed in several high-yielding small-scale inland fisheries in Africa, where the relative proportion of the components in the fish community has been largely maintained by a balanced reduction of all species and size groups (Misund et al. 2002; Kolding et al. 2003a, 2003b; Kolding and van Zwieten 2011, 2014). This less selective fishing pattern is achieved by combining a large range of different mesh sizes and gear types, often with a strong focus on small species and sizes (Kolding et al. 2015a) as they are the most productive and return the highest relative catch per unit effort for the individual fisher. Such a fishing pattern, which typically involves ‘indiscriminate’ fishing methods, however, is under current management paradigms considered unethical, destructive and often technically illegal, and as a consequence there are often strong conflicts within and between fishers and managers, even under co-management situations (Kolding et al. 2014). Actually, artisanal inland fisheries are considered the least successfully managed fisheries in a recent global meta-analysis (Gutiérrez et al. 2011).

The aim of this paper is to examine the consequences of selective and less-selective fishing patterns in terms of total yield and community structure. We use the case of man-made Lake Kariba (Fig. 1) which for historic and political reasons has experienced very different management regimes on its two shores in

Zimbabwe and Zambia respectively (Kolding et al. 2003a): while Zimbabwe successfully enforced gear regulations and effort control until recently, the Zambian side can be considered an open access fishery with no enforcement of technical regulations. We therefore have an example where one half of the same ecosystem is managed by enforcing a selective fishing pattern (Zimbabwe) and the other half employs a less-selective fishing pattern (Zambia). We apply a recent trait- and size-based multi-species model of the fish community (Andersen and Pedersen 2010) which is particularly suited to make an impact assessment of size-selective fisheries in diverse communities (Andersen and Rice 2010) as it specifically accounts for individual energy budgets, and thus captures the indirect effects of the change in community structure a fishery might cause. The model is calibrated to the fishing pattern, effort and community structure observed on the two shores of Lake Kariba. We use the model to calculate the yield and community structure under different fishing patterns and levels of fishing mortality. The results confirm the observations that high fishing mortality on small and juvenile fish can give high yields with limited changes to the community structure.

## Methods

### *Lake Kariba*

The data are from Lake Kariba (5300 km<sup>2</sup>), on the Zambezi River, Southern Africa, which is the world's largest man-made reservoir by volume (180 km<sup>3</sup>) and approximately equally shared between Zambia on the Northern bank and Zimbabwe on the Southern (Fig.1). The Zambezi River provides about 80% of the water inflow and there is a natural limnological gradient in the lake ecosystem from riverine characteristics in the shallow effluent east, which gradually change into a more lacustrine environment near the 120 m dam wall to the west. The gradient in the lake is also reflected in the fish communities which are dominated by potamodromous species in the east (Cyprinidae and Distichodontidae) and by more sedentary cichlids in the western basins (Begg 1974). For cultural and political reasons, the two sides of the lake have been exposed to very different management regimes, which in retrospective can be

considered a grand-scale ecological experiment (Kolding et al. 2003a). While the Zimbabwean side has been strictly managed and controlled in terms of licensed fishers, restricted fishing grounds, and minimum mesh-size regulations, the Zambian side has virtually been an open access fishery with no enforcement of regulations since its independence in 1964. The result has been two very different scenarios of development of the inshore stocks (Fig. 2), which can be considered homologous but mutually independent as very few of the demersal, originally riverine, species venture across the deep pelagic zone created by the lake (Ngalande 1995; Kolding et al. 2003a). Actually, the pelagic middle of the lake was uninhabited by fish until the introduction of the Tanganyika clupeid (*Limnothrissa miodon* or kapenta) in 1967-68 to fill out this vacant niche. Presently, the kapenta fishery is the largest on the lake, yielding about 30,000 metric tons per year, and has virtually no bycatch of the inshore species (Nyikahadzoi and Råkjær 2014). While the overall fish biomass has been fluctuating due to environmental climate driven variation (Karengere and Kolding 1995a, 1995b), the long-term trend (measured as standardized catch per unit effort, CPUE) in the Zimbabwe inshore fishery is stable (Fig. 2A) whereas it has declined exponentially in Zambia (Fig. 2B) in accordance with the usual expectations of increased effort. Total number of recorded nets over the period under investigation (1980-1994) is about 7 times higher in Zambia compared to Zimbabwe and the corresponding average annual yield is approximately 6000 metric tons in Zambia versus 1200 tons in Zimbabwe (Kolding et al. 2003a). The average catch rates of the fishers (kg per 50 m net) are about 2.7 in Zimbabwe compared to 2.0 in Zambia (Fig. 2). The relatively small difference in catch rates despite the large differences in effort and biomass is obtained by the Zambian fishers using a suite of smaller mesh sizes starting from around 2 inch (50 mm), while the Zimbabwean fishers are obeying the minimum legal mesh size of 4 inch (102 mm) stretched mesh and above (Fig. 3).

Experimental fishing from the respective management institutions on each side (the Department of Fisheries in Zambia and Department of Natural Park and Wildlife Services in Zimbabwe) has been

performed regularly over the whole period in i) a protected area with no other fishing near the town of Kariba in Zimbabwe, and ii) on the fishing grounds close to Sinazongwe in Zambia from 1980 and onwards (Fig. 1). These data are described in detail in Karengu (1992), Musando (1996) and Songore (2002) and summarized in Kolding et al. (2003a). The experimental fishing consists of standardized multifilament gillnet fleets with 13 mesh sizes ranging from 1 to 7 inches in half inch (13 mm) steps. All fish from the experimental fishing are recorded by length, weight, sex, gonadal stage and mesh size they were caught in. The experimental fish data, covering the period 1980-1994, where the sampling design was homogenous and standardized on both sides of the lake consists of nearly 75,000 fish from 1059 samples from the unfished area in Zimbabwe and close to 50,000 fish from 958 samples from the fished area in Zambia. Both data sets are trimmed to cover the 9 mesh sizes (13 mm increments) in the 50-152 mm range to correspond with the artisanal fishery. Thus, in summary, we have four separate time series of information (Fig. 2): artisanal catch and effort from two different and separate management regimes in the same lake and experimental catch and effort with individual species demographic data, from an unfished area (serving as baseline) and a heavily fished area. The fish species diversity has gradually increased in the lake since its creation (Kolding and Songore 2003), with no significant differences between the two sides (Musando 1996; Kolding et al. 2003a), and the species composition in both the experimental fishery (Fig. 4) and the artisanal fishery (Fig. 5), is practically identical on both sides along the gradient, albeit the Zambian fishery contains a higher proportion of small species due to smaller mesh sizes. Thus the only significant difference between the two sides of the lake is the standing fish density and total landings.

#### *Size-based model*

The model is size- and trait-based and calculates the number-distribution of fish as a function of their size  $w$  and their maximum asymptotic size  $W_{\infty}$  as:  $N(w, W_{\infty})$ . The model is based on a few ecological assumptions, which are formalized in a set of mathematical equations (Table 2). The general model is



described in detail in Hartvig et al (2011) and the specific setup used here in Jacobsen et al (2014) with a set of parameters calibrated to Lake Kariba (Table 1). Assumptions are made only at the level of the individuals in terms of their physiology, their encounter with prey, and their reproductive capability. The central assumption is that big individuals eat smaller individuals with a log-normal size-preference (Ursin 1973; M1). The size-preference is used to determine the amount of food that an individual encounters, which depends on a search rate that scales with individual weight (M2) and the available prey (M3). Encountered prey is consumed with a functional response that sets the feeding level of an individual (M4-5), which is a dimensionless number between 0 and 1 and a measure of satiation. Consumed food is channeled into growth (M6), and, if the individual is mature (M7), energy is used for reproduction (M8-9). To maintain coexistence of all asymptotic size groups, recruitment is limited by a Beverton-Holt stock-recruitment relationship (M10). The consumption of the larger individuals is translated into corresponding predation mortality on the smaller individuals (M11), such that there is a mass-balance between consumption (and thus growth) and mortality. Prey for the smallest individuals are accounted for by a resource spectrum of plankton with semi-chemostatic growth (M14-15). The individual-level processes are scaled up to the community level by means of the McKendrick-von Foerster equation (M16).

The model is calibrated to Lake Kariba by 1) adjusting the carrying capacity of the resource  $\kappa$  such that the simulated yields are in the correct range, and 2) correcting the maximum uptake rate ( $h$ , eq. M4) to fit the growth rates in the model to observed growth trajectories in the lake (Kolding et al. 1992, Fig. 6). This calibration causes all fish of the same weight class to have equal growth and mortality, and thus does not distinguish between slow and fast growing varieties, but as Figure 6 shows, the estimated growth of the actual species in Lake Kariba does not diverge much relative to size. The model consists of 19 different ‘asymptotic size groups’, so that the community consist of a ‘species’ within each group with asymptotic sizes ranging from 12 grams to 10 kg. Fishing is composed of a large number of

gillnets with different mesh size (Fig. 3), each with their own bell-shaped size-selection curves (Fig. A1). Fishing is therefore only selecting for size, not for species. The fishing patterns used in the simulations are estimated by using the observed mesh size distribution from Zambia and Zimbabwe (Fig. 3). A fitted log-normal curve represents the selectivity of each mesh size (see appendix). To move from individual mesh size selectivity to the total fishing pattern, the selectivity for each mesh size is weighed by the number of corresponding nets and summed (Fig. A3). The total selection pattern by weight is modeled by estimating the parameters  $w_m$  (maximum retention weight) and  $\sigma_m$  (standard deviation) in eq. M13 for Zambia and Zimbabwe respectively by converting length (Fig. A3) to weight from a standard length-weight relationship  $w(g) = aL(cm)^3$ , where  $a = 0.01$ . Both selectivity patterns have a hard cut-off,  $w_F$ , at 10 and 50 g for Zambia and Zimbabwe respectively, to avoid catch of unreasonably small fish.

Table 1.

Table 2.

## Results

The slopes of the modelled size spectra (from  $\approx 20$ -100 cm) are similar to both the unfished (Lakeside) and the fished (Zambia) experimental sampling stations (Fig. 7A). The main difference between the fished and the unfished areas is that the density of fish by number is approximately 10 times lower in the Zambian area. The size spectra from the community model show a remarkably good fit with the observed size spectra in the catch curves of the experimental nets (Fig. 4 and 7A), even though the model has only been calibrated with few parameters (Table 2). The resemblance between observations and simulations is limited to fish larger than  $\approx 25$  cm, which largely corresponds with the size at which the observed data are underrepresented due to gear selectivity (Figs. A1, A2). The fished Zambian size-spectrum is obtained by applying the modeled fishing pattern (Figs. 7B and A3) corresponding with the number of mesh sizes observed in Zambia (Fig. 3). The Zimbabwean selection pattern is regulated towards highest retention at larger sizes (Figs. 3 and 7B).

Figure 8 shows the total yield from the Zambian and Zimbabwean side respectively under increased effort using the fishing patterns from Figure 7B. The fishing effort used to simulate the observed spectrum in Figure 7A indicates that the Zambian fishery was still not fully exploited under the observed fishing pattern (mesh sizes and number of nets). Since the Zimbabwean side yielded five times less (about 1200 tons per year) on average, we can deduce from the model that this fishery was only lightly exploited in relation to the maximum potential yield at the time of the observations. We also see that the fishing effort must be approximately 5.5 times higher in Zambia to get a yield that is 5 times higher (Fig. 9). The number of fishers in Zambia was on average 3 times higher than in Zimbabwe, but they had about 7 times more nets (Kolding et al 2003a).

To evaluate the impact of fishing on the fish community structure we use the size spectrum slope, calculated for fish between 10 and 7000 g. A low change in slope indicates little impact on the relative size structure on the community. We find that the Zambian fishery is not changing the slope significantly more than the Zimbabwean fishery (Fig. 10), even though the yield is much higher. The observed slope in the experimental catches from Zambia is also not significantly different from the unfished area in Zimbabwe (Figs. 4 and 7A). But we also find that the yield extracted from the Zambian side is closer to a point, where yield stops increasing and the slope steepens if effort expands without changing the fishing pattern. Moving beyond this point without decreasing the mesh sizes further means that large fish in the system are fished out relatively faster than the small, and that the community structure will change towards a less desirable state from an ecosystem approach or diversity point of view. Nevertheless, given the particular fishing patterns of the two fisheries, the point where the slope deteriorates is reached at a much lower effort and yield in the selective fishery in Zimbabwe compared to the less-selective fishery in Zambia.

## Discussion

With a conceptually relatively simple size-based model we are able to closely reproduce the observed fished and unfished community structure in Lake Kariba and thereby explain how the less-selective fishery in Zambia is able to provide higher yield than the more selective fishery in Zimbabwe, while still conserving the relative community structure. The main points that emerge from the model, and are validated by the observations, are that focusing the fishing pattern under high effort on predominantly small individuals produces little impact on the community and the largest maximum yield, while at low effort the highest individual catch rates is obtained by focusing on larger individuals. These findings are important, as the development of the uncontrolled fishery on the Zambian side of Lake Kariba with increasing effort, decreasing catch rates, and subsequently decreasing mesh sizes in order to compensate for decreasing returns, is conventionally interpreted as emergent signs of overfishing. Despite producing a higher yield while conserving relative community structure, the less-selective fishery in Zambia are conforming to conventional indicators of destructive and unsustainable fishing patterns such as increased use of illegal small meshed gears, strongly reduced stock abundance and decreased mean size of fish in catches (Tweddle et al. 2015).

The paradox, however, as shown both by the empirical observations and theoretical results here, is that the uncontrolled open access fishery on the Zambian side of Lake Kariba appears to attain the desired goals set in international agreements. By ignoring the minimum mesh size regulations the Zambian fishery produces the highest sustainable yield (UNCLOS 1982), while maintaining the relative fish community structure (CBD 1992). These positive counter-intuitive results of non-compliance are created by a rational individual response to the open access regime. When effort grows, and catch per unit effort decreases, it is a logical and necessary reaction of individual fishers to gradually decrease their mesh sizes in order to maintain an acceptable catch rate, albeit the result is increasing amounts of small fish over a larger species diversity as an increasing number of small species enter the fishery (Kolding et al.

2015a). Thus, the increased effort is distributed over a wider range of the fish community so that catch rates are maintained with limited change to the overall size-structure of the community (Fig. 10). This, so-called “fishing down process” (Welcomme 1999) is generally considered as a sign of a deteriorating and harmful situation (Pauly et al. 2008; Tweddle et al. 2015), with the added problem that an increasing number of fishing methods become technically illegal as they target smaller and smaller fish (Kolding et al. 2015a). Our results, however, indicate a need to reconsider this traditional evaluation.

In African inland fisheries food is the major objective and small fish often have the same price per unit weight as large (Brummett 2000) confirming the high demand. Small fish, either juveniles or species, have a higher productivity per unit biomass than large, and are generally lower in the trophic chain (Lorentzen 1996; Jennings et al. 2001; Brown et al. 2004). In many fishes studied the somatic growth of adults contributes less than one third, and seldom more than half, to the total production (Morgan et al. 1980). In terms of food production this means that harvesting small fish and juveniles is most efficient as energy is lost in metabolic costs when targeting large fish at higher trophic levels. Furthermore, the Zambian fishing pattern does not impair sustainability in terms of renewed recruitment of large slow growing species. In Lake Kariba, as in most other African inland fisheries, the predominant gear is gillnets with a bell-shaped selectivity curve (equation M13). Thus a decrease in mesh-sizes will not affect the adults with a relatively large maximum size, the so-called BOFFFs (Big Old Fat Fecund Females, Hixon et al. 2013), as more of these will escape being caught (Fig. 7B) securing continued reproduction. Adjusting the fishing mortality according to productivity, and thereby shift the fishing mortality towards small fish as the Zambian fishers do by decreasing the average mesh sizes (Fig. 3), is in accordance with the ‘Balanced Harvest’ principle suggested by Garcia et al. (2012) in order to mitigate the adverse effects of fishing on community structure and address food security.

While there is increasing evidence of the demographic, structural and genetic effects of selective fishing on adults, resulting in age-truncations, species loss, increased instability, and possible induced evolutionary effects (Rice and Gislason 1996; Andersen and Brander 2009; Jørgensen et al. 2007), there are very few known examples of balanced fishing across species and sizes. Nearly all comprehensive observations on fished communities come from managed fisheries, and these all have strong elements of size selective restrictions. In fact, for fisheries with limited information and lack of regular stock assessments, the cheapest and easiest option for managers is to regulate the fishing pattern through gear or size limitations (Misund et al. 2002; Kolding et al. 2014). Examples of less selective fishing therefore have to be found among fisheries where limited or no enforcement of formal regulations exists. Among the latter are many small-scale fisheries in developing countries that lack the resources for effective compliance. In the few cases where selectivity have been studied in such fisheries, the results show that the rapidly adapting multi-gear, multi-species artisanal fisheries often seem to be producing an overall species-, abundance-, and size composition in their catches that closely matches the ambient ecosystem structure (Misund et al. 2002; Jul-Larsen et al. 2003; van Zwieten et al. 2011; Kolding and van Zwieten 2014).

Harvesting natural ecosystems will inevitably make an impact on abundance and selective exploitation on targeted species and sizes will change the community structure and composition. The international agreements of keeping fish communities at the levels of maximum sustainable yields (UNCLOS 1982; WSSD 2002), while at the same time make the least structural and functional disturbance to the ecosystem (UNEP 2000) are therefore difficult objectives to reconcile (Hilborn 2006; Law et al. 2013; Kolding et al. 2015b). The fishing mortality on a population is shaped by a combination of 'how' we fish (fishing pattern) and 'how much' we fish (fishing pressure), but often the distinction between these two separate factors are ignored and the effects become merged (Kolding and van Zwieten 2011, 2014). The minimum size regulations imposed in Lake Kariba are typical for a large number of industrial and small-

scale fisheries, but as this study shows, such regulations are difficult to implement unless enforced when the market has no particular size preferences. The inherent tendency for many small-scale fishers to violate size-based regulations has an economic basis and the resulting universal conflict between managers and fishers over size regulations is therefore largely futile, and has no ecological justification (Kolding and Zwieten 2011).

Our results call for a re-evaluation of the size based management regulations that are ubiquitous in most fisheries if the Convention on Biodiversity principle of maintaining ecosystem structure is to be taken seriously. In contrast to conventional expectations from standard fisheries theory, the unregulated fishing pattern that has evolved on the Zambian side of Lake Kariba, seems to fulfill most of our goals: it is high yielding, community structure conserving, and sustains the livelihood of many fishers. The negative sides are that the standing biomass in the fished areas is typically low, with corresponding low individual catch rates, and consequently low individual revenue (Burgess et al. 2015). The negative aspects, however, is more a question of fishing effort (“how much” fishing) than of size-regulations (“how” to fish). If regulations are needed it would therefore be better to control access, than to regulate the fishing pattern. Fisheries management is always a balance of trade-offs (Link 2010; Andersen et al. 2014), and for many fisheries, particularly in the Northern hemisphere, the value of the catch is strongly correlated with size of the fish, in which case size-restrictions combined with low effort may be appropriate. In the developing world, however, food production, and in particular healthy food containing essential micronutrients, is still of major importance (FAO 2014, HLPE 2014) and in such situations a fishing pattern like the Zambian side of Lake Kariba seems to be optimal from both an ecological, socio-political and nutritional aspect (Kolding et al. 2015a), the latter because small fish are usually sundried and eaten whole, in contrast to large fish which are filleted or smoked and thereby lose many essential micronutrients (Longley et al 2014) in addition to being more expensive to process. We hope that this

study will inspire more research into how local communities develop fishing patterns and how these affect the fish community they depend on.

**Acknowledgements.** The fishery data used in this study was collected by the Lake Kariba Fisheries Research Institute (Zimbabwe), and by Lake Kariba Research Unit and the Sinazongwe Fisheries Training Center (Zambia). Much of the empirical data compilation and background analyses were performed during the Zambia/Zimbabwe SADC Fisheries project, sponsored by Norad (Norway) and Danida (Denmark) and a four year research project on freshwater fisheries development in the SADC area (Management, co-management or no management? Major dilemmas in southern African freshwater fisheries) funded by the Norwegian Research Council. We are indebted to all these institutions for help and assistance. NSJ and KHA were supported by the Centre for Ocean Life, a VKR Centre of Excellence supported by the Villum Foundation.



## References

- Andersen, K.H., and Beyer, J.E. 2006. Asymptotic Size Determines Species Abundance in the Marine Size Spectrum. *Am. Nat.* **168**: 54–61.
- Andersen, K.H., and Pedersen, M. 2010. Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. B-Biological Sci.* **277**: 795–802. doi: 10.1098/rspb.2009.1512.
- Andersen, K.H., and Rice, J.C. 2010. Direct and indirect community effects of rebuilding plans. *ICES J. Mar. Sci.* **67**: 1980–1988. doi: 10.1093/icesjms/fsq035.
- Andersen, K.H., Brander, K., and Ravn-Jensen, L.J. 2014. Trade-offs between objectives for ecosystem management of fisheries. *Ecological Applications* 25:390-1396. doi: 10.1890/14-1209.1
- Anderson, C.N.K., Hsieh, C.-H., Sandin, S.A., et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* 452: 835-839
- Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.* **41**: 137–160. doi: 10.1111/j.1095-8649.1992.tb03875.x.
- Beverton, R.J.H., and Holt, S. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food. Available from <http://www.worldcat.org/isbn/1930665946>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. 2004. Toward a Metabolic Theory of Ecology. *Ecology* **85**: 1771–1789. doi: 10.1890/03-9000.
- Brummett, R.E. 2000. Factors influencing fish prices in Southern Malawi. *Aquaculture* 186:243-251.

- Burgess, M.G, Diekert, F.K, Jacobsen, N.S., Andersen, K.H & Gaines, S.D. Remaining questions in the case for balanced harvesting. *Fish and Fisheries*. Published online June 2015. Doi: 10.1111/faf.12123
- Caddy, J. F. 1999. Fisheries management in the twenty-first century: will new paradigms apply? *Rev in Fish Biol and Fisheries* 9:1-43.
- CBD, 1992. Convention on Biological Diversity, Rio de Janeiro, Brazil. Available from <http://www.cbd.int/rio/> [accessed 17 February 2015]
- Daan, N., Gislason, H., G. Pope, J., and C. Rice, J. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar. Sci. J. du Cons.* **62**: 177–188. doi: 10.1016/j.icesjms.2004.08.020.
- FAO 2014. The State of World Fisheries and Aquaculture. Opportunities and Challenges. Rome, FAO. <http://www.fao.org/3/a-i3720e/index.html> [Accessed 24 April 2015]
- Frank, K.T., Petrie, B., Choi, J.S., and Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**: 1621–3. doi: 10.1126/science.1113075.
- Garcia, S.M., Kolding, J., Rice, J., Rochet, M.J., Zhou, S., Arimoto, T., Beyer, J.E., Borges, L., Bundy, A., Dunn, D., and others. 2012. Reconsidering the consequences of selective fisheries. *Science* **335**: 1045–1047.
- Gutiérrez, N.L., Hilborn, R., and Defeo, O. 2011. Leadership, social capital and incentives promote successful fisheries. *Nature* **470**: 386–389.
- Hartvig, M., Andersen, K.H., and Beyer, J.E. 2011. Food web framework for size-structured populations. *J. Theor. Biol.* **272**: 113–122.

- Hilborn, R. 2006. Defining success in fisheries and conflicts in objectives. *Marine Policy* 31:153-158
- Hixon, M.A., Johnson, D.W. and Sogard, S. 2013. BOFFFs: on the importance of conserving old-growth age structure in fishery population. *ICES Journal Mar. Sci.* doi:10.1093/icesjms/fst200
- HLPE, 2014. Sustainable fisheries and aquaculture for food security and nutrition. A report by the High Level Panel of Experts on Food Security and Nutrition of the Committee on World Food Security, Rome 2014. Available from <[www.fao.org/3/a-i3844e.pdf](http://www.fao.org/3/a-i3844e.pdf)> [accessed 17 February 2015]
- Houle, J.E., Andersen, K.H., Farnsworth, K.D., and Reid, D.G. 2013. Emerging asymmetric interactions between forage and predator fisheries impose management trade-offs. *J. Fish Biol.* **83**: 890–904
- Hsieh, C., Yamauchi, A., Nakazawa, T., and Wang, W.-F. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquat. Sci. - Res. Across Boundaries* **72**: 165–178. doi: 10.1007/s00027-009-0122-2.
- Jacobsen, N.S., Gislason, H., and Andersen, K.H. 2014. The consequences of balanced harvesting of fish communities. *Proc. R. Soc. B Biol. Sci.* **281**: 20132701.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., and Boon, T.W. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J. Anim. Ecol.* **70**: 934–944.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gårdmark A. G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. & Rijnsdorp, A. D. (2007). Ecology: Managing Evolving Fish Stocks. *Science* 318:1247-1248. doi: 10.1126/science.1148089
- Karenga, L.P. 1992. Inshore fish population changes at Lakeside, Kariba, between 1969-1991. MPhil. thesis, Department of Biology, University of Bergen, Norway.

- Karenga, L., and Kolding, J. 1995a. Inshore fish population and species changes in Lake Kariba, Zimbabwe. *In* The impact of species changes in African lakes. *Edited by* T.J. Pitcher and P.J.B. Hart. Chapman & Hall, London. pp. 245–275.
- Karenga, L., and Kolding, J. 1995b. On the relationship between hydrology and fisheries in man-made Lake Kariba, Central Africa. *Fish. Res.* **22**: 205–226.
- Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a Bioenergetics Model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Canada* **34**: 1910–1921. doi: 10.1139/f77-258.
- Kolding, J. and Songore, N. 2003. Diversity, disturbance, and ecological succession of the inshore fish populations in Lake Kariba, Zimbabwe from 1960 to 2001. Paper presented for The Linnean Society of London Symposium on the use of long-term databases for the prediction of ecological change. London. October 23rd-24th, 2003  
[https://www.academia.edu/14642691/Diversity\\_disturbance\\_and\\_ecological\\_succession\\_of\\_the\\_inshore\\_fish\\_populations\\_in\\_Lake\\_Kariba\\_Zimbabwe\\_from\\_1960\\_to\\_2001](https://www.academia.edu/14642691/Diversity_disturbance_and_ecological_succession_of_the_inshore_fish_populations_in_Lake_Kariba_Zimbabwe_from_1960_to_2001)
- Kolding, J., Tirasin, E. M., and Karenga, L. 1992. Growth, mortality, maturity and length-weight parameters of fishes in Lake Kariba, Africa. *Naga, the ICLARM Quarterly* 15.4: 39-41.
- Kolding, J., Musando, B., and Songore, N. 2003a. Inshore fisheries and fish population changes in Lake Kariba. *FAO Fish. Tech. Pap* 426/2: 67–99. FAO, Rome.
- Kolding, J., Ticheler, H., and Chanda, B. 2003b. The Bangweulu swamps-A balanced small-scale multispecies fishery. *FAO Fish. Tech. Pap.* 426/2: 34–66. FAO, Rome.
- Kolding, J., Béné, C and Bavinck, M. 2014. Ch. 22 Small-scale fisheries - importance, vulnerability, and deficient knowledge. pp 317-331 *In* S. Garcia, J. Rice and A. Charles (eds). *Governance for Marine*

- Fisheries and Biodiversity Conservation. Interaction and coevolution. Wiley-Blackwell. DOI: 10.1002/9781118392607.ch22
- Kolding, J., and van Zwieten, P.A.M. 2014. Sustainable fishing of inland waters. *J. Limnol.* **73**: 132-148. DOI: 10.4081/jlimnol.2014.818
- Kolding, J., and van Zwieten, P.A.M. 2011. The Tragedy of Our Legacy: How do Global Management Discourses Affect Small Scale Fisheries in the South? *Forum Dev. Stud.* **38**: 267–297. doi: 10.1080/08039410.2011.577798.
- Kolding, J., van Zwieten, P.A.M and Mosepele, K. 2015a. “Where there is water there is fish” – Small-scale inland fisheries in Africa: dynamics and importance. *In A History of Water, Series 3, Volume 3. Water and Food: From hunter-gatherers to global production in Africa. Edited by T. Tvedt and T. Oestigaard .I.B. Tauris. London. (in press)*
- Kolding, J., Law, R. Plank, M. and van Zwieten, P.A.M. 2015b. The Optimal Fishing Pattern. Chapter 5.5 *In Freshwater Fisheries Ecology. Edited by J. Craig. Wiley-Blackwell.*
- Law, R., Kolding, J., and Plank, M.J. 2013. Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries.* Doi: 10.1111/faf.12056
- Law, R., Plank, M.J., and Kolding, J. 2012. On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES J. Mar. Sci. J. du Cons.* doi: 10.1093/icesjms/fss031.
- Law, R., Plank, M.J and Kolding, J. 2014. Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish and Fisheries.* DOI: 10.1111/faf.12098
- Link, J. S. 2010. *Ecosystem-Based Fisheries Management: Confronting Tradeoffs.* Cambridge University Press, Cambridge.

- Longley, C., Haraksingh Thilsted, S., Beveridge, M; Cole, S.; Banda Nyirenda, D., Heck, S. and Hother, A.-L. 2014. The Role of Fish in the First 1,000 Days in Zambia. IDS Special Collection. Institute of Development Studies, Brighton BN1 9RE, UK [www.ids.ac.uk](http://www.ids.ac.uk)
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* 49: 627-647.
- Misund, O.A., Kolding, J., and Fréon, P. 2002. Fish capture devices in industrial and artisanal fisheries and their influence on management. *In Handbook of fish Biology and Fisheries*. **2**. Edited by P.B.J. Hart and J.D. Reynolds. Blackwell Publishing, UK. pp. 13–36.
- Morgan, N.C., Backiel, T., Bretschko, G., Duncan, A., Hillbricht-Ilkowska, A., Kajak, Z., Kitchell, J.F., Larsson, P., Lévêque, C., Nauwerck, A., Schiemer, F. and Thorpe, J.E. 1980. Secondary production. *In The Functioning of Freshwater Ecosystems*. International Biological Programme Synthesis Series (No. 22). Edited by E. D. Le Cren and R. H. Lowe-McConnell. Cambridge University Press, Cambridge. pp. 247-340
- Musando, B. 1996. Inshore fish population changes in the Zambian Waters of Lake Kariba from 1980 to 1995, MPhil thesis, Department of Biology, University of Bergen, Norway .
- Ngalande, P. 1995. Assessment of the Tanganyika clupeid, *Limnothrissa miodon*, in Lake kariba by hydroacoustics. MPhil thesis, Department of Biology, University of bergen, Norway.
- Nyikahadzoi, K. and Råkjær, J. 2014. The myths and realities in the management of the Kapenta fishery at Lake Kariba (Zimbabwe). *Lakes and reservoirs: Research and Management* 19: 1-10.
- Pope, J.G. 1991. The ICES Multispecies Assessment Working Group: evolution, insights and future problems. *ICES Marine Science Symposium* **193**, 22-33.

- Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., and Charnov, E.L. 2004. Effects of body size and temperature on population growth. *Am. Nat.* **163**: 429–441.
- Scholtz, U. 1993. The development of inshore fish stocks and small-scale fishery on the Zambian side of Lake Kariba 1960-1990. PhD thesis, University of Kiel, 162 pp. Kiel, Germany.
- Songore, N. 2002. Fish Diversity Development in Lake Kariba Zimbabwe from 1960 to 2001, MPhil thesis, Department of Biology, University of Bergen, Norway.
- Tweddle, D., Cowx, I.G., Peel, R.A., and Weyl, O.L.F. 2015. Challenges in fisheries management in the Zambezi, one of the great rivers of Africa. *Fisheries Management and Ecology*, 22:99-111
- UNCLOS, 1982. United Nations Convention on the Law of the Sea (UNCLOS) of 10 December 1982. Available from [http://www.un.org/depts/los/convention\\_agreements/convention\\_overview\\_convention.htm](http://www.un.org/depts/los/convention_agreements/convention_overview_convention.htm). [accessed 17 February 2015]
- UNEP. 2000. Decisions adopted by the Conference of the Parties to the Convention on Biological Diversity at its fifth meeting Nairobi. Available from [www.cbd.int/doc/decisions/COP-05-dec-en.pdf](http://www.cbd.int/doc/decisions/COP-05-dec-en.pdf). [accessed 17 February 2015]
- UNEP/CBD/COP. 1998. Convention of Biological Diversity. Report of the Workshop on the Ecosystem Approach. Lilongwe, Malawi, 26 - 28 January 1998. Available from <http://www.cbd.int/doc/meetings/cop/cop-04/information/cop-04-inf-09-en.pdf>. [accessed 17 February 2015]
- Ursin, E. 1973. On the prey size preferences of cod and dab. *Medd. Danm. Havunders. N.S.* 7: 85–98

- Welcomme, R.L. 1999. A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. *Fisheries Management and Ecology* 6:1-19.
- West, G.B., Brown, J.H., and Enquist, B.J. 1997. A General Model for the Origin of Allometric Scaling Laws in Biology. *Science* **276**: 122–126. doi: 10.1126/science.276.5309.122.
- Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. *Fish. Res. Bd Can., Trans. Ser.* **194**: 1–202.
- WSSD (2002). World Summit of Sustainable Development, Plan of Implementation, § 31 a, Johannesburg 2002. Available from:  
[www.un.org/esa/sustdev/documents/WSSD\\_POI\\_PD/English/WSSD\\_PlanImpl.pdf](http://www.un.org/esa/sustdev/documents/WSSD_POI_PD/English/WSSD_PlanImpl.pdf) [accessed 17 February 2015]
- Zhou, S., Smith, A.D.M., Punt, A.E., Richardson, A.J., Gibbs, M., Fulton, E.A., Pascoe, S., Bulman, C., Bayliss, P., and Sainsbury, K. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proc. Natl. Acad. Sci.* **107**: 9485–9489.



Table 1: Model equations. Units are in brackets.

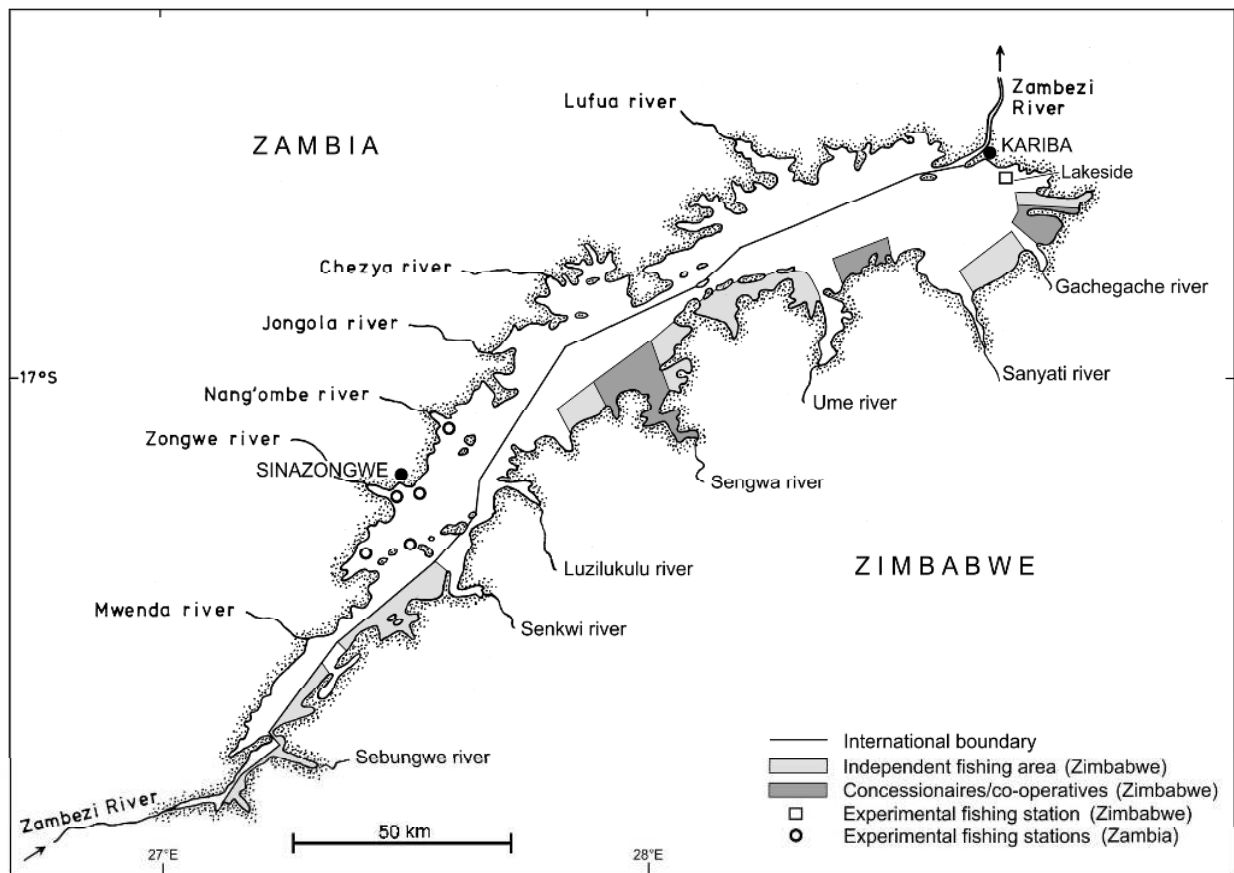
<i>Encounter and consumption</i>		
Prey size selection (-)	$\phi\left(\frac{w}{w_{\text{prey}}}\right) = \exp\left[-\left(\ln\left(\frac{w}{\beta w_{\text{prey}}}\right)\right)^2 / (2\sigma^2)\right]$	M1
Volumetric search rate (	$V(w) = \gamma w^q$	M2
Encountered food (g yr <sup>-1</sup> )	$E(w) = V(w) \int_0^{\max(W_{\infty})} w_{\text{prey}} \phi\left(\frac{w}{w_{\text{prey}}}\right) \left(\sum N_{i(w_{\text{prey}})} + N_r(w_{\text{prey}})\right) dw_{\text{prey}}$	M3
Maximum consumption rate	$I_{\max} = h w^n$	M4
Feeding level (-)	$f(w) = \frac{E(w)}{E(w) + I_{\max}}$	M5
<i>Growth and reproduction</i>		
Somatic growth (g yr <sup>-1</sup> )	$g_i(w) = (\alpha f(w) h w^n - k w^p)(1 - \psi(w))$	M6
Maturity ogive (-)	$\psi_i(w) = \left[1 + \left(\frac{w}{\eta W_{\infty,i}}\right)^{-10}\right]^{-1} \left(\frac{w}{W_{\infty,i}}\right)^{1-n}$	M7
<i>Recruitment</i>		
Egg production (eggs yr <sup>-1</sup> )	$R_p(W_{\infty,i}) = \frac{\epsilon}{2w_0} \int_{w_0}^{W_{\infty,i}} (\alpha f(w) h w^n - k w^p) \psi(w) N_i dw$	M8
Max. recruitment (eggs yr <sup>-1</sup> )	$R_{\max}(W_{\infty,i}) = K \kappa_r (\alpha f_0 h w_0^n - k w_0^p) W_{\infty,i}^{2n-q-3+a} \Delta W_i$	M9
Recruitment (eggs yr <sup>-1</sup> )	$R(W_{\infty,i}) = R_{\max}(W_{\infty,i}) \frac{R_p(W_{\infty,i})}{R_p(W_{\infty,i}) + R_{\max}(W_{\infty,i})}$	M10
<i>Mortality</i>		
Background mortality (yr <sup>-1</sup> )	$\mu_{b,i} = \mu_0 W_{\infty,i}^{n-1}$	M11
Predation mortality (yr <sup>-1</sup> )	$\mu_p(w_{\text{prey}}) = \sum_i \int_{w_0}^{\infty} \phi\left(\frac{w}{w_{\text{prey}}}\right) (1 - f(w)) V(w) N_i(w) dw$	M12
Fishing mortality (yr <sup>-1</sup> )	$F = F_0 \exp\left(\frac{-\ln\left(\frac{w}{w_m}\right)^2}{2\sigma_m}\right)$	M13
<i>Resource spectrum</i>		
Resource dynamics (g yr <sup>-1</sup> )	$\frac{\partial N_r(w)}{\partial t} = r_0 w^{n-1} (\kappa(w) - N_r(w)) - \mu_p(w) N_r(w)$	M14
Carrying capacity (g <sup>1-n</sup> )	$\kappa(w) = \kappa_r^{-2-q+n} \text{ for } w < w_{\text{cut}}$	M15
Conservation equation	$\frac{\partial N(w, W_{\infty,i})}{\partial t} + \frac{\partial g_i(w) N(w, W_{\infty,i})}{\partial w} = -\mu_p(w) N(w, W_{\infty,i})$	M16

Table 2: Parameters used in the size based model.

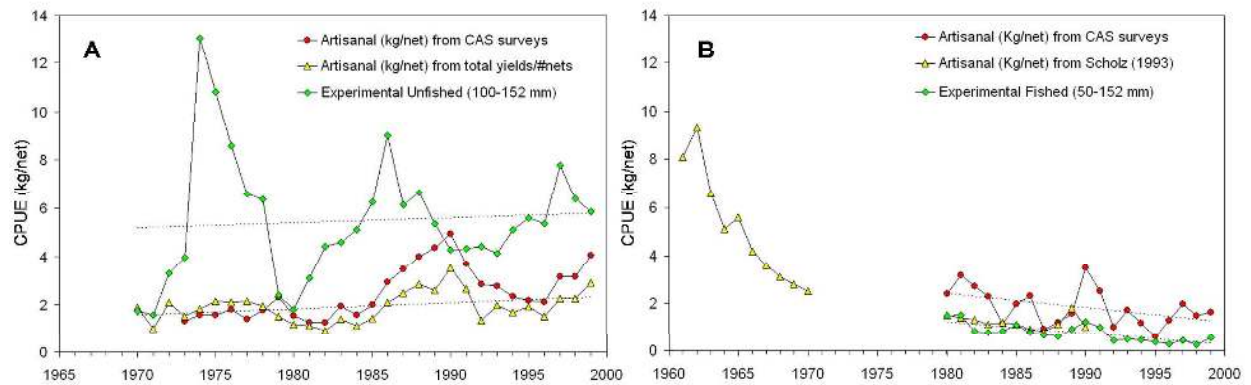
<i>Encounter and growth</i>			<i>Unit</i>
$\alpha$	Assimilation efficiency <sup>a</sup>	0.6	-
$n$	Exponent of max. consumption <sup>b</sup>	0.75	-
$h$	Factor of max. consumption <sup>c</sup>	28*	$\text{g}^{1-n}\text{yr}^{-1}$
$q$	Exponent of search volume <sup>d</sup>	0.75	-
$p$	Exponent of standard metabolism <sup>e</sup>	0.75	-
$k$	Factor of standard metabolism <sup>f</sup>	2.4	$\text{g}^{1-n}\text{yr}^{-1}$
$\gamma$	Factor for volumetric search rate <sup>g</sup>	5e-9	$\text{g}^{-q}\text{yr}^{-1}$
$\beta$	Preferred predator-prey mass ratio <sup>h</sup>	100	-
$\sigma$	Width of size-selection function <sup>i</sup>	1.3	-
$\eta$	Size at maturation relative to asymptotic size <sup>j</sup>	0.25	-
$f_0$	Expected feeding level <sup>k</sup>	0.6	-
$K$	Maximum recruitment factor <sup>l</sup>	1e4	-
<i>Mortality</i>			
$\mu_0$	Factor for background mortality <sup>m</sup>	3	$\text{g}^{1-n}\text{yr}^{-1}$
$a$	Physiological mortality <sup>n</sup>	0.58	-
<i>Resource spectrum</i>			
$r_0$	Productivity of resource spectrum <sup>o</sup>	4	$\text{g}^{1-p}\text{yr}^{-1}$
$\kappa_r$	Carrying capacity of resource spectrum	3.3e9 *	$\text{g}^{\lambda-1}$
$w_{\text{cut}}$	Cut-off size of resource spectrum	1	g
<i>Fishing mortality</i>			
$F_0$	Level of effort	Free	$\text{yr}^{-1}$
$w_F$	Smallest size caught	Free	g

<sup>a</sup>Kitchell *et al.* (1977), <sup>b</sup>Jobling (Brown *et al.* 2004) states that  $2/3 < n < 3/4$ . <sup>c</sup>We have used  $n = 3/4$  to be consistent with von Bertalanffy growth curves. <sup>d</sup>Adjusted such that emergent growth rates are in the range of those observed.

<sup>e</sup>Considerations on the bioenergetic budget of swimming predict a value of  $q$  between 2/3 and 1 (Andersen and Beyer 2006). <sup>f</sup>West *et al.* (1997). <sup>g</sup>The data of Winberg ((1956)) indicate a standard (resting) metabolism factor for fish of about  $4 \text{ g}^{0.25} \text{ yr}^{-1}$  at 10°C. <sup>h</sup>Calculated from the other parameters as specified in Andersen and Pedersen (2010). <sup>i</sup>Ursin (1973) and Jennings *et al.* (2001). <sup>j</sup>Ursin (1973) finds  $\sigma \approx 1$  for a single species. To account for species diversity within trait class classes, this has been increased to  $\sigma = 1.3$ . <sup>k</sup>Beverton (1992). <sup>l</sup>Andersen and Pedersen (2009). <sup>m</sup>Determines the relation between piscivory and zooplanktivory in early life stages (Houle *et al.* 2013). <sup>n</sup>Adjusted to lead to a background mortality of the same order (but lower) than the predation mortality. <sup>o</sup>The physiological mortality describes the relative strength of predation, for derivation see Andersen and Beyer (2006). <sup>p</sup>Hartvig *et al.* (2011). \* means that the parameter is specifically calibrated to Lake Kariba.



**Figure 1.** Map of Lake Kariba on the Zambezi River between Zambia and Zimbabwe. Designated fishing areas in Zimbabwe are indicated with the rest being protected, while the whole Zambian side is open to fishing. Experimental fishing stations are shown in Zambia around Sinazongwe (open circles), and from the protected non-fished Lakeside area in Zimbabwe near Kariba town (open square). Modified from Kolding et al. 2003a.



**Figure 2.** Catch per unit effort time series in Lake Kariba inshore demersal fishery. A) Zimbabwe:

Artisanal mean annual kg per net from Catch Assessment Surveys - CAS (circles), total annual yield / total number of nets (triangles, trend n.s.), and mean annual experimental kg per 45 m net set (diamonds, trend n.s.) in the mesh range 100-152 mm (comparable with artisanal mesh range) from an unfished area.

B) Zambia: Artisanal mean annual kg per net from CAS surveys (circles, trend n.s.), mean annual kg per net from Scholtz (1993, triangles), and mean annual experimental kg per 45 m net set (diamonds, trend \*\*\*) in the mesh range 50-152 mm (comparable with artisanal mesh range) from the fished area.

Redrawn from Kolding et al. (2003a).

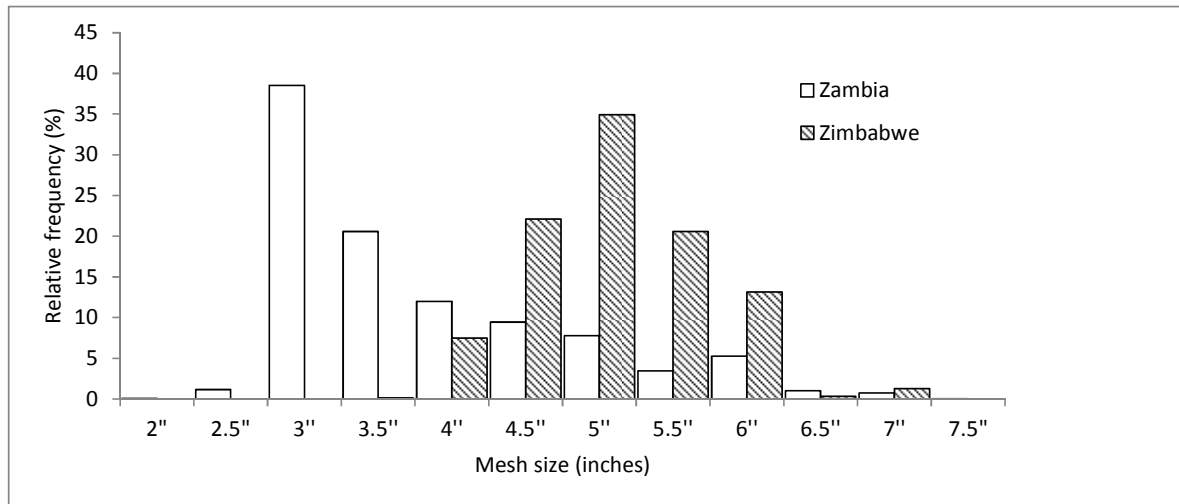
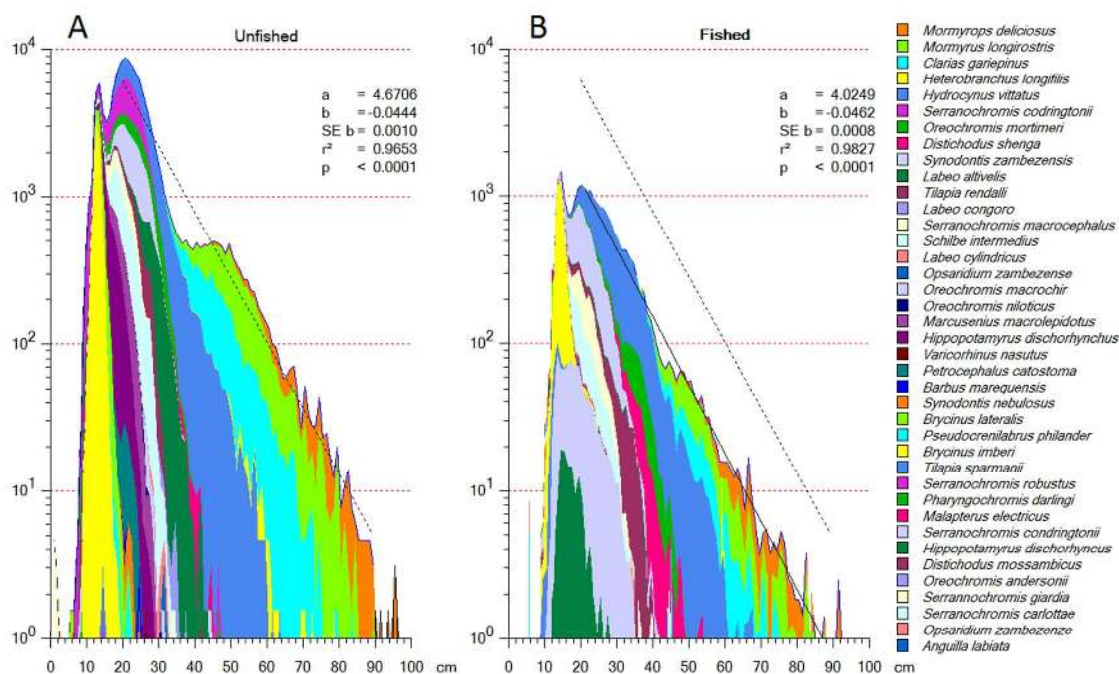
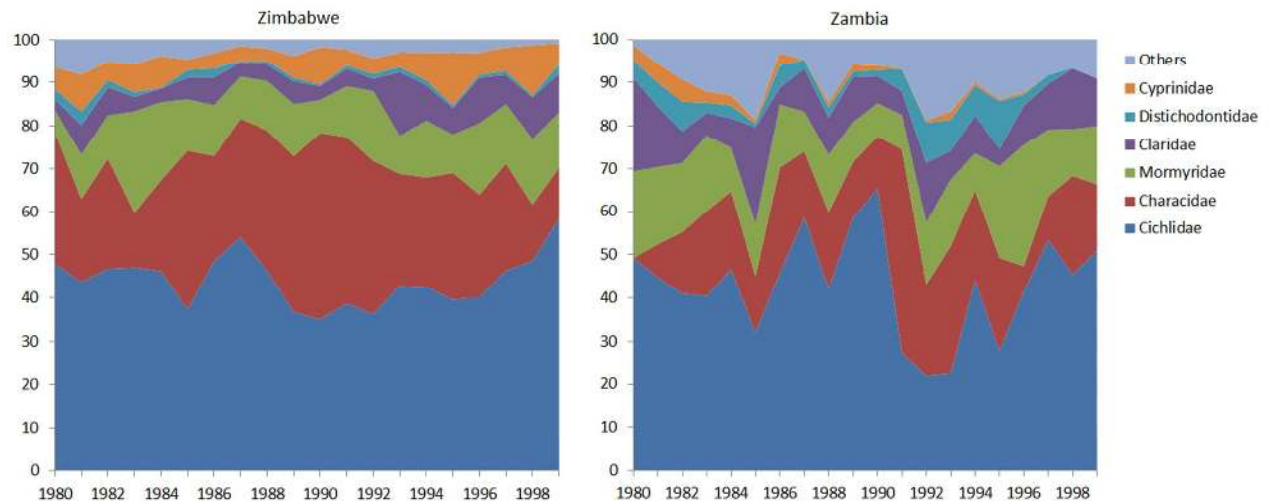


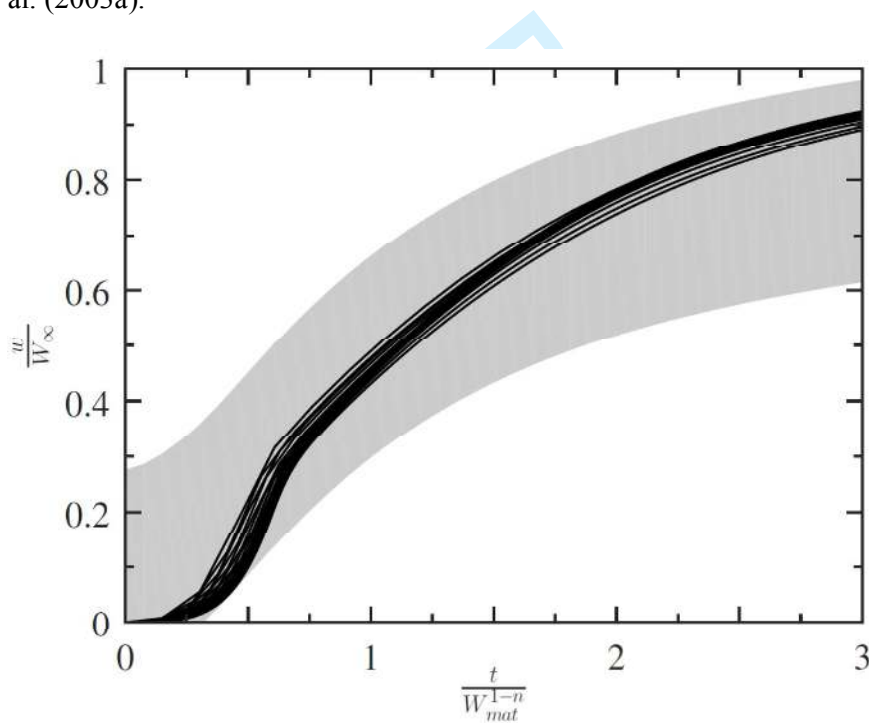
Figure 3. Observed artisanal fishing pattern in Lake Kariba Zambia (open bars) and Zimbabwe (hatched bars) as relative distribution of recorded mesh sizes in the 1980-1994 Catch Assessment Surveys (Zambia) and a 1993 Frame survey (Zimbabwe). Data from Department of Fisheries (Zambia) and Department of National Parks and Wildlife (Zimbabwe).



**Figure 4.** Standardized biomass-size distributions by species in Lake Kariba from demersal experimental gillnet surveys 1980-1994. A: unfished area, Zimbabwe; B: heavily fished Zambian fishing grounds (ref. Fig 1 for locations). No significant difference between the slopes (regression lines) of the unfished (dashed) and the fished (full) community indicates a significantly lower standing biomass but almost equal species (relative to the natural limnological gradient) and size compositions in the fished area. Modified from Kolding et al. (2003a) and Kolding and van Zwieten (2014).



**Figure 5.** Relative catch composition (% weight) in the inshore fishery between 1980 to 1999 by major families in Zimbabwe and Zambia based on catch assessment surveys (CAS). Modified from Kolding et al. (2003a).



**Figure 6:** Averaged estimated von-Bertalanffy growth curves from 22 fish species in Lake Kariba (Kolding et al. 1992)  $\pm 1$  SD (gray area) and the emergent growth of 19 species in the size-based model (black lines). The y-axis is scaled by the asymptotic weight and the x-axis is time scaled by  $W_{mat}^{1-n}$  which is proportional to age at maturity.

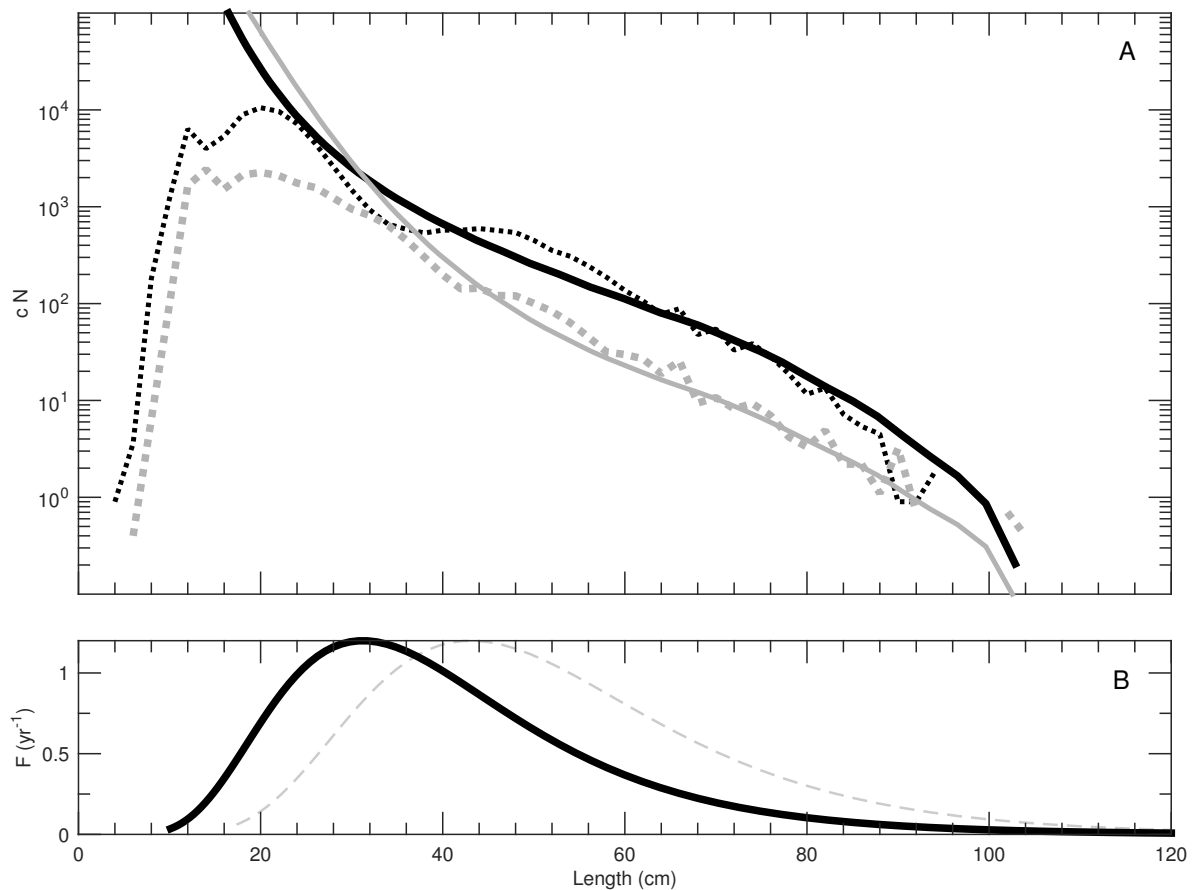


Figure 7: A) The observed size spectra (standardised number of fish caught) from the 1980-1994 experimental gillnet surveys in Lake Kariba from the unfished (dotted black) Lakeside area in Zimbabwe, and the fished (dotted gray) area in Zambia (Figure 4), and the modeled unfished (solid black) and fished (solid gray) size spectra (scaled with a constant factor  $c$  to get comparable units with observations). Fish below  $\approx 25$  cm in the observed size spectra are not well sampled due to gear selectivity (see Appendix). There is no significant difference in the descending slopes between the fished and unfished distributions (Kolding et al. 2003a). B) Modeled fishing selectivity pattern in Zambia (solid black) and in Zimbabwe (dashed gray). The Zambian fishing pattern was used to generate the fished size-spectrum in A.



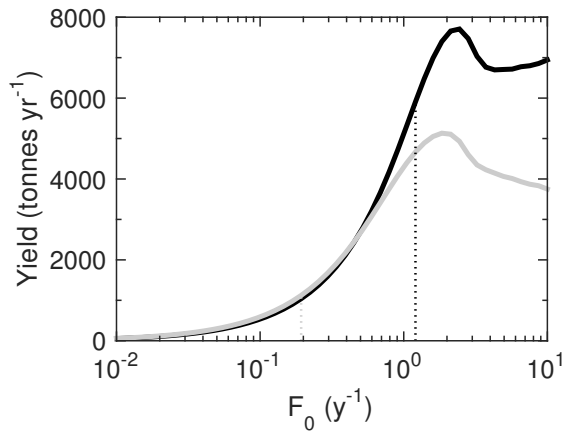


Figure 8: Yield from the less-selective fishery on the Zambian side (black) and the selective fishery on the Zimbabwean side (gray), as a function of effort ( $F_0$ ) using the fishing patterns in figure 5. Dotted lines are the expected  $F_0$  corresponding to the observed  $\approx 6000$  tons/year in Zambia and  $\approx 1200$  tons/year in Zimbabwe.

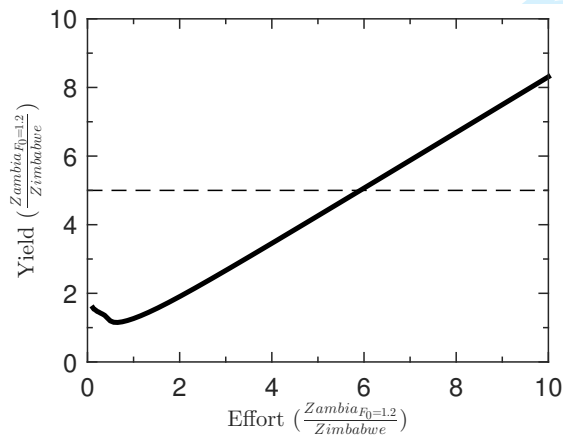


Figure 9. The difference in yield between Zambia and Zimbabwe as a function of relative effort. The yield and effort from Zambia are held constant with  $F_0 = 1$ , corresponding to the effort level used to model the Zambian fished spectrum in figure 5A. To obtain a fivefold higher yield in Zambia than Zimbabwe, the relative effort is  $\approx 5.5$  times higher.

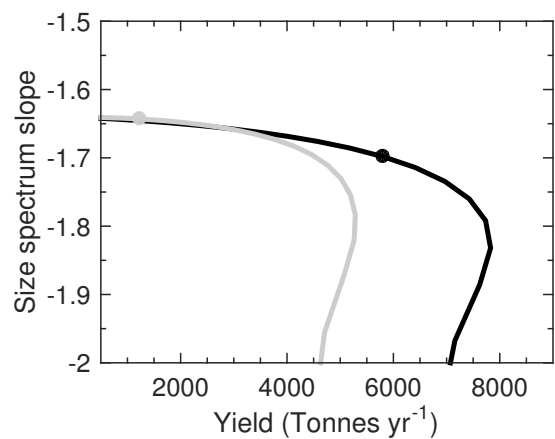


Figure 10: The size spectrum slope from Zambia (black) and Zimbabwe (gray) under increasing yield and given the different size selection pattern from each fishery (Figures 3 and 5). The black and the gray dot represent the average observed yields from Zambia and Zimbabwe, respectively. Yield can increase up to a maximum achievable with only small change in slopes, after which increased effort will mainly affect slope without gain in yield. Thus, using a less selective fishing pattern as in Zambia gives significantly higher yields with only small changes in the slope.

## Appendix

### Fisheries selectivity patterns in Lake Kariba

#### 1. Estimated selectivity in experimental nets:

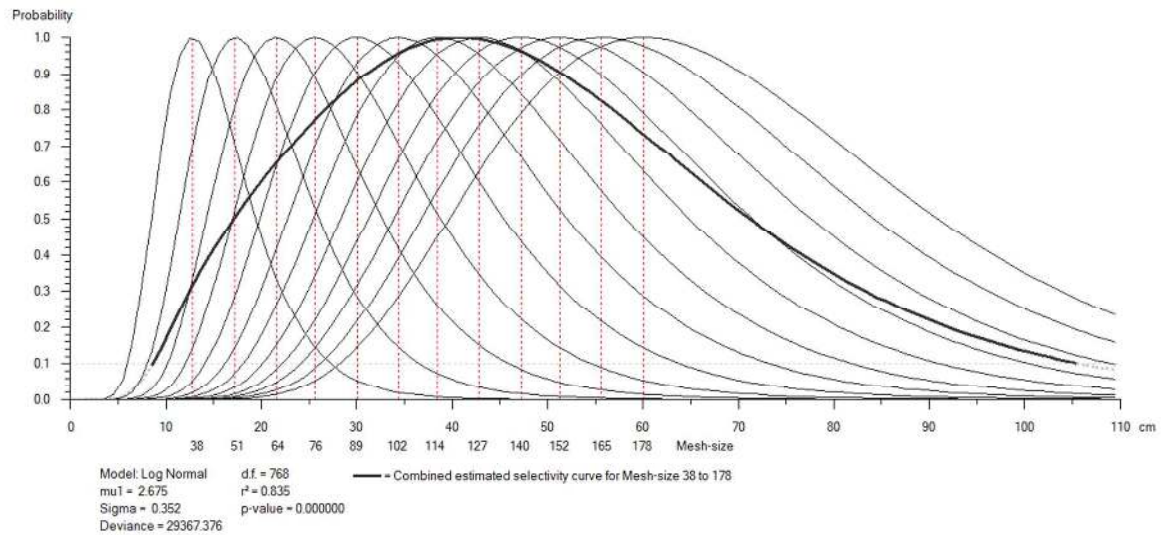


Figure A1. Estimated log-normal selectivity curves on the experimental gillnet catches on the Zimbabwean side of Lake Kariba (1980-1994) from mesh size 38 mm to 178 mm and the combined estimated selectivity (thick black line). Estimation done in Pasgear II (Kolding and Skålevik 2011) using the SELECT method (Millar and Holt 1997).

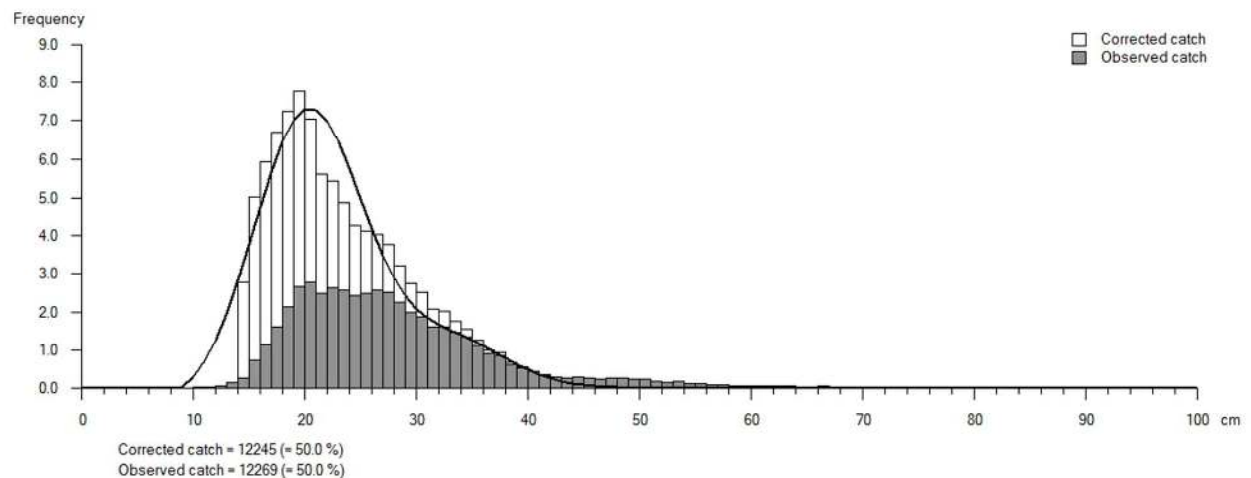


Figure A2. The observed (gray bars) and corrected for selectivity (open bars) catches (relative frequencies by 1 cm intervals) in the experimental gillnets catches on the Zambian side of Lake

Kariba (1980-1994) from mesh size 50 mm to 152 mm. Superimposed (black line) is the estimated overall log-normal selectivity curve. Catches of small fish are underrepresented relative to abundance due to selective catchability from less than around 20 cm TL.

## 2. Calculated selectivity in the artisanal fishery:

The calculated selectivity patterns in Lake Kariba are based on the predominant fishing gear: a gill-net with a log-normal bell-shaped selectivity (Fig A1). The individual mesh selectivity functions are formulated as (Millar and Holt, 1997)

$$\frac{1}{L} \exp \left[ \mu_1 + \log \left( \frac{m_i}{m_1} \right) - \frac{\sigma^2}{2} - \frac{\left( \log(L) - \mu_1 - \log \left( \frac{m_i}{m_1} \right) \right)^2}{2\sigma^2} \right] \quad (\text{A1})$$

Where  $L$  is fish length,  $\mu_1$  is a constant estimated by the SELECT method,  $m_1$  the smallest mesh size in the series,  $m_i$  is mesh size  $i$  and sigma is the spread. Parameters used are estimated in figure A1. To obtain the total selection pattern, the relative heights of the individual curves are adjusted by the number of observed nets of each mesh size and summed for Zambia and Zimbabwe, respectively (Fig. A3).

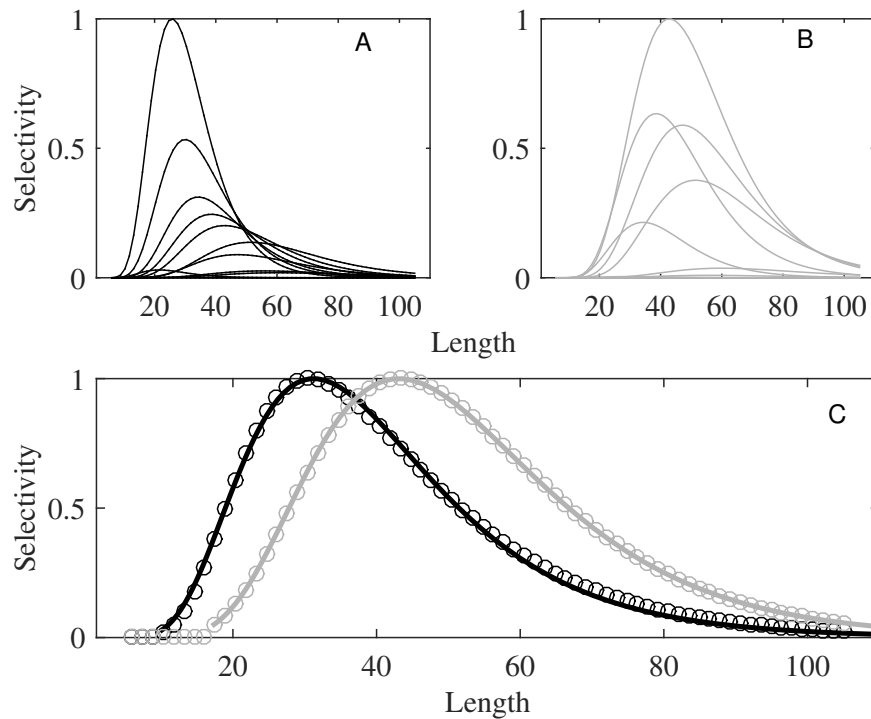


Figure A3. The overall selectivity of artisanal gill-nets in Zambia (A) and Zimbabwe (B) (spread and length parameters from figure A1, height from each mesh size from figure 3, main text). C) The sum of length specific gill-net selectivities gives the total selectivity, or fishing pattern, for Zambia (black circles) and Zimbabwe (gray circles). The full line is the modeled selectivity (eq. M13) in Zambia (black) and Zimbabwe (gray).

#### References:

- Kolding, J. and Skålevik, Å. 2011. PasGear II. A database package for experimental or artisanal fishery data. University of Bergen, Norway. Available from [http://www.imr.no/forskning/bistandsarbeid/nansis/pasgear\\_2/en](http://www.imr.no/forskning/bistandsarbeid/nansis/pasgear_2/en) [accessed 10 January 2015]
- Millar, R.B. and Holst, R. 1997. Estimation of gillnet and hook selectivity using log-linear models. *ICES Journal of Mar. Sci.*, **54**:471-477