Implications of using small meshed gillnets for the sustainability of fish populations: a theoretical exploration based on three case studies

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Abstract The study explores the impacts of varying gillnet mesh size and fishing level on yield per recruit (Y/R), escapement spawning stock (ESS) and mega-spawners (MS) of three widely distributed freshwater fishery target species. Y/R is maximised when the optimal length of capture (L_{cap}) is above the size of maturity (L_{50}). However, the unimodal shape of gillnet selectivity results in lower impacts to ESS and MS with both smaller and larger mesh sizes. Under conditions of moderate exploitation, the fraction of MS was significantly larger if small meshed gillnets were used. This is due to the relatively smaller cumulative vulnerability from small mesh sizes through time, as they target a smaller size range of fish, which also grow more quickly through the vulnerable window due to higher growth rates. Therefore, unlike trawls and beach seines, which select all size classes beyond the minimum length of capture (L_c), small meshed gillnets are not necessarily destructive and may rather promote sustained production by allowing a higher proportion of the spawning biomass to remain in the stock. The work also helps to explain the observation of sustained fish production in many developing countries despite the persistent use of gillnets of small mesh size that target small, under-sized individuals.

KEYWORDS: balanced harvest, mega-spawner, optimum length of capture, selectivity, spawning stock, yield per recruit.

Introduction

The catch volume and size distribution of any fisheries resource depends on fishing effort, gear type, mesh size and other factors (e.g. time of year, location, catchability, quotas). When Beverton and Holt (1957) invented their yield per recruit (Y/R) model and yield isopleth diagram (YID), fisheries managers had the theoretical tool they had long been waiting for. It was now possible to estimate the yield for any recruit that entered the fishery, as a function of two variables that can be determined by the fishery: the fishing mortality, which is proportional to the fishing effort, and the mesh size of the gear, which determines the sizes of the fish that are caught by the fishery. Using this tool, one can theoretically explore how fishing effort (more precisely the fishing mortality F or exploitation rate E) ought to be changed to optimise the Y/R at a given mesh size (fish age at entry). In addition, the mesh size could be determined that optimises Y/R at a given fishing effort. The Y/R model was thus a

breakthrough in fisheries science and is still widely used (Pauly 1998; Caddy 1999).

However, the model is based on two basic assumptions that need to be revised here: (1) independent of the combination of fishing mortality (F) and mesh size (if beyond size at maturity of fishing target), there will be sufficient recruits coming into the fishery every year, so fishing is not expected to affect recruitment substantially; (2) gear selection follows a sigmoid selection curve, with all fish larger than the size at first capture (inflection point of the curve) being retained by the net. Both assumptions were quite reasonable for the target stocks of the North Atlantic trawl fishery at that time (such as plaice and haddock in the North Sea).

Over the years, it has been shown, however, that the first assumption may, in many cases, be wrong and a substantial reduction of the spawning stock under conditions of heavy fishing, may eventually lead to recruitment failure and collapse of the fishery (Cushing

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1971). As a consequence of these fishing failures, fishing mortality (F) and stock biomass reference points had to be developed to allow for a more sustainable harvesting regime (see Caddy (1999) for a comprehensive description of the development of the 21st Century fisheries management). Despite the assumption of independent recruitment processes, the second assumption of a sigmoid selection curve in a trawl fishery led to the 'rule' that the mesh size should be larger than the size at first maturity to avoid catching fish before they have grown to their size at first maturity. A great number of studies have therefore been conducted to estimate the size at first maturity of the fisheries target species to set the size at first capture (and the corresponding mesh size of the gear). Hereby, it is usually assumed that the year class surviving to spawn in their first year of maturity makes the major contribution to reproduction and, thus, can be safely captured thereafter (Law 1991). This paradigm implies that large spawners are the legitimate targets of the fishery, while smaller immature sizes are protected.

In gillnet fisheries, the selection curve of this passive gear differs fundamentally from a trawl that is actively pulled over the ocean bottom, as the small fish pass through the meshes and larger fish may bounce off without being entangled ('gilled') by the net. The curve is thus rather unimodal, and the peak of this curve represents the maximum retention size, here called optimal length of capture (L_{cap}) (Holt 1963; Hamley 1975; Millar & Holst 1997; Sparre & Venema 1998). This means that the larger fish beyond this size has a decreased vulnerability to the gear and for the largest ones, the so-called mega-spawners or BOFFFs – Big Old Fat Fecund Females (Hixon *et al.* 2014), the vulnerability may even be zero. The question thus arises, if fishing with gillnets of mesh size smaller than the size at first maturity (L_{50}) is more harmful than using a larger mesh size – that is in terms of remaining spawners, also called escapement spawning stock (ESS) (Caddy & Mahon 1995). An answer to this question is considered to be important as the argument – gear mesh size should catch sizes >L_{50} as a measure to protect the fish stock – is often used to prohibit fishing with small mesh sizes (Garcia *et al.* 2012). As also emphasised by Kolding and van Zwieten (2014), small-scale unregulated African lake fisheries, with a high diversity of seasonally adapted fishing methods, have persisted over a long time despite using gears with small mesh sizes.

This study explores this question using three case studies, for which growth parameters, size–weight relationships, size at maturity and gear selectivity estimates were available for gillnets with mesh sizes selecting for fish larger and smaller than L_{50}. With these data and given values for the natural (M) and fisheries mortality

Table 1. Input data used for computations of Y/R, ESS and mega-spawners

Parameter*	*Oreochromis niloticus*	*Cyprinus carpio*	*Clarias gariepinus*
K [year^{-1}]	0.41	0.28	0.16
L_∞ [cm]	44.5	74.1	121.9
a	0.0195	0.0228	0.0062
b	2.9679	2.9314	3.039
M [year^{-1}]	0.82	0.55	0.33
L_{50} [cm] (w)	24.6 (5.72)	30.6 (8.53)	53.4 (12.74)
Selectivity function†	LN ($m_1 = 60$ mm, $\mu_1 = 2.7977$, $\sigma = 0.1175$)	LN ($m_1 = 60$ mm, $\mu_1 = 2.8782$, $\sigma = 0.1292$)	LN ($m_1 = 60$ mm, $\mu_1 = 3.4655$, $\sigma = 0.1290$)

* Growth and gillnet selectivity parameters were obtained from Tesfaye and Wolff (in press) and Tesfaye *et al.* (unpublished data), respectively.
† Selectivity functions and parameters as described by Millar and Holst (1997). K = von Bertalanffy growth constant, L_∞ = average maximum length a fish can attain if a fish allowed to live indefinitely, a and b = parameters from length–weight relationship, M = rate of natural mortality; L_{50} = the length at which 50% of the population becomes mature (in parenthesis, w, equalling the width [cm] between the 25% and 75% quantiles), LN = Lognormal model.

(F), the widely used Thompson and Bell (1934) Y/R approach was used to compare the overall yield (Y) and escapement spawning stock (ESS) obtained for both gears.

Materials and methods

Case studies – data input

Three widely distributed fishery target species of African lakes that have different size and growth rates were used as case study species. These include small fast-growing tilapia, *Oreochromis niloticus* (L.), medium size moderately growing common carp, *Cyprinus carpio* L. and large slow-growing African catfish, *Clarias gariepinus* (B.). The summary of input data used for the computation is given in Table 1.

Simulation of fishing

A modification of the Thompson and Bell (1934) model was applied to simulate the fishing regime with gillnets of different mesh sizes. In its original version, it follows a cohort of fish that enters the fishery from its first age at capture (t_c) to its maximum age assuming full vulnerability of all fish >t_c. As gillnets typically have a unimodal selection function (Holt 1963; Hamley 1975; Millar & Holst 1997; Sparre & Venema 1998), the highest probability of capture is at L_{cap}, while fish

smaller and larger than L_{cap} have a lower probability of capture. Thus, the numbers of fish that are harvested at each age depends on two factors: (1) the fishing effort and (2) the probability of capture. In the current model, fishing effort is directly related to fishing mortality, F, while the effect of this mortality is scaled by the gillnet selectivity function (e.g. the probability of capture, which ranges from 0 to 1, is multiplied by the F value).

By modifying F (assuming a constant rate of natural mortality, M, for the sizes vulnerable by the fishery), it can be explored how many fish at each age are removed by gillnets with different but known selection curves and how the total catch over the cohort's lifespan would change. At the same time, the model allows for the estimation of the biomass of fish beyond the size/age at first maturity (L_{50}) (ESS). Furthermore, the study also assessed the effect of the variable F and L_{cap} combinations on the fraction of so-called mega-spawners (MS); that is fish that are at least 10% larger than the size at which an unfished stock ($F = 0$) maximises cohort biomass (L_{opt}) (Froese 2004). The rationale is that larger, older fish often have disproportionate spawning success due to increased fecundity, experience and egg quality and that a high fraction of MS would be indicative of population health.

For each of the case study species, combinations of F and L_{cap} (corresponding to fishing intensity and mesh size) were used to simulate the development of a single cohort. F was simulated over a range corresponding to exploitation rates, $E = F/(M + F)$, of 0.0–0.8. Cohorts were simulated until the maximum age, t_{max}, corresponding to the age at $L_\infty \times 0.95$ (Taylor 1958).

Growth

Growth in length is modelled using the von Bertalanffy growth function,

$$L_t = L_\infty (1 - e^{(-K*(t-t_0))}) \qquad 1$$

where L_t is length [cm] at age t, L_∞ is the asymptotic length, K [year^{-1}] is the von Bertalanffy growth constant and t_0 is the time when the function crosses the time axis at length equalling zero. Individual weight, W_t [g], can then be calculated given the length to weight relationship as described by a power function:

$$W_t = a \times L_t^b \qquad 2$$

where a and b are constants and the units are centimetres for length and grams for weight. Growth parameters

were estimated by Tesfaye and Wolff (2015) using a large number of individual samples from Lake Koka, Ethiopia (*O. niloticus*, $n = 7933$; *C. gariepinus*, $n = 6025$; *C. carpio*, $n = 6139$).

Natural and fishing mortality

The shape of the selectivity function for the probability of capture by length can be described by various density functions. A method called 'SELECT (**S**hare **E**ach **Le**ngth class **C**atch **T**otal)' is widely used and became popular in gillnet selectivity studies (Millar & Holst 1997; Millar & Fryer 1999). With SELECT, the expected catch proportions are fitted to the observed catch using maximum likelihood, under the assumption that catches are Poisson random variables (Millar & Holst 1997; Millar & Fryer 1999). It comprises several models and estimates selection curves (i.e. retention probabilities) from comparative gillnet catches within a single model, which increases statistical precision and power. It is thus considered to be the most robust indirect method to estimate gear selectivity (for details, see Millar & Holst 1997; Millar & Fryer 1999).

For the three species modelled here, gillnet selectivity parameters were derived from experimental fishing experiments using gillnets of differing mesh sizes (60, 80, 100 and 120 mm), which caught all species across a wide range of sizes (*O. niloticus,* 14-38 cm, $n = 286$; *C. gariepinus,* 24-80 cm, $n = 257$; *C. carpio*, 11-50 cm, $n = 395$) and included both immature and mature individuals (G. Tesfaye, unpublished data). The results indicated that a lognormal distribution best described the experimental gillnet selectivity data for all three species. The lognormal model as described by Millar and Holst (1997) was used to fit the selection curves and estimate L_{cap} values:

$$\frac{1}{L_i}\exp\left(\mu_1 + \log\left(\frac{m_j}{m_1}\right) - \frac{\sigma^2}{2} - \frac{\left(\log(L_i) - \mu_1 - \log\left(\frac{m_j}{m_1}\right)\right)^2}{2\sigma^2}\right) \qquad 3$$

where L_i is mid-length of the ith length class in the catch of gillnet j, m_j is the mesh size of gillnet j, m_1 is the size of the smallest mesh size gillnet, and μ_1 and σ are model parameters.

The decrease in a cohort's population size over time t is assumed to follow a negative exponential function, whose slope is determined by the summation of natural and fishing mortality:

$$N_{t2} = N_{t1} * e^{(-(M + F * pCAP_t) * (t2 - t1)))} \qquad 4$$

where N_{t2} and N_{t1} are the population sizes (in numbers) at times t_2 and t_1, M [year^{-1}] is the rate of natural mortality, F [year^{-1}] is the fishing mortality, which is scaled by the probability of capture at length L, pCAP$_L$. Likewise, the number of caught individuals at age t, C_t, can be obtained calculating the decrease in numbers due to fishing mortality alone:

$$C_{t2} = N_{t1} * \left(1 - e^{(-(F * pCAP_t) * (t2 - t1))}\right) \qquad 5$$

Yield, spawning stock biomass and indices of population health

Yield to the fishery can be calculated for each age t, Y_t, by multiplying the catch in numbers by their individual weight (from Eq. 2):

$$Y_t = C_t \times W_t \qquad 6$$

By summing up the fishing yield across all ages, and dividing by the number of starting recruits, one is able to calculate the yield per recruit, *Y/R*:

$$Y/R = \left(\sum_{t=0}^{t_{max}} Y_t\right) \Big/ N_{t0}, \qquad 7$$

where N_{t0} is the initial number of recruits at t = 0, and t_{max} is the maximum age. Likewise, the population biomass at age t, B_t, can be calculated by multiplying the population size in numbers by their individual weight (from Eq. 2):

$$B_t = N_t * W_t \qquad 8$$

Information on the age of maturity is required to describe the effects of fishing on the reproductive capacity of the population. The probability of maturity is described by the logistic regression after Heino *et al.* (2002):

$$pMAT_t = 1 \Big/ \left(1 + e^{-(L_t - L_{50})/\delta}\right), \qquad 9$$

where L_{50} is the length at 50% maturation probability, and the parameter δ defines the steepness of the transition between immature and mature as defined by the width, w, between lower and upper probability bounds, p_l and p_u:

$$\delta = \frac{w}{\log itp_u - \log itp_i} \qquad 10$$

where $\log itp = \log_e(p/(1 - p))$. The 25% and 75% quartiles were used to calculate w ($p_i = 0.25$; $p_u = 0.75$).

The logistic regression model is an adaptation of that presented by Heino *et al.* (2002) for probabilistic maturation reaction norms.

Using $pMAT_t$, one can calculate the spawning biomass, SB_t, as the proportion of the population biomass, B_t, that is mature:

$$SB_t = B_t \times pMAT_t \qquad 11$$

The sum of the spawning biomass over all ages is referred to as the ESS:

$$ESS = \left(\sum_{t=0}^{t_{max}} SB_t\right) \Big/ t_{incr} \qquad 12$$

where t_{max} is the maximum age, and t_{incr} is the time increment used; this standardisation is necessary if model time steps differ from the growth, K, and mortality, M and F, rate units (e.g. year^{-1}).

Froese (2004) defined mega-spawners as fish that are +10% larger than the size when the cohort's biomass, B_t, is at a maximum, L_{opt}, under conditions of natural mortality only (i.e. $F = 0$). Here, due to the unimodal selection of gillnets, this indicator was adapted to reflect the fraction of mega-spawners, fracMS, in the whole population rather than in the catch alone:

$$\text{fracMS} = \left(\sum_{t=0}^{t_{max}} (N_t * MS_t)\right) \Big/ \sum_{t=0}^{t_{max}} N_t \qquad 13$$

where N_t is the number of individuals in the population at time t, MS_t is conditional vector defining whether the corresponding size is greater than L_{opt}: if $L_t > L_{opt} *$ 1.1, then $MS_t = 1$, else $MS_t = 0$.

Results

For the large, relatively slow-growing African catfish, *Y/R* increases with mesh size, even if this was beyond L_{opt} at the level of full exploitation ($E = 0.5$) and beyond (Fig. 1). However, the ESS is significantly larger if a small L_{cap} (even $< L_{50}$) was used. At extreme high fishing rates, either very small or very large mesh sizes would allow for maintenance of a larger ESS. Also, the fraction of mega-spawners remaining in the stock would – under conditions of moderate to extreme exploitation rates – be significantly larger if gillnets of small mesh sizes ($<L_{50}$) were used.

The time vulnerable to the fishing gear increases exponentially with mesh size, as larger fish need far more time to grow through the vulnerable size window (Fig. 2). In particular, the vulnerability in relation to size increases in a linear manner, while the same data

presented versus age indicates the exponential increase in the vulnerability window.

For the large, moderately growing carp, while the isolines of Y/R and ESS differ a bit from those of the above example of the catfish, the general tendencies are very similar with larger mesh sizes optimising Y/R and smaller mesh sizes optimising ESS (Fig. 3). The same holds for the plot of the proportion of mega-spawners (Fig. 3, right panel).

For the fast-growing, relatively small tilapia, the tendencies are similar as for the other two species with regard to the relationship between Y/R, ESS and mega-spawners and L_{cap} and E (Fig. 4); however, the Y/R does not increase as strongly with the mesh size as in the other slow- and moderate-growing species.

Discussion

The results show that the use of gillnet mesh sizes that select fish below the size at maturity (L_{50}) of the target resources is, opposite of what is generally believed, less reducing the spawning stock (Figs 1, 3 and 4). Instead, small mesh sizes select fish during a short time window of their life cycle only (Fig. 2) and allow more spawners to remain in the stock. Of special relevance is that the large 'mega-spawners' are particularity favoured by those gillnets of small mesh sizes. The reason is that large fishes cannot penetrate deep enough into the small mesh to be gilled or wedged and, thus, are less vulnerable to the small mesh (Hamley 1975; Pope *et al.* 1975; Millar & Fryer 1999). However, as the three case study results also show, the down side of this strategy of using small mesh sizes in gillnets is that the overall Y/R of those species is suboptimal (Figs 1, 3 and 4).

Often fishery regulations rely mainly on minimum-size regulations that give legitimate right to target larger individuals (sizes beyond L_{50} or sizes at L_{opt}). However, if only large mesh sizes were used (a common measure to implement minimum-size regulations), the larger predatory fish and/ or old larger individuals, which are often highly fecund and produce quality eggs, would be targeted more heavily and would result in a substantial alteration of the size spectrum and trophic structure of the ecosystem. Law *et al.* (2013) also noted that targeting only larger individuals cause truncation of age and size structures and destabilisation of the fish stocks. On the other hand, old larger individuals are not only an indicator of population health, but also maintain and transfers desirable genes to their descendants. However, persistent removal of large individuals causes directional selection of genes resulting in earlier maturation and slower growth, setting the stage for fisheries-induced evolution of maturation at younger ages and smaller sizes (Law 2000; Sharpe & Hendry 2009; Borrell 2013; Law *et al.* 2013). This has been observed in heavily exploited stocks such as Northeast Arctic cod *Gadus morhua* and British Columbia Coho salmon *Oncorhynchus kisutch* & Pink salmon *Oncorhynchus gorbuscha* (Jørgensen *et al.* 2007). Therefore, fisheries-induced evolution not only diminishes yield, but also degrades ecological services, having an impact on species, ecosystems and societies (Jørgensen *et al.* 2007).

Experience has also shown a high resistance of fishers to follow minimum-size regulations particularly in small-
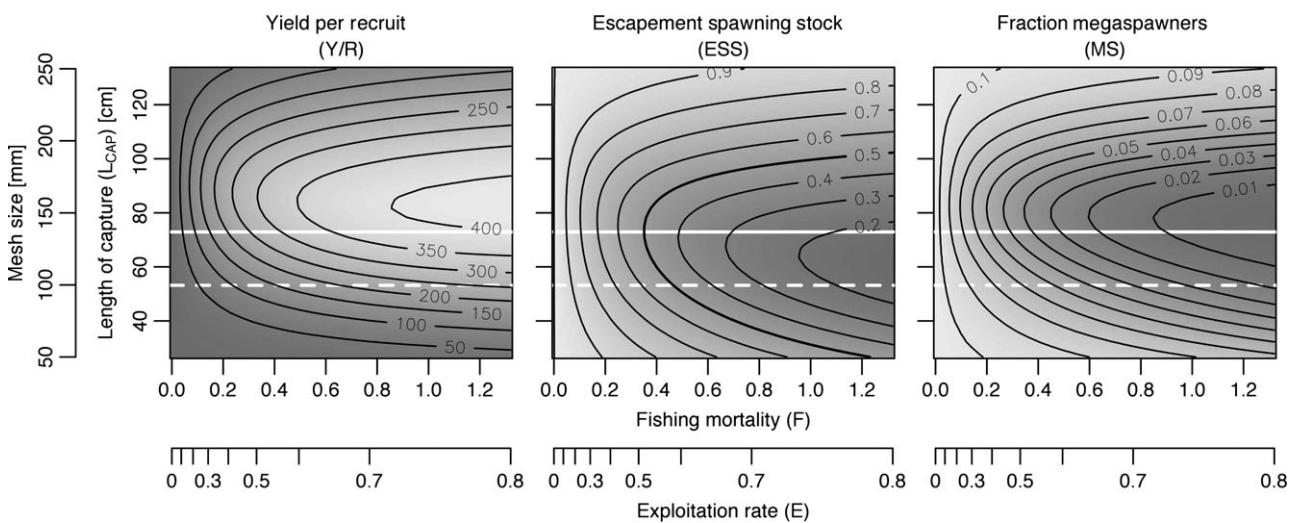

Figure 1. *Clarias gariepinus* – yield and spawning stock exploration at different gillnet mesh sizes. Yield per recruit (*Y/R*) (left), escapement spawning biomass (ESS) relative to the unfished stock (middle), and fraction of population classified as mega-spawners (right) as a function of fishing mortality (*F*) and optimal length of gillnet capture (L_{cap}). Body lengths of maximum cohort biomass (L_{opt}, solid white line) and maturity (L_{50}, dashed white line) are shown for reference.
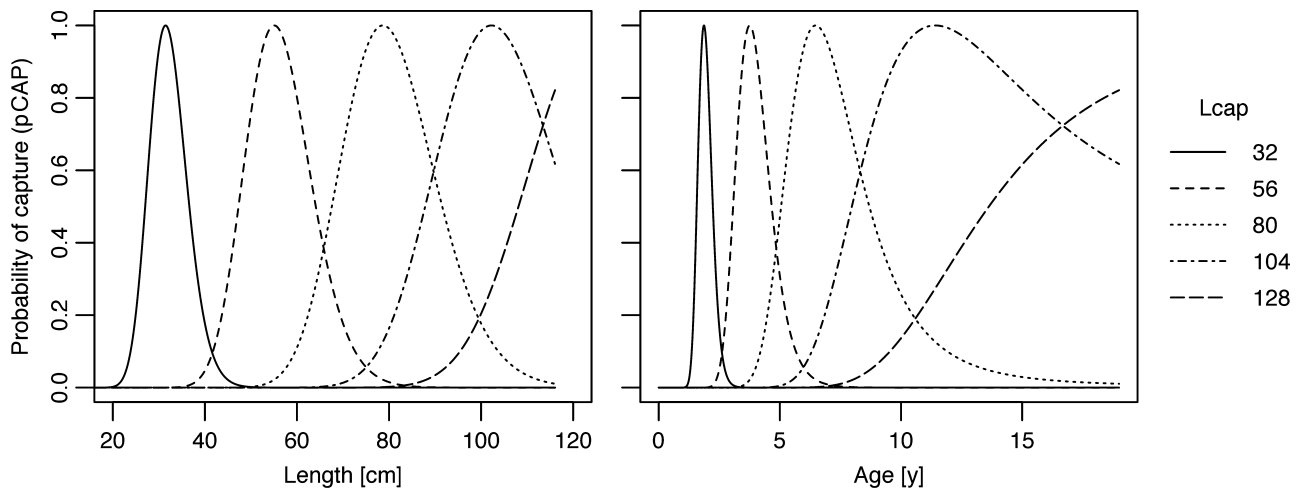
Figure 2. Probability of capture as a function of fish length and age for *Clarias gariepinus*. Probability of capture (*pCAP*) as a function of fish length (left) and age (right) for different gillnet L_{cap}. The time spent vulnerable to capture increases exponentially with the length of optimal capture (L_{cap}).
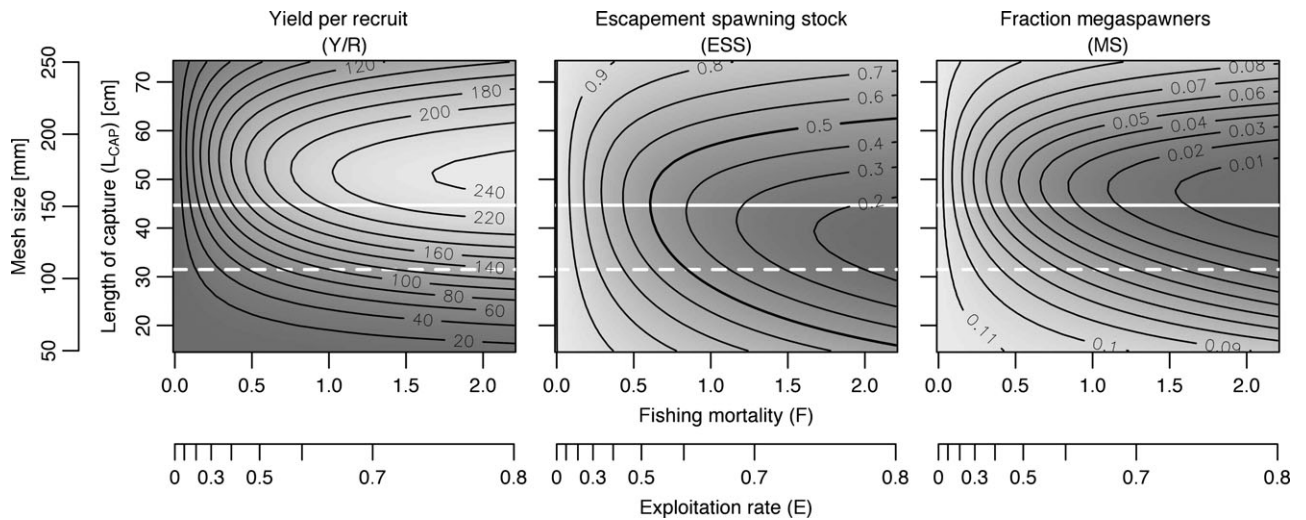

Figure 3. *Cyprinus carpio* – yield and spawning stock exploration at different gillnet mesh sizes. Yield per recruit (*Y/R*) (left), escapement spawning biomass (ESS) relative to the unfished stock (middle) and fraction of population classified as mega-spawners (right) as a function of fishing mortality (*F*) and optimal length of gillnet capture (L_{cap}). Body lengths of maximum cohort biomass (L_{opt}, solid white line) and maturity (L_{50}, dashed white line) are shown for reference.

scale fisheries where fishing serves as a means of livelihoods and social security. Kolding and van Zwieten (2011) observed that most fishers of African lakes would not follow the recommendations for increasing the mesh sizes of their gears beyond the fish's size at first maturity. This often caused strong conflicts between fishers and the fisheries authorities. The reason for this fishermen behaviour is that their small nets allow for larger catch volumes (see Fig. 5 for an illustration of this). As small fish are generally more abundant, grow faster and have higher overall biomass and turnover in the system (Sweeting *et al.* 2009; Rochet & Benoît 2012), a gillnet

that targets this part of the size spectrum would allow for a higher overall yield (in terms of extracted biomass) than a gillnet entirely targeting the larger sizes alone (see also Law *et al.* (2014) for a discussion of *Y/R* models in a size-spectrum perspective). In addition, small fish contain more nutrients (being eaten whole) than large fish (Roos *et al.* 2003; Kawarazuka & Bene 2011).

While catch (weight) maximisation by the use of small gillnets may thus be the primary goal of many subsistence fishers, larger fish species often have a higher market value and may additionally be targeted using other gillnets with larger mesh sizes. A diversification of
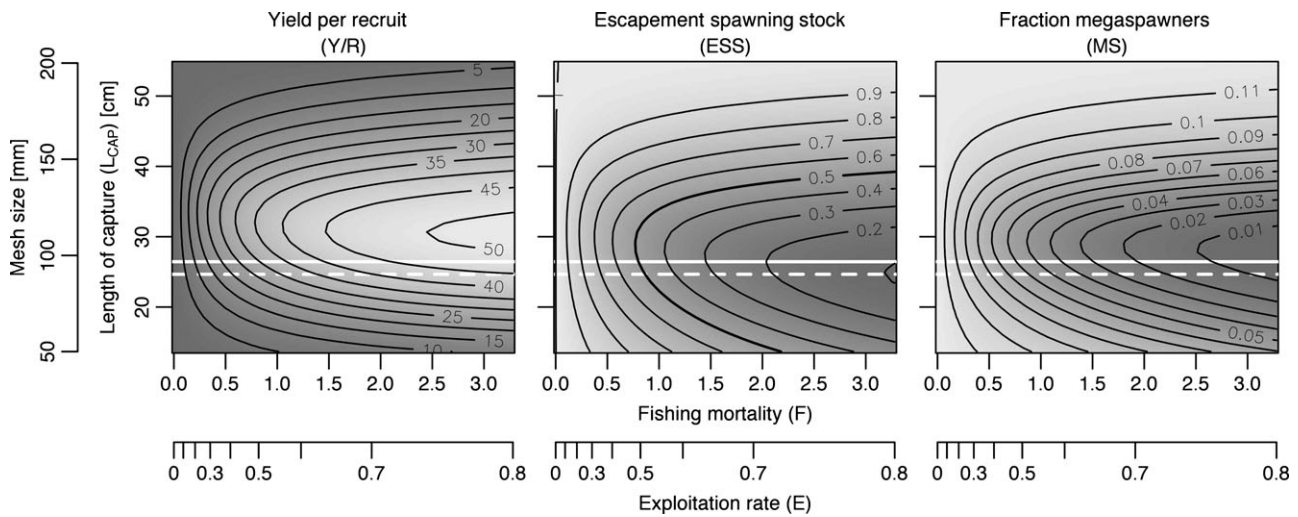
Figure 4. *Oreochromis niloticus* – yield and spawning stock exploration at different gillnet mesh sizes. Yield per recruit (*Y/R*) (left), escapement spawning biomass (ESS) relative to the unfished stock (middle) and fraction of population classified as mega-spawners (right) as a function of fishing mortality (*F*) and optimal length of gillnet capture (L_{cap}). Body lengths of maximum cohort biomass (L_{opt}, solid white line) and maturity (L_{50}, dashed white line) are shown for reference.
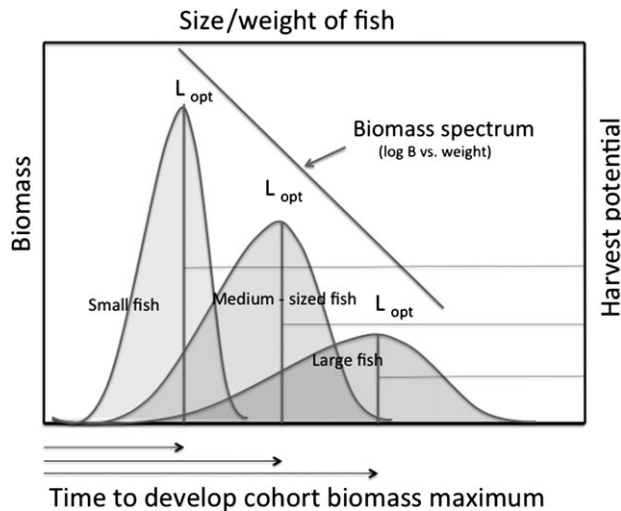

Figure 5. Fish size – biomass spectrum and harvest potential for different sizes of fish. The figure shows that cohorts of large fish need longer time to grow in order to maximise biomass; this time is inversely related to biomass productivity and harvest potential.

gillnet types and the use of other gears such as longlines and traps to target different parts of the size spectrum thus seems to be the logical – and apparently used – approach for a multigear, multispecies fishery to optimise the overall resource use along the natural size spectrum of the ecosystem. This idea that exploitation should be balanced across trophic levels to maintain the ecosystem trophic structure has already been put forward by Misund *et al.* (2002) and Bundy *et al.* (2005) and was called 'balanced harvest' by Garcia *et al.* (2012). It not only allows for the most efficient use of the ecosystem's

resources, but it also leads to a splitting of the overall fishing effort over different gears, target species and sizes thereby reducing the exploitation rate over any single size fraction of the system. By this diversification, competition between fishers is also reduced. Moreover, as Law *et al.* (2012) and Rochet and Benoît (2012) demonstrated via a modelling simulation, 'biomass oscillations have wider amplitude when fishing is selective (removes a narrow size range) and/or when large fish are targeted, than when fishing is more balanced (catching a larger size range) or when small fish are targeted'. In this context, Kolding and van Zwieten (2011) showed that the exploitation rate of many African lake fish stocks increased with size and trophic level, which confirms that the assumption that small, illegally used gillnets would heavily impact the stocks of small fish species is not necessarily correct.

In this study, the consequences of using gillnets with different mesh sizes were assessed, but the potential problems associated with the use of other gears that are frequently used in tropical coastal areas, such as beach seines or trawls, were not explicitly addressed. Trawls target fish beyond the size at first capture, which means that, if fishing effort is high and mesh size is small, most of the fish of an area along the whole size spectrum may be removed by the fishery, with no chance for the larger spawners to escape. This is shown in Figure 6, where the effect of a trawl (knife edge) selection on the African catfish used in Figure 1 was explored. It is evident that at smaller length of capture (around or below the dashed line of L_{50}), ESS and MS would be very low for almost any exploitation rate, while a gillnet would not have this detrimental effect (Fig. 1).
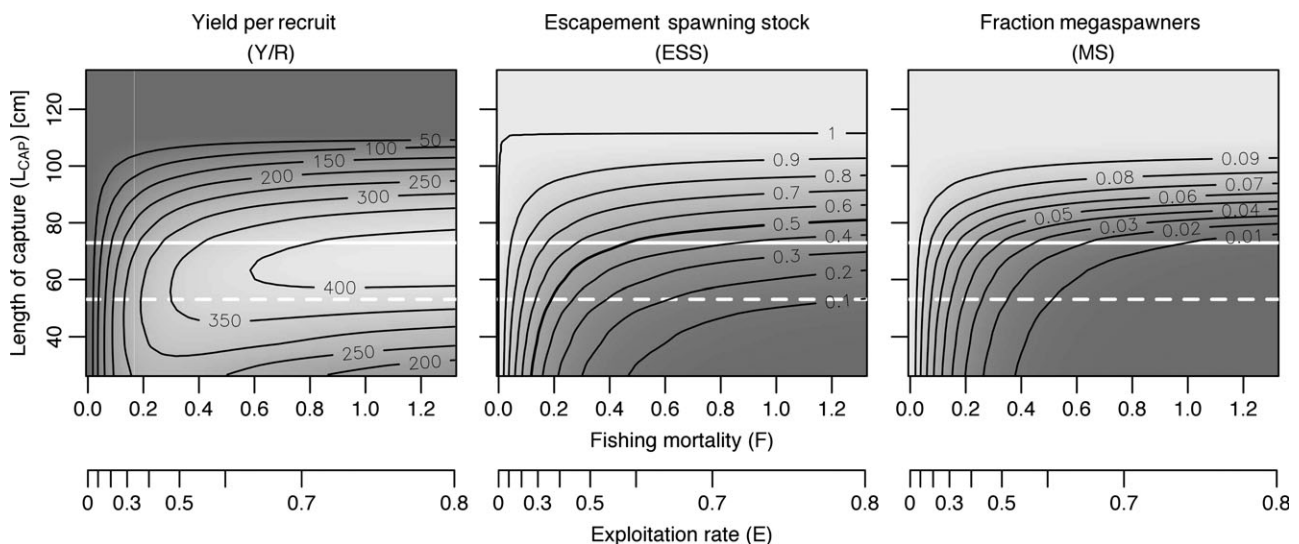
Figure 6. *Clarias gariepinus* – yield and spawning stock explorations under conditions of trawl selection (assuming knife-edge selection). Yield/recruit (left), escapement spawning biomass (ESS) relative to the unfished stock (middle) and fraction of population classified as mega-spawners (right) as a function of fishing mortality (F) and length at first capture assuming trawl selection. Body lengths of maximum cohort biomass (L_{opt}, solid white line) and maturity (L_{50}, dashed white line) are shown for reference.

In conclusion, gillnets with small mesh sizes are not necessarily destructive and may rather promote sustained production by allowing a higher proportion of the spawning biomass (both ESS and MS) to remain in the stock. Nevertheless, these results cannot be extrapolated to trawls and beach seines, as these gears have different selection properties (selectivity curves) and disturb and alter the substrate. In addition, for a sound overall fishing strategy to be implemented in a specific fishing area, the selectivity of the gears employed needs to be known as well as the fishing mortalities caused by the multigear fishery along the whole fish size spectrum of the system. Based on this knowledge, a 'system fishery strategy' should be developed that allows for harvesting all size fractions according to their productivities.

Acknowledgments

References

Beverton R.J.H. & Holt S.J. (1957) *On the Dynamics of Exploited Fish Populations*. UK: Ministry of Agriculture, Fisheries and Food, 533 pp.

Borrell B. (2013) Ocean conservation: a big fight over little fish. *Nature* **493**, 597–598.

Bundy A., Fanning P. & Zwanenburg C.T.K. (2005) Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *Ices Journal of Marine Science* **62**, 503–510.

Caddy J.F. (1999) Fisheries management in the twenty-first century: will new paradigms apply? *Reviews in Fish Biology and Fisheries* **9**, 1–43.

Caddy J.F. & Mahon R. (1995) Reference points for fisheries management. *FAO Fisheries Technical Paper* **347**, 83.

Cushing D.H. (1971) The dependence of recruitment on parent stock in different groups of fishes. *Journal du Conseil* **33**, 340–362.

Froese R. (2004) Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries* **5**, 86–91.

Garcia S.M., Kolding J., Rice J., Rochet M.J., Zhou S., Arimoto T. *et al.* (2012) Reconsidering the consequences of selective fisheries. *Science* **335**, 1045–1047.

Hamley J.M. (1975) Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada* **32**, 1943–1969.

Heino M., Dieckmann U. & Godø O.R. (2002) Measuring probabilistic reaction norms for age and size at maturation. *Evolution* **56**, 669–678.

Hixon M.A., Johnson D.W. & Sogard S.M. (2014) BOFFFs: On the importance of conserving old-growth age structure in fishery populations. *Ices Journal of Marine Science* **71**, 2171–2185.

Holt S.J. (1963) A method for determining gear selectivity and its application. *International Commission for the Northwest Atlantic Fisheries (ICNAF) Special Publication* **5**, 106–115.

Jørgensen C., Enberg K., Dunlop E.S., Arlinghaus R., Boukal D.S., Brander K. *et al.* (2007) Managing evolving fish stocks. *Science* **318**, 1247–1248.

Kawarazuka N. & Bene C. (2011) The potential role of small fish species in improving micronutrient deficiencies in developing countries: building evidence. *Public Health Nutrition* **14**, 1927–1938.

Kolding J. & van Zwieten P.A.M. (2011) The tragedy of our legacy: How do global management discourses affect small scale fisheries in the south? *Forum for Development Studies* **38**, 267–297.

Kolding J. & van Zwieten P. (2014) Sustainable fishing of inland waters. *Journal of Limnology*. **73**, 132–148. doi:10.4081/jlimnol.2014.818.

Law R. (1991) Fishing in evolutionary waters. *New Scientist* **129**, 35–37.

Law R. (2000) Fishing, selection, and phenotypic evolution. *Ices Journal of Marine Science* **57**, 659–668.

Law R., Plank M.J. & Kolding J. (2012) On balanced exploitation of marine ecosystems: results from dynamic size spectra. *Ices Journal of Marine Science* **69**, 602–614.

Law R., Kolding J. & Plank M.J. (2013) Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries* **16**, 160–174.

Law R., Plank M.J. & Kolding J. (2014) Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish and Fisheries*. doi:10.1111/faf.12098.

Millar R.B. & Fryer R.J. (1999) Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries* **9**, 89–116.

Millar R.B. & Holst R. (1997) Estimation of gillnet and hook selectivity using log-linear models. *Ices Journal of Marine Science* **54**, 471–477.

Misund O.A., Kolding J. & Freon P. (2002) Fish capture devices in industrial and artisanal fisheries and their influence on management. In: P.J.B. Hart & J.D. Reynolds (eds) *Handbook of Fish Biology and Fisheries*. London: Blackwell Science, pp 13–36.

Pauly D. (1998) Beyond our original horizons: the tropicalization of Beverton and Holt. *Reviews in Fish Biology and Fisheries* **8**, 307–334.

Pope J.A., Margetts A.R., Hamley J.M. & Akyüz E.F. (1975) Manual of methods for fish stock assessment. Part III, Selectivity of fishing gear. *FAO Fisheries Technical Paper* **41–1**, 65.

Rochet M.J. & Benoît E. (2012) Fishing destabilizes the biomass flow in the marine size spectrum. *Science* **279**, 284–292.

Roos N., Islam M.M. & Thilsted S.H. (2003) Small indigenous fish species in bangladesh: contribution to vitamin A, calcium and iron intakes. *Journal of Nutrition* **133**, 4021S–4026S.

Sharpe D.M.T. & Hendry A.P. (2009) Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications* **2**, 260–275.

Sparre P. & Venema S.C. (1998) Introduction to tropical fish stock assessment: Part 1-manual. *FAO Fisheries Technical Paper* **306-1**, rev. 2, 407.

Sweeting C.J., Badalamenti F., D'Anna G., Pipitone C. & Polunin N.V.C. (2009) Steeper biomass spectra of demersal fish communities after trawler exclusion in Sicily. *Ices Journal of Marine Science* **66**, 195–202.

Taylor C.C. (1958) Cod growth and temperature. *Journal du Conseil* **23**, 366–370.

Tesfaye G. & Wolff M. (2015) Stock assessment of fishery target species in Lake Koka, Ethiopia. *Revista de Biología Tropical* **63**(3): 755–770.

Thompson W.F. & Bell F.H. (1934) Biological statistics of the Pacific halibut fishery. Effect of changes in intensity upon total yield and yield per unit of gear. *Report of the International Fisheries Commission* **8**, 49.