# **Ecological Consequences of Alternative Gill Net Fisheries for Nile Perch in Lake Victoria**

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Abstract: Both harvest rates and food web interactions may be altered through use of different gill net mesh sizes in the fisheries of Lake Victoria, East Africa. Thus, conservation of the native ichthyofauna is intimately linked to patterns of exploitation in the fisheries. We used bioenergetics modeling to estimate the harvest rates of introduced Nile perch (Lates cf. niloticus) and changes in their predation rates on other important fishes that would result from the implementation of various restrictions on gill net mesh size. Total mass of harvested Nile perch was predicted to vary more than three-fold over the range of minimum gill net mesh size from 3 to 16 inches. Maximum harvest is expected to result from minimum mesh size restrictions between 6 and 10 inches. Predation rates on all prey fishes would increase with all increases in minimum mesh size. Universal enforcement of a 5-inch minimum mesh size would reduce both Nile perch cannibalism and predation on other important fishes, such as tilapiines, haplochromine cichlids, and Rastrineobola argentea by as much as 44%, with little decrease (10%) in Nile perch yield. But, if fishers respond to a 5-inch minimum mesh size by concentrating all fishing effort on the smallest gill nets (5- and 6-inch mesh), a substantially larger reduction in predation on native haplocbromines will result, but at the expense of large ( $\sim$ 35%) decreases in Nile perch barvest. Our analyses demonstrate that fisheries in Lake Victoria will play an active role in the restoration of a diverse fish community and fishery resource, thus benefiting both many native fish species and the sustainability of the fishery.

Consecuencias Ecológicas de Pesquerias de Redes Agalleras Alternativas para la Perca del Nilo en el Lago Victoria

Resumen: Tanto las tasas de cosecha como las interacciones de la cadena alimenticia pueden ser alteradas mediante el uso de diferentes tamaños de luz de malla de las redes agalleras en las pesquerías del lago Victoria, en el este de Africa. Por lo tanto, la conservación de la ictiofauna nativa esta íntimamente ligada a los patrones de explotación de las pesquerías. Utilizamos un modelado bioenergético para estimar las tasa de cosecha de la perca del Nilo introducida (Lates cf. niloticus) y los cambios en sus tasas de depredación sobre otras especies de peces importantes, mismos que podrìan resultar de la implementación de varias restricciones en el tamaño de la luz de malla de redes agalleras. Se predijo que la masa total cosechada de perca del Nilo variará mas de tres veces sobre un rango minimo de luz de malla de entre 3 y 16 pulgadas. Las cosechas máximas se esperan como resultado de restricciones en el tamaño minimo de luz de malla entre 6 y 10 pulgadas. Las tasas de depredación en todas las presas de peces podría incrementarse con todos los incrementos en el tamaño de luz de malla. La aplicación estricta de un mínimo de luz de malla de 5 pulgadas podría reducir tanto el canibalismo de la perca del Nilo así como su depredación sobre otras especies importantes de peces, como son las tilapias, los cíclidos baplocrominos y Rastrineobola argenta por basta un 44%, con una pequeña disminución (10%) en la cosecha de la perca. Sin embargo, si los pescadores responden a un tamaño mínimo de luz de malla de 5 pulgadas al concentrar todo el esfuerzo pesquero en las redes mas pequeñas (i.e., 5 y 6 pulgadas de luz de malla), podría obtenerse una reducción sustancialmente grande en la depredación de los peces haplocrominos, pero a expensas de un disminución considerable ( $\sim$ 35%) en la cosecha de la perca. Nuestro análisis demuestra que las

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pesquerías del lago Victoria jugarán un papel activo en la restauración de la comunidad diversa de peces y recursos pesqueros, beneficiando tanto a varias especies nativas de peces, como a la sustentabilidad de la pesquería.

### Introduction

Changes in the food web of Lake Victoria (East Africa) during the last 40 years are among the most dramatic known to ecology (Kaufman 1992; Lowe-McConnell 1994). Nile perch (Lates cf. niloticus, Centropomidae) and several tilapia species (especially Nile tilapia—Oreochromis niloticus, Cichlidae) were introduced to Lake Victoria from neighboring sources in the 1950s (Ogutu-Ohwayo 1990a), and their populations have subsequently shown exponential growth. Rapid increase of the piscivorous Nile perch was accompanied by an equally spectacular decline in the diversity and abundance of the endemic haplochromine cichlid species (Barel et al. 1985; Witte et al. 1992), an event considered the most rapid vertebrate mass extinction in recent history (Kaufman 1992). The loss of many endemic species appears related primarily to Nile perch predation, although other factors including overfishing with fine-mesh nets, eutrophication and associated hypoxia, and extreme fluctuations in lake level—have also contributed to the decline of the native ichthyofauna (Kaufman 1992; Kaufman & Ochumba 1993).

The Lake Victoria fisheries have also changed radically from a focus on native species before 1970 to current dominance by catches of Nile perch, introduced tilapiines, and the native pelagic cyprinid Rastrineobola argentea (Cyprinidae) (Ogutu-Ohwayo 1990b, 1994). Total fishery yield has increased at least four-fold during this time and currently supports a prosperous industry based largely on gill net fishing for Nile perch and Nile tilapia (Greboval 1990). Because gill nets are highly sizeselective, changes in fishery practices are likely to alter the predatory effects of Nile perch on the remnant native species by altering both total Nile perch biomass and the population size-structure (Kitchell et al. 1997). Thus, humans are currently a dominant component of the Lake Victoria food web, and fisheries have the potential to further alter community structure and dynamics. Means for conserving the remaining haplochromine species in the context of the changing fishery are not well understood (Bruton 1990).

Growing concern that the current gill net fisheries in Lake Victoria might lead to overexploitation and potential collapse of the commercially important stocks (Ogutu-Ohwayo et al. 1997) has prompted management proposals that seek to sustain both the Nile perch and Nile tilapia populations. The fisheries of Lake Victoria could be regulated in at least two distinct ways. One option is to con-

trol fishing effort as a means to regulate exploitation, but, this would be difficult to implement given that no effective mechanism exists to regulate fishing effort from the riparian communities of Uganda, Tanzania, and Kenya. The fisheries have always been managed with an open access policy that is typically the predecessor of overexploitation (Hilborn et al. 1995). An alternative to regulating total effort is to regulate the allocation of effort through gear restrictions—particularly enforcement of allowable gill net mesh sizes (Greboval 1990; Ogutu-Ohwayo et al. 1997). Through restrictions on retail distribution of gill nets and confiscation of nets outside allowable size ranges, successful implementation of gill net mesh size regulations may be possible with adequate funding for enforcement. Although the realized success of such a strategy is likely to be the most acceptable and enforceable from a management standpoint, its potential ecological consequences on both the target species and the endangered haplochromine cichlids remain unexplored.

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Ogutu-Ohwayo et al. (1998) compared the size at maturity of Nile perch and Nile tilapia with vulnerability to gill nets. They recommended that a minimum gill net mesh size be enforced at 5 inches (127 mm, stretched mesh) in Lake Victoria and in other nearby lakes (Kyoga and Nabugabo) where these species have also been introduced. This management strategy has unexplored consequences for potential Nile perch harvest, for its effects on Nile perch predation rates on other commercially important stocks, and consequently for the remnant haplochromine species that are prey of Nile perch and the focus of conservation goals (Kitchell et al. 1997). We combined a bioenergetics model of Nile perch growth and predation rates with a simple population model. We estimated the likely changes in Nile perch predation and harvest that would result from various scenarios of gill net mesh size regulation. We showed that the potential effects of Nile perch predation in the Lake Victoria food web are sensitive to the way in which fishing effort is allocated in future gill net fisheries.

# **Methods**

### **General Approach**

Quantitative measures of Nile perch abundance and population size-structure do not exist for Lake Victoria. Population dynamics can only be inferred from records of fish-

ery landings whose dynamics have largely been driven by the development of the fishery itself (Pitcher & Bundy 1993; Ogutu-Ohwayo 1994). Our approach was to estimate the relative changes in predation and harvest that would result from gill net mesh size regulation by simulating the dynamics of an initial population  $(n = 10^6)$  of juvenile fish over a reasonable extent of the cohort's lifespan (Stewart et al. 1981). We used a bioenergetics model (Hewett & Johnson 1992) with parameters derived for Nile perch (Kitchell et al. 1997) to estimate the predatory impact of an average fish as it grows through a characteristic 10-year life span. Effects of population level were estimated by linking the bioenergetics model predictions of per capita predation rates to a simple population model that accounts for natural mortality and alternative rates of harvest by the fisheries.

#### **Model of Growth and Predation Rates**

Kitchell et al. (1997) developed a detailed bioenergetics model of Nile perch growth, prey consumption, and metabolism from information about Nile perch thermal tolerance (Thompson et al. 1977) and previous models for warmwater piscivores (Hewett & Johnson 1992). Accordingly, only a brief description of the model is presented here. The bioenergetics model is simply a mass balance of energy that is allocated to growth and loss processes according to

where SDA is specific dynamic action (the energy required for digestion). To determine a daily balance of energy, all mass units of predator and prey were converted to caloric values (Kitchell et al. 1997). Daily respiration rates (grams/grams/day) were modeled as a function of body mass (grams) according to

respiration = 
$$0.0086 \times \text{mass}^{-0.2}$$
. (2)

This allometric function accounts for active metabolism and is corrected for a nearly constant 25°C thermal environment characteristic of Lake Victoria (Hecky et al. 1994; Kitchell et al. 1997). The allometric effect on maximum consumption rate was accounted for by

$$consumption_{max} = 0.282 \times mass^{-0.27},$$
 (3)

which is also corrected for by a 25°C thermal environment. Excretion, egestion, and SDA were estimated as 6%, 10%, and 16% of consumed energy, respectively (Kitchell et al. 1997). Production of gametes was set at 2% of body mass per year, and individuals matured halfway through their third year of life (Ogutu-Ohwayo 1994). Using growth as input, the software of Hewett and Johnson (1992) iteratively estimates the prey consumption rates that satisfy equation 1. Predation rates were determined by apportioning total consumption to prey categories de-

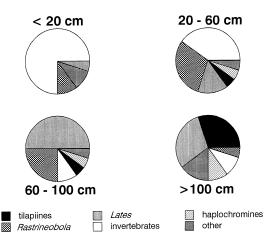


Figure 1. Diet composition, as percentage of wet mass, of four size classes of Nile perch from Lake Victoria between 1988 and 1992. The "other" category accounts for a mixture of fishes not characterized by the alternative diet categories. Data from Ogutu-Ohwayo (1994).

termined from extensive size-specific diet analyses of Nile perch from Lake Victoria (Ogutu-Ohwayo 1994; Fig.1).

We used the growth curve of Hughes (1992) to estimate Nile perch length-at-age from day 118 in the first year of growth (age 0+) through the end of the tenth year (10+). Length-at-age estimates were converted to mass (grams) estimates according to Ogutu-Ohwayo (1994):

mass = 
$$0.0079 \times TL^{3.12}$$
, (4)

where TL is total length in centimeters.

#### Gill Net Selectivity and Mortality Schedules

We determined the average size of Nile perch vulnerable to various gill net sizes according to

$$TL = 8.9 \times \text{mesh size} + 2,$$
 (5)

where TL is the total length of the average Nile perch retained by nets with a stretched mesh size equal to mesh-size in inches (Ligtvoet & Mkumbo 1990). We report mesh sizes in inches because nets are sold in these units and, therefore, management decisions will be formulated on the basis of imperial net sizes.

We determined the age of vulnerability to certain fishery restrictions based on the growth curve of Hughes (1992, Fig. 2) and the mean vulnerable size calculated from equation 5. We assumed that annual, natural mortality of Nile perch was 75% in their first year of life and 30% for all older ages (Pitcher & Bundy 1993; Kitchell et al. 1997).

#### **Model Simulations**

We simulated two possible fishery scenarios to estimate the potential effects of gill net mesh size regulations on

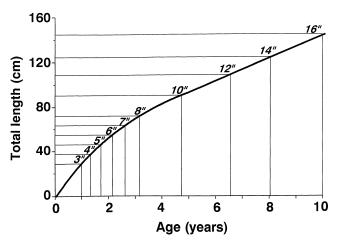
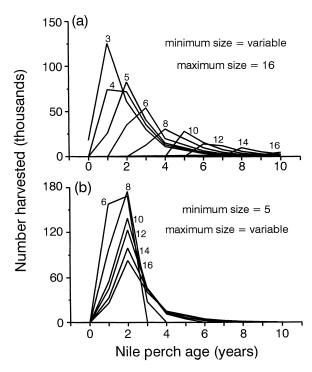


Figure 2. Length-at-age curve for Nile perch from Lake Victoria (from Hughes 1992) and associated average size and age vulnerable to gill nets of various mesh sizes ranging from 3 to 16 inches (").

Nile perch harvest and predation rates. The first scenario evaluated Nile perch harvest and predation rates in response to changes in the minimum allowable gill net mesh size in the fishery. The second scenario investigated how a concentration of fishing effort on small mesh sizes would alter harvest and predation rates. For each scenario we altered harvest rates and size of vulnerability according to the management option to be simulated; all other parameters were held constant across simulations.

Our first analysis simulated a fishery where regulation only limited the minimum mesh size of gill nets and where Nile perch were harvested at a constant annual rate after reaching the minimum vulnerable size. The maximum gill net mesh size currently used is about 16 inches (Ligtvoet & Mkumbo 1990), which we set as our maximum mesh size in the fishery. We set annual harvest rates for all vulnerable sizes of fish at 30%, which is equal to our assumed background natural mortality rate (Gulland 1971). Total harvest of Nile perch and their predation on tilapiines, other Nile perch, *Rastrineobola*, and haplochromines were determined for minimum mesh sizes set at 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 inches (Fig. 3a).

In the simulations described above we assumed that fishers would continue to allocate fishing effort across the range of mesh sizes from the enforced minimum up to 16 inches. But, total effort in the fishery is not likely to decline with decreases in the range of allowable mesh sizes. Instead, we should expect that fishers will concentrate their effort with smaller mesh gill nets and no longer use the largest mesh sizes (Ligtvoet & Mkumbo 1991). Therefore, we expect that the harvest rates on Nile perch of vulnerable sizes will be inversely related to the overall range of mesh sizes used in the fishery. Specifically, if a 5-inch minimum mesh size were enforced



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Figure 3. Age distributions of Nile perch caught under various gill net mesh size restrictions in Lake Victoria: the maximum mesh size is set at 16 inches, and catches are shown for minimum mesh sizes set at 3, 4, 5, 6, 8, 10, 12, 14, and 16 inches (a); the minimum mesh size is set at 5 inches and the maximum mesh size is set at 6, 8, 10, 12, 14, and 16 inches (b). In (b) the exploitation rate is inversely related to the length of time Nile perch are vulnerable to the fishery.

(Ogutu-Ohwayo et al. 1997), a possible fisher response would be to concentrate fishing effort on smaller mesh sizes down to the enforced minimum of 5 inches. We simulated this potential response by holding the total number of fish harvested constant at a value equal to the number harvested with the entire suite of 5- to 16-inch gill nets being employed at an annual harvest rate of 30%. We then held the minimum gill net size at 5 inches and varied the maximum mesh size from 16 down to 6 inches. Harvest rates were altered to account for the variation in time that fish were vulnerable to the fishery, depending on the range of mesh sizes used (Fig. 3b).

#### Results

#### Responses to Changes in Minimum Gill Net Mesh Size

We estimated that regulation of minimum gill net mesh size will cause the biomass of Nile perch harvested to change as much as three-fold and as a uni-modal function of minimum mesh size (Fig. 4a). Harvest was maximized

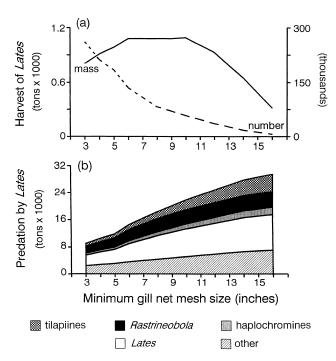


Figure 4. Estimated total barvest as mass (solid line) and number of individuals (dashed line) of an initial cobort of 10<sup>6</sup> Nile perch subjected to various minimum gill net mesh size restrictions (a), and estimated total predation on four dominant fish prey that result from each of these management strategies (b). Maximum gill net mesh size was held constant at 16 inches. Annual barvest rates are 30% for all fish greater than or equal to the minimum vulnerable size.

by fishing with a minimum gill net mesh size between 6 and 10 inches, with little or no change in yield over this range. The number of Nile perch harvested declined exponentially as a function of the minimum mesh size (Fig. 4a).

Predation by Nile perch declined with reduction in minimum gill net mesh size (Fig. 4b). The strongest responses were for predation on Nile perch (i.e., cannibalism) and on tilapiines. Total predation on *Rastrineobola* did not change with minimum mesh sizes set at 8 inches or greater (Fig. 4b), largely because of its reduced importance in the diets of the largest class of predators (Fig. 1). Although the native haplochromines constitute a small component of current Nile perch diets, larger minimum mesh sizes always produced higher rates of predation on these fishes.

# Effects of Enforcing a 5-Inch Minimum Mesh Size

Fishers targeting Nile perch in Lake Victoria currently employ a range (3–16 inches) of gill net mesh sizes with a strong mode at 8 inches (Ligtvoet & Mkumbo 1990). The 5-inch minimum mesh size recommended by Ogutu-Ohwayo et al. (1997) is intended to minimize Nile perch

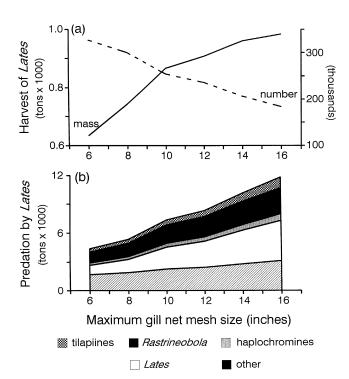


Figure 5. Estimated total harvest as mass (solid line) and number of individuals (dashed line) (a) and predation by an initial cobort of  $10^6$  Nile perch (b) when the minimum gill net mesh size is set at 5 inches and the maximum mesh size is varied between 6 and 16 inches. Harvest rates are inversely related to the range of mesh sizes used (i.e., harvest rate is highest when the fishery only uses 5- and 6-inch gill nets). These simulations reflect a concentration of fishing effort dependent on the total range of mesh sizes used in the fishery.

predation on other commercially important fishes (especially *Rastrineobola* and tilapia) and the endemic haplochromine cichlids without compromising Nile perch harvest. By initiating harvest with 5-inch mesh nets instead of 8-inch mesh nets, we estimate that predation rates by Nile perch will decrease substantially, relative to estimates of current conditions. The largest decreases in predation rates were predicted for prey that dominate the diets of the largest Nile perch, tilapiines (44%) and juvenile Nile perch (40%). Predation by Nile perch on haplochromine cichlids and *Rastrineobola* were estimated to decrease by 38% and 31%, respectively. Change from current conditions to a minimum gill net mesh size of 5 inches resulted in less than a 10% reduction in harvest of Nile perch.

# Effects of Changing Maximum Gill Net Size with a 5-Inch Minimum

When we simulated harvest rates as a function of the range of mesh sizes used above the minimum of 5 inches,

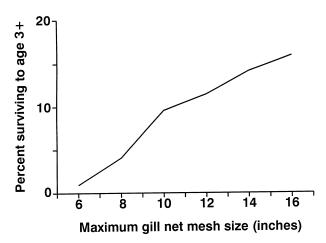


Figure 6. Percentage of the original cohort of 10<sup>6</sup> Nile perch that would survive to maturity (85 cm length) if the minimum mesh size was set at 5 inches and the maximum mesh size varied between 6 and 16 inches.

harvest of Nile perch increased asymptotically as larger mesh sizes were included in the fishery (Fig. 5a). Predation rates on all important fishes increased as the range of mesh sizes was increased (Fig. 5b). For example, we estimate that Nile perch predation rates on haplochromines would be three times higher when gill nets spanning the range from 5 to 16 inches are used than when only 5- and 6-inch gill nets are included in the fishery.

We also investigated how the range of mesh sizes would affect the number of Nile perch that survive to a length of 85 cm—the size at which females become reproductively mature (Ogutu-Ohwayo 1994). The percentage of Nile perch reaching 85 cm decreased rapidly (Fig. 6) with reductions in the maximum mesh size in the fishery. If all fishing effort was concentrated on mesh sizes between 5 and 6 inches, we estimate that about 1% of the initial cohort would survive from day 118 of life to sexual maturity.

### **Discussion**

Our analyses demonstrate that changing the gill net mesh sizes in the Nile perch fishery of Lake Victoria will (1) have direct implications for Nile perch harvest rates; (2) alter predatory impact on other species, including the remnant haplochromines; and (3) have major effects on the abundance of mature Nile perch. By enforcing the minimum gill net mesh size at 5 inches, we estimate that total Nile perch harvest will decline by approximately 10% and that predation rates on other fishes will decline between 30% and 40% from that of current conditions in the fishery (Fig. 4). This estimate assumes that fishing effort will be allocated equally across all allowable sizes of gill nets. If fishers respond to this minimum gill net size

by allocating more effort to small-mesh gill nets (Ligtvoet & Mkumbo 1991), the decrease in both harvest and predation rates will be accentuated. Harvest will decrease by an additional 12% and total predation by an additional 38% from the rates estimated for the 5-inch minimum if fishing effort changes to concentrate on gill nets up to and including 10-inch nets. Because substantial decreases in predation by Nile perch should result, more tilapiines and *Rastrineobola* should become available to fisheries. From the standpoint of minimizing predation impacts on cichlids, including both haplochromines and commercially important tilapiines, the greater the focus on small-mesh gill nets (as small as 5-inch mesh) in the fishery, the greater the reduction of predation pressure on the remnant cichlids (Fig. 5).

#### **Assumptions of the Model**

We estimated individual, size-specific predation rates by Nile perch with a bioenergetic modeling approach that has been applied to a variety of fishery problems (Ney 1993). This model has proven valuable in estimating the effects of different management scenarios on the impact of predatory fishes in aquatic food webs (Kitchell et al. 1977; Kitchell & Breck 1980; Stewart et al. 1981; Rudstam et al. 1993; Hansson et al. 1996). When both allometric scaling of respiration and consumption and observed ontogenetic diet composition are accounted for, the bioenergetics model can be used to estimate the predatory impacts on specific prey taxa.

The general form of this model has undergone extensive error and sensitivity analyses and has proven to be generally robust (Kitchell et al. 1977; Rice & Cochran 1984; Bartell et al. 1986). An alternative approach would have been to estimate total prey consumption based on observed growth rates and a fixed assimilation efficiency (Moreau et al. 1993). But, fish energy budgets can be dynamic because of variation in type and quality of prey consumed and the allometric scaling of metabolism. Therefore, assuming a constant assimilation efficiency is likely to cause the differences in consumption rates between small and large fish to be underestimated. Because different gill net mesh restrictions are likely to have large effects on the size structure of the Nile perch population, our approach is especially appropriate in that we explicitly account for the metabolic and diet changes that occur as these fish change size through their lifetime.

We have assumed that the diet composition of Nile perch will not change as a result of population changes due to gill net mesh restrictions. Ogutu-Ohwayo (1994) documented strong diet shifts in the Nile perch of Lake Victoria between the early 1970s and the early 1990s, which were largely a function of a changing prey resource base. Haplochromine prey dominated Nile perch diets in the 1970s when they were abundant in Lake Victoria. As the Nile perch populations increased, haplo-

chromine abundances declined and cannibalism became a dominant component of Nile perch feeding. There is evidence for a recent resurgence of some populations of cichlids and consequent increases in the importance of cichlids in the diet of Nile perch, especially in nearby Lake Kyoga (R. Ogutu-Ohwayo, personal observation). Current increases in some cichlid species may indicate overfishing of Nile perch and a resulting decrease in predation on cichlids. Nile perch diets in the future will be a function of their numerical responses to a changing fishery and their functional responses to changes in prey availability. Management plans for the Nile perch fishery must be adaptive in order to respond to the highly dynamic nature of this system.

The most liberal assumptions in our analysis involve estimation of natural and harvest mortality rates of Nile perch in Lake Victoria. Because these parameters are poorly quantified, our interpretation remains fairly general. We have stressed the relative differences between possible management scenarios and estimated the likely fishery responses. Better knowledge of the current population parameters and how these would be altered under different fishery strategies would allow a refinement of our analyses and more precise empirical conclusions.

We have not explicitly considered how recruitment patterns might change with changes in the gill net fishery. Intense harvest of juvenile Nile perch will decrease the number of fish surviving to reproductive age (Fig. 6). This result suggests that intense harvest of juveniles might increase the risk of a critical reduction in the spawning stock. This concern is argued forcefully by Pitcher and Bundy (1993). But given the enormous fecundity of adult Nile perch (adult females produce about 140 eggs/g body mass; Ogutu-Ohwayo 1984), the stock is probably resilient to large reductions in spawner biomass. The controls on recruitment of Nile perch in Lake Victoria and the implications of exploitation for recruitment are important arenas for future research and management.

#### Implications for Management of the Lake Victoria Fishery

Adequate determinations of stock size, population structure, and mortality rates do not exist for Lake Victoria fish stocks. As a result, estimating sustainable fishery yields involves enormous uncertainty. Nevertheless, managers need guidance regarding the potential costs and benefits of management strategies for the regulation of the multi-species fishery now dominated by Nile perch.

Pitcher and Bundy (1993) have estimated sustainable yields of Nile perch at approximately 300,000 tons per year based of analyses of surplus production and yield per recruit analyses. Pitcher and Bundy (1993) also recommended that optimal harvest rates of Nile perch would result if fish were not vulnerable to the fishery before reaching a minimum 3-5 years of age. Based on their

growth curve, this would correspond to fish between about 85 and 130 cm in length, which are vulnerable to 9- and 14-inch gill nets, respectively. Our analyses suggest that Nile perch harvest will be maximized by beginning to harvest with gill nets 6-10 inches. This result is valid only if critical reductions in spawning stock do not occur. We also demonstrate that predation by Nile perch will increase with all increases in the minimum gill net mesh size used in the fisheries. Our results indicate that Nile perch harvest strategies commencing with gill nets 5-6 inches will provide relatively high fishery yields and minimize predation rates on other important species.

The intensive stock assessments currently being carried out will undoubtedly improve analyses such as ours and those of Pitcher and Bundy (1993). But given the rates at which the fisheries and the biota have changed in the past (Kaufman 1992), the system is likely to show equally dynamic changes in the near future. Thus, management decisions must be made promptly if reasonable goals are to be achieved (Ludwig et al. 1993). Regulation of the allocation of effort through gear restrictions (i.e., allowable gill net mesh sizes) has been suggested as a possible management alternative (Greboval 1990; Ogutu-Ohwayo et al. 1998). At present, resources for enforcement are low and implementation of regulation is poor. Increased resources for enforcement will undoubtedly increase the probability of successful implementation of policy. Our analyses offer some indication of the possible ecological effects of gill net mesh size restrictions in the Lake Victoria fisheries.

The fisheries of Lake Victoria have undergone massive changes in the past and will likely change in the future. Environmental conditions are in flux (Mugidde 1993; Hecky et al. 1994), fish populations and predator-prey interactions are changing rapidly (Ogutu-Ohwayo 1990a, 1994), and humans continue to become more efficient top predators in this ecosystem and their effects extend beyond the lakeshores (Riedmiller 1994). For the more than 30 million people who live in the Lake Victoria basin, many of whom are dependent on the fishery, management for a productive and sustainable harvest should be a primary goal. Conserving the remnant species flock of haplochromines depends in many ways on the successes of the Nile perch fishery (Ribbink 1987; Kitchell et al. 1997). Our analyses suggest that management through gear regulation will have important consequences for the Nile perch fishery and Nile perch prey. If Nile perch are efficiently harvested at relatively small sizes, predation rates on haplochromines will decrease and their populations should begin to recover. This would coincide, however, with some reduction in the sustainable harvest of Nile perch. Nile perch harvest, predation pressure on other commercially important fishes (e.g., tilapia and Rastrineobola), and the dynamics of the native haplochromine fishes may be a function largely of how humans respond to changing fishery regulations. Although restoration of Lake Victoria's biodiversity and

its historic food web is impossible, fisheries management can control exploitation in ways that should benefit both the people that depend on the Nile perch fishery for their livelihood and those that are concerned with conserving and sustaining a diverse fish community (Bruton 1990; Kitchell et al. 1997).

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#### **Literature Cited**

- Barel, C. N. D., R. Dorit, P. H. Greenwood, G. Fryer, N. Hughes,
  P. B. N. Jackson, H. Kawanabe, R. H. Lowe-McConnell, M. Nagoshi,
  A. J. Ribbink, E. Trewavas, F. Witte, and K. Yamaoka. 1985. Destruction of fisheries in Africa's lakes. Nature 315:19-20.
- Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 43: 160-168.
- Bruton, M. 1990. The conservation of the fishes of Lake Victoria, Africa: an ecological perspective. Environmental Biology of Fishes 27:161-175
- Greboval, D. 1990. Socio-economic issues for planning in support of fisheries management. In CIFA report of the 5th Session of the subcommittee for the Development and Management of the Fisheries of Lake Victoria, Mwanze, Tanzania, 12–14 September 1989. Food and Agriculture Organization of the United Nations Fisheries Report 430:75–97.
- Gulland, J. A. 1971. The fish resources of the ocean. Fishing News Books, Surrey, England.
- Hansson, S., L. G. Rudstam, J. F. Kitchell, M. Hildén, B. L. Johnson, and P. E. Peppard. 1996. Predation rates by North Sea cod (*Gadus morbua*): predictions from models of gastric evacuation and bioenergetics. International Council for Exploration of the Sea (ICES) Journal of Marine Science 53:107-114.
- Hecky, R. E., F. W. B. Bugenyi, P. Ochumba, J. F. Talling, R. Mugidde, M. Gophen, and L. Kaufman. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnology and Oceanography 39: 1476-1481.
- Hewett, S. J., and B. L. Johnson. 1992. Fish bioenergetics model 2. Technical report WIS-SG-92-250. Sea Grant Institute, University of Wisconsin, Madison.
- Hilborn, R., C. J. Walters, and D. Ludwig. 1995. Sustainable exploitation of renewable resources. Annual Review of Ecology and Systematics 26:45-67.
- Hughes, N. F. 1992. Growth and reproduction of the Nile perch, Lates

- *niloticus*, an introduced predator, in the Nyanza Gulf, Lake Victoria, East Africa. Environmental Biology of Fishes **33:**299–305.
- Kaufman, L. 1992. Catastrophic changes in species-rich freshwater ecosystems: the lessons of Lake Victoria. BioScience 42:846–858.
- Kaufman, L., and P. Ochumba. 1993. Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria. Conservation Biology 7:719–730.
- Kitchell, J. F., and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 37:2159–2168.
- Kitchell, J. F., D. J. Stewart, and E. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Reserach Board of Canada 34:1922-1935.
- Kitchell, J. F., D. E. Schindler, P. M. Reinthal, and R. Ogutu-Ohwayo. 1997. The Nile perch in Lake Victoria: strong interactions between fishes and fisheries. Ecological Applications 7:653–664.
- Ligtvoet, W., and O. C. Mkumbo. 1990. Synopsis of ecological and fishery research on Nile perch (*Lates niloticus*) in Lake Victoria, conducted by HEST/TAFIRI. Food and Agriculture Organization of the United Nations (FAO) Fisheries Report 430:35-74.
- Ligtvoet, W., and O. C. Mkumbo. 1991. A pilot sampling survey for monitoring the artisinal Nile perch (*Lates niloticus*) fishery in southern Lake Victoria (East Africa). Pages 349–360 in I.G. Cowx, editor. Catch effort sampling strategies. Their application in freshwater fisheries management. Fishing News Books, Surrey, England.
- Lowe-McConnell, R. 1994. The changing ecosystem of Lake Victoria, East Africa. Freshwater Forum 4:76–89.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260: 547-549.
- Moreau, J., W. Ligtvoet, and M. L. D. Palomares. 1993. Trophic relationship in the fish community of Lake Victoria, Kenya, with emphasis on the impact of Nile perch (*Lates niloticus*), Pages 144–152. V. Christensen and D. Pauly, editors. Trophic models of aquatic ecosystems. Conference proceedings 26. International Center for Living Aquatic Resources Management, Manila.
- Mugidde, R. 1993. Changes in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Verhandlungen der Internationalen Vereingung für Theoretische und Angewandte Limnologie 25: 846-849
- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122: 736-748.
- Ogutu-Ohwayo, R. 1984. Reproductive potential of the Nile perch, *Lates niloticus* L., and the establishment of the species in Lakes Kyoga and Victoria (East Africa). Hydrobiologia **162**:193–200.
- Ogutu-Ohwayo, R. 1990a. Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). Journal of Fish Biology 37:55-63.
- Ogutu-Ohwayo, R. 1990b. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes 27:81–96.
- Ogutu-Ohwayo, R. 1994. Adjustments in fish stocks and life history characteristics of the Nile perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo. Ph.D. thesis. University of Manitoba, Winnipeg, Canada.
- Ogutu-Ohwayo, R., S. W. Wandera, and J. Kamanyi. 1998. Fishing gear selectivity of *Lates niloticus* L. (Nile perch), *Oreochromis niloticus* L. (Nile tilapia) and *Rastrineobola argentea* Pellegrin (Mukene) in lakes Victoria, Kyoga and Nabugabu. Uganda Journal of Agricultural Sciences. In Press.
- Pitcher, T. J., and A. Bundy. 1993. Successful species introductions in the African Lakes: assessment, uncertainties, and strategies for fishery management. Pages 545-570. G. Kruse, D. M. Eggers, R. J.

Marasco, C. Pautzke, and T. J. Quinn, II, editors. Proceedings of the international symposium on management strategies for exploited fish populations. College program report no. 93–102. Alaska Sea Grant, University of Alaska, Fairbanks.

- Ribbink, A. J. 1987. African lakes and their fishes: conservation scenarios and suggestions. Environmental Biology of Fishes 19:3-26.
- Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology **65:**732–739.
- Riedmiller, S. 1994. Lake Victoria fisheries: the Kenyan reality and environmental implications. Environmental Biology of Fishes 39:329-338.
- Rudstam, L. G., R. C. Lathrop, and S. R. Carpenter. 1993. The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. Ecology 74:303-319.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110:751-763.
- Thompson, K. W., C. Hubbs, and B. W. Lyons. 1977. Analysis of potential environmental factors, especially thermal, which would influence the survivorship of exotic Nile perch if introduced into artificially heated reservoirs in Texas. Technical series no. 22. Texas Parks and Wildlife Department, Austin.
- Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34:1-28.

