

THE NILE PERCH IN LAKE VICTORIA: INTERACTIONS BETWEEN PREDATION AND FISHERIES

JAMES F. KITCHELL,¹ DANIEL E. SCHINDLER,¹ RICHARD OGUTU-OHWAYO,² AND PETER N. REINTHAL³

¹Center for Limnology, 680 North Park Street, University of Wisconsin, Madison, Wisconsin 53706 USA

²Fisheries Research Institute, Box 343, Jinja, Uganda

³Department of Biology, Eastern Michigan University, Ypsilanti, Michigan 48197 USA

Abstract. Introduction of the exotic Nile perch (*Lates niloticus*) into Africa's Lake Victoria accelerated decline of the diverse, endemic ichthyofauna, altered food web structure, and created valuable fisheries. As the Nile perch population expanded and predation rates increased, many of the endemic fish species disappeared, total fishery yield increased nearly fourfold, and fishery-related employment approximately doubled. Ecological changes in this system now occur rapidly, are due largely to human actions, and have profound socioeconomic effects.

We used a bioenergetics model of Nile perch predation rates to evaluate the consequences of previous, current, and future fishery exploitation patterns and their ecological implications. The analysis produced three main conclusions: (1) Development of fisheries based on large-mesh gill nets reduced total predation by Nile perch to $\approx 40\%$ of that estimated during the late 1970s, when Nile perch densities were greatest. (2) Expansion of recent intensive beach seine and small-mesh gill net fisheries for juvenile Nile perch could reduce total predation to $\approx 25\%$. (3) The combination of fishing methods could reduce total predation to $\approx 10\%$ of previous levels.

Reduction in estimated predatory impact corresponds with recent reports of recovery by haplochromine populations and increased fish species diversity in regions (e.g., Napoleon Gulf, Mwanza Gulf, and Winam Gulf) where fisheries are locally intense.

Key words: Africa; fish; fisheries; haplochromines; Lake Victoria; *Lates niloticus*; Nile perch; predator-prey interactions; Uganda.

INTRODUCTION

Review of recent ecological changes

Africa's Lake Victoria, the world's largest tropical lake, is the site of rapid ecological changes due to the effects of cultural eutrophication, introduced species, and intensive fishery exploitation. For three decades, nutrient loading has increased due to a burgeoning human population (currently 35×10^6) in the catchment that includes parts of Burundi, Rwanda, Kenya, Tanzania, and Uganda. Major limnological changes include twofold increases in phytoplankton biomass and primary production (Hecky and Bugenyi 1992, Mugidde 1993). Bloom-forming cyanobacteria replaced diatoms as the dominant algae (Ochumba and Kibara 1989); subsequently, the rate of oxygen depletion for deeper water masses increased (Hecky 1993, Hecky et al. 1994).

The fish community was highly diverse (>400 species), including perhaps 350 species ($>95\%$ endemic to Lake Victoria) within the haplochromines of the family Cichlidae (Greenwood 1966, Witte et al. 1992). Artisanal fisheries harvested many of these species from littoral regions. Fishing intensified as outboard motors and nylon nets became more readily available during

the 1950s; large members of the piscivorous guilds and potadromous species were exploited heavily. Although many haplochromine species remained abundant under continuing exploitation, these generally small-bodied species supported fisheries of only modest economic value. In an attempt to increase the economic value and use of fishes from the lake (Graham 1929), the piscivorous Nile perch (*Lates niloticus*) and the rapidly growing omnivorous Nile tilapia (*Oreochromis niloticus*) were introduced from their native habitats in Lake Albert and Lake Turkana (Ogutu-Ohwayo 1993). The precise dates of those introductions are not known. Nile perch and Nile tilapia populations grew slowly at first, then increased exponentially during the 1970s through the 1980s. Major fisheries developed in concert with the increase of Nile perch as an improved distribution system linked new processing plants to foreign markets. Total yields climbed to 4 times the maximum of previous fisheries for native species. In the view of human communities on Lake Victoria's shores, Nile perch was "the saviour" (Greboval 1990).

As intended, Nile perch was a very successful predator. In these productive and warm tropical waters it grows to 1 kg during its first year of life, is primarily piscivorous at that age, and can reach sizes of 100 kg, although the most commonly harvested sizes are 2–4 kg at ages 2+ or 3+. Although the small juveniles are

Manuscript received 2 August 1995; revised 8 March 1996; accepted 19 March 1996; final version received 6 May 1996.

restricted to shallow and/or nearshore environments, larger juvenile and adult Nile perch occupy all habitats of the lake where oxygen concentrations are sufficient (Ogutu-Ohwayo 1994). Increasing cultural eutrophication has caused recent development of seasonal anoxia in deeper waters, which has restricted that habitat for all fishes (Kaufman 1992).

In the early phases of Nile perch population growth, haplochromine species comprised 80–90% of their diets (Ogutu-Ohwayo 1994). Many haplochromines are trophic specialists; most mature at a small size and have low reproductive potential due to small clutch sizes and extended parental care. This type of life history pattern makes them particularly vulnerable to the effect of a voracious and widely distributed predator such as Nile perch (Ribbink 1987).

Most haplochromine stocks declined to low levels and eventually experienced lakewide extirpation as the Nile perch population increased. Although the rate of extirpation is not well documented for the lake as a whole, Ligotvoet and Mkumbo (1990) offer an excellent local example; the catch rate of haplochromines in fishery assessment trawls of Tanzania's Mwanza Gulf declined from 70–75 to <1 kg/h during 1986 through 1987 while Nile perch populations were increasing. Nile perch diets were almost exclusively haplochromine prey initially, then gradually shifted to other fishes as haplochromines disappeared. Similar changes in haplochromine abundance and Nile perch diets occurred earlier in Ugandan waters (Ogutu-Ohwayo 1994). By 1987, Nile perch in Tanzanian waters of Lake Victoria had reached a biomass of 150 kg/ha (Ogutu-Ohwayo 1994).

Analogous events transpired throughout the lake and around its many islands (Ogutu-Ohwayo 1994). Conservative estimates hold that 150–200 of the endemic fish species—most of which had not been fully described by systematists—are now gone (Witte et al. 1992). In addition to the depletion of littoral and demersal species that exhibited a wide range of trophic specialization (Goldschmidt et al. 1993), those haplochromines that were pelagic zooplanktivores and insectivores declined as well. The Nile perch in Lake Victoria has been claimed to have effected the greatest vertebrate extinction known in recent times (Kaufman 1992, 1993).

Whereas conservation biologists decry the loss of endemic species and of the previous extraordinary fish diversity in Lake Victoria, the social and economic benefits of the current fisheries are undeniable. Before the Nile perch, total annual fisheries yield was $\approx 100\,000$ Mg (1 Mg = 1 metric ton) (Greboval 1990). Yields during the recent past were 300 000–500 000 mt, 80–90% of which was Nile perch. At present, $\approx 19\,000$ fishing canoes plus 100 000 fishermen and crew members are directly engaged in the fisheries. An additional 250 000 other persons are employed in the marketing and distribution system resulting from the

fisheries. According to Greboval (1990), advent of the Nile perch fishery produced 150 000 new jobs and a threefold increase in net economic benefits. Further, these increases occurred in regions where unemployment was particularly high.

While a substantial literature has developed around the dynamics of Lake Victoria, select recent sources provide a contemporary perspective. Pitcher and Bundy (1994) offer a review of traditional fishery analyses. Witte et al. (1992) and Kaufman (1992) provide the most complete overview of the biodiversity issues. The forecasts of Ribbink (1987) and the anecdotal accounts of Riedmiller (1994) offer strong evidence of the complex socioeconomic context for the most powerful ecological force operating in this ecosystem—human activities.

Dominant components of the fish community are now Nile perch, Nile tilapia, and a small zooplanktivorous cyprinid, *Rastrineobola argentea* (Ogutu-Ohwayo 1994). The life history strategies of Nile tilapia and *Rastrineobola* allow their persistence. Nile tilapia was sympatric with Nile perch and appears resistant to predation due to its rapid growth rate and large adult size (>30 cm total length). Gill net fisheries for Nile tilapia are now very productive and profitable. In contrast, *Rastrineobola* has a small adult size (maturity at 4.5–5.0 cm). Its evasive and schooling behaviors allow it to occupy surface waters of the pelagic zone. Local fishermen estimate that its abundance has increased 4–5 times since Nile perch appeared (S. B. Wandera, Fisheries Research Institute, Jinja, Uganda, *personal communication*). *Rastrineobola* fisheries are expanding; they are pursued using night-light systems and fine-mesh purse seines or Lampara lift-net systems. Most *Rastrineobola* are sun-dried and sold as a protein supplement for livestock feeds.

From a socioeconomic perspective, the Lake Victoria fisheries are in a highly desirable state. There is modest need for capital investment, effort and benefits are broadly distributed, and markets remain receptive to even greater yields. However, from a fishery management perspective, the current state is problematic. Regulatory policies are difficult to define because they require international agreements. Fish populations change more rapidly than the policy-making process. Regulations are difficult to implement due to the dispersion of fishing effort and of the responsibility for regulatory enforcement.

From an ecological perspective, the trophic system is now relatively simple. Increased nutrient loading fuels algal blooms, increasing the detritus base consumed by the extraordinarily abundant prawn *Caridina nilotica*. This prawn is the main prey of juvenile Nile perch, which is the primary prey of adult Nile perch. In the nearshore environment, the omnivorous Nile tilapia flourishes. *Rastrineobola* grows rapidly on the increased abundance of large zooplankton and emerging insects. Based on experiences in great lakes elsewhere,

this much-simplified ecosystem is unlikely to remain in its current state (Kaufman 1993).

Rationale for a modeling approach

Lake Victoria appears to be entering yet another period of rapid ecological changes. Nile perch catches peaked in the period of 1985–1990 and are now declining while fishing effort is still increasing (Pitcher and Bundy 1994, Riedmiller 1994). Fishermen are switching to progressively smaller meshes in gill nets. Juvenile Nile perch are increasingly exploited by beach seine fisheries in many areas. Some haplochromine populations are recovering in those areas where fisheries are most intense (e.g., Winam Gulf in Kenya; L. Kaufman, Boston University, *personal communication*).

While sustained fishery yields are an obvious goal, sustainable fishery management practices are based on knowledge of stock size and age structure (Ludwig et al. 1993). Reliable quantitative measures of the abundance or age structure do not exist for the Nile perch population in Lake Victoria, or for any of the sympatric fish species. These shortcomings will not be resolved before management actions are taken. Decisions will be based on the best extant information. The current state of knowledge is summarized by Riedmiller (1994: 332): “The maximum sustained yield of the lake is not known, nor is it known whether an equilibrium could be reached between the Nile perch and other species.” Accordingly, we adopted an empirical modeling approach designed to employ available information as a guide to evaluating alternative management scenarios.

We analyzed scenarios representing previous, current, and future levels of predation and fishery effects, and their consequent influence on both food web structure and the native fishes. We use a bioenergetics modeling approach to estimate predation rates by Nile perch and fishery yields under conditions that existed (1) before the advent of the Nile perch fishery, (2) as a result of the fishery at its current state, and (3) with the full effects of overexploitation that might develop if the fisheries were unrestricted. In sum, these analyses revealed the strong effect of adding another predator to this system—fisheries—which has reduced the impact of Nile perch predation and offers encouragement for some recovery of the native fish community.

METHODS

We used the bioenergetics model of Hewett and Johnson (1992) to develop a quantitative assessment of predation rates. Analogous applications have been employed in developing estimates of ecological effects and fisheries management approaches in North America's Laurentian Great Lakes (Stewart et al. 1981, Jones et al. 1993, Kitchell et al. 1994). At present, several dozen publications exist describing the development of parameters for this modeling approach (Kitchell et al. 1977, Kitchell 1983), detailed error and sensitivity

analysis (Bartell et al. 1986, Rice and Cochran 1984) and a user's guide that explains the software (Hewett and Johnson 1992). Accordingly, we will not detail components of the model structure except as they pertain to development of a model for Nile perch in Lake Victoria.

The bioenergetics model is simply a means for estimating daily energy budgets based on five basic kinds of information: (1) a set of physiological parameters defining the temperature and size dependence of growth and metabolic rates, (2) estimates of temperatures experienced during the annual cycle, (3) growth curves (size at age) for the species in that site, (4) proportions by mass of prey in the diet and estimates of energy densities for both predator and prey, and (5) estimates of population parameters (natural and fishery mortality rates). The software calculates all terms of the daily budget in energy units (calories or Joules, where 1 calorie = 4.184 joules), and then converts them to units of mass.

For Lake Victoria, the temperature dependence functions are readily implemented because water temperatures change little (24°–26°C) during the year and thermal stratification is minimal. We employed a constant 25°C for all calculations. The paucity of physiological studies on Nile perch required that we make general estimates for rates of anabolic and catabolic processes. We used the nonlinear Model 2 approach for temperature dependence, which is recommended for applications to warmwater fishes (Hewett and Johnson 1992). Experimental studies of Nile perch temperature tolerance (Thompson et al. 1977) were used to estimate the optimum temperature for feeding ($T_{\text{opt}} = 27.5^\circ\text{C}$) and the upper lethal temperatures ($T_{\text{max}} = 38^\circ\text{C}$). The modeling approach involves specifying boundary conditions for energy-budgeting processes. This requires an estimate of maximum feeding rates (C_{max}) and routine metabolic rates, R_r , as a function of fish size. Accordingly, we used parameters that represent the modal values for the 11 large piscivorous fishes summarized in the appendix tables of Hewett and Johnson (1992). Thus, for maximum feeding rates:

$$C_{\text{max}} = 0.30W^{-0.27}, \quad (1)$$

where W is fish mass (g) and C_{max} is the mass-specific maximum rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). These parameter estimates were comparable to those for other large warmwater piscivores such as largemouth bass, *Micropterus salmoides*, and striped bass, *Morone saxatilis* (Hewett and Johnson 1992).

Equation 1 defines the upper limit of the scope for growth. Based on the observed growth, the model then calculates a parameter, ρ , that scales from 0 to 1.0 and represents the proportion of the maximum feeding rate required for the predator to grow at observed rates. For example, if $\rho = 0.50$, the predator is growing at rates that indicate feeding at 50% of maximum capacity. This parameter synthesizes the dynamics of energy budget-

TABLE 1. Parameter values and their literature sources in the bioenergetics model for Nile perch, *Lates niloticus*. Symbols and units are presented in the format developed by Kitchell et al. (1977).

Symbol	Parameter description	Value	Source
Respiration			
RA	Intercept for standard respiration	0.011	Hewett and Johnson (1992)
RB	Slope for standard respiration	-0.20	Hewett and Johnson (1992)
RTO	Optimal temperature for standard respiration	38.0°C	Thompson et al. (1977)
RTM	Maximum temperature for standard respiration	43.0°C	Hewett and Johnson (1992)
RQ	Slope for temperature dependence	2.5	Hewett and Johnson (1992)
ACT	Activity respiration multiplier	2.0	Boisclair (1991)
S	Specific dynamic action coefficient	0.163	Hewett and Johnson (1992)
Consumption			
CA	Intercept for maximum consumption	0.30	Hewett and Johnson (1992)
CB	Slope for maximum consumption	-0.27	Hewett and Johnson (1992)
CTO	Optimal temperature for maximum consumption	27.5°C	Thompson et al. (1977)
CTM	Maximum temperature for maximum consumption	38.0°C	Thompson et al. (1977)
CQ	Slope of temperature dependence	2.65	Hewett and Johnson (1992)
Waste losses			
FA	Fecal loss coefficient	0.104	Hewett and Johnson (1992)
UA	Urinary loss coefficient	0.068	Hewett and Johnson (1992)

ing in a single value that facilitates comparisons among cohorts, populations, etc. The energetics calculations are not strongly influenced by the precision of parameter estimates for Eq. 1 unless the predator is feeding at or near maximum feeding rates (Bartell et al. 1986).

Using the same approach (modal values for parameters), we estimated the mass-specific metabolic parameters for routine metabolism, R_r , as:

$$R_r = 0.011W^{-0.20}, \quad (2)$$

which expresses the cost of metabolic processes in their mass equivalents ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$). In keeping with the general conclusion of Winberg (1960) and the more recent discussion of this issue (Boisclair and Leggett 1991), we increased metabolic output by setting the activity parameter (ACT) of the Hewett and Johnson (1992) model at a value of 2.0. This simply means that swimming activity of the predator roughly doubles the expenditure of energy over that estimated as routine metabolic rate. As for most piscivores (Hewett and Johnson 1992), the energetic cost of digesting, absorbing, and assimilating food (SDA or specific dynamic action), was set at a constant percentage (16%) of total food consumed. Total metabolic output, R_t , by Nile perch was therefore:

$$R_t = 2R_r + 0.16C.$$

As recommended by Hewett and Johnson (1992) for piscivorous fishes, we estimated losses to egestion (E) and excretion (U) as 10% and 7% of consumed energy, respectively. Parameter estimates for this bioenergetics model are summarized in Table 1.

Growth rates of Nile perch in Lake Victoria were calculated from the total length (TL, measured in centimeters) – mass (W , measured in kilograms) equation developed by Ogutu-Ohwayo (1994), where $W = 0.0076\text{TL}^{3.12}$. Length at age estimates came from the most recent and complete work by Hughes (1992). Nile

perch diets, which demonstrate substantial trophic ontogeny, were taken from the 1988–1992 studies of Ogutu-Ohwayo (1994). Diets of fish <20 cm TL are dominated by invertebrates, especially the prawn *Caridina nilotica*. Fish of 20–60 cm TL eat equal proportions of invertebrates and fish, with *Rastrineobola* and juvenile *Lates* among the most common fish prey. Diets of Nile perch in the size range of 60–100 cm TL are 80% fish, with juvenile *Lates* as the main component. Large Nile perch (>100 cm TL) are exclusively piscivorous; small *Lates*, juvenile *Tilapia*, and haplochromines are their main prey. We used the literature summary of Hewett and Johnson (1992) and wet : dry mass ratios for prey fishes (Ogutu-Ohwayo 1984) to estimate energy densities in seven diet categories: *Caridina* and Anisoptera = 3.35 kJ/g; *Rastineobola* and other fishes = 4.6 kJ/g; and *Tilapia*, *Lates*, and haplochromines = 5.0 kJ/g. As *Lates* get older and larger, the muscle tissue increases in oil content and mesenteric fat deposits increase. This type of ontogenic change in energy density is reported in many fishes and is particularly well documented for some piscivorous members of the Salmonidae (Stewart et al. 1983). Accordingly, we estimated the energy density of the predator's growth to increase according to age, with age 0+ = 4.6 kJ/g, and to increase 0.42 kJ/g for each age up to age 5+. We assumed energy density of all fish age 6+ and older to be 6.7 kJ/g.

Energy expended in reproduction is included in the Hewett and Johnson (1992) model by estimating the age at maturity, the mass of gonads at the time of spawning, and the frequency and timing of spawning in a given year. At spawning, energy accumulated through growth is decremented and the fish's mass reduced accordingly. The reproductive biology of *Lates* includes some unusual features. Based on the extensive work of Ogutu-Ohwayo (1994), male *Lates* mature at an age of 2+ and TL of 50–55 cm. Virtually all mature

TABLE 2. Total length and wet mass at different ages for Nile perch cohorts and the consequent parameter values[†] used to simulate growth in the bioenergetics model. Nile perch abundance is presented for each of the four fishery scenarios described in the *Methods* section and presented in Fig. 1. Simulation of growth of age 0+ fish began on day 118 after hatching.

Cohort	Age (yr)	Total length (cm)	Mass (kg)	ρ^{\dagger}	Fishery scenario			
					Historical	Gill nets	Beach seines	Gill nets and beach seines
1	0+	10	0.0096	NA [‡]	1.0×10^6	1.0×10^6	1.0×10^6	1.0×10^6
2	1+	28.7	0.28	0.46	5.0×10^5	5.0×10^5	3.9×10^5	3.9×10^5
3	2+	51.8	1.76	0.43	3.5×10^5	3.5×10^5	9.8×10^4	9.8×10^4
4	3+	69.4	4.39	0.37	2.4×10^5	1.7×10^5	5.6×10^4	3.9×10^4
5	4+	82.8	7.62	0.35	1.7×10^5	6.9×10^4	3.9×10^4	1.6×10^4
6	5+	93.0	10.95	0.38	1.4×10^5	3.4×10^4	3.1×10^4	7.9×10^3
7	6+	105.4	16.17	0.35	8.4×10^4	1.1×10^4	1.9×10^4	2.5×10^3
8	7+	115.7	21.66	0.34	5.9×10^4	4.4×10^3	1.3×10^4	1.0×10^3
9	8+	126.1	28.31	0.34	4.1×10^4	1.8×10^3	9.4×10^3	4.0×10^2
10	9+	136.5	36.22	0.35	2.9×10^4	7.0×10^2	6.6×10^3	1.6×10^2
11	10+	146.8	45.58	0.35	2.0×10^4	2.8×10^2	4.6×10^3	64
12	11+	157.2	56.31	0.35	1.4×10^4	1.1×10^2	3.2×10^3	25

[†] The parameter value ρ represents the proportion of the maximum feeding rate required for the predator to grow at observed rates.

[‡] NA denotes "not applicable."

fish <80 cm TL are male. Females mature at 85–100 cm TL and approximately age 5+. Fish >100 cm TL are predominately mature females. Similar results can be derived from Hopson's (1972) study of *L. niloticus* in Lake Chad. According to Ogutu-Ohwayo (1984, 1994), Nile perch spawn over a protracted period, but each mature adult spawns only once per year and the energy lost as gametes is equivalent to 2% of adult mass for both males and females. Nile perch engage in broadcast spawning in marshes and the littoral areas of shallow bays. A 100-cm female produces $\approx 2 \times 10^6$ eggs at her first spawning, and fecundity increases as the cube of length (Ogutu-Ohwayo 1994). No estimates exist for hatching success or for the causes and rates of mortality in the early life history stages. Nile perch do not engage in parental care.

Estimates of total predation require estimates of abundance and age structure of the predator population. While we have evidence for Nile perch size at age in Lake Victoria, no estimates exist for relative abundance at age. Following the example of Stewart et al. (1981), we estimated the relative changes in predation effects by simulating the dynamics of an initial population of 10^6 juvenile fish over their life span. To evaluate the interaction of fishery effects and changes in predation rates, we constructed a model including 12 cohorts and 11 age classes. Because little is known of the early life history stages of Nile perch, we began our simulations with age 0+ fish, which weighed 9.6 g on day 118 of the first year simulated and grew to 280 g by day 365 (Hughes 1992). We estimated natural mortality rates (M) for this cohort (cohort 1) as 50% from day 118 to day 365. Each subsequent cohort corresponded with an age class of known length and mass on day 1 of the year. Using the work of Pitcher and Bundy (1994), we estimated natural mortality rates as 0.3 (30% per year) for all other cohorts. To assess the effects of fishery practices, we followed the general suggestion of Gul-

land (1971) that fishing mortality (F) should approximate that of natural mortality so that total mortality (Z) would be $Z = M + F$ for each cohort. This approach was used by Pitcher and Bundy (1994) for estimating sustainable yields of Nile perch in Lake Victoria and serves as the baseline for our analyses. In the model, mortality rates are converted from annual percentages to instantaneous daily rates (Hewett and Johnson 1992).

As the basis for comparative study, we simulated fishing scenarios that represent the extremes of conditions in Lake Victoria. Natural mortality was held at 50%/yr for cohort 1 (age 0+) and 30%/yr for cohorts 2–12 (ages 1+ to 11) in all cases. First, we estimated predation effects in the absence of fishing mortality, chosen to represent the early 1970s when the Nile perch population was expanding and haplochromine fishes were still abundant (Ogutu-Ohwayo 1994). Next, we estimated the effects of the current fishery, which is primarily based on large-mesh (152–229 mm stretch measure) gill nets that capture fish >50 cm TL (age 2+) and added fishing mortality (F) as 30%/yr to the mortality schedule for all cohorts from age 2+ and older. Beach seine fisheries are known to have increased rapidly in recent years, but they are unregulated and poorly monitored. To simulate the effect of intensive beach seine fisheries, we set fishing mortality at 30%/yr for the two juvenile cohorts (age 0+ and 1+), then allowed no fishing mortality for ages 2+ and older. To simulate an intense, fully effected fishery, we added mortality from the beach seine fishery and the large mesh gill net fishery so that fishing mortality was 30%/yr for all cohorts. Thus, total mortality was 80% for cohort 1 and 60% per year for all other cohorts when both fisheries are operating.

Combining physiological parameters, known growth rates, and 1988–1992 diets for Nile perch in Lake Victoria, we calculated values for the model parameter ρ for the average individual in each cohort (Table 2).

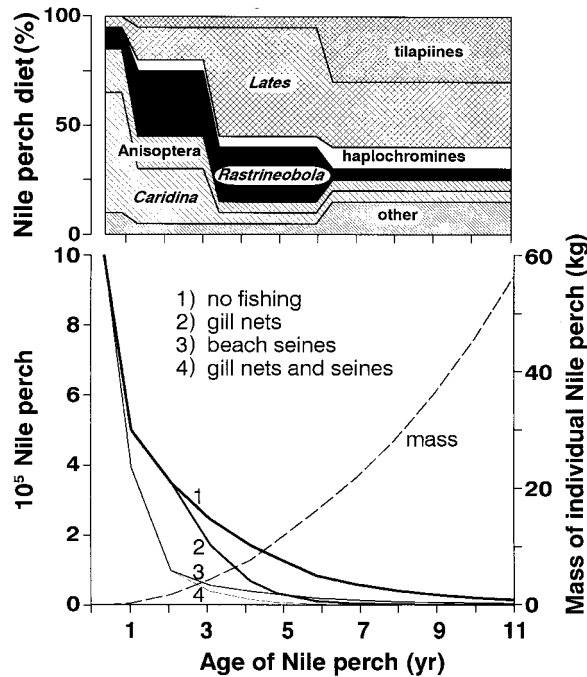


FIG. 1. Upper panel: diet components (percentage of mass in stomachs) as a function of age for Nile perch, *Lates niloticus*, in Lake Victoria (from Ogutu-Ohwayo 1994). Lower panel: individual mass and survivorship curves for a cohort of 10^6 Nile perch as a function of age. Each survivorship curve represents one of the scenarios simulated in the modeling analysis: (1) natural mortality rates in the absence of fishing, (2) fishing with large mesh gill nets, (3) fishing with beach seines, and (4) fishing with gill nets plus beach seines.

Adding the natural mortality rates for each cohort and alternative fishery practices yields the estimates of total predation rates and total fishery yields under each of the selected scenarios: no fishing, large mesh gill nets only, beach seines only, and the combined effect of large mesh gill nets and beach seines.

RESULTS

As an independent evaluation of the energy budget calculations, we compared the distribution of the balanced budget with that from other studies. From the model, a 1-kg Nile perch growing at $\rho = 0.43$ has a specific growth rate of $0.0059 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. Tagging studies conducted by Ogutu-Ohwayo (1994) revealed that Nile perch of this size range were growing at $0.0060 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in Lake Victoria. The distribution of the normalized energy budgeting rates (percentage per day) for a 1-kg Nile perch when food consumption, C , is set to 100% would be growth = 32%, egestion = 10%, excretion = 6%, SDA = 15%, and routine plus active metabolism = 37%. In other words, when feeding at $\approx 43\%$ of its maximum capacity, this fish absorbs 90% of the food energy consumed, loses 16% to wastes, expends 52% of its energy in metabolic processes (routine + active + SDA), and has a growth efficiency of 32%. Results from the model compare favorably with

results of a general review of energy budget components for rapidly growing carnivorous fishes, which yielded an average growth efficiency of 29% (Brett and Groves 1979).

As is generally observed, specific growth rates decline with fish size, and values for ρ are greatest for age 0+ fish, then decline with increasing fish size (Table 2). Simulated decline in fish abundance corresponded with the independent and additive effects of size-selective fisheries (Fig. 1). Greatest mortality occurred when both beach seine and large-mesh gill net fisheries are employed. The product of average individual mass (calculated from a standard growth curve) and survivorship curves (Fig. 1) form the basis for many traditional fishery management models (Pitcher and Bundy 1994). As an addition to that approach, the bioenergetics model combined growth rates, survivorship curves, and diet composition with the temperature- and size-dependent rules of energy allocation, then calculated total predation rates on each prey type.

In the absence of exploitation, peak predation occurred 4–6 yr after a cohort was formed (Fig. 2A). Addition of the gill net fishery shifted peak of predation to 2 yr earlier and reduced total predation by Nile perch to $\approx 40\%$ of that in the absence of fishing. An intensive beach seine fishery would reduce the population in its early stages and thereby reduce total predation to 25%

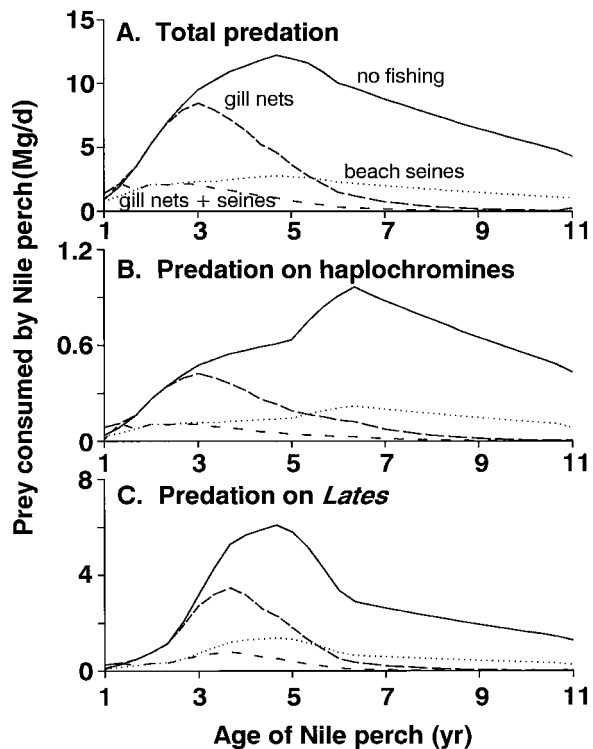


FIG. 2. (A) Simulated total predation rates, (B) predation on haplochromines, and (C) predation on juvenile *Lates niloticus* as a function of cohort age of Nile perch for each of the four fishery scenarios (as Fig. 1).

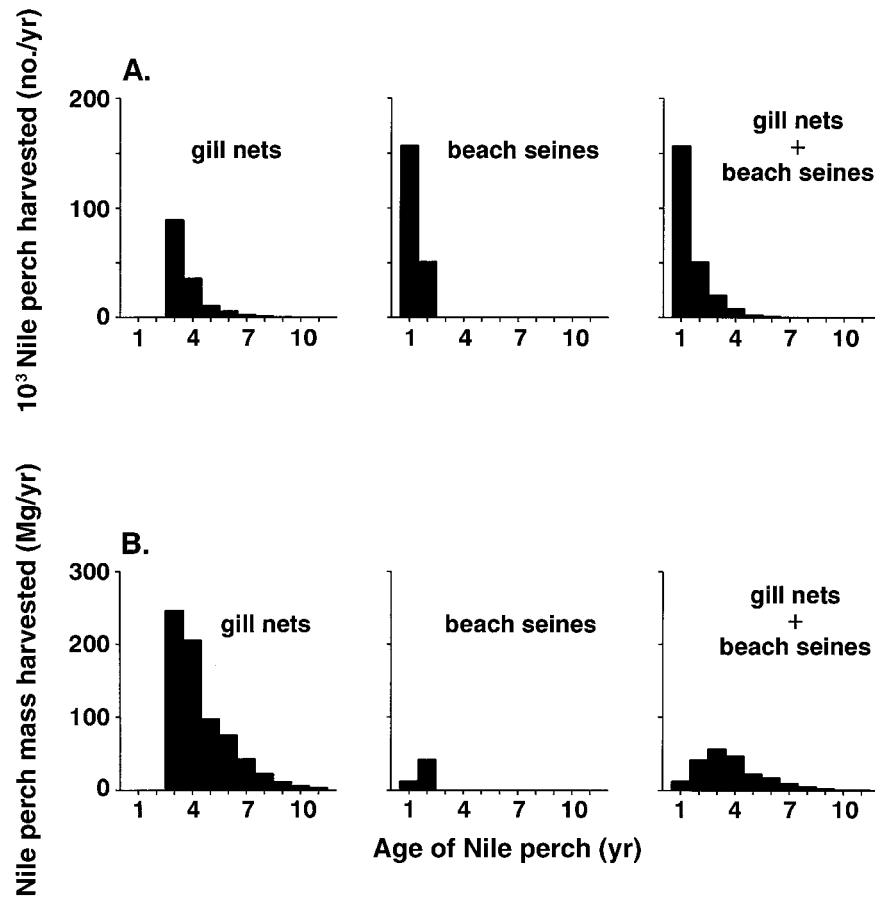


FIG. 3. (A) Simulated harvest of numbers and (B) biomass of Nile perch under each of three fishery scenarios: gill net fishery, beach seine fishery, and gill nets plus beach seine fisheries.

of its previous levels. Beach seine plus gill net fisheries reduced total predation effects to <10% of those estimated for an unexploited Nile perch population.

As expected, fisheries for *Lates* led to a reduction in haplochromine and juvenile *Lates* mortality (Fig. 2B and C). Large *Lates* imposed the greatest predation on haplochromines. Differences in the scales of panels A, B, and C (Fig. 2) demonstrate the effects of *Lates* on the formerly dominant haplochromine stocks and illustrate the important role of cannibalism in the current food web.

Peak predation on juvenile *Lates* was due to persistence of older age classes of Nile perch, while the converse was true for haplochromine prey. Any fishery for the predator benefited all prey species, while addition of the gill net fishery appeared to favor survival for juvenile *Lates*. Addition of the beach seine fishery offered greater relative survival for haplochromines. The first reports of reappearance of haplochromines came from Kenya's Winam Gulf, where beach seine fisheries for juvenile Nile perch originated and have been most intensively pursued (Riedmiller 1994).

Our three fishery scenarios produced very different yields from the simulated cohorts (Fig. 3). Number of

fish harvested was lowest when large gill nets were employed, but the total mass of harvest (and price per fish) would be much greater if the Nile perch were allowed to grow. Total biomass of *Lates* harvested was clearly reduced if beach seine fisheries depleted the population before growth allowed accumulation of biomass by the cohort. Fishing with gill nets alone provided three- to fourfold greater biomass yields than those that derived from the combined fishery.

Among the important components of current fisheries, adult tilapia (*Oreochromis niloticus*) commands the highest market prices per kilogram. Ogutu-Ohwayo (1994) does not distinguish that species from other tilapias, so we calculated effects of fisheries on consumption by Nile perch for all tilapiines combined. In fact, Nile tilapia is essentially the only tilapiine still abundant in Lake Victoria, as it currently comprises >95% of commercial catches and Nile perch diets (Ogutu-Ohwayo 1994).

Fisheries had substantial, but contrasting, effects on the three major components of Lake Victoria's food web (Fig. 4). Harvest of *Lates* biomass was greatest under conditions of the large-mesh gill net fisheries. Beach seine fisheries alone provided very low biomass

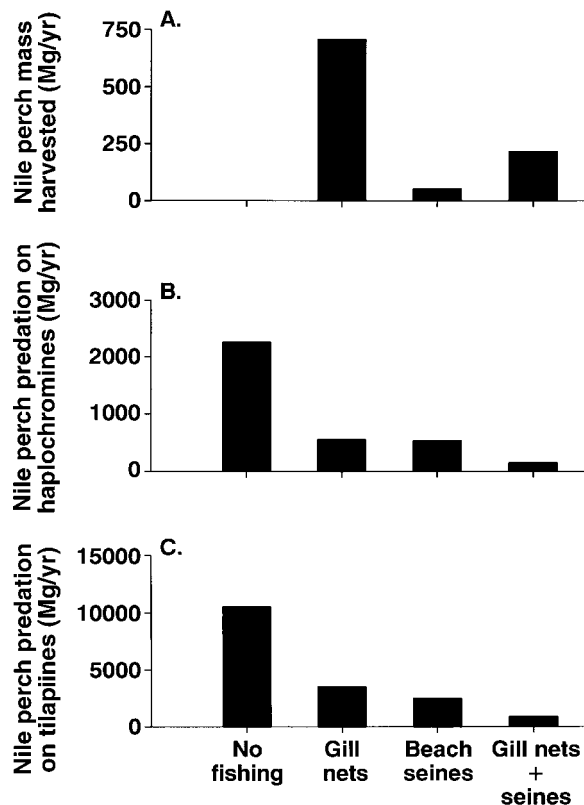


FIG. 4. (A) Summary of total harvest of Nile perch, and its effects on prey populations of (B) haplochromine and (C) tilapiine fishes in Lake Victoria under each of the four fishery scenarios (as in Fig. 1).

yields. Their combination produced fishery yields less than one-third of those derived from a large-net fishery, thus the effect of fishing for juveniles substantially diminished total yields. Predation on haplochromines (Fig. 4B) was greatest in the absence of fishery exploitation. Due to the reduction in large fish accomplished in each of the fishery scenarios, predation effects on haplochromines were reduced to very low levels. Similarly, predation on the tilapiines was reduced under each of the fishery scenarios, with the large-mesh gill net fisheries having the least effect.

DISCUSSION

Comparisons with other systems

Events described for Lake Victoria were partially anticipated. Among the native habitats of Nile perch is Lake Albert (Uganda–Zaire), where its prey assemblage is dominated by *Alestes* spp., which include ecological analogues of *Rastrineobola* and tilapia species. Nile perch was introduced to Uganda's Lake Kyoga and Lake Nabugabo in an attempt to evaluate the prospect for introduction to Lake Victoria (Ogutu-Ohwayo 1990, 1993). The resultant changes in community structure of both systems were similar to those observed in Lake Victoria. These fish assemblages in-

clude *Rastrineobola* and tilapias as the primary sympatric forms; other species, including some haplochromines, persist in all three lakes. The lessons from lakes Kyoga and Nabugabo did not guide the management decision, as Nile perch appeared in Lake Victoria before its effects were evaluated elsewhere. Lessons from Lake Kyoga also include a rapid expansion of the Nile perch fishery, overexploitation, and the gradual recovery of many prey species populations. Current Nile perch yields from Kyoga are half or less of those at their highest, and haplochromines have become more abundant (Ogutu-Ohwayo 1994). Most recent events in Lake Victoria suggest a similar trajectory.

Lake Victoria is now heavily influenced by its apical predator—humans—and the factors that regulate their behavior. This ecosystem cannot be restored to its ancestral condition because many endemic species are gone, habitats have changed due to continuing cultural eutrophication, and the inertia of the current fishery is enormous. Management focused solely on complete recovery of the lake's historical species diversity would probably reduce total fishery yields and diminish economic benefits to the hundreds of thousands of people who depend on the lake's fishery resources. Increased social and political tensions would be a probable consequence of the resultant economic stress. In fact, the interests of European and North American conservation biologists might best be served through maintenance of a sustained, closely regulated fishery for Nile perch. Where the fisheries are particularly intense, native species are recovering and fish community diversity is increasing. Similarly, ecologists and limnologists must recognize that fisheries and the cascade of food web effects they induce are a major cause of changes in this ecosystem (Goldschmidt et al. 1993) and many others (Kitchell 1992, Christensen and Pauly 1993). Fisheries should be viewed as a trophic level and gill nets as a species or size-selective predator fully as effective as those known from the principles of predation outlined in textbooks (Ricklefs 1990, Diana 1994, Stone 1995). In an ecological sense, fishermen exhibit a steep functional response to populations of their prey and have a rapid numerical response (Johnson and Carpenter 1994). Preventing overexploitation requires a constraint on their numerical response (limited entry) and/or reduction of their capture efficiency (e.g., gear, season, and mesh size restrictions or size limit and total catch quota systems).

The conflict of sustainable, high fishery yields and restoration of native haplochromine stocks is clear from our results. If the goal is to maintain high yields of *Lates* (and the many socioeconomic benefits they bring), then a strictly regulated large-mesh gill net fishery would provide the most likely means to that end. Given the growth rate of the gill net fishery in the past decade, regulatory policy must develop a means for constraining exploitation and/or regulating fishing effort. Expansion of the beach seine fishery encourages

recruitment overfishing and is clearly disadvantageous to the prospects for developing sustained, high-value yields from the *Lates* fisheries.

A compromise of interests and benefits may be effected if the riparian governments can agree upon and enforce restriction of the Nile perch fishery. Based on experience in scores of other fisheries (Ludwig et al. 1993), regulations must be established to prevent yet another tragedy of the commons and the "pauperization" that typically accompanies overexploitation of a fishery resource (Greboval 1990). Among the regulations most likely to be effective (i.e., enforceable) would be those that provide a uniform regulation for gill net mesh size. Large-mesh gill nets provide greatest yields to the fisheries, with their associated socioeconomic benefits, and a substantial reduction in predation effects. Those should allow some recovery of the haplochromine species and maintenance or enhancement of the tilapia populations.

All fishery scenarios bring a severalfold reduction in the intensity of predation on haplochromines. Management goals based on recovery of native species have obvious allies in the fisheries for Nile perch. Further, the effects of fishery practices are similar for the tilapiines. Their current abundance, as made evident in the diets of Nile perch, is roughly 5 times greater than that of the haplochromines. Although tilapia populations are probably heavily influenced by Nile perch predation, they persist and maintain relatively high abundances in the presence of this predator. The large-mesh gill net fisheries reduce predation on prey of large Nile perch (haplochromines and tilapiines) as well as cannibalism on juvenile *Lates*. This is most apparent in the greater survival of larger prey, the tilapiines. To the extent that resource-based competition occurs in this system, the introduction of the omnivorous Nile tilapia may have created an impediment to recovery of some of the trophic specialists among the haplochromine species.

Modeling caveats

Our modeling approach is simply an empirical analysis of growth and population effects for one predator. It is only as precise and accurate as its inputs. This application employed well-defined inputs for growth rates and diet components. Although the physiological parameters and costs of swimming activity were estimated from those typical for other piscivores, the calculated ρ values did not approach the upper or lower limits of energy budgeting constraints and were all within the range least influenced by bias or error in parameter estimates. Thus, the model has potential error effects analogous to those presented by Rice and Cochran (1984) and parameter sensitivities similar to those outlined by Bartell et al. (1986). We also made general estimates of energy density values for the predator and its prey. If those are in error, their effect would be represented as a proportional and equivalent bias in

all calculations. Thus, the conclusions based on comparison of results would not be substantially altered. The general correspondence of energy budget components with those known from other, ecologically analogous fishes lends greater credence to this analysis.

The major assumptions and the most important prospect for error in this analysis revolves around the estimates of mortality rates. Knowing that, we adopted a strategy based on comparisons of strongly contrasting conditions, i.e., intense fisheries vs. none, and effects based on very different modes of exploitation. We also interpret the results in general terms rather than making specific, empirical conclusions. If and when better estimates of mortality rates become available, they will apply to all four of our scenarios. That will improve, but not radically change, the consequent interpretations. Where Nile perch fisheries are locally intense, recovery of haplochromine stocks serves as an independent indicator of the effects and mechanisms we describe.

Our approach assumes a stable age distribution and evaluates the consequences of different kinds of mortality effects on predator-prey interactions. It did not include the functional response of the predator or the numerical dynamics of prey or predator in response to changing mortality schedules (e.g., Johnson and Carpenter 1994, Walters and Juanes 1994). Implementing those prospects in any empirical or theoretical analysis will require some accounting for three key unknowns: the stock-recruit relationships for Nile perch and their prey, the size-selective basis of predation processes or fisheries, and the density dependence of the predator-prey interaction. Given the logistics and financial constraints of field studies in Lake Victoria, resolving those unknowns is a major challenge.

High levels of cannibalism are evident for *Lates* in Lake Victoria. This raises an interesting, but unresolved, question about the trade-off of predation and fishery effects. Intense large-mesh gill net fisheries reduce the extent of cannibalism, thereby fostering survival of juvenile *Lates*. However, the beach seine fisheries harvest many immature fish, including a by-catch of other species, and diminish the future reproductive potential of both predator and prey populations through recruitment overfishing. The steady state or equilibrium solution to this problem can only be found if the fisheries remain static and if the *Lates* population exhibits no compensatory changes in growth rate or age and size at sexual maturity. None of those conditions is likely to hold (Hilborn and Walters 1992). In other systems where cannibalism constrains recruitment, fish populations exhibit irruptive responses, and the consequent food web dynamics are attuned to a frequency approximating that of the typical adult life span for the piscivore (Carpenter 1993).

Given their enormous fecundity and the many unknowns associated with the early life history of Nile perch, a pragmatic alternative for establishing expect-

tations and management policies might focus on measures of juvenile abundance (e.g., abundance of 15–20 cm TL, age 0+ fish in assessment trawls) and their relationship to that of the adults. If general patterns become apparent, a monitoring program based on standard catch indices of juveniles might be implemented at little cost to the management agencies. This would allow some indicator of recruitment to the fisheries at age 2+ and older and a forecast of the relative strength of predation effects as the new cohort ascends the trophic hierarchy.

Under sponsorship of the European Community, a lakewide fisheries stock assessment program is currently underway. This effort may produce the information required to establish analyses based on population dynamics of Nile perch and the complex feedback pathways for this predator–prey system. Considering the rapid rates of change exhibited by both predation and fisheries effects, future research also should attend to the prospect of density-dependent, compensatory responses in the life history characteristics of both the Nile perch and its prey (Ogutu-Ohwayo 1994). Our familiarity with analogues elsewhere (e.g., the Laurentian Great Lakes; Smith 1968) are based on response rates for populations, communities, and food webs in lakes of the temperate zone. As in other tropical systems (Zaret and Paine 1973, Christensen and Pauly 1993), those in Lake Victoria will undoubtedly be more rapid.

The future

Attempts to forecast the equilibrium, sustainable, or steady-state condition of Lake Victoria can derive from two traditional approaches. The assemblage of fishery yield models presented by Pitcher and Bundy (1994) demonstrates substantial differences among the alternatives. The best estimates of maximum sustainable yields (MSY) for Nile perch range from 93×10^3 to 690×10^3 Mg per year, and differ largely as a result of the assumptions and uncertainties associated with each. Pitcher and Bundy (1994) point out that the 1990 catch (500×10^3 Mg) exceeds the majority of estimates for MSY and their “best guess” MSY estimate of 300×10^3 Mg per year.

An alternative approach derives from the “bottom-up” view of traditional limnological studies, which argues that fundamental research will provide a means for forecasting fish yields in large lakes. Among those methods, the morpho-edaphic index (MEI) approach has gained greatest application (Ryder 1982) and has been used to estimate fish production rates in a diversity of African lakes (Fryer and Iles 1972). The MEI estimate of fishery yield for Lake Victoria was $10 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ before Nile perch was introduced. Conventional ecotrophic wisdom would hold that addition of a top predator to the system should reduce yield to the fisheries. In fact, addition of Nile perch to the Lake Victoria food web caused fishery yields to rise to ≈ 80

$\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Pitcher and Bundy 1994). The calculated MEI for Lake Victoria would produce a sustained fishery yield that is substantially below the current harvest rates.

Although nutrient loading has increased in the recent past and there is reason to be concerned about oxygen depletion in deep-water habitats (Hecky et al. 1994), the reported doubling in primary production rates is insufficient to account for the disparities in fishery yield estimates. Our view is that neither of the conventional approaches to estimating sustainable yields offer much guidance in forecasting the future of the Lake Victoria ecosystem. Its dynamics are now, and will likely continue to be, most strongly influenced by the rapidly growing populations of humans whose incentives to catch fish are generally in conflict with the goals of sustainable management policies (Ludwig et al. 1993) and whose behavior as a predator defies expectations based on equilibrium models.

Another ominous exotic has appeared in Lake Victoria. The water hyacinth (*Eichhornia crassipes*) recently invaded from the Kagera River in Rwanda, spread rapidly throughout the lake, and now clogs bays and landings, fouls fishing nets, causes anoxia beneath its dense mats in the littoral zone, and creates a habitat where snails and the resulting schistosomiasis may be enhanced, to the detriment of human health (Twongo 1991). It also provides refuge from predation for the juvenile stages of many fishes in both the littoral and pelagic habitats. The potential for water hyacinth increase is unknown. Thus, its ecological and economic impacts remain a major question. A water hyacinth reduction program is currently being evaluated based on biological control through introduction of two insect species (weevils) that feed on water hyacinth. In the interim, mechanical removal seems the only alternative for dealing with water hyacinth mats at landing beaches, water intakes, and the major hydroelectric dam at the source of the Victoria Nile, Owen Falls near Jinja, Uganda, which is a primary source of power to much of the region.

Our analyses of predation and fishery effects in Lake Victoria are based on extensions of current conditions to their likely maximum. The present state of this system is most like that represented by the conditions simulated under fisheries based on large-mesh gill nets. Reports of declining catch rates and the consequent response by the apical predator (fisheries are switching to smaller mesh nets [Riedmiller 1994]) indicate that the system is in a transient state characterized by declining piscivory, diminishing fishery yields, intensifying socioeconomic stressors, and the continuing recovery by populations of those species that serve as primary prey of the Nile perch.

Estimating the future state of Lake Victoria will require greater and continuing resolution of the status of fish populations, attention to the ominous portent of deepwater oxygen depletion as it relates to nutrient

loading and cycling (Hecky et al. 1994, MacIntyre and Melack 1995), and development of a combination of conceptual, empirical, and modeling approaches for characterizing food web interactions (Reinthal and Kling 1994). Included among the latter must be an evaluation of the consequences of alternative fishery management policies (Kitchell 1992). Fishing is a potent ecological force and is clearly among the most important regulators of trophic dynamics in the Lake Victoria ecosystem.

ACKNOWLEDGMENTS

We thank Fred Bugenyi, Director of the Fisheries Research Institute in Jinja, and our colleagues at FIRI for their continued diligence in securing information and for their willingness to share insights. We thank Les Kaufman, Boston University, and Bill Cooper, Michigan State University, for their foresight in catalyzing an expanded research effort on Lake Victoria. Dave Beauchamp, Utah State University, Steve Carpenter, University of Wisconsin-Madison, Les Kaufman, Roy A. Stein, Ohio State University, and an anonymous reviewer provided valuable suggestions for improvement of the manuscript. We thank our co-investigators George Kling and Patricia Ramlal, both from the University of Michigan, for their advice, encouragement, and hospitality during the time that J. F. Kitchell, D. E. Schindler, and P. N. Reinthal visited Jinja. Research by J. F. Kitchell, D. E. Schindler, and P. N. Reinthal was supported by the Ecosystem Analysis Program of the National Science Foundation, while the primary data collection by RO-O was supported by the Canadian International Development Research Centre (IDRC).

LITERATURE CITED

- 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.
- Boisclair, D., and W. C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). *Canadian Journal of Fisheries and Aquatic Sciences* **48**:1337–1344.
- Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pages 279–352 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*. Volume VIII. Academic Press, New York, New York, USA.
- Carpenter, S. R. 1993. Statistical analysis of the ecosystem experiments. Pages 26–42 in S. R. Carpenter and J. F. Kitchell, editors. *The trophic cascade in lakes*. Cambridge University Press, New York, New York, USA.
- Christensen, V., and D. Pauly, editors. 1993. *Trophic models of aquatic ecosystems*. International Center Living Aquatic Resource Management Conference Proceedings 26. ICLARM, Manila, Philippines.
- Diana, J. 1994. *Biology and ecology of fishes*. Cooper, Carmel, Indiana, USA.
- Fryer, G., and T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh, UK.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* **7**:686–700.
- Graham, M. 1929. *The Victoria Nyanza and its fisheries. A report on the fish survey of Lake Victoria 1927–1929*. Crown Agents for the Colonies, London, UK.
- Greboval, D. 1990. Socio-economic issues for planning in support of fisheries management. In CIFA report of the 5th session of the Sub-committee for the Development and Management of the Fisheries of Lake Victoria, Mwanze, Tanzania, 12–14 September 1989. FAO Fisheries Report **430**:75–97.
- Greenwood, P. H. 1966. *The fishes of Uganda*. The Uganda Society, Kampala, Uganda.
- Gulland, J. A. 1971. *The fish resources of the ocean*. Fishing News Books, Surrey, UK.
- Hecky, R. E. 1993. Peter Kilham Memorial Lecture. The eutrophication of Lake Victoria. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **25**:39–48.
- 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.
- Hecky, R. R., and F. W. B. Bugenyi. 1992. Hydrology and chemistry of the African Great Lakes and water issues: problems and solutions. *Mitteilungen, Internationale Vereinigung für theoretische und angewandte Limnologie* **23**:45–54.
- Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin Sea Grant Institute, WIS-SG-92-250, Madison, Wisconsin, USA.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, New York, New York, USA.
- Hopson, A. J. 1972. A study of the Nile Perch (*Lates niloticus* (L.), Pisces: Centropomidae) in Lake Chad. Overseas Research Publication 19, Overseas Development Administration, London, UK.
- 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.
- Johnson, B. M., and S. R. Carpenter. 1994. Functional and numerical responses: a framework for fish-angler interactions? *Ecological Applications* **4**:808–821.
- Jones, M. L., J. F. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Transactions of the American Fisheries Society* **122**:1002–1018.
- Kaufman, L. S. 1992. Catastrophic change in species-rich freshwater ecosystems, the lessons of Lake Victoria. *BioScience* **42**:846–852.
- . 1993. The challenge of the world's Great Lakes. *Conservation Biology* **7**:447–449.
- Kitchell, J. F. 1983. Energetics. Pages 312–338 in P. W. Webb and D. Weihs, editors. *Fish biomechanics*. Praeger, New York, New York, USA.
- , editor. 1992. *Food web management: a case study of Lake Mendota*. Springer-Verlag, New York, New York, USA.
- Kitchell, J. F., E. A. Eby, X. He, D. E. Schindler, and R. M. Wright. 1994. Predator-prey dynamics in an ecosystem context. *Journal of Fish Biology* **45**:209–226.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). *Journal of the Fisheries Research Board of Canada* **34**:1922–1935.
- 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. In CIFA report of the 5th session of the Sub-committee for the Development and Management of the Fisheries of Lake Victoria, Mwanza, Tanzania, 12–14 September 1989. FAO Fisheries Report **430**:35–74.
- Ludwig, D., R. Hilborn, and C. J. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* **260**:547–549.
- MacIntyre, S., and J. M. Melack. 1995. Vertical and hori-

- zontal transport in lakes: linking littoral, benthic and pelagic habitats. *Journal of the North American Benthological Society* **14**:599–615.
- Mugidde, R. 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). *Internationale Vereinigung für theoretische und angewandte Limnologie* **25**:846–849.
- Ochumba, P. B. O., and D. I. Kibara. 1989. Observations on the blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African Journal of Ecology* **27**:23–34.
- Ogutu-Ohwayo, R. 1984. Predation by Nile perch, *Lates niloticus* (Linné), introduced into Lake Kyoga (Uganda) and its effects on the populations of fish in the lake. Thesis (Fisheries and Aquatic Sciences), University of Dar es Salaam, Dar es Salaam, Tanzania.
- . 1990. 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.
- . 1993. The effects of predation by the Nile perch, *Lates niloticus* L., on the fishes of Lake Nabugabo, with suggestions for the conservation of endangered endemic cichlids. *Conservation Biology* **7**:701–711.
- . 1994. Adjustments in fish stocks and in life history characteristics of the Nile perch, *Lates niloticus* L., in lakes Victoria, Kyoga and Nabugabo. Thesis. University of Manitoba, Winnipeg, Manitoba, Canada.
- Pitcher, T. J., and A. Bundy. 1994. Successful species introductions in the African lakes: assessment, uncertainties and strategies for fishery management. Pages 545–570 in B. David and E. Baldwin, editors. *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations*. AK-SG-93-02. Alaska Sea Grant Program, Fairbanks, Alaska, USA.
- Reinthal, P. N., and G. W. Kling. 1994. Exotic species, trophic interactions and ecosystem dynamics: a case study of Lake Victoria. Pages 295–313 in D. Stouder, K. Fresh, and R. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia, South Carolina, USA.
- 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.
- Ricklefs, R. E. 1990. *Ecology*. W. H. Freeman, New York, New York, USA.
- Riedmiller, S. 1994. Lake Victoria fisheries: the Kenyan reality and environmental implications. *Environmental Biology of Fishes* **39**:329–338.
- Ryder, R. A. 1982. The MEI—use, abuse and fundamental concepts. *Transactions of the American Fisheries Society* **111**:154–164.
- Smith, S. H. 1968. Species success and fishery exploitation in the Great Lakes. *Journal of the Fisheries Research Board of Canada* **25**:667–693.
- 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.
- Stewart, D. J., D. Weininger, V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:681–698.
- Stone, R. 1995. Taking a new look at life through the functional lens. *Science* **269**:316–317.
- Thompson, K. W., C. Hubbs, and B. 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. Texas Parks and Wildlife Department, Technical Series Number 22, Austin, Texas, USA.
- Twongo, T. 1991. Implications of the water hyacinth infestation for fisheries, with particular reference to Lake Kyoga. Pages 19–23 in K. Thompson, editor. *The water hyacinth in Uganda*. United Nations Food and Agricultural Organization, Jinja, Uganda.
- Walters, C. J., and F. Juanes. 1994. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2058–2070.
- Winberg, G. G. 1960. Rate of metabolism and food requirements of fishes. Belorussian University, Minsk, Belorussia. Fisheries Research Board of Canada Translation Series **164**.
- 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.
- Zaret, T. M., and R. T. Paine. 1973. Species introduction in a tropical lake. *Science* **182**:449–455.