



Predator Removal: Effect on Fisheries Yields in Lake Victoria (East Africa)

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Thermoluminescence, a two-step process in which electrons are first excited into metastable states in cold materials and later stimulated to decay by heating of the materials, has been proposed by Nelson and Hapke (2) to explain Io's post-eclipse brightening. They showed that this process would be consistent with the correlation they found between solar flare activity and Io's post-eclipse brightening. There were solar flares of importance 2N on 8 February 1978 and of importance 2B on 22 November 1977, both within 10° in heliographic longitude of the sub-Jupiter point (16). (Flares of importance 2 cover 5.2 to 12.4 square degrees on the solar disk. Smaller flares are much more common. The term "N" refers to "normal" and "B" to "rather bright" appearance.) Unfortunately, our knowledge of thermoluminescence, like ordinary luminescence, suffers from a lack of data in the 5- μ m region. The possible relation of the 5- μ m Io brightening to the solar flare could support any of the above explanations based on energetic particle bombardment.

To examine the reasonableness of the luminescence hypotheses, let us carry out a "black box" analysis in which we compare the observed excess amount of emitted energy with likely amounts of energy contained in high-energy particles striking Io's surface. We require then that the energy flux hitting the surface exceeds the energy emitted. If the observed excess flux originates from the entire hemisphere facing Earth, then it corresponds to an energy flux of about 5×10^2 erg cm⁻² sec⁻¹ at Io's surface. The surface of Io is being bombarded by high-energy magnetospheric electrons and protons (17) as well as thermal plasma protons and electrons that have been accelerated by a plasma sheath thought to exist about Io (12). Of these four possibilities, the highest energy flux would be expected from thermal plasma electrons accelerated through the positive sheath (12). Using a typical unidirectional flux of 5×10^9 electron cm⁻² sec⁻¹ and a potential drop of 300 kV across the sheath (12, 18), we obtain an energy flux of about 2×10^3 erg cm⁻² sec⁻¹ striking the surface of Io in the region beneath the positive plasma sheath. Thus, accelerated plasma electrons represent a plausible energy source for the postulated luminescence provided that the efficiency of conversion of particle impact energy to luminescence is 0.25. Values for luminescence efficiency for electron impact rarely exceed 0.2, but very few data exist at 5 μ m. Typical values of luminescence efficiency in visible

wavelengths for lunar materials (19) are below 10^{-2} for excitation by ultraviolet light and lower still for excitation by protons.

The occurrence of the postulated luminescence at one rotational phase angle but not at others could be attributed to several factors. First, if thermal luminescence is responsible for the effect observed, the rate of excitation out of metastable states could depend strongly on temperature, so that either nighttime cooling or eclipse cooling might delay the release of the observed photons. Second, only a portion of Io's surface is exposed to bombardment by the accelerated thermal plasma electrons so that the observed excess can be seen only when this portion of Io is facing Earth. Third, the plasma density and therefore the amount of luminescence may depend on Io's position relative to the jovian magnetic equator (20). Finally, the surface composition and therefore the efficiency of luminescence may vary with position on Io.

On the basis of the above discussion, we conclude that the observed excess flux near 5 μ m was probably the result of emission excited by an interaction with Jupiter's magnetosphere. Further observations will be needed, however, to rule out internal heat sources or to relate the brightening to a specific magnetospheric phenomenon.

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22. We thank L. Lebofsky, U. Fink, and H. Larson for discussions of their observations prior to publication. We are also grateful to members of the LPL/NASA Mount Lemmon Observatory staff from both the Lunar and Planetary Laboratory and the Ames Research Center for their work in preparing the telescope for our observations.

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Predator Removal: Effect on Fisheries Yields in Lake Victoria (East Africa)

Abstract. *Lake Victoria's artisanal fishery has an overfishing problem. A possible solution is suggested by records showing that fish catches are best where predator populations have been reduced by fishing. It may be possible to remedy overfishing by increasing fishing effort, provided the additional effort is directed toward predators.*

Harvesting the predator of an exploited animal population should theoretically release more of that population's production for human consumption (1). I recently encountered an example of this while analyzing records of the artisanal, inshore fishery of Lake Victoria.

My analysis of Lake Victoria was motivated by symptoms of overfishing

such as low catches and reduced fish sizes, which have been particularly conspicuous during the past decade (2). It has been proposed that this problem could be solved by (i) reducing the fishing effort and (ii) eliminating fishing gear that captures juvenile fish (3). The purpose of my analysis was to evaluate the effectiveness of these two proposed solutions, but it became apparent that an al-

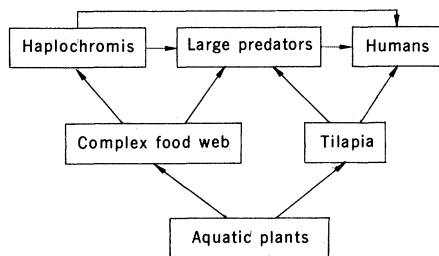


Fig. 1. Food web for the major commercial genera in Lake Victoria. The diagram is oversimplified for *Haplochromis*, as a few of the more than 150 species of *Haplochromis* eat plants.

ternative solution—directing fishing toward large predators—was also worthy of consideration. This solution involves more, rather than less, fishing.

Lake Victoria has a complex fishery of 200 species, with adults ranging in length from 6 cm to 2 m. Fishing gear that is optimal for one species may be disastrous for others. The food web relationships of the major commercial genera are shown in Fig. 1.

Fishing intensities in different parts of the lake range from 3 to 35 canoes per mile of shoreline. The proportions of different kinds of fishing gear (such as hooks, fine-mesh seines, and gill nets with mesh sizes ranging from 3.8 to 20 cm in stretch length) also vary considerably from one part of the lake to another in accord with local tastes for fish and fishing techniques.

Since environmental conditions and the array of species present are similar throughout the inshore area of Lake Victoria, the conspicuous variation in abundance and composition of fish catch from one place to another can be attributed largely to variation in the quantity and quality of fishing effort. The result is a series of "experiments" that show the effects of human-induced differences in fish populations on the yield of the fishery. The independence of each locality is reinforced by the fact that inshore fish typically travel only a few miles in their lifetime (4).

A curvilinear multiple regression equation was fitted to catch figures for 1972 and 1973 from 50 recording stations distributed over the 2000-mile shoreline of Lake Victoria (5, 6). Including only the linear terms, which reflect the contributions of six categories of fishing gear to the total weight yield summed over all species in the fishery, the equation is

$$Y = 48X_{SM} + 50X_L + 10X_E + 110X_H \quad (1)$$

where Y is the yield (kilograms per year); X_{SM} is the contribution of small gill nets (3.8 to 5.1 cm); X_L , large gill nets (10 to

12 cm); X_E , extra large gill nets (13 to 20 cm); and X_H , hooks.

Gill nets of intermediate size (6.2 to 9.8 cm) and seines are not included because their regression coefficients are not significantly different from zero, indicating no contributions to overall yield. That is, the negative effects of seines and intermediate gill nets—due, for example, to premature harvesting of the larger species (or destruction of spawning grounds in the case of seines)—cancel out the positive effects from their more appropriate harvesting of smaller species such as the *Haplochromis*.

I have analyzed the complete regression equation (5, 7) and demonstrated that Lake Victoria's fishing problem is due to the quality and not the quantity of fishing. The equation suggests that more intense fishing efforts could lead to higher yields, provided (i) mesh sizes are large enough to permit the herbivorous *Tilapia* to reach maturity before harvest and (ii) the large predators (*Clarias*, *Bagrus*, and *Protopterus*) are fished heavily by means of hooks. The optimal strategy for the fishery as a whole corresponds to fishing optimally for the larger fish, especially *Tilapia* (5, 8).

The large positive contribution of hooks in Eq. 1 was not expected before the analysis, because the large predators caught by hooks represent only a minority of the commercial fish in Lake Victoria. An explanation is suggested by the yields (Y_T and Y_H) of the cichlid genera *Tilapia* and *Haplochromis*, which are not only the principal prey of the adult stages of these predators but also account for most of the commercial catch (5, 9).

$$Y_T = -4.8X_{SM} + 6.2X_L + 8.8X_E + 29X_H \quad (2)$$

$$Y_H = 21X_{SM} + 8.8X_H + 124X_{SE} \quad (3)$$

where X_{SE} is the contribution of seines.

Since *Tilapia* and *Haplochromis* are not themselves caught by hooks, I hypothesize that the stimulatory effect of hooks is due to the reduction of predator populations that is observed to accompany heavier hook fishing. The effect of predators on the yields of their prey is indicated by the estimate (based on stomach analyses) that *Bagrus* consumes more than ten times as many *Haplochromis* as are caught by fishermen (10).

The significance of *Bagrus* is further suggested by catch records (Fig. 2), which indicate an inverse relation between *Tilapia* catches and *Bagrus* abundance. (The points in Fig. 2 are present-

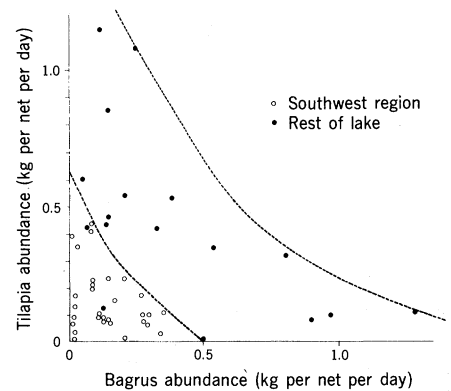


Fig. 2. *Tilapia* abundance (measured as catch per unit effort) at various landings throughout Lake Victoria during 1972 and 1973, as a function of the abundance (catch per unit effort) of one of its predators, *Bagrus docmoc*. Effort units are gill nets of mesh size exceeding 50 mm in stretch length.

ed separately for two regions of Lake Victoria that have different *Tilapia* catches because of factors other than predation. Each region manifests the same pattern, however.) Although *Tilapia* catches at a particular *Bagrus* abundance vary considerably with fishing practices, the maximum catch that can be made is reduced as *Bagrus* increases. *Bagrus* seems to place a ceiling on sustainable *Tilapia* yields (11).

A strategy of waiting for the large herbivorous fish to mature before harvesting becomes particularly lucrative if natural mortality due to predation is low. Because the large predators in Lake Victoria are generally underfished (12), fishing them more intensely will not only increase the yields of the predators themselves but could also increase the yields of their prey.

Despite overfishing symptoms, it appears the total harvest of Lake Victoria can be increased by increasing the fishing effort, provided the additional effort is properly directed. This conclusion is fortunate, since the high human population pressure along the shoreline of the lake, coupled with the difficulty of imposing unpopular restrictions on thousands of autonomous fishermen, rule out reduction of fishing effort from a practical point of view (13).

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natural mortality during the exploitation phase if natural mortality is significantly greater than fishing mortality. Even more drastically, recruitment to the exploitation phase varies inversely with the exponent of mortality rate before exploitation. (That is, each doubling of mortality can theoretically reduce yield to approximately one-seventh of what it otherwise would be.) Although such a simplistic view does not take into account the compensatory relations between predation, other sources of mortality, and growth, some of which may reduce the impact of natural predation in a real fishery, the potential effect is nonetheless striking.

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5. G. G. Marten, *J. Fish Res. Board Can.*, in press.
6. The complete regression equation is

$$Y = 48X_{SM} - 1.8X_{SM}^2 + 50X_L - 1.1X_L^2 + 10X_E - 0.2X_E^2 + 110X_H - 6.4X_H^2 - 23X_{SM}X_L - 2.2X_LX_H - 4.0X_{SM}X_{SE} - 8.0X_HX_{SE} - 1.0X_LX_E - 1.6X_{SM}X_E$$

All units are per mile of shoreline. Fishing gear is in terms of "canoe loads" (one seine, 40 gill nets, or 800 hooks per canoe). The equation was originally fitted separately to data from 1972 and 1973. As the 2 years gave almost identical results, they were pooled for the equation presented here. Negative square and cross-product terms reflect diminishing returns with higher fishing gear densities.

7. The optimum for Eq. 1 is no use at all of seines and small, intermediate, and extra large gill nets, accompanied by intensive use of hooks (4600 per mile) and large gill nets (660 per mile). The current average and maximum densities of hooks on Lake Victoria are 2000 and 3900 per mile, respectively. The current average and maximum densities of large gill nets are 160 and 645 per mile. Although the optimum is not very precise because of the numerous errors in the method, it should be valid for qualitative comparison with the present fishery.
8. Indulging in some ecological speculation, the larger species seem to deserve priority for optimal management because some of them (the tilapias) are herbivorous and have a high potential production per unit area, and others (the large predators) are mostly free of natural predation that would compete with predation by humans. The smaller species are primarily insectivorous and piscivorous predators at the end of long food chains and therefore lack the energy input to sustain heavy harvests by both humans and the larger predators.
9. The complete equations are

$$Y_T = -4.8X_{SM} + 6.2X_L + 0.8X_L^2 + 8.8X_E + 0.4X_E^2 + 29X_H - 3.2X_H^2 - 0.7X_{SE}^2 - 2.0X_EX_L - 0.2X_{SM}X_L - 0.4X_{SM}X_{SE} - 0.4X_EX_{SE}$$

$$Y_H = 21X_{SM} - 1.0X_{SM}^2 - 9.6X_M + 9.6X_M^2 - 20X_E + 8.8X_H - 0.26X_H^2 + 124X_{SE} - 9.0X_{SE}^2 - 5.6X_{SM}X_{SE}$$

where X_M represents medium gill nets.

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11. The explanation for Fig. 2, presented in the text is based on predation, that is, causality from *Bagrus* to *Tilapia*. There are other possible explanations, including ones based on causality in the opposite direction. *Bagrus* is insectivorous until it reaches a length of approximately 15 cm and is piscivorous thereafter. It may be that in areas where *Tilapia* populations have been decimated by destructive fishing, more of the lake's primary production is channeled through food chains leading to aquatic insects, insectivorous fish, and eventually *Bagrus*. Such alternative explanations are not necessarily mutually exclusive.
12. G. G. Marten, B. Wanjala, R. Scully, J. N. Rinne, *Afr. J. Trop. Hydrobiol. Fish.*, in press.
13. Additional fishing effort might be directed by use of economic incentives. In any one region of the lake, one of the large predators is typically considered a delicacy and fished very heavily, whereas another is considered unfit for human consumption and remains underfished and very

abundant. Which predator plays which role depends on tribal tastes in the region. If the infrastructure were available to market "trash" predators in areas where they are worth many times what they are locally, it should be possible to encourage heavy fishing of all the large predators.

14. This study was conducted under the auspices of the East African Freshwater Fisheries Research Organization (EAFFRO) with support from the U.S. Agency for International Development.

Fisheries records were provided by the fisheries departments of Kenya, Tanzania, and Uganda. My EAFFRO colleagues J. Okedi, B. Wanjala, J. Rinne, L. Guluka, R. Scully, G. Ssentongo, and W. Kudhongania made numerous contributions. P. Larkin and H. Regier provided valuable comments on the manuscript.

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Carbon-13 Depletion in a Hydrothermal Vent Mussel: Suggestion of a Chemosynthetic Food Source

Abstract. *Tissues of a mytilid mussel from the Clambake I hydrothermal vent in the Galápagos Rift zone are strikingly depleted in carbon-13 relative to the tissues of other marine organisms. The stable carbon isotope composition of this mussel suggests that chemoautotrophic bacteria present in the hydrothermal waters are a major food source for filter-feeding organisms in this abyssal environment.*

Investigations of warm-water anomalies along the axis of the Galápagos Rift west of Ecuador led in 1977 to the unprecedented discovery of colonies of benthic marine organisms clustered around active hydrothermal vents (1, 2). These abyssal communities include dense populations of clams, mussels, and other filter feeders which are found only in the immediate proximity of the vents. This profusion of filter feeders is thought to result from locally high fluxes of particulate organic matter (2). Possible ultimate sources of this food are (i) photosynthetically produced organic matter introduced from overlying waters and carried through the vent regions by convection currents near the ocean floor and (ii) sulfur-oxidizing bacteria and possibly other chemoautotrophs that are present in this sulfide-rich environment (2).

Limited evidence that marine chemoautotrophic bacteria fractionate carbon isotopes to a greater extent than marine phytoplankton (3) and general evidence for minimal fractionation of carbon isotopes along food chains (4-6) suggest

that the distributions of stable carbon isotopes in the soft tissues of hydrothermal vent organisms might be used to discriminate between photosynthetic and chemosynthetic food sources. We report here a preliminary test of this hypothesis based upon carbon isotope analyses of tissues from a mytilid mussel collected at the Clambake I hydrothermal vent on the Galápagos Rift.

A mytilid mussel of unknown species 15 cm long was collected at a water depth of approximately 2500 m by the submersible *Alvin*. A specimen of *Mytilus californianus* 5 cm long from Freshwater Bay, Washington, and a specimen of *Mytilus edulis* 4 cm long from the Quiberon Peninsula of France were also analyzed. Entire specimens were frozen upon collection. Mantle and foot tissues were later excised and freeze-dried. Subsamples of 5 to 10 mg were taken from these tissues and combusted by the method of Buchanan and Corcoran (7). The resultant CO_2 was purified and isolated as described by Rau (8). The carbon isotope composition of the CO_2 was determined with a Nuclide 6-60 ratio

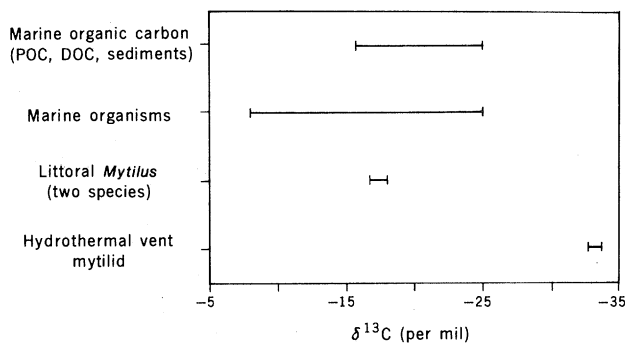


Fig. 1. The $\delta^{13}C$ of organisms and major organic carbon reservoirs in temperate ocean environments including pelagic and bathypelagic animals (3, 4), particulate organic carbon (POC), dissolved organic carbon (DOC), and sediments (4, 5). Also shown is the range of seven $\delta^{13}C$ determinations of foot and mantle tissues from two littoral *Mytilus* species and the range of eight determinations on the same types of tissue from a hydrothermal vent mytilid.