

The Origins of the Nile Perch in Lake Victoria

ROBERT M. PRINGLE

*The ways in which economic, social, and political forces lead to species introductions are an important, if overlooked, aspect of ecology and conservation. The nonnative Nile perch (*Lates niloticus*) in Lake Victoria, and the ecological changes associated with the species' establishment and expansion there, has elicited tremendous attention from biologists. Yet it has never been clear why, when, or by whom the fish was introduced. Here I outline the history of fishery research and management in East Africa and explore the circumstances that led to the introduction of the Nile perch. The evidence suggests that repeated secretive introductions were made in the mid-1950s by members of the Uganda Game and Fisheries Department as part of a bifurcated effort to improve sport fishing on the one hand and to bolster fisheries on the other. Fisheries scientists affiliated with the East African Fisheries Research Organization opposed the introduction, but were ineffective; I suggest that this failure stemmed partially from their inability to engage effectively with political processes.*

Keywords: African cichlids, exotic species introductions, extinction, invasive species, *Haplochromis*

Most ecologists and evolutionary biologists are familiar with the saga of the introduced Nile perch (*Lates niloticus*) in Lake Victoria. The explosion of the lake's Nile perch population in the 1980s was monitored closely, because it coincided both with a fivefold increase in the economic value of the fishery (Reynolds et al. 1995) and with a halving of the lake's 500-species haplochromine cichlid flock (Ogutu-Ohwayo 1990). This reduction in species and functional diversity restructured the lake's ecology; for example, the disappearance of zooplanktivorous haplochromines coincided with a dramatic sixfold increase in biomass of the zooplanktivorous cyprinid *Rastrineobola argentea* (Wanink 1999). By the early 1990s, what had been a diverse multispecies fishery rested on only three species: the nonindigenous Nile perch, the nonindigenous Nile tilapia *Oreochromis niloticus*, and the diminutive *R. argentea*. Although some of the blame for the cichlid extinction spasm has been shifted from the Nile perch to other anthropogenic factors, such as overfishing and eutrophication (Seehausen et al. 1997), the Nile perch was certainly a major contributor.

The lucrative fishery that developed for Nile perch has itself had diverse impacts. Around the lakeshore, enthusiasm over the increase in the value of the fishery has been tempered by concerns about species loss, increased economic stratification, and the fact that most Nile perch is exported and locally unaffordable (Pringle 2005). Ecologically, the intense fishing pressure on Nile perch has depressed its populations to the extent that certain species of the remnant cichlid fauna are resurging (Witte et al. 2000).

These events have spawned hundreds of publications, making the Nile perch in Lake Victoria one of the best-

studied invasive species in history (for a recent review, see Balirwa et al. 2003). Yet despite this wealth of knowledge, there remains confusion about exactly when, why, and by whom the Nile perch was introduced into Lake Victoria. The literature offers a range of dates for the introduction, from the 1920s to the 1960s; tracing the tortuous citation chain to the origins of these dates reveals a fundamental uncertainty about when the Nile perch was first introduced. Likewise, the motivations for this anthropogenic introduction, often ambiguously ascribed to a desire to "increase productivity," have not been thoroughly explored.

Unlike many introductions, which occur by accident or are made quietly by private citizens, the introduction of Nile perch into Lake Victoria was hotly debated at the highest levels of the British administration in colonial East Africa. As today's ecologists often note, colonial ecologists opposed the proposal (Fryer 1960). The eventual introduction of the Nile perch therefore represents the failure of ecologists to communicate and implement their vision for Lake Victoria. Although this failure was at least partially due to the familiar problem of trying to regulate a common resource, I suggest that there were two additional factors at play.

Robert M. Pringle (e-mail: pringle@stanford.edu) was a Thouron Fellow in the program in Economic and Social History at the University of Oxford when this research was conducted; he is now a doctoral student in the Department of Biological Sciences at Stanford University, Stanford, CA 94305. Although his current focus is tropical ecology (especially of African savannas), he maintains an active interest in history and its applications to ecology and environmental policy. © 2005 American Institute of Biological Sciences.

The first of these factors stems from the nature of British colonialism in East Africa and the role of science within it. The colonial enterprise underwent a transformation in the late 1930s. The Great Depression had highlighted human vulnerability and prompted new concern for the welfare of Britain's "dependents" in the colonies. Likewise, confrontation with Nazi Germany had made clear, among other things, the true ugliness of imperialism. Hence the shift to what historians have called "the second colonial occupation" (Low and Lonsdale 1976): the paternalistic attempt to guide Africa through development and into modernity, in which eventual self-government was a stated aim. But administrators in this new developmental bureaucracy lacked the patience of their predecessors for basic ecological research. They wanted immediate results, practical scientific means of running an efficient transitional empire. The scientists who opposed the introduction of the Nile perch into Lake Victoria failed to engage effectively with these emergent political trends; as a result, they were considered too cautious and their research too pure. They were thus kept to the political margins, where they found it difficult to influence policy.

The second factor relates to the history of ecology and evolutionary biology as disciplines. The late 1950s and 1960s were a particularly fertile time for ecological and evolutionary ideas; several conceptual developments of that period would arguably have enabled fisheries scientists in East Africa to make a more forceful case against the Nile perch introduction, had the debate taken place a few years later than it actually did.

Whether or not it was "right" to introduce the Nile perch into Lake Victoria is a contentious and subjective question (Pringle 2005). I do not wish to take a stand on that issue here. Neither am I interested in apportioning blame—or credit—for the Nile perch's introduction, the haplochromine extinctions, or the economic growth of Lake Victoria's fisheries. My only intention is to shed light on the social, economic, scientific, and political processes that led to these important events. Thus, although I speak of the "failure" of scientists to prevent the introduction, I do not mean it in a pejorative sense. It was simply the failure of a stated objective.

The origins of fishery research and management, 1921–1950

To the British in East Africa, Lake Victoria's 70,000 square kilometers (km²) seemed capable of supporting outstanding fisheries. The 1901 completion of the railroad from Mombasa to Kisumu, which enabled the transport of lake fish to Nairobi marketplaces, provided an added incentive to maximize fishery production. Yet by 1921 there was concern that fish yields, especially of *ngege* (*Oreochromis esculentus*), were declining. One observer, assistant surgeon E. J. H. Oorloff, complained that Africans were overfishing the lake with the aid of imported equipment—"the better class of natives use English nets"—and recommended that a closed season be implemented (Oorloff 1921). However, administrators were hesitant to regulate fishing, principally because their ignorance of fish

biology left them unsure whether "any good results would accrue from putting fishermen to the hardship of a general close season" (Caldwell 1923); it was suggested that museum experts be recruited to survey "the finny denizens of our premier pool" (Anonymous 1923).

To that end, Michael Graham and Edgar Barton Worthington traveled from Britain in 1927 and spent a year steaming around Lake Victoria. Their work resulted in Graham's (1929) *The Victoria Nyanza and Its Fisheries*. In that book, Graham recommended that a permanent fisheries research institute be erected to continue scientific study of the lake. This led to the construction in 1947 of a research laboratory in Jinja, Uganda, which became home to the East African Fisheries Research Organization (EAFRO). Crucially, however, an earlier warning by Worthington—that "it would be a mistake to separate administration from research in the matter of fisheries" (Worthington 1940)—was ignored. "I suppose difficulties are bound to go on," Worthington had written, "so long as fisheries in Uganda are directly under the Game Department, while in Kenya they are ? [sic] Agriculture, and in Tanganyika are directly under the Administration" (Worthington 1940). Ultimately, however, research and administration were indeed separated; the Lake Victoria Fisheries Service was created as an interterritorial administrative body distinct from EAFRO in 1948.

In 1950, the East African High Commission implemented the Lake Victoria Fisheries Act. The act initiated several conservation measures, one of which was the stricture that "any person who introduces, puts or places into Lake Victoria any fish, or the spawn thereof, of a species other than that in Lake Victoria...shall be guilty of an offense against this Act." Significantly, EAFRO and Lake Victoria Fisheries Service personnel were exempt from these provisions. And although a 1953 amendment to the 1950 act extended its legislative reach one mile up "each river and stream entering Lake Victoria," the rest of East Africa's inland water remained under territorial control.

These provisions reflected a growing debate over whether fishery productivity might be increased by introducing non-indigenous species into Lake Victoria. Colonial officials were frustrated that Africa's largest lake contained relatively small fish, mostly cichlids of the genus *Haplochromis*. Haplochromine cichlids were widely utilized by local fishermen, but the British disdained them, labeling them "trash fish." In *The Victoria Nyanza and Its Fisheries*, Graham (1929) wrote, "It has been suggested to me frequently that Lake Victoria would be improved if its fish fauna contained some of the Lake Albert species, such as the Nile perch (*Lates*) or the Tiger fish (*Hydrocyon*)" (p. 23). Graham conceded that this was a reasonable idea, but he urged caution: "In the *ngege* fishery of Lake Victoria we have an extremely valuable established fishery for a very desirable fish. The introduction of a large predatory species from another area would be attended with the utmost danger, unless preceded by extensive research into the probable effects of the operation" (Graham 1929, p. 23).

Of course, the introduction of nonindigenous fish was a common practice in colonial East Africa. Beginning in the 1890s, colonial administrators stocked dozens of Kenya's rivers with trout, both to entertain themselves and to entice prospective settlers. Later, in an attempt to stem tilapia declines, EAFRO blessed the introduction of four nonindigenous tilapiines (*Oreochromis leucostictus*, *O. niloticus*, *Tilapia rendalli*, and *Tilapia zillii*) in 1953. Although legal under the 1950 Fisheries Act's exemption of fisheries officials, these tilapia introductions were controversial. The British Museum's Ethelwynn Trewavas, who saw her opportunity to map Africa's ichthyogeography slipping away, had complained that people were moving tilapia around the continent "in a slap-happy fashion" (Trewavas 1952). Much later, one-time EAFRO director Peter Jackson lamented the introductions as "woolly-headed" and "useless" (Jackson 2000). At the time, however, the move was rationalized by EAFRO's "seemingly paradoxical conclusion that under tropical conditions the more animals, particularly herbivorous animals, living in a lake, the more animals that lake can support" (EAFRO 1953).

However, the introduction of a large predatory fish was viewed with considerably more skepticism by fishery biologists. Because of the possibility that the Nile perch might ruin Lake Victoria's important tilapia fishery, Worthington (1929) echoed Graham's caution, urging that "the *recommendation made by Mr. Graham that no such project be put in hand must be endorsed here* [italics in original] until extensive research has been carried out into the effects of the introduction." He later suggested an experimental introduction into nearby Lake Nabugabo and concluded that "if the introduction is effected and a natural balance is struck between the Nile Perch and the Lake Nabugabo fishes, the introduction of the Nile Perch into Lake Victoria may be considered" (Worthington 1932).

The cautious stance of Graham and Worthington found support in other quarters. Kenya fish warden Hugh Copley (1940) wrote that

the question of a predatory fish in Lake Victoria is an inter-territorial matter and any introduction should take place only after a most exhaustive and searching investigation. It has always been a worry to myself having [American] Black Bass in Lake Naivasha, for it is always possible some irresponsible person will take this fish and stock a dam having an outflow (possibly during the season of heavy rains) to some stream with an ultimate access to Lake Victoria, and thereby introducing a predatory fish whether it was advisable or not.

This memo captures the essence of the management dilemma that took shape in the years following World War II. First, the lake was shared by three territories, and different aspects of its administration fell to different organizations, all of which were disjunct from fisheries research. Second, trying to regulate the species composition of a lake the size of Victoria in an era obsessed with bolstering production was a

monumental job. It implied both monitoring the numerous rivers and swamps that abutted the lake and policing a 3500-km shoreline to prevent any unilateral introductions.

Fisheries management in a developmental empire: 1948–1963

The consecutive ravages of depression and war brought food supply to the fore of the colonial mind. EAFRO, which owed its existence to the beneficence of the High Commission and the Colonial Office, was often pressed to aid in the undertaking. In 1948, EAFRO director Robert Beauchamp received an inquiry from the East African Industrial Research Board in Nairobi about the prospects for an industry, based on the lake, to "make fishmeal to supplement the animal protein ration which is deficient to the [tune] of some 1,000 tons per annum" (EAIRB 1948). Beauchamp's lukewarm response prompted chastisement from an official at the Colonial Development Corporation in London, who urged that "if we keep bashing at these problems, I think we will find some field for commercial development!" (CDC 1949). In one extreme attempt to boost production, London-based colonial fisheries adviser C. F. Hickling (1953) recommended that the fishery be totally deregulated: "It is possible to exterminate stocks of game, hence the need for game sanctuaries; but it is in fact impossible to exterminate stocks of fish except in a few special cases.... It would seem a wise principle to assume that a fishery is in a sound condition, requiring no regulation, unless the contrary can be proven."

EAFRO's reluctance to throw its weight behind such "practical" measures, and the tendency of its scientists to work on problems that had no immediate economic application, was almost its undoing. In 1954, Worthington received a letter from the High Commission. "Sir," it began, "I have the honour to address you on the question whether or not there still exists an economic need for fisheries research in the East African territories" (EAHC 1954). Copley (1954), frustrated at the political naïveté of the EAFRO scientists, begged Worthington to give him something with which he could justify further research to his superiors:

Literally I stand between the Kenya Government withdrawing its support from Jinja, and Jinja, if you understand me. The Kenya Government would withdraw their support tomorrow morning with the greatest of pleasure.... Tanganyika would do so the next day. What one is fighting for is to get all these Governments to believe that...a lot of the work has practical application NOW; if we cannot, then good-bye to Jinja.

As far as the scientists were concerned, their various investigations needed no special justification. Administrators, however, expected scientists in the colonies to be responsive to political and economic imperatives. In one revealing episode, Colonel S. P. Fearon of the High Commission dispatched a directive to EAFRO director Beauchamp: "You will undertake a fishing survey of the deeper waters of the Lake,"

it instructed, and “you will exercise the strictest economy” (Fearon 1955). This wording was so dictatorial that even the Colonial Office blanched, but Fearon would not budge:

We are merely trying to lay down what the Council expects Beauchamp to do, both for his benefit and the Council's.... Today the successful scientist is a man commanding a handsome salary with a host of lesser scientists beneath him and a large, expensive and complicated organization to manage.... The scientist of today, in fact, cannot expect to have his cake and eat it. He must either accept the restrictions which the expenditure of public money entails, or he must be content to remain a scientist pure and simple. (Fearon 1955)

Thus, EAFRO scientists were not in a particularly strong position to influence policy when the idea of introducing Nile perch was revisited in the 1950s. Despite considerable effort, the British had not been able to discover a commercial value for the “trash” haplochromines. Graham (1929) had suggested that they might be made into fertilizer; others posited that their function was simply to die, thereby enhancing the fertility of the lake (Greenwood 1966). Still others suggested that they were vermin, in that some preyed on economically valuable tilapia fry, and should therefore be exterminated (Provincial Commissioner, Nyanza 1939).

The impetus for the revival of the Nile perch introduction proposal was the Uganda Game and Fisheries Department (UGFD), which brought together two men who advocated the idea for different reasons. Bruce Kinloch, chief game warden from 1950 to 1960, was a devoted big-game hunter and sport fisherman, and he worked hard to expand the range of the Nile perch, a “fine sporting and very edible fish” (UGFD 1951, Kinloch 1972). Kinloch's chief fisheries officer Don Rhodes believed, according to a contemporary, “that anything whatsoever was justified if it could conceivably advance the weal of the common man” (Jackson 2000). Yet UGFD was hamstrung by “certain influential and conservative-minded quarters” at EAFRO, which opposed any Nile perch introductions (Kinloch 1972).

However, when the Owen Falls Dam was constructed in 1954, putatively sealing off Lake Victoria from the Nile, UGFD came into sole regional jurisdiction over the upper Nile and the attached Lake Kyoga. Within the year, UGFD officials and local African fish guards had transferred a handful of Nile perch from the base to the top of Murchison Falls (which separates Lake Albert from the upper Nile). In 1955, UGFD officer John Stoneman led a “proper” stocking expedition, transferring 47 Nile perch from Butiaba on Lake Albert to the Victoria Nile below the dam, and 100 more to Lake Kyoga at Masindi Port (Kinloch 1972).

After these steps had already been taken, the debate over whether to stock Lake Victoria grew louder, with the lines drawn between EAFRO and UGFD. At a 1955 meeting, Kinloch requested consideration of the issue, arguing that although the Nile perch would probably affect “various species

of fish which were of little or no commercial value,” it would have minimal impact on tilapia (EAIFAC 1955). Opposition from EAFRO hinged on the argument that the outcome of the “experiment” with Nile perch in Lake Kyoga should be known before an introduction into Lake Victoria could be considered.

Adopting a different tack, UGFD employees seized on a paleontological study showing that a congener of the Nile perch (*Lates* sp.) had occurred, and gone extinct, in the Lake Victoria region during the Miocene (Greenwood 1951). Thus, UGFD officials began calling for the reintroduction of the Nile perch, while also alluding to “vague reports” that Nile perch had already been seen in Lake Victoria near Port Bell (EAIFAC 1957). In face of stubborn resistance from EAFRO, UGFD officer Alec Anderson agreed to a hiatus on stocking operations within Uganda, although he grumbled that he would “prefer to see some such device as an electrical fence installed rather than that there should be a complete prohibition on stocking” (EAIFAC 1957). Anderson also engaged in a debate in the *East African Agricultural Journal* with EAFRO scientist Geoffrey Fryer. Fryer (1960) appealed to the “common-sense” principle of trophic inefficiency (Lindeman 1942) and argued that to assume Nile perch would feed only on *Haplochromis* species to the exclusion of tilapia was “wishful thinking.” Anderson (1961) countered that Nile perch certainly *would* feed on “*les indésirables Haplochromis*,” which “is [sic] generally regarded as a [sic] ‘trash fish’ of very little value.”

EAFRO, perhaps recognizing that the Nile perch question would not disappear, had belatedly begun to arrange for a study of Nile perch biology, which they had long stated was a prerequisite for considering the introduction. This work was not begun until 1959 (EAFRO 1960), in part because of budget constraints (themselves due to niggardly funding from the High Commission, which had decided in 1958 to disband the Lake Victoria Fisheries Service and distribute its duties to the three territories). And almost before the work could get under way, Nile perch began turning up in Lake Victoria. The 1960 EAFRO annual report stated that the need for the Nile perch study had become all the more urgent, “since during the year it became apparent that Nile perch had already gained access to the lake by some means” (EAFRO 1960). In October of 1961, a Nile perch caught near Mwanza, Tanganyika, was brought to fisheries officials there by an engineer who, having worked for years on Lake Albert, was familiar with the fish (Mwanza Fisheries Officer 1961).

These discoveries transformed the debate, and nobody objected when Don Rhodes said in 1962 that “in view of the evidence that Nile perch were already breeding in Lake Victoria and spreading rapidly, [I] would therefore like to stock more fish immediately as these become available at Port Bell, Kaazi, and Entebbe to satisfy the long-standing demands of important sporting and commercial efforts in these areas” (UFD 1962). Thereafter, the anthropogenic dispersal of Nile perch did indeed spread rapidly (figure 1). Thirty-five were introduced into Lake Victoria at Entebbe Harbor in May 1962; by November 1963, that total had reached 339. In 1963, Nile perch were stocked “in the Kagera River, Lake Salisbury,

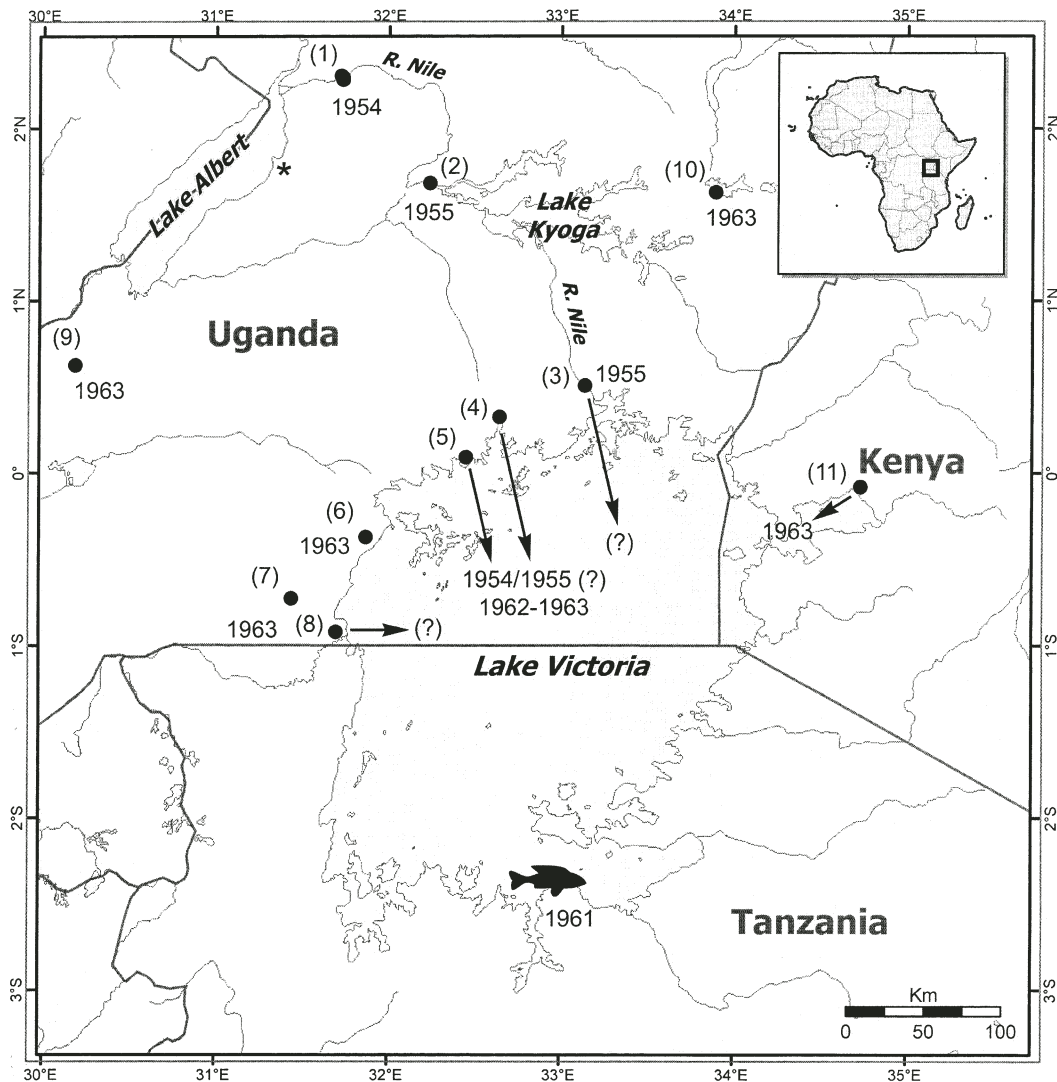


Figure 1. Map of the Lake Victoria region, showing the range expansion of the Nile perch in East Africa during the 1950s and 1960s. Dots show locations and years of deliberate introductions: (1) Murchison Falls; (2) Masindi Port; (3) the upper Nile below the Owen Falls Dam; (4) Port Bell; (5) Entebbe Pier; (6) Lake Nabugabo; (7) Lake Kijanebalola; (8) the Kagera River; (9) Lake Saka; (10) Lake Salisbury; (11) Kisumu. Arrows indicate entry of Nile perch into Lake Victoria; question marks indicate uncertainty. The asterisk shows the point of origin of Nile perch introduced into the Ugandan waters of Lake Victoria, at Butiaba on Lake Albert; the Nile perch introduced at Kisumu in 1963 came from Lake Turkana in northern Kenya (not shown). The fish icon represents the point of furthest advance, near Mwanza, Tanganyika, by 1961.

Lake Saka, Lake Nabugabo, Lake Kijanebalola, and various dams” (UFD 1962/1963). Fishery officials in Kenya introduced eight more Nile perch (from Lake Turkana) at Kisumu in 1963.

It remains impossible to say with absolute certainty that somebody within UGFD introduced Nile perch directly into Lake Victoria before 1960. However, the available evidence points strongly in that direction (although both Kinloch and Rhodes denied having done so personally in interviews with the author). Kinloch’s 1972 memoir and numerous official documents from the time certainly evince a steadfast resolve to spread Nile perch and a disdain for those who opposed the idea, as does a report by American economist James A. Crutch-

field (1959), who worked closely with UGFD during his tenure as a Fulbright fellow.

Most compelling, however, is the testimony of two Africans who worked for UGFD in the 1950s. On 25 February 1978—shortly before the Nile perch boom—John Ofulla Amaras published the following in a letter to the *East African Standard*: “Please take note that Nile perch...were stocked in Lake Victoria and Kioga [sic] from Lake Albert in August, 1954...by myself assisted by fish scouts at that time Augustino Kyomya, Benwa Magadu, Peter Karakaba and others—under the directive of the then Senior Fisheries Officer, Mr. Alex [sic] M. Anderson.”

Amaras, a Kenyan, was indeed a UGFD fisheries assistant from 1954 to 1955 (UGFD 1955); in a 2003 interview with the author, he claimed that multiple introductions of Nile perch from Lake Albert had been made into Lake Victoria at Port Bell and Entebbe Pier over several months in 1954 (these are the same locations subsequently proposed by Don Rhodes in 1962). Peter Karakaba, named in Amaras's letter, also stated in a 2003 letter to the author that Nile perch had been introduced directly into Lake Victoria, although he gave the date as 1955. Former UGFD officer John Stoneman, in an interview with the author, remembered Amaras's having been involved in the stocking of Lake Victoria, which would mean that the introduction took place in either 1954 or 1955, as Amaras was dismissed from UGFD in October 1955 (UGFD 1955).

It is unlikely that any existing evidence could conclusively prove whether the initial introduction into Lake Victoria itself was intentional or accidental. UGFD officials have always maintained that Nile perch must have entered the lake through the turbines in the Owen Falls Dam when the dam was shut down for cleaning, a claim that many scientists considered implausible (Jackson 2000). In any case, it made little practical difference whether the Nile perch was introduced directly into the lake or into a river behind a penetrable dam.

Conclusions

Although a number of factors and individuals clearly contributed to the Nile perch's introduction, it is perhaps most interesting historically to ask why EAFRO's research biologists failed in their attempts to prevent it. This is neither a criticism nor an attempt to downplay the considerable importance of EAFRO's basic research during these years—much of it conducted under difficult conditions. It is merely an attempt to learn from history.

It is true that it would have been difficult for EAFRO to prevent determined UGFD officials from transferring Nile perch at least to the source of the Nile. However, it is possible that if they had made a stronger attempt to push their agenda through political channels from the beginning, the interterritorial organizations of research and administration might have been fused, as originally advocated by E. B. Worthington. Such an arrangement would have provided scientists direct control over policy. Alternatively, EAFRO might have been afforded a stronger intraterritorial role, such that moving Nile perch from Lake Albert to Lake Kyoga or the upper Nile would at least have required EAFRO oversight.

A third possibility is that more funding would have been forthcoming if EAFRO had more skillfully manipulated administrative sentiment within the High Commission. As early as Graham's 1929 survey, EAFRO scientists had maintained that "extensive research" was required before Nile perch introductions could be considered. Yet they were slow to undertake such a study, and by the time they did, they found it difficult to obtain funding from an administration convinced that their work was too esoteric. It is tempting to speculate what would have happened if, as Worthington suggested in

1932, an experimental introduction had been made into Lake Nabugabo. What ultimately happened in Lake Nabugabo was similar to what happened in Lake Victoria, with approximately 50 percent of indigenous fishes disappearing from open waters (Chapman et al. 2003). This is hardly the "natural balance" that Worthington (1932) was looking for.

However, it is not clear that even this would have provided EAFRO biologists with a compelling argument against further introductions. Biologists such as the British Museum's Ethelwynn Trewavas and Humphrey Greenwood valued haplochromine cichlids as evolutionary curiosities, but the argument that these cichlids had some intrinsic value was never raised in fishery policy discussions. Instead, biologists such as Fryer (1960) appealed principally to economics, arguing that the Nile perch would devastate valuable established fisheries. This turns out not to have been the case—indeed, the Nile perch vastly increased the economic value of every lake where it was introduced. To modern biologists, who generally believe that biological diversity is a good in itself, the term "trash fish" sounds odd, even offensive. But modern ecology's preoccupation with diversity and its benefits only really began in the late 1950s (e.g., Hutchinson 1959). While EAFRO biologists clearly believed that species were interesting things to study, they would have found it hard to articulate policy arguments based on the value of biodiversity. Simply, no such "value" had yet been attributed to biodiversity.

Similarly, the study of biological invasions was in its infancy in the 1950s (Elton 1958) and later drew heavily on the observations that predator–prey, parasite–host, and mutualist–mutualist relationships are coevolved (Ehrlich and Raven 1964), and that invasive species can exploit or disrupt those relationships. Whereas Fryer (1960) and others at EAFRO clearly recognized that the introduction of a nonindigenous apex predator could endanger fisheries, their arguments could have been much stronger in, say, 1970 than they could possibly have been in the period 1954–1960.

It might be argued that no amount of cogent scientific reasoning would have made a difference—that government agencies like UGFD tend to introduce nonindigenous species regardless of scientific concerns, and that such introductions, once proposed, are so difficult to prevent as to be almost inevitable. However, the history of the Nile perch in Lake Victoria also offers an instructive example of applied science being used to forestall such an introduction. In the late 1980s, it was proposed to introduce the Nile perch into still-water bodies of tropical Queensland, Australia. After a detailed study of the thermal tolerances of Nile perch, and careful scrutiny of the consequences of the introductions in Lakes Victoria and Kyoga, it was concluded that the introduction "would be potentially disastrous for Australian aquatic fauna.... Consequently, the agency responsible for the evaluation program has abandoned the concept of introducing the Nile perch to Australia" (Barlow and Lisle 1987). The Nile perch remains classified as a noxious species in Queensland.

It is also possible that the secretive introduction of a handful of fish would have been inadequate to establish the Nile

perch in Lake Victoria, and that the legally sanctioned mass introductions after 1960 were crucial to its subsequent success. A growing literature suggests that multiple introductions can increase the genetic diversity of invading populations and lessen the probability of stochastic extinction (Kolbe et al. 2004).

Incipient conflicts between biodiversity and economic or infrastructural development persist today in various manifestations: new roads, new dams, new species introductions. Thus, ecologists and evolutionary biologists might profitably take several lessons from this story. The first is that there is an important role for scientists who are willing to grapple with policy, and with politics. While science itself should obviously be apolitical, the systems that scientists study (and the economic, legal, and social matrix in which they must operate) are politically contested arenas. Thus, scientists who desire the persistence of the systems they study (and the unfettered ability to study them) are justified in being advocates in matters on which their science can be brought to bear. Taking this reasoning one step further, it is not unreasonable for scientists to consider how they might position themselves to exert political influence if and when it becomes necessary.

By the same token, this story highlights the importance of both applied and basic research: a thorough and persuasive argument against the introduction of the Nile perch would have required both empirical data on the probable effects of the introduction and a cogent theoretical framework to express generally why the introduction of nonindigenous species can be ecologically disastrous.

Acknowledgments

I am deeply indebted to those who discussed these events with me: John Amaras, Peter Karakaba, Bruce Kinloch, Rosemary Lowe-McConnell, Don Rhodes, John Stoneman, and Robin Welcomme. John Balirwa and the staffs of Rhodes House Library, the Public Record Office, and the Kenya National Archives kindly helped me locate archival material. Financial support was provided by the Thouron family and by St. John's College, Oxford. Finally, I am grateful to Dave Anderson, William Beinart, Kai Chan, Paul Ehrlich, John Fay, and Jessica Shors for advice and help with the manuscript.

References cited

Anderson AM. 1961. Further observations concerning the proposed introduction of Nile perch into Lake Victoria. *East African Agricultural and Forestry Journal* 26: 195–201.

Anonymous. 1923. Letter to Kenya game warden, 9 December 1923. Nairobi: Kenya National Archives File KP/4/7/18.

Balirwa JS, et al. 2003. Biodiversity and fishery sustainability in the Lake Victoria Basin: An unexpected marriage? *BioScience* 53: 703–715.

Barlow CG, Lisle A. 1987. Biology of the Nile perch *Lates niloticus* (Pisces: Centropomidae) with reference to its proposed role as a sport fish in Australia. *Biological Conservation* 39: 269–289.

Caldwell K. 1923. Letter to Colonial Secretary, Nairobi, 3 December 1923. Nairobi: Kenya National Archives File KP/4/7/17.

[CDC] Colonial Development Corporation. 1949. Letter to EAFRO director, 6 December 1949. Jinja (Uganda): Fisheries Resources Research Institute File FSH/1.

Chapman LJ, Chapman CA, Schofield PJ, Olowo JP, Kaufman L, Seehausen O, Ogutu-Ohwayo R. 2003. Fish faunal resurgence in Lake Nabugabo, East Africa. *Conservation Biology* 17: 500–511.

Copley H. 1940. Letter to Kenya game warden, 10 May 1940. Nairobi: Kenya National Archives File KP/6/7/100.

———. 1954. Letter to E. B. Worthington, 26 May 1954. Oxford (United Kingdom): Edgar Barton Worthington Papers File 3/10/5, Rhodes House Library.

Crutchfield JA. 1959. Report to the Government of Uganda on Fish Marketing in Uganda. Rome: Food and Agriculture Organization of the United Nations.

[EAFRO] East Africa Fisheries Research Organization. 1953. Report on Fisheries Research. Nairobi: Kenya National Archives File VF/5/9/2/5.

———. 1960. Annual Report. Kampala (Uganda): Uganda Argus.

[EAHC] East Africa High Commission. 1954. Letter to E. B. Worthington, 27 March 1954. Oxford (United Kingdom): Edgar Barton Worthington Papers File 3/10/69, Rhodes House Library.

[EAFAC] East Africa Inland Fisheries Advisory Committee. 1955. Meeting minutes, 22 August 1955. Nairobi: Kenya National Archives File KL/24/31/1/1.

———. 1957. Meeting minutes, 7 July 1957. Nairobi: Kenya National Archives File KL/24/31/25.

[EAIRB] East Africa Industrial Research Board. 1948. Letter to EAFRO director, 19 March 1948. Jinja (Uganda): Fisheries Resources Research Institute File Res/E.15/22.

Ehrlich PR, Raven PH. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18: 586–608.

Elton CS. 1958. *The Ecology of Invasions by Plants and Animals*. London: Methuen.

Fearon SP. 1955. Letters to EAFRO director (4 November 1955) and London Colonial Office (2 December 1955). Kew (United Kingdom): Public Record Office File CO/927/562.

Fryer G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. *East African Agricultural Journal* 25: 267–270.

Graham M. 1929. *The Victoria Nyanza and Its Fisheries: A Report on the Fishing Survey of Lake Victoria, 1927–1928, and Appendices*. London: Crown Agents for the Colonies.

Greenwood PH. 1951. Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Annals and Magazine of Natural History* 4: 1192–1201.

———. 1966. *The Fishes of Uganda*. Kampala (Uganda): Uganda Society.

Hickling CF. 1953. Memorandum on fisheries legislation. Oxford (United Kingdom): Edgar Barton Worthington Papers File 3/10, Rhodes House Library.

Hutchinson GE. 1959. Homage to Santa Rosalia; or, why are there so many kinds of animals? *American Naturalist* 93: 145–159.

Jackson PBN. 2000. Freshwater fishery research organizations in central and eastern Africa. *Transactions of the Royal Society of South Africa* 55: 1–81.

Kinloch B. 1972. *The Shamba Raiders*. London: Collins and Harvill.

Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, Losos JB. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431: 177–181.

Lindeman R. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399–418.

Low DA, Lonsdale JM. 1976. Introduction: Towards the new order, 1945–1963. Pages 1–63 in Low DA, Smith A, eds. *The Oxford History of East Africa*. Oxford (United Kingdom): Clarendon Press.

Mwanza Fisheries Officer. 1961. Letter to EAFRO director. Jinja (Uganda): Fisheries Resources Research Institute File RS/7/57.

Ogutu-Ohwayo R. 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.

- Oorloff EJH. 1921. Letter to Nyanza senior commissioner, 5 September 1921. Nairobi: Kenya National Archives File KP/4/7/1.
- Pringle RM. 2005. The Nile perch in Lake Victoria: Local responses and adaptations. *Africa* 75. Forthcoming.
- Provincial Commissioner, Nyanza. 1939. Letter to East Africa High Commission, 28 December 1939. Nairobi: Kenya National Archives File KP/6/7/87.
- Reynolds JE, Greboval DF, Mannini P. 1995. Thirty years on: The development of the Nile perch fishery in Lake Victoria. Pages 181–214 in Pitcher TJ, Hart PJB, eds. *The Impact of Species Changes in African Lakes*. London: Chapman and Hall.
- Seehausen O, van Alphen JJM, Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808–1811.
- Trewavas E. 1952. Letter to E. B. Worthington, 21 March 1952. Oxford (United Kingdom): Rhodes House Library. Edgar Barton Worthington Papers File 3/8/19.
- [UFD] Uganda Fisheries Department. 1962. Meeting minutes, 24 April 1962. Jinja (Uganda): Fisheries Resources Research Institute File RS/7/82.
- . 1962/1963. Annual Report. Kampala (Uganda): Makerere University Library Africana Collection.
- [UGFD] Uganda Game and Fisheries Department. 1951. Annual Report. Kampala (Uganda): Makerere University Library Africana Collection.
- . 1955. Annual Report. Kampala (Uganda): Makerere University Library Africana Collection.
- Wanink JH. 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. *Hydrobiologia* 407: 183–189.
- Witte F, Maku BS, Wanink JH, Seehausen O, Katunzi EFB, Goudswaard PC, Goldschmidt T. 2000. Recovery of cichlid species in Lake Victoria: An examination of factors leading to differential extinction. *Reviews in Fish Biology and Fisheries* 10: 233–241.
- Worthington EB. 1929. A Report on the Fishing Survey of Lakes Albert and Kyoga, March to July, 1928. London: Crown Agents for the Colonies.
- . 1932. A Report on the Fisheries of Uganda: Investigated by the Cambridge Expedition to the East African Lakes, 1930–31. London: Crown Agents for the Colonies.
- . 1940. Letter to Kenya game warden, 22 April 1940. Nairobi: Kenya National Archives File KP/6/7/100.