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# THE NILE PERCH IN LAKE VICTORIA: LOCAL RESPONSES AND ADAPTATIONS

*Robert M. Pringle*

In 1962, offshore of Lwanika, a fishing village forty kilometres south-east of Jinja, Uganda, fisherman Lawrence Makhoha hauled a surprise into his canoe. It was a fish that he had never encountered in twenty years on the lake. He was surprised, then curious. What was this fish, and where had it come from? Was it dangerous, or was it safe to eat?[1] The fish was *mputa*, Nile perch (*mbuta* to Luos; Table 1), and Makhoha's experience was to be replayed hundreds of times around the shores of Lake Victoria.

TABLE 1 *Fish names: Latin, English, Dholuo and Luganda*

| *TAXONOMY* | *ENGLISH* | *DHOLUO* | *LUGANDA* |
|---|---|---|---|
| *Alestes* | – | Osoga | Nsoga |
| *Bagrus* | Catfish | Seu | Semutundu |
| *Barbus* | Barbel | Fwani | Kisinja |
| *Haplochromis/Neochromis* | Cichlid | Fulu | Nkejje |
| *Labeo* | – | Ningu | Ningu |
| *Lates* | Nile perch | Mbuta | Mputa |
| *Mormyrus* | Elephant-snout fish | Suma | Kasulubana |
| *Rastrineobola* | Minnow | Omena | Mukene |
| *Synodontis* | Squeaker | Okoko | Nkolongo |
| *Tilapia/Oreochromis* | Tilapia spp. | Ngege, Mbiru | Ngege, Mbiru |

The Nile perch is a large (up to two metres), piscivorous fish native to the River Nile and to Lakes Albert in Uganda and Turkana in Kenya. During the 1950s and early 1960s, hundreds of these fish were introduced into Lake Victoria and its adjoining rivers and lakes. This was part of a bifurcated effort by colonial fisheries officials in Uganda to widen the range of a 'fine sporting and very edible fish' and to bolster the economic productivity of Lake Victoria's fisheries, which had until then rested on two species of native tilapia (UGFD 1952: 66; Anderson 1961).

In what some British colonials had considered a bothersome irony, Africa's largest lake contained some of Africa's smallest fish, many of them cichlid species of the genus *Haplochromis*. Colonial fisheries managers could not find an economic use for what came to be called 'trash fish', and they saw the introduction of the Nile perch, which they

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[1] Interview with Lawrence Makhoha, age 81. Lwanika Landing, Uganda, 10 July 2003.

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hoped would feed on these small species and convert them into something more palatable, as the solution to the problem (Kinloch 1972). However, research scientists at Jinja's East African Fisheries Research Organization (EAFRO) objected to the proposed introduction, arguing conservatively that the introduction of a large predator into an ecosystem that had evolved in its absence would have unpredictable and potentially untoward effects upon the established tilapia fishery (Fryer 1960).

In 1960, eight Nile perch of mysterious origin were caught in Lake Victoria and brought in to EAFRO by Ugandan fishermen (EAFRO 1960). In the light of UGFD's long-standing advocacy of the introduction, EAFRO scientists charged that UGFD had unilaterally and illegally introduced Nile perch into the lake (Jackson 2000), an accusation bolstered in 1978 when former UGFD fish guard John Ofulla Amaras wrote the following in a letter to the editor of the *East African Standard*:

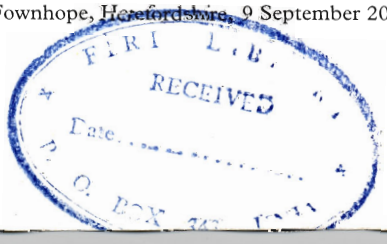
> Please take note that Nile perch ... were stocked in Lake Victoria and Kioga from Lake Albert in August, 1954 ... by myself assisted by fish scouts at that time Augustino Kyomya, Benwa Magadu, Peter Karakaba and others – under the directive of the then Senior Fisheries Officer, Mr Alex M. Anderson.[2]

1954 has therefore become the date most often cited by academics writing on the Nile perch introduction (Reynolds et al. 1995; Goldschmidt 1996). However, UGFD officials have always maintained that the introduction was unintentional and that Nile perch must have entered the lake via the turbines of the Owen Falls Dam at the source of the Nile, where the fish was legally and officially introduced in 1955.[3] In any case, the discovery that Nile perch were established and breeding in the lake diminished opposition to further stocking, and official introductions were made in 1962 at Port Bell and Entebbe Harbour and in 1963 at Kisumu (EAFRO 1963; for further detail, see Pringle 2005).

For about twenty years after the introductions, the plan seemed to have flopped. The Nile perch established itself in Lake Victoria, but at very low densities, and it was infrequently caught. Then, in the mid-1970s, for reasons that biologists do not fully understand, Nile perch populations suddenly spiked. The total annual catch of fish from Lake Victoria rose from a fairly steady 100,000 tons per year in the early 1970s to about 500,000 tons in 1989, which translated to an increase in landing

[2] *East African Standard*, 25 February 1978. Former EAFRO biologist Robin Welcomme (interview, Stoke-by-Clare, Suffolk, 5 September 2003) also asserted that UGFD had purposely introduced the Nile perch into Lake Victoria. Likewise, the author's personal correspondence with former fish guard Peter Karakaba, cited in Amaras's letter as having been involved in the introduction, corroborated the allegation that UGFD had placed the Nile perch directly into Lake Victoria, although Karakaba stated that the date of the introduction was 1955 rather than 1954.

[3] Uganda Fisheries Department Meeting Minutes, 24 April 1962. Fisheries Research Institute Archives, Jinja, Uganda, File RS/7/82; interview with Bruce Kinloch, former Chief Game Warden of Uganda. Fownhope, Herefordshire, 9 September 2003.



value from around 17 to more than 80 million 1989 $ (Reynolds et al. 1995: 199). This population explosion, termed the 'Nile perch boom', had a transformative effect on the regional economies of southern Uganda, western Kenya and northern Tanzania. As elsewhere in Africa (e.g. Sarch 2001), the fishing economy around Lake Victoria has long been complemented by land-based agricultural and pastoral enterprises (Geheb and Binns 1997); and, in the pre-colonial artisanal fishery, fish were a pillar of a barter-based system of exchange (Geheb 1995). The colonial period – and in particular the completion of the Mombasa-to-Kisumu railway – sowed the seeds of a cash-based economy with the attendant need to produce marketable surplus. However, it was the Nile perch that laid the foundation for what has become, since the 1970s, a globally significant fishing industry. Lake Victoria's native fish had been small and bony, unsuitable for export. In contrast, the Nile perch was large and fleshy and could be filleted. Processing facilities sprang up around the lakeshore, and fillets were exported to Israel and Europe in return for valuable foreign exchange. This rapid integration with the global economy has transformed lifestyles, societies and economies around the periphery of the lake.

The Nile perch also precipitated profound ecological changes in Lake Victoria. In the mid-1970s, just as the Nile perch population was exploding, scientists determined that what the British colonials had called 'trash fish' were what biologists call a 'species flock', an evolutionary phenomenon in which numerous species evolve rapidly from a common ancestral species (Greenwood 1974). As Nile perch increased in number, they did what they had been introduced to do: prey voraciously on the haplochromines. In fact, they did this so efficiently that entire species began to disappear before the eyes of frustrated ichthyologists; many species vanished before they could even be formally described (Goldschmidt 1996). Biologists deplored this loss of biodiversity, and the Nile perch in Lake Victoria has been treated as a textbook example – literally – of the disastrous consequences of environmental mismanagement (Primack 1998: 164). While this assessment has been mitigated by the more recent realization that other factors, such as commercial trawl-fishing and the intensification of commercial agriculture on the lakeshore, contributed to the extinction spasm (Seehausen et al. 1997; Verschuren et al. 2002), the Nile perch is still considered to have been a major culprit.

Whereas biologists have generally been of one mind in lamenting the damage to the lacustrine ecosystem, social scientists have come to more varied conclusions: some have celebrated the economic growth that has accompanied the Nile perch's rise to dominance (Reynolds and Greboval 1988; Reynolds et al. 1995), while others have dubbed Lake Victoria a 'casualty of capitalism' (MacDougall 2001), noting the proletarianization of fishermen and the increased concentrations of wealth and productive power that have accrued to processing facilities and middlemen under the Nile perch regime (Harris et al. 1995; Jansen 1997).

The biological aspects of the Nile perch phenomenon have received a great deal of academic attention, as have the fish processing and export sectors. Some contributors have attempted to indicate how fishermen themselves have responded to these wide-ranging ecological and economic changes, but these assessments have often been based either on anecdotal evidence or on inferences from ecological or economic statistics. While such metrics may be useful indicators of local feeling, they tend to represent static temporal cross-sections of opinion and to overlook the dynamism intrinsic to people's responses to major changes. To capture the latter, and thus a more accurate understanding of local responses to the Nile perch introduction and its sequelae, a historical approach is required. This article is an attempt, based on oral and archival sources, to trace the evolution of fishermen's opinions about the Nile perch phenomenon and to analyse the degree to which local perceptions coincide with the assessments of academics.

A brief note is needed on the methods used to gather the oral-historical data on which much of this article is based. The history of the Lake Victoria fisheries from the pre-colonial era to the present, and especially the development therein of local and national regulatory frameworks, has been well documented in previous studies based on archival research and numerous surveys (Geheb 1995, 1997; Geheb and Binns 1997; Gibbon 1997; Geheb and Crean 2003). Likewise, economic and marketing aspects of the fish trade around Lake Victoria have received considerable quantitative and qualitative attention (Reynolds and Greboval 1988; Reynolds et al. 1995; Abila and Jansen 1997; Jansen 1997; Abila 2000). The reader is referred to these works for historical and socio-economic context. My intention here is not to provide a thoroughgoing account of Lake Victoria's multi-faceted fishery, but rather a more narrowly focused narrative account of the evolution of the Nile perch fishery, local attitudes towards biological diversity, and the interface of these two phenomena.

The twin goals of depth and specificity dictated my choice of interview technique. I travelled to six fishing beaches (three in Kenya and three in Uganda; Fig. 1) with translators who were familiar with the areas and their fishing communities. Upon arrival at a beach, we requested an audience with the beach chairman, a locally elected representative in charge of coordinating and administering fishing activity. The first interview was always with this individual; upon completion of the interview, we asked to speak with any additional fishermen with knowledge about the pre-Nile perch fishery and the changes effected by the Nile perch. In one case (Kikondo Landing, Uganda), a group of senior fishermen asked to be interviewed jointly; in all other cases, interviews were conducted with one individual at a time.

The interviews lasted between one and three hours and were tape-recorded with the permission of the interviewees. Interviews were conducted in Dholuo, Luganda, English, or a combination of English and the local language at the discretion of the interviewee. In each interview, I asked a standardized set of questions about the Nile perch fishery and individual and community responses to its development;

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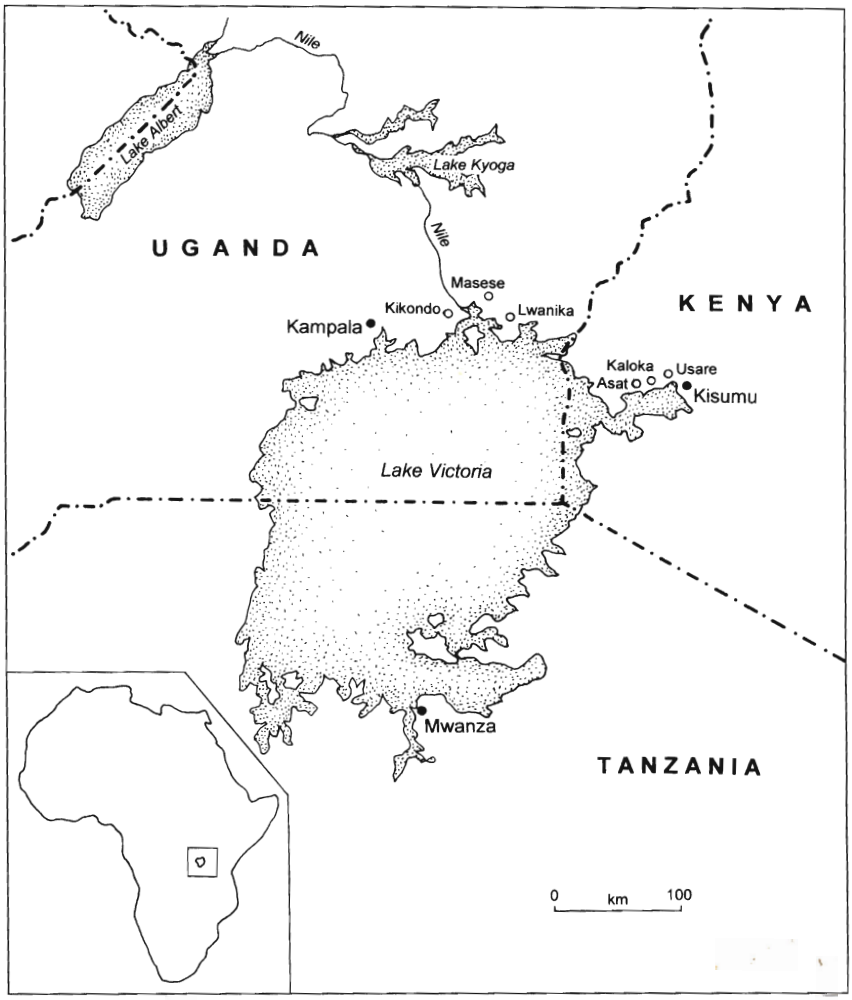



FIGURE 1 Map of the Lake Victoria region, showing sites (*) where interviews were conducted

however, the interviews invariably took on a more conversational form, and interviewees were asked to elaborate on various points of interest (although efforts were made to centre the discussion on the Nile perch). All interviews were subsequently transcribed verbatim by the author with assistance from the translator where necessary. In total, fifteen fishermen and three former fisheries officials were interviewed in this way.

The methodology employed did impose several limitations on my study, notably the brief interview period and the relatively small sample of interviewees. However, two factors justify these limitations. With respect to interview length, there is a trade-off between the amount of information gathered and the degree to which the researcher imposes on

the interviewee: because my interviews were fairly short and directed, a substantial amount of detailed and relevant information could be collected without taking so long as to exhaust the interviewees or keep them from their daily duties. With respect to sample size, there is again a trade-off between statistical power/generality and the amount of detail and nuance that can be woven into a narrative. Because I wanted to evince the qualitative, subjective and emotional responses of fishermen, a smaller number of in-depth interviews was more appropriate than the large number of survey-style interviews or questionnaires that would have been required for quantitative analysis (e.g. Geheb and Crean 2003).

The absence of women among my informants also warrants mention. I discuss only incidentally the differential impacts of the Nile perch fishery on men and women. This by no means implies that gender roles and gender relations are unimportant parts of the Lake Victoria fishery, for quite the reverse is true (Asiimwe 1994). Indeed, the gendered aspects of the fishing economy deserve separate treatment and are a promising avenue for further research; my decision to interview only men (who are exclusively active in fishing) reflects my desire to restrict the scope of this study to the reactions to an introduced fish by those who fished it, and what their perceptions reveal about local attitudes towards lacustrine biodiversity in East Africa.

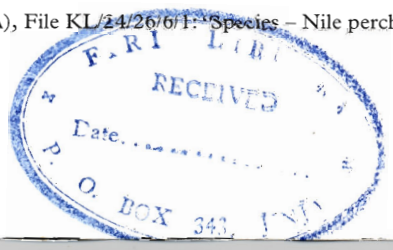
I show that fishermen have overcome an initial aversion to the Nile perch and now greatly appreciate the fish for its economic potential; however, underlying this appreciation is an ambivalence about its overall effect on life in the fishing communities. In particular, I highlight local concerns about biodiversity loss and environmental degradation and situate them in relation to the critical literature on conservation in Africa's terrestrial ecosystems, where conservation efforts have often been considered oppositional to the interests of Africans themselves. I then discuss the consequences of this analysis for the discourse on biodiversity and its conservation in Africa.

## FIRST IMPRESSIONS

In early 1964, EAFRO scientist J. M. Gee cruised around the northern lakeshore to consult with fishermen at various beaches and determine how far and how fast the Nile perch was spreading. He learned that Nile perch had been caught as far west as Entebbe and as far east as Ugowe Bay, Kenya, but that the fish's distribution was spotty, and that fishermen at many of the intervening beaches had neither seen nor heard of it.[4] In fact, the precise year in which different communities first began seeing the fish varied considerably, from the early 1960s to the late 1970s.

With some exceptions, the initial reactions of most fishermen to Nile perch were distaste and apprehension. Their wariness is understandable.

[4] Kenya National Archives (KNA), File KL/24/26/6/1: 'Species – Nile perch'.



Many animals are unsafe to approach, much less to handle or consume. 'That thing was foreign', explained one old fisherman. 'A foreign thing you cannot just start eating.'[5] At first, these fears seemed well founded. As word of the new fish spread around the lake, so did ugly rumours. 'Before I had seen it, the other fishermen who had had the chance to see it . . . didn't talk so well about it', related a fishermen from Kikondo Landing in Uganda. 'They used to say that there's an *mputa* fish and it can cause diseases.'[6] It was alleged that those who ate Nile perch would develop nausea, skin rashes or even leprosy.[7] It was perhaps this scepticism about the Nile perch's quality as food that fuelled early speculation by Kenyans that the fish had been introduced by the British to poison them (Geheb 1997: 59).

That the Nile perch was also suspected of being a man-eater, or at least a child-eater, also retarded its acceptance by lakeshore communities. One respondent, a third-generation Luo fisherman from Uganda's Masese Landing, had been warned by his parents that Nile perch ate children. He therefore always observed Nile perch from a healthy distance, even when they lay dead on the beach.[8] These assertions took on a more grisly tinge when wristwatches found in the bellies of Nile perch caught in Kenya during the 1970s led to the belief that Nile perch were feeding on corpses, victims of Idi Amin's genocide in Uganda (Geheb 1997: 59).

Yet the Nile perch was not universally reviled in these early years. Some fishermen, especially those who began catching the fish relatively late, had either seen it elsewhere during their travels or heard flattering things about it from fishermen who had already adopted the fish into their lives. On Buvuma Island, Uganda, people used to sing a song about the types of food that were available. 'At first they didn't sing about *mputa*. But after some time they began to include *mputa* in the song, as part of the food we had':

> *Enva tulina yingi eza bulingeri, tulina soya beani, tulina kawo, tulina enyama.*
>
> We have many types of sauce: we have soybeans; we have cowpeas; we have meat.
>
> *Tulina enkejje eyo nayo ewoma*
>
> We have *nkejje*, which are also sweet.
>
> *Kyoka mubenyanja, tulina emputa.*
>
> Surprisingly, we have *mputa*.
>
> *Tetunalaba kiwoma kisinga emputa.*
>
> We have never seen anything as sweet as *mputa*.[9]

[5] Interview with Daniel Obonyo Ominda, age 60. Asat Beach, Kenya, 25 July 2003.
[6] Interview with Kasumba Ahamed, age 52. Kikondo Landing, Uganda, 14 July 2003.
[7] Interview with Ntege Bakali, age 68. Kikondo Landing, Uganda, 14 July 2003.
[8] Interview with Haruna Opio, age 30. Masese Landing, Uganda, 11 July 2003.
[9] Interview with Andrea Kakoza, age 91. Masese Landing, Uganda, 11 July 2003.

Ntege Bakali, who was operating out of Masese Landing in 1968, recalled the promotional efforts of government officials who visited the beach: 'They would explain that this fish . . . was very beneficial and its production potential was very high, and that it would be more beneficial to our families as a whole'.[7]

It is also possible that EAFRO's research activities helped to prompt local re-evaluation of the Nile perch. Several informants in Kenya and Uganda noted that they were remunerated for returning tagged Nile perch – the subjects of migration studies – to scientists.[7,8,15] According to Bakali, 'Back then [five shillings] was a lot of money. So the privilege of five shillings, in case somebody caught ten of the tagged fishes, he would have made a lot of money compared to having caught a number of *ngege*.'

It is unclear which process – internal acclamation or external promotion – had the greater impact on communities' perceptions. The fishermen interviewed for this study laid more emphasis on their own internal processes of trial and discovery, but it is also possible that official propaganda worked in subtle, subconscious or indirect ways.

Thus, Nile perch was no longer perceived as a threat, but there was a lingering feeling among many that it was something of a nuisance. For one thing, it stank. Several fishermen noted that the fish's fatty flesh had a strange and offensive smell, which kept potential consumers at arm's length.[6,16] Compounding this problem was the disconcerting tendency of that odour to work its way into the glands of its human predators: those who regularly ate Nile perch found that when they sweated, they smelled like Nile perch. This was not an insuperable problem. Immature Nile perch are less oily than the adults, and they have a milder smell; many villagers began tentatively by eating the smallest individuals in the catch and later, once they were accustomed to the taste, moved on to eating fully grown specimens. This process was also hastened by a change in the fish itself. In the early years, Nile perch had grown particularly blubbery off huge quantities of easily caught food, 'more like pigs than fish' according to EAFRO's 1964 report (EAFRO 1964: 7). When this superabundance of food disappeared, the predator grew leaner and less smelly. A sterner problem than the odour – and it would have been difficult for anyone to predict how dramatically this would soon change – was that there was very little market for Nile perch. EAFRO commonly financed its field surveys in part by selling its by-catch in local markets; however, in the early 1970s, the institute was forced to unload Nile perch very cheaply if it were to unload them at all.[17]

In fact, there was a fairly tight correlation between the growth of a commercial market for Nile perch and fishing communities' burgeoning

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[15] Interview with Morris Opinya Asura, age 68. Usare Beach, Kenya, 25 July 2003.

[16] Interview with Joseph Ogutu, age 62. Usare Beach, Kenya, 25 July 2003.

[17] Interview with Ocen Odong, former EAFRO research officer. Jinja, Uganda, 14 July 2003.

school, and then to pay the tax, and so on'.[18] Daniel Ominda was even more effusive, reeling off the various blessings bestowed by *mbuta* on Asat Beach:

> Before *mbuta*, the kind of life we were leading was very low. We were living in these thatched-roof houses. And nowadays, the majority have permanent structures because of *mbuta* ... [*Mbuta* also] has introduced this issue of weighing machines. [Purchasers] used just to approximate the price of fish – 'This one, I'm giving you forty shillings' – which, of course, is a problem for fishermen ... Again [thanks to] *mbuta*, we as fishermen have now lived in the line of the employed class ... So there is no gap between a fisherman nowadays and the employed class.[5]

*Mbuta* was also a multi-purpose fish. It produced copious quantities of oil, which could then be used to fry other fish. Fishermen from Lake Albert, where the Nile perch occurred naturally, have even found that this oil can be distilled into a medicine useful for curing coughing fits.[19]

Joseph Ogutu of Kenya's Usare Beach summarized these sentiments: 'Economically, *mbuta* is of high value. *Mbuta* supports families. *Mbuta* is an economic earner. *Mbuta* spreads wide.' Most importantly, he said, *mbuta* is a boon because fishermen can keep on harvesting it, unlike some other species, which have disappeared.[16]

It was perhaps these economic developments, as much as the gradual processes of persuasion and acclamation described above, that prompted a re-evaluation of the Nile perch from stinky to savoury. Fishermen at Kikondo Landing unanimously concurred that Nile perch was now the best fish for eating. 'One kilo of *mputa* can be eaten by five people', one said. 'Besides, it is very sweet, and there are fewer bones in *mputa*' than in the lake's more diminutive species, which made it easier for children to eat.[20] Daniel Ominda offered another interesting interpretation, that as something that is sent abroad to foreign dinner tables, Nile perch flesh has come to be regarded as a status symbol. 'This *mbuta* is used as an export commodity', he said. 'So [people] believe it is being eaten by *wazungu*, *wazungu* overseas. So that's why the majority are nowadays taking it.'[5]

The observation that foreigners were fond of Nile perch spurred speculation that Europeans were responsible for introducing it. Most fishermen professed not to know the details of the introduction, although they were curious and felt that they deserved to be informed – the chairman of Masese Landing had even petitioned the Ugandan government for an explanation, to no avail. Villagers at Kenya's Kaloka Beach assumed that Europeans were somehow involved, perhaps in cahoots with Asian middlemen, who started turning up with remarkable

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[18] Interview with Okidi Wakimon, age 38. Masese Landing, Uganda, 11 July 2003.

[19] Interview with John Ofulla Amaras, age 71, former UGFD fish guard. Ebulukulu, Kenya, 26 July 2003.

[20] Interview with Hanza Sebabatya, age 46, Local Council I Chairman. Kikondo Landing, Uganda, 14 July 2003.

reported bypassing the problem by selling off the larger Nile perch in his catch and keeping the smaller ones, which the factories disdain, to eat.[18]

However, it is possible that even this practice might have negative repercussions for food security. When Wakimon began fishing in 1982, it was with nets. But he discovered that the bigger Nile perch – those weighing upwards of twenty kilogrammes – inhabit the deeper waters of the lake, and that 'if you send a net around the deep water, you'll not get the big fish'. Therefore, he switched to using a floating rig, from which dangled multiple baited hooks. The result was bigger, more valuable fish, but fewer of them. In Kenya, a large Nile perch can bring multiple thousands of shillings, and the temptation to go after the fifty-kilogramme whopper is substantial. 'We are now doing fishing for us to get money', said the chairman of Kaloka beach, 'not to consume'.[10]

As suggested by Wakimon's account, the logistics of fishing also changed as the Nile perch established itself. In particular, new boats and nets were needed. To reach the open waters that contained the biggest fish, one needed a sturdy boat and preferably a motor. Nile perch has also forced fishermen 'to fish with a strong net, because the Nile perch, it grows big, and big, and big, and *bigger*. And even the smaller one has *power*!'[10] Fishermen who want to keep their gear intact now must use heavier nets or employ a technique known as double-netting.

New gear is expensive, and that expense has become a capital barrier to entry into the industry. The most successful Nile perch fishermen were those who could afford outboard motors and high-quality nets. Ntege Bakali of Kikondo beach, who claimed to have owned twenty motor-boats and 100 nets at the peak of his career, often had such a surplus of *mputa* that he simply gave away any fish smaller than five kilograms.[7] Others, like Bakali's Kikondo colleague Kasakya Hassan, were forced to aim for smaller fish: 'The costs of the nets used for catching *mputa* are very high. I can only afford to buy nets for *nkejje*. That is why I started fishing for *nkejje*.'[23]

In this vein, Geheb and Binns (1997) have shown that the Nile perch regime has initiated a cascade of changes in the traditional Luo 'tri-economy' based on fishing, farming and pastoralism. During the lucrative boom years of the 1980s, farming was increasingly neglected and many fishermen over-invested in expensive fishing equipment. The declining fishery productivity of the 1990s led fishermen to reassert the importance of a diversified economy, but indebted individuals found that small-scale farming in the intrinsically poor Nyanza soils could not generate the cash incomes that they had come to require.

Another problem was that a fat Nile perch could not be sun-dried in the same way as the smaller species. Nile perch that were not smoked or frozen within hours of death quickly rotted. This problem was ameliorated to some extent by the influx of aid from foreign development agencies, which, during the boom years, financed refrigeration facilities

[23] Interview with Kasakya Hassan, age 30. Kikondo Landing, Uganda, 14 July 2003.

at some (fortunate) beaches. Yet most landings still lacked this capacity in mid-2003, and the constant demand for a dwindling supply of firewood for fish-smoking has prompted concern about deforestation around the lakeshore (Riedmiller 1994). Moreover, smoked fish are no good for filleting. The lack of ice therefore distressed fishermen, because it allowed middlemen to dictate prices: 'If he comes with fifty shillings per kilo, you just give him or her *mbuta* to go with it. Because if you denied to give him or her *mbuta, mbuta* will [go] rotten and you will get nothing.'[24] Likewise, poor road quality meant that more isolated beaches were unlikely to receive visits from more than one buyer, further enhancing buyers' market power.

There are also indications that the Nile perch industry has restructured family and gender relations. Asowa-Okwe (1989) and Asiimwe (1994) have noted that a system of labour migrancy evolved around the peripatetic Nile perch during the 1980s, especially among casual fishermen. Asiimwe's female respondents from Bugala Island, Uganda, declared that their husbands now departed for months at a time and frequently neglected to remit food or money to their families. In addition, many fishermen took new wives at the landings they visited, often without informing the first wife. This led some women to remain single; one is said to have spat:

> My child! Movement of fishermen in search of fish has led them into marrying many wives. I am an able-bodied old woman. I will work for myself and my children. I will not stand having a man who cannot even feed his family. What is he for? (Asiimwe 1994)

For other women, the consequences were even more serious, as the taking of additional wives at distant landings facilitated the spread of HIV. These marital strains led some wives to disparage their husbands as 'prostitutes' to *mputa*.

The impact of the Nile perch boom on the gender division of labour was less straightforward. Respondents in both Kenya and Uganda affirmed that men retain exclusive rights to the act of fishing itself, while women dominate the trading of fish on the shore and may own boats or fishing gear.[16,25] However, the commercial sector has increasingly dominated processing, which has stripped many women of these sources of independent income (Abila and Jansen 1997: 30). Moreover, although women have presided over fish trading generally, men have come to predominate in the trading of the important export commodity, Nile perch (Lwenya et al. 2000). This recalls Guyer's (1980) finding among West African farming communities that men came to dominate production of the flagship export commodity (in that case, cocoa), regardless of the traditional system of labour division.

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[24] Interview with John Okise Ochola, note 10. See also Awori 2003.

[25] Interview with Hanza Mugenya, age 41, Chairman of Kikondo Landing, Uganda, 14 July 2003.

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reduced so much in number, and it's time that the issue is addressed by the relevant authorities ... In case *mukene* wasn't in the lake, then there would be no Nile perch, because Nile perch feeds on the *mukene*.'[7]

Other communities lamented biodiversity loss simply 'because the species which got lost were the sweetest for consumption'.[10] 'It concerns and bothers us that they are no longer seen', said the Local Council Chairman of Kikondo beach, 'because we want to have variety. These fishes, especially *semutundu* and *kisinja* ... are very delicious.'[20]

As for the cause of this decline in species richness and abundance, fishermen, like scientists, cited a combination of factors. There were now more people, and more fishermen, around the lake than in years past, which meant more competition for fewer fish.[5,7,16,22] Meanwhile, fishing gear had proliferated and improved, while more and more unscrupulous fishermen were violating customary prohibitions against fishing in the inshore breeding grounds.[26] Some fishermen, noting the coincidence of species disappearance and the proliferation of the Nile perch, inferred that the Nile perch had cleared out the smaller types.[8,10] Broader macro-environmental factors were also cited. One Kenyan remembered that the decline of many species had begun in 1963, when a bad flood disturbed spawning areas, while another contended that the weather had become increasingly hot and dry, which breeding fishes found distasteful.[5,16]

Still, there was hope that many desirable species could be induced to return. Kikondo's Hanza Sebabatya recalled that in 1979, the villagers had thought that *nkejje* were extinct. But when *mputa* appeared, they needed bait and searched harder for *nkejje*. They discovered that *nkejje* could still be found in some areas, 'which shows that even these other rare fishes, like *semutundu* and *kasulubana*, are still there in the water'.[20] Andrea Kakoza, while acknowledging that *mputa* had reduced the numbers of many species, argued that it was impossible for it to 'finish them', especially species like *nkolongo* that have sharp protective spines.[9] In the late 1990s, when Kenya's Kaloka beach was invaded by water hyacinth (*Eichornia crassipes*), fishermen noticed a resurgence of species that had been missing for years, leading them to speculate that vegetation was important to species preservation. The community therefore initiated a campaign to preserve the papyrus along the lakeshore, so that fishes would have shade in which to breed.[10]

Potent as these concerns about biodiversity loss were, however, other species were clearly perceived to be of secondary importance to Nile perch. According to John Okise Ochola:

> Even if the *mbuta* is the one which eats the *ningu* and the *osogas* and so forth, that's good, because it eats the *ningus*, and the *mbuta* itself is here. So we can thank the Almighty, because he's not left us without anything ... Other species here, we can be happy because we can eat [them]. But with our

[26] See Geheb and Crean (2003) for a fuller discussion of access controls and local self-regulation of fishing activity on Lake Victoria.

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country of today, it needs *money*. But the species, if they come again here, cannot give us money.[10]

But if, as often asserted, Nile perch is gold, then the Nile perch fishery has been a gold rush. Since 1990, Nile perch have been decreasing in number and size, a phenomenon noted by fishermen and biologists alike (Ogutu-Ohwayo 1999; Balirwa et al. 2003). This was a rude shock to communities that had just adapted to a new regime: 'After [the] experience that *mbuta* is money, the *mbuta* itself . . . disappeared'.[10] Again, fishermen were quick to blame increased fishing effort and use of destructive methods as the causes of the decline (Riedmiller 1994). This, they pointed out, operated both directly, as more Nile perch were removed from the lake, and indirectly, as stocks of small prey fish were depleted. Going a step further, some argued that macro-economic instability created crowded fisheries. In Kenya, a shortage of jobs in other sectors has prompted many to enter the fishery, which was perceived to be more accessible. Even educated youngsters could not find jobs, reported the Chairman of Kaloka beach. 'So you just decided to have a short cut: instead of going to school, you just start fishing here.'[10]

Another factor mentioned in relation to the decreasing Nile perch stocks was corruption among fisheries authorities, some of whom allegedly allowed the use of illegal nets in return for bribes.[27] These practices were partially responsible for *mputa's* decline, declared one fisherman, adding: 'The Government must protect *mputa*!'[27] This desire for more efficient regulation was not new. As early as 1978, Kisumu fisherman Agum Onege had written to the editor of the *Standard* that the destructive 'mosquito' seine was being 'used throughout the year after [fisheries] officers have been given "tea" [bribes] by the greedy fishermen. There is no period left where the small fish can breed.'[28]

Ultimately, despite universal avowals of enthusiasm for the Nile perch itself, there appeared to be a deep-seated ambivalence about its overall effect on life. Asked to speak for the members of his community, Kaloka chairman John Ochola paused. 'The community are happy,' he concluded, 'and on the other hand they're not happy.'[10]

## CONCLUSIONS

Thus far, I have provided a descriptive account of local responses and adaptations to the Nile perch in Lake Victoria. I will conclude by considering this narrative in the context of the social and historical literatures on African environments and their conservation.

[27] Interviews in Kenya and Uganda, kept anonymous to protect the respondents.

[28] *East African Standard*, 27 July 1978. Likewise, Kim Geheb's survey of 128 Kenyan fishermen found that 58 per cent would, if they were director of fisheries, 'establish a permanent minimum mesh size' (Geheb 1997: 90).

To date, one of the most thorough examinations of African biodiversity from a social and epistemological perspective is that of Guyer and Richards (1996). They argued that biodiversity as a concept, while 'not entirely ludicrous', is too vaguely defined and is 'quantitative without necessarily being quantifiable'. The definition of biodiversity adopted at the 1992 Earth Summit in Rio de Janeiro – the total genetic variation present in living things – *is* too broad for precise quantification, although that does not invalidate the concept; we conceptualize the Pacific Ocean and acknowledge its importance without knowing or caring how many water molecules constitute it. Nevertheless, this definition may indeed be too broad to have much functional conservation significance. Strictly speaking, it would impossible to 'preserve' biodiversity at this level, because a small portion of it is lost each time an organism dies.[29] Thus, most in the scientific community have settled on species diversity as the subset of total biodiversity with the greatest functional importance. Biodiversity at this level is quantifiable in theory if not yet in practice, and it is reasonable to speak of conserving as much of it as possible.

A central thrust of Guyer and Richards' argument was that we must 'scrutinize the level of phenomenal resolution' that biodiversity has in different cultural settings, and that in African contexts, biodiversity might need conversion into 'a notion congenial to the popular imagination' (Guyer and Richards 1996). To the contrary, I contend that biodiversity at the level of species diversity has been both highly resolved in and congenial to the imaginations and indeed to the lifestyles of Lake Victoria fishing communities through time. It was congenial to the African fishermen who, in 1927, patiently explained to confused Western scientists the difference between an *ngege* tilapia and an *mbiru* tilapia (Worthington 1983: 14). It was congenial to the Kenyan Luo who, according to Michael Graham's 1929 study, were 'rather exceptional in distinguishing different species of *Haplochromis*' (Graham 1929: 27 fn). It was congenial to Okidi Wakimon of Uganda's Masese Landing, who believed that without a diverse fish fauna, he would ultimately not be able to catch the big Nile perch that send his son to school.[18] It was congenial to Kasakya Hassan of Uganda's Kikondo Landing, who relied on a diverse fauna because he could not afford the nets needed to catch the big commercial species.[23] It was congenial to John Okise Ochola of Kaloka, who felt that the maintenance of healthy papyrus fringe swamps was essential to inducing long-lost fish to return (a conclusion also emphasized in recent biological studies: Chapman et al. 2003).[10] It was congenial to the numerous fishermen who wanted haplochromines for medicine, and for 'feasts and weddings' (Jackson 2000).[9,20] And it was congenial to the elders of Kikondo Landing who said simply: 'We want to have variety'.[20] Indeed, I suggest that the

[29] That said, it is biologically important that enough intraspecific diversity be conserved to avoid inbreeding depressions. Likewise, isolated subspecific populations warrant conservation as 'species in waiting' in evolutionary time.



metropolitan West has only tardily re-realized the congeniality of wild species diversity – those who lived off the lake never lost sight of it.

Yet most African peasants are not fishermen, but instead derive their livelihoods primarily from agriculture and pastoralism. The critical literature that has grown up around biological conservation efforts in Africa, many of which are thought to have been implemented from afar without regard for local desires and needs, has focused almost entirely on these terrestrial systems (e.g. Anderson and Grove 1987). This primacy of the terrestrial speaks to the level of phenomenal resolution at which biodiversity has traditionally operated for both international conservationists and Africanist scholars: rhinos, elephants and leopards are more highly resolved in most human psyches than are small fish in a murky lake. However, so far as a strict conception of species diversity is concerned, the endangered cichlid *Haplochromis lividus* is as important as any of the more charismatic beasts *Diceros bicornis*, *Loxodonta africana* or *Panthera pardus*.

My argument here – that recognition and appreciation of species diversity is a phenomenon that cuts across geographical and cultural boundaries – is not novel, although scholars in the biological and social sciences have generally sought different explanations for it. For many biologists such as Edward Wilson (1984), appreciation of species diversity in different societies is an outgrowth of common evolutionary heritage, a human universal he calls 'biophilia'. Wilson supports the biophilia hypothesis with cross-cultural studies indicating common preferences for/reactions to certain landscape features and wild organisms, and, importantly, the finding that people from entirely different socio-cultural settings often classify organisms in similar ways. For example, he recounts biologist Ernst Mayr's travels to New Guinea's Arfak Mountains in the 1920s, where he found that local hunters had devised a taxonomy for birds that corresponded almost perfectly to that devised by museum taxonomists working with reference specimens (Wilson 1992: 39).

Evidence supplied by other naturalists through time corroborates a certain universality of taxonomic classification and indicates that people in various times and places have often developed roughly parallel systems for the categorization of species diversity. When the nineteenth-century Scottish traveller Henry Forbes travelled to the Malay Archipelago in 1878, he rejoiced in his discovery that in Jakarta, 'every man was a naturalist':

> In regard to every thing around them, they were marvellously observant and intelligent. Not one or two only, but every individual among them seemed equally stored with natural history information. There was not a single tree or plant or minute shrub, but they had a name for, and could tell the full history of; and not a note in the forest but they knew from what throat it proceeded. Every animal had a designation, not a mere meaningless designation, but a truly binomial appellation as fixed and distinctive as in our own system, differing only in the fact that their's [sic] was in their own and not in a foreign language. Often enough this designation has so close a resemblance and sound to Latin, that it has been accepted by Western naturalists as if it

> had been so. One of the liveliest and most obtrusive of the squirrels in Java and Sumatra is a little red-furred creature called by the natives *tupai*, and to distinguish it from its more arboreal congeners they add, from its habit of frequenting branches near the ground, the word *tana* (for earth); and *Tupaia tana* is the accepted scientific term among European naturalists ... In this respect they excel far and away the rural population of our own country, among whom without exaggeration scarcely one man in a hundred is able to name one tree from another. (Forbes 1885: 54)

Jared Diamond had a similar experience in New Guinea. He recounts querying his New Guinean friends about whether a mushroom he had been brought was safe to eat:

> At that point my companions got angry and told me to shut up and listen while they explained some things to me. After I had been quizzing them for years about names of hundreds of trees and birds, how could I insult them by assuming they didn't have names for different mushrooms? Only Americans could be so stupid as to confuse poisonous mushrooms with safe ones. They went on to lecture me about 29 types of edible mushroom species, each species' name in the Foré language, and where in the forest one should look for it. (Diamond 1998: 144)

In contrast, social scientists have tended to view appreciation of local biological diversity as outgrowths of unique social and cultural values. Often, for example, it is pointed out that animal and plant species have some religious or totemic value to the society in question and are thus venerated and protected. Kandeh and Richards' (1996) intriguing exploration of 'rural conservationists' in Sierra Leone explains the persistence of the endangered white-necked Picathartes (*Picathartes gymnocephalus*) in terms of its spiritual value to Mende and Gola communities: 'Picathartes nesting areas, as conduits to the world beyond, are sites at which annual rituals are performed to seek ancestral blessing on hunters, farmers and childless women'. Fairhead and Leach (1996: 5–7), in reference to the construction and maintenance of a forest–savanna matrix in Kissidougou, discuss 'cycles of birth, growth, maturity and death common to people, land spirits and termites, and to animals, crops and plants'; they go on to suggest that such constructions may be unfamiliar or unacceptable to Western ecologists. Thus, Guyer (1996) has laudably initiated an empirical effort to elucidate what diversity itself (biological and otherwise) means in different cultural settings, the better to reconcile different cultural constructions of the concept.

At first glance, these differences in explanatory framework for what is apparently the same phenomenon – folk appreciation of species diversity – might be taken for yet another example of contrast between universalizing Western bioscience and particularizing Western anthropology. However, it is not at all clear why these superficially divergent explanatory frameworks should be considered mutually exclusive, as any innate human tendency to appreciate non-human organisms and their ecologies would be subsequently moulded and manifested (or perhaps muted) via culturally specific networks.



Many social anthropologists and historians are wary of biological explanations for human behaviour, but if we look beneath the divergent vocabularies of these disciplines, we might find unexpected commonalities between them. For example, Wilson (1975) was famously criticized by social anthropologists (and socialist biologists) for his book *Sociobiology*, the final chapter of which attempts to infer lessons about human social organization using the methods and tenets of behavioural ecology. Yet, in exploring ecological thought in West Africa, Fairhead and Leach (1999) make peasant farmers sound for all the world like Wilsonian sociobiologists:

> Analogies between people's and termites' manipulation of ecology gain further plausibility in local thought from the analogies in their social organization. Kissia and Kuranko recognize in termite organization a social world parallel to their own: one of male and female chiefs, and of different categories of worker, all living within a village. Kissia describe termite society as led by two *Kolatio* (leaders) which lie on an east–west axis; a male on the east, and a female on the west. They inhabit the heart of the mound (*telekotin* in Kissie). They and the majority of termites are protected by *Kangua*, the soldiers ... Let us conclude by discussing the baga-baga, a kind of ant ... The society of this animal is a well-organized natural republic.[30]

Such unacknowledged common ground between social and biological assessments further opens the door for the kind of interdisciplinary collaboration on conservation in the developing world that is often called for and rarely accomplished (e.g. Mascia et al. 2003).

Returning to the issue of species diversity and what it means in different cultural contexts, I want to draw attention to another assumption common to many works of biological and social science, illustrated in the quotations above: that non-Western people value biological diversity only to the extent that it is directly useful to them. In some cases, this assumption is made explicit, as in Terborgh's (1999: 12) contention that 'for many residents of the tropics, nature has only utilitarian value'. In the social scientific literature, this assumption tends to be more equivocal, but it is ubiquitous nonetheless. For example, there is by now a voluminous literature on 'local' ecological knowledge, which documents the savvy and adaptability of indigenous peoples in coping with the vagaries of harsh environments (e.g. Kjekshus 1977; Richards 1983; Giblin 1990; Tiffen et al. 1994; Iliffe 1995; Fairhead and Leach 1996; Maddox et al. 1996; Schoenbrun 1998; MacKenzie 2003; this study). Almost invariably, these works describe pragmatic adaptations that have enabled indigenous peoples to excel variously

[30] Comparing hymenopteran and human societies in *Sociobiology*, Wilson (1975: 549) wrote: 'In honeybees and in ants of the genera *Formica* and *Pogonomyrmex*, "personality" differences are strongly marked even within single castes. Some individuals, referred to by entomologists as the elites, are unusually active, perform more than their share of work, and incite others to work through facilitation. Other colony members are consistently sluggish. The controls governing human societies are not nearly so strong, and the effects of deviation are not so dangerous.'

diversity, and in what form. This may be difficult, as understanding non-use values in non-Western cultures is likely to prove at least as intractable as understanding them in our own more familiar economic and social contexts. We must take care methodologically, for the wrong questions will prompt the wrong answers: it is important to know for other reasons how people felt about being forcibly resettled during the gazetting of a national park (e.g. Collett 1987; Neumann 1998; Brockington 2002), or about their troubles with crop-raiding elephants and stock-raiding lions; but sole reliance on these types of question will perpetuate the idea that conservation and rural livelihoods are intrinsically oppositional.

One way to bring out the nuance in local valuations of species diversity might be through social histories (or ethnographies) of extinction (or extirpation). Stearns and Stearns (1999) have, journalistically, compiled what amount to ethnographies of extinction for the scientists who study endangered species, but similar studies of African non-scientists are glaringly absent. The advantage to such an approach would be in separating fundamental feelings about environmental quality from today's pressing concerns about livelihood. In the West, we hold axiomatically that amenities are not truly appreciated until they have been lost. If the same is true in rural African societies, social histories of extinction may greatly enhance our understanding of complex local knowledges and environmental ethics. The salient questions would be: what have been the consequences in local thought patterns and lifestyles where native species have disappeared? Have people been indifferent to such losses, or have they felt somehow deprived? Is it likely that, even where human–wildlife conflict is a mundane fact of life, entire rural populaces would prefer to live in biotically depauperate landscapes?

I hypothesize that the answer to this last question is no. Undoubtedly there are rural Africans, as there are rural and urban Americans and Europeans, who would profess to have no personal stake in the survival of a given plant or animal species, or who would opine that as long as their crops are left unraided and their livestock unharried, little else matters. But I suspect that many – if not most – others would reject such a simplistic world-view.

By extension, it follows that if we are to have a productive discussion about the social role and conservation of biological diversity in Africa, we must broaden our conception to include all manifestations of species diversity (whether charismatic plains megafauna or obscure lake fish) and their importance to a widely dispersed set of stakeholders (both within rural Africa and internationally). Like air and water, the diversity of biological species (however defined) is arguably a global resource that should know no national borders. Most or all local subsets of biodiversity will be important to the lives of some stakeholder somewhere, and the eradication of any of these subsets will therefore disenfranchise someone somewhere. Thus, the goal becomes to conserve as much of biodiversity as possible without further disenfranchising anyone in the process. This will be no easy feat, but it must be the focus of our collective enterprises. We might even take the idea of species diversity as a global resource one

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ABSTRACT

Introduced into Lake Victoria in the 1950s, the Nile perch has gained fame for prompting rapid regional economic growth and for driving scores of endemic fish species into extinction. This study uses oral and archival data to trace the historical development of the Nile perch fishery on Lake Victoria. Particular emphasis is placed on local responses and adaptations to (1) the Nile perch itself; (2) the abrupt integration of the Lake Victoria fishery with the global economy; and (3) the ecological changes that the Nile perch has precipitated. I also attempt to situate Lake Victoria's history in the larger debate about environment and African livelihoods. Because so much of Lake Victoria's species diversity has been lost within one generation – biologist E. O. Wilson (1992) has called this process 'the most catastrophic extinction episode of recent history' – the lake is an ideal case study with which to examine 'local' perceptions of biodiversity. The data suggest that species diversity is important and highly resolved in the worldviews of Lake Victoria's fishermen; yet, although the will for conservation is present, poverty obstructs its realization. These findings are discussed in relation to other work on indigenous environmental knowledge and ecological ethics. I argue that 'intrinsic' valuation of species diversity and ecological processes may be more widespread in rural societies than has traditionally been assumed by natural and social scientists, and that the preponderance of social studies highlighting oppositions between Western science and ethno-science, and between conservation concerns and local livelihoods, may have blinded us to synergies between them. More effort is needed to understand fully the nuances in these complex local ecological worldviews, perhaps via 'social histories of extinction' that explore the local consequences of species loss.

RÉSUMÉ

Introduite dans le lac Victoria dans les années 50, la perche du Nil est célèbre pour avoir insufflé une croissance économique régionale rapide et pour avoir entraîné l'extinction de quantités d'espèces de poissons endémiques.

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Cette étude se sert de données orales et d'archives pour retracer l'évolution historique de la pêche de la perche du Nil sur le lac Victoria. Elle met l'accent sur les réponses et adaptations locales à (1) la perche du Nil elle-même, (2) la brusque intégration de la pêche du lac Victoria dans l'économie mondiale et (3) les changements écologiques précipités par la perche du Nil. L'étude tente également de situer l'histoire du lac Victoria dans le débat plus large de l'environnement et des moyens de subsistance en Afrique. Compte tenu de l'ampleur de la perte de diversité d'espèces du lac Victoria en une génération (processus que le biologiste E. O. Wilson (1992) a qualifié d'«épisode d'extinction le plus catastrophique de l'histoire récente»), le lac est une étude de cas idéale pour examiner les perceptions «locales» de la biodiversité. Les données suggèrent que la diversité des espèces est importante et fortement résolue dans la vision du monde qu'ont les pêcheurs du lac Victoria; néanmoins, même si le désir de conservation est présent, la pauvreté gêne sa réalisation. L'article présente ces observations en les rapprochant d'autres travaux menés sur la connaissance de l'environnement et l'éthique écologique. Il affirme que la valorisation «intrinsèque» de la diversité des espèces et des processus écologiques peut être plus répandue dans les sociétés rurales que ne le suggèrent traditionnellement les scientifiques naturels et sociaux, et que la prépondérance des études sociales soulignant des oppositions entre la science occidentale et l'ethnoscience d'une part, et entre le souci de conserver et les moyens de subsistance locaux d'autre part, peut nous avoir empêché de voir les synergies qui les animent. D'autres études sont nécessaires pour comprendre pleinement les nuances de ces visions du monde écologiques locales complexes, peut-être à travers des «histoires sociales de l'extinction» qui examineraient les conséquences locales de la perte d'espèces.

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Although not all the predictions have been tested yet, the results obtained so far are interesting in view of the current session theme.

## METHODS

Sampling was done from March till May each year, at station G in the Mwanza Gulf (see Witte 1981). Haplochromines were caught by bottom trawling during daytime. Only adults were used in the analyses. Nightly surface trawls were performed to sample the adult dagaa population (see Wanink 1990). Since haplochromines and dagaa were caught with different gear, their catch rates are not directly comparable.

Ripe females, caught by trawling all over the Mwanza Gulf, throughout the year, were used to assess fecundity. Absolute fecundity (AF) was determined by the total number of eggs per female. Relative fecundity (RF) was defined as: $RF=10\times AF\times SL^{-3}$, where SL is standard length of fish in centimetres.

## RESULTS

### Survival of the zooplanktivores

In line with Witte & Goudswaard's (1985) prediction, the percentage of zooplanktivores within haplochromine catches increased in the years following the Nile perch population boom. Values of 34% ($n=494$) and 98% ($n=85$) were established during 1985 and 1987 respectively. A significant increase ($\chi^2$ test) in comparison with the value of 30% which has been reported for the period 1978–1979 by Witte (1981).

From the absolute catch rates, however, a dramatic fall in haplochromine zooplanktivores is obvious (Table 1). Though they have not disappeared as completely as many other haplochromine species, zooplanktivores, too, have been brought close to extinction since the upsurge in the Nile perch. On the contrary, the density of dagaa rose sharply (Table 1).

**Table 1** — Rise of dagaa, and fall of haplochromine zooplanktivores. Values for 1982, 1983 and 1985, from unpublished work by F. Witte, W. Hoogenboezem, and P. C. Goudswaard respectively. Spearmen rank correlation coefficient of year versus catch rate is −0.9439 ($n=10$, $P<0.01$) for haplochromies, and 0.7857 ($n=13$, $P<0.01$) for dagaa

| Year | Mean catch rate (*N*/h) | | Standard deviation | | Number of trawlshots | |
|---|---|---|---|---|---|---|
| | Dagaa | Haplochr. | Dagaa | Haplochr. | Dagaa | Haplochr. |
| 1982 | 851 | | 384 | | 4 | |
| 1983 | 556 | | 246 | | 3 | |
| 1985 | | 36000 | | 23500 | | 3 |
| 1986 | 3132 | 4275 | 965 | 6427 | 4 | 3 |
| 1987 | 8715 | 42 | 1200 | 72 | 2 | 4 |

**Reproductive tactics**

Dwarfing of haplochromines has become a striking feature during recent years (Witte & Witte-Maas 1987). Also for dagaa, a significant decrease in length was found (one-tailed Kolmogorov–Smirnov test; $P<0.01$) between all successive years, except for 1982–1983 ($P>0.05$) (Fig. 1). However, that dwarfing contributed to

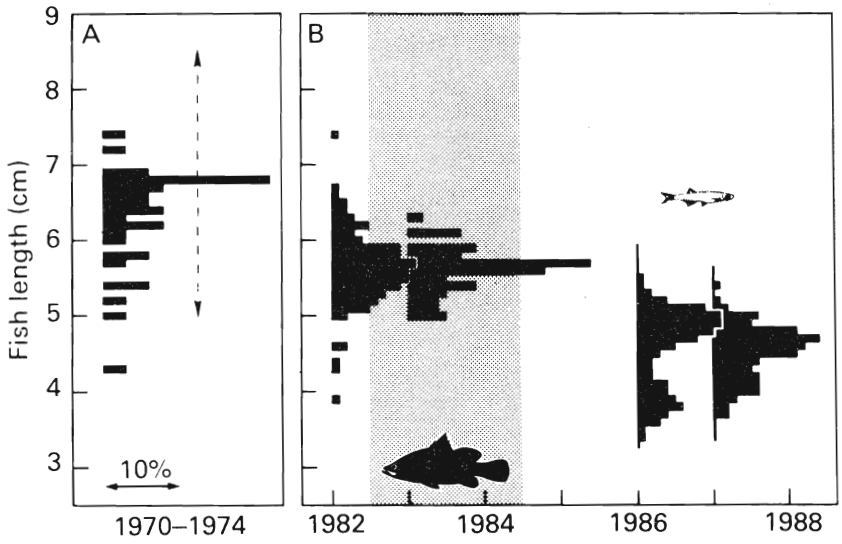



Fig. 1 — Changes in standard length of *Rastrineobola argentae*. A: Distribution based on ripe females only ($n=36$). Samples from the Mwanza Gulf and three other areas (after Okedi 1974). The dotted line represents the range for adult dagaa published by Okedi (1981). B: Distributions based on unsexed fishes from station G. Data for 1982 ($n=190$) and 1983 ($n=55$) from F. Witte (unpublished) and W. Hoogenboezem (unpublished) respectively. Sample sizes were 1522 in 1986 and 1311 in 1987. The grey bar indicates the Nile perch boom.

accelerated maturation cannot be demonstrated, since time to first maturity is not known for dagaa. In the haplochromines, Witte & Witte-Maas (1987) found that it did not change.

In contrast to the predictions, indications for slower growth were found in the haplochromines (Witte & Witte-Maas 1987). The growth rate of dagaa could only be determined for the period after the upsurge of Nile perch.

Absolute fecundity of dagaa amounted to $1073\pm313$ eggs ($n=22$) during 1987. A value of $2282\pm1065$ ($n=36$) was established for the period 1970–1974, by recalculation from Okedi (1974). The difference is significant (Mann–Whitney $U$ test; $P<0.01$). This may be attributed to dwarfing, since a positive correlation exists between size of dagaa and absolute fecundity (Okedi 1974, J. H. Wanink unpublished). To rule out the size effect, relative fecundity was taken as the parameter to be tested. This appeared to be identical (Mann–Whitney $U$ test; $P>0.05$) during 1970–1974 ($87.1\pm31.8$; $n=36$) and 1987 ($86.6\pm26.9$; $n=22$).

Haplochromine fecundity patterns were more complex. Spearman rank correlations showed a decrease in mean standard length of ripe females over the period 1983–1986 (Fig. 2A), for *H. laparogramma* ($r=-0.25$, $n=72$, $P<0.05$) and *H.*

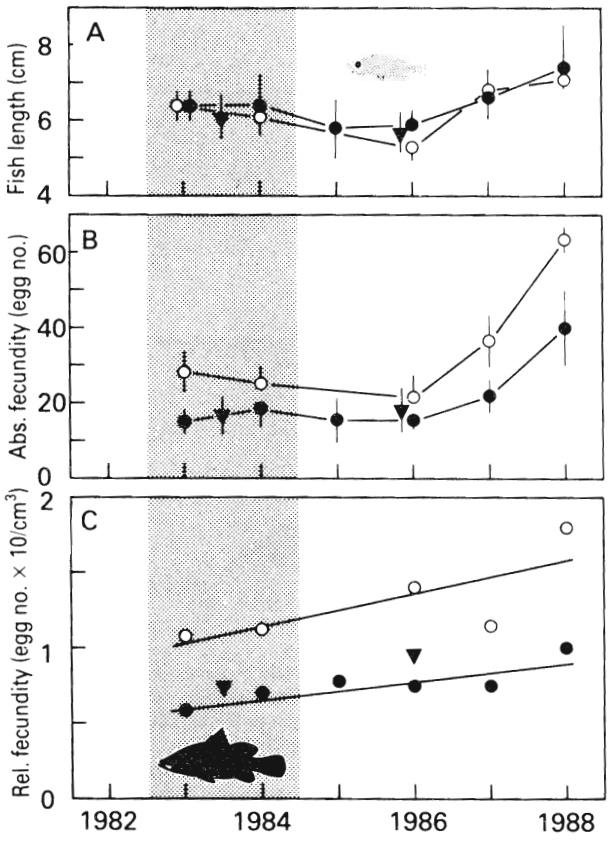



Fig. 2 — Changes in standard length of ripe females, absolute and relative fecundity of *Haplochromis laparogramma* (black dots), *H. pyrrhocephalus* (open circles) and *H. heusinkveldi* (black triangles), during and after the Nile perch boom (grey bar). Values for 1983–1985 were determined from a sample of the fishes used by Goldschmidt & Witte (in press). *H. heusinkveldi* values for 1983/84 are from Goldschmidt (1986). Panels A and B show means and standard deviations. Successive sample sizes: *H laparogramma*: 9, 11, 27, 25, 14, 3; *H. pyrrhocephalus:* 18, 37, 18, 5, 6; *H. heusinkveldi:* 41, 7. Values plotted in panel C were calculated from the means given in A and B.

*pyrrhocephalus* ($r=-0.66$, $n=73$, $P<0.01$). From 1986 onwards, size increased again (*H. laparogramma*: $r=0.63$, $n=42$, $P<0.01$; *H. pyrrhocephalus*: $r=0.83$, $n=29$, $P<0.01$). A positive correlation ($P<0.01$) between size and absolute fecundity was found for both species, in each period. Absolute fecundity (Fig. 2B) did not change during 1983–1986 in *H. laparogramma* ($P>0.05$), whereas a moderate decrease was found in *H. pyrrhocephalus* ($r=-0.38$, $P<0.01$). A strong increase in absolute

fecundity was apparent in the two species from 1986 onwards (*H. laparogramma*: $r=0.74$, $P<0.01$; *H. Pyrrhocephalus*: $r=0.85$, $P<0.01$). Relative fecundity increased significantly over the years 1983–1988 (least-squares linear regression; $P<0.01$) (Fig. 2C). The yearly increment (straight lines in Fig. 2C) amounted to 0.05 in *H. laparogramma* ($n=89$, $R^2=0.11$) and to 0.12 in *H. pyrrhocephalus* ($n=84$, $R^2=0.38$). The data for *H. heusinkveldi* were not enough for analysis, but looked comparable to those for the other species.

It is not yet known whether the life-span of the the zooplanktivores has decreased, following the Nile perch boom.

## DISCUSSION

### Testing the predictions

Witte & Goudswaard (1985) correctly predicted the relative rates of population decline in demersal versus more pelagic species. From their point of view, dagaa should be almost unaffected by Nile perch predation, since the species was commonly believed to occupy the surface layers only. The superior survival of dagaa cannot, however, be attributed to its restriction to surface waters, since it has recently been demonstrated that adults move downward during daytime (Wanink 1990).

Of the tested predictions, only the increase of relative fecundity in haplochromines agreed directly with life-history theory. Nevertheless these species have almost vanished, whereas dagaa is flourishing Goldschmidt & Barel (pers. comm.) suggest an evolutionary trap: the buccal cavity volume of the mouthbrooding female haplochromines setting a limit to the increase in fecundity. Their idea could be the explanation for the unexpected increase of female standard length during 1987–1988 (Fig. 2A): increased body size also means a larger buccal cavity.

The haplochromines produce less than 50 eggs per spawning (Goldschmidt & Witte in press). Considerably more eggs are released by dagaa, which have no parental care. According to classic *r*/*K* dichotomy in life-history strategies (MacArthur & Wilson 1967), this would classify the cichlids as relatively *K*-selected and dagaa as a more *r*-selected species. Theory predicts a selective advantage for the more *r*-selected species in a disturbed habitat, which nicely fits in with the developments observed in the Mwanza Gulf. However, the *r*-and *K*-selection model has been criticized for its assumption of age-independent mortality (Wootton 1990).

### The need for theory

The work presented in this chapter supports the view that ecological theory can to a certain extent predict the outcome of perturbation in an ecosystem. Simple models gave the best practical results, although they might not have been very realistic. The more complex modern life-history may give a better fit with the real world when all the parameters involved will have been analysed. So far, application in the field only raises new questions, which ask for further development of the theory.

Ecological field research is indispensible in theory-building. Models have to be tested in the field, after which the results should be used to adjust the theory if necessary. To test and develop ecological theory, large-scale 'natural' experiments,

*the Seventh Pan-African Ornithological Congress, Nairobi, 28 August–5 September 1988* (in press).

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