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# Hypoxia Tolerance in Twelve Species of East African Cichlids: Potential for Low Oxygen Refugia in Lake Victoria

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**Abstract:** *The species flock of haplochromine cichlid fishes in Lake Victoria is one of the most extensive and recent radiations of vertebrates known. Over the past 15 years, however, many of the haplochromine cichlid species have vanished, and predation by the introduced Nile perch (*Lates niloticus*) is thought to be one of the most significant factors underlying this mass extinction. Information on the hypoxia tolerance of haplochromines from Lake Victoria is valuable for predicting their response to the increasing anoxia within the lake and in evaluating their potential use of low oxygen regions as refugia from predation by introduced Nile perch. This study examines the response of nine cichlid species from Lake Victoria (eight indigenous, one introduced) and three cichlid species from Lake Tanganyika to different low-oxygen regimes under laboratory conditions. Fish were exposed to progressive and acute hypoxia, with and without access to the surface. All species used aquatic surface respiration at very low  $P_{O_2}$ . Buccal bubble holding and active swimming at the surface during aquatic surface respiration were used by many species and may serve to increase its efficiency. Lacustrine cichlids endemic to Lake Victoria were more tolerant of hypoxia than ecologically similar species from Lake Tanganyika. The two species examined that are widespread in a variety of aquatic habitats exhibited a relatively high tolerance to hypoxia, with well-developed aquatic surface respiration and bubble-holding capabilities and no loss of equilibrium during progressive hypoxia. Species strongly affected by recent changes in Lake Victoria were not consistently poorer in their hypoxia tolerance than less-affected species. But, two of the less-affected species are inhabitants of shallow, rocky habitats, an environment that may be both rich in oxygen and well defended against the Nile perch because of the structural complexity of the rocky, littoral area. The generally high levels of hypoxia tolerance in the cichlid species examined from Lake Victoria suggest that these species potentially could use low-oxygen refugia to escape Nile perch predation. Some species that are thought to have disappeared may currently inhabit low-oxygen refugia that have not been adequately sampled.*

Tolerancia a la hipoxia en cíclidos del Africa oriental: Refugios con bajo contenido de oxígeno en el lago Victoria

**Resumen:** *El grupo de especies de peces cíclidos haplocromínidos del lago Victoria es una de las radiaciones de vertebrados más recientes y extensas de la que se tenga conocimiento. Sin embargo, a lo largo de los últimos 15 años, muchas de las especies de cíclidos haplocromínidos han desaparecido, y la predación por una especie introducida, la perca del Nilo (*Lates niloticus*) es considerada como uno de los factores más significativos que contribuyeron a esta extinción masiva. La información sobre la tolerancia a la hipoxia de los haplocromínidos del lago Victoria es valiosa para predecir sus respuestas a la anoxia en aumento dentro del lago y*

en la evaluación del uso potencial de regiones con bajo contenido de oxígeno como refugios contra la predación por parte de la perca del Nilo. Este estudio examina la respuesta de nueve especies de cíclidos del lago Victoria (ocho indígenas y una introducida) y tres especies de cíclidos del lago Tanganica bajo distintos regímenes de bajo contenido en oxígeno en condiciones de laboratorio. Los peces fueron expuestos a una hipoxia progresiva y aguda, con o sin acceso a la superficie. Todas las especies usaron respiración de superficie cuando los niveles de  $P_{O_2}$  eran muy bajos. Muchas especies usaron la retención de burbujas en la boca y la natición activa en la superficie durante la respiración de superficie, las cuales podrían servir para aumentar su eficiencia. Los cíclidos lacustres endémicos al lago Victoria fueron más tolerantes a la hipoxia que las especies ecológicamente similares del lago Tanganica. Las dos especies examinadas que tienen amplia distribución en una variedad de hábitats acuáticos exhibieron una tolerancia relativamente alta a la hipoxia, con respiración de superficie y capacidad para la retención de burbujas bien desarrolladas y sin ninguna pérdida en el equilibrio durante la hipoxia progresiva. Las especies fuertemente afectadas por cambios recientes en el lago Victoria no fueron consistentemente más pobres en su tolerancia a la hipoxia que las especies menos afectadas. Sin embargo dos de las especies menos afectadas son residentes de hábitats rocosos someros, un ambiente que podría ser rico en oxígeno y podría estar resguardado de la perca del Nilo debido a la complejidad estructural del área litoral rocosa. Los niveles generalmente altos de tolerancia a la hipoxia en las especies de cíclidos del lago Victoria examinadas sugiere que estas especies podrían usar en forma potencial los refugios con bajo contenido de oxígeno para escapar de la predación por parte de la perca del Nilo. Algunas de las especies que se piensa han desaparecido podrían, en la actualidad, residir en refugios con bajo contenido de oxígeno que no han sido muestreados adecuadamente.

## Introduction

The species flock of haplochromine cichlid fishes in Lake Victoria represents one of the most rapid, extensive, and recent radiations of vertebrates known (Greenwood 1966, 1979). Over 50% of the over 400 species of fishes (90% haplochromine cichlids) native to the lake, however, are thought to have gone extinct in the last 15 years (Ogutu-Ohwayo 1990a; Kaufman 1992; Witte et al. 1992; Kaufman & Ochumba 1993). Although several factors may have contributed to the precipitous decline in Lake Victoria's indigenous fishes, predation by the introduced Nile perch is thought to be one of the most significant (Barel et al. 1985, 1991; Balon & Bruton 1986; Bruton 1990; Ogutu-Ohwayo 1990a, 1990b, 1990c; Ogutu-Ohwayo & Hecky 1991; Witte et al. 1992). Nile perch were first introduced to the lake beginning in 1954 and persisted as a minor component of the fauna until the early 1980s, when their populations increased dramatically. As recently as 1980 about 90% of the native species and about 80% of the fish biomass consisted of haplochromine cichlids (Kudhongania & Cordone 1974; Witte 1981, 1984, 1987; Witte et al. 1992). By 1990, much of the native fish community is thought to have vanished; Nile perch (*Lates niloticus*) comprised 80% of the catch, with the remaining 20% consisting of introduced Nile tilapia (*Oreochromis niloticus*), the native omena (*Rastrineobola argentea*), and a small remnant of other indigenous fishes, including haplochromine cichlids (Ogutu-Ohwayo 1990a; Kaufman 1992; Witte et al. 1992).

Decline of the native fishes has also been attributed to the effects of a number of other factors, including the introduction of other exotics (Ogutu-Ohwayo 1990a),

overfishing (Cadwalladr 1965; Coulter et al. 1986; Ogutu-Ohwayo 1990a), and changes in the physical environment of the lake (Hecky 1993). Formerly, Lake Victoria was well mixed, and the deeper waters contained more oxygen than they do now (Hecky 1993). Talling (1966) found that Lake Victoria was subject to hypoxia in the open waters only on a seasonal basis below 60 m, although severe hypoxia characterized the dense interior of the marginal swamps (Carter 1955). Now, anoxia below 45 m is common and affects 50% of the lake's bottom area for extended periods (Hecky 1993). Dense algal blooms occur more frequently now in the shallow regions and open waters of the lake and are often characterized by low-oxygen conditions (Ochumba 1987; Ochumba & Kibaara 1989; Ochumba 1990). Fish kills also occur frequently now (Ochumba & Kibaara 1989; Ochumba 1990) and are thought to be related to the widespread anoxia in the bottom waters interacting with hydrodynamic movements of the lake and the massive algal blooms (Ochumba 1990; Hecky 1993). Increasing anoxia in the deeper waters may have reduced available habitat for hypoxia-intolerant species, resulting in distributional shifts or loss of deep-water species, including large numbers of demersal haplochromine fishes (Kudhongania & Cordone 1974; Hoogerhoud et al. 1983).

The fishes of Lake Victoria currently experience hypoxia under three circumstances: (1) anoxia is now widespread in deeper waters (Hecky 1993); (2) chronic hypoxia also occurs in the shallow, heavily vegetated peripheral wetlands, lagoons, and papyrus-choked river mouths (Carter 1955; Welcomme 1970); and (3) acute hypoxia can occur anywhere in the typically oxygenated zone as a result of upwellings of deoxygenated hypolim-

netic water and dense algal blooms (Ochumba & Kibara 1989; Ochumba 1990). This spatial distribution of hypoxic water is potentially an important factor influencing the distribution, species interactions, and survival of fishes in Lake Victoria. Certainly, recent changes in the oxygen conditions in the deeper waters of the lake and local upwellings of anoxic waters may have contributed to the recent history of species loss. But because the Nile perch is thought to be relatively intolerant of low-oxygen conditions, low-oxygen regions may also serve as refugia for prey species. Variation in hypoxia tolerance may help to explain why some species of haplochromine cichlids have persisted with Nile perch, while others have gone extinct.

Papyrus swamps, which dominate the peripheral swamp regions of Lake Victoria, are characterized by severe oxygen depletion, high structural heterogeneity, and a succession of habitats from the dense interior of the swamps to the open water, with oxygen increasing toward the open water (Carter 1955; Chapman & Liem 1995). For example, Carter (1955) reported oxygen levels averaging only 0.07 mg/L in the shore region of a papyrus swamp near Jinja, with average values increasing to 3.5 mg/L for surface waters in the outer part of the papyrus zone. We speculate that these wetlands may play an important role as refugia from Nile perch predation for some species of haplochromine cichlids because Nile perch seem to be relatively intolerant of extreme hypoxia, and it is unlikely that Nile perch can prey as effectively in the structurally complex littoral swamps as in more open water areas. Fish (1956) found that Nile perch require water with high levels of dissolved oxygen (> 5 mg/L) because their blood has a low affinity for oxygen. The large proportion of Nile perch in fish kills in Lake Victoria (Ochumba 1990) and Lake Turkana (Kolding 1993) also suggest that Nile perch are more sensitive to low oxygen than some cichlids. In addition to marginal wetland refugia, deep-water haplochromines tolerant of low oxygen may find refuge near the oxycline (Kaufman & Ochumba 1993). Knowledge of the response of individual species of haplochromine cichlids to hypoxia is essential to assess the consequences of anthropogenic impacts on aquatic biodiversity and to identify the potential value of low-oxygen areas as refugia for endemics from the introduced Nile perch.

Oxygen scarcity has produced varied evolutionary responses by fishes, including such adaptations as anaerobic metabolism, the development of air-breathing organs, and the ability to carry out aquatic respiration at the air-water interface, where diffusion produces a thin layer of well-oxygenated water, despite oxygen scarcity in the rest of the water column (aquatic surface respiration [ASR]; Kramer 1983*a*, 1983*b*, 1987; Liem 1987). In response to severe hypoxia, some cichlids have been observed to use ASR (Kramer & McClure 1982; Kramer

1983*a*, 1983*b*; Verheyen et al. 1994). This widespread strategy (Kramer & McClure 1982; Kramer 1983*b*) requires open water surface, but can be used over prolonged periods by some species (Kramer & Mehegan 1981; Kramer & McClure 1982; Weber & Kramer 1983; Gee & Gee 1991). There are few studies that assess the hypoxia tolerance of cichlids from Lake Victoria, but studies of the gill morphology in a variety of haplochromine cichlids from Lake Victoria suggest high tolerance in some species (Galis & Barel 1980; Hoogerhoud et al. 1983).

We examined the response of nine species of cichlids from Lake Victoria (eight indigenous, one introduced) to different low-oxygen regimes under laboratory conditions. We compared the hypoxia tolerance of species that have been heavily affected by recent changes in the Lake Victoria ecosystem to species that were less affected. Species were selected from a wide range of trophic and habitat niches. In addition, we compared the general responses of the species of haplochromine cichlids from Lake Victoria to those of three ecologically similar cichlid species endemic to Lake Tanganyika. The cichlid faunas of the three great lakes of East Africa (Lakes Tanganyika, Malawi, and Victoria) are strikingly similar (Fryer & Illes 1972; Witte 1984; Eccles & Trewavas 1989), but Lake Victoria is a much younger, shallower lake in a swampy basin (maximum depth = 93 m) that may have dried up as recently as 14,000 years ago (Schotz et al. 1990). Lakes Tanganyika and Malawi are much deeper (Tanganyika, maximum depth = 1600 m; Malawi, maximum depth = 722 m), and these harbor fish faunas that are much older (the age of radiation = <1,500,000 years for Malawi and >3,000,000 years for Tanganyika; Kaufman 1992). Having evolved in a shallow, swampy, broad basin, cichlids from Lake Victoria may differ from cichlids endemic to Lake Tanganyika in their response to hypoxia.

## Materials and Methods

### Study Species

Species were chosen to shed light on possible relationships between hypoxia tolerance and five attributes: morphometry of the lake basins in which they evolved (shallow and broad Lake Victoria versus steep and deep Lake Tanganyika); habitat specialization (lacustrine-limited versus widespread distribution in lakes and rivers); level of impact on population by recent changes in Lake Victoria (not affected to highly negatively affected), trophic groups (pelagic zooplanktivore, piscivore, phytoplanktivore, pharyngeal-crushing molluscivore, rock grazer); and evolutionary lineage (haplochromine, tilapine; Table 1). All of the selected species from Lake Victoria are generally found in shallow waters. Of the species

of cichlids from Lake Victoria, six species are endemic to the lake, and one species, *Astatoreochromis alluaudi*, is widespread in the Lake Victoria-Nile Basin. The endemic tilapiine, *Oreochromis esculentus*, previously a major food fish in the Lake Victoria fishery, was included because this species has also become scarce. The decline of this species coincided with earlier perturbations, however, most likely overfishing and the introduction of other tilapiine competitors. *O. esculentus* was compared to *O. niloticus*, which was introduced to the lake in the 1950s and is now the most abundant tilapiine in the system. Three endemic cichlid species that occur in the well-oxygenated rocky areas of Lake Tanganyika and belong to functional/trophic groups similar to three of the haplochromine species from Lake Victoria were selected for comparison with the cichlid species from Lake Victoria (Table 1).

*Prognathochromis perrieri*, *Pyxichromis orthostoma*, *Yssichromis argens*, *Neochromis nigricans*, *Labrobromis ishmaeli*, "Haplochromis" "rock kribensis", *Astatoreochromis alluaudi*, *Oreochromis niloticus*, and *Oreochromis esculentus* were obtained through the assistance of the Lake Victoria Fishes Species Survival Plan (IUCN/AZA). The three cichlid species from Lake Tanganyika (*Cyprichromis leptosoma*, *Tropheus moorii*, *Neolamprologis tredocephalus*) were purchased from Old World Exotics, Inc. (Florida). When possible, fish of approximately the same size were used (Table 1); but we were unable to obtain very small *O. esculentus* or *O. niloticus*.

To quantify the behavioral response of the cichlids to oxygen scarcity, detailed observations of respiratory behavior were recorded during progressive hypoxia tests where oxygen was lowered slowly over a three-hour period and 10 experimental fish had access to the surface. Use of peripheral swamps or swamp ecotones would re-

quire prolonged tolerance to low-oxygen conditions. Fish were also exposed to acute hypoxia, with and without access to the surface. Local upwellings of anoxic water from deeper sections of the lake would entail sudden exposure to low-oxygen conditions; fish might not be able to adjust buoyancy rapidly enough to reach the surface before the effects of the anoxic water were felt. In contrast, where anoxic water sweeps into relatively shallow bays, fish would experience acute oxygen drops but would potentially have access to the water surface.

#### Experimental Protocol: Progressive Hypoxia

Fish were held in well-oxygenated aquaria maintained at 23–26°C and were fed Tetramin food flakes. The night before the trial, fish were transferred to an experimental tank with comparable oxygen and temperature conditions. The experimental tank (90 × 30 × 37 cm, maintained at a depth of 32 cm) was divided into three compartments: two side compartments of 10 × 30 × 37 cm and a large central compartment of 70 × 30 × 37 cm. The central compartment contained the fish, and the two smaller compartments contained heaters and airstones and were separated from the main compartment by screen partitions that rose above the surface of the water but permitted water exchange. At the water surface, the aquarium was marked off into 10-cm intervals to permit estimates of the speed of movement during aquatic surface respiration.

Nitrogen was bubbled into the two side compartments to lower the oxygen content (Gee & Gee 1991; Chapman et al. 1994) without disturbing the water surface in the central compartment. To create extreme hypoxia (<1.0 mg/L), small amounts of sodium sulfite were added to the water (Lewis 1970; Kramer & Mehe-

Table 1. A description of the source lake and functional group of 12 species of cichlids (10 individuals/species) considered in hypoxia tolerance experiments.

Species (Lake)	Functional Group	Impact	Body Mass (g; mean ± SD)	Total Length (cm; Mean ± SD)
<b>Lake Victoria</b>				
<b>Haplochromines</b>				
<i>Prognathochromis perrieri</i>	Piscivore	heavily impacted	5.78 ± 2.00	7.94 ± 0.80
<i>Yssichromis argens</i>	Zooplanktivore	heavily impacted	2.72 ± 1.63	6.23 ± 0.95
<i>Labrobromis ishmaeli</i>	Molluscivore	heavily impacted	3.92 ± 0.97	6.81 ± 0.57
<i>Pyxichromis orthostoma</i>	Piscivore	not heavily impacted	1.94 ± 4.43	5.27 ± 0.58
<i>Neochromis nigricans</i>	Rock Scraper	not heavily impacted	5.38 ± 1.53	7.22 ± 0.59
"Haplochromis"				
"Rock kribensis"	Molluscivore	not heavily impacted	3.37 ± 1.37	5.83 ± 0.90
<i>Astatoreochromis alluaudi</i>	Molluscivore	not heavily impacted	3.88 ± 0.97	6.45 ± 0.58
<b>Tilapiines</b>				
<i>Oreochromis esculentus</i>	Phytoplanktivore	heavily impacted	21.17 ± 5.13	11.10 ± 0.88
<i>Oreochromis niloticus</i>	Phytoplanktivore	not heavily impacted	40.07 ± 9.11	13.69 ± 1.13
<b>Lake Tanganyika</b>				
<i>Cyprichromis leptosoma</i>	Zooplanktivore	—	8.76 ± 2.05	9.62 ± 0.49
<i>Tropheus moorii</i>	Rock Scraper	—	4.11 ± 0.57	6.04 ± 0.24
<i>Neolamprologis tredocephalus</i>	Molluscivore	—	4.11 ± 0.57	6.04 ± 0.24

gan 1981; Gee & Gee 1991). Oxygen content was measured with a YSI (Model 57) oxygen meter and converted to  $P_{O_2}$  using standard tables (Davis 1975). Oxygen was lowered over a three-hour period (average duration 191 minutes; SD = 20.9, range = 150–210, for species that did not lose equilibrium), and then the fish were held at under 0.2 mg/L for 30 minutes.

A blind was set up that permitted observations through a small viewing port but prevented the fish from being disturbed by the observers. The following response variables were recorded from behind the blind every 15 minutes and after the final 30-minute interval: activity level (number of active fish recorded 10 times at 5-second intervals), gill ventilation rate (number of ventilations in a 15-second period, repeated for six fish), number of fish using ASR (recorded every 10 seconds for 100 seconds), the percentage of fish holding a bubble in their buccal cavity (estimated), elapsed time between successive bubble exchanges from the buccal cavity ( $n = 10$  repetitions), and, when appropriate, surface speed of the fish (number of 10-cm increments traversed in 15 seconds). The oxygen levels at which 10% ( $ASR_{10}$ ), 50% ( $ASR_{50}$ ), and 90% ( $ASR_{90}$ ) of the fish performed ASR were estimated from curves of the percentage of fish using ASR plotted against the  $P_{O_2}$  (following Kramer & McClure 1982).

Fish were closely monitored for any sign of equilibrium loss. If this occurred, the time was noted and the fish was quickly removed from the experimental tank and placed in well-oxygenated water. The experiment was terminated if 80% of the fish lost equilibrium. Video recordings were used to describe details of the respiratory behavior at low oxygen levels.

### Rapid Oxygen Drop

To examine the response of fish to acute hypoxia with access to the surface, five of the 10 fish from a well-oxygenated aquarium were quickly transferred into the experimental tank that had only trace amounts of oxygen in the water (mean  $P_{O_2} = 2.2 \pm 1.2$  mm Hg, SD, range = 0.9–5.5, <0.2 mg/L). To assess the impact of the capture and transfer of the fish between tanks, we transferred the five other fish to a control tank, where the oxygen was high (mean  $P_{O_2} = 138.8 \pm 10.7$  mm Hg, SD, range = 132.2–157.4).

Time to loss of equilibrium was used to assess relative tolerance between species. If a fish started exhibiting signs of equilibrium loss, the animal was closely monitored. When the fish lost equilibrium, the time was recorded and the animal was quickly removed from the experimental tank and placed in well-oxygenated water. If four of the five fish in the experimental tank lost equilibrium, the experiment was terminated. In all cases the fish quickly recovered. Because equilibrium loss generally did not occur, the other response variables were re-

corded five minutes after introduction to the aquarium and after 30 minutes under experimental conditions.

To examine the response of fish to acute hypoxia in which immediate access to the surface is difficult or impossible, a plastic sheet was suspended 5 cm below the surface of the water to prevent surface access. The previous protocol was followed in all other respects. Time to loss of equilibrium was recorded and, again, when four of the five fish lost equilibrium, the experiment was terminated. The other response variables were not recorded because fish generally lost equilibrium within the 30-minute time frame.

## Results

### Comparative Response to Progressive Hypoxia

All species performed ASR when oxygen became scarce ( $ASR_{10}$  range in  $P_{O_2} = 7.4$ –35.3 mm Hg; Table 2, Fig. 1). There was no significant difference between the haplochromine cichlids from Lake Victoria (tilapiines excluded) and the endemic cichlids from Lake Tanganyika in their  $ASR_{10}$  (Lake Victoria: mean  $P_{O_2} = 16.4$  mm Hg; Lake Tanganyika: mean  $P_{O_2} = 22.8$  mm Hg, Mann-Whitney  $U$  test,  $U = 6.0$ ,  $p = 0.383$ ; Table 2) or  $ASR_{50}$  (Lake Victoria: mean  $P_{O_2} = 11.6$  mm Hg; Lake Tanganyika: mean  $P_{O_2} = 14.9$  mm Hg;  $U = 6.5$ ,  $p = 0.383$ ; Table 2).  $ASR_{90}$  could not be compared because fish from Lake Tanganyika typically lost equilibrium prior to this point.

The cichlids from Lake Victoria were more tolerant of progressive hypoxia than the three species of cichlids from Lake Tanganyika. Among the Lake Victoria haplochromines and the tilapiines, only *Neochromis nigricans* lost equilibrium during the progressive experiment. In contrast, individuals from all the species from Lake Tanganyika lost equilibrium during progressive hypoxia exposure. *Neochromis nigricans* individuals lost equilibrium during the 30-minute period at the end of the experiment when fish were held at under 0.2 mg/L. The species from Lake Tanganyika lost equilibrium prior to this point (*Neolamprologis tredocephalus* at an average  $P_{O_2}$  of 13.9 mm Hg, *Cyprichromis leptosoma* at 8.0 mm Hg, and *Tropheus moorii* at 5.4 mm Hg).

During ASR, all species, except *Pyxichromis orthostoma*, were observed to hold buccal bubbles. Water was passed around the bubble during ASR, potentially increasing the oxygen content of the ventilated water. Bubble holding may also contribute to lift. Bubbles were generally released through the mouth. Although occasional bubbles escaped during ASR, bubble exchange in most species was a well-defined behavior characterized by a distinct spitting action for bubble release. Bubbles seemed to have a positive effect on head buoyancy because a portion of the snout was emersed during bubble holding in some species. Buccal bubbles were held only

during ASR and were released when fish moved below the surface.

There was variation among species in both the frequency of bubble exchange and in the initiation of bubble holding during progressive hypoxia. Mean bubble exchange frequency at the end of the progressive experiment varied from 4.5 seconds in *Tropheus moorii* to 113.5 seconds in *Oreochromis niloticus* (Table 2). Mean bubble exchange frequencies (calculated over all P<sub>O<sub>2</sub></sub> levels where exchange rates could be recorded) exhibited the same trends (Table 2). Initiation of bubble holding varied among species from 2.9 mm Hg in *Prognathochromis perrieri* to 45.8 mm Hg in *Oreochromis niloticus*. In most species, fish did not hold bubbles immediately upon commencing ASR, but the percentage of fish holding bubbles increased with decreasing P<sub>O<sub>2</sub></sub> and, with the exception of *Tropheus moorii*, eventually included all individuals. Bubble exchange (mean for the final sample interval) averaged 9.1 seconds for the cichlids

from Lake Tanganyika and 41.9 seconds for the haplochromine cichlids from Lake Victoria (Mann-Whitney *U* test, *U* = 0.0, *p* = 0.074, tilapiines excluded, Table 2). There was no difference in the bubble exchange frequency between species from Lake Victoria that have been heavily affected by recent changes in the lake (mean = 59.6 sec) and fish that seem to have been less affected (mean = 50.8, *U* = 4.0, *p* = 0.248, including both tilapiines, Table 2).

Whenever possible, gill ventilation rates were recorded for fish using ASR and fish not at the surface during the same observation period (same P<sub>O<sub>2</sub></sub>). In all of the haplochromine species from Lake Victoria, except *Astatoreochromis alluaudi*, gill ventilation rates decreased with the initiation of ASR (Fig. 1). Across a broad range of oxygen concentrations (46 to 4 mm Hg), *Oreochromis niloticus* using ASR exhibited lower gill ventilation rates than did fish below the surface (Fig. 1). In *Oreochromis esculentus*, gill ventilation rate exhibited only a

**Table 2.** The response of cichlids from Lake Victoria and Lake Tanganyika and *Oreochromis niloticus* (introduced into Lake Victoria) to progressive hypoxia.

Species	Oxygen Tension (mm Hg) <sup>a</sup>			Loss of Equilibrium	Bubble <sup>b</sup> Exchange (mean/final)	Speed <sup>c</sup> (cm/15 sec)	Percent Forward <sup>d</sup>	Effort to Stay at the Surface	Body Position (angle in degrees, fish to surface)
	ASR <sub>10</sub>	ASR <sub>50</sub>	ASR <sub>90</sub>						
Lake Victoria									
Haplochromines									
<i>Prognathochromis perrieri</i>	15.2	11.0	7.0	no	50.8/50.8	39.2	0	minimal	45
<i>Yssichromis argens</i>	20.7	17.4	16.5	no	51.2/53.0	45.8	20	minimal	35
<i>Labrobromis ishmaeli</i>	17.0	8.5	1.5	no	57.4/58.0	35	30	moderate	45-55
<i>Pyxichromis orthostoma</i>	17.0	13.2	7.2	no	—	11.2	70	minimal	45
<i>Neochromis nigricans</i>	10.1	7.6	3.0	yes	23.9/27.7	36.7	60	moderate	35-55
"Haplochromis" "rock kribensis"	14.6	10.5	8.4	no	17.8/17.3	20.0	50	minimal	45
<i>Astatoreochromis alluaudi</i>	20.1	13.2	9.9	no	23.5/44.5	< 5	—	minimal	55
Tilapiines									
<i>Oreochromis esculentus</i>	7.4	6.1	5.1	no	68.5/76.7	< 5	—	minimal	40
<i>Oreochromis niloticus</i> (introduced)	35.3	6.9	4.5	no	113.5/113.5	< 5	—	minimal	35
Lake Tanganyika									
<i>Cyprichromis leptosoma</i>	12.0	8.5	—	yes	20.3/13.7	< 5	—	intense	45
<i>Tropheus moorii</i>	29.5	19.0	15.0	yes	9.9/4.5	41.7	100	very intense	80
<i>Neolamprologis tretocephalus</i>	26.8	17.2	—	yes	—	< 5	—	moderate	45

<sup>a</sup>The oxygen level at which 10% (ARS<sub>10</sub>), 50% (ARS<sub>50</sub>), and 90% (ARS<sub>90</sub>) of the fish performed ASR was estimated from plotted curves of the percentage of the fish using ASR and P<sub>O<sub>2</sub></sub>.

<sup>b</sup>The mean bubble exchange rate (in seconds) represents the average rate over all sampling periods where bubbles were exchanged. The final bubble exchange rate represents the average rate in the final sample interval.

<sup>c</sup>"Speed" is the average distance traveled (cm) per 15-second interval during the last observation trial.

<sup>d</sup>% Forward is the percentage of the movements during the last observation that was in a forward direction; this was not recorded if the species moved very slowly.

marginal decline with the initiation of ASR. If a decline in gill ventilation rates indicates enhancement of oxygen intake, the decrease in gill ventilation rates with initiation of ASR demonstrates the efficiency of ASR for these species. In the three species from Lake Tanganyika, gill ventilation rate did not show a consistent decline associated with ASR. In the final sample interval there was no difference in gill ventilation rate between the haplochromine cichlids from Lake Victoria (mean gill ventilations/15 seconds = 32.5; tilapiines excluded) and the species of cichlids from Lake Tanganyika (mean gill ventilations/15 seconds = 31.9, Mann-Whitney  $U$  test,  $U = 9.0$ ,  $p = 0.833$ ). In addition, there was no difference in gill ventilation rate between species from Lake Victoria that have been heavily affected by recent changes in the lake (mean = 31.9) and fish that have not been affected by the changes (mean = 33.3,  $U = 8.5$ ,  $p = 0.730$ , both tilapiines included).

Activity levels associated with ASR could be divided into two distinct categories based on the degree of surface activity. Of the Lake Victoria species, *Astatoreochromis alluaudi* and the two tilapiines remained relatively sedentary at the surface. The other species moved

actively at the surface during ASR using both active forward and backward motion. Of the three species from Lake Tanganyika, only *Tropheus moorii* used active forward motion during ASR. Those species moving actively at the surface varied both in the speed of movement and in the time when ASR surface activity was initiated. In general, horizontal speeds during ASR were lower just after surface swimming was initiated than in the final sample interval when surface swimming was not initiated (Wilcoxon test,  $z = -2.366$ ,  $p = 0.018$ ; Table 2, Fig. 2). Final speeds for species that moved actively at the surface during ASR varied from 11.2 cm/15 seconds to 45.8 cm/15 seconds (Fig. 2).

**Comparative Response to Acute Hypoxia**

The response of fish to acute hypoxia with surface access varied markedly among species, although all species used ASR. Time to loss of equilibrium was used to assess relative hypoxia tolerance between species. The Lake Victoria haplochromines were very tolerant of acute hypoxia within the framework of this experimental design.

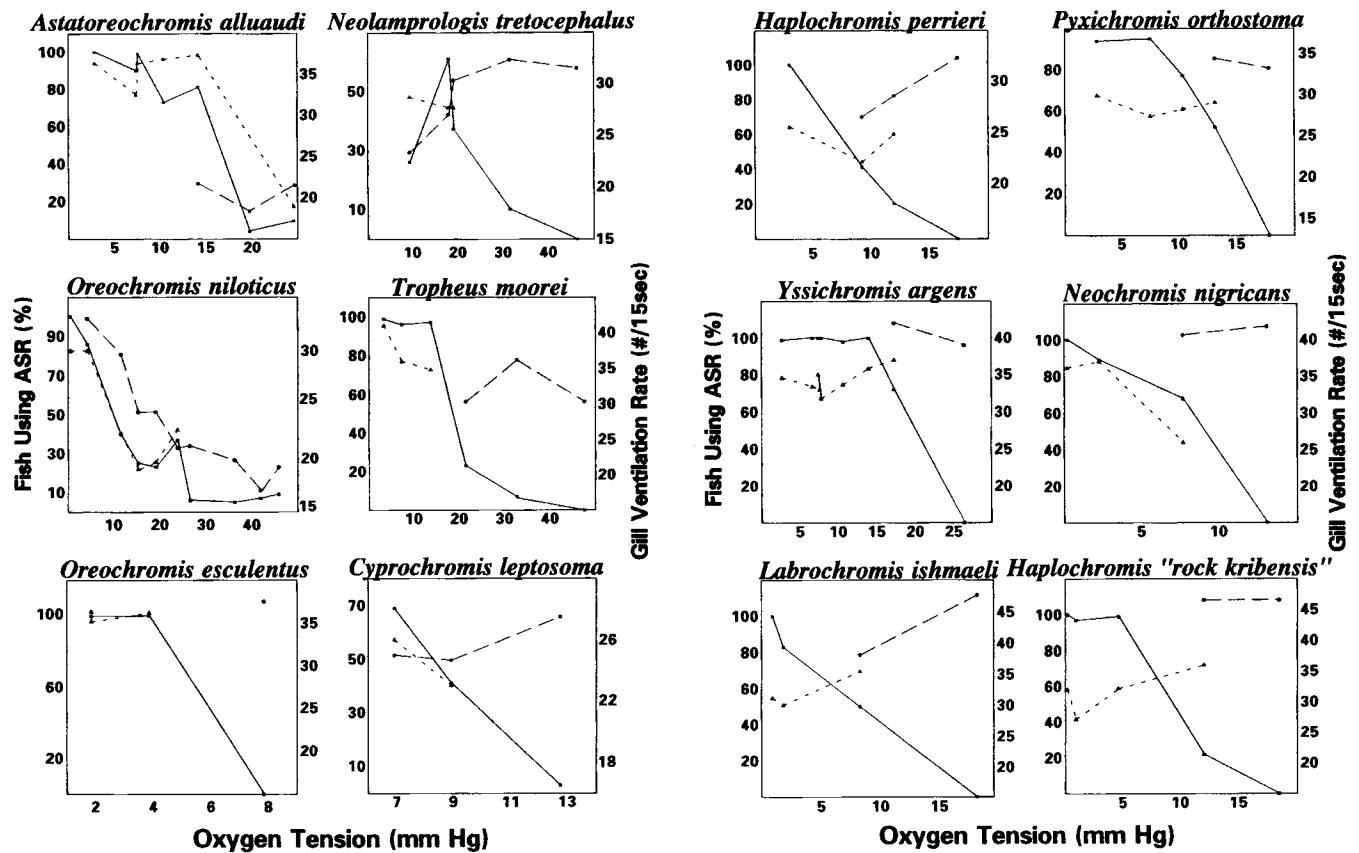


Figure 1. Reactions of 12 species of East African cichlids to progressive hypoxia. Both the time spent at the surface (solid line/squares) and gill ventilation rate are indicated in relation to subsurface  $P_{O_2}$ . Gill ventilation rate is indicated for fishes not using ASR (dashed line, circles) and fishes using ASR (dotted line, triangles).

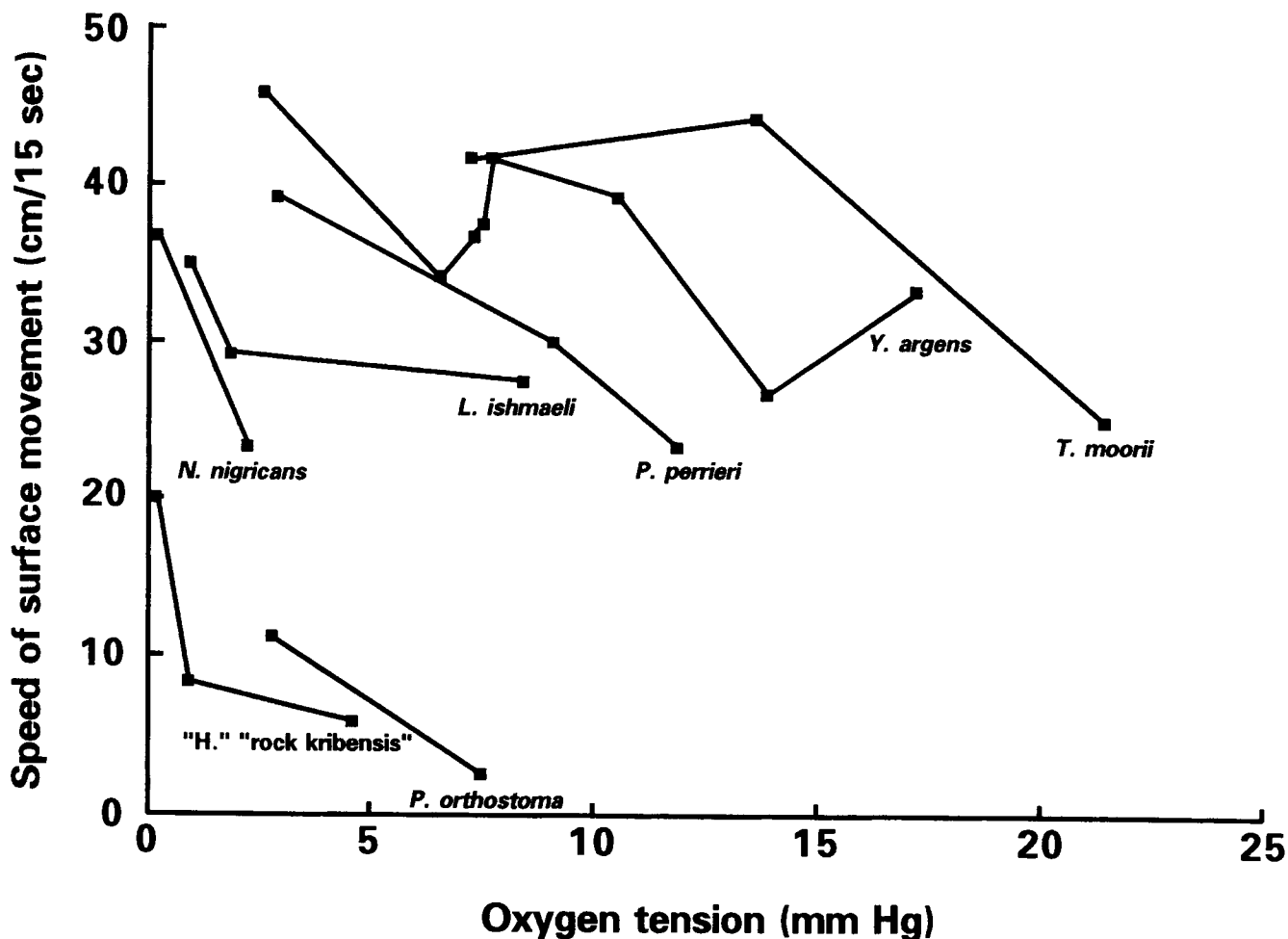


Figure 2. The relationship between subsurface  $P_{O_2}$  and the speed of surface movement for seven species of East African cichlids using aquatic surface respiration.

Among them, only *Neochromis nigricans* lost equilibrium, with its time to loss of equilibrium averaging 1504 seconds after introduction (25 minutes; Fig. 3). Similarly, the two tilapiines showed no loss of equilibrium. In contrast, all of the Lake Tanganyikan fish lost equilibrium during this experiment (mean times to loss of equilibrium: *Cyprichromis leptosoma*, 187 seconds; *Neolamprologis tredocephalus*, 326 seconds; *Tropheus moorii*, 597 seconds; Fig. 3a). None of the fish in the control treatments lost equilibrium or showed obvious signs of distress.

We compared response variables (bubble exchange frequency, gill ventilation rate, and speed of surface movement) between the end of this acute experiment (after 30 minutes at  $<0.2$  mg/L) and at the end of the progressive hypoxia experiment (after 30 minutes at  $<0.2$  mg/L). There was no difference in gill ventilation rate between progressive hypoxia (32.2 gill ventilations/15 seconds) and acute hypoxia (31.4 gill ventilations/15 seconds, Wilcoxon test,  $z = -0.840$ ,  $p = 0.401$ ). Similarly, speed at the surface during ASR did not differ be-

tween the two experimental conditions (progressive hypoxia: mean = 30.2 cm/15 seconds; acute hypoxia: mean = 21.8 cm/15 seconds,  $z = -1.75$ ,  $p = 0.080$ ). The most notable difference in the response of fishes to acute versus progressive hypoxia was observed in the shorter bubble exchange time under conditions of acute hypoxia (progressive hypoxia: mean = 59.1 seconds; acute hypoxia: mean = 36.9 seconds,  $z = -2.366$ ,  $p = 0.018$ ).

With the exception of *Oreochromis niloticus* and *O. esculentus*, individuals of all species lost equilibrium when exposed to acute hypoxia without access to the surface. But the time to loss of equilibrium ranged between an average of 85 seconds for *Cyprichromis leptosoma* and 1596 seconds for *Astatoreochromis alluaudi* (Fig. 3b). The haplochromines from Lake Victoria maintained equilibrium significantly longer than the cichlids from Lake Tanganyika (Mann-Whitney  $U$  test,  $U = 0.0$ ,  $p = 0.0167$ , Lake Victoria: mean = 1005 seconds; Lake Tanganyika: mean = 298 seconds). Within the group of haplochromine cichlids from Lake Victoria, *Neochromis*



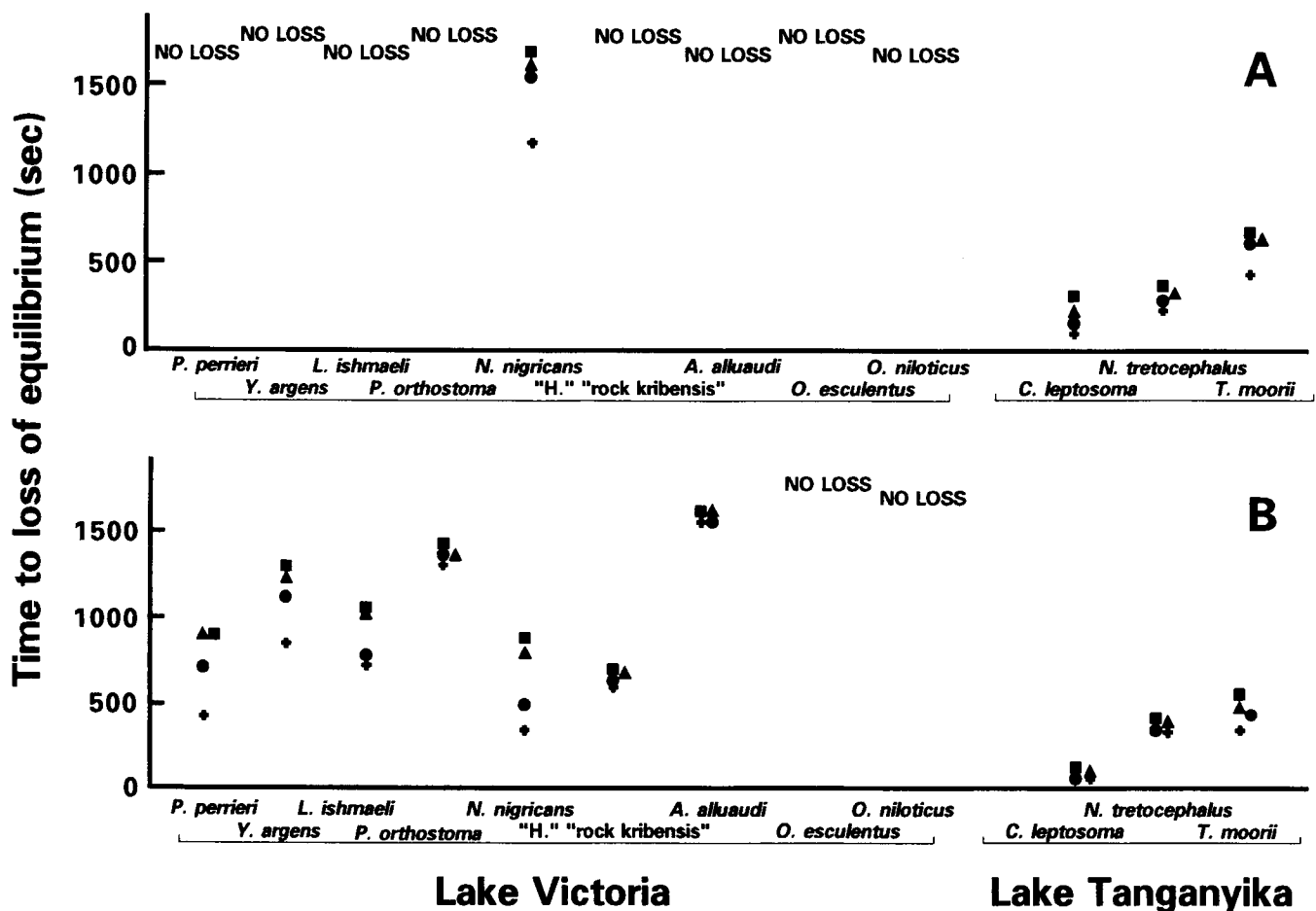


Figure 3. Time to loss of equilibrium for individuals of 12 species and East African cichlids when exposed to acute hypoxia with access to the surface (a) and time to loss of equilibrium for individuals of 12 species of East African cichlids when exposed to acute hypoxia without access to the surface (b). Each symbol represents an individual fish.

*nigricans* and "Haplochromis" "rock-kribensis" lost equilibrium more quickly than the others. There was no difference in the mean time to loss of equilibrium between the species from Lake Victoria that have been heavily affected by the recent changes in the lake (mean = 1068 seconds) and those that have not been heavily affected by the changes (mean = 921 seconds;  $U = 6.0$ ,  $p = 1.00$ , Fig. 3b).

Neither *O. esculentus* nor *O. niloticus* lost equilibrium when exposed to acute hypoxia without access to the surface (Fig. 3b). These species quickly became inactive, lay on their ventral surfaces or on their sides on the bottom of the tank, and exhibited extremely slow and shallow gill ventilations (mean gill ventilation rate = 6/15 seconds). The fish were left under these conditions for 50 minutes and quickly recovered normal activity levels upon being placed in well oxygenated water. Although this suggests a capacity for anaerobic metabolism, such a mechanism cannot be determined from the tests performed. Again, none of the fish in the control experiments lost equilibrium or showed obvious signs of distress.

## Discussion

The spatial distribution of hypoxic water is potentially an important factor influencing fish species distributions and interactions. This is particularly relevant in Lake Victoria, where intense predation by the Nile perch and increasing anoxia greatly affect the indigenous fauna. Relatively high hypoxia tolerance may be important in permitting some indigenous fishes in Lake Victoria to adjust to the recent changes in the physical and biological environment of the lake because (1) it may permit endangered species to use hypoxic regions as refugia from the Nile perch, which may have higher oxygen requirements; (2) it may allow prey species to use structured in-shore habitats as refugia from the Nile perch without adverse affects from the low-oxygen conditions that can occur there; and (3) it may allow indigenous species to survive periodic occurrences of poorly oxygenated water in the open lake, a situation that is becoming more common because of changes in the limnological conditions of the lake.

### Respiratory Behavior and Variation in Hypoxia Tolerance

All species examined used aquatic surface respiration in response to hypoxia when there was access to the surface. When denied access to the surface all species lost equilibrium, with the exception of *Oreochromis niloticus* and *O. esculentus*. This points out the survival value of aquatic surface respiration. Aquatic surface respiration is a widespread adaptation to hypoxia (Gee et al. 1978; Kramer & McClure 1982; Kramer 1983a, 1983b, 1987; Gee & Gee 1991) and increases the probability of survival under low-oxygen conditions for a variety of fishes (Kramer & McClure 1982). There is much variation among species, however, in their efficiency at using this strategy. Kramer (1983b) found evidence to suggest that aquatic surface respiration is more common among species from potentially hypoxic habitats in Panama than in consistently well-oxygenated habitats. Similarly, in a study of the metabolic rate and hypoxia tolerance of 10 species of East African cichlids (five from Lake Tanganyika, three from Lake Malawi, one from Stanley Pool of the Zaire River, and *Oreochromis niloticus*), Verheyen et al. (1994) found that six species that naturally occur in well-aerated water were not able to perform ASR when subjected to severe hypoxia.

Seven of the 12 species examined in the hypoxia experiments with access to the surface were observed to swim continuously across the surface during ASR while continuing to actively ventilate their gills. Much of this movement was directed backward. Chapman et al. (1994) suggested that the continuous active forward motion at the surface during ASR in *Synodontis afrofischeri* forces more well-oxygenated surface water over the gills than could be achieved by gill ventilation alone and contributes to lift. Backward motion is not likely to contribute to lift or force more well-oxygenated water over the gills, but it does expose the fish to new surface film. Over the range of species examined there was an increase in the speed of surface movement with decreasing  $P_{O_2}$ , suggesting that the movement may be a response to the need for more effective utilization of the surface waters. In addition, buccal bubble holding, which was observed in all but one species (*Pyxichromis orthostoma*), may increase the efficiency of ASR. This behavior has been advocated as a buoyancy compensation mechanism for negatively buoyant fish (such as gobies, Gee & Gee 1991) and also as a mechanism to increase the oxygen in the water passing over the bubble (Burggren 1982; Kramer 1983b). Despite these strategies for increasing the efficiency of ASR, there was still much variation among species in hypoxia tolerance.

Trophic adaptations may relate to hypoxia tolerance and account for some of the variation among species due to covariation between feeding habit and habitat selection. For example, *Neochromis nigricans* was the only haplochromine from Lake Victoria to lose equilib-

rium during progressive exposure to hypoxia. Like *Tropheus moorii*, its ecological counterpart from Lake Tanganyika, *N. nigricans* grazes algae from rocks in shallow, clear, turbulent water, where high oxygen levels are typical.

High tolerance to low oxygen may have contributed to the widespread distribution of many species in the Lake Victoria Basin because it would have facilitated their dispersal through extensive papyrus swamps and permitted broader habitat use. *Oreochromis niloticus* is a widespread species that occupies the entire Nile basin. It was successfully introduced to Lake Victoria in the 1950s. *Astatoreochromis alluaudi* is also a widespread species and still occupies its historic range in Lake Victoria and its satellite lakes and affluent streams. These two species exhibited a relatively high tolerance to hypoxic conditions, with well-developed ASR and bubble-holding capabilities and no loss of equilibrium during prolonged hypoxia. *Astatoreochromis alluaudi* showed the highest tolerance of all the haplochromines when subjected to acute hypoxia without access to the surface, and *Oreochromis niloticus* did not lose equilibrium when exposed to acute hypoxia with no surface access. Verheyen et al. (1994) also found high tolerance and use of ASR in *Oreochromis niloticus* when fish were exposed to low oxygen under experimental conditions, which they attribute to the common occurrence of this species in hypoxic habitats.

Cichlids endemic to Lake Victoria were more tolerant of hypoxia than ecologically similar species from Lake Tanganyika, and they appeared to use ASR to greater advantage than those from Lake Tanganyika, based on the assumption that decline in gill ventilation rates with onset of ASR indicates enhancement of oxygen intake. Having evolved in a shallow, swampy, broad basin, it is not surprising that the haplochromines from Lake Victoria may be, as a fauna, more tolerant of hypoxia than the fauna from Lake Tanganyika. It should be noted, however, that the cichlids from Lake Tanganyika that were considered in this study were species that occur in well-oxygenated rocky habitats in shallow or moderate depths. In a study of deep-water fishes in Lake Tanganyika, Coulter (1967) captured a variety of species in deep-water nets (150–200 meters down) in anoxic or extremely hypoxic waters, suggesting that some deep-water species in the lake have remarkably high tolerance to low oxygen, which permits their exploitation of benthic slopes of the lake. Verheyen et al. (1994) presents data on the metabolic rate and hypoxia tolerance for five cichlids from Lake Tanganyika, four from well-oxygenated rocky littoral habitats (*Tropheus moorii*, *Eretmodus cyanostictus*, *Neolamprologus brichardi*, *Julidochromis marlieri*) and one (*Astatotilapia burtoni*) from less-aerated water (over sand/mud between littoral vegetation). *A. burtoni* showed higher survival rates under experimentally induced gradual hypoxia and

was the only species to exhibit ASR under acute hypoxia. These studies demonstrate the important link between hypoxia tolerance and spatial distribution patterns within fish communities.

### Low Oxygen Refugia

Wetlands, dominated by papyrus, are widespread throughout the Lake Victoria Basin and may protect some fishes from Nile perch predation for two reasons. First, they may provide both structural and low-oxygen refugia for prey species tolerant of the hypoxic conditions that prevail in the dense interior of many wetland areas. Second, papyrus swamps may serve as barriers to the dispersal of Nile perch, permitting shallow-water species tolerant of chronic exposure to hypoxia to persist in open lagoon areas behind the fringing swamp, in papyrus choked tributaries, or in small satellite lakes. The wetland areas of Lake Victoria have not been well explored. Ogutu-Ohwayo (1993) notes, however, that many surviving haplochromine cichlids are found associated with marginal macrophytes, where they can find protection from Nile perch. In addition, preliminary survey data in Lake Nabugabo, where native populations have declined or disappeared since the introduction of the Nile perch in 1960, indicate that some of the species thought to be rare or extinct in Nabugabo can be found in wetland areas around the lake, where Nile perch are rare (Ogutu-Ohwayo 1993; Chapman & Chapman, unpublished data). If papyrus swamps are barriers to the dispersal of Nile perch, the extensive areas of fringing swamp in Lakes Victoria and Kyoga may permit species to persist in the lagoons and satellite lakes (Kaufman & Ochumba 1993) separated from the main lake by these wetland areas. Welcomme (1970) studied the fish populations that colonized lagoons that formed behind the fringing swamp of Lake Victoria with the abnormally high water levels between 1961 and 1964. His studies demonstrated that many species are capable of colonizing and surviving in wetland lagoons. Welcomme (1970) suggested that the deoxygenated conditions of the water under the floating vegetation that isolated the lagoons accounted for the drop in species number with increasing isolation from the main lake. All lagoons experienced a nocturnal reduction in dissolved oxygen, and thus species that survived were those that could tolerate low dissolved oxygen (Welcomme 1970). Twenty-seven species were recorded from these lagoons, but the greater the separation of the lagoon from the lake the fewer species of haplochromine cichlids recorded. The rapid colonization of these lagoons under high water-level conditions and the variety of species that were found suggests the potential value of wetland lagoons as refugia if Nile perch are unable to penetrate fringing swamps. On a larger scale, populations of the highly endangered *Oreochromis esculentus* and *Oreochromis*

*variabilis* can still be found in small satellite lakes of Lake Victoria and Lake Kyoga (Ogutu-Ohwayo 1993; Kaufman & Chandler, unpublished data). Many of these satellites are connected by papyrus swamps to the main lakes that harbor introduced Nile perch. It is conceivable that the papyrus swamps are serving as barriers to the dispersal of the Nile perch, permitting populations of endangered species such as *Oreochromis esculentus* and other potential prey species to survive in these peripheral lakes.

Wetland areas may serve as refugia for prey species from introduced predators if the low oxygen conditions that prevail in many swamps are unsuitable for exploitation by the predator or because of their structural complexity, which may reduce predatory efficiency. Many fishes, particularly at juvenile stages, select shallower or more structurally complex portions of the habitat to minimize predation (Mittlebach 1981; Werner et al. 1983; He & Kitchell 1990; Brown & Moyle 1991). The presence of structural refugia may be critical for the maintenance of fish faunal structure and diversity in systems where nonnative predators have been introduced. In Florida, for example, the introduced pike killifish (*Belonesox belizanus*) has been documented as a major source of mortality among native forage populations (Taylor et al. 1984); however, predation by the pike killifish is reduced in the presence of heavy vegetative cover (*Hydrilla verticillata*), which may serve as a structural refugium for prey species (Miley 1978; Taylor et al. 1984).

If wetland refugia exist, they may be inhabited by remnants of larger populations that had a broader distribution pattern prior to the introduction of the predator. Alternatively, fish may shift their habitat use from open-water habitats into marginal areas. Shifts in habitat use due to the presence of predators are well documented for a variety of species. He and Kitchell (1990) conducted a whole-lake manipulation in which northern pike, a piscivorous predator, was introduced into a piscivore-free lake. Four fish species showed significant shifts between habitats in response to the presence of the introduced predator. When a substantial density of planktivorous minnows was introduced into a lake with a small population of predatory fish, Carpenter et al. (1987) found that the minnows largely abandoned the pelagic zone and retreated to littoral refugia. Brown and Moyle (1991) found that the introduction of squawfish to the Eel River resulted in dramatic changes in the habitat and microhabitat partitioning of the resident fish assemblage. Other studies in streams and experimental ponds have demonstrated marked effects of predatory fish on the spatial structure of the fish community (Werner et al. 1983; Power et al. 1985; Schlosser 1987). Because habitat shifts in response to predator risk are not uncommon, it is not unreasonable to expect similar distributional shifts by some indigenous species in Lake Victoria

from open waters to more marginal habitats, but exploitation of marginal refugia will depend on the abilities of the species to adjust to the conditions that prevail in the new habitat.

In addition to the potential of wetland refugia, hypoxia-tolerant deepwater species may find refuge from hypoxia-intolerant predators by inhabiting the deeper waters of stratified lakes near the oxycline. In Lake Victoria, use of these areas could be a short-term response to the incidence of Nile perch, which demands an acute tolerance of hypoxic or anoxic waters, or a longer-term pattern of use. Recent trawl data from greater than 30 meters deep in Lake Victoria contained numerous haplochromines (Kaufman & Ochumba 1993). But the fish kills associated with upwellings of anoxic water suggest that use of this region may impose a high risk for some species (Kaufman & Ochumba 1993; Kolding 1993). In addition, there is the possibility that Nile perch can dive beneath the oxycline to forage because they have been found to feed heavily on *Caridina nilotica*, a native detritivorous shrimp, that is abundant below the oxycline (Kaufman & Ochumba 1993).

Within the range species tested hypoxia tolerance per se appeared to be unrelated to the extent to which particular species had declined since the major demographic and limnological changes in the lake. The number of species considered in this study was small, however, and several factors (for example, trophic status, habitat) may covary with tolerance. Differences in hypoxia tolerance were probably not a significant factor in the replacement of *Oreochromis esculentus* by *Oreochromis niloticus* in Lake Victoria. Both species exhibited impressive ASR and bubble-holding capabilities, and neither lost equilibrium during prolonged hypoxia, even when denied access to the surface. Haplochromine cichlids that are currently common (*Neochromis nigricans*, "Haplochromis" "rock kribensis", *Pyxichromis orthostoma*, *Astatoreochromis alluaudi*) were not consistently more tolerant to hypoxia than species that have nearly or totally disappeared from the lake (*Yssichromis argens*, *Prognathochromis perrieri*, *Labrochromis ishmaeli*). This may be a result of the fact that both *Neochromis nigricans* and "Haplochromis" "rock kribensis" are inhabitants of shallow, rocky environments, a habitat that is both rich in oxygen and of sufficient structural complexity to decrease the risk of Nile perch predation. Witte et al. (1992) provide quantitative data on the decline of haplochromine cichlids in the Mwanza Gulf of Lake Victoria. They found that most stenotypic rock-dwelling species have survived and note that species with reduced habitat-overlap with the Nile perch have shown lower rates of disappearance. *Pyxichromis orthostoma*, a species common in inshore vegetated areas, was the most tolerant of the endemic haplochromines from Lake Victoria when exposed to acute hypoxia without access to the surface. We expect that as other

littoral species from vegetated habitats and remnant deep-water haplochromines become available for study, they may prove to be highly tolerant of low oxygen levels. Some rare species or species that are thought to have disappeared (such as *Yssichromis argens*, *Prognathochromis perrieri*, *Labrochromis ishmaeli*) may be currently present in low-oxygen refugia in wetlands or deeper waters that have not been adequately sampled in many areas of the lake. The generally high levels of hypoxia tolerance under both acute and progressive exposure in the species of cichlids from Lake Victoria suggests the potential for use of low-oxygen refugia. Future experiments that examine a broader range of species, longer-term chronic exposure to low oxygen, and acclimation to hypoxia may permit a finer assessment of the potential for long-term utilization of low-oxygen refugia and response to increased anoxia in Lake Victoria by different haplochromine cichlid species.

The introduction of nonnative species into new habitats is a common practice throughout the world and is difficult to regulate. In a conservation context biologists face several critical questions with respect to the consequences of introductions, and some of the most significant issues relate to the introduction of predators into ecosystems. Knowledge of the types of refugia used by prey species when confronted with exotic predators is important to the development of effective conservation strategies. It may be possible to minimize biodiversity loss through the management or manipulation of refugia. For Lake Victoria, for example, it has been recommended that "fish parks" be established to protect the native fish and maintain spawning stocks of commercially important species. This can be achieved only if there is sufficient data on the characteristics and distribution of refugia and understanding of the biological characteristics of species that permit exploitation of these refugia. In Lake Victoria low-oxygen tolerance may permit endangered cichlid species to use structured inshore habitats or deeper waters near the oxycline as refugia from Nile perch and to adjust to the increasing levels of anoxia in the lake.

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