



Respiratory characters of three species of haplochromine cichlids: Implications for use of wetland refugia

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Respiratory characters of three east African haplochromine cichlid species that differ in their use of hypoxic wetlands were examined to consider the potential of dissolved oxygen as one factor affecting habitat use. All three species had a large gill surface area, ranging from the 67th (*Pseudocrenilabrus multicolor victoriae*) to 98th (*Astatotilapia velifer*) percentile of the known gill size range for freshwater fishes. *Pseudocrenilabrus multicolor victoriae* was the most tolerant to hypoxia exhibiting the lowest aquatic surface respiration (R_S) thresholds and lowest critical oxygen tension of the three species. *Astatotilapia velifer* had the highest ASR thresholds, gill ventilation rates, and level of surface activity of the three species, indicating a relatively low tolerance to hypoxia. *Prognathochromis venator* was intermediate in its response to hypoxia. These findings are discussed in light of survivorship and distribution patterns of these species following Nile perch introduction into Lake Nabugabo. © 2000 The Fisheries Society of the British Isles

Key words: haplochromine cichlids; respiratory characteristics; hypoxia; wetlands; refugia; species introductions.

INTRODUCTION

The species flock of endemic haplochromine cichlids in Lake Victoria (600+ species) is well-known as one of the most recent and extensive radiations of vertebrate taxa (Greenwood, 1980; Kaufman, 1992; Kaufman *et al.*, 1997). In addition, a diverse assemblage of non-cichlids inhabits the lake (Greenwood, 1966). Basin diversity is supplemented by smaller lakes (e.g. lakes Kyoga, Nabugabo, Nwampassa) with faunas similar, though less rich, than Lake Victoria.

In the late 1950s and early 1960s, Nile perch *Lates niloticus* (L.) was introduced into Lake Victoria and some of its surrounding lakes in an attempt to convert the vast numbers of small haplochromine cichlids into a large, exportable food product (Fryer, 1960; Ogutu-Ohwayo, 1990; Witte *et al.*, 1992). The species comprised a small portion of the fishery until the early 1980s when its numbers increased dramatically (Kaufman, 1992). This rapid increase in Nile perch coincided with rapid loss of fish diversity in the lake (Ogutu-Ohwayo, 1990; Kaufman, 1992). In Lake Victoria, an estimated 50% of the endemic

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haplochromine cichlids as well as many indigenous non-cichlids have declined or disappeared during the last 20 years (Ogutu-Ohwayo, 1990; Kaufman, 1992; Witte *et al.*, 1992; Kaufman *et al.*, 1997). Similar changes have also occurred with the introduction of Nile perch into Lake Kyoga (Ogutu-Ohwayo, 1994) and Lake Nabugabo (Ogutu-Ohwayo, 1993).

Studies aimed at identifying faunal refugia have documented remnant populations of haplochromines and other indigenous non-cichlids (Witte *et al.*, 1992; Chapman *et al.*, 1996a, b; Kaufman *et al.*, 1997). Refugia have been identified in the rocky shores of the Mwanza Gulf, where rock crevices shelter endemic haplochromines from predation (Witte *et al.*, 1992; Seehausen, 1996). Though small in assemblage diversity, satellite lakes that have not experienced introductions by Nile perch (e.g. lakes Nwampassa, Kayugi, and Manywa) contain threatened species extirpated from lakes with Nile perch (Ogutu-Ohwayo, 1993; Kaufman *et al.*, 1997). Finally, wetland areas may protect prey species by limiting exploitation by Nile perch (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999; Schofield & Chapman, 1999).

Extensive areas of fringing wetland in the Lake Victoria basin, dominated by papyrus *Cyperus papyrus* and *Miscanthidium violaceum*, permit remnant populations of some species to persist in the small lagoons, satellite lakes, and tributaries separated by swampy divides from open water areas with Nile perch (Chapman *et al.*, 1996a, b; Kaufman *et al.*, 1997; Chapman & Chapman, 1998). Thick macrophyte growth may inhibit the hunting efficiency and dispersal of Nile perch. In addition, the extremely low levels of dissolved oxygen that characterize the dense interior of papyrus and *Miscanthidium* swamps (Carter, 1955; Chapman *et al.*, 1998; Chapman & Chapman, 1998) may also limit exploitation by Nile perch since this species has a low tolerance to hypoxia (Schofield & Chapman, 2000).

The wetlands of Lake Nabugabo, a small satellite lake of Lake Victoria, hold a unique suite of species, many of which have disappeared from the open waters of the lake since the introduction of Nile perch in the early 1960s (Chapman *et al.*, 1996b; Rosenberger & Chapman, 1999). However, these wetlands harbour only a sub-set of Lake Nabugabo's former diversity (Chapman *et al.*, 1996b; Rosenberger & Chapman, 1999). Some haplochromine cichlids, such as *Prognathochromis venator* (Greenwood), and other non-cichlids that have disappeared from Lake Nabugabo, are not found in wetland refugia.

This study builds on previous research in the Lake Victoria basin to explore the potential of chronic hypoxia as one factor that might explain interspecific variation in the use of the wetland refugia. It is focused on species from the Lake Nabugabo region and examines the low-oxygen tolerance of three phylogenetically similar species (Cichlidae, haplochromine lineage) that differ in persistence with Nile perch and their use of hypoxic wetlands as refugia. First, the behavioral response of these species to progressive and acute hypoxia is compared. Second, differences in physiological response to hypoxia are examined by measuring their metabolic rate and critical oxygen tension. Finally, the total gill filament length, gill lamellar density, and total gill surface area are compared among the three species as indicators of their relative capacities to extract oxygen from the water.

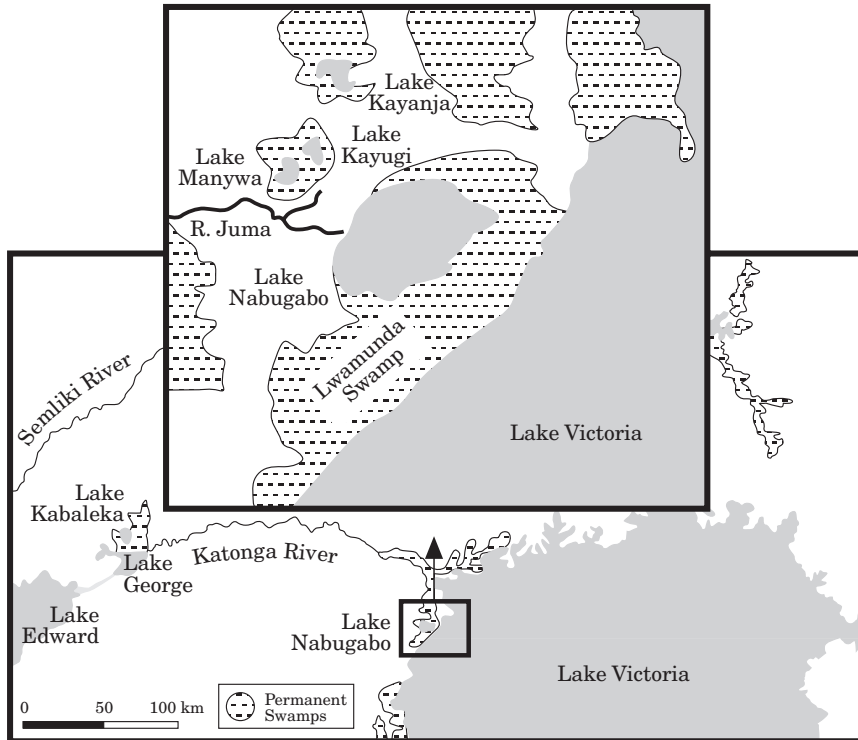


FIG. 1. Map of Lake Nabugabo, a small satellite lake of Lake Victoria in Uganda, East Africa. Nearby satellite lakes Kayanja, Kayugi, and Manywa are also shown.

MATERIALS AND METHODS

STUDY SITE

Lake Nabugabo is a small satellite lake (24 km², 5 km in diameter, mean depth 4.5 m) of Lake Victoria. The lake lies within an extensive wetland that was formerly a bay on the western shore of Lake Victoria (Fig. 1) (Worthington, 1932; Greenwood, 1965; Ogutu-Ohwayo, 1993). Long shore bars that isolate Lake Nabugabo from Lake Victoria were created during water-level fluctuations about 4000 years ago (Greenwood, 1965, 1966). The lake margin is primarily marsh, dominated by hippo grass *Vossia cuspidata*, *M. violaceum*, and water lilies *Nymphaea lotus* and *N. caerulea*, with small stands of papyrus. Its main tributary, the Juma River, along with numerous small springs that discharge along the lakeshore, feed Lake Nabugabo (Greenwood, 1965). Outflow from the lake is eastward via the Lwamunda Swamp, with seepage through the sandbar that forms the eastern barrier separating Lake Nabugabo from Lake Victoria (Greenwood, 1965). The Lwamunda Swamp is an extensive wetland surrounding much of the lake (c. 4 km wide) and contains permanent lagoons and small intermittent streams (Fig. 1).

STUDY SPECIES

Pseudocrenilabrus multicolor victoriae (Schoeller) is a widespread haplochromine cichlid in the Nile River basin (Schierwater & Mrowka, 1987). In Lake Nabugabo, *P. multicolor victoriae* has declined coincident with the increase in Nile perch numbers, but persists in high abundance in wetland refugia such as the Juma River and wetland lagoons of the Lwamunda Swamp (Chapman *et al.*, 1996b; Rosenberger & Chapman, 1999). For this study specimens of *P. multicolor victoriae* were captured from upstream regions of the Juma River with metal minnow traps (0.63 cm mesh) set overnight. This area is dominated by papyrus, and oxygen content is chronically low (Chapman

et al., 1996b; Rosenberger & Chapman, 1999). Greenwood (1965) considered *Prognathochromis venator* and *Astatotilapia velifer* (Trewavas) as endemic to Lake Nabugabo. Later work has indicated that their distribution includes Lake Nabugabo and other small satellite lakes near Nabugabo (Lakes Manywa and Kayanja, Kaufman & Ochumba, 1993; Ogutu-Ohwayo, 1993). *Prognathochromis venator* is a piscivorous haplochromine (Greenwood, 1965) that disappeared from Lake Nabugabo subsequent to the introduction of Nile perch (Ogutu-Ohwayo, 1993; Chapman *et al.*, 1996b) and is not found in associated wetland refugia (Chapman *et al.*, 1996a, b). Specimens were collected using a small mesh seine from the open waters of Lake Kayanja, a small lake (1.6 km in diameter) in the Lake Nabugabo region surrounded by a narrow wetland margin dominated by *M. violaceum*. Lake Kayanja has no Nile perch and has a fauna similar to the pre-Nile perch fauna of Lake Nabugabo. *Astatotilapia velifer* has declined in the open waters of Lake Nabugabo since the introduction of Nile perch, but still occurs in ecotonal wetlands (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999). For this study *A. velifer* specimens were collected in metal minnow traps set overnight in the ecotone of the Juma River. Waters of the ecotone, dominated by hippo grass, have a high amount of interaction with the open waters of Lake Nabugabo, high variation in oxygen content, and a unique, though unstable, species assemblage (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999).

RESPIRATORY BEHAVIOUR

To quantify the behavioural response of *P. multicolor victoriae*, *P. venator*, and *A. velifer* to progressive hypoxia, captured fish were held in large plastic containers aerated periodically with a battery operated bubbler [dissolved oxygen (0600–0800 hours) = 3.5 ± 1.1 mg l⁻¹, s.d. temperature = 19.7 ± 0.5 °C; dissolved oxygen (1500–1700 hours) = 3.5 ± 1.5 mg l⁻¹, temperature = 22.6 ± 1.9 °C]. To minimize the number of fish collected, a group of eight individuals was selected for each species, and behavioural trials were repeated six times on each group of fish. To minimize the effects of dependence among trials, experiments were separated by at least 48 h, and results from individual fish were averaged for each trial. Individuals were transferred to a plexiglas aquarium (50 × 22 × 30 cm, average water temperature = 22.9° C) and acclimated for 1 h. This seemed sufficient to permit fish to settle in the aquarium. After the acclimation period, oxygen was lowered slowly with the addition of small amounts of sodium sulphite (following Chapman & Liem, 1995; Olowo & Chapman, 1996) over 3.5 h, and then held at levels <0.03 mg l⁻¹ for 30 min. The remoteness of the field site precluded the use of nitrogen gas to lower dissolved oxygen levels. However, Lewis (1970) found no observable differences in the behavioural responses of fishes to water freed of oxygen with sodium sulphite and water freed of oxygen by bubbling with nitrogen gas. A blind positioned in front of the aquarium permitted observations through a small viewing port.

Many cichlids are known to use aquatic surface respiration (R_S ; Kramer & Mehegan, 1981) in response to hypoxia, ventilating their gills with water from the air-water interface where diffusion produces a very thin layer of well-oxygenated water (Kramer & McClure, 1982; Chapman *et al.*, 1995). In addition, some species hold bubbles in their buccal cavities during periods of oxygen stress, which may increase the oxygen content of water passing over the gills or increase buoyancy at the water surface. Observations were taken every 15 min. The following parameters were recorded from behind the blind: gill ventilation rate (number of ventilations in a 15-s period recorded for each fish), number of fish using R_S (recorded every 10 s for 100 s), aggressive interactions (recorded every 10 s for 100 s), number of individuals using buccal bubble holding, and speed of movement at the surface during R_S (distance moved in 10 s for each of the eight fish). Gill ventilations were recorded when deep enough to be clearly visible. The outline of buccal bubbles could be observed clearly when an individual's mouth was extended to obtain air at the surface. Aggressive interactions usually involved fish pursuing other individuals, sometimes nipping at fins or tails. On rare occasions, the fishes would lock mouths during these interactions. The edge of the experimental aquarium was marked at regular intervals in order to gauge movement of fishes at the surface. If any individual

lost equilibrium, it was removed quickly from the experimental tank and placed in well-oxygenated water to recover.

The level of oxygen at which 10% ($R_{S_{10}}$), 50% ($R_{S_{50}}$), and 90% ($R_{S_{90}}$) of the fish performed R_S was estimated by fitting curves to plots of PO_2 and per cent R_S . Per cent R_S was calculated as the number of fish in a group using R_S divided by the total number of fish, averaged over the 10 observations in a given sample. Recorded concentrations of dissolved oxygen were converted to PO_2 using tables in Davis (1975). Because data violated normality assumptions, the Kruskal–Wallis test and the K-W multiple comparisons test (Conover, 1980) were used to detect differences in oxygen levels at which R_S was initiated, speed at the surface, aggression, and per cent bubble holding among species. The Wilcoxon signed-ranks test was used to detect differences in gill ventilation rates just before and after the initiation of R_S .

To examine the response of species to acute hypoxia with access to the surface, five fishes were transferred quickly from well-oxygenated holding tanks to an experimental tank that had only trace amounts of oxygen in the water (dissolved oxygen = 0.17 ± 0.06 mg l^{-1} , s.d.). Behavioural data were taken immediately after introduction to the aquarium and at 15-min intervals for 30 min. The Kruskal–Wallis test and the K-W multiple comparisons test were used to detect differences in R_S thresholds, speed at the surface, and per cent bubble holding among species.

The response of fish to acute hypoxia without surface access was observed by suspending a plastic sheet 2 cm below the surface of the water to prevent that access. Again, five fish from well-oxygenated holding tanks were transferred quickly to the experimental tank that had only trace amounts of oxygen (mean dissolved oxygen = 0.17 ± 0.06 mg l^{-1} , s.d.). Only time to loss of equilibrium (L_E) was recorded. When the five fish lost equilibrium, the experiment was terminated, and fish were revived immediately in well-oxygenated water. Other behavioural data were not recorded because the fish generally lost equilibrium within the 30-min time frame. The Kruskal–Wallis and the K-W multiple comparisons tests were used to test for differences among species in time to L_E .

METABOLIC RATE AND CRITICAL OXYGEN TENSION

Tolerance to low oxygen may relate in part to the metabolic rate of a fish (Verheyen *et al.*, 1994). Fishes will regulate their metabolic rate over a range of dissolved oxygen concentrations; however, at some point, a further reduction in oxygen tension will produce a shift from a metabolic rate that is independent of oxygen concentration to one that is dependent on oxygen level. The point is referred to as the critical oxygen tension (Ultsch *et al.*, 1978). Both metabolic rate and critical oxygen tension were measured for each species using a closed respirometer. Metabolic rate was determined as routine oxygen consumption (rates during random movement under experimental conditions, Saint-Paul, 1984) for a range of body sizes for each species (Table I). Total metabolic rate was calculated using data collected at least 30 min after the container was sealed with the probe and prior to estimated critical oxygen tension. Winberg (1956, 1961) derived a standard curve for the relationship between total metabolic rate (at 20° C) and body size for freshwater fishes, and Q_{10} values based on literature data. The observed metabolic rates were adjusted to 20° C using Q_{10} values in Winberg (1956) to permit comparison among the three species and with Winberg's standard curve. Critical oxygen tension was determined through graphic interpretation and a BASIC program by Yeager & Ultsch (1989) designed to fit two regression lines to a data set by least squares method.

The closed respirometer setup was designed for use at remote sites with no electricity. An individual fish was placed in a dark chamber with a battery-operated bubbler at least 1 h before an experimental trial. Overnight acclimation periods were limited by site logistics. The chamber was held in a larger water-filled cooler in a shaded facility to minimize variation in water temperature during and among runs. Water temperature averaged 18.6 ± 1.4 ° C (s.d.) for *P. multicolor victoriae*, 18.8 ± 1.0 ° C for *P. venator*, and 18.1 ± 0.8 ° C for *A. velifer*. At the start of each experiment, the chamber was sealed with an oxygen probe (YSI Model 600) connected to a data collection system run on solar power. The meter was programmed to take measurements of water temperature and

TABLE I. Sample size and body size (total length, L_T) of individuals used in respiratory experiments

Species	Respiratory behaviour	Metabolic rate and CPO ₂	Gill morphology
<i>Pseudocrenilabrus multicolor victoriae</i>			
<i>n</i>	8	12	10
Mean L_T (cm), S.D.	5.9 ± 0.8	5.0 ± 1.0	5.0 ± 1.1
Range L_T (cm)	4 to 9.5	3.6 to 6.9	4.3 to 7.8
<i>Prognathochromis venator</i>			
<i>n</i>	8	9	10
Mean L_T (cm), S.D.	7.5 ± 1.1	7.1 ± 1.9	7.8 ± 1.4
Range L_T (cm)	4 to 9.5	5.8 to 10.3	6.2 to 9.0
<i>Astatotilapia velifer</i>			
<i>n</i>	8	10	10
Mean L_T (cm), S.D.	4.2 ± 1.0	7.5 ± 1.8	7.1 ± 0.9
Range L_T (cm)	4.5 to 10.5	6.0 to 8.4	5.9 to 9.3

dissolved oxygen at 10-min intervals and to display plotted values throughout the trial. Once the critical oxygen tension was detected on the computer-generated plots, the experiment was terminated, and the water in the chamber was returned quickly to normoxia with the battery-powered bubbler. Following each trial, the total length and weight of the fish were recorded. Metabolic rates were measured on post-absorptive fish within 3 weeks of capture. During this time the fish were held in large plastic containers bubbled periodically with battery-operated bubblers [dissolved oxygen (0600–0900 hours)=4.1 ± 0.8 mg l⁻¹, S.D., temperature=18.1 ± 0.8° C; dissolved oxygen (1600–1800 hours)=5.3 ± 1.8 mg l⁻¹, temperature=20.7 ± 1.7° C].

Analysis of covariance was used to compare the total metabolic rate among species with body weight (total weight of preserved specimens) as the covariate. Both variables were log₁₀ transformed. Adjusted mean total metabolic rates (sample means adjusted for a common mean body weight and a common regression line) and their standard errors were calculated from the ANCOVA analysis, and the *a posteriori* Sidak test was used to test for significant differences between pairs of species. ANOVA and the Scheffe's multiple comparisons test were used to detect differences among species in critical oxygen tension and metabolic rate expressed as a percentage below the standard curve for freshwater fishes.

GILL MORPHOLOGY

Total gill filament length was measured for 10 specimens of each species (Table I). Specimens were preserved in paraformaldehyde (35 g l⁻¹), and total gill filament length was estimated following standard methods (Muir & Hughes, 1969; Hughes, 1980, 1984). For each fish, the four gill arches of the left side of the branchial basket were removed and separated. For each hemibranch of the gill arches, the length of every fifth gill filament was measured. Two successive measurements along a hemibranch were averaged and multiplied by the number of filaments in the section between the two filaments. Filament lengths were summed for the four hemibranchs and multiplied by 2 to produce an estimate of total gill filament length (L_{TF}). Average lamellar density (D_L) was also estimated for ten specimens of each species. Lamellar density was measured on every tenth filament in the dorsal, middle, and ventral parts of the second gill arch on the left side (Muir & Hughes, 1969; Hughes & Morgan, 1973). For five specimens of each species, the length and height of the secondary lamellae were measured a number of times over the length of every 10th filament (Galis & Barel, 1980). The average lamellar length multiplied by the average lamellar width for each filament was converted to an estimate

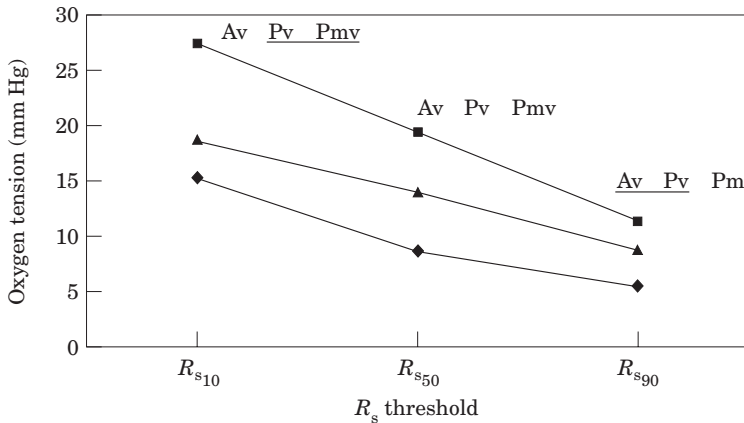


FIG. 2. R_s thresholds (10, 50 and 90) for three species of haplochromine cichlids from the Lake Nabugabo region of Uganda [*Pseudocrenilabrus multicolor victoriae*—Pmv (◆), *Prognathochromis venator*—Pv (▲), and *Astatotilapia velifer*—Av (■)]. Underlined species are not significantly different (R_{s10} , $\chi^2=9.7$, $P<0.01$; R_{s50} , $\chi^2=12.6$, $P<0.01$; R_{s90} , $\chi^2=9.2$, $P=0.01$; Kruskal–Wallis, multiple comparisons, $P<0.05$).

of lamellar area using a regression determined through the dissection of secondary lamellae from various sections of arch II from two specimens of each species (*P. multicolor victoriae*, $n=50$, area=(length \times width) $0.733+0.0004$, $r^2=0.77$, $P<0.01$; *P. venator*, $n=32$, area=(length \times width) $1.1989+0.0001$, $r^2=0.82$, $P<0.01$; *A. velifer*, $n=25$, area=(length \times width) $1.2611+0.0009$, $r^2=0.56$, $P=0.03$). Lamellar area was multiplied by 2 to produce an average bilateral surface area (A_L) on one side of the filament for the fish. Total gill surface area (A_G) was determined using the formula: $A_G=L_F \times 2 \times \bar{D}_L \times \bar{A}_L$.

ANCOVA was used to compare among populations total gill filament length, average lamellar density, and total gill surface area with body weight (total weight of preserved specimens) as the covariate. Variables were \log_{10} transformed. Adjusted means and their standard errors were calculated from the ANCOVA analysis, and the *a posteriori* Sidak test was used to test for significant differences between pairs of sites. Palzenberger & Pohla (1992) reviewed literature data available on the gill morphology of fishes. From their data set for 28 non-air-breathing freshwater species, they extracted the mean slope of significant regressions for total gill filament length, lamellar density, and total gill surface area versus body weight. They set the lowest and highest mean values within each parameter range to 0 and 100%, respectively, to create a range of values for each gill parameter. This permitted them to express the gill size of a species as a percentile within the range of freshwater fishes and permits comparison among species controlling for differences in body size. The Kruskal–Wallis test was used to examine differences among species in mean values of gill morphological characters expressed as a percentile of the range for freshwater fishes.

RESULTS

RESPIRATORY BEHAVIOUR

All species used aquatic surface respiration (R_S) when subjected to progressive hypoxia. However, each species differed in the oxygen level at which they initiated R_S . *Astatotilapia velifer* exhibited the highest R_{S10} , R_{S50} , R_{S90} thresholds, suggesting a lower tolerance to hypoxia than the other two species. *Pseudocrenilabrus multicolor victoriae* had the lowest R_S thresholds, suggesting relatively high tolerance to hypoxia (Fig. 2). In both *P. multicolor victoriae* and

P. venator, gill ventilations decreased after the initiation of R_S , demonstrating the effectiveness of this behaviour for these two species (Wilcoxon signed-ranks test: *P. multicolor victoriae*, mean before $R_S = 30.1 \pm 3.3$, s.d., vents 15 s^{-1} , mean after $R_S = 23.7 \pm 2.7$ vents 15 s^{-1} , $z = 2.6$, $P = 0.01$; *P. venator*, mean before = 28.4 ± 9.7 vents 15 s^{-1} , mean after = 23.7 ± 0.1 vents 15 s^{-1} , $z = 2.2$, $P = 0.03$). Gill ventilations did not drop in *A. velifer* (Wilcoxon signed-ranks test: mean before = 27.7 ± 2.8 vents 15 s^{-1} , mean after = 28.26 ± 2.6 , $z = 0.32$, $P = 0.81$). None of the three species lost equilibrium during progressive hypoxia trials.

Buccal bubble holding was frequently observed in both *A. velifer* and *P. venator* during the last 15 min of the experimental trials, when only trace amounts of oxygen were present (Table II). This behaviour was not observed as frequently in *P. multicolor victoriae* (Table II). All three species moved actively at the surface during R_S , but differed in the speed of movement (Table II). Aggressive behaviour was more frequent in *P. venator* and *A. velifer* than in *P. multicolor victoriae* under hypoxia (Table II). However, when the percent time at the surface was >90%, aggressive behaviour was infrequent and did not differ among species (Table II).

The response of fish to acute hypoxia with surface access varied among species, although all species used R_S and did not lose equilibrium within the 30-min trial. When fishes were first placed into the tank, *A. velifer* and *P. venator* initiated R_S almost immediately. *Pseudocrenilabrus multicolor victoriae* spent less time at R_S during the first sampling interval than *P. venator* and *A. velifer* (Table III). This suggests less urgency for surface access in *P. multicolor victoriae* than in the other species. However, after the initial sampling interval, there was no difference among species in time spent at the water surface (Table III). As with the progressive hypoxia trials, buccal bubble holding was more frequently observed in *P. venator* and *A. velifer* than in *P. multicolor victoriae* (Table III). All species moved actively at the surface during R_S ; however, the speed of movement was higher in *A. velifer* than in the other two species (Table III). In acute hypoxia trials without access to surface water, all individuals lost equilibrium within 35 min of exposure (range 6.2–31.6 min) and did not differ in their average time to loss of equilibrium (*P. multicolor victoriae*, mean $L_E = 15.7 \pm 9.9$ min; s.d.; *P. venator*, mean $L_E = 11.7 \pm 2.0$ min; *A. velifer* mean $L_E = 12.4 \pm 2.1$ min; Kruskal–Wallis, $\chi^2 = 0.38$, $P = 0.83$).

METABOLIC RATE AND CRITICAL OXYGEN TENSION

Total metabolic rate ranged from 0.05 to 0.23 ml $\text{O}_2 \text{ h}^{-1}$ for *P. multicolor victoriae* (body weight range 0.63–9.68 g), 0.11–0.72 ml $\text{O}_2 \text{ h}^{-1}$ for *P. venator* (body weight range 0.74–8.53 g), and 0.14–0.89 ml $\text{O}_2 \text{ h}^{-1}$ for *A. velifer* (body weight range 0.78–12.87 g). For all species total metabolic rate increased with body size (*P. multicolor victoriae*: $r^2 = 0.52$, $P = 0.04$; *P. venator*: $r^2 = 0.75$, $P = 0.01$; *A. velifer*: $r^2 = 0.67$, $P = 0.02$). The slopes of the relationships did not differ (ANCOVA, $F_{2,26} = 0.003$, $P = 0.997$); however, there was a significant difference among the intercepts ($F_{2,28} = 15.94$, $P < 0.001$). Adjusted mean total metabolic rate (adjusted to 2.68 g) was higher in *A. velifer* (mean = 0.47 ml $\text{O}_2 \text{ h}^{-1}$) than in both *P. multicolor victoriae* (0.20 ml $\text{O}_2 \text{ h}^{-1}$) and *P. venator* (0.25 ml $\text{O}_2 \text{ h}^{-1}$; Sidak test, $P < 0.05$).

TABLE II. The behavioural response of three haplochromine cichlids species from the Lake Nabugabo region of the Lake Victoria basin to progressive hypoxia

Parameter	Trials tested	Species			Kruskal–Wallis	
		<i>P. multicolor victorinae</i> (Pmv)	<i>P. venator</i> (Pv)	<i>A. velifer</i> (Av)	χ^2	<i>P</i> -value
% Bubble holding	Last interval	21.3	83.30	100.00	16.5	<0.01
Speed at surface (cm 10 s ⁻¹)	Last interval	11.0	19.80	28.10	16.7	<0.01
% Aggression	<90% <i>R</i> _S	0.4	1.70	1.60	12.8	0.02
% Aggression	>90% <i>R</i> _S	0.0	0.07	0.05	0.25	0.85

Species underlined are not significantly different (Kruskal–Wallis, multiple comparisons, *P*>0.05).

TABLE III. The behavioural response of the three haplochromine species examined in this study from the Lake Nabugabo region of the Lake Victoria basin to acute hypoxia with access to surface water

Parameter	Sampling period	Species			Kruskal–Wallis		
		<i>P. multicolor victorinae</i> (Pmv)	<i>P. venator</i> (Pv)	<i>A. velifer</i> (Av)	χ^2	<i>P</i> -value	
% R_s	First interval	22.2	76.3	88.2	17.1	<0.01	<u>Pmv</u> <u>Pv</u> <u>Av</u>
% R_s	Last two intervals	96.0	100.0	100.0	6.83	0.13	<u>Pmv</u> <u>Pv</u> <u>Av</u>
Loss of equilibrium	All intervals	None	None	None			<u>Pmv</u> <u>Pv</u> <u>Av</u>
% Bubble holding	All intervals	6.7	80.4	100.0	10.8	0.03	<u>Pmv</u> <u>Pv</u> <u>Av</u>
Speed at surface cm 10 s ⁻¹	Last two intervals	1.0	1.4	2.4	16.7	<0.01	<u>Pmv</u> <u>Pv</u> <u>Av</u>

Species underlined are not significantly different (Kruskal–Wallis multiple comparisons, $P > 0.05$).

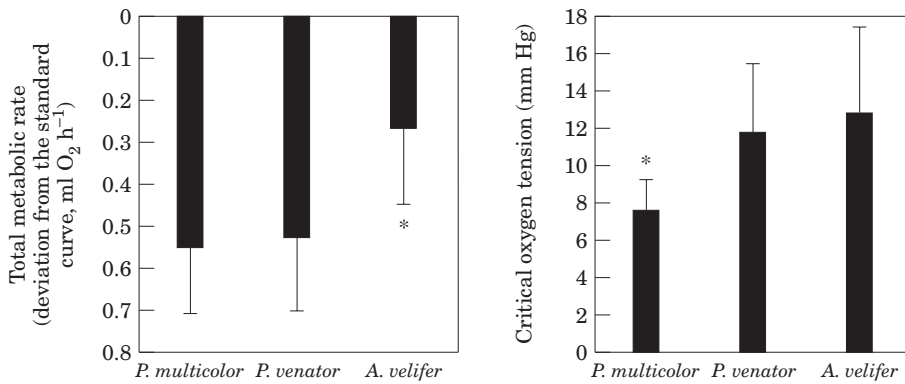


FIG. 3. Routine metabolic rate (expressed as a percentage below the expected values based on the standard curve for freshwater fishes; Winberg, 1956, 1961) and critical oxygen tension (mm Hg) of three species of haplochromine cichlids. *Species significantly different (ANOVA, Scheffé's multiple comparisons, $P < 0.05$).

The total metabolic rate (expressed as the mean per cent deviation from the standard curve) of all three haplochromine cichlids falls well below the predicted values based on Winberg's (1961) equation (Fig. 3). The metabolic rate of *A. velifer* was closer to the standard curve than the other two species (ANOVA, $F_{2,29} = 9.00$, $P = 0.001$, Scheffé's multiple comparisons, $P < 0.05$, Fig. 3).

Values of critical oxygen tension based on visual estimates and values derived from the BASIC program (Yeager & Ultsch, 1989) were strongly correlated ($r^2 = 0.74$, $P < 0.01$). Therefore only values derived from the BASIC program are presented. All three species exhibited very low critical oxygen tensions; however, the tension of *P. multicolor victoriae* was lower than the other two species (ANOVA, $F_{2,24} = 6.2$, $P = 0.007$, Scheffé's multiple comparisons, $P < 0.05$, Fig. 3).

GILL MORPHOLOGY

Total gill filament length of *P. multicolor victoriae* (body weight range 0.72–5.2 g) ranged between 76.5 and 220 cm. For *P. venator* (1.2–15.96 g) L_{TF} ranged between 99.4 and 369 cm, and for *A. velifer* (2.3–8.3 g), L_{TF} ranged between 145 and 243 cm. For all species, total gill filament length increased with body size (*P. multicolor victoriae*: $r^2 = 0.95$, $P < 0.01$; *P. venator*: $r^2 = 0.98$, $P < 0.01$; *A. velifer*: $r^2 = 0.89$, $P < 0.01$). However, the slopes of the relationships differed among the three species (ANCOVA, $F_{2,24} = 6.29$, $P = 0.006$), and therefore differences among the adjusted mean total gill filament length of the three species could not be tested. Total gill filament length expressed as a percentile of the range for freshwater fishes did not differ among the three species (Table IV). In addition, for all three species, total gill filament length fell within the upper range for freshwater fishes (Table IV). Both adjusted mean lamellar density and lamellar density expressed as a percentage of the range for freshwater fishes (Palzenberger & Pohla, 1992) were higher in *A. velifer* than in *P. multicolor victoriae* and *P. venator* (Table IV).

Total gill surface area ranged from 9.6 and 34.0 cm² in *P. multicolor victoriae*, 25.0 to 73.1 cm² in *P. venator*, and 41.8 to 76.9 cm² in *A. velifer*. Adjusted mean total gill surface area and total gill surface area expressed as a percentage of

TABLE IV. Gill morphological characters for three haplochromine cichlid species from the Lake Nabugabo region (*P. multicolor victorinae*, *Astatotilapia velifer*, and *Prognathochromis venator*)

Gill character	Species		Kruskal-Wallis		ANCOVA		Multiple comparisons ($P < 0.05$)
	<i>P. multicolor victorinae</i> (Pmv)	<i>P. venator</i> (Pv)	χ^2	<i>P</i>	<i>F</i> _{df}	<i>P</i>	
Total gill filament length (% fw fishes \pm s.d.)	62.32 \pm 2.30	63.92 \pm 3.71	2.64	0.27	—	—	<u>Pmv Pv Av</u>
Average lamellar density (\log_{10} lam mm ⁻¹ \pm s.d.) [antilog adjusted mean]	1.45 \pm 0.03 [28.18]	1.48 \pm 0.03 [30.20]	—	—	13.42 _{2,11}	<0.001	<u>Pmv Pv Av</u>
Average lamellar density (% fw fishes \pm s.d.)	51.44 \pm 1.54	57.87 \pm 6.43	15.11	0.001	—	—	<u>Pmv Pv Av</u>
Total gill surface area (\log_{10} cm ² \pm s.d.) [antilog adjusted mean]	1.46 \pm 0.06 [28.84]	1.61 \pm 0.05 [40.74]	—	—	13.87 _{2,11}	0.001	<u>Pmv Pv Av</u>
Total gill surface area (% fw fishes \pm s.d.)	53.88 \pm 28.91	88.00 \pm 25.10	12.5	0.002	—	—	<u>Pmv Pv Av</u>

Species underlined are not significantly different (Kruskal-Wallis multiple comparisons tests, $P < 0.05$, ANCOVA/Sidak's t-test, $P < 0.05$).

the range for freshwater fishes (Palzenberger & Pohla, 1992) was lower in *P. multicolor victoriae* than in both *P. vendator* and *A. velifer* (Table IV).

DISCUSSION

RESPIRATORY PROFILES OF THREE HAPLOCHROMINE CICHLID SPECIES

Pseudocrenilabrus multicolor victoriae, *P. venator* and *A. velifer* differed in a variety of respiratory characters including thresholds for R_S , gill ventilation rates, metabolic rate, critical oxygen tension, and gill surface area. Hypoxia tolerance was highest in *P. multicolor victoriae*, a species that persists in abundance in deep wetland refugia (Chapman *et al.*, 1996b; Rosenberger & Chapman, 1999). The low oxygen levels at which this species initiated R_S and its low surface water speeds, metabolic rate, and critical oxygen tension indicate efficiency in oxygen uptake and low oxygen demand. In addition, *P. multicolor victoriae* had a large total gill surface area in relation to the range of freshwater fishes (67th percentile of the range), which, given its very low metabolic rate, may reflect a requirement of hypoxic waters rather than metabolic demand.

Astatotilapia velifer persists in abundance in the wetland ecotones of Lake Nabugabo but is very rare in the more hypoxic waters beyond the marginal swamps (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999; Schofield & Chapman, 1999). This species initiated R_S at higher oxygen levels than *P. multicolor* and *P. venator* and exhibited a high metabolic rate and critical oxygen tension relative to the other two species, suggesting a lower tolerance to hypoxia and higher oxygen demand. The large gill surface area of *A. velifer*, which was higher than *P. multicolor victoriae*, may reflect oxygen demands associated with a higher metabolic rate in a habitat where oxygen conditions are more variable (Rosenberger & Chapman, 1999).

For *A. velifer*, the chronic low-oxygen conditions characteristic of the deeper swamps potentially would demand prolonged R_S to maintain its relatively high metabolic rate. Rosenberger & Chapman (1999) reported average dissolved oxygen levels of 1.56 ± 1.0 mg l⁻¹ deep in the Juma river, a level below oxygen levels at the $R_{S_{10}}$ threshold for *A. velifer* ($R_{S_{10}} = 1.6$ mg l⁻¹). Oxygen concentration of lagoon areas in the Lwamunda swamp are extremely low (0.7 mg l⁻¹, Chapman & Chapman, 1998), a level at which *A. velifer* spends 90% of its time at the water surface. Prolonged R_S in these areas could lead to increased aerial predation risk (Kramer *et al.*, 1983) or limit important behaviours. However, *A. velifer* is capable of handling short-term low oxygen conditions characteristic of the ecotonal wetlands in Lake Nabugabo where there is interaction between main lake and wetland waters (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999). Dissolved oxygen concentration averaged 2.2 mg l⁻¹ in the ecotonal wetland at the mouth of the Juma River (Rosenberger & Chapman, 1999) and is higher in other ecotonal areas of the lake (Schofield & Chapman, 1999). On occasions when ecotonal oxygen levels fall below the R_S threshold for *A. velifer*, access to the more highly oxygenated main lake may minimize time at the surface.

Although *P. venator* was less tolerant of low oxygen than *P. multicolor victoriae*, this species initiated R_S at lower oxygen levels and exhibited a lower metabolic rate and critical oxygen tension than *A. velifer*. In addition, its total

gill surface area was relatively large. This suggests that this species has the respiratory capacity to exploit wetland areas in Lake Nabugabo; however, *P. venator* is not found in the Lwamunda swamp, the Juma River, or the wetland ecotones of Lake Nabugabo (Chapman *et al.*, 1996a, b; Rosenberger & Chapman, 1999; Schofield & Chapman, 1999).

IMPLICATIONS FOR USE OF HYPOXIC REFUGIA

Respiratory characteristics of *P. multicolor victoriae* and *A. velifer* may help to explain their current distribution pattern and permit them to persist in Lake Nabugabo with the predatory Nile perch. In their survey of Lake Nabugabo prior to the increase in the introduced Nile perch population, the Cambridge Nabugabo Biological Survey (CNBS, 1962, preliminary report) found *P. multicolor victoriae* to be abundant in inshore habitats, the Juma River, and the Lwamunda Swamp. Since Nile perch are most abundant in open waters and rare in wetlands, the historical and current distribution of *P. multicolor victoriae* may minimize interaction with the predator.

Prior to the increase in introduced Nile perch, *A. velifer* was widely distributed in the lake and abundant offshore, but not found in the deep swamp habitats (Greenwood, 1965; CNBS, unpubl. data). *Astatotilapia velifer* may persist today by continued use of wetland ecotones, where Nile perch are rare (Schofield & Chapman, 1999), but its modest tolerance to extreme hypoxia may limit exploitation of areas beyond the fringing swamp. However, proximity of ecotonal refugia to open waters with Nile perch could threaten the long-term viability of ecotonal refugia (Rosenberger & Chapman, 1999; Schofield & Chapman, 1999).

Hypoxia has been extremely important in determining fish assemblage structure in other systems. For example, Tonn & Magnuson (1982) demonstrated that Wisconsin lakes were dominated by a predator assemblage (centrarchid-*Esox*) if winter oxygen levels were high, while *Umbra*-cyprinid prey assemblages dominated lakes with low winter oxygen levels. Rahel & Kolar (1990) noted that localized pockets of normoxia (such as that might be found in ecotonal wetlands) in lakes with widespread winter hypoxia may provide refugia for less tolerant species during winter months. Hypoxia associated with refugia from predation has also been extremely important in invertebrate distribution and assemblage structure (Rahel & Kolar, 1990; Kolar & Rahel, 1993; Rahel & Nutzman, 1994). Invertebrate species capable of tolerating low oxygen conditions may be able to use hypoxic benthic areas in stratified lakes to avoid fish predation (Rahel & Kolar, 1990; Kolar & Rahel, 1993). However, when fish predators are capable of tolerating lethal levels of low oxygen for short periods, they can forage in hypoxic waters when food abundance is low in waters with high oxygen levels (Rahel & Nutzman, 1994). These findings may be applied easily to what is known of ecotonal wetland refugia, where tolerant species seeking refuge may be threatened by short-term foraging from less tolerant Nile perch (Rosenberger & Chapman, 1999; Schofield & Chapman, 1999).

The respiratory profile of *P. venator* indicates that it is capable of exploiting wetland areas around Lake Nabugabo. Further, distributions of *P. venator* in Lake Manywa (a small satellite lake near Nabugabo without introduced Nile perch) suggest that this species has the capacity to use dense wetlands (L. J.

Chapman & C. Chapman, unpubl. data). Greenwood (1965) noted that *P. venator* was once widely distributed in Lake Nabugabo, and, though abundant in open, offshore areas, it was often found close to benthic areas where hypoxia and anoxia can occur due to benthic productivity. The respiratory profile of *P. venator* and its distribution in another satellite lake suggest factors other than hypoxia tolerance must have contributed to its disappearance from Lake Nabugabo subsequent to the introduction of Nile perch.

Adult *P. venator* are predominantly piscivorous (Greenwood, 1965). Haplochromine cichlids and small *Barbus* species, which declined or disappeared in Lake Nabugabo after the introduction of Nile perch (Ogutu-Ohwayo, 1993), comprised its most common prey taxa (Greenwood, 1965). A strict piscivore like *P. venator*, although able to exploit wetlands to avoid predation by Nile perch, may be unable to feed effectively in the structural complexity of dense swamps. In addition, adult Nile perch are likely to compete with native predators for food resources. A combination of these two factors may have contributed to the disappearance of *P. venator* from Lake Nabugabo.

HYPOXIA TOLERANCE OF EAST AFRICAN CICHLIDS

Chapman *et al.* (1995) used behavioural studies to describe the hypoxia tolerance of nine cichlids from Lake Victoria (eight indigenous, one introduced) and three cichlids from Lake Tanganyika. As with the cichlids from the Nabugabo region, the Victorian and Tanganyikan cichlids all used R_S in response to extreme hypoxia. However, they varied clearly in their degree of hypoxia tolerance. Chapman *et al.* (1995) found relatively high tolerance to hypoxia in some of the haplochromines, and not surprisingly, tolerance was greater in the widely distributed swamp specialists than in the more stenotypic lacustrine forms. Also, they found that lacustrine cichlids endemic to Lake Victoria were more tolerant to hypoxia than ecologically similar species from Lake Tanganyika. Methods used in these studies are comparable with this study. The R_S oxygen thresholds of *P. multicolor victoriae* and *P. venator* are comparable with the thresholds reported by Chapman *et al.* (1995), and fall well below the thresholds for Nile perch (Schofield & Chapman, 1999), *Oreochromis niloticus* L., and two of the three cichlids from Lake Tanganyika (Chapman *et al.*, 1995, Table V). *Astatotilapia velifer* thresholds are comparable to *Tropheus moorii* (Boulenger) and *Neolamprologis tretocephalus* (Boulenger), which occur in well-oxygenated rocky areas of Lake Tanganyika. All three species of cichlids examined in this study had a large total gill surface area (67th to 98th percentile of the range for freshwater fishes). These values fall above many of the values reported by Galis & Barel (1980) for several cichlids from Lake Victoria.

Verheyen *et al.* (1994), described the metabolic rate and critical oxygen tension of four species of cichlids from Lakes Malawi and Tanganyika and one widespread species found in Lake Victoria. Cichlids from Lakes Victoria and Nabugabo, with the exception of *A. velifer*, have lower metabolic rates than four of the five cichlids examined from Lakes Malawi and Tanganyika. In addition, the critical oxygen tensions of the Lake Nabugabo cichlids fall markedly below the values given by Verheyen *et al.* (1994), for fishes from lakes Malawi and Tanganyika (Table VI). Also, Chapman *et al.* (1995) found Victorian cichlids to be far more tolerant than their Tanganyikan counterparts. Having evolved in a

TABLE V. R_S thresholds (mm Hg) for progressive hypoxia trials and time to loss of equilibrium for acute hypoxia trials with and without surface access for East African cichlids

Species	$R_{S_{10}}$	$R_{S_{50}}$	$R_{S_{90}}$	Mean time to equilibrium loss (min)	
				With surface access	Without surface access
Nile perch <i>Lates niloticus</i>	25.3	17.2	11.1	10.2	4.92
Study species from Lake Nabugabo					
<i>Pseudocrenilabrus multicolor victoriae</i>	15.2	8.5	5.4	*	15.7
<i>Astatotilapia velifer</i>	27.5	19.4	11.6	*	11.7
<i>Prognathochromis venator</i>	19.7	14.0	8.8	*	12.4
Cichlids from Lake Victoria					
<i>Prognathochromis perrieri</i> (Greenwood)	15.2	11.0	7.0	*	12.3
<i>Yssichromis argens</i> (Greenwood)	20.7	17.4	16.5	*	18.9
<i>Labrochromis ishmaeli</i> (Boulenger)	17.0	8.5	1.5	*	14.9
<i>Pyxichromis orthostoma</i> (Greenwood)	17.0	13.2	7.2	*	23.0
<i>Neochromis nigricans</i> (Regan)	10.1	7.6	3.0	25.1	10.5
<i>Astatoreochromis alluaudi</i> (Pellegrin)	20.1	13.2	9.9	*	26.6
'Haplochromis' rock kribensis	14.6	10.5	8.4	*	11.1
<i>Oreochromis esculentus</i> (Graham)	7.4	6.1	5.1	*	*
<i>Oreochromis niloticus</i> (introduced)	35.3	6.9	4.5	*	*
Cichlids from Lake Tanganyika					
<i>Cyprichromis leptosoma</i> (Boulenger)	12.0	8.5	—	3.1	1.4
<i>Tropheus moorii</i>	29.5	19.0	15.0	10.0	7.5
<i>Nelamprologis tredocephalus</i>	26.8	17.2	—	5.4	6.0

*No loss of equilibrium within the 30 min time frame. Data are presented for three haplochromine species from Lake Nabugabo that differ in their use of wetland refugia, Nile perch from Lake Nabugabo (Schofield, 1997), nine cichlid species from Lake Victoria (Chapman *et al.*, 1995), and three cichlid species from Lake Tanganyika (Chapman *et al.*, 1995).

shallow swampy basin, haplochromine cichlids from the Lake Victoria region are possibly, as a fauna, more tolerant of hypoxia than cichlids from Lakes Tanganyika and Malawi, where marginal wetlands are far less extensive.

Although tolerance certainly varies among species in the Lake Victoria basin, the results from this and previous studies (Chapman *et al.*, 1996a, b) suggest that some cichlids have the respiratory tolerance to allow exploitation of wetland areas that may be important refugia from Nile perch. In addition, cichlid species from Lake Victoria are likely to encounter anoxia in the hypolimnetic zone (Hecky, 1993), during upwellings and in dense algal blooms which are now widespread in the lake (Ochumba & Kibaara, 1989; Ochumba, 1990). Although the recent eutrophication of Lake Victoria (Kaufman *et al.*, 1997; Ochumba, 1995; Hecky *et al.*, 1994; Kaufman, 1992) may threaten many species, hypoxia-tolerant deepwater species may find refugia from Nile perch. Use of these areas could be a short-term evasive response demanding an acute tolerance of hypoxic or anoxic waters, or longer-term use, which would demand tolerance to chronic hypoxia or anoxia without access to surface waters. However, fish kills associated with upwellings of anoxic water suggest that the use of deepwater

refugia may impose a high risk for some species (Ochumba, 1987, 1990; Kaufman & Ochumba, 1993; Kolding, 1993).

In summary, *Pseudocrenilabrus multicolor victoriae*, *P. venator*, and *A. velifer* differed in a variety of respiratory characters including thresholds for R_s , gill ventilation rates, metabolic rate, critical oxygen tension, and gill surface area. Respiratory characteristics of *P. multicolor victoriae* and *A. velifer* may help to explain their current distribution pattern and persistence in Lake Nabugabo with the predatory Nile perch. The respiratory characteristics of *P. venator* suggest that factors other than hypoxia tolerance must have contributed to its disappearance from Lake Nabugabo subsequent to the introduction of Nile perch.

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