

Hypoxia Tolerance of the Mormyrid *Petrocephalus catostoma*: Implications for Persistence in Swamp Refugia

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The introduction of Nile perch into the Lake Victoria basin of East Africa has led to dramatic changes in fish faunal structure and diversity. Though catches of many species had declined by the 1960s due to overexploitation (Kudhongania et al., 1992), the dramatic increase in Nile perch in the 1980s in Lake Victoria was followed by a drastic decline in the populations of several indigenous species (Kaufman, 1992). Most notable has been the disappearance of over 50% of the endemic haplochromine cichlids from Lake Victoria (Kaufman, 1992; Kaufman et al., 1997). However, many indigenous noncichlids, some of which were important in the pre-Nile perch fishery, have also declined or disappeared (Kaufman, 1992; Kudhongania et al., 1992). Similar trends have been observed in other lakes in the basin (e.g., Lakes Kyoga and Nabugabo, Ogotu-Ohwayo, 1990a, 1993). Initially, haplochromine cichlids and mormyrids were the main prey ingested by Nile perch until their numbers declined to the point where Nile perch switched to other prey items (Hamblyn, 1966; Gee, 1969; Ogotu-Ohwayo, 1990b).

The tremendous loss of biodiversity led to studies directed at the identification of faunal refugia. Rocky crevices appear to be important refugia for rock-dwelling haplochromine cichlids in the Mwanza Gulf of Lake Victoria (Witte et al., 1992). In Lakes Victoria, Kyoga, and Nabugabo, wetlands also protect some fishes from Nile perch predation by providing both structural and low-oxygen refugia for prey species that can tolerate the hypoxic conditions that prevail in their dense interior (Chapman et al., 1996a,b). In addition, wetlands may serve as barriers to the dispersal of Nile perch. Wetlands in the basin are dominated by papyrus (*Cyperus papyrus*) and the grass *Miscanthidium violaceum*. Little light or wind penetrate the swamp canopy, and both growth and decomposition proceed at high rates. This results in extremely low levels of oxygen in the swamp interior (Chapman and Liem, 1995; Chapman et al., 1996a). Laboratory experiments have demonstrated a relatively high tolerance to hypoxia in some haplochromine cichlids. This permits use of marginal wetlands by some species, particularly ecotonal wetlands where hypoxia is moderated by interaction with the main lake waters (Chapman et al., 1995, 1996b). Air-breathing noncichlids (e.g.,

Protopterus aethiopicus, *Clarias* spp., *Ctenopoma muriei*) withstand extreme hypoxia by virtue of their ability to use atmospheric oxygen, and many species are still common in wetlands though their numbers have declined dramatically in the main lakes. However, very little is understood about the respiratory biology of water-breathing noncichlids in the Lake Victoria basin. Of particular interest are the seven species of mormyrids that declined or largely disappeared from the open waters of Lakes Victoria, Kyoga, and Nabugabo. Their benthic feeding habits and habitat use led Okedi (1972) to suggest that some lake-dwelling mormyrids withstand very low-oxygen tensions. This may predispose them to persistence in wetland refugia.

A Cambridge expedition to Lake Nabugabo in 1962 [Cambridge Nabugabo Biological Survey (CNBS), unpubl.] reported four mormyrid species in the main lake. *Gnathonemus victoriae*, *G. longibarbus*, and *Marcusenius nigricans* were common in areas near overhanging marsh vegetation, whereas *Petrocephalus catostoma* was found in the open lake. In later surveys of the main lake (1991-1994, Ogotu-Ohwayo, 1993; Chapman et al., 1996a,b), *G. victoriae* was extremely rare, and the other three mormyrid species were not found. However, *P. catostoma* can still be found in some lagoons and small tributaries in the Lwamunda swamp, an extensive wetland surrounding Lake Nabugabo (Chapman et al., 1996a). In surveys of 12 lagoons (and associated tributaries) in 1995 and 1996, we found *P. catostoma* to be abundant in one lagoon and its tributary (site 1) and present in a nearby chain of lagoons in the Lwamunda Swamp (site 2), located approximately 3 km from the open waters of Lake Nabugabo. Oxygen levels in the lagoons showed nocturnal reduction, but even peak values during the day were very low averaging 0.9 mg l⁻¹ (Table 1). High tolerance to low oxygen permits use of these wetlands by *P. catostoma*; however, mechanisms for tolerating hypoxia in this species are unknown. This study examines the low-oxygen tolerance of *P. catostoma* collected from the lagoons in the marginal wetlands of Lake Nabugabo, Uganda. To facilitate comparison with published results on mechanisms leading to hypoxia tolerance in other fishes, we examined behavioral, morphological, and physiological

TABLE 1. DISSOLVED OXYGEN CONCENTRATION (mg l^{-1} , MEAN \pm SD) AND WATER TEMPERATURE (C, MEAN \pm SD) OF SITES IN THE LWAMUNDA SWAMP, UGANDA WHERE *Petrocephalus catostoma* WERE CAPTURED IN JUNE 1996. Dissolved oxygen and water temperature were measured in the upper 20 cm of the water column. Oxygen partial pressure (mm Hg) is indicated in parentheses.

Site	Water depth (cm)	Time (h)	Dissolved oxygen in mg l^{-1} (mm Hg)	Water temperature in C
Kisasa Lagoon 1 (n = 10)	41	0840	0.6 ± 0.4 (10.1)	19.6 ± 0.2
		1445	1.3 ± 0.6 (22.6)	21.5 ± 0.6
Kisasa Lagoon 1 tributary (n = 6)	29	0855	0.4 ± 0.1 (6.7)	19.0 ± 0.04
		1410	0.7 ± 0.1 (12.2)	21.4 ± 0.1
Chain 2 Lagoon (n = 10)	63	0825	0.5 ± 0.1 (8.5)	20.3 ± 0.1
		1245	0.8 ± 0.5 (13.9)	21.8 ± 0.2

adaptations that may promote survival in hypoxic waters. These included behavioral response to progressive hypoxia, oxygen consumption rate, critical oxygen tension, total gill filament length, and total gill surface area.

MATERIALS AND METHODS

Lake Nabugabo is a small satellite lake (24 km^2) of Lake Victoria, lying within a former bay of Lake Victoria that was isolated approximately 4000 years ago (Greenwood, 1965). Lake Nabugabo is surrounded by an extensive peat, grass, and papyrus swamp (Lwamunda Swamp). Small lagoons (mean depth generally less than 2 m) are situated in low-lying depressions behind or within the fringing wetlands.

Petrocephalus catostoma is a small mormyrid (maximum total length = 120 mm) with a scattered but wide distribution in east, central, and south Africa. It feeds primarily on insects both from the bottom (e.g., chironomid and ephemeropteran larvae) and from marginal vegetation (plants, chaoborids, Corbet, 1961; Okedi, 1972). Little is known about its habitat use or other aspects of its ecology.

To quantify the behavioral response of *P. catostoma* to progressive hypoxia, fish were collected from the Lwamunda Swamp (mean total length = 4.4 ± 0.24 cm, SD, mean total weight = 0.92 ± 0.15 g) and held in a large plastic container aerated with a battery operated bub-

bler. The experiment was repeated twice on a group of 10 fish selected randomly from the holding tank and transferred to a Plexiglass aquarium (50 cm \times 22 cm \times 30 cm, average water temperature = 23 C) for behavioral observations. Oxygen was slowly lowered with the addition of small amounts of sodium sulfite (following Chapman and Liem, 1995) over 3.5 h, and then held at levels averaging $< 0.02 \text{ mg l}^{-1}$ for 30 min. Lewis (1970) found no observable differences in the behavioral responses of fishes to water freed of oxygen with sulphite and water freed of oxygen by bubbling with nitrogen. A blind positioned in front of the aquarium permitted observations through a small viewing port. The following variables were recorded at 15-min intervals: gill ventilation rate (number of opercular beats in a 15-sec period recorded for five fish); number of fish using aquatic surface respiration (recorded every 10 sec for 100 sec); orientation at the surface during ASR; and the presence or absence of buccal bubble holding. Gill ventilations were not recorded until of sufficient amplitude to be clearly visible. Dissolved oxygen concentration and water temperature were also recorded every 15 min using a YSI Model 51B oxygen probe. The level of oxygen at which 10% (ASR_{10}) and 50% (ASR_{50}) of the fish performed ASR was estimated by fitting curves to plots of PO_2 and percent ASR. Percent ASR was calculated as the number of fish in a group using ASR divided by the total number of fish, averaged over the 10 observations in a given sample.

Total gill filament length was measured for 10 *P. catostoma* (3.4–7.0 cm TL, 0.34–3.20 g) preserved in paraformaldehyde (35 g/L) using standard methods (Muir and Hughes, 1969; Hughes, 1984). For each fish, the branchial basket was removed, and the four gill arches from the left side of the basket were 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 (TFL). Lamellar density and lamellar area were estimated for the nine largest fish. Lamellar density was measured on every 10th filament in the dorsal, middle, and ventral parts of the second gill arch on the left side. The total number of lamellae (on one side of the filament) and average lamellar density (ALD) were estimated using a weighted mean method, which takes into account the difference in length of differ-

ent filaments (Muir and Hughes, 1969; Hughes and Morgan, 1978). For every 10th filament, the length and height of the secondary lamellae were measured a number of times over the filament (Galis and Barel, 1980). The average lamellar length multiplied by the average lamellar width for each filament was converted to an estimate of lamellar area using a regression determined through the dissection of 60 lamellae from various sections of the second gill arch from two specimens [area = (length \times width) $0.646 + 0.0096$, $r^2 = 0.83$, $P < 0.001$]. The sum of the total lamellar area for all sections of the second arch was divided by the total number of lamellae and multiplied by 2 to produce a weighted average bilateral surface area on one side of the filament (ALA) for the fish. Total gill surface area (TGA) was determined using the following formula:

$$\text{TGA} = \text{TFL} \times 2 \times \text{ALD} \times \text{ALA}.$$

Oxygen consumption and critical oxygen tension (the level of oxygen concentration where metabolic rate becomes dependent on oxygen concentration) were measured using a closed respirometer. Metabolic rate was determined as routine oxygen consumption (rate including spontaneous activity), and critical oxygen tension was determined through graphic interpretation. The setup for the measurement of metabolic rates was designed for use at remote sites with no electricity. Nine *P. catostoma* (6.6–7.8 cm TL, 2.54–3.44 g) were collected from the lagoons of the Lwamunda Swamp and transferred to the Makerere University Biological Field Station in western Uganda, where they were held in small outdoor ponds. An individual fish was placed in a dark chamber with a battery-operated bubbler at least 1 h before an experimental trial. 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 19.4 ± 0.68 C. At the start of each experimental run, the chamber was sealed with a YSI Model 600 multiparameter oxygen probe connected to a data collection system run on solar power. The meter was programmed to take measurements of water temperature and 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 quickly returned to normoxia. Following each trial, the total length and weight of the fish were recorded. Oxygen consumption rates were measured within two weeks of capture. Oxygen consumption

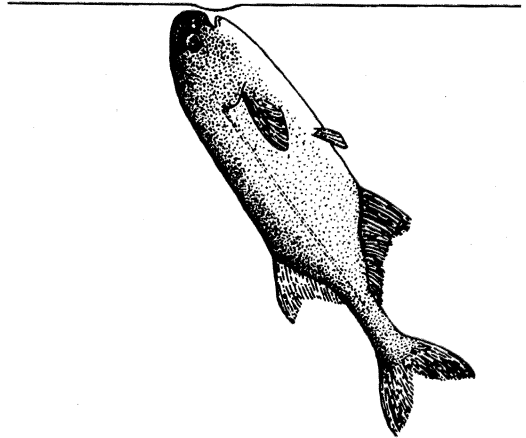


Fig. 1. Posture used by *Petrocephalus catostoma* during aquatic surface respiration.

rate was calculated for each fish using data collected at least 30 min after the container was sealed with the probe and prior to estimated critical oxygen tension. To calculate mass-corrected oxygen consumption rates we used the exponent of the general equation $\text{MR} = kW^{0.81}$ of Winberg (1956, 1961) for freshwater fishes. Values were corrected following the relationship, $\text{MR}_c = (\text{W}_o^{0.19})$ (mean mass of the sample $^{-0.19}$) (MR_o), where MR_c is the mass-corrected oxygen consumption and M_o is the observed oxygen consumption for an individual of weight W_o (Ultsch et al., 1978). The critical oxygen tension (or critical partial oxygen pressure) was estimated by visual interpretation of the relationship between metabolic rate and P_{O_2} (mm Hg).

RESULTS

The response of *P. catostoma* to progressive hypoxia under experimental conditions was very similar between the two trials, and results were combined in the following description. In response to severe hypoxia, *P. catostoma* uses aquatic respiration at the air-water interface (aquatic surface respiration, ASR, Kramer and Mehegan, 1981), ventilating its gills with water from the surface film where diffusion maintains a micro-layer of well-oxygenated water. Unlike most other fishes that use ASR, *P. catostoma* swims inverted when breathing at the surface ($\sim 45^\circ$ angle to the surface), thus placing its subterminal mouth into proximity with the oxygen-rich surface layer (Fig. 1). This posture is maintained through ASR bouts, during which *P. catostoma* swims continuously. ASR_{10} and ASR_{50} occurred at approximately 13 mm Hg and 3 mm Hg, respectively. Gill ventilation rates in-

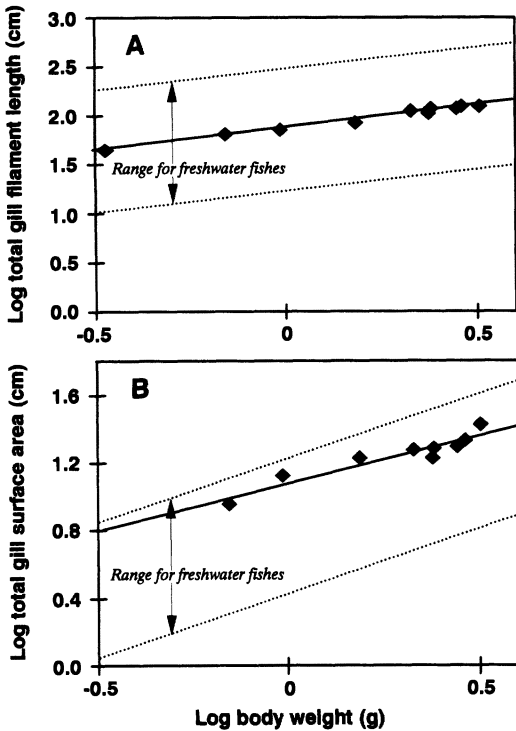


Fig. 2. Bilogarithmic (\log_{10}) plot of (A) total gill filament length (TGFL; for all arches combined) and body weight and (B) total gill surface area (TGA) and body weight for *Petrocephalus catostoma* from the Lwamunda Swamp, Uganda. Regressions: $\log \text{ TGFL} = 0.47 (\log \text{ body weight}) + 1.87$, $r^2 = 0.98$, $P < 0.001$; $\log \text{ TGA} = 0.55 (\log \text{ body weight}) + 1.08$, $r^2 = 0.89$, $P < 0.001$. The range for water-breathing freshwater fishes is indicated for each morphological character based on the regressions provided by Palzenberger and Pohla (1992).

creased with decreasing PO_2 from an average of 21.5 ventilations per 15 sec at 40–60 mm Hg ($2.2\text{--}3.4 \text{ mg l}^{-1}$) to 94.5 ventilations per 15 sec at 8–20 mm Hg ($0.45\text{--}1.1 \text{ mg l}^{-1}$). At lower oxygen levels, gill ventilations were too fast to be recorded with the naked eye. We observed no buccal bubble holding during ASR.

The total gill filament length (TFL) of *P. catostoma* (body weight range = 0.34–3.2 g) ranged between 43.5 and 123.0 cm and was positively correlated with body size ($r^2 = 0.98$, $P < 0.001$, Fig. 2A). Palzenberger and Pohla (1992) reviewed the literature on gill morphology of fishes. From their dataset for 28 water-breathing freshwater species, they extracted the mean slope of significant regressions for gill morphological parameters (total filament length, lamellar density, gill surface area) and 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 values of a species as a percentage within the range of values for freshwater fishes. For total gill filament length, *P. catostoma* averaged 52% of the range for freshwater fishes (± 2.0 , SD, range = 48–55%, Fig. 2A). Lamellar density (ALD) averaged 28.5 lamellae per millimeter and ranged between 26.4 and 31.6 lamellae per millimeter. There was no relationship between lamellar density and body size ($r^2 = 0.26$, $P = 0.16$). Average lamellar density for *P. catostoma* falls within the middle ($47 \pm 9\%$) of the total range for freshwater fishes reviewed by Palzenberger and Pohla (1992). Total gill surface area (TGA) was relatively large reflecting a large lamellar area which averaged 0.015 mm^2 . TGA ranged between 9.0 and 27.0 cm^2 and increased with body size ($r^2 = 0.89$, $P < 0.001$, Fig. 2B). TGA fell within the upper ($75 \pm 8\%$, SD) of the range for freshwater fishes (Fig. 2B).

The total oxygen consumption rate for *P. catostoma* (body weight range = 2.54–3.44 g, 20 C) averaged $0.36 \pm 0.07 \text{ mg O}_2/\text{h}$ (SD), and mass-specific oxygen consumption rate averaged $0.13 \pm 0.02 \text{ mg O}_2/\text{g/h}$. Mass-corrected oxygen consumption rates (corrected to the mean weight of 3.06 g) also averaged $0.13 \pm 0.02 \text{ mg O}_2/\text{h}$. Winberg (1956, 1961) derived a standard curve for the relationship between total metabolic rate and body size for freshwater fishes based on literature data. The total oxygen consumption rate for *P. catostoma* averaged 36% ($\pm 7\%$) of the predicted values for freshwater fishes based on Winberg's line (1956, 1961). Winberg (1961) also presents an equation for poeciliid fishes which have metabolic rates below his predicted values for freshwater fishes. The oxygen consumption rate of *P. catostoma* averaged 61% ($\pm 1\%$) of the predicted values based on the poeciliid line. Critical oxygen tension (P_c) averaged 9.1 mm Hg (± 1.09 , SD) and ranged from 7.0–11.0 mm Hg.

DISCUSSION

The inverted swimming posture exhibited by *P. catostoma* during aquatic surface respiration is unusual but should increase the efficiency of ASR for a fish with a subterminal mouth. Some catfishes in the genus *Synodontis* and allied genera of the family Mochokidae also swim upside down. Though it is clear that inverted swimming in some mochokids is used for surface feeding (Bishai and Abu Gideiri, 1963; Lowe-McConnell, 1975), Chapman et al. (1994) found that inverted swimming in *S. nigriiventris* was associated with surface breathing in hypoxic

water. The inverted behavior in *S. nigriventris* and *P. catostoma* places the subterminal mouth in a position to efficiently pump water from the oxygen-rich surface film over the gills. In *P. catostoma*, inverted swimming seems to be exclusively respiratory in function; inverted swimming was never observed in association with feeding during our field observations or laboratory studies.

The thresholds for aquatic surface respiration (13 and 3 mm Hg for ASR_{10} and ASR_{50} , respectively) were very low relative to other tropical freshwater fishes. Kramer and McClure (1982) found an average ASR_{10} level of 21 mm Hg and an ASR_{50} level of 16 mm Hg in their study of 26 species of water-breathing tropical fishes. Increased time at the surface may be energetically expensive, particularly for species like *P. catostoma* that swims continuously during ASR, and may increase exposure to predators (Kramer et al., 1983). In *P. catostoma*, a low metabolic rate, a low critical oxygen tension, and relatively large gills may permit a low threshold for aquatic surface respiration minimizing both the predator risk and energy costs associated with surface swimming. Oxygen values at *P. catostoma* sites in the Lwamunda Swamp were always above the 50% ASR threshold for *P. catostoma* during the day but not above the 10% threshold, suggesting that ASR may be required at a minimal level during the day. ASR may occur more frequently associated with nocturnal oxygen reduction (Table 1).

A low metabolic rate and a low critical oxygen tension may permit fish to withstand extreme hypoxia. There are few data available on oxygen consumption rates and critical tensions of water-breathing fishes from African swamps; however, recent data on the swamp-dwelling African cichlid, *Pseudocrenilabrus multicolor victorae* indicate that this species has a low routine metabolic rate (30% of expected values based on Winberg's 1961 equation) and a low critical oxygen tension (6.6 mm Hg, Rosenberger, 1997). The metabolic rate of *P. catostoma* is also low, averaging only 35% of the expected values based on Winberg's equation (1961). Ultsch et al. (1978) compared metabolic rates for freshwater fishes reported in the literature between 1962 and 1975 to values predicted by Winberg's equation and found that metabolic rates averaged only 52% of the predicted values. However, given that the oxygen consumption rate of *P. catostoma* falls far below predicted values for freshwater fishes and the poeciliid fishes derived from Winberg's equations (1961) falls below the average value reported by Ultsch et al. (1978) for the more recent studies, we conclude that *P. catos-*

toma has a relatively low metabolic rate. The low critical oxygen tension of *P. catostoma* (9 mm Hg) reflects high oxygen uptake efficiency even at very low levels of dissolved oxygen. Based on field data of oxygen availability in the Lwamunda lagoons, *P. catostoma* may only experience levels below its critical tension during the night and early morning. Midday values fell above the critical tension at all sites (Table 1).

There are few comparative data on hypoxia tolerance of mormyrids. However, Fish (1956) found that the hemoglobin content of the blood of *Mormyrus kannume* from Lake Albert was high, and oxygen dissociation curves indicated high tolerance to low-oxygen conditions. In a recent study, Nilsson (1996) found that the mormyrid *Gnathonemus petersii* is very tolerant of low oxygen levels. The metabolic rate of *G. petersii* averaged 47% of the predicted values based on the equation derived by Winberg (1961) and was maintained to an oxygen level of 0.77 mg l⁻¹. Mormyrids have an exceptionally large cerebellum, related at least in part to their remarkable electrogenic and electrolocation capabilities (Kramer 1990). Nilsson (1996) found that, in *Gnathonemus petersii*, the brain accounts for approximately 60% of the total oxygen consumption, a larger fraction than reported for any other vertebrate brain. Nilsson (1996) notes that the ability of mormyrids to utilize oxygen efficiently under extreme hypoxia and regulate oxygen uptake at very low ambient levels may be important in protecting the brain from hypoxia damage.

In *P. catostoma*, a low threshold for aquatic surface respiration and a low critical oxygen tension may reflect very efficient oxygen uptake mechanisms including a large respiratory surface area. The gill surface area of fishes is assumed to correlate with the ratio of metabolic oxygen demands to the oxygen content of their environment (Palzenberger and Polha, 1992). *Petrocephalus catostoma* has a relatively low routine metabolic rate and a relatively large total gill surface area, which suggests that increased oxygen uptake efficiency afforded by large gills may reflect a requirement of the environment, rather than sustaining high activity levels. However, data on the active metabolic rate of *P. catostoma* will be necessary to fully understand the interaction of gill size, metabolic rate, and oxygen availability in this species.

Wetlands in the Lake Victoria basin may be critical to the protection of some species from Nile perch predation because they provide both low-oxygen and structural refugia. Fish (1956) found that Nile perch require water with high dissolved oxygen (> 5 mg l⁻¹) since their blood

has a low affinity for oxygen. In addition, in a comparison of ecotone areas of Lake Nabugabo, Chapman et al. (1996b) found that Nile perch were less abundant in wetland ecotones relative to exposed inshore areas. Thus, the expansion of Nile perch from lakes into river systems and wetlands in the Lake Victoria region may be limited by their low tolerance to hypoxia and the structural complexity of dense wetlands. For *P. catostoma*, a high tolerance of extreme hypoxia permits exploitation of wetland habitats like the lagoons and tributaries of the Lwamunda Swamp. In the Lake Nabugabo region, *P. catostoma* populations may persist today only by continued use of wetland lagoons and tributaries and nearby satellite lakes where Nile perch are absent (e.g., Manywa, Kayugi, Ogutu-Ohwayo, 1993). It is not likely that the *P. catostoma* of the Lwamunda swamp have shifted their distribution into the swamp in response to Nile perch predation. Rather, the current distribution may represent a remnant of a much broader pre-Nile perch distribution. The Cambridge expedition to Lake Nabugabo in 1962 (CNBS, unpubl.) recorded *P. catostoma* in the main lake but also in a few small pools of the Lwamunda Swamp where they have persisted since that time.

For *P. catostoma*, a suite of characters may contribute to its ability to persist in the hypoxic waters of the Lwamunda Swamp including its efficient use of aquatic surface respiration, a low oxygen consumption rate, a low critical oxygen tension, and large gills. It is likely that other adaptations to low oxygen conditions (e.g., high hemoglobin concentration) compliment this suite and interact with environmental pressures to contribute to the current pattern of *P. catostoma* distribution.

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