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Why Swim Upside Down?: A Comparative Study of Two Mochokid Catfishes

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Some catfishes in the genus *Synodontis* and its allied genera (family Mochokidae) swim upside down and exhibit reverse countershading. We demonstrate a potential respiratory function for this behavior through laboratory observations of upside down (*Synodontis nigriventris*) and right side up (*Synodontis afrofisheri*) species exposed to low PO₂. Both species used aquatic surface respiration (ASR) at the air-water interface when PO₂ was <15 mm Hg. With decreasing PO₂, *S. nigriventris* increased the percentage of ASR time spent upside down, did not emerge its body during ASR, and had very modest surface activity levels. *Synodontis afrofisheri* used a vertical posture for ASR that caused emersion of its snout and required constant swimming to maintain position; it used active forward motion during ASR at very low PO₂ and made repeated trips to the bottom. The vertical posture and increased swimming activity associated with ASR by *S. afrofisheri* is probably less efficient than the inverted ASR of *S. nigriventris*.

MANY catfishes of the family Mochokidae are benthic in habit, feeding on bottom-dwelling organisms or detritus with their ventral mouths (Lowe-McConnell, 1975). A few species, however, can be found swimming inverted, a habit often associated with exploitation of the water surface. Although similar morphologically to the other mochokids, some species that exhibit upside down habits, such as *Synodontis nigriventris* and *Hemisyndontis membranaceus*, are characterized by reverse countershading (Daget, 1948; Poll, 1971). This pat-

tern may allow the fish to merge with their background of light when their ventral surface is directed upward. Apparently, swimming with the ventral surface uppermost is used in a feeding context, facilitating the exploitation of plankton and fine detritus from the surface waters (Bishai and Abu Gideiri, 1963; Holden and Reed, 1972; Lowe-McConnell, 1975). However, a respiratory function has also been ascribed to this unusual behavior (Holden and Reed, 1972; Roberts, 1975).

Many fish species use aquatic respiration at

the surface (Aquatic Surface Respiration, ASR; Kramer and Mehegan, 1981) when inhabiting hypoxic waters. ASR works because diffusion from the atmosphere provides a thin, well-oxygenated microlayer of surface water, even though deeper waters may be hypoxic (Gee et al., 1978; Kramer and McClure, 1982; Kramer, 1983). The upside down habit of certain mochokid fishes could also provide surface access for purposes of ASR, an activity that would otherwise be difficult for a fish having a ventral mouth. There is little quantitative data on the respiratory responses of the upside down catfishes to hypoxia or their use of ASR.

Here we compare the behavioral responses to hypoxia of two mochokid catfish (*Synodontis nigriventris* and *Synodontis afrofischeri*). Unlike *S. nigriventris*, *S. afrofischeri* does not habitually swim upside down and, thus, may not respond to hypoxia by swimming ventrally at the surface. The percentage of time spent at the surface and the behavior of both species is described in relation to PO_2 . In addition, we examine behavioral parameters related to efficiency of respiratory use of the surface layer.

METHODS

Study species.—Wild-caught *S. afrofischeri* were obtained from Old World Exotics of Florida from a private collector who works on the northern shoreline of Lake Victoria between Entebbe and Jinja. The four smallest individuals were captive spawned from the wild-caught group in the Lake Victoria exhibit at the Franklin Park Zoo, Boston, Massachusetts. *Synodontis nigriventris* used in this work were purchased from Metro Pets, New Jersey.

Synodontis afrofischeri occurs in the Nile basin, primarily in Lake Victoria and its affluent rivers; the Victoria Nile; and lakes Nabugabo, Kyoga, and Ihema (Greenwood, 1966; Poll, 1971). It is benthic, retains a normal orientation, feeds on insect larvae and molluscs (Corbet, 1961), and rarely attains a total length of over 15 cm. *Synodontis nigriventris* reaches a maximum total length of 9.6 cm and occurs in streams and rivers of the central Congo (Poll, 1971). It has reversed countershading related to its habit of routinely swimming inverted.

The effect of PO_2 .—Four small *S. afrofischeri* (mean Total Length = 64.9 ± 4.7 mm) and four *S. nigriventris* (mean Total Length = 64.3 ± 4.1 mm) were selected from a stock aquarium ($59 \times 37 \times 39$ cm, 23–26 C). To determine the effect of hypoxia on the behavior of the two

species, an experimental tank ($90 \times 30 \times 37$ cm, maintained at 32 cm of depth) was divided into two major compartments ($36 \times 30 \times 37$ cm) using a screen partition that limited visibility and eliminated fish movement between compartments but permitted some water exchange. Two additional partitions divided the major compartments from the two ends of the tank. These smaller end compartments contained heaters and air stones. Each major compartment contained a box filter and two pieces of cover that consisted of strips of plastic connected to a small plexiglass tube. The two species were placed in separate compartments, maintained at 23–26 C, and fed Tetramin food flakes.

Fish were exposed to various concentrations of oxygen between 0.15 and 8.3 mg/L at 23–26 C (3–154 mm Hg). Twenty-one trials were conducted over 16 days, with the level of oxygen concentration selected randomly from predetermined values. No more than two trials were conducted each day, with an average of 3 h between trials on the same day. Fish were maintained at normoxia overnight, and PO_2 was returned to normoxic levels between trials conducted on the same day. Fish were starved for several hours before a trial to ensure that trips to the surface were not associated with feeding at the surface. PO_2 was reduced by bubbling N_2 through an air stone in each of the two end compartments. To create extreme hypoxia (<1 mg/L), small amounts of sodium sulfite were added to the water (Lewis, 1970; Kramer and Mehegan, 1981; Gee and Gee, 1991). Oxygen content was measured (± 0.1 mg/L) with a YSI (Model 57) O_2 meter and converted to PO_2 using standard tables (Davis, 1975). For each trial, oxygen concentration was reduced over 40–90 min. Fish were then allowed to acclimate for 30 min.

The average amount of time spent at the surface was determined for each species by an observer who sat behind a blind 0.5 m from the tank. The blind was necessary to prevent disturbance that would result in fish retreating to cover. A continuous record was kept of the number of fish and their orientation at the surface for 30 min. Video recordings were used for assessment of posture, positioning of the barbels, and emersion of the snout.

Gill ventilation rates/15 sec were determined in relation to the method of ASR employed by the fish. Oxygen was lowered slowly. Gill ventilation rates were recorded four times on each fish just prior to the ASR threshold level and after ASR was initiated for each species in different postures.

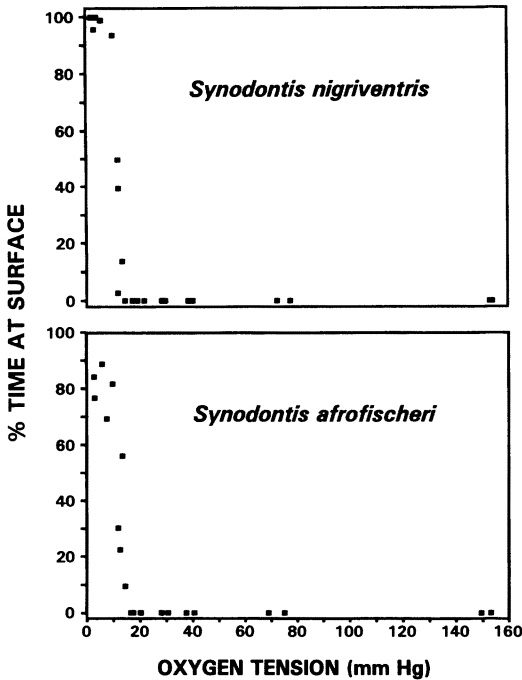


Fig. 1. Relationship between the percentage of time engaged in aquatic surface respiration and sub-surface PO_2 (mm Hg) for *Synodontis nigriventris* and *Synodontis afrofisheri*.

RESULTS

Relationship between PO_2 and ASR.—At low PO_2 , both *S. nigriventris* and *S. afrofisheri* used ASR. There was no evidence for regular inspiration of atmospheric air. On very rare occasions, *S. afrofisheri* was observed to take a bubble into its mouth. Although this behavior may have been used to adjust buoyancy (Gee and Gee, 1991), it was not a regular event associated with ASR. Nor were bubbles regularly released when fish left the surface after ASR.

PO_2 had a very strong effect on the amount of time both species spent using ASR. ASR was initiated in both species at approximately 15 mm Hg, and the occurrence of this activity increased rapidly with decreasing PO_2 until ASR occupied most of their time (Fig. 1). *Synodontis nigriventris* spent an average of 98% of their time engaged in ASR at 3–10 mm Hg. For *S. afrofisheri*, the percent of time at the surface averaged only 83% at 3–10 mm Hg (Fig. 1).

During ASR, *S. afrofisheri* made frequent short trips to the bottom. This was reflected in frequent changes in the number of individuals at the surface. For *S. nigriventris*, ASR was less frequently interrupted by trips to the bottom, and group composition remained stable over a longer period. Over the nine trials where both species used ASR, mean bout length (time at the surface without a change in the number of

individuals at the surface) was significantly higher for *S. nigriventris* (mean = 116 sec) than for *S. afrofisheri* (mean = 22 sec, paired t-test, $t = 3.80$, $P = 0.005$).

Respiratory behavior.—*Synodontis afrofisheri* was never observed to swim on its back. ASR was achieved by positioning the body nearly perpendicular to the surface (Fig. 2A). Active movements were required to maintain this posture. ASR was performed in two ways. The first was to perform ASR while hovering in a vertical position against the wall of the aquarium. We refer to this as “pump ASR,” because water passing over the gills is pumped by mouth and opercular movement. Pump ASR was more common at the initiation of ASR and at higher oxygen levels. The second way was to perform ASR in a vertical posture while swimming back and forth across the tank (Fig. 2A). Although the fish actively ventilated their gills while moving across the tank through buccal and opercular movement, this method presumably forces more well-oxygenated surface water over their gills than could be achieved by active respiratory movements in a static position. By constantly moving along the water surface, the fish continuously exposes the buccal area to a new region of the surface layer. Forward motion may also contribute to lift. Active movement across the tank during ASR was greater when PO_2 was low (<6 mm Hg). We postulate that O_2 uptake enhancement via forward motion is obligate at very low PO_2 s in this species and tentatively refer to this as “ram-assisted ASR” (Fig. 2A). Although ram-assisted ASR was used more when oxygen was very low, mean gill ventilation rates showed no significant increase over pump ASR rates (no./15 sec: ram-assisted ASR—43.1, pump ASR—41.6, $t = 1.3$, $P = 0.19$), suggesting that ram-assisted ASR may facilitate more efficient use of the surface layer. The use of either method resulted in a decrease in gill ventilation rates from prethreshold levels (no./15 sec: pump ASR—41.6, prethreshold—59.9, $t = 10.9$, $P < 0.001$; ram-assisted ASR—43.1, prethreshold—59.9, $t = 9.8$, $P < 0.001$).

Only the single pair of maxillary barbels were in contact with the surface when *S. afrofisheri* performed either method of ASR. The two pairs of mandibular barbels were generally held together approximately 2–3 mm under the surface of the water forming a scoop that may have aided in directing water into the mouth (Fig. 2A). The snout was often emersed during ASR, increasing the weight of the fish. This may account to some degree for the activity necessary for maintenance of position during ASR. For *S. afrofisheri*, movement toward the surface was often a slow upward creep in close proximity to

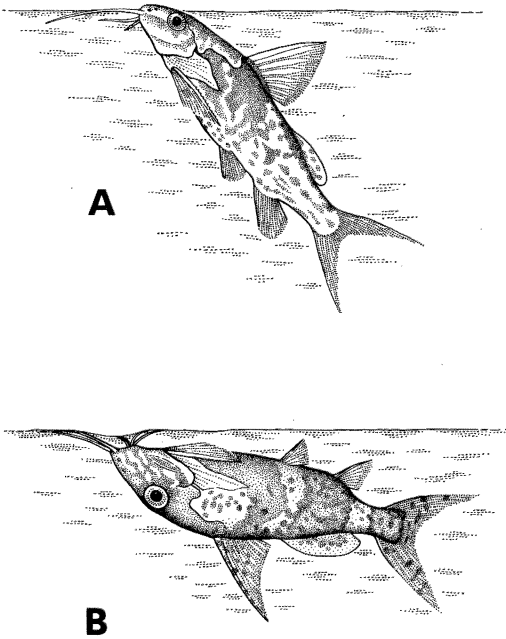


Fig. 2. Postures used by *Synodontis afrofischeri* (A) and *Synodontis nigriventris* (B) during ASR.

a side of the compartment. External stimuli (e.g., a hand moving across the tank) generally produced a quick diving response. When PO_2 was very low, the fish returned to the surface within seconds.

Synodontis nigriventris exhibited two patterns of ASR. It was common to find *S. nigriventris* swimming inverted at the surface using ASR, with all sets of barbels in contact with the surface (Fig. 2B). Often, the fish remained motionless, floating inverted for several seconds, with no active movement necessary for continued use of the surface layer. This was periodically followed by the fish swimming slowly upside down to a new location, where, again, the fish might stay for several seconds in the same position. Pelvic fins were used in maneuvering and maintenance of position. The second posture was similar to *S. afrofischeri* in that *S. nigriventris* would also hang in a vertical position against an upright structure (glass or divider) using ASR, with only the maxillary barbels at the surface. However, unlike *S. afrofischeri*, *S. nigriventris* often remained in the vertical position without active movement. The use of either posture resulted in a decrease in mean gill ventilation rates from prethreshold levels (no./15 sec: vertical posture—42.7, prethreshold—62.9, $t = 12.4$, $P < 0.001$; inverted posture—43.1, prethreshold—62.9, $t = 11.0$, $P < 0.001$).

At PO_2 s below the threshold for ASR, the percentage of time that *S. nigriventris* swam upside down during ASR increased rapidly with

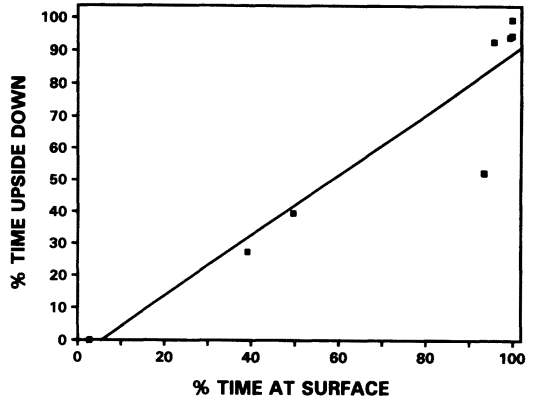


Fig. 3. The relationship between the percent time *Synodontis nigriventris* spends inverted during ASR and the percent time at the surface (ASR).

decreasing PO_2 ($r = -0.93$, $P < 0.001$), producing a strong correlation between the time spent upside down during ASR and the time spent at the surface ($r = 0.94$, $P < 0.001$, Fig. 3). At the lowest oxygen level (< 3 mm Hg), *S. nigriventris* spent 100% of its time at the surface swimming upside down, supporting the hypothesis that inverted swimming is used to increase the efficiency of oxygen extraction from the surface waters. Although the inverted posture was used more when the PO_2 was very low, gill ventilation rates remained the same as those in the vertical posture (no./15 sec: vertical posture—42.7, inverted posture—43.1, $t = 0.3$, $P = 0.79$), again suggesting that the inverted posture facilitates more efficient use of the surface layer. In *S. nigriventris*, both postures were characterized by only modest activity and could be classified as “pump” ASR. As with *S. afrofischeri*, movement toward the surface was often slow and secretive.

We used a simple procedure to assess relative differences in buoyancy between the two *Synodontis* species. Four *S. afrofischeri* and four *S. nigriventris* that were resting at the bottom of the stock aquarium maintained under normoxic conditions were removed from the tank, quickly anesthetized with MS-222 (tricaine methanesulfonate), and gently placed back in the surface waters of the aquarium. All four *S. afrofischeri* were negatively buoyant and quickly sank. Three *S. nigriventris* were only slightly negatively buoyant, sinking very slowly, whereas one fish was positively buoyant. Within the limits of this procedure, this suggests that *S. afrofischeri* is more negatively buoyant than *S. nigriventris*.

Frequent trips to the bottom during ASR bouts by *S. afrofischeri*, even at low PO_2 , and qualitative observations of this species' behavior during ASR suggest that respiration in the surface waters is energetically expensive. *Synodontis*

afrofischeri clearly works at maintaining its vertical position at the surface, which may reflect both negative buoyancy and difficulties associated with maintenance of the posture. As an index of energetic cost, we recorded the number of strong beats of the caudal peduncle in 30-sec intervals for each of the species during ASR. Although *S. nigriventris* used delicate movements of the caudal fin and pectoral fins at times when at the surface, distinct, strong beats of its caudal peduncle were far fewer than in *S. afrofisheri* (*S. nigriventris*: mean = 6.0, n = 26; *S. afrofisheri*: mean = 44.2, n = 20, Mann-Whitney test, $z = -5.5$, $P < 0.001$).

DISCUSSION

Because most fishes rarely turn upside down, the question of why some mochokids are commonly found swimming inverted has been of interest for some time. That reversed countershading is often associated with the inverted behavior suggests that there has been selection for traits minimizing predation for fish assuming the upside down posture. There are laboratory and field observations, and stomach content data, demonstrating that inverted swimming is an adaptation for feeding on surface plankton (Bishai and Abu Gideiri, 1963; Poll, 1971; Lowe-McConnell, 1975). *Hemisynodontis membranaceus* has been observed feeding on micro-organisms from the surface waters with its ventral surface uppermost (Poll, 1971; Lowe-McConnell, 1975). In *Hemisynodontis membranaceus* and *Brachysynodontis batensoda*, both inverted swimmers, the gill rakers are longer and more densely placed than those of other benthic feeding mochokids, producing an efficient sieving organ for the exploitation of plankton (Bishai and Abu Gideiri, 1963). Both of these species are surface feeders, but they will readily feed on bottom food when surface food is not available (Bishai and Abu Gideiri, 1963).

Although it is clear that swimming upside down has advantages for feeding, this does not preclude a respiratory function, nor is it necessarily the case that feeding at the surface predisposed these species to use inverted swimming for efficient ASR. Our study provides several lines of evidence consistent with the idea that, for *S. nigriventris*, inverted swimming increases the efficiency of ASR for a fish with a subterminal mouth. These include the use of inverted swimming for ASR at low PO_2 , no emersion of the snout, an increase in the percentage of surface time spent upside down with a decrease in PO_2 , and only modest activity when using ASR. Field observations of *Hemisynodontis membrana-*

ceus and *Brachysynodontis batensoda* in dry season pools also suggest that inverted surface swimming may be used in a respiratory context (Roberts, 1975; Holden and Reed, 1972). Green (1977) notes that, for *H. membranaceus*, the habit of swimming upside down in the open water while feeding on plankton close to the surface also tends to keep the fish in well-aerated water.

There are a variety of behavioral and morphological features of various fishes that are viewed as adaptations to permit or increase the efficiency of ASR. Lewis (1970) demonstrated how the dorsally oriented mouth and dorsoventrally flattened head of fishes such as *Fundulus*, *Poecilia*, and *Gambusia* are adaptations for ASR. The dermal protuberances of the lower lip that develop in certain Amazonian characids are viewed as adaptations to facilitate ASR by reducing mixing between the oxygenated surface film and the hypoxic water beneath (Braun and Junk, 1982; Winemiller, 1989). Gee and Gee (1991) found that nine species of benthic negatively buoyant gobies held a bubble in the buccal chamber during ASR, which appeared to function in providing lift to the head or body, facilitating ASR and potentially adding oxygen to buccal water prior to gill ventilation.

For *Synodontis nigriventris*, *Hemisynodontis membranaceus*, *Brachysynodontis batensoda*, and other mochokid catfish that are habitually inverted, a combination of behavioral and morphological features seem to be related to their utilization of ASR. The inverted behavior places the subterminal mouth in a position to efficiently pump surface water over the gills. The placement of all three pairs of barbels in contact with the surface, which was observed in *S. nigriventris*, may function in an analogous manner to the characid dermal protuberances. Reversed countershading potentially minimizes the threat of predation during time at the surface.

The comparative study of *S. afrofisheri*, a species that retains a normal orientation, and the upside down catfish, *S. nigriventris*, provides further support for the respiratory function of inverted swimming. In *S. afrofisheri*, emersion of the snout during ASR, constant swimming to maintain position at the surface, the use of ram-assisted ASR at very low PO_2 , and repeated trips to the bottom during ASR suggest that the vertical posture and associated ASR performance by *S. afrofisheri* is less efficient than the inverted strategy of *S. nigriventris*. At low PO_2 , ram-assisted ASR may be necessary to maintain lift and to extract sufficient oxygen from the surface layer because the position of the mouth is not flat against the surface layer. Positioning of the mandibular barbels in a scooplike formation under the water surface could facilitate more

directed flow of the upper water layer toward the mouth. The vertical posture, in combination with the subterminal position of the mouth in *S. afrofischeri*, often results in emersion of the snout during ASR. This both increases the weight of fish and potentially increases the stimuli for aerial predators.

Whether feeding inverted at the surface pre-disposes upside down mochokid catfish to more efficient utilization of the well-oxygenated surface waters, or whether the original adaptation was to low oxygen, is not clear. However, our results do suggest that inverted swimming may increase the efficiency of ASR for fishes with a subterminal mouth, permitting exploitation of hypoxic waters or prolonging survival in such habitats. We believe that the apparent controversy over the primary function of inverted swimming, i.e., feeding versus respiration, is moot. To the inverted catfishes, the water's surface is just another substratum. The cluster of morphological and behavioral traits exhibited by upside down catfishes reflects an extension of simple mochokid and more generally siluroid adaptations to life at structural interfaces. Surface feeding and surface respiration go hand in hand, just as feeding and refuge from predators do in benthic environments. Nonetheless, it is odd that so few benthic fishes exploit surface waters and that they may exist only in Africa, despite the high diversity of catfishes of similar morphology in South America. The answer to the first question may lie in the high risk of aerial predation. The apparent restriction of upside down catfishes to Africa is more puzzling.

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