COORDINATION OF RESPIRATORY AND HYDROSTATIC FUNCTIONS OF THE SWIMBLADDER IN THE CENTRAL MUDMINNOW, *UMBRA LIMI*

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**SUMMARY**

1. Observations of behaviour and changes in buoyancy of *Umbra limi*, a facultative air-breathing fish, were studied to understand coordination of respiratory and hydrostatic functions of the swimbladder.

2. Fish were exposed to either normoxic or hypoxic water in either undisturbed or disturbed (simulating predator presence) conditions. Declines in swimbladder volume occurred between air-breaths as O₂ was removed. These varied between treatments averaging 1.3% in disturbed normoxic conditions, 4.1% and 6.4% in undisturbed treatments (normoxic and hypoxic conditions respectively), and 8.3% in disturbed hypoxic conditions.

3. To minimize the extent and rate of such changes and thereby reduce energy costs of a non-optimal buoyancy, fish either maintained a continuous positive buoyancy at the water surface, compressed the swimbladder gases after inspiration and gradually reduced the pressure to compensate for O₂ uptake, or increased their reliance on aquatic O₂. The use of any of the above mechanisms was determined by the amount of dissolved O₂ and presence or absence of disturbance.

4. In normoxic water fish without access to the surface maintained neutral buoyancy despite a very limited ability to secrete swimbladder gases.

5. The frequency of air-breathing in normoxic water was independent of swimbladder O₂ levels, indicating that fish breathe air in normoxic water in response to a decline in swimbladder volume.

6. The potentially conflicting roles of the swimbladder are well coordinated.

**INTRODUCTION**

The advantages to fishes of using air as a respiratory medium are well known (Johansen, 1970) but only recently (Kramer et al. 1978) have the disadvantages, particularly those of an ecological or behavioural nature, received attention. One cost of breathing air is the potential loss of hydrostatic control between air-breaths. This arises because O₂ is removed from the air-breathing organ without equivalent replacement of CO₂ (Johansen, 1970), leading to a decline in buoyancy and ultimately a greater expenditure of energy in both movement and maintenance of vertical position. To make the opposing roles of hydrostatic control and respiration com-
patible, the extent and rate of buoyancy change between air-breaths should be minimized.

A number of behavioural, morphological and physiological adaptations are possible to reduce this conflict. These include (a) adopting a mode of life at the water surface where continuous positive buoyancy is maintained such that changes in buoyancy would have little effect as long as it remained above neutral; (b) adopting a benthic mode of life to counter costs of maintaining vertical position at negative buoyancy (but not costs of locomotion); (c) gulping in a large volume of air, compressing it to provide the appropriate buoyancy and gradually releasing the pressure to compensate for uptake of O\textsubscript{2} from the respiratory organ thus keeping buoyancy constant; (d) in hypoxic water, reducing perfusion of air-breathing organ to restrict uptake of aerial O\textsubscript{2} and increase reliance on aquatic respiration as much as possible, thereby reducing the rate of buoyancy change; and (e) utilization of hydrodynamic compensation whereby lift created from the body shape and paired fins during swimming is used to compensate for a negative buoyancy.

Detailed information on buoyancy changes between air-breaths and on mechanisms used to minimize such changes are lacking. The purpose of this study is to provide an understanding of the strategies used by the central mudminnow, *Umbra limi* (Kirkland) to minimize the conflict between serial respiration and hydrostatic control.

The mudminnow is a common fish in central North America occupying still waters that vary greatly in temperature and dissolved O\textsubscript{2}. It is most abundant in areas of dense aquatic vegetation where organic debris accumulates (K. A. Martin, personal communication). It is exposed to a variety of aquatic and terrestrial predators and is very secretive in its habits. A relatively inactive fish, it stalks its prey by hovering, and then approaching very slowly before striking. Precise buoyancy control is critical. Mudminnows are continuous but facultative air-breathers using the swimbladder as an accessory respiratory organ (Gee, 1980). In normoxic water aquatic respiration is the primary mode regardless of temperature (5–30 °C) although air-breaths are taken every 1–2 h. When levels of dissolved O\textsubscript{2} fall below 50 torr, aerial respiration becomes the dominant mode, with the level of dissolved O\textsubscript{2} at which it becomes dominant decreasing with lower temperatures (Gee, 1980). The reason for periodic air-breaths in normoxic water is unclear but Gee (1980) suggested that they may be necessary to maintain the swimbladder at the appropriate volume to provide optimal buoyancy. If this explanation is correct then it suggests that the stimulus to take an air-breath in normoxic water may well be in response to a decline in buoyancy and not to a change in composition of gases in the swimbladder. However, such a mechanism of buoyancy control is limited during winter when ice cover, restricting access to air, is present from late October until early April. Under such conditions alternate mechanisms such as gas secretion would have to function. The secretory ability of respiratory swimbladders is unclear (Fange, 1976).

Specific objectives of this study were to determine: (1) the amount, range, and rate of change in buoyancy between air-breaths and to elucidate the mechanisms used to minimize such changes, (2) whether buoyancy control can be maintained without access to the surface by gas secretion into the swimbladder, and (3) whether fish breathe air in normoxic water in response to a decline in buoyancy or changes swimbladder O\textsubscript{2} levels.
Functions of the swimbladder in Umbra limi

MATERIALS AND METHODS

Fish (66–101 mm total length) were collected from Hazel Creek, Brokenhead and Bog Rivers, Manitoba, in September and October of 1976–78, with observations made in the laboratory between December and April of each year. Prior to observation fish were held in tanks (90 × 45 × 45 cm) at 25 (± 1) °C, in a 12 L: 12D photoperiod, and were fed frozen brine shrimp and trout starter (no. 3). The mudminnow is ideally suited to laboratory observation as it tolerates confined conditions, is responsive to disturbance, is relatively inactive and hovers at neutral buoyancy or rests either on the bottom or in contact with the water surface.

Buoyancy change between air-breaths

Measurements of buoyancy and observations of respiratory behaviour were made concurrently on fish held individually. Four treatments were chosen to represent extremes in conditions that mudminnows encounter in the field. These were the presence and absence of predator disturbance which were created in normoxic (partial pressure of O₂ (Pω₀) ca. 150 torr) and hypoxic (Pω₀ < 25 torr) water. In each treatment 5–7 fish were observed.

Observations were carried out within an aquarium balance system (Fig. 1) where Pω₀ was controlled by gently bubbling either compressed air or N₂ into the water creating either normoxic or hypoxic conditions. Simulated predator disturbance was created every 5 min by turning the light source off–on rapidly three times to represent the shadow of an aerial predator. This was followed by a strong rap on the table supporting the aquarium. Observations provided information at regular intervals on buoyancy, vertical position (surface resting, midwater hover, bottom resting) and number of opercular movements over 15 s. Time of air-breaths was recorded to the nearest second and buoyancy was measured immediately after each air-breath. Pω₀ and water temperature were monitored on a Yellow Springs Instrument O₂ meter. In normoxic water these data were recorded every 5 min and on some fish in the disturbed treatment every 2 min. In hypoxic water observations were made every 1 min and on some fish in the disturbed treatment every 2 min, and on one fish in the undisturbed treatment observations on buoyancy only were made every 10 s to provide a more complete record of buoyancy change.

Observations were made on individual fish at 25 (± 1) °C with a 12L:12D light regime. Fish were introduced into the cylinder of the aquarium balance system and allowed to adjust to it for at least 48 h. Observations (from behind a blind) followed over a 1–3 d period and were made during the period of illumination. Fish were not fed during this period. Duration of a daily period of observation was from 90 to 285 min in normoxic treatments and from 33 to 114 min in hypoxic treatments.

Each fish was exposed to only one treatment except for four that were exposed to two treatments and two that were exposed to three treatments. Fish exposed to multiple treatments were observed on consecutive days with observations in normoxic water preceding those in hypoxic water, and undisturbed treatments preceding disturbed treatments.

Buoyancy was determined by recording, at appropriate intervals, either the weight 0.001 g; recorded instantaneously) of a negatively buoyant fish resting on the bottom screen, or the lift of a positively buoyant fish resting against the top screen.
Fig. 1. Aquarium balance system used to measure changes in buoyancy between air-breaths. Fish were contained in a plexiglas cylinder (15 cm inside diameter) that was supported by the walls of the aquarium (40 x 20 x 24 cm). Top and bottom stainless steel screens contained fish in the cylinder but were supported independently from aquarium and the cylinder from a below-the-balance hook of a Sartorious balance (model 2250). Five holes (2 cm diameter) in the top screen permitted access to the surface for air-breathing. A number of 2 cm diameter holes were placed in the cylinder wall to ensure circulation of water.

Changes in weight over time can be equated to volume because 1 ml of gas at a given depth will support 1 g in fresh water (Gee, 1970). At the end of a period of observation and just after the last recording of weight or lift, anaesthetic (MS 222, ethyl m-aminobenzoate methanesulphanate) was introduced into the aquarium balance system, and once the fish was immobilized, it was removed, its swimbladder exposed and all gas expelled, the fish returned to the aquarium balance system, and after removing any bubbles from the body cavity, mouth, or opercula, the weight of the gas-free fish in water was recorded. The difference between the last recording of weight or lift of the intact fish in water and the weight of the gas-free fish in water equals the volume of the swimbladder (± 0-001 ml). Buoyancy was expressed by dividing the swimbladder volume by the weight of the gas-free fish in water (1-0 ml.g⁻¹ = neutral buoyancy; < 1-0 ml.g⁻¹ = negative buoyancy; > 1-0 ml.g⁻¹ = positive buoyancy). All previous measures of weight or lift in water were then converted into the swimbladder volume of the fish at that particular time and buoyancy values were then calculated.

Maintenance of neutral buoyancy and gas secretion

To determine if mudminnows could maintain neutral buoyancy without access to the surface, fish were divided into two batches of 10 and each batch put into a small
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These were placed within a single larger one at different levels; the higher to provide access to the surface (control), the lower to be submerged below the water surface and covered with stainless steel screen. Initially each small aquarium was filled to just below the top and provided with a supply of normoxic water at 25 (± 1) °C. After 3 days of acclimation to surroundings all fish were observed to be close to neutral buoyancy. The water level was raised in the large aquarium to cover the surface and screen of the lower aquarium, leaving no bubbles trapped within. Fish were fed each morning and then observed from behind a blind for 20 min daily each afternoon for four days and then once after nine days. The number of neutrally buoyant fish (surface or midwater hovering or touching the bottom lightly with tip of caudal fin; negatively buoyant fish rest with body contacting bottom), the number of fish active (moving through the water as opposed to hovering; recorded instantaneously), and the number of fish in the top, middle and bottom thirds of the aquaria were recorded four times at 5 min intervals.

Two experiments were completed to describe the rate of gas secretion into the swimbladder. In each, mudminnows were exposed to a reduced pressure (281 torr in the first and 540 torr in the second) to induce fish to spit gas. When these fish had attained neutral buoyancy under these conditions, pressure was returned to atmospheric and the now negatively buoyant fish were transferred to aquaria without access to the surface. In the first experiment, five fish were placed individually in the aquarium balance system (no access to surface) in normoxic water at 20 (± 1) °C and left for a day. Their weight in water was recorded 30 min after introduction and then one day later. Any decrease in weight (g) could be equated to volume of gas secreted (ml) assuming that there was no change in internal pressure of swimbladder gases. In the second experiment eight negatively buoyant fish were placed into a small aquarium, covered with a stainless steel screen and submerged within a larger aquarium and supplied with normoxic water at 25 (± 1) °C. The number of neutrally buoyant fish was recorded daily for 22 days.

Influence of swimbladder O₂ levels on air-breaths

To determine if the frequency of air-breathing was influenced by a particular level of swimbladder O₂, fish were observed when breathing from a gas phase of either air, N₂ (hypoxic) or O₂ (hypoxic). Fish were held in an aquarium (55 x 30 x 25 cm) with the surface covered by a 5 cm thick styrofoam plate to prevent access to air. The plate was fitted with a plexiglass cylinder (95 mm diameter) protruding 2 cm below the plate and 12 cm above. The cylinder was capped and fitted with an exhaust valve so that a continuous supply of any gas could be maintained. Normoxic water flowed through the aquarium at 25 (± 1) °C and a 100 W bulb above the aquarium illuminated the gas phase.

Ten fish were introduced into the aquarium through the cylinder 2 days before observations began. They were observed first breathing air, followed by N₂, then O₂. In the latter two treatments fish were breathing the particular gas for 2 days prior to observation. In each treatment fish were observed for either 12 or 14 periods of 30 min. These were separated by at least 30 min with no more than three observation periods made on one day. Observations were made from behind a blind and
Table 1. Extent, rate and range of buoyancy change between air-breaths

The mean inter-breath interval was calculated from the mean frequency of air-breaths (Table 2) and the mean rate of decrease was calculated by dividing the mean extent of change by the mean inter-breath interval.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. fish observed; total air-breaths taken</th>
<th>Mean buoyancy (ml.g⁻¹)</th>
<th>Mean inter-breath interval (min)</th>
<th>Mean rate of decrease (ml.g⁻¹.h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>After breath</td>
<td>Prior to breath</td>
<td>Difference (extent of change)</td>
</tr>
<tr>
<td>Normoxic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undisturbed</td>
<td>7; 13</td>
<td>0.931</td>
<td>0.990</td>
<td>0.041</td>
</tr>
<tr>
<td>Disturbed</td>
<td>6; 10</td>
<td>0.985</td>
<td>0.972</td>
<td>0.013</td>
</tr>
<tr>
<td>Hypoxic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undisturbed</td>
<td>6; 55</td>
<td>1.071</td>
<td>1.007</td>
<td>0.064</td>
</tr>
<tr>
<td>Disturbed</td>
<td>5; 55</td>
<td>1.002</td>
<td>0.919</td>
<td>0.083</td>
</tr>
</tbody>
</table>

included the number of breaths at the gas phase, the frequency of branchial breathing (recorded on five fish at the beginning, midway and end of each observation period), and the number of fish active at 5 min intervals.

RESULTS

Buoyancy change between air-breaths

Buoyancy declined between air-breaths in all treatments but the pattern of change varied between treatments (Table 1). In normoxic water, undisturbed fish were mostly positively buoyant, resting at the water surface and showing a gradual but marked decrease in buoyancy between infrequent air-breaths (Fig. 2A; Table 1). Occasional abrupt increases and decreases in buoyancy were observed. Fish exposed to simulated predator disturbance in normoxic water were mostly negatively buoyant but remained close to neutral buoyancy and showed only a slight decline in buoyancy between infrequent air-breaths (Fig. 2B; Table 1). On four observations, fish were observed to have a high positive buoyancy immediately after an air-breath, which dropped sharply to near neutral buoyancy within 2 min. As these abrupt changes in buoyancy resulted from alterations to the internal pressure of swimbladder gases (no additional gas was gained or lost by the swimbladder) the four values were not used to calculate mean buoyancy after an air-breath in this treatment. Instead, they were replaced by the next buoyancy value recorded. In hypoxic water, undisturbed fish remained positively buoyant and showed rapid declines in buoyancy between frequent and regular air-breaths taken just before neutral buoyancy was reached (Fig. 2C; Table 1). Disturbed fish were mostly negatively buoyant and displayed marked decreases in buoyancy between frequent and irregular air-breaths (Fig. 2D; Table 1).

An estimate of the internal pressure observed in the normoxic disturbed treatment was made on nine fish held individually in the aquarium balance system by observing their buoyancy before and after a single disturbance. The following mean buoyancy values (ml.g⁻¹) and 95% confidence limits were found: prior to disturbance, 1.046 (± 0.032); following disturbance, 0.981 (± 0.018). The difference between means was significant (P < 0.005 ANOVA) and, as no gas was lost, indicates that the intern
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Pressure was increased by an average of 50.2 torr. Such an increase in pressure would reduce buoyancy to a similar extent as that shown in Fig. 2B which occurred between 36 and 37 min, just after the air-breath was taken.

Disturbance affected the extent of buoyancy decline between air-breaths in normoxic water as undisturbed fish showed a significant \( P < 0.005 \); ANOVA) change in buoyancy while the change in buoyancy for disturbed fish was not significant \( P > 0.10 \); ANOVA). In hypoxic water significant \( P < 0.005 \) declines in buoyancy in both undisturbed and disturbed fish were similar and exceeded those in normoxic water (Fig. 3; Table 1). Disturbance reduced the rate of decline in buoyancy in both normoxic and hypoxic water and rates of decline in the latter

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*Fig. 2.* Typical patterns of buoyancy change between air-breaths for undisturbed and disturbed fish in normoxic and hypoxic water. The dotted lines represent neutral buoyancy, the triangles the time of an air-breath.
Fig. 3. Extent and range over which buoyancy changes occurred between air-breaths by undisturbed and disturbed fish in normoxic and hypoxic water. The solid vertical line represents the extent of change, with upper and lower circles representing mean buoyancy just after and before an air-breath respectively. The vertical lines represent 95% confidence limits on these means. The horizontal line of each triangle represents the mean time between breaths and the slope of the remaining line represents the rate of change in buoyancy.

were much more rapid than in the former (Fig. 3; Table 1). In normoxic water the interval between air-breaths was similar for disturbed and undisturbed fish. This interval was greatly reduced in hypoxic water, and here undisturbed fish had a much shorter interval between air-breaths than did disturbed fish (Fig. 3; Table 1).

Disturbance had a profound effect on vertical distribution. In both normoxic and hypoxic water disturbed fish were most frequently observed on the bottom (Table 2). Differences in $P_{O_2}$ had a lesser influence and fish in hypoxic water were more frequently observed at the surface in both disturbed and undisturbed treatments than fish in normoxic water. The four ratios of the number of fish in the three vertical zones of the aquarium were dissimilar ($P < 0.005$; test of independence using an $r \times c$ contingency table).

In normoxic water the mean frequency of air-breaths by disturbed and undisturbed fish was similar, but the mean frequency of branchial breathing increased with disturbance (Table 2). In hypoxic water, undisturbed fish breathed air much more frequently than disturbed fish and many showed no perceptible branchial movement. Occasionally, however, these fish showed rapid bursts of branchial breathing just prior to taking an air-breath. Disturbed fish in hypoxic water showed an extremely high frequency of branchial breathing (Table 2). Using the relative frequency of both modes of respiration the primary mode can be determined in each treatment. In normoxic water both undisturbed and disturbed fish used aquatic respiration as the primary mode, as air-breaths were infrequent. In hypoxic water, undisturbed fish were primarily air-breathers as the frequency of branchial pumping was greatly reduced. But disturbed fish were bimodal, with an extremely rapid frequency branchial breathing.
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<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean air-breaths (fish⁻¹ h⁻¹)</th>
<th>Mean branchial breaths (fish⁻¹ min⁻¹)</th>
<th>Fish position (%)</th>
<th>Total observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normoxic</td>
<td>0.68 ± 0.06</td>
<td>47.6 ± 9.6</td>
<td>Surface</td>
<td>419</td>
</tr>
<tr>
<td>Undisturbed</td>
<td>0.82 ± 0.38</td>
<td>47.2 ± 3.6</td>
<td>Hovering</td>
<td>175</td>
</tr>
<tr>
<td>Disturbed</td>
<td>2.76 ± 1.32</td>
<td>51.9 ± 5.2</td>
<td>Bottom</td>
<td>954</td>
</tr>
</tbody>
</table>

Numbers in parentheses are 95% confidence limits on means. The frequency of branchial breathing of each fish was based on at least 13 observations.
Mudminnows maintained neutral buoyancy when denied access to the surface. One fish became negatively buoyant on day 2 but regained neutral buoyancy by the next day. During the first two days fish without access were more active than those with access and were observed frequently in the top third of the aquarium, where they probed the screen with their snouts.

Four of the five fish held individually in the aquarium balance system at negative buoyancy (about 0.276 ml.g\(^{-1}\)) showed an increase in swimbladder volume over 24 h. At the average rate of increase, 0.022 ml.day\(^{-1}\), these fish would require 24.3 days to reach neutral buoyancy. Six of the 8 fish established in a group without access to the surface at a negative buoyancy of about 0.539 ml.g\(^{-1}\) attained neutral buoyancy at an average time of 9.3 days (range 2-13 days). The remaining two were resting heavily on the bottom after 22 days. When the screen was removed they darted to the surface, gulped air and attained neutral buoyancy in 5 s.

**Influence of swimbladder O\(_2\) levels on air-breathing**

Within each of the air, N\(_2\) and O\(_2\) gas phase treatments there was considerable variation in activity between observation periods. Regression coefficients of the frequency of air-breathing with activity were significant \((P < 0.05)\). Fish utilizing N\(_2\) were generally more frequent gas-breathers than those utilizing air, while those breathing O\(_2\) were less frequent. However, there was considerable overlap between treatments (Fig. 4) and hence the effect of O\(_2\) levels in the swimbladder had no clear effect on the frequency of air-breathing.

**DISCUSSION**

Respiration and hydrostatic control generally are well coordinated in the central mudminnow, particularly when fish are undisturbed in normoxic or hypoxic water. Under conditions of disturbance that simulate the presence of a predator, coordination is less perfect and more energy is expended in the maintenance of vertical position and locomotion. Such expenditures appear greatest when in hypoxic water. Several mechanisms reduce the extent and rate of buoyancy change between air-breaths, thus reducing conflict between respiration and hydrostatic control. This
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Use of any one of these is influenced by the availability of dissolved $O_2$ and the presence or absence of predator disturbance.

**Mechanisms minimizing buoyancy change**

Maintenance of continuous positive buoyancy was used by undisturbed fish in normoxic water for 64% of the time and for 90% of the time in hypoxic water. This strategy minimizes the expenditure of energy in travelling to the surface and in maintaining vertical position. In normoxic water the rate of change in buoyancy between air-breaths was very slow, as aquatic respiration was the dominant mode, and buoyancy sometimes dropped below neutral. This provided the fish with time at near neutral buoyancy when it could move efficiently in the water away from the surface where other activities such as feeding could be undertaken. In hypoxic water, where air-breathing is the dominant mode, undisturbed fish are tied more to the surface because of the rapid decline in buoyancy between frequent air-breaths. In nature, hypoxia is common in summer from late evening to dawn in environments occupied by mudminnows (K. A. Martin, personal communication). A position at the surface at this time is not disadvantageous as mudminnows are opportunistic feeders and can capture invertebrates at the surface when illumination is low (K. A. Martin, personal communication). This combined with its very cryptic coloration, its inactivity, and a strong preference for vegetation and cover at the surface reduces its vulnerability to predation. If disturbed, mudminnows dart rapidly to the bottom, either compressing or spitting swimbladder gases, and burrow into the substrate. The use of continuous positive buoyancy is probably common amongst aquatic air-breathing animals. Graham, Kramer & Pineda (1977) observed the characin *Piabucina festae* to use this strategy in hypoxic water, and the sea snake *Pelamis platurus* remains at positive buoyancy for extensive periods (Graham, Gee & Robison, 1975).

Maintaining optimal buoyancy by compression of inspired gas and then altering excess internal pressure of the swimbladder as $O_2$ is resorbed was evident only in disturbed fish in normoxic water. Such a mechanism provides a buoyancy close to neutral for prolonged periods, allowing for the efficient and rapid movements necessary for escape from predators. This strategy may have been used to reduce the extent and rate of decrease in buoyancy between air-breaths among disturbed fish in hypoxic water, but there is no direct evidence to support this idea. Many fishes maintain an excess internal pressure of gas in either the swimbladder or air-breathing organ (Gee, 1976; Gee, Machniak & Chalanchuk, 1974; Gee & Gee, 1976) which can be altered to provide precise adjustments to buoyancy (Gee, 1970). Changes in excess internal pressure could be used to provide precise adjustment to swimbladder volume and buoyancy under all conditions. Such control would be particularly critical when stalking prey. This strategy involves energy costs, as compression of gas in the swimbladder results from contraction of muscles in either the wall of the swimbladder or the body wall of the fish.

Disturbed fish in hypoxic water increased their reliance on aquatic $O_2$ when compared with undisturbed fish as detected by a marked increase in frequency of branchial breathing. In doing so fish would most likely decrease perfusion of the swimbladder, reducing $O_2$ uptake from it. Johansen, Hansen & Lenfant (1970)
showed that *Amia* diverted a portion of the blood flow away from the swimbladder when aquatic respiration became the primary mode. Such blood shunts appear common in air-breathing fishes (Farrell, 1978). This would not influence the extent of adjustment but would reduce the rate of decrease in buoyancy between breaths and ultimately the frequency of air-breathing, saving some time and energy in swimming to the surface and reducing potential exposure to predators. The strategy itself would be inefficient as the energy costs of extracting O₂ from hypoxic water are high. Most of the undisturbed fish did not use aquatic respiration in hypoxic water. Disturbed fish in hypoxic water were negatively buoyant and remained on the bottom. Movement through the water column as well as breathing at the surface could expose fish to terrestrial and aquatic predators. Under such conditions mudminnows move to surface waters and breathe air in synchrony. That is, a breath by one fish is immediately followed by one or more other fish (Gee, 1980). Such clumping in time does not occur with undisturbed fish, supporting the hypothesis of Kramer & Graham (1976) that it is an anti-predator adaptation.

The mudminnow is not well adapted to a benthic mode of life, and resting on the bottom was only used by disturbed fish in hypoxic water. This counters the energy costs required to maintain vertical position but does not reduce costs of surfacing to breathe air. Some air-breathing species such as *Corydoras* (Kramer & McClure, 1980) and *Brochis* (Gee & Graham, 1978) rely on this strategy exclusively and have adapted to a benthic mode of life. In *Brochis*, air-breaths occur regularly with extensive (13-2%) declines in volume of the respiratory organ. In the latter part of the inter-breath period a constant low buoyancy is often maintained during periods of inactivity, indicating no immediate advantage in regaining a higher buoyancy. When fish are actively moving along the bottom, more precise control of buoyancy may be required to move efficiently and the frequency of air-breaths is increased (Gee & Graham, 1978). Environments occupied by mudminnows are characterized by soft silty substrates with accumulations of detritus and as such are not suitable for a visual benthic feeder.

Mudminnows make limited use of hydrodynamic compensation to correct for buoyancy. Undulatory movements of the dorsal, anal and paired fins are used to maintain precise vertical position when hovering. These appear to offset a buoyancy that is either slightly too high or too low.

**Gas secretion**

In normoxic water undisturbed fish lost gas from the swimbladder at an average rate of 0.028 ml.g⁻¹.h⁻¹, but this loss was made up by periodic gulping of air. When denied access to air in normoxic water fish maintained neutral buoyancy. It is most unlikely that fish secreted gas into the swimbladder to maintain this buoyancy, as rates of secretion (two estimates gave means of 0.001 and 0.002 ml.g⁻¹.h⁻¹ at 20 and 25 °C respectively) were considerably less than the above rate of gas lost. Gas secretion by physostomes is variable between species. Wittenberg (1958) showed that rainbow and brown trout required at least 13 days to completely fill an emptied swimbladder. Cyprinidae are considerably faster. Goldfish (Wittenberg, 1958), longnose dace (Gee, 1968), and fathead minnows (Gee, 1977) secreted gas at rates sufficient to fill an emptied swimbladder in 5-7 days, 3-4 days, and less than 2 days.
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respectively. Thus, to maintain neutral buoyancy without access to the surface, mudminnows must have greatly restricted perfusion of the swimbladder. Such control must be costly as mudminnows rely on additional strategies to maintain buoyancy control in normoxic water. Corydoras aeneus were unable to maintain buoyancy control in normoxic water when denied access to the surface (Kramer & McClure, 1980) and presumably are unable to prevent loss of gas from the accessory respiratory organ (intestine).

In nature mudminnows are denied access to a gas phase once a complete ice cover forms in autumn, and control of buoyancy by preventing loss of gas from the swimbladder may be necessary for several days. However, bubbles of gas do accumulate under the ice from photosynthesis, anaerobic decomposition within the substrate, and from mammal (e.g. muskrat) activity. Once established these bubbles could provide a source of gas which could be inspired periodically, maintaining buoyancy. Klinger (1978) has shown that bubbles produced by anaerobic decomposition can strip O_2 from hypoxic water, and that this source of O_2 can be used by mudminnows to prolong their survival.

Composition of gases

The frequency of air-breathing in normoxic water with a gas phase of either N_2 or O_2 was similar to that with an air phase. Thus neither hyperoxic or hypoxic conditions in the swimbladder appeared to influence strongly the frequency of air-breathing. This supports the idea that the stimulus to take in air-breath in normoxic water may result from a decline in swimbladder volume. Such a change could be detected by mechanoreceptors in the swimbladder wall or else occur as a result of density changes. Mudminnows were observed to be very sensitive to changes in atmospheric pressure, and when it was altered, spitting and gulping gas occurred readily. The striking regularity at which undisturbed fish in hypoxic water took an air-breath just before the declining buoyancy reached neutral level is also strong evidence for this idea. A number of air-breathing species respond to decreases in swimbladder volume by rising to the surface and gulping air (Gee & Graham, 1978; Farrell & Randall, 1978; Johansen, 1970). It is likely that other stimuli (partial pressures of gases, or pH of blood) also play an important role in the regulation of air-breathing, particularly under conditions of disturbance in hypoxic water. Obligate air-breathers are responsive to changes in the composition of gases within the respiratory organ while most facultative air-breathers do not respond to such changes but are more sensitive to conditions in the surrounding water (Hughes & Singh, 1970b; Lomholt & Johansen, 1974; Johansen, Hanson & Lenfant, 1970). For mudminnows to breathe air independently of the composition of gases inspired would be advantageous during winter. Fish could maintain buoyancy by gulping gas from bubbles under the ice. Klinger (1978) has shown that such bubbles vary greatly in gas composition containing N_2 from 42·6 to 96·8%, O_2 from 1·2 to 9·3%, and CH_4 from 0 to 55·2%.

Facultative air-breathers, whose respiratory organ also plays a hydrostatic role, face the problem of preventing leakage of gas (O_2) from the respiratory organ when aerial respiration is not required. The dual functioning of the organ creates a strong conflict: to be an efficient respiratory organ it must develop the capacity for rapid
Table 3. Occurrence of air-breathing in normoxic water by facultative air-breathers whose accessory respiratory organ has a hydrostatic function

<table>
<thead>
<tr>
<th>Species</th>
<th>Respiratory; hydrostatic organ</th>
<th>Comments</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepisosteidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lepisosteus osseus</em></td>
<td>Swimbladder</td>
<td>Irregular air-breaths in normoxic water, becoming more frequent at higher temperatures</td>
<td>Rahn <em>et al.</em> 1971</td>
</tr>
<tr>
<td>Amiidae</td>
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<tr>
<td><em>Amia calva</em></td>
<td>Swimbladder</td>
<td>Irregular air-breaths in normoxic water at higher temperatures</td>
<td>Johansen, Hanson &amp; Lenfant, 1970</td>
</tr>
<tr>
<td>Ceratodontidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Neoceratodus forsteri</em></td>
<td>Swimbladder</td>
<td>Sporadic air-breaths in normoxic water, becoming more frequent at night and with increased activity</td>
<td>Grigg, 1965</td>
</tr>
<tr>
<td>Umbridae</td>
<td></td>
<td></td>
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<tr>
<td><em>Umbra limi</em></td>
<td>Swimbladder</td>
<td>Regular, infrequent air-breaths in normoxic water at all temperatures (5-30 °C)</td>
<td>Gee, 1980</td>
</tr>
<tr>
<td>Erythrinidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Erythrinus erythrinus</em></td>
<td>Swimbladder</td>
<td>Bimodal respiration sometimes occurs in normoxic water</td>
<td>Stevens &amp; Holeton, 1978</td>
</tr>
<tr>
<td><em>Hoploerythrinus unitaeniatus</em></td>
<td>Swimbladder</td>
<td>Bimodal respiration sometimes occurs in normoxic water</td>
<td>Stevens &amp; Holeton, 1978</td>
</tr>
<tr>
<td>Lebiasinidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Piaubucina festae</em></td>
<td>Swimbladder</td>
<td>Frequent air-breaths taken in normoxic water</td>
<td>Graham, Kramer &amp; Pineda, 1977</td>
</tr>
<tr>
<td>Claridae*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Clarias batrachus</em></td>
<td>Supra-branchial cavity</td>
<td>Irregular air-breaths in normoxic water, becoming more frequent at night</td>
<td>Jordan, 1976</td>
</tr>
<tr>
<td>Saccobranchidae*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Saccobranchus fossils</em></td>
<td>Diverticulum of opercular cavity</td>
<td>Irregular air-breaths taken in normoxic water</td>
<td>Hughes &amp; Singh, 1971</td>
</tr>
<tr>
<td>Callitrichidae*</td>
<td></td>
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<tr>
<td><em>Hoplosternum thoracatum</em></td>
<td>Intestine</td>
<td>Regular frequent air-breaths taken in normoxic water which increase with activity</td>
<td>Gee &amp; Graham, 1978</td>
</tr>
<tr>
<td><em>Brochis splendens</em></td>
<td>Intestine</td>
<td>Regular, infrequent air-breaths in normoxic water</td>
<td>Gee &amp; Graham, 1978</td>
</tr>
<tr>
<td><em>Corydoras aeneus</em></td>
<td>Intestine</td>
<td>Irregular air-breaths in normoxic water</td>
<td>Kramer &amp; McClure, 1980</td>
</tr>
<tr>
<td>Anabantidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anabas testudineus</em></td>
<td>Supra-branchial cavity; swimbladder</td>
<td>Irregular air-breaths in normoxic water</td>
<td>Hughes &amp; Singh, 1970(a, b)</td>
</tr>
</tbody>
</table>

* Fishes in these families are characterized by having a swimbladder of greatly reduced volume (Bridge & Haddon, 1894) and thus has little hydrostatic function. In those species examined the volume of the swimbladder constitutes less than 5% of the lift required to attain neutral buoyancy (Gee, 1976; Gee & Graham, 1978).
Functions of the swimbladder in *Umbra limi*  

...take of O₂; as a hydrostatic organ it must be impermeable to gas diffusion. It is not possible to resolve this conflict completely. Hence, most facultative air-breathers remain in contact with air, gulping at the surface even in normoxic water (Table 3). In some species this use of aerial O₂ serves to increase the metabolic scope beyond the limits set by aquatic respiration permitting bursts of activity, but in many species, particularly when inactive, it is most likely that air-breaths in normoxic water are required to maintain hydrostatic control. Facultative air-breathers in normoxic water that maintain hydrostatic control by regular air-breaths potentially place themselves under double jeopardy; under such conditions they do not receive the advantages of breathing air, yet expose themselves to all the disadvantages. To completely resolve the problem either exclusive air or aquatic respiration must be used. However, Kramer & McClure (1981) have pointed out that fishes efficient in both modes of respiration have the advantage of being able to exploit that source of O₂ that is the most efficient to use. The mudminnow possesses such dual efficiency (Gee, 1980) and can switch rapidly from one mode to the other or can use both. To coordinate the two opposing functions, mudminnows must minimize the extent and rate of decrease in buoyancy between air-breaths. They use primarily the strategies of continuous positive buoyancy, compression of inspired gas combined with precise regulation of internal pressure of swimbladder gases, and the utilization of aquatic respiration to supplement aerial respiration in hypoxic water. The strategy used is determined by the availability of dissolved O₂ and the presence or absence of predators.

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**REFERENCES**


