

Journal of Fish Biology (2014) **4** $\frac{d}{dx}$:10.11111/ .12323, $\frac{d}{dx}$ $\frac{d}{dx}$ $\frac{d}{dx}$ $\frac{d}{dx}$ $\frac{d}{dx}$

REVIEW PAPER

Breaking wind to survive: fishes that breathe air with their gut

J. A. Nelson

Department of Biological Sciences, Towson University, Towson, MD 21252-0001, U.S.A.

 2 $\qquad \qquad$ $\qquad \qquad$ \qquad \qquad

Aquatic hypoxical and anoxial and another due to various combinations of \mathbf{a}_1 and \mathbf{a}_2 aquatic combinations of \mathbf{a}_1 respiratory rates exceeding photosynthetic rates, (2) poor to 1 at the non-mixing at the non-mixing at the \mathbf{r} aerial–aquatic interfacerial, interfacerial, interfacerial, interfacerial, interfacerial, interfacerial, inter **a** (4) **is the particle particle paraceles paracels (Junk, 1984; Diaz** α **, 2001;** α **,** α **,** β 2009). These conditions of \mathbf{z} and \mathbf{z} is probably in frequently in frequently in \mathbf{z} is probably in \mathbf{z} not a coincidence that most air-breathing fishes as well as well as well as \mathbf{a} $(A \bullet A)$ fishes are free free final fields (Graham, 1997). In temperature to polar regions, \bullet the most common scenarios resulting in hypoxia and anoxia involve isolation of \mathcal{F} the water body from the oxygen-rich atmosphere. Other temperate fish habitats \mathcal{F} \mathbf{s} ubiect to hypoxical include soft sediments that do not mix well with the water that do not mix well with the water \mathbf{s} c_0 imn and swamp habitats. Hypoxic and anoxic waters for \mathbf{z}_1 and another in tropical waters for \mathbf{z}_1 through a diversity of processes that generally dependent of \mathcal{G}_1 are harder and **the** c_{haract}erize than temperate that $(1, \mathbb{k}, 1984)$. \bullet **d** (1) \bullet (1) temperature, (2) nutrient-rich waters, (3) dense terrestrial vegetation that can be can sunlight and wind, (4) dense surface vegetation that can not only block sunlight and wind but can also contribute photosynthetic oxygen to the water and \mathcal{B} and \mathcal{B} and \mathcal{B} and \mathcal{B} β iota that can influence the water chemistry as β as β as β mosaic of \mathfrak{g}_1 and another another tropics. It is common for \mathfrak{g}_2 the tropics. It is common for \mathfrak{g}_1 is common for \mathfrak{g}_2 , \mathfrak{g}_3 is common for \mathfrak{g}_4 , \mathfrak{g}_5 is common for \mathfrak{g}_7 i \mathbf{t} , $\overline{\mathbf{a}}$, $\overline{\mathbf{w}}$, ence the $\overline{\mathbf{a}}$ source $\overline{\mathbf{a}}$, $\overline{\mathbf{a}}$, $\overline{\mathbf{a}}$, $\overline{\mathbf{a}}$, $\overline{\mathbf{w}}$, $\overline{\mathbf{w}}$ 1995). It is also not uncommon to find waters that cycle between $\frac{1}{2}$ is $\frac{1}{2}$ \mathbf{s} and \mathbf{a} and \mathbf{a} and \mathbf{a} at \math Antipogenic climate distruption is predicted to expand the predicted to expand the predicted to expand the prevalence of \mathcal{A} \vec{a} a, \vec{a} , \vec{b} , \vec{b} , \vec{a} , \vec{a} , \vec{c} , \vec{c} , \vec{a} , \vec{c} , \vec 2010).

EVOLUTION OF AIR BREATHING IN FISHES

 \circledcirc 2014 \rightarrow Fisheries Society of the British Isles, $J = \angle$ \rightarrow F , $B = \angle$ 2014, doi:10.1111/ \rightarrow 12323

 $\frac{1}{2}$ 1987). (1976) **4 depen after the oxygen is dependent on the oxygen is dependent of the oxygen is depend** $M \times 3 \& 111 \& 1987$. $\sqrt{24} \times 1976$ \mathbf{b}_i attributable to \mathbf{b}_i ancy attribute to a \mathbf{F} and \mathbf{F} attribute to respiration. Thus, but represents a significant component of an animal's buoyancy budget and could be envisioned as a target for selection. Certainly for the loricariids, where many species use an oral sucker to remain inverted under logs or rocks, a gut ABO would seem advantageous to a head \mathbf{A} head region \mathbf{A} above. A head \mathbf{A} extensive vascularization of both dorsal and ventral buccal or pharyngeal surfaces to accommodate extraction of oxygen in both normal and inverted positions, respectively. The inverted positions, respectively. The inverted position of \mathbf{z}_1 tively. Thus, buoyancy and positioning issues may explain the frequent evolution of \mathfrak{F}_1 , \mathfrak{F}_2 , \mathfrak{F}_3 , \mathfrak{F}_4 , \mathfrak{F}_5 , \mathfrak{F}_6 , \mathfrak{F}_7 , \mathfrak{F}_8 , \mathfrak{F}_8 , \mathfrak{F}_9 , $\mathfrak{F$ $\frac{y}{H}$ $\frac{1}{A}$

 \mathcal{F} PERCEIVED As \mathcal{H}_A in \mathbf{C}_F of \mathcal{G}_F and \mathcal{H}_A Among the perceived changes of \mathscr{F} and \mathscr{F} are that digestive function could be compromised. Vertebrate digestion is generally and an anaerobic process (van Soester, 1994) \mathbf{A} find many \mathbf{A} are herbivorous \mathbf{A} find \mathbf{A} and \mathbf{A} and \overline{a} , curve \overline{a} equation from from from \overline{a} extraction from \overline{a} equation from from from \overline{a} 2009 . Thus, $\frac{3}{4}$ regions $\frac{3}{4}$ and $\frac{3}{4}$ bial activity. Additionally, the regions of the gut specialized for respiration are not \mathcal{A} thought to \mathcal{A}_1 the secretory or the secretory or the absorption facets of digestions of digestions of digestions of \mathcal{A}_2 $(2, 2006),$ $\frac{1}{4}$
 $\frac{1}{4}$ $\frac{1}{4}$ λ regions of two λ regions \mathbb{R} final \mathbb{R} final \mathbb{R} final \mathbb{R} and \mathbb{R} in \mathbb{R} , 2002; $\mathbf{G} = \begin{bmatrix} \mathbf{G} & \mathbf{F} & \mathbf{$ $\ddot{\bm{c}}$ and $\ddot{\bm{c}}$ and $\ddot{\bm{c}}$ and $\ddot{\bm{c}}$ accomplish adequate to accomplish additional structure to accomplish adequate $\frac{1}{4}$ digestion. \mathbf{C} conversely, food and digestive secretions in the gradient comparison in the gradient compromise gas \mathbf{C} exchange by the ABO. The thin epithelium necessary for efficient diffusive gas Φ of efficient diffusive gas exchange would seemingly be vulnerable to damage by the acid, alkali, digestive enzymes and dietary items that are normal constituents of the vertebrate gut. In addition, the physical presence of food, protective mucus and digestive juices would tend to increase the diffusive distance for oxygen, potentially limiting oxygen \mathcal{R}_{max} , use \mathbf{A}_{max} as an ABO seemingly places of the guitar places digestion and respiration in competition for available blood (Fig. 2). Generally, full perfusion for available blood (Fig. 2). Generally, full perfusion for available blood (Fig. 2). Generally, full perfusion for available blood (F $\frac{1}{2}$ of the fishes post-pranetary in water-breathing fishes (Thomas in water-bre & Farrell, 2006). Although ventilation–perfusion matching has not been studied in GAB fishes, presumably perfusion of gut ABOs is maximized when fresh air is present as $\overline{3}$, $\overline{1}$, $\overline{2}$, $\overline{3}$, $\overline{4}$, $\overline{5}$, $\overline{4}$, $\overline{5}$, $\overline{5}$, $\overline{6}$, $\overline{5}$, $\overline{6}$, $\overline{5}$, $\overline{6}$, $\overline{5}$, divert blood from digestive regions of the gut during air breathing, thus prolonging \overrightarrow{a} \overrightarrow{a} \overrightarrow{b} \overrightarrow{c} \overrightarrow{a} $\overrightarrow{$

MORPHOLOGICAL INDICATORS OF THE GUT AS AN ABO

 G_1 above \mathbf{G}_1 , \mathbf{G}_2 is the \mathbf{G}_3 consistent with reduced digestive \mathbf{G}_2 and \mathbf{G}_3 and \mathbf{G}_4 and \mathbf{G}_5 function and facilitation of gas exchange. More indicates that are indicated features that are indicated for \mathbf{g}_i $\overline{\phi}$ increased as exchange increased increased increased variant ϕ increased variant ϕ (2) capital increases of ϕ

 \bigcirc 2014 \bigcirc \bigcirc _{is} \bigcirc \bigcirc **Society 3** \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc F \bigcirc B \bigcirc 2014, \bigcirc \bigcirc \bigcirc 10.1111/ \bigcirc .12323

 F_1 IG. 2. Circulatory design of guidal fishes. Composite drawing incorporation in composite drawing incorporation \mathbf{E}_1 f_{ϵ} the different Ga $\begin{array}{c} \mathbf{G} & \mathbf{G} & \mathbf{G} \ \mathbf{G} & \mathbf{D} & \mathbf{G} & \mathbf{G} \end{array}$ (*e.g. Dallia* and *Ancistrus*) is *via* the coeliac artery, whereas the more posterior intestinal ABOs tend to be supplied by the anterior mesenteric artery (*e.g. Misgurnus*) or directly from the dorsal aorta (*e.g. Callichthysis and Hoplosternum* in the heart of the heart *via the heart in the heart of the heart* portal vein $(\mathbb{C}[\mathfrak{F}_i,\mathfrak{F}_i])$ or the interrenal vein $(\mathfrak{F}_i,\mathfrak{F}_i)$ or anterior mesenteric arterior connection to the dorsal aorta through multiple vessels; DA, dorsal aorta; G, gills; H, heart; HPV, hepatic portal veining p , interventing p is an interventing \mathbf{A}_i vertex \mathbf{B}_i .

embedded in the epithelium with a concomitant reduced blood-lumen distance, (3) increased luminosity area, (4) presence of surfactant-producing lamellar bodies of surface of surface \emptyset , and and (5) presence of muscular sphincters is equal to region from other region from other region from other region \mathfrak{F} $\begin{array}{c}\n\begin{array}{c}\n\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2}\n\end{array} \\
\begin{array}{c}\n\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2}\n\end{array} \\
\begin{array}{c}\n\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2}\n\end{array} \\
\begin{array}{c}\n\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2} \\
\sqrt{2} & \sqrt{2}\n\end{array} \\
\begin{array}{c}\n\sqrt{2$

 $\begin{bmatrix} \mathbf{F} & \mathbf{S} \\ \mathbf{F} & \mathbf{S} \end{bmatrix}$ **One umbrid (Crawford, 1971, 1974) and one blenning (Laming et al.**, 1982; Pelsterniid (Pal. *et al.*, 1988) are reported to use their oesophagus as a respiratory organ (Table I). The umbrid is the Alaska blackfish *Dallia pectoralis* Bean 1880, which has a highly vascularized swimbladder, but without capillaries that penetrate the inner epithelial lining. In contrast, the oesophagus of *D*. *pectoralis* is also highly vascularized, but with extensive capital lining. The extensive capital lining into the epithelial lining. Crawford's (1974) histological analysis of *D*. *pectoralis* revealed an oesophageal blood–air barrier of *<*1 mm, similar to that reported for the ABO gas bladders of the bowfin *Amia calva* L. 1766 **a**nd the longitudinal decrees and the longitudinal control (L. 1758) (Crawford, 1971; Table II). \mathbf{G}_i absorption in *D.* p_{max} *is probably limited* to the oesophagus because of \mathbf{F}_i a stricture between the oesophagus and storach and because the oesophagus and because the is no epithelial and because the capillary penetration and gastric glands are presented in the latter (Crawford, 1974). $\left(\begin{array}{ccc} H^1 & \mathbf{a}_1 & \mathbf{a}_2 & \mathbf{a}_2 & \mathbf{a}_3 & \mathbf{a}_4 & \mathbf{a}_5 & \mathbf{a}_4 & \mathbf{a}_5 & \mathbf{a}_6 & \mathbf{a}_7 & \mathbf{a}_7$ \blacksquare , \blacksquare , \blacksquare , \blacksquare , \blacksquare , \blacksquare , 1982), extensive vascularization, longitudinal folding and separation from the buccopharynx and stomach by sphincters. Laming *et al.* (1982) did not report a blood–air diffusion distance, but capillaries were reported to be embedded in the oesophageal folds and were described as \mathbf{w}_i as \mathbf{w}_i as \mathbf{w}_i

 $\textcircled{2014} \rightarrow \text{F}_\text{F} \rightarrow \text{F}_\text{F} \rightarrow \text{F}_\text{F} \rightarrow J \rightarrow F \rightarrow B \rightarrow \text{2014\%} \text{ (i0.1111/} \text{ .12323)}$

 $(200296 - 1.1)$

 8 . A. \mathbb{F} $\left\{ \frac{1}{2} \right\}$ the corpus compared to the cardiac and pyloric regions. In *Ancistrus*, capillaries $\mathbf{w} = \mathbf{w}$ embedded in the much much much experimental in the corpus (Satora, 1998), further targeting the site of O₂ uptake. Carpus as the site of O2 uptake. Cruz **et al.** (2009) **report that i** *goplichthys* has also reduced gastric gland density in the corpus region, coincident with a high degree of longitudinal folding of the mucosalistic state of the mucosa. Other authors report the m complete absence of digestive glands in the ABO stock \mathbf{a}_1 1935; Oliveira *et al.*, 2001). Surfactant-producing lamellar bodies have also been documented in the stomach epithelial cells and gastric glands of *Ancistrus* (Satora & Winnicki, 2000), *Hypostomus* (Podkowa & Goniakowska-Witalinska, 2003) and *P_{tery}* (C_{ruz} *et al.*, 2009).

INTEST INAL BREATHERS \mathcal{F}_max , and callichthyids and callichthyids and callichthyids are generally described as generally described as $\mathcal{F}_\text{tot}=\mathbb{R}^{\P_1}$, thin walled, translaused. In cobiting, the isolation of this is approximately defined and \mathcal{F}_tot \mathcal{F} , ded of the interstal two-thirds of the interstinance (\mathcal{F} defined), \mathcal{F} and \mathcal{F} $1987; \mathbf{M}$ onta and \mathbf{W} , \mathbf{W} and \mathbf{W} approximately the posterior \mathbf{W} and \mathbf{W} **3** decrease is involved in the intervalse in gas exchange α (Huebner α , α , 1978; Kramer α M_{\odot} , 1980; Podkowa \mathbb{R} in \mathbb{R} in \mathbb{R} in \mathbb{R} , 2002). Capitalinska, \mathbb{R} **into the interval muchosa is reported from** M_1 (Jasinski, 1973), *Hoplosternum* (Huebner & Chee, 1978) and *Corydoras* (Podkowa & Goniakowska-Witalinska, 2002; Table III). Surfactantente la mediante in the respiratory in the respiratory internal bodies in the respirator epithelia have been described in M_{ν} in \mathcal{L} (\mathcal{L} , 1973) and C_{ν} and \mathcal{L} (Podkowa \mathbb{K} \mathbb{K} \mathbb{K} \mathbb{K} and \mathbb{K} and \mathbb{K} amplibious \mathbb{K} and $\frac{1}{2}$ (987; 664 $\frac{1}{3}$, $\frac{1}{2}$, \frac $\frac{1}{2}$ (987; 664 $\frac{1}{3}$, $\frac{1}{2}$, \frac

10 $\mathbf{A} \cdot \mathbf{F}$ \mathbf{S}

contraction of viscosities of the respiratory stock muscle and (3) positive \mathbb{R}^n \overrightarrow{a} nis skeletal muscle, but there was no experimental differentiation amongst these alternatives. $F_{\rm eff}$ intertain \mathbf{A} of $\mathbf{C}_{\rm eff}$ and \mathbf{A} and $\mathbf{C}_{\rm eff}$ and $\mathbf{C}_{\rm eff}$ are entirely the entire length of the gut and exhale through the grad throu 411 , 1987). $\epsilon = \frac{a_1}{2}$ of co-ordinating transport of air and digesta. Both these families have a transitional zone between the digestive and respiratory portions of the α 4111 , 1987; **Person**, 2006) that a_1 and a_2 and possibly encompacting the digest This compacted digesta would then minimally interfere with gas exchange in the **r**
(b) $r_1 = \frac{1}{2}$ segment of the interstinance interstine. Persaud $\frac{1}{2}$ (2006), in callichthyids that air transport is necessary for normal digesta transport and that $\mathcal{F}=\left[\begin{array}{ccc} 0& \frac{\pi}{2} & \frac$ **i** \overline{Z} . (2006) \overline{Z} positive pressure generated by the buccal and opercular pump provides the force for inspiration, and any transport and the respiratory \mathbf{a} the intertwine of \mathbf{a}_1 and \mathbf{a}_2 and \mathbf{a}_3 and \mathbf{a}_4 and \mathbf{a}_5 and \mathbf{a}_7

 $\begin{array}{c} \mathbf{A} \end{array}$ $\begin{array}{c} \mathbf{C} \end{array}$ $\begin{array}{c} \mathbf{F} \end{array}$ $\begin{array}{c} \mathbf{A} \end{array}$ $\begin{array}{c} \mathbf{H} \end{array}$ $\begin{array}{c} \mathbf{A} \end{array}$ $\begin{array}{c} \mathbf{A} \end{array}$ $\begin{array}{c} \mathbf{A} \end{array}$ $\begin{array}{c} \mathbf{A} \end{array}$ The general pattern of branchinal ventilation in $\mathbf{z} = \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix}$ is to $\mathbf{z} = \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix}$ is to hypoxial ventilation in fig. $\frac{1}{2}$ P 2 (**d**₁ c regulation) by increasing given P in $\frac{1}{2}$ (H₄^c d₎, 1980; Fig. 3). This is many figures in vertice $\frac{1}{2005}$ and $\frac{1}{40}$ in vertice $\frac{1}{2007}$ or $\frac{1}{40}$ in $\& \left(\begin{array}{cc} 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right)$ $\& \left(\begin{array}{cc} 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right)$ **a** $(\mathbf{M}^2, 200)$ **e** \mathbf{M}^3 1998; Fig. 3). As \mathbf{A}^3 is breathing the start using atmospheric start using atmosph oxygen, energy conservation would dictate that gill ventilation should diminish or stop. Fishes expenditure around \mathbf{z}_1 resting methods of the intervals methods of the intervals of give (H $\frac{3}{4}$, $\frac{4}{3}$, $\frac{1980}{5}$, $\frac{6}{5}$, $\frac{80}{100}$, $\frac{909}{5}$, $\frac{90}{100}$, $\frac{3}{4}$ $\frac{1}{2}$, $\frac{1}{2}$, $\frac{1}{2}$, $\frac{1}{2}$, $\frac{1}{2}$, $\frac{1}{2}$ ally still use their gills or skin to eliminate CO2 (α and potential loss of potential loss of potential loss $\overline{\mathbf{a}}$ to the given the gill lamellae would see make a \mathbf{a} and \mathbf{a} in hypoxic water a poor physiological strategy. Indeed, fishes from one of the GAB taxa (*Lipophrys*) have been reported to cease branchial ventilation upon leaving the $w = \frac{1}{2}$, 1982), **although Pelster et al.** (1988) claim that ventilation **et al.** (1988) claim that ventilation **a** continues during emersion. The situation is also unclear in other GAB fishes. Some investigators have reported cessation of branchial ventilation in loricariids (Gradwell, 1971; Wood *et al.*, 1979), but these were visual observations and appear to the visual observations and a have **ded e**rroredus. Graham (1983) **d**. 20% d_r in air-breathing in air-breathing in air-breathing in air-breathing in an air-breathing *Ancistrus* when acclimated to hypoxic water, but Gee & Graham (1978) report a 33% increase in *Hoplosternum* gill *f* ^v when induced to increase its frequency of air breathing through and Affonso \mathbf{A} and \mathbf{A} and \mathbf{A} and \mathbf{A} and \mathbf{A} are positive and \mathbf{A} and $\$ in hypoxic *Hoplosternum* gill *f* ^v breathing air. Finally, both foregut breathers, *e*.*g*. *H*_y (1, 3, 2007), **a**nd **a**₁, *e*. *i*₁, *e.*, *M_{is}* (MoM_a) $\&$ and been reported to \bullet . The change to not change their rate of a \bullet and \bullet and \bullet and \bullet and \bullet when air breathing is induced with a single variable \mathfrak{g}_i , and \mathfrak{g}_i , and \mathfrak{g}_i , and \mathfrak{g}_i $\mathbf{F}[\mathbf{A}\cup\mathbf{A}]=\mathbf{F}_{\mathbf{A}}\cup\mathbf{F}_{\mathbf{A}}$ and $\mathbf{F}_{\mathbf{A}}$ is a finite alone for $\mathbf{F}_{\mathbf{A}}$ and $\mathbf{F}_{\mathbf{A}}$ is alone for $\mathbf{F}_{\mathbf{A}}$

 G_{A} A_{B} A_{B} A_{B} B_{C} A_{C} A_{D} B_{C} B_{C} B_{C} B_{C} C_{D} 11

is that reduced gill ventilation while air breathing is not a general strategy GAB fishes have employed to the same energy of \mathbf{F}_1 , \mathbf{F}_2 is to \mathbf{F}_3 , \mathbf{F}_4 , \mathbf{F}_5 , \mathbf{F}_6 , \mathbf{F}_7

 GA S except FA C G_F A_F is a A_F in A_F is a A_F in A_F is a set A_F is a set A_F is a set of A_F is a set of At the characterize the gas composition of GABOS date to the 19th century of GABOS da (3) $(3, 1877)$, yet there is a surprisingly small and $(3, 3, 3, 3, 3)$, and changes \mathbf{C} and changes with time in GaBOs. A general finding is that \mathbf{C} is not contained in GaBOs. released *via* the ABO. This observation holds for both foregut breathers, *e*.*g*. *Pterygoplichthys* (Carter & Beadle, 1931; Graham, 1983), and hindgut breathers, *e*.*g*. *Misgurnus* (**McMa** 13 & Burgen, 1987). The high capacitance of water for C₂ $(Sc_n, \overset{\bullet}{\bullet} \overset{\bullet}{\bullet}_{\lambda,1}, \ldots, 1997)$ means that C_2 will $\overset{\bullet}{\bullet}_\lambda$ or $\overset{\bullet}{\bullet}_\lambda$ or $\overset{\bullet}{\bullet}$ or $\overset{\bullet}{\bullet}_\lambda$ or $\overset{\bullet}{\bullet}_\lambda$ permeable skin in fishes submerged in low carbon dioxide partial pressure (*P*CO2) water. Blennies are the only GAB fishes that are classified as a amphibious and *L.* $p_{\rm c}$, $p_{\rm c}$, $p_{\rm c}$ measured $p_{\rm c}$ and $p_{\rm c}$ measured when $P_{\rm c}$ and $P_{\rm c}$, $r_{\rm B}$ 53% rⁱse (**f** 2·43 **3**·3·71 **d**), $r_{\rm B}$ **P**_C 2 in emersed *L*. *p*_C in did not report ABO *P*CO2. Based on this limited physiology, GABOs do not appear **t** be significant organism of \mathbf{z} except \mathbf{z}

 ${\sf A}_1$. Given with expose to ${\sf A}_2$ final do not become to ${\sf A}_3$ final do not be come become to ${\sf A}_4$ final do not be come to ${\sf A}_4$ final do not be come to ${\sf A}_4$ final do not be come to ${\sf A}_4$ final do not be c hypometabolic when allowed access to air and instead retain oxygen regulation and normal levels of air breathing \mathbf{F} are thus complex functions of air breathing are thus complex functions \mathbf{F} $\overline{\mathbf{a}}$ that contribute to metabolic rate as well as well as well as well as $\overline{\mathbf{a}}$ and behavioural factors. Metabolic rate in fishes depends on size, species and multiple additional factors such as social situation, stress level, diet, temperature and water chemistry (nelson $\mathbf{3}$, 2011). As the information is only sports in formation in $\mathbf{4}$ $\mathbf{F}[\mathbf{A}^{\dagger}, \ldots, \mathbf{A}^{\dagger}, \mathbf{A}^{\dagger}, \ldots, \mathbf{A}^{\dagger}, \mathbf{A}^{\dagger}, \ldots, \mathbf{A}^{\dagger}, \mathbf{A}^{\dagger}]$ partitioning (the fraction of all f and f and f and f are rates of \mathcal{I} and f or \mathcal{I} and f are f and f and f**rom the ABO active Across GA**BO and **A**_{cist}rus at 25° C **A** MAY **4** $\&$ \cdots (1987) **A** $\&$ M \cdots 20° \cdots **4** details of compositions of A and \tilde{a} , \tilde{a} , \tilde{a} and \tilde{a} and \tilde{a}

ES, HGEAL A GASE HAGE Crawford (1971) showed that three individual *D*. *pectoralis* maintained normal metabolic rates below and $\frac{1}{2}$ of $2 \frac{1}{2}$ mg l $\frac{1}{2}$ mg l_y supplementing and $\frac{1}{2}$ mg lines with $\frac{1}{2}$ air breathing. Likewise, metabolic rates of *L*. *pholis* stayed relatively constant through cycles of immersion and \mathbf{S} immersion and skin oxygen consumption \mathbf{S} , such and support \mathbf{S} ing the GABO is able to maintain normal resting \mathbf{a} is able to \mathbf{a} is able to \mathbf{a} in emergent members of this species (Laming *et al.*, 1982).

 S MA^H A^G A₂S_p H_AC₅_F Cala *et al.* (1990) report that the trichomycterid *Eremophilus* must increase its and frequency to survive and \mathfrak{F}_n to survive and \mathfrak{F}_n . But there have been no studies been no studies there have been no studies and \mathfrak{F}_n . But the studies of \mathfrak{F}_n of actual gas exchange in this family. Lorical family \mathbb{Z}_p is follow the general FAB pattern \mathbb{Z}_p $(\Box F \cdot \mathbf{3})$: as environmental $(\Box F \cdot \mathbf{3})$ drops, $(\Box F \cdot \mathbf{3})$ and $(\Box F \cdot$ lation units, a specific and environment-specific orientations of the water of the water of the water of the w (P_2) between 25 **a**nd 60 **to** in **canded (Braham & Baird), 1982; Graham 1983;**

oxygen levels reported by Carter \mathbb{Z} and \mathbb $A \cdot (2007)$ **for** *H* $A \cdot (n-1)$ increases of \mathcal{A} , \mathcal{A} , water by increasing (*f* v; air breaths (f v; and f v; and f v; and f v; and the changes increases increasing f v; and f demand (Graham, 1983). Interestingly, *Ancistrus* acclimated to hypoxia by expanding the size of \mathbf{A} and 25% and increasing the effective \mathbf{A} extraction (Graham, 1983). Most authors report no air breathing from local property in a indicate from local property in \mathbf{J} , \mathbf{c} , \mathbf{J} , \mathbf{c} , \mathbf{c} , \mathbf{c} , \mathbf{c} , \mathbf{c} , \mathbf{c} , \mathbf{a} , \mathbf{a} , \mathbf{e} , \mathbf{b} , \mathbf{a} , \mathbf{b} , \mathbf{e} , air breathing) behaviour that was independent of environmental \mathfrak{B}_1 in telemeter \mathfrak{B}_2 in telemetered \mathfrak{B}_3 *Glyptoperichthys*.

INTESTINAL ABO GAS EXCHANGE $\mathcal{F}=\mathcal{B}=\mathcal{$ **to be continuously be continuously be continuously by the continuously be co** $\mathbf{M}\epsilon$, 1980; McMas $\mathbf{A}\ \&$ and ϵ , 1987), and ϵ claim $\&$ claim (1945) c_{laim} that *Misgurnus* abandons CAB at low temperature. This implies that some other as pect of air ingestion such as buoyancy (Gee, 1976), digesta transport (Persaudion such as \mathcal{C} *et* al., 2006) **3 dee ended scope for all** \mathcal{C} **c** \mathcal{C} **c** $\mathcal{$ \mathbf{F}_1 , 1996) in proves fitness (done so in the past). As representatives from the past \mathbf{F}_2 $\mathbf{B}_{\mathbf{r}}$, $\mathbf{a}_{\mathbf{r}}$, ventilation of the \mathcal{A} defined \mathcal{A} and \mathcal{A} rate \mathcal{A} and \mathcal{A} $\&$ aritic to a 1987), it is particularly to a factors were secondary to a secondary secondary were $t = \sum_{i=1}^{n}$ in driving the evolution of \mathbf{z}_i in driving the evolution of \mathbf{z}_i $B_{\rm eff}$ urnus (1987) **found that when** M **singurnus confronted with a quatic hypoxical confronted with a** M **singurnus** \mathbf{d} it increased the rate of intestinal ventilation entirely through increases in *f* v. Changes in all were not involved, similar to \mathbf{S}_i , \mathbf{S}_i for storaghed, similar to \mathbf{S}_i for stomachbreathing *Ancistrus*. Three species of callichthyids also increase *f* ^v with progressive and \mathbf{G} , \mathbf{G} , \mathbf{G} , \mathbf{G} , \mathbf{G} , \mathbf{G} , 1978; Kramer & McClure, 1980; Affonso & Rantin, 2005). Man \mathcal{X} & \mathcal{Y} (1987) estimated a \mathcal{Y} of \mathcal{Y} subsequent breath in *Misgurnus* intestines. Interestingly, they report no correlation between gas composition of the ABO and breath interval durations ranging from 5 min to 1 h, such that the air rapidly with a variable oxygen is extracted from the air rapidly with \mathfrak{F} and \mathfrak{F} are rapidly with \mathfrak{F} and \mathfrak{F} are rapidly with \mathfrak{F} and \mathfrak{F} are rapid very little subsequent gas exchange. Interestingly, July 2004) $\frac{1}{\sqrt{3}}$ reports that $\frac{1}{\sqrt{3}}$ the intestinal breathing *Hoplosternum* can extract more oxygen per unit body mass from an air breath than either a gas bladder breathing erythrinid (*Hoplerythrinus*) or the lungfish *L*. *paradoxa*.

 $\mathbf{F} = \mathbf{A} \mathbf{U} = \mathbf{U}_1 \mathbf{F} + \mathbf{G}_2 \mathbf{A} \mathbf{U} + \mathbf{I} \mathbf{F} \mathbf{A}$. Here \mathbf{S} Gee \mathcal{A} (1978) and McMahon $\mathcal{B}^{\prime\prime}$ & and the through $\mathcal{B}^{\prime\prime}$ (1987) showed the showed through manips ulations of the aquatic and aerial medium that intestinal air breathers do not sense the c_{max} chemical composition of the gas in the A BO to set A BO \rightarrow although ABO ventilation, although ABO ventilation, and although ABO ventilation, although ABO ventilation, although ABO ventilation, although ABO ve volume may play a role of \mathbb{C} for \mathbb{C} and \mathbb{C} to set \mathbb{C} and \mathbb{C} for set \mathbb{C} set $\mathbb{C$ \mathcal{F} **8** and **4** and **6** and **metabolic rate (K**_r & M_{\odot} , 1980; Graham & Baird, 1982; McMahon & Burger, 1987). McMahon & $\&$ and the sensitivity of \bullet **f** M_{ν} for \bullet \bullet \bullet \bullet **f** \bullet *P_C* 2 **as de** R_p_c & **B**_i (1982) **for** *A_{ncist}ra B_i <i>H*_i (iii), but the primary state primary \mathbf{A} drive to \mathbf{A} as \mathbf{A} as

 $\qquad \qquad$ \qquad \qquad

 15

16 $\mathbf{A} \cdot \mathbf{F} = \begin{bmatrix} 1 \\ 1 \end{bmatrix}$

saturates haemoglobin (*p*50) with coincident low erythrocyte nucleoside triphosphate concentration $\mathbf{A} = \begin{bmatrix} 1 & 1 \end{bmatrix}$ ($\mathbf{A} = \begin{bmatrix} 1 & 1979 \end{bmatrix}$, 1979; Marcon **et al.**, 1999). As many of the GAB fishes accelerate to hypoxia by increasing blood oxygen affinity at \mathbf{a} least particle in the control of the cont \mathcal{E} & $^{\prime\prime}$, 1983; \mathcal{E} val 1990), \mathcal{E} published values will be dependent on \mathbf{S} . The dependent on \mathbf{S} $\mathcal{F}^{\text{tr}}_{\text{cav}}$ and animals blood collections prior to blood collection. The high blood oxygen blo affinity makes sense considering the general occupancy of \mathbb{Z}_p and \mathbb{Z}_p by these fishes. On the other hand, the evolutionary prediction for air breathing is a right shift shift of \mathbf{z}_1 affinity to facilitate oxygen affinity to facilitate oxygen delivery as oxygen affinity of \mathbf{z}_1 **i** is not all (1979) summarized and (1979) of Amazonian fishes and concluded that there was no evidence for right shifting in air-breath morris and morris \mathbb{R}^n , and data set and \mathbb{R}^n expanding that data set and data s provided some modest evidence for right shifting of haemoglobin–oxygen affinity across all air-breathing fields α $\mathcal{F}_\mathbf{z}$ fishes can be further generalized as $\mathbf{g}_\mathbf{z}$ as having as $\mathbf{g}_\mathbf{z}$ moderate to strong as $\mathbf{g}_\mathbf{z}$ as $\mathbf{g}_\mathbf{z}$, $\mathbf{g}_\mathbf{z}$, $\mathbf{g}_\mathbf{z}$, $\mathbf{g}_\mathbf{z}$, $\mathbf{g}_\mathbf{z}$, Bohr effect and no Root effect (Focesi *et al.*, 1979; Powers *et al.*, 1979; Bridges *et al.*,

1984). The Bohr effect appears manufacture, at least in one genus, that is $L \rightarrow L$ $H'(\frac{1}{\epsilon}, \frac{1}{\epsilon}, \frac{1}{\epsilon}, \frac{1}{\epsilon}, 2004).$ When L acidotic, the Bohr effect would exact would be desired the desired \mathbf{A} effluent and increase the potential loss of \mathbf{C}_2 to \mathbf{C}_3 to \mathbf{C}_4 to \mathbf{C}_5 to \mathbf{C}_6 to \mathbf{C}_7 (Fig. 2). The general absence of a Root effect in the GAB fishes is consistent with G \mathcal{F}_c reduction in swimbland \mathcal{F}_c and the lack of a choroid reternal reternal reternal reternal reternal reternal returns \mathcal{F}_c 1976; Schaefer & Lauder, 1986; Berenbrink, 2011).

 \mathbf{M} and \mathbf{M} and \mathbf{M} is a \mathbf{M} is a water, and \mathbf{M} is a water, and \mathbf{M} is a water, and bimodal breather (Domenici *et al.*, 2007). The increased aquatic ventilation required in hypoxic habitats will increase an animal increase and potentially requirements and potentially requirements its concealment from both potential predators and prey. Certainly, the diminished $\&$ $\frac{1}{2008}$ predator–prey performance; however, the diminished feeding activity and scope for \mathbf{g} in \mathbf{g} in \mathbf{g} in \mathbf{g} as in the important on \mathbf{g} in \mathbf{g} is important on $\mathbf{$ longer time scales. The evolution of air breathing solved some of these hypoxia issues for GAB fishes but \mathbf{A} is new characteristic (Kramer, 1987). Air breathing can expose animals to new predation regimes. In a direct test of this hypothesis, Kramer *et al.* (1983) showed that air-breathing fishes \mathbf{A} finds for \mathbf{A} finds from a striated to predation from a striated to predation from a striated to predation from a strict of \mathbf{A} heron *Butorides striatus* when forced to breathe air than water-breathing fishes under $\frac{\&\mathbf{M}\&\mathbf{q}}{\mathbf{r}}$ (1980) it \mathbf{q} (1984) less likely to deep to deep the deeper the deeper theorem are, and Power (1984) provides evidence from \mathcal{A} the field that \mathbf{A} lorically will avoid shallow waters where the total shallow waters where the vulnerable to \mathbf{r} avian predation despite the predation of abundant for abundant for \mathcal{B} fishes of G fishes of G a_1 behaviour a_2 in synchronized at \mathbf{K} (Kramer \mathbf{K} , 1976; Gee \mathcal{S} , 1978; S₁ and the suppliers suggest that evolution of G₁ 3 \mathcal{S} A₁ may have necessitated concomitant evolution of anti-predator behaviours to compen $s=3$ sate for increased visibility of surfaced visibility of s surfaced, many G a note the set of the set \mathcal{R} are less lifestyle to be visual predators. Bout- $\frac{d_1}{dt}$, (1990) $\frac{1}{t}$, $\frac{d}{dt}$, $\frac{d_1}{dt}$, $\frac{d_2}{dt}$ in *Hoplosternum* that very quickly tracked experimental changes to the timing of the $\begin{bmatrix} \mathbf{w} & \mathbf{b} & \mathbf{d} \\ \mathbf{w} & \mathbf{c} & \mathbf{d} \\ \mathbf{w} & \mathbf{d} & \mathbf{e} \end{bmatrix}$ (ρ,\mathbb{R}) and (ρ,\mathbb{R}) are loricariid (*Glyptoperichthysis*). Considering the potential interactions between digestive and respiratory function the Pebrea404onor beach $\frac{3}{2}$, $\frac{3}{2}$

20
\n
$$
A. = \frac{5}{5}
$$

\n $H_2 = 1.445$
\n $A. = \frac{5}{5}$
\n $A. = \frac{1}{5}$
\n $A. = \frac{1}{5$

$$
\mathbf{G}_{\mathbf{A}} = \mathbf{A}_{\mathbf{A}} \mathbf{I} \quad \text{and} \quad \mathbf{H}_{\mathbf{A}} \mathbf{G}_{\mathbf{A}} = \mathbf{A}_{\mathbf{A}} \mathbf{S} \mathbf{H}_{\mathbf{A}} \mathbf{S} \tag{21}
$$

MAY $\mathbf{3}$, $\mathbf{4}$. $\&$ air $\mathbf{1}$, $\mathbf{5}$, $\mathbf{6}$, $\mathbf{7}$, $\mathbf{8}$, in the teleost fish *Misgurnus anguillicaudatus*.

22 \ldots \ldots \ldots \ldots \ldots

- Riggs, A. (1979). Studies of the hemoglobins of Amazonian fishes: an overview. *Comparative Biochemistry and Physiology A* **62,** 257–272. \mathbf{S} . S.t. (1998). Histological and ultrastructural study of the stock of the stock of the air-breathing of the *Ancistrus multispinnis* (Siluriformes, Teleostei). *Canadian Journal of Zoology* **76,** 83–86. \mathbf{S} Since \mathcal{S} , L. (2000). Stomach as an additional respiratory organization respiratory organization organization respiratory organizations of \mathbf{S} A_{c} A_{c} A_{c} A_{c} A_{c} A_{c} A_{c} A_{c} A_{c} *Ichthyologica Piscatoria* **30,** 73–79. Schaefer, S. A. & Participation of Function of function of function of \mathbb{F}_q . The function of function of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. *Systematic Biology* **35,** 489–508. **Sc_hmidt-Night-Night-Nielsen, K. (1997).** *Animal Physiology: Adaptation and Environment* bridge: Cambridge University Press. S loman, K. A., S loman, R. D., D., D., B., B., S., S., S., S., I., \mathbb{R} , \mathbb{R} , \mathbb{R} , \mathbb{R} , A., \mathbb{R} \mathbf{M} , \mathbf{M} , \mathbf{M} , \mathbf{M} , \mathbf{M} , \mathbf{M} , \mathbf{M} . \mathbf{M} and \mathbf{M} are air breathing of synchronous and \mathbf{M} , \mathbf{M} and \mathbf{M} are a synchronous and \mathbf{M} are a synchronous and $\mathbf{M$
- *Hoplosternum littorale*. *Physiological and Biochemical Zoology* **82,** 625–634. $S_{1} = 0.5, N.$ (1986). Ventilatory and cardiac reflex responses to $1.3, 1.4, 1.5$
- L_{ℓ} , and μ , $^{-1}$ 21 $^{-1}$.58330 $^{-8}$ 81-382 $\%$.)-50087.0001 ϵ (A_{nimal})-&b 0.5(.5 μ ϵ 1-38

$$
\mathbf{C}_{\mathbf{A}_{\mathbf{B}}^{\mathbf{A}}\mathbf{A}_{\mathbf{B}}^{\mathbf{B}}}\mathbf{A}_{\mathbf{B}}^{\mathbf{B}}\mathbf{A}_{\mathbf{B}}^
$$

Electronic References

$$
\begin{array}{c|ccccccccc}\n\mathbf{A} & \mathbf{I} & \mathbf{I} & \mathbf{I} & \mathbf{A} & \mathbf{A} & \mathbf{I} & \
$$