Oxygen and fish behaviour

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One of the basic principles of good aquarium maintenance is to make sure that the water is well aerated, so that enough dissolved oxygen is available for fish respiration. This oxygen can be produced by the photosynthesis of aquatic plants and algae, or it can simply diffuse from air to water. In most environments it is diffusion from air that represents the main source of dissolved oxygen. That's certainly the case for most aquaria. (In that respect, one should know that filtration systems are useful not only for cleaning the water but also for stirring it, bringing bottom water to the surface where it can take up oxygen from the air before being pushed back to lower levels where the fish can enjoy it. Air bubblers perform the same function and, as an additional benefit, they increase the area of the air-water interface.)

In contrast to the ideal conditions that normally prevail in the home aquarium, wild fishes are sometimes faced with situations where little oxygen is present in the water. In places such as swamps and pools, the absence of wind and water currents prevents the mixing of the oxygen-rich upper layer with the rest of the water column.[1] In other places, an overabundance of aquatic animals or decomposing matter depletes oxygen because of increased consumption. These conditions are not uncommon, and therefore it is not surprising to learn that fishes have evolved special behaviours to cope with low oxygen levels. Good aquarists should have no cause to ever witness these behaviours, but biologists, being the curious lot that they are, have sought or created hypoxic (low oxygen) conditions and catalogued the reactions of fishes to them. Here is what they found.

Increased ventilation

A universal reaction to low oxygen is increased ventilation of the gills. In the same way that people start to breathe faster in order to bring more air to their lungs, fishes increase the rate of water flow through their gills. A convenient measure is the rate at which gill covers open and close under different levels of dissolved oxygen. Thus three-spined sticklebacks have been reported to increase their rate of gill cover movements from 95 to 165 per minute after the oxygen content of their water was experimentally cut down to half of its normal level.[2] One could also hypothesize that ram-ventilating sharks (fishes that bring oxygenated water to their gills by swimming with their mouths open) would increase their swimming speed and would open their mouths wider when oxygen is scarce. This is indeed what has been observed.[3]

In the lab, researchers normally reduce oxygen levels by blowing bubbles of a physiologically neutral gas – usually nitrogen – into the water; nitrogen then becomes much more abundant than oxygen and displaces it as a dissolved gas.[4] One has to be mindful of confounding variables in experiments of this kind: disease, stress and strenuous activity can also make fishes – like people – breathe faster. To eliminate the potential effect of these variables, it is important to work with animals that are consistently healthy, calm and not fidgety. Moreover, fishes are ectotherms (cold-blooded), which means that warm temperatures can raise their metabolism and consequently their breathing rate also. Comparisons between oxygen levels must therefore be done at similar water temperatures.

Decreased activity

After encountering an area of low oxygen content, fish often start to swim rapidly and to zig-zag all over the place. This is probably an adaptive response to escape the danger zone. However, if hypoxic conditions persist, most fish will greatly curtail their general activity. The advantage of inactivity in the face of hypoxia is simple: less muscular work means less need for oxygen. As part of his doctoral research at Laval University in Quebec City, Fred Whoriskey observed sticklebacks breeding in tide pools along the St-Lawrence Estuary, and he reported that during periods when dissolved oxygen levels dropped, the fish became very sluggish, even failing to show normal fright responses when an object flew over the pool (the object could be a bird or, if nature did not oblige, a frisbee thrown by the resourceful researcher). In the same vein but this time in a lab at McGill University in Montreal, Don Kramer and his students observed that guppies swim less, eat less, and court less when oxygen levels are lower than normal.[5] Inactivity can even reach extremes, as in the case of the South American cichlid *Biotodoma cupido* (the greenstreaked eartheater) which appears to fall “asleep” when oxygen is scarce.[6]

Aquatic surface respiration

Another common response to low oxygen is aquatic surface respiration. In this behaviour, fish stay just below the surface, put their snout at the air-water interface, and breathe in the film of water that is in direct contact with the air. This thin layer of water is comparatively rich in oxygen. Once I have seen this behaviour done by wild sticklebacks in a tide pool. It was a very warm summer night without wind. The water in the pool did not hold its normal load of dissolved oxygen because it was warm, the absence of wind prevented mixing, and aquatic plants could not photosynthesise in the dark and therefore did not produce any oxygen.[7]

In the lab, Don Kramer and Martha McClure studied 24 species of tropical fish common to the pet trade, from tetras to barbs to cichlids. They found that all of these fishes performed aquatic surface respiration when oxygen was deficient.[8] Typically, the fishes waited until a very low threshold of oxygen concentration was reached – less than 2 ppm[9], or about 25% of well aerated freshwater at room temperature – before starting surface respiration. This reluctance to breathe near the surface is easy to understand when we consider that, in nature, many predators of fishes are terrestrial or aerial animals that attack from above, and therefore being close to the surface is risky.

Air-breathing

Some fishes can switch from water-breathing to air-breathing when there is not enough oxygen in the water. These fishes break the surface and trap air inside their mouth. Then they use their mouth, pharynx, oesophagus, swimbladder or even in some cases their stomach like we use lungs, that is, as a site where oxygen can diffuse into the blood. Examples of such fishes include gouramis, goldfish, loaches, catfishes, the algae-consuming suckermouth catfish so common in home aquaria, and the lungfishes.[10]

Air breathing allows many fishes to lead an amphibious lifestyle, or to temporarily move out of the water if they are bothered by predators, competitors, or the threat that their water world will disappear because of a drought. Among the most amphibious of these fishes are the mudskippers, which spend most of their active lives in the air on intertidal mudflats where they feed and mate and bicker with their territorial neighbours. They are skittish creatures though, and at the slightest hint of danger they will retreat into water-filled burrows dug in the mud (see page: Can fishes build things?). At least two species – the giant mudskipper *Periophthalmodon schlosseri* and the walking goby *Scartelaos histophorus* – exhibit the interesting behaviour of storing air inside their burrow. They take air into their mouth, dive into their water-filled burrow, and release the air into special chambers. If researchers experimentally extract air from the special chambers, the fish diligently replenish it. The significance of this behaviour stems from the facts that at high tide, when water covers the mudflats, the fish stay in their burrow to avoid predators, and water inside the confined burrow is often poorly oxygenated. At such times these air-breathing fishes can tap into the air reserve of their special chambers.[11]

There are several physiological advantages to using air as a source of oxygen. Per unit volume, air contains about 30 times more oxygen than water (the exact value depends on water temperature). Moreover, air is 1000 times less heavy and 50 times less viscous than water, and therefore easier to move through the respiratory system. To grasp the difficulty of breathing in water rather than air we need only consider the fact that to survive, a fish of 100 g typically must move 30 to 65 g of water per minute through its gills – that is 1/3 to 2/3 of its own body weight, a substantial exercise! Only the incredibly large surface area of the gills can compensate for this disadvantage. But breathing in air also carries a major disadvantage: air cannot support the gills. Gills are thin to facilitate gas exchange and to maximise their number and surface area. Because of their thinness, the gills usually are not self-supporting. For a strictly water-breathing fish this is not a problem because water provides support for the gills. However, if such a fish finds itself out of water, the gills are not supported anymore. The collapse of gills and the limited surface area of other possible breathing organs are the reasons why most fishes ultimately choke outside water, despite the abundance of oxygen in air. Only air-breathing fishes can manage, and among their anatomical adaptations are thicker, self-supporting (but, consequently, less numerous) gills, as well as modified swimbladders, mouths, gill chambers, guts, or skin which have more blood vessels and are more gas-permeable than in other species.

Some species of fishes have become so specialized for air-breathing that their capacity for water breathing is impaired and they cannot meet all of their oxygen demand even in normally oxygenated water. They must breathe in air at least once in a while. Surprisingly for a fish, they will "drown" if they are forced to stay in water. Among such fishes are the South American pirarucu *Arapaima gigas* (this fish can get huge, at 4.5 m and 200 kg, and 95% of its large oxygen demand is provided by air-breathing), the freshwater butterflyfish *Pantodon buchholzi* (popular in the aquarium trade), the adult *Lepidosiren paradoxa* (a South American lungfish), the electric eel *Electrophorus electricus*, the three-spot (=blue) gourami *Trichogaster trichopterus*, and the climbing perch *Anabas testudineus*.

Some air breathers, like the European eel (*Anguilla anguilla*) or the trahiras (family Erythrinidae), are capable of overland treks that take them deep into forests. Others can catch insects on land, like the afore-mentioned mudskippers (subfamily Periophthalminae), the mangrove rivulus *Rivulus marmoratus*, the reedfish *Erpetoichthys (=Calamoichthys) calabaricus*, and the eel catfish *Channallabes apus*. Mudskippers and the eel catfish can even bend their head downward to facilitate the capture of prey lying on the ground, an anatomical adaptation – shared with the salamanderfish *Lepidogalaxias salamandroides* – that is exceptional among fishes.[12] Other amphibious fishes, like the North African catfish *Clarias gariepinus* (= *lazera*) and the climbing perch, take advantage of their ability to live on land to include grain in their diet.[13] Others, like the goby *Lentipes concolor*, can surmount waterfalls as high as 130 m (about 425 feet) by climbing on the rocks behind or next to the falls, using a special suction cup formed by the fusion of their pelvic fins to cling to the vertical surfaces. They do this amazing feat not as adults, but as fry no more than 2.5 cm (1 inch) long![14]

The mangrove rivulus lives in streams that are prone to drying up, so air breathing is a definite advantage. A recent study done in Belize and Florida has found that these fish can find out-of-water refuge in an odd place: the inside of rotting logs. These logs have long galleries inside them that were originally bored by terrestrial insects. The rivulus, which normally are very aggressive towards one another, agree to a truce and pack themselves tight inside those galleries. There they can remain, without food, breathing moist air, for up to 66 days.[15]

When it comes to living out of water for a long time, the undisputed champions are the African lungfishes (four species in the genus Protopterus). As the swamp in which they live dries up, they dig a burrow, coil up into it, and secrete mucus around themselves to form a cocoon. Then they become dormant. Their metabolism is very low, yet they still need to breathe a little bit, and they do so with air. This estivation goes on for the whole of the African dry season, and we're talking 7-8 months here. Even more impressively, some estivating African lungfishes have been forced experimentally to remain in this state for 4 years, and survived.

The eggs of some fish can also survive in air, as long as the air is well laden with humidity. The splash tetra *Copella arnoldi* – itself an air-breather – can jump straight out of the water and deposit eggs or sperm on the underside of leaves. Then from below the males splash water onto the eggs every 10-15 minutes to keep them moist and oxygenated. In an aquarium, splash tetras can lay eggs on glass above the waterline, or even on the underside of the tank lid.

Other species, even though they are not air breathers, are known to lay eggs in places that get exposed to air.[16] For example, in Australia and New Zealand, several species of *Galaxias* deposit their eggs in vegetation above the waterline. The eggs hatch only when floodwaters rise high enough to submerge them.[17] In Canada, populations of "white" sticklebacks lay their eggs in filamentous algae or even on bare rocks in the intertidal zone, places that get exposed to the air at low tide; exceptionally for a stickleback, the eggs receive no parental care.[18] Sites chosen for terrestrial egg laying are naturally moist – or kept moist, as in the case of the splash tetra – so that the eggs won't dry up and die. By developing in air, eggs may benefit from higher temperatures, more oxygen available, and protection against aquatic predators.

Oxygen and predation

As with aquatic surface respiration, air-breathing entails a substantial risk of predation because of the fish's necessary proximity to the surface. To demonstrate this risk of predation, Don Kramer and his students hand-reared a green heron until it was 1 year old and allowed it to forage in pools stocked with various kinds of fishes (10 species of tropical fishes, as well as bluegill sunfish and central mudminnows). The researchers experimentally reduced dissolved oxygen to either 1.6 or 0.5 ppm. As expected, the fishes came to the surface, albeit not as much as they would have if the heron had not been there – they were aware of the bird's presence and the danger it represented. Yet they were still forced to come up once in a while to perform aquatic surface respiration or air-breathing, especially at 0.5 ppm. The heron caught more fishes at 0.5 ppm than at 1.6 ppm because of the prey's greater use of the surface at that concentration. The danger inherent to aquatic surface respiration and air-breathing was thus confirmed.[19]

With this risk in mind, it is worth mentioning that in many species of air-breathing fishes, individuals can synchronize the time at which they break the surface to gulp air.[20] Presumably, the fishes are wary of predators and delay air gulping until they see another fish get away with it. The link between predation and synchronous air-breathing has been demonstrated experimentally by John Gee of the University of Manitoba. He simulated a heron strike by plunging the wooden model of a heron head into the water of a tank housing central mudminnows, *Umbra limi*, and saw that the mudminnows started to synchronise their air breaths after such a disturbance. Instead of each individual breaking the surface at any time as they did before, the mudminnows experimentally scared by Gee's fake heron tended to break the surface more simultaneously.[21]

Other students and colleagues of Don Kramer have investigated the risk of predation by piscivorous fishes rather than birds. Robert Poulin has found that guppies did not run a greater risk of being caught by oscars under hypoxia, probably because the predatory oscars were just as affected by the lack of oxygen as their prey. In contrast, Nancy Wolf has observed that giant snakeheads, *Channa micropeltes*, were more successful at capturing dwarf gouramis, *Colisa lalia*, at 1 ppm than at 3 or 8 ppm, because the gouramis had to leave the cover of submerged plastic plants to go near the surface. The difference between the two studies may be that predatory air breathers, such as snakeheads, are not as adversely affected by hypoxia as predatory water breathers, such as oscars.[22]

Findings of this kind allow us to predict that oxygen-poor habitats could provide a refuge to hypoxia-tolerant prey species relative to their not-so-tolerant predators. This idea has been put forward to explain the disappearance of indigenous species from the open waters but not from swamps in waters infested by the predatory Nile perch in Africa,[23] and to explain the boldness of minnows in the presence of visibly distressed yellow perch under hypoxic conditions.[24]

When pursued by predators, tolerant species could do more than just seek hypoxic refuges. They could simply jump out of the water and spend some time on land. This predator-evasion behaviour has been observed in rivulines (family Aplocheilidae), killifishes (family Cyprinodontidae), and the bald sculpin *Clinocottus recalvus*.

Winterkill

In northern lakes, whole fish populations are sometimes wiped out during the winter. Following a fierce winter, very few fishes are found alive in the lake. Such massive die-offs – called winterkill – take place when the surface of the lake gets covered by ice, with snow on top. The ice isolates the water from the air, while the snow screens the aquatic plants from much of the already short daylight, curtailing photosynthesis. Oxygen eventually runs out, and the fishes start to die. They cannot use aquatic surface respiration or unrestricted air-breathing because of the ice. They are reduced to gathering around air bubbles trapped underneath the ice, as witnessed in the field by John Magnuson and his team from the University of Wisconsin.[25] But this, obviously, can only be a short-term measure. The fish's only hope for long-term survival – beside physiological adaptations such as the use of anaerobic metabolism, see below – is to congregate near the mouths of inflowing tributaries that discharge well-oxygenated water (if the current is strong enough, ice does not form over the stream, and oxygen can diffuse into it). Such streams, unfortunately, cannot always be found, hence the winterkill.

Bringing oxygen to the eggs

Another aspect of behaviour very much affected by low oxygen is parental care. Many species lay their eggs on the surface of rocks and fan them. Fanning is an activity whereby the parent maintains a flow of water over the eggs by rhythmically moving its fins near them. This water movement is necessary because without it the breathing eggs would use up all of the oxygen present in the layer of water that immediately surrounds them, and thus would eventually suffocate. The flow created by the parent guarantees that well oxygenated water is in constant contact with the eggs. Given this, one would expect fishes to fan more when dissolved oxygen levels are low. This prediction is borne out. I have taken a battery-operated oxygen meter to tide pools where male threespine sticklebacks tended their nests full of eggs, and have found that lower oxygen levels coincided with higher percentages of time spent fanning by the fish.[26] Dutch ethologists working in the lab have also been able to coerce male sticklebacks into fanning more by connecting a tube to their nest and pumping deoxygenated water through it.[27] Higher fanning levels caused by low oxygen represent a great expenditure of energy by parental males, to the point that they may lose weight and be unable to successfully breed a second time after the first stressful attempt. This was recently demonstrated in common gobies, *Pomatoschistus microps*, by Jackie Jones and John Reynolds from the University of East Anglia.[28]

A peculiar behaviour has been documented in one species of cichlid, the rainbow cichlid *Herotilapia multispinosa*. Working in the lab of Miles Keenleyside at the University of Western Ontario, Simon Courtenay exposed parental rainbows to oxygen concentrations of only 2 ppm. When the eggs hatched, the parents did not gather the emerging wrigglers into pits dug in gravel as usual. Instead they sucked the wrigglers into their mouth and spat them into vegetation, onto which the wrigglers attached themselves thanks to glue-producing glands on their head. Courtenay showed that this behaviour, called "wriggler-hanging", was more prevalent when oxygen concentration was low. Presumably, wrigglers benefited from being close to vegetation because of the oxygen released by photosynthesis and also because the plants were often closer to the surface. Wriggler-hanging has also been reported in other cichlids, such as the angelfish, the red discus, the severum and the festivum.[29]

One of my students has told me about another peculiar behaviour, this time in the convict cichlid. He had a pair of convicts tending their eggs inside a ceramic skull (one of those aquarium decorations sold in pet shops). The female, instead of fanning her eggs in the usual way, used to go to the airstone, take air into her mouth, bring it back to the nest and release it at the bottom so that the air bubble would float upwards along the egg batch. She did this repeatedly, to the extent that air was gathering at the top of the skull, threatening to raise the nest and its content all the way to the surface! Did she carry air bubbles to provide oxygen to her eggs in the face of localised hypoxic conditions? George Barlow has provided another interpretation, which may be better: he has observed a similar behaviour in orange chromides, *Etroplus maculatus*, and he saw this as an expression of fry-retrieving behavior (see the page: Are fishes good parents?). The small bubbles are about the same size as fry. The parent may be fooled into thinking that the air bubbles are fry (even though its eggs have not hatched yet), and it tries to bring back those incredibly mobile fry back into the nest. [30]

There is another similar case, but one in which an oxygen-supply explanation seems more likely. Some gouramis take in air, move below their bubble nest, and with strong opercular action they squirt bubbles up through the nest. [31] This behaviour probably brings oxygen to the eggs and must have evolved as an adaptation to the warm, stagnant and therefore oxygen-poor waters in which these species eke out a living.

The ease of ventilating eggs may be influenced by nest shape. In the common goby, males build a nest for their future eggs by dumping sand over down-turned mussel shells. In the lab they may do it over a clay flower pot. The accumulated sand partially occludes the object's opening. Normally the males try to make the opening relatively small because this impedes the entry of egg predators such as crabs. But small openings also mean less potential for circulating water. It has been observed that the owners of nests with smaller openings fan more than others. Also, if the oxygen content of the water is experimentally reduced, then the males build nests with larger openings. Obviously the fish adapt their nest building and nest tending behaviour to oxygen levels.[32]

In many fish species, females prefer to lay eggs in nests that already contain other eggs, perhaps a form of copying the choice that previous females have made for particular high-quality males. But considerations relating to oxygen must be taken into account. In sticklebacks for example, females prefer to spawn in nests that already contain two or three clutches, but they disregard nests that are packed with four or five clutches.[33] This may be related to the fact that eggs in an overcrowded nest have trouble getting enough oxygen for optimal development. In the same vein, female common gobies normally prefer nests that already have eggs in residence, but if the fish are kept in oxygen-poor water the females reverse their preference and now favour nests that are empty. This new choice is probably adaptive because competition for oxygen is fiercer in a nest with many eggs, and such a nest should therefore be avoided when oxygen is already in short supply.[34]

The South American lungfish *Lepidosiren paradoxa* lives in swamps where hypoxia is common. In this species the male guards eggs and developing larvae within a nest. At such a time, the male grows long filaments on his pelvic and pectoral fins. Work in the 1930s has shown that oxygen is released from these filaments into the water. It is thought that the filaments act as oxygenators for the nest and its content. The male breathes air at the surface, oxygen passes into his blood, and from there it is released into the nest through the thin surface of the filaments.[35]

Physiological adaptations to low oxygen levels

Adaptations to low oxygen can be not only behavioural but also physiological. Fishes that live in frequently hypoxic habitats may have more haemoglobin in their red blood cells, and more of those cells in their blood, and therefore a higher blood capacity to take up and transport oxygen. Their body tissues may contain more myoglobin, a molecule that can bind up oxygen and therefore act as an oxygen store.[36] But their main adaptation is anaerobic metabolism, a set of biochemical pathways that do not require oxygen to yield energy. This type of metabolism is not very efficient and can lead to the accumulation of relatively toxic by-products, such as lactic acid, and therefore when oxygen is present anaerobic metabolism is put aside in favour of its more efficient aerobic counterpart. But when oxygen is rare and metabolic demand is low, as in a cold water fish for example, anaerobic metabolism can contribute to survival for days, weeks, or even months. For example, through the use of anaerobic metabolism, goldfish can survive for up to 9 days at 4 ^{o}C in only 0.5 ppm of oxygen. Similarly, from February to April there is virtually no oxygen at the bottom of northern lakes, and yet crucian carp, *Carassius carassius*, survive there because of their anaerobic metabolism and the cold winter temperatures that lower their energy requirements.[37] Finally, drought is another ecological condition that selects for anoxia tolerance via anaerobic metabolism. For example, the killifish *Austrofundulus limnaeus* lives in ephemeral ponds in Venezuela and the eggs it produces can enter diapause and survive for up to 60 days in the complete absence of oxygen.[38]

Last word

Behavioural and physiological responses are not sufficient to allow fishes to live indefinitely in severely hypoxic waters, but they can contribute to survival for significant periods of time. It is a comforting thought, one to which fish keepers can cling next time they are away from home on an extended leave, worrying about their air pumps suddenly failing.

[1] Chapman, L.J., Chapman, C.A., Nordlie, F.G., and Rosenberger, A.E., 2002, Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region, Comparative Biochemistry and Physiology A – Molecular and Integrative Physiology 133, 421-437; Congleton, J.L., 1980, Observations on the response of some southern California tidepool fishes to nocturnal hypoxic stress, Comparative Biochemistry and Physiology A 66, 719-722.

[2] Jones, J.R.E., 1952, The reactions of fish to water of low oxygen concentration, Journal of Experimental Biology 29, 403-415.

[3] Carlson, J.K., and Parsons, G.R., 2001, The effects of hypoxia on three sympatric shark species: physiological and behavioral responses, Environmental Biology of Fishes 61, 427-433.

[4] The amount of gas that can be dissolved in water depends on four factors: (1) the intrinsic solubility of the gas (for example the solubility of oxygen is twice that of nitrogen but 30 times less than CO_2); (2) the water temperature (the warmer it is, the less gas can be dissolved); (3) the salt content of the water (the more solutes present, the less gas can be dissolved); and (4) the partial pressure of the gas (partial means relative to other gases; for example, the more dissolved nitrogen and CO_2 there is in the water, the less the partial pressure of oxygen, even for a fixed quantity of it, and the less oxygen can be dissolved). By bubbling nitrogen into the water, it is possible to drive out as much as 90% of the oxygen already there just by reducing its partial pressure. To lower the concentration of dissolved oxygen even further (to less than 1 ppm), it is possible to dissolve small quantities of sodium sulphite in the water, without harm to the fish. To check oxygen concentration, scientists use oxygen meters (Yellow Spring Instruments is a popular brand) or chemical methods (for example, the well-known Winkler Titration).

[5] Kramer, D.L., and Mehegan, J.P., 1981, Aquatic surface respiration, an adaptive response to hypoxia in the guppy, *Poecilia reticulata* (Pisces, Poeciliidae), Environmental Biology of Fishes 6, 299-313. Kramer has done a lot of work on the effect of low oxygen levels on fish behaviour, and has written a good review on the topic: Kramer, D.L., 1987, Dissolved oxygen and fish behavior, Environmental Biology of Fishes 18, 81-92.

[6] Cichocki, F., 1977, Tidal cycling and parental behavior of the cichlid fish, *Biotodoma cupido*, Environmental Biology of Fishes 1, 159-169.

[7] Reebs, S.G., Whoriskey, F.G., and FitzGerald, G.J., 1984, Diel patterns of fanning activity, egg respiration, and the nocturnal behavior of male three-spined sticklebacks, *Gasterosteus aculeatus* L. (f. *trachurus*), Canadian Journal of Zoology 62, 329-334.

[8] Kramer, D.L., and McClure, M., 1982, Aquatic surface respiration, a widespread adaptation to hypoxia in tropical freshwater fishes, Environmental Biology of Fishes 7, 47-55. The species tested were of different shapes, but it is worth mentioning here that the flattened head shape of poeciliids and other tropical fishes common to the pet trade could be viewed as an adaptation for aquatic surface respiration because it allows better access to the thin layer of oxygen-rich water near the surface. Water is often hypoxic in the tropics because of its high temperature and, consequently, its low oxygen solubility. This, however, does not mean that aquatic surface respiration is limited to tropical species. It can be found at any latitude; for example, see: Gee, J.H., Tallman, R.F., Smart, H.J., 1978, Reactions of some Great Plains fishes to progressive hypoxia, Canadian Journal of Zoology 56, 1962-1966; Congleton, J.L., 1980, Observations of the responses of some southern California tidepool fishes to nocturnal hypoxic stress, Comparative Biochemistry and Physiology A 66: 719-722;

[9] ppm means part per million, which in this case is equivalent to milligrams of O_2 per litre of water.

[10] For a thorough review, including a list of all groups of fish that breathe air, see: Graham, J.B., 1997, Air-breathing Fishes: Evolution, Diversity, and Adaptation, Academic Press, San Diego. Also: Martin, K.L.M., 1995, Time and tide wait for no fish: intertidal fishes out of water, Environmental Biology of Fishes 44, 165-181; Martin, K.L.M., and Bridges, C.R., 1999, Respiration in water and air, pp. 54-78 in: Intertidal Fishes: Life in Two Worlds (Horn, M.H., Martin, K.L.M., and Chotkowski, M.A., eds.), Academic Press, San Diego; Sayer, M.D.J., 2005, Adaptations of amphibious fish for surviving life out of water, Fish and Fisheries 6, 186-211.

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