
Review

Tribute to P. L. Lutz: respiratory ecophysiology of coral-reef teleosts

Göran E. Nilsson^{1,*}, Jean-Paul A. Hobbs² and Sara Östlund-Nilsson³

¹*Department of Molecular Biosciences, University of Oslo, N-0316 Oslo, Norway,* ²*ARC Centre of Excellence for Coral Reef Studies and School of Marine and Tropical Biology, James Cook University, Townsville, Australia and*

³*National Library of Norway, Oslo, Norway*

*Author for correspondence (e-mail: g.e.nilsson@imbv.uio.no)

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Summary

One of the most diverse vertebrate communities is found on tropical coral reefs. Coral-reef fishes are not only remarkable in color and shape, but also in several aspects of physiological performance. Early in life, at the end of the pelagic larval stage, coral-reef fishes are the fastest swimmers of all fishes in relation to body size, and show the highest specific rates of maximum oxygen uptake. Upon settling on the reef, coral-reef fishes have to adopt a demersal lifestyle, which involves coping with a habitat that can become severely hypoxic, and some fishes may even have to rely on air breathing when their coral homes become air exposed. Oxygen availability appears to be a major ambient selection pressure, making respiratory

function a key factor for survival on coral reefs. Consequently, hypoxia tolerance is widespread among coral-reef fishes. Hypoxia can even be a factor to gamble with for those fishes that are mouthbrooders, or a factor that the coral inhabitants may actively seek to reduce by sleep-swimming at night. Here, we summarize the present knowledge of the respiratory ecophysiology of coral-reef teleosts. From an ecophysiological perspective, the coral reef is an exciting and largely unexplored system for testing existing hypotheses and making new discoveries.

Key words: hypoxia, coral reef, fish larvae, Pomacentridae, Gobiidae, Apogonidae.

Introduction

This review is dedicated to our late friend, colleague and long-term collaborator, Peter Lutz, who devoted much of his scientific life to the hypoxia tolerance and respiratory physiology of various animals in various parts of the world. Like two of us, Peter came from the North but loved life in the tropics. He was a true explorer, and had Peter still physically been with us, we know that he would have been delighted to join us in the exploration of the respiratory physiology of coral-reef teleosts, and to share our beers in the evening.

Animals that take up their oxygen from water run a much greater risk of experiencing hypoxia than air breathers. This is because the concentration of oxygen in air-saturated water is only about 3–5% of that in air, and because oxygen diffuses some 10 000 times faster in air than in water. Thus, aquatic organisms may use up the oxygen in their surroundings before it is replenished by diffusion or photosynthesis. Hypoxia is particularly likely to occur at night, when the lack of light stops photosynthesis and forces plants to rely on respiration for their energy supply. While it is well known that hypoxia has a great influence on tropical freshwater habitats (e.g. Val et al., 2006), it has only recently become apparent that hypoxia also shapes

the teleost fauna on tropical coral reefs. Thus, in the areas with the most diverse fish faunas, which include tropical freshwater systems, such as that of the Amazon river, and tropical coral reefs, hypoxia is a major abiotic selection pressure. Still, the exploration of how hypoxia has shaped coral-reef fishes has just begun, and the high complexity and biodiversity of this ecosystem indicate that we can expect to find a wealth of adaptations to hypoxia. In this review, we will summarize our present understanding of the respiratory challenges that coral-reef teleosts have to cope with. We begin with an overview of the prevalence of hypoxia tolerance in coral-reef fishes and identify where and when coral-reef fishes are likely to experience hypoxia. Following this, we highlight specific cases of respiratory adaptation and examine the respiratory abilities of larval fish and the ontogeny of respiratory physiology. We attempt to link physiological adaptations with the environment that presumably promoted their evolution.

Hypoxia tolerance in coral-reef fishes

Hypoxia tolerance appears to be widespread in coral-reef fishes. In an initial survey carried out on the coral reef at Lizard

Table 1. Hypoxia tolerance of coral-reef fishes in the lagoon at Lizard Island Research Station, Great Barrier Reef

Family/Species	N	Mass (g)	Normoxic \dot{M}_{O_2} (mg kg ⁻¹ h ⁻¹)	[O ₂] _{crit}	[O ₂] _{out}
Cardinalfishes (Apogonidae)					
<i>Apogon compressus</i>	4	7.0±1.2	179±67	19±5	6.7±1.9
<i>Apogon cyanosoma</i>	1	2.2	259	30	
<i>Apogon doederleini</i>	1	4.4	288	31	
<i>Apogon exostigma</i>	1	3.7	218	26	11.4
<i>Apogon fragilis</i>	14	1.9±0.1	255±17	17±1	7.2±1.0
<i>Apogon leptacanthus</i>	14	1.5±0.1	239±19	19±1	7.0±1.2
<i>Archamia fucata</i>	1	5.8	225	34	
<i>Cheilodipterus quinquelineatus</i>	2	1.8–7.4	244–263	23–31	7.2–11.1
<i>Sphaeramia nematoptera</i>	1	7.3	131	17	10.0
Damsel-fishes (Pomacentridae)					
<i>Acanthochromis polyacanthus</i>	1	15.4	197	26	6.5
<i>Acanthochromis polyacanthus</i> juv	7	0.13±0.02	1561±185	29±6	12.4±2.9
<i>Chromis atripectoralis</i>	5	8.4±2.5	358±84	22±2	8.8±0.8
<i>Chromis viridis</i>	6	2.5±1.1	555±108	23±1.2	7.4±0.9
<i>Chrysiptera flavipinnis</i>	1	2.4	384	30	12.0
<i>Dascyllus aruanus</i>	3	4.1±1.3	306±37	19±0	5.9±0.6
<i>Neoglyphidodon melas</i>	6	32.1±8.8	216±32	25±2	5.6±0.7
<i>Neoglyphidodon nigroris</i>	6	14.9±2.4	162±21	22±3	8.9±1.5
<i>Neopomacentrus azysron</i>	1	3.2	493	32	
<i>Pomacentrus amboinensis</i>	4	12.6±1.7	201±11	22±4	7.1±2.0
<i>Pomacentrus bankanensis</i>	1	7.8	237	19	
<i>Pomacentrus coelestis</i>	6	7.8±3.0	387±85	22±4	9.3±1.0
<i>Pomacentrus lepidogenys</i>	5	3.1±0.6	516±73	31±2	12.5±1.1
<i>Pomacentrus moluccensis</i>	4	5.2±4.0	397±85	25±3	10.4±1.9
<i>Pomacentrus philippinus</i>	2	2.2–6.9	320–348	26–33	9.3–10.5
Gobies (Gobiidae)					
<i>Amblygobius phalaena</i>	1	2.4	333	21	2.8
<i>Amblygobius rainfordi</i>	2	1.0–1.5	209–352	18–26	6.7–10.4
<i>Amblygobius rainfordi</i> juv	3	0.23±0.09	874±353	20±5	6.5±1.6
<i>Asterropteryx semipunctatus</i>	1	1.4	403	26	1.4
<i>Gobiodon axillaris</i>	6	0.94±0.25	250±26	18.9±1.5	3.3±0.5
<i>Gobiodon erythrospilus</i>	11	0.56±0.10	260±58	17.5±3.2	2.9±1.1
<i>Gobiodon histrio</i>	5	0.53±0.08	263±83	19.3±6.5	3.0±1.4
<i>Gobiodon unicolor</i>	7	1.7±0.7	302±58	25.0±5.8	0.9±0.7
<i>Gobiodon acicularis</i>	6	0.84±0.24	188±28	19.6±3.2	2.8±0.9
<i>Gobiodon ceramensis</i>	6	0.90±0.27	230±35	14.7±2.1	0.4±0.5
<i>Gobiodon okinawae</i>	11	0.72±0.32	298±72	21.8±8.2	5.3±1.6
<i>Paragobiodon xanthosomus</i>	6	0.69±0.18	266±42	24.3±5.2	5.7±1.5
<i>Valenciennesia strigata</i>	1	28.2	157	19	5.3
Blennies (Blenniidae)					
<i>Atrosalarias fuscus</i>	3	7.3±1.9	208±34	18±2	1.6±0.7
<i>Atrosalarias fuscus</i> juv	1	0.29	552	13	1.5
Sandperches (Pinguididae)					
<i>Paraperca cylindrica</i>	1	3.06	381	26	1.6
Filefishes (Monacanthidae)					
<i>Paramonacanthus japonicus</i>	1	1.7	486	23	9.5
Brems (Nemipteridae)					
<i>Scolopsis bilineatus</i> juv	1	1.9	375	28	12.8
Wrasses (Labridae)					
<i>Halichoeres melanurus</i>	1	1.8	394	25	6.8
<i>Labroides dimidiatus</i> juv	3	0.56±0.09	736±35	24±5	7.8±0.9

Table 1. Continued on next page.

Table 1. Continued

Family/Species	<i>N</i>	Mass (g)	Normoxic \dot{M}_{O_2} (mg kg ⁻¹ h ⁻¹)	[O ₂] _{crit}	[O ₂] _{out}
Surgeonfishes (Acanthuridae)					
<i>Acanthurus grammoptilus</i> juv	1	7.45	474	21	11.0
Scorpionfishes (Scorpaenidae)					
<i>Caracanthus unipinna</i>	5	1.8±0.9	238±58	22±3	2.4±0.6
<i>Parascorpaena mossambica</i>	1	3.19	193	17	3.0
<i>Sebastapistes cyanostigma</i>	1	14.4	228	27	2.9

[O₂]_{crit} + [O₂]_{out} values are % of air saturation.

(Normoxic \dot{M}_{O_2} = routine rate of O₂ consumption at a water [O₂] >70% air saturation; [O₂]_{crit} = critical [O₂]; below this level \dot{M}_{O_2} starts falling and is no longer independent of ambient [O₂]; [O₂]_{out} = [O₂] at which the fish showed signs of agitation or balance problems.

Values for 3 or more fish are means ± s.d.; juv, juvenile.

Taxonomic nomenclature follows Munday et al. (Munday et al., 1999) for *Gobiodon* and Randall et al. (Randall et al., 1997) for all other fishes. Most values are from Nilsson and Östlund-Nilsson (Nilsson and Östlund-Nilsson, 2004) with additional values from Nilsson et al. (Nilsson et al., 2007a; Nilsson et al., 2007b) and from new measurements (Pinguipedids and Acanthurids) made under identical conditions. Measurements were made at 28–30°C.

Island (Great Barrier Reef, Australia), we used closed respirometry to determine critical oxygen concentrations ([O₂]_{crit}) in 31 species of teleost fish from several families (Nilsson and Östlund-Nilsson, 2004). [O₂]_{crit} is the lowest oxygen level where a fish is able to maintain its routine rate of oxygen consumption (Prosser and Brown, 1961), and is a frequently used indicator of hypoxia tolerance. To our immediate surprise, all species examined were found to be strikingly hypoxia tolerant, showing [O₂]_{crit} values between 13 and 34% of air saturation, the mean being about 24% (Table 1).

At the time of our first experiments, we did not think of coral reef fishes as inhabitants of hypoxic habitats, except in the special case of the epaulette shark on shallow tidal flats (reviewed by Nilsson and Renshaw, 2004), which are known to periodically become large hypoxic tide pools at night (Orr, 1933). Tolerating hypoxia in warm water, like the 30°C water of a tropical coral reef, should be more challenging than in colder water. Thus, it seems to be a considerable physiological achievement of coral-reef fishes to maintain O₂ uptake in hypoxia, due to the combined effects of a low solubility of O₂ in warm seawater, and the high rate of oxygen consumption of a small fish at such a high temperature. Most of the fishes studied weighed less than 10 g and had routine rates of oxygen consumption (\dot{M}_{O_2}) of 200–700 mg O₂ kg⁻¹ h⁻¹, which is about 2–5 times higher than that of fishes living at 10–20°C in temperate waters (see Clarke and Johnston, 1999).

The [O₂]_{crit} values shown by the coral-reef fishes were similar to those of tropical freshwater fishes that inhabit hypoxic waters and are renowned for their hypoxia tolerance. For example, African cichlid species, including tilapia (*Oreochromis niloticus*), show [O₂]_{crit} values of about 20% of air saturation at 25°C (Verheyen et al., 1994). The elephant nose fish (*Gnathonemus petersii*) from central Africa has a [O₂]_{crit} as low as 10% at 26°C (Nilsson, 1996), while adults of the hypoxia tolerant oscar cichlid (*Astronotus ocellatus*) of the Amazon river have an [O₂]_{crit} value of 30% (Sloman et al.,

2006). In those measurements, like in our measurements on reef fish, closed respirometry was used. This method mimics the hypoxic situation in nature, where oxygen is used up by aerobic organisms converting O₂ into CO₂, thereby creating hypoxia as well as hypercapnia. Moreover, a closed respirometer is relatively simple, lightweight and transportable, making it ideal to use in the field.

Although hypercapnia (high P_{CO_2}) is associated with low oxygen environments, both in a closed respirometer and in the field, we have focused our research on hypoxia, since hypercapnia is unlikely to be a major challenge in warm seawater because it is well buffered (see Kalle, 1972) and holds relatively little O₂ that can be converted into CO₂ even when air saturated. Thus, in marine tide pools that are supersaturated (200–300%) with O₂ in the day, P_{CO_2} does not reach levels much higher than 2 mmHg, and pH stays above 7.5, when all this O₂ has been consumed at night (Truchot and Duhamel-Jouve, 1980). Consequently, P_{CO_2} values in the respirometer should not reach higher values than about 1 mmHg, which should not be a major threat to the CO₂ excretion of fishes, which normally have a blood P_{CO_2} near 4 mmHg (Ishimatsu et al., 2005).

Anaerobic energy production – the second line of defence

Low oxygen environments pose significant challenges to an animal's physiology, and without specialized adaptations hypoxia is likely to lead to death. When ambient oxygen levels fall below [O₂]_{crit}, the tissues become starved for oxygen. At low cellular oxygen levels, the ATP production from oxidative phosphorylation slows down and eventually stops. A fall in [ATP] rapidly becomes life threatening to fish, like to most animals, since ion-pumps stop, leaving the cells in a depolarized state (Nilsson et al., 1993; Nilsson and Lutz, 2004). Still, most of the coral-reef fishes we studied did not show any signs of distress or loss of coordination until the O₂ level in the

closed respirometer had fallen well below $[O_2]_{crit}$. In fact, these signs were usually not seen until water $[O_2]$ had fallen below 10% of air saturation, or even as low as 1–3% of air saturation in several gobiids, blenniids, scorpaenids and a pinguipedid. These are the values denoted $[O_2]_{out}$ in Table 1 (at which point the fish was taken out of the respirometer and allowed to recover). After $[O_2]$ had fallen below $[O_2]_{crit}$, it often took 1–2 h before $[O_2]_{out}$ was reached (see Nilsson et al., 2004). Thus, our data indicate that when the $[O_2]$ in water falls below the $[O_2]_{crit}$, coral-reef fishes are, at least temporarily, able to maintain ATP levels in spite of the impaired oxidative ATP production. This is likely to be achieved by boosting anaerobic ATP production (i.e. glycolysis), and it may also involve mechanisms for reducing ATP demand (metabolic depression) (see Hochachka and Somero, 2002; Lutz and Nilsson, 2004). Suppressing ATP demand has been found in other fish to involve suppressed brain activity (Johansson et al., 1995; Nilsson, 2001) correlated with increased levels of inhibitory neurotransmitters (Nilsson et al., 1991; Nilsson, 1992; Lutz and Nilsson, 2004). To what extent coral-reef teleosts are utilizing anaerobic glycolysis and metabolic depression when faced with critically low O_2 levels remains to be studied.

Where is the hypoxia?

The low $[O_2]_{crit}$ of coral-reef fishes clearly indicates that hypoxia is an important selective pressure on coral reefs. However, identifying hypoxic habitats utilized by coral-reef fishes was not obvious at first. The clear, well-lit waters of coral reefs is as far as one can imagine from the turbid or shaded waters normally associated with hypoxic waters. So where and when do coral-reef fishes encounter hypoxia? The fishes that exhibited hypoxia tolerance were collected in close proximity to living coral on 2–5 m deep reefs (Fig. 1) in the lagoon at Lizard Island, and were indicative of the coral-reef

fish community present in this habitat. During the daytime, we found that these coral-reef waters have oxygen levels around 100% of air saturation. However, at night these waters may become hypoxic because photosynthesis ceases while the reef inhabitants will continue to consume oxygen.

By focusing on the possibility of nocturnal hypoxia, we envisaged two major scenarios that could result in coral-reef fishes experiencing hypoxia (Nilsson and Östlund-Nilsson, 2004): (i) when fishes hide from predators at night by moving into the coral colonies and residing between coral branches, or (ii) when fishes get trapped in tidal pools during nocturnal low tides. While the first situation could be a ubiquitous cause of hypoxia in coral reef environments, the latter situation is of course only possible on shallow reefs. It is well known that hypoxia can occur in tide pools in all kinds of marine ecosystems (e.g. Horn et al., 1999), and with regard to coral reefs, it was noted by European expeditions to Australia and Java in the 1920s that oxygen levels could fall to about 20% of air saturation during the dark hours in tidal pools on shallow reefs, or in reef lagoons temporarily cut off from the ocean (Verwey, 1931; Orr, 1933).

To test the first hypothesis, we collected live colonies of *Acropora nasuta* from the Lizard Island reef, placed these colonies in outdoor aquaria, and monitored the water oxygen levels between the coral branches. The recordings showed a progressive reduction in $[O_2]$ during the night, with the average $[O_2]$ between the branches falling to 20% of air saturation just before sunrise (Fig. 2) and, for short periods, $[O_2]$ as low as 2% of air saturation was measured (Nilsson et al., 2004).

Similarly, in colonies of *Stylophora pistillata* from the Red Sea, kept in the laboratory, Goldshmid et al. (Goldshmid et al., 2004) showed that water oxygen levels can fall to 10–20% of air saturation in the dark. They also made the interesting suggestion that piscine inhabitants of the *Stylophora* colonies (three damselfish species: *Chromis viridis*, *Dascyllus aruanus* and *D. marginatus*) perform nocturnal ‘sleep-swimming’ (Fig. 3), apparently to increase the water flow through the coral, thereby reducing nocturnal hypoxia. It was found that the presence of sleep swimming fish increased the flow of water through coral colonies on the reef. In the laboratory, sleep-swimming fish reduced the hypoxia occurring in coral colonies kept in the dark (Goldshmid et al., 2004). It remains to be studied in the field if the presence of fish in coral does reduce the level of hypoxia within the coral colonies.

To confirm that the nocturnal hypoxia



Fig. 1. Coral reef at Lizard Island, Great Barrier Reef, Australia. This picture depicts daytime behaviour of damselfishes (here mainly represented by the genera *Pomacentrus* and *Chromis*) hovering above a colony of *Acropora nasuta*. At night, these fishes shelter between branches in the coral, a microhabitat that can be severely hypoxic. Photo by G. E. Nilsson.

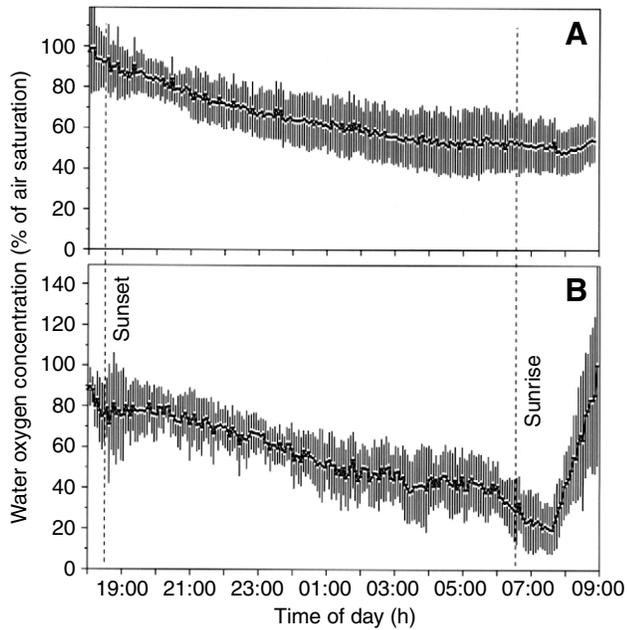


Fig. 2. Coral colonies can be severely hypoxic habitats at night. The graphs show the oxygen levels (A) outside and (B) between branches of *Acropora nasuta* colonies from dusk to dawn. Values are means \pm s.e.m. from six measurements on three corals in an outdoor tank at Lizard Island Research Station. Sunset and sunrise are indicated by broken lines. From Nilsson et al. (Nilsson et al., 2004).

detected between branches in coral colonies in the laboratory was indicative of oxygen levels on coral reefs, we conducted night-time field measurements of oxygen levels on the reef in the Lizard Island lagoon. The measurements were done between 02:00 h and 05:00 h on (austral) summer low tides (G.E.N., J.-P.H. and S.Ö.-N., unpublished observations). Inbetween the branches of coral colonies, where numerous

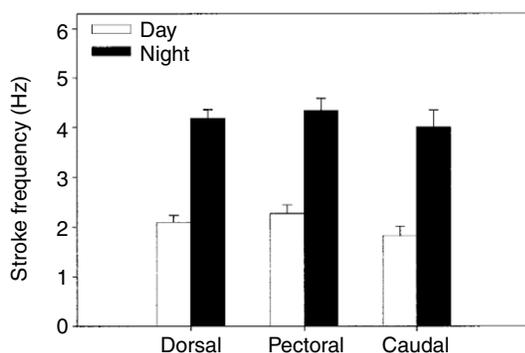


Fig. 3. Sleep swimming in the damselfish *Dascyllus marginatus* measured by video filming them in infrared light on a coral reef in Eilat, Red Sea. The stroke frequencies of the dorsal, pectoral and caudal fins are about doubled at night when the fish hide inside coral (*Stylophora pistillata*) compared to the 'normal swimming' performed outside the coral during the day. From Goldshmid et al. (Goldshmid et al., 2004). Reproduced with permission from *Limnology and Oceanography*.

fishes were seen to hide, oxygen levels between 12 and 20% of air saturation were recorded (Fig. 4), confirming that the water inside coral colonies becomes hypoxic at night.

These nocturnal surveys confirmed that fishes do reside in these hypoxic environments. For example, one coral colony (*Acropora yongei*; about 1.3 m in diameter and with a water [O₂] of about 13% between the branches), was sprayed with clove-oil to temporarily anaesthetize some of its inhabitants so that they would drift out of the coral and be positively identified. We counted 77 *Chromis viridis*, two *Pomacentrus pavo*, and one each of *Pomacentrus mollucensis*, *Dascyllus aruanus*, *Acanthochromis polyacanthus*, *Chelmon rostratus* and *Ostracion cubicus*. The first five species are damselfishes (Pomacentridae), while the latter are a butterflyfish (Chaetodontidae) and a boxfish (Ostraciidae), respectively. It was clear that these fishes only made up a fraction of the fishes hiding in this coral colony and that there may have been

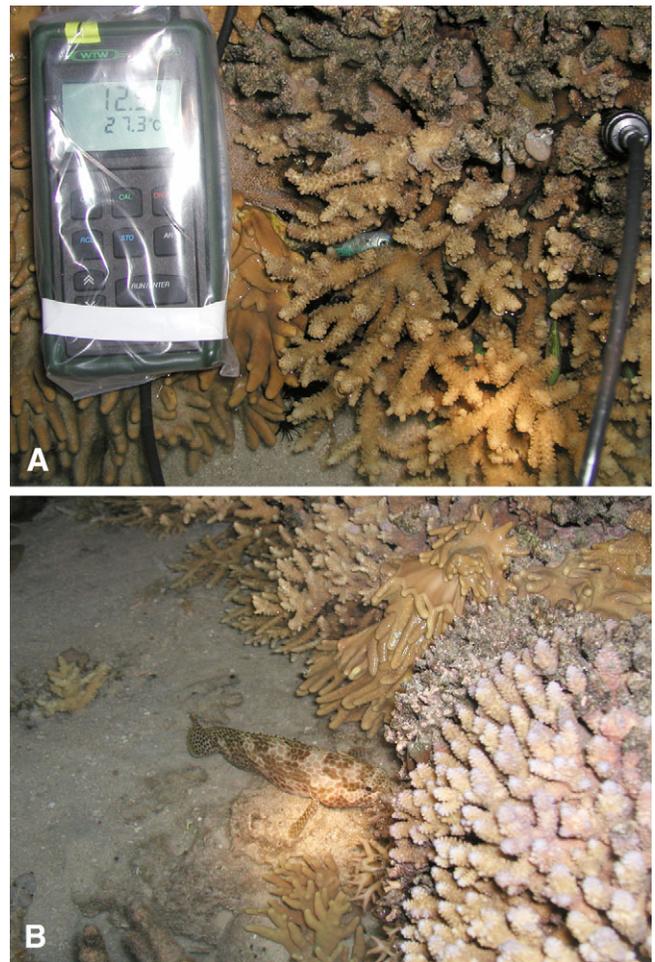


Fig. 4. (A) Fishes (*Chromis viridis*) sheltering in the hypoxic water inside a coral colony (*Acropora* sp.) on the Lizard Island reef at night during low tide. Oxygen levels between the coral branches varied between 12 and 20% of air saturation. (B) A predatory rockcod (*Epinephelus spilotoceps*) lies outside the coral and provides a good reason for the smaller fishes to use the coral as nocturnal shelter. Photo G. E. Nilsson.

hundreds of fishes residing in about 1 m² of living coral. It is probable that these fishes are sheltering in corals at night to avoid predators. This habit of hiding in coral at night has previously been described (Fishelson et al., 1974; Hixon, 1991; Holbrook and Schmitt, 2002; Goldshmid et al., 2004), and is well known to many night divers. Apparently, to use these nocturnal shelters, the fishes need the capacity to endure severely hypoxic environments.

The second scenario where coral-reef fish would experience hypoxia is through nocturnal occupation of tide pools. The stop of inflow of oceanic water combined with continued respiration and the lack of photosynthesis at night will result in tidal pools becoming hypoxic. Oxygen levels as low as 17.8% of air saturation were registered in tide pools at Low Isles (Great Barrier Reef) at nocturnal low tide (Orr, 1933). However, it has been unclear to what extent fishes remain in such hypoxic tide pools. We found the tidal pools formed at nocturnal low tides at Lizard Island to be severely hypoxic, with oxygen levels typically within the range of 8–12% of air saturation. A range of coral-reef fishes were seen occupying these hypoxic tidal pools, including surgeonfish (*Acanthurus grammoptilus*), emperors (*Lethrinus* sp.), coral bream (*Scolopsis bilineatus*), rockcod (*Epinephelus spilotoceps*), damselfishes (*Chromis viridis*, *Pomacentrus ambionensis*, *P. nagasakiensis*, *P. wardi*), butterflyfishes (*Chaetodon auriga*), wrasses (*Coris batuensis*), shrimp goby (*Amblyeleotris steinitzi*), sandperch (*Parapercis cylindrica*) and cardinalfishes (*Apogon* spp.). This appears to be a fairly random selection of coral-reef fishes, rather than a subset of species particularly well adapted to survival in tide pools. (The exceptions may be the shrimp goby and the sandperch, which both live in sand burrows on shallow water.) Thus, in addition to residing within hypoxic coral colonies at night, some coral-reef fishes also run the risk of encountering severe hypoxia when they venture into shallow water and get trapped in nocturnal tidal pools.

Further research is likely to unveil coral-reef fishes living in other hypoxic microhabitats. Many gobiids and blenniids live in sand burrows close to coral reefs, and are likely to be exposed to hypoxia in their burrow. These include *Amblygobius phalaena* (Table 1), *Asterropteryx semipunctatus* (Table 1), *Valenciennesa longipinnis* (studied by Takegaki and Nakazono, 1999) and *V. strigata* (Table 1), which all show a considerable hypoxia tolerance. Interestingly, *Amblygobius rainfordi*, which live in sandy areas but does not reside in burrows, shows the highest [O₂]_{out} of the gobiids examined (Table 1). With regard to parrotfishes (Scaridae) and wrasses (Labridae), their habit of spending the night in a mucus-cocoon or buried in the sand may lead to impaired oxygen exchange that demands hypoxia tolerance. Both wrasse species that we have examined (*Halichoeres melanurus*, which we observed burrowing in the aquarium, and *Labroides dimideatus*, which makes a cocoon at night) showed a level of hypoxia tolerance that was similar to that of most other coral reef fishes examined (Table 1).

Overall, to live on a coral reef means more or less regular encounters with hypoxia for many teleosts. As we shall see next, some may have to endure more than others.

The obligate coral-dwellers: hypoxia tolerant air breathers

It is well known that many fishes living in tropical freshwaters, estuarine habitats, or rocky intertidal zones have evolved air-breathing capacities to cope with hypoxia or air exposure (Graham, 1997; Martin and Bridges, 1999). Also recently some fishes intimately connected to living coral have been found to be excellent air-breathers. Apparently, for some fishes, it is not enough to be hypoxia tolerant to survive in a coral habitat, they also need the ability to breathe air. The need for air breathing probably does not relate to aquatic hypoxia. It appears to have evolved to allow the fishes to endure air exposure during the lowest of tides. In contrast to fishes inhabiting intertidal rocky shores, air exposure in coral dwellers is a rare event, and may only occur a few times a year during the lowest of tides.

Coral-dwelling gobies of the genera *Gobiodon* are obligate inhabitants of coral colonies, particularly species of branching *Acropora* (Munday et al., 1997). Some of these coral colonies not only become hypoxic at night (see above) but can also become air exposed during very low tides. At Lizard Island we have observed that colonies of *Acropora* can become air exposed for up to 4 h during spring tides. To test if coral-dwelling gobies can tolerate severe hypoxia and air exposure we initially focused on *Gobiodon histrio*, whose preferred coral (*Acropora nasuta*) (Munday et al., 1997; Hobbs and Munday, 2004) is often exposed to air. It was found that *G. histrio* could not only tolerate hypoxia ([O₂]_{crit} was around 19% of air saturation, Table 1), but also endured hours of air exposure (Nilsson et al., 2004). The ability to remain in the coral during periods of hypoxia and air exposure would be a distinct fitness advantage, given the risk of predation outside the coral and the potential loss of this limited habitat to other competing gobies (Munday et al., 2001; Hobbs and Munday, 2004).

Air-breathing ability and habitat choice

To determine if the hypoxia tolerance and air breathing abilities observed in *G. histrio* are indicative of all obligate coral-dwelling fishes, we repeated the same experiments on a range of species. These obligate coral-dwelling species included coral gobies of the genera *Paragobiodon* and *Gobiodon*, as well as the coral croucher (also known as velvetfish; *Caracanthus unipinna*, family Scorpaenidae) (Fig. 5). Preferences for host coral species (Lassig, 1976; Munday et al., 1997; Wong et al., 2005) may overlap and preferred corals are often a limiting resource, resulting in intense intra- and interspecific competition (Munday et al., 2001; Hobbs and Munday, 2004). Therefore, tolerance to hypoxia and the ability to breathe air would be adaptive in this habitat. However, these coral dwellers vary in their preference for coral species, water depth and reluctance to leave their host coral. Some of them inhabit coral species that occur in shallow water where they will become air exposed for several hours at the lowest tides, whereas others live in coral species that occur in slightly deeper water and never become air exposed.

By using closed respirometry to compare hypoxia tolerance

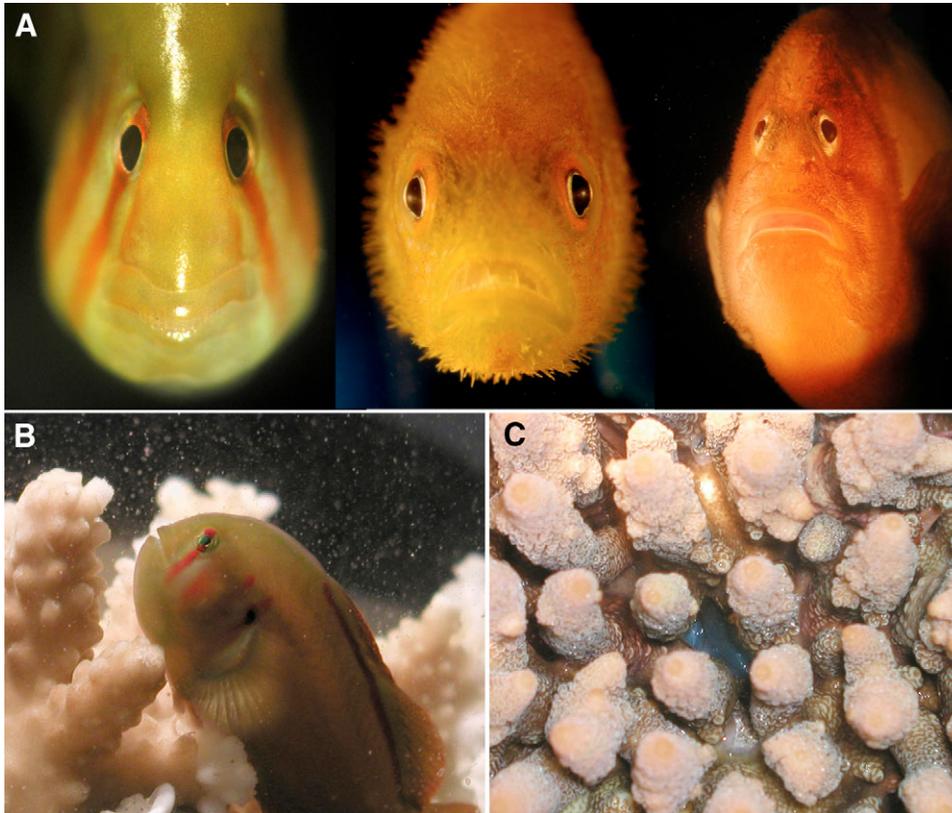


Fig. 5. Obligate coral dwellers represented by *Gobiodon axillaris* (A, left, B), *Paragobiodon xanthosomus* (A, middle), *Caracanthus unipinna* (A, right), and *Gobiodon histrio* (C). These fishes spend virtually their whole life between branches of coral, and show a high degree of hypoxia tolerance. Moreover, *G. axillaris*, *G. histrio* and *C. unipinna* have excellent abilities for air breathing, apparently through their scaleless skin. Air breathing is needed if their coral home becomes air exposed. C shows *G. histrio* in a coral colony that has become air exposed during a nocturnal low tide at the Lizard Island reef. Photos by G. E. Nilsson.

and air-breathing capacity among *Paragobiodon xanthosomus*, *Caracanthus unipinna* and seven species of *Gobiodon* we found a significant variation in hypoxia tolerance, and that air-breathing ability was correlated with habitat use (Nilsson et al., 2007a). The four *Gobiodon* species (*G. axillaris*, *G. erythrospilus*, *G. histrio* and *G. unicolor*) that inhabit *Acropora* corals, which often occur in shallow water where they may become air exposed at low tide, were all found to be excellent air breathers. Also *C. unipinna*, which live in *Acropora* and *Pocillopora* species that extend into shallow water, showed an equally good air-breathing capacity. By contrast, *Gobiodon acicularis* and *G. ceramensis*, which occupy corals of the genera *Echinopora*, *Hydnophora* and *Stylophora* that do not usually become air exposed, could only maintain oxygen uptake from air for short periods (an hour or less). Also *G. okinawae*, which deviates from other *Gobiodon* by often venturing relatively far from the host coral, and probably leaving it during air exposure, was found to be a poor air breather. Finally, *Paragobiodon xanthosomus*, which inhabits *Seriatopora hystrix* in areas that do not usually become air exposed, was unable to take up oxygen from air.

Cutaneous air-breathing and toxin production

For the coral dwellers, the results suggested that oxygen uptake in air occurs primarily through the skin, which is scaleless in both *Gobiodon* and *Caracanthus* (Nilsson et al., 2007a). This conclusion is based on the observation of a 50% fall in the rate of oxygen uptake when one body half of the fish

was stuck to the wall of the respirometer. Moreover, oxygen uptake was found to be maintained even if ventilatory movements stopped in some individuals, indicating that oxygen uptake over the gills or oral mucosa were of minor importance. In the five best air breathers (*G. axillaris*, *G. erythrospilus*, *G. histrio*, *G. unicolor* and *C. unipinna*), the rate of oxygen uptake was similar in water and in air and could continue in air for at least 4 h, which corresponds to the longest periods that their coral hosts may be air exposed around Lizard Island. It was striking that the unrelated genera *Gobiodon* and *Caracanthus* were found to have a similar capacity for air breathing, most likely taking up the oxygen through their scaleless skin, while *Paragobiodon*, a close relative to *Gobiodon*, has retained its scales and is unable to breathe air. Martin and Bridges (Martin and Bridges, 1999) suggested that for the skin to function as a respiratory organ in fish, it must be relatively free of scales or other obstructions. Our finding on the air-breathing abilities of the scaleless *Gobiodon*, *contra* the closely related scaled *Paragobiodon*, certainly supports this view, but being scaleless is apparently not a pre-requisite for air-breathing in all fishes since a well vascularised epidermis can be present outside the scales (Feder and Burggren, 1985).

It can be concluded that a high capacity for air breathing has evolved at least twice in coral-dwelling fishes, and at least in the gobies, this is probably a relatively late evolutionary event that probably involve the loss of scales. In contrast to air-breathing fishes in freshwater habitats, marine air-breathing fishes occupying intertidal zones have generally not evolved specialized air-breathing organs (Graham, 1976; Graham,

1997). Similarly, except for the loss of scales, specialized organs for oxygen uptake in air appear to be lacking in the obligate coral dwellers.

While a scaleless skin probably improves cutaneous gas exchange, it is also likely to make the fish particularly vulnerable to ectoparasites. The species of the genus *Gobiodon* secrete a toxic mucus through glands in their skin. This mucus is highly toxic to other fish attempting to eat them, indicating a function in predator avoidance (Schubert et al., 2003). However, the scaled skin of *Paragobiodon* does not contain toxin glands, which has led to the speculation that the toxin secreted through glands in the scaleless skin of *Gobiodon* may be aimed at fighting off cutaneous parasites. Indeed, a study has suggested that the scales of *Paragobiodon* and the toxin of *Gobiodon* are equally effective in fighting off ectoparasites, since exposing these gobies to gnathiid isopods leads to similar infection rates in both genera (Munday et al., 2003). Interestingly, the same study showed that in *Gobiodon*, body regions with fewer toxin glands were more vulnerable to these ectoparasites. Thus, in *Gobiodon*, evolving a capacity for cutaneous air breathing may have triggered the evolution of toxin glands to protect the scaleless skin from parasites.

Close association with coral correlate with hypoxia tolerance

The nine species of obligate coral-dwelling fish studied (Nilsson et al., 2007a) were found to have an average $[O_2]_{crit}$ of 20.4%, and did not show any signs of distress until the ambient oxygen level fell to 3% of air saturation, with two species doing well down to 1% of air saturation (genera *Gobiodon*, *Paragobiodon* and *Caracanthus* in Table 1). These values revealed a significantly higher degree of hypoxia tolerance than that of coral-reef fish with a somewhat less intimate connection with living coral (fishes of the families Apogonidae, Labridae, Monacanthidae, Nemipteridae, and Pomacentridae). Thus, an obligate association with living coral appears to demand a particularly well developed tolerance to hypoxia. As mentioned, measurements of nocturnal oxygen levels between branches in *A. nasuta* colonies inhabited by *Gobiodon* show that these may fall well below 20% of air saturation (even as low as 2% for short periods) (Fig. 2). A physiological heritage allowing a high degree of hypoxia tolerance may have been a prerequisite for these gobiids and scorpaenids to acquire an obligate coral-dwelling life style. This is suggested by the particularly well developed hypoxia tolerance (low $[O_2]_{crit}$ and $[O_2]_{out}$ values) shown by other members of these two families that live in reef habitats but do not show such a close association with living coral (exemplified by genera *Amblygobius*, *Asterropteryx*, *Valenciennea*, *Parascorpaena* and *Sebastapistes* in Table 1).

Hyperoxia – an additional challenge?

Coral-reef fishes may not only need physiological adaptations that enable them to utilize a hypoxic and air

exposed environment. They may also have to tolerate very high oxygen levels (hyperoxia) in the daytime due to oxygen produced by various plants and algae, including the coral's symbiotic photosynthesizing algae (zooxanthellae). Oxygen levels as high as 278% of air saturation were measured in enclosed areas rich in coral at Low Isles (Great Barrier Reef) (Orr, 1933). Similarly, between the branches of *A. nasuta* colonies kept in sun-exposed outdoor tanks on Lizard Island, we measured supersaturated oxygen levels around 200% of air saturation during the middle of the day (G.E.N., J.-P.A.H. and S.Ö.N., unpublished observation). These corals were inhabited by *Gobiodon* species, suggesting that hyperoxia is a factor that these coral dwellers have to cope with. High levels of oxygen can be a challenge for fish, since it may cause cellular damage through the formation of reactive oxygen species (reviewed by Lushchak and Bagnyukova, 2006). It appears that the life of these coral dwellers, from a respiratory point of view, is in some aspects similar to that of many marine tide-pool fishes, which are also exposed to highly variable oxygen levels (Truchot and Duhamel-Jouve, 1980). Whether coral-dwelling fishes have particularly well developed mechanisms for counteracting oxygen induced damage remains to be explored.

Tackling hypoxia with a mouth full of eggs

Cardinalfishes (Apogonidae), a species-rich family on coral reefs, are faced with a particular respiratory challenge. All species of this family are mouthbrooders, and it is always the males that take care of this task. They keep the brood in their mouth for about 2 weeks after fertilization (Fig. 6A). This egg mass can make up a quarter of the male's body mass (Östlund-Nilsson and Nilsson, 2004), and it is virtually filling up his whole oral cavity, which constitutes about 20–30% of the body volume and is significantly larger in males compared to females (Barnett and Bellwood, 2005). There is a central channel in the egg mass, rendering it doughnut shaped (Fig. 6B). This channel probably serves to let some water through to the gills, and aides in the ventilation of the gills as well as the egg clutch. Still, one may assume that the egg mass will reduce the ability of the fish to ventilate its gills, which could be a problem when they face hypoxia at night. Moreover a reduced ability to ventilate the gills could affect the capacity for sustained aerobic swimming.

We compared the respiratory consequences of mouthbrooding in two *Apogon* species occurring at Lizard Island: the fragile cardinalfish (*A. fragilis*) and the longspine cardinalfish (*A. leptacanthus*) (Östlund-Nilsson and Nilsson, 2004). The resting metabolic rate was not significantly affected by the presence of the egg clutch in the mouth (if the oxygen consumption of the clutch itself was accounted for). By contrast, $[O_2]_{crit}$ of the mouthbrooding males was increased, being about 32% of air saturation, as compared to 18% in non-brooding males or females. Thus, their hypoxia tolerance was clearly reduced by having the mouth full of eggs. Moreover, their ability for sustained aerobic swimming was also diminished: while non-mouthbrooding males of *A.*

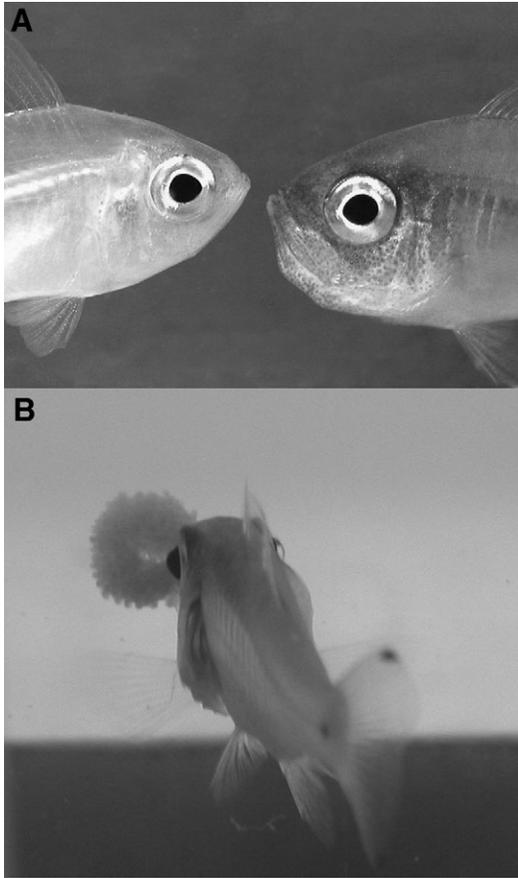


Fig. 6. A female (A, left) and male (A, right) of the cardinalfish *Apogon leptacanthus*. The male is mouthbrooding, as revealed by its expanded lower jaw. The egg mass of this species makes up about 14% of the body mass of the male, and constitutes a considerable respiratory obstacle. (B) A male of *Apogon fragilis* spitting his brood when exposed to hypoxia in a closed respirometer, thereby significantly increasing his ability to take up oxygen. Photos by G. E. Nilsson.

leptacanthus could maintain a maximal aerobic swimming speed of 5.1 BL s^{-1} (where BL is body length), the same value for mouthbrooding males was reduced to 3.5 BL s^{-1} . By contrast, the time that the males could swim anaerobically against water moving at speed of 14 BL s^{-1} was not affected by mouthbrooding, both groups being able to do this for about 50 s (Östlund-Nilsson and Nilsson, 2004). Of course, there is no obvious reason to expect that anaerobic capacity would be significantly affected by having eggs in the mouth.

The two species studied were found to differ in the mean brood mass, with males of *A. fragilis* and *A. leptacanthus* having broods that corresponded to 20% and 14% of the body mass, respectively. This difference clearly affected their performance in hypoxia. When faced with a continuous decrease in the ambient oxygen level in the closed respirometer, both species eventually spat out the clutch (Fig. 6B), thereby sacrificing their offspring while significantly increasing their ability to take up oxygen (i.e. increasing their

own chance of hypoxic survival). However, in *A. fragilis* (the species with the larger egg mass), the brood spitting occurred at a less severe level of hypoxia, 22% of air saturation, compared to *A. leptacanthus*, which spat out the eggs at 13% of air saturation. Moreover, while mouthbrooding *A. leptacanthus* were able to increase their ventilatory frequency in response to a falling ambient oxygen level, mouthbrooding *A. fragilis* were already performing at their maximal ventilatory rate during normoxic conditions. These results clearly indicate a trade-off situation between brood size and hypoxia tolerance. Being able to successfully brood a larger clutch should mean a correspondingly larger increase in fitness. *A. fragilis* appears to be gambling on a brooding period without any severely hypoxic episodes, attempting to maximize the fitness gained from each brood, while *A. leptacanthus* does not take this risk. Interestingly, both species occur in the same habitat at daytime, often schooling together, which suggest that these different strategies are not the result of different environmental constraints in the preferred habitat. However, we do not presently know how the different mouthbrooding strategies correlate with their nocturnal habits.

Ontogeny and respiration: from record swimmers to hypoxia tolerance

Most coral-reef fishes have planktonic larvae (Thresher, 1984). Thus, after hatching, their larvae spend a few weeks drifting in the open water before they settle on the reef. Research in the last decade has revealed that coral-reef fish larvae develop very impressive capacities for high-speed sustained swimming (i.e. for hours or even days) at the end of their pelagic phase when they need to reach and settle on suitable coral habitats (Stobutzki and Bellwood, 1994; Leis and Carson-Ewart, 1997; Pain, 1997; Fisher et al., 2005). Indeed, coral-reef fish larvae may have more influence on their movement and distribution in the ocean than previously assumed (Leis, 2006).

Many of the late stage pre-settlement larvae are capable of reaching maximal sustained swimming speeds (U_{crit}) of $30\text{--}50 \text{ BL s}^{-1}$ (Stobutzki and Bellwood, 1994; Leis and Carson-Ewart, 1997; Fisher et al., 2005). To put this into perspective, it can be mentioned that larvae of temperate fishes do not usually reach a U_{crit} higher than $4\text{--}5 \text{ BL s}^{-1}$ (Blaxter, 1986; Meng, 1993). Similarly, most adult fishes, including salmonids, cannot attain higher sustained swimming speeds than $5\text{--}7 \text{ BL s}^{-1}$. In fact, not even the fishes best known for exceptional swimming performance, including swordfish (*Xiphias*), tunas (*Thunnus* and *Euthynnus*), and the inconnu (*Stenodus leucichthys*), which can reach maximal sustained speeds of $12\text{--}20 \text{ BL s}^{-1}$ (Aleyev, 1977; Beamish, 1978), come close to the swimming performance of many coral-reef fish larvae. Scaling can be used to explain the extraordinary swimming performance of coral-reef fish larvae. It appears that the smaller a fish is, the faster it can swim in relation to body size (i.e. in BL s^{-1}). However, this relationship only exists for fish that have developed a capacity for forceful swimming, and

coral-reef fish larvae are probably the smallest fishes that have such capacities (Bellwood and Fisher, 2001).

Swimming can only be sustained if it is fully aerobic and does not lead to a build up of lactate (Goolish, 1991). Therefore, one may assume that the extremely high, sustained (and therefore aerobic) swimming speeds of coral-reef fish larvae must require very high rates of maximum oxygen uptake ($\dot{M}_{O_{2max}}$). We recently constructed a miniature swim respirometer that allowed us to measure $\dot{M}_{O_{2max}}$ during high-speed swimming in larvae and juveniles of two species of damselfish, *Chromis atripectoralis* and *Pomacentrus ambionensis* (Nilsson et al., 2007b). Our results showed that pre-settlement larvae of *C. atripectoralis* and *P. ambionensis*, swimming at maximal sustained speeds, reach $\dot{M}_{O_{2max}}$ values of about 5000 and 4000 mg O₂ kg⁻¹ h⁻¹, respectively, which to our knowledge is the highest $\dot{M}_{O_{2max}}$ values ever measured in cold-blooded vertebrates.

C. atripectoralis is one of the fastest swimming coral-reef fish larvae both in nature and in laboratory race tracks. Thus, Leis and Carson-Ewart (Leis and Carson-Ewart, 1997), who had divers swim after released coral-reef fish larvae in nature, found that pre-settlement larvae of damselfish have some of the highest maximum sustained swimming speeds. The 17 damselfish species they examined reached an average maximum speed of 34 BL s⁻¹, with the 10 mm long *C. atripectoralis* larvae being the fastest swimmers observed, reaching maximal *in situ* swimming speeds of 53 BL s⁻¹. Similar results have later been obtained in swim tunnels (Fisher et al., 2005), although it appears that mean U_{crit} values are generally a bit higher than the average speeds seen *in situ*. Still, observations of spontaneous swimming of pre-settlement larvae suggest that they are almost constantly swimming at high speeds, although they rarely swim at their U_{crit} (Fisher and Bellwood, 2003). In comparison with *C. atripectoralis*, *P. ambionensis* is a more average performer among pre-settlement larvae, with a U_{crit} of about of 30 BL s⁻¹ (Stobutzki and Bellwood, 1994).

We also carried out comparative measurements of $\dot{M}_{O_{2max}}$ in *Acanthochromis polyacanthus*, which is one of very few coral-reef damselfishes showing parental care, thus lacking a planktonic larval stage (Randall et al., 1997). The $\dot{M}_{O_{2max}}$ of resident *A. polyacanthus* juveniles weighing 30 mg, corresponding to the pre-settlement size of other damselfishes, was about 2000 mg O₂ kg⁻¹ h⁻¹, which was significantly lower than the $\dot{M}_{O_{2max}}$ of 4000–5000 mg O₂ kg⁻¹ h⁻¹ that we measured in *C. atripectoralis* and *P. ambionensis* (Nilsson et al., 2007b). This low $\dot{M}_{O_{2max}}$ in juvenile *A. polyacanthus* coincides with a comparatively poor swimming performance of these juveniles, which at a size that is equivalent to pre-settlement larvae of other damselfishes, only reach a U_{crit} of 12 BL s⁻¹ (Fisher et al., 2005).

We may conclude that the extraordinarily high, sustained swimming speeds of pre-settlement damselfish larvae are paralleled by extraordinarily high capacities for rapid oxygen uptake, and that these traits are important because they enable the larvae to reach a suitable reef at the end of their planktonic period. However, high aerobic capacities of very active fish

species appear to preclude hypoxia tolerance, and *vice versa* (for a review, see Burggren et al., 1991). Thus, fishes with highly active life styles and top swimming performance cannot tolerate low oxygen levels. Salmonids, for example, display $[O_2]_{crit}$ values around 50% of air saturation (Davis, 1975), and tuna die when water $[O_2]$ falls below 60% of air saturation (Gooding et al., 1981). The underlying reasons are probably the opposing demands that a high $\dot{M}_{O_{2max}}$ and hypoxia tolerance put on the oxygen-carrying properties of haemoglobin. Oxygen uptake in hypoxia require haemoglobins with high O₂ affinities, which leads to relatively low rates of O₂ downloading in the tissues (O₂ has to be downloaded at a low partial pressure, leading to a small pressure gradient from blood into the mitochondria and therefore a slow O₂ delivery). Therefore, haemoglobins of highly active fish show lower O₂ affinities than those of sedentary species (reviewed by Burggren et al., 1991).

As discussed earlier, coral-reef fishes probably need to cope with hypoxia when they shelter in corals at night to avoid predators. An obvious question therefore is: have coral-reef fishes found a unique way to combine extremely high rates of oxygen uptake with hypoxia tolerance? Or, could it be that they change their respiratory performance when they settle on the reef?

To answer these questions, we measured $[O_2]_{crit}$ and $\dot{M}_{O_{2max}}$ with closed respirometry in pre-settlement larvae, post-settlement larvae, and juveniles of *C. atripectoralis* and *P. ambionensis*, as well as in juvenile *A. polyacanthus* of different sizes (Nilsson et al., 2007b). For the two species with planktonic larvae, the results revealed a striking, almost transient, reduction in $\dot{M}_{O_{2max}}$ and $[O_2]_{crit}$ within the first 5–10 days of settlement, which is illustrated by data for *C. atripectoralis* in Fig. 7. Thus, upon settlement, larval *C. atripectoralis* and *P. ambionensis* adjust their respiratory capacities to increase their hypoxia tolerance at the expense of rapid oxygen uptake. Our results indicate that it takes about a week for the settled larvae to attain low $[O_2]_{crit}$ values, and that high anaerobic capacities allow them to survive hypoxic episodes during this period. Measurements of U_{crit} in two species of developing damselfish (*P. ambionensis* and the clown-fish *Amphiprion melanopus*) also reveal a transient drop in swimming capacity when the fishes reach settlement size (Bellwood and Fisher, 2001) (Fig. 8). Thus, after settlement, these fishes are no longer exceptionally fast swimmers with high $\dot{M}_{O_{2max}}$ values, but instead become hypoxia-tolerant fishes that can utilize the shelter provided by coral colonies at night.

At present, we can only hypothesize on the mechanisms responsible for the rapid change in respiratory properties displayed by settling coral-reef fish larvae. An obvious possibility is that the transition involves changes in blood oxygen affinity. Many fishes are known to possess multiple haemoglobin isoforms, and there are examples of ontogenetic changes in haemoglobin isoform expression in fishes (reviewed by Jensen et al., 1998). Thus, when fish larvae settle on a coral reef, they may change the expression of haemoglobin isoforms to types with higher O₂ affinity that allow hypoxia tolerance at

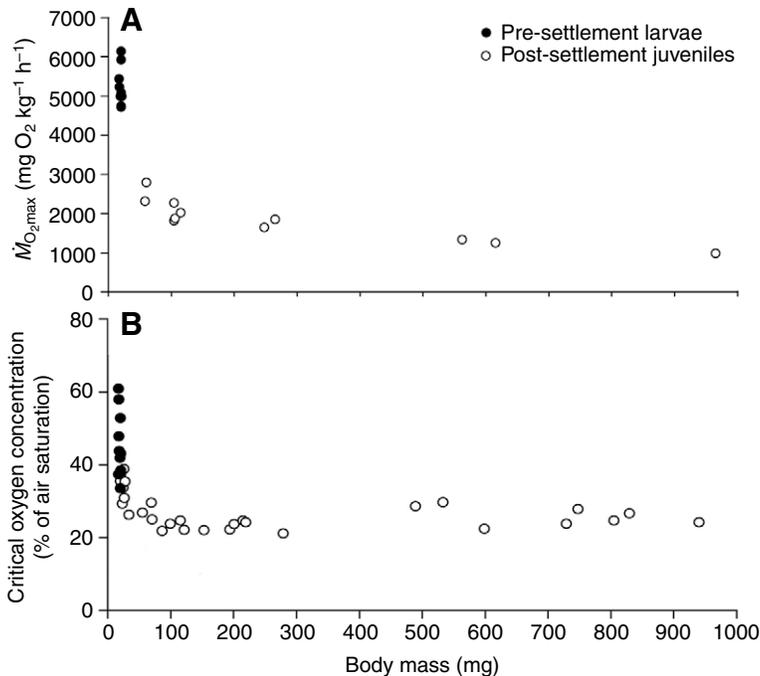


Fig. 7. Coral-reef fish larvae need to make a transition from top swimming performance to hypoxia tolerance when they settle on a reef. Relationship between body mass and (A) oxygen consumption at maximal swimming speed, and (B) hypoxia tolerance (measured as $[O_2]_{crit}$) in larvae and juveniles of *Chromis atripectoralis*. Note the transient drop in maximum oxygen uptake and simultaneous increase in hypoxia tolerance (seen as a drop in $[O_2]_{crit}$) that occur when the larvae settle on the reef and become post-settlement juveniles. Data from Nilsson et al. (Nilsson et al., 2007b).

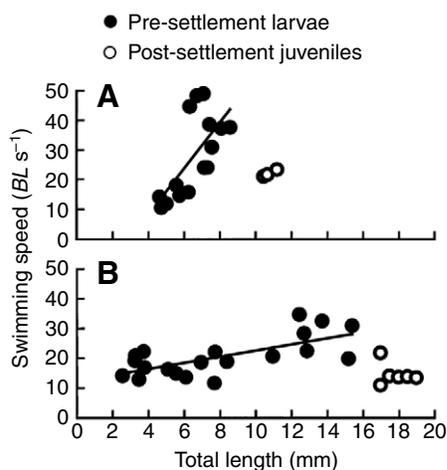


Fig. 8. Transient fall in maximum sustained swimming speed (U_{crit}) when post-settlement size is reached in two species of damselfish, *Amphiprion melanopus* (A) and *Pomacentrus ambionensis* (B). The fishes were reared in the laboratory and tested in a swimming flume. From Bellwood and Fisher (Bellwood and Fisher, 2001). Reproduced with permission from *Marine Ecology Progress Series*.

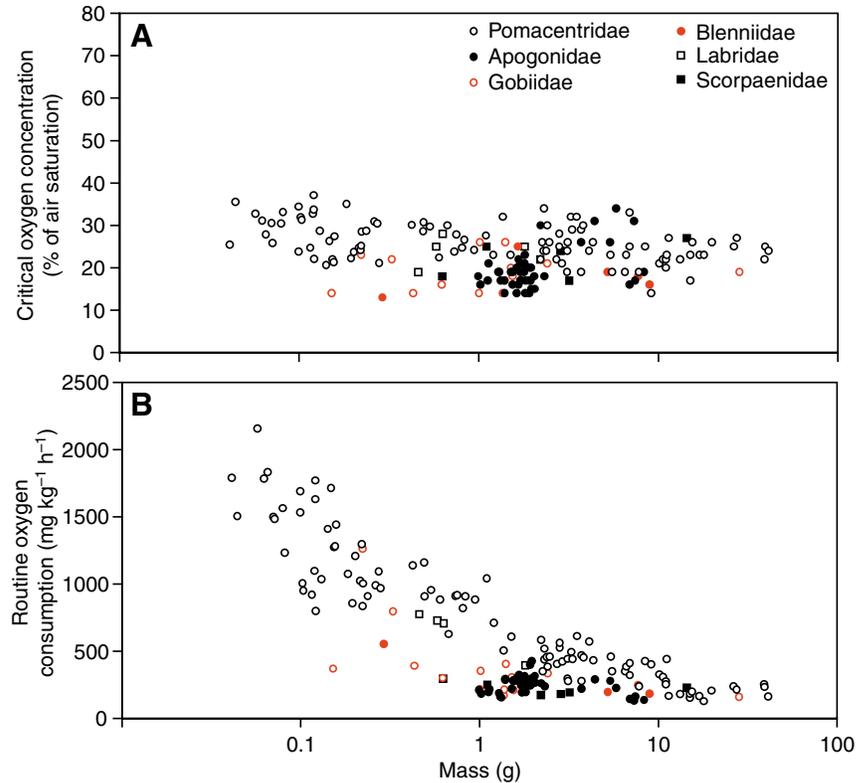
the expense of fast O_2 downloading in the tissues. Unfortunately, the small size of the larvae (generally less than 50 mg) would preclude a study of haemoglobin's oxygen binding properties and isoform expression pattern using electrophoresis, but it may be possible to measure changes in mRNA expression of haemoglobin isoforms using quantitative PCR.

Body size and hypoxia tolerance

After the transition to hypoxia tolerance has occurred upon settling on the reef, coral-reef fishes maintain a steady level of hypoxia tolerance throughout life, as seen from the lack of any change in $[O_2]_{crit}$ with size in juvenile and adult fishes from the Lizard Island reef (Fig. 9A). This suggests that the level of hypoxia tolerance needed is constant throughout life. This is not unexpected since they probably continue to use the coral colonies as shelter after settlement, and may also continue to run the risk of being temporarily confined in nocturnal tide pools. Nevertheless, the role of size in hypoxia tolerance is not an uncontroversial issue. Fig. 9B shows that in coral-reef fishes (like in all organisms) mass-specific metabolic rate (measured as routine rate of oxygen consumption) falls as body size increases. An adult coral-reef fish has a mass-specific rate of oxygen consumption that is about 10% of what it had when it settled on the reef (Nilsson and Östlund-Nilsson, 2004; Nilsson et al., 2007b). Arguably, because adults need that much less oxygen, acquiring a low $[O_2]_{crit}$ should be less of a challenge for adults than for juveniles.

Thus, life in hypoxia may become relatively easy as coral-reef fishes reach adult size. In the hypoxia-tolerant oscar cichlid of the Amazon river system, large individuals do indeed show a lower $[O_2]_{crit}$ (about 30% of air saturation) than smaller ones (near 50% of air saturation) (Sloman et al., 2006). On the other hand, it has been argued that the scaling of respiratory factors such as gill-surface area and branching of blood vessels should make smaller individuals more hypoxia tolerant than larger ones (e.g. Robb and Abrahams, 2003), and a higher degree of hypoxia tolerance in small individuals has been seen in some fish species (Burlison et al., 2001; Robb and Abrahams, 2003). Still, one may expect that the degree of hypoxia tolerance displayed by a fish reflects its need for survival under hypoxic conditions, rather than being a factor that passively follows scaling relationships. Thus, the prime reason why coral-reef fishes (at least those represented in Fig. 9) maintain a constant level of hypoxia tolerance once they have settled on the reef, is probably that the hypoxic environment inside coral colonies continues to be an important nocturnal refuge from predators. At present we have no $[O_2]_{crit}$ measurements on coral-reef teleosts larger than 40 g, but one may expect that larger fishes in this habitat are also hypoxia tolerant. As mentioned above, at nocturnal low tides we have observed rockcods and emperors,

Fig. 9. Relationship between body mass and (A) hypoxia tolerance (critical oxygen concentration), and (B) metabolic rate (routine oxygen consumption) in juvenile and adult coral-reef fishes (excluding pre-settlement larvae). Note that while hypoxia tolerance does not change with body mass, metabolic rate shows the 'classical' scaling relationship with body mass. The dataset includes 174 individuals weighing between 40 mg and 40 g and representing 35 species from six families, and is largely the same as that presented in Table 1 [mostly from Nilsson and Östlund-Nilsson (Nilsson and Östlund-Nilsson, 2004), with additional individuals from Östlund-Nilsson and Nilsson (Östlund-Nilsson and Nilsson, 2004) and Nilsson et al. (Nilsson et al., 2007b)]. For the whole dataset, the mass-specific metabolic rate was related to $\text{mass}^{-0.367}$ (which translates into a scaling exponent of $1-0.367=0.633$ for absolute metabolic rate; $r=0.80$). For the best represented family, Pomacentridae with 99 individuals from 14 species, the same scaling exponents were -0.347 (mass-specific metabolic rate) and 0.653 (absolute metabolic rate) ($r=0.94$). Temperature was 28–30°C.



weighing a few hundred grams, trapped in shallow hypoxic tide pools with oxygen levels around 10% of air saturation. Thus, fishes of all sizes that stay in shallow water on coral reefs, even if they do not reside inside coral colonies, probably have to be quite hypoxia tolerant.

Conclusions

Nocturnal hypoxia is probably a ubiquitous phenomenon on coral reefs, and recent studies indicate that hypoxia tolerance is widespread among coral-reef teleosts. While many coral-reef fishes spend their day in the well-oxygenated water above the coral, they may encounter hypoxia as they shelter in the coral at night, probably to avoid nocturnal predators. Coral-reef fishes may also experience hypoxia if they get trapped in temporary pools formed during nocturnal low tides. The combination of a cessation of photosynthesis and a lack of water movements can in both cases make these habitats severely hypoxic. In the field as well as in the laboratory, oxygen levels have been found to fall below 20% of air saturation in these situations.

Studies on obligate coral dwellers (coral gobies and coral crouchers) show that an intimate connection with coral demands a particularly well-developed hypoxia tolerance, and in several cases also a capacity for air breathing, as the coral colonies that they inhabit may become fully air exposed at low tides. It appears that these fishes are able to maintain oxygen uptake in air mainly *via* cutaneous respiration.

The reproductive modes of some reef fishes may impose additional demands on the respiratory systems. When male

cardinalfishes are mouthbrooding, this clearly affects both their hypoxia tolerance and the capacity for sustained aerobic swimming. These males are confronted with a trade-off situation between hypoxia tolerance and brood size.

The planktonic larvae produced by most coral-reef fishes are faced with having to rapidly change their respiratory properties when settling on the reef. From being the fastest swimmers of all fish, with record high rates of oxygen uptake, they have to become hypoxia tolerant upon settlement, so that they can seek shelter in coral colonies at night to avoid predators. After settlement, coral-reef teleosts retain about the same degree of hypoxia tolerance throughout life. Thus, the ability for oxygen uptake in hypoxia appears to be size-independent in fishes inhabiting coral reefs.

Fishes living on coral reefs have been suggested to form the most diverse vertebrate community in the world (Jones et al., 2002). In this habitat, oxygen availability is clearly a major ambient selection pressure, making respiratory function a key factor for survival on coral reefs. We can be certain that a wealth of respiratory adaptations remain to be discovered among coral-reef fishes. Presently, we have only a rudimentary understanding of how oxygen shapes coral-reef habitats and of hypoxia adaptations in coral-reef inhabitants. The need for more knowledge does not only apply to fishes, and not only to respiration, so the scope for future physiological research on coral reefs is broad.

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