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Intragel oxygen promotes hypoxia tolerance of scyphomedusae

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Summary

Populations of jellyfish are known to thrive in many low oxygen environments, however, the physiological mechanisms that permit these organisms to live in hypoxia remain unknown. The oxyregulatory abilities of four species of scyphomedusae were investigated, and it was found that *Aurelia labiata, Phacellophora camtschatica, Cyanea capillata* and *Chrysaora quinquecirrha* maintain steady oxygen consumption to below 20 hPa oxygen (<10% air saturation). Oxygen content of the mesoglea of *A. labiata* was measured using a fibre optic oxygen optode, and oxygen profiles through the gel are characterised by a gradient that decreases from just below normoxia at the aboral subsurface to ~85% air saturation near the subumbrellar musculature. This gradient sustains oxyregulation by scyphomedusae, and it is demonstrated that *A. labiata* must be using intragel oxygen to meet its metabolic needs. Gel can also be used as an oxygen reservoir when *A. labiata* moves into hypoxia. Gel oxygen is depleted after about 2 h in anoxia and recovers to 70% of normal after 2.5 h in normoxia. Behaviour experiments in the laboratory showed that *Aurelia labiata* behaves similarly in normoxia and hypoxia (30% and 18% air saturation). The acute threshold for provoking behavioural changes in *A. labiata* is somewhere near its critical partial pressure, and oxygen stratification stimulates swimming back and forth across the oxycline. Intragel oxygen dynamics are recognised as a fundamental component of medusan physiology.

Key words: critical partial pressure, gel, hypoxia, jellyfish, metabolic rate, oxyregulation, scyphomedusae.

Introduction

An emerging paradigm in marine science is the elastic ability of gelatinous zooplankton to dominate in stressed marine environments, and several studies have raised the possibility that gelatinous zooplankton populations are increasing worldwide (CIESM, 2001; Mills, 2001). Possible explanations for this phenomenon include increased ecological space due to overfishing (Brodeur et al., 2002; Gücü, 2002), introductions of exotic species (Kideys, 1994; Graham et al., 2003), and climatic changes (Lynam et al., 2004). Gelatinous zooplankton populations also appear to be increasing due to increased eutrophication resulting in hypoxia (Keister et al., 2000; Arai, 2001; Purcell et al., 2001). Scyphomedusae are known to be present in waters with very low oxygen concentrations and in some cases anoxic waters (Mackie and Mills, 1983; Thuesen and Childress, 1994; Benović et al., 2000; Kideys and Romanova, 2001; Purcell et al., 2001; Dawson and Hamner, 2003), but the physiological mechanisms that allow jellyfish with no specialised oxygen uptake systems to thrive in low oxygen environments remain unknown.

Pelagic organisms such as shrimps, cephalopods and fishes that can easily move in and out of low oxygen conditions typically tolerate hypoxia through primarily aerobic metabolic adaptations (Childress and Seibel, 1998), therefore the existing paradigm suggests that estuarine medusae should also live in hypoxia through aerobic adaptations. A study on the enzymatic activities of medusae found that both hydromedusae and scyphomedusae lack several of the -opine dehydrogenases, suggesting they lack much anaerobic capacity (Thuesen and Childress, 1994). These enzymes are typically used by invertebrates when tolerating low oxygen conditions (Hochachka and Somero, 2002) and are present in sea anemones (Walsh, 1981) that experience episodic night-time hypoxia in tide pools. To investigate the hypothesis that medusae live in hypoxia by means of aerobic adaptations, we measured the mass-specific oxygen consumption rate ($\dot{V}_{O_2}$) under declining oxygen concentrations and determined the critical partial pressure of oxygen (P_{crit}) on *Aurelia labiata* and three other species of scyphomedusae. Measurements of intragel oxygen content were taken to begin elucidating the role of gelatinous tissue in medusan physiology, and laboratory experiments were conducted to determine the influence of oxygen conditions on the behaviour of *A. labiata*.

Materials and methods

Specimens

All specimens of *Aurelia labiata* Chamisso and Eysenhardt 1821, *Phacellophora camtschatica* Brandt 1838 and *Cyanea capillata* (L.) were hand-dipped from southern Puget Sound, USA using 1- or 2-litre containers. *Chrysaora quinquecirrha* (Desor 1848) was collected from the dock at the Academy of Natural Sciences Estuarine Research Center in western Chesapeake Bay, USA. Specimens were transported to the laboratory and maintained individually in 1-litre containers of filtered seawater (FSW, 10 μm filter). Specimens were maintained at 10°C and 30 psu, except for *C. quinquecirrha*, which was kept at 25°C and 12 psu. If necessary, salinity was adjusted using Instant Ocean® aquarium salts or deionized water. These temperature and salinity conditions were also used in the respiration experiments described below.

Oxygen measurements

Oxygen measurements made during experiments on *C. quinquecirrha* from Chesapeake Bay used a PreSens Microx 8 oxygen meter (Precision Sensing, GmbH, Germany); however, all other oxygen measurements in this study were made using a fibre optic oxygen optode connected to a PreSens Microx TX3 temperature-compensated oxygen meter (Precision Sensing, GmbH, Germany). Type B2-NTH optodes were housed in 80 mm stainless steel needles. Optical fibres had probe tips ~55 μm in diameter. Respiration experiments were carried out in glass chambers containing FSW (0.2 μm filter, containing 50 mg each of streptomycin and ampicillin) and kept in the dark at a constant temperature on an orbital shaker at 85 r.p.m. to facilitate mixing in the respiration chambers. Experiments were continued until specimens exhausted all of the oxygen in the respirometry chamber or had ceased to consume oxygen. For intragel oxygen profiles, specimens of *A. labiata* were harnessed to paraffin platforms in open chambers of well-stirred FSW (10 μm filter) using dome-shaped harnesses constructed of tempered 0.222 mm nylon netting. Oxygen optodes were inserted through a 1 cm circular opening in the top of the harness using a Narishige, Tokyo, Japan micromanipulator while viewing specimens under a dissecting microscope. Intragel oxygen measurements on unharnessed specimens were also taken at the surface of open cylindrical tanks under five oxygen conditions: normoxia, hypoxia (30% air saturation), anoxia (for 1 h and 2 h) and anoxia followed by a recovery period (2 h in anoxia followed by 2.5 h in normoxia). Specimens were allowed to swim freely during the incubation period; afterwards, optodes were inserted by hand into specimens restrained against the clear acrylic tanks until oxygen measurements stabilised (~1 min). Oxygen measurements were made in three easily replicated locations: the aboral subsurface gel, the mid-point of the mesoglea and the gonad (Fig. 1).

Behavioural observations

Observations of the response of *Aurelia labiata* to different oxygen conditions were made in tanks in a laboratory coldroom. 80 cm water columns were prepared in cylindrical tanks (1 m×15 cm, clear acrylic) with oxygen levels of either 100, 30, 18 or 0% air saturation by bubbling FSW (10 μm filter) with nitrogen gas to remove oxygen. Oxygen stratified tanks were prepared by gently adding small amounts (~100 ml) of FSW supersaturated with oxygen (~400% air saturation) to the surface of an anoxic water column. Tanks with reduced oxygen were covered during experiments to slow gas exchange across the surface, but stratified tanks were allowed to de-gas freely. Oxygen profiles of tankwater were made before and after all experiments. Oxygen stratified tanks were ~130% oxygen in the surface 20 cm, and the bottom 40 cm contained <3% air saturation oxygen. Only experiments whereby tanks contained at least 20 cm of normoxic or hyperoxic surface water and 40 cm of 'anoxic' bottom water (0–5% air saturation oxygen) remaining at the end of experiments are reported in this study. Position in the tanks and whether or not the specimen was swimming were recorded every minute in each tank. Bell pulsation rate was noted at the start of the experiment and after each 10 min period over the following 1 h. All observations were made under constant vertical lighting in a constant-temperature cold room at 10°C. Previous experiments demonstrated that *Aurelia labiata* does not have an intrinsic biological clock (Mackie et al., 1981); nevertheless, all experiments were conducted during daylight hours. Experiments were conducted on specimens within 48 h of collection and following at least 6 h of laboratory acclimation. With the exception of the 30% hypoxia experiments (N=7), all specimens were fed *ad libitum* with *Artemia franciscana* nauplii prior to experiments and eight specimens were run per oxygen condition. Similar sized specimens were selected for these experiments (mean diameter ± S.D., 3.9±0.8 cm).

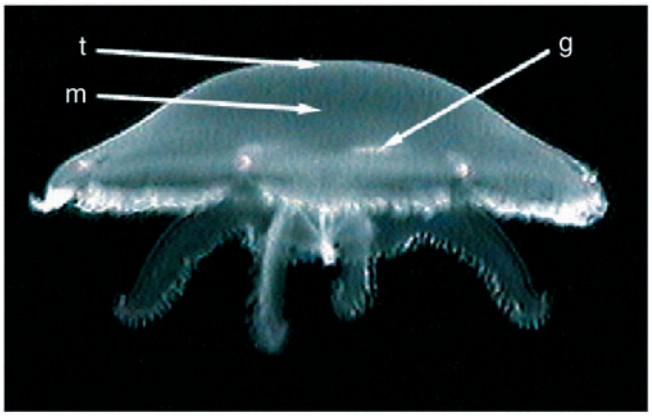

Fig. 1. Intragel oxygen characteristics of *Aurelia labiata*. An image of *A. labiata* showing the location of intragel oxygen measurements. The points labeled t, m and g represent measurements taken in the immediate subsurface of the aboral side mesoglea, the midgel, and the oral subsurface tissue (gonad), respectively.

Data analysis

Oxygen consumption rates were compared using two-tailed *t*-tests. Linear regression was used to determine P_{crit}.

Comparisons of behavioural data were made using analysis of variance (ANOVA) followed by a Fisher PLSD *post-hoc* analysis. The possible influence of animal size on intragel oxygen comparisons was checked using multivariate ANOVA (MANOVA) with diameter as the size parameter, and comparisons of intragel oxygen partial pressures were also performed using MANOVA. The SPSS general linear model MANOVA was evaluated using Pillai's Trace statistic followed by Dunnett T3 *post-hoc* analyses for data sets with unequal variances. All other analyses were performed using the Statview II computer program. Significance was determined at $P<0.05$.

Results

Oxyregulation

All specimens of the four species in this investigation maintained their $\dot{V}_{O_2}$ under declining oxygen concentrations to below 18.1 hPa oxygen (Table 1, Fig. 2). The $\dot{V}_{O_2}$ values of *Aurelia labiata* were significantly higher than those of *Phacellophora camtschatica* (*t*-test, $P<0.01$), even though the specimens of the latter were all smaller (Table 1). Interestingly, the P_{crit} values of these two species were not significantly different (*t*-test, $P>0.05$). The lowest recorded individual P_{crit} values for *A. labiata* and *P. camtschatica* are 3.7 and 2.5 hPa, respectively.

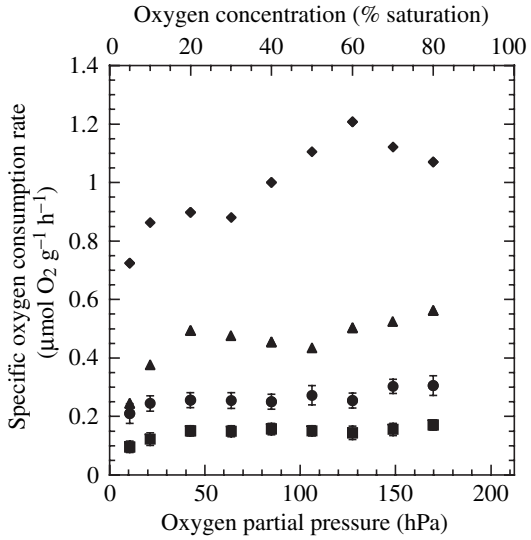

Fig. 2. Mass-specific oxygen consumption rates in progressive hypoxia for four species of scyphomedusae. Squares, *Phacellophora camtschatica* (*N*=7); circles, *Aurelia labiata* (*N*=7); triangles, *Cyanea capillata* (*N*=1); diamonds, *Chrysaora quinquecirrha* (*N*=1). Critical partial pressures of oxygen were determined to be 9.1±1.4, 9.0±1.9, 14.6 and 12.3 hPa for *P. camtschatica, A. labiata*, *C. capillata* and *C. quinquecirrha*, respectively. Values are means ± S.E.M. Temperature and salinity were 10°C and 30 psu for experiments with *P. camtschatica, A. labiata*, and *C. capillata*; for *C. quinquecirrha*, 25°C and 12 psu, respectively.

Intragel oxygen

Oxygen concentrations through the gel of *A. labiata* were measured on 25 harnessed specimens. Striking differences were seen between profiles made in the aboral to oral direction and those in the oral to aboral direction, and typical examples are shown in Fig. 3. In specimens harnessed with the oral side down, the upper section of the exumbrellar gel displays a typical Fickian diffusion gradient (Crank, 1975). The diffusion gradient intensifies in the subumbrellar region of the medusa due to increased tissue heterogeneity and metabolic use of intragel oxygen. In specimens harnessed with the oral side up, oxygen supply through the outer bell surface was almost entirely eliminated, oxygen content was lower, and the oxygen profile of the mesoglea was reversed (Fig. 3). The similarities in intragel oxygen contents between specimens harnessed with the aboral side down (Fig. 3) and unharnessed specimens held in hypoxia and anoxia (Fig. 4) demonstrate that intragel oxygen concentration was affected within the time frame of the harnessing preparation (~1 h). Gel becomes depleted of oxygen within the time it takes to harness the specimen and align the probe as animal metabolism consumes oxygen and exumbrellar oxygen diffusion is repressed. These profiles demonstrate clearly that diffusion from the subumbrellar cavity by itself is insufficient to supply oxygen to the metabolically active tissues of the organism, and jellyfish must be using intragel oxygen to meet their metabolic needs.

Intragel oxygen experiments demonstrated the capacity of *Aurelia labiata* to use intragel oxygen as a reservoir to support its metabolic needs when it migrates from higher oxygen

Table 1. *Oxygen consumption rates at 60% oxygen saturation and critical oxygen partial pressures for four species of scyphozoan jellyfish*

Genus and species	Wet mass (g)	(*N*)	Metabolic rate, V_{O_2} (μmol O_2 g^{-1} h^{-1})	Critical P_{O_2}, P_{crit} (hPa)
Aurelia labiata	7.126±2.309	(7)	0.255±0.025	9.0±1.9
Cyanea capillata	1.166	(1)	0.501	14.6
Phacellophora camtschatica	0.873±0.175	(7)	0.156±0.021	9.1±1.4
Chrysaora quinquecirrha	1.082	(1)	1.210	12.3

Values are means ± S.E.M. (± S.D. for mass).

Temperature and salinity conditions were 10.0°C and 30.0 psu for *A. labiata*, *C. capillata* and *P. camtschatica*, and 25.0°C and 12.0 psu for *C. quinquecirrha*, respectively.

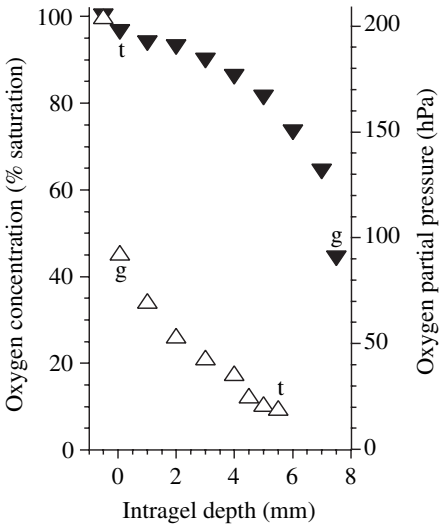

Fig. 3. Typical intragel oxygen profiles of two harnessed specimens of *Aurelia labiata* in normoxia. Solid triangles, specimen was harnessed exumbrellar side up. Open triangles, specimen was harnessed with the exumbrellar surface firmly pressed to the bottom of the chamber. Locations of points t and g as in Fig. 1.

waters into low oxygen waters (Fig. 4). Using bell diameter as the size parameter, there was no effect of size on the intragel comparisons (MANOVA, $P>0.20$). Intragel oxygen becomes significantly reduced in the bell surface, mid-gel and gonad tissues after 1 h in hypoxia (30% air saturation, $N=7$) and anoxia ($N=4$) (Fig. 4, MANOVA, $P<0.001$; Dunnett T3 *post-hoc* analyses, $P<0.02$). However, the oxygen content in the

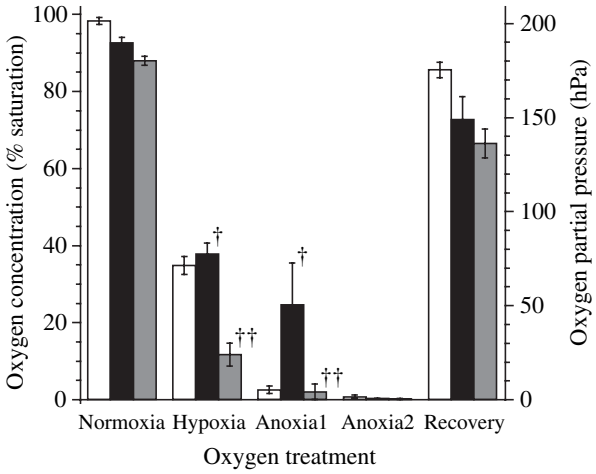

Fig. 4. Intragel oxygen measurements of unharnessed specimens of *Aurelia labiata* under different oxygen conditions. Values are means ± S.E.M. White, black and shaded bars represent measurements made in points t, m and g, respectively (see Fig. 1). Hypoxia=30% air saturation. Anoxia1 and Anoxia2, 1 and 2 h in anoxia, respectively. Recovery, 2 h in anoxia followed by 2.5 h in normoxia. All differences in intragel oxygen partial pressures between treatments are significant, except that † and †† are not significantly different from each other. For N and P values, see text.

midgel and gonad tissues were not significantly different between the hypoxia and 1 h anoxia treatment (Fig. 4; Dunnett T3 *post-hoc* analyses, $P>0.05$). After 2 h in anoxia ($N=6$), gel oxygen reached environmental levels (Fig. 4). When specimens that had been held for 2 h in anoxia were transferred to normoxic seawater, intragel oxygen recovered to ~70% of normal after 2.5 h ($N=4$), but oxygen contents in all three tissues still remained significantly lower than in specimens in normoxia (Fig. 4, MANOVA, $P<0.001$; Dunnett T3 *post-hoc* analyses, $P<0.001$). When *A. labiata* is transferred to lower oxygen environments, oxygen is depleted from the exumbrellar surface due to the reversal of the direction of oxygen diffusion, and the mesoglea continues to supply oxygen to metabolically active tissues.

Behaviour experiments

Aurelia labiata displayed different behaviour patterns under different oxygen regimes in the laboratory (Fig. 5). In air-saturated, hypoxic and anoxic tanks, *A. labiata* typically swims against the tank bottom or water surface with occasional vertical up and down forays. In stratified oxygen conditions, *A. labiata* travels the greatest distance as it swims back and forth through the oxycline. The vertical distance that *A. labiata* travelled while swimming in the stratified oxygen conditions was significantly higher than the other conditions (ANOVA, Fisher's PLSD, $P<0.01$, Fig. 6A). The time spent swimming was not significantly different in the tanks with oxygen, but swimming period was significantly reduced in anoxia (ANOVA, Fisher's PLSD, $P<0.01$, Fig. 6B). The apparent contradiction between distance travelled (Fig. 6A) and time spent swimming (Fig. 6B) can be explained due to the individuals that were actively swimming against either the surface or bottom of the normoxia and hypoxia tanks (Fig. 5). *Aurelia labiata* is least active when under anoxia, and bell pulsation rate was significantly reduced in the anoxia tanks (ANOVA, Fisher's PLSD, $P<0.01$, Fig. 6C).

Discussion

Although a number of investigators have previously measured metabolic rates of medusae (Vernon, 1895; Thill, 1937; Mangum et al., 1972; Larson, 1987; Childress and Thuesen, 1993; Thuesen and Childress, 1994), none until now have used techniques that allow for the observation of the critical partial pressure of oxygen. The ability to detect oxyregulation demonstrates that our method of using a shaker table to mix seawater in the chamber is effective, since poor mixing of the chamber seawater would result in apparent oxyconformation (Shick, 1991). A pronounced ability to regulate $\dot{V}_{O_2}$ is counterintuitive for coelenterates, because they have not evolved specialised structures for oxygen uptake and circulation. All four species of scyphomedusae were able to oxyregulate well below ~25% air saturation, the oxygen level considered to be environmentally significant hypoxia because of the detrimental effects on most organisms (Rabalais and Turner, 2001). The P_{crit} values of the three Puget Sound species

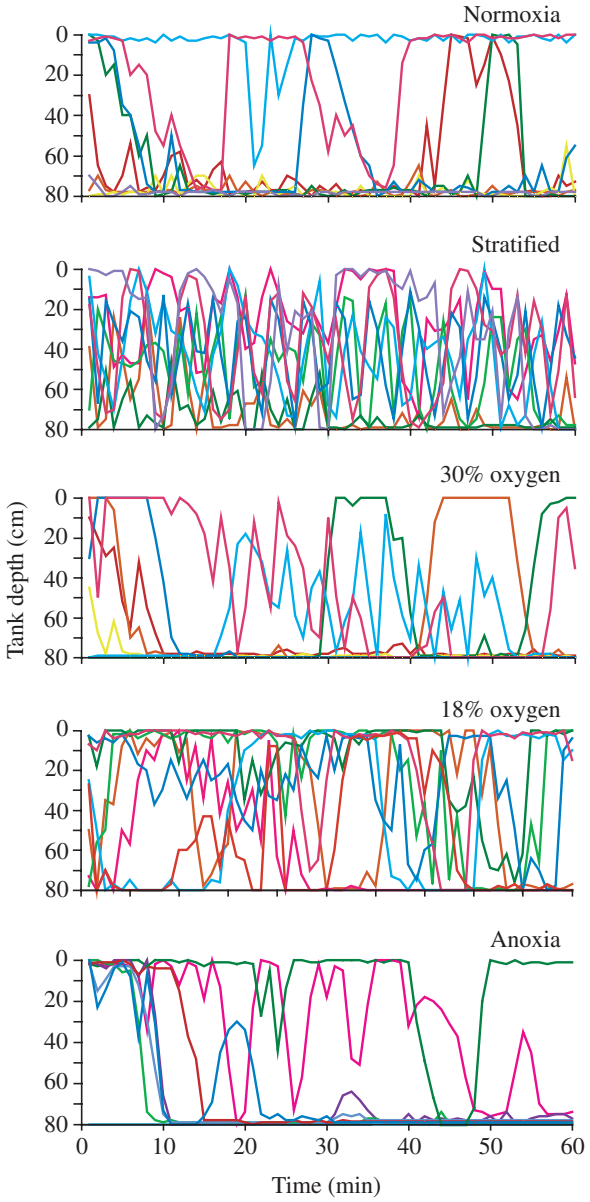

Fig. 5. Depth profiles of *Aurelia labiata* in 80 cm water columns under five oxygen conditions. Each coloured line is the track of an individual specimen over a 1 h period. The five tank conditions were normoxia (100% air saturation oxygen), stratified (with ending oxygen concentrations of 100–130% air saturation oxygen in the surface 20 cm and 0–5% air saturation oxygen in the bottom 40 cm), 30% air saturation oxygen, 18% air saturation oxygen, and anoxia.

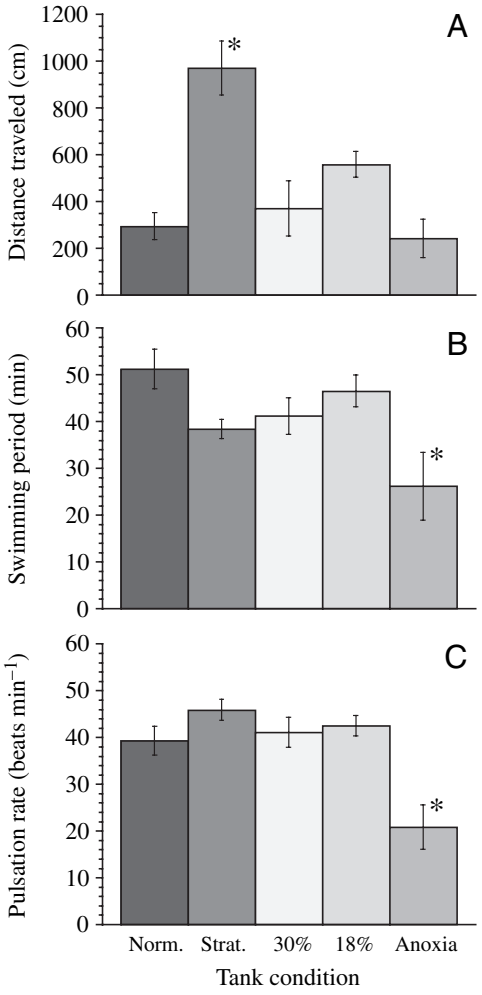

Fig. 6. Swimming characteristics of *Aurelia labiata* in 1 h tank experiments. (A) Vertical distances travelled. (B) Time (min) swimming. (C) Bell pulsation rates. Values are means ± S.E.M. *Significant difference from all other treatments (P<0.01). Tank conditions as in Fig. 5.

indicate that the medusae of these species will not be directly affected by continuing eutrophication, and the P_{crit} of *Chrysaora quinquecirrha* from Chesapeake Bay demonstrates its capability to tolerate hypoxia in that eutrophic ecosystem. Physiological studies on the benthic stages of these organisms are needed to further elucidate their abilities to thrive in stressed estuarine environments.

The critical oxygen partial pressures for the medusae of these four species of Scyphozoa and our behavioural observations indicate that they can endure all but the most severely hypoxic environments without undergoing any major metabolic transition to anaerobiosis. Other recent observations indicate that some species of hydromedusae (Rutherford and Thuesen, 2005) and ctenophores (Thuesen et al., 2005) can also tolerate very low oxygen conditions. However, some hydromedusae displayed oxyconformation and had higher P_{crit} values than the scyphomedusae in this study (Rutherford and Thuesen, 2005). The ability of scyphomedusae to function aerobically is similar to that displayed by pelagic crustaceans (Childress, 1975; Cowles et al., 1991), cephalopods (Seibel et al., 1997) and fishes (Torres et al., 1979) in the midwater oxygen minimum layer off California, where oxygen partial pressures below 30 hPa persist over millennia (Childress and Seibel, 1998).

Intragel oxygen

The majority of the metabolically active tissues of

scyphomedusae is sandwiched between the largely acellular gel of the aboral mesoglea and the seawater of the subumbrellar space, and we investigated whether overlying gel supports oxygen diffusion to these metabolically active tissues. Scyphomedusae swim through sustained contractions of the subumbrellar musculature and the myofibril layer of this muscle tissue is heavily interdigitated with the mesogleal gel (Gladfelter, 1972; Anderson and Schwab, 1981). These myofibrils contain neither microtubles nor sarcoplasmic reticulum, and it has been proposed that the mesoglea must be directly responsible for supplying calcium to the myofibril cells (Anderson and Schwab, 1981). Our intragel oxygen measurements indicate that the mesoglea is also supplying oxygen to the musculature and other metabolically active tissues in the subumbrellar region. Nevertheless, in some large species of scyphomedusae, a coronal swimming muscle also hangs free in the water of the subumbrellar space (Russell, 1970). This indicates that there are limits on intragel oxygen supply to the subumbrellar musculature, and oxygen supply may have been an important factor in the evolution of medusan morphology.

Scyphomedusae can regulate their oxygen consumption down to very low oxygen partial pressures due to the suite of diffusion gradients that exist between the surrounding seawater and mesogleal gel with metabolically active tissues. Oxygen diffusion gradients are described by Fick's first law: $F=-D\delta C/\delta x$, where F=transfer rate per unit area of section, D is the diffusion coefficient, C is the oxygen concentration and x is the space coordinate perpendicular to the section (Crank, 1975). If oxygen declined in both the umbrellar gel and the subumbrellar seawater at the same rate, δC across the subumbrellar tissue would be maintained and F across these tissues would remain unchanged. The rate that oxygen diffuses into subumbrellar tissue (F_1) is dependent on the magnitude of two general oxygen gradients. F_2 is the diffusion of oxygen from aboral surrounding seawater into mesogleal gel. F_3 is the gradient from oxygen in the subumbrellar seawater into the oral mesogleal gel. As long as F_2 and F_3 are both large enough to maintain oxygen partial pressures in gel above those needed to support F_1, the jellyfish oxyregulates. If F_2 or F_3 fall below that level, the critical partial pressure of oxygen is reached, the oxygen gradient is inadequate to allow sufficient oxygen to diffuse into the tissue to meet aerobic metabolic demand, and a transition to anaerobiosis would be expected (Grieshaber et al., 1988).

Behaviour under different oxygen conditions

The observations of the behaviour of *Aurelia labiata* made in normoxia are similar to those made in much larger tanks (Mackie et al., 1981). *Aurelia labiata* is not as active in anoxia. When compared to the other oxygen treatments, the visually apparent difference in the swimming tracks of the medusae in oxygen-stratified tanks is striking (Fig. 5). Although no significant differences in the three behaviour parameters between specimens in normoxia or hypoxia were observed, the distance traveled by specimens in 18% air saturation (Figs 5 and 6) is slightly elevated. It appears that 18% oxygen saturation is approaching a level of hypoxia that begins to induce behavioural changes. Experiments conducted at 30% air saturation used animals that were starved prior to observations, and this conditioning also complicates definitive interpretation of these behavioural data. Nevertheless, these experiments demonstrated that the acute threshold for provoking behavioural changes in *A. labiata* is somewhere near its P_{crit} and that oxygen stratification stimulates swimming across the oxycline.

Our laboratory observations of the behaviour of *A. labiata* in stratified tanks are in agreement with those made on the distribution of *Chrysaora quinquecirrha* in oxygen-stratified areas of Chesapeake Bay (Keister et al., 2000). Stratified oxygen levels in eutrophic estuarine environments can have pronounced impacts on the trophic interactions of planktonic organisms (Breitburg et al., 1994, 1999). Stimulation of intra-oxycline swimming behaviour by oxygen stratification may augment the impact of scyphozoans on planktonic prey, since currents generated while swimming also function to move prey items within the tentacle capture zone of medusae (Costello and Colin, 1994). Breeding aggregations (Hamner et al., 1994) of *Aurelia labiata* occur in the near-surface seasonal oxycline in southern Puget Sound where oxygen concentrations range from 20% to 150% air saturation over a distance of just 2.0 m (P.L.B. and E.V.T., manuscript in preparation), and successful transfer of sperm in breeding aggregations of *A. labiata* may also be promoted. Even in severe (sub-P_{crit}) hypoxia, *A. labiata* has sufficient oxygen in its gel to support aerobic metabolic needs for up to several hours, and this study suggests that jellyfish will only be affected by hypoxia when they swim into waters with oxygen concentrations below their P_{crit} and remain there for over several hours.

Role of gel in jellyfish biology

The great diversity of histological characteristics of mesoglea has been recognized for many years (Kölliker, 1865). In jellyfish, its primary role is usually considered to be that of a supporting tissue. It provides hydrostatic skeletal support for musculature (Alexander, 1964; Chapman, 1966) and supports the development of complex tissues (Schmid et al., 1991). Gel may also be an energy storage tissue, albeit a poor one, and it can provide energy to metabolically active tissues during periods of starvation (Hamner and Jenssen, 1974). The internal gel milieu is a dynamic environment. It accommodates buoyancy changes due to salinity shifts (Mills, 1984; Wright and Purcell, 1997), and gel likely provides important ions to musculature (Anderson and Schwab, 1981). We now know that gel also plays a key role in supporting oxygen delivery to tissues. Jellyfish were some of the first mobile metazoans, and they evolved in early seas with low oxygen levels (Brenchley and Harper, 1998). Our study suggests that the evolution of gelatinous tissue that supports oxygen diffusion may have played a role in the success of pelagic cnidarians in those early hypoxic oceans. Diffusion gradients in mesoglea represent the first hurdles jumped in the

evolution of oxygen delivery systems that are found in more complex metazoan animals.

List of symbols and abbreviations

F_1	oxygen diffusion rate into subumbrellar tissues
F_2	oxygen diffusion rate into aboral gel
F_3	oxygen diffusion rate into subumbrellar gel
FSW	filtered seawater
P_{crit}	critical partial pressure of oxygen
$\dot{V}_{O_2}$	mass-specific oxygen consumption rate

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