Ocean Acidification

And Animal Physiology

$$CO_2 + H_20 \text{ <--> } HCO_3^- + H^+$$

$$pH = pK + \log \frac{[HCO_3^-]}{[CO_2]}$$

Outline for Today's Lecture

1. **Introduction to acid-base physiology**

    -Buffering capacity and Ion transport

    -Correlation with metabolic rate

2. **What processes (and organisms) are sensitive?**

    -enzyme-mediated processes

    -blood-oxygen binding

    -Metabolic rate as CO_2-sensitive indicator?

3. **Dosidicus gigas as a canary in the coalmine.**
4. **Does a broadly-applicable critical CO_2 level exist?**

Organisms can control intracellular PCO_2 and pH

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decompressor
are needed to see this picture.

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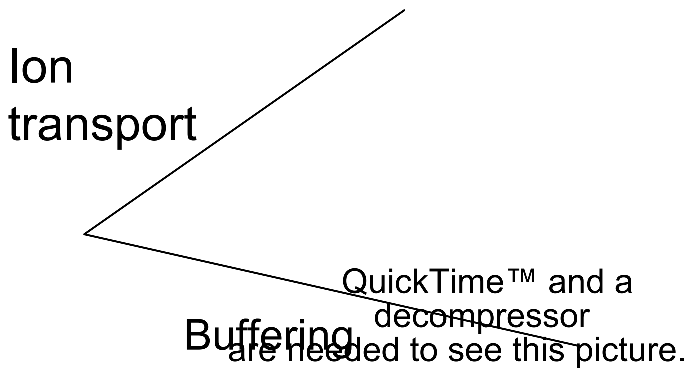
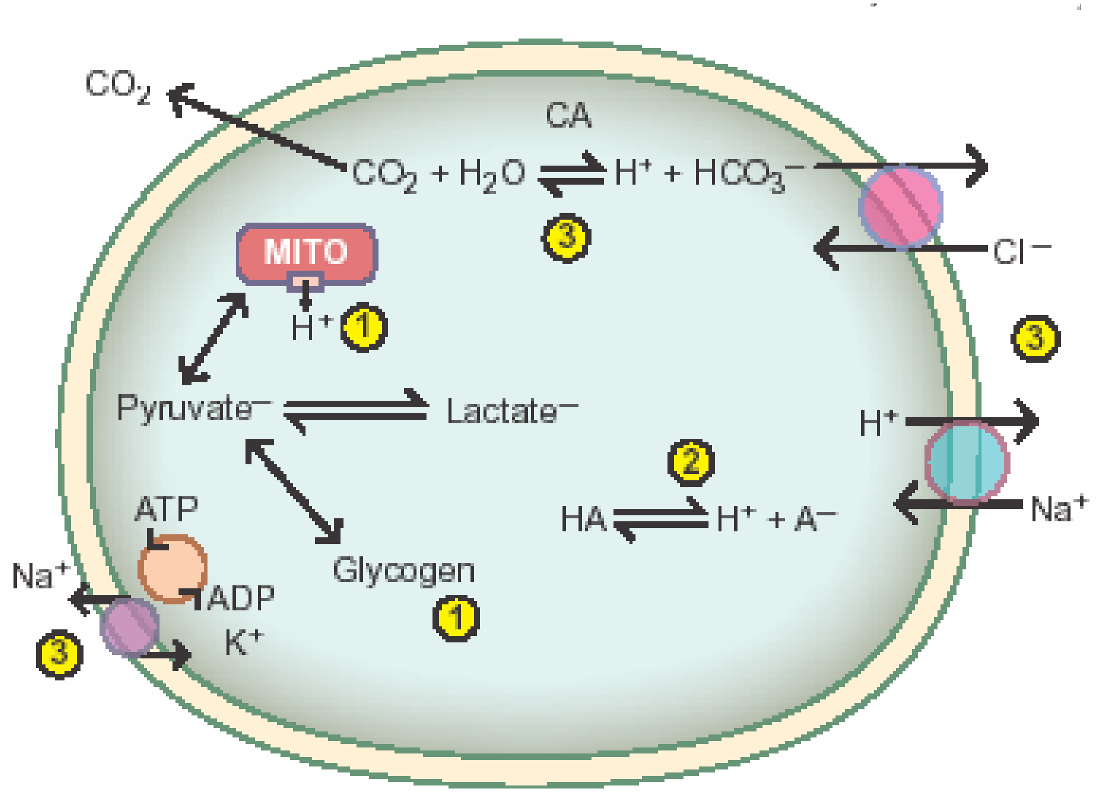
Buffering moderates pH imbalance on short term (minutes), ion transport compensates on longer time scales (hours-days).



PERSPECTIVES: CARBON CYCLE

Potential Impacts of CO_2

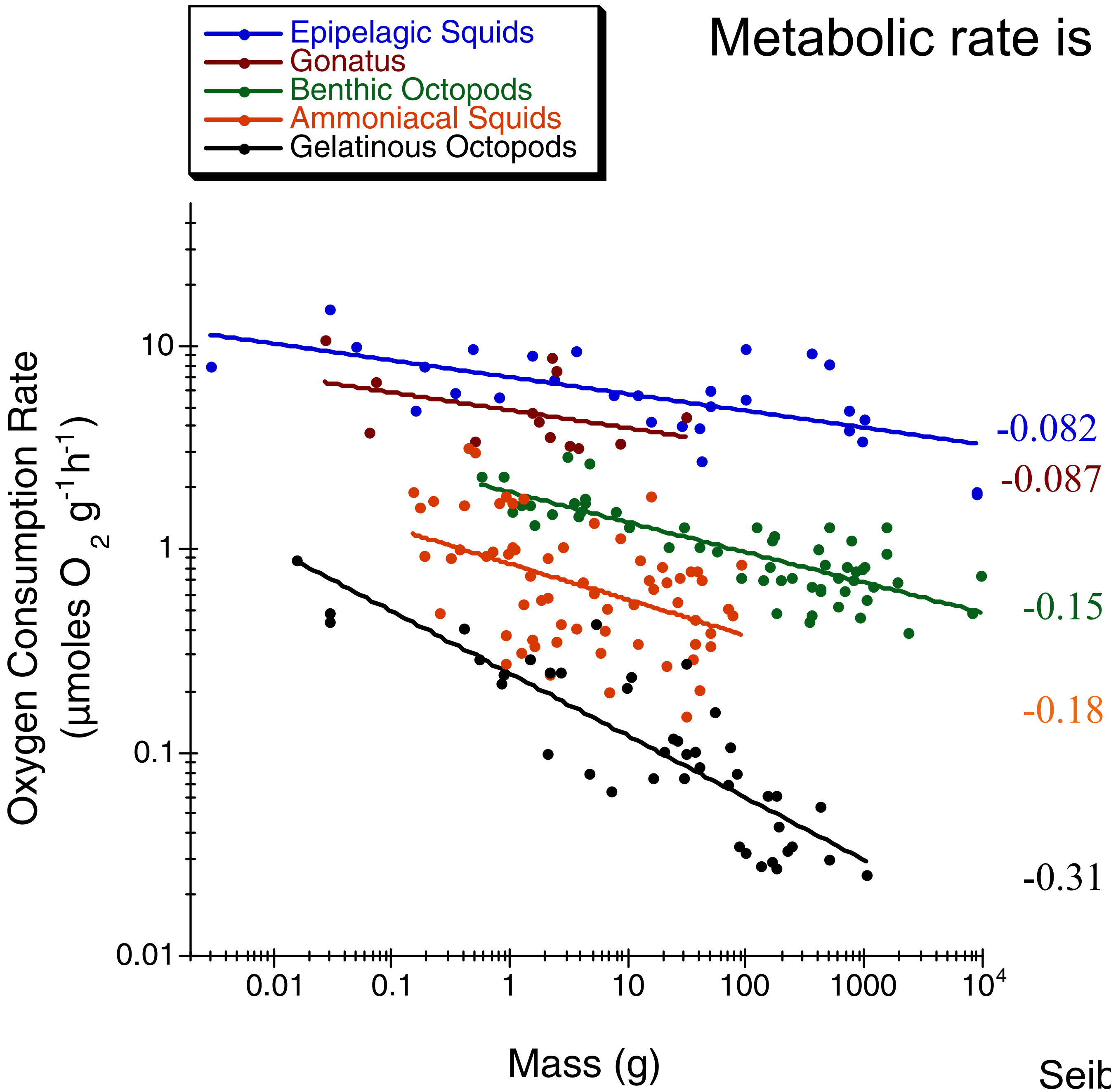
Brad A. Seibel and Patrick J. Walsh



Organisms capacity to control intracellular pH is an evolved function of the rate of production of acid-base equivalents (i.e. Dependent on metabolic rate).

Melzner et al., 2009. Biogeosciences

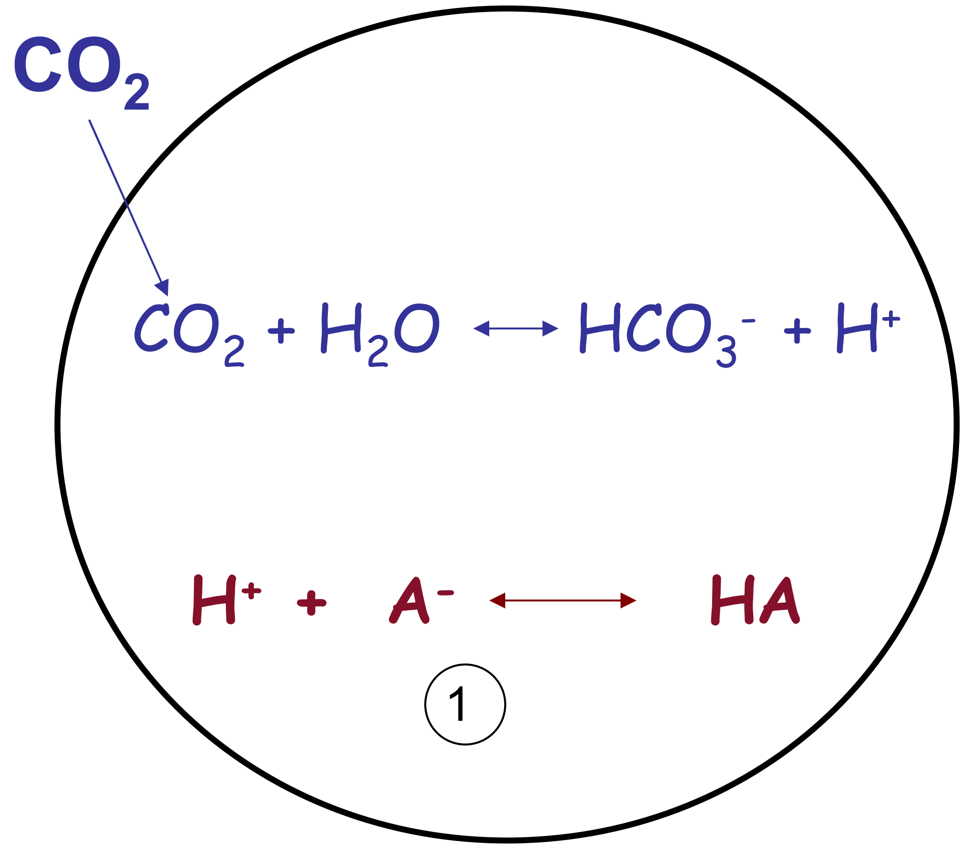
Metabolic rate is highly variable



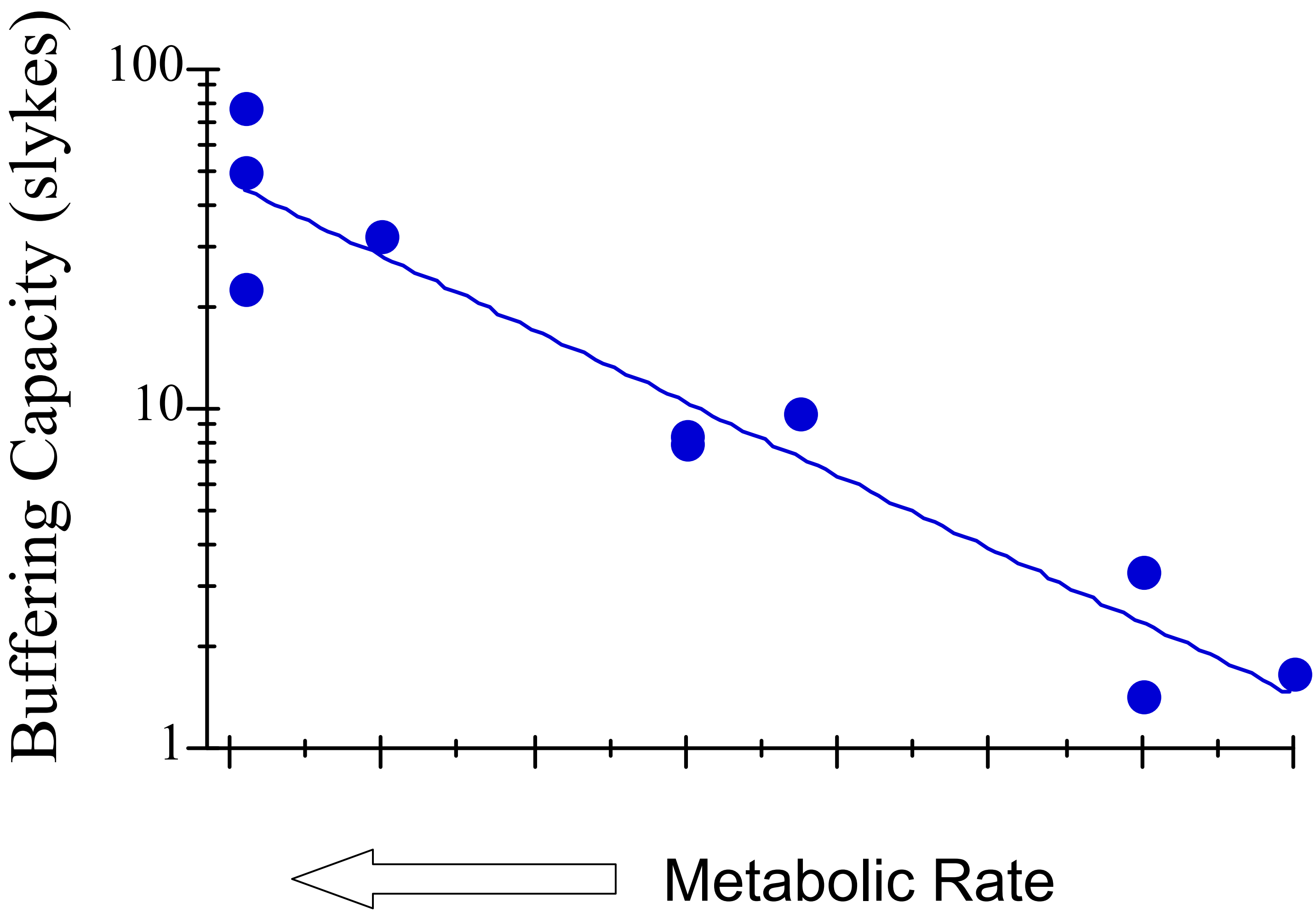
Seibel and Drazen 2007

Combating Acidosis

1. Buffering

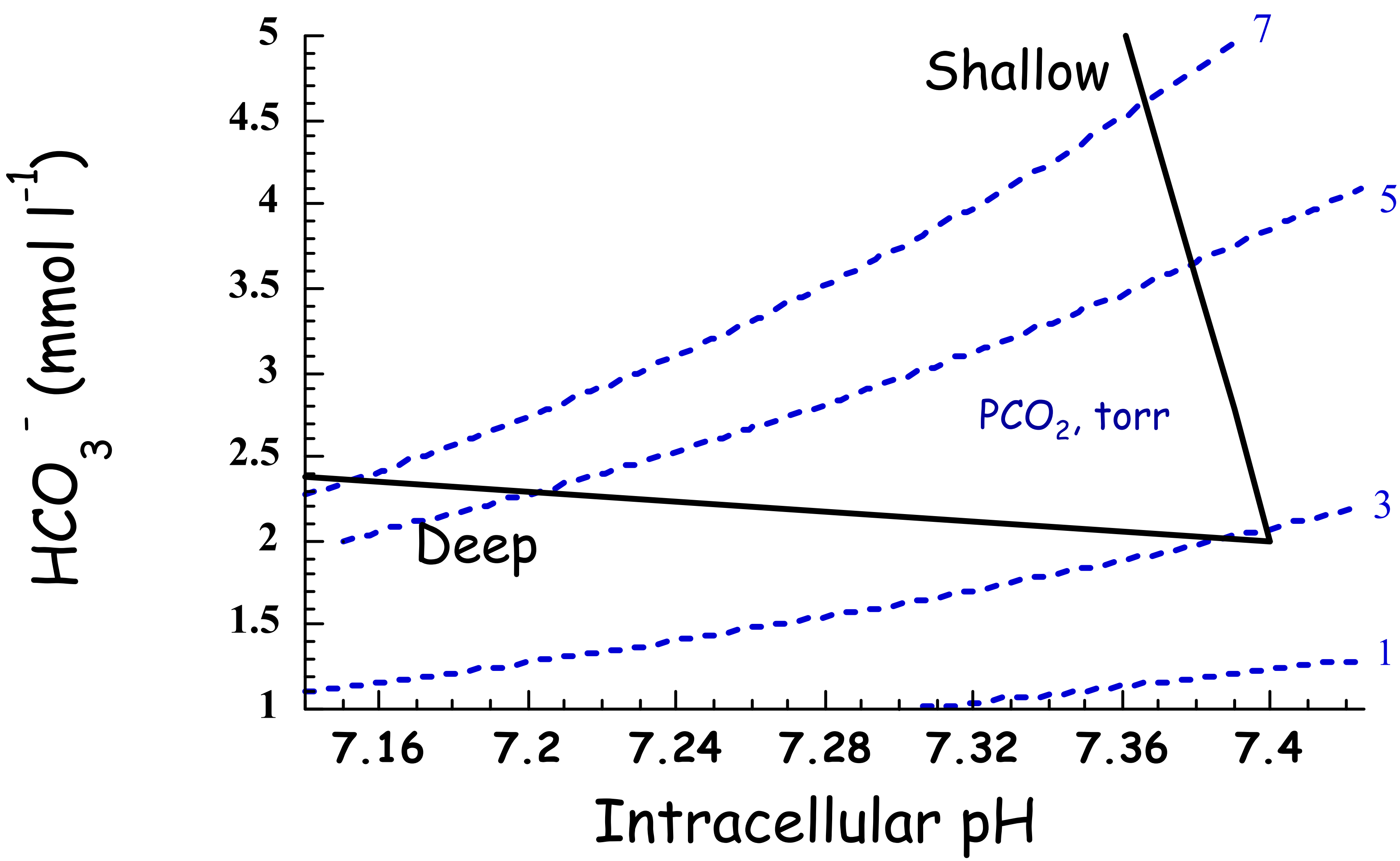


Buffering Capacity is correlated with metabolic rate



Seibel and Walsh, 2003

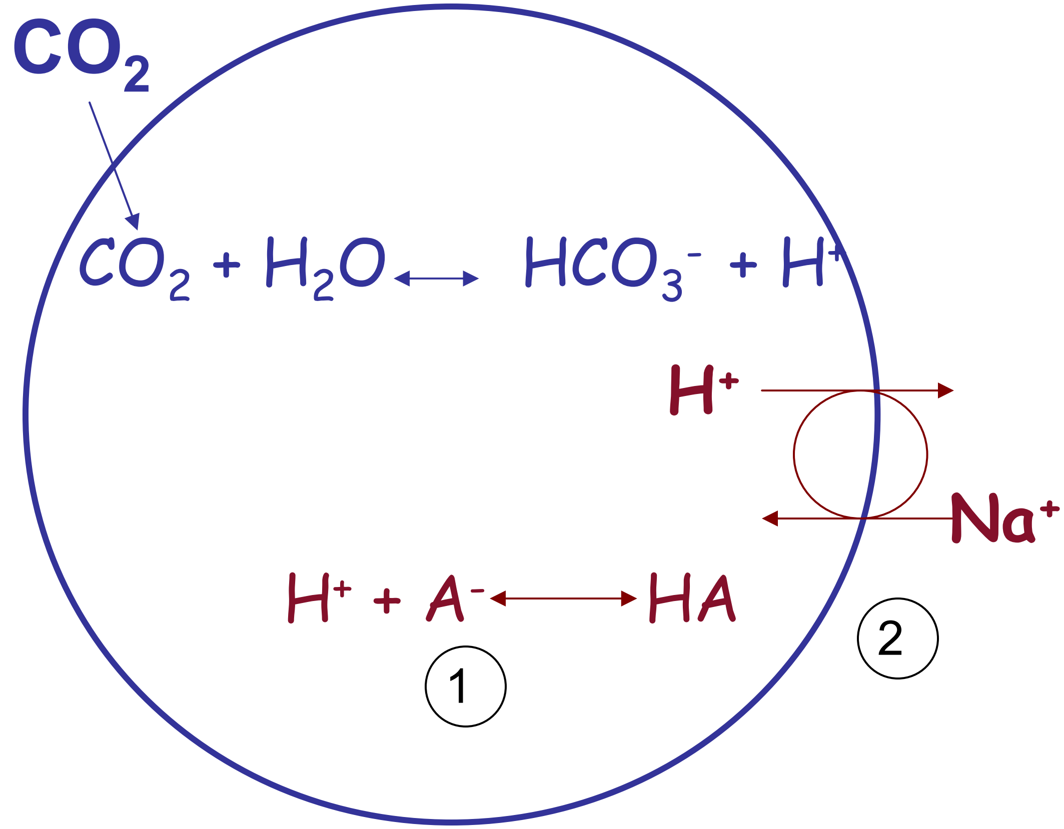
$$pH = pK + \log \frac{[HCO_3^-]}{CO_2}$$



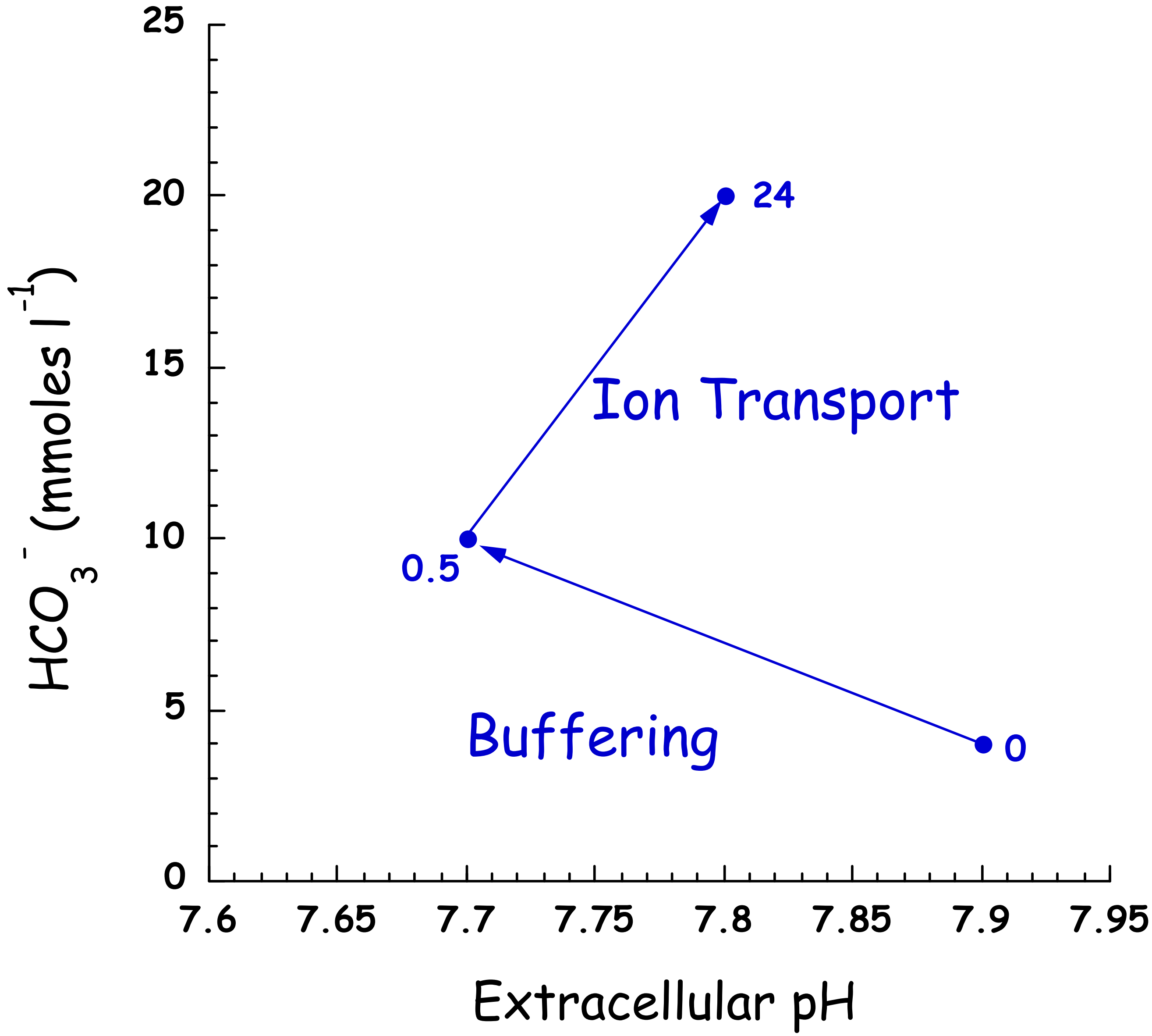
Combating Acidosis

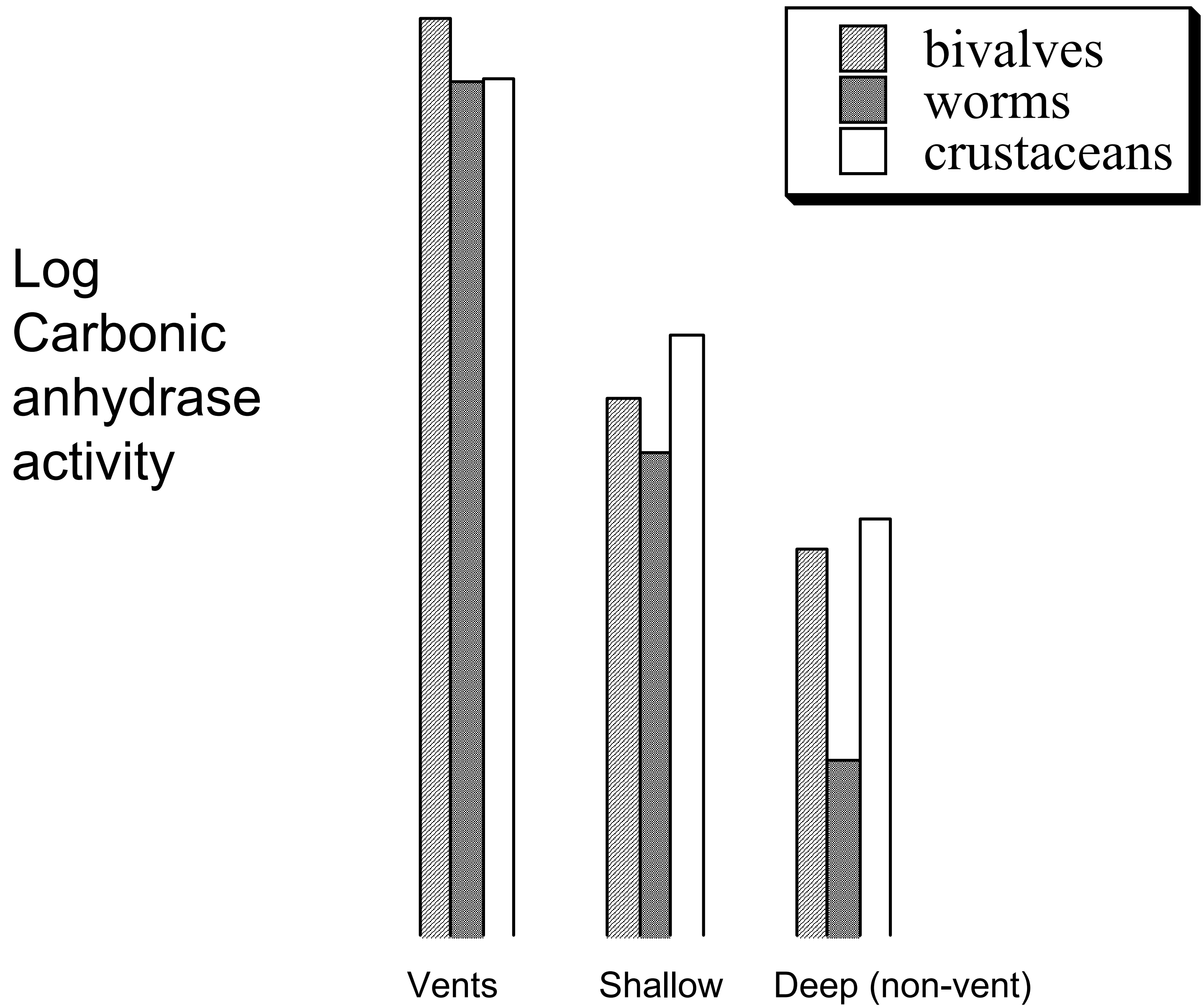
1. Buffering

2. Ion transport



Typical timecourse for acid-base compensation in the blood




Log
Carbonic
anhydrase
activity
bivalves
worms
crustaceans
Vents
Shallow
Deep (non-vent)

1989

QuickTime™ and a
decompressor
are needed to see this picture.

Pörtner, H. O. et al. Respiration Physiology 1990. 81(2):255-73. Determination of intracellular pH and PCO2 after metabolic inhibition by fluoride and nitrilotriacetic acid.

Pörtner, H. O. Respiration Physiology 1990. 81(2) 275-288. Determination of intracellular buffer values after metabolic inhibition by fluoride and nitrilotriacetic acid.

Baker et al. 2009. J. Fish Biol. A validation of intracellular pH measurements in fish exposed to hypercarbia: the effect of duration of tissue storage and efficacy of the metabolic inhibitor tissue homogenate method.

QuickTime™ and a
decompressor
are needed to see this picture.

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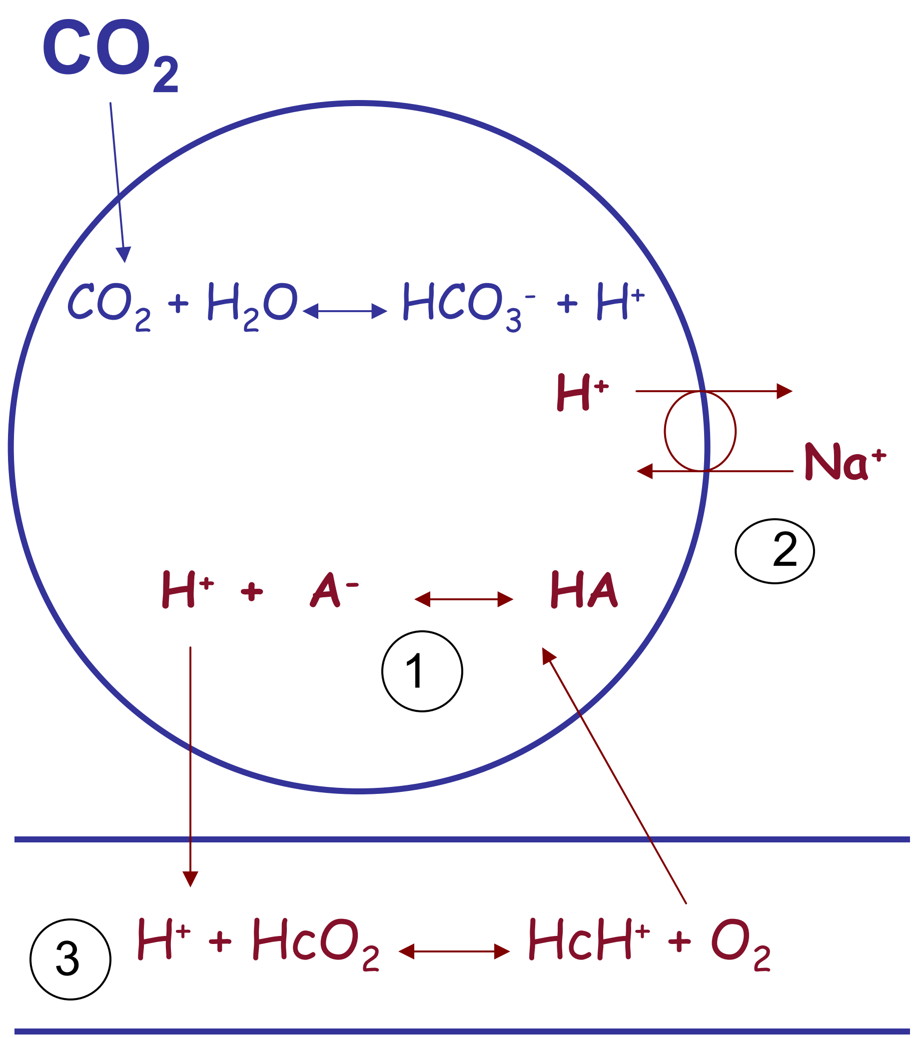
Combating Acidosis

1. Buffering
2. Proton transport
3. Blood-oxygen binding



Seibel and Walsh, 2001

Is a (partially) compensated acidosis good enough?

Time-scale dependent?

Trade-off between ionic- and acid-base balance?

Is there an energetic cost?

Capacity for acclimation?

can organisms produce new isozymes or higher concentrations of relevant enzymes?

What happens when acid-base regulation fails?

-Enzyme-mediated processes have an evolved pH optimum

QuickTime™ and a
decompressor
are needed to see this picture.

-May enhance enzymes quantitatively or qualitatively

What about at a whole-organism level?

Energetics (Complex, interconnected processes)

QuickTime™ and a
decompressor
are needed to see this picture.

Metabolic rate as a *cost* to organisms

QuickTime™ and a
Photo - JPEG decompressor
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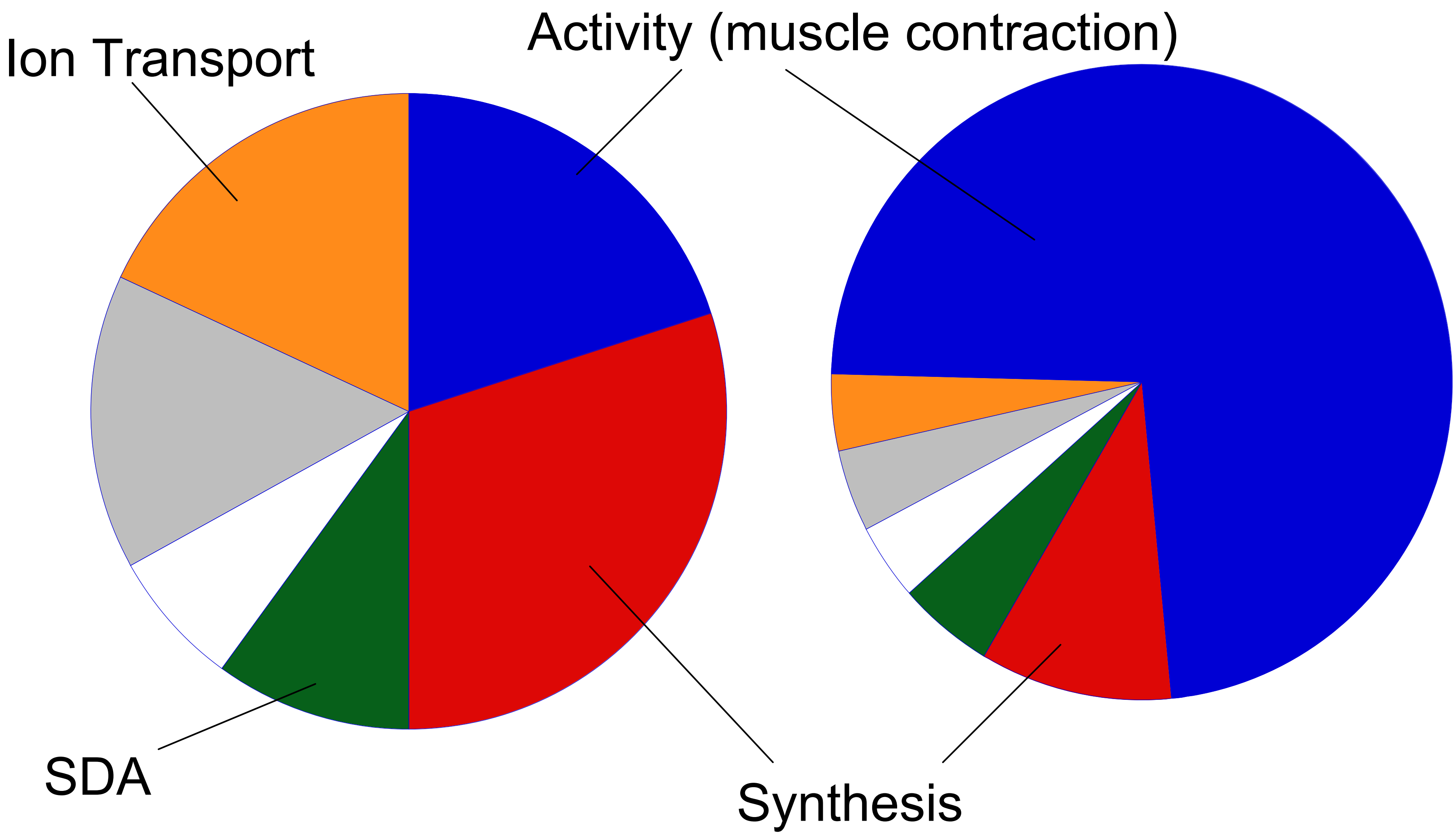
"Evolution tends to maximize metabolic rate, because metabolism produces the energy required to sustain and reproduce life"

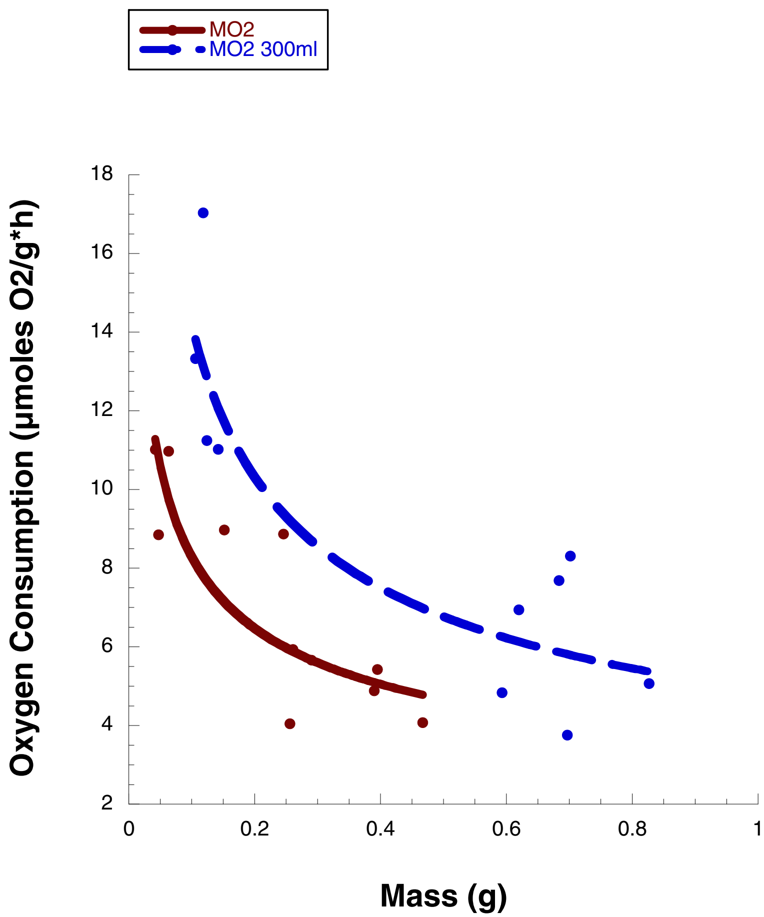
West et al., 1999, Science

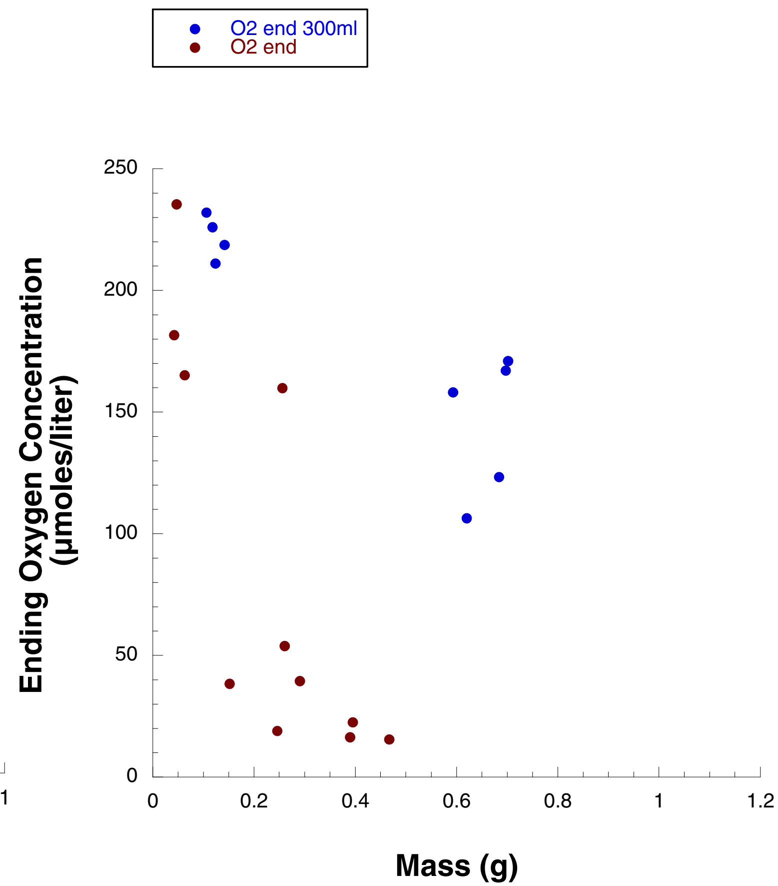
Metabolic rate: sum of all costs



How Do You Measure Metabolic Rate?

1. Duration of experiment (>12 hours)
2. Maintain oxygen well above critical PO_2 (species-specific)
   - Pcrit typically > 50% saturation
   - Respiratory quotient ~0.7 to 1.0 (CO2:O2)
3. Temperature within habitat range (Q_{10} = 2-3)
4. Control activity level (Aerobic scope ~ 5-10X)
   - Basal, Routine, Active, Maximal MR
5. Control feeding (SDA ~ 2-5X BMR)
6. Chamber volume and flow are critical


MO2
MO2 300ml
Oxygen Consumption (µmoles O2/g*h)
Mass (g)


O2 end 300ml
O2 end
Ending Oxygen Concentration (µmoles/liter)
Mass (g)

Measuring Metabolic Rates

1. Oxygen electrodes vs Optodes
   -expense
   -simplicity
   -stirring

2. Calibration

3. Flow through, static, end-point, or intermittent flow

Closed (static)

Flow-through

QuickTime™ and a
decompressor
are needed to see this picture.

Intermittent Flow

Measuring Metabolic Rates:

A manual for scientists

QuickTime™ and a
decompressor
are needed to see this pictur

John R. B. Lighton

"It is possible to measure metabolic rates without understanding what you are doing. In doing so you may think, or hope, that the data you acquire are accurate. In fact, this approach is pretty much the rule….but my hope is that this text will discourage this approach"

www.respirometry.org

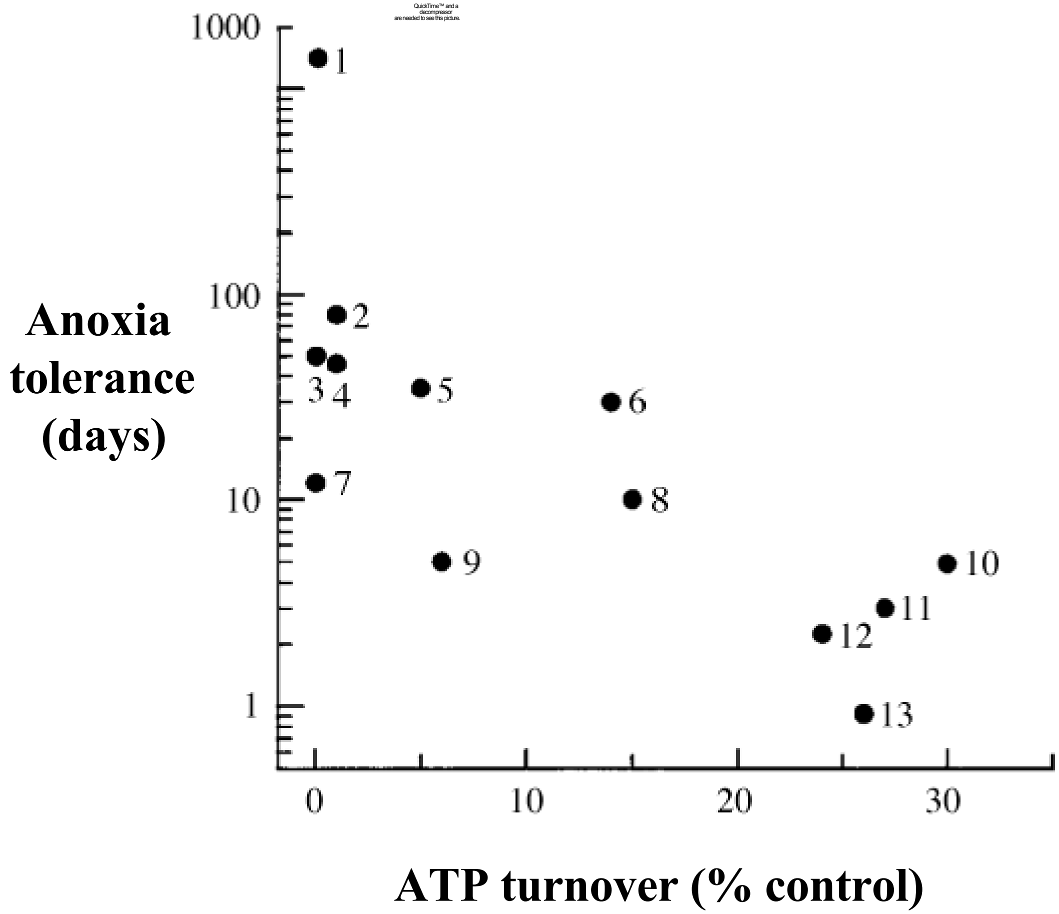
Two cases where CO_2 may reduce MO_2:

1. Metabolic Suppression as an adaptive response to oxygen limitation - often triggered by CO_2 or pH.

2. Oxygen transport limitation due to pH effect on respiratory protein in blood.

Metabolic Suppression

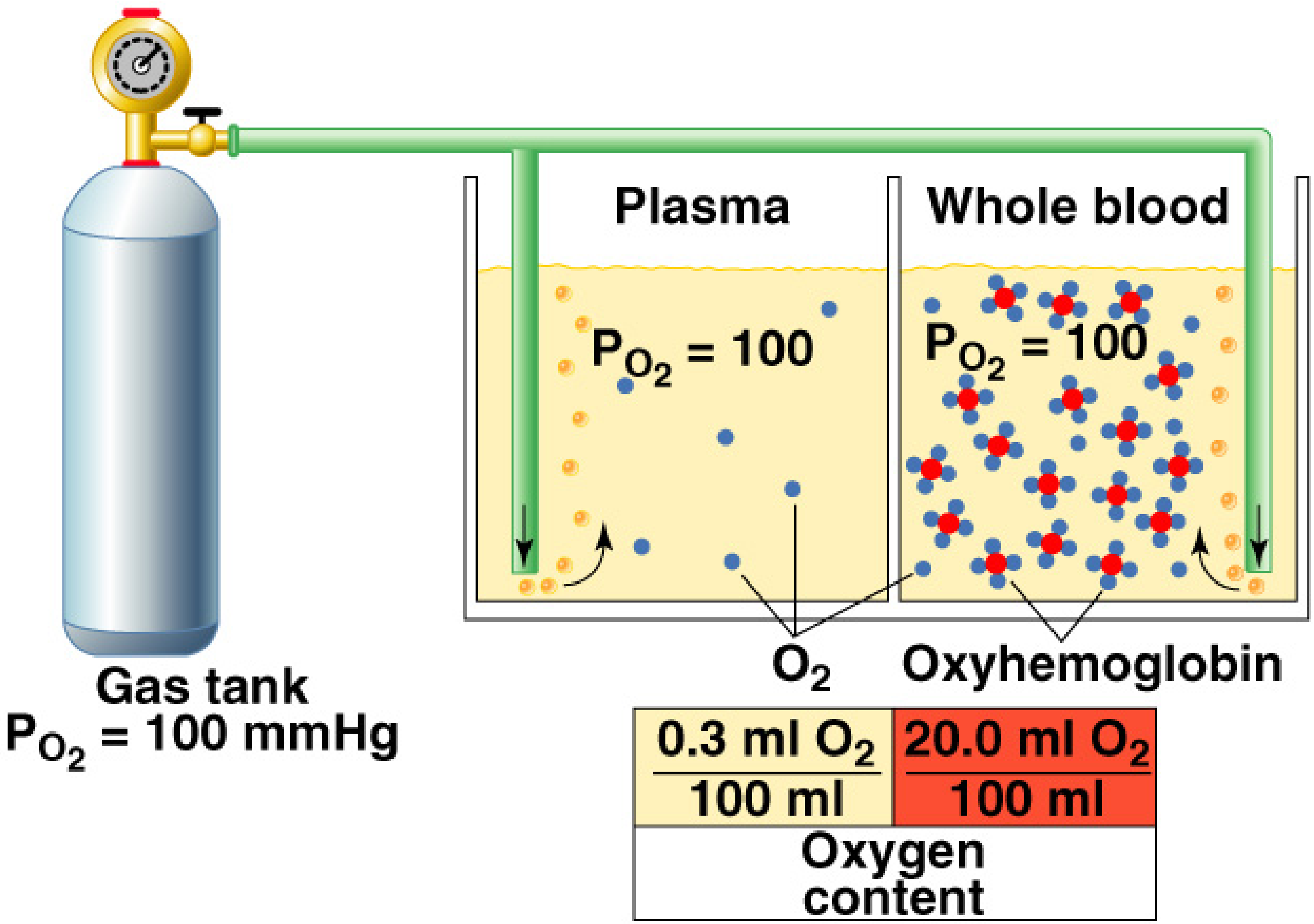
Anoxia tolerance correlates with metabolic suppression



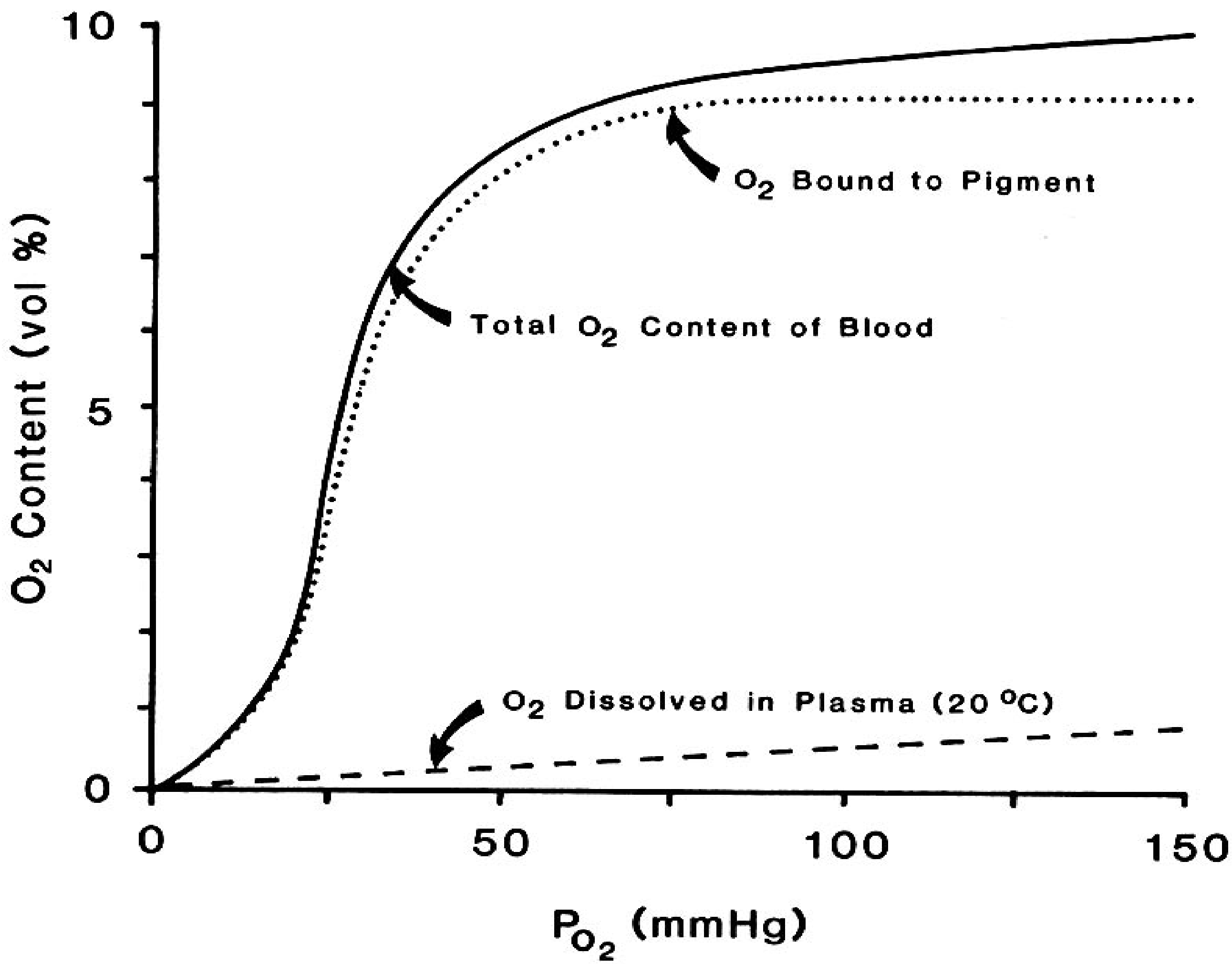
Hand, 1998

Oxygen-limitation of metabolism due to pH effect on protein

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

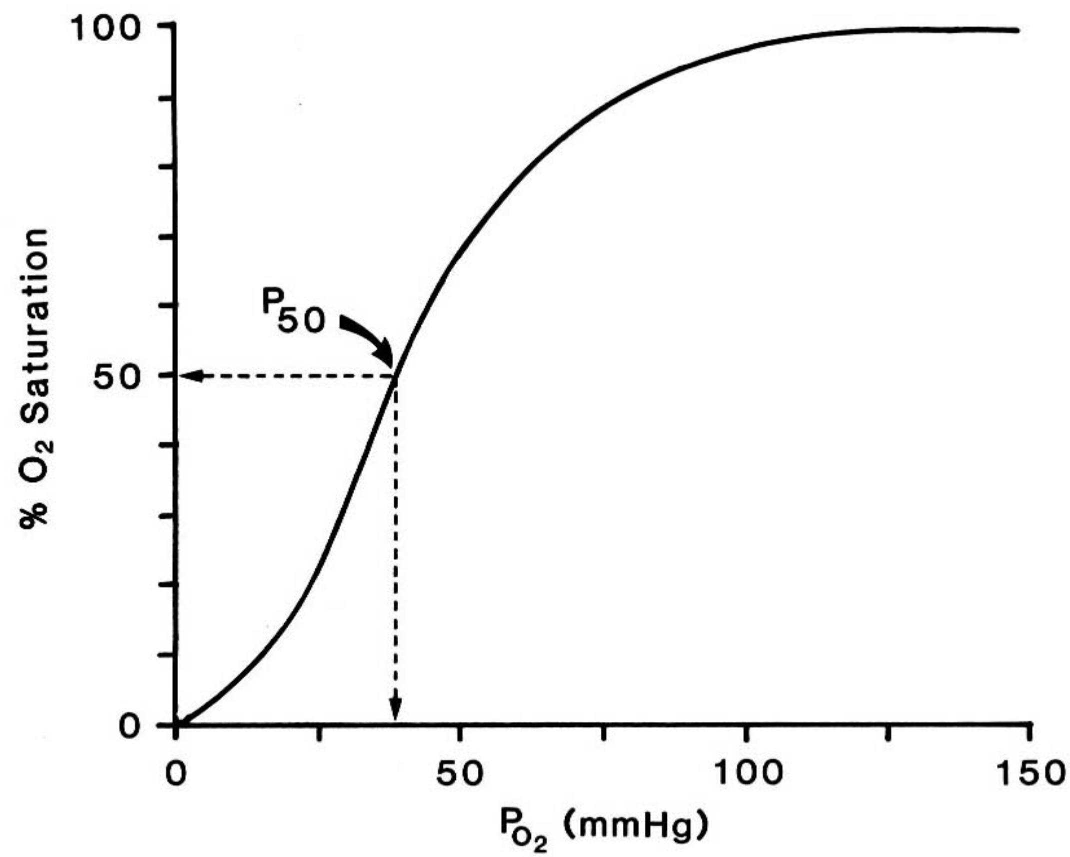

Plasma
Whole blood
P_{O_2} = 100
P_{O_2} = 100
O_2
Oxyhemoglobin
Gas tank
P_{O_2} = 100 mmHg
0.3 ml O_2 / 100 ml
20.0 ml O_2 / 100 ml
Oxygen content

RESPIRATORY PIGMENT FUNCTION

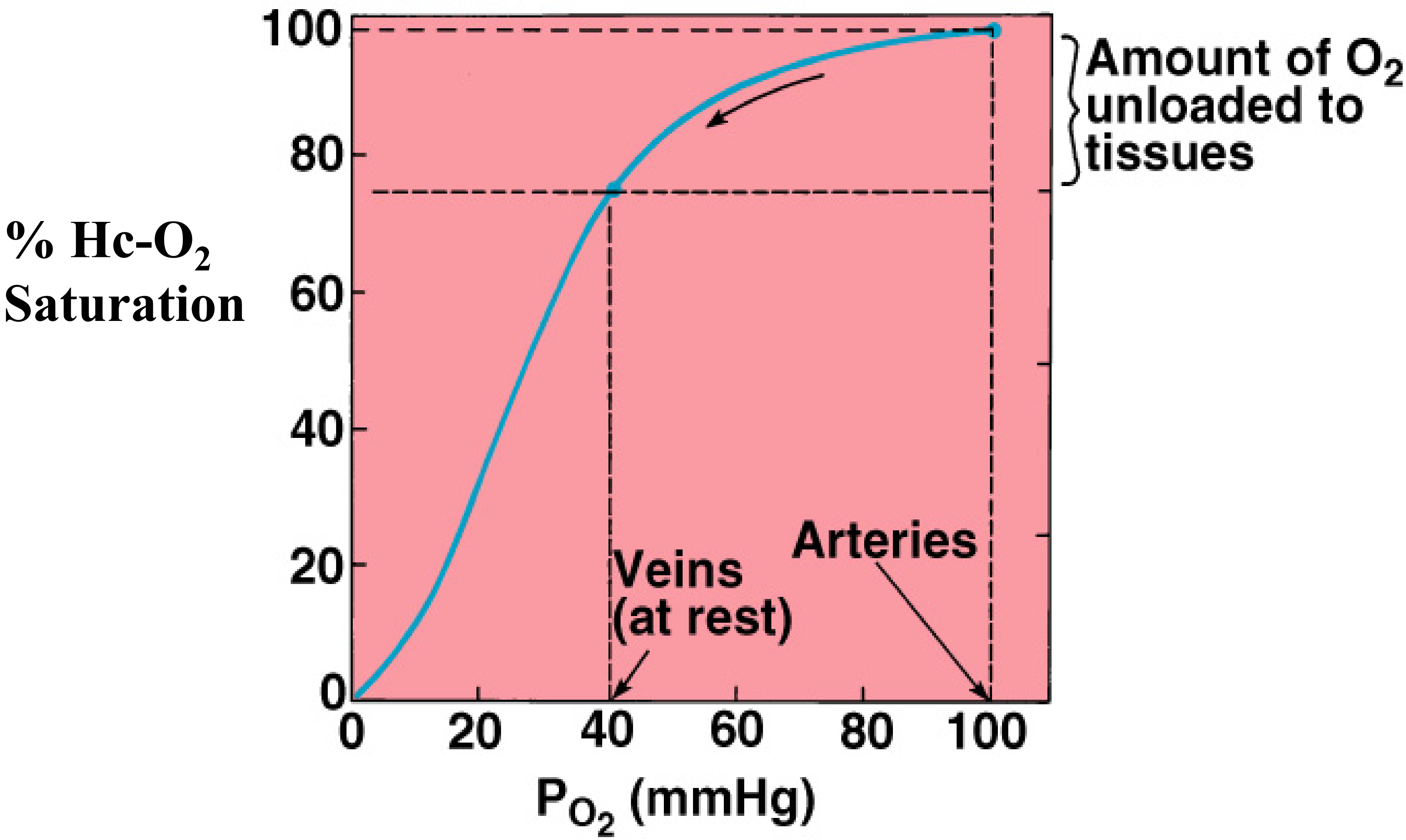


Oxygen Binding Curves

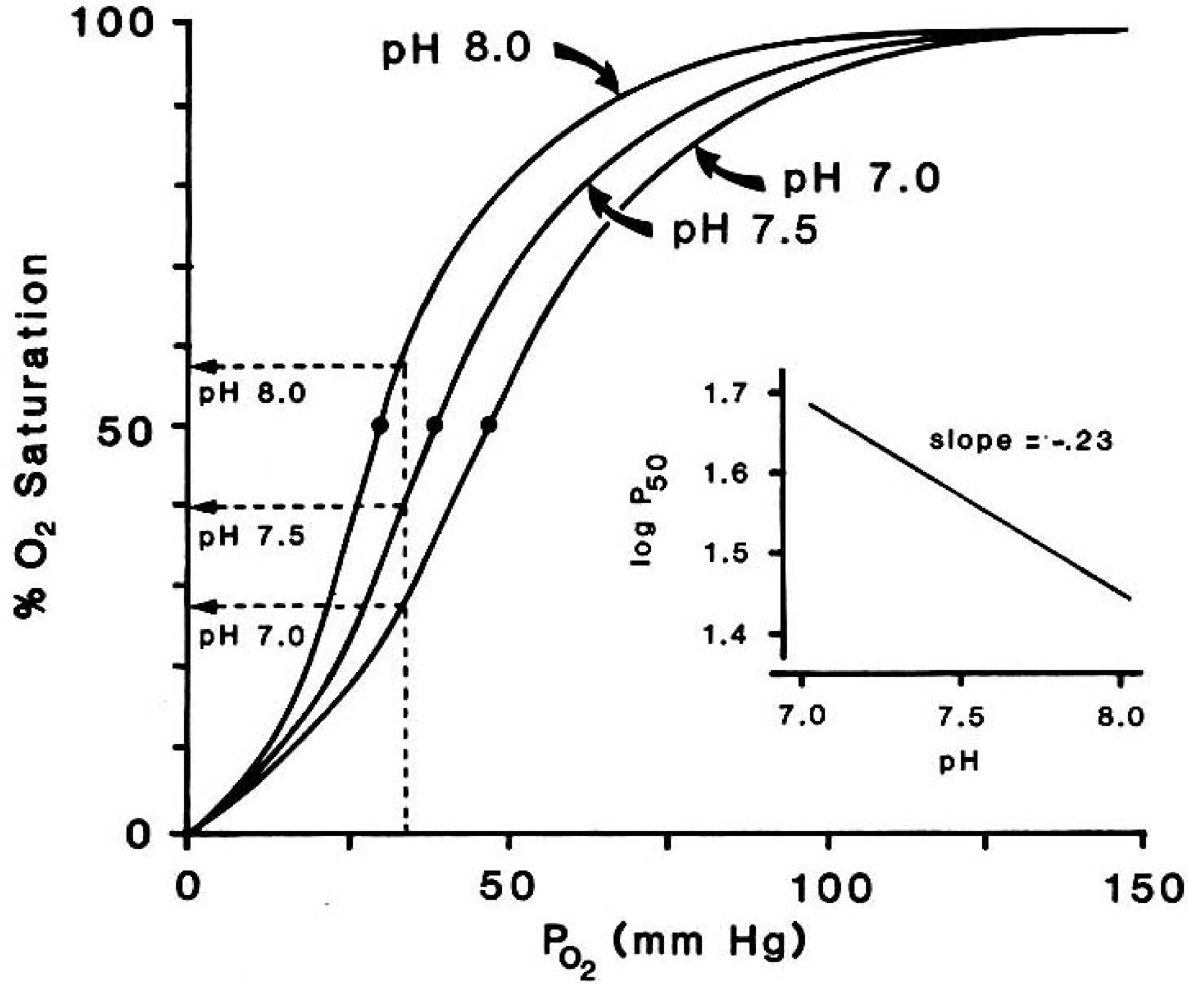
The affinity of an oxygen-binding pigment for O_2 is given as the P_{50}, the PO_2 required to saturate half the O_2 binding sites.



Oxygen Binding Curves

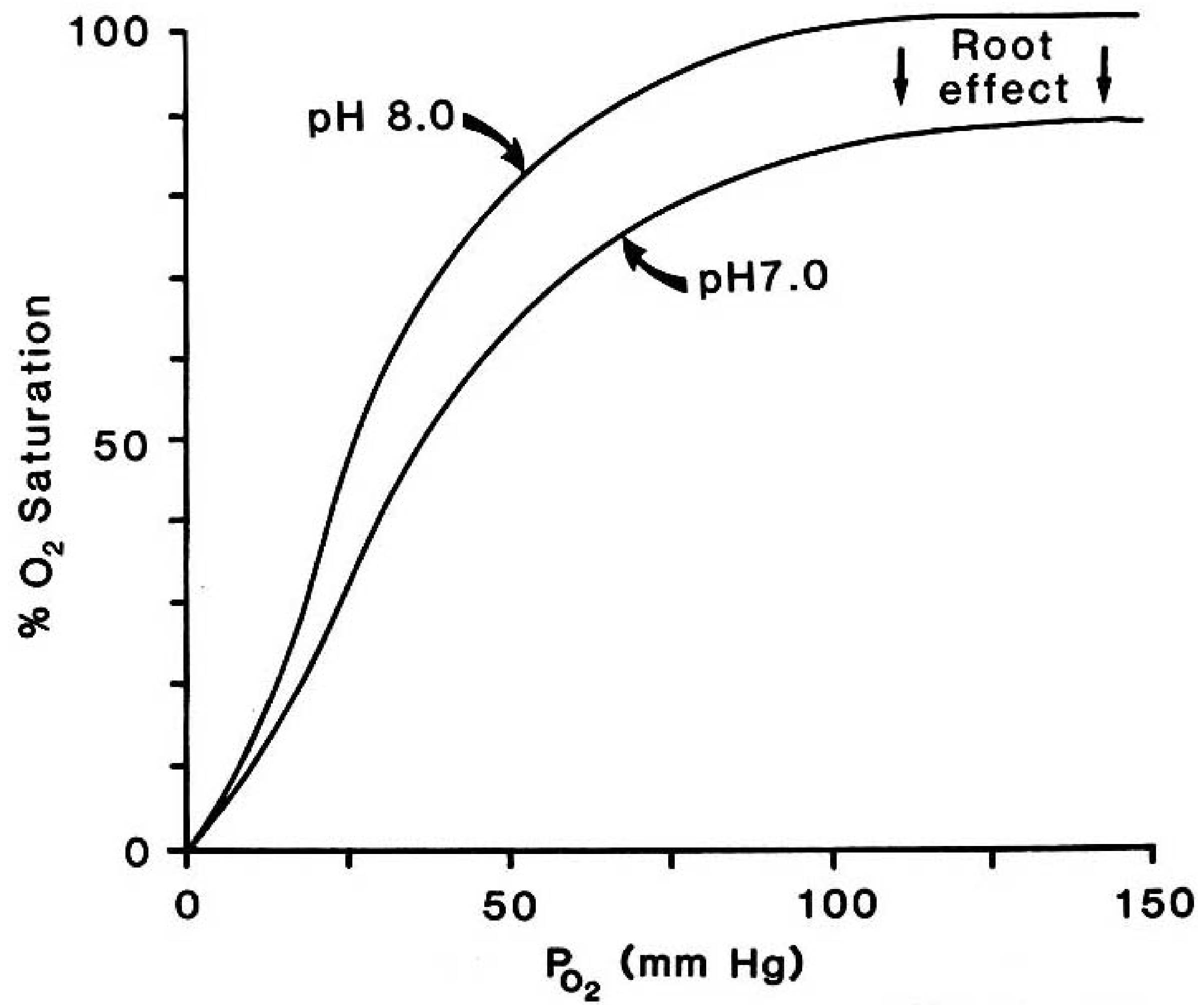


pH: THE BOHR EFFECT



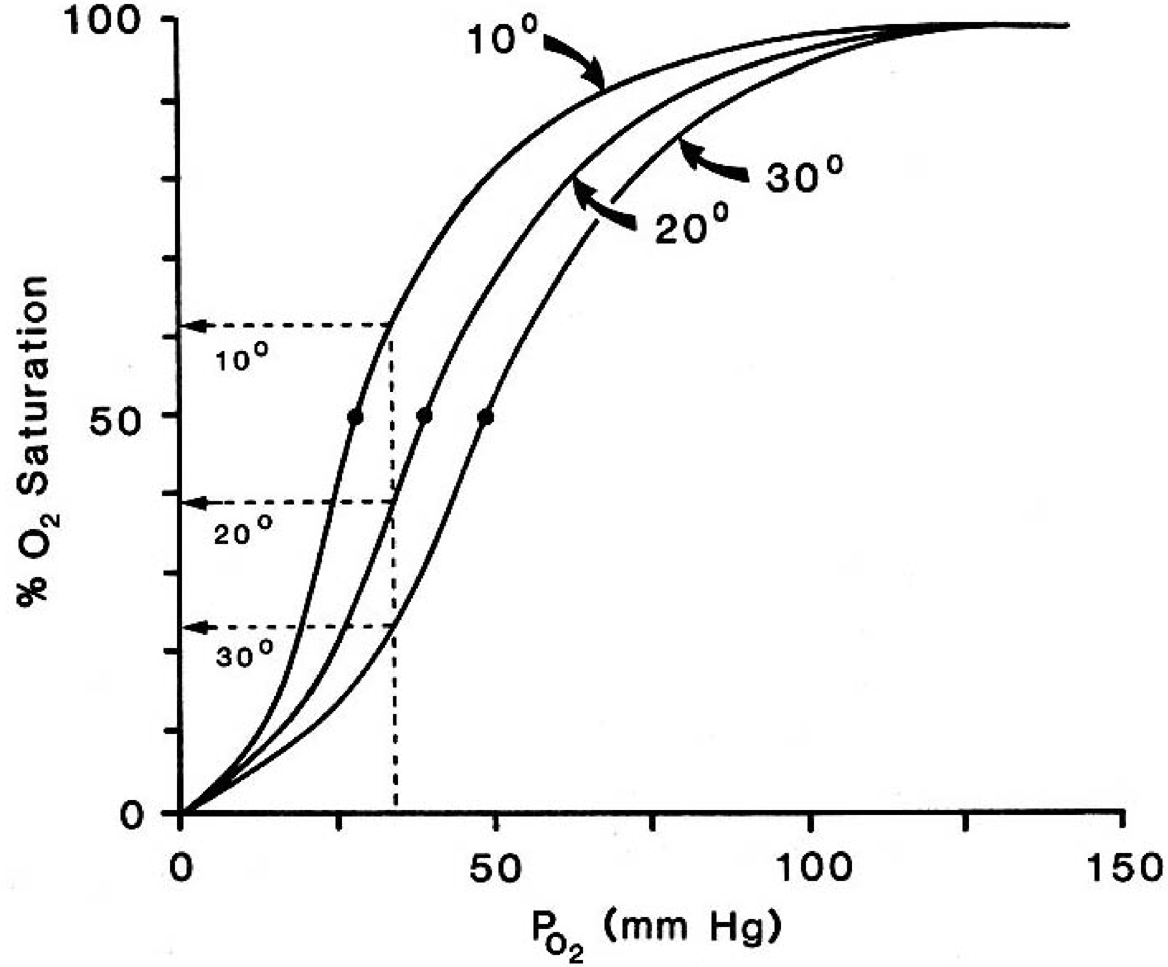
(From Burggren *et al.* 1993)

pH: THE ROOT EFFECT

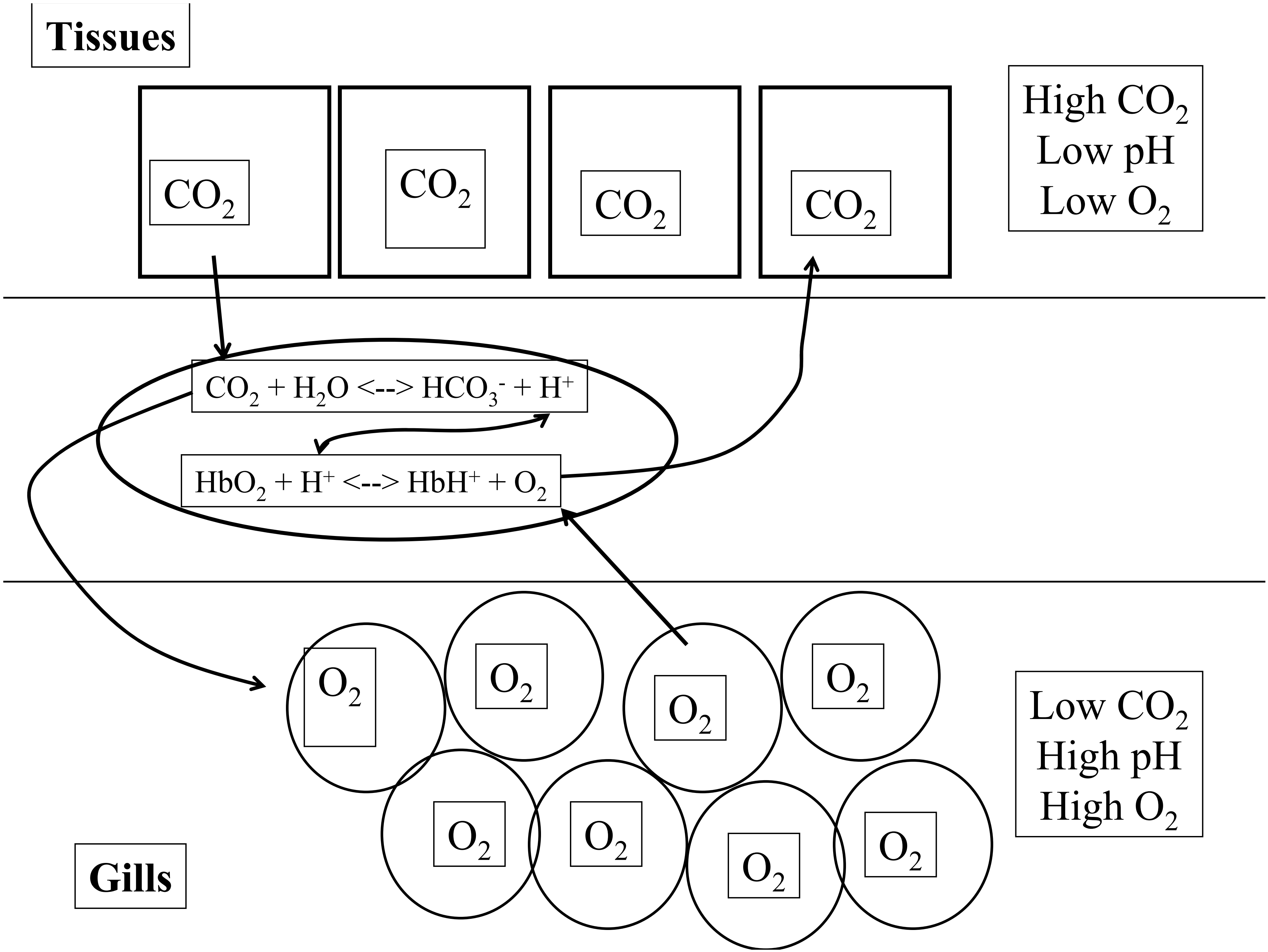


(From Burggren *et al.* 1993)

TEMPERATURE EFFECTS



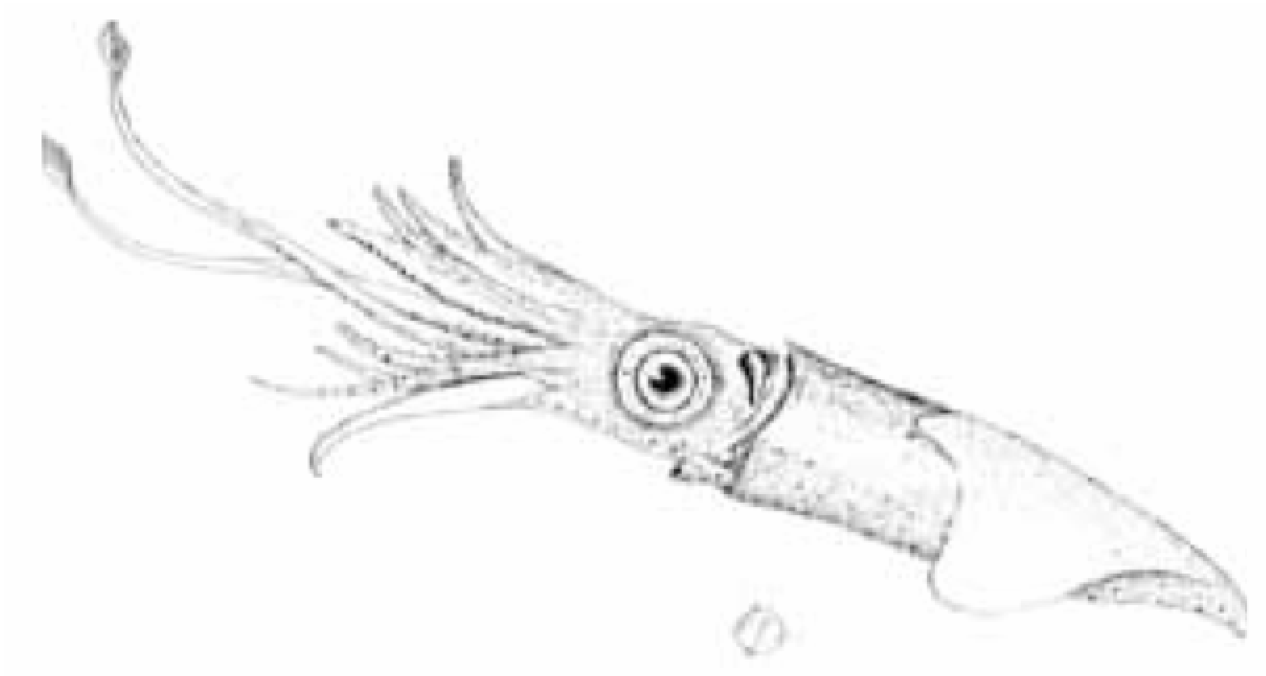
(From Burggren *et al.* 1993)


Tissues
CO2
CO2
CO2
CO2
High CO2
Low pH
Low O2
CO2 + H2O <--> HCO3- + H+
HbO2 + H+ <--> HbH+ + O2
O2
O2
O2
O2
O2
O2
O2
O2
Low CO2
High pH
High O2
Gills

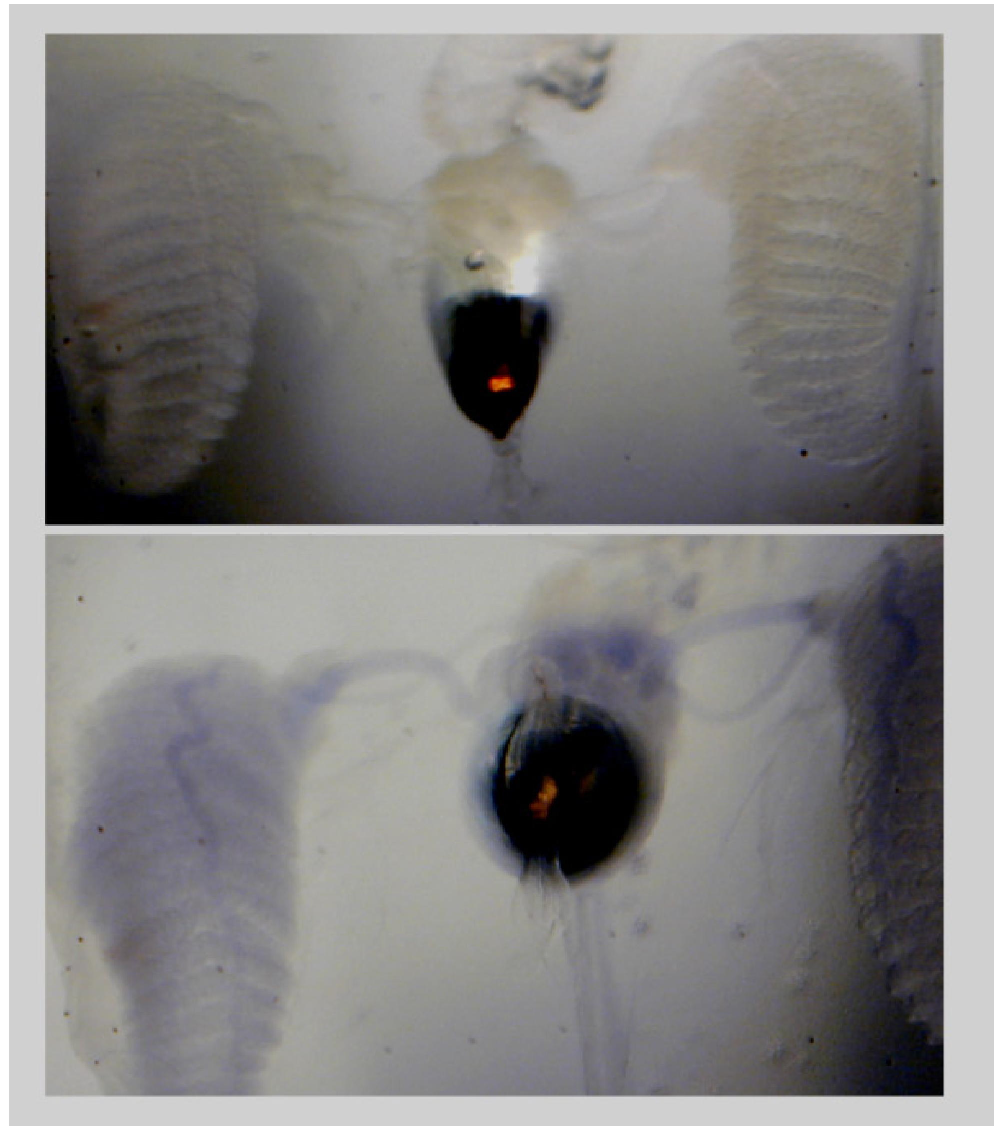
Squids as extreme animal models

"The fine-tuning of hemocyanin function underlines the dependence of squid on low environmental CO2"

Pörtner and Reipschläger, 1997



Squids as extreme animal models: "The edge of oxygen limitation"



-High O_2 Demand

-Low carrying capacity

-No venous reserve

Squids vs Fishes:
Similar thrust, less efficient

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

Fins move more water slowly

QuickTime™ and a
TIFF (Uncompressed) decompressor
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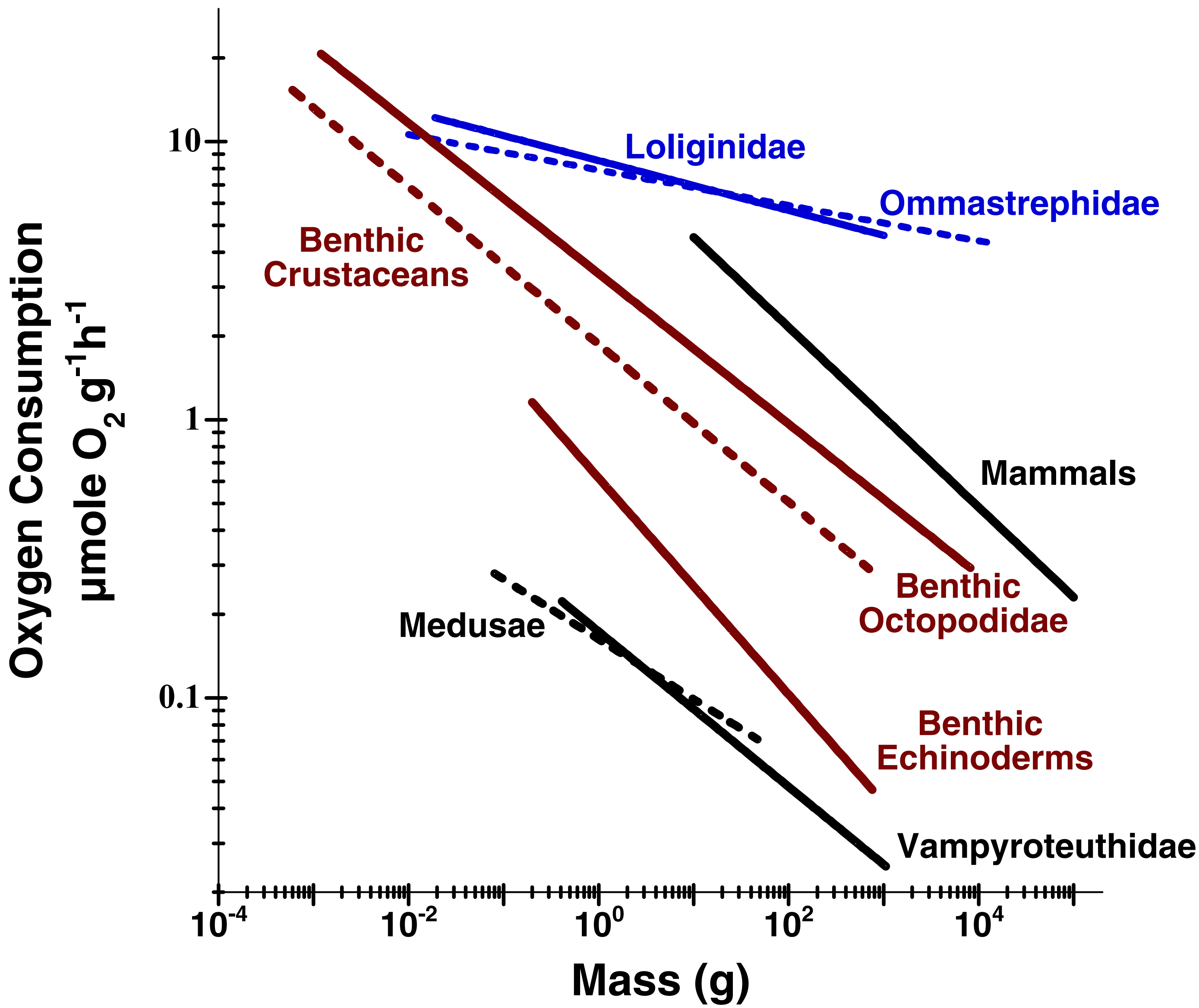
Jet propulsion moves less water at greater speeeds.

Squids must consume twice as much oxygen to go half as fast as a similar sized fish

-O'Dor and Webber, 1986

High metabolic rates in squids



Squids may operate at environmental limits of temperature, oxygen availability and body size

-Pörtner, 2002

Dosidicus gigas: Extreme animal in an Extreme Environment

QuickTime™ and a
H.264 decompressor
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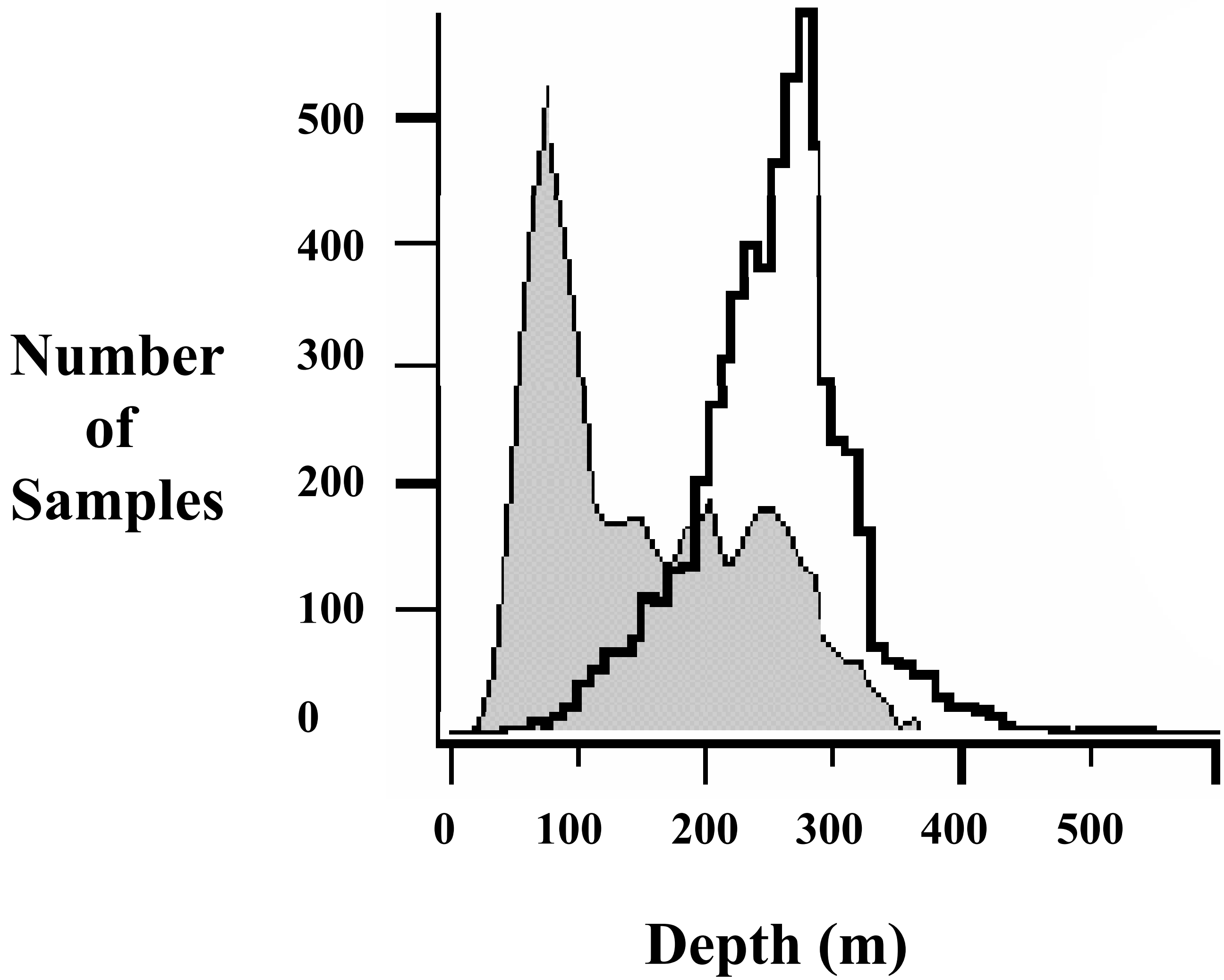
Day and Night Depth Distribution of *Dosidicus gigas*



Gilly et al., 2006, MEPS

Oxygen Minimum also a CO_2 *Maximum* Zone

pCO_2 (ppmv)

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decompressor
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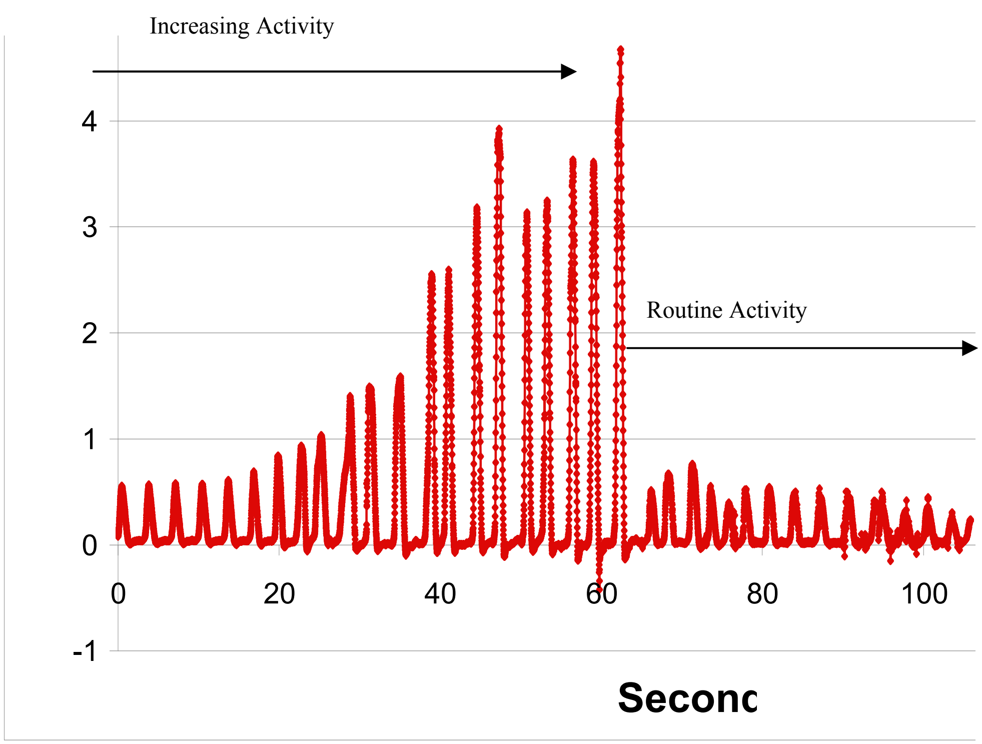
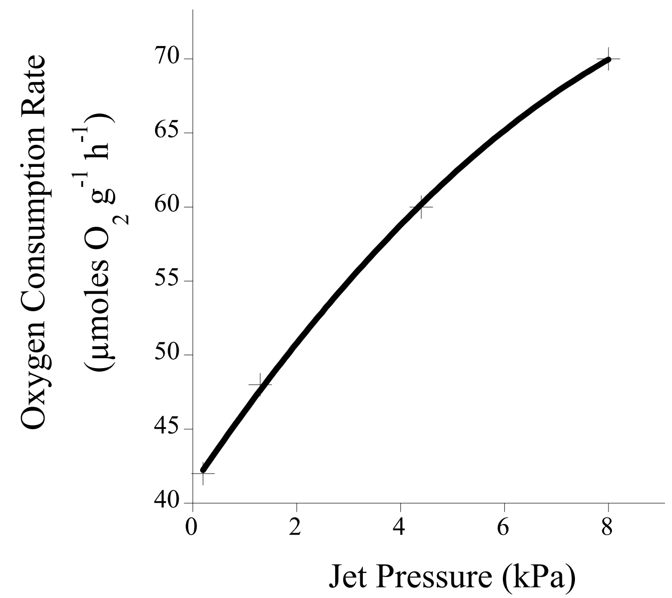
Depth (m)

HOtTUB
Humbolt Oxygen Temperature Utilization Basin

Generating Field Metabolic Rates

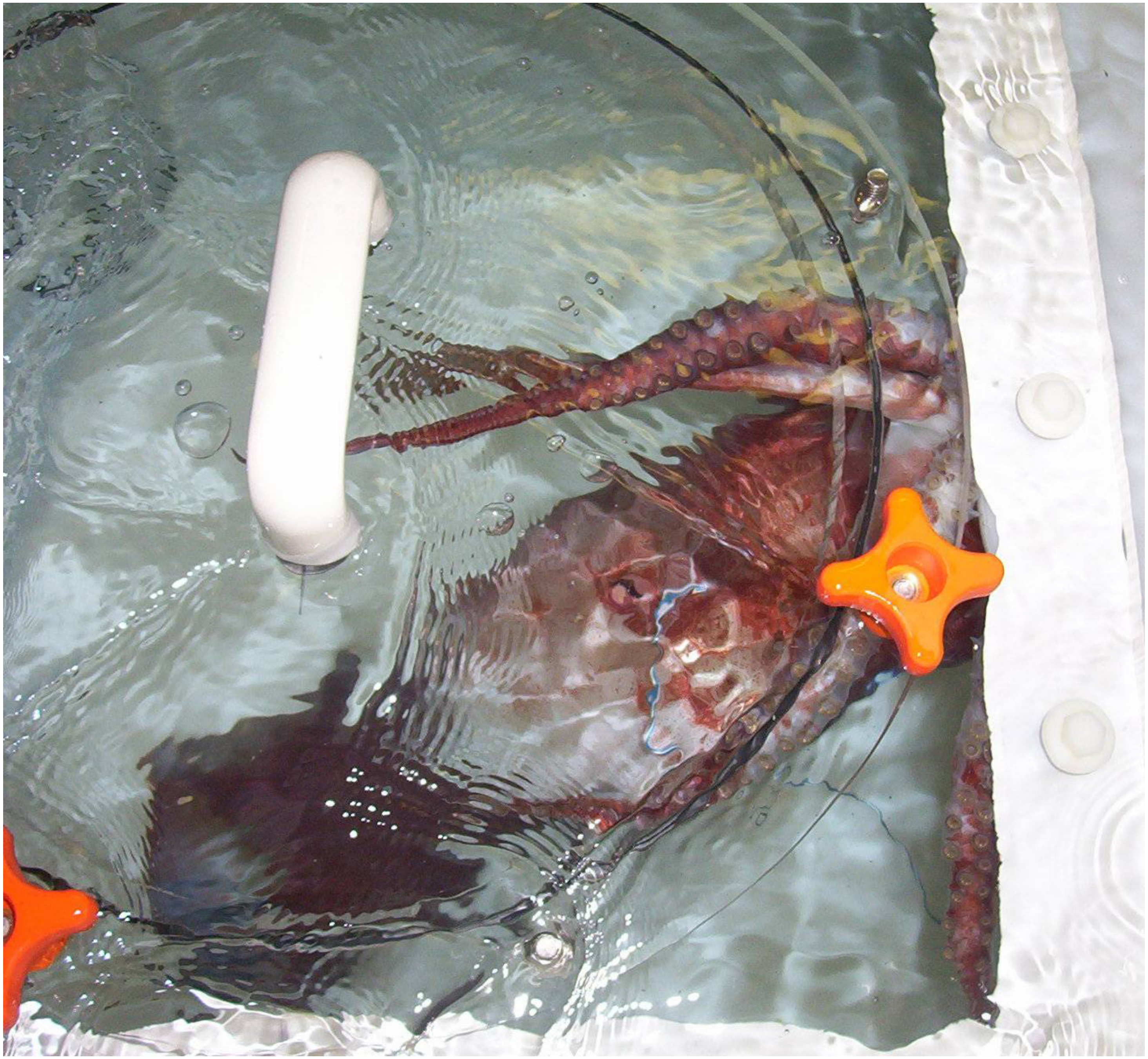




The pressure generated by mantle contractions during swimming is correlated with metabolism

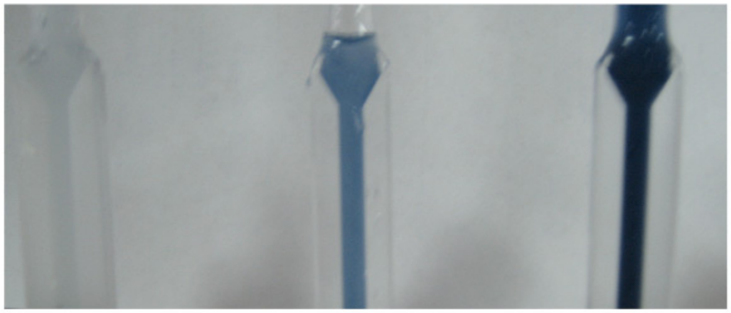
QuickTime™ and a
YUV420 codec decompressor
are needed to see this picture.

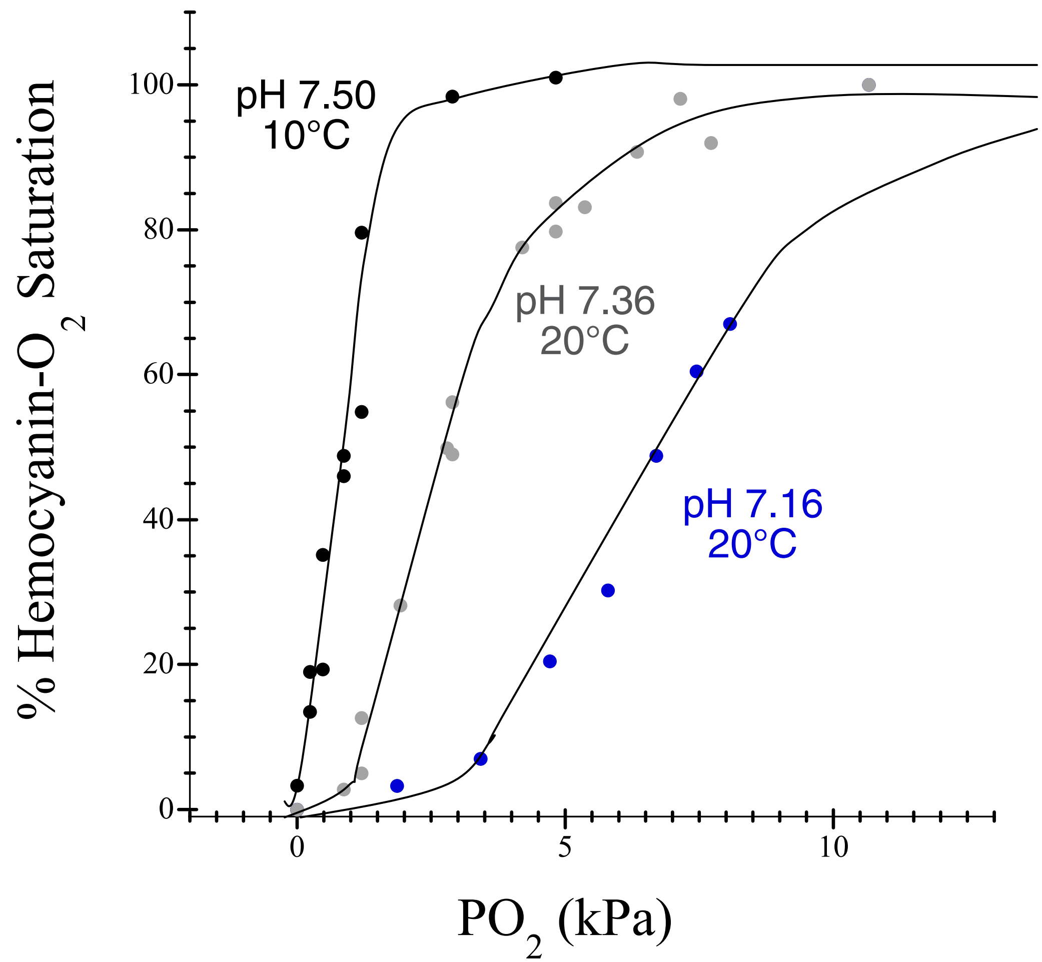

16 11:39PM



Dr. Rui Rosa

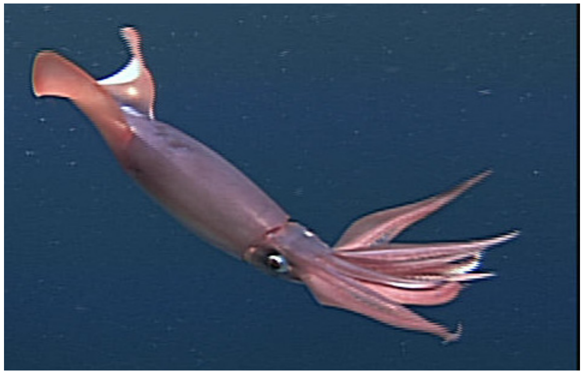
Metabolic depression at high CO_2?

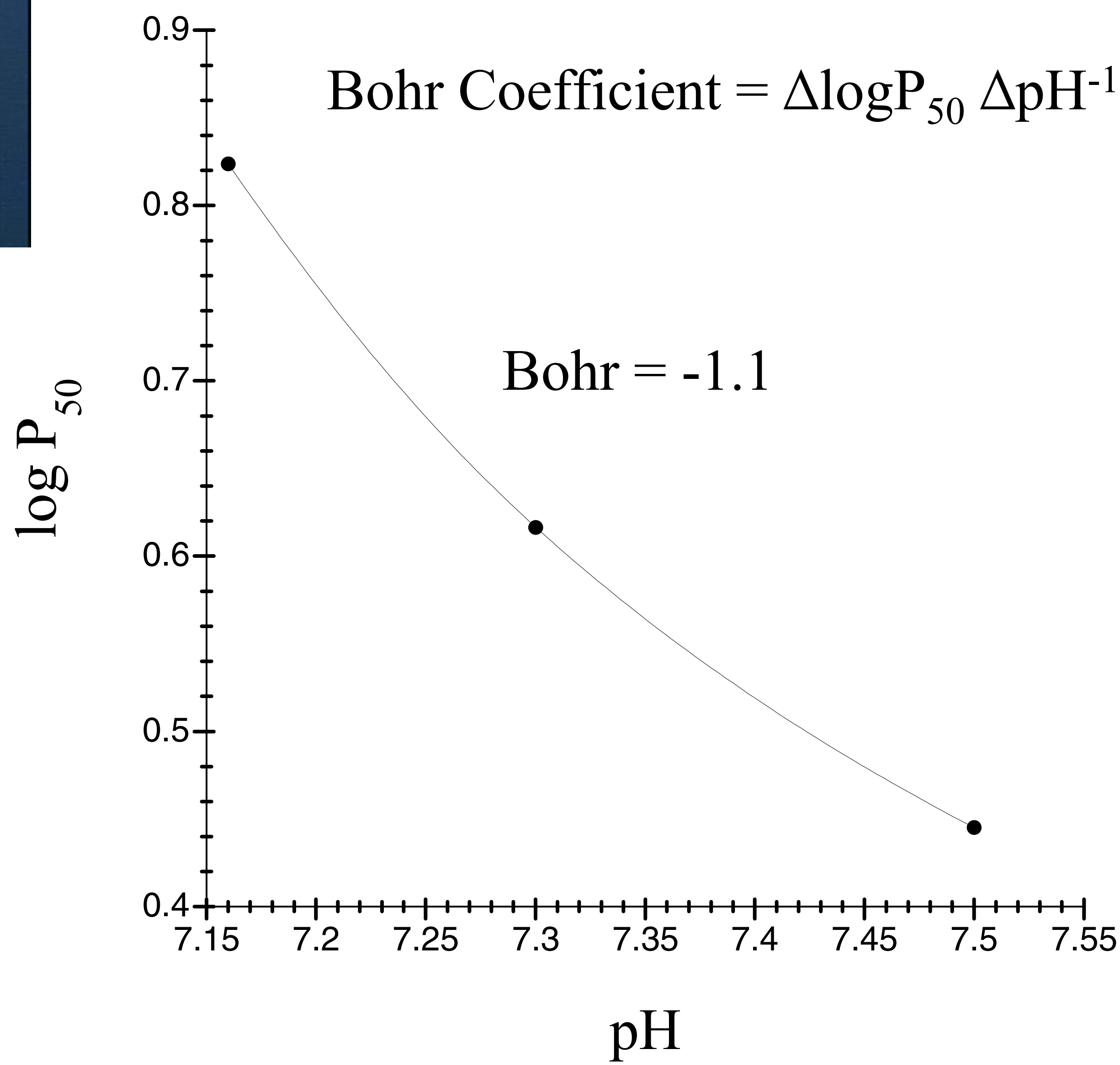


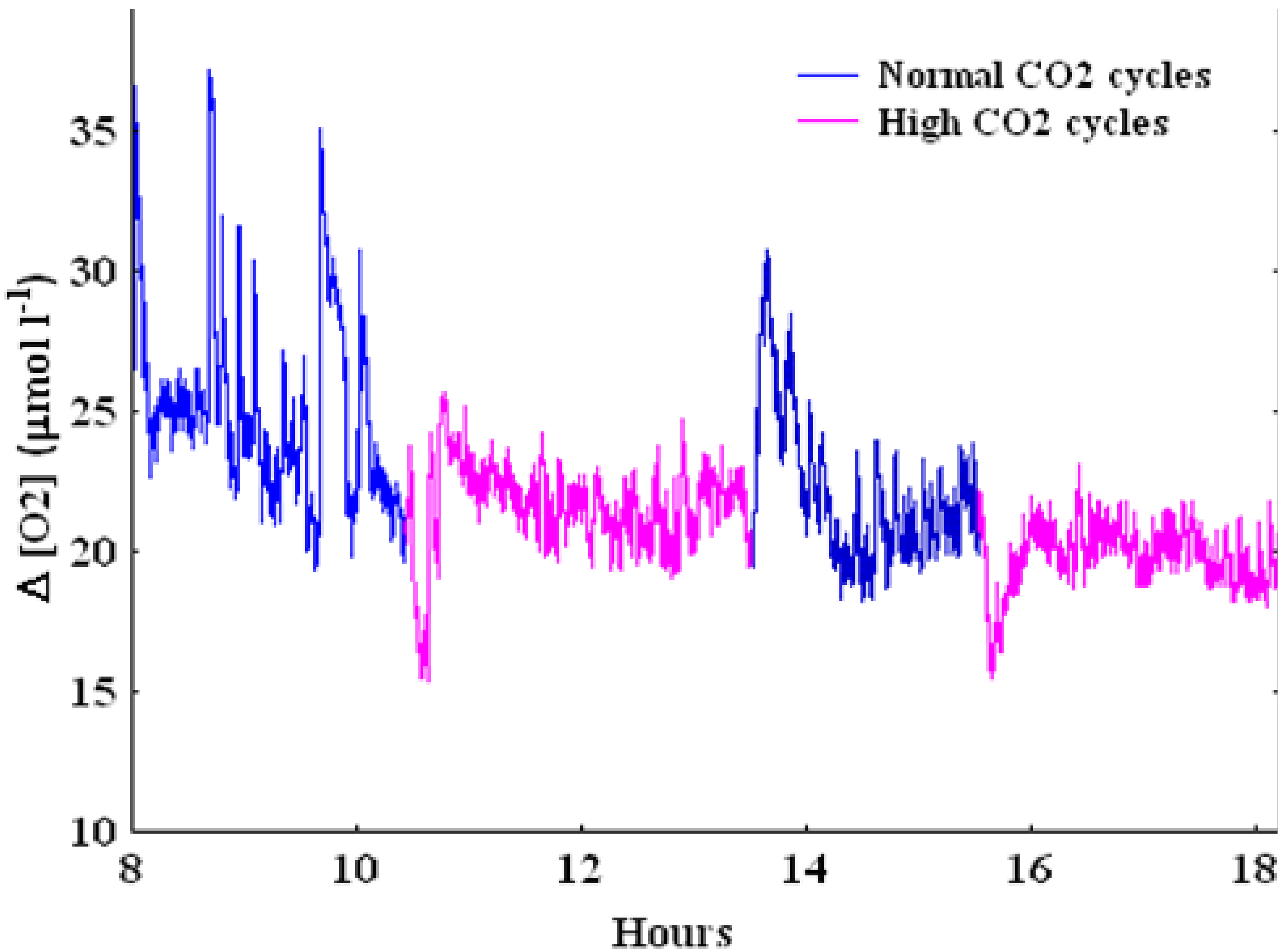


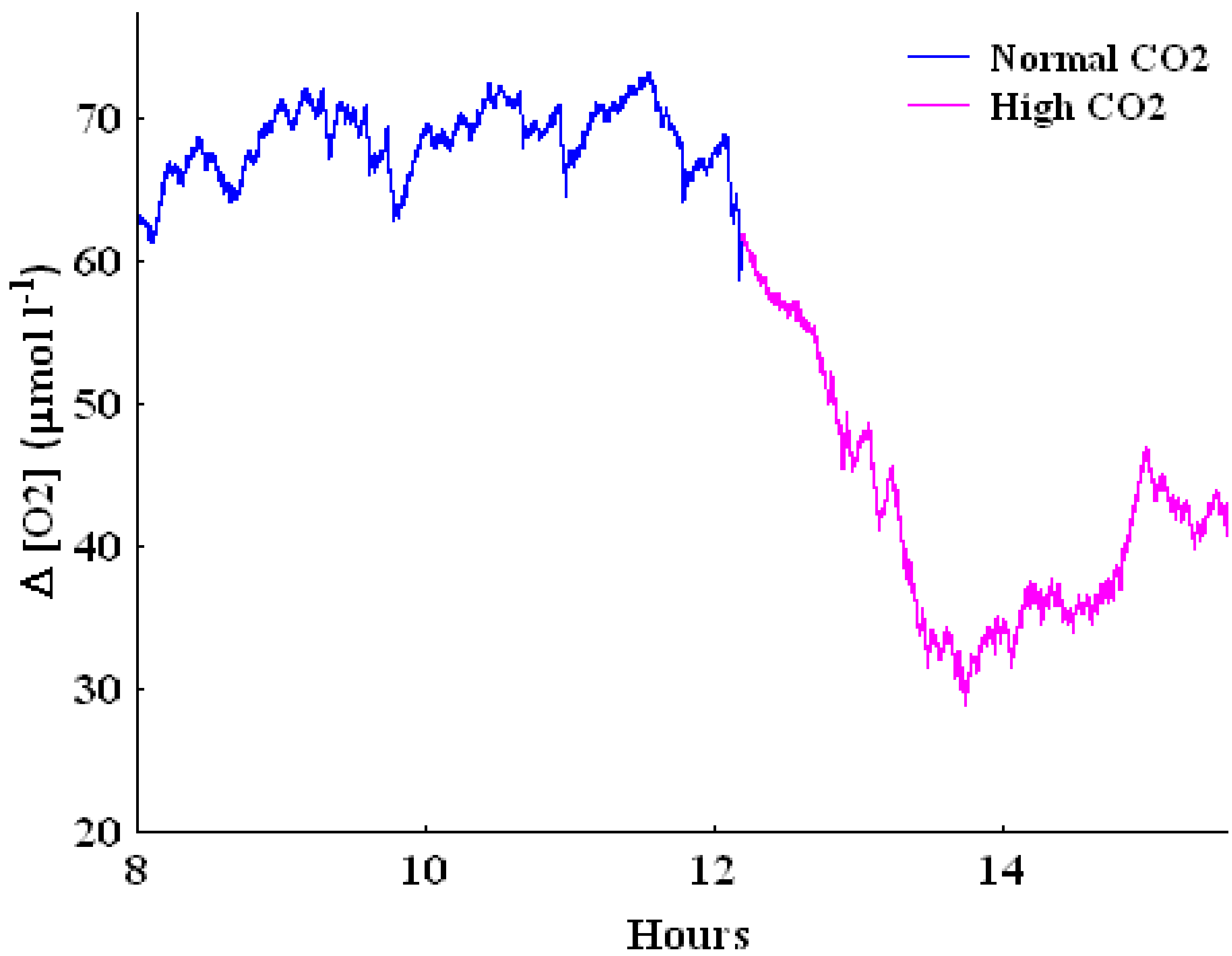
% Hemocyanin-O_2 Saturation
100
80
60
40
20
0
0
5
10
PO_2 (kPa)
pH 7.50
10°C
pH 7.36
20°C
pH 7.16
20°C

Highly pH-sensitive oxygen binding

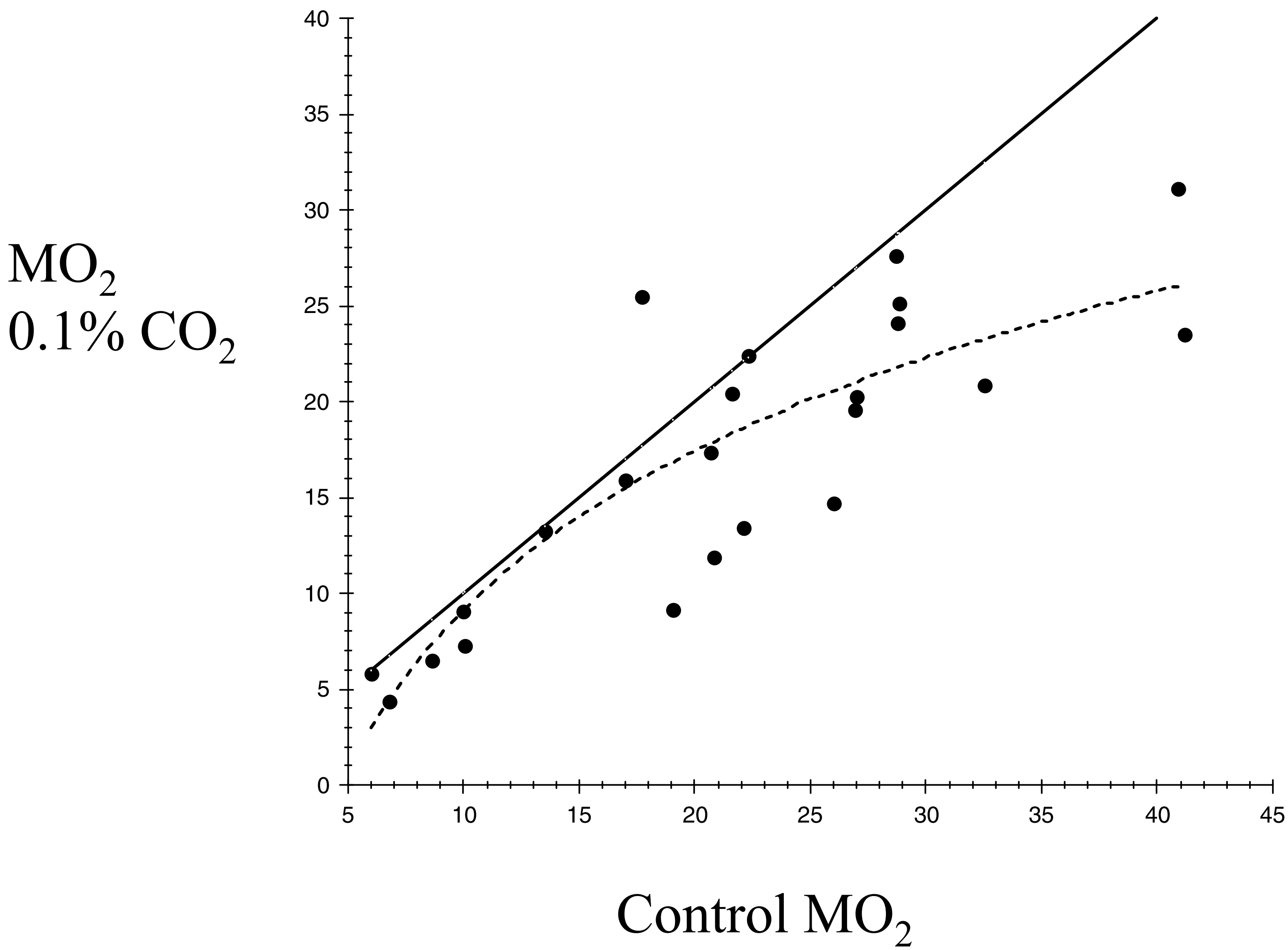




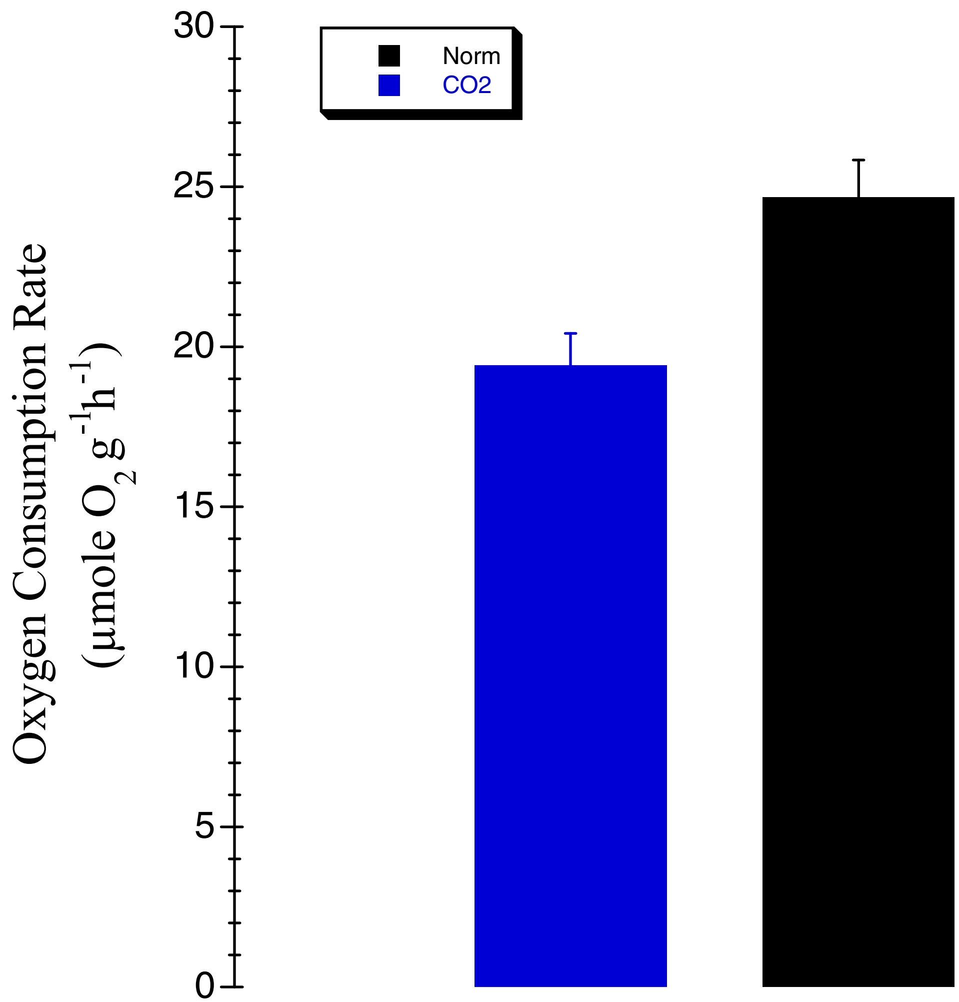

Normal CO2 cycles
High CO2 cycles
Δ [O2] (μmol l-1)
35
30
25
20
15
10
8
10
12
14
16
18
Hours


Normal CO2
High CO2
Δ [O2] (µmol l-1)
70
60
50
40
30
20
8
10
12
14
Hours

CO_2 effect on oxygen consumption rates
Most pronounced at high activity levels

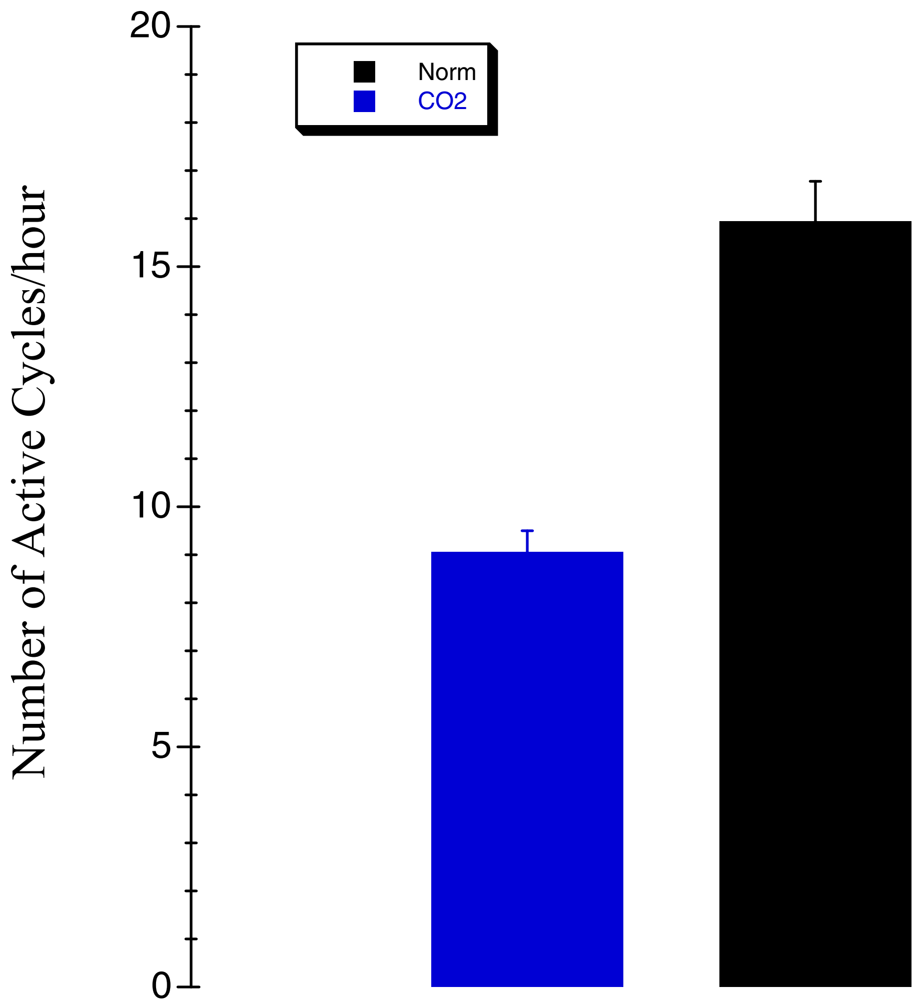


Metabolism is reduced at 0.1% CO2 and 20° C



Not significant at 10° C

Activity is reduced at 0.1% CO_2



The synergistic effect of these three climate-related variables (O_2, T°C and CO_2) may be to vertically-compress the habitable night-time depth range of the species

-Rosa and Seibel, 2009 PNAS

QuickTime™ and a
decompressor
are needed to see this picture.

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decompressor
are needed to see this picture.

QuickTime™ and a
decompressor
are needed to see this picture

ure.

$$C_{org} + O_2 \rightarrow CO_2$$

$$\Delta G = \Delta G° * \ln \{(fCO_2/(C_{org})(fO_2)\}$$

$$\mathrm{Log}_{10}\ (pO_2/pCO_2) = \text{Respiration Index}$$

"*A simple numerical constraint linearly related to available energy*"

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decompressor
are needed to see this picture

Two faulty assumptions:

1) That the respiration equation proceeds toward Equilibrium as if in a closed system.

2) That gas partial pressures inside cells resemble Those in the environment.

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decompressor
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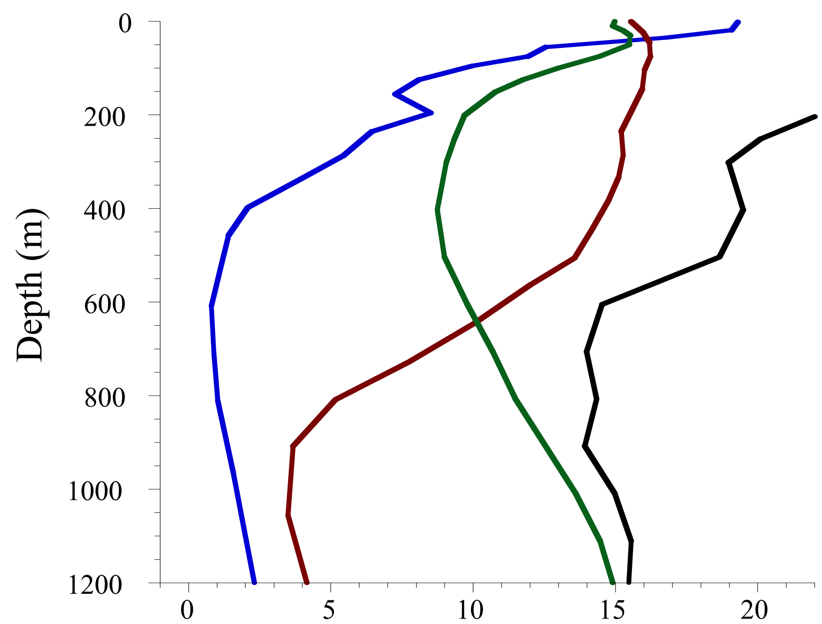
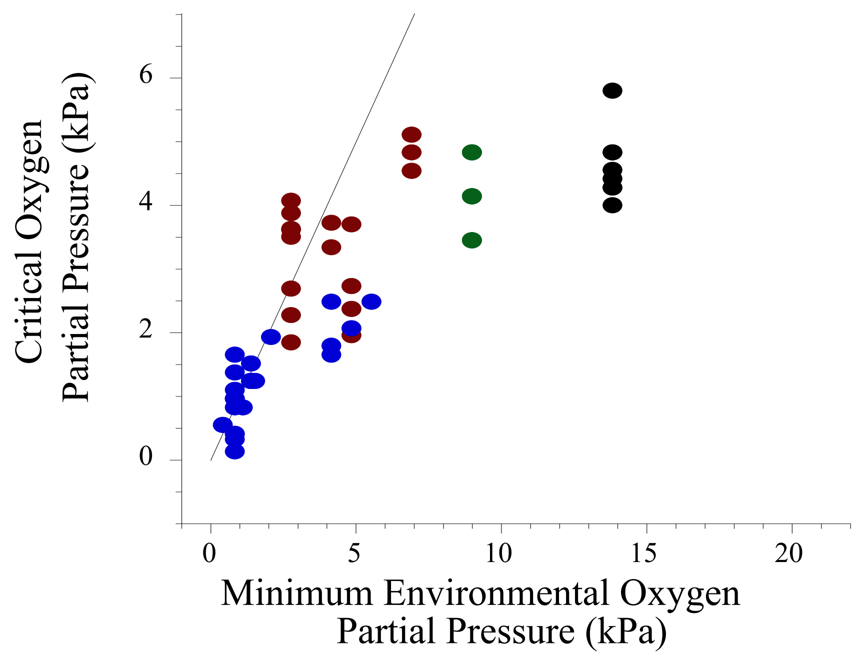
Leading to faulty conclusions:

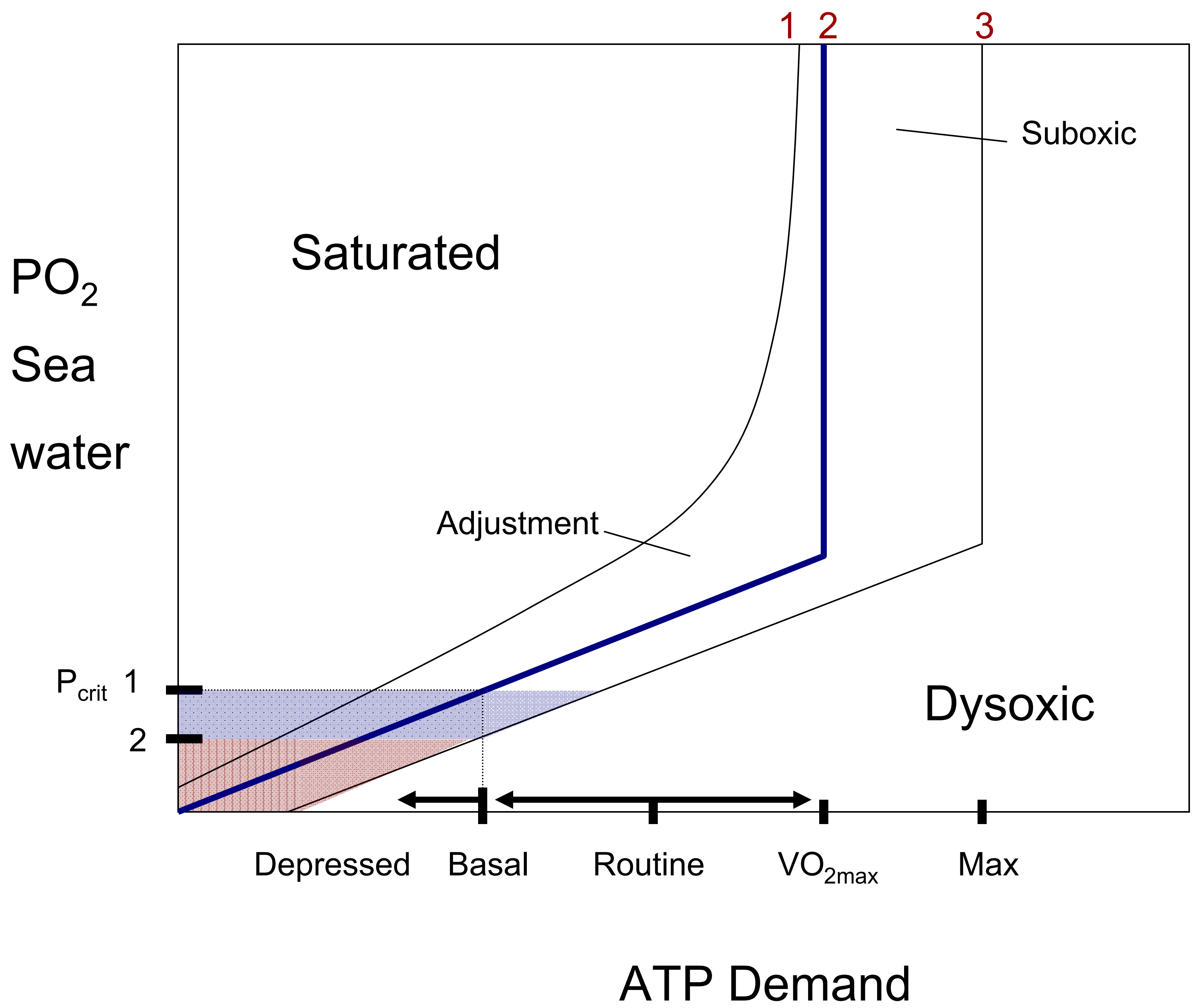
"For the vast areas of the ocean that are well-oxygenated, the rise in oceanic CO_2 concentrations will exert a negligible effect on the normal aerobic functioning of adult marine animals".

"Even if oxygen levels do not decline, the oceanic dead zones will expand as a result of rising CO_2 concentrations".

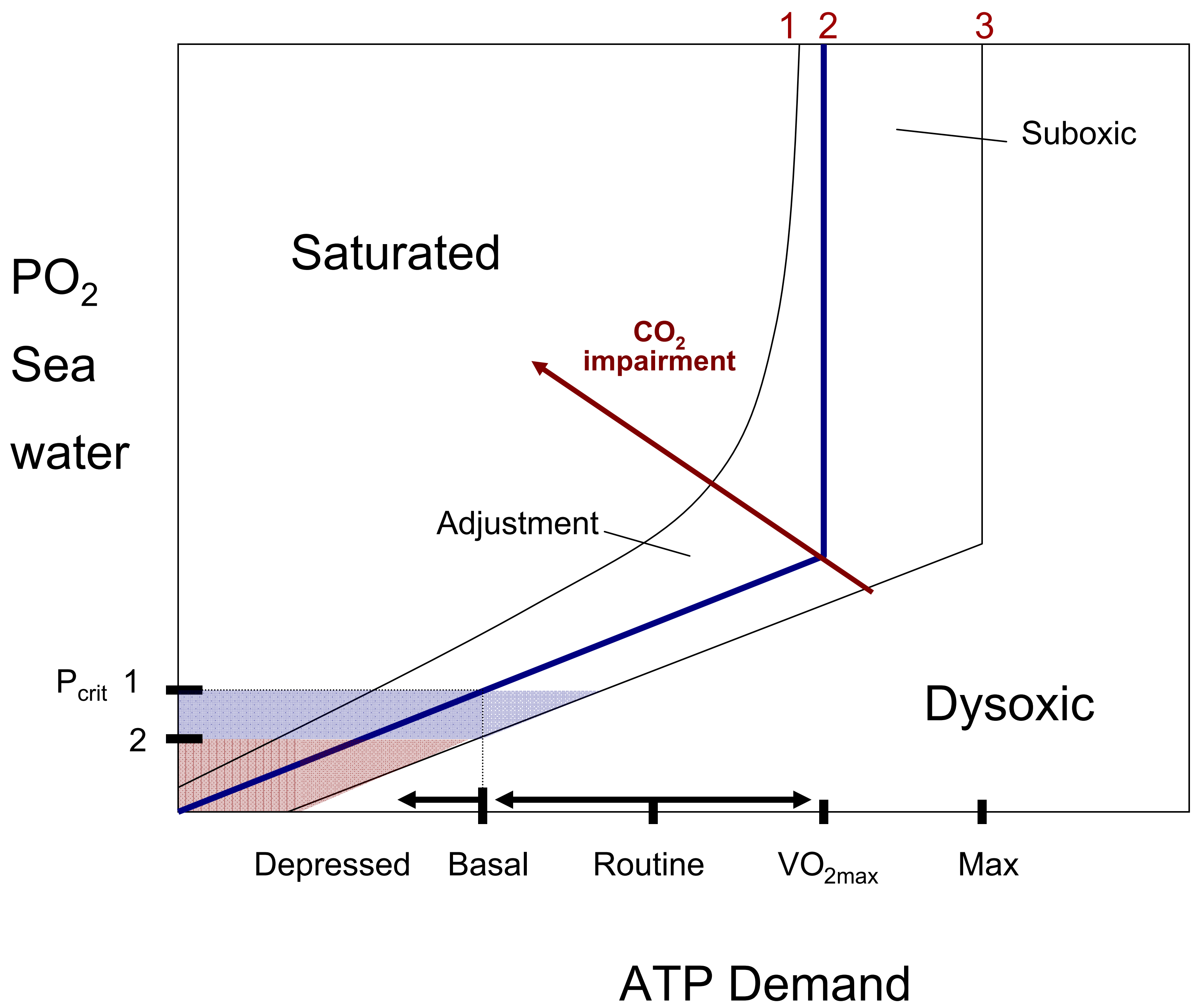
Evolved response to environmental oxygen







1
2
3
Suboxic
Saturated
PO2
Sea
water
Adjustment
Pcrit 1
2
Dysoxic
Depressed
Basal
Routine
VO2max
Max
ATP Demand



1
2
3
Suboxic
Saturated
PO2
Sea
water
CO2
impairment
Adjustment
Pcrit 1
2
Dysoxic
Depressed
Basal
Routine
VO2max
Max
ATP Demand

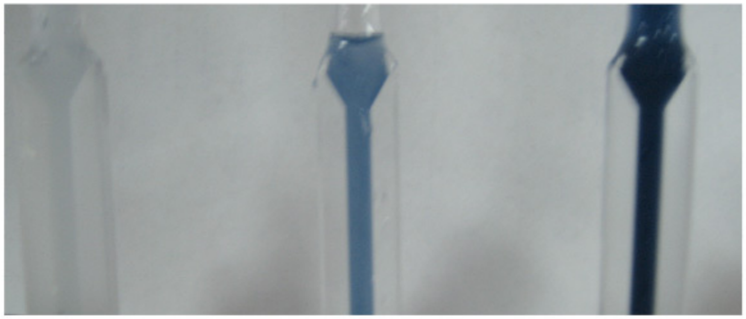
Ocean Acidification Research

What is the goal?

To determine critical CO_2 levels?

To demonstrate that CO_2 is a problem?

Funding to investigate interesting questions?



Dosidicus has high oxygen affinity

QuickTime™ and a
decompressor
are needed to see this picture.

Calcification

Controlled by $[CO_3^{=}]$? Or too simplistic?

QuickTime™ and a
decompressor
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