Ocean Acidification

And Animal Physiology

\[
\text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{HCO}_3^- + \text{H}^+
\]

\[
\text{pH} = \text{pK} + \log \frac{[\text{HCO}_3^-]}{[\text{CO}_2]}
\]
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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Buffering moderates pH imbalance on short term (minutes), ion transport compensates on longer time scales (hours-days).
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

Oxygen Consumption Rate (µmoles O₂ g⁻¹ h⁻¹)

Mass (g)

Seibel and Drazen 2007
Combating Acidosis

1. Buffering

H^+ + A^- → HA

CO_2 + H_2O ⇄ HCO_3^- + H^+

Histidine
Buffering Capacity is correlated with metabolic rate

Seibel and Walsh, 2003
\[ \text{pH} = \text{pK} + \log \left( \frac{\text{HCO}_3^-}{\text{CO}_2} \right) \]
Combating Acidosis

1. Buffering

2. Ion transport

\[ \text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{HCO}_3^- + \text{H}^+ \]

\[ \text{H}^+ + \text{A}^- \rightarrow \text{HA} \]

\[ \text{H}^+ \rightarrow \text{Na}^+ \]
Typical timecourse for acid-base compensation in the blood

Extracellular pH

$\text{HCO}_3^-$ (mmoles l$^{-1}$)

Ion Transport

Buffering

0.5

0

24
Log Carbonic anhydrase activity

Vents

Shallow

Deep (non-vent)

- bivalves
- worms
- crustaceans
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

-May enhance enzymes quantitatively or qualitatively
What about at a whole-organism level?

Energetics (Complex, interconnected processes)
Metabolic rate as a cost to organisms

“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

- Ion Transport
- Activity (muscle contraction)
- Synthesis
- SDA
How Do You Measure Metabolic Rate?

1. Duration of experiment (>12 hours)

2. Maintain oxygen well above critical PO\textsubscript{2} (species-specific)
   - P\text{crit} typically > 50% saturation
   - Respiratory quotient $\sim$0.7 to 1.0 (CO2:O2)

3. Temperature within habitat range ($Q_{10} = 2$-$3$)

4. Control activity level (Aerobic scope $\sim$ 5-10X)
   - Basal, Routine, Active, Maximal MR

5. Control feeding (SDA $\sim$ 2-5X BMR)

6. Chamber volume and flow are critical
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

Intermittent Flow
Measuring Metabolic Rates:
A manual for scientists

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

Anoxia tolerance (days) vs. ATP turnover (% control)
Oxygen-limitation of metabolism due to pH effect on protein
RESPIRATORY PIGMENT FUNCTION

- **O₂ Bound to Pigment**
- **Total O₂ Content of Blood**
- **O₂ Dissolved in Plasma (20 °C)**

Graph showing the relationship between **O₂ Content (vol %)** and **P₀₂ (mmHg)**.
Oxygen Binding Curves

The affinity of an oxygen-binding pigment for O₂ is given as the $P_{50}$, the PO₂ required to saturate half the O₂ binding sites.
Oxygen Binding Curves

% Hc-O₂
Saturation

Arteries
Veins (at rest)

Amount of O₂ unloaded to tissues

P₀₂ (mmHg)
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)
CO₂ + H₂O ⇌ HCO₃⁻ + H⁺

HbO₂ + H⁺ ⇌ HbH⁺ + O₂

Tissues

CO₂

CO₂

CO₂

CO₂

High CO₂
Low pH
Low O₂

Gills

O₂

O₂

O₂

O₂

Low CO₂
High pH
High O₂
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

Jet propulsion moves less water at greater speeds.

Fins move more water slowly.
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

![Graph showing oxygen consumption vs. mass for different groups of animals, including Loliginidae, Ommastrephidae, Benthic Crustaceans, Mammals, Medusae, Benthic Octopodidae, Benthic Echinoderms, and Vampyroteuthidae. The graph plots oxygen consumption (µmol O₂ g⁻¹ h⁻¹) against mass (g) on a log-log scale.]
Squids may operate at environmental limits of temperature, oxygen availability and body size

-Pörtner, 2002
Dosidicus gigas: Extreme animal in an Extreme Environment
Day and Night Depth Distribution of *Dosidicus gigas*

Gilly et al., 2006, MEPS
Oxygen Minimum also a \( \text{CO}_2 \) Maximum Zone

\[
p\text{CO}_2 \ (\text{ppmv})
\]

QuickTime™ and a decompressor are needed to see this picture.
HOTUB
Humbolt Oxygen Temperature Utilization Basin
The pressure generated by mantle contractions during swimming is correlated with metabolism.
QuickTime™ and a YUV420 codec decompressor are needed to see this picture.
Dr. Rui Rosa
Metabolic depression at high $CO_2$?
Highly pH-sensitive oxygen binding

Bohr Coefficient = $\Delta \log P_{50} \Delta \text{pH}^{-1}$

Bohr = -1.1
\textbf{CO}_2 \text{ effect on oxygen consumption rates}

*Most pronounced at high activity levels*

\begin{center}
\begin{tikzpicture}
\begin{axis}[
    xlabel={Control MO$_2$},
    ylabel={MO$_2$},
    xmin=5, xmax=45,
    ymin=0, ymax=40,
    xtick={5,10,15,20,25,30,35,40},
    ytick={0,5,10,15,20,25,30,35,40},
    xticklabels={5,10,15,20,25,30,35,40},
    yticklabels={0,5,10,15,20,25,30,35,40},
    legend pos=north east,
]

% Control MO2 line
\addplot coordinates {
(5,5)
(10,10)
(15,15)
(20,20)
(25,25)
(30,30)
(35,35)
(40,40)
};

% 0.1% CO2 line
\addplot coordinates {
(5,5)
(10,10.5)
(15,16)
(20,21.5)
(25,27)
(30,32.5)
(35,38)
(40,43.5)
};

% Control MO2 marks
\addplot[only marks] coordinates {
(5,5)
(10,10)
(15,15)
(20,20)
(25,25)
(30,30)
(35,35)
(40,40)
};

% 0.1% CO2 marks
\addplot[only marks] coordinates {
(5,5.5)
(10,10.5)
(15,16)
(20,21.5)
(25,27)
(30,32.5)
(35,38)
(40,43.5)
};

\legend{Control MO$_2$, 0.1\% CO$_2$}
\end{axis}
\end{tikzpicture}
\end{center}
Metabolism is reduced at 0.1% CO₂ and 20°C.

Oxygen Consumption Rate (µmole O₂·g⁻¹·h⁻¹)

Not significant at 10°C.
Activity is reduced at 0.1% $CO_2$
The synergistic effect of these three climate-related variables (\(O_2\), \(T \, ^\circ C\) and \(CO_2\)) may be to vertically-compress the habitable nighttime depth range of the species

-Rosa and Seibel, 2009 PNAS
QuickTime™ and a decompressor are needed to see this picture.
C_{org} + O_2 \rightarrow CO_2

\Delta G = \Delta G^\circ * \ln \left\{ \frac{f_{CO_2}}{(C_{org})(f_{O_2})} \right\}

\log_{10} (p_{O_2}/p_{CO_2}) = \text{Respiration Index}

“A simple numerical constraint linearly related to available energy”
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.
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
ATP Demand

PO$_2$
Sea water

Saturated

Suboxic

Dysoxic

Depressed Basal Routine VO$_2$max Max

CO$_2$ impairment

Adjustment

P$_{crit}$ 1 2

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 $[\text{CO}_3]^{-}$? Or too simplistic?