The effects of ocean acidification on organisms: an ecophysiological perspective

Jim Barry, MBARI, UCSC, 2011

- Ocean acidification, warming, hypoxia related to $CO_2$ emissions
- Environmental changes can affect the physiological performance of many marine organisms
- Potential for large effects on ocean ecosystems and society
CO$_2$ emissions cause Ocean Acidification.
Change in ocean pH over 25 million years

- Estimated from boron isotopes in seabed foraminifera
- Note speed and size of current pH change

Turley et al 2005
A worrisome storyline

Rising atmospheric CO₂

Decreasing ocean pH, Ω, [CO₃²⁻]

Altered physiology, population changes

Changing benefits

Food web changes, ecosystem shifts

Socioeconomic consequences
How do animals cope with changing ocean conditions?

- Migration
- Acclimation
- Adaptation
- Extinction

What to do..?
Environmental Stress, Ecosystems, and Society

Ocean Acidification
Warming
Hypoxia

Physiological processes (acclimation)
Metabolic Performance
Survival Growth Reproduction

Abundance Distribution Productivity
Biological Interactions (food web)
Energy Flow

Ecosystem Function
Resilience
Stability
Productivity

Fisheries
Other Ecosystem Services
Physiological processes affected by high CO₂

- Photosynthesis
- Calcification
- Respiration
- Acid - Base Balance
- Metabolic Rate

Vampire Squid
Stress increases the 'cost of living'

Energy budgets - If the cost of living (e.g. shells) increases, less is available for growth and reproduction.
Reduced Calcification

Environmental hypercapnia may affect calcification for many species

- Clams, snails, sea stars, urchins, crabs, shrimps, corals, ...
- Calcareous echinoderms largely absent from vent sites

Riebesell et al 2000
Calcification is most costly in a high CO2 ocean

Model of Coral Calcification

Brownlee, 2009
What is Coral Bleaching?
Threshold temperature – above which bleaching manifests itself (1-2°C above the long-term summer maximum temperatures)

WHAT DOES THE FUTURE HOLD?

Hoegh-Guldberg (1999)
Coral calcification is reduced in high-CO2 ocean

Low aragonite saturation associated with low calcification rate

Hoegh-Guldberg et al. 2007
Ocean chemistry and the future of coral reefs?

Predicted aragonite saturation ($\Omega$) [a measure of the amount of minerals available to make coral skeletons] is shown over a global map of existing coral reef locations (pink dots) for various atmospheric CO2 levels. Note that $\Omega$ decreases drastically with higher CO2 levels.

280 ppm is the preindustrial level of CO2 in the atmosphere. During 2011 CO2 is ~390 ppm. Most climate models indicate that we will reach ~800 ppm CO2 by 2100.

Corals grow best when carbonate minerals are abundant ($\Omega >3$), and cease to grow at low mineral levels ($\Omega \sim 2$) and can dissolve at very low levels ($\Omega < 1$).

On the right, there is a count of the mineral conditions for the locations of all global coral reefs. Note that the preindustrial climate (280 ppm CO2) all reef locations had mineral conditions favorable to growth (high $\Omega$). As CO2 levels rise through this century, ALL existing reef are expected to have marginal or poor conditions for coral growth.

Cao and Caldeira 2008
Are $CO_2$-related stresses severe for deep-sea animals?

Deep-Sea Animals

1. Reduced metabolic rates
2. Reduced enzyme function
3. Evolved in highly stable deep-sea environment
4. Food-limited –
   "Living on the edge"

Deep-sea Octopus
Deep-Sea CO$_2$ - Release Experiments

- 3600 m (~12,000 ft.)
- Effects of CO$_2$-rich seawater on animals
- Initial studies of effect of deep-sea CO$_2$ storage
Depth-related trends in O2, T, pH

Oxygen & Temp. vs. Depth

Oxygen (ml/l) or Temp. (C)

pH variation in the Pacific Ocean

pH

Future Ocean

Depth (m)

Depth (m)

Oxygen (ml/l) or Temp. (C)

- Temperature
- North Pacific
- California Current
- North Atlantic

Central Pacific
- Western Pacific
- North Pacific
- Antarctic Pacific
- Eastern Pacific
Are $CO_2$-related stresses severe for deep-sea animals?

- Strong A-B regulation evolves in aquatic animals from naturally variable environments
- The deep sea is one of the most invariant environments on Earth

**General hypothesis:** Hypometabolic deep-sea animals will be particularly sensitive to respiratory acidosis associated with hypercapnia
Controlled-gas Aquarium System for lab-based studies of CO$_2$ tolerance

Barry et al. 2008
Acid-Base Regulation in Crabs

- Deep-sea vs. shallow-living crab
- Normoxic vs. hypoxic conditions

**Chionoecetes tanneri**
The grooved Tanner crab
(~ 500 to 1500 m)

**Cancer magister**
The Dungeness crab
(~ 10 to 200 m)

- Metabolic Rates
- Acid-base regulatory capacity
- Ion exchange
- Role of oxygen
Metabolic rates

- Crabs collected from field (tanner crab) or purchased (dungeness)
- Acclimated to 95% O2 saturation, in situ temperature (3.5, 10 C) for 3 weeks
- Metabolic rates measured in closed cell respirometers

**Metabolic Rates**

Dungeness = 4.5 X Tanner
Acute (24 h) High-Level (~ 1% CO2) Hypercapnic Exposure

Experimental Conditions
- Atmospheric pressure
- 3.5°C Tanner
- 10°C Dungeness
- 95% O2 saturation
- 3 weeks acclimation
- Hemolymph sampled through carapace above heart
Dungeness crab is tolerant of CO₂ stress

Effects of ambient oxygen levels?

Pane and Barry, 2007
### Hypercapnic compensation after 24 h

<table>
<thead>
<tr>
<th></th>
<th>Tanner, High O₂</th>
<th>Dungeness</th>
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<tbody>
<tr>
<td><strong>pH Drop</strong></td>
<td>0.32 units</td>
<td>0.08 units</td>
</tr>
<tr>
<td><strong>Increase in [H⁺]</strong></td>
<td>111%</td>
<td>21%</td>
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<tr>
<td><strong>Increase in [HCO₃⁻]</strong></td>
<td>28%</td>
<td>174%</td>
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![Tanner crab](image1.jpg) ![Dungeness crab](image2.jpg)
Hypoxia reduces hypercapnic compensation

“High” O$_2$ (95% saturation) (Hyperoxia) vs. “Low” O$_2$ (10-15% saturation) (In situ)
# Hypercapnic compensation after 24 h

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<td>0.08 units</td>
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<td>140%</td>
<td>111%</td>
<td>21%</td>
</tr>
<tr>
<td><strong>Increase in [HCO₃⁻]</strong></td>
<td>-3.9%</td>
<td>28%</td>
<td>174%</td>
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Post-branchial Ion Exchange

- Hypercapnia inhibits ATPase activity
  - Dungeness only

- Dungeness > High O2 Tanner
  - Ion transport more effective in dungeness

- High O2 Tanner ~ > Low O2 Tanner
  - Ion transport in tanner too energetically costly?

**Carbonic anhydrase activity**

<table>
<thead>
<tr>
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<th>Muscle</th>
<th>Heart</th>
<th>Posterior Gill</th>
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<tr>
<td>Dungeness (C. magister) normoxia</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tanner (C. tanneri) Hypoxia</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Posterior Gill**

- Total ATPase
  - Control
  - CO₂

- Na⁺-K⁺-ATPase
- Amiloride-sensitive ATPase

**Carbonic Anhydrase Activity**

- Mol H⁺ mg protein⁻¹ min⁻¹
Tanner Crab: HCO₃⁻ infusion helps pH compensation

8 days of recovery after postbrachial infusion (low O₂)

- HCO₃⁻ elevation not sustainable
- Weak pH compensation after 8d
Conclusions – Crab physiology

Deep vs. Shallow Habitats

• Acid-base regulation in hypometabolic deep-sea crabs is weak
  - Shallow water crab compensated in 24 h, but little recovery in deep crab

• Supports hypothesis of slow ion exchange at gill in deep-sea animals
  - Reduced rates of key enzymes in deep-sea animals
  - Ion-regulation is energetically costly, difficult for hypometabolic taxa

Effects of Oxygen

• Hyperoxia led to improved extracellular pH compensation, bicarbonate accumulation.
  - Oxygen limitation on metabolic rate may be responsible.

• Synergistic effects of hypercapnia and hypoxia for A-B regulation indicates potential for greater OA related stress in future
Deep-Sea Urchins to are vulnerable to ocean acidification

Allocentrotus fragilis
Measuring sea urchin respiration rates in the deep-sea
Urchins are oxygen-stressed in the OMZ

Given more oxygen, respiration increases

Fragile Urchin – Allocentrotus californiensis
Expansion of hypoxia likely to affect deep-sea urchins and other animal populations

Urchin $O_2$ Consumption vs. Available $O_2$
Deep-sea urchin capable of pH compensation under mild ocean acidification

- Tank pH = 7.5
- Tank O₂ ~100 uM
- Moderate compensation after mild acidosis

Fragile Urchin

Moderate pH recovery

31 days
pH compensation weak under moderate ocean acidification

- Tank pH = 7.1
- Tank O₂ ~100
No pH compensation under severe ocean acidification

- Tank pH = 6.7
- Tank O₂ ~100 uM
Urchin physiological performance impaired by ocean acidification

- Deep-sea urchin metabolism
  - Low, limited by hypoxia

- Acid-base compensation
  - Weak

- Consequences for performance?
  - Survival
  - Growth
  - Reproduction
EFFECTS OF OCEAN ACIDIFICATION ON METABOLISM AND ACID-BASE BALANCE IN BRACHIOPODS (LAQUEUS SP.): IMPLICATIONS FOR THE FOSSIL RECORD AND THE FUTURE

J. P. Barry; K. Buck; E. F. Pane; C. Lovera; P. J. Whaling; C. Tanner
MBARI, Moss Landing, CA, United States.
Laqueus californianus

Morphology

Continental Shelf aggregation

Lophophore

Pennington et al. 1999
Mass Extinctions and Brachiopods

Permian – Triassic Boundary (~250 mya)
- Siberian Traps volcanism
- ~85-95% extinction of marine life
- “Kill mechanisms (Knoll et al 2007)
  - Hypoxia / Anoxia
  - Ocean acidification
  - Hydrogen sulfide
  - Global warming
  - Productivity collapse

Brachiopoda
- 12,000+ fossil species
- High rates of extinction
- Survivors smaller, generalist taxa

Are extant brachiopods sensitive to OA stress?

Harper & Jia-Yu (2001)
Laqueus californianus Studies

Field Collections

Metabolic Chambers

Monterey Bay
**Metabolic Rate Measurements**

- High survival, apparently good health for most animals
- No effect of pH on metabolic rate until day 14
  - Increase in O2 consumption with low pH
- 4 days acclimation
Microbial Fouling of Lophophore

- Healthy animal
  - thin microbial film on tentacles
  - no shedding of tentacles

- Unhealthy brachiopod
  - high microbial load on tentacles
  - degraded tentacles, shedding
Acid-Base Balance

- Normal pH poise ~0.2 – 0.3 units below ambient
- Become isoprotic with SW near pH=7.2

Unhealthy animals?
Metabolic Consequences of poor ion-regulatory control

- Ion Regulation possible, but costly
  - Increased metabolic cost of pH compensation
- Ion Regulation ineffective
  - Metabolic depression?
  - Respiratory stress
  - Ineffective enzyme function
  - Metabolic inefficiency

- Growth
- Aerobic scope
- Reproduction
- Survival

Manwell 1960
Brachiopod hemerythrin (Bohr Effect)

- Population dynamics
- Extinction?
- Community interactions
Implications for Brachiopod Fossil Record and Future

Fossil Record – PT boundary (high pCO2, low O2, low productivity)

• Lack of ion-regulatory control probably caused severe problems for many brachiopods
  • Acid-base disruption, weaker gas exchange capacity
  • Respiratory stress
  • Reduced activity?

• Multiple stressors (hypoxia, low food availability)
  • Respiratory stress would cause severe problems (pO2(atm) dropped from 35% to 15%)
  • Reduced food for specialists vs. generalist

Future Ocean Acidification

• pH, pCO2 levels used correspond to likely future scenarios
• Results suggest that brachiopods may have acid-base problems in future

• But:
  • They already live in a highly variable environment
  • Acclimation? Adaptation?
Biodiversity is reduced in natural CO2 vents

51 percent reduction in species richness per 1 pH unit

Data from Hall-Spencer et al. 2008
Acid-base disruption affects enzyme activity

Consequences?

- Reduced enzyme activity under OA

Deep-Sea Taxa

- Narrower optimal pH range?
- Lower enzyme activity in general
- More severe OA stress for deep taxa
Stress affects animal performance
Multiple stressors can interact to affect animal performance

Modified from Portner (2008)
<table>
<thead>
<tr>
<th>Stage</th>
<th>Duration</th>
<th>Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertilization</td>
<td>Seconds</td>
<td>High?</td>
</tr>
<tr>
<td>Embryo</td>
<td>Hours - Days</td>
<td>High?</td>
</tr>
<tr>
<td>Larva</td>
<td>Days - Months</td>
<td>Mod. - High?</td>
</tr>
<tr>
<td>Juvenile</td>
<td>Mo. - Yr.</td>
<td>Moderate?</td>
</tr>
<tr>
<td>Adult</td>
<td>Yr. - Cent.</td>
<td>Low - Mod.?</td>
</tr>
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**Tuna Life Cycle**

- Egg (4 hours)
- Egg (1 hour)
- Egg (20 hours)
- Egg (30 hours)
- Mature fish (7-9 years)
- Immature fish
- Larvae
Field Survey of Natural CO$_2$ Venting Sites in Italy

- Echinoderms conspicuously absent, shell dissolution
- Seagrasses thrive

Jason Hall-Spencer et al. 2008
Outside the vents – abundant calcifiers e.g. sea urchins
At high CO$_2$ there are almost no calcifiers, fleshy algae and invasive species dominate

250 taxa now examined including macroalgae (Porzio in press, JEMBE), seagrasses, foraminifera, sponges, nematodes, polychaetes, molluscs, crustaceans, chaetognaths, bryozoans.
Biodiversity is reduced in natural CO2 vents

51 percent reduction in species richness per 1 pH unit

Modified from Barry et al. 2011
Marine Communities are Biological Networks

Primary Production

Phytoplankton

Zooplankton

Detritus / Bacteria

Large zooplankton

Seabirds

Seafloor Animals

Squid

Fish

Mammals

Humans

Marine Food Web
Effects of Ocean Acidification on Ocean Food Webs

Ocean Acidification:
• Reduced shell formation in pteropods
• Reduced growth & survival of pteropods

Disruption of Salmon Food Web
Cascading effects for higher predators (mammals, humans)

Pteropod = Salmon food

Sockeye Salmon
Summary

What we know:

- OA can cause physiological stress
  - More severe for taxa with:
    - low metabolic rates
    - limited respiratory capacity
    - deep-sea taxa
  - Variation in sensitivity among taxa (winners and losers)
  - Calcification is most consistent and widespread impact
  - Acid-base disruption can affect overall cellular function
  - Reduced physiological function leads to reduced performance

What we expect:

- Food webs will be affected
- Ecosystem services (e.g. fisheries) will change

What we don’t know:

- Long term (i.e. lifelong) effects
- Developmental bottlenecks, cumulative impacts
- Capacity for acclimation and adaptation
- Interaction with other environmental changes (warming, pollution)
- Effects on marine communities, ecosystems - tipping points?
Society has choices for adaptation to a changing ocean

- Ocean change is a problem for society
- Food and energy needs for society linked to ocean health
- How to balance ocean health and societal demands?
- Can we avoid ocean tipping points?
- Early action reduces severity of impacts
Reasons for Hope?

High-efficiency cars and trucks

Wave and Tidal Energy

Photovoltaic Energy (Solar)

Wind Power
Value the Oceans