Multiple stressors on upwelling margins: Untangling biological effects of hypoxia, hypercapnia and temperature (on benthos)

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Multiple Stressors: San Diego Coastal Expedition – UC Ship Funds
https://sites.google.com/site/sandiegoseaflex/home

Oxygen Minimum Zone
Benthos

Methane release
Sulfide!!

Oxygen dynamics

pH/Omega
Calcifier responses

CO₂ dynamics
Ca dissolution
Understanding Multiple Stressors

– What is a stressor?

– Generating hypotheses about multiple stressor impacts
  • Multiple stressor dynamics (time)
  • Stressor biogeography (space)
  • Stressor interactions – physico-chemical & biological

– Testing and untangling stressor effects
  • Space for time translation – OMZ Benthos
  • Laboratory exposure experiments – disentangling pH and O₂
  • Geochemical proxies for multiple stressor exposure
Defining A Stressor

*External factors that disrupt homeostasis*
(equilibrium of biochemical factors)

*Temperature
*Oxygen
*Carbonate System
\[(pH, \text{pCO}_2, \text{DIC, Omega})\]
*Food Supply
Defining Stress Level - Temperature Stress

- **Thermal windows** for aerobic performance (Oxygen capacity-limited thermal tolerance)
- **Optimum temperature** (performance maxima)
- **Pejus temperature** (limits to long-term tolerance)
- **Critical temperature** (transfer to anaerobic metabolism)
- **Denaturation temperature** (onset of cell damage)
- **Thermal specialization** (performance curves/reaction norms)
- **Phenology shifts** (timing of Biol. Processes)
- **Biogeographic shifts**

*Portner et al. 2009*
Oxygen Stress

- **Oxygen windows** for aerobic performance (Oxygen capacity-limited oxygen tolerance)
- **Optimum oxygen** (performance maxima)
- **Pejus oxygen** (limits to long-term tolerance)
- **Critical oxygen** (transfer to anaerobic metabolism)
- **Mortality** (onset of cell damage)
- **Hypoxia specialization** (performance curves/reaction norms)
- **Temporal and Vertical shifts** (migration, distribution, zonation)
- **Biogeographic shifts** (OMZ)

*Modified from Portner et al. 2009*
Oxygen thresholds for sublethal and lethal effects vary by taxon

Coastal Studies: Vaquer-Sunyer & Duarte 2008

Mean $\mu\text{mol}$

Lethal

Sublethal

Crustacea

Mean (μmol)

76

48

44

47

Fishes

184

147

103

50

46

25

Bivalva

Gastropoda

Median Lethal Concentration (mg O$_2$/L)

Sublethal thresholds (mg O$_2$/liter)

Sublethal oxygen concentrations 2-4 mg/L (125-250 μmol)

Lethal oxygen concentrations 1-2 mg/L (32-63 μmol)

OMZ oxygen concentrations <0.7 mg/L (<22 μmol)
The physiologists view: (CO$_2$) stress response

Portner 2008 (MEPS)
The Ecologists View: Biotic/Functional Responses to Stressors

**Structural Attributes**
- **Diversity** (richness, evenness, taxonomic distinctness, rarity, turnover, $\alpha$, $\beta$, $\gamma$ diversity, Bray-curtis similarity)
- **Abundance** (density, biomass)
- **Size**: distributions, mean
- **Composition** (taxon-specific responses, assemblage structure)
- Reproductive Mode
- Metazoan:protozoan ratios
- Eukaryote:prokaryote ratios
- Representation of calcareous species
- Depth of midslope diversity maximum

**Physiological Attributes**
- Calcification rates, form of carbonate
- Metabolic Rates: $O_2$ consumption
- Extracellular Enzyme activity
- Growth Rate, Reproductive Rate
- Survival

**Functional Attributes**
- **Production** – primary, heterotrophic prokaryotes, metazoans
- **Habitat provision**
- **Bioturbation**, C burial
- **Remineralization** of C, N and P
- Community Respiration
- Nutrient fluxes
- C and N Fixation
- Trophic Structure and Diversity
- Functional/Lifestyle diversity
- Metazoan vs protozoan vs prokaryote C consumption, respiration
- Colonization/recruitment/recovery potential
Eastern Boundary Upwelling Regions

Continental Margins, Bathyal and Shelf Depths
The Oxygen Minimum as Carbon Maximum Zone

Paulmier et al. 2011  Low oxygen/high CO$_2$ conditions persist over a range of depths

[Graphs and maps showing oxygen and DIC distributions across different depths and locations]
Low oxygen is linked to low pH in the Eastern Pacific Ocean. Both are controlled by respiration and CO2 production.

GLODAP DATA

$O_2$ - $CO_2$ (pH) relationships in eastern Pacific

Oxygen Depth Profile

pH Depth Profile
ALL upwelling margins are not equal with respect to temperature

Oxygen at 800 m

Temperature at 800 m

Low Oxygen
High CO2 (low pH)
Variable T
Guiding concepts for evaluating multiple stressor effects

- *Environmental (stressor) variation* can occur on diurnal/semidiurnal, seasonal, interannual, interdecadal time scales. These are superimposed on longer-term climate change.

- There is *geographic variation in action of climate stressors*.

- *Climate (stressor) variables interact* such that the effects of one (or more) modify absolute values of and biotic responses to other variables.

- *Space for time translation* - Can we use biotic response to existing gradients to predict future responses to changing environments?

- *Time series are required to document response to climate stressors*. These can come from the geological, historical or modern records.
What are the time scales of stress exposure?

CO$_2$

O$_2$

Temperature
LONG-TERM FLUCTUATIONS:
Episodic Anoxia (red) and Extinction Events

Figure courtesy Ariel Anbar and Timothy Lyons.

Periodic Fluctuations in Open Ocean pH
DECADAL VARIATION

Temperature Regimes

Oxygen Regimes?

Modified from McClatchie et al. 2010

So. California – Cowcod Conservation Area
Continuous monitoring reveals short-term dynamics of multiple stressors in coastal upwelling regions.

Sea-pHOx
(S, T, pH, O₂, pressure)
INTERANNUAL - ENSO
Anomalies at Del Mar Buoy - 35 m, So. California

(Nam et al. 2011)
SEASONALITY: Spring Low pH-Oxygen Stress

Send & Nam
2012
EVENT-SCALE (week-long) variation associated with wind reversals

Send and Nam 2012
Tight pH/DO relationships
La Jolla kelp forest, southern California

but with broad temperature signals

Frieder et al., Biogeosciences Discussion, In review
Power spectrum for a year of data – 7 m La Jolla kelp forest

Strong Diurnal and Semidiurnal Signals

Frieder et al., Biogeosciences Discussion, In review
Short-term semidiurnal/diurnal sources of pH variability at 7 m

Upwelling Phase – Internal Tidal Effects

Relaxation Phase: Kelp Respiration/Photosynthesis Effects

Green – kelp forest/inshore      Blue – 1.5 km offshore of kelp forest
LONG-TERM DEOXYGENATION in the NORTHEAST PACIFIC OCEAN

Whitney et al. 2007

20-30% decline in oxygen at 200-300 m off southern CA over the past 22 y

Bograd et al. 2008

Oxygen loss of 0.67μM O₂/y
GLOBAL AOU & OXYGEN CHANGE (200-700m)  
1964-70 vs 1990-2008

At 200 m the area with $< 70 \mu M$ $O_2$ has increased by 4.5 million km² area 

*Are these new zones of acidification?*

Stramma et al. 2010
A relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions. Negative Dsy represents hypoxic waters shallower than 200m.

Hofmann et al. 2011 Deep-sea Research
Change in pH in the N. Pacific (1991-2006)

Byrne et al. 2010

**TOTAL**

Effects of anthropogenic C on pH are detectable mainly to 150 m.

Change in pH have occurred down to 800 m

**NATURAL VARIATION**

**ANTHROPOGENIC CARBON**
Physical/Chemical Stressor Interactions
The Oxygen and Carbonate System Are Sensitive to Temperature

Oxygen concentration at 100% saturation

\[ S = 35 \] (solubility eqn. of Garcia & Gordon 1992)

Courtesy of T. Martz

\[ S = 35 \text{ (solubility eqn. of Garcia & Gordon 1992)} \]

Courtesy of T. Martz
Temperature regulates biological tolerances to stressors

Elevated temperature reduces hypoxia tolerance time

Elevated temperature raises threshold oxygen concentrations

Vaquer Sunyer & Duarte 2010
Space for Time Translation

Strong gradients on upwelling margins preview effects of changing oxygen, $pCO_2$, $\Omega_{aragonite}$ and temperature on benthos.
**OMZ BENTHIC TRANSECTS**

*Depth range: 122 – 3400m*

<table>
<thead>
<tr>
<th>Study Region</th>
<th>Number of Stations</th>
<th>Oxygen</th>
<th>Temp</th>
<th>pCO$<em>2$ &amp; $\Omega</em>{\text{arag}}$</th>
<th>Macrofauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>NE Arabian</td>
<td>14</td>
<td>x</td>
<td>x</td>
<td>nd</td>
<td>Hughes et al. 2009; Levin et al. 2009</td>
</tr>
<tr>
<td>NW Arabian</td>
<td>6</td>
<td>x</td>
<td>x</td>
<td>GLODAP*</td>
<td>Levin et al. 2000</td>
</tr>
<tr>
<td>Oregon</td>
<td>5</td>
<td>x</td>
<td>x</td>
<td>NACP*</td>
<td>Levin et al. 2010/unpub.</td>
</tr>
<tr>
<td>N. California</td>
<td>4</td>
<td>x</td>
<td>x</td>
<td>NACP*</td>
<td>Levin et al. 2010/unpub.</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>5</td>
<td>x</td>
<td>x</td>
<td>Frieder unpub.</td>
<td>Levin unpub.</td>
</tr>
<tr>
<td>Peru</td>
<td>4</td>
<td>x</td>
<td>x</td>
<td>GLODAP*</td>
<td>Levin et al. 2003</td>
</tr>
<tr>
<td>Central Chile</td>
<td>4</td>
<td>x</td>
<td>x</td>
<td>nd</td>
<td>Gallardo et al. 2004</td>
</tr>
</tbody>
</table>

**Total Stations**  
42  
42  
33  
24

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*NACP West Coast Cruise 2007; [http://cdiac.ornl.gov/oceans/Coastal/NACP_West.html](http://cdiac.ornl.gov/oceans/Coastal/NACP_West.html)*
**Diversity Indices**

**Shannon Diversity – \( H' \)**  
(species richness)  
\[
H' = - \sum_{i=1}^{K} p_i \log p_i 
\]

Low \( H' \)  
High \( H' \)

**Pielou’s Evenness – \( J' \)**  
(dominance)  
\[
J' = \frac{H'}{H'_{\text{max}}} 
\]

Low \( J' \)  
High \( J' \)  
(high dominance)
Is there a relationship between macrofaunal $H'$, $J'$ and oxygen, $pCO_2$, $\Omega_{\text{aragonite}}$ or temperature?
Diversity is reduced at the lowest oxygen levels, largely where temperatures are highest. pCO₂ is not clearly linked to diversity.

Elevated temperature may exacerbate oxygen effects on diversity and evenness.
Variation in macrofaunal diversity (H’) & evenness (J’) associated with depth, oxygen, pCO$_2$, Ω$_{aragonite}$ and temperature on OMZ margins?

Regression Tree

- Diversity (H’) most influenced by O$_2$, and at higher O$_2$ levels, by PCO$_2$
- Evenness (J’) most influenced by temperature, and at lower temperatures, by pCO$_2$
Does $\text{pCO}_2$ or $\Omega_{\text{aragonite}}$ influence density of major taxa?

**IN OMZs:**
- Little effect of $\text{pCO}_2$ or Omega-Ar on Density of any group
- High densities persist at carbonate undersaturation
CALCIFYING ECHINODERMS (*Allocentrotus fragilis* and *Brisaster latifrons*) dominate at 300 m off La Jolla (So. California)

300 m: Oxygen 0.84 ml/L   pCO$_2$ 1267
pH (in situ T): 7.57 (total scale)
DIC: 2277 umol/kg
Omega-Ar: 0.70
Temperature: 9.3$^\circ$C   Sal: 34.3

(Data Courtesy of Y. Takeshita, C. Frieder
Trawl by M. Navarro)
Controlled laboratory experiments
to distinguish different stressor influences

Market Squid – *Doryteuthis opalescens*

California Mussel – *Mytilus californianus*
Bay Mussel – *Mytilus galloprovincialis*

M. Navarro

C. Frieder
Controlling Multiple Stressors
Dickson/Bockman Experimental Facility
Can we detect exposure to multiple stressors in larval carbonates?

Larval structures retained after recruitment

Otoliths  Statoliths  Prodissococonchs

Hypoxia in Baltic cod otoliths

Temperature: Sr, Mg, $^{18}/^{16}O$, $^{88}/^{87}Sr$

pH

Hypoxia: $\delta^{11}B$, B:Ca

Mn:Ca

B:Ca in planktonic Foraminifera tests reflects pH and Temperature (via Mg:Ca)

Yu et al. 2007
CLIDEEP
Climate Change Impacts on Ecosystem Function of the Deep Sea Floor
(A. Sweetman, A. Thurber, C. Smith, L. Levin + 20 others)

• Temperature, temperature variation
• Oxygen (hypoxia – $O_2$, $pO_2$, % saturation)
• Carbonate system
  (DIC/pCO2, pH, Alkalinity, aragonite/calcite saturation, CCD)
• POC Flux (quantity & quality), surface production/chlor a, seasonality

Co-locate major sites of multiple stressors, predict changes and impacts on ecosystem function

Support from:
Norwegian Research Council
INDEEP
Deep Sea Responses to Climate Change

Gas Hydrates

Aragonite Saturation Depth

Norwegian corals

OMZ “corals”
Climate stressors interact with anthropogenic stressors on the upper slope and shelf

Modified from Levin et al. 2009, Biogeosciences
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