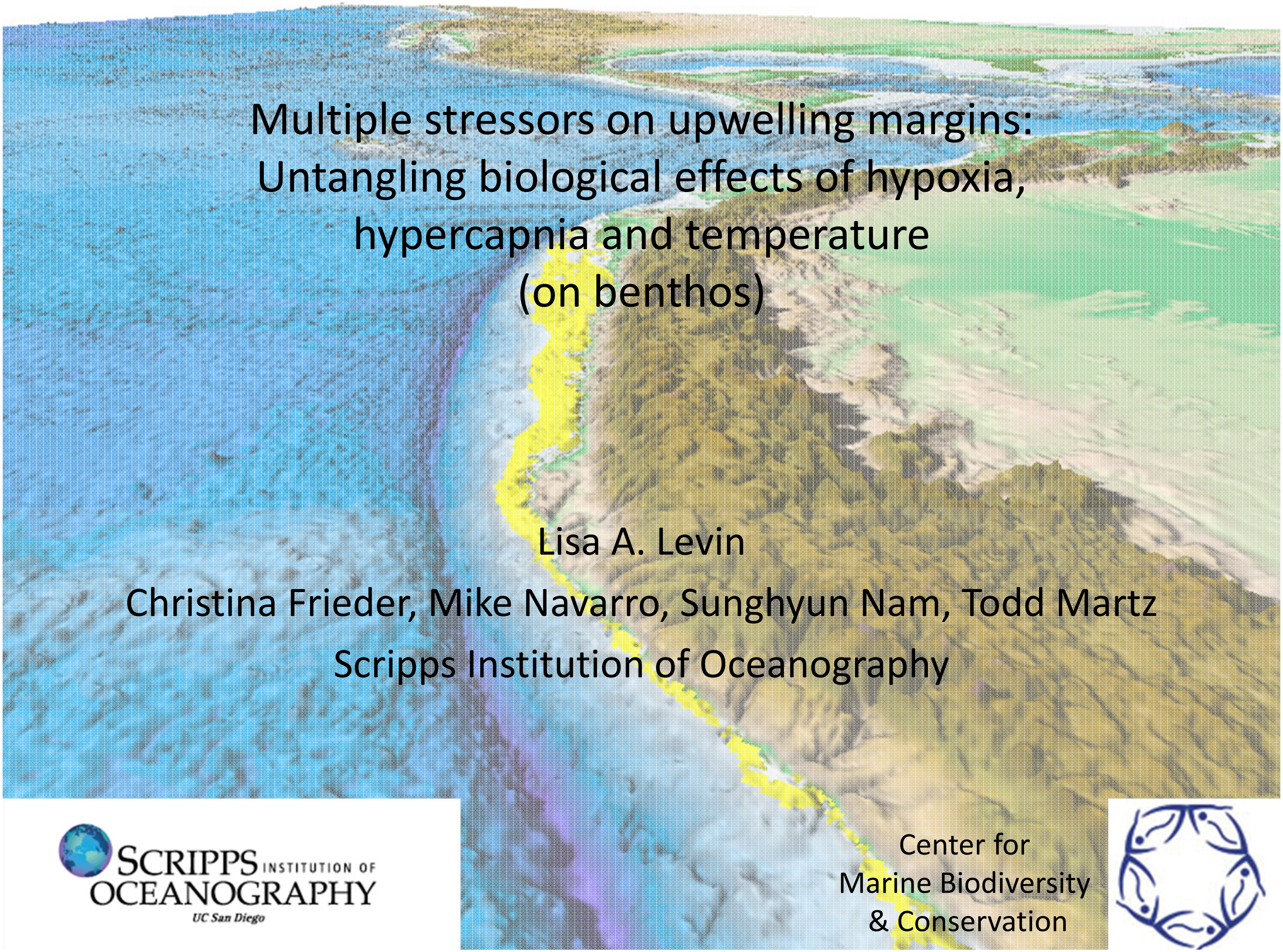


Multiple stressors on upwelling margins: Untangling biological effects of hypoxia, hypercapnia and temperature (on benthos)

Lisa A. Levin

Christina Frieder, Mike Navarro, Sunghyun Nam, Todd Martz

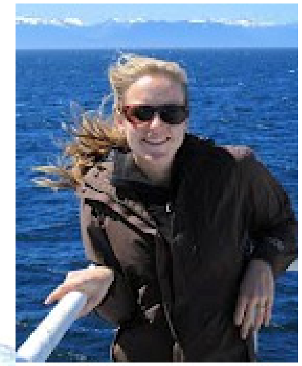
Scripps Institution of Oceanography

SCRIPPS INSTITUTION OF OCEANOGRAPHY
UC San Diego

Center for
Marine Biodiversity
& Conservation

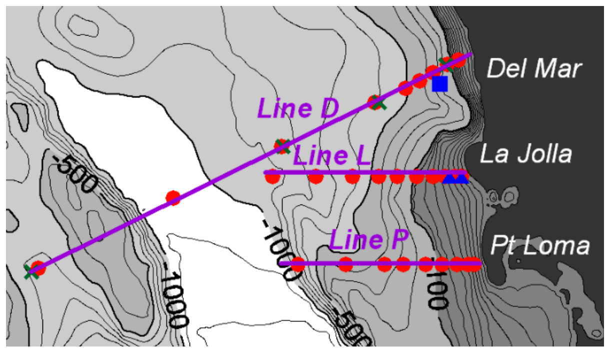
Multiple Stressors:San Diego Coastal Expedition – UC Ship Funds
https://sites.google.com/site/sandiegoseaflex/home

RV Melville



Chief Sci
C. Frieder

Oxygen Minimum Zone
Benthos



Mud
Artist

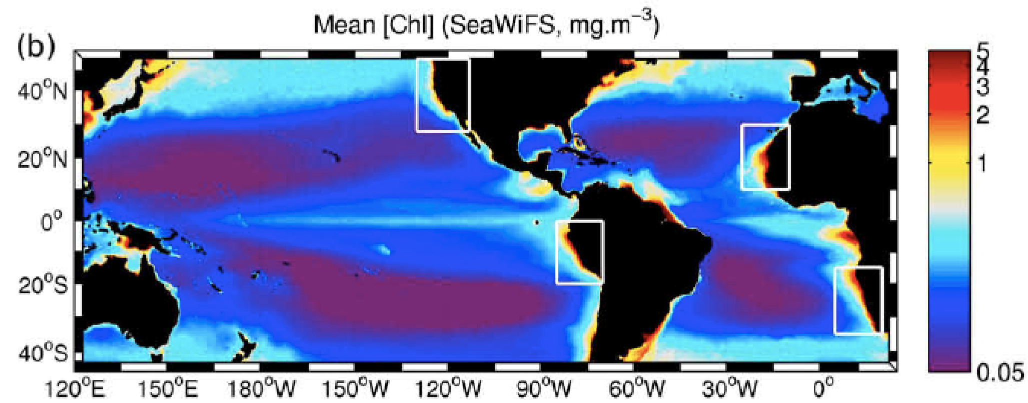
Oxygen dynamics

Methane release
Sulfide!!

pH/Omega
Calcifier responses

CO_2 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 O_2
  - Geochemical proxies for multiple stressor exposure

Defining A Stressor

External factors that disrupt homeostasis

(equilibrium of biochemical factors)

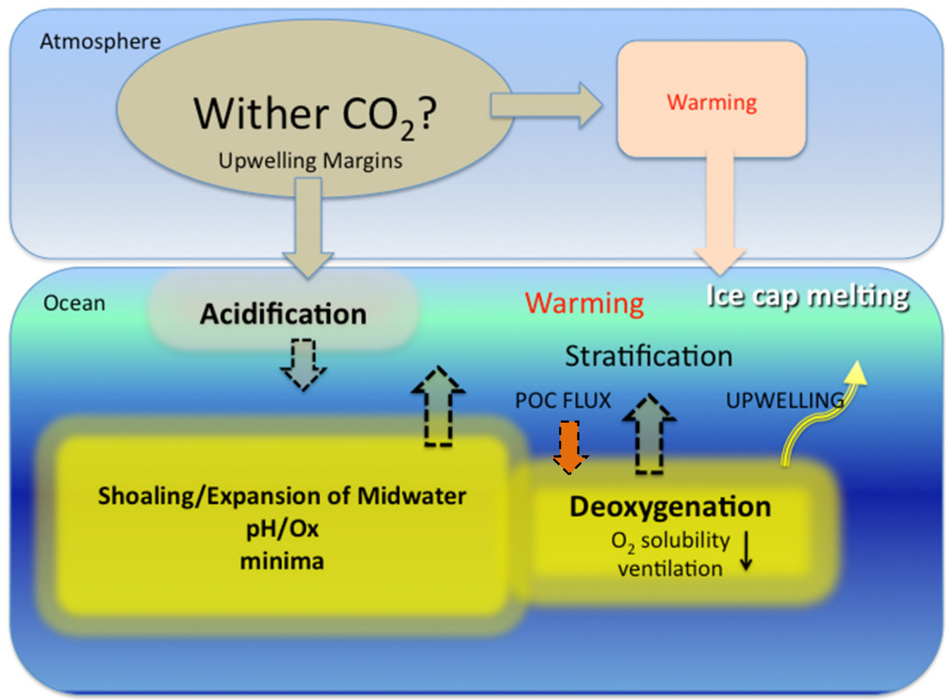
***Temperature**

***Oxygen**

***Carbonate System**

(pH, pCO_2, DIC, Omega)

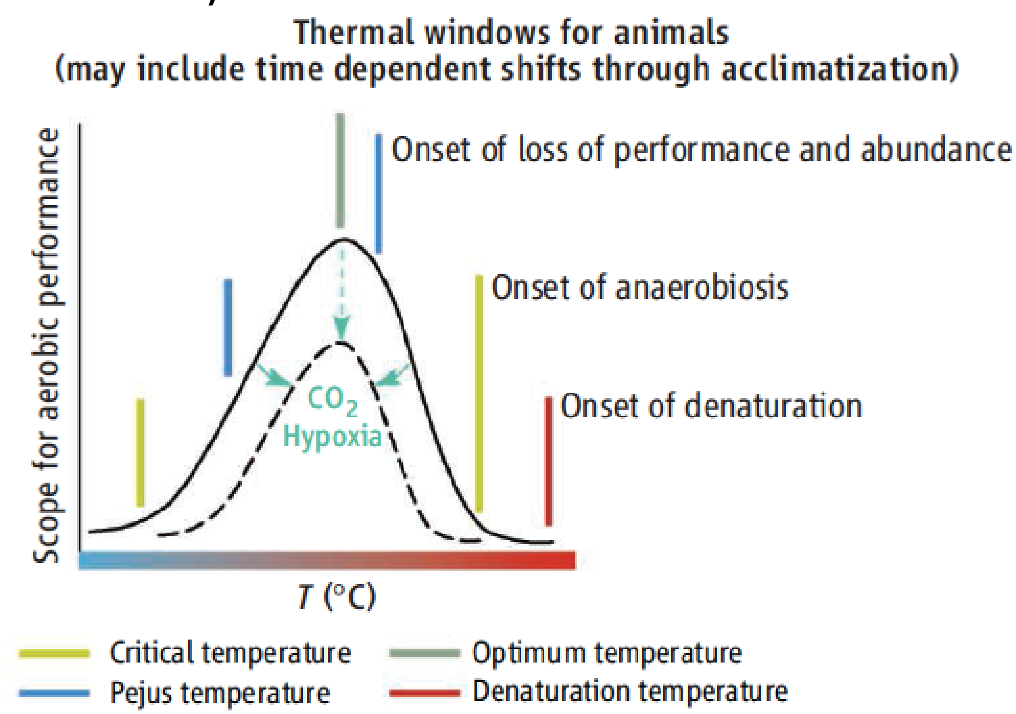
*Food Supply



Defining Stress Level - Temperature Stress

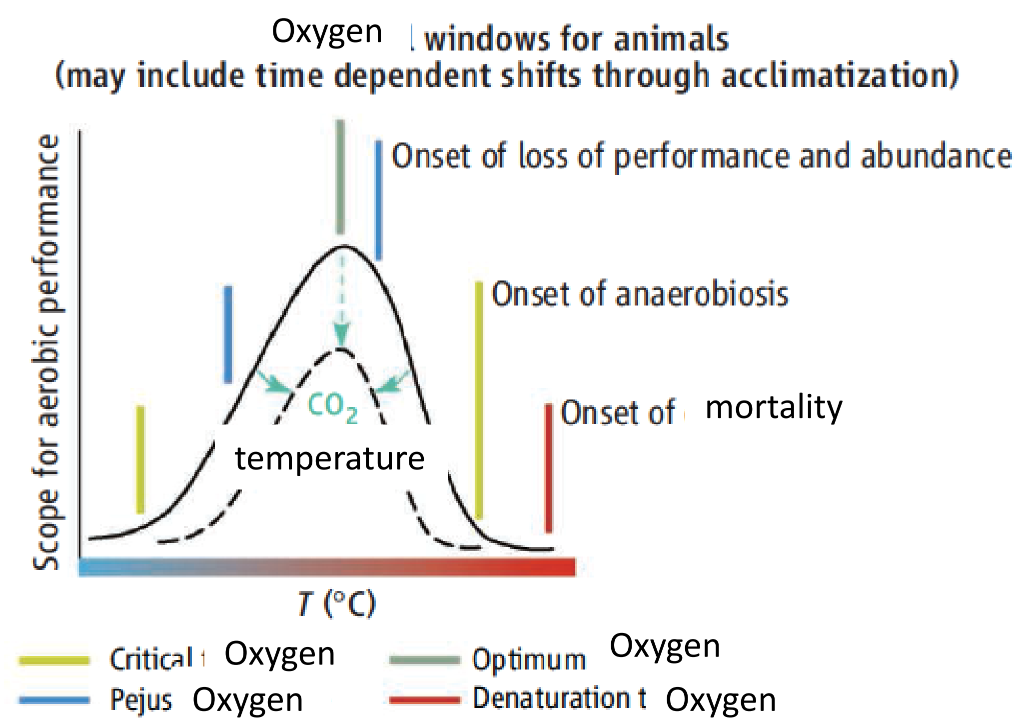
- **Thermal *windows*** for aerobic performance
  (Oxygen capacity-limited thermal tolerance)
- ***Optimum* temperature** (performance maxima)
- ***Pejus* temperature** (limits to long-term tolerance)
- ***Critical* temperature** (transfer to anaerobic metabolism)
- **Denaturation temperature** (onset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

Portner et al. 2009



Oxygen Stress

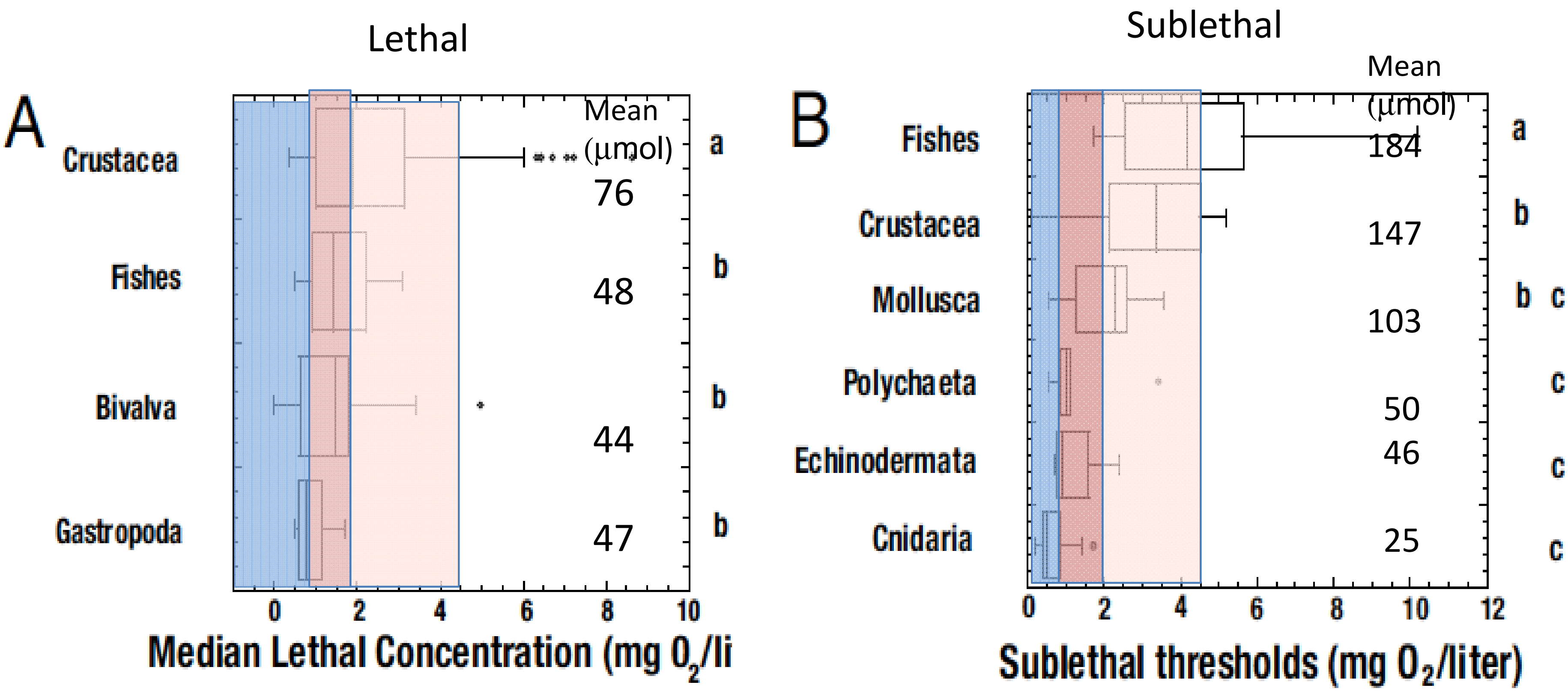
- **Oxygen *windows*** for aerobic performance
  (Oxygen capacity-limited oxygen tolerance)
- ***Optimum* oxygen** (performance maxima)
- ***Pejus* oxygen** (limits to long-term tolerance)
- ***Critical* oxygen** (transfer to anaerobic metabolism)
- **Mortality** (onset of cell damage)
- **Hypoxia specialization** (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*

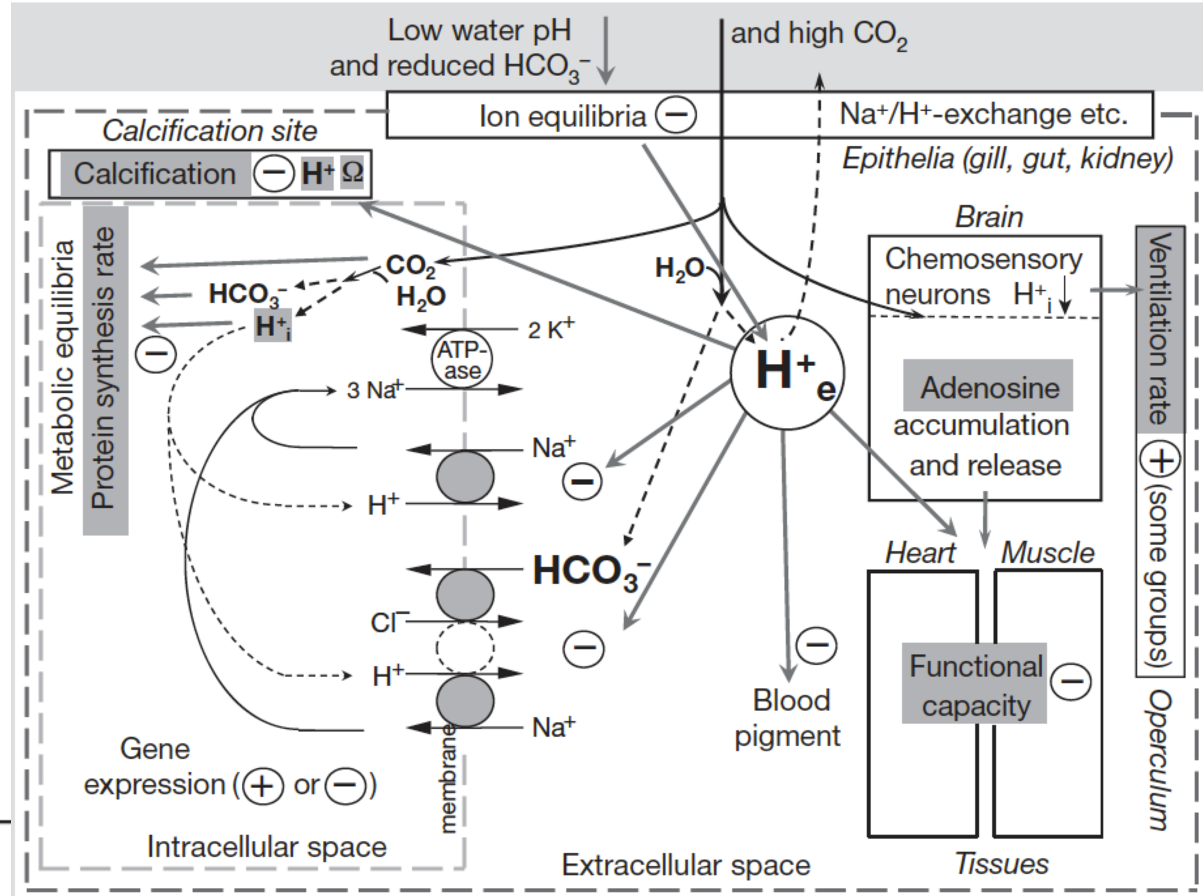


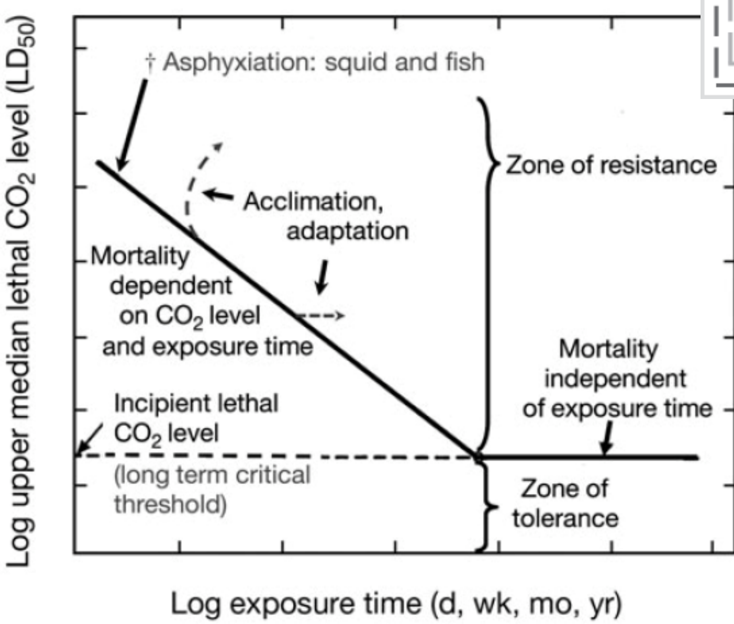
Sublethal oxygen concentrations 2-4 mg/L (125-250 µmol)

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, α, β, γ 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

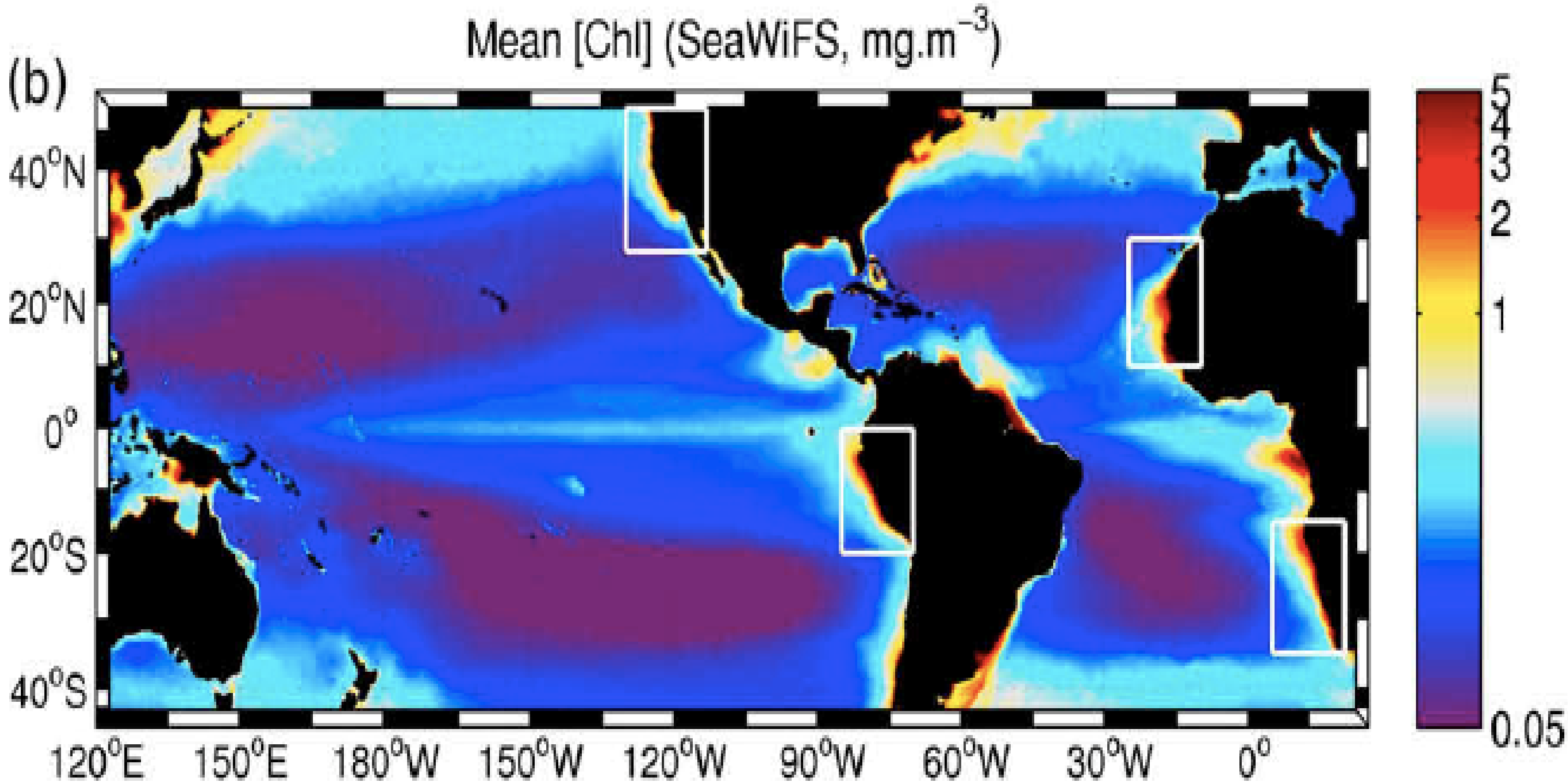
Physiological Attributes

- 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

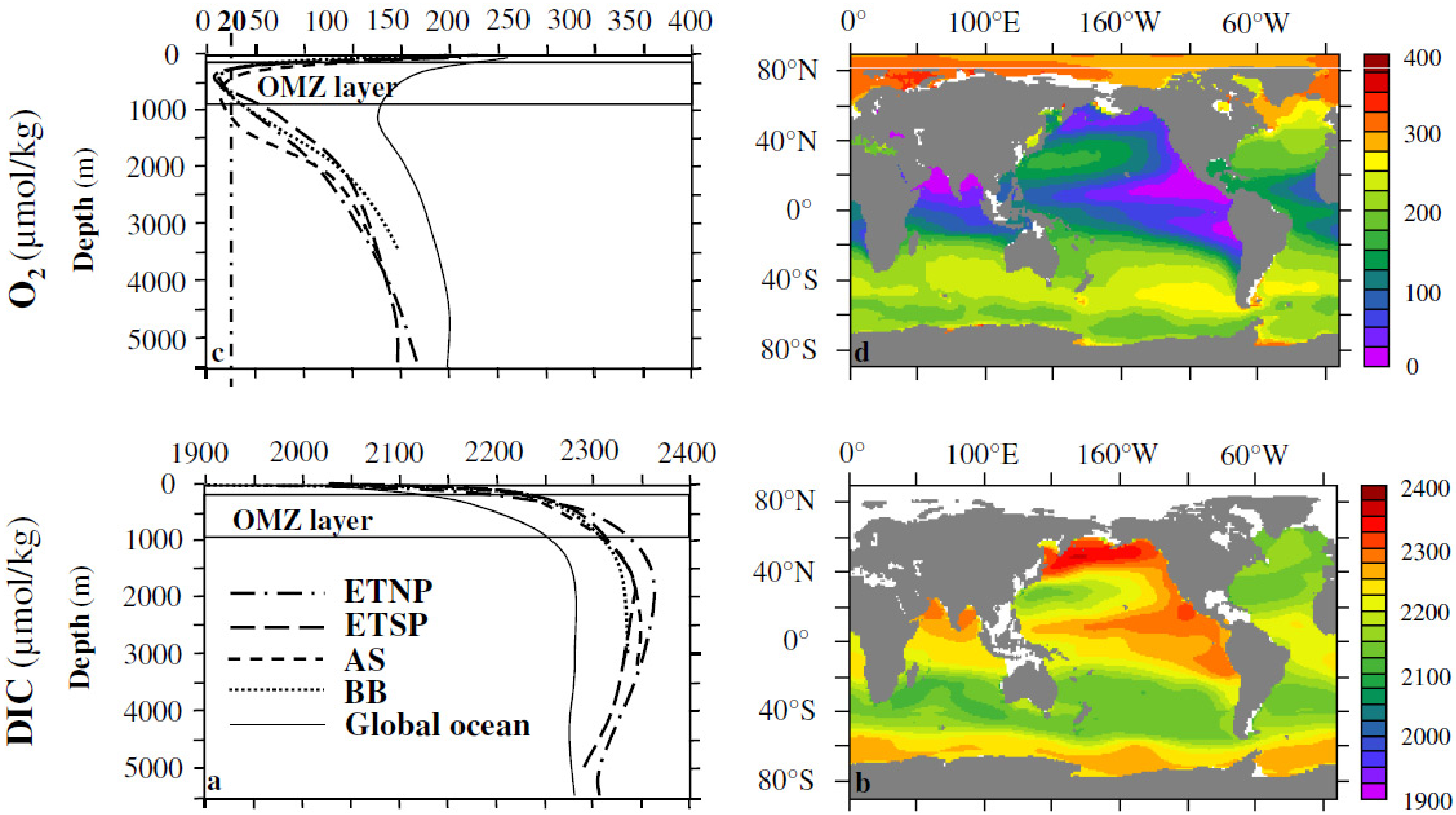
Eastern Boundary Upwelling Regions

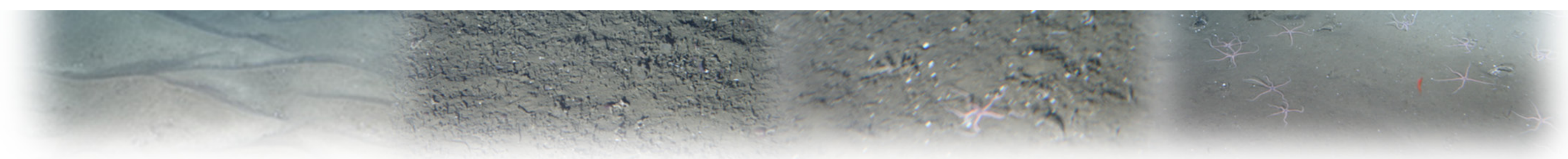


Continental Margins, Bathyal and Shelf Depths

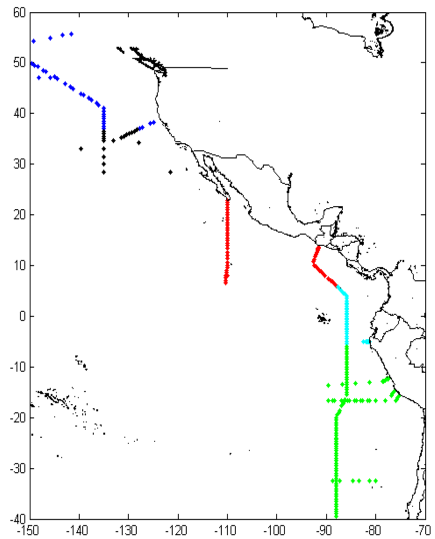
The Oxygen Minimum as Carbon Maximum Zone

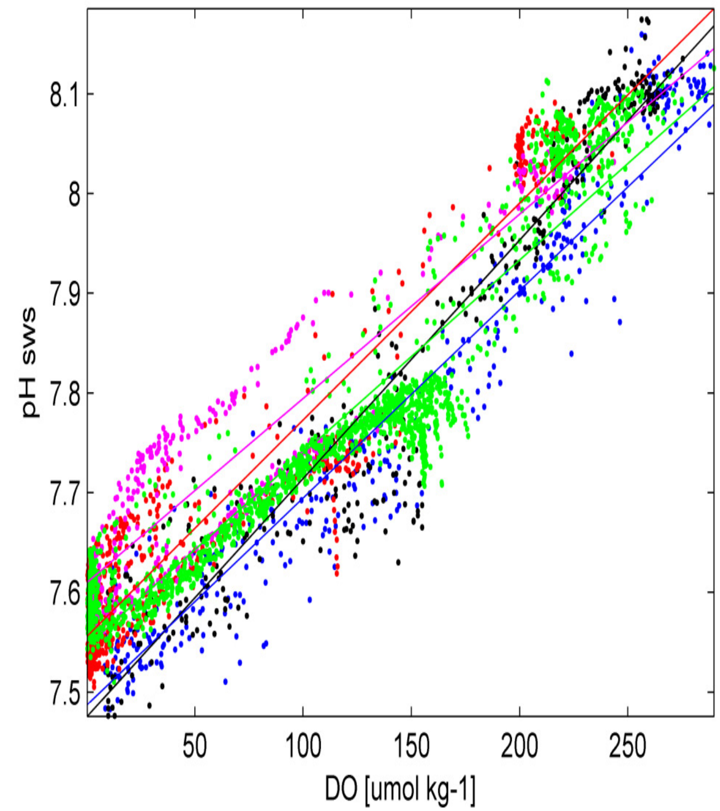
Paulmier et al. 2011 Low oxygen/high CO_2 conditions persist over a range of depths

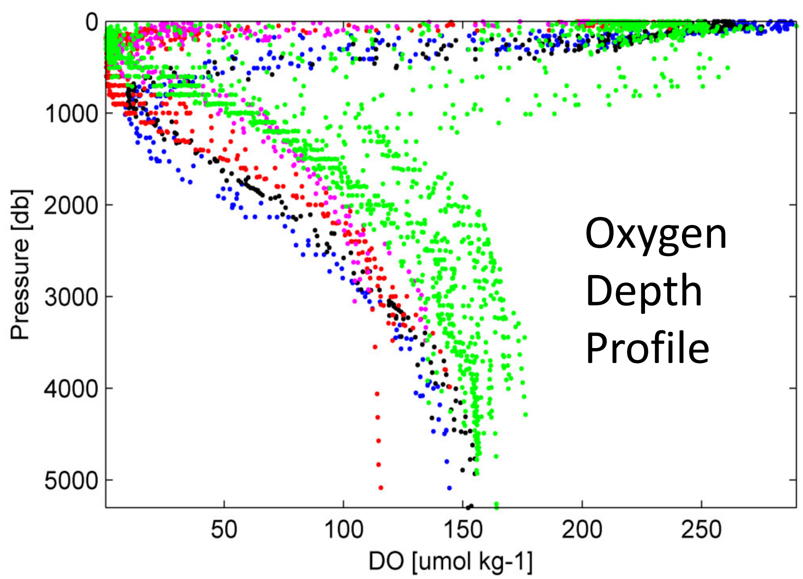


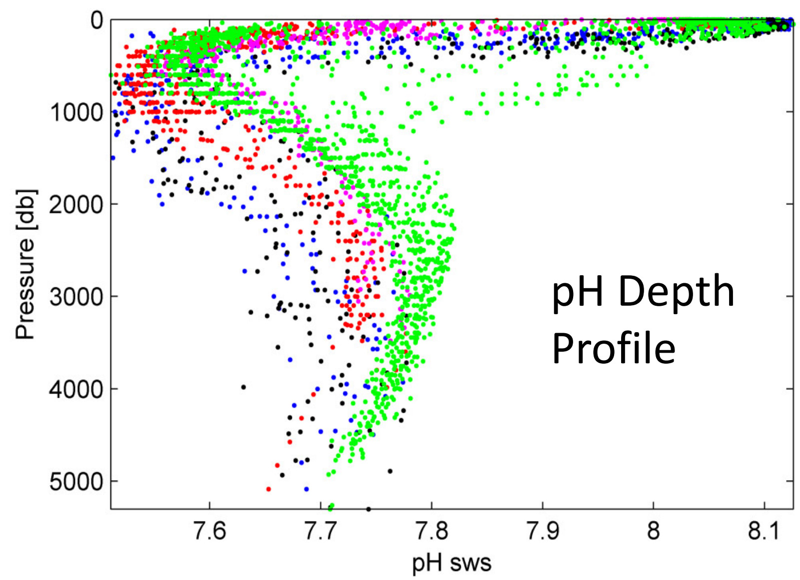


GLODAP DATA
O_2-CO_2 (pH) relationships in eastern Pacific



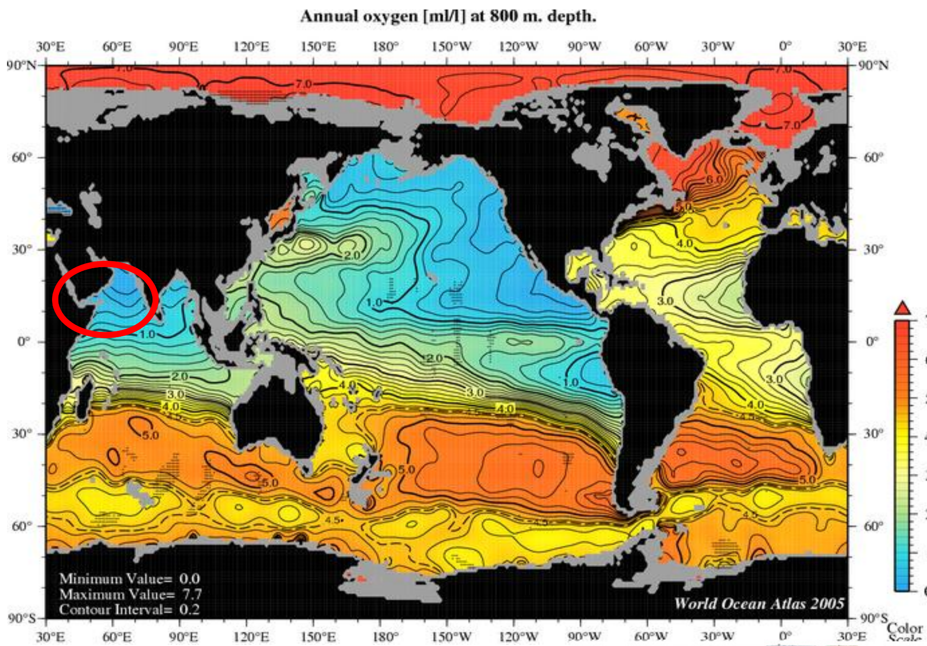




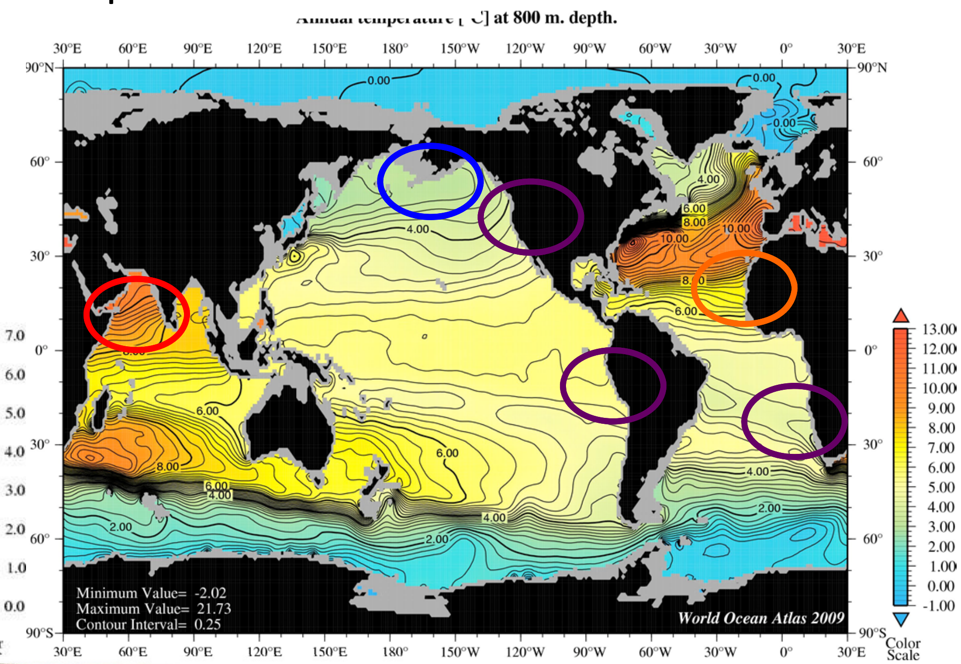


ALL upwelling margins are not equal with respect to temperature

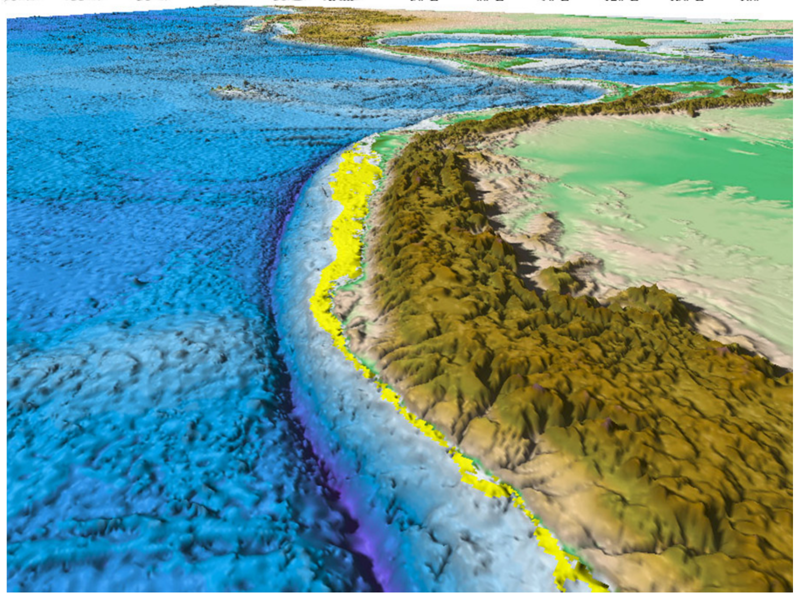
Oxygen at 800 m



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

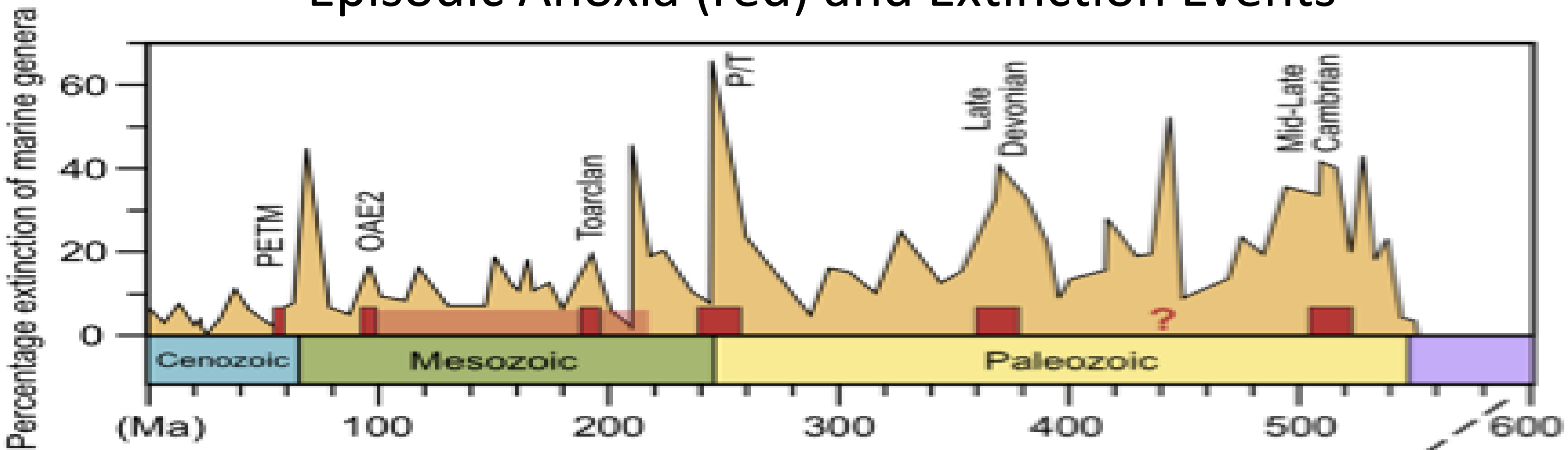
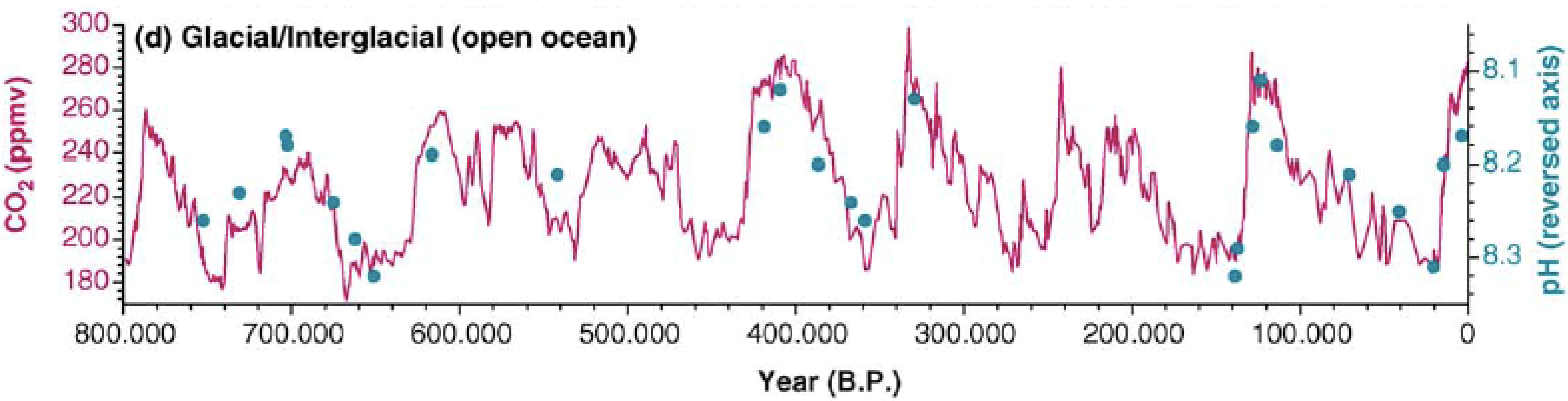


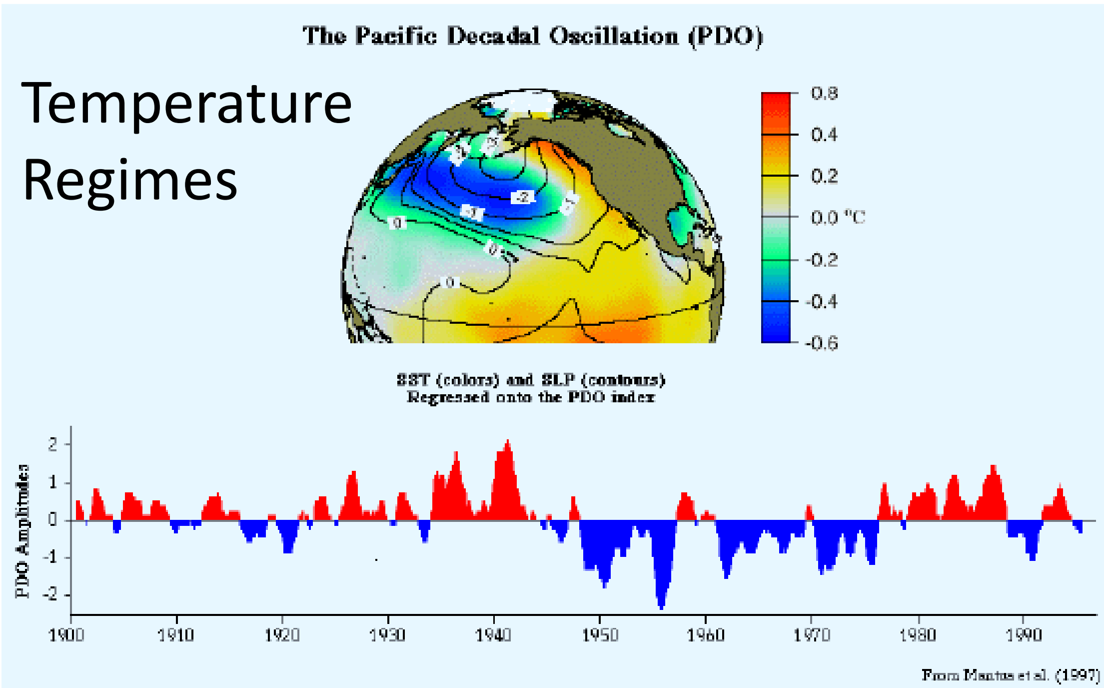
Figure courtesy Ariel Anbar and Timothy Lyons.

Periodic Fluctuations in Open Ocean pH



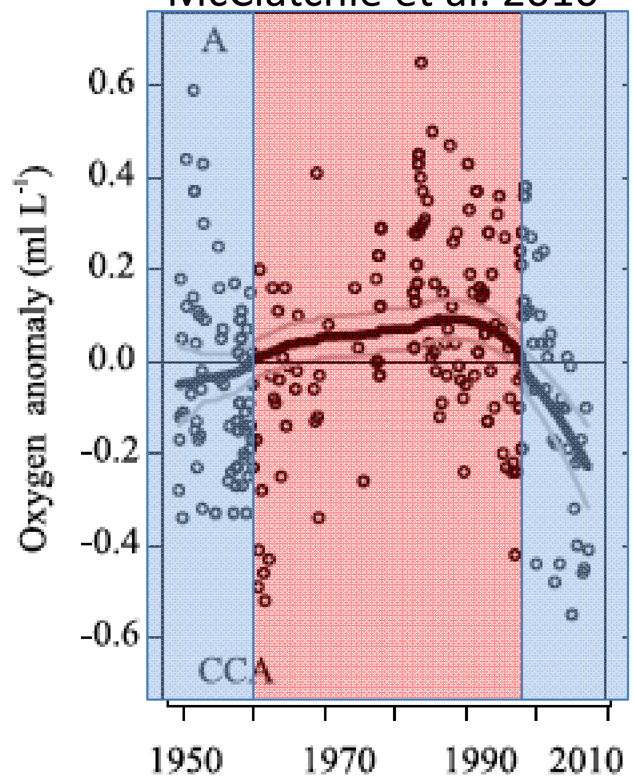
TRENDS in Ecology & Evolution

DECADAL VARIATION



Oxygen Regimes?

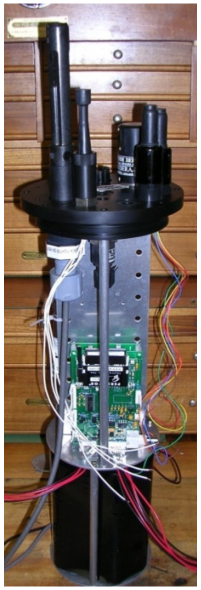
Modified from McClatchie et al. 2010

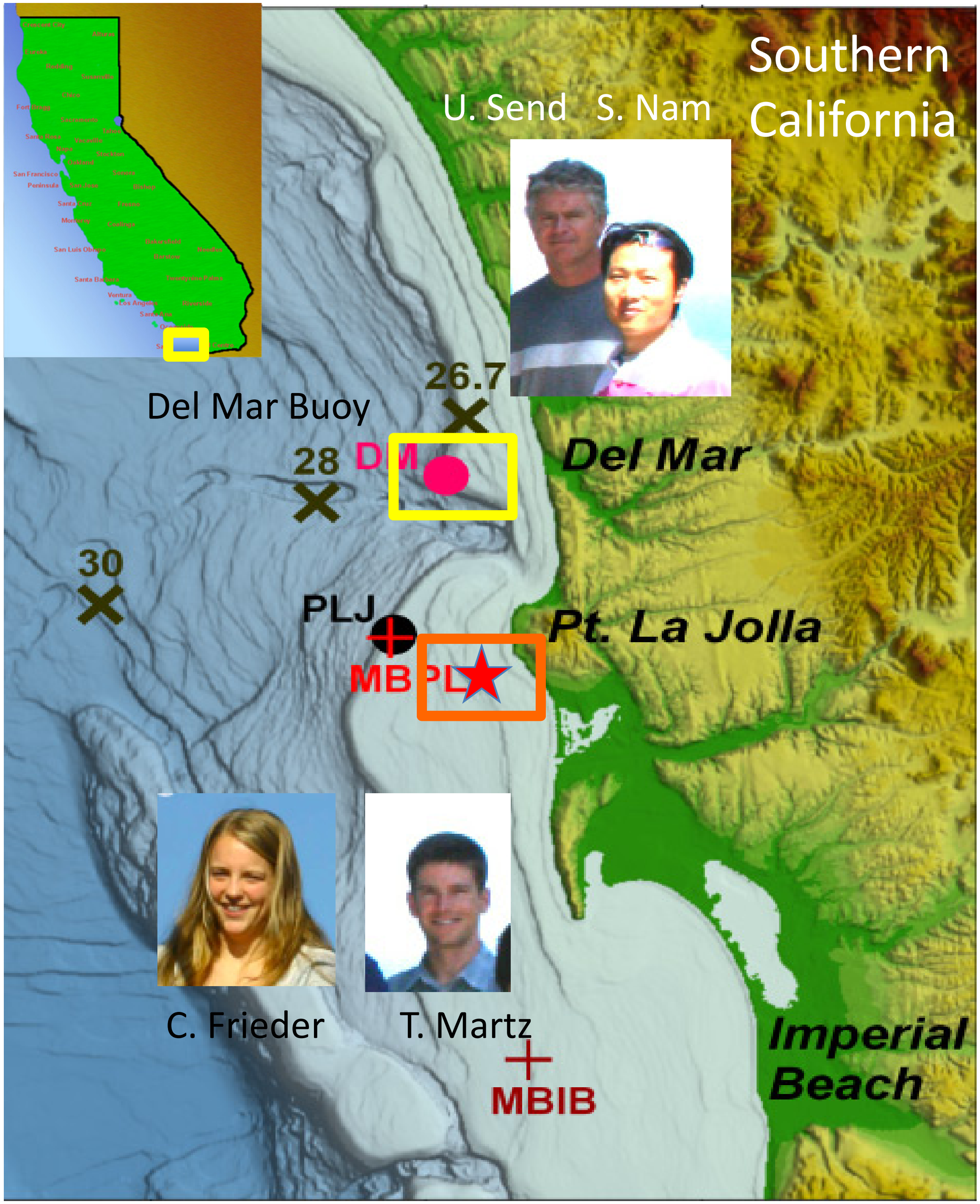


So. California – Cowcod Conservation Area

Continuous monitoring
reveals short-term dynamics
Of multiple stressors
in coastal upwelling regions

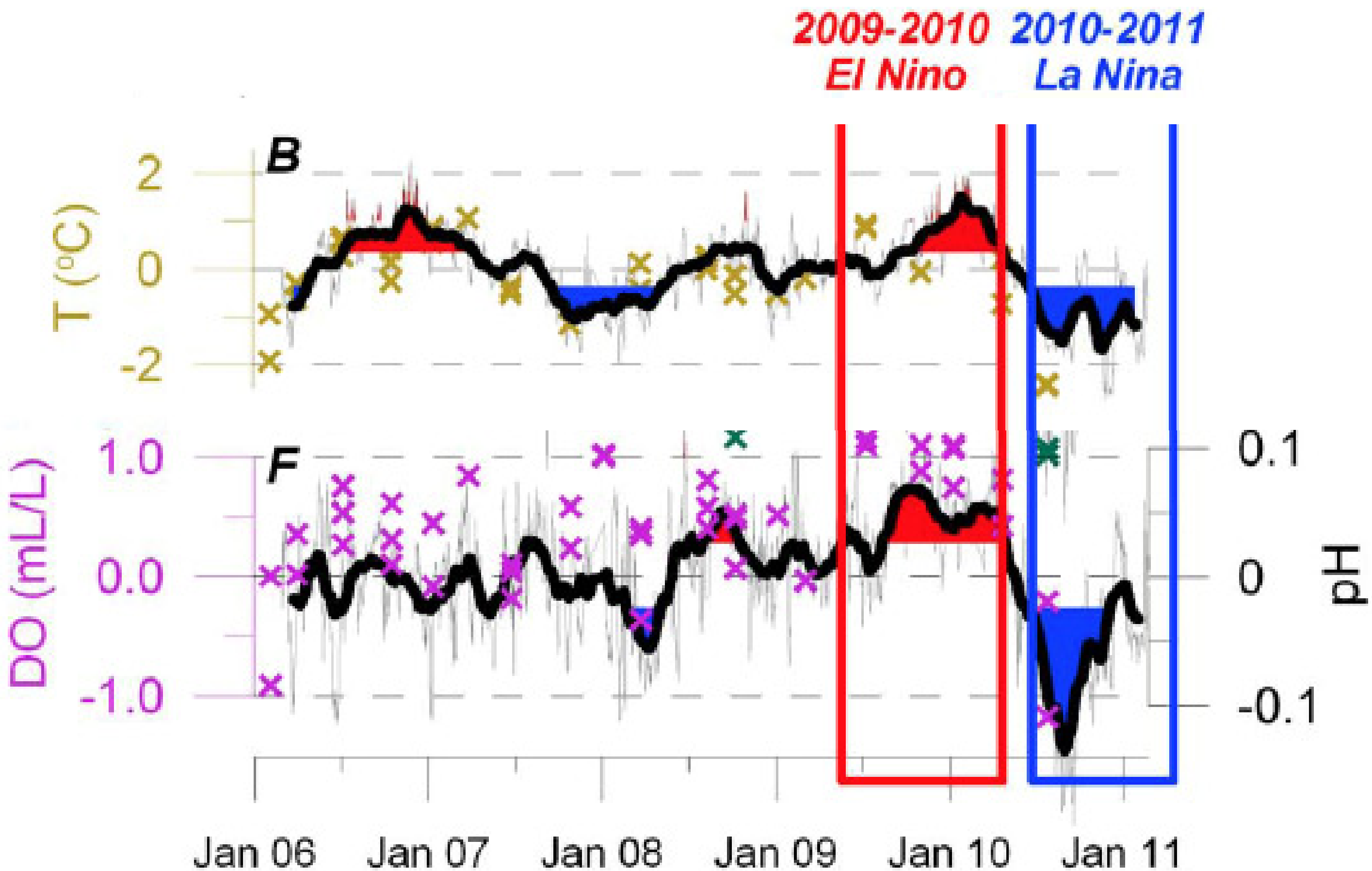
Sea-pHOx
(S, T, pH,
O_2, pressure)





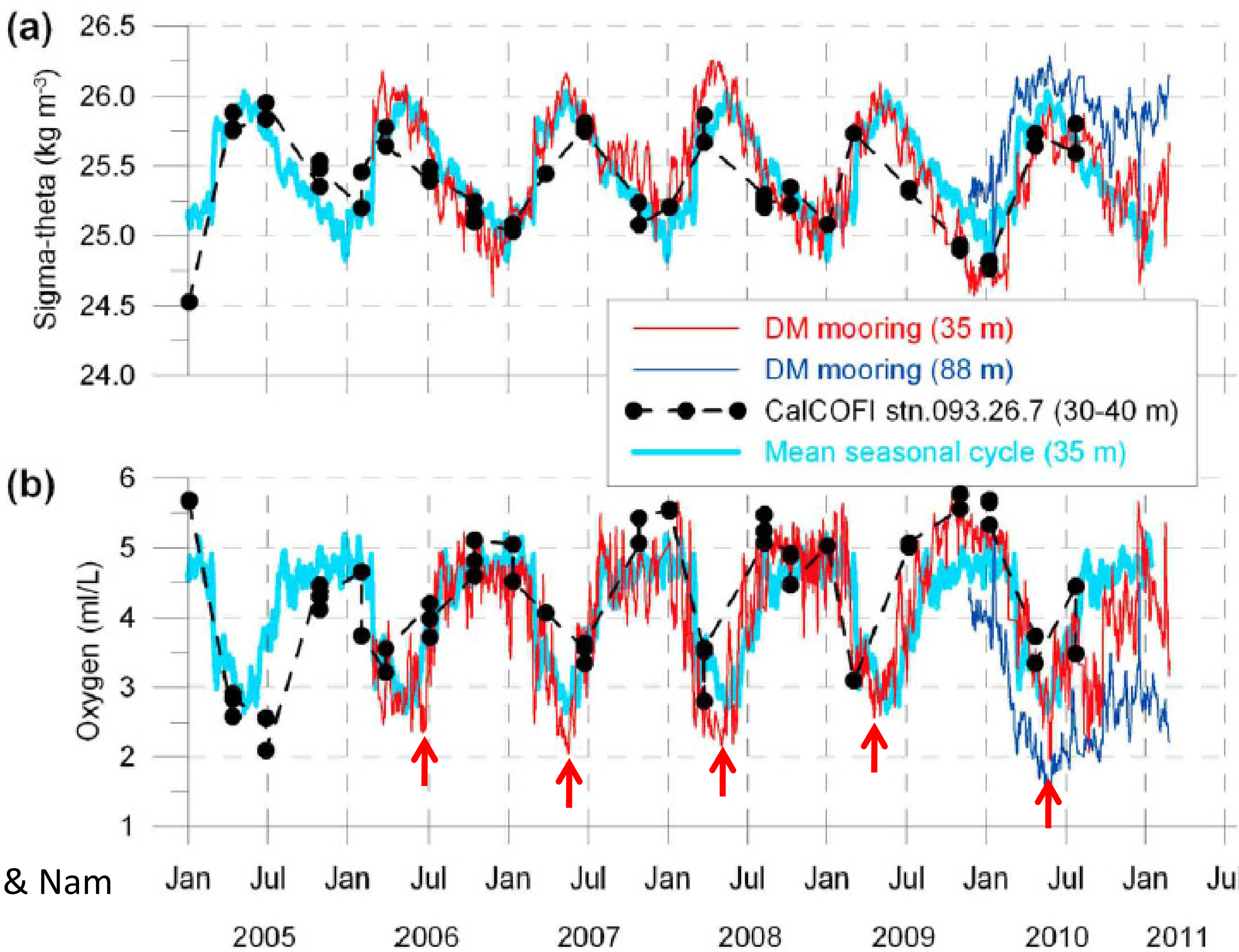
INTERANNUAL - ENSO

Anomalies at Del Mar Buoy - 35 m, So. California



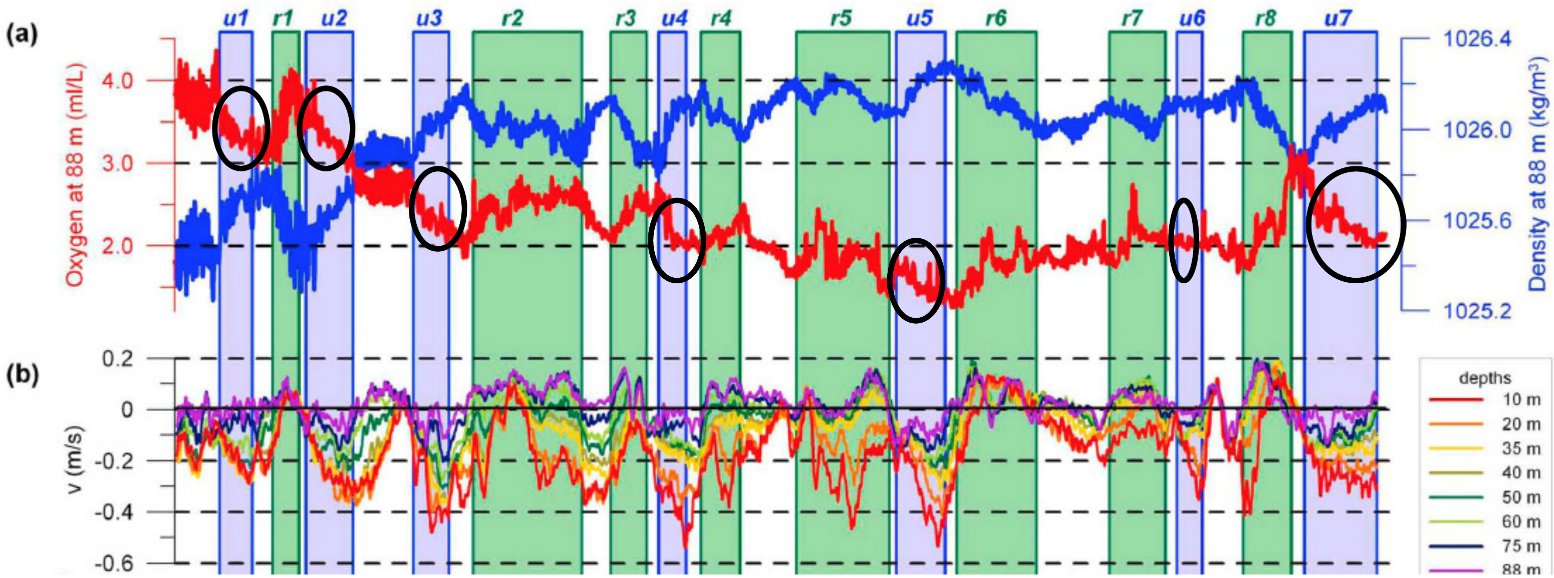
(Nam et al. 2011)

SEASONALITY: Spring Low pH-Oxygen Stress



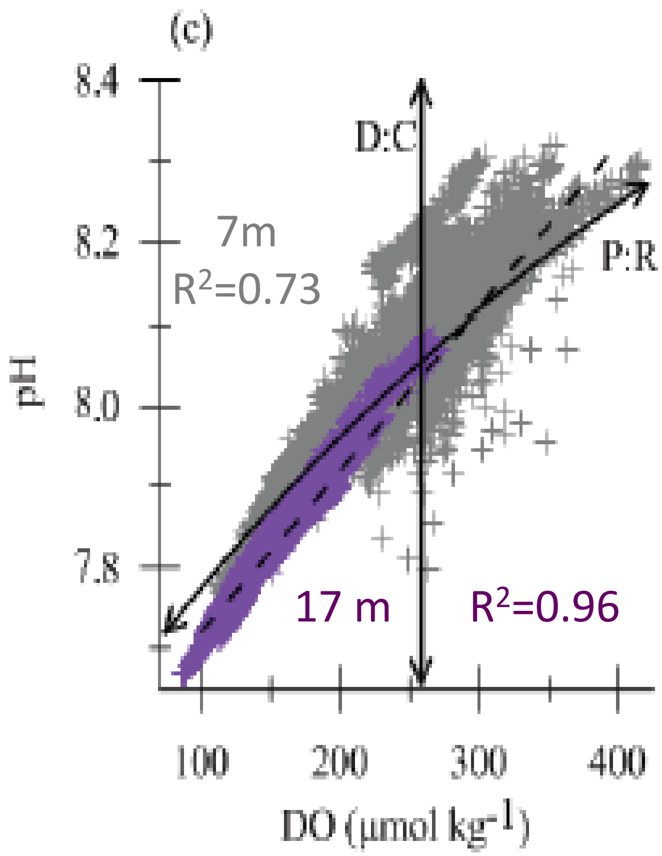
Send & Nam 2012

EVENT-SCALE (week-long) variation associated with wind reversals

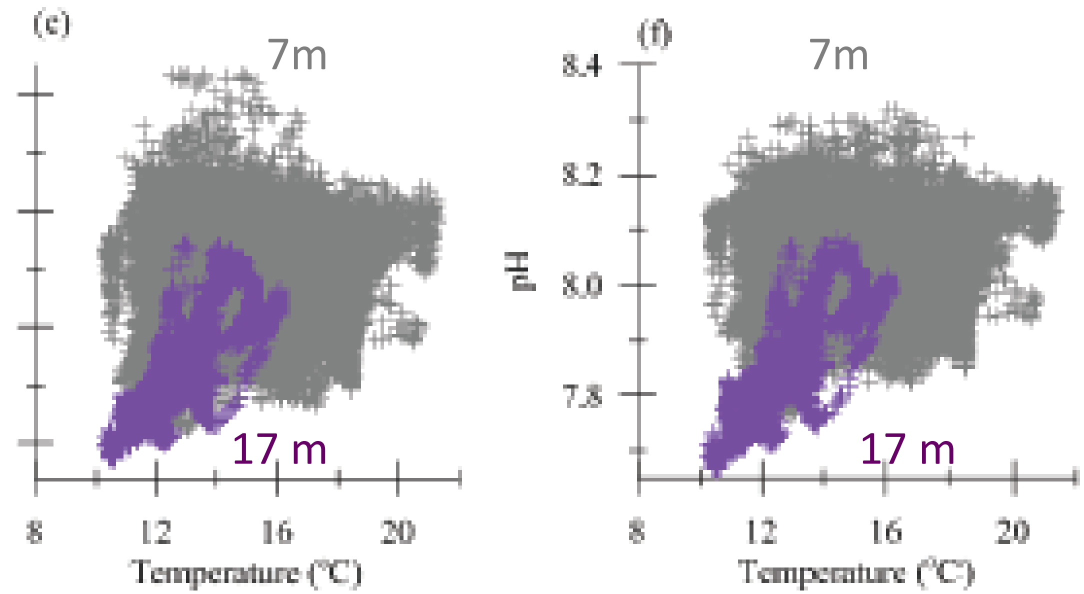


Send and Nam 2012

Tight pH/DO relationships
La Jolla kelp forest , southern California

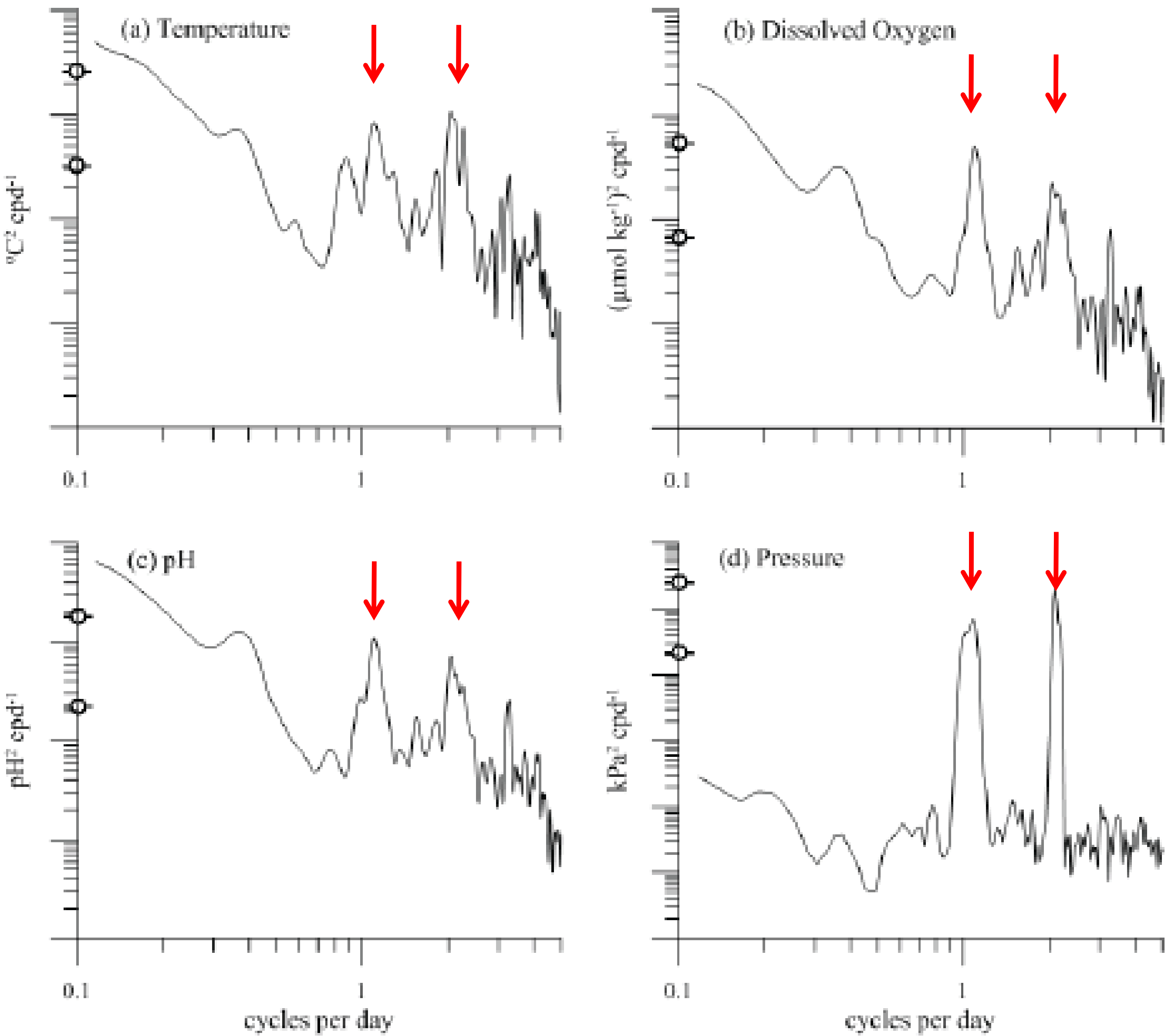


but with
broad temperature signals



Frieder et al., Biogeosciences Discussion, In review

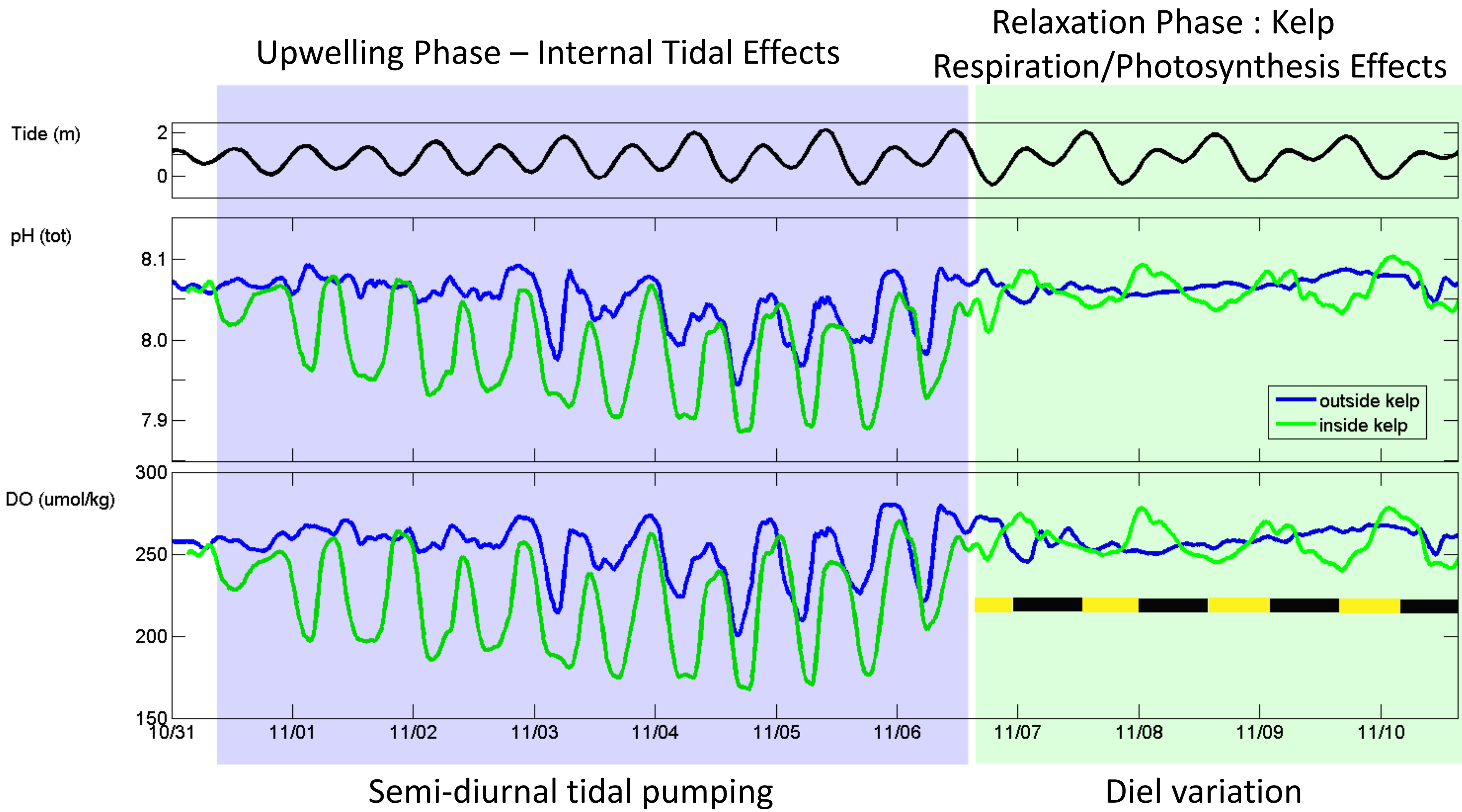
Power spectrum for a year of data – 7 m La Jolla kelp forest



Strong **Diurnal** and **Semidiurnal** Signals

Frieder et al., Biogeosciences Discussion, In review

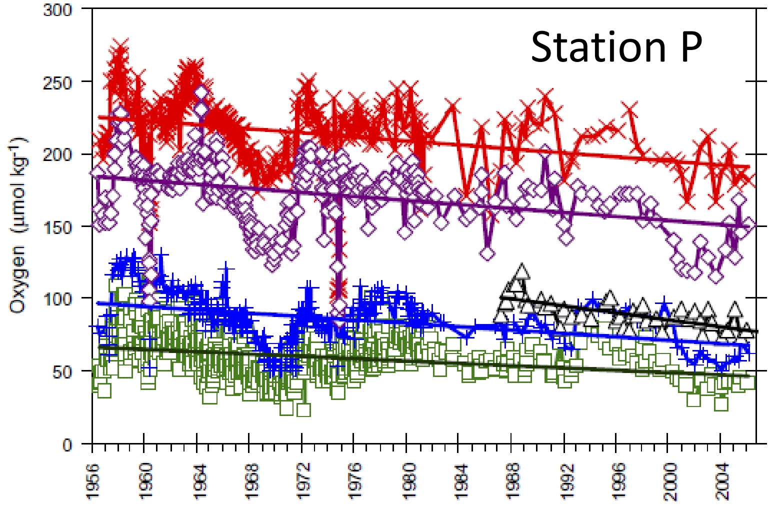
Short-term semidiurnal/diurnal sources of pH variability at 7 m



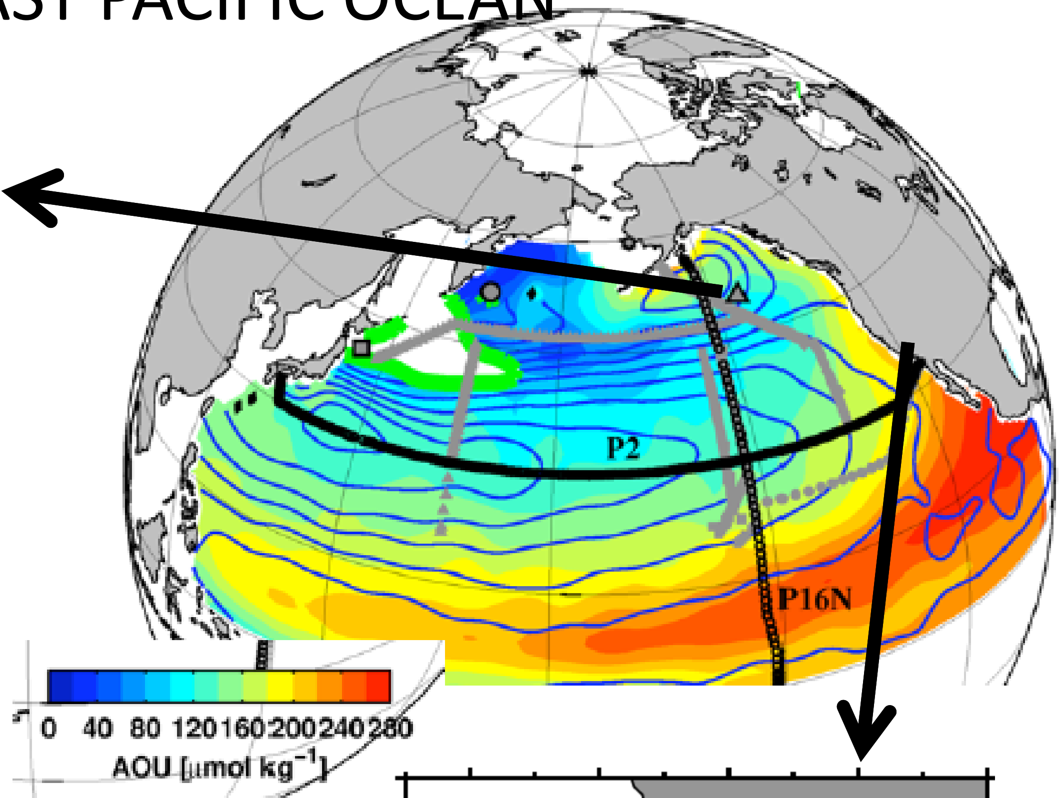
Green – kelp forest/inshore Blue – 1.5 km offshore of kelp forest

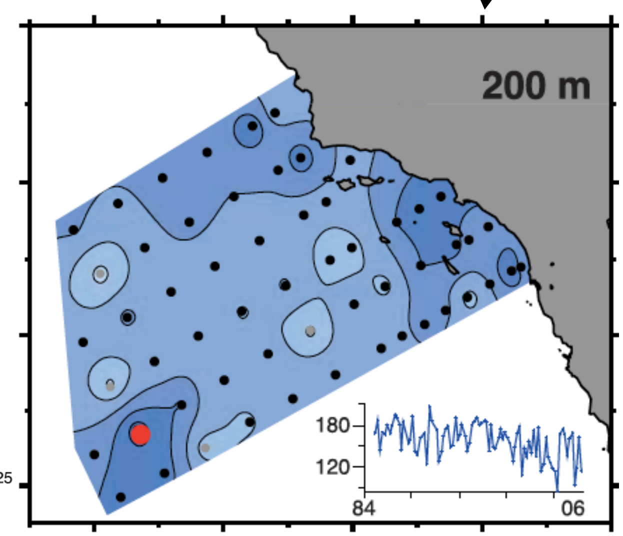
LONG-TERM DEOXYGENATION in the NORTHEAST PACIFIC OCEAN

Oxygen loss of 0.67µM O_2/y



Whitney et al. 2007

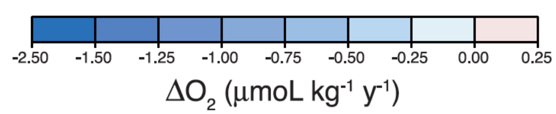




20-30% decline in oxygen at 200-300 m

off southern CA over the past 22 y

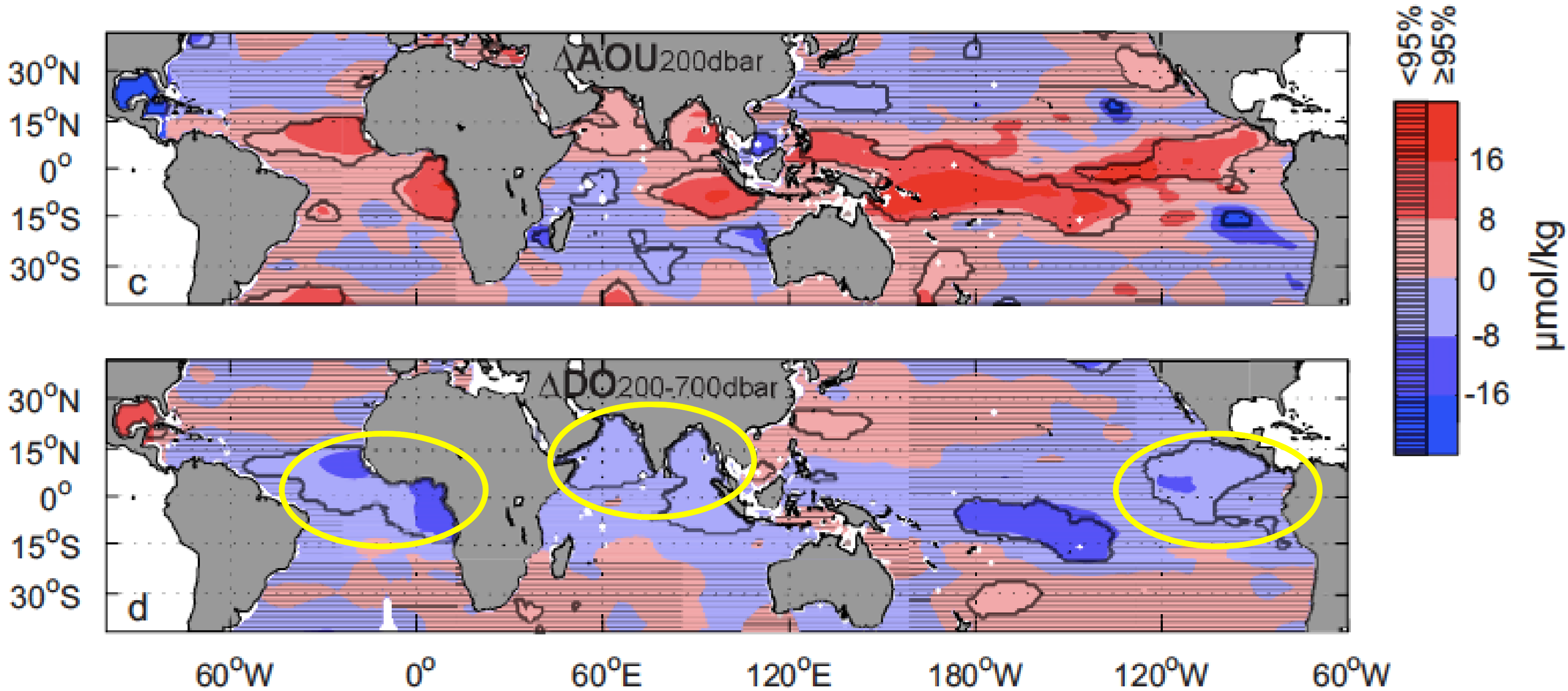
Bograd et al. 2008



GLOBAL AOU & OXYGEN CHANGE (200-700m)
1964-70 vs 1990-2008

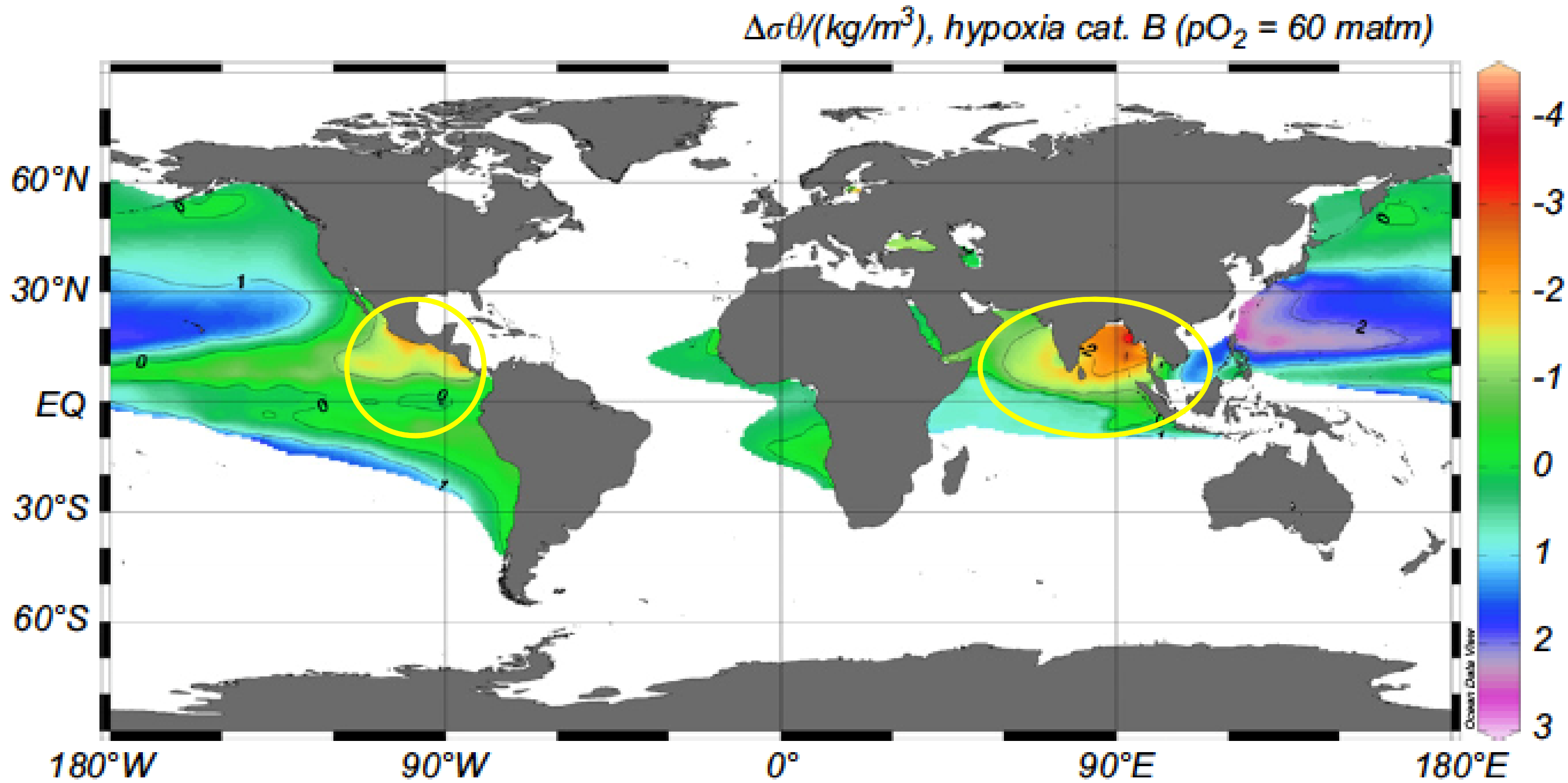
At 200 m the area with < 70 µM O_2 has increased by 4.5 million km^2 area

Are these new zones of acidification?



Stramma et al. 2010

The Biogeography of Hypoxia Stress

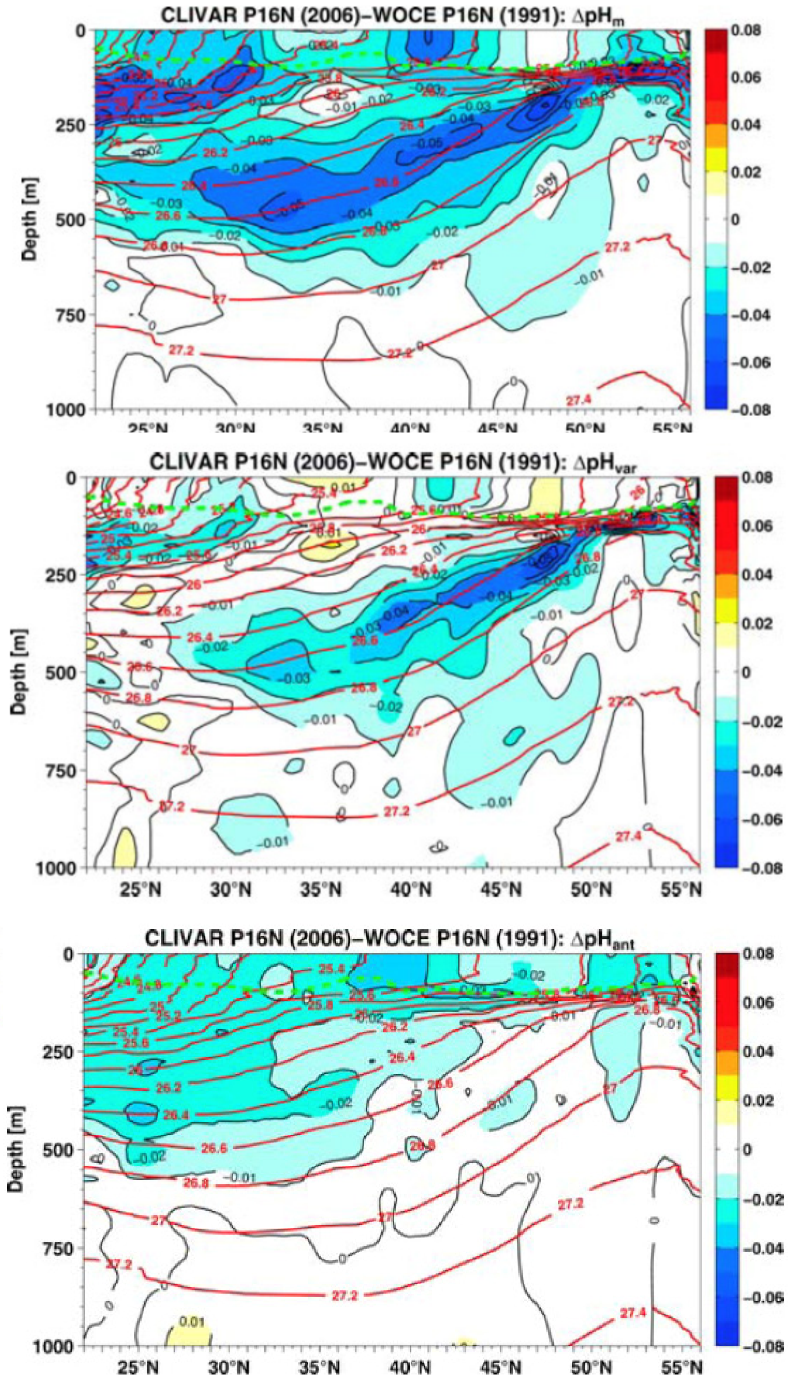


A relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions. Negative Dsy represents hypoxic waters shallower than 200m.

Hofmann et al. 2011 Deep-sea Research

Change in pH in the N. Pacific (1991-2006)

Byrne et al. 2010



TOTAL

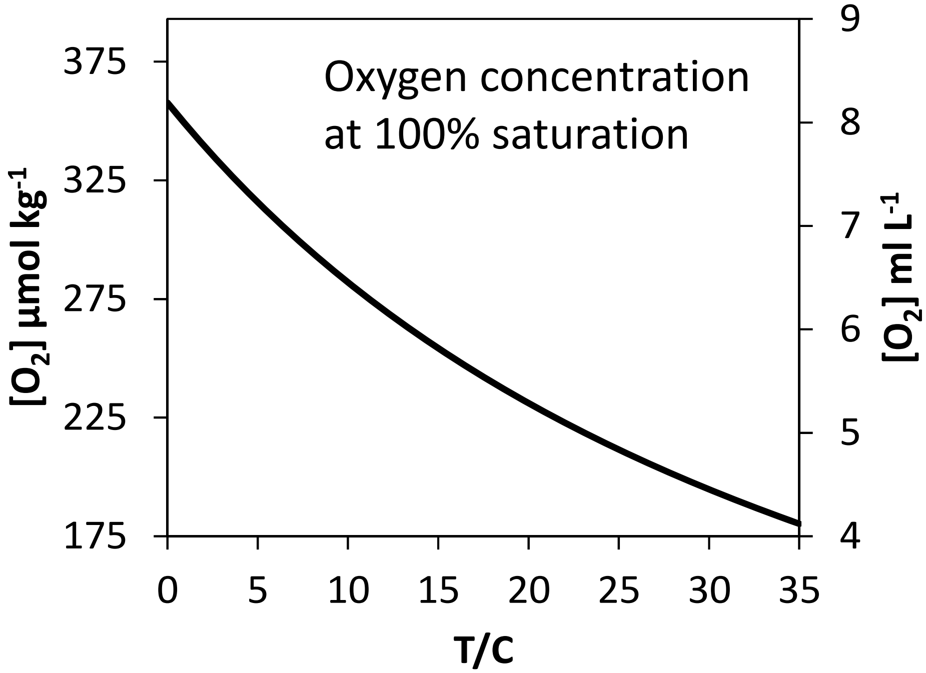
Effects of anthropogenic C on pH are detectable mainly to 150 m.

Change in pH have occurred down to 800 m

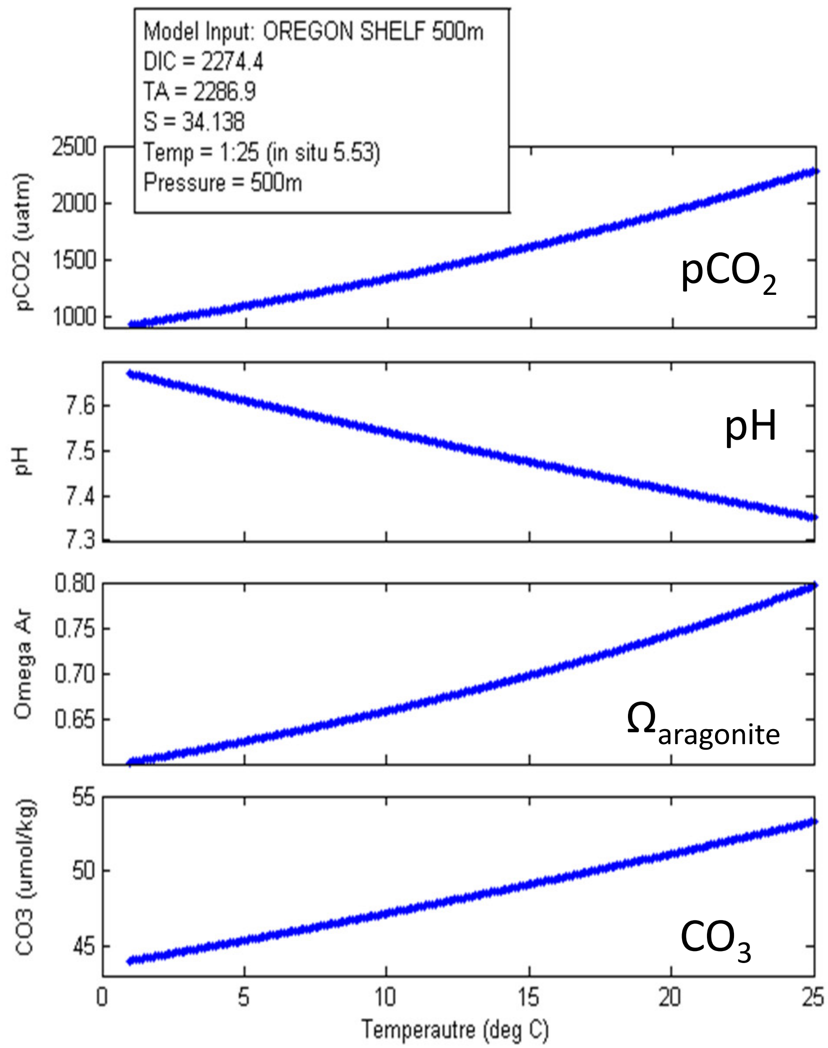
NATURAL VARIATION

ANTHROPOGENIC CARBON

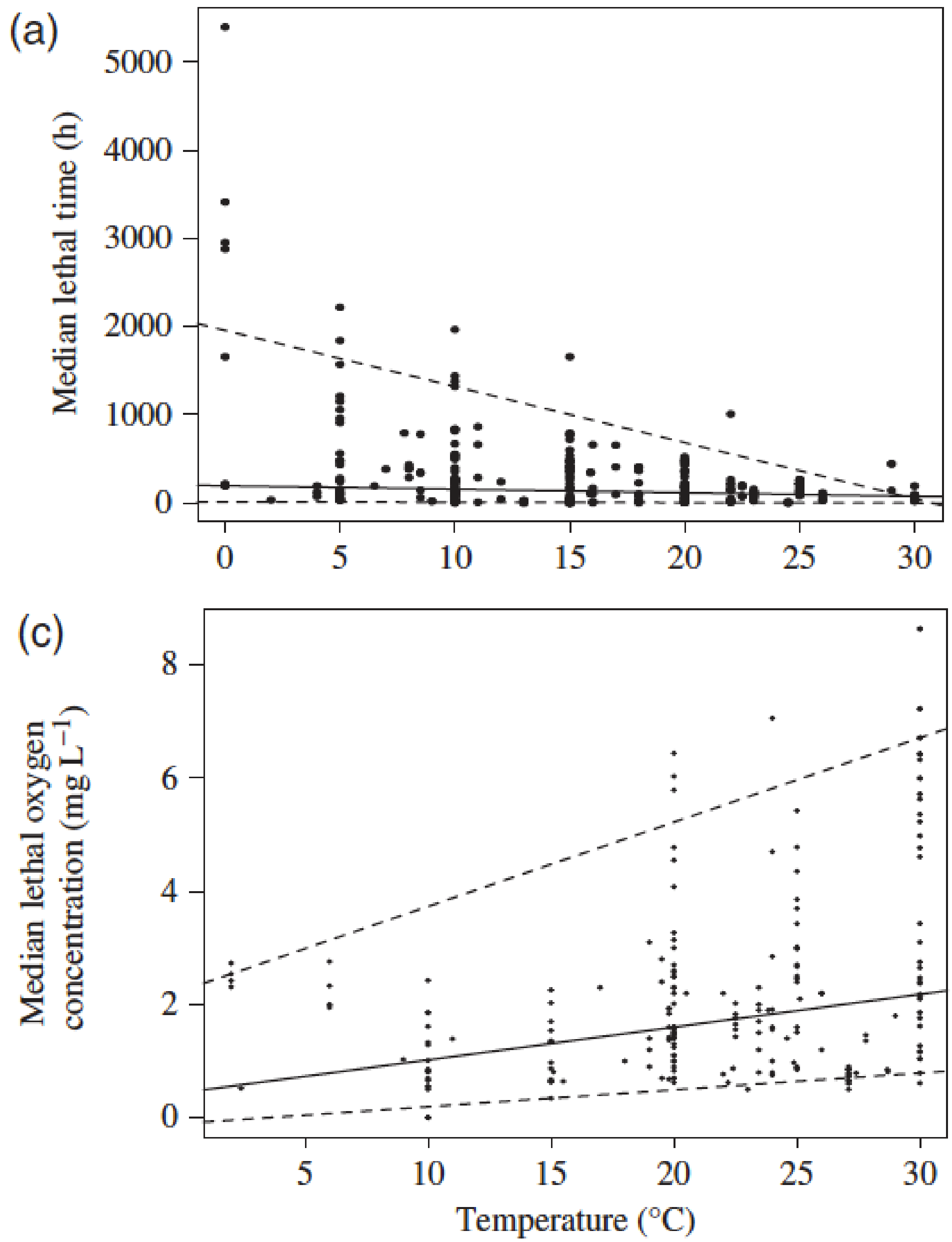
Physical/Chemical Stressor Interactions
The Oxygen and Carbonate System Are Sensitive to Temperature



S = 35 (solubility eqn. of Garcia & Gordon 1992)
Courtesy of T. Martz



Temperature regulates biological tolerances to stressors



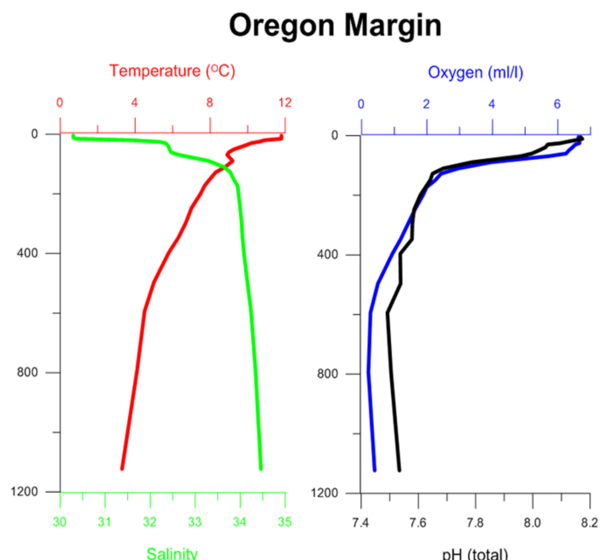
Elevated temperature
reduces hypoxia tolerance time

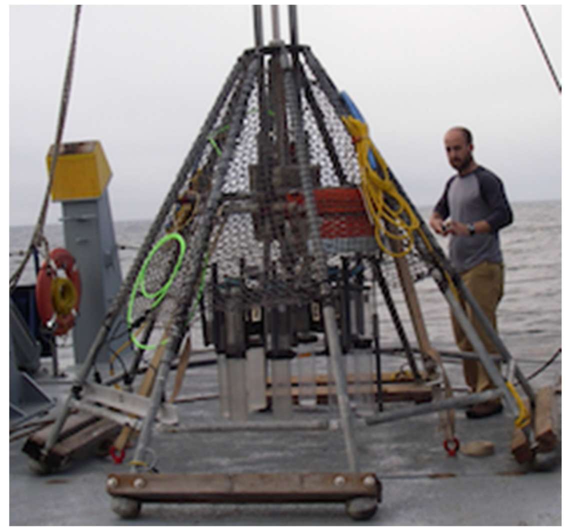
Elevated temperature raises
threshold oxygen concentrations

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

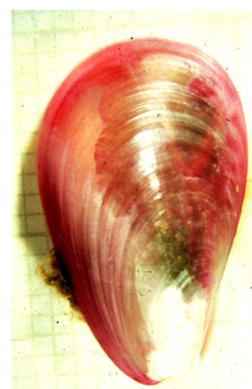




echinoderms

crustaceans

molluscs

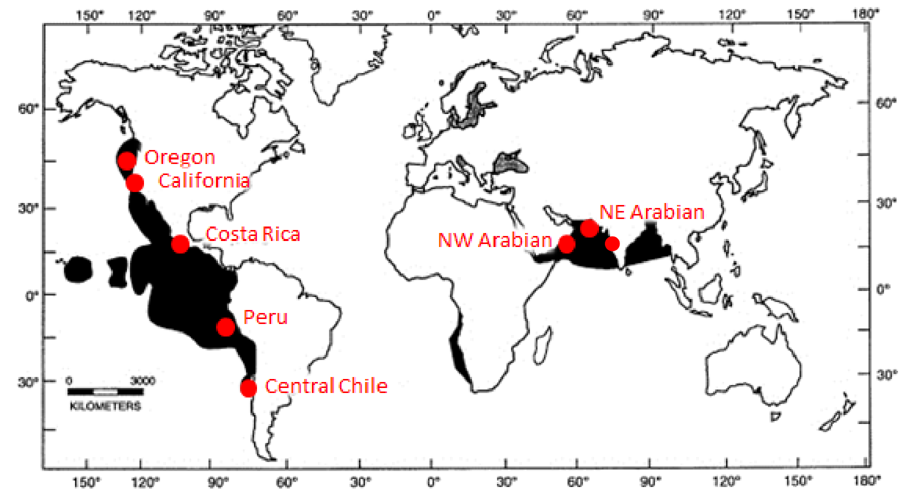


annelids

Levin & Frieder, unpublished

OMZ BENTHIC TRANSECTS

*Depth range: 122 – 3400m



Study Region	Number of Stations	Oxygen	Temp	pCO_2 & Ω_{arag}	Macrofauna
NE Arabian	14	x	x	nd	Hughes et al. 2009; Levin et al. 2009
NW Arabian	6	x	x	GLODAP*	Levin et al. 2000
Oregon	5	x	x	NACP*	Levin et al. 2010/unpub.
N. California	4	x	x	NACP*	Levin et al. 2010/unpub.
Costa Rica	5	x	x	Frieder unpub.	Levin unpub.
Peru	4	x	x	GLODAP*	Levin et al. 2003
Central Chile	4	x	x	nd	Gallardo et al. 2004
Total Stations	**42**	**42**	**33**	**24**	

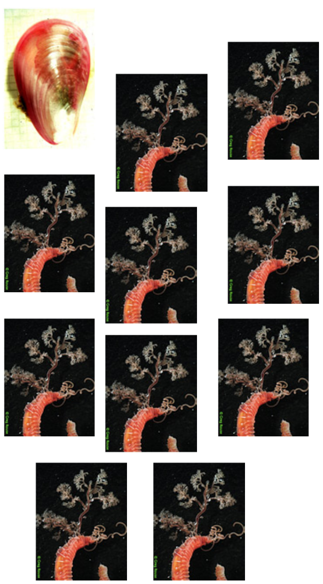
*GLODAP – Global Ocean Data Analysis Project; http://cdiac.ornl.gov/oceans/glodap/
*NACP West Coast Cruise 2007; http://cdiac.ornl.gov/oceans/Coastal/NACP_West.html

Diversity Indices

Shannon Diversity – H'
(species richness)

$$H' = -\sum_{i=1}^{R} p_i \log p_i$$

Low H' → High H'



2 species

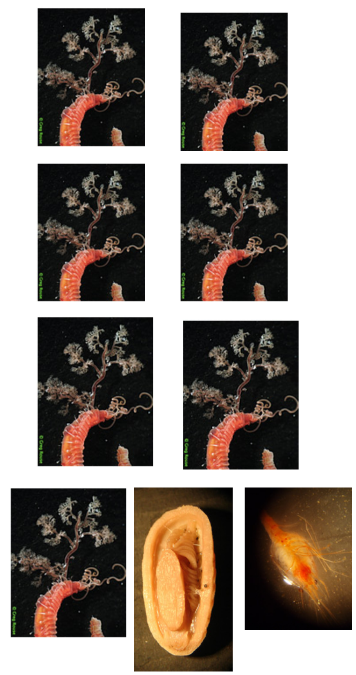
5 species

Pielou's Evenness – J'
(dominance)

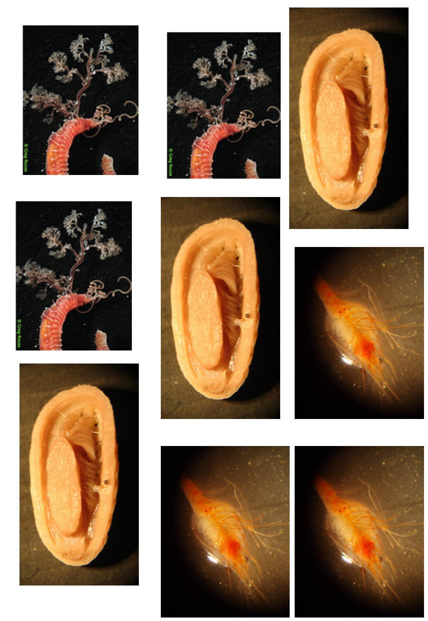
$$J' = \frac{H'}{H'_{\max}}$$

Low J' → High J'

(high dominance)

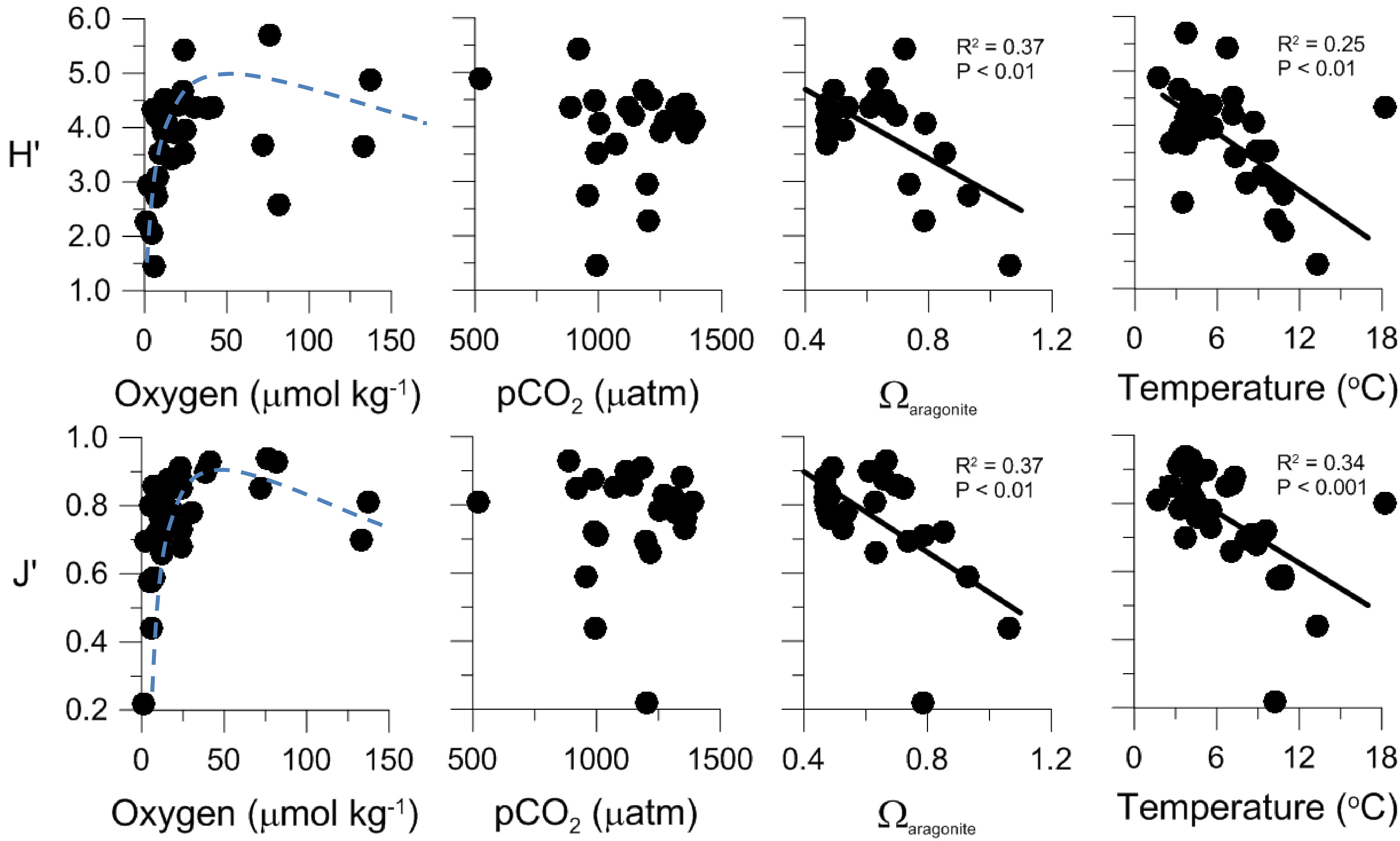


3 species

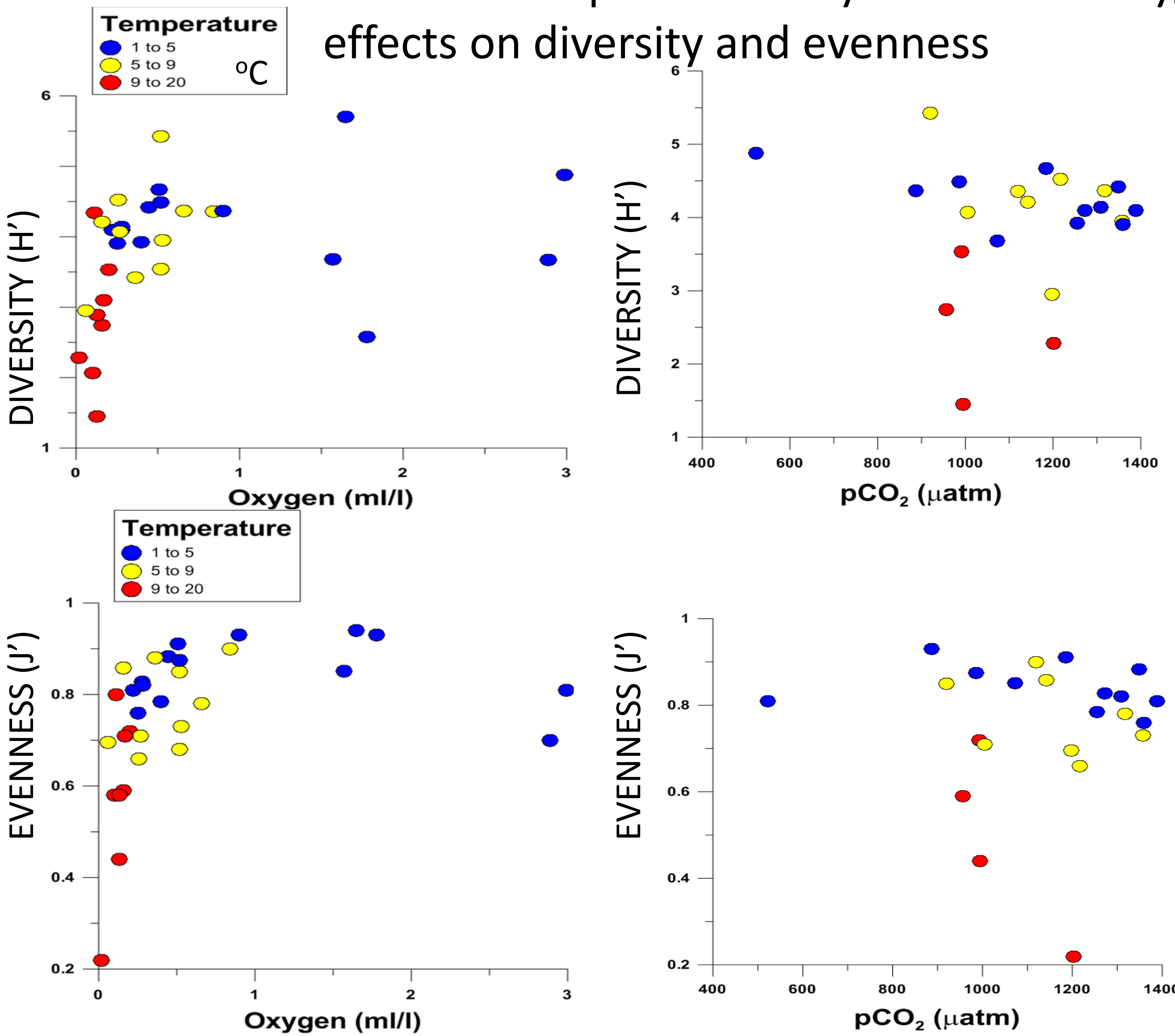


3 species

Is there a relationship between macrofaunal H', J' and oxygen, pCO_2, $\Omega_{aragonite}$ or temperature?



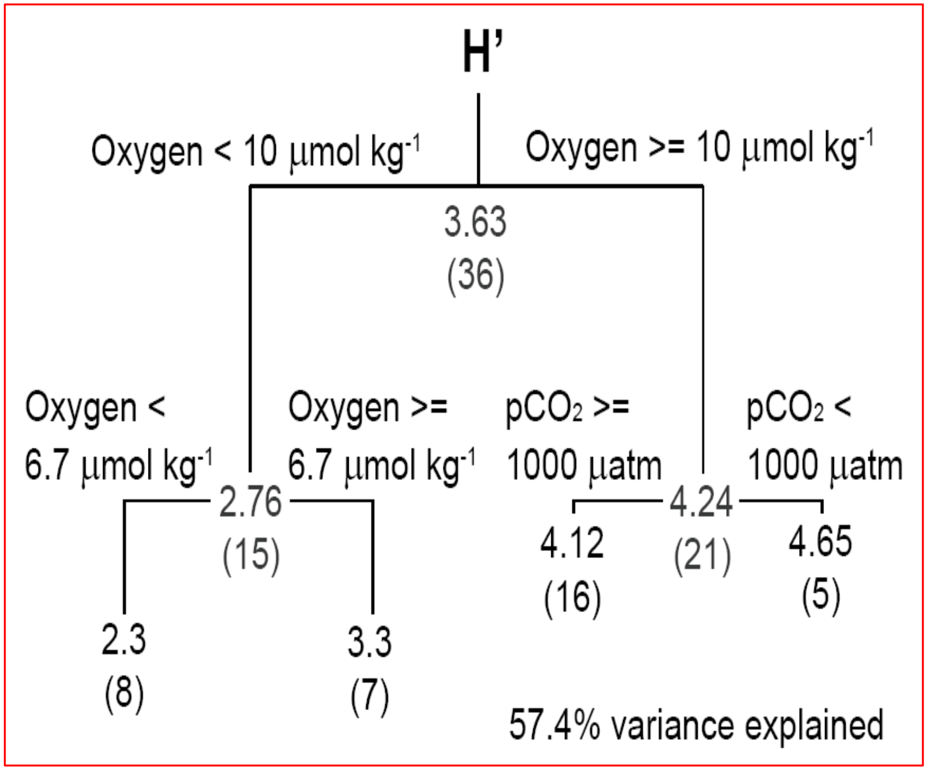
Elevated temperature may exacerbate oxygen effects on diversity and evenness

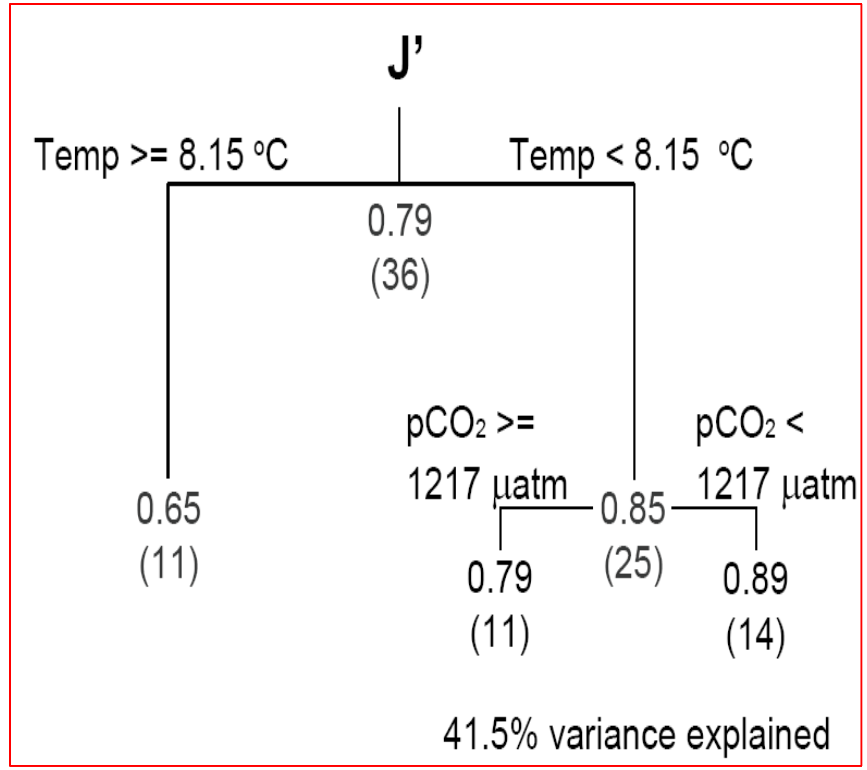


Variation in macrofaunal diversity (H') & evenness (J') associated with depth, oxygen, pCO_2, $\Omega_{aragonite}$ and temperature *on OMZ margins*?

Regression Tree

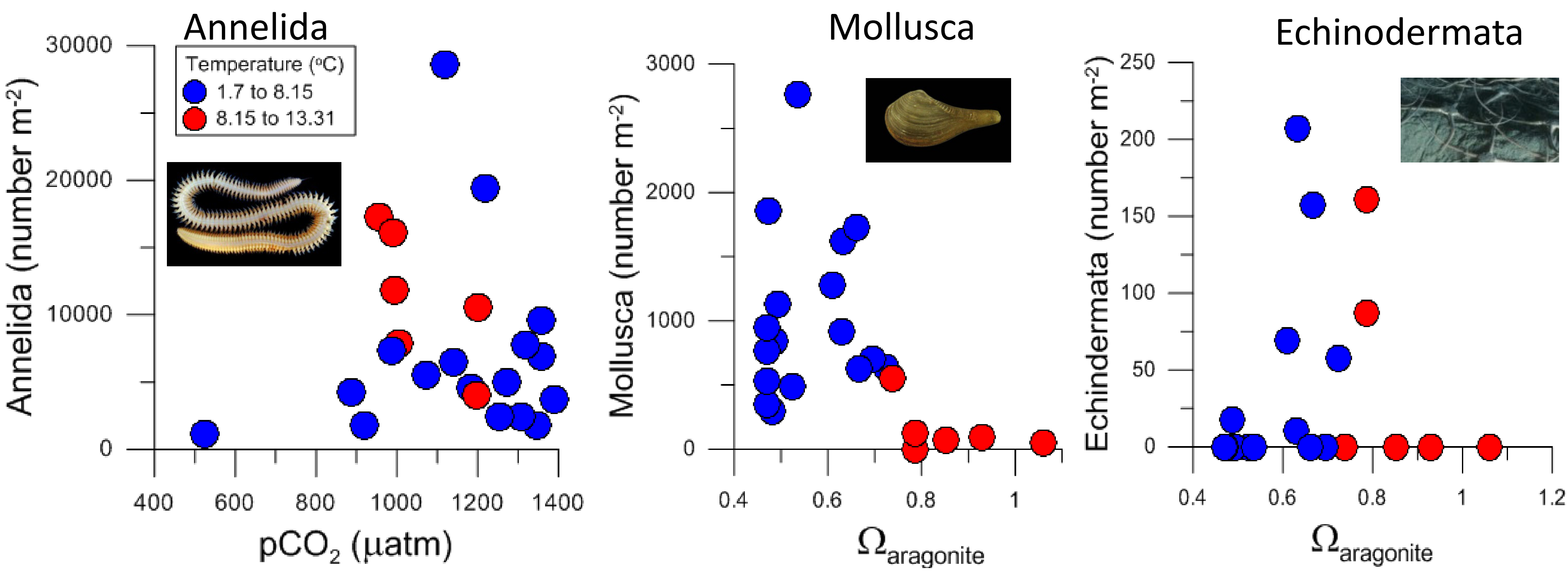
Levin & Frieder, unpubl.





- 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 pCO_2 or $\Omega_{aragonite}$ influence density of major taxa?

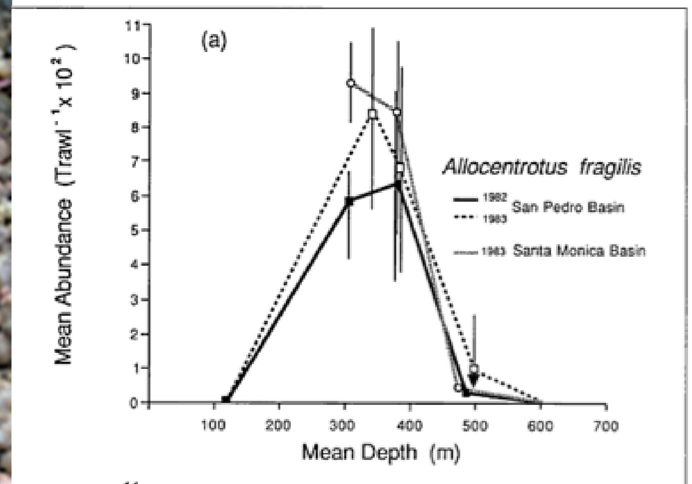


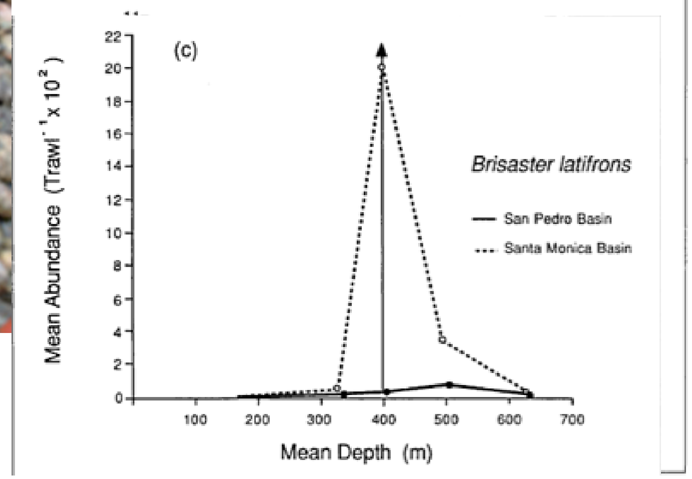
IN OMZs:

- Little effect of 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)

Dailey et al. 1993



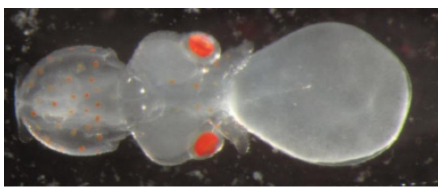


300 m: Oxygen 0.84 ml/L pCO$_2$ 1267
pH (in situ T): 7.57 (total scale)
DIC: 2277 umol/kg
Omega-Ar: 0.70
Temperature: 9.3^{o}C Sal: 34.3

(Data Courtesy of Y. Takeshita, C. Frieder
Trawl by M. Navarro)

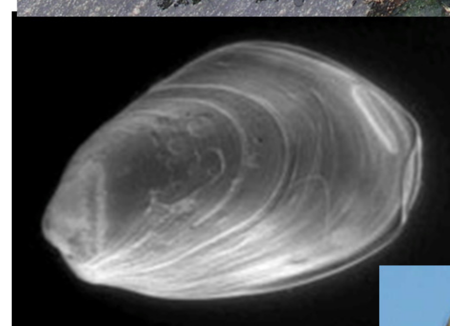
Controlled laboratory experiments
to distinguish different stressor influences

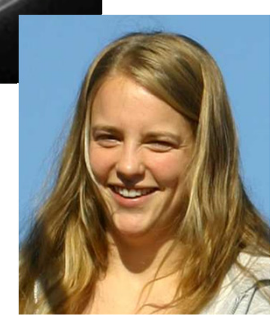
Market Squid – *Doryteuthis opalescens*



M. Navarro

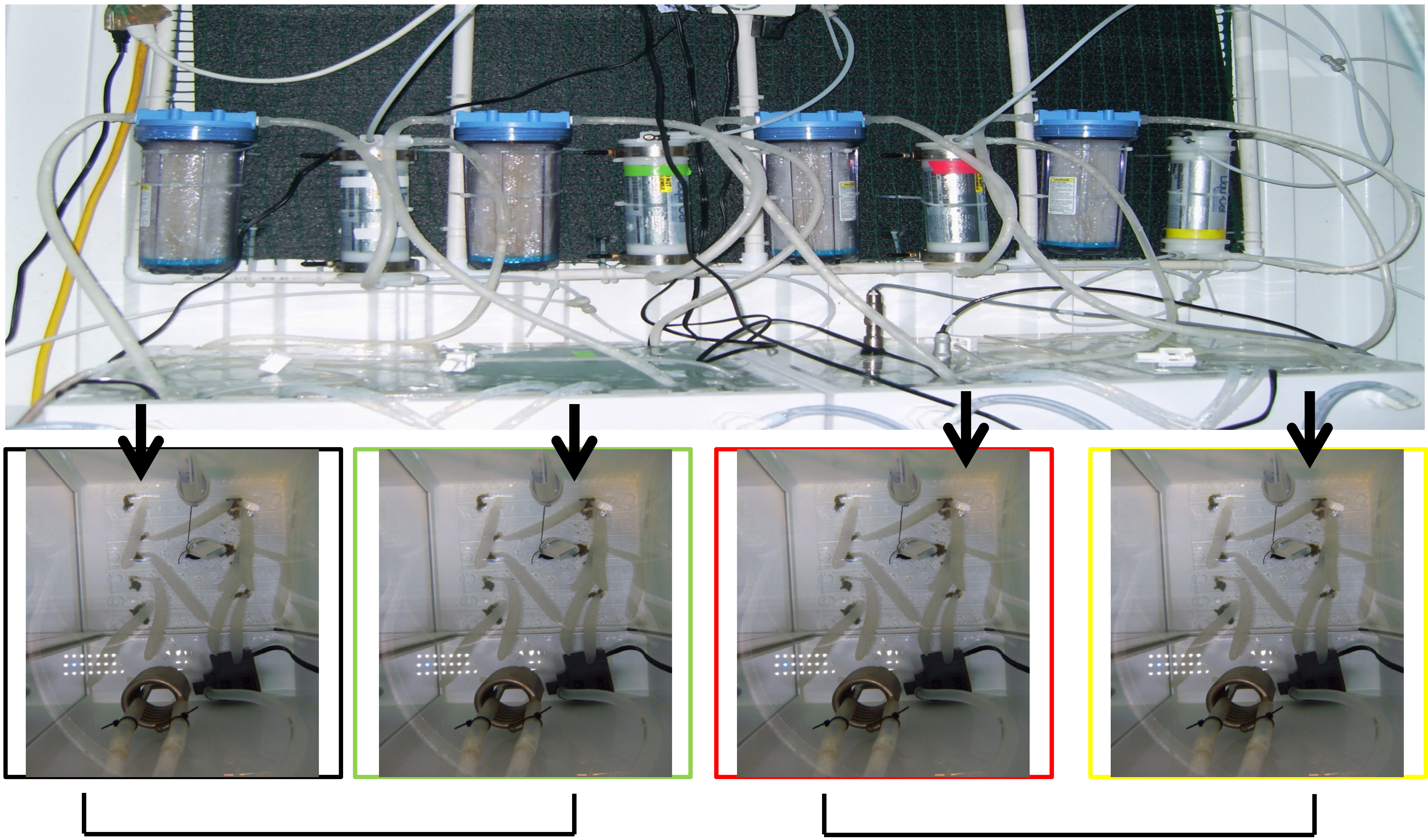
California Mussel – *Mytilus californianus*
Bay Mussel – *Mytilus galloprovincialis*





C. Frieder

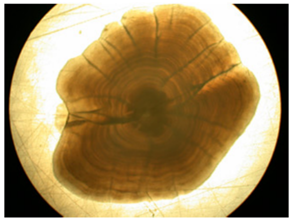
Controlling Multiple Stressors
Dickson/Bockman Experimental Facility



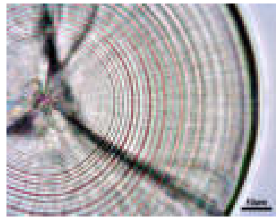
Can we detect exposure to multiple stressors in larval carbonates?

Larval structures retained after recruitment

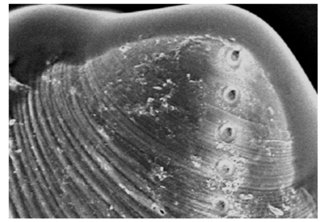
Otoliths



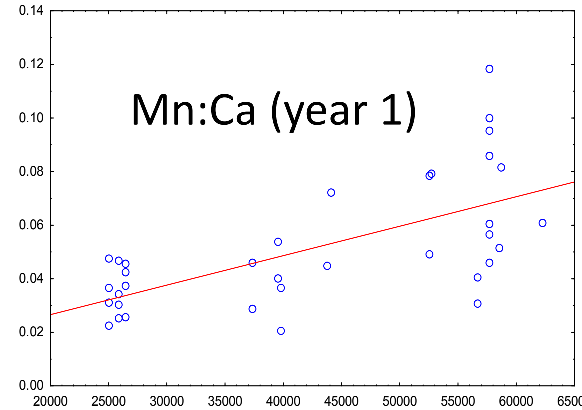
Statoliths



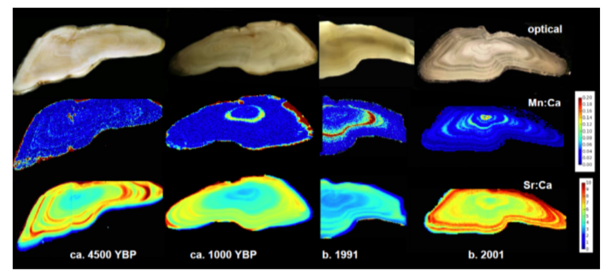
Prodissoconchs



Hypoxia in baltic cod otoliths

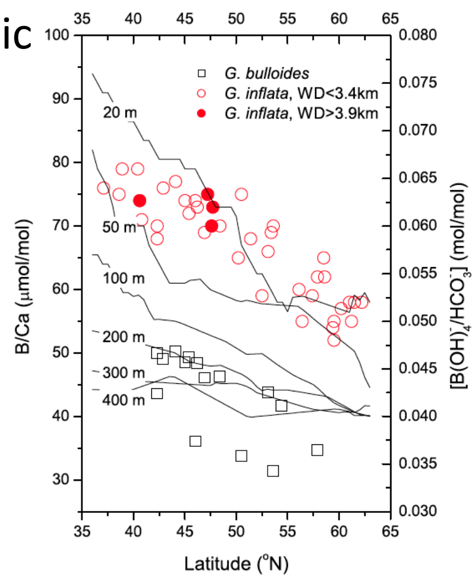


Temperature:	Sr, Mg, $^{18/16}O$, $^{88/87}$ Sr
pH	$\delta^{11}B$, B:Ca
Hypoxia:	Mn:Ca

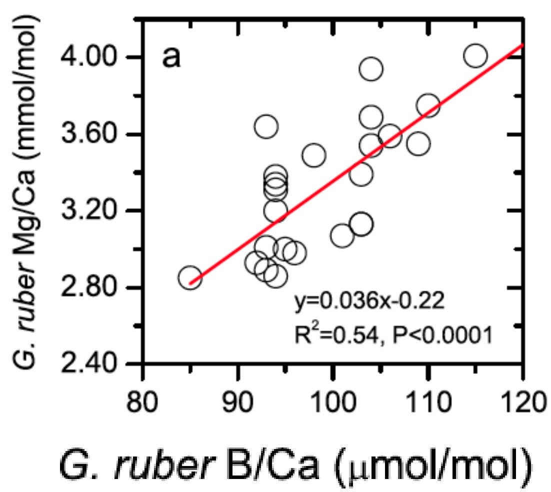


Limburg et al. 2011

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



Yu et al. 2007



LA-ICPMS

CLIDEEP
Climate Change Impacts on Ecosystem Function of the Deep Sea Floor

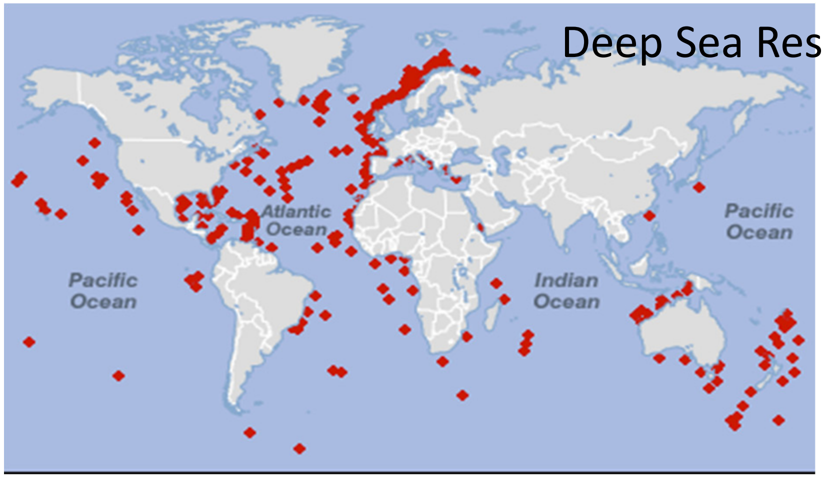
(A. Sweetman, A. Thurber, C. Smith, L. Levin + 20 others)

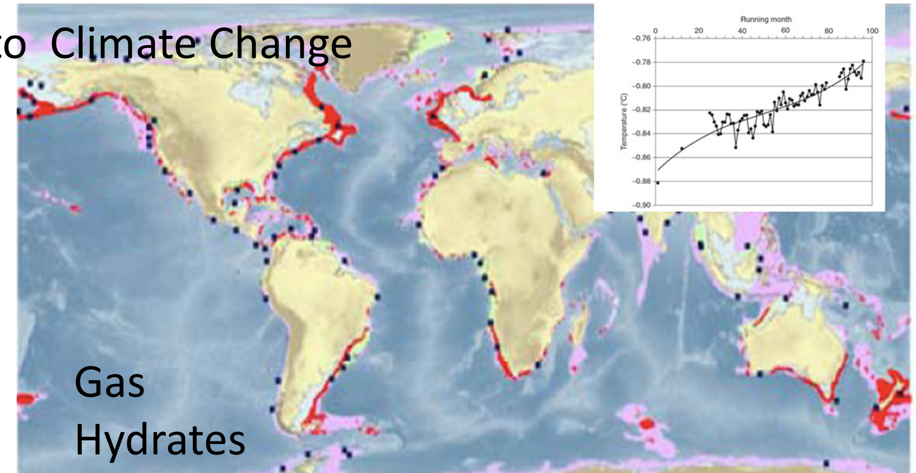
- Temperature, temperature variation
- Oxygen (hypoxia – O_2, pO_2, % saturation)
- Carbonate system
  (DIC/pCO2, pH, Alkalinity, aragonite/calcite saturation, CCD)
- POC Flux (quantity & quality), surface production/chlor a, seasonality

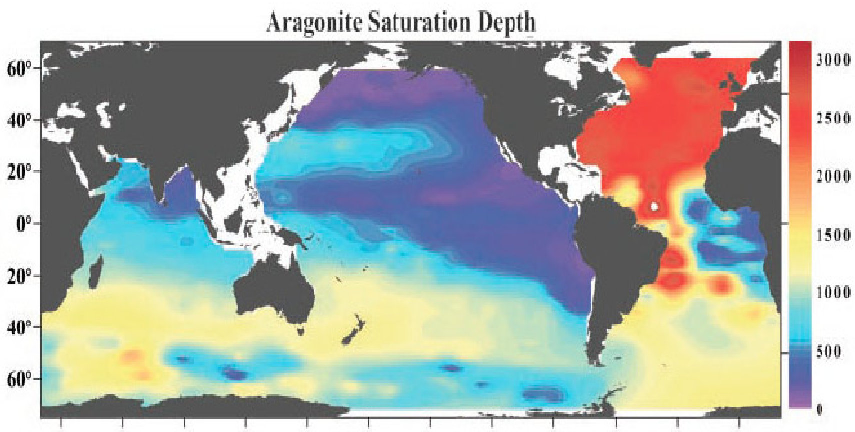
Co-locate major sites of multiple stressors, predict changes and impacts on ecosystem function

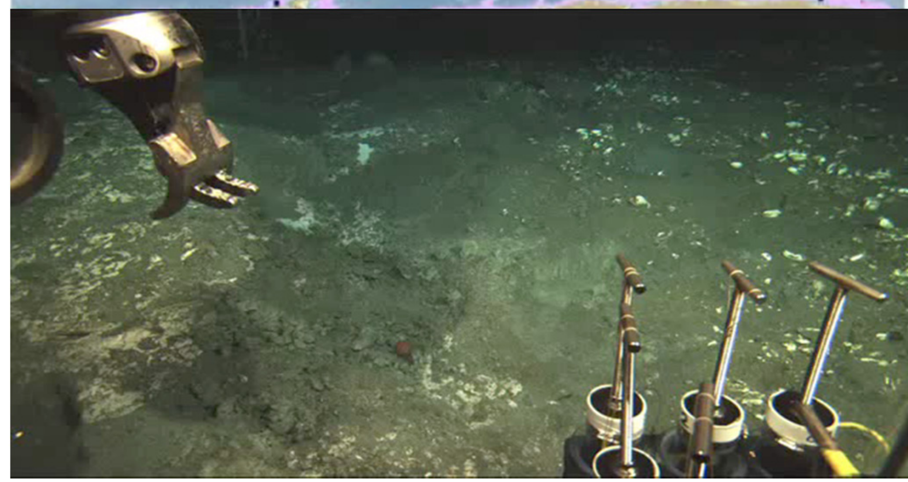
Support from:
Norwegian Research Council
INDEEP

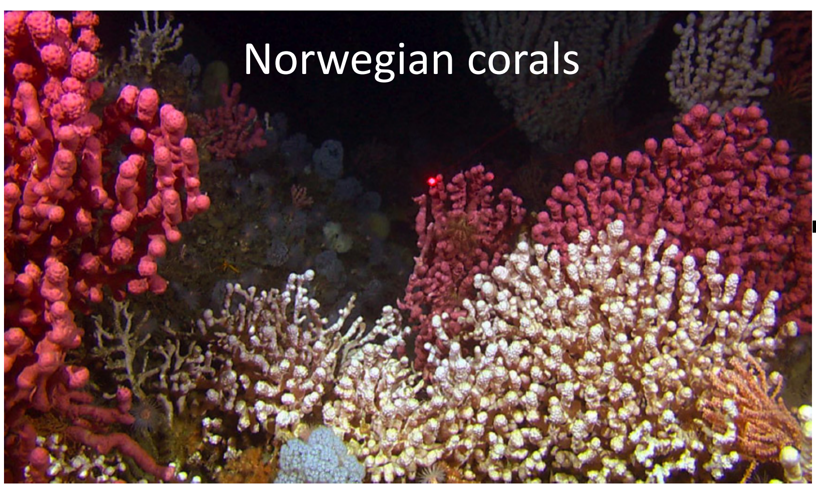
Deep Sea Responses to Climate Change

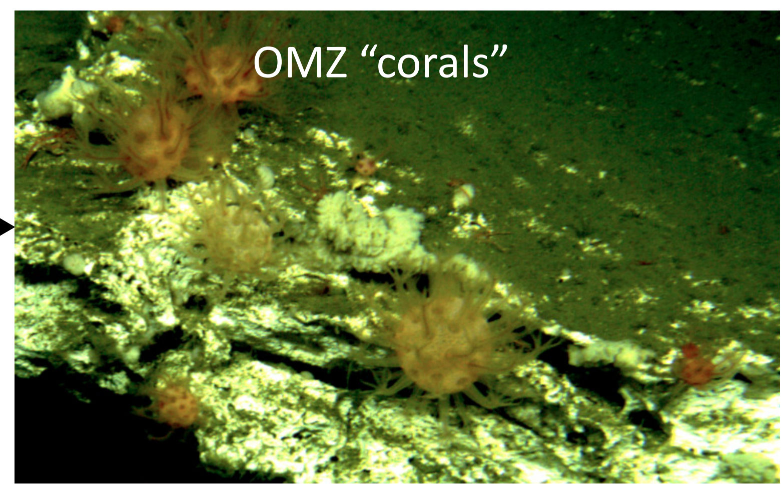




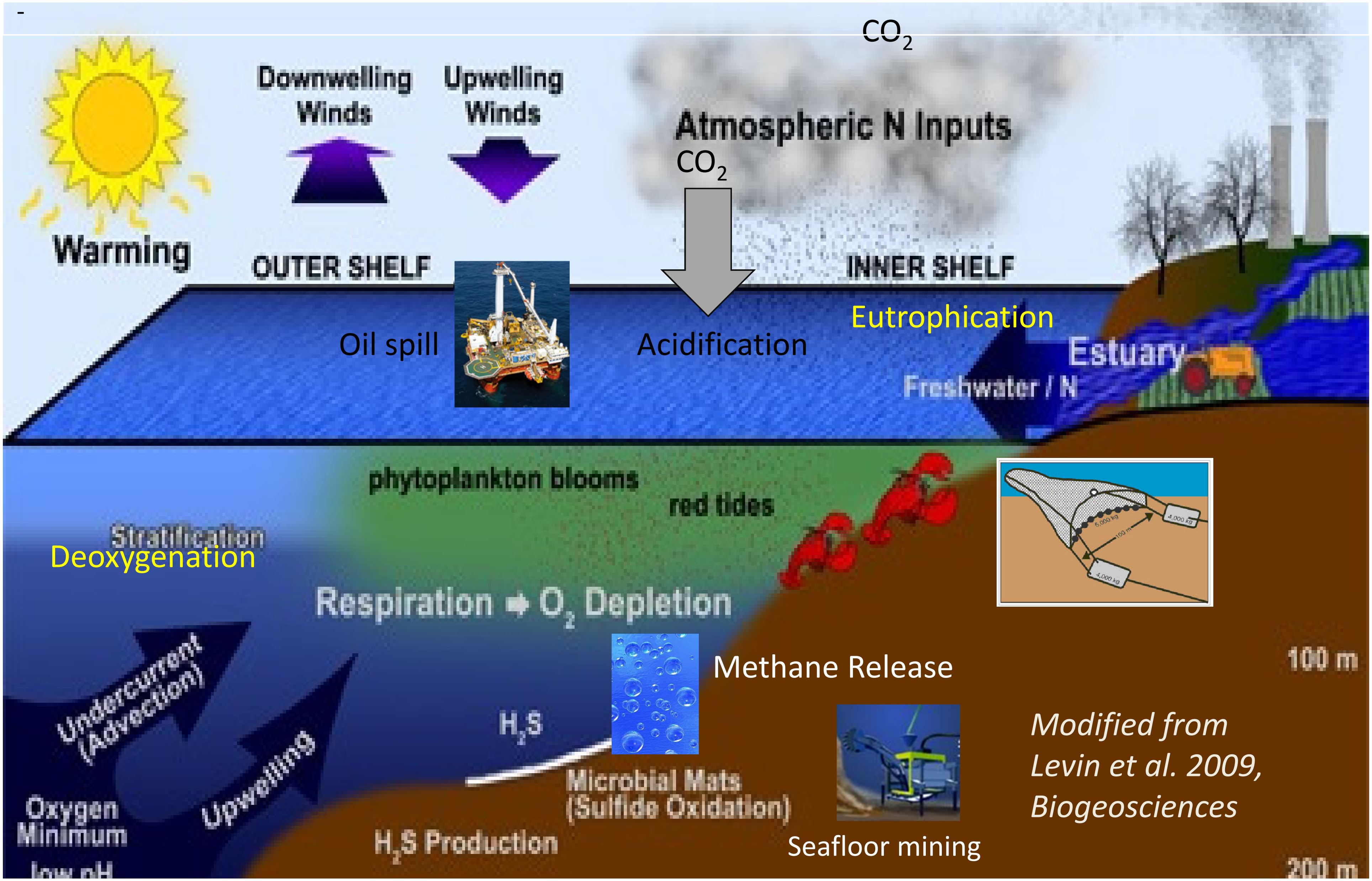








Climate stressors interact with anthropogenic stressors on the upper slope and shelf



Modified from Levin et al. 2009, Biogeosciences

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