Oxygen and capacity limitation of thermal tolerance (OCLT):

a matrix for integrating climate related stressor effects in marine ecosystems

Hans Pörtner

Physiological mechanisms linking climate to ecosystem change
Trends and projections of ocean warming:

Many open questions ....however...
...clear ecological impact is observed
...physiological knowledge which explains ecological impact is available and emerging

Temperature anomalies in different oceans between 1906 and 2005 compared to 1901 to 1950. Projections until 2100 according to emission scenarios B1, A1B, A2.
The „emerging“ danger: Ocean Acidification (through CO₂ enrichment)...

...associated with a pH-decrement in surface water by 0.02 units per decade since 1980

Even more questions....
...ecological impact setting in (calcification)
...emerging hypotheses and knowledge about physiological basis BEYOND calcification

RELEVANCE emphasized by:
- present atmospheric CO₂ accumulation beyond IPCC (2007) scenarios.
- possibility of coral reef marginalization by combined temperature and CO₂ (>350 ppm) effects.
Future scenario: fossil fuel reserve: 5000 Gto C → 18 000 Gto CO₂

Pre-industrial → Today

\[ \Delta pH = -0.12 \]

→ 32 % more acidification

→ 2100

\[ \Delta pH = -0.45 \]

→ 2.8 fold more ....

→ 2300

\[ \Delta pH = -0.77 \]

→ 5.9 fold more ...

Caldeira and Wickett, 2003, 2005
**Expanding oxygen minimum layers**

**Hypoxia effects....**

...ecological impact setting in (...dead zones)

...combined with CO$_2$ effects

...some knowledge about physiological basis

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**Unifying principles in ecosystem effects of ocean warming, acidification, hypoxia?**

Physiology and climate change:

(Quantitative) evidence linking physiological responses to ecosystem change in various climate scenarios is scarce

Solutions?

Patterns identified by long-term Field data (!), Macrophysiology, Meta-Analyses using statistical tools.... However,......this remains insufficient...
To be complemented by:
.... mechanism based projections linking physiological and ecological processes.

What would we need? To develop....

• an integrative understanding of the mechanisms, benefits, functional tradeoffs of adaptation
• an understanding of the interdependence of mechanisms at various levels of biological organisation, molecular to whole organism and.... ecosystem
• an integrative picture of synergistic or antagonistic effects of abiotic and biotic factors

Expected result:
• Reliable projections of ecosystem change
• High predictive power for realistic scenarios
Current ecological phenomena:

East Atlantic species are moving North
……to various degrees (!)

Shifting biogeographies
~ Different thermal sensitivities
→ Changes in community composition

Cod
*(Gadus morhua)*

Anglerfish
*(Lophius piscatorius)*

Snake blenny
*(Lumpenus lampretaeformis)*

Perry A.L. *et al.*, 2005
Thermal specialization explaining sensitivity, productivity and ecological phenomena?

The climate-induced “regime shift” from sardines to anchovies (Japanese Sea) is linked to the thermal windows of growth of the two species.

Takasuka et al. 2007
Explaining climate specialization from (animal) physiology: Concept of oxygen and capacity limited thermal tolerance (OCLT)

Climate sensitivity is based on the specialization of animals on limited thermal windows set by (aerobic) performance capacity: the first level of thermal limitation!

Are these physiological principles suitable to explain ecological phenomena?

Eelpout (Zoarces viviparus) abundance in the German Wadden Sea falls at high summer mean temperatures.

Early loss of LARGE individuals due to the allometry of oxygen limitation.
Climate effects in the field…..

Abundance

Eelpout

At the limits of acclimation capacity the loss of fitness (performance capacity) beyond pejus limits causes reduced growth and field abundance!

Blood flow

O₂-deficit

Not all thermal windows are the same:
Temporal dynamics and climate dependence

Life history
Thermal window widths across life stages (fishes, crustaceans)

- Spawners
- Growing adults
- Juveniles
- Eggs, early larvae

Aerobic thermal window

Climate zone

Performance

Eury-therm
Steno-therm

T clines

There are metabolic and functional consequences of adaptation to various climate regimes:
Co-defining sensitivity to CO₂, hypoxia… and vice versa?

Acclimation capacity differs between species according to climate zones: defining the thermal niche

Warm acclimation in Antarctic fish

Seasonal acclimation in temperate lugworms

Genomic basis: (Cold) acclimation capacity even differs between populations

Less in temperate eurythermal North Sea cod (NSC) than in cold eurythermal Barents Sea cod (NEAC)

White muscle citric synthase & cytochrome oxidase

Tradeoff: High cost of eurythermal cold adaptation causing lower growth
Integrating hypoxia sensitivity into thermal tolerance
Patterns of critical $P_{O_2}$ at standard metabolic rate (SMR):
Transition to anaerobic metabolism characterizes $P_c$ in oxyregulators,
may cause metabolic stimulation in hypoxia

Bufo marinus (toad), Palaemon elegans (shrimp)

Pörtner et al. 1991
A different look at Pc:
Upon warming (and cooling) the level of excess oxygen availability shrinks from supporting aerobic scope to setting thermal limits.

Pc equals normoxic Po₂ at high (and low?) Tc‘s

(Zakhartsev et al. 2003, Pörtner and Knust 2007)
Integrating hypoxia effects into O$_2$ limited thermal tolerance:

at MMR: $P_c^{\text{max}}$

at SMR and $T_{\text{opt}}$: $P_c^{\text{min}}$

$P_c^{\text{max}} = \text{Normoxia}$

$P_c$ (kPa)

Rate of aerobic performance,

Temperatures

MMR: maximum metabolic rate
SMR: standard metabolic rate

Pörtner, J. exp. Biol. 2010
**Hyas araneus**

**Leftward shift of upper Tc sets in**
under expected CO₂ accumulation scenarios:

**Highest CO₂ sensitivity at thermal extremes,**
→ Narrowing of thermal windows

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CO$_2$ causes enhanced hypoxemia at thermal extremes

BUT not necessarily lower performance optima, e.g. in fish (Melzner et al. 2009)

Hypothesis confirmed in Crustaceans (Metzger et al. 2007, Walther et al. 2009), coral reef fishes (Munday et al. 2009)

Which mechanisms define CO$_2$ sensitivity?

Acclimation to high CO₂ tensions occurs via gene expression of pH-regulation mechanisms in fish gills, alleviating sensitivity in apparently insensitive fish?

Eelpout (Z. viviparus)

Expression studied by real-time PCR

Deigweiher et al. 2008
At high CO₂ levels (>3000 ppm) uncompensated acidosis and metabolic depression in several lower invertebrates contribute to reduced calcification, lower performance, and enhanced mortality on long time scales.

Compensated acidosis, and, therefore, non-metabolic depression in most fish contribute to maintained performance, enhanced resistance.

Acidosis causes performance decrements... …a link to modulating thermal tolerance?

Regulation of extracellular acid-base status as a major factor in defining different sensitivities?

HYPOTHESES to be tested under ocean acidification scenarios...
Mechanism based projections of ecosystem implications:

CO₂ (and hypoxia) affect species interactions due to differential sensitivities.

Differential sensitivities

Relative changes in performance:
- Δ competition
- Δ susceptibility to predation

THERMAL WINDOWS as defined by the OCLT concept: a suitable matrix for understanding changes in food web dynamics and ecosystem functioning.

Addressing CO$_2$ and hypoxia effects in warming oceans, hypotheses

First lines of sensitivity (with ecological relevance) likely depend on

- effects on OCLT (oxygen and capacity limited thermal tolerance)
- compensation capacity for extracellular acid-base status in relation to levels of CO$_2$ accumulation and OA.

Implications to be considered:

- seasonal shifts in performance windows
- climate dependent functional specialization
- temperature dependent biogeography
- climate dependent growth, fecundity
- synergistic interactions with further factors in addition to temperature, hypoxia, CO$_2$ (e.g. various pollutants, …)
- effects on biogeography and species interactions
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