Can we infer organismal physiology from geochemical proxies?

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Proxies are stand-ins for environmental parameters that can no longer be measured directly.
The B/Ca proxy for past seawater-pH or \([\text{B(OH)}_4^-]/[\text{HCO}_3^-]\)

\[
\text{CaCO}_3 + \text{B(OH)}_4^- \rightleftharpoons \text{Ca(HBO}_3) + \text{HCO}_3^- + \text{H}_2\text{O}
\]

The boron isotope proxy for past seawater-pH

Hemming & Hanson, GCA, 1992
B/Ca and boron isotope proxies for reconstructing past seawater-pH

Allen et al. (2011)
pH modification in response to physiological processes: photosynthesis, respiration, calcification

- Photosynthesis: DIC → CO$_2$ → pH increase
- Respiration: CO$_2$ →DIC → pH decrease
- Calcification: Ca$^{2+}$ → 2H$^+$ → pH decrease

Foraminifer shell: pH increase
Coral skeleton: pH decrease
ΔpH (site of calcification - ambient, TS)

- O. universa (California)
- O. universa (Caribbean)
- G. sacculifer
- A. lobifera (fluorescent dye)
- M. vertebralis, A. lobifera, A. hemprichii
- G. fascicularis
- Favia sp.
- Acropora sp.

light (μmol photons m⁻² s⁻¹)

Rink et al. 1998
Köhler-Rink & Kühl 2005
Jørgensen et al. 1985
Köhler-Rink & Kühl 2000
Bentov et al. 2009
Al-Horani et al. 2003
Kühl et al. 1995
Larger symbiont-bearing foraminifers often record higher $\delta^{11}$B - i.e. greater pH elevation.

$\delta^{11}$B (‰)

size (µm)

- G. ruber, coretops and sediment traps
- G. sacculifer, coretop sediments
- G. sacculifer, Pliocene age sediments

Hönisch & Hemming, 2004
Bartoli et al., 2011
Henehan et al., 2013
Ocean acidification at the PETM (56 million years ago)

Penman et al., Paleoceanography, 2014
No apparent effect of symbiont-bleaching on the $\delta^{11}$B record at the PETM

Penman et al. (EPSL, 2014)
But what about pH-elevation differences between species?

Allen et al. (2011)
Dyez & Hönisch, unpubl.
Assessment of algal photosynthesis in planktic foraminifers by fast repetition rate fluorometry

Fujiki et al. (2014)
Globigerinoides sacculifer

photochemical efficiency ($F_v/F_m$) foraminiferal shell size (µm) days to gametogenesis

maximum fluorescence ($F_m$) foraminiferal shell size (µm) days to gametogenesis

Fish et al., unpubl.
Globigerinoides ruber

G. ruber

photochemical efficiency ($F_v / F_m$)
g cultivating shell size ($\mu m$)
days to gametogenesis

Fish et al., unpubl.
Orbulina universa

photochemical efficiency ($F_v/F_m$)

maximum fluorescence ($F_m$)

foraminiferal shell size ($\mu$m)

days to gametogenesis

Fish et al., unpubl.
Orbulina universa

Fish et al., unpubl.

Allen et al., 2011
Foraminiferal shell size (µm)

- G. ruber
- G. sacculifer
- O. universa

Fish et al., in prep.
Physiological processes – photosynthesis, respiration and calcification – modify pH in the microenvironment of foraminifers.

Taking B/Ca and boron isotope values at face value, pH-elevation due to symbiont photosynthetic activity and/or depth range in the water column should rank *G. ruber* > *G. sacculifer* > *O. universa*.

This prediction is not verified by symbiont density and fluorescence measurements, which are similar for all species, if not even highest for *O. universa*.

Alternative processes must be responsible for the difference in shell geochemistry, most likely including the biomineralization process and related ion transport.

Inferring physiological processes from geochemical proxies may be misleading, unless all details of the organismal biology are known.
Coral resilience to ocean acidification and global warming through pH up-regulation?
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- pH estimated from $\delta^{11}B$
  - Krief et al., 2010 (apical)
  - Holcomb et al., 2014 (apical)
  - Holcomb et al., 2014 (lateral)
  - Sanyal et al., 2000 (synthetic calcite)

- pH measured with fluorescent dye
  - Venn et al., 2013 (lateral)
  - Holcomb et al., 2014 (lateral)

$\Delta$pH inferred from $\delta^{11}B$ synthetic calcite

pH at the site of calcification (TS)

Seawater pH (TS)
pH up-regulation has been measured directly and via $\delta^{11}B$ in *S. pistillata* follow a similar pH-slope. This may indicate greater resilience to ocean acidification.

$\delta^{11}B$ in all marine carbonate calibrated over a wide pH range show lesser sensitivity to pH than predicted from $\delta^{11}B$ in aqueous borate, including synthetic calcite.

Biology is not involved in synthetic calcite precipitation, suggesting that the $\delta^{11}B$ vs. pH sensitivity of marine carbonates may not be due to active pH up-regulation, but instead reflect an incomplete understanding of the boron isotope proxy systematics.

Unless proxy systematics are understood in their entirety, interpretations of deviations from theory should be approached with caution.

Inorganic CaCO$_3$ precipitation experiments should be replicated to confirm or revise the calibration.
Thanks!