Coral and foraminifera calcification mechanisms in view of high CO$_2$ ocean (Monaco 2008)

Jonathan Erez
Institute of Earth Sciences,
The Hebrew University of Jerusalem Israel.

Shmuel Bentov, Jack Silverman, Kenny Schneider, Alon Braun, Mor Grinstein and Boaz Lazar

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Introduction and questions

• Ocean acidification is well documented in terms of \( \Omega \) or \( \text{CO}_3^{2-} \), past, present, and future (Orr, Feely, Kleypas, Caldeira, Tyrell and others)

• However, calcifying organisms are not little pieces of \( \text{CaCO}_3 \) floating in the ocean. “they are protected by membranes”, so why are they sensitive to \( \Omega \)?

• Why is there a different response in different organisms? If we ignore experimental artifacts, why some respond strongly and other do not?
Introduction and questions 2

• More specifically: the calcification response of foraminifera and corals is different from that of coccolithophores why is that?

• Environmental variability in carbonate chemistry of ambient seawater (diurnal and seasonal) is larger then ocean acidification, so why are they responding to changes of 0.2 pH units or less?
A plate from the book of Winter and Seisser on Coccolithophores

33 Emiliania huxleyi var. corona
known range: Late Pleistocene - Recent
known distribution: Pac (NE,C); Atl (N)

J. Alcober

35 Gephyrocapsa ericsonii
known range: Pleistocene - Recent
known distribution: Pac (NE,C); Atl (N); Ind; Med; Red

S. Kling

36 Gephyrocapsa muelleroe
known range: Late Pleistocene - Recent
known distribution: Atl (N); Med

37 Gephyrocapsa oceanica
known range: Early Pleistocene - Recent
known distribution: Pac (NW,NE,C,S); Atl (N,C,S); Ind; Med; Car; Red; Wed
1. The most diverse and most productive ecosystem in the oceans
2. Precipitate ~ 50 % of the net CaCO3 accumulation in the ocean
3. Coral skeletons provide excellent oceanic paleo-archives
Riebesell et al. 2000, Nature

The graph shows the relationship between Calcite/POC and [CO$_2$] (μmol l$^{-1}$) and [CO$_3^{2-}$] (μmol l$^{-1}$) with values at 280, 365, and 750 indicated. The data points and trend lines illustrate the decrease in Calcite/POC with increasing [CO$_2$] and [CO$_3^{2-}$].
Fig. 2. Coccolith volume and CaCO₃ per cell. Increasing coccolith volume is closely coupled with increasing CaCO₃ per cell, indicating down-core measurement of coccolith mass to be representative of CaCO₃ production. Scanning electron microscope (SEM) images show typical coccoliths from each culture with Pco₂ values from 280 to 750 ppmv of CO₂, of where the measured volume was converted to length using the formula for a heavily calcified coccolith (27).
Fig. 4. Average mass of CaCO$_3$ per coccolith in core RAPID 21-12-B and atmospheric CO$_2$. The average mass of CaCO$_3$ per coccolith in core RAPID 21-12-B (open circles) increased from $1.08 \times 10^{-11}$ to $1.55 \times 10^{-11}$ g between 1780 and the modern day, with an accelerated increase over recent decades. The increase in average coccolith mass correlates with rising atmospheric $p$CO$_2$, as recorded in the Siple ice core (gray circles) (26) and instrumentally at Mauna Loa (black circles) (38), every 10th and 5th data point shown, respectively. Error bars represent 1 SD as calculated from replicate analyses. Samples with a standard deviation greater than 0.05 were discarded. The smoothed curve for the average coccolith mass was calculated using a 20% locally weighted least-squares error method.
Foraminifera and corals are major CaCO$_3$ producers in the ocean. Both groups show light enhanced calcification suggesting that symbionts are involved.
Constant $C_T$ experiment

Schneider and Erez, 2006
Limnol & Oceanog
Calcification response to changes in the carbonate system

CONSTANT pH

CONSTANT pCO$_2$

Schneider and Erez, 2006
Limnol & Oceanog
Summary of Constant temperature experiments

Schneider and Erez, L&O (2006)
Decoupling of photosynthesis from calcification

Constant $C_T$

![Graph showing the relationship between Oxygen Flux and pH with $C_T$ as a constant.]

Oxygen Flux
($\mu$mol O$_2$ ml$^{-1}$ coral h$^{-1}$)

pH

Constant $pCO_2$

![Graph showing the relationship between Oxygen Flux and $C_T$ with $pCO_2$ as a constant.]

Oxygen Flux
($\mu$mol O$_2$ ml$^{-1}$ coral h$^{-1}$)

$C_T$ (µmol kg$^{-1}$)

Constant pH

![Graph showing the relationship between Oxygen Flux and $C_T$ with pH as a constant.]

Oxygen Flux
($\mu$mol O$_2$ ml$^{-1}$ coral h$^{-1}$)

$C_T$ (µmol kg$^{-1}$)

Schneider and Erez, 2006 Limnol & Oceanog
Acropora Sp. Laboratory Experiments at constant $C_T$

Schneider and Erez, 2006
Limnol & Oceanog
Calcification Using internal pH (light + 0.2, dark - 0.3 pH units)

\[ y = 1.667x - 12.918 \]

\[ R^2 = 0.6787 \]

Schneider and Erez, 2006
Limnol & Oceanog
Live *Globigerinoides sacculifer* and its symbiotic algae (Dinoflagellates)
planktonic foraminifera response

![Graph showing the relationship between shell wall thickness and carbonate concentration](image)

Russel et al. 2004
Constant $C_T$, variable pH

$G. \ ruber$ (at 27$^\circ$C and 35 psu)

A v. calcification rate (µg/day)

Data of B. Kisakurek project
Cassiopea, EC
Constant $C_T$, variable pH

Foraminifera: (A. lobifera)

Uptake (µg C/mg foram/48 h)

Erez 2003

pH
Fig. 7. *Amphisorus hemprichii*. Ci uptake as a function of pH.
Growth of Amphistegina at constant pH (8.15) with variable C\textsubscript{T}.

- Shell weight increase factor for:
  - A. lobifera: 250, 375, 125
  - A. lessoni: 250, 375

\[ \text{CO}_3^{2-} (\mu\text{mole Kg}^{-1}) \text{ or } C\text{T (mmole/Kg)} \]
Fig. 1. (A) Shell weights of four species of planktonic foraminifera from the North Atlantic between 60° and 30°N latitude plotted against modern sea surface temperature (SST) at the core sites (28). Also shown are corresponding values of surface water $[\text{CO}_3^{2-}]$ (based on the linear relation between temperature and $[\text{CO}_3^{2-}]$) corrected to preindustrial values (20). Solid circles, *Globorotalia bulloides*.
Fig. 2. (A) Measured shell weight and (B) size-normalized shell for *G. bulloides* plotted with $\delta^{18}O$ [data from (32)] for the same species in NEAP 8K [age model from (33)].

Barker and Elderfield, Science 2002
Two steps of biomineralization relevant to ocean acidification

• The supply of ions needed ($\text{Ca}^{2+}$ and $\text{CO}_3^{2-}$): cellular channels, pumps, or other?

• Control of the chemical micro-environment at the site of biomineralization: e.g. pH, ionic composition, supersaturation, rate of precipitation
Why are foraminifera and corals so sensitive to atmospheric CO$_2$ increase while coccolithophores are not?

- In foraminifera and corals calcification is extracellular and the main source of Ca$^{2+}$ and CO$_3^{2-}$ in both groups is **ambient seawater** which is brought to the site of biomineralization.

- Coccolithophores calcify inside vesicle that is intracellular and are using channels and pumps.
Self vacuolization in foraminifera and the formation of delimited calcification space

v – vacuole
s – symbionts
ic- intralocullar cytoplasm
ec- extralocullar cytoplasm
d- delimited calcification space
p- pseudopods

Erez 2003
Seawater vacuolization using FITC-Dex

Bentov et al unpublished
Two problems associated with \( \text{CaCO}_3 \) precipitation from seawater

- Mg:Ca ratio in seawater is 5:1. Under these conditions, aragonite is the preferred mineral (e.g., corals). How can foraminifera precipitate low Mg calcite?

- \( \text{Ca:CO}_3^{2-} \) ratio in seawater is well above 10 (even at pH 9). Obviously, the foraminifera are not Ca limited but carbon limited. They need a \textbf{carbon concentrating mechanism.}
$\text{CO}_2$ dynamics in foraminifera

Erez et al
unpublished
• Acidic vacuoles supply CO$_2$ both to symbionts and to the host’s basic vacuoles.

• Metabolic CO$_2$ is also a source of DIC for the vacuoles.

• Mg is probably removed into the cytosol and then pumped out.
Jerusalem coral reef
Horizontal growth
Erez and Braun in prep. *P. damicornis* incubated with Calcein
More evidence for direct seawater supply to the calcification site

- In addition to calcein, FITC dextran (MW 10,000, was also incorporated into skeleton of completely covered colonies
- Fluorescent plastic beads (20 nm) were incorporated into the skeleton of completely covered colonies

Erez and Braun in prep.
Pumping mechanism

Erez and Braun in prep.
Celenteron cavity
modified seawater
Aragonite skeleton CaCO$_3$

Hermatypic coral anatomy

Seawater route between polyps

Oral epithelium

Gastrodermis & symbionts

Celenteron cavity

Aboral epithelium

Chalicoblastic epithelium

Paracellular pathway
modified seawater

High pH and Ca

Ca$^{2+}$ATPase

Aragonite skeleton CaCO$_3$

Seawater

Erez and Braun in prep.
Summary

• Both foraminifera and corals bring seawater directly to the site of biomineralization. This is a new calcification pathway not described before.
• Both groups elevate the pH at the biomineralization site (above 9).
• Ocean acidification makes it harder to elevate the pH.
• This may not be the case in coccolithophores which calcify internally (in vesicles). Note that they are not labeled with Calcein.
• If all the calcification in the oceans stops it will produce a CO2 sink of 0.2 (net) to 1 (gross) GTC/y. But coral reefs ecosystems will disappear.