

Coral Population Biology

Growth, Dynamics, Yield, and Connections with
Ocean Warming and Acidification

Stefano Goffredo, PhD

The ocean acidification transplant experiment at Panarea Island

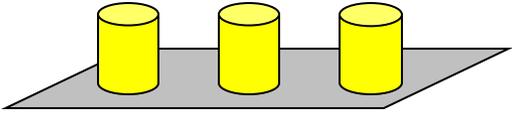
www.CoralWarm.eu



Ecological modes in corals

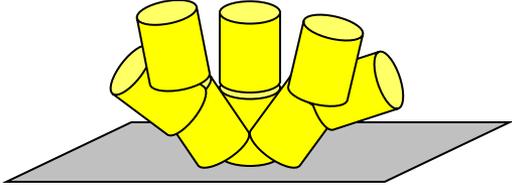
Growth types

Solitary



Single modules living separated
one from each other

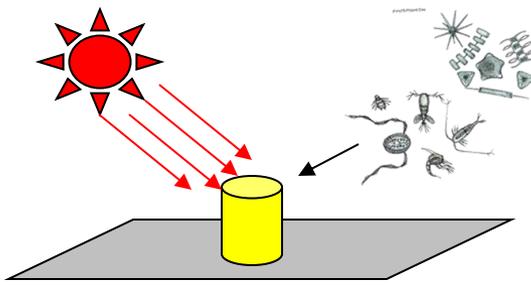
Colonial



Multiple cloned modules living in close connection
(physical and physiological) one to each other

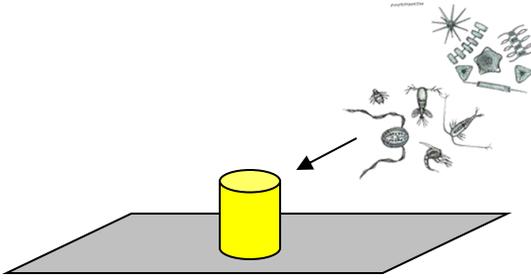
Energetic supplying types

Zooxanthellate



Nourishment from symbiont photosynthesis and from
zooplankton capture

Non-zooxanthellate

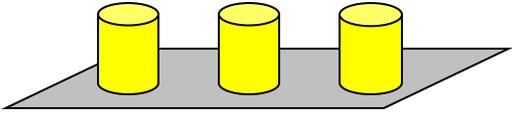


Nourishment only from zooplankton capture

Ecological modes in corals

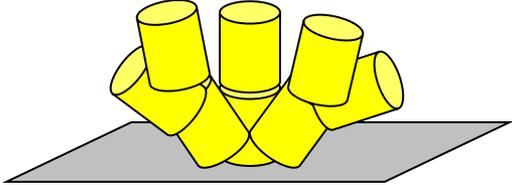
Growth types

Solitary



Single modules living separated one from each other

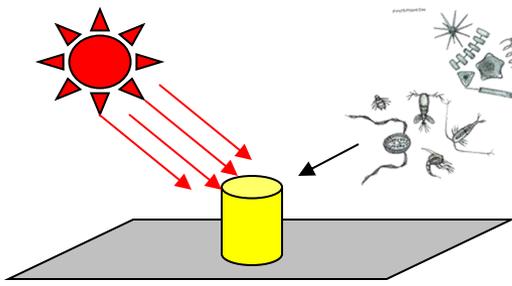
Colonial



Multiple cloned modules living in close connection (physical and physiological) one to each other

Energetic supplying types

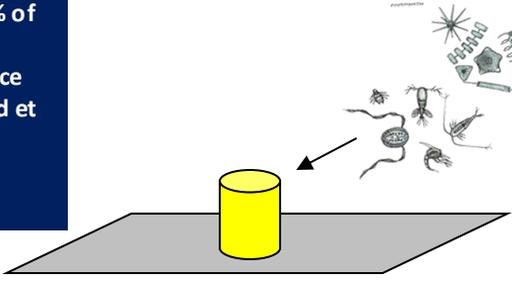
Zooxanthellate



Nourishment from symbiont photosynthesis and from zooplankton capture

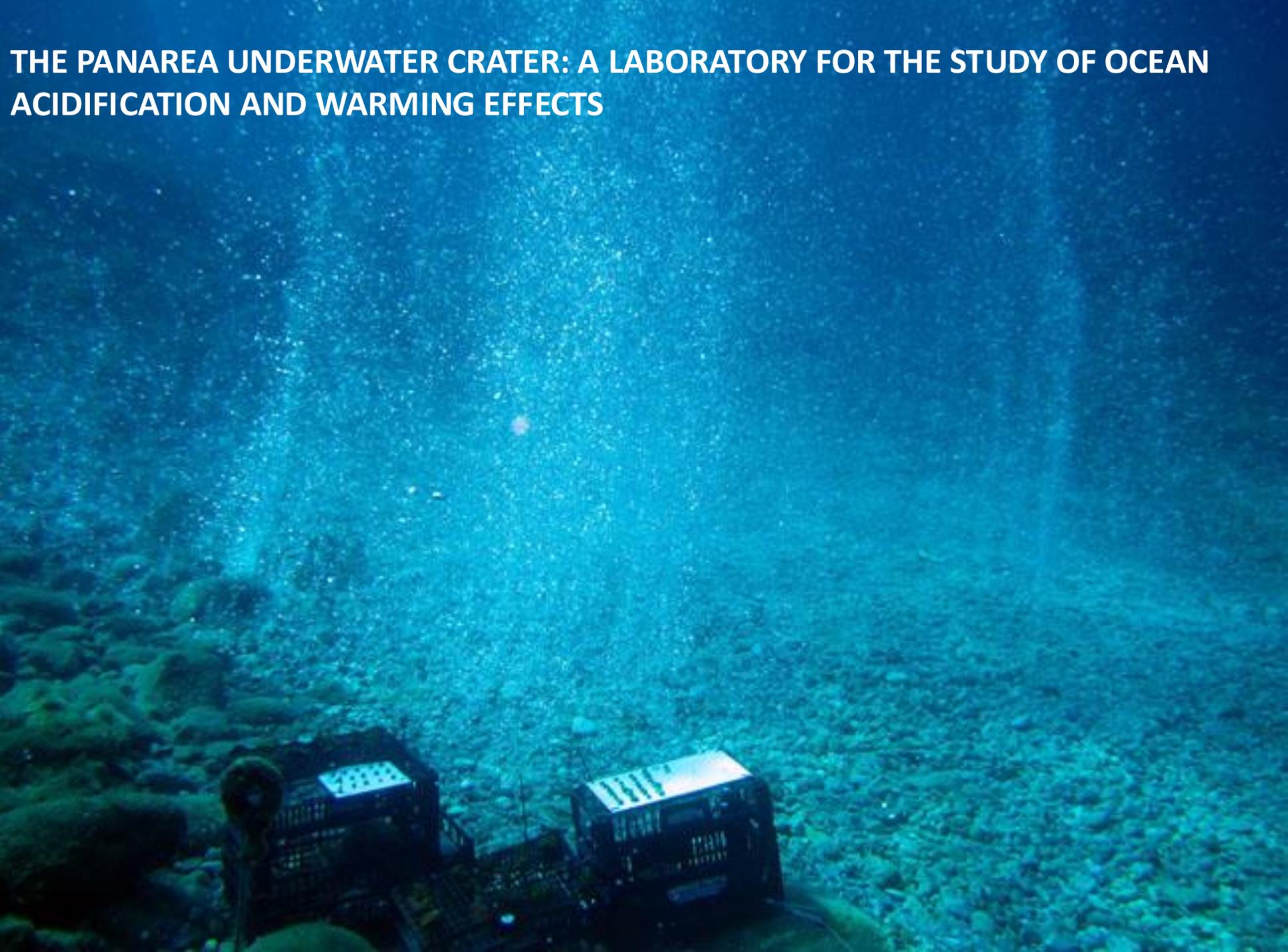
“Under normal conditions, ZOOXANTHELLAE translocate up to 95% of their photosynthetically fixed carbon to the coral host. They also cover 30% of the host’s nitrogen requirements for growth, reproduction and maintenance from dissolved nutrient uptake” (Wild et al. 2011, *Marine and Freshwater Research*, 62: 205-215)

Non-zooxanthellate



Nourishment only from zooplankton capture

THE PANAREA UNDERWATER CRATER: A LABORATORY FOR THE STUDY OF OCEAN ACIDIFICATION AND WARMING EFFECTS



THE PANAREA UNDERWATER CRATER: A LABORATORY FOR THE STUDY OF OCEAN ACIDIFICATION AND WARMING EFFECTS



Zvy Dubinsky,
The Mina and Everard Goodman
Faculty of Life Sciences



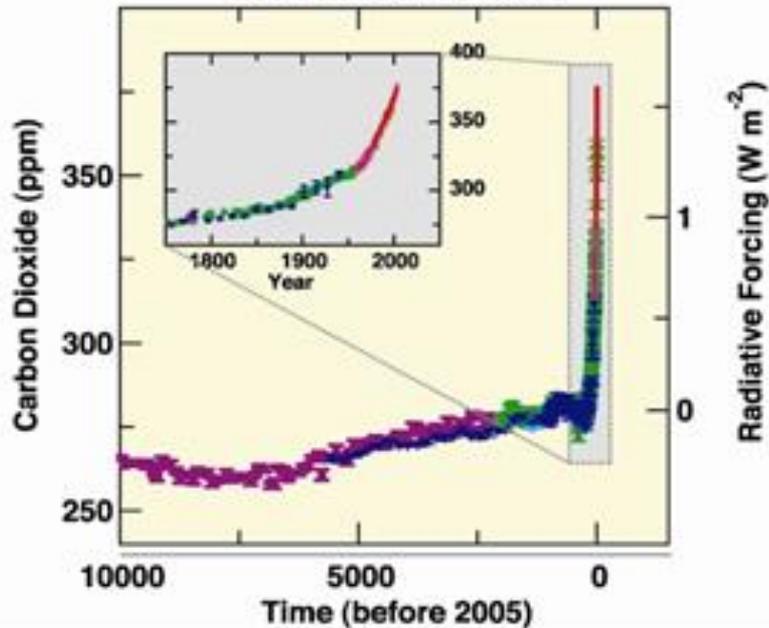
Stefano Goffredo,
Marine Science Group, Department of
Evolutionary and Experimental Biology

Giuseppe Falini,
Department of Chemistry "G. Ciamician"



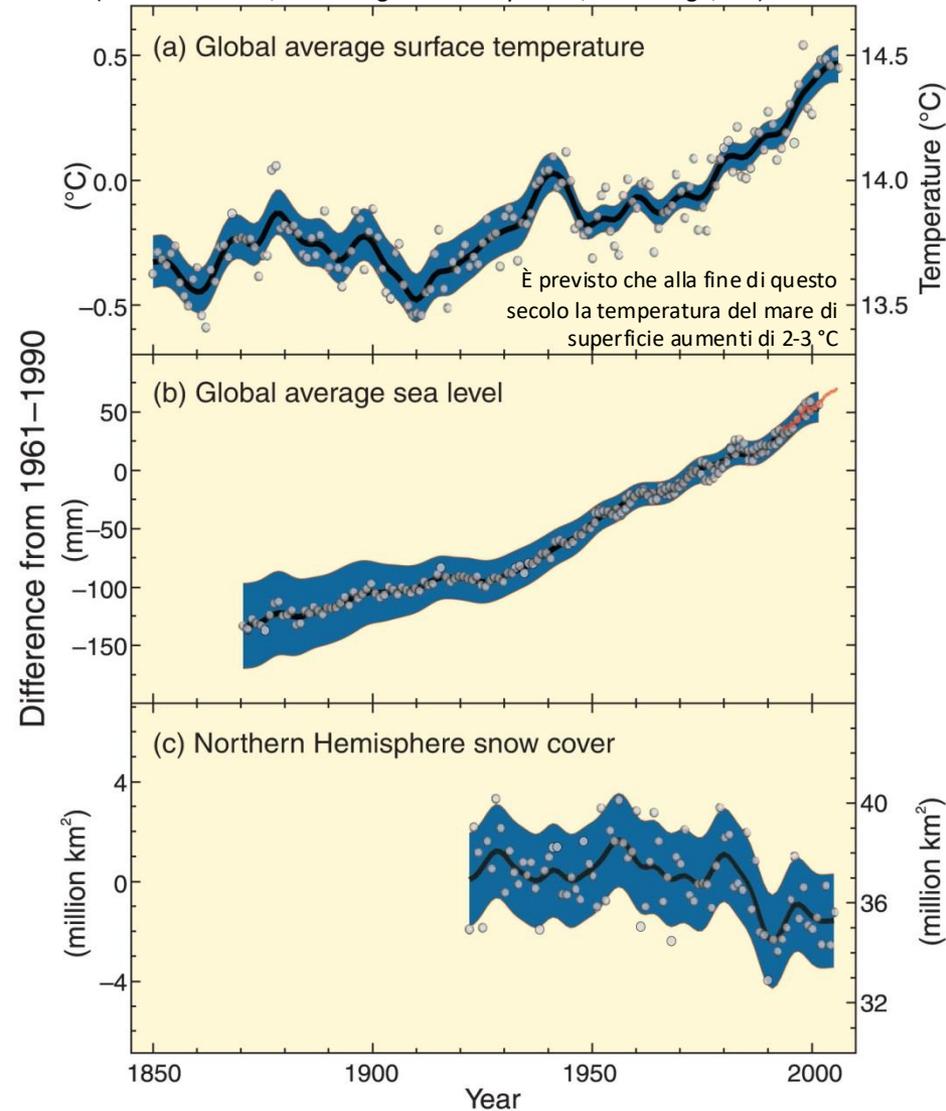
Oggi siamo arrivati a 380 ppm, la più alta concentrazione degli ultimi 800 mila anni (Luthi et al. 2008, *Nature*, 453: 379-382). Un tasso di incremento di CO₂ così rapido come quello di oggi non si è mai verificato nel corso dei tempi geologici (Pandolfi et al. 2011, *Science*, 333: 418-422).

Change in greenhouse CO₂ gas from ice core and modern data



“Atmospheric concentration of CO₂ over the last 10,000 years (large panel) and since 1750 (inset panel). The corresponding radiative forcing is on the right axis of the large panel; positive forcing warms the Earth’s surface” (IPCC 2007, Cambridge University Press, Cambridge, UK).

Changes in temperature, sea level and Northern Hemisphere snow cover (from IPCC 2007, Cambridge University Press, Cambridge, UK)



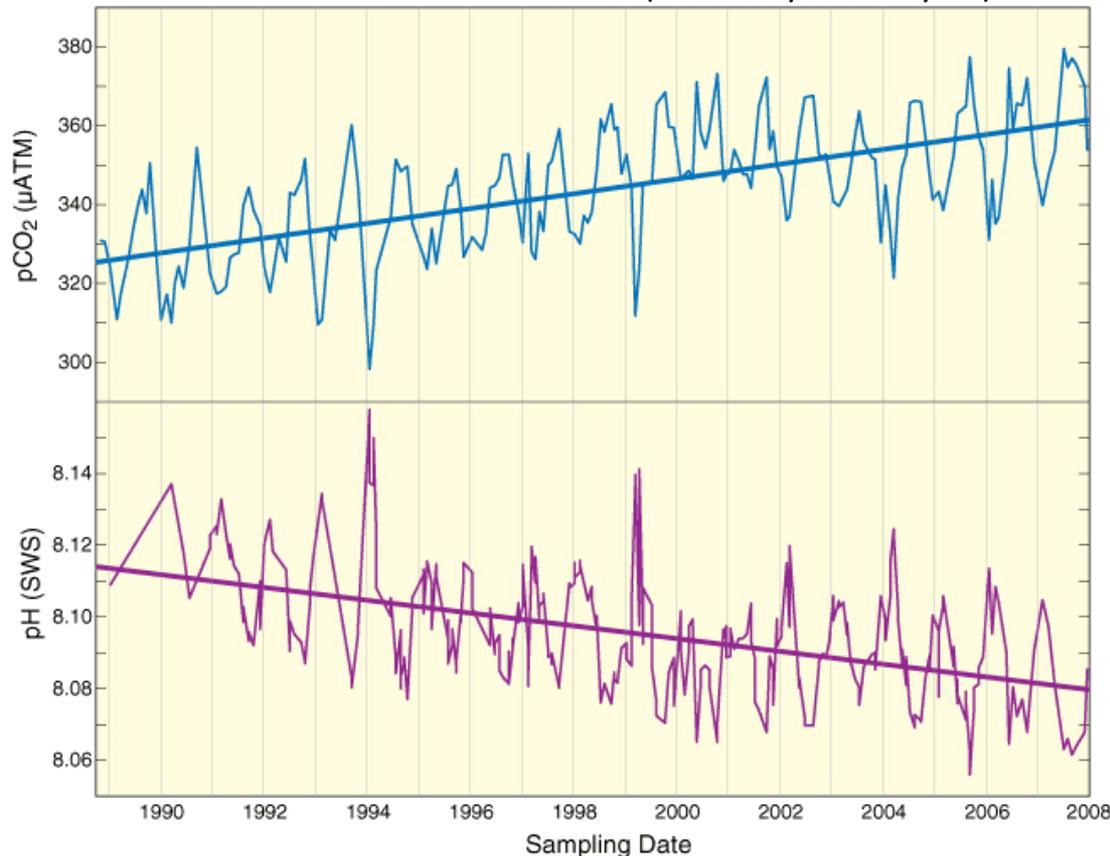
THE OCEAN ACIDIFICATION



Il 25% della CO₂ antropogenica viene assorbita dagli oceani (Canadell et al. 2007, *PNAS*, 104:18866-18870).

The Station ALOHA Curve

Center for Microbial Oceanography: Research and Education (The University of Hawai'i System)



“One of the least-understood consequences of increasing carbon dioxide concentrations in the atmosphere is that the oceans are becoming more acidic. This is because CO₂ in the air dissolves in seawater to form carbonic acid — a weak acid that makes the oceans slightly more acidic” (Center for Microbial Oceanography: Research and Education. The University of Hawai'i System) .



Acidificazione dell'oceano: il progressivo decremento di pH dell'acqua

“We are changing ocean chemistry too much too fast” (Caldeira, 2007, *Oceanography*, 20: 188-195)

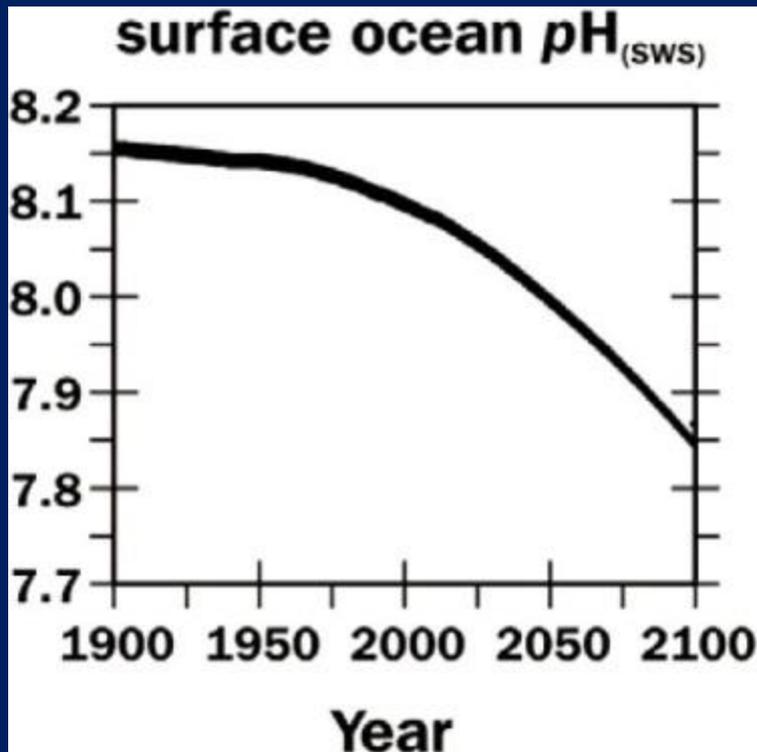
pH



today, **8.1** -> **7.8**, at the end of this century

(Caldeira e Wickett , 2005, *Journal of Geophysical Research* , 110: C09S04)

This represents an extremely rapid rate of change, which will lead to a decrease in seawater pH up to levels never reached in the past 20 millions years (Pearson and Palmer, 2000, *Nature* 406: 695-699)



Change of H⁺ concentration
+ 99.5%

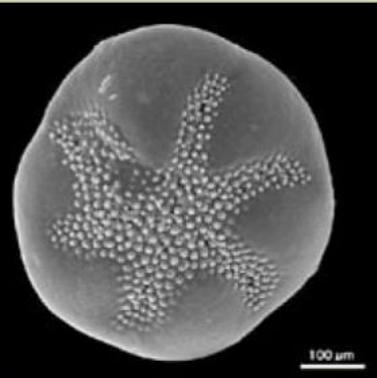
(Orr et al., 2005, *Nature* 437: 681-686)

Turley et al., 2010, *Marine Pollution Bulletin*, 60: 787-792

Calcifiers may be particularly threatened by ocean acidification



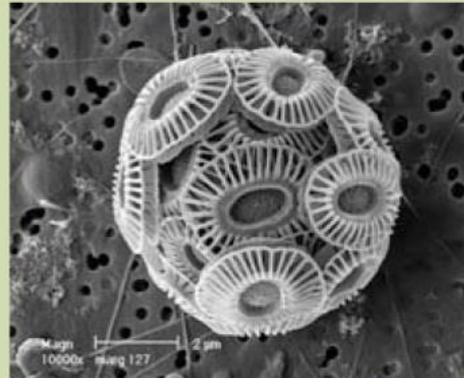
PELAGIC



A. Foraminifera



B. Pteropod

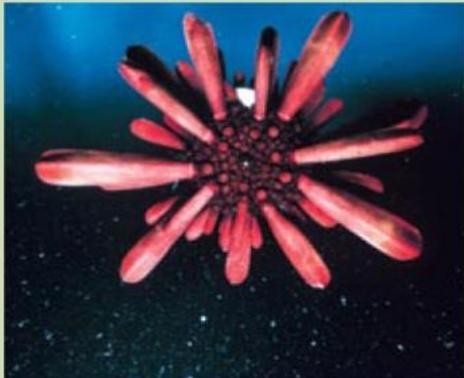


C. Coccolithophore

BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral

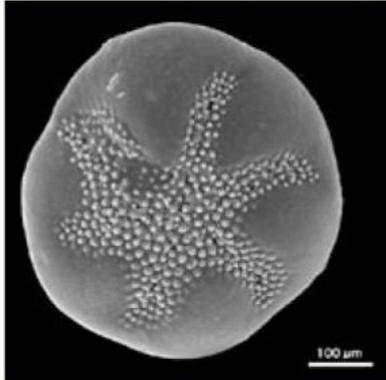
Many marine organisms make shells or skeletons out of calcium carbonate. Upper row: pelagic organisms that live in the open ocean. Lower row: benthic animals that live in shallow habitats (D and E) or in deep waters (F). All of these organisms are threatened by ocean acidification, but the corals and pteropods appear to be most at risk. (Caldeira, 2007, *Oceanography* 20: 188-195)

Acidification determines two potential problems to calcifying organisms: **dissolution** of calcium carbonate, and the **non-precipitation** of new calcium carbonate

Calcifiers may be particularly threatened by ocean acidification



PELAGIC



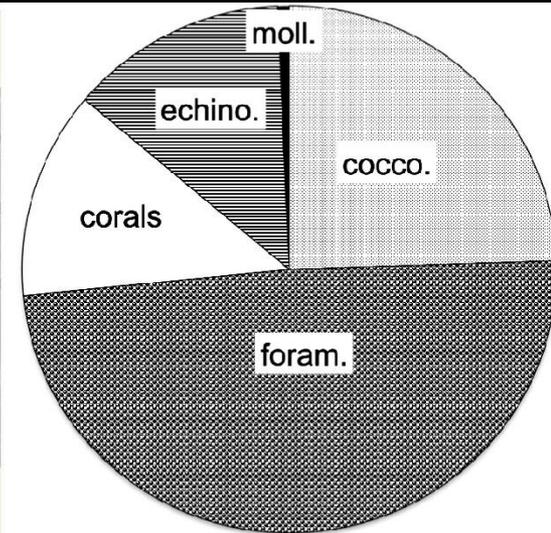
A. Foraminifera



B. Pteropod



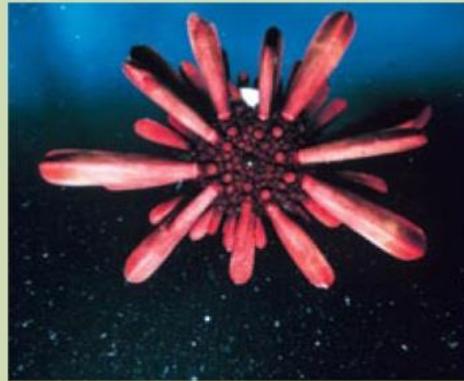
C. Coccolithophore



BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral

Calcium carbonate global production by the major marine calcifiers (Tambutté et al. 2011, *J. Exp. Mar. Biol. Ecol.*, 408: 58–78).

Coccolithophores: 1.6 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; foraminifera: 1.3–3.2 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; coral reefs: 0.65–0.83 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; molluscs: 0.047 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; echinoderms: 0.86 Gt $\text{CaCO}_3 \text{ yr}^{-1}$

Calcifiers may be particularly threatened by ocean acidification



PELAGIC



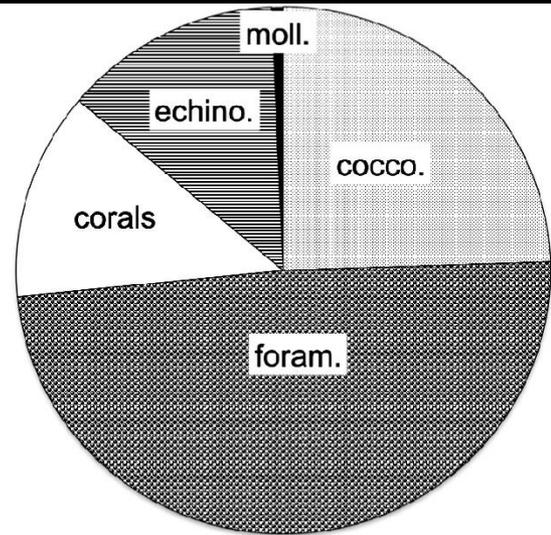
A. Foraminifera



B. Pteropod



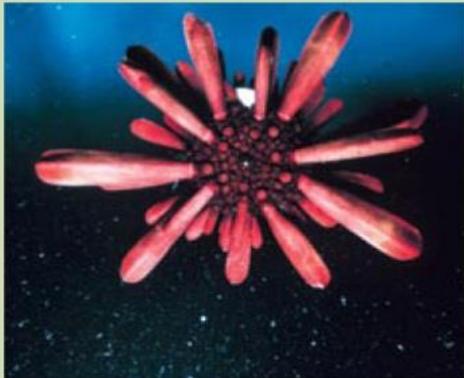
C. Coccolithophore



BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral

Calcium carbonate global production by the major marine calcifiers (Tambutté et al. 2011, *J. Exp. Mar. Biol. Ecol.*, 408: 58–78).

Coccolithophores: 1.6 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; foraminifera: 1.3–3.2 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; coral reefs: 0.65–0.83 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; molluscs: 0.047 Gt $\text{CaCO}_3 \text{ yr}^{-1}$; echinoderms: 0.86 Gt $\text{CaCO}_3 \text{ yr}^{-1}$

Totale: 5.2 miliardi di tonnellate di CaCO_3 per anno

Calcifiers may be particularly threatened by ocean acidification



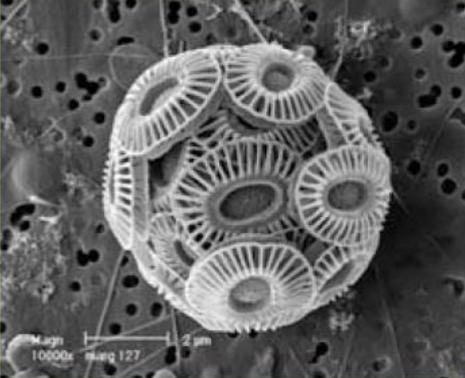
PELAGIC



A. Foraminifera



B. Pteropod

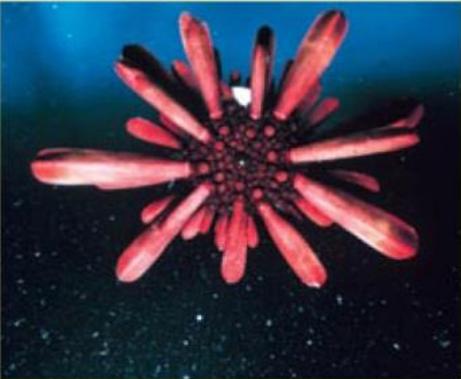


C. Coccolithophore

BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral



Great Barrier Reef



Maldives Atolls

Calcifiers may be particularly threatened by ocean acidification



PELAGIC



A. Foraminifera



B. Pteropod

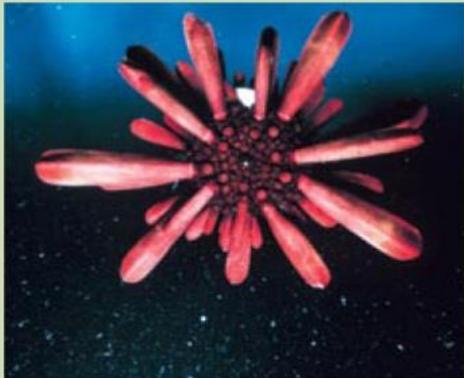


C. Coccolithophore

BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral

The *Cladocora caespitosa* bank in the Mljet National Park (Southern Adriatic Sea)



Reef built by the cold water coral *Lophelia pertusa*, off the coast of Norway



Calcifiers may be particularly threatened by ocean acidification



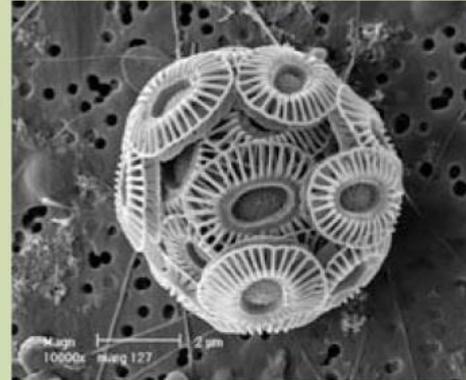
PELAGIC



A. Foraminifera



B. Pteropod



C. Coccolithophore

BENTHIC



D. Reef Coral



E. Sea Urchin



F. Deep Sea Coral



Le Dolomiti nelle Alpi Orientali

Calcifiers may be particularly threatened by ocean acidification



PELAGIC



A. Foraminifera



B. Pteropod

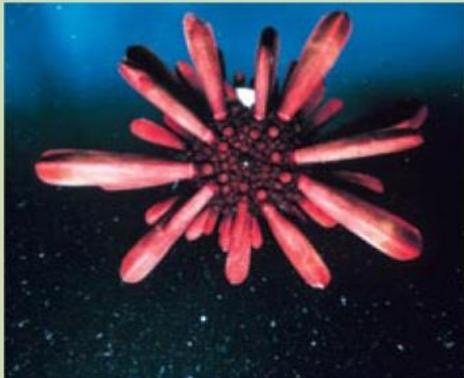


C. Coccolithophore

BENTHIC



D. Reef Coral



E. Sea Urchin

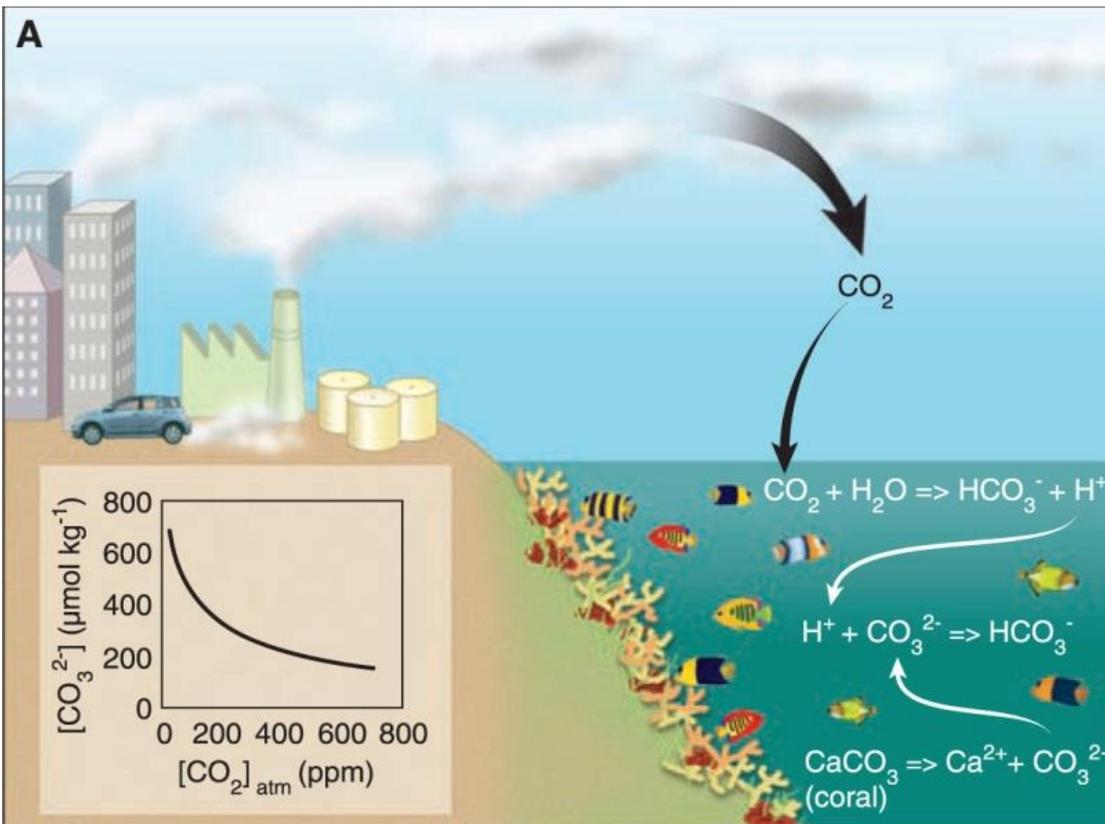
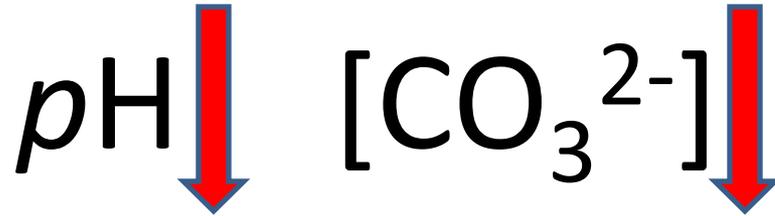


F. Deep Sea Coral

Many marine organisms make shells or skeletons out of calcium carbonate. Upper row: pelagic organisms that live in the open ocean. Lower row: benthic animals that live in shallow habitats (D and E) or in deep waters (F). All of these organisms are threatened by ocean acidification, but the corals and pteropods appear to be most at risk. (Caldeira, 2007, *Oceanography* 20: 188-195)

Acidification determines two potential problems to calcifying organisms: **dissolution** of calcium carbonate, and the **non-precipitation** of new calcium carbonate

All'aumento della acidità dell'acqua del mare è associato il decremento della concentrazione dello ione carbonato



“Linkages between the buildup of atmospheric CO_2 and the slowing of coral calcification due to ocean acidification. Approximately 25% of the CO_2 emitted by humans in the period 2000 to 2006 was taken up by the ocean where it combined with water to produce carbonic acid, which releases a proton that combines with a carbonate ion. This decreases the concentration of carbonate, making it unavailable to marine calcifiers such as corals” (Hoegh-Guldberg et al. 2007, *Science*, 318: 1737-1742).



L'abbassamento della concentrazione dello ione carbonato nell'acqua di mare può sostanzialmente impattare gli organismi calcificanti, come i coralli duri (Scleractinia), abbassando la saturazione dell'acqua di mare relativamente alla mineralogia carbonatica dei loro scheletri (Marubini et al. 2008, *Coral Reefs*, 27: 491-499)

Lo stato di saturazione dell'aragonite è definito come:

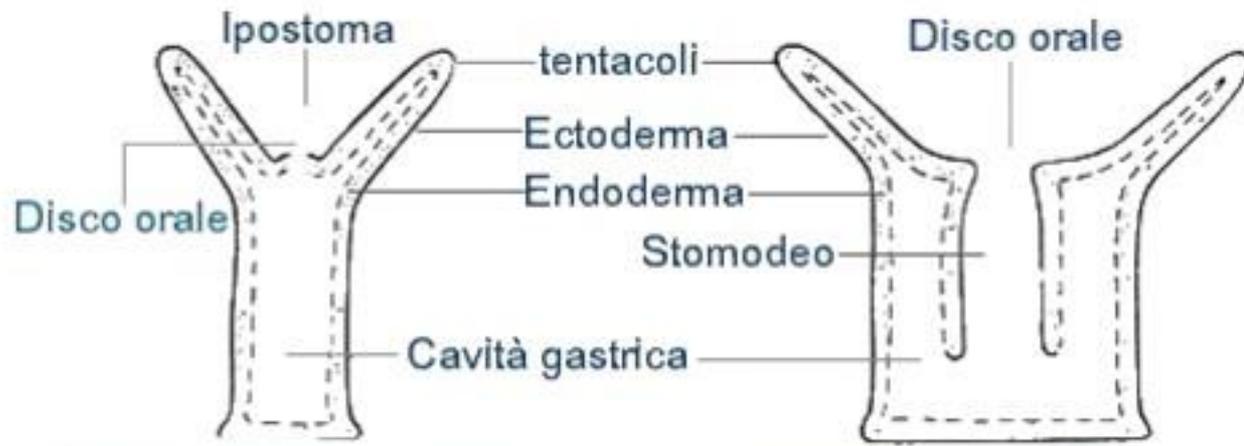
$$\Omega_{\text{arag}} = \frac{[\text{Ca}^{2+}] * [\text{CO}_3^{2-}]}{K'_{\text{arag}}}$$

Dove K'_{arag} è il prodotto di solubilità apparente del minerale

Valori di $\Omega_{\text{arag}} > 1$ indicano supersaturazione

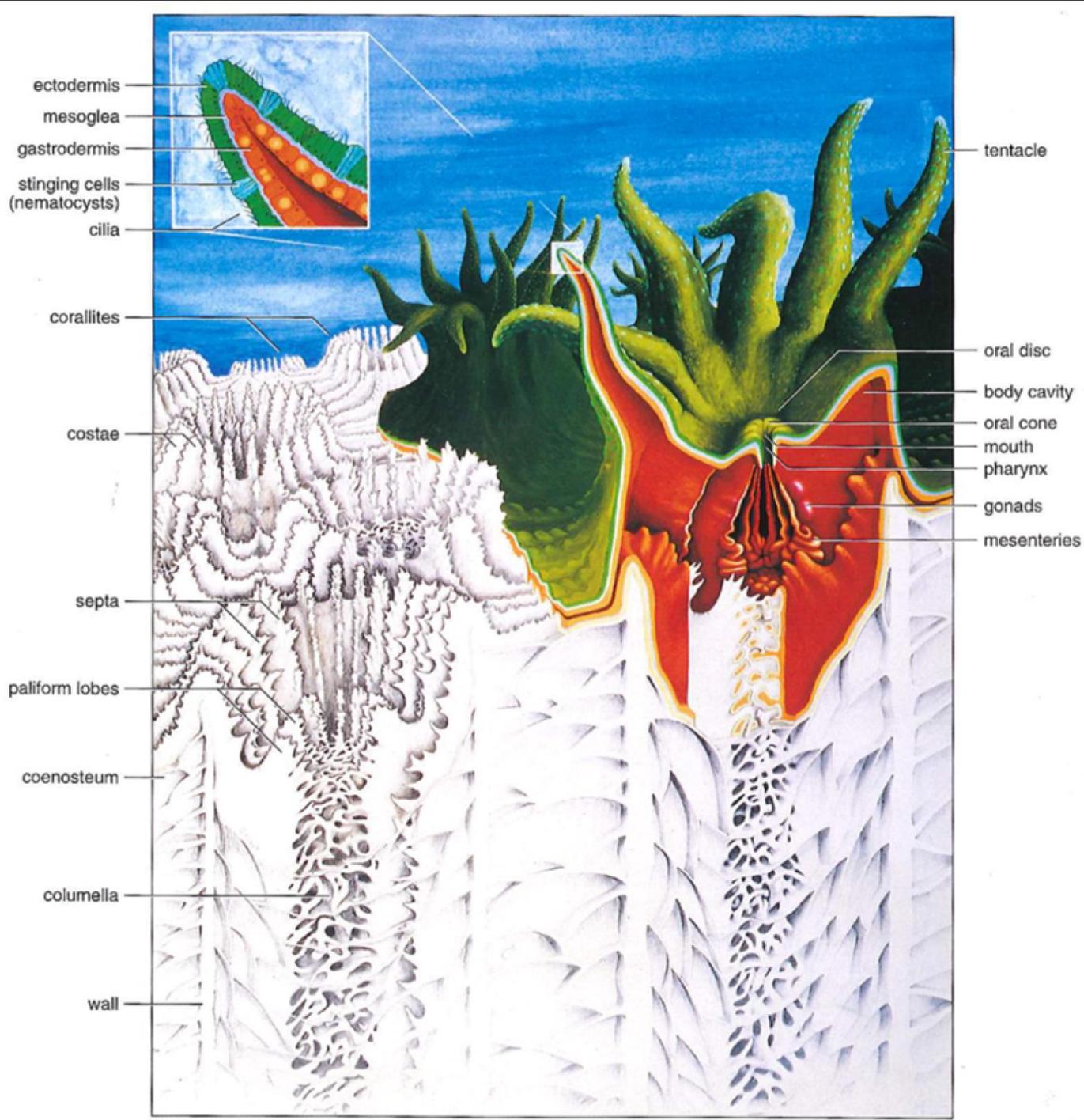
Valori di $\Omega_{\text{arag}} < 1$ indicano sottosaturazione

Siccome $[\text{Ca}^{2+}]$ è circa cento volte maggiore di $[\text{CO}_3^{2-}]$ ed è un elemento conservativo dell'acqua di mare (10 mM nell'acqua di superficie dal Precambriano; Kempe e Kazmierczak 1994, *Bull Inst Oceanogr Monaco*, 13: 61-117; Marubini et al. 2001; *Mar. Ecol. Prog. Ser.*, 220: 153-162), Ω_{arag} è largamente determinato da $[\text{CO}_3^{2-}]$ (Reynaud et al. 2003, *Glob. Change Biol.*, 9: 1660-1668).

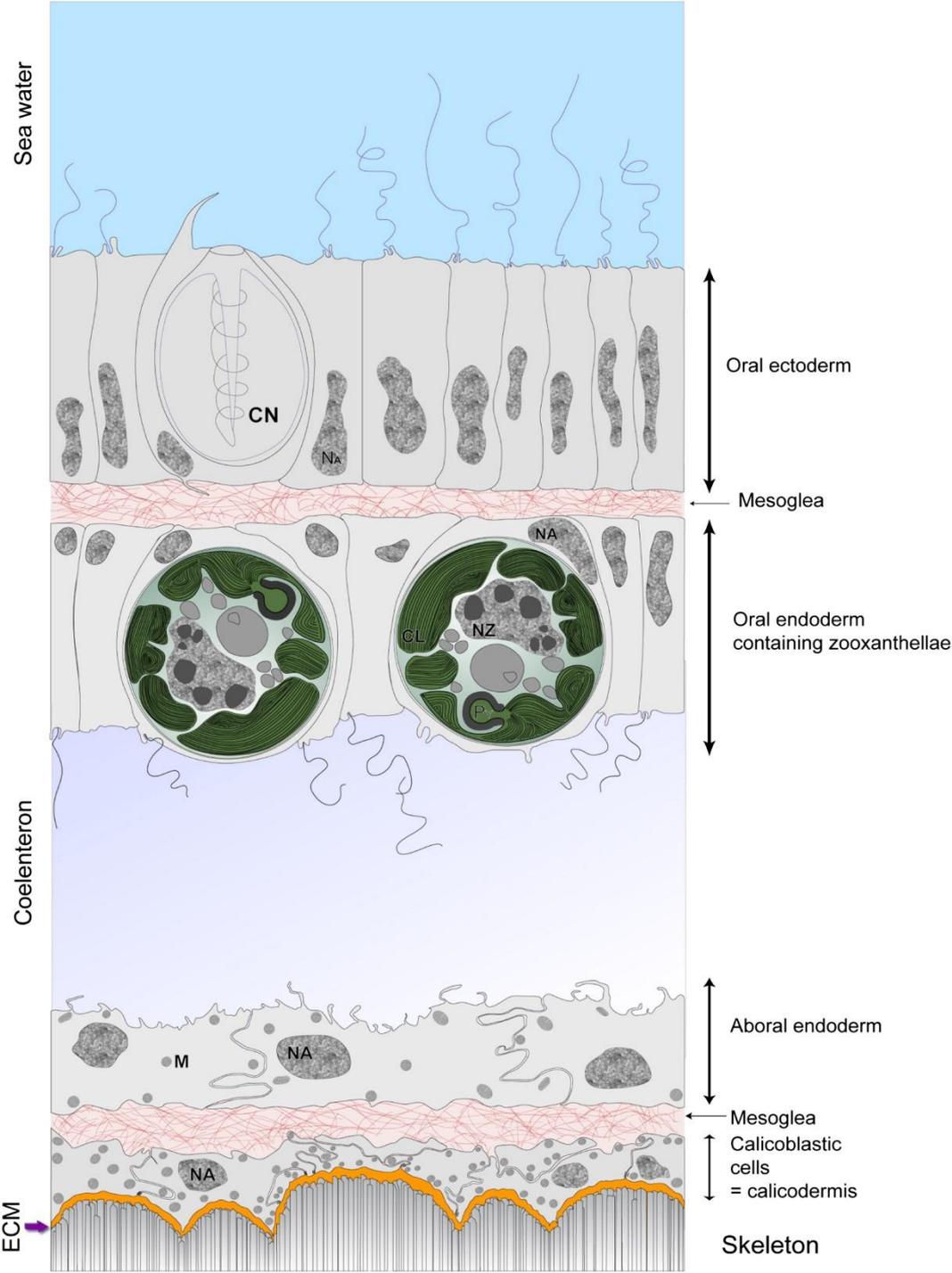


Polipo Classe Hydrozoa

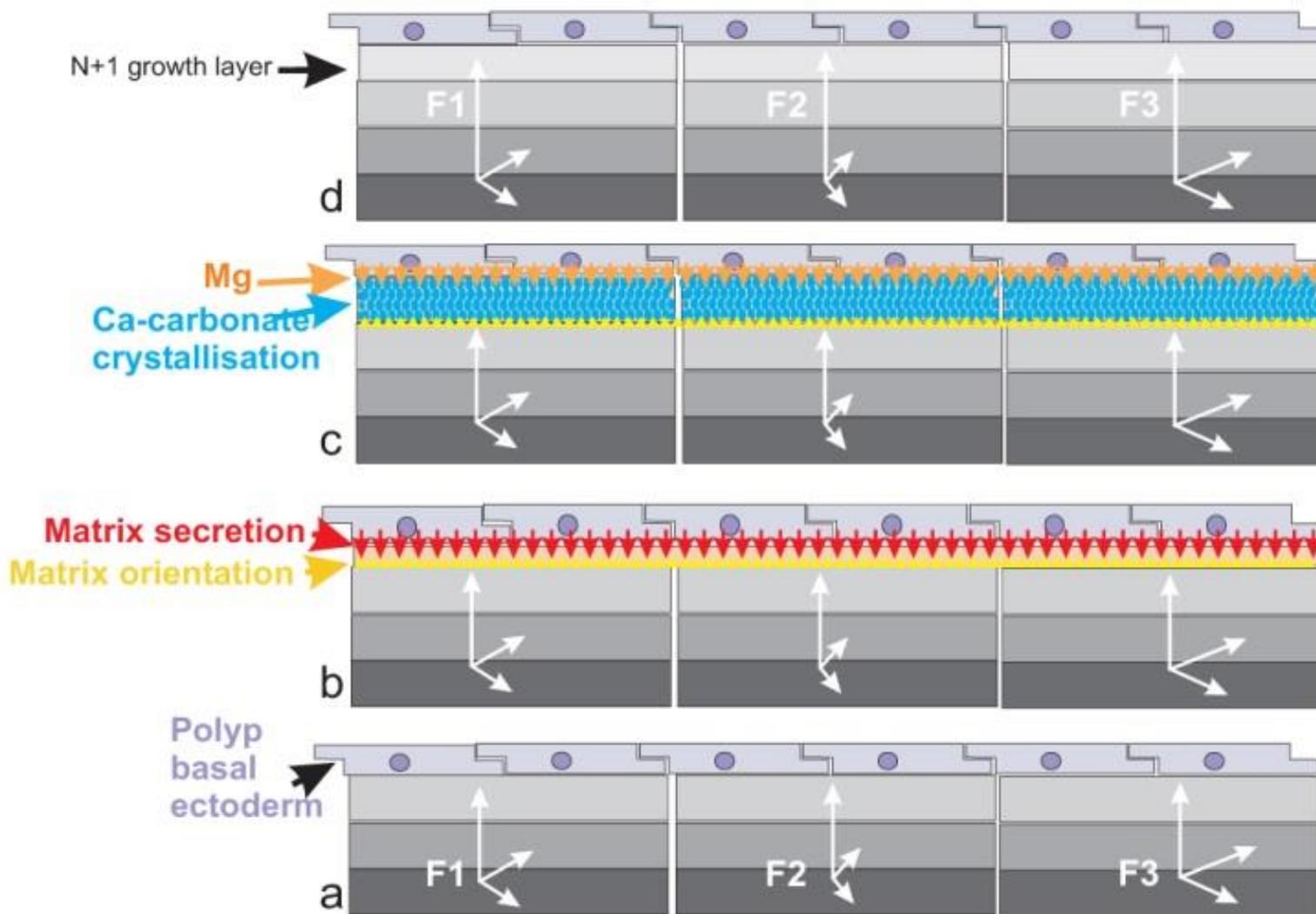
Polipo Classe Anthozoa



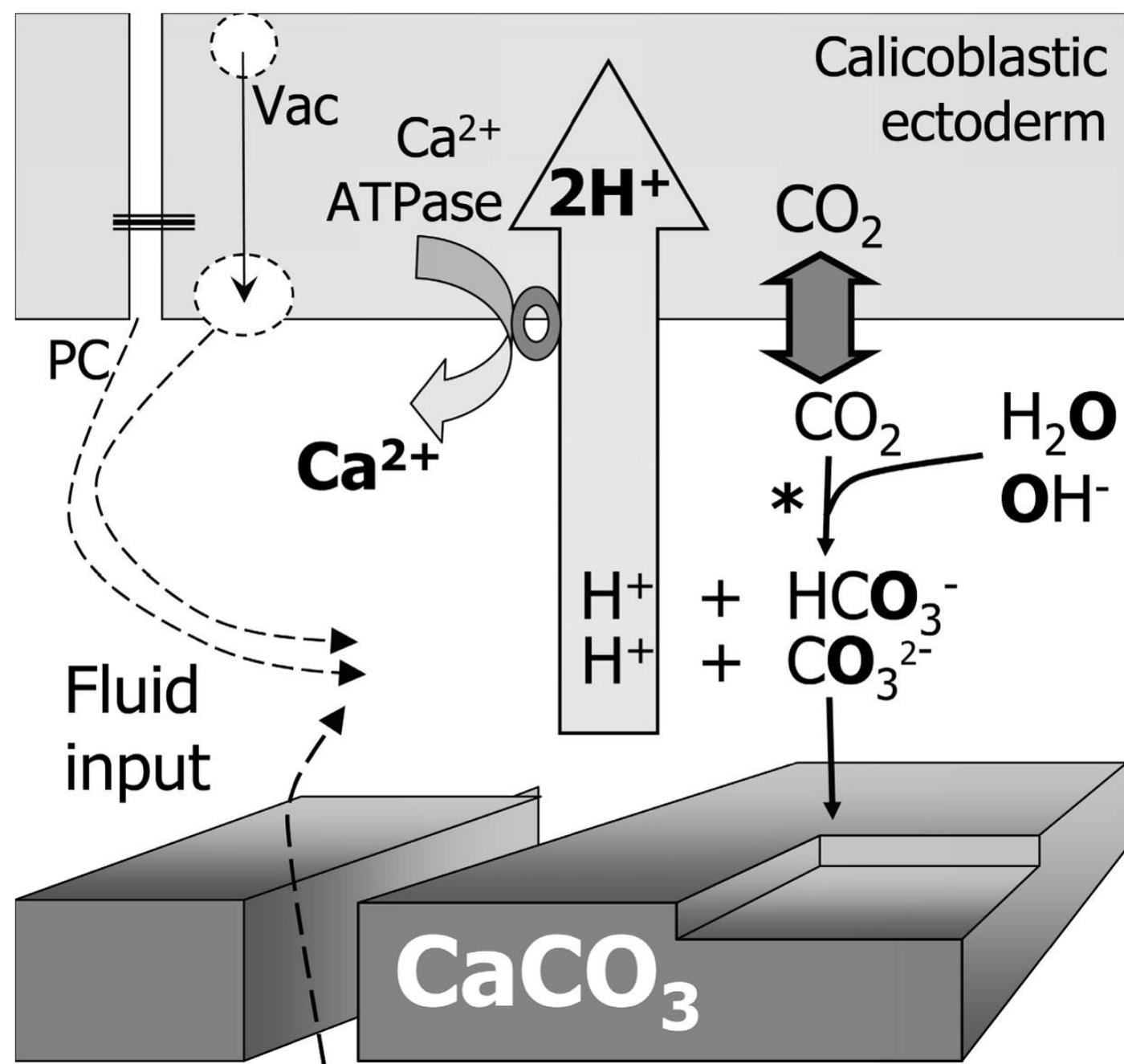
The general structure of a polyp and underlying skeleton. The corallite is a tube enclosed by a wall, which is intercepted by flattened plates, the septa radiating out from the tube center. The paliform lobes are outgrowths of the septa. Extensions of the paliforms lobes meet in the center to form the columella [reproduced from Veron 1986, with permission; from Reggi, Fermani, Levy, Dubinsky, **Goffredo**, Falini, 2016, in: Goffredo, Dubinsky (eds), *The Cnidaria, past, present and future*. The world of Medusa and her sisters, Springer, Cham, *in press*]



Schematic representation of the histology of the coenosarc (drawn from a picture in transmission electronic microscopy of the coral *S. pistillata*). CL = Chloroplast. CN = Cnidocyte. M = Mitochondria. NA = Nucleus of animal cell. NZ = Nucleus of zooxanthella. PY = Pyrenoid. ECM = **Extracellular Calcifying Medium** (Tambutté et al. 2011, *J. Exp. Mar. Biol. Ecol.*, 408: 58–78).



Scheme of a growth layer formation in a coral skeleton, summarizing the structural, chemical and biochemical data. F1, F2, F3: upper mineralized layers in three adjacent fibres; arrows: overall crystallographic orientations (Cuif and Dauphin 2005, *Biogeosciences*, 2: 61-73)



Physiological model for coral calcification. Ca^{2+} -ATPase adds Ca^{2+} and removes protons from calcifying fluid, raising its pH. CO_2 diffuses in and reacts with H_2O and OH^{-} to produce CO_3^{2-} . Much of this ion transport may actually take place across the membranes of vacuoles (vac) that transfer seawater through the cells of the basal epithelium. Seawater may also reach the calcifying space by diffusion through the porous skeleton and pericellular channels (PC) between the epithelial cells. **From Cohen & McConnaughey 2003, Rev. Mineral. Geochem. 54, 151–187**



GOAL OF THE PANAREA TRANSPLANT EXPERIMENT:

Verify the effects of ocean acidification on Mediterranean corals, taking into consideration different responses between colonial and solitary, zooxanthellate and non-zooxanthellate forms, in order to detect possible different sensitivities

Test the hypotheses that temperature influences the degree by which ocean acidification affects coral growth parameters

THE INTERACTIVE EFFECTS OF HIGH LEVELS OF $p\text{CO}_2$ AND TEMPERATURE HAVE BEEN LITTLE INVESTIGATED (Antony et al., 2008, *Proceedings of the National Academy of Sciences of the United States of America* 105: 17442-17446)



Today I want to show data on growth of *Balanophyllia europaea*, *Leptopsammia pruvoti*, and *Astroides calycularis* along a natural pH gradient, created by CO₂ volcanic emissions, at different temperatures

Class: Anthozoa
Order: Scleractinia
Family: Dendrophylliidae

Balanophyllia europaea

Leptopsammia pruvoti

Astroides calycularis

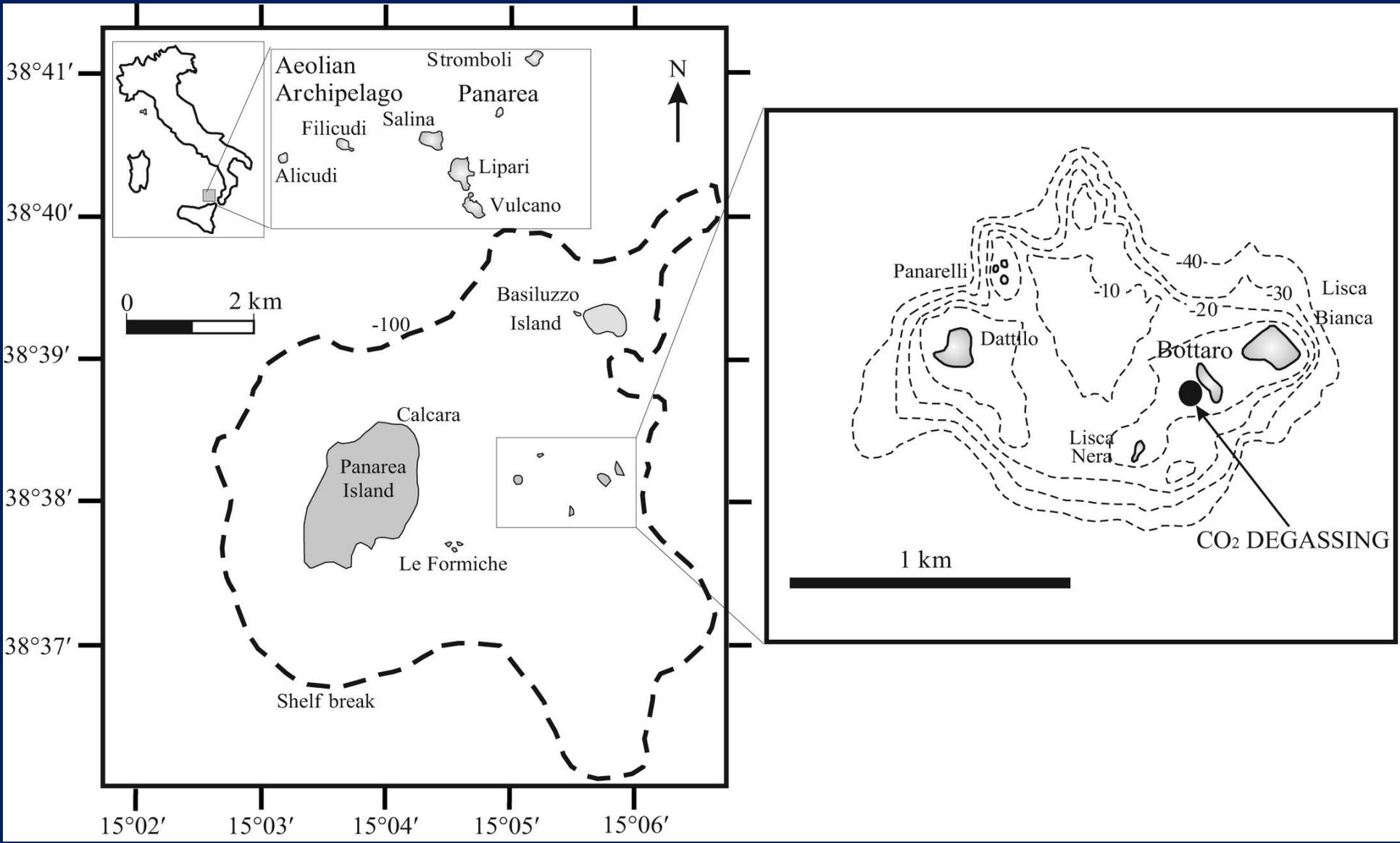


**SOLITARY,
ZOOXANTHELLATE**

**SOLITARY,
NON-ZOOXANTHELLATE**

**COLONIAL,
NON-ZOOXANTHELLATE**

Map of the study area, showing the CO₂ emissions site at Bottaro (Panarea Island) and the surrounding islets





The Panarea Experiment

In-situ transplants, along a natural pH gradient generated by CO₂ volcanic emissions

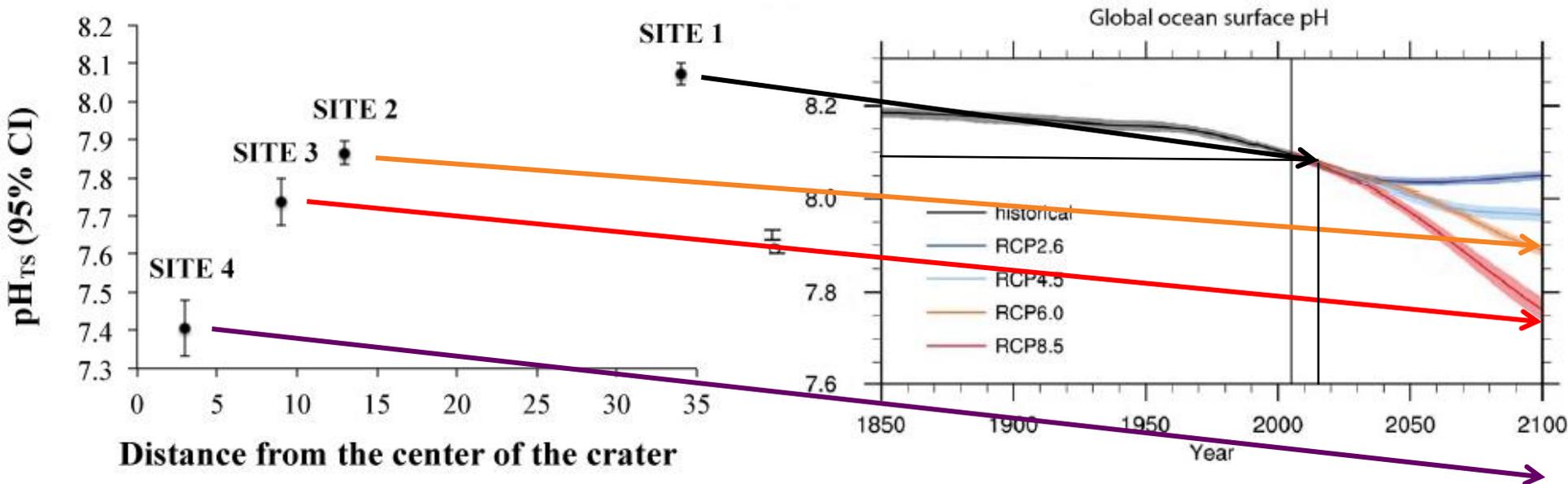


Panarea CO₂ vent

Panarea Experiment^{1,2}

pH Gradient (July 2010-May 2013)

IPCC scenarios for year 2100³



1. Goffredo et al., 2014, *Nature Climate Change*, 4: 593-597

2. Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, Goffredo, 2015, *Nature Communications*, 6: 7785

3. Stocker, Qin, Plattner et al. (eds.) (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge

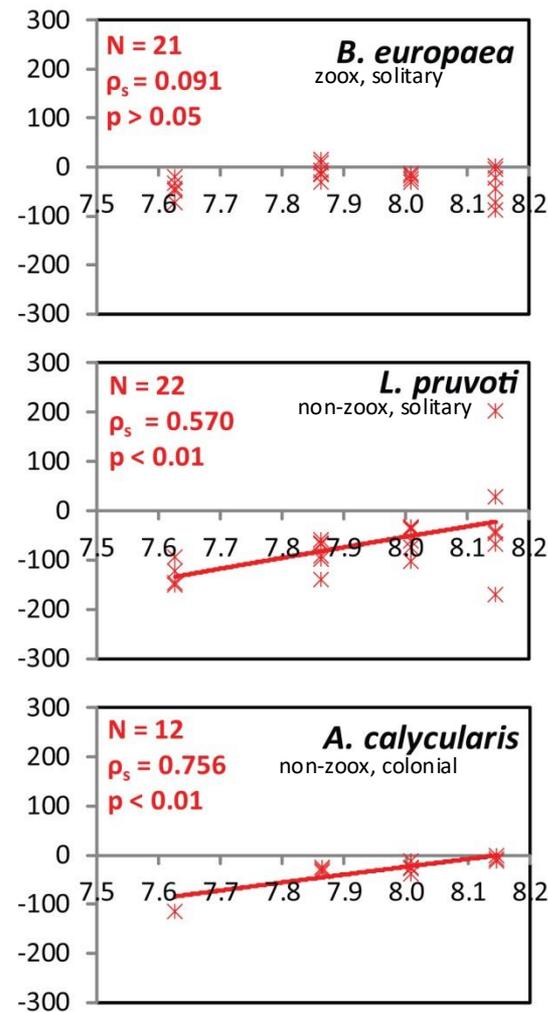
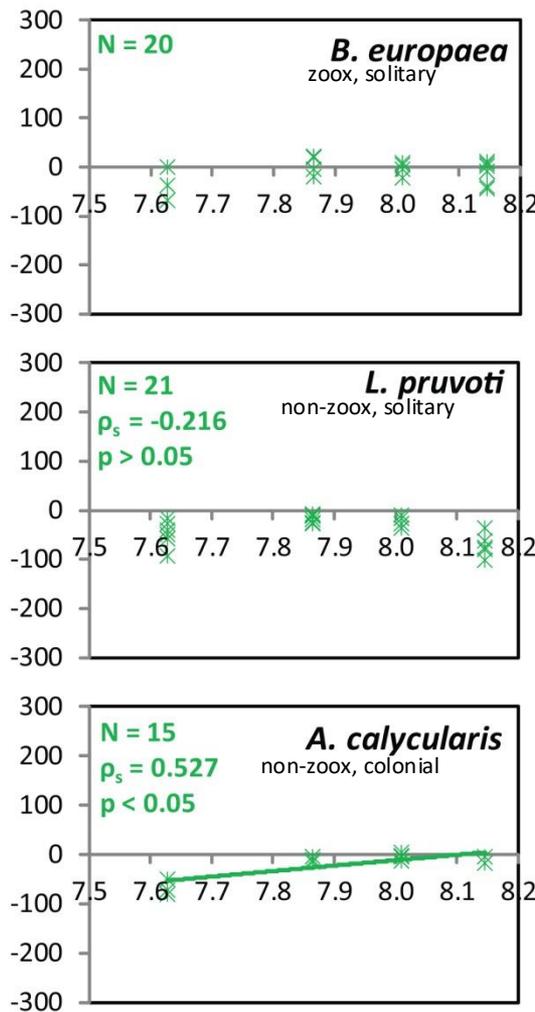
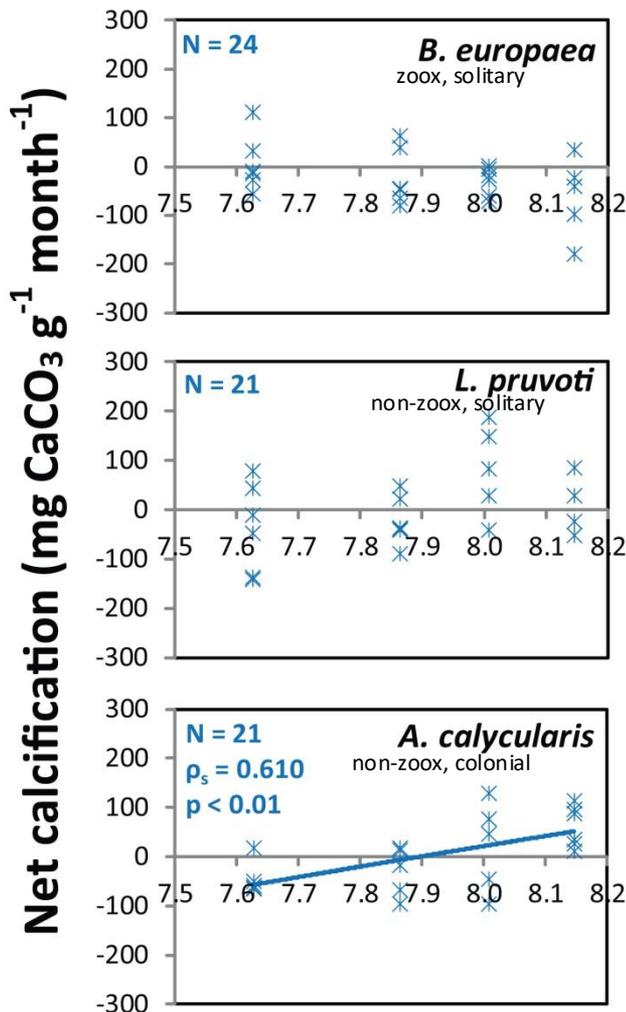
GROWTH RATE



November 2010-March 2011
15.0-18.9 °C

March 2011-June 2011
17.3-19.6 °C

June 2011-August 2011
22.7-24.6 °C



Average pH

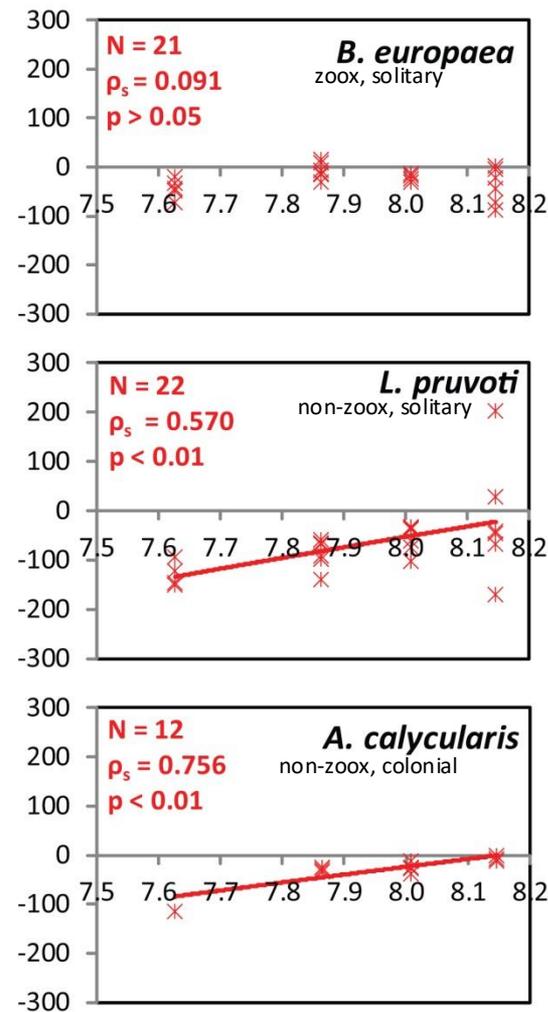
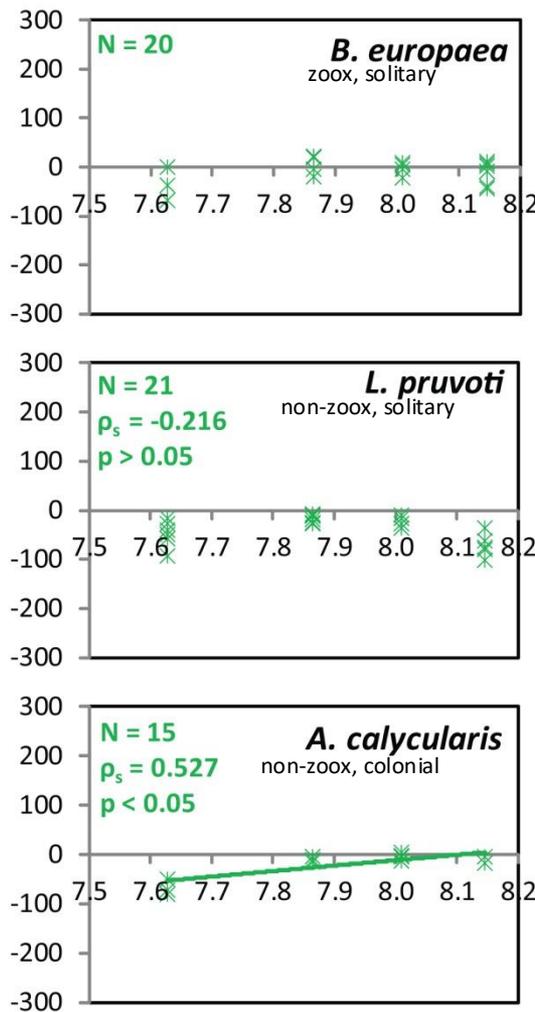
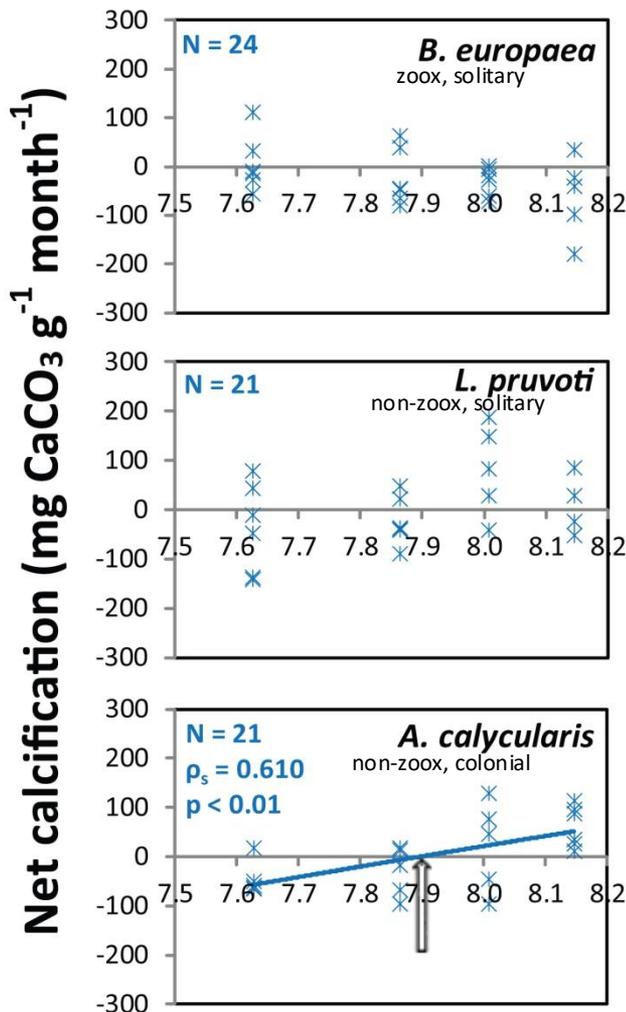
GROWTH RATE



November 2010-March 2011
15.0-18.9 °C

March 2011-June 2011
17.3-19.6 °C

June 2011-August 2011
22.7-24.6 °C



Average pH

GROWTH RATE



November 2010-March 2011

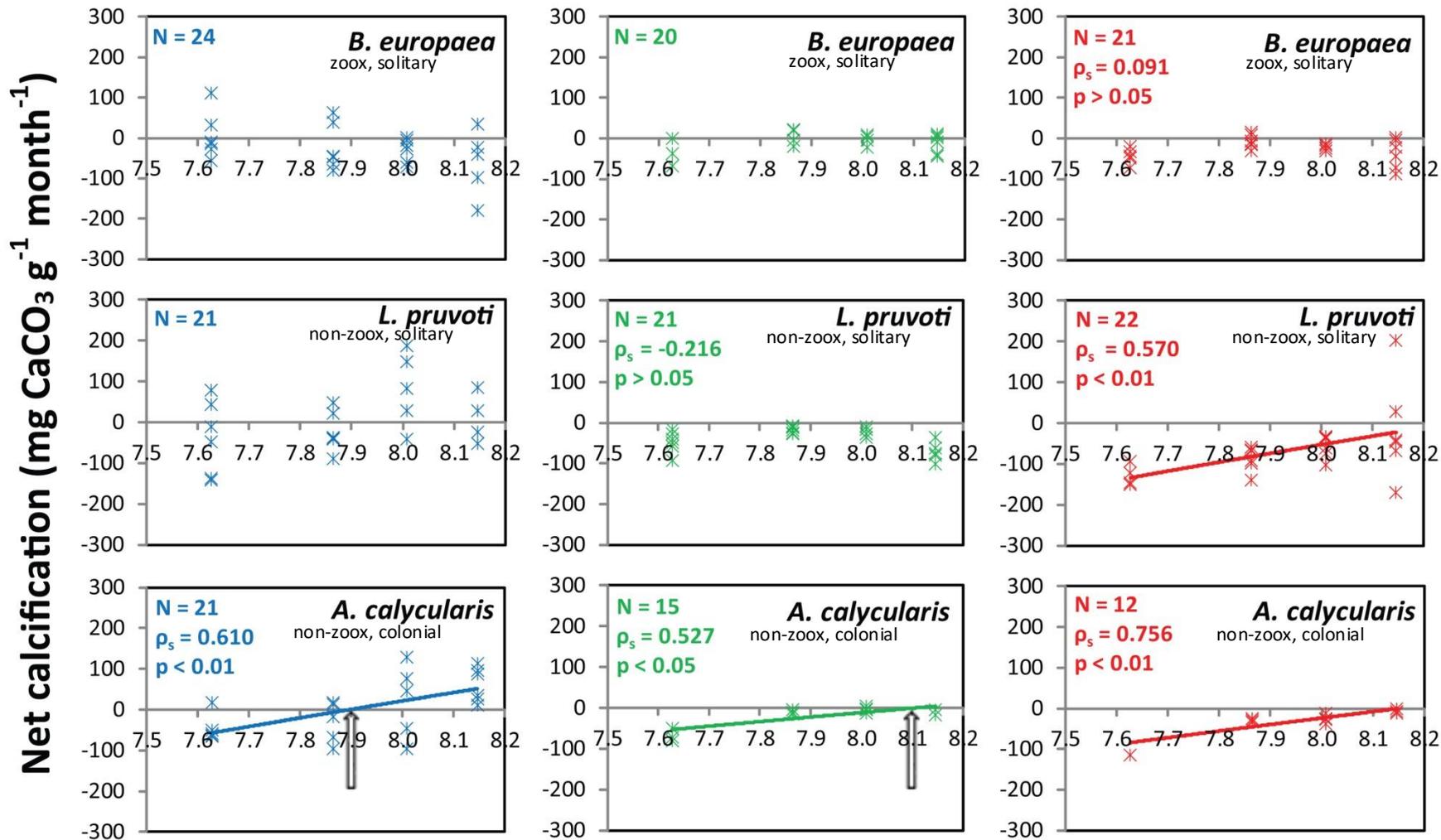
15.0-18.9 °C

March 2011-June 2011

17.3-19.6 °C

June 2011-August 2011

22.7-24.6 °C



Average pH

GROWTH RATE



November 2010-March 2011

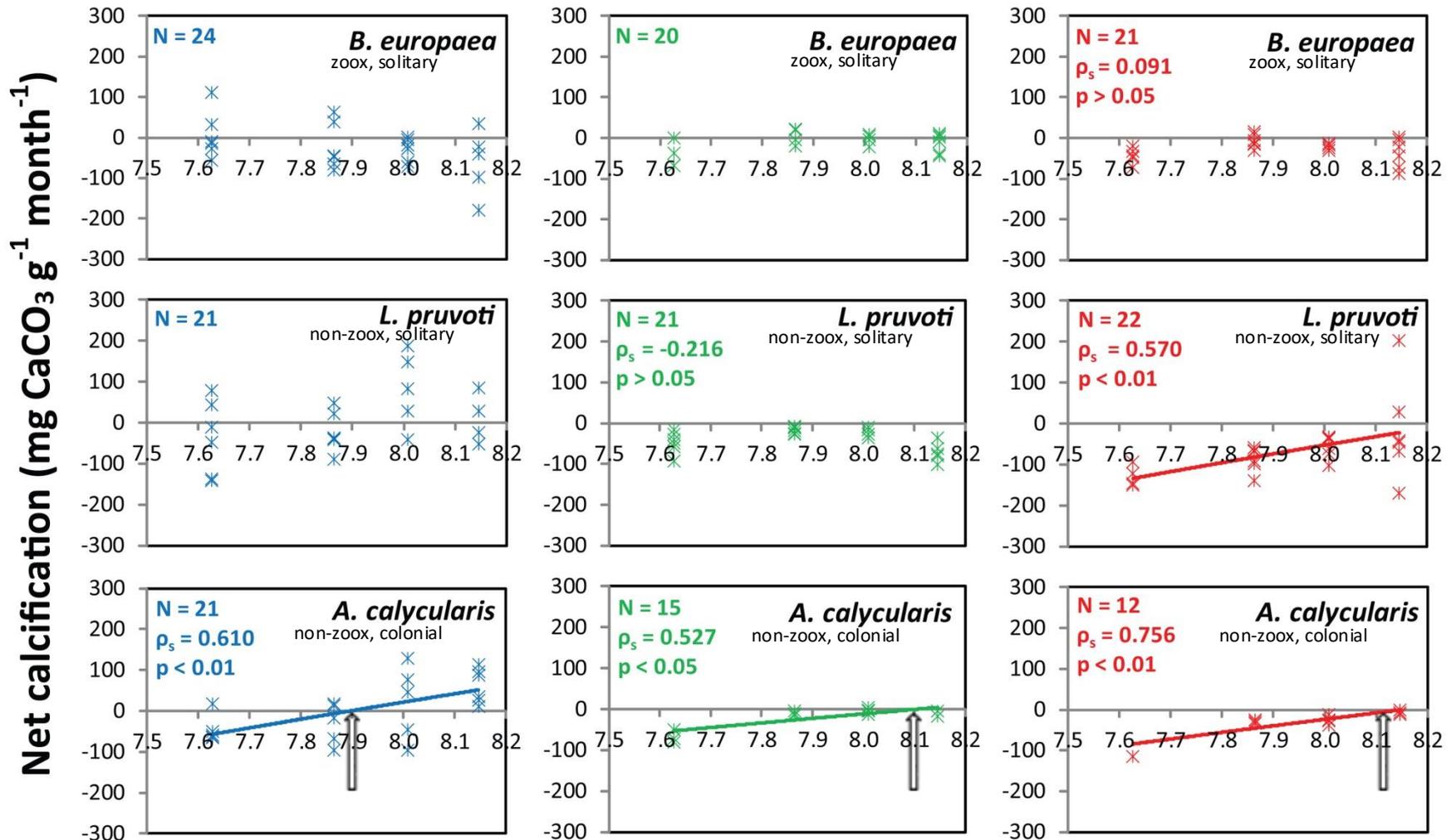
15.0-18.9 °C

March 2011-June 2011

17.3-19.6 °C

June 2011-August 2011

22.7-24.6 °C



Average pH

Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate species**, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate species**, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?

A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

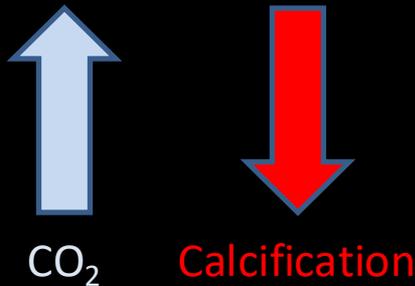
Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate species**, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate species**, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?



A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate species**, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate species**, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?



CO₂



Calcification



Photosynthesis

In zooxanthellate corals

A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate species**, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate species**, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?



A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

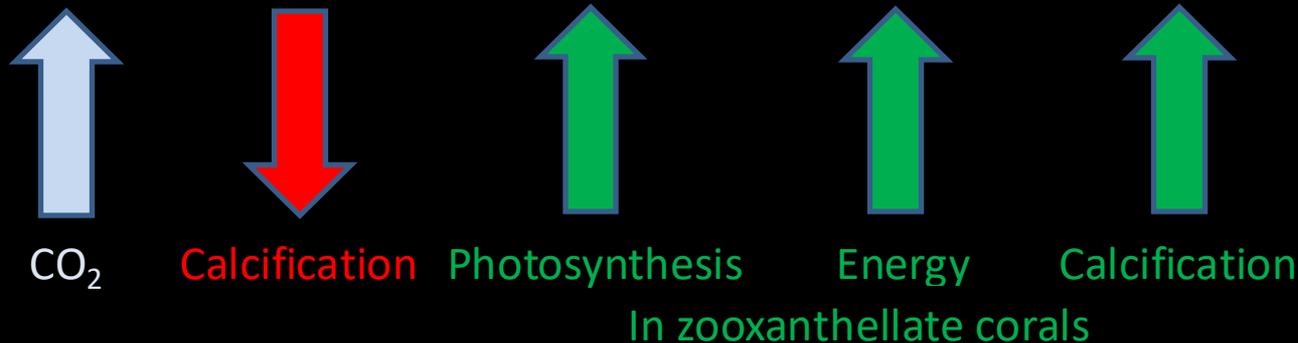
Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate** species, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate** species, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?



A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

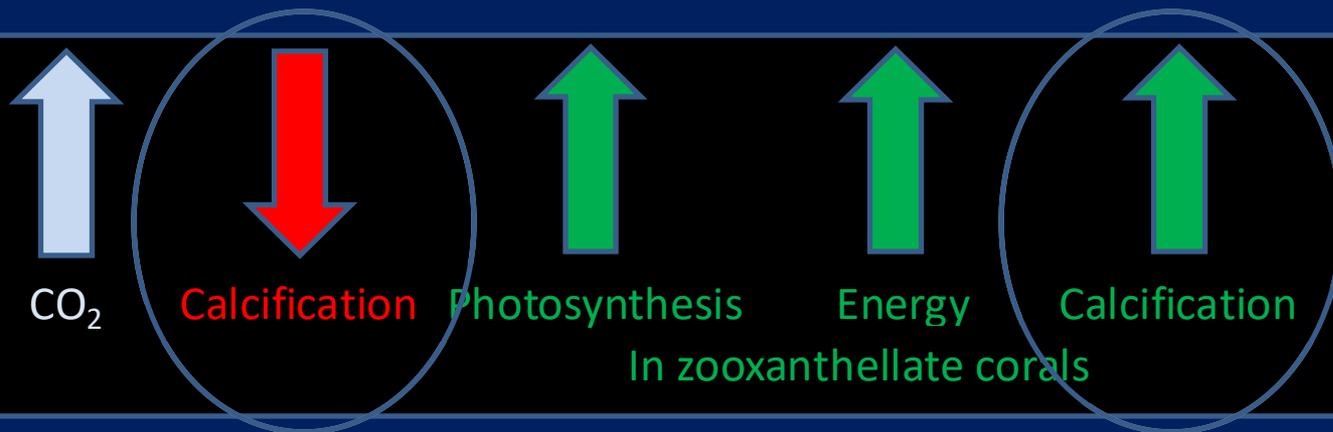
Discussion



While the growth rates of *L. pruvoti* and *A. calycularis*, the **non-zooxanthellate species**, are negatively affected by water acidity, those of *B. europaea*, the **zooxanthellate species**, result unaffected.

From aquarium studies, other two scleractinian **zooxanthellate** species exhibited unaffected calcification rates with increased acidity (Jury et al. 2010, *Global Change Biology* 16: 1632-1644; Metalpa et al. 2010, *Biogeosciences* 7: 289-300). To the best of my knowledge, examples of **non-zooxanthellate** scleractinian corals with unaffected calcification rates in acidic water conditions are not known.

Does a physiological connection exist between growth resistance to acidity and the symbiosis with zooxanthellae? Does symbiont photosynthesis play a role?



A zooxanthellate coral (mixotrophic) has two modalities of energetic intake, compared to a non-zooxanthellate coral (heterotrophic): the trophic plasticity (phototrophy/heterotrophy) of zooxanthellate corals is a mechanism to enlarge the physiological niche and resist stresses (Anthony and Fabricius 2000, *Journal of Experimental Marine Biology and Ecology*, 252: 221-253).

Discussion

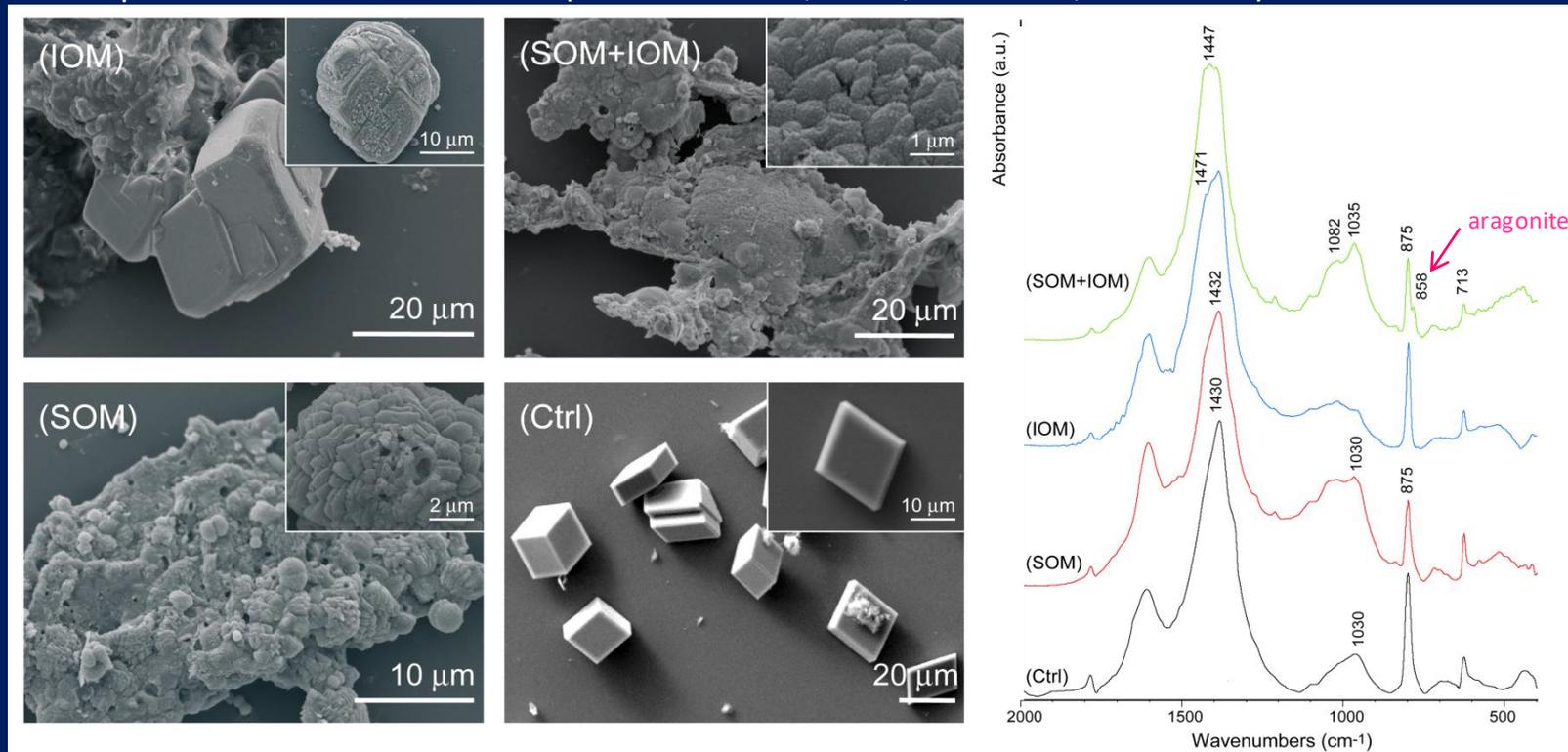


In-vitro crystallization experiments demonstrate that the intra-skeletal organic matrix (OM) of *B. europaea* determines the precipitation of CaCO_3 in the form of aragonite even in the absence of Mg (Goffredo et al., 2011, *PLoS ONE*, 6: e22338). The intra-skeletal organic matrix of *L. pruvoti* does not.

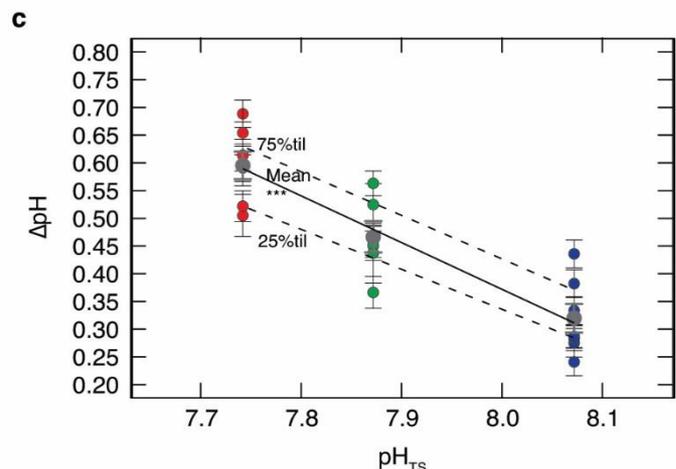
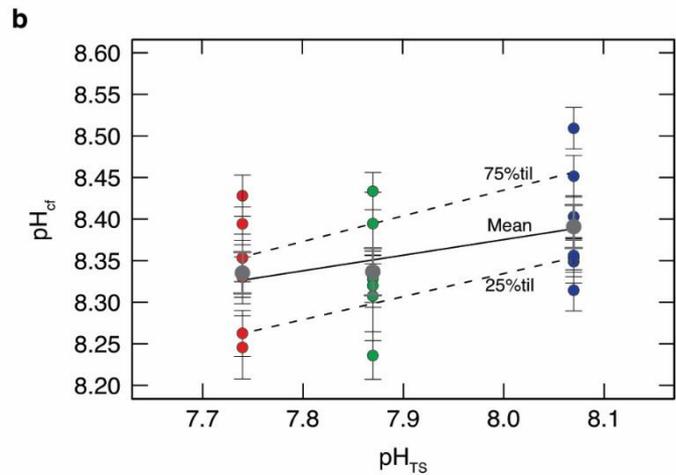
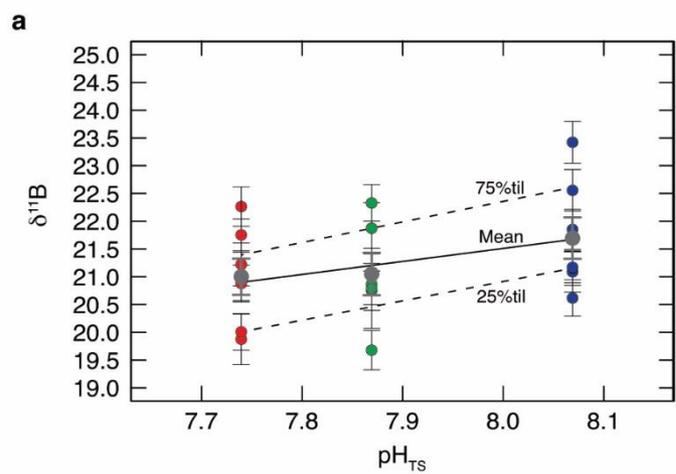
These experiments suggest that *B. europaea* may perform a higher biological control over the mineralization process, displaying a reduced sensitivity to environmental conditions compared to *L. pruvoti*.

Balanophyllia europaea

Precipitation in calcium solution (Goffredo et al., 2011, *PLoS ONE*, 6: e22338).



Experiments of crystallization of calcium carbonate from a solution of CaCl_2 10 mM in absence of additives (Ctrl), and in presence of Soluble Organic Matrix (SOM), Insoluble Organic Matrix (IOM) or both (SOM+IOM). In the right side the FTIR (Fourier Transform Infrared Spectroscopy) spectra of precipitated are reported. The main absorption bands of calcium carbonate are indicated.

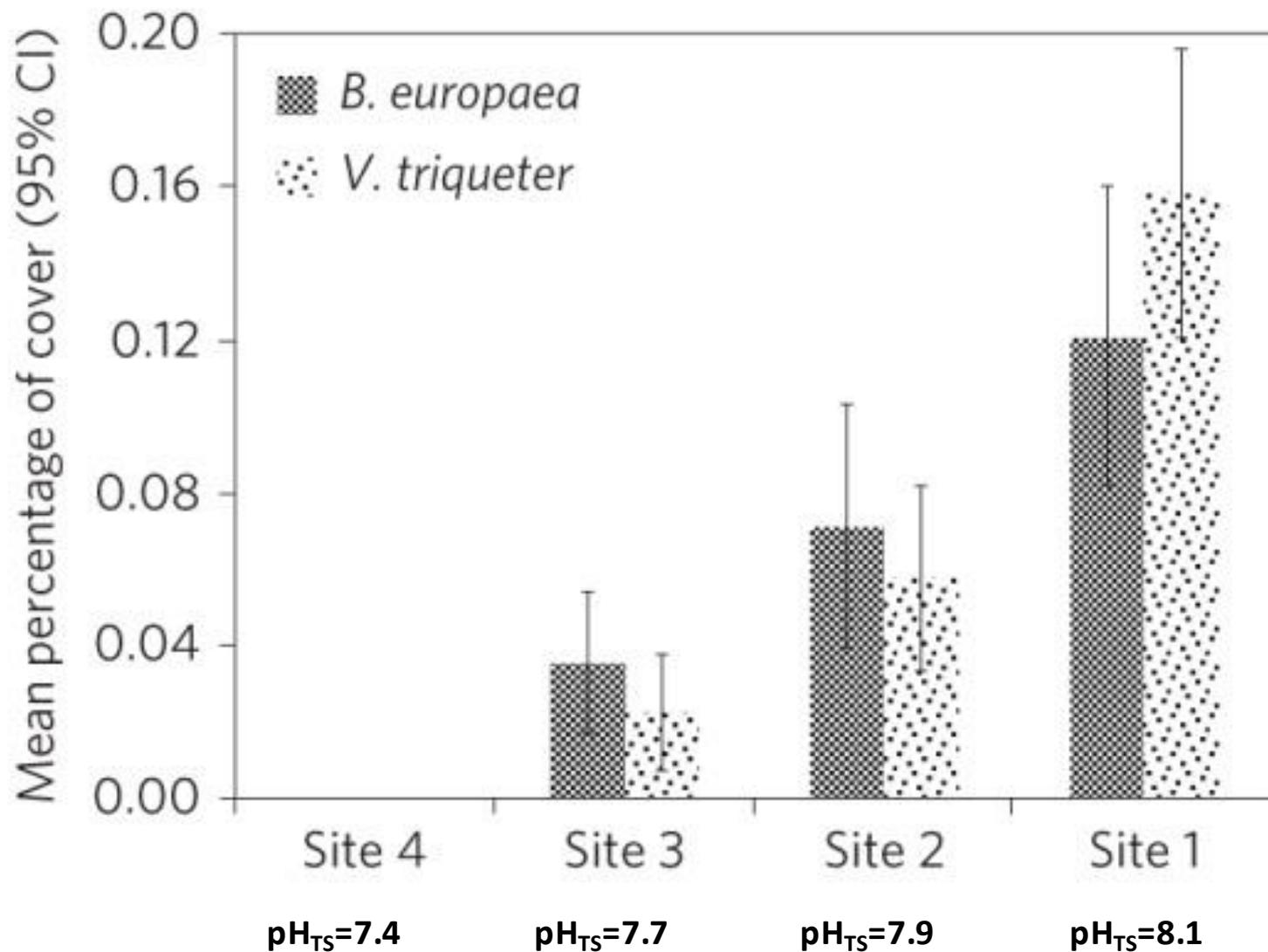


Boron isotopic signature ($\delta^{11}\text{B}$), $\delta^{11}\text{B}$ -derived internal calcification pH (pH_{cf}) and pH up-regulation intensity (ΔpH) of *Balanophyllia europaea* corals from the CO_2 seeps near Panarea Island, Italy. Data published in: Wall M., Prada F., Fietzke J., Caroselli E., Dubinsky Z., Brizi L., Fantazzini P., Franzellitti S., Mass T., Montagna P., Falini G., Goffredo S. 2019: Linking Internal Carbonate Chemistry Regulation and Calcification in Corals Growing at a Mediterranean CO_2 Vent. *Frontiers in Marine Science* 6: 699. doi: 10.3389/fmars.2019.00699.

(a) $\delta^{11}\text{B}$ values were measured in total 20 *B. europaea* samples collected at three different sites along a natural pH gradient (pH_{TS} in total scale; site 1 = blue, site 2 = green, site 3 = red). From the boron isotopic signature (b) pH_{cf} and (c) ΔpH ($= \text{pH}_{\text{cf}} - \text{pH}_{\text{TS}}$) were calculated. Filled circles and error bars represent individual colony means ± 1 sem per colony. Dark grey filled circles show average per site (\pm sem). Black solid line indicates linear regression and the dashed lines the 25% and 75%-quantile range of the regression.

Long term effects of acidification on
growth of *B. europaea* naturally living
along the pH gradient

B. europaea abundance decreases along the $p\text{CO}_2$ gradient



Mean percentage of cover for *Balanophyllia europaea* and *Vermetus triqueter* along the $p\text{CO}_2$ gradient (Goffredo et al., 2014, *Nature Climate Change*, 4: 593-597).

With increasing pCO₂:

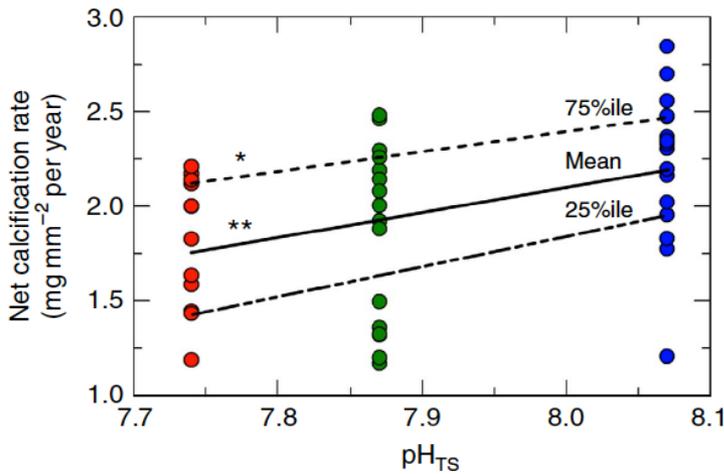
Site 1: $d=34$ m
 pCO₂=423 μatm
 pH=8.07
 N=16

Site 2: $d=13$ m
 pCO₂=698 μatm
 pH=7.87
 N=16

Site 3: $d=9$ m
 pCO₂=922 μatm
 pH=7.74
 N=12



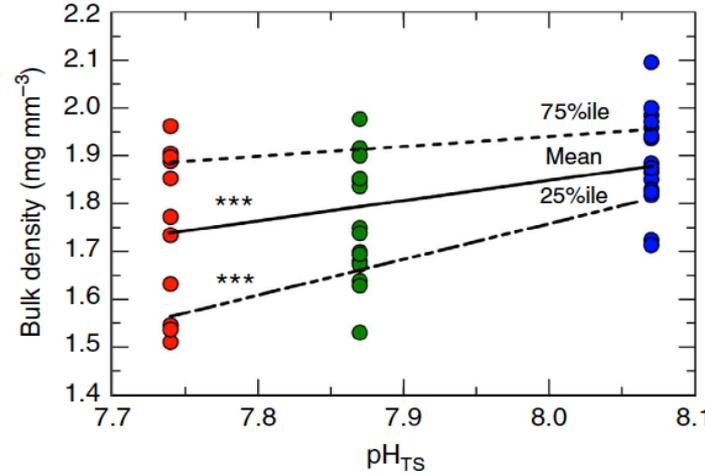
	mean	se	mean	se	mean	se	statistical significance
Net calcification rate (mg mm ⁻² yr ⁻¹)	2.2	0.1	1.9	0.1	1.8	0.1	*
Linear extension rate (mm yr ⁻¹)	1.17	0.05	1.04	0.05	1.03	0.05	NS
Skeletal bulk density (d_b) (mg mm ⁻³)	1.89	0.03	1.77	0.03	1.76	0.05	*



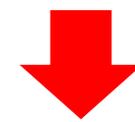
Net calcification rate



Linear extension rate



Skeletal bulk density



With increasing pCO₂:

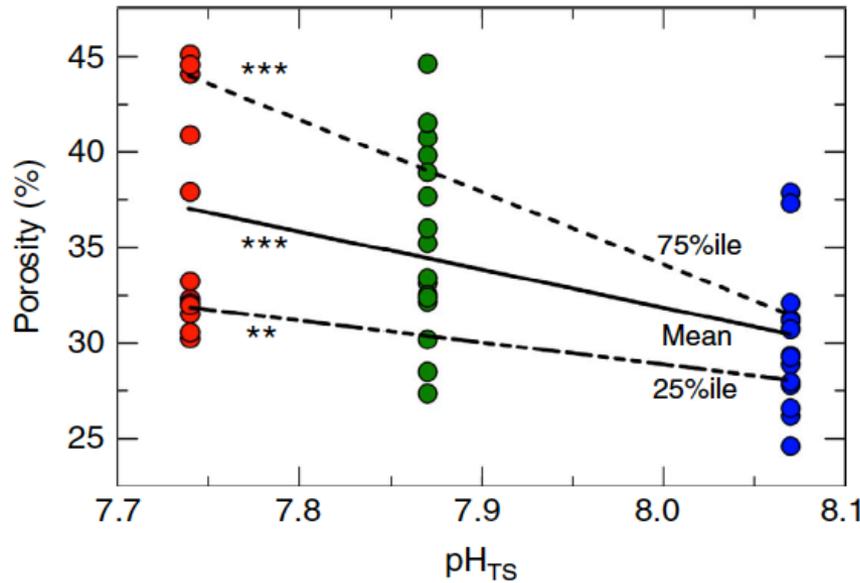
Site 1: $d=34$ m
 pCO₂=423 μatm
 pH=8.07
 N=16

Site 2: $d=13$ m
 pCO₂=698 μatm
 pH=7.87
 N=16

Site 3: $d=9$ m
 pCO₂=922 μatm
 pH=7.74
 N=12



	mean	se	mean	se	mean	se	statistical significance
Skeletal porosity (P_A) (%) [§]	30.0	0.9	35.3	1.2	36.2	1.7	**

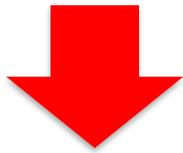


 Porosity

$$\begin{array}{ccc} \text{Net calcification} & = & \text{linear} \\ \text{rate} & & \text{extension rate} \\ (\text{mg mm}^{-2} \text{ yr}^{-1}) & & (\text{mm yr}^{-1}) \end{array} \times \begin{array}{c} \text{skeletal} \\ \text{bulk density} \\ (\text{mg mm}^{-3}) \end{array}$$

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:

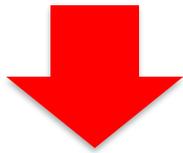


$$\begin{array}{l} \text{Net calcification} \\ \text{rate} \\ (\text{mg mm}^{-2} \text{ yr}^{-1}) \end{array} = \begin{array}{l} \text{linear} \\ \text{extension rate} \\ (\text{mm yr}^{-1}) \end{array} \times \begin{array}{l} \text{skeletal} \\ \text{bulk density} \\ (\text{mg mm}^{-3}) \end{array}$$

Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:

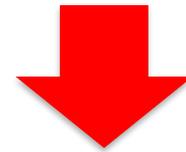
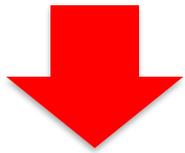


$$\begin{array}{l} \text{Net calcification} \\ \text{rate} \\ (\text{mg mm}^{-2} \text{ yr}^{-1}) \end{array} = \begin{array}{l} \text{linear} \\ \text{extension rate} \\ (\text{mm yr}^{-1}) \end{array} \times \begin{array}{l} \text{skeletal} \\ \text{bulk density} \\ (\text{mg mm}^{-3}) \end{array}$$

Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:



**Net calcification
rate**



**linear
extension rate**



**skeletal
bulk density**

(mg mm⁻² yr⁻¹)

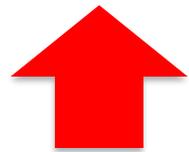
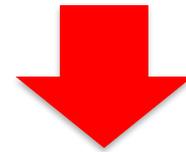
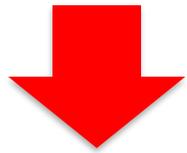
(mm yr⁻¹)

(mg mm⁻³)

Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:



**Net calcification
rate**



**linear
extension rate**



**skeletal porosity
bulk density**

(mg mm⁻² yr⁻¹)

(mm yr⁻¹)

(mg mm⁻³)

Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

Biological significance of the *B. europaea* growth strategy in acidified conditions, and depleted calcification

Biological significance of the *B. europaea* growth strategy in acidified conditions, and depleted calcification

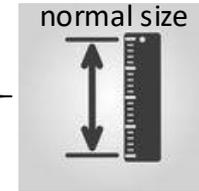
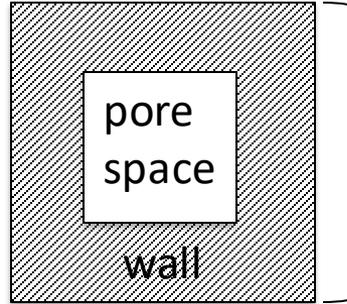
normal calcification

normal phenotype

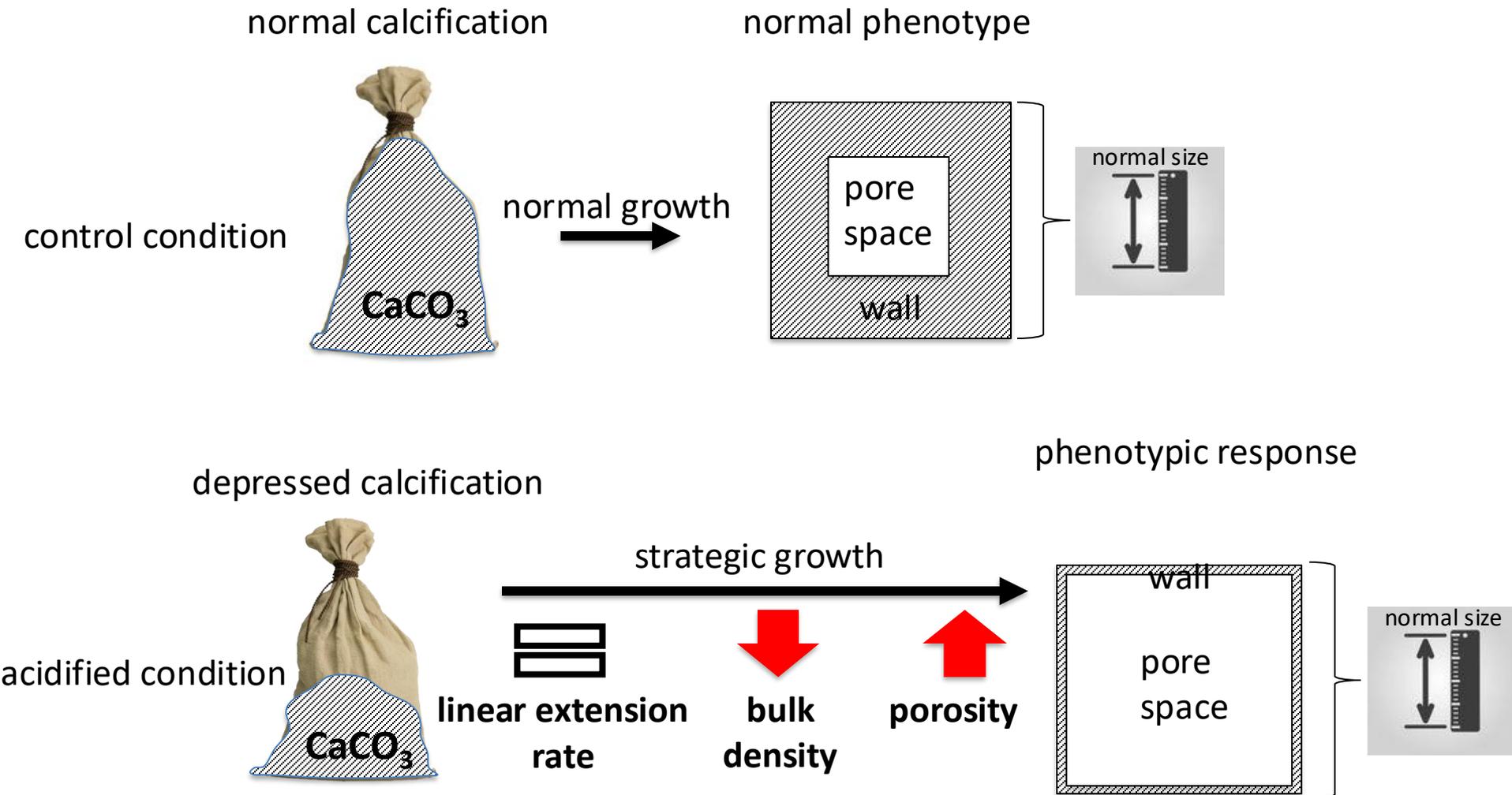
control condition



normal growth



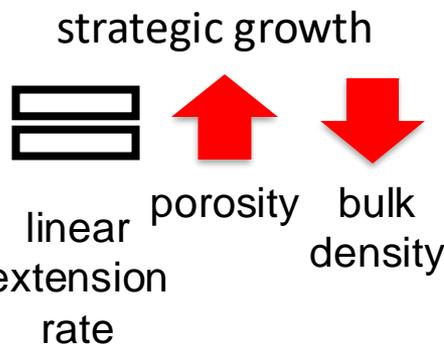
Biological significance of the *B. europaea* growth strategy in acidified conditions, and depleted calcification



With increasing pCO₂:



depressed
calcification



GAIN



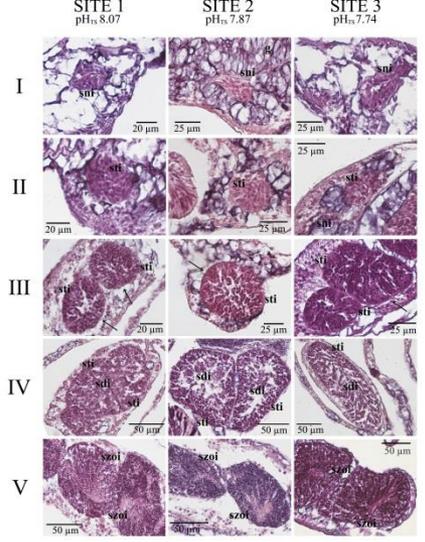
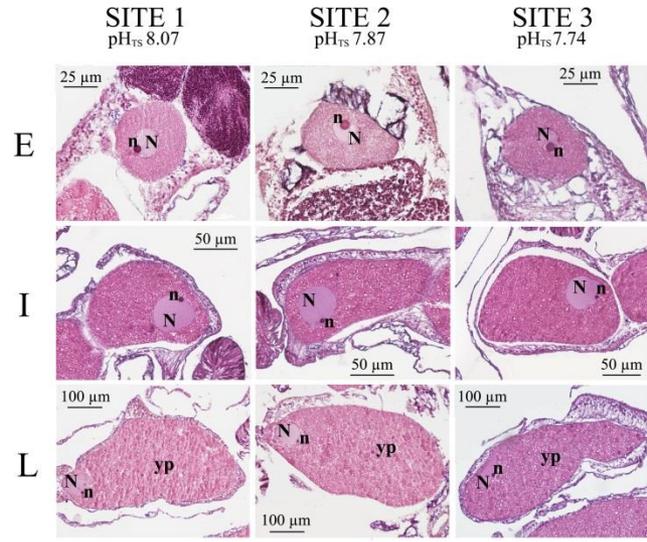
LOSS



With increasing pCO₂:



depressed calcification



Gizzi e Marchini, 2016, *Tesi di Dottorato*

Size at sexual maturity



strategic growth



linear extension rate



porosity

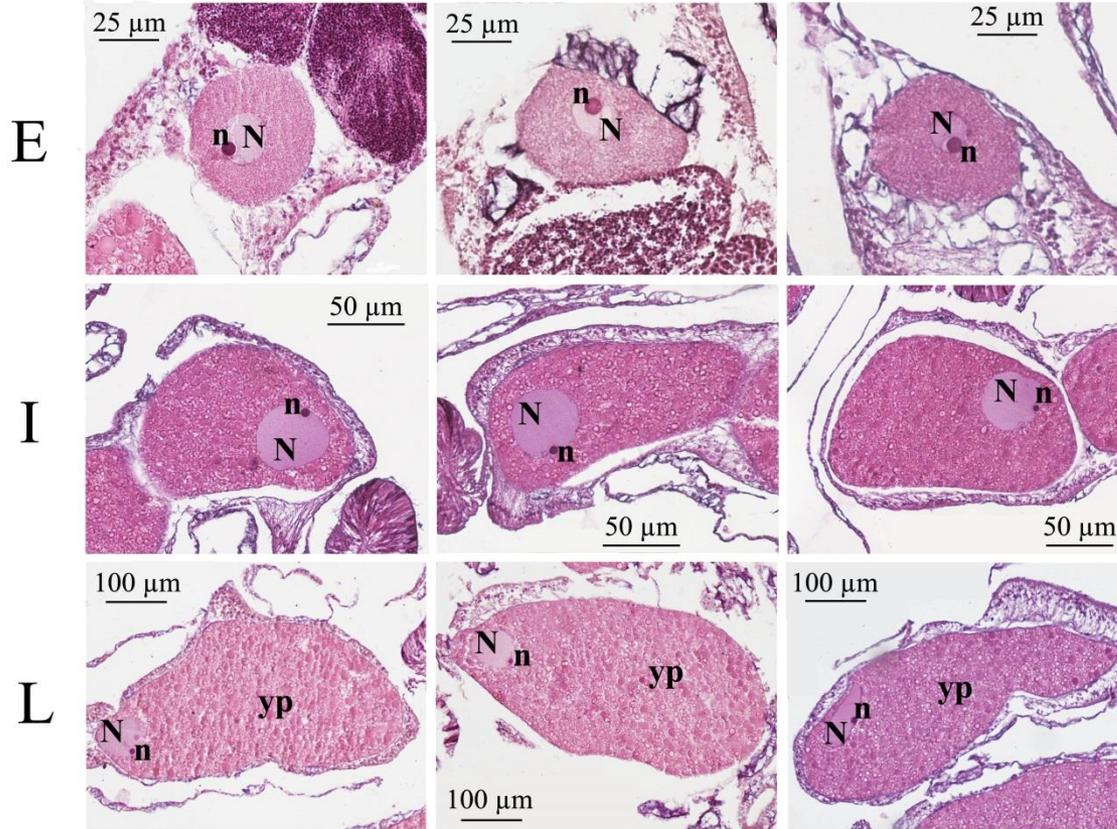


bulk density

SITE 1
pH_{TS} 8.07

SITE 2
pH_{TS} 7.87

SITE 3
pH_{TS} 7.74

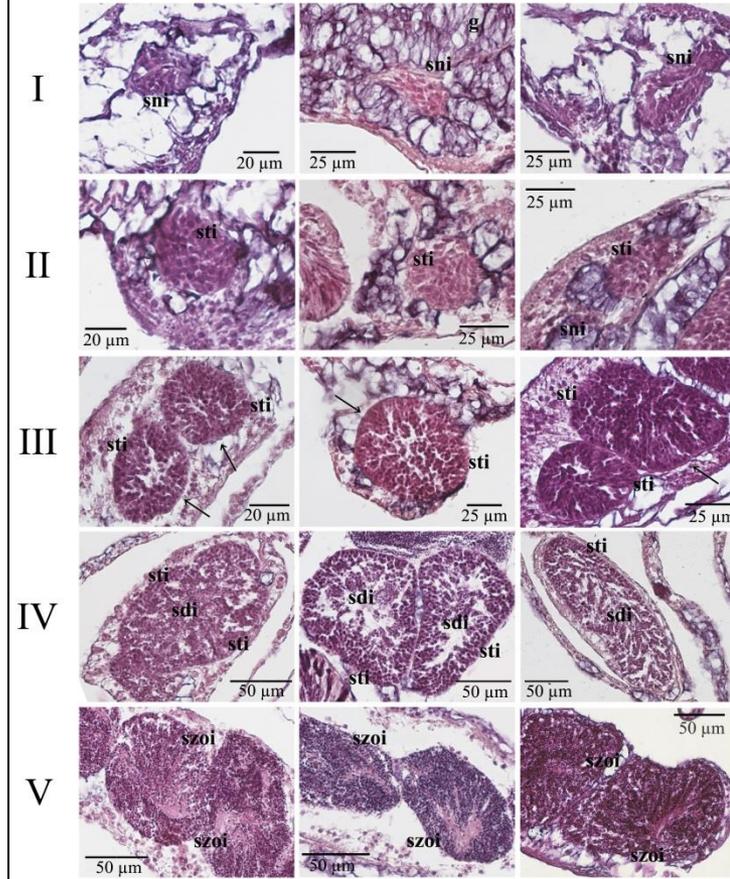


Balanophyllia europaea. Oogenesis. E: Earlier stage oocytes. The spherical nucleus is located centrally and contains a single nucleolus. I: Intermediate stage oocytes. The spherical-shaped nucleus has started to migrate toward the cell's periphery. L: Late mature stage: the nucleus is now located in the outer portion of the oocyte. The ooplasm is full of small yolk plates. [N: nucleus; n: nucleolus; yp: yolk plates].

SITE 1
pH_{TS} 8.07

SITE 2
pH_{TS} 7.87

SITE 3
pH_{TS} 7.74

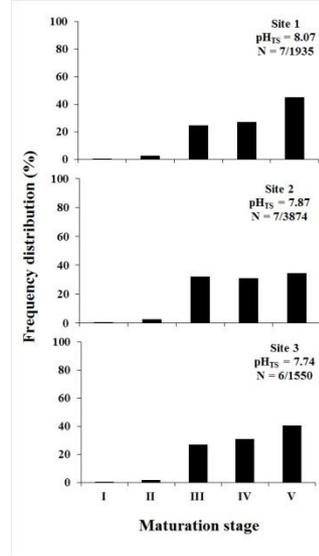
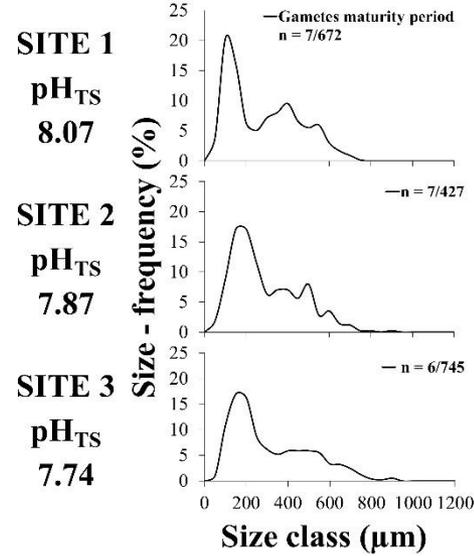
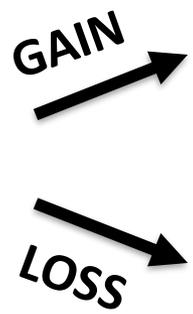
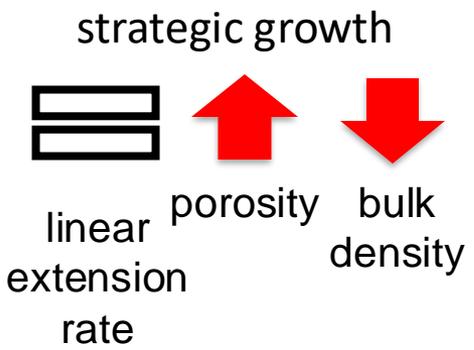


Balanophyllia europaea. Spermatogenesis. Five spermary maturation stages (I, II, III, IV, V) in the three study sites along the pCO₂ gradient. Stage I: undifferentiated spermaries. Stage II: the spermary is made up of a group of spermatocytes involved in the meiosis process. Stage III: the spermaries are delineated by a wall that has arisen from the mesoglea (arrows). Stage IV: the spermary presents an external layer of spermatocytes and an internal mass of spermatids. Stage V: the spermary is made up of a mass of spermatozoa. [g: gastrodermis; sni: spermatogonia; sti: spermatocytes; sdi: spermatids; szoi: spermatozoa].

With increasing pCO₂:



depressed calcification

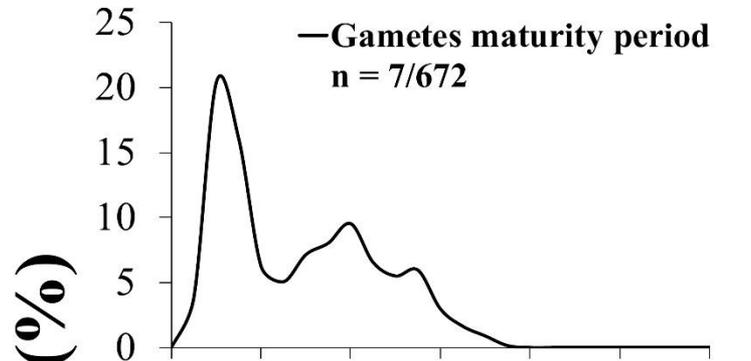


Size at sexual maturity

Gizzi e Marchini, 2016, *Tesi di Dottorato*

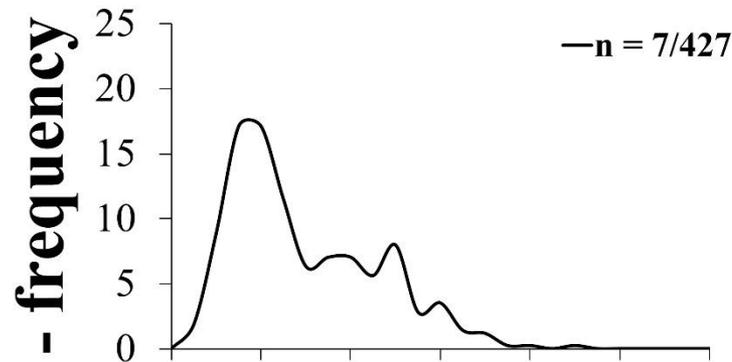
SITE 1

pH_{TS}
8.07



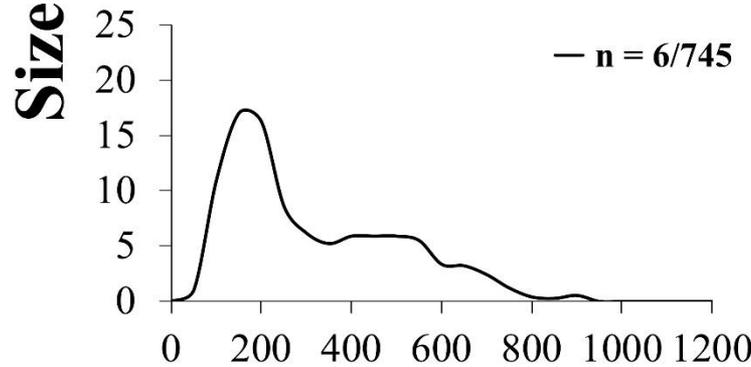
SITE 2

pH_{TS}
7.87



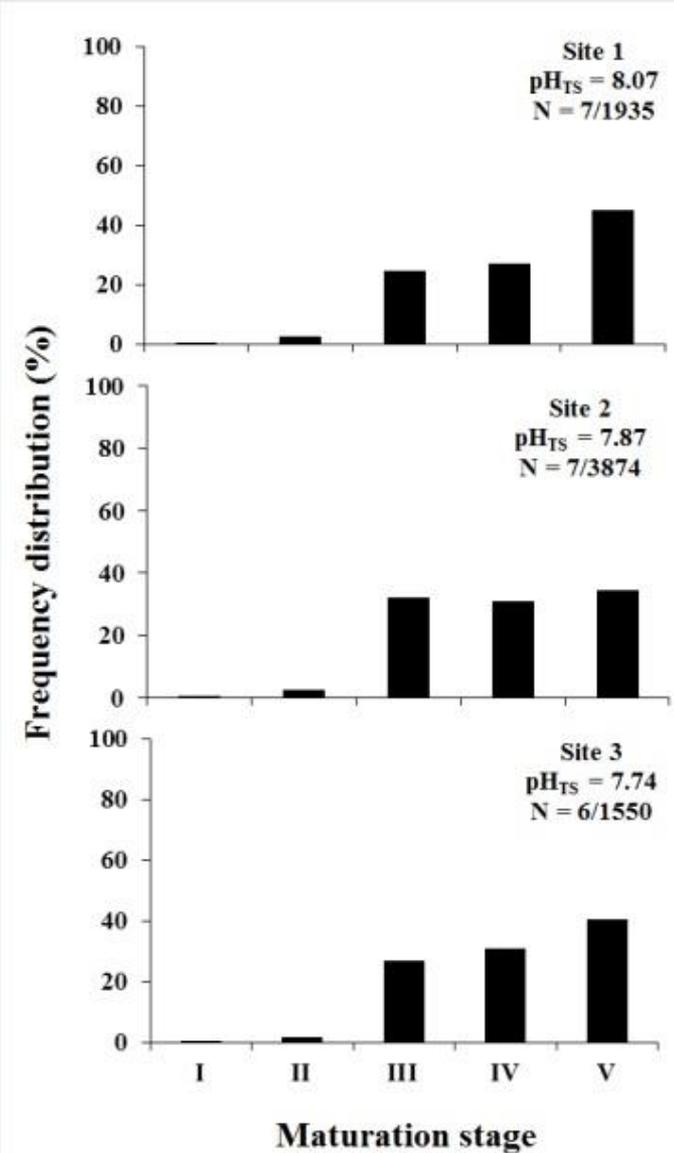
SITE 3

pH_{TS}
7.74



Size class (µm)

Balanophyllia europaea. Size–frequency distribution of oocytes in the three sites. N = number polyps/number oocytes

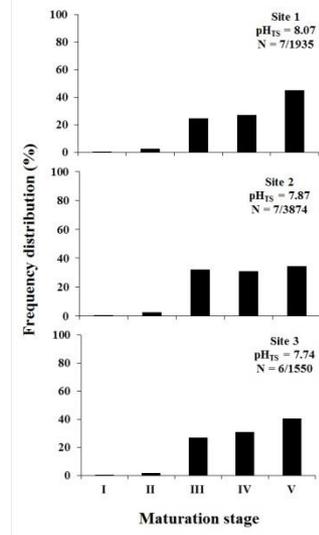
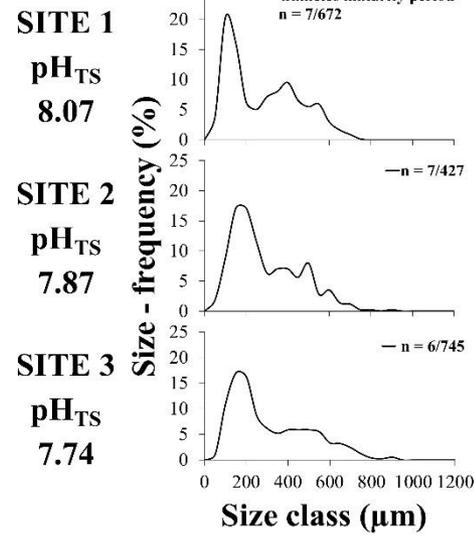
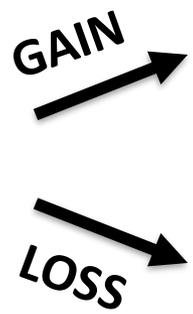
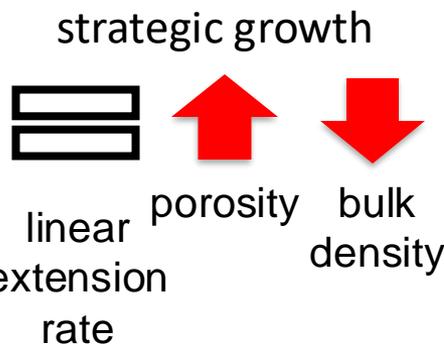


Balanophyllia europaea. Distribution of the five stages of spermary maturation in the three sites along the pCO₂ gradient. N indicate the number of polyps/the total number of spermaries measured per site.

With increasing pCO₂:



depressed calcification



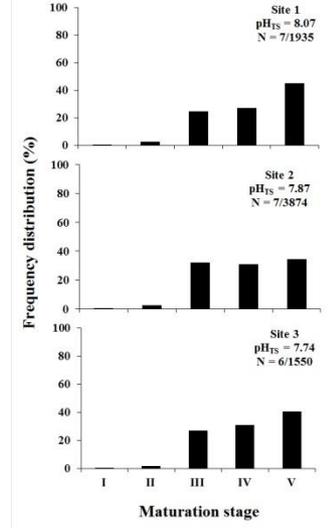
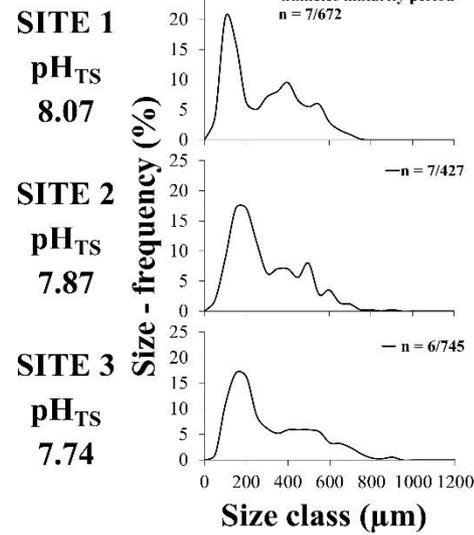
Size at sexual maturity

Gizzi e Marchini, 2016, *Tesi di Dottorato*

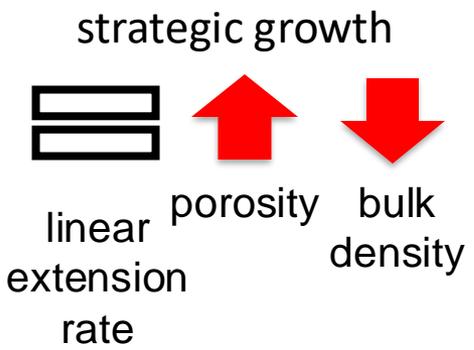
With increasing pCO₂:



depressed calcification



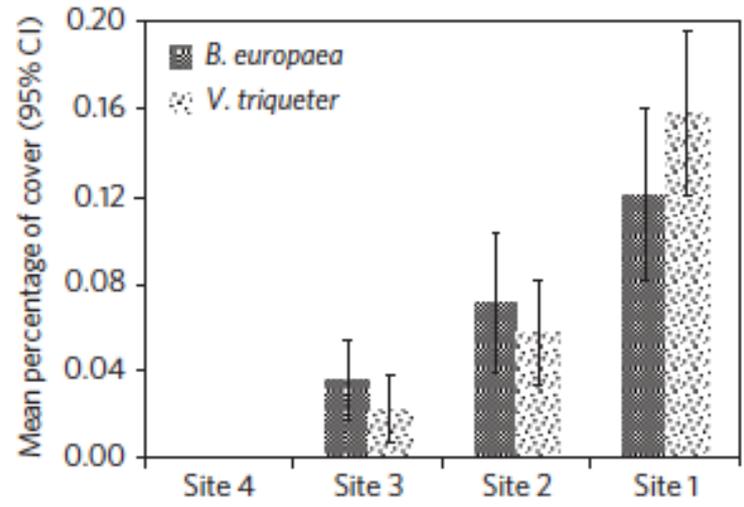
Gizzi e Marchini, 2016, Tesi di Dottorato



GAIN
LOSS

mechanical strength

Size at sexual maturity

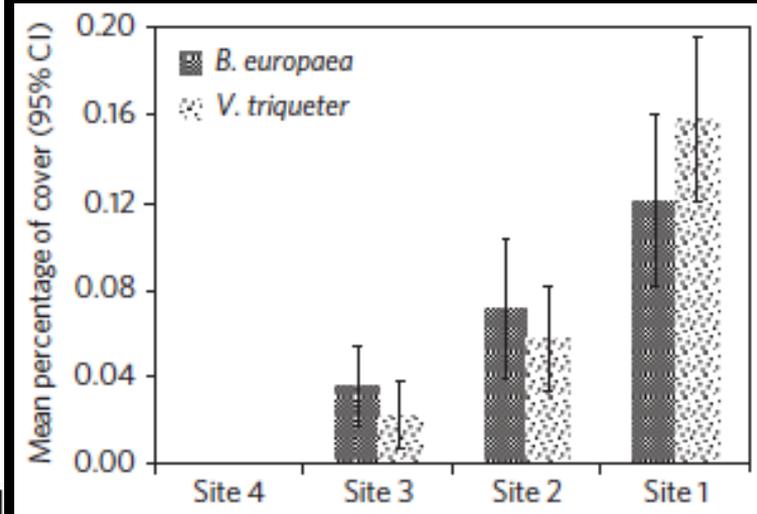
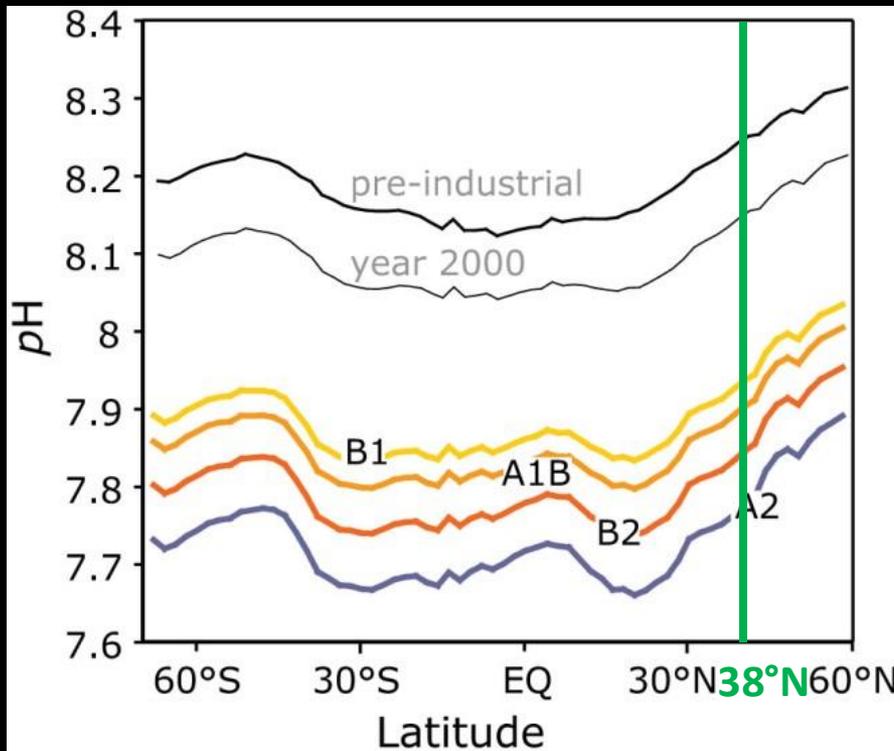


pH_{TS}=7.4 pH_{TS}=7.7 pH_{TS}=7.9 pH_{TS}=8.1

Goffredo et al., 2014, Nature Climate Change, 4: 593-597

Predictions for 2100

(Caldeira, 2007, *Oceanography*, 20: 188-195)

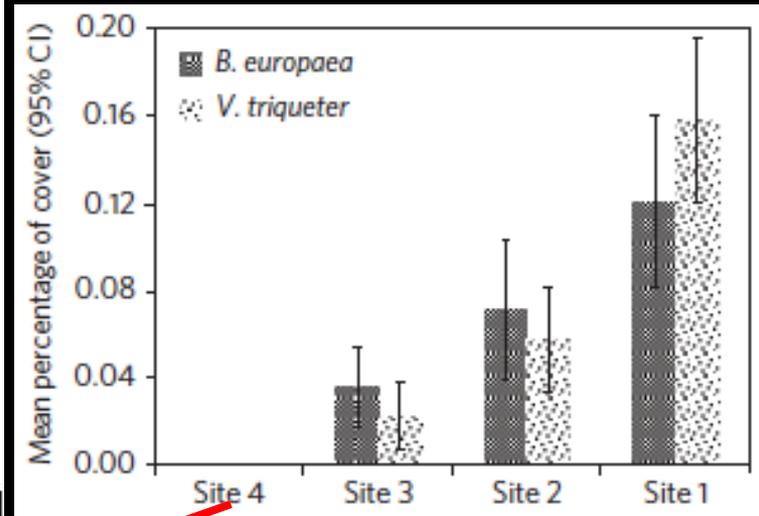
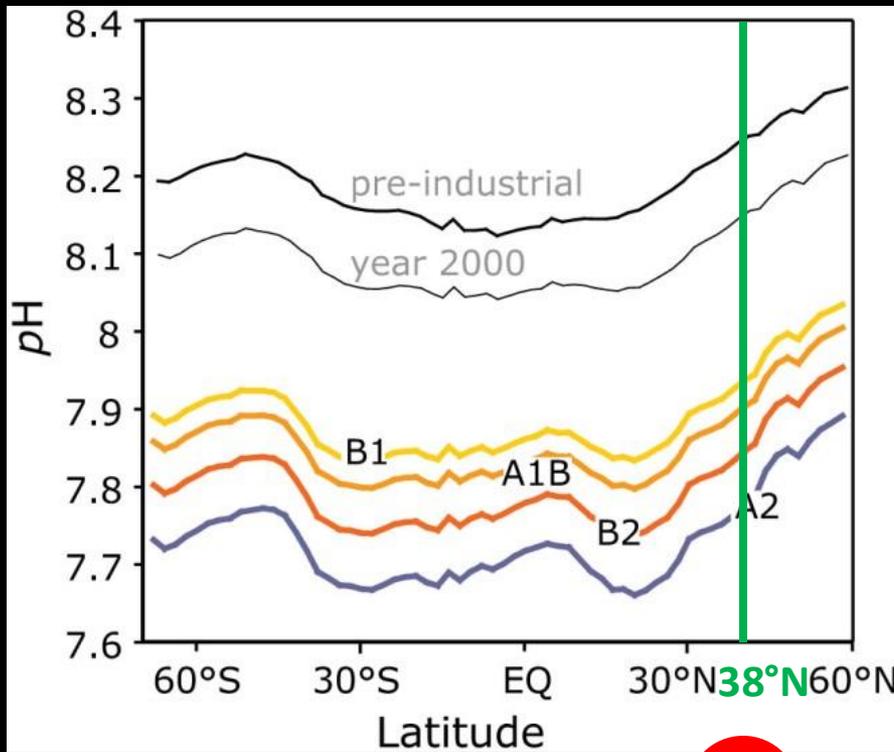


$pH_{TS}=7.4$ $pH_{TS}=7.7$ $pH_{TS}=7.9$ $pH_{TS}=8.1$

Goffredo et al., 2014, *Nature Climate Change*, 4: 593-597

Predictions for 2100

(Caldeira, 2007, *Oceanography*, 20: 188-195)



pH_{TS}
7.4

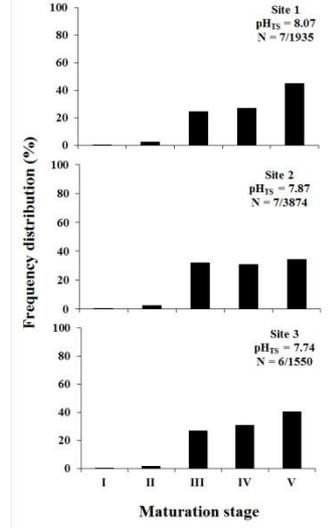
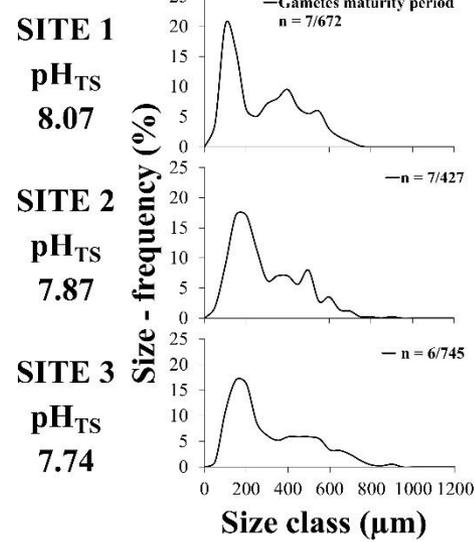
$pH_{TS}=7.4$ $pH_{TS}=7.7$ $pH_{TS}=7.9$ $pH_{TS}=8.1$

Goffredo et al., 2014, *Nature Climate Change*, 4: 593-597

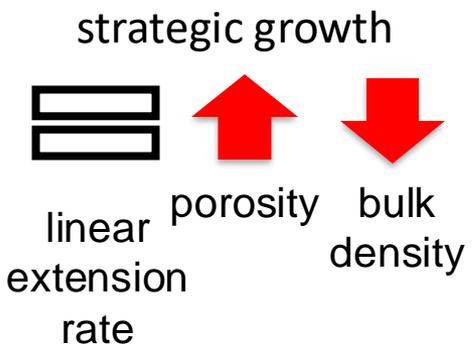
With increasing pCO₂:



depressed calcification



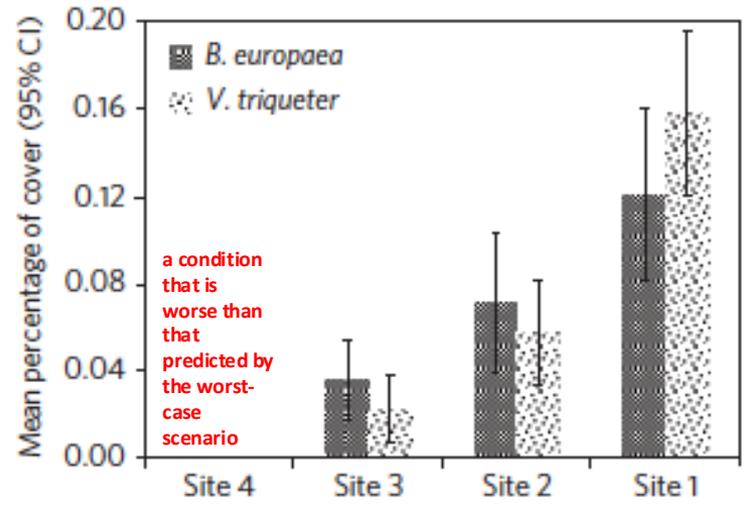
Gizzi e Marchini, 2016, Tesi di Dottorato



GAIN
LOSS

mechanical strength

Size at sexual maturity



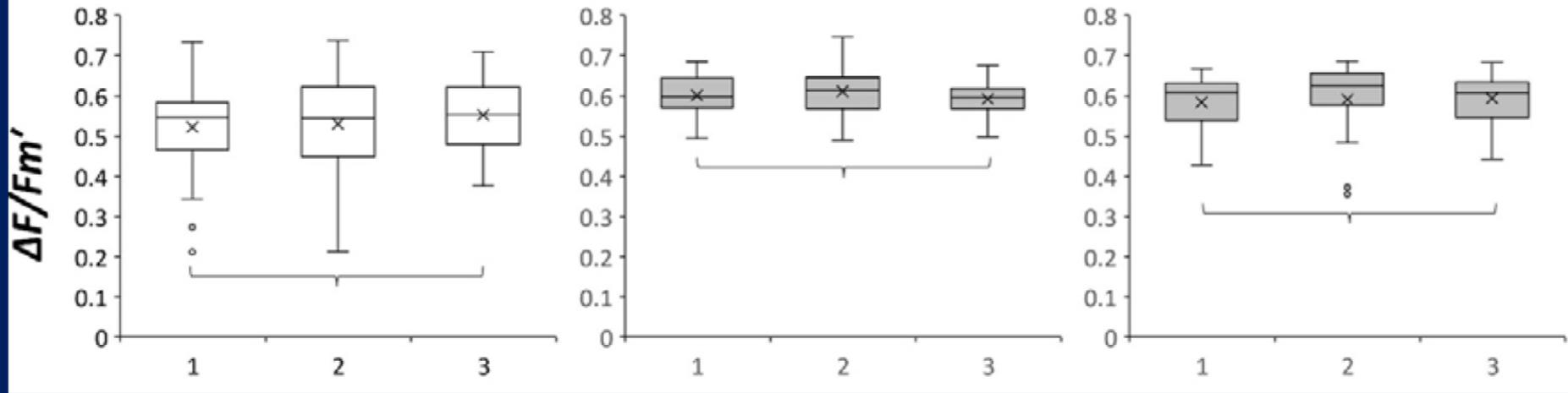
pH_{TS}=7.4 pH_{TS}=7.7 pH_{TS}=7.9 pH_{TS}=8.1

Goffredo et al., 2014, Nature Climate Change, 4: 593-597

9:00-13:00

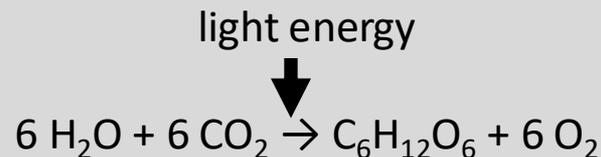
18:00-20:00

20:00-22:00

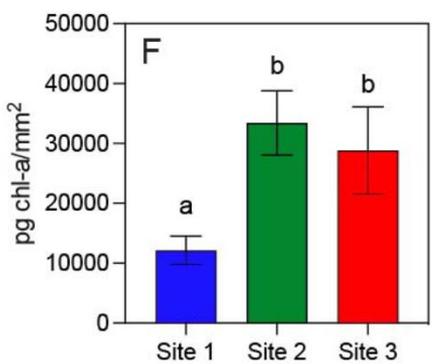
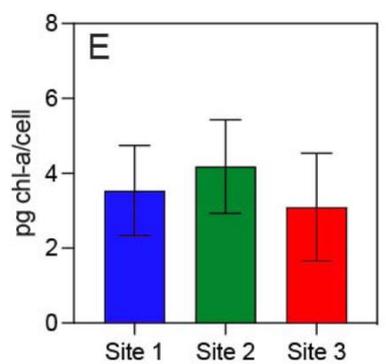
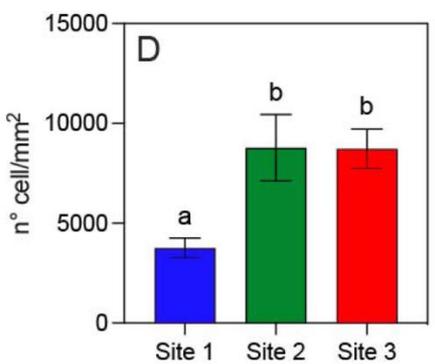
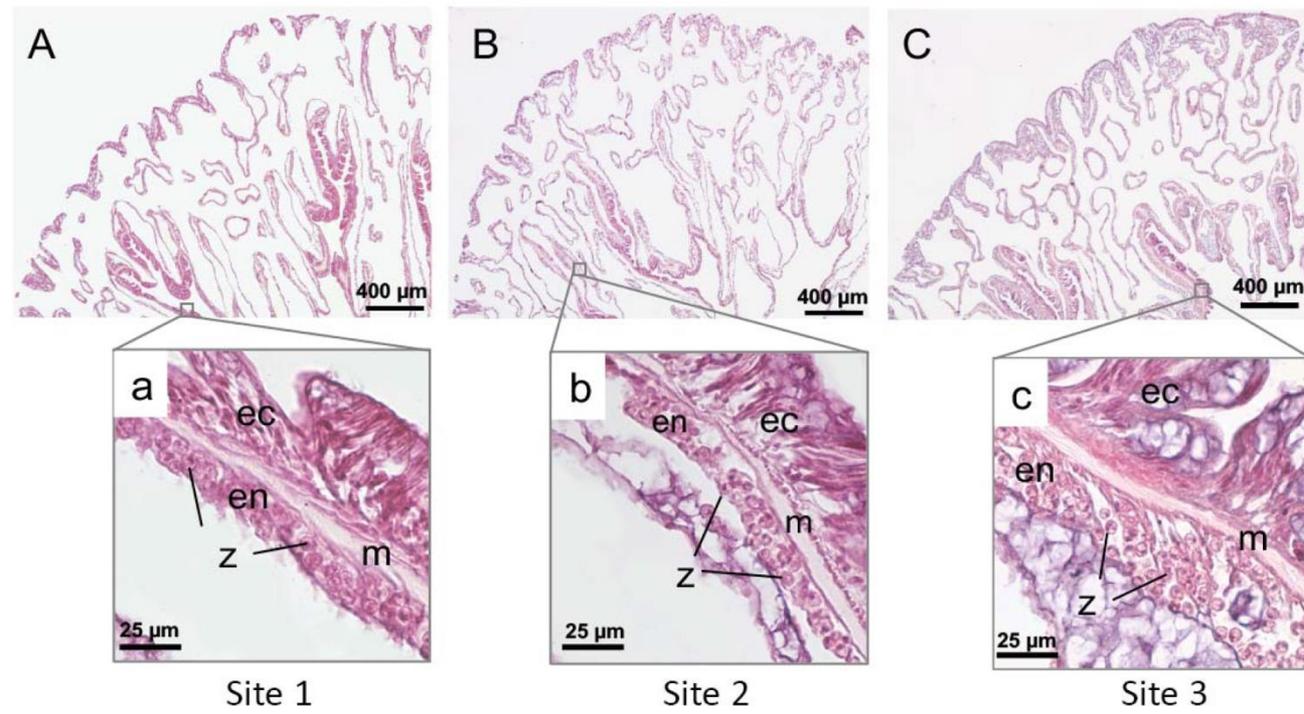


Boxplots of photosynthetic efficiency (= photosynthetic yield) obtained by PAM measurements at the three sites and at three time intervals. Significant differences ($p < 0.01$) between time intervals are indicated by different colors (significantly higher mean value is ranked as white->gray->black). Within each panel, thin branches group study sites with a homogeneous parameter value ($p > 0.05$). The boxes indicate the 25th and 75th percentiles and the line within the boxes mark the medians. Whisker length is equal to $1.5 \times$ interquartile range (IQR). Circles represent outliers. From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO_2 vent. *Communications Biology*, *submitted*.

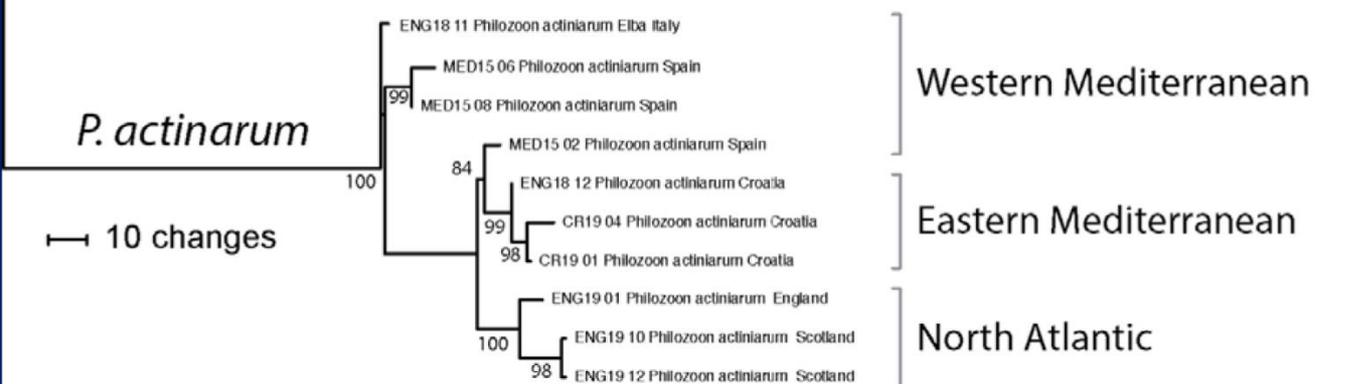
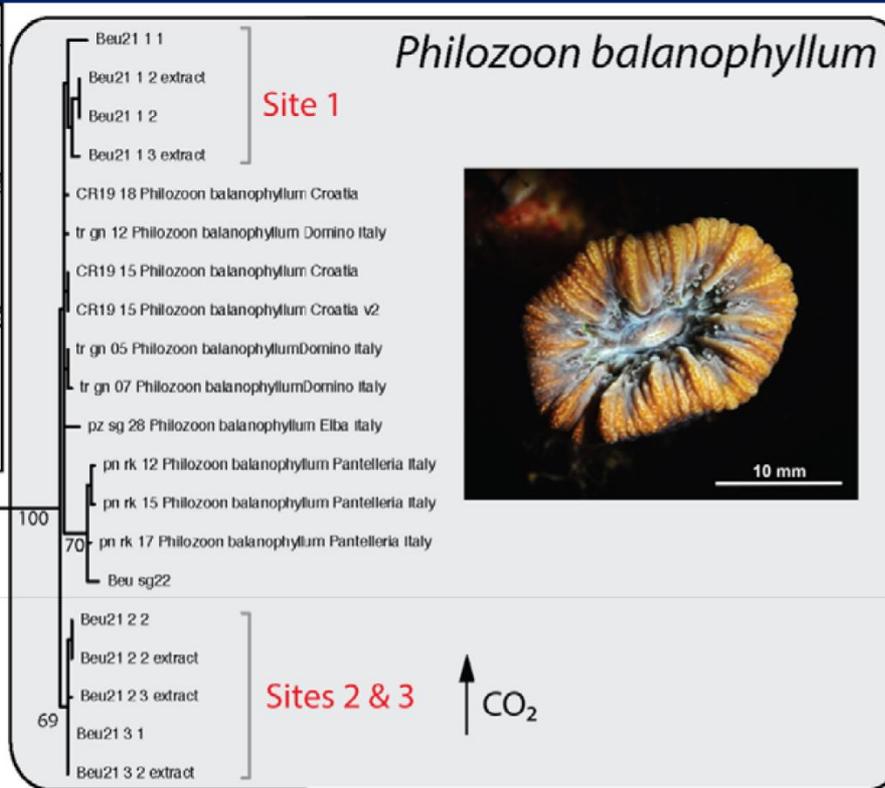
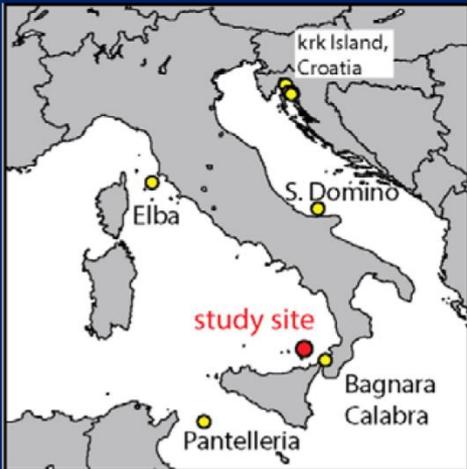
The photosynthetic efficiency is the fraction of light energy converted into chemical energy during photosynthesis. Photosynthesis can be described by the simplified chemical reaction



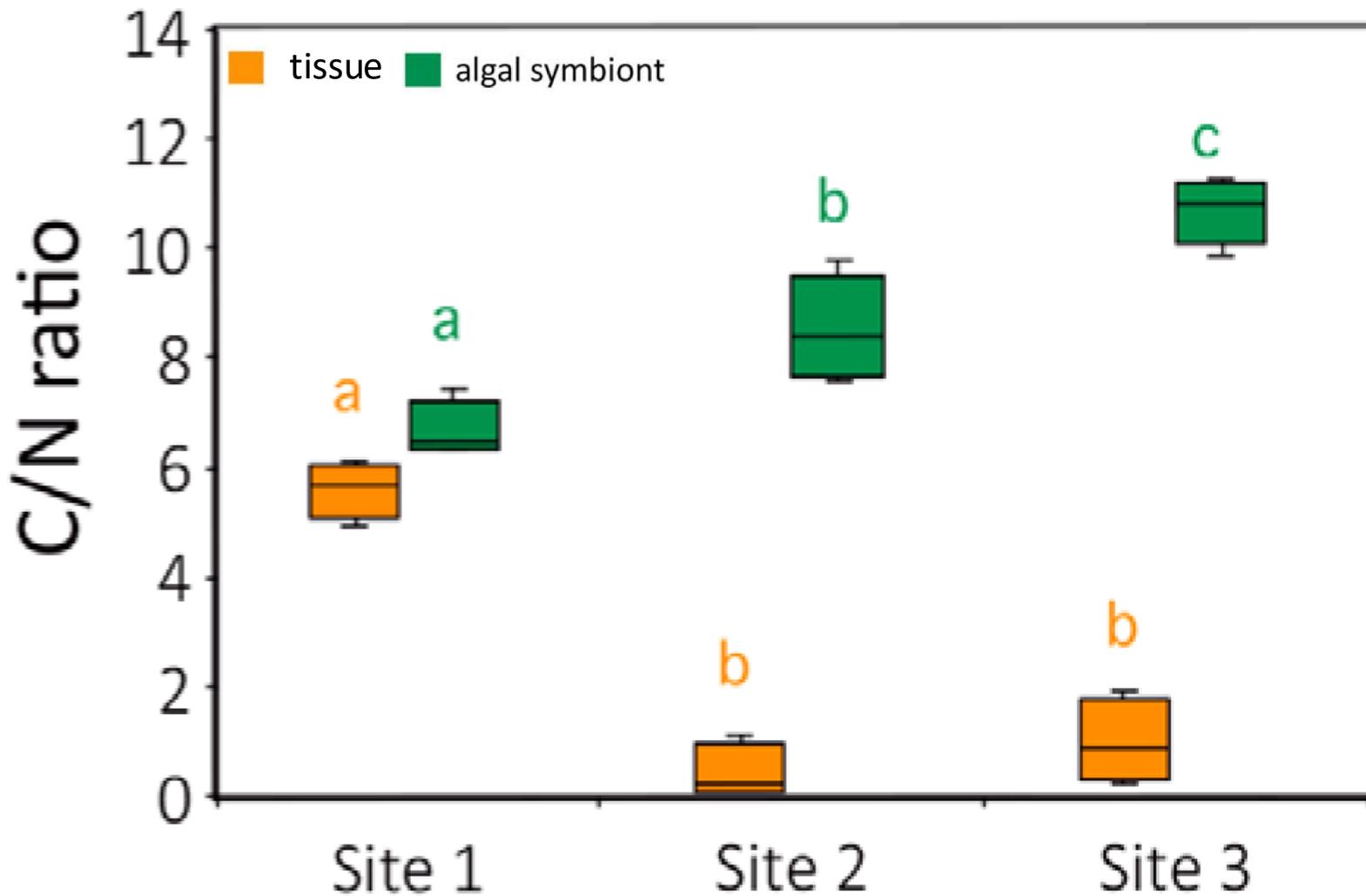
where $\text{C}_6\text{H}_{12}\text{O}_6$ is glucose (which is subsequently transformed into other sugars, starches etc.).



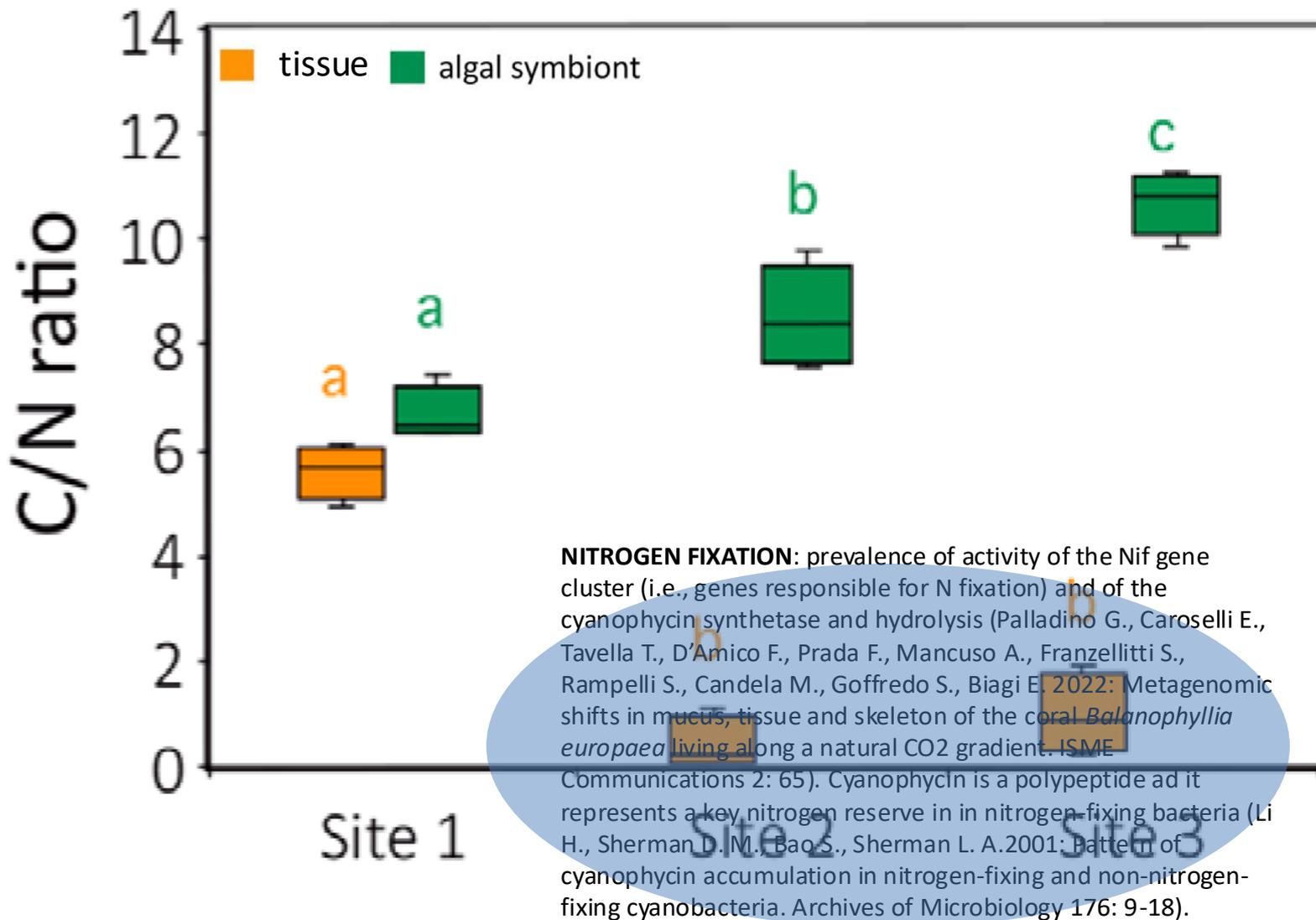
Zooxanthellae algae in tissues of *Balanophyllia europaea* polyps sampled along the natural pH gradient of Panarea. (A-C) Histological transverse sections of representative polyps in Sites 1-3 (x 4 magnification). (a-c) Zooxanthellae within the endoderm of the mesentery highlighted by x 40 magnification. z: zooxanthellae; ec: ectoderm; m: mesoglea; en: endoderm. (D) Zooxanthellae algae density and (E) chlorophyll-a (chl-a) concentration normalized over cell count or (F) polyp area. Values are reported as mean ± sem (N = 4 per Site). Different letters indicate statistical differences ($p < 0.05$). From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. Communications Biology, *submitted*.



Philozoon balanophyllum phylogeny. *Philozoon balanophyllum* haplotypes in *B. europaea* specimens from Sites 1-3 along the Panarea pH gradient and from around the Tyrrhenian and Adriatic Seas. (Photograph by Francesco Sesso). From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., Lajeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. *Communications Biology*, *submitted*.



C/N ratios in *B. europaea* tissue and algal symbionts from Sites 1 (control), 2 (intermediate pH) and 3 (low pH). The boxes indicate the 25th and 75th percentiles and the line within the boxes mark the medians. Whisker length is equal to 1.5 × interquartile range (IQR). Different letters indicate statistical differences ($p < 0.05$) between sites. From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. Communications Biology, submitted.



C/N ratios in *B. europaea* tissue and algal symbionts from Sites 1 (control), 2 (intermediate pH) and 3 (low pH). The boxes indicate the 25th and 75th percentiles and the line within the boxes mark the medians. Whisker length is equal to $1.5 \times$ interquartile range (IQR). Different letters indicate statistical differences ($p < 0.05$) between sites. From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. Communications Biology, submitted.

NITROGEN FIXATION

Nitrogen fixation is a chemical process by which molecular nitrogen (N_2) is converted into ammonia (NH_3) or related nitrogenous compounds. Atmospheric nitrogen is molecular dinitrogen, a relatively nonreactive molecule that is metabolically useless. Biological nitrogen fixation or diazotrophy is an important microbially mediated process that converts dinitrogen (N_2) to ammonia (NH_3) using the **nitrogenase protein complex (Nif)**. Nitrogen fixation is essential to life because fixed inorganic nitrogen compounds are required for the biosynthesis of all nitrogen-containing organic compounds, such as amino acids and proteins, nucleoside triphosphates and nucleic acids. Nitrogen fixation is carried out naturally by bacteria microorganisms termed **diazotrophs**. Some nitrogen-fixing bacteria have symbiotic relationships.

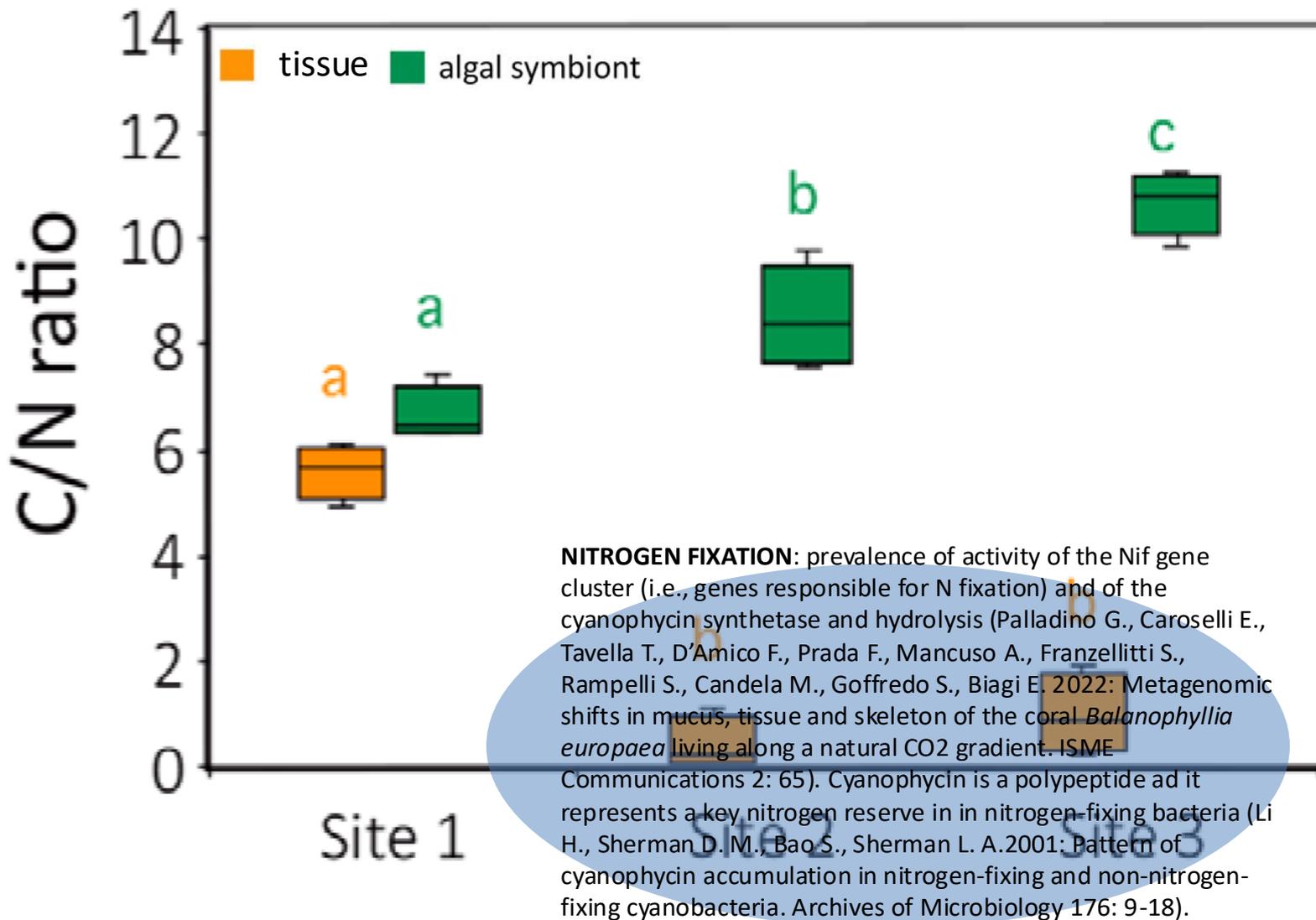
Biological nitrogen fixation (BNF) occurs when atmospheric nitrogen is converted to ammonia by a nitrogenase enzyme. The overall reaction for BNF is:



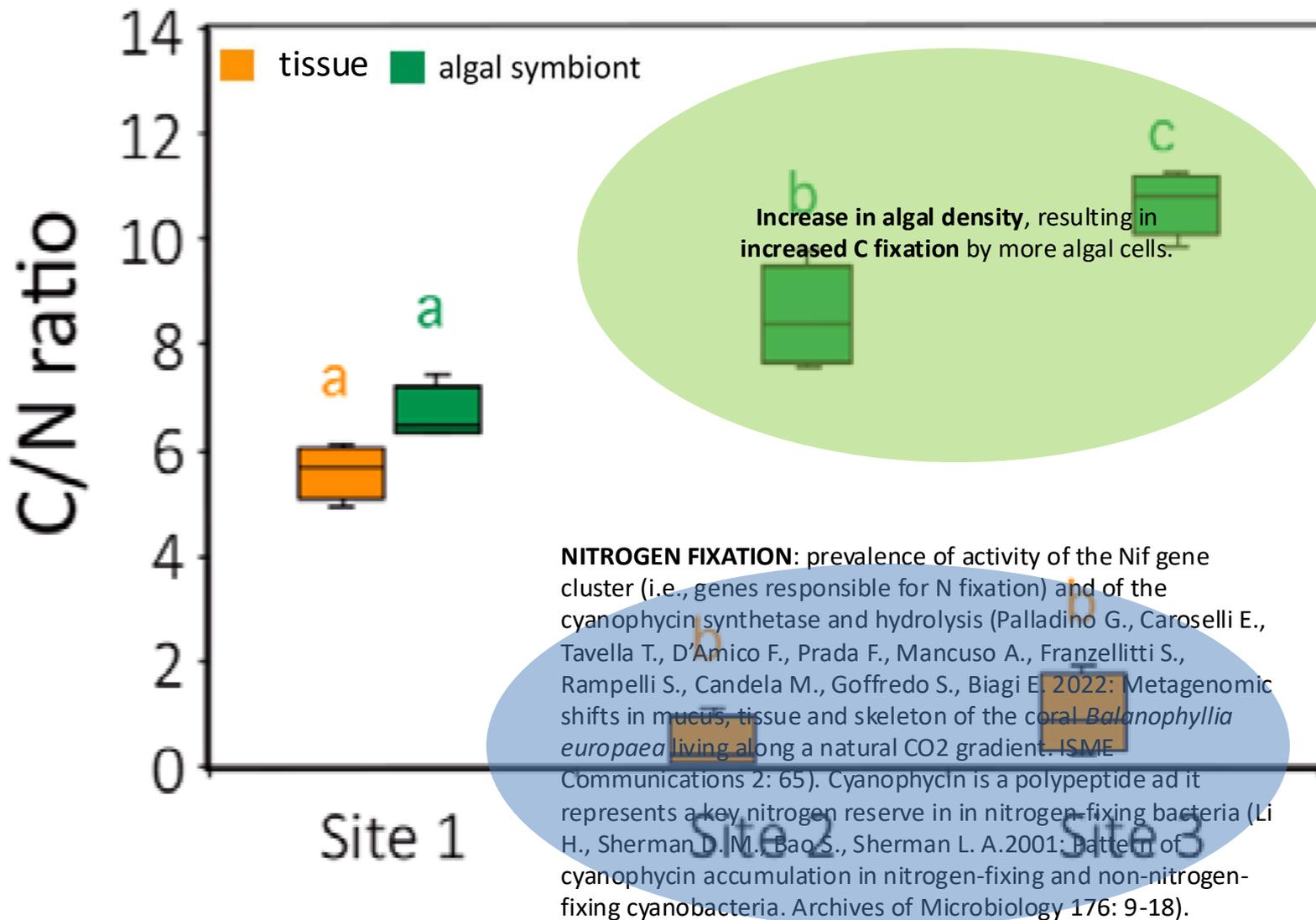
The process is coupled to the hydrolysis of 16 equivalents of ATP and is accompanied by the co-formation of one equivalent of H_2 . In diazotrophs, nitrogenase-generated ammonia is assimilated into glutamate through the glutamine synthetase activity. Glutamine synthetase is an enzyme that catalyzes the formation of the amino acid glutamine, starting from glutamate, ammonia and ATP.

The microbial Nif genes required for nitrogen fixation are widely distributed in diverse environments.

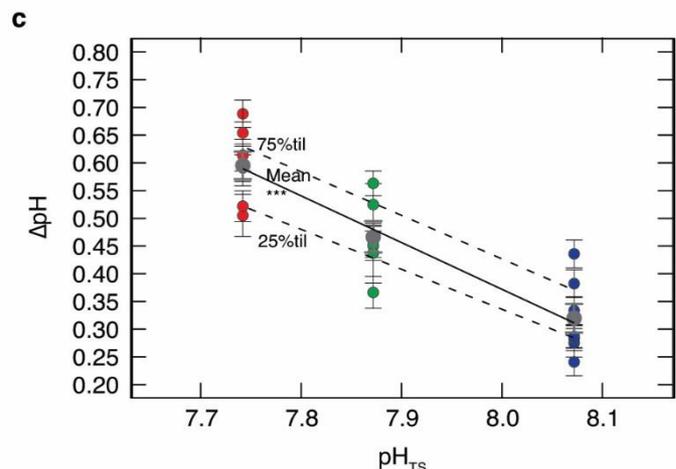
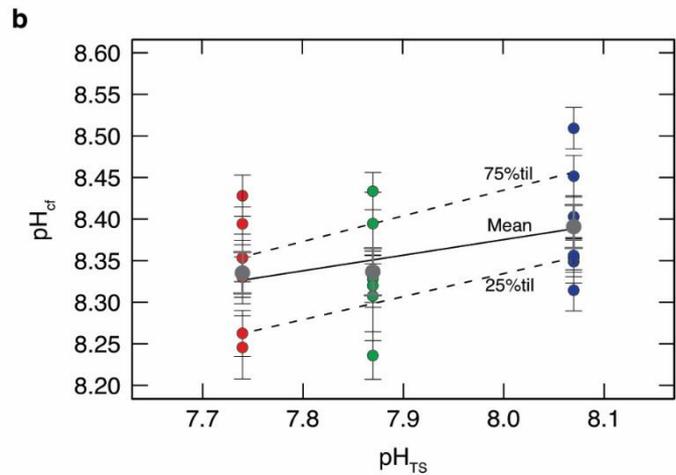
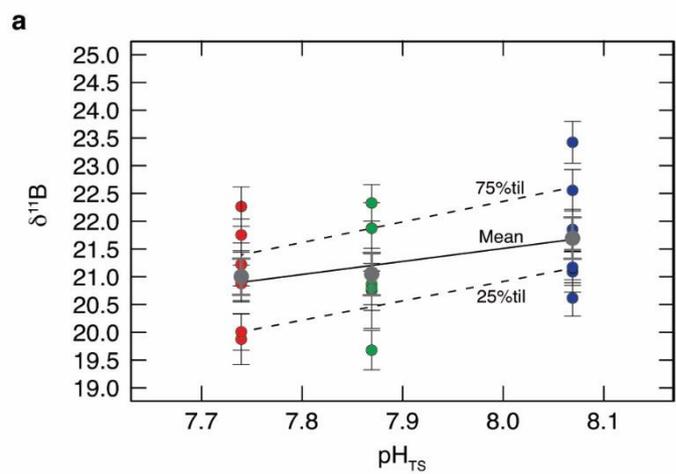
In general, considering atom acquisition in organisms, for every 100 atoms of carbon, roughly 2 to 20 atoms of nitrogen are assimilated. The atomic ratio of carbon (C) : nitrogen (N) : phosphorus (P) observed on average in planktonic biomass was originally described by Alfred Redfield. The Redfield Ratio, the stoichiometric relationship between C:N:P atoms, is 106:16:1



C/N ratios in *B. europaea* tissue and algal symbionts from Sites 1 (control), 2 (intermediate pH) and 3 (low pH). The boxes indicate the 25th and 75th percentiles and the line within the boxes mark the medians. Whisker length is equal to 1.5 × interquartile range (IQR). Different letters indicate statistical differences (p < 0.05) between sites. From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. Communications Biology, submitted.



C/N ratios in *B. europaea* tissue and algal symbionts from Sites 1 (control), 2 (intermediate pH) and 3 (low pH). The boxes indicate the 25th and 75th percentiles and the line within the boxes mark the medians. Whisker length is equal to $1.5 \times$ interquartile range (IQR). Different letters indicate statistical differences ($p < 0.05$) between sites. From: Prada F., Franzellitti S., Caroselli E., Cohen I., Marini M., Campanelli A., Sana L., Mancuso A., Marchini C., Puglisi A., Candela M., Mass T., Tassi F., LaJeunesse T., Dubinsky Z., Falini G., Goffredo S. 2022: Acclimatization of a coral-algal mutualism at a CO₂ vent. Communications Biology, *submitted*.



Boron isotopic signature ($\delta^{11}\text{B}$), $\delta^{11}\text{B}$ -derived internal calcification pH (pH_{cf}) and pH up-regulation intensity (ΔpH) of *Balanophyllia europaea* corals from the CO_2 seeps near Panarea Island, Italy. Data published in: Wall M., Prada F., Fietzke J., Caroselli E., Dubinsky Z., Brizi L., Fantazzini P., Franzellitti S., Mass T., Montagna P., Falini G., Goffredo S. 2019: Linking Internal Carbonate Chemistry Regulation and Calcification in Corals Growing at a Mediterranean CO_2 Vent. *Frontiers in Marine Science* 6: 699. doi: 10.3389/fmars.2019.00699.

(a) $\delta^{11}\text{B}$ values were measured in total 20 *B. europaea* samples collected at three different sites along a natural pH gradient (pH_{TS} in total scale; site 1 = blue, site 2 = green, site 3 = red). From the boron isotopic signature (b) pH_{cf} and (c) ΔpH ($= \text{pH}_{\text{cf}} - \text{pH}_{\text{TS}}$) were calculated. Filled circles and error bars represent individual colony means ± 1 sem per colony. Dark grey filled circles show average per site (\pm sem). Black solid line indicates linear regression and the dashed lines the 25% and 75%-quantile range of the regression.



L'abbassamento della concentrazione dello ione carbonato nell'acqua di mare può sostanzialmente impattare gli organismi calcificanti, come i coralli duri (Scleractinia), abbassando la saturazione dell'acqua di mare relativamente alla mineralogia carbonatica dei loro scheletri (Marubini et al. 2008, *Coral Reefs*, 27: 491-499)

Lo stato di saturazione dell'aragonite è definito come:

$$\Omega_{\text{arag}} = \frac{[\text{Ca}^{2+}] * [\text{CO}_3^{2-}]}{K'_{\text{arag}}}$$

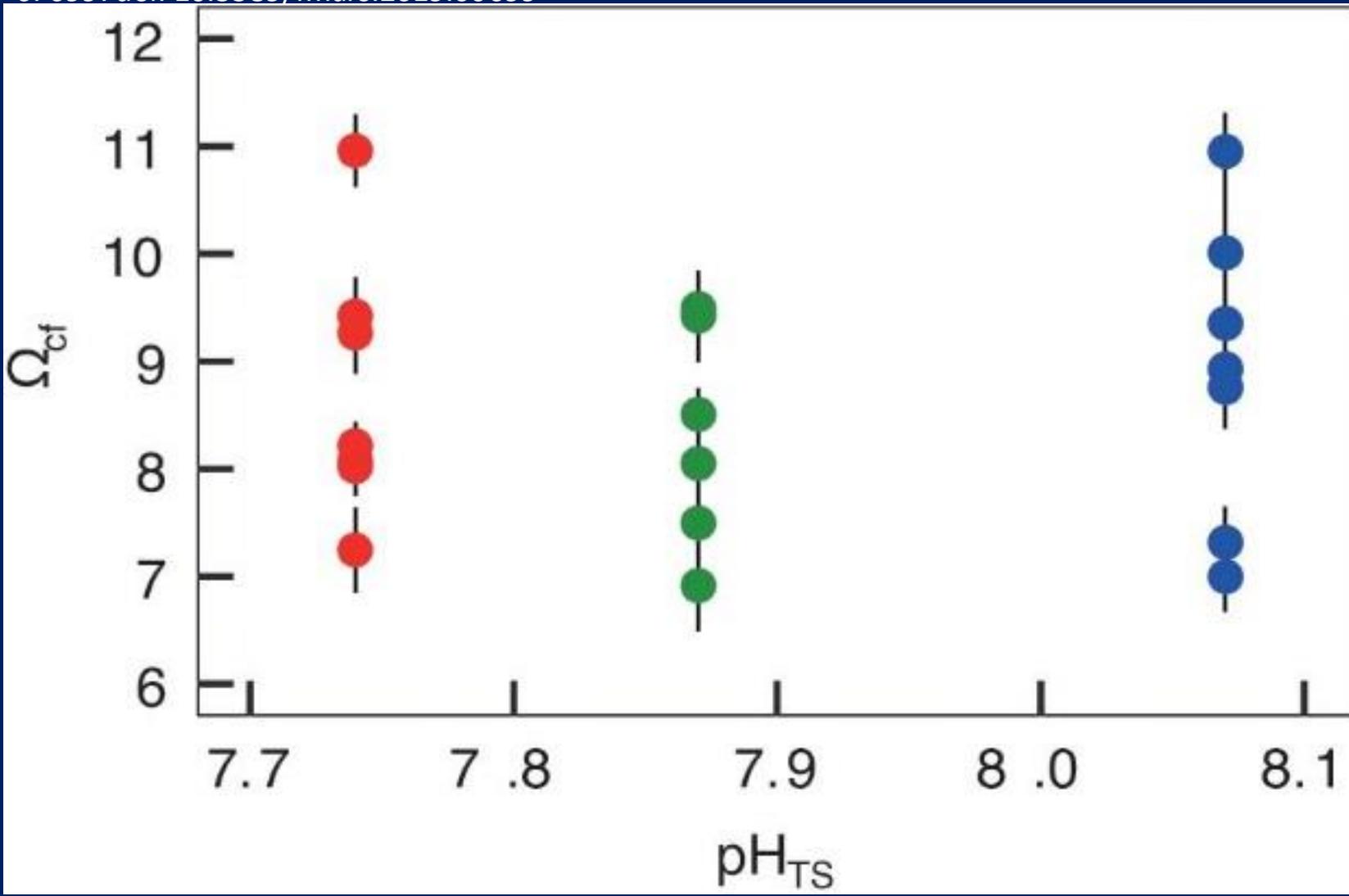
Dove K'_{arag} è il prodotto di solubilità apparente del minerale

Valori di $\Omega_{\text{arag}} > 1$ indicano supersaturazione

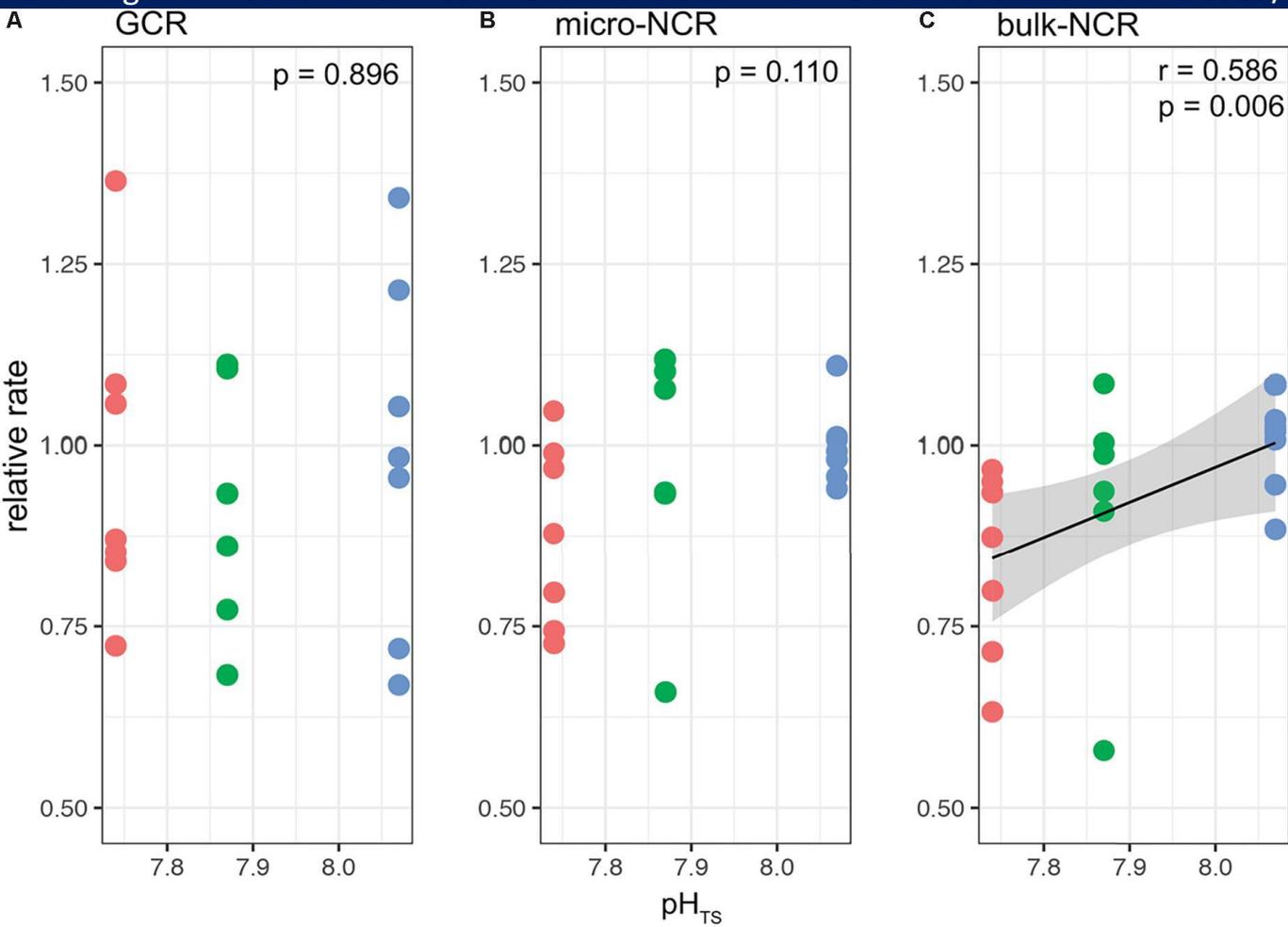
Valori di $\Omega_{\text{arag}} < 1$ indicano sottosaturazione

Siccome $[\text{Ca}^{2+}]$ è circa cento volte maggiore di $[\text{CO}_3^{2-}]$ ed è un elemento conservativo dell'acqua di mare (10 mM nell'acqua di superficie dal Precambriano; Kempe e Kazmierczak 1994, *Bull Inst Oceanogr Monaco*, 13: 61-117; Marubini et al. 2001; *Mar. Ecol. Prog. Ser.*, 220: 153-162), Ω_{arag} è largamente determinato da $[\text{CO}_3^{2-}]$ (Reynaud et al. 2003, *Glob. Change Biol.*, 9: 1660-1668).

Skeletal aragonite saturation state (Ω_{cf}) assessed in *Balanophyllia europaea* corals growing along the pH_{TS} gradient at Panarea Island. Ω_{cf} was calculated from the average internal pH_{cf} of the individual corals and the DIC_{cf} concentration. Circles represent values for each individual coral (mean \pm SEM). Color denotes the different sampling sites: Site 1 = blue, Site 2 = green, Site 3 = red. From: Wall M., Prada F., Fietzke J., Caroselli E., Dubinsky Z., Brizi L., Fantazzini P., Franzellitti S., Mass T., Montagna P., Falini G., Goffredo S. 2019: Linking Internal Carbonate Chemistry Regulation and Calcification in Corals Growing at a Mediterranean CO_2 Vent. *Frontiers in Marine Science* 6: 699. doi: 10.3389/fmars.2019.00699



Modeled gross calcification rates (GCR) and comparisons with measured micro and bulk net calcification rates (NCR) in *Balanophyllia europaea* corals growing along the pH_{TS} gradient at Panarea Island. **(A)** GCRs were calculated following the IpHRAC model (McCulloch et al., 2012a) (internal pH regulation and abiotic calcification): Gross calcification = $k \times (\Omega_{\text{cf}} - 1)^n$ and presented as relative rates (setting average control growth as 1). **(B)** micro-NCR and **(C)** bulk-NCR were derived from micro-density, bulk density and linear extension rates taken from Fantazzini et al. (2015). Circles represent values for each individual coral. Color denotes the different locations: Site 1 = blue, Site 2 = green, Site 3 = red. Black dashed line indicates linear regression and the gray area the 95%-CI band of the significant regression ($p < 0.01$; $N = 7$ for Sites 1 and 3, and $N = 6$ for Site 2). From: Wall M., Prada F., Fietzke J., Caroselli E., Dubinsky Z., Brizi L., Fantazzini P., Franzellitti S., Mass T., Montagna P., Falini G., Goffredo S. 2019: Linking Internal Carbonate Chemistry Regulation and Calcification in Corals Growing at a Mediterranean CO₂ Vent. *Frontiers in Marine Science* 6: 699. doi: 10.3389/fmars.2019.00699



Perché la net calcification cala nei siti più acidificati?

$$\begin{array}{l} \text{Net calcification} \\ \text{rate} \\ (\text{mg mm}^{-2} \text{ yr}^{-1}) \end{array} = \begin{array}{l} \text{linear} \\ \text{extension rate} \\ (\text{mm yr}^{-1}) \end{array} \times \begin{array}{l} \text{skeletal} \\ \text{bulk density} \\ (\text{mg mm}^{-3}) \end{array}$$

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

$$\text{Net calcification rate} = \text{Gross calcification rate} - \text{Dissolution rate}$$

(mg mm⁻² yr⁻¹) (mg mm⁻² yr⁻¹) (mg mm⁻² yr⁻¹)

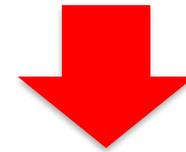
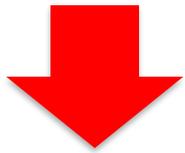
From: Rodolfo-Metalpa R., Houlbrèque F., Tambutté É. 3 et al. (2011) Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nature Climate Change* 1: 308–312

$$\text{Net calcification rate} = \text{linear extension rate} \times \text{skeletal bulk density}$$

(mg mm⁻² yr⁻¹) (mm yr⁻¹) (mg mm⁻³)

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:



**Net calcification
rate**



**linear
extension rate**



**skeletal
bulk density**

(mg mm⁻² yr⁻¹)

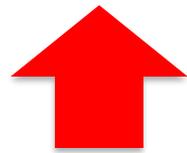
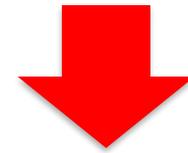
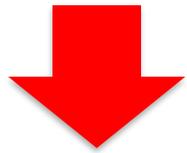
(mm yr⁻¹)

(mg mm⁻³)

Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

With increasing pCO₂:



**Net calcification
rate**



**linear
extension rate**



skeletal bulk density **porosity**

(mg mm⁻² yr⁻¹)

(mm yr⁻¹)

(mg mm⁻³)

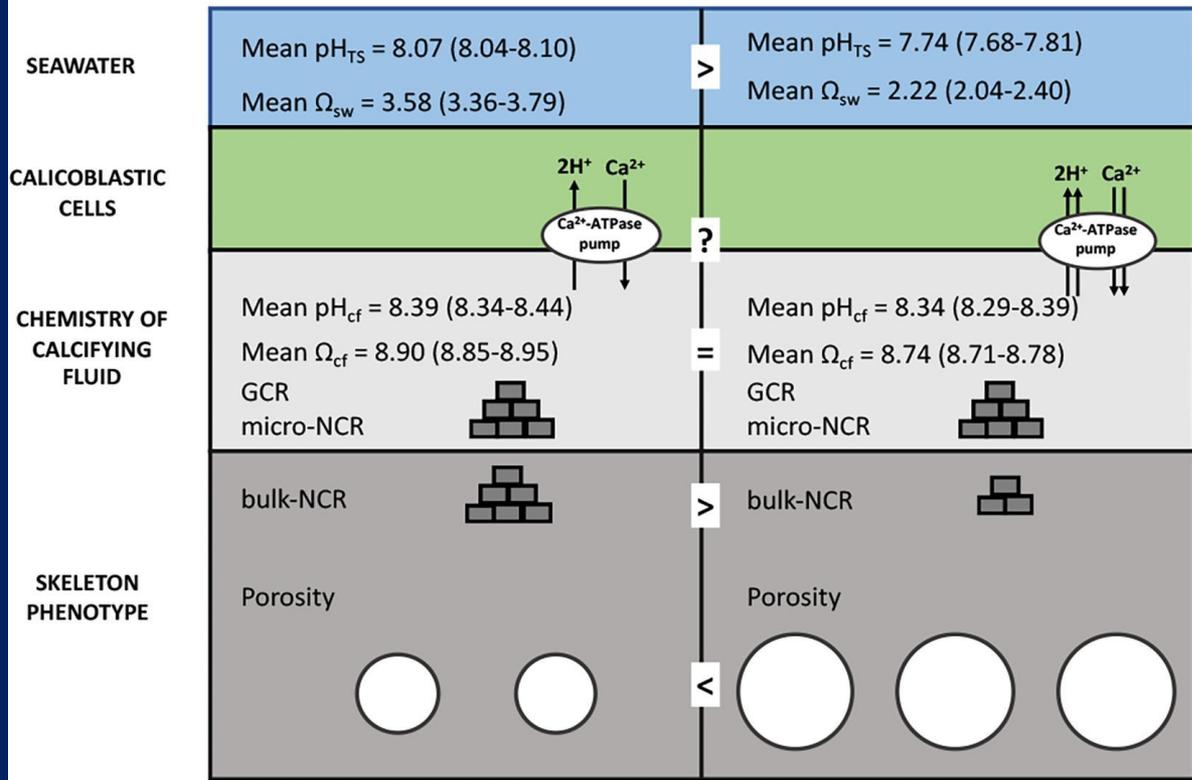
Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

Lough and Barnes, 2000, *Journal of Experimental Marine Biology and Ecology*, 245: 225–243; Carricart-Ganivet, 2004, *Journal of Experimental Marine Biology and Ecology*, 302: 249–260

Perché aumenta la porosità nei siti più acidificati? / Come si forma la porosità/il poro?

Present day seawater chemistry
(Site 1 at Panarea)

2100 IPCC projected seawater chemistry
(Site 3 at Panarea)



Schematic summary showing the hypothesized impacts of life-long acclimation to low pH on skeletal growth in *Balanophyllia europaea* along the gradient of Panarea. At the current seawater pH (Site 1), *B. europaea* up-regulates pH and carbonate chemistry of the calcifying fluid compared to seawater levels. At low pH_{TS} as those projected for 2100 (Site 3), seawater acidification did not significantly affect pH_{cf} and DIC_{cf} showing comparable values to those of Site 1. Under these conditions, the bio-inorganic model projects no changes of aragonite saturation state (Ω_{cf}), thus unmodified GCR and micro-NCR, compared to present-day conditions (Site 1), suggesting that *B. europaea* performs an effective biological control over the calcification process. Nevertheless, with increased energy expenditure which is likely needed to maintain calcification, *B. europaea* changes its skeleton phenotype to a morphology characterized by decreased bulk density and increased porosity at the macro-scale, and reduced (measured) bulk-NCR, while maintaining unchanged linear extension rates (Fantazzini et al., 2015). No increases in production of organic matrix proteins (OM) per unit mass of $CaCO_3$ are observed (Fabry et al., 2008). We postulate a tradeoff in energetic balance in which internal carbonate chemistry is homeostatically compensated at the expenses of calcicoblastic cell and organic matrix functioning/organization and macro-scale skeleton structure to maintained coral growth (i.e., linear extension rates) and the reproductive output (Andersson and Mackenzie, 2012; Fantazzini et al., 2015). From: Wall M., Prada F., Fietzke J., Caroselli E., Dubinsky Z., Brizi L., Fantazzini P., Franzellitti S., Mass T., Montagna P., Falini G., Goffredo S. 2019: Linking Internal Carbonate Chemistry Regulation and Calcification in Corals Growing at a Mediterranean CO₂ Vent. *Frontiers in Marine Science* 6: 699. doi: 10.3389/fmars.2019.00699



Conclusions

Comparison between zoox and non-zoox temperate corals under climate change stresses (↓ negative effects; = no effects)

	ZOOXANTHELATE CORALS	NON-ZOOXANTHELATE CORALS
Temperature gradient - long term	↓	=
pH gradient - short term CO ₂ exposure	=	↓
pH gradient - long term CO ₂ exposure	↓	?

