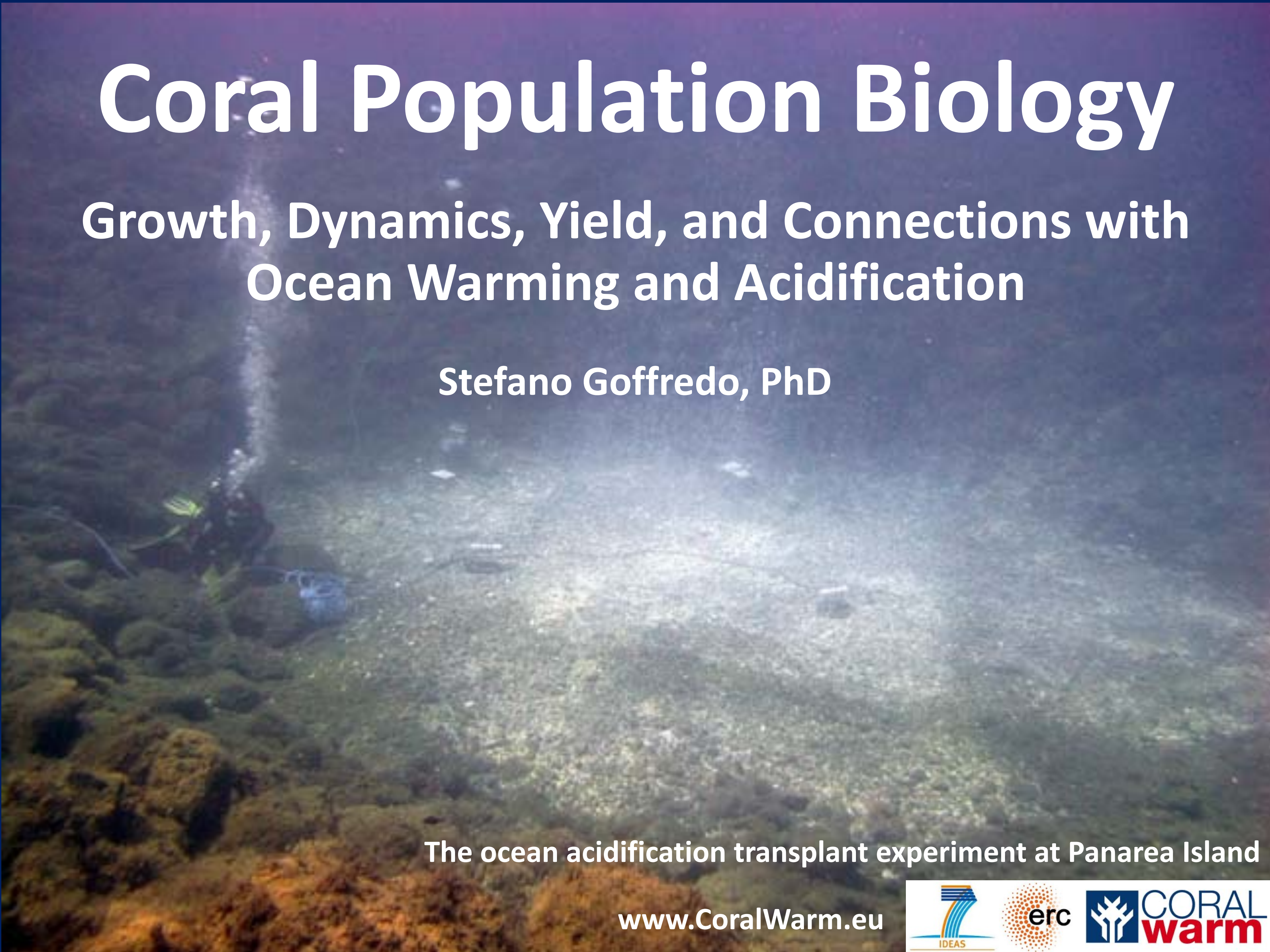
Coral Population Biology

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

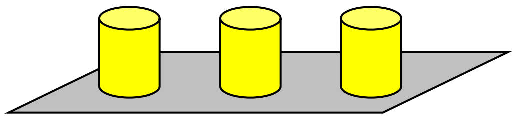
Stefano Goffredo, PhD



Ecological modes in corals

Growth types

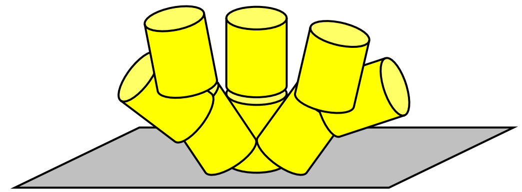
Solitary



Single modules living separated

one from each other

Colonial

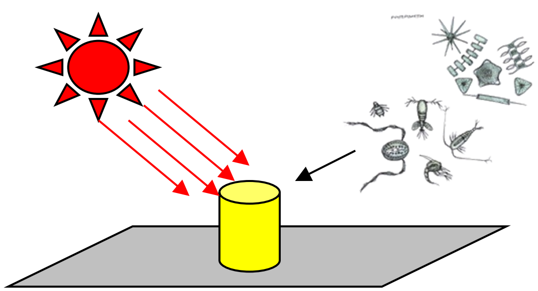


Multiple cloned modules living in close connection

(physical and physiological) one to each other

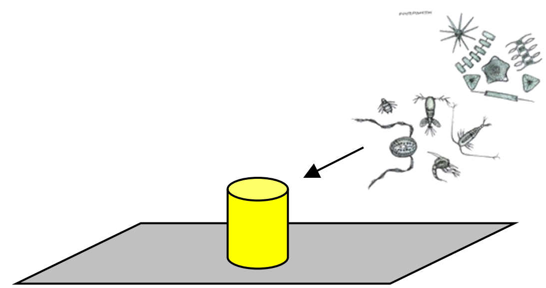
Energetic supplying types

Zooxanthellate



Nourishment from symbiont photosynthesis and from zooplankton capture

Non-zooxanthellate

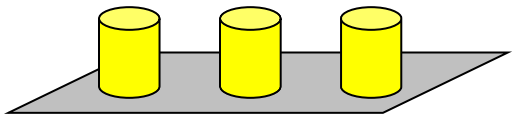


Nourishment only from zooplankton capture

Ecological modes in corals

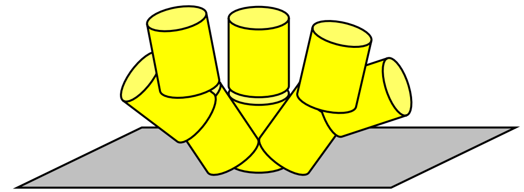
Growth types

Solitary



Single modules living separated one from each other

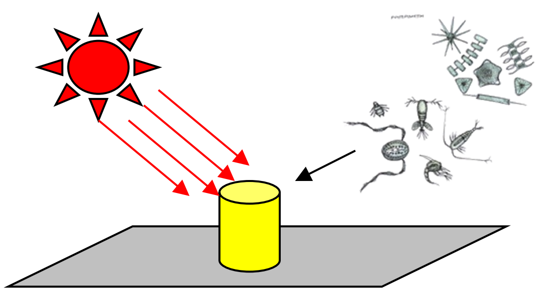
Colonial



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

Energetic supplying types

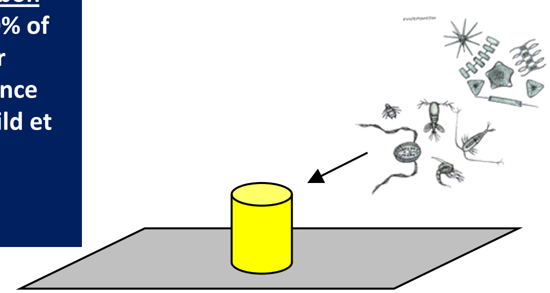
Zooxanthellate



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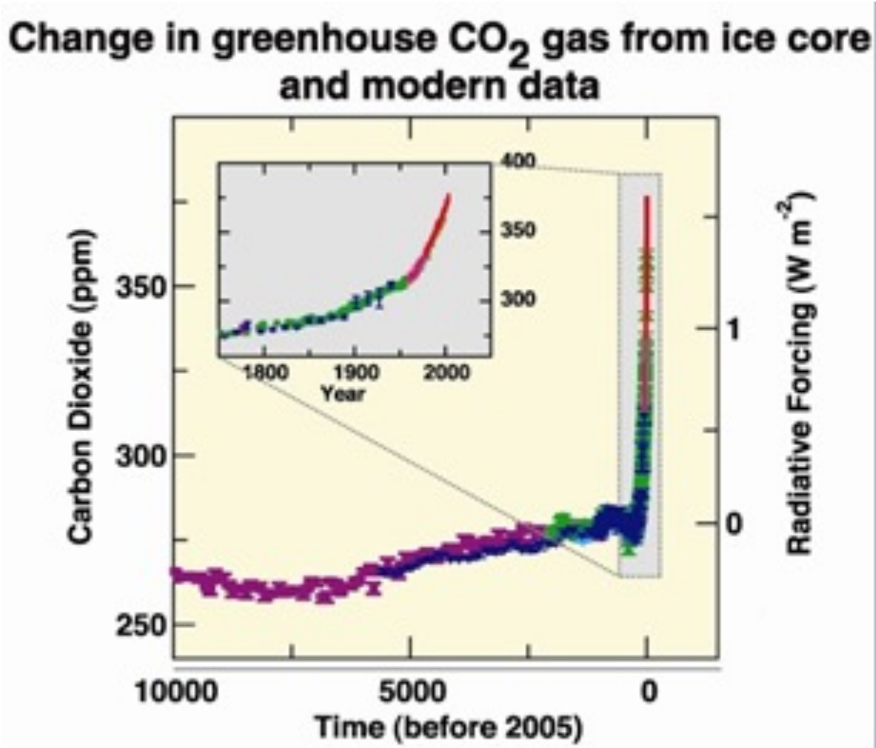
Stefano Goffredo,
Marine Science Group, Department of
Evolutionary and Experimental Biology

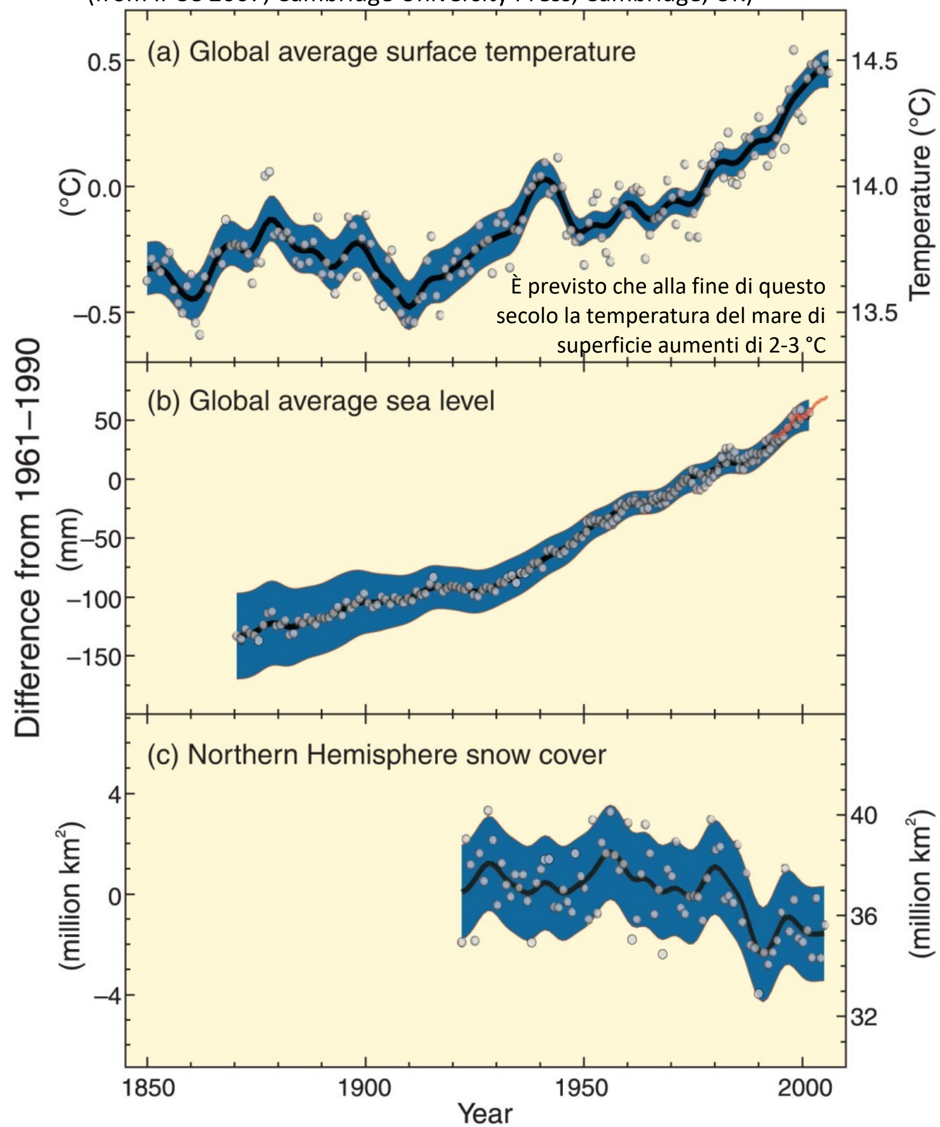
Giuseppe Falini,
Department of Chemistry "G. Ciamician"

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 CO_2 così rapido come quello di oggi non si è mai verificato nel corso dei tempi geologici (Pandolfi et al. 2011, *Science*, 333: 418-422).



"Atmospheric concentration of CO_2 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)

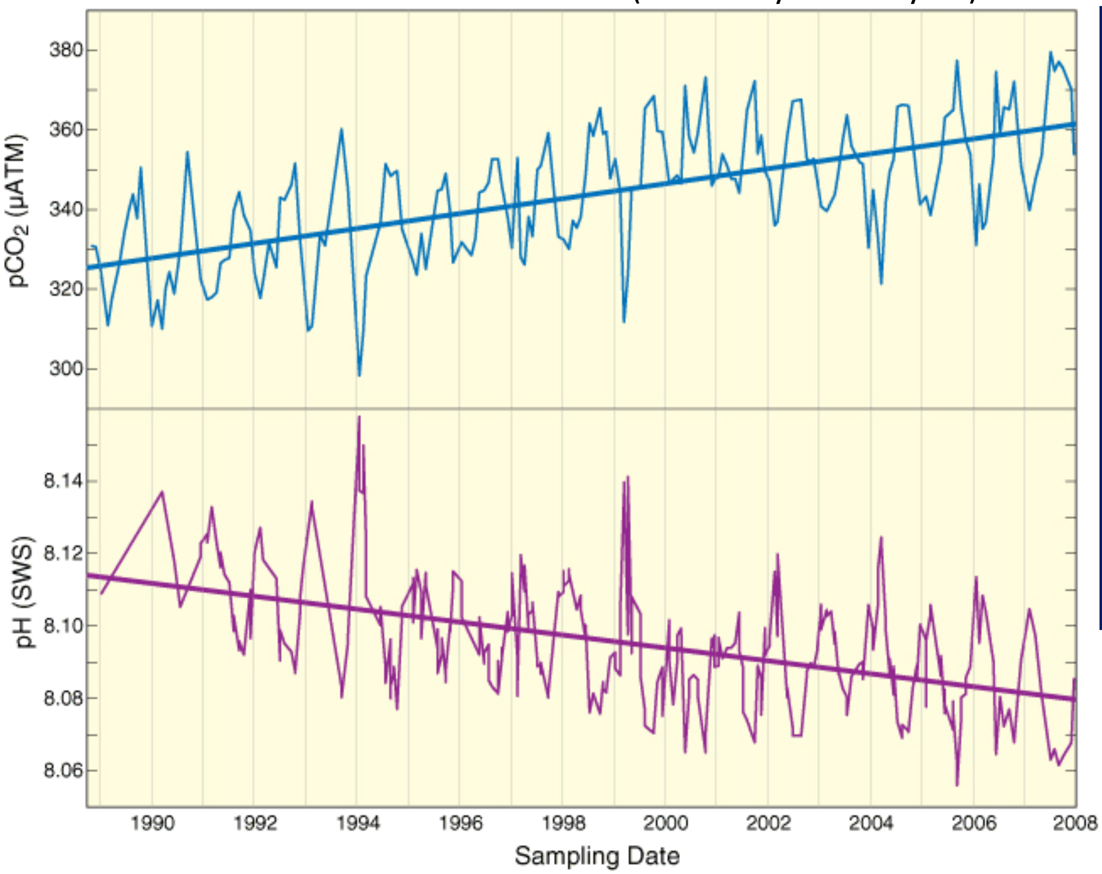


THE OCEAN ACIDIFICATION

Il 25% della CO_2 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 CO_2 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) .

$$CO_2 + H_2O \Rightarrow HCO_3^- + H^+$$

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

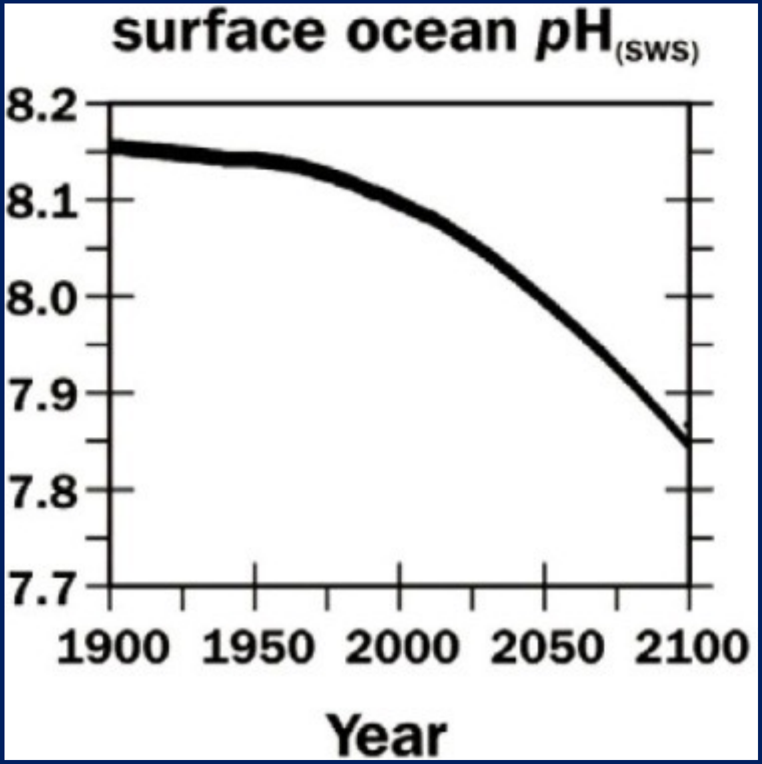
"We are changing ocean chemistry too much too fast "(Caldeira, 2007, *Oceanography*, 20: 188-195)

*p*H

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)



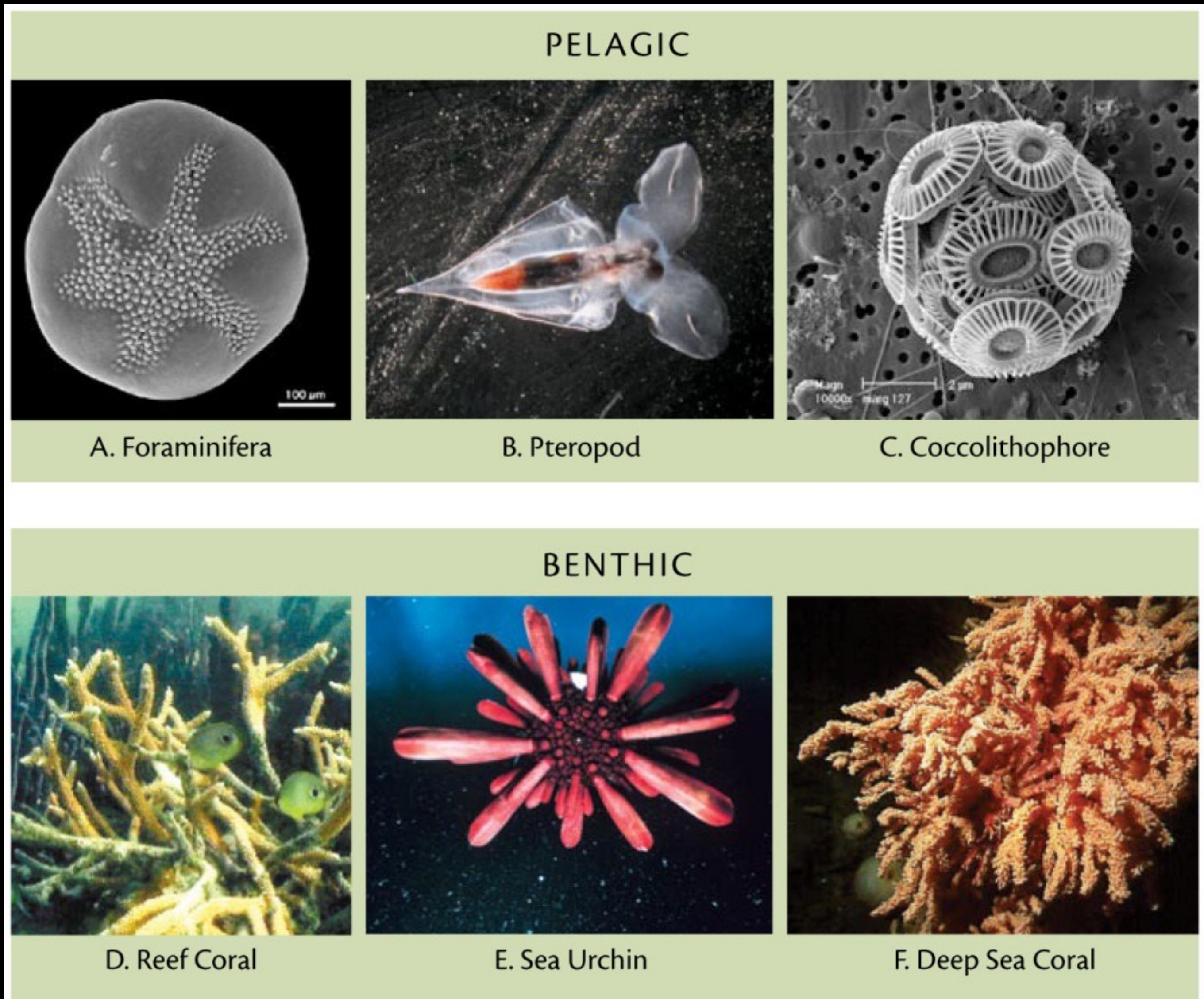
Change of H^+ concentration

+ 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



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

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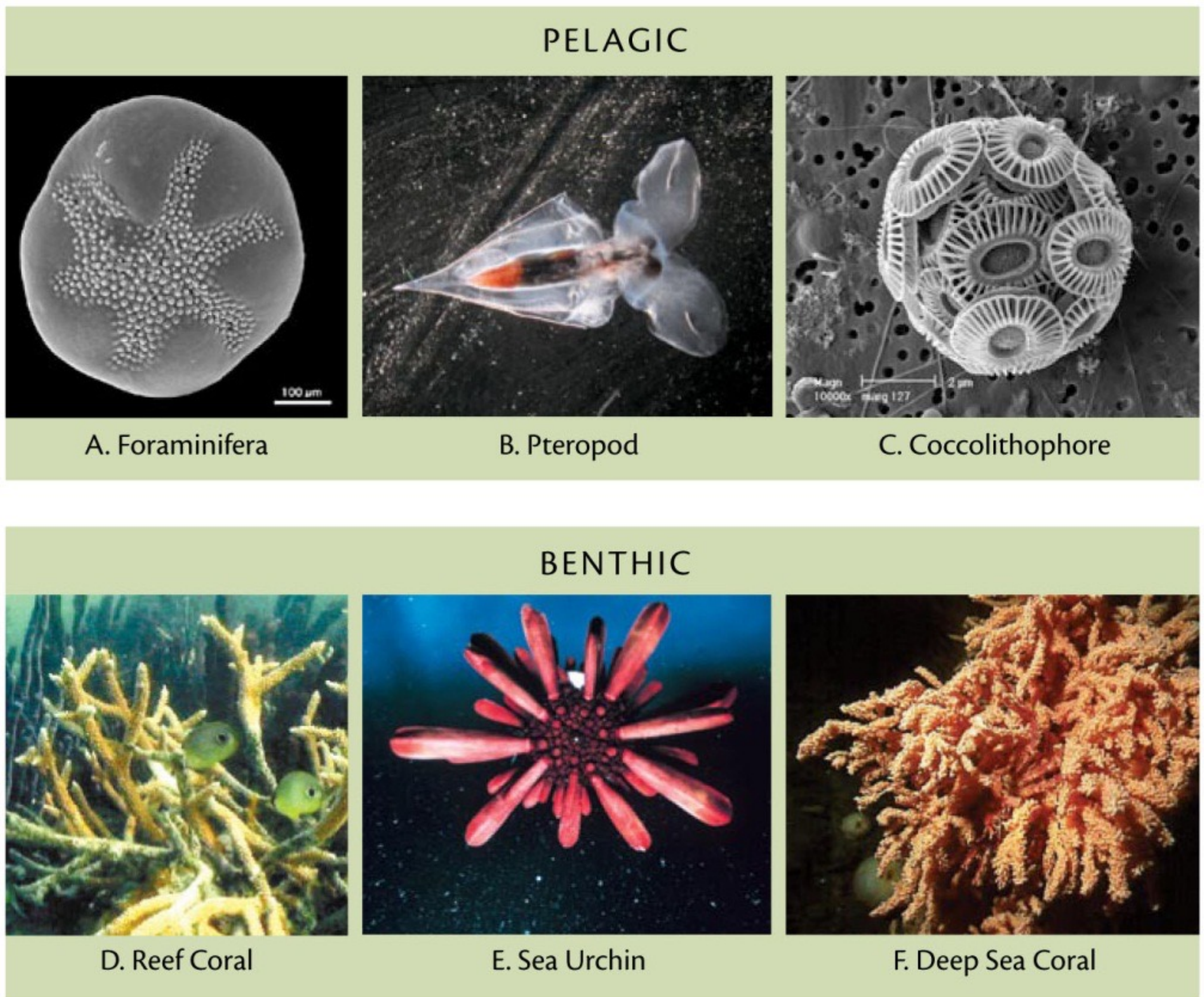

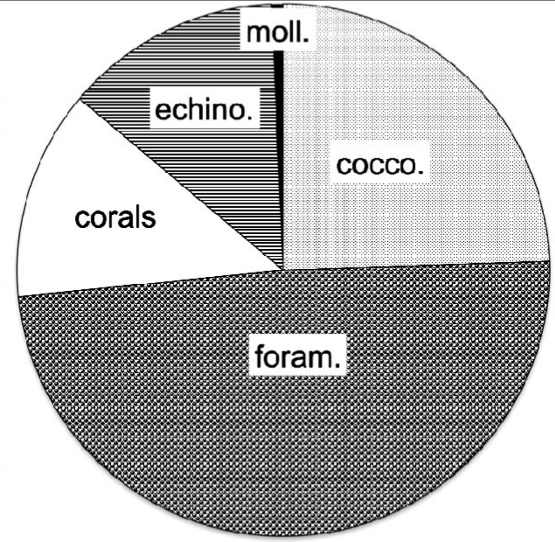

Calcium carbonate global production by the major marine calcifiers (Tambutté et al. 2011, *J. Exp. Mar. Biol. Ecol.*, 408: 58–78).

Coccolithophores: 1.6 Gt $CaCO_3$ yr^{-1}; foraminifera: 1.3–3.2 Gt $CaCO_3$ yr^{-1}; coral reefs: 0.65–0.83 Gt $CaCO_3$ yr^{-1}; molluscs: 0.047 Gt $CaCO_3$ yr^{-1}; echinoderms: 0.86 Gt $CaCO_3$ yr^{-1}

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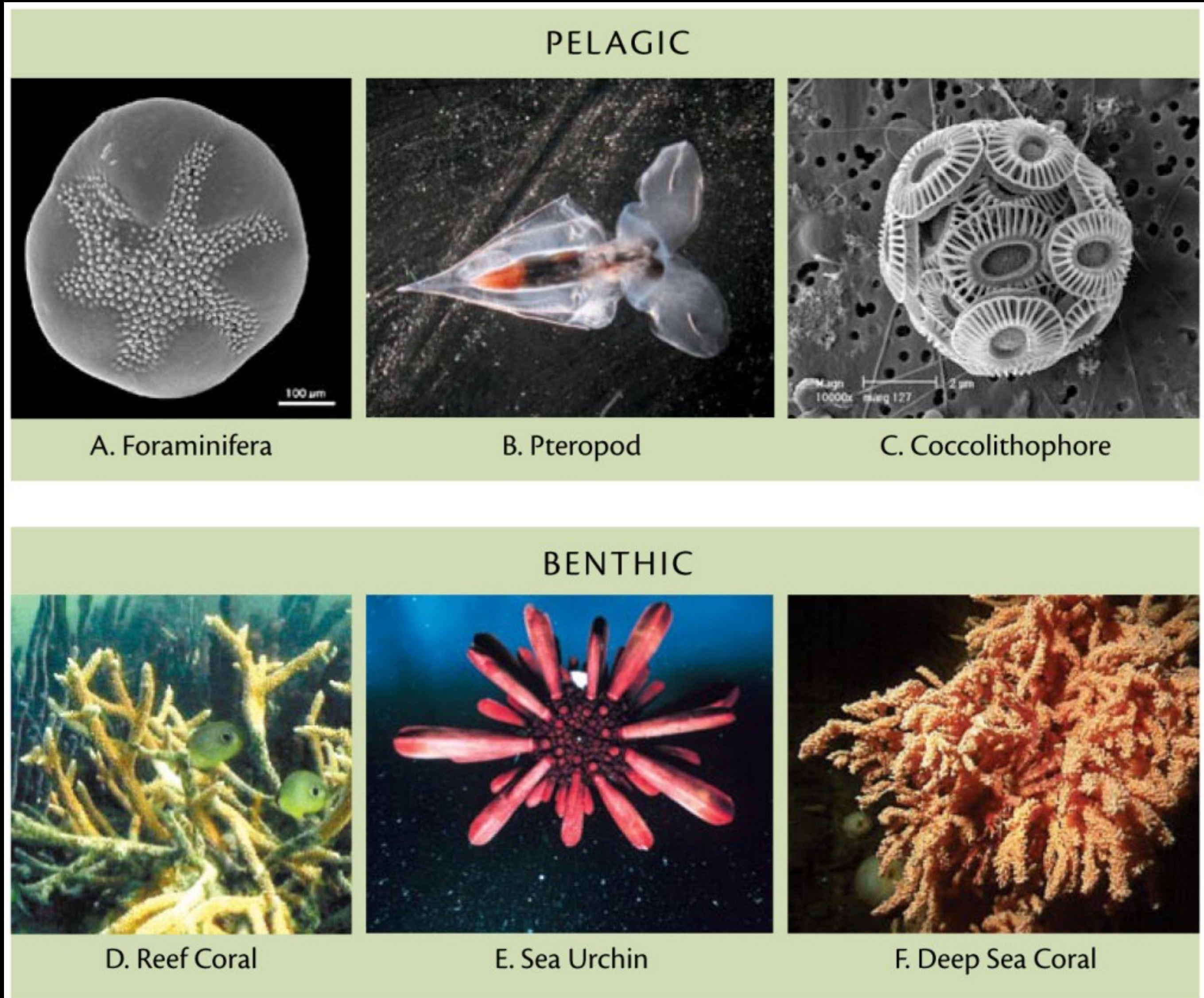

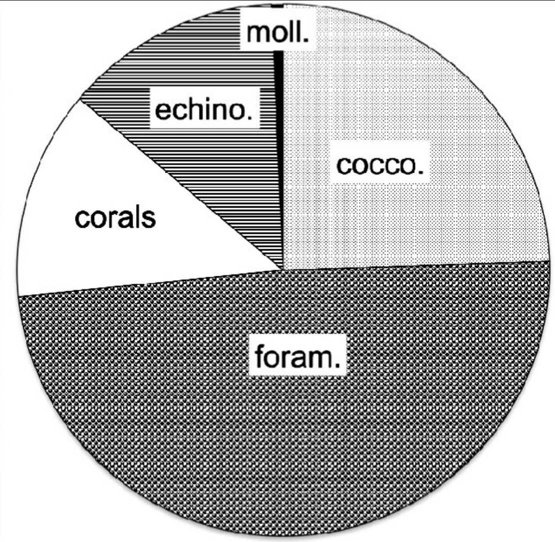

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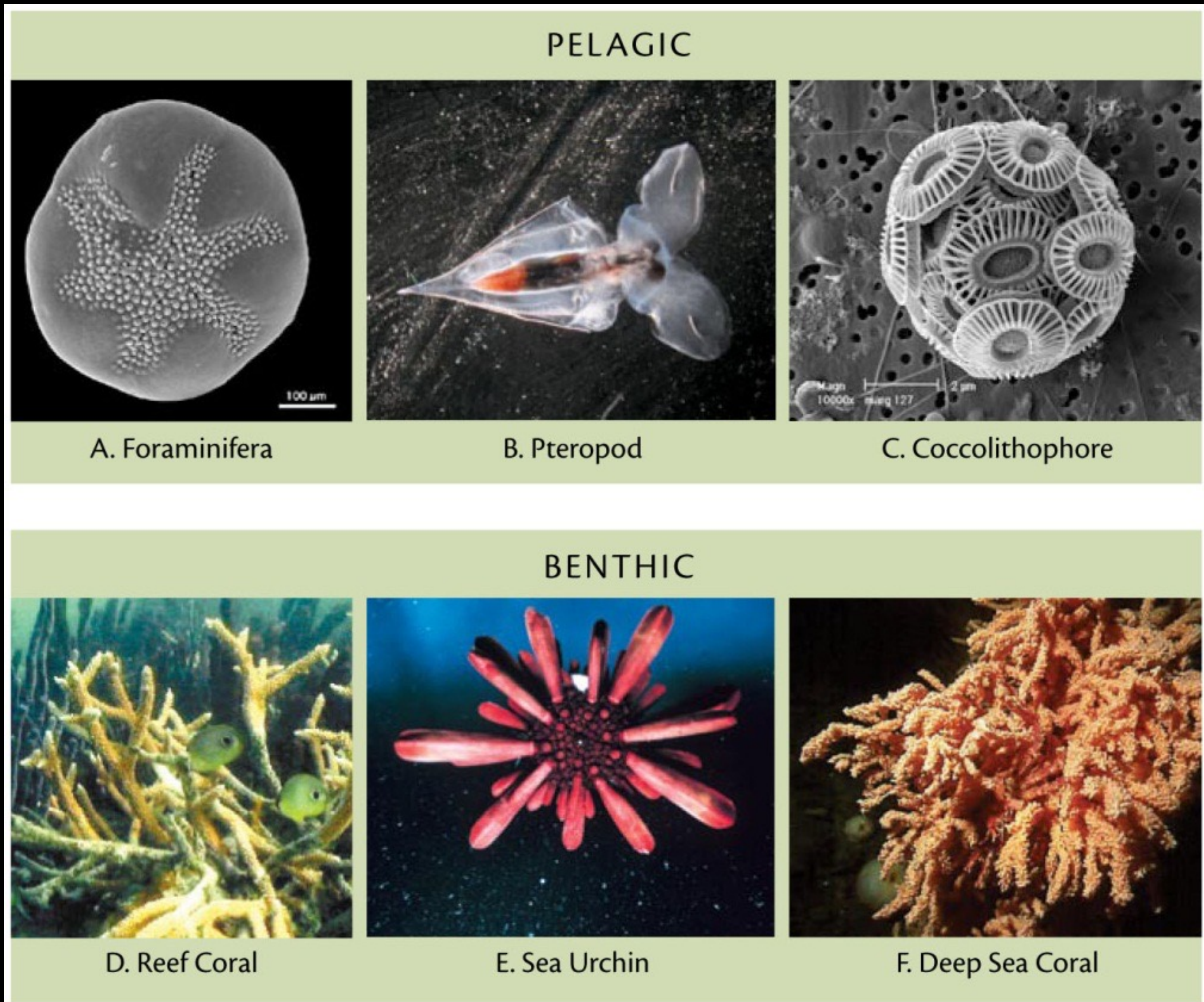
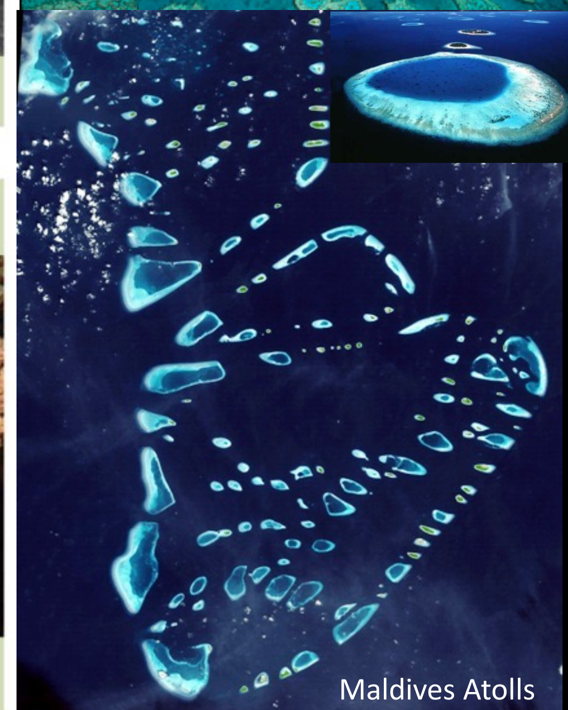
Totale: 5.2 miliardi di tonnellate di $CaCo_3$ per anno

Calcifiers may be particularly threatened by ocean acidification





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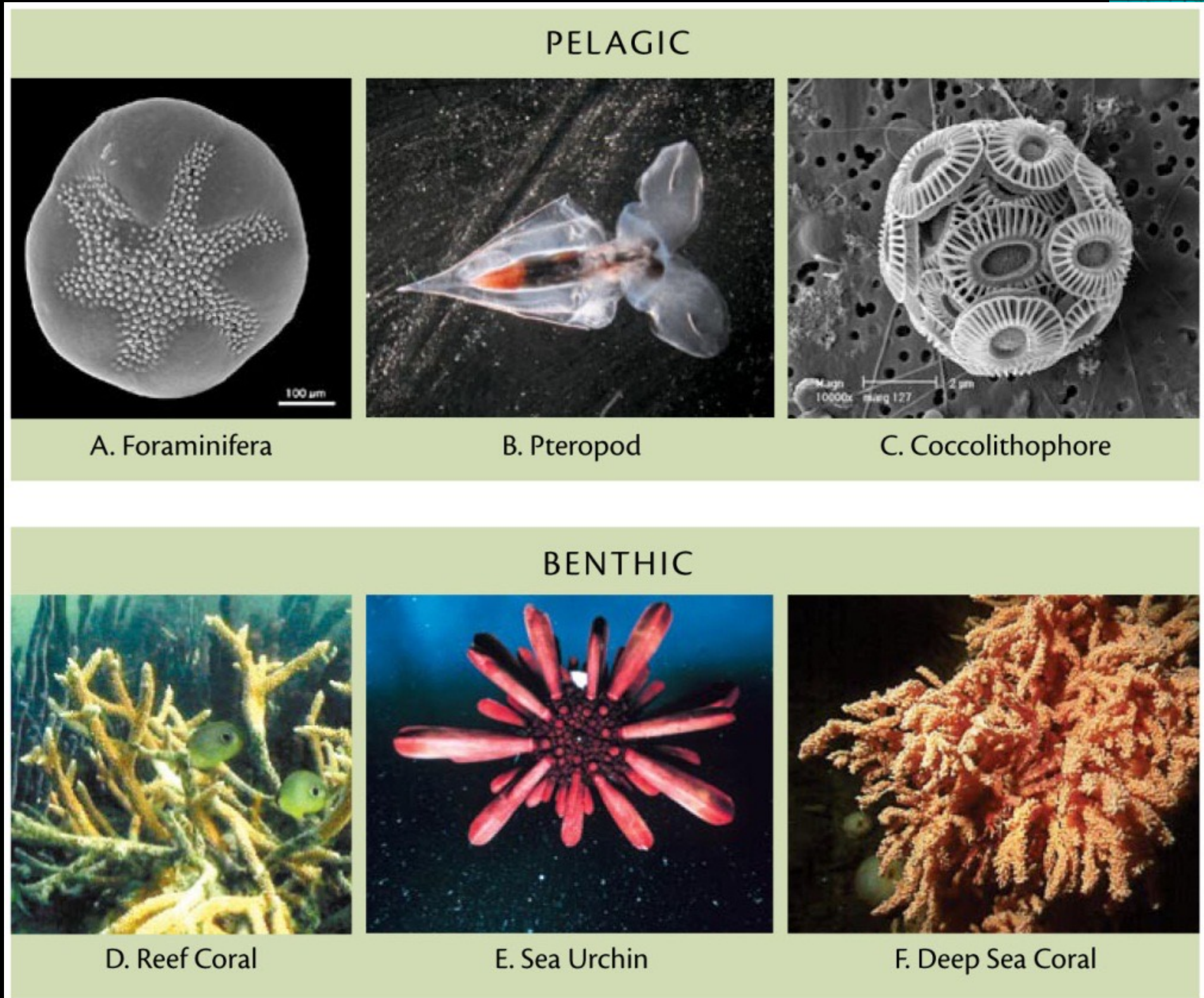
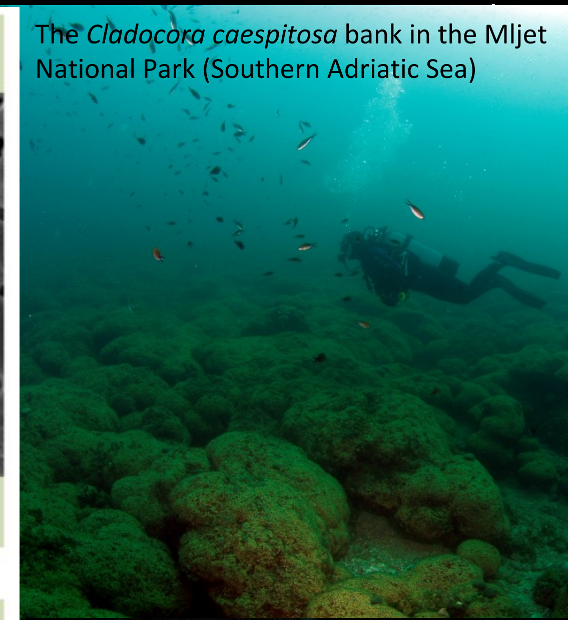
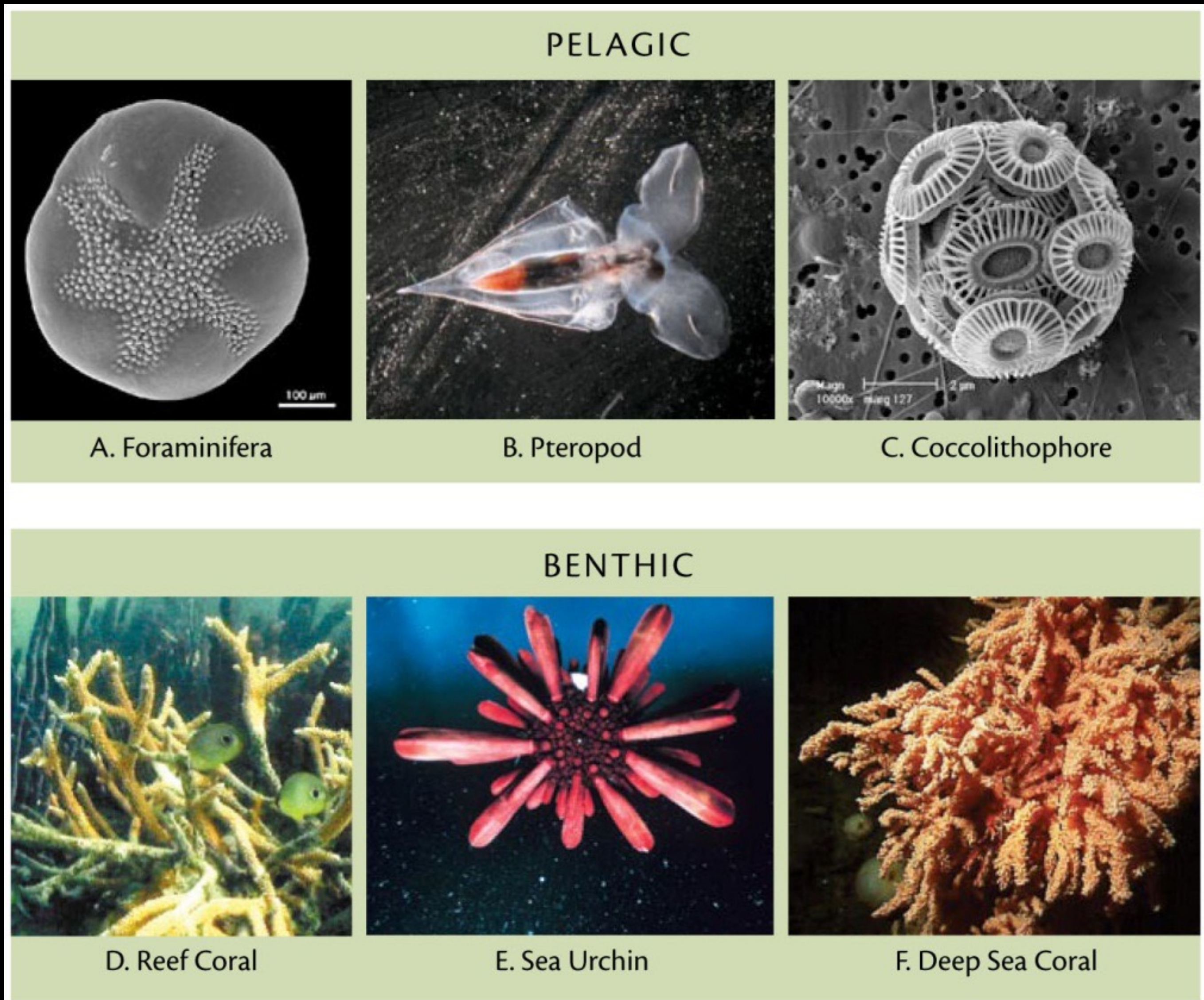




The *Cladocora caespitosa* bank in the Mljet National Park (Southern Adriatic Sea)

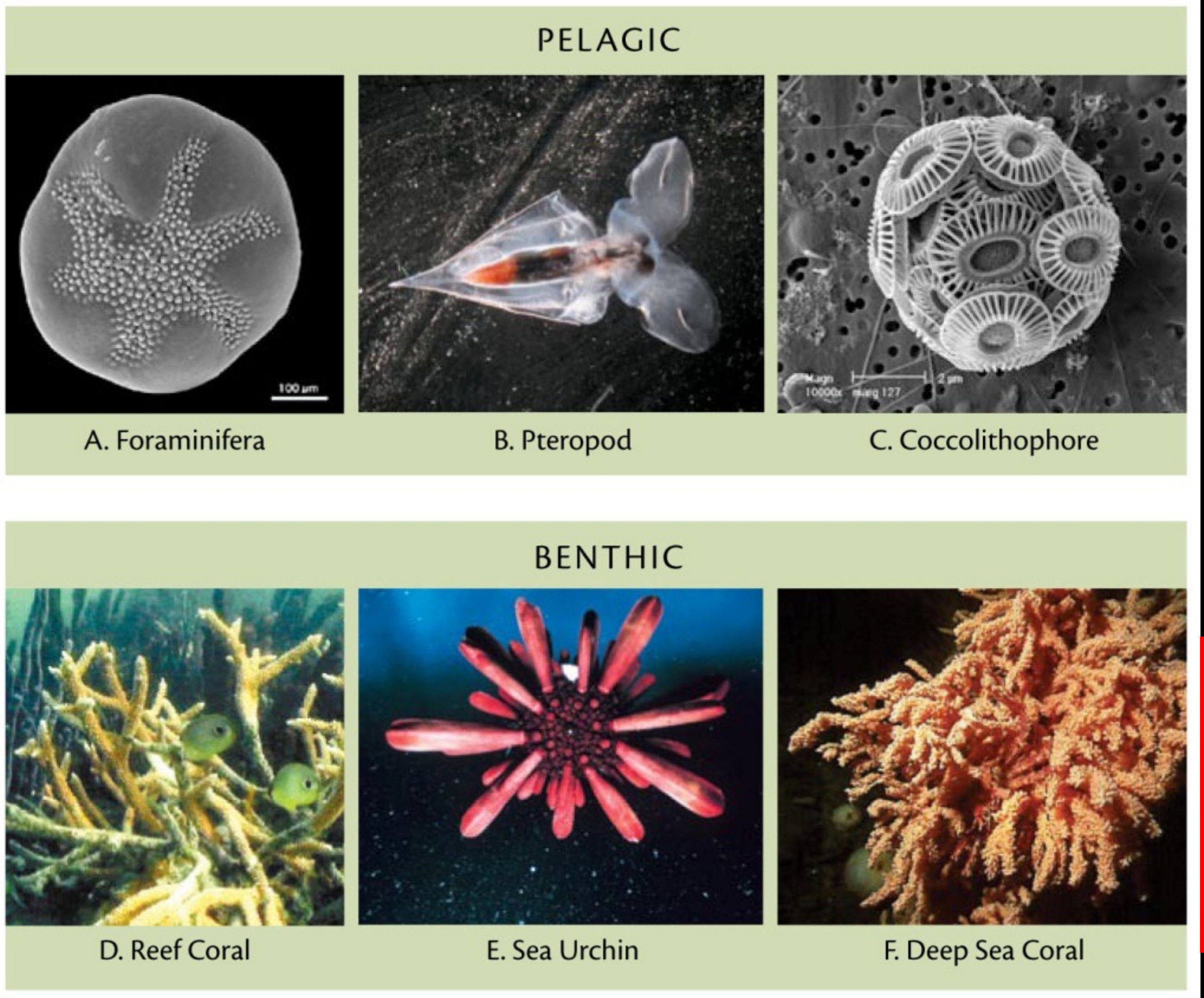
Reef built by the cold water coral *Lophelia pertusa*, off the coast of Norway

Calcifiers may be particularly threatened by ocean acidification



Le Dolomiti nelle Alpi Orientali

Calcifiers may be particularly threatened by ocean acidification



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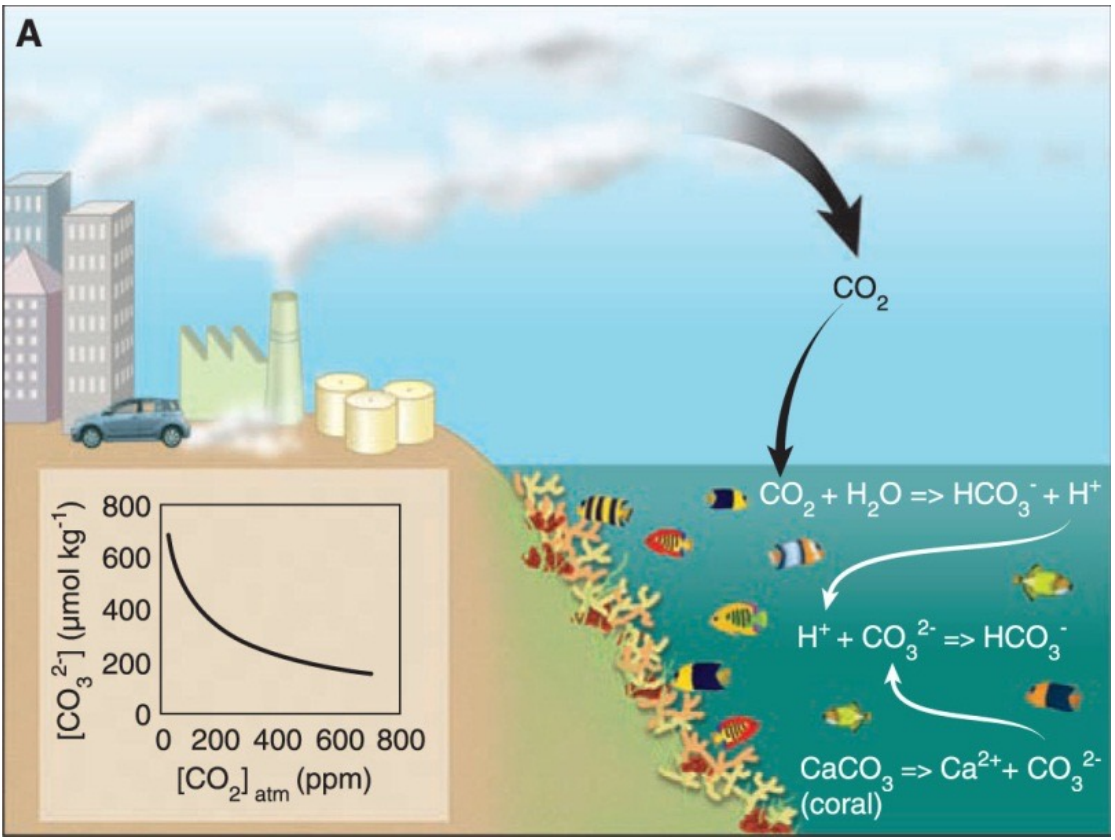
Acidification determines two potential problems to calcifying organisms: **dissolution** of calcium carbonate , and the **non-precipitation** of new calcium carbonate

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

pH ↓ $[CO_3^{2-}]$ ↓



"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:

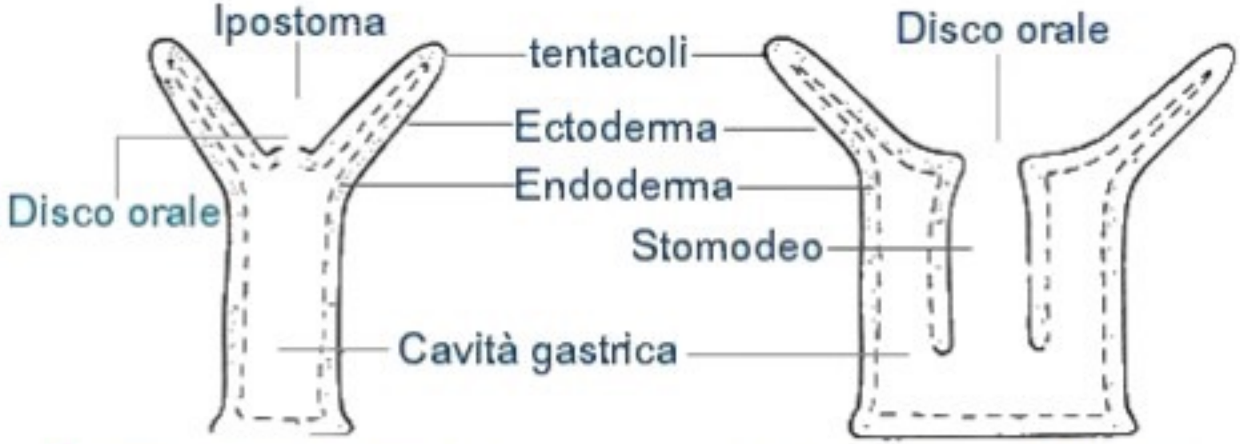
$$\Omega_{arag} = \frac{[Ca^{2+}]*[CO_3^{\ 2-}]}{K'_{arag}}$$

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

Valori di Ω_{arag} > 1 indicano **supersaturazione**

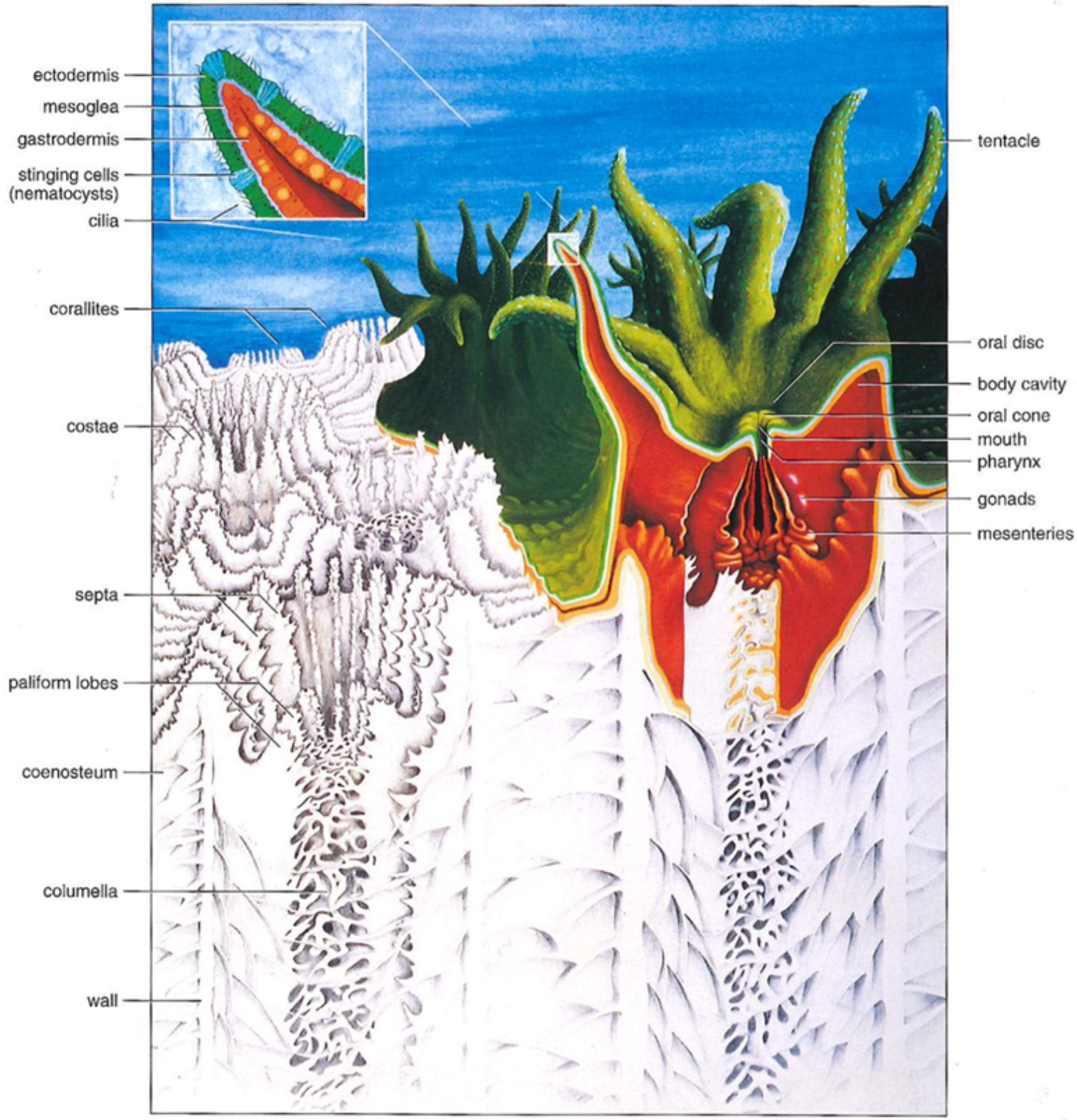
Valori di Ω_{arag} < 1 indicano **sottosaturazione**

Siccome $[Ca^{2+}]$ è circa cento volte maggiore di $[CO_3^{2-}]$ 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 $[CO_3^{2-}]$ (Reynaud et al. 2003, *Glob. Change Biol.*, 9: 1660-1668).

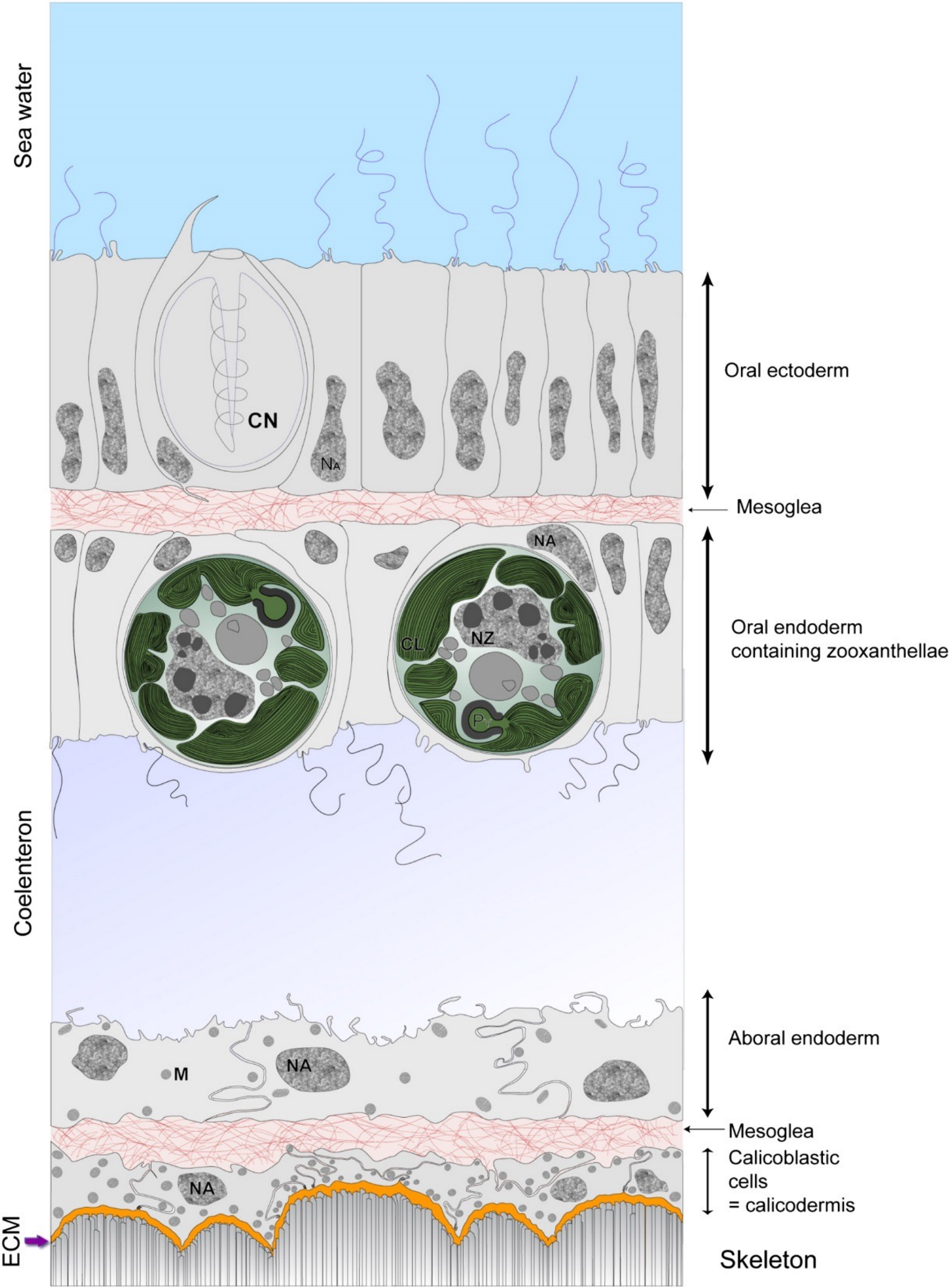


Polipo Classe Hydrozoa

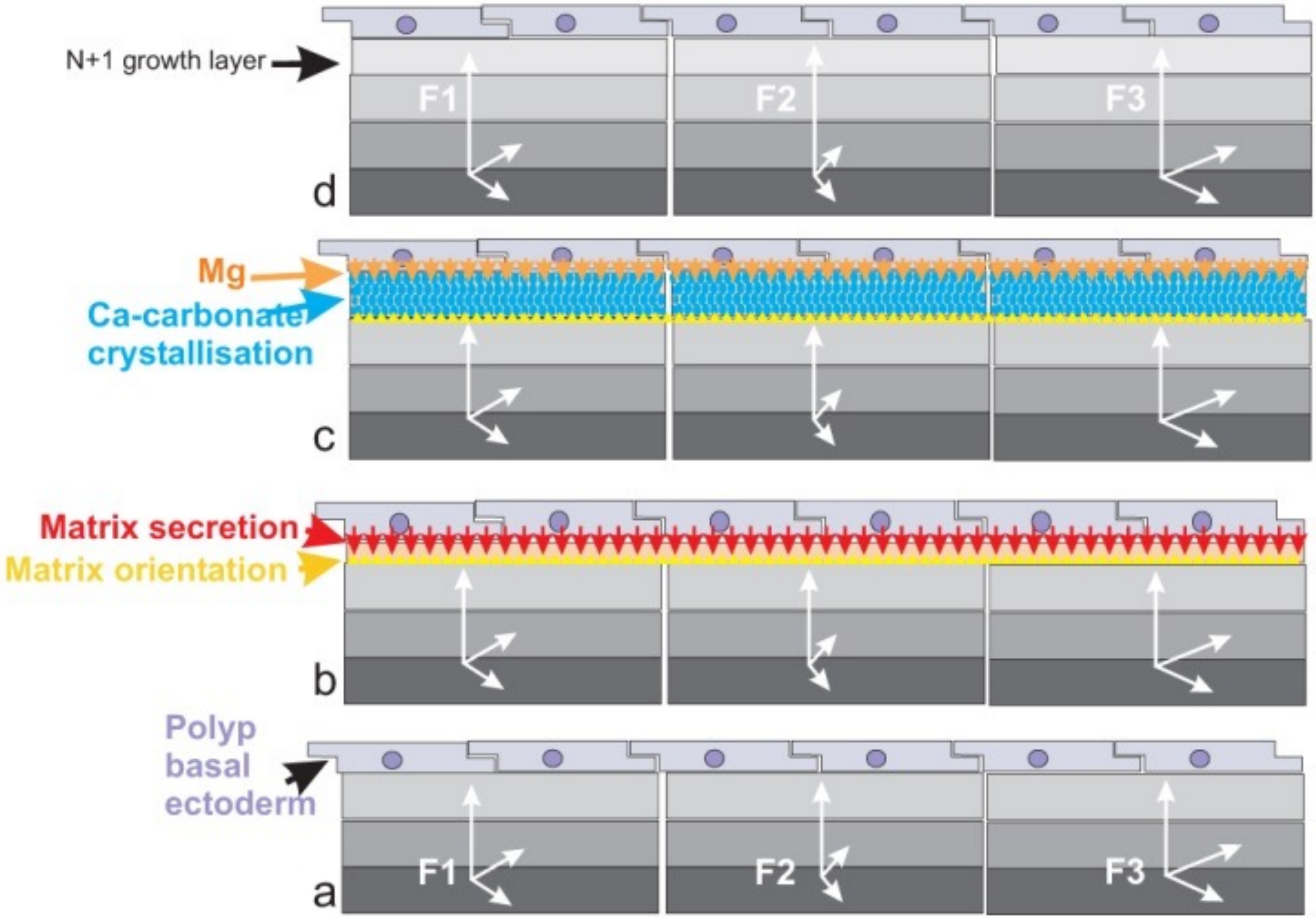
Polipo Classe Anthozoa



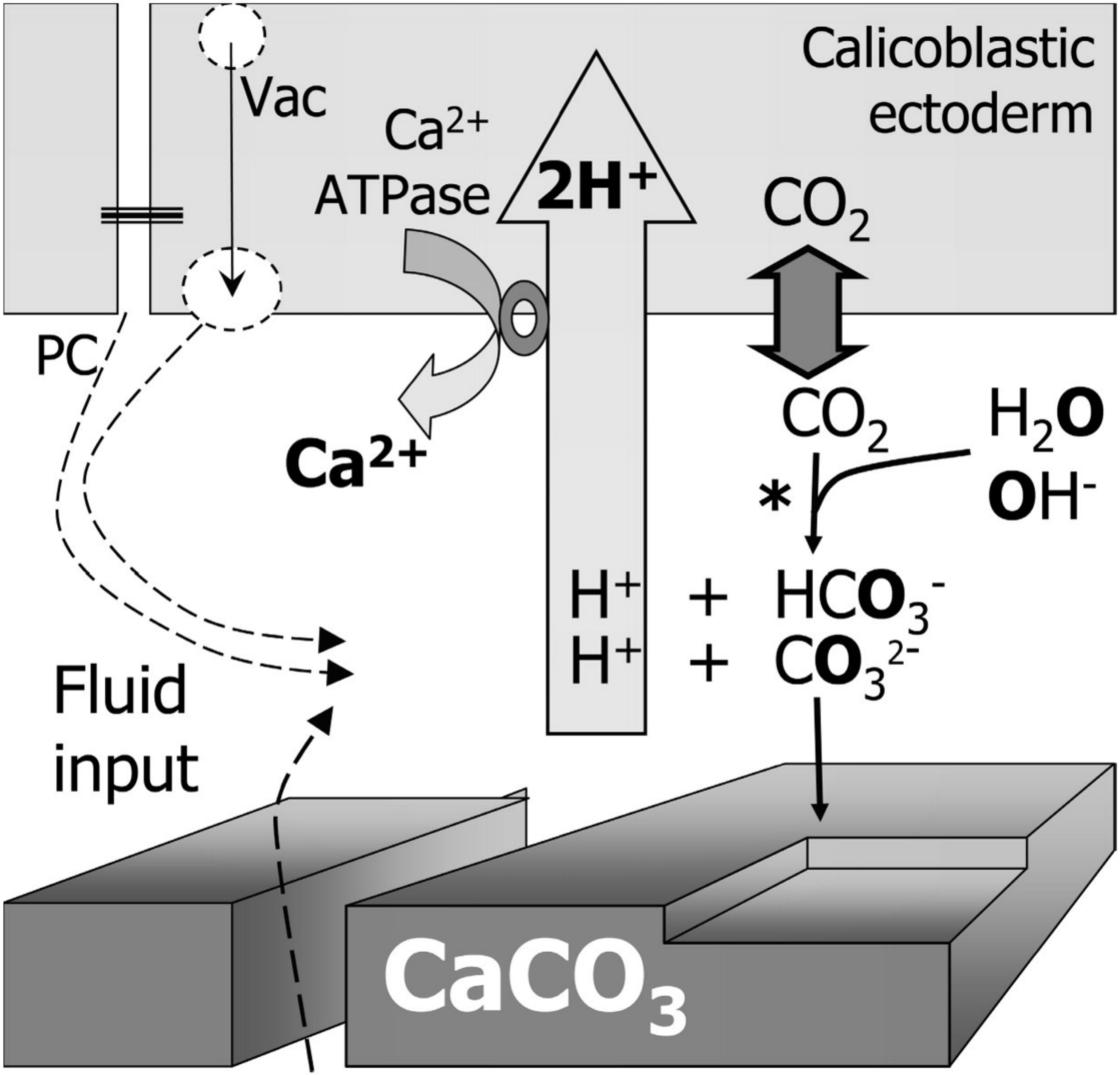
The general structure of a polyp and underlying skeleton. The corallite is a tube enclosed by a wall, which is intercepted by flattened plates, the septa radiating out from the tube center. The paliform lobes are outgrowths of the septa. Extensions of the paliforms lobes meet in the center to form the 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 pCO_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 CO_2 volcanic emissions, at different temperatures

Class: Anthozoa
Order: Scleractinia
Family: Dendrophylliidae

Balanophyllia europaea

SOLITARY, ZOOXANTHELLATE

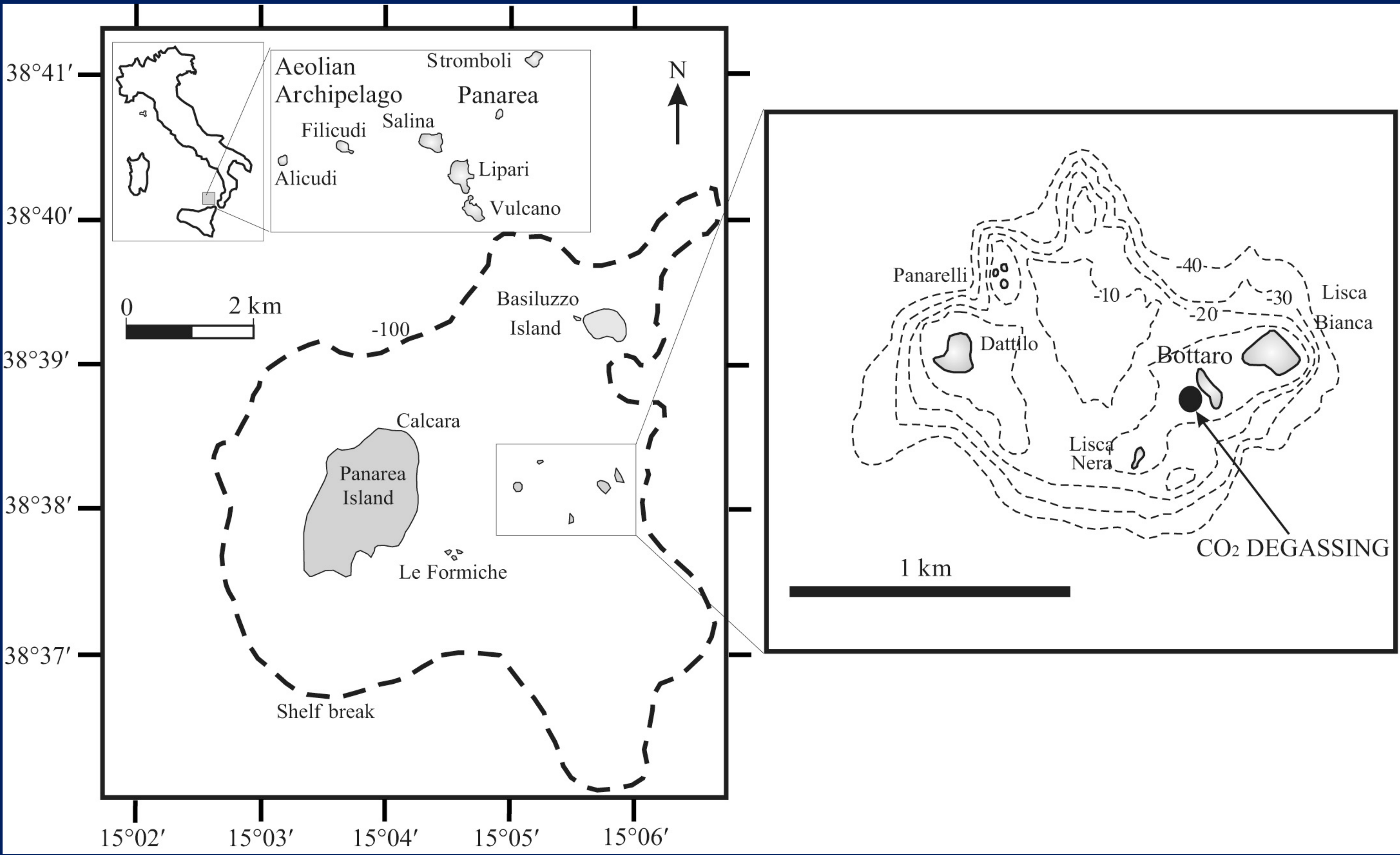
Leptopsammia pruvoti

SOLITARY, NON-ZOOXANTHELLATE

Astroides calycularis

COLONIAL, NON-ZOOXANTELLATE

Map of the study area, showing the CO_2 emissions site at Bottaro (Panarea Island) and the surrounding islets



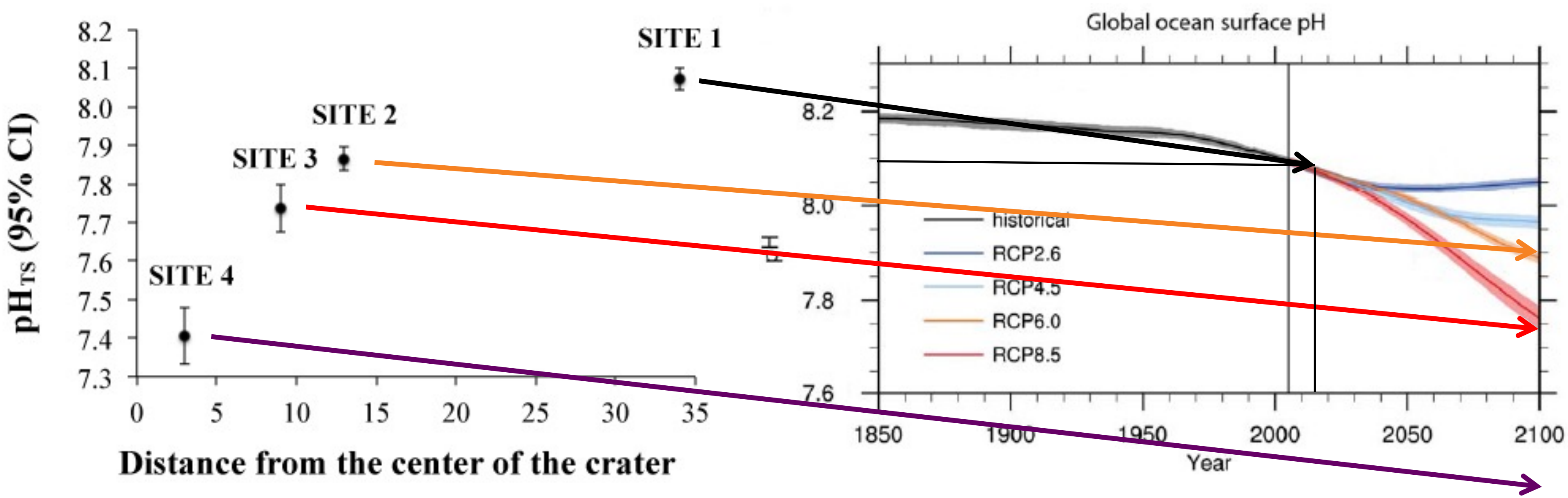
The Panarea Experiment

In-situ transplants, along a natural *p*H gradient generated by CO_2 volcanic emissions

Panarea CO_2 vent

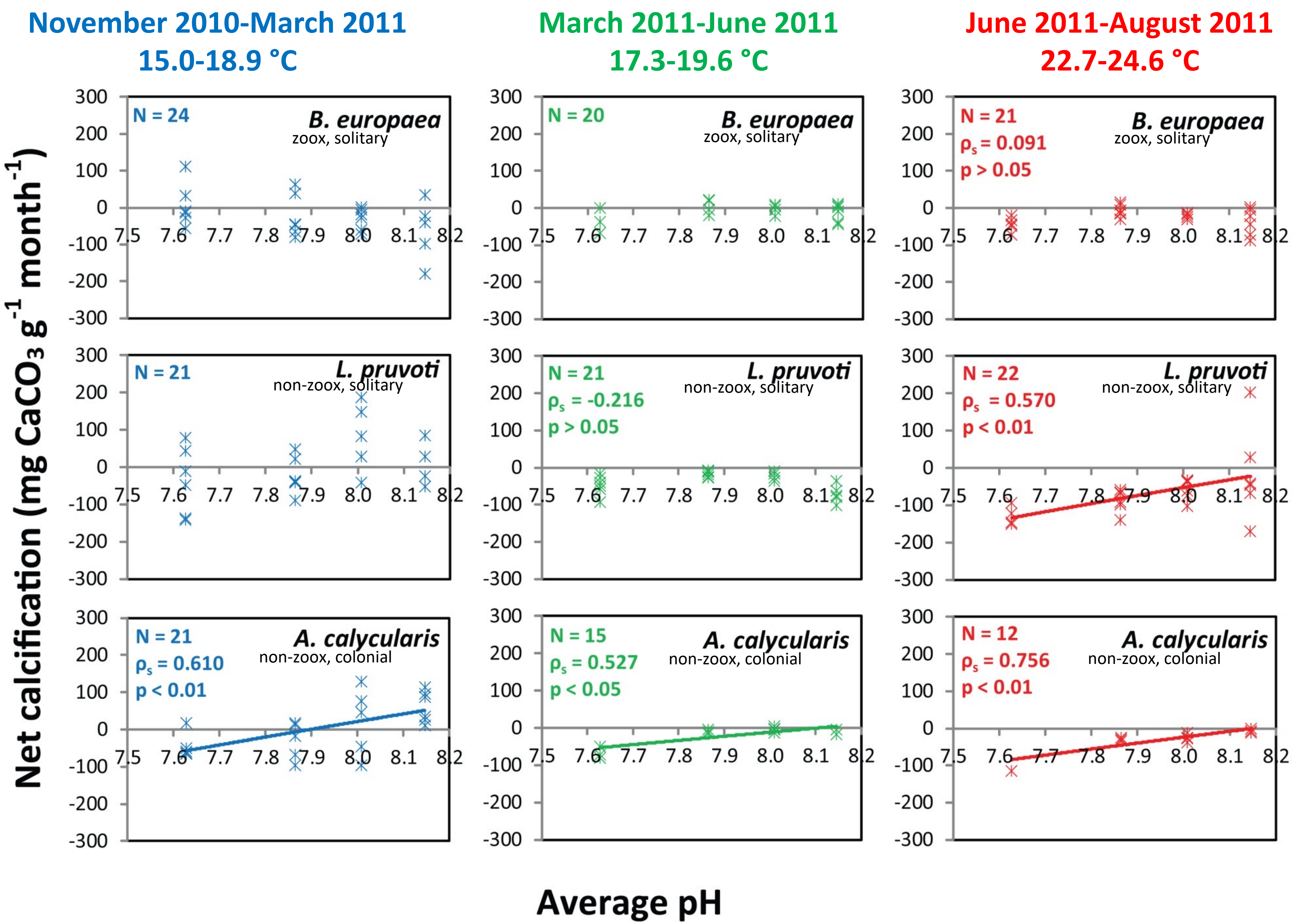
Panarea Experiment[1,2]
pH Gradient (July 2010-May 2013)

IPCC scenarios for year 2100[3]

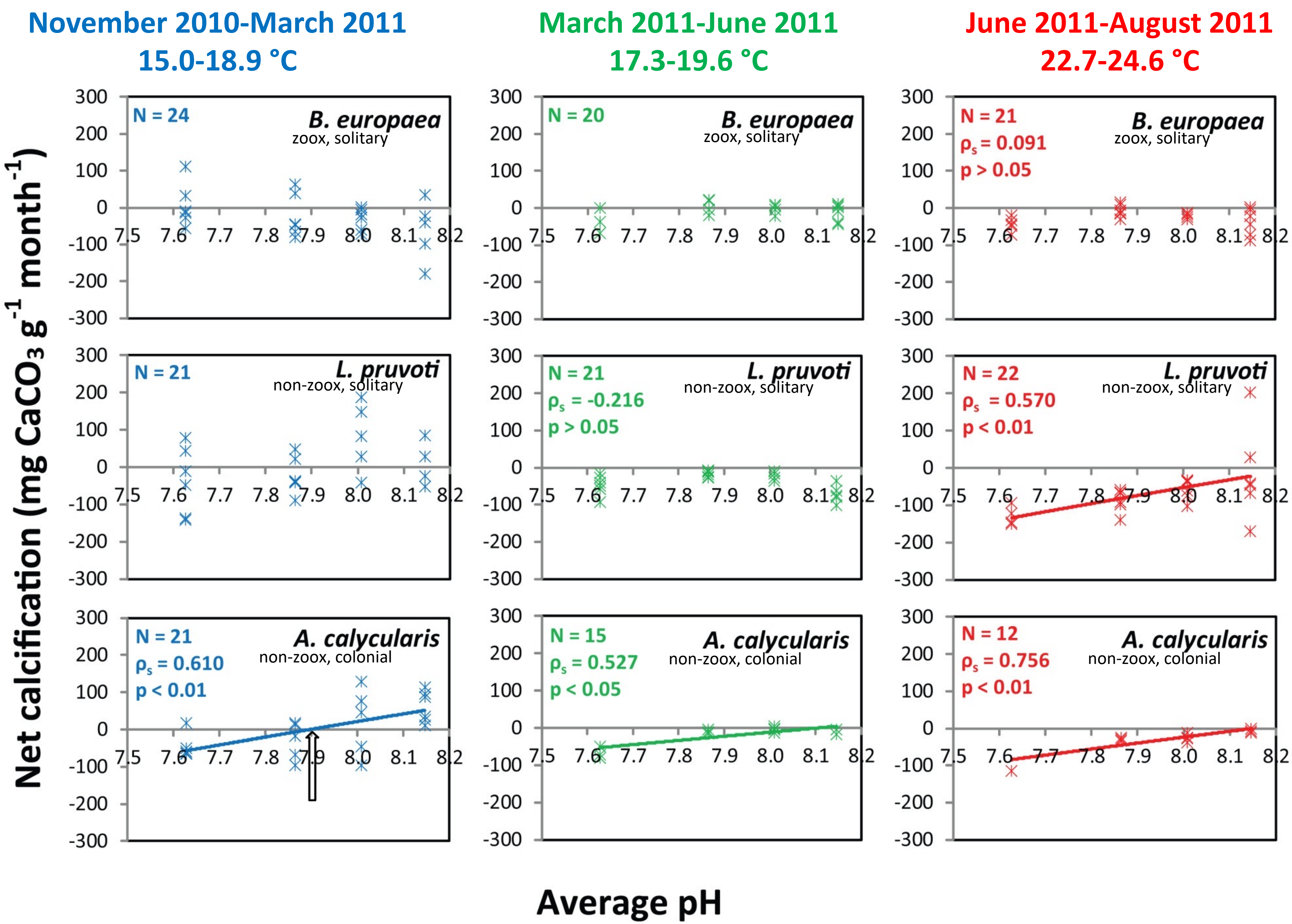


1. **Goffredo** et al., 2014, *Nature Climate Change,* 4: 593-597
2. Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 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
Net calcification (mg CaCO3 g-1 month-1)
Average pH
N = 24
B. europaea
zoox, solitary
N = 20
B. europaea
zoox, solitary
N = 21
ρs = 0.091
p > 0.05
B. europaea
zoox, solitary
N = 21
L. pruvoti
non-zoox, solitary
N = 21
ρs = -0.216
p > 0.05
L. pruvoti
non-zoox, solitary
N = 22
ρs = 0.570
p < 0.01
L. pruvoti
non-zoox, solitary
N = 21
ρs = 0.610
p < 0.01
A. calycularis
non-zoox, colonial
N = 15
ρs = 0.527
p < 0.05
A. calycularis
non-zoox, colonial
N = 12
ρs = 0.756
p < 0.01
A. calycularis
non-zoox, colonial
300
200
100
0
-100
-200
-300
7.5
7.6
7.7
7.8
7.9
8.0
8.1
8.2

GROWTH RATE



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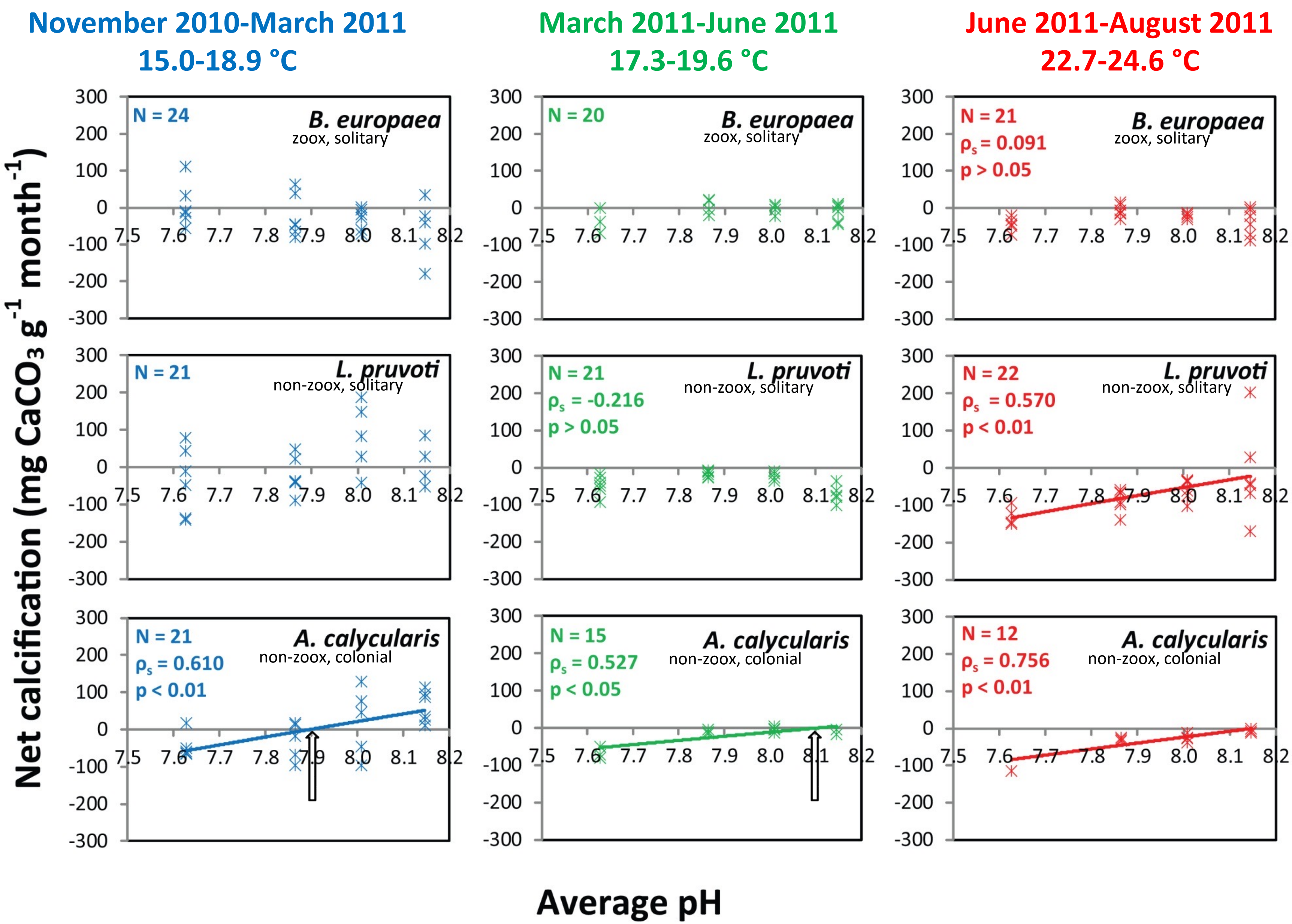
Average pH

GROWTH RATE



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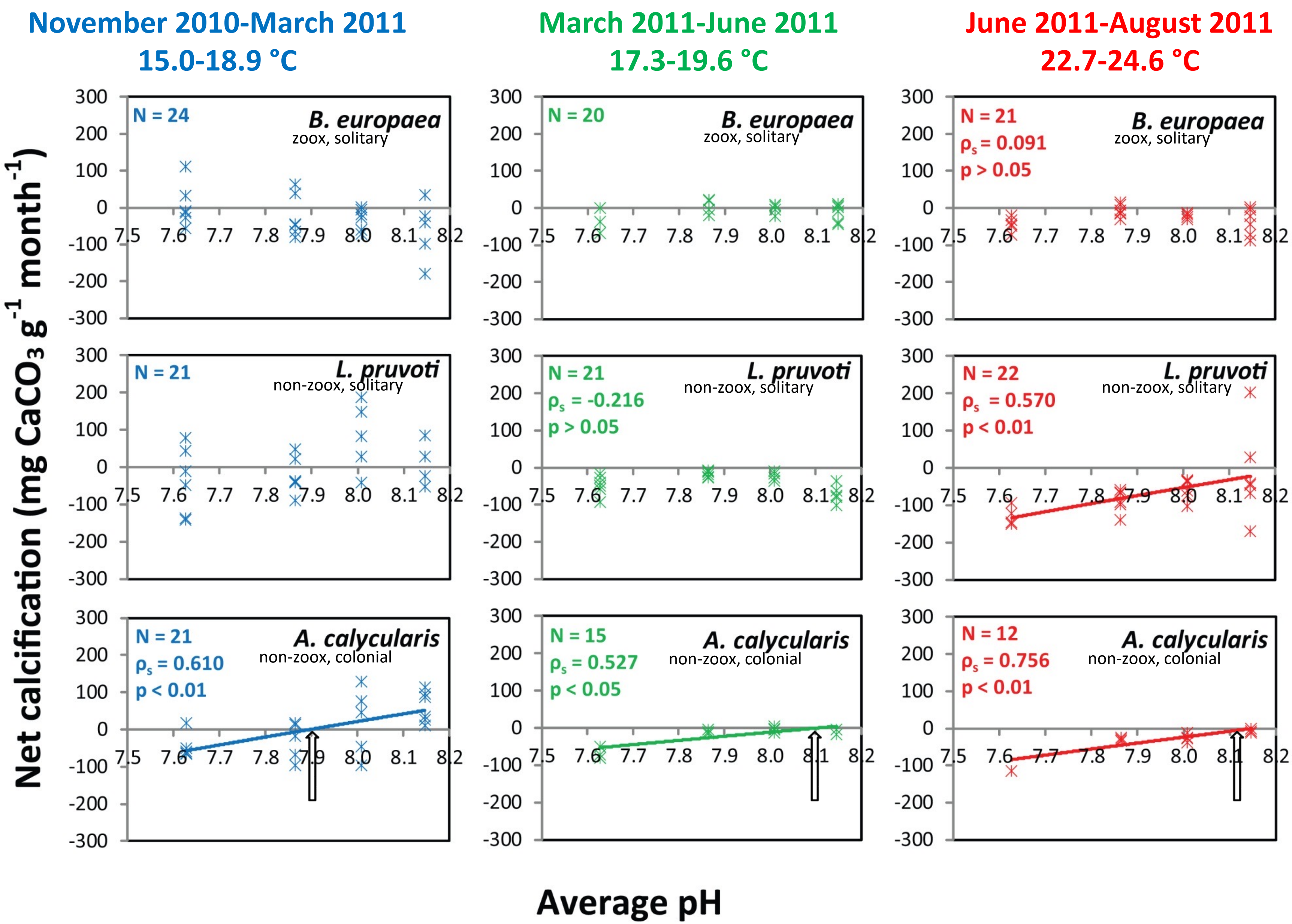
non-zoox, colonial
N = 15
ρs = 0.527
p < 0.05
A. calycularis
non-zoox, colonial
N = 12
ρs = 0.756
p < 0.01
A. calycularis
non-zoox, colonial

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
Net calcification (mg CaCO3 g-1 month-1)
N = 24
B. europaea
zoox, solitary
N = 20
B. europaea
zoox, solitary
N = 21
ρs = 0.091
p > 0.05
B. europaea
zoox, solitary
N = 21
L. pruvoti
non-zoox, solitary
N = 21
ρs = -0.216
p > 0.05
L. pruvoti
non-zoox, solitary
N = 22
ρs = 0.570
p < 0.01
L. pruvoti
non-zoox, solitary
N = 21
ρs = 0.610
p < 0.01
A. calycularis
non-zoox, colonial
N = 15
ρs = 0.527
p < 0.05
A. calycularis
non-zoox, colonial
N = 12
ρs = 0.756
p < 0.01
A. calycularis
non-zoox, colonial
300
200
100
0
-100
-200
-300
7.5
7.6
7.7
7.8
7.9
8.0
8.1
8.2
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).

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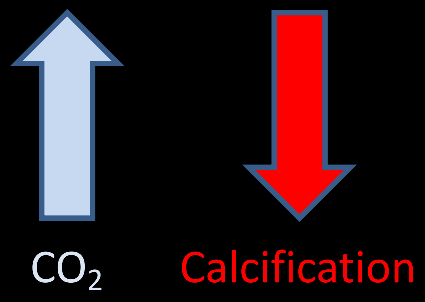

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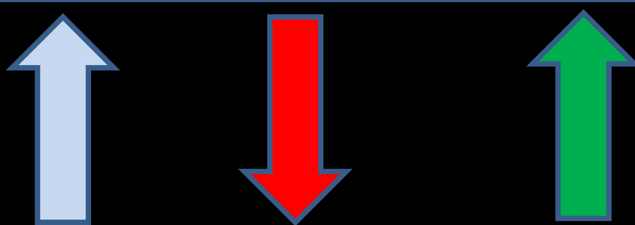

CO_2 Calcification Photosynthesis

In zooxanthellate corals

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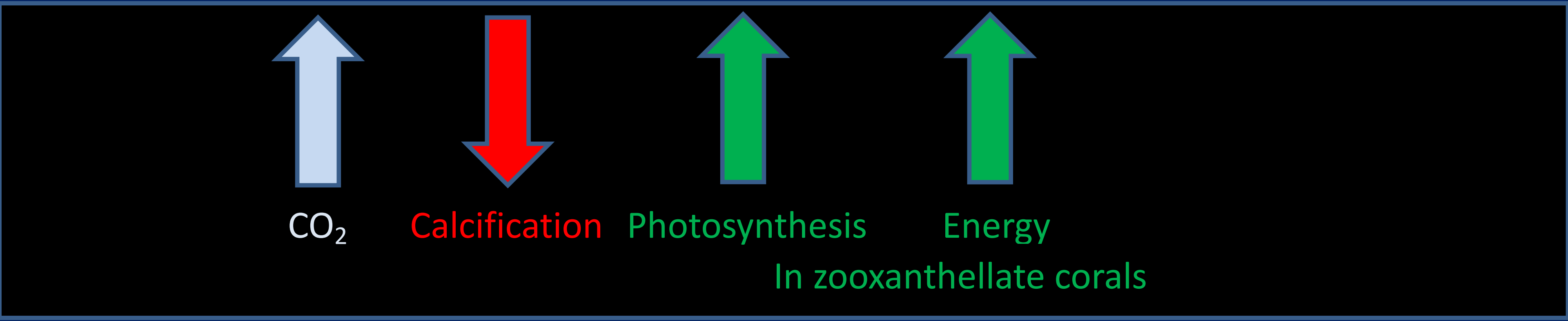

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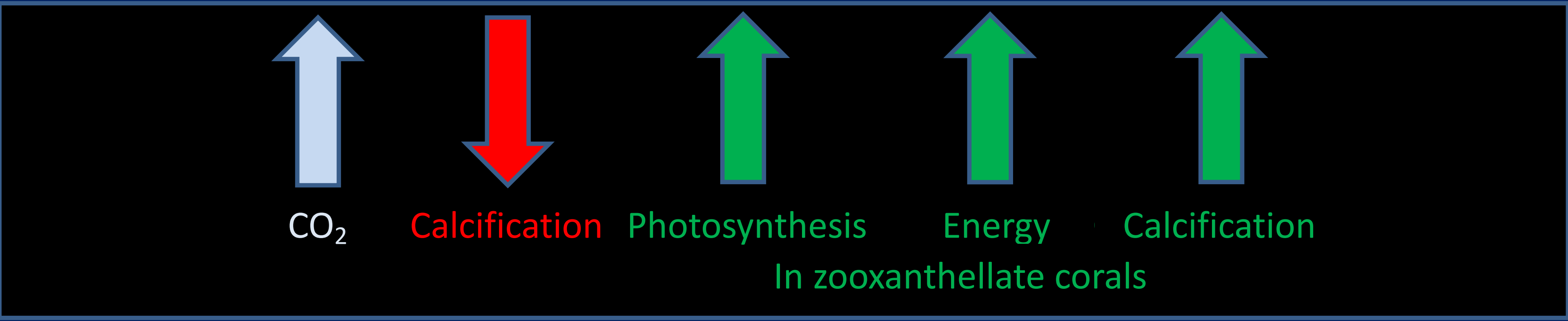

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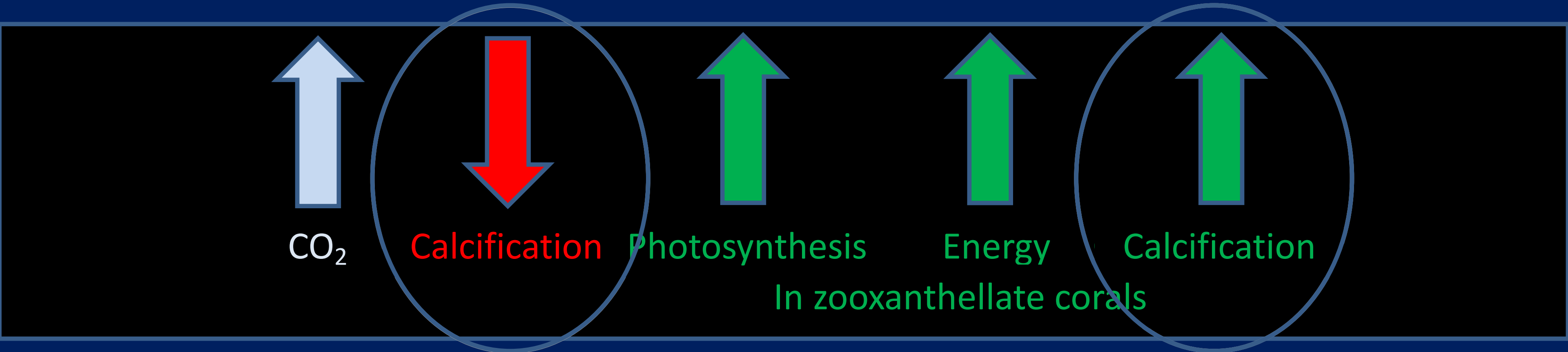

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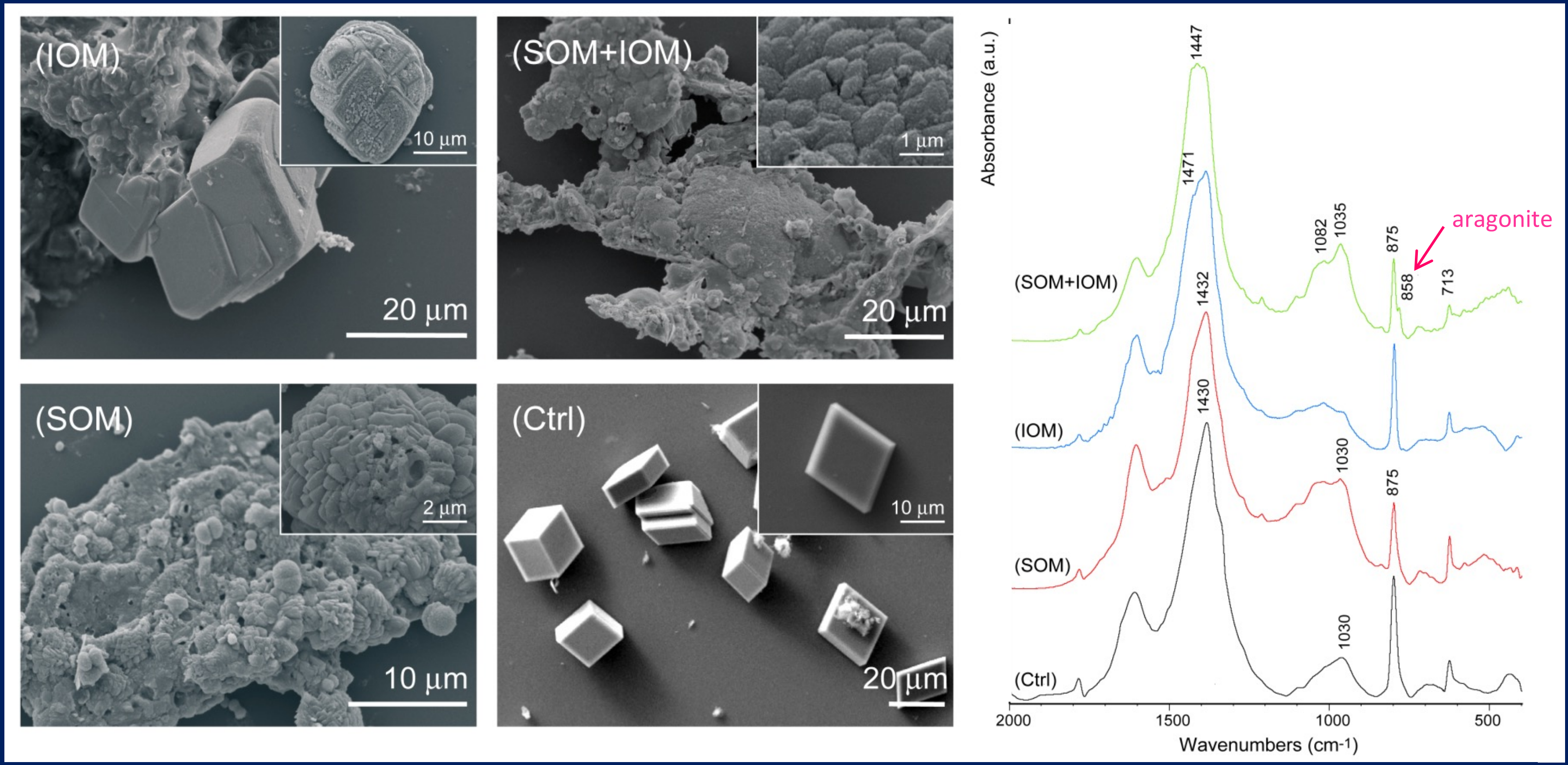
Discussion

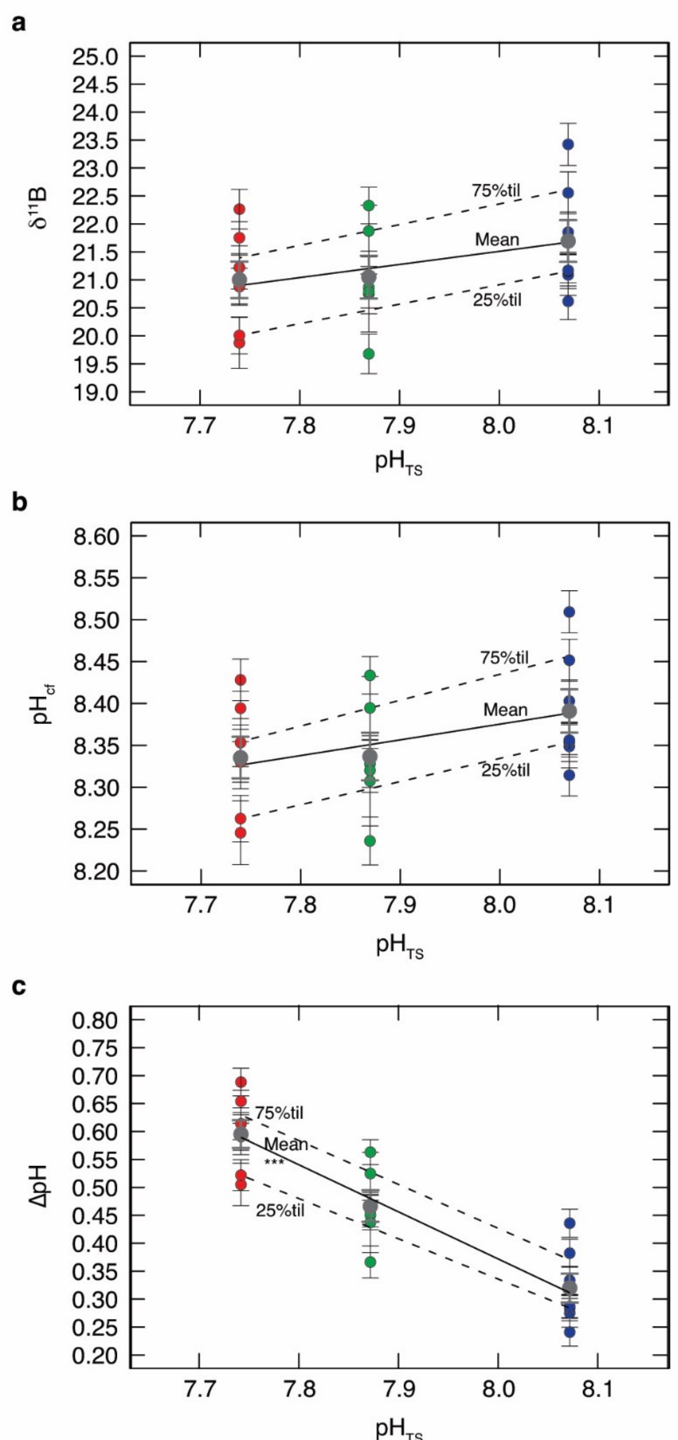
In-vitro crystallization experiments demonstrate that the intra-skeletal organic matrix (OM) of *B. europaea* determines the precipitation of $CaCO_3$ in the form of aragonite even in the absence of Mg (Goffredo et al., 2011, *PLoS ONE,* 6: e22338). The intra-skeletal organic matrix of *L. pruvoti* does 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.

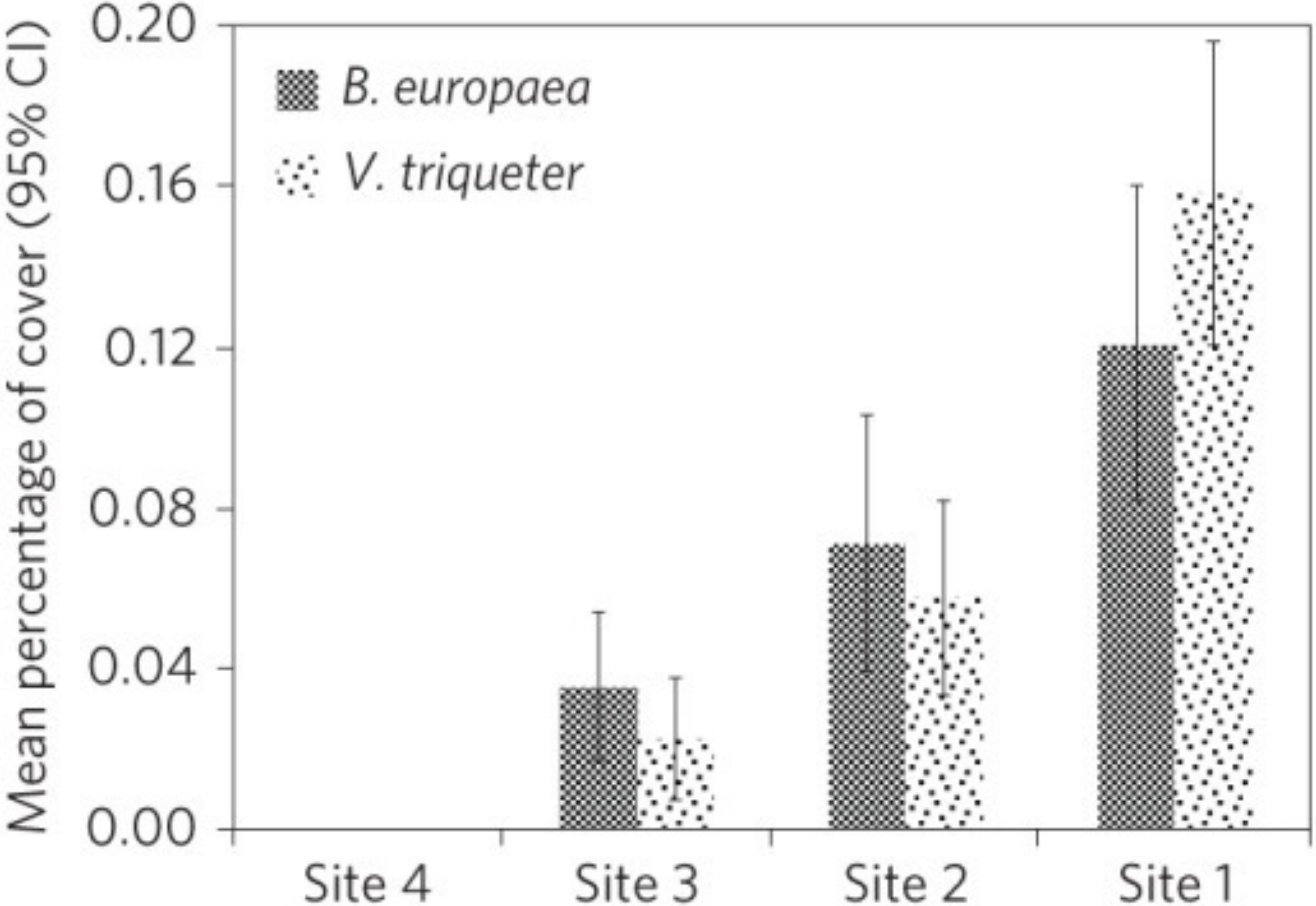


Boron isotopic signature ($\delta^{11}B$), $\delta^{11}B$-derived internal calcification pH (pH_{cf}) and pH up-regulation intensity (ΔpH) of *Balanophyllia europaea* corals from the CO_2 seeps near Panarea Island, Italy (Wall et al., manuscript in preparation).

(a) $\delta^{11}B$ values were measured in total in 20 *B. europaea* coral colonies 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 (= pH_{cf} – pH_{TS}) were calculated. Filled circles and error bars represent individual colony means ± 1 sem per colony. Dark grey filled circles show average per site (± 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 pCO_2 gradient

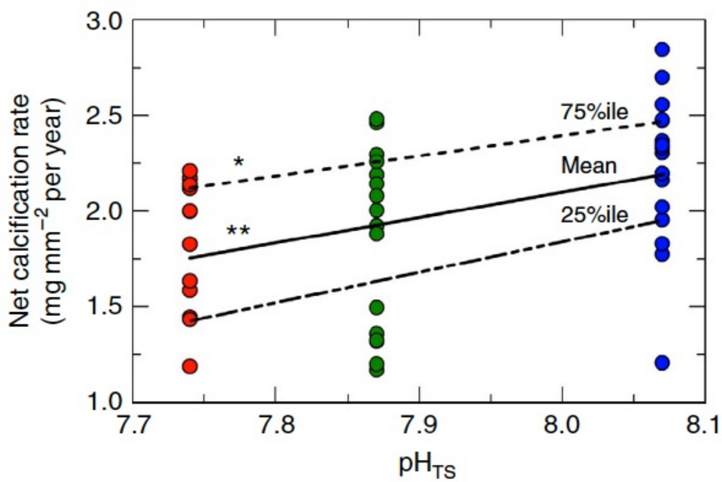


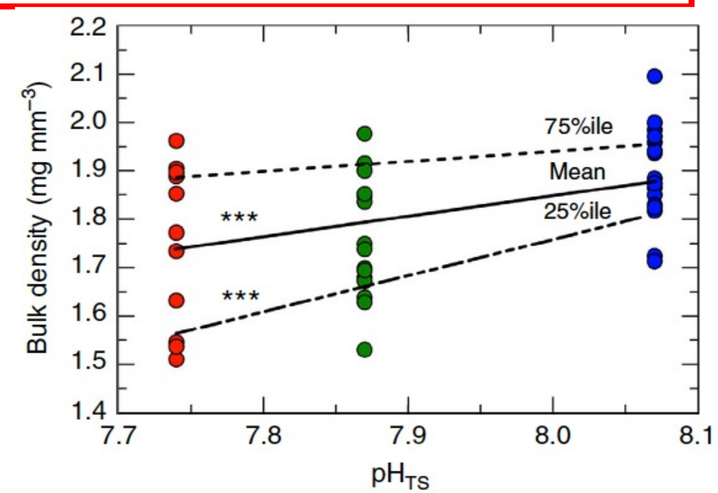
pH_{TS}=7.4 **pH_{TS}=7.7** **pH_{TS}=7.9** **pH_{TS}=8.1**

Mean percentage of cover for *Balanophyllia europaea* and *Vermetus triqueter* along the *p*CO**2** gradient (Goffredo et al., 2014, *Nature Climate Change,* 4: 593-597).

With increasing pCO_2:

	Site 1: *d*=34 m pCO_2=423 μatm pH=8.07 *N*=16		Site 2: *d*=13 m pCO_2=698 μatm pH=7.87 *N*=16		Site 3: *d*=9 m pCO_2=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 ↓

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

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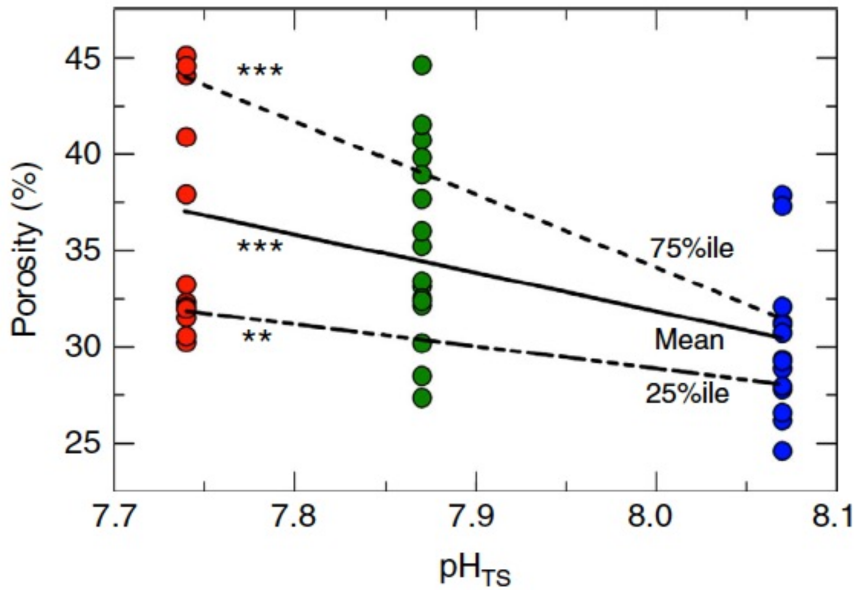
	mean	se	mean	se	mean	se	statistical significance
Skeletal porosity (P_A) (%)[$]	30.0	0.9	35.3	1.2	36.2	1.7	**



Porosity

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

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

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

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Net calcification rate ($mg\ mm^{-2}\ yr^{-1}$) **=** **linear extension rate** ($mm\ yr^{-1}$) **×** **skeletal bulk density** ($mg\ mm^{-3}$)

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With increasing pCO_2:

↓ **Net calcification rate** ($mg\ mm^{-2}\ yr^{-1}$) = (unchanged) **linear extension rate** ($mm\ yr^{-1}$) × ↓ **skeletal bulk density** ($mg\ mm^{-3}$)

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

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With increasing pCO_2:

Net calcification rate (mg mm^{-2} yr^{-1}) ↓ **=** **linear extension rate** (mm yr^{-1}) = **×** **skeletal bulk density** (mg mm^{-3}) ↓ **porosity** ↑

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

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

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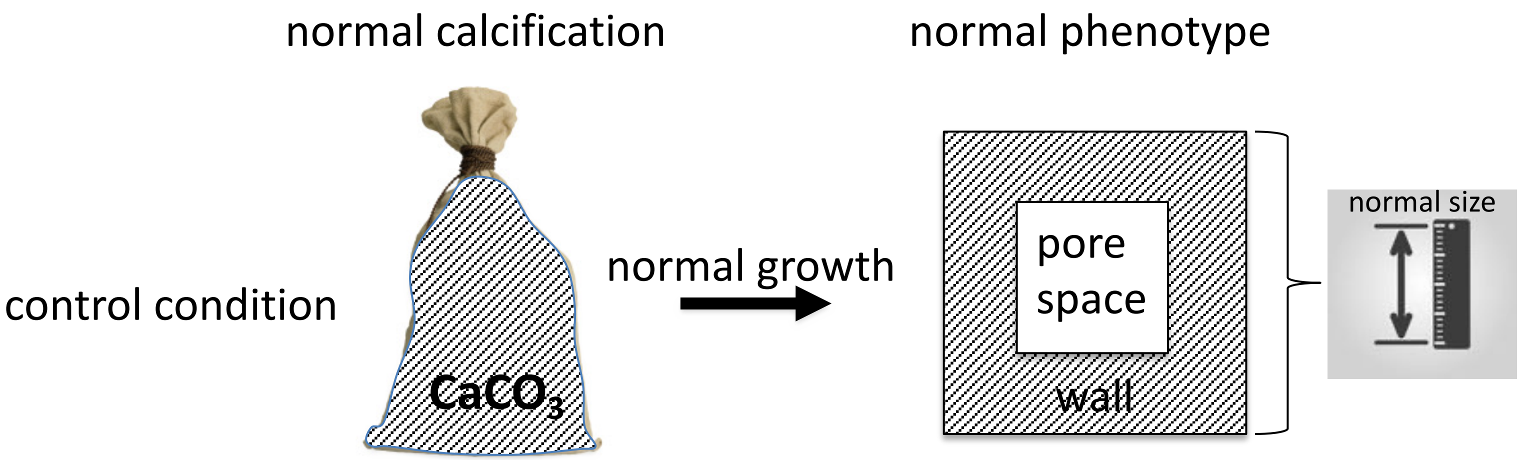

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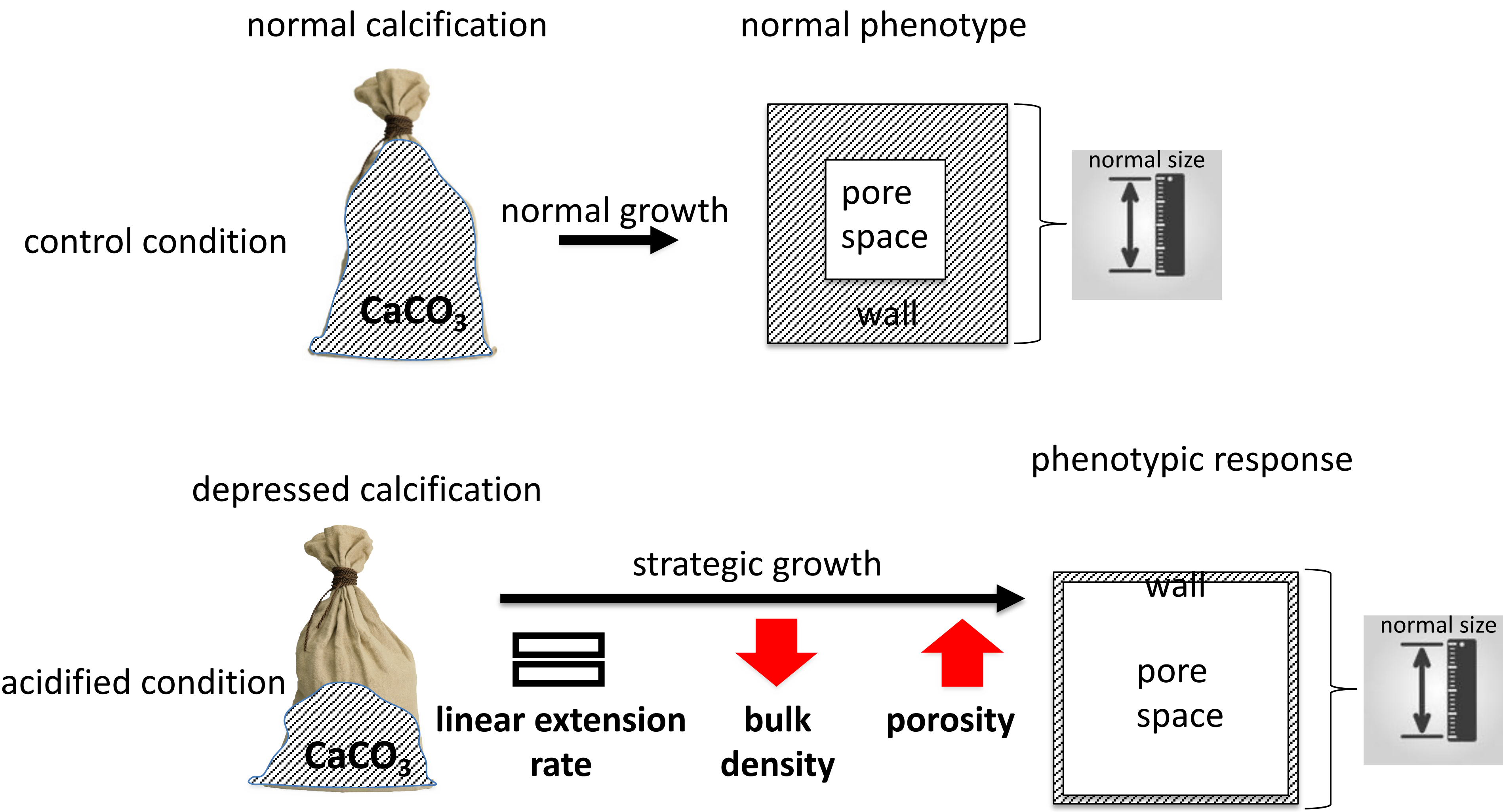
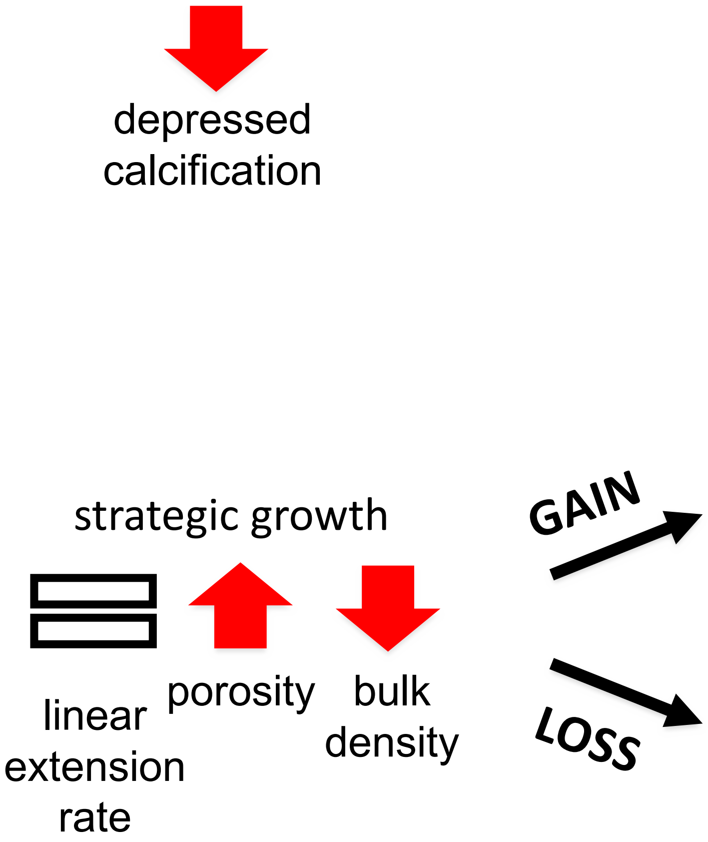


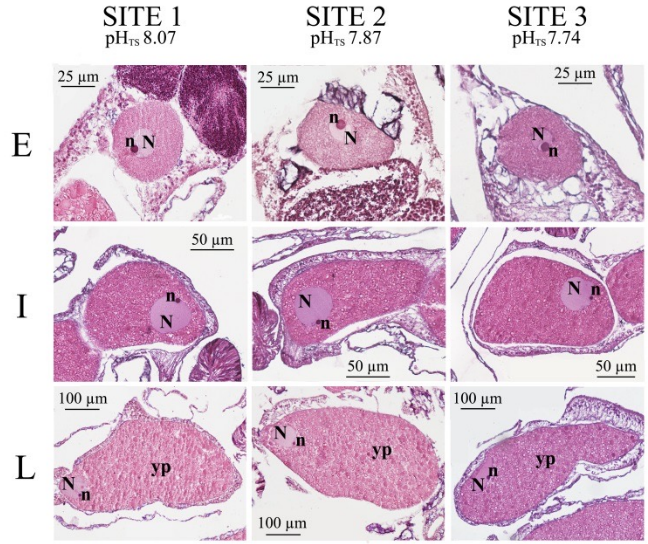
Fantazzini, Mengoli, Pasquini, Bortolotti, Brizi, Mariani, Di Giosia, Fermani, Capaccioni, Caroselli, Prada, Zaccanti, Levy, Dubinsky, Kaandorp, Konglerd, Hammel, Dauphin, Cuif, Weaver, Fabricius, Wagermaier, Fratzl, Falini, **Goffredo**, 2015, *Nature Communications*, 6: 7785

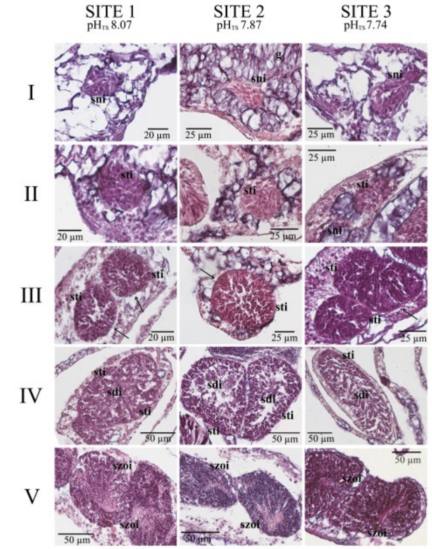
With increasing pCO_2:



With increasing pCO_2:

depressed calcification





Gizzi e Marchini, 2016, *Tesi di Dottorato*

strategic growth

linear extension rate

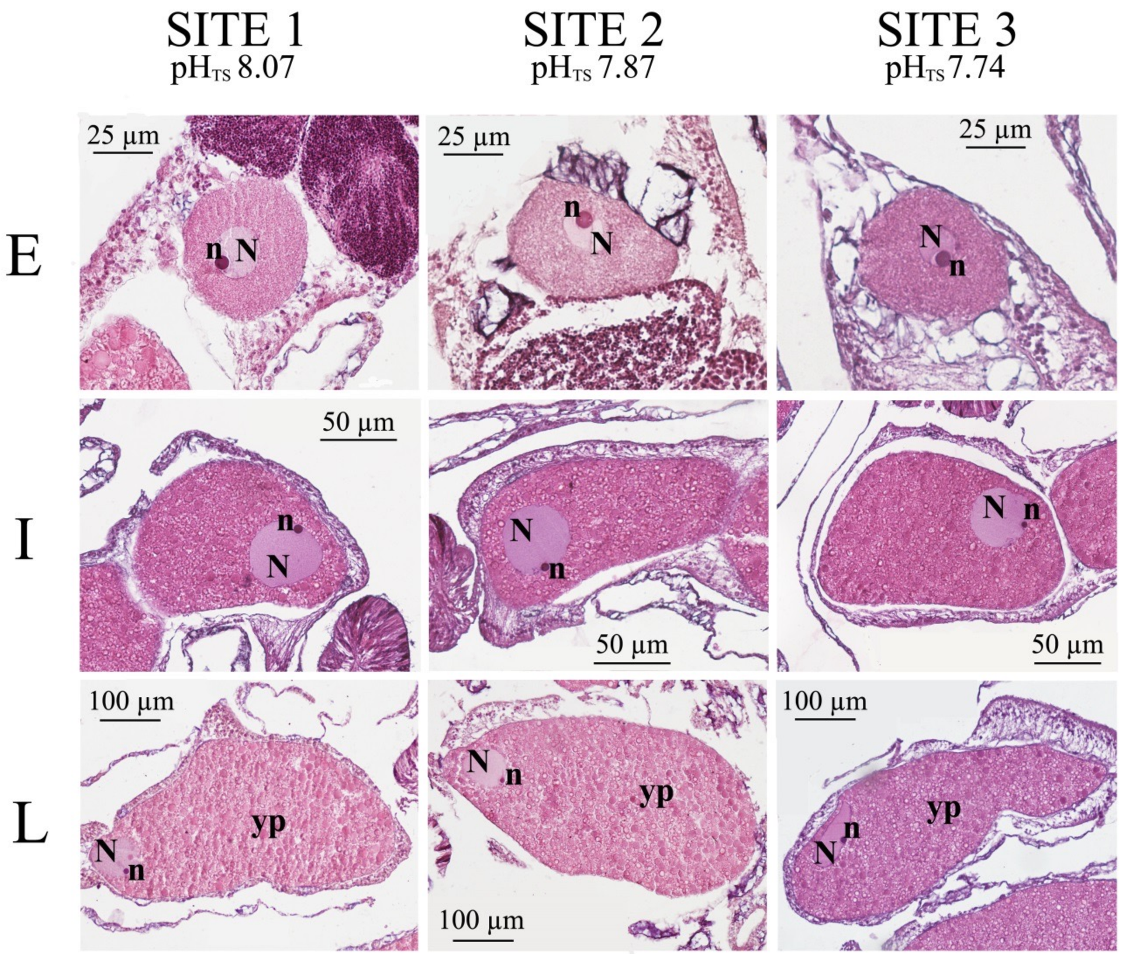
porosity

bulk density

GAIN

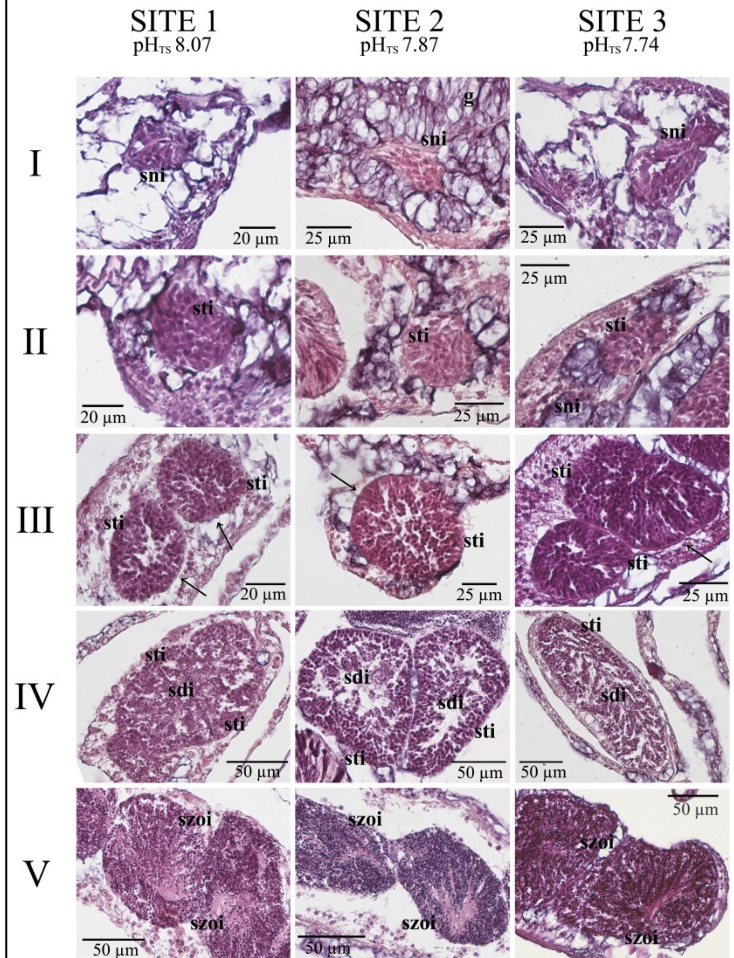
LOSS

Size at sexual maturity



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].

Gizzi *Tesi di Dottorato*

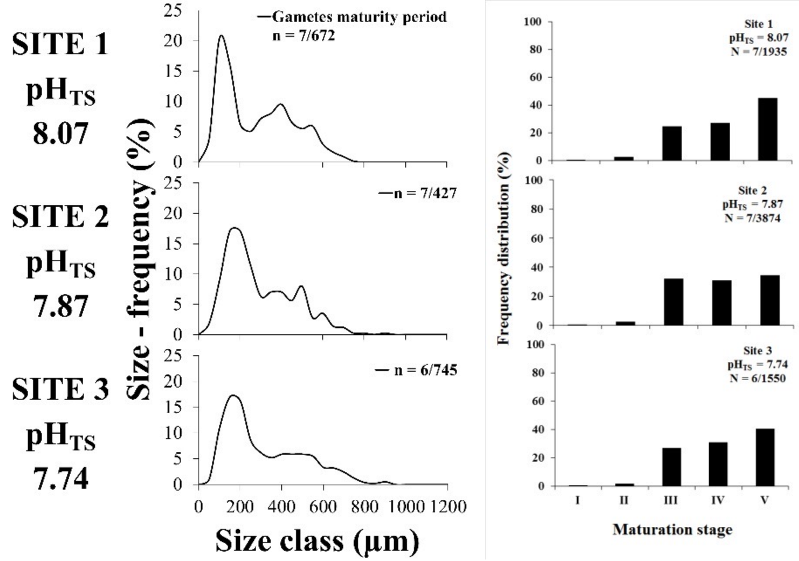


Balanophyllia europaea. Spermatogenesis**.** Five spermary maturation stages (I, II, III, IV, V) in the three study sites along the *p*CO_2 gradient. Stage I: undifferentiated spermaries. Stage II: the spermary is made up of a group of spermatocytes involved in the meiosis process. Stage III: the spermaries 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].

Marchini *Tesi di Dottorato*

With increasing pCO_2:

depressed calcification



Gizzi e Marchini, 2016, *Tesi di Dottorato*

strategic growth

linear extension rate

porosity

bulk density

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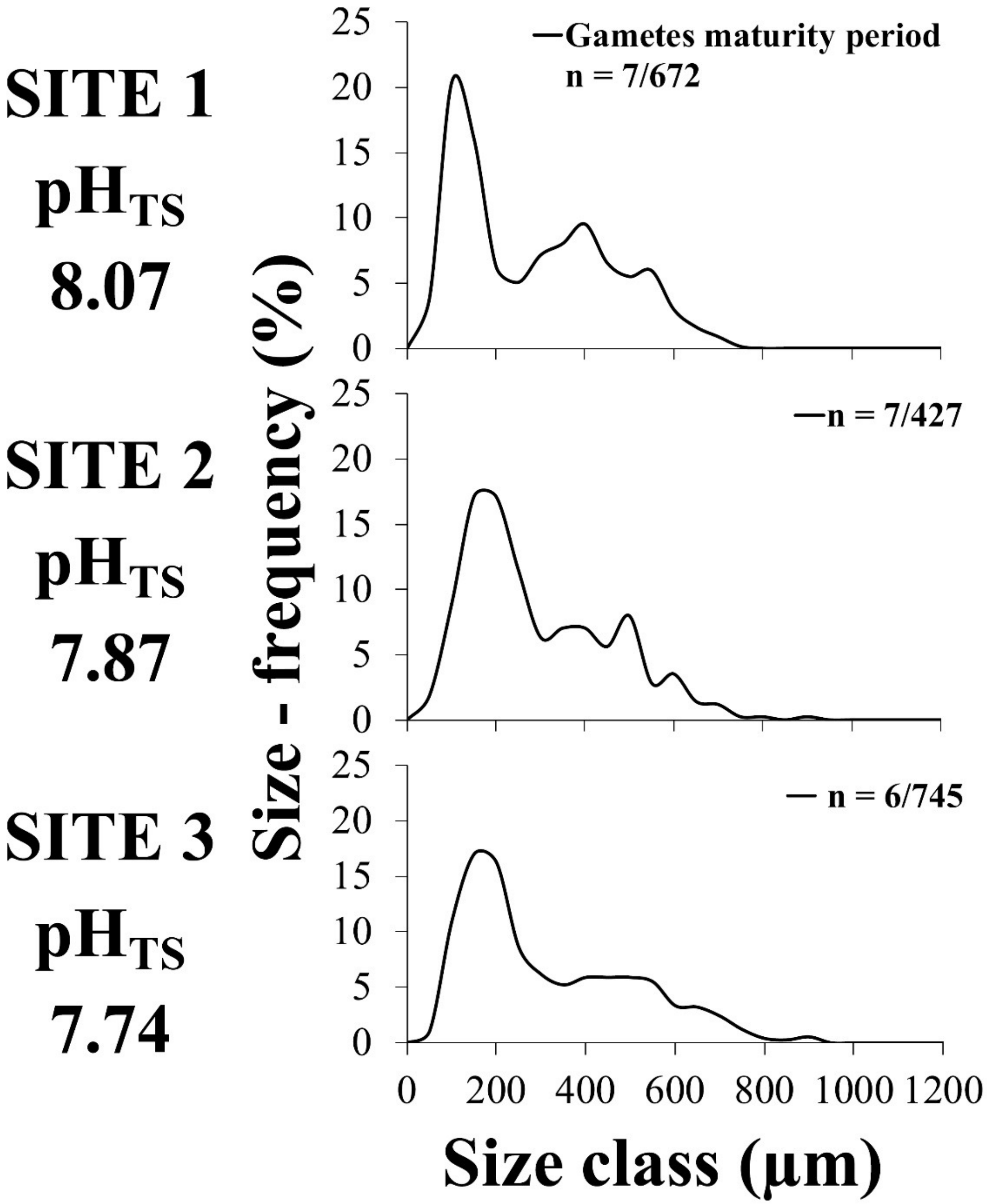
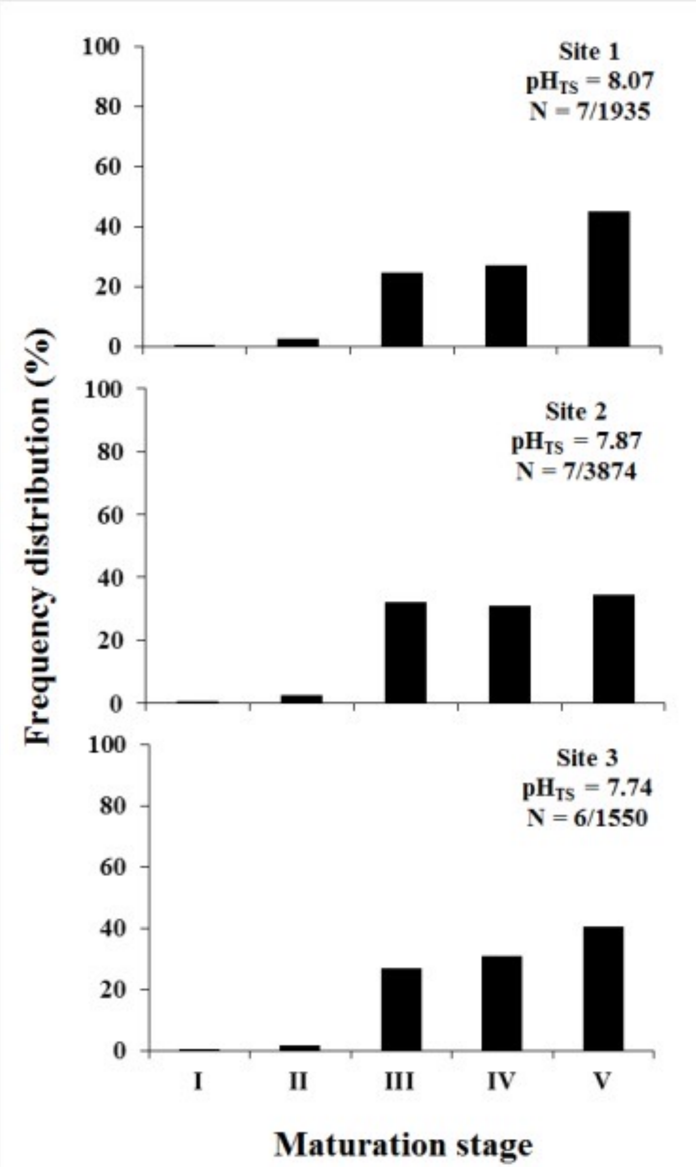
LOSS

Size at sexual maturity



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

Gizzi *Tesi di Dottorato*

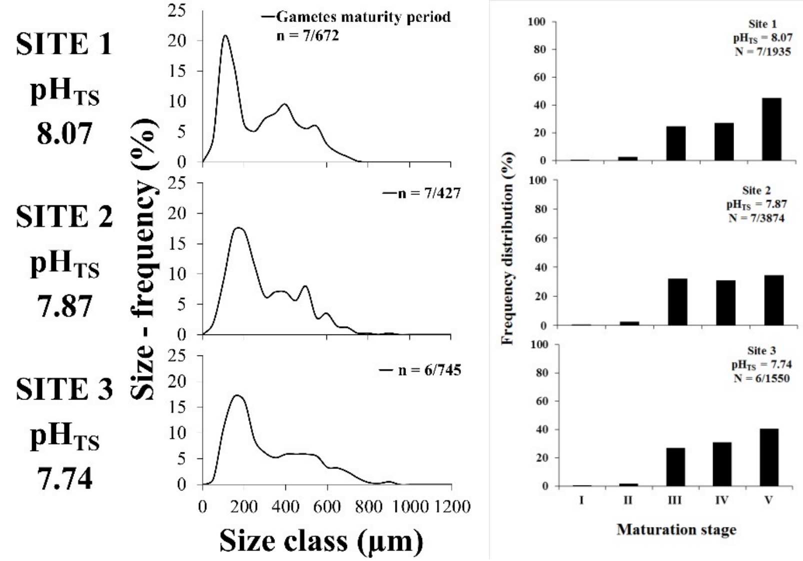


Balanophyllia europaea. Distribution of the five stages of spermary maturation in the three sites along the pCO_2 gradient. N indicate the number of polyps/the total number of spermaries measured per site.

Marchini *Tesi di Dottorato*

With increasing pCO_2:

depressed calcification



Gizzi e Marchini, 2016, *Tesi di Dottorato*

strategic growth

linear extension rate

porosity

bulk density

GAIN

LOSS

Size at sexual maturity

With increasing pCO_2:

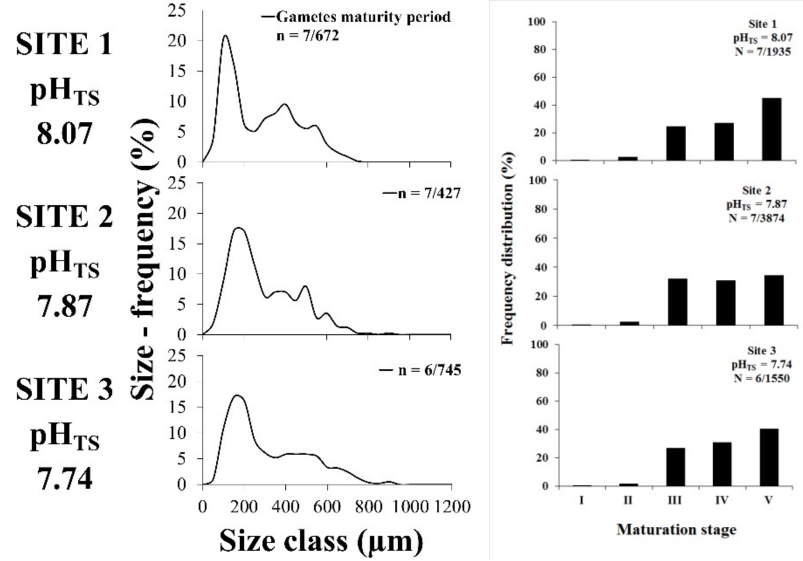
depressed calcification

strategic growth

linear extension rate

porosity

bulk density



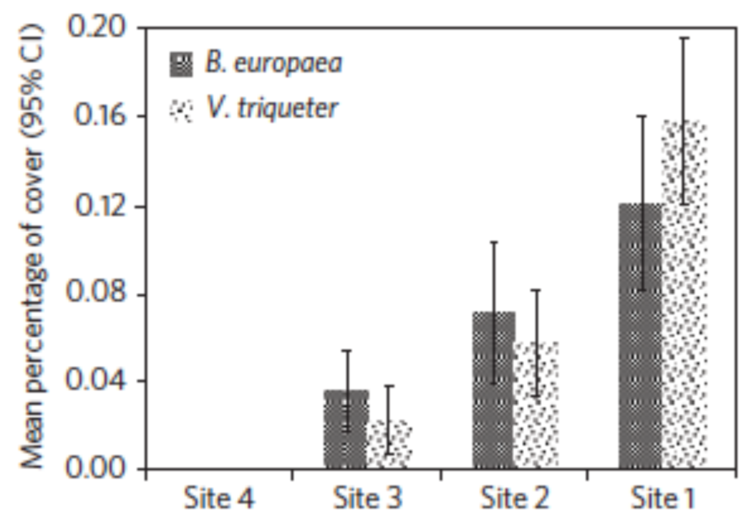
Gizzi e Marchini, 2016, *Tesi di Dottorato*

GAIN

Size at sexual maturity

LOSS

mechanical strength

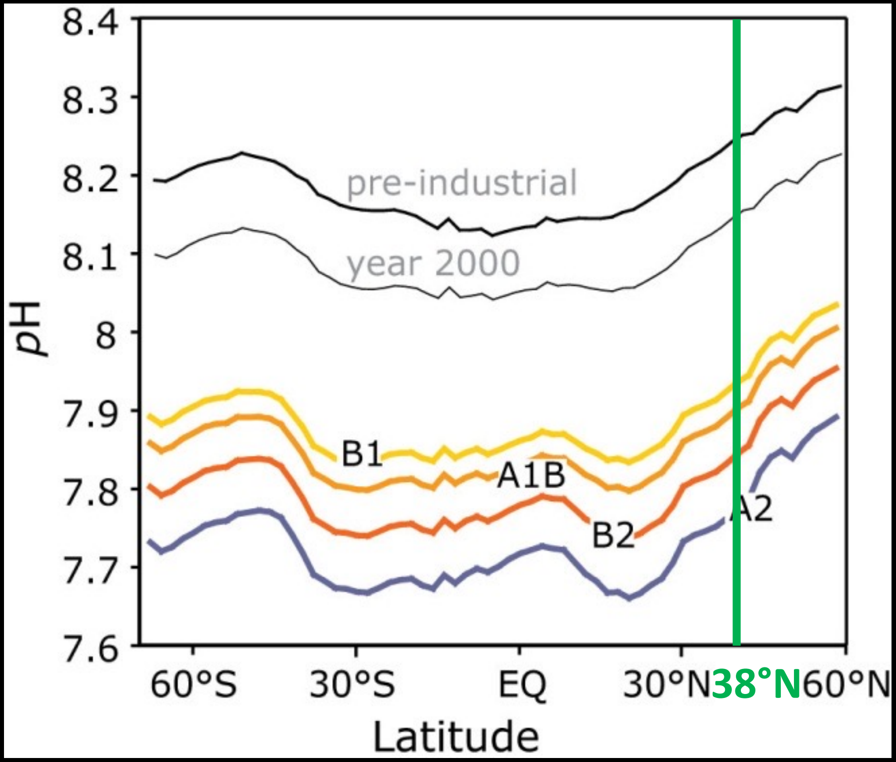


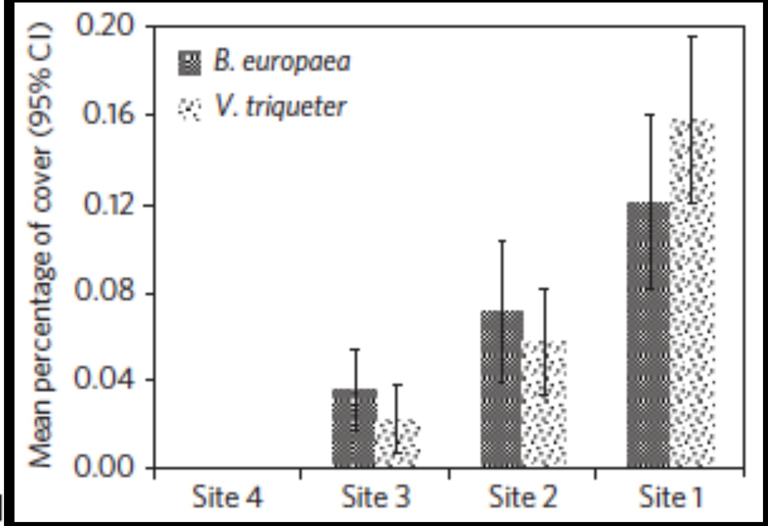
pH_{TS}=7.4 pH_{TS}=7.7 pH_{TS}=7.9 pH_{TS}=8.1

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

Predictions for 2100

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



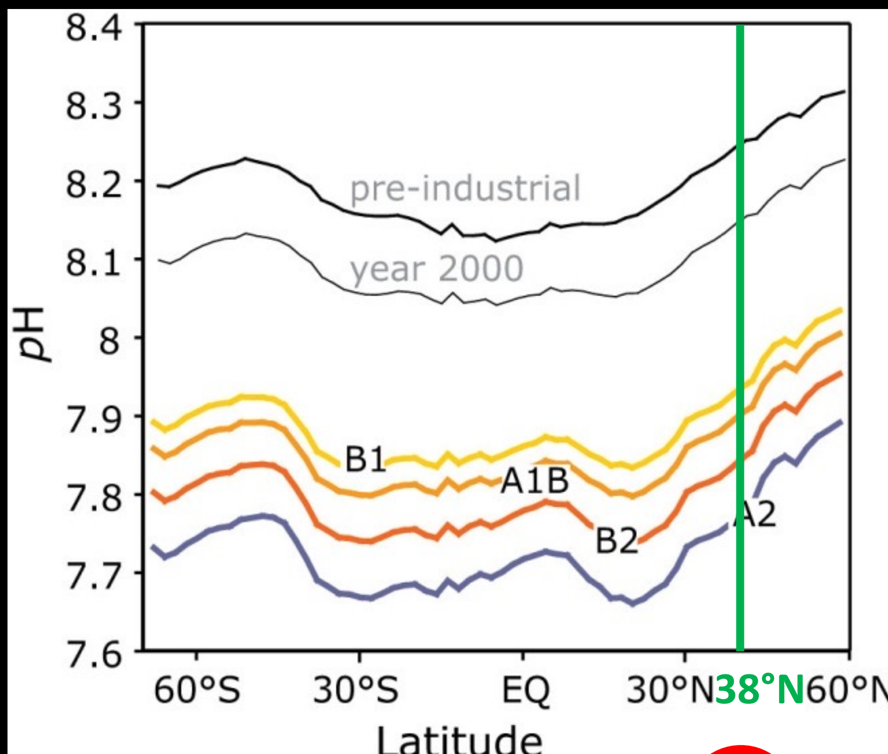


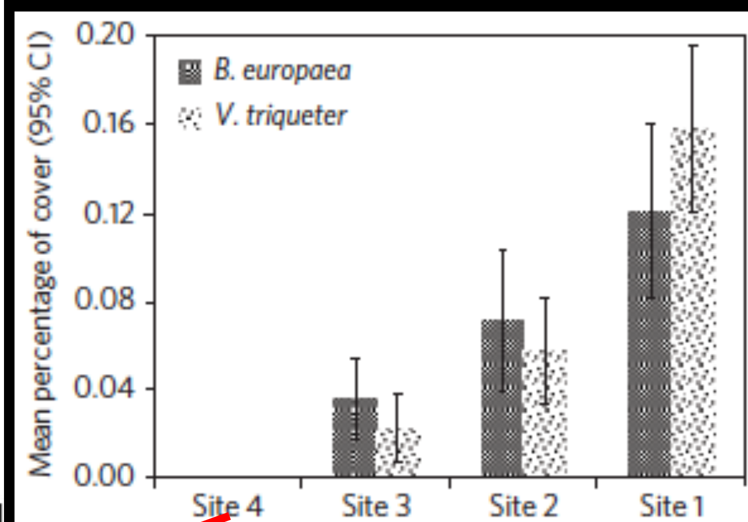
pH_{TS}=7.4 pH_{TS}=7.7 pH_{TS}=7.9 pH_{TS}=8.1

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

Predictions for 2100

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





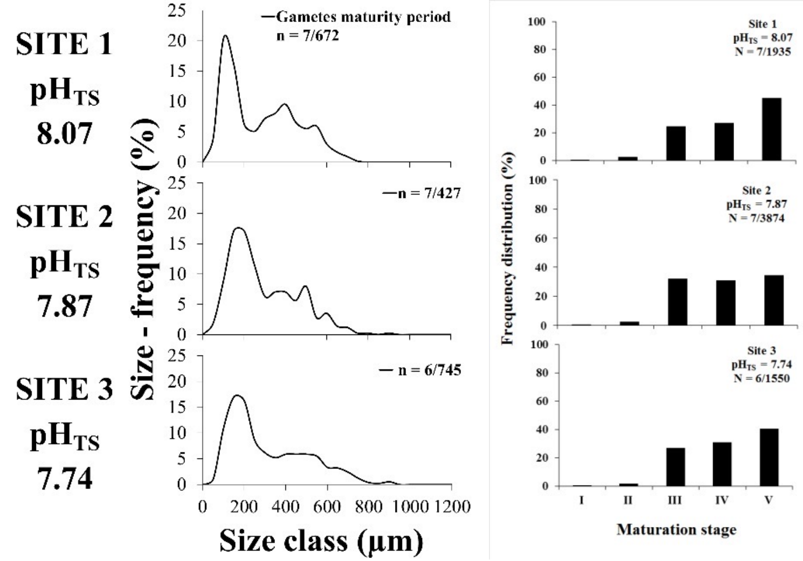
pH_{TS} 7.4

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 pCO_2:

depressed calcification



Gizzi e Marchini, 2016, *Tesi di Dottorato*

strategic growth

linear extension rate

porosity

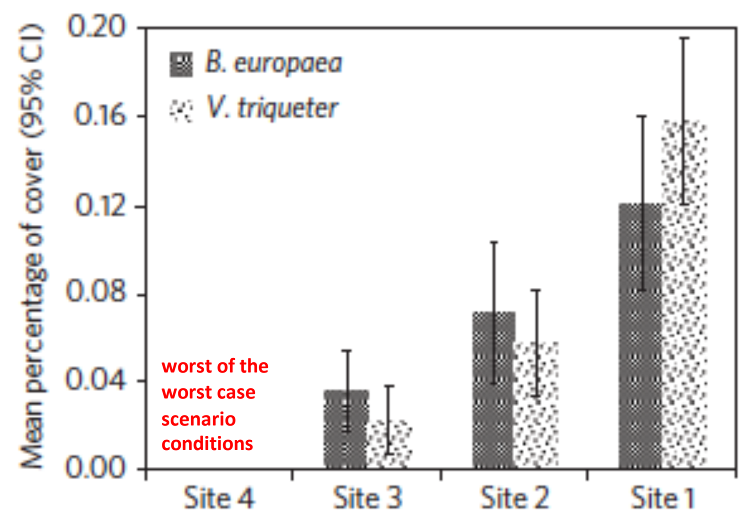
bulk density

GAIN

Size at sexual maturity

LOSS

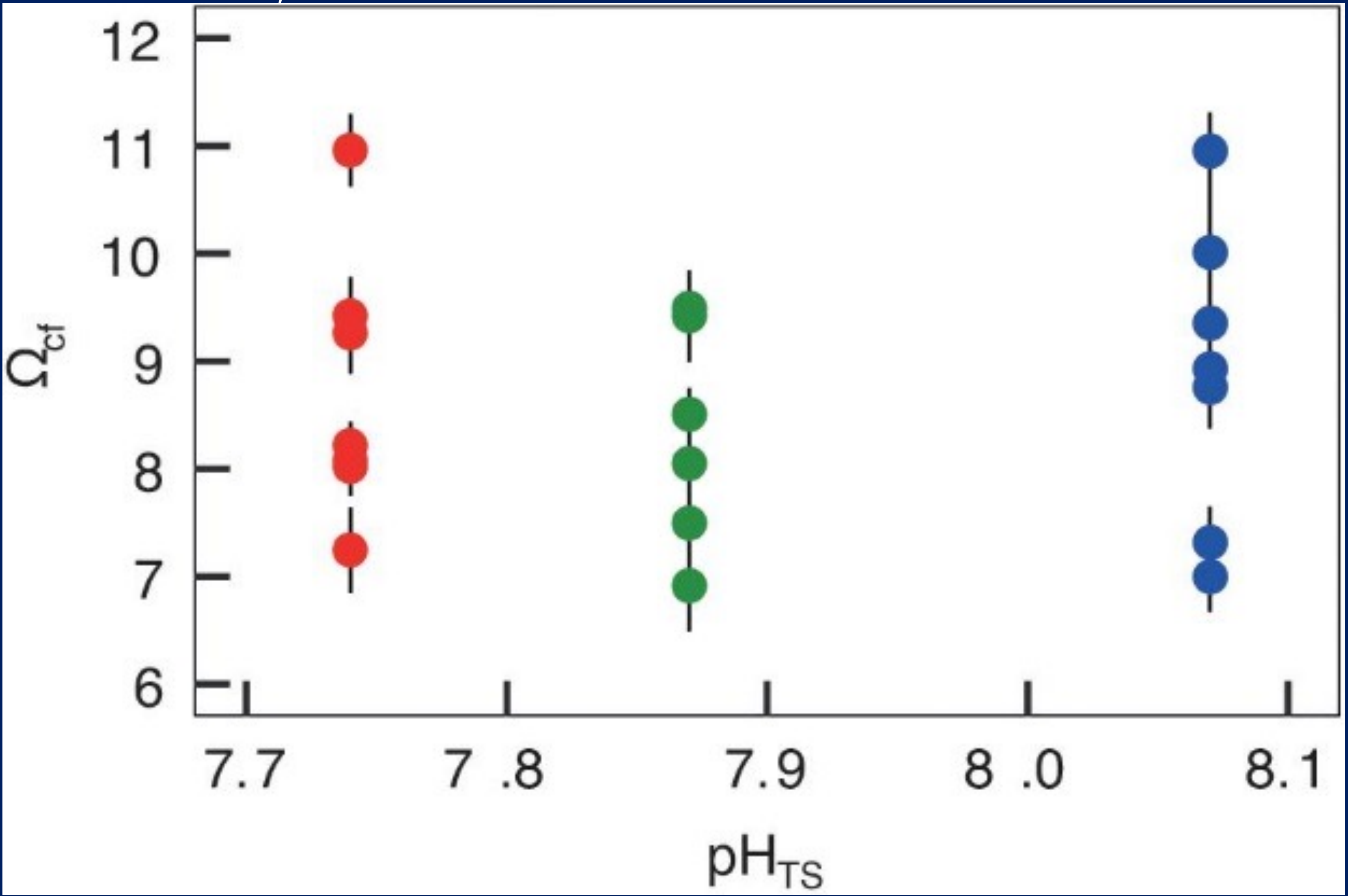
mechanical strength



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

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 ± 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 CO2 Vent. Frontiers in Marine Science 6: 699. doi: 10.3389/fmars.2019.00699



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:

$$\Omega_{arag} = \frac{[Ca^{2+}]*[CO_3^{\ 2-}]}{K'_{arag}}$$

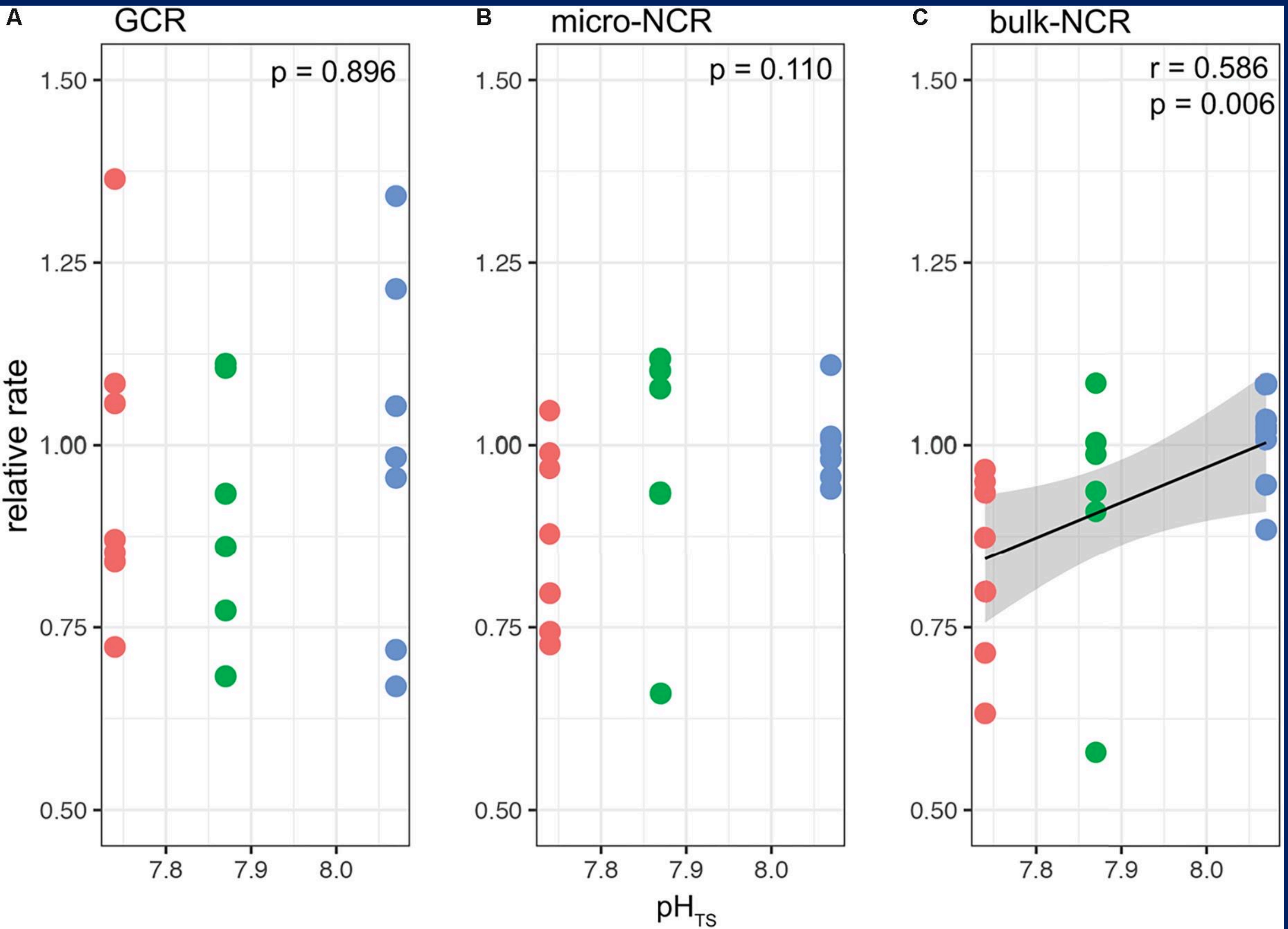
Dove K'_{arag} è il prodotto di solubilità apparente del minerale

Valori di Ω_{arag} > 1 indicano **supersaturazione**

Valori di Ω_{arag} < 1 indicano **sottosaturazione**

Siccome [Ca^{2+}] è circa cento volte maggiore di [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 [CO_3^{2-}] (Reynaud et al. 2003, *Glob. Change Biol.*, 9: 1660-1668).

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 = $k \times (\Omega_{cf}-1)^n$ and presented as relative rates (setting average control growth as 1). **(B)** micro-NCR and **(C)** bulk-NCR were derived from bulk density, micro-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



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

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

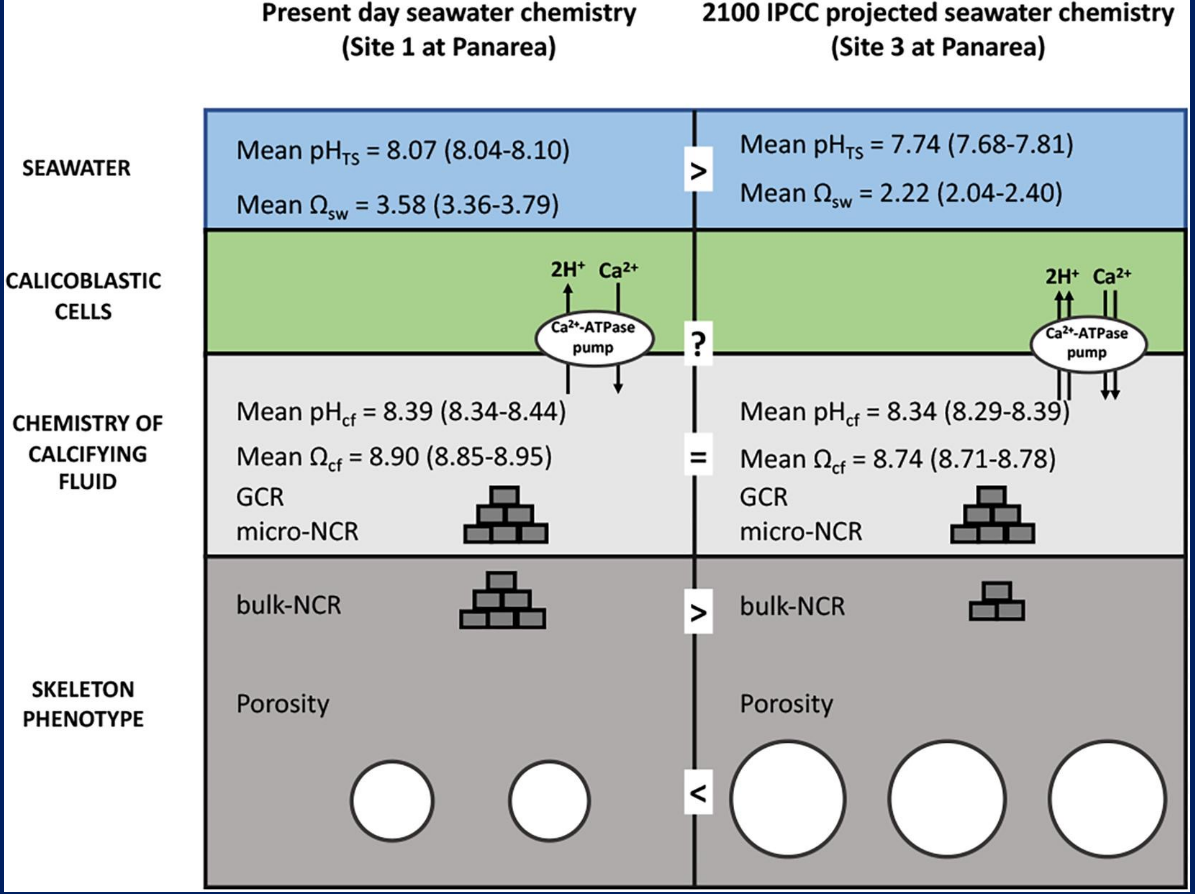
Net calcification rate = Gross calcification rate – Dissolution rate

($mg\ mm^{-2}\ yr^{-1}$) ($mg\ mm^{-2}\ yr^{-1}$) ($mg\ mm^{-2}\ yr^{-1}$)

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

Net calcification rate ($mg\ mm^{-2}\ yr^{-1}$) **=** **linear extension rate** ($mm\ yr^{-1}$) **×** **skeletal bulk density** ($mg\ mm^{-3}$)

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



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 CaCO3 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 calicoblastic 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	↓	?