Frederic Bassemayousse

Broad Phyletic Adaptation/Exaptation to Thermal Stress in Corals, and Implications for Extinction

by

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and

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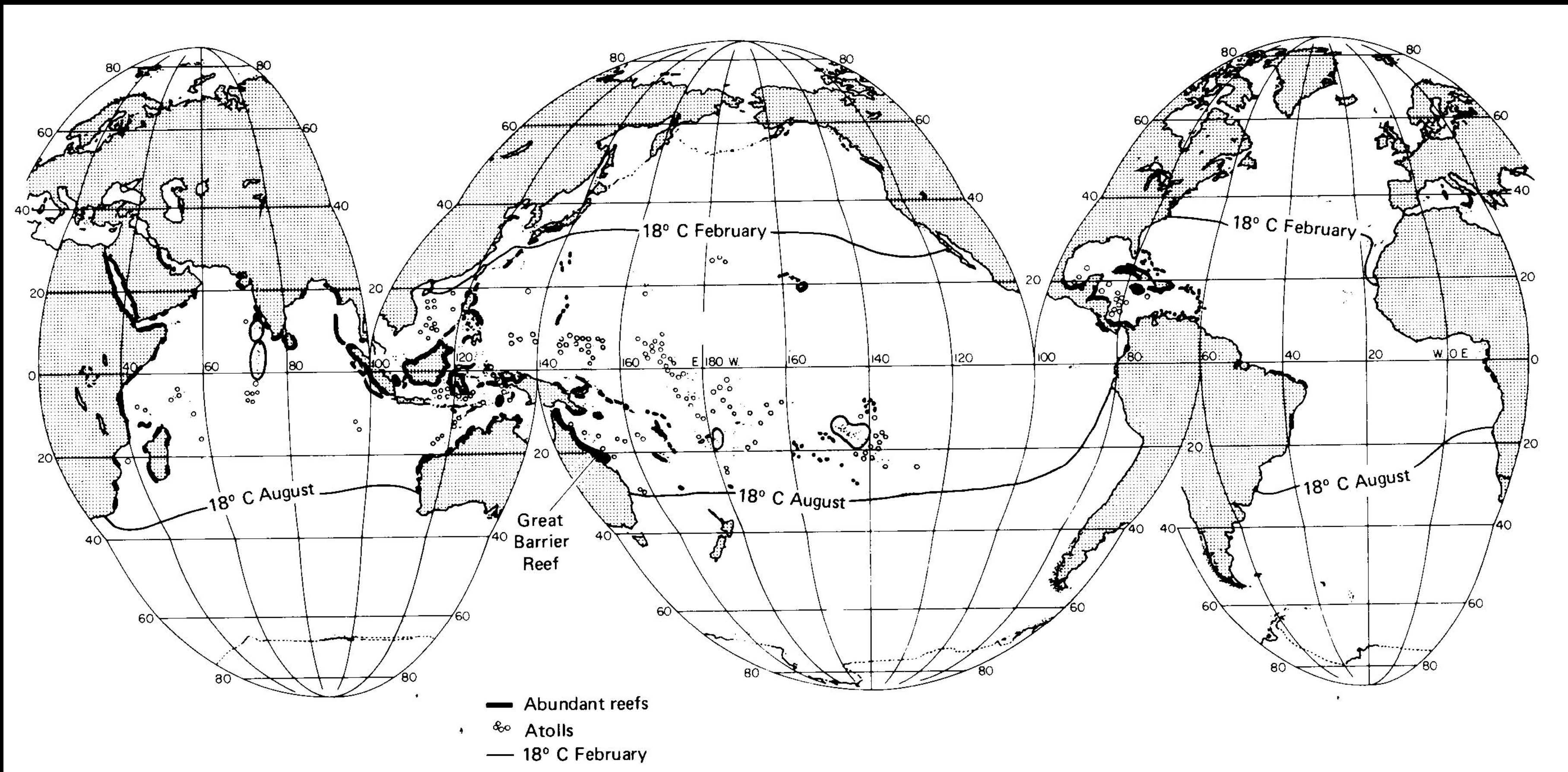
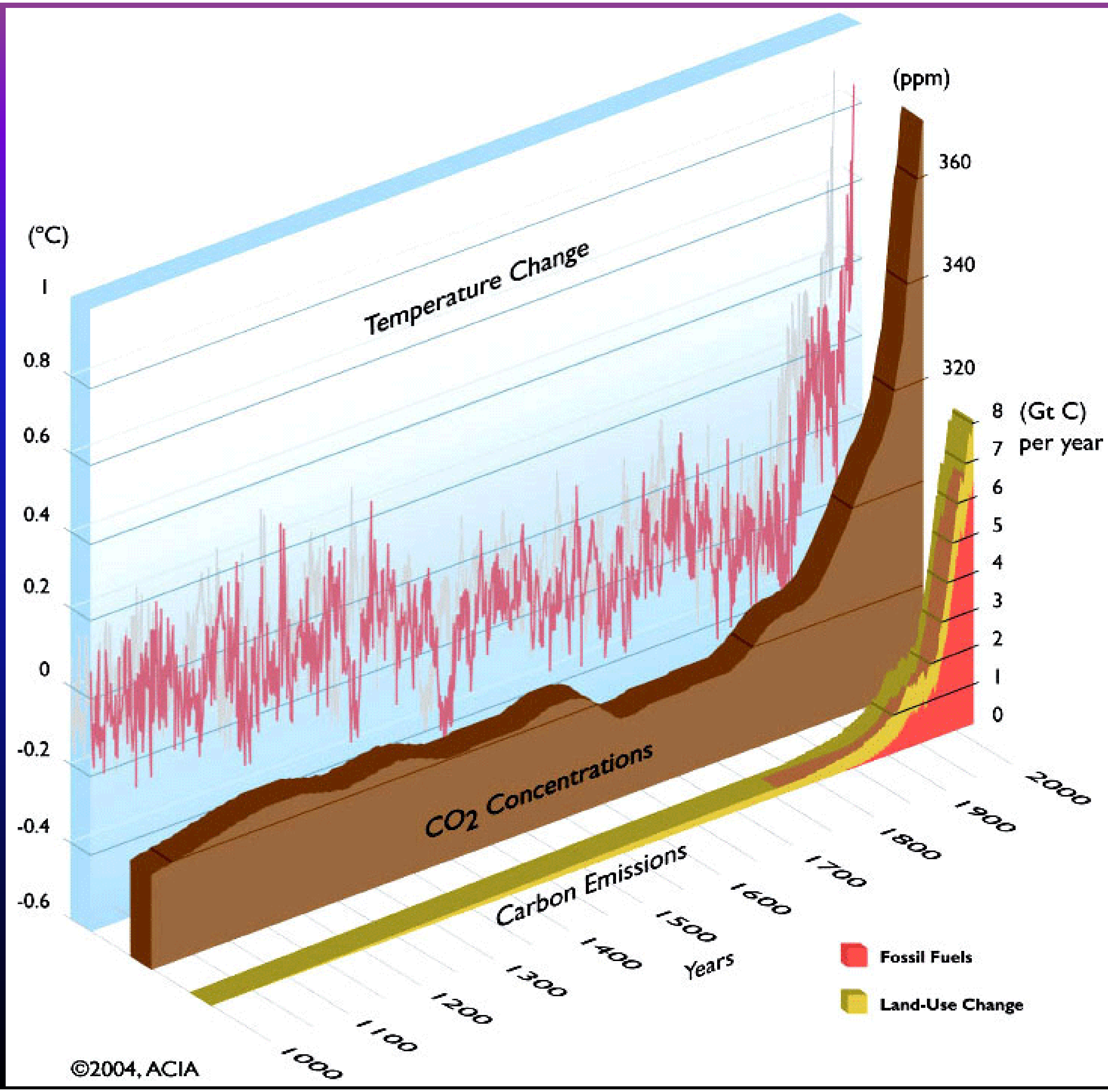
Muskegon, MI, USA

Hermatypic Coral Temperature Limits



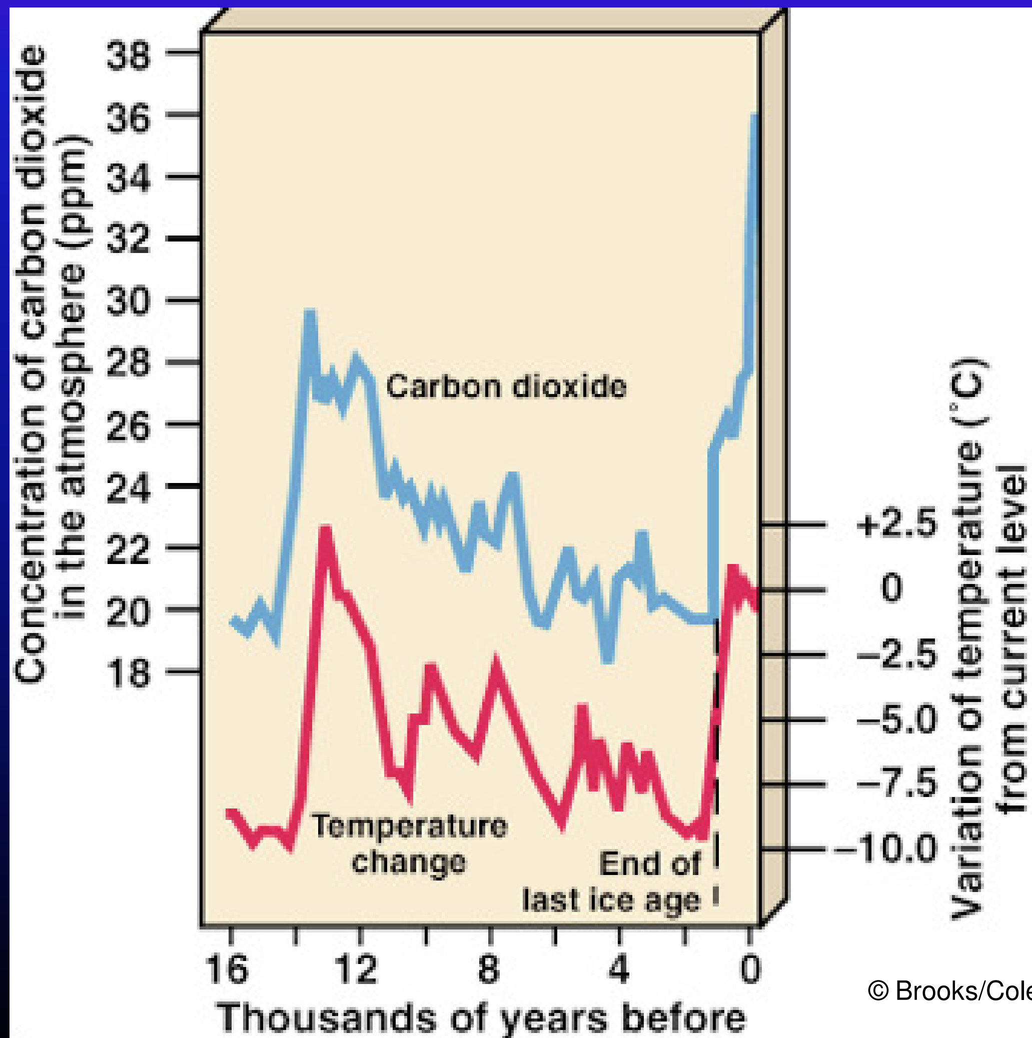
(Gross, 1977)



(°C)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Temperature Change
(ppm)
360
340
320
8 (Gt C)
per year
7
6
5
4
3
2
1
0
CO2 Concentrations
Carbon Emissions
Years
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
Fossil Fuels
Land-Use Change
©2004, ACIA

Atmospheric CO_2 and Temperature

Over the Past 160,000 Years



Mt. Hood
Oregon, USA

Glacier National Park

- 1910 – 150 glaciers
- 2004 – 30 glaciers, each reduced by 2/3 in size

Climate Change / Global Warming

. Between 1960s and 1985-1994, 10^{o}-24^{o} N lat.

- Pacific – increase of 1.79×10^8 J m^{-2} (Wong et al., 2001)

. Energy required to lift an apple to a table = One (1) Joule (J)

. 500 MW power plant produces 5×10^8 J per second

. Since the 1950s, our oceans have absorbed an extra 15×10^{22} J

. If warming ceased today, the temperature of the ocean

would not begin to reverse until the year 2075 (Church, 2007).

Outline

I. Coral Reefs and Bleaching – Background

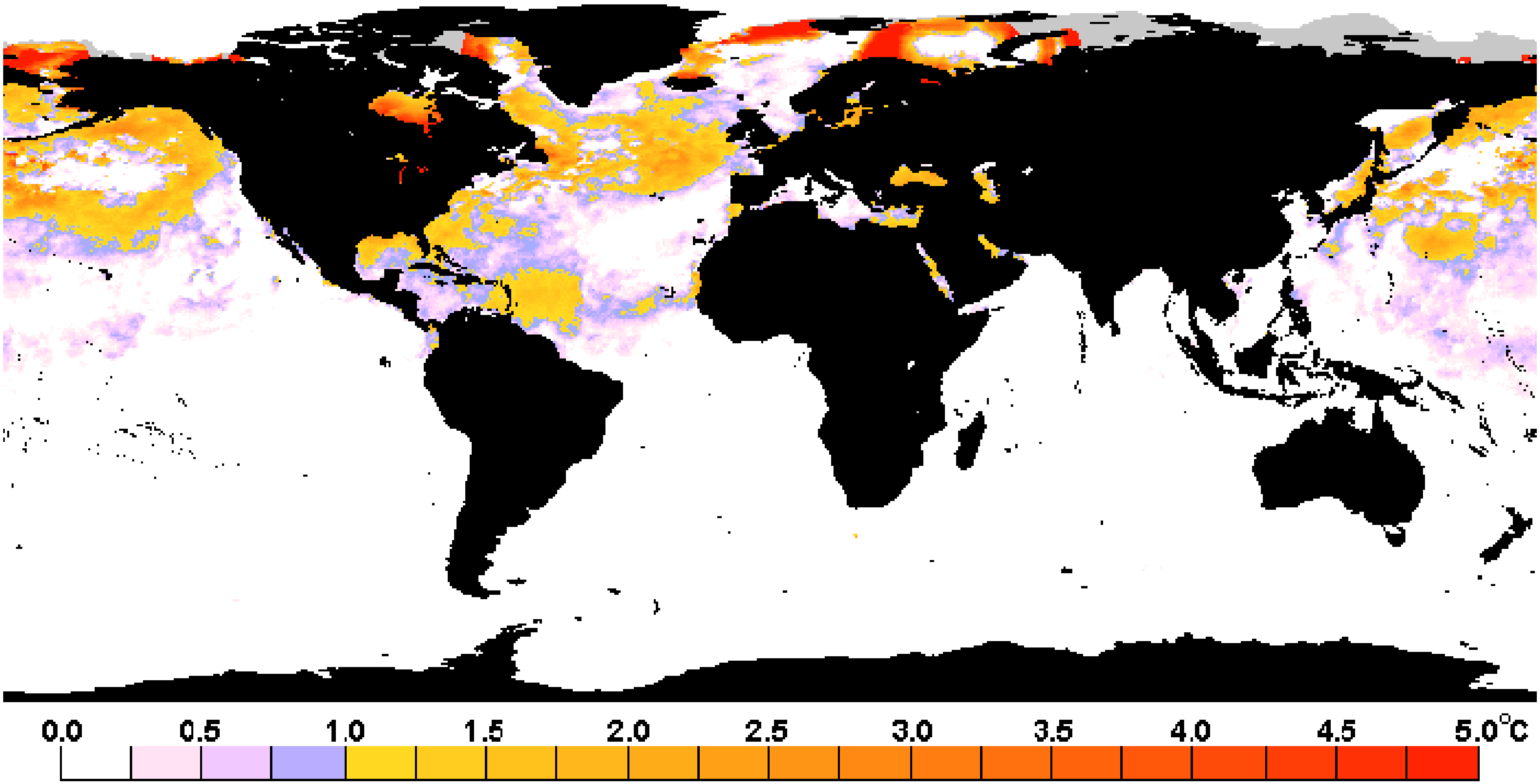
II. Experimentation and Results

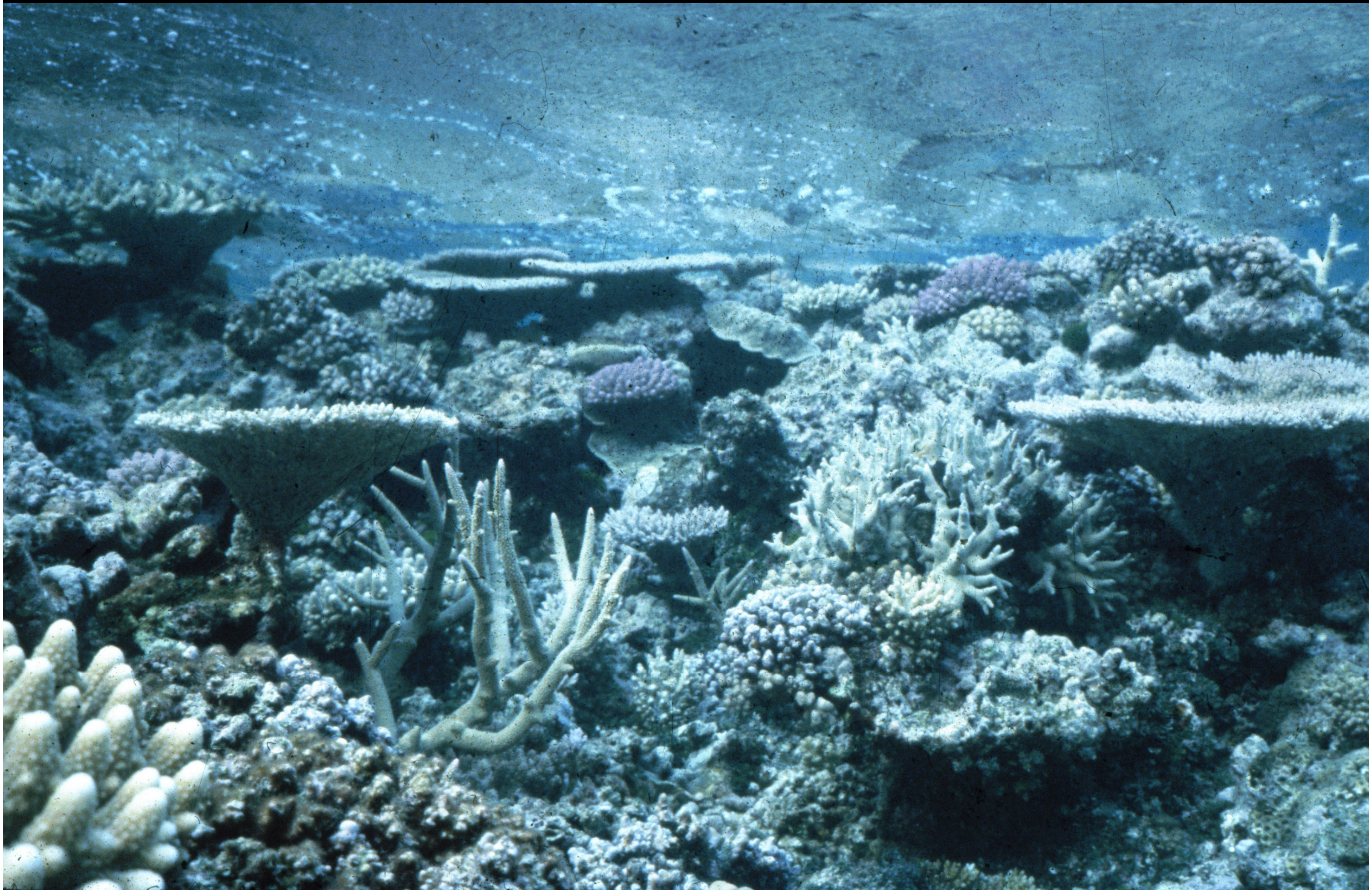
III. Questions and New Experimentation

IV. Implications

V. Predictions for Extinction of Zooxanthellate Organisms

Coral Bleaching Hotspots
(8/27/05)





Endosymbiotic Zooxanthellae

Present in Hermatypic Corals

NOAA

Reef Prior to Bleaching

www.cosmos.ne.jp/~kamiyama/full.htm

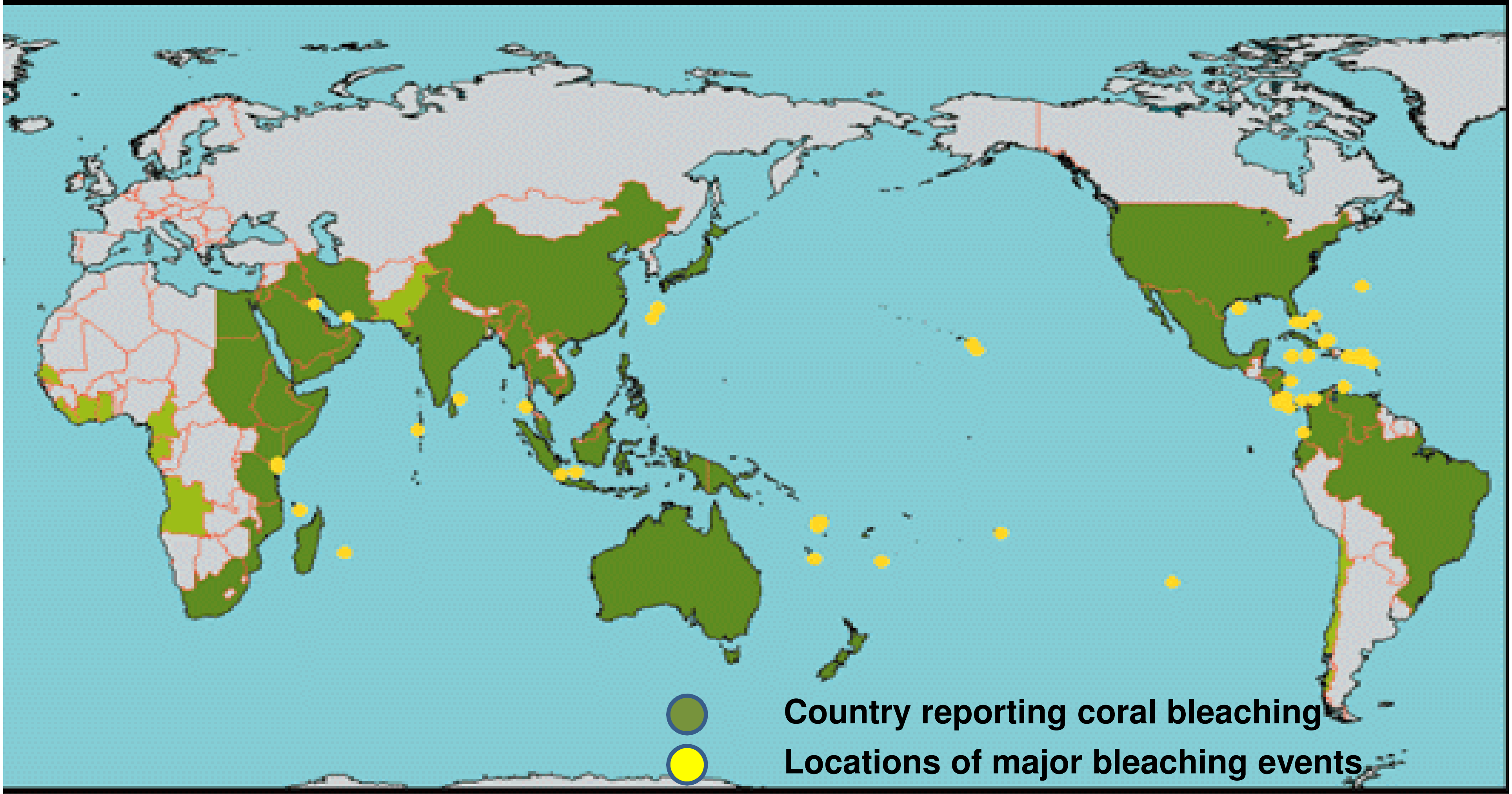
Reef During the Bleaching Process

www.cosmos.ne.jp~kamiyama/full.htm

1-2 Months after Bleaching

www.cosmos.ne.jp~kamiyama/full.htm

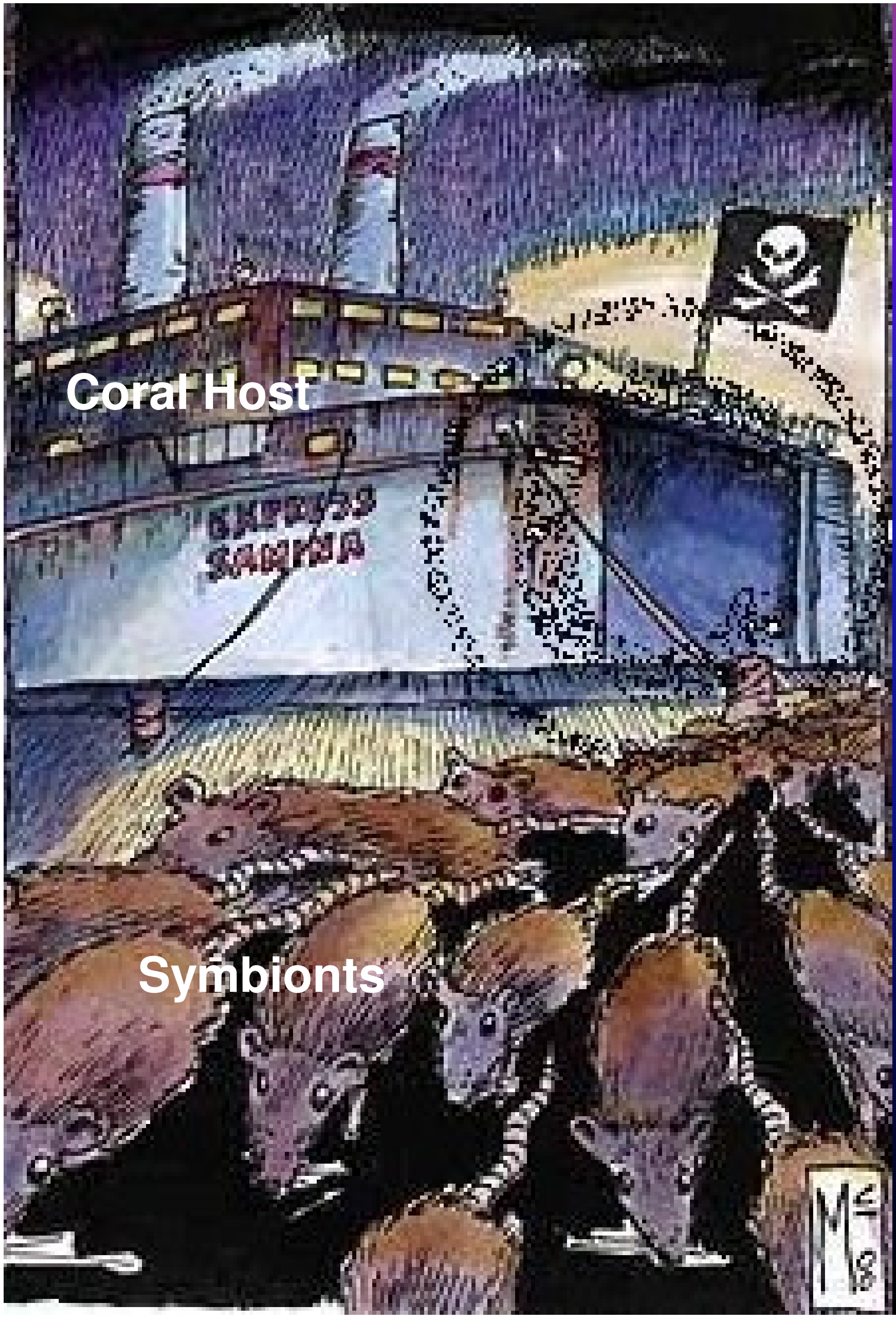
Regions of bleaching over the past 15 years



http://www.ncdc.noaa.gov/paleo/outreach/coral/sor/images/map7-large.gif

Coral Bleaching

- 1979 - First recorded coral bleaching event
- 1998 - El Nino yr - 48% of reefs in the W. Indian Ocean suffered bleaching;
  16% of the world's reefs appeared to have died.
- 2002 - 60-95% of the 110,000 sq mi of the Great Barrier Reef bleached



Coral Bleaching

Question:

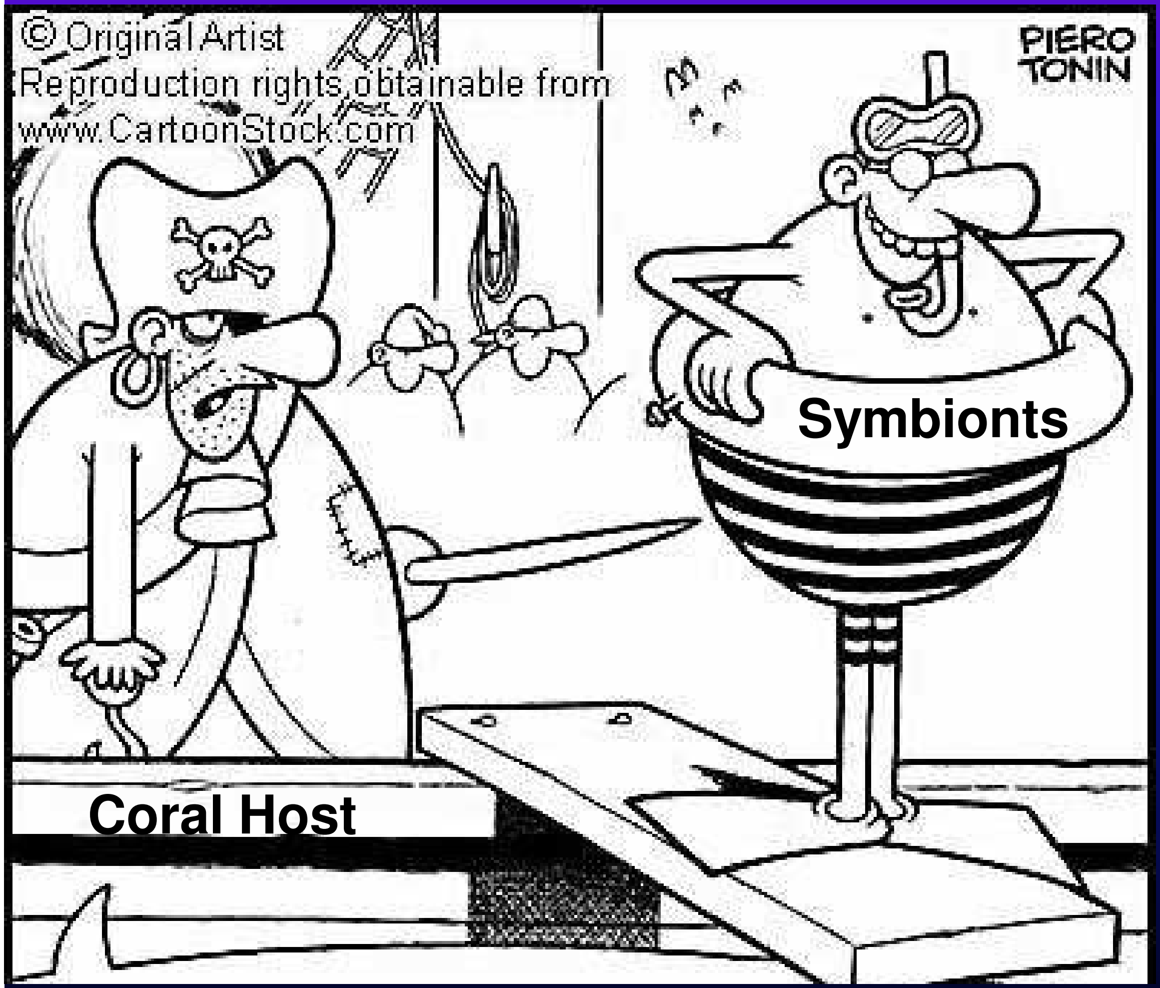
Are the zooxanthellae -

1) Rats Leaving a

Sinking Ship?

OR…

Media.photobucket.com/image/rats%20leaving%20sinking%20
ship/Freedonian/rats.jpg



Or -

2) Are the zooxanthellae

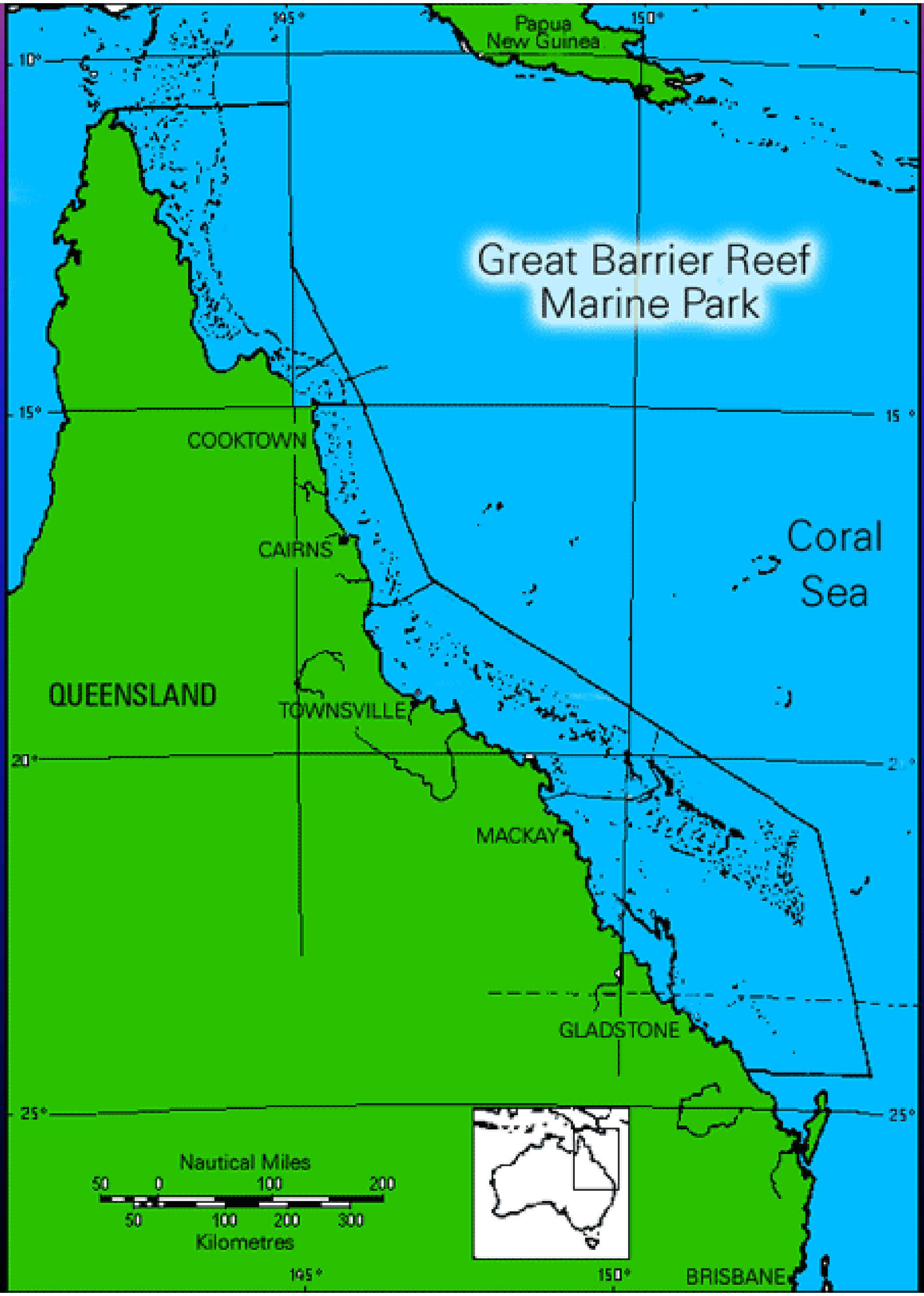
being made

to walk the plank?

http://www.cartoonstock.com/newscartoons/cartoonists/pto/lowres/pton182l.jpg

Experimentation with Scleractinian Corals –

Great Barrier Reef


Papua
New Guinea
Great Barrier Reef
Marine Park
Coral
Sea
COOKTOWN
CAIRNS
QUEENSLAND
TOWNSVILLE
MACKAY
GLADSTONE
BRISBANE
Nautical Miles
Kilometres

Programmed Cell Death

Apoptosis

- Series of biochemical events leading to characteristic cell morphology and death (incl. blebbing, cell membrane changes, shrinkage, nuclear fragmentation, chromatin condensation, and c-DNA fragmentation.)

- e.g., Differentiation of human fingers and toes in development of a fetus.

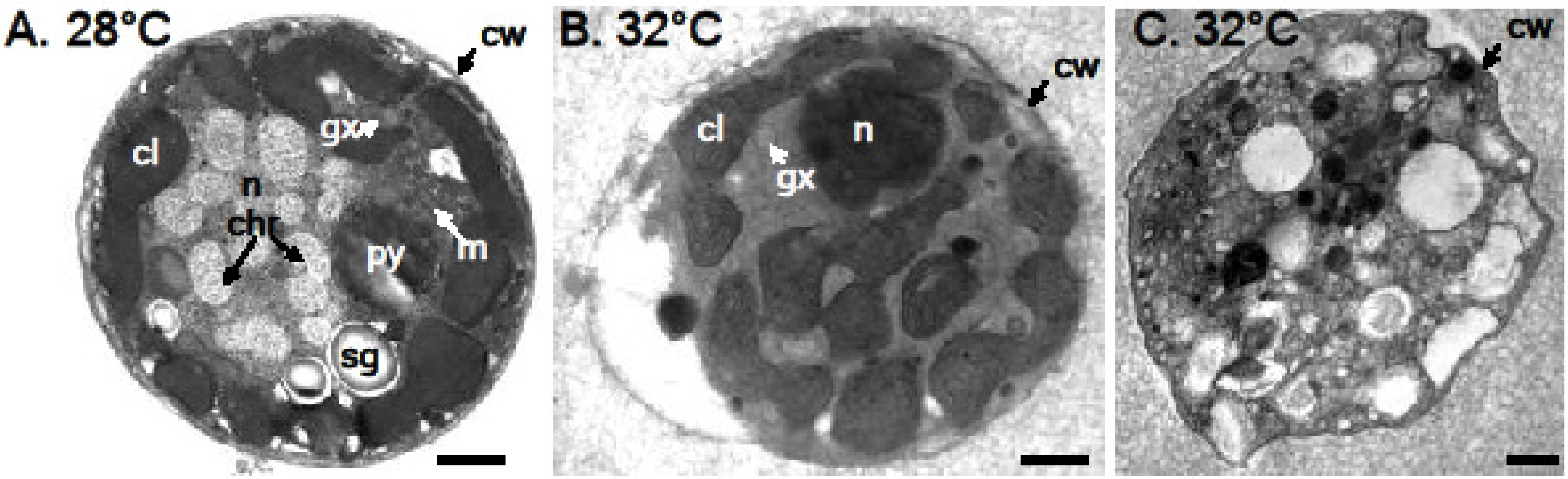
Necrosis

- Premature death of cells caused by acute cellular injury by external factors, such as infection, toxins, or trauma.

- e.g., Necrotic tissue resulting from a recluse spider bite (LA).

Symbiodinium sp. cells *in situ* within the coral *Acropora hyacinthus*

Control | Experimentally Increased Temperature



1 µm | 500 nm | 500 nm

Normal Cell | Apoptotic Cell | Necrotic Cell

Phycologia (2004) Volume 43 (6), 768–777

Published 30 December 2004

Apoptotic and necrotic stages of *Symbiodinium* (Dinophyceae) cell death activity: bleaching of soft and scleractinian corals

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[2]Louisiana Universities Marine Consortium (LUMCON), 8124 Highway 56, Chauvin, LA 70344, USA
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K.B. Strychar, P.W. Sammarco and T.J. Piva. 2004. Apoptotic and necrotic stages of *Symbiodinium* (Dinophyceae) cell
death activity: bleachi

Mechanisms which re
rently proposed mech
zooxanthellae of soft
croscopy (TEM) and
diagnostic characteris
blebbing, the formatio
and burst, followed b
showed that apoptotic
reduce the likelihood of recolonization upon expulsion from the host.

ELSEVIER

Journal of Experimental Marine Biology and Ecology
304 (2004) 99 121

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Bleaching as a pathogenic response in scleractinian corals, evidenced by high concentrations of apoptotic and necrotic zooxanthellae

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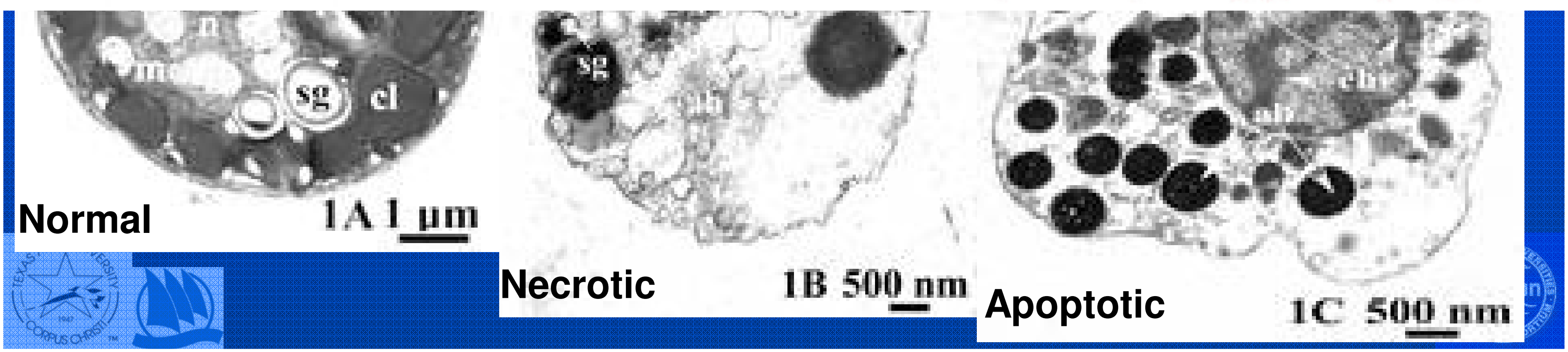
Abstract

yacinthus, Favites
sp., and *Xenia* sp.
rosis. Despite the
of apoptotic and
e cells decreases
temperatures by
y described, since
eath. The fraction
32 °C was greater
Xenia sp. fell but
rature tolerances.
sistant symbionts
d previously for
n, particularly for
an octocoral. Many of the viable cells, determined using Trypan blue staining techniques, are in fact

90% of the zooxanthellae in bleaching corals have been found in various stages of cell death



Answer:

The corals are the pirates.

The zooxanthellae are being made to

“Walk the Plank”.

Adapatation or Exaptation in the Coral Hosts?

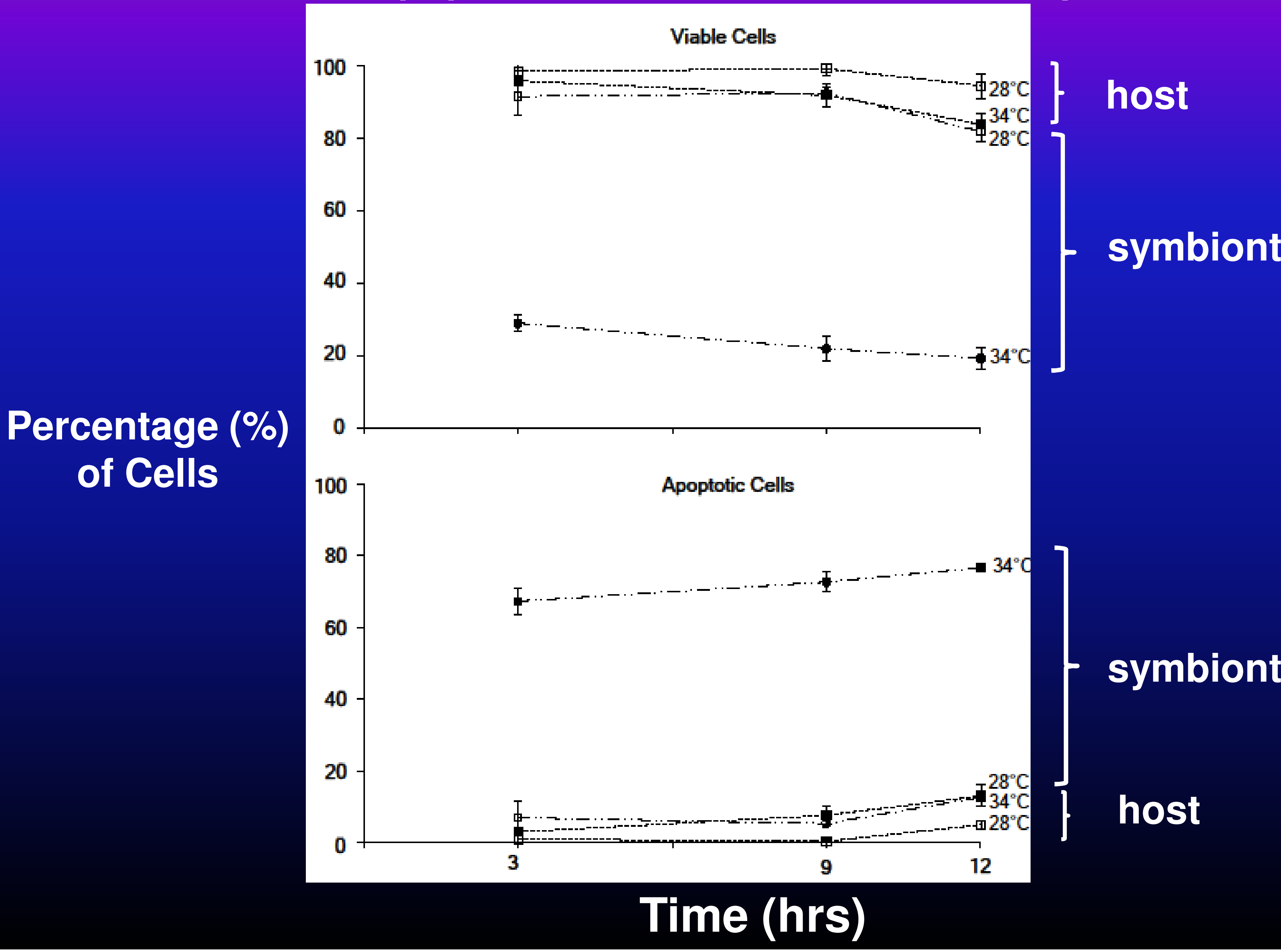
- Adaptation
  - Requires natural selection by these temperature conditions in the evolutionary history of this group
- Exaptation
  - Requires that some other physiological trait, previously existing, function known or unknown, serves to enhance temperature tolerance.
- “Pre-adaptation”
  - Synonymous with “exaptation”; pre-dates that term; but is no longer used due to its adoption by Creationists.

Acropora hyacinthus
(Acroporidae)

www.starfish.ch/c-invertebrates/corals.html

Acropora hyacinthus (host - Acroporidae)

Viable vs. Apoptotic Cells as a Function of Temperature

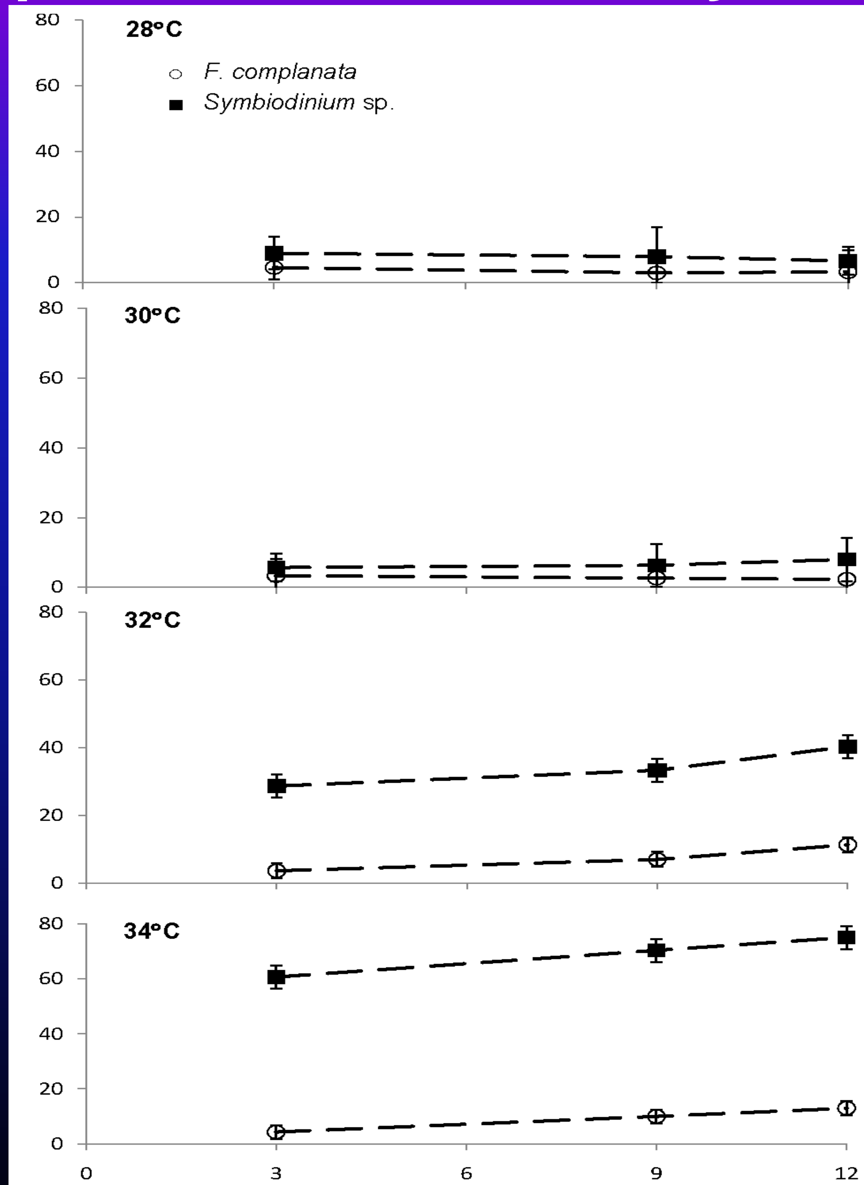


Favites complanata
(Faviidae)

Morze Koralowe
Pl.reeflex.net/tiere/a756_Favites_complanata.htm

Favia complanata
Apoptotic Cells, Host *vs.* Symbiont

Percentage (%) of Cells



Time (hrs)

F. complanata (Faviidae - coral)

Symbiodinium sp. (symbiont)

Porites solida
(Poritidae)

Similar Response to

Same Experimental Treatments

Zoo2.zool.kyoto-u.ac.jp/~hirose/Marine/corals/porites.htm

Questions -

- Is this temperature adaptation / exaptation restricted to only the zooxanthellate scleractinian corals?

- Does it extend to other coelenterate groups?

Different Cnidarian Taxonomic Group

- Cnidaria
  - Octocorallia
    - Alcyonacea
      - Alcyoniidae
      - Xeniidae

- Cnidaria
  - Anthozoans
    - Scleractinia

- Split off > 200-240 Mya

Sarcophyton ehrenbergi
(Alcyoniidae)

www.korallenfarm.de/Weiche.htm

Sarcophyton sp. bleached

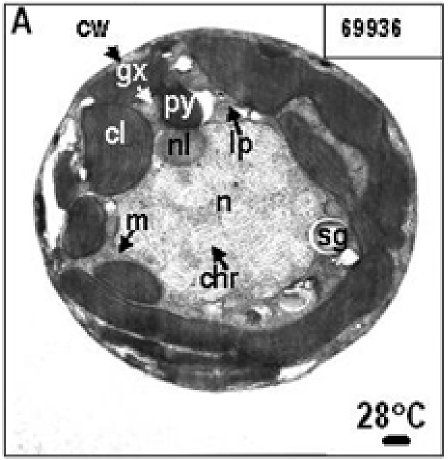
www.ratemyfishtank.com/friendemail.php/13611

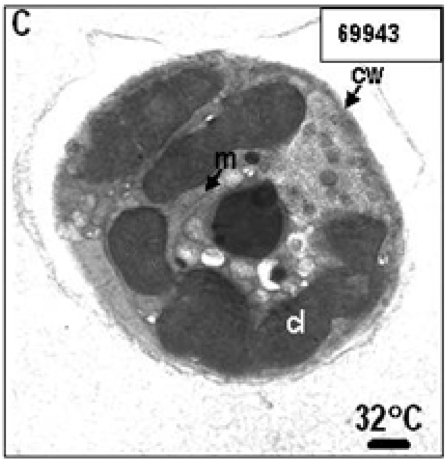
Sinularia lochmodes

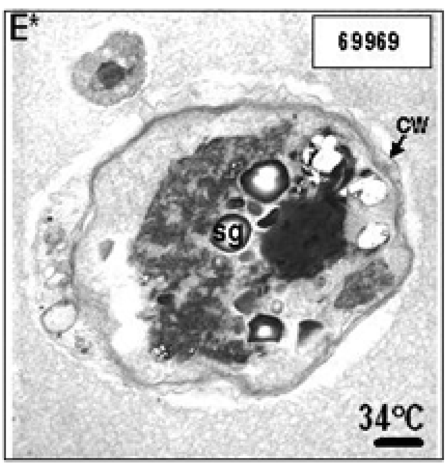
(Alcyoniidae)

Xenia elongata
(Xeniidae)

David Robb
www.davidrobb.me.uk/Marine/Invertebrates.htm







Sarcophyton ehrenbergi

Symbiodinium cells

Apoptosis

28°C – Normal

32°C - Early Apoptosis - Reversible

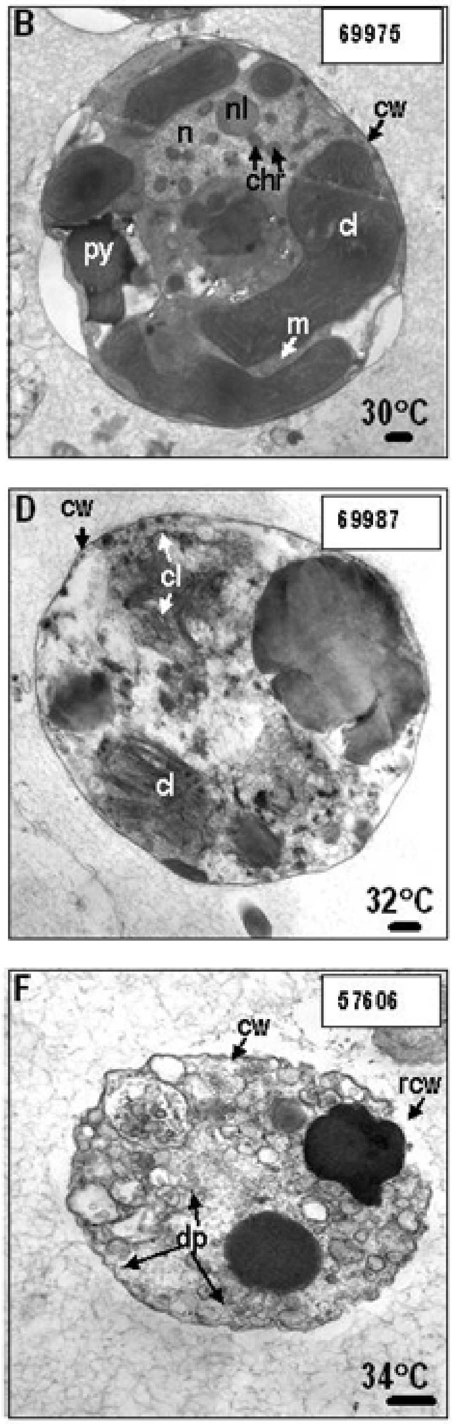
34°C - Late Apoptosis - Irreversible

Bar = 500 µm

Sarcophyton ehrenbergi

Symbiodinium cells

Necrosis



28°C – Normal

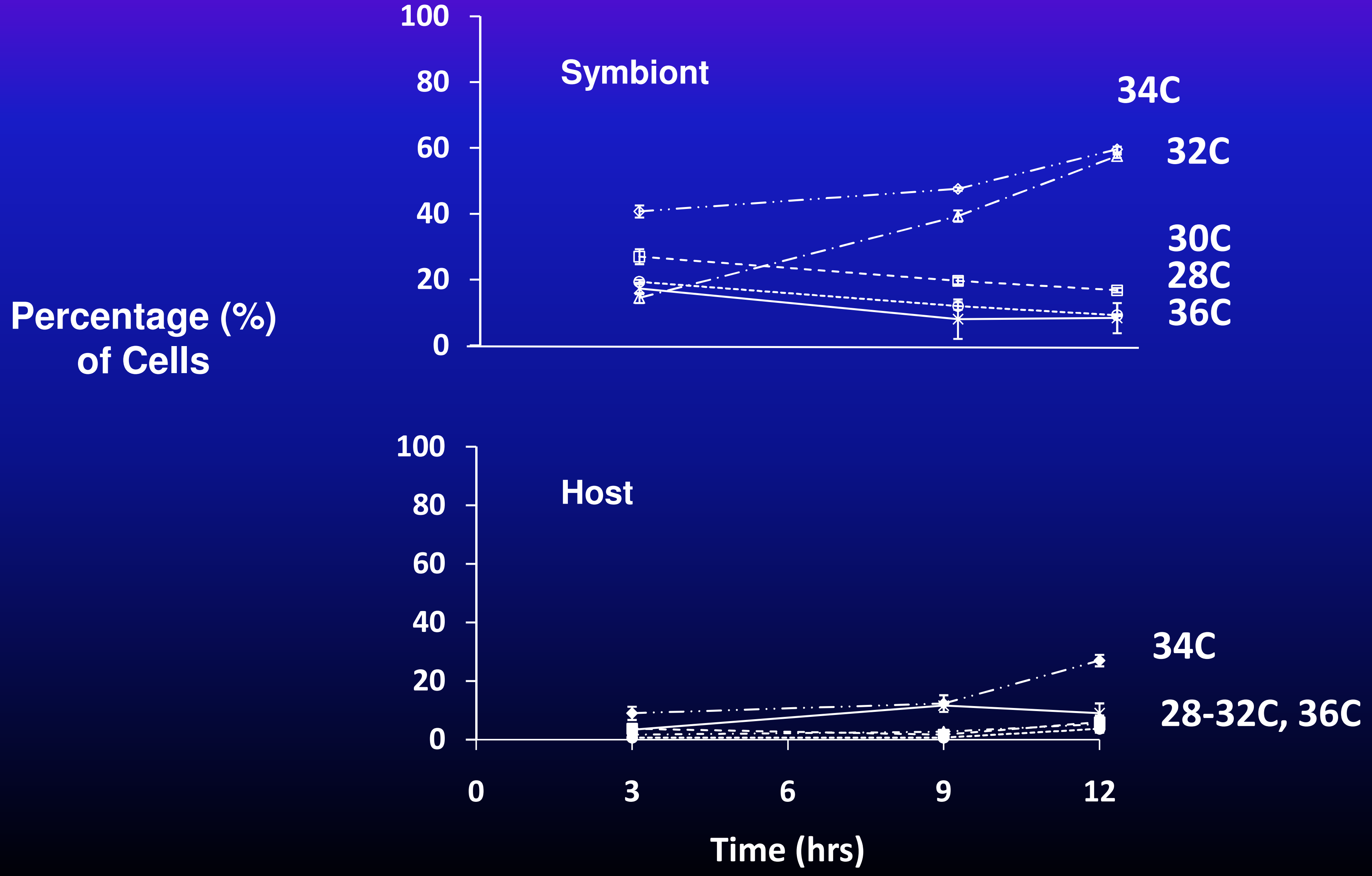
32°C - Early Necrosis

34°C - Late Necrosis

Bar = 500 µm

Sarcophyton ehrenbergi

Necrotic Cells



Similar Responses in the

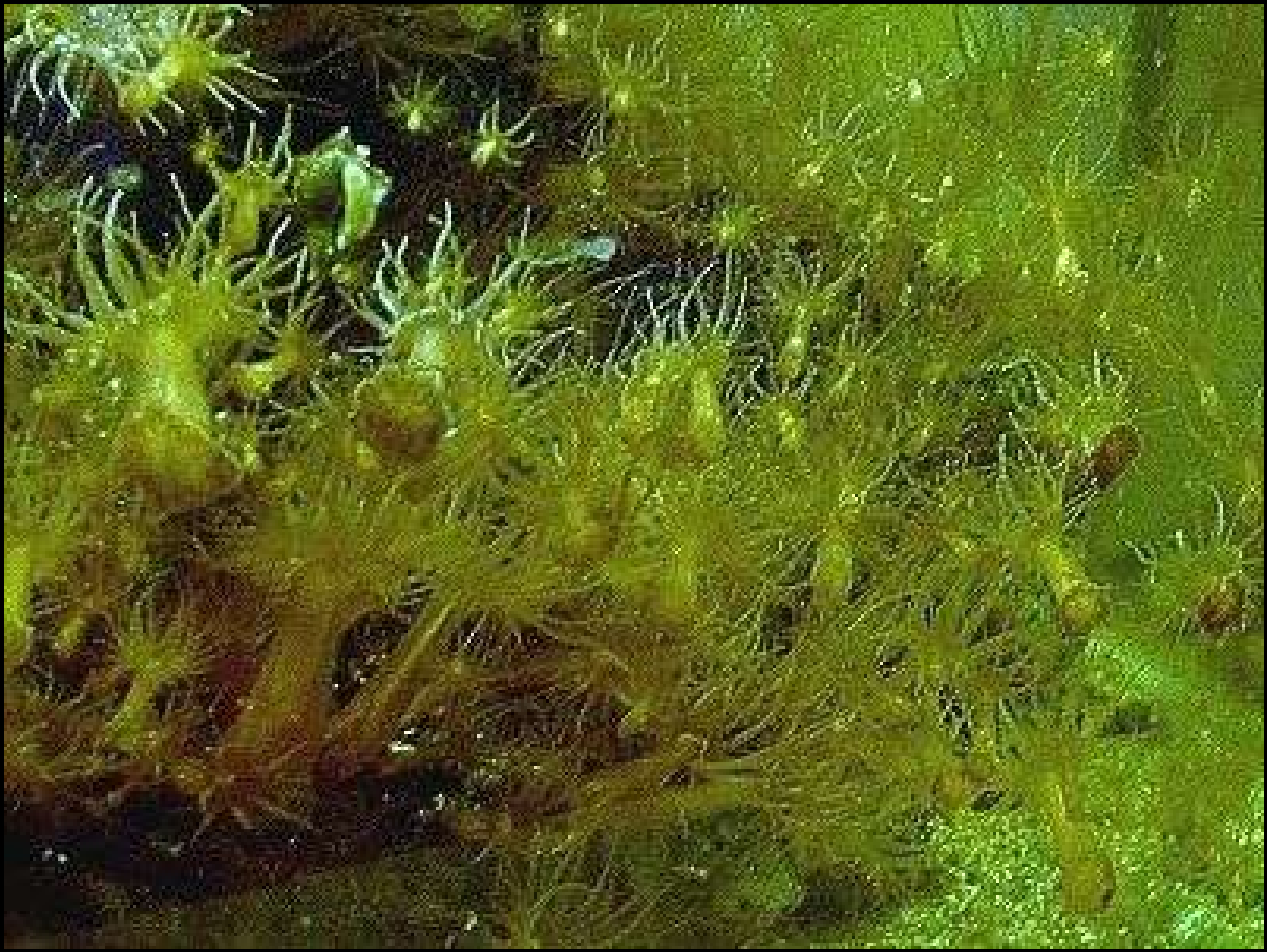
Other two Alcyonacean Species

(with variance)

Implications

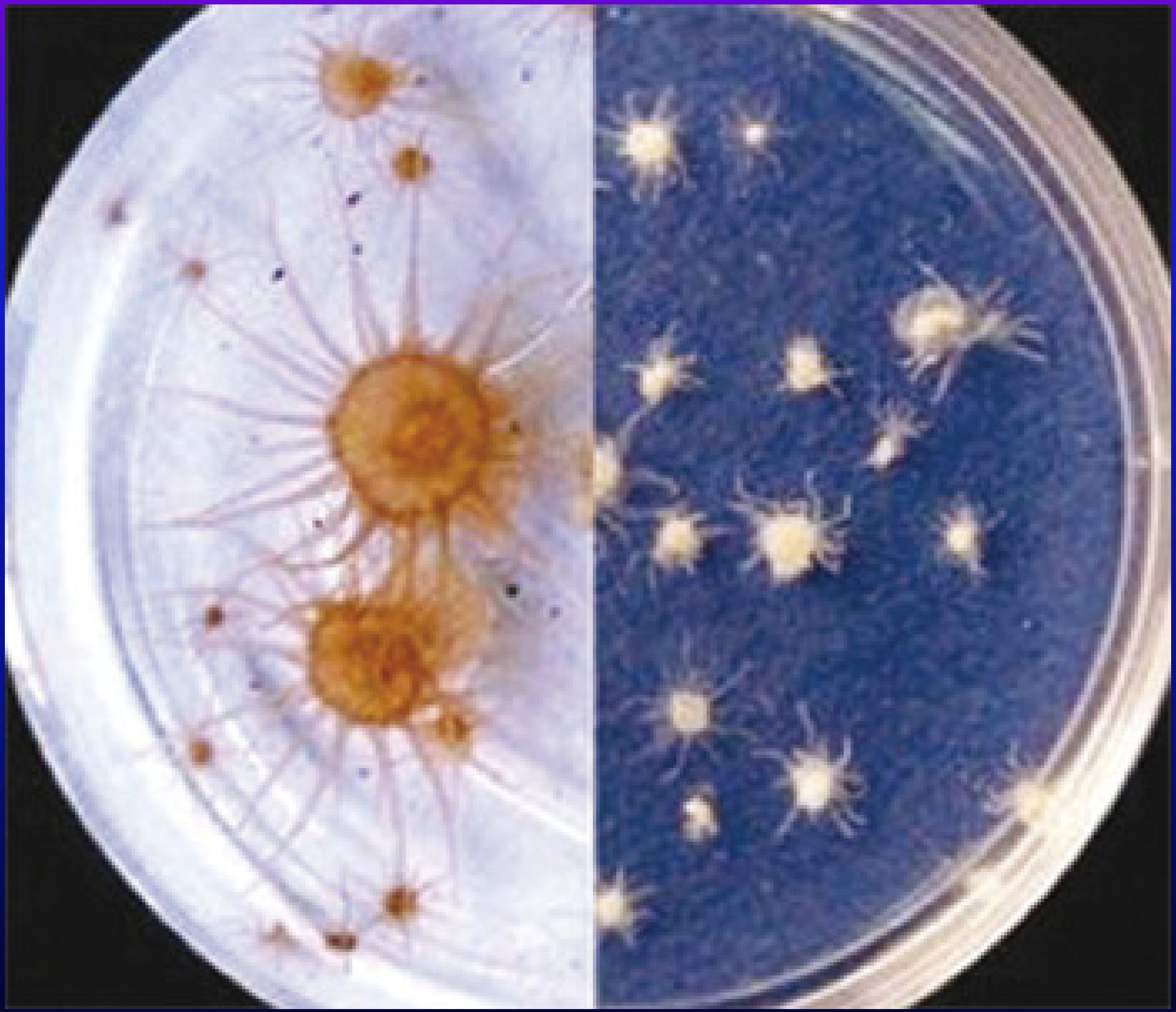
Zooxanthellae occur in hundreds of marine invertebrate species

Aiptasia patella
(Anthozoa, Actiniaria)



http://www.berghia.net/aiptasiaBiology.html

Aiptasia pallida, bleached



Jessie Kershner
www.coralscience.org/main/articles/symbiosis-3/aiptasia-a-bleaching

Cassiopeia xamachana

Scyphozoa

Jonathan Dunder

www.freeinfosociety.com/site.php?postnum=833

Amphiscolops langerhansi

(Platyhelmenthes)

Nanozine.blogspot.com/ 2007_05_01_archive.html

Tricacna gigas
(Mollusca, Bivalvia)

Ewa Barska
commons.wikimedia.org/wiki/File:Tridacna_gigas_by_Ewa_Barska.jpg

Tricacna gigas
Bleaching

James W. Fatheree
www.advancedaquarist.com/2010/8/inverts

Primary Conclusions

. Alcyonaceans

- Zooxanthellae are more sensitive to temperature than their hosts
- Same as in scleractinian corals
- Differences - more subtle

. Broad-scale phyletic character of exaptation in host cnidarians

- Verified across sub-classes
- Anthozoa, Scleractinia, and
- Octocorallia, Alcyonacea

Primary Conclusions

. Application to other cnidarians?

- Most likely, yes
- To varying degrees – dependent upon calcification
- Will affect nutritional status of organisms

Predictions (cont.)

- Latitudinal Expansion of Corals and other temperature-limited symbiotic organisms
  - e.g., *Acropora cervicornis* off Broward County, FL
- Similar observations made in Japan

http://www.cryofthewater.org/images/2.jpg

Predictions – (cont.)

- Emergence of a “Hyper-Tropical Oceanic Climatic Zone”
- Decrease in species diversity of corals and other zooxanthellate organisms
  - Due to species-specific sensitivity to increasing seawater temperatures

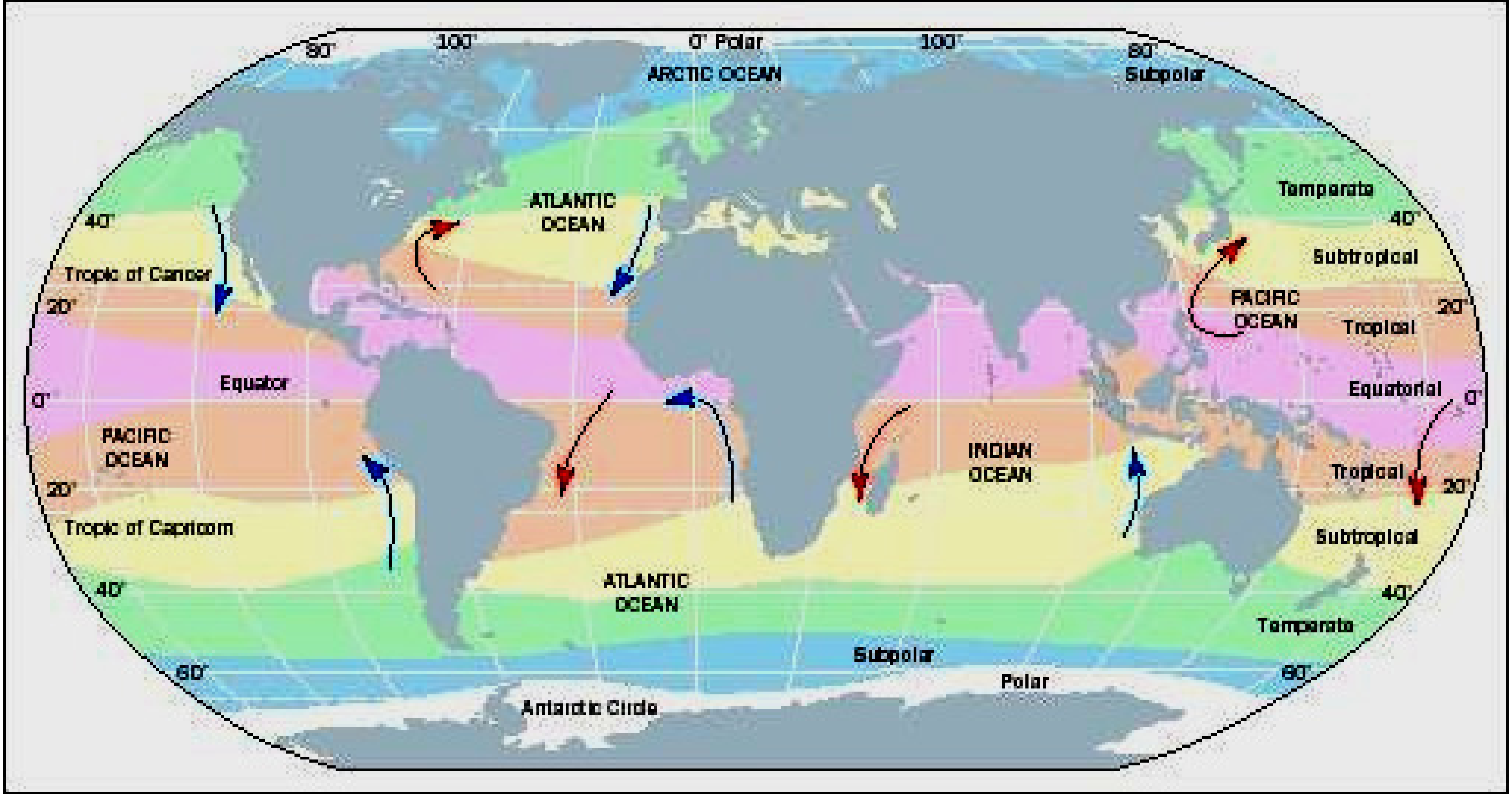
Predictions (cont.)

. No net gain in coral reef cover or numbers with time

- Increase in higher latitudes, but –

- High coral mortality in the warmer regions – lower latitudes

Oceanic Climatic Zones Today

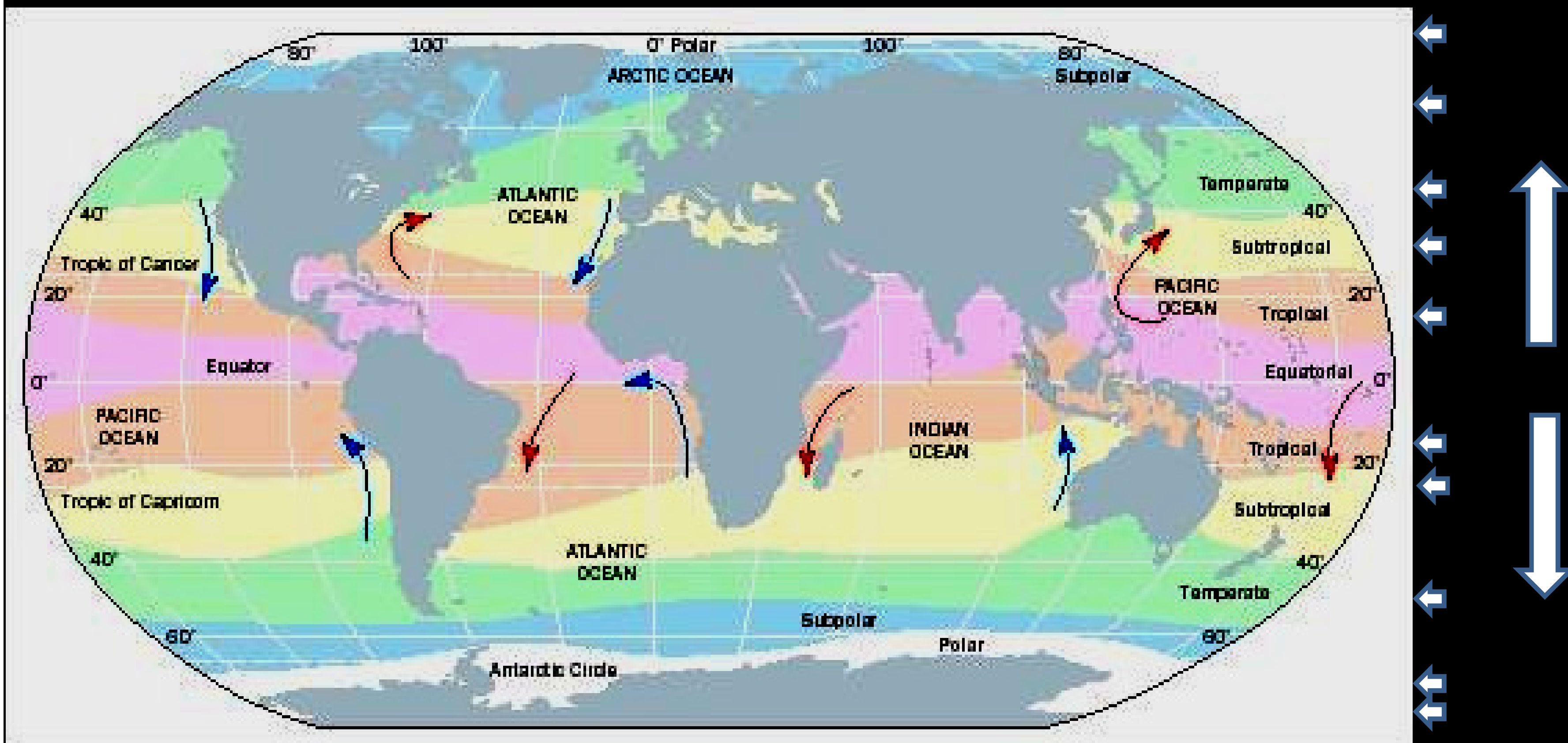


http://www.waterencyclopedia.com/images/wsci_01_img0100.jpg

Shrinking of Arctic Polar Cap and Permafrost Boundary

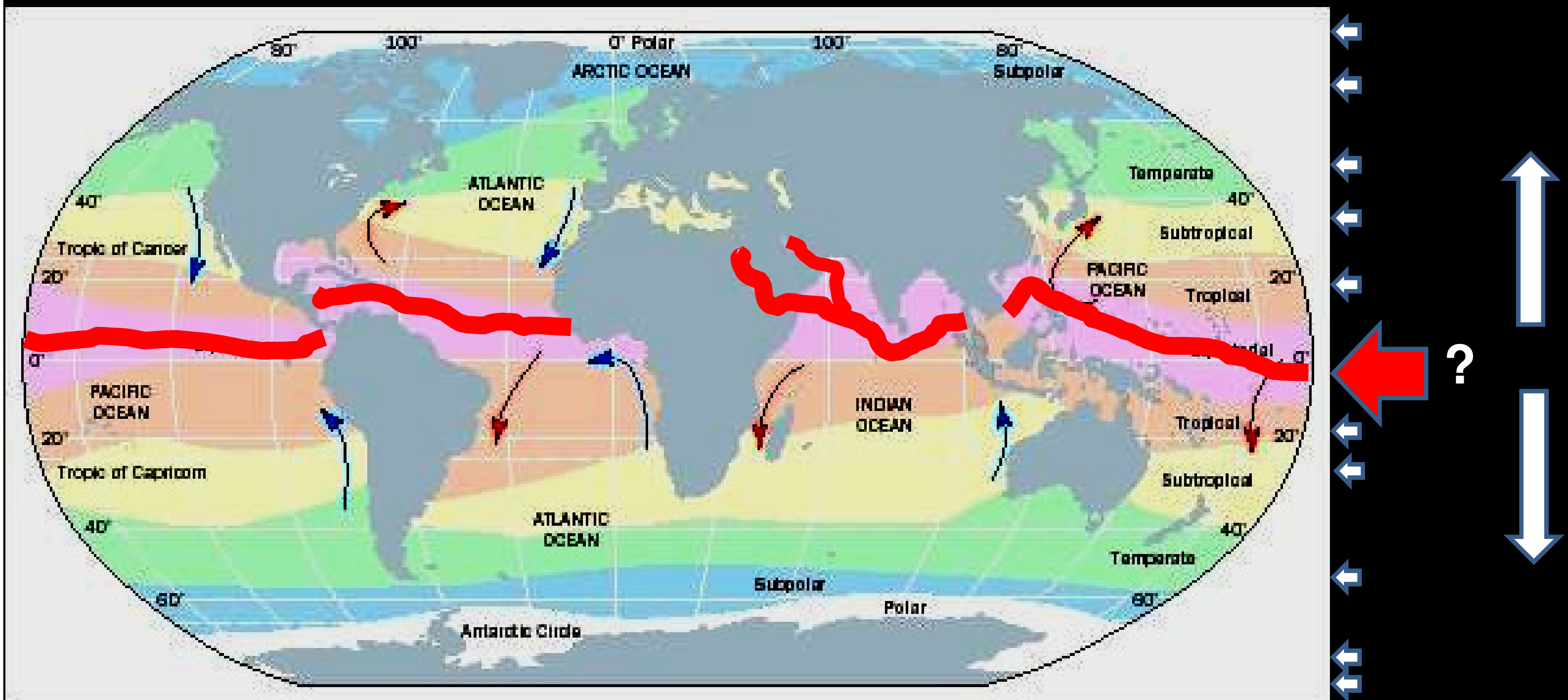
Maps.grida.no/go/graphic/shift-in-climatic-zones-arctic-scenario

Poleward Migration of Oceanic Climatic Zones



Expansion of Tropical Zone; Movement of Sub-Tropical, Temperate, and Sub-Polar Zones; Compression of Polar Zones

Possible Creation of a Hyper-Tropical Zone



Possible introduction of new Hyper-Tropical Zone, and decrease in species of diversity of corals and other zooxanthellate organisms therein


Thank you
www.panamainfo.com

Predictions (cont.)

. **Acquisition of replacement symbionts**

- e.g., *Prochloron*
- Would require host to recognize new symbiont as “self”
- Would require the same in new symbiont
- Would require new symbiont to reproduce inside host tissue
- Three known precedents of replacement

  Ectomycorrhizal fungi replacing arbuscular mycorrhizal fungi on tree roots

  Yeasts replacing *Buchnera* bacteria in aphids

  Endosymbiotic algae replacing plastids w. peridinin in some dinoflagellates.

- Possible, but tall order.

Sinularia sp., bleached

Kenneth K. Uy
Kensreef.tripod.com/reefdiary6.htm

Xenia sp., bleached

www.thereeftank.com/forums/f6/my-29-gallon-biocube-correct-pictures-134031-4.html

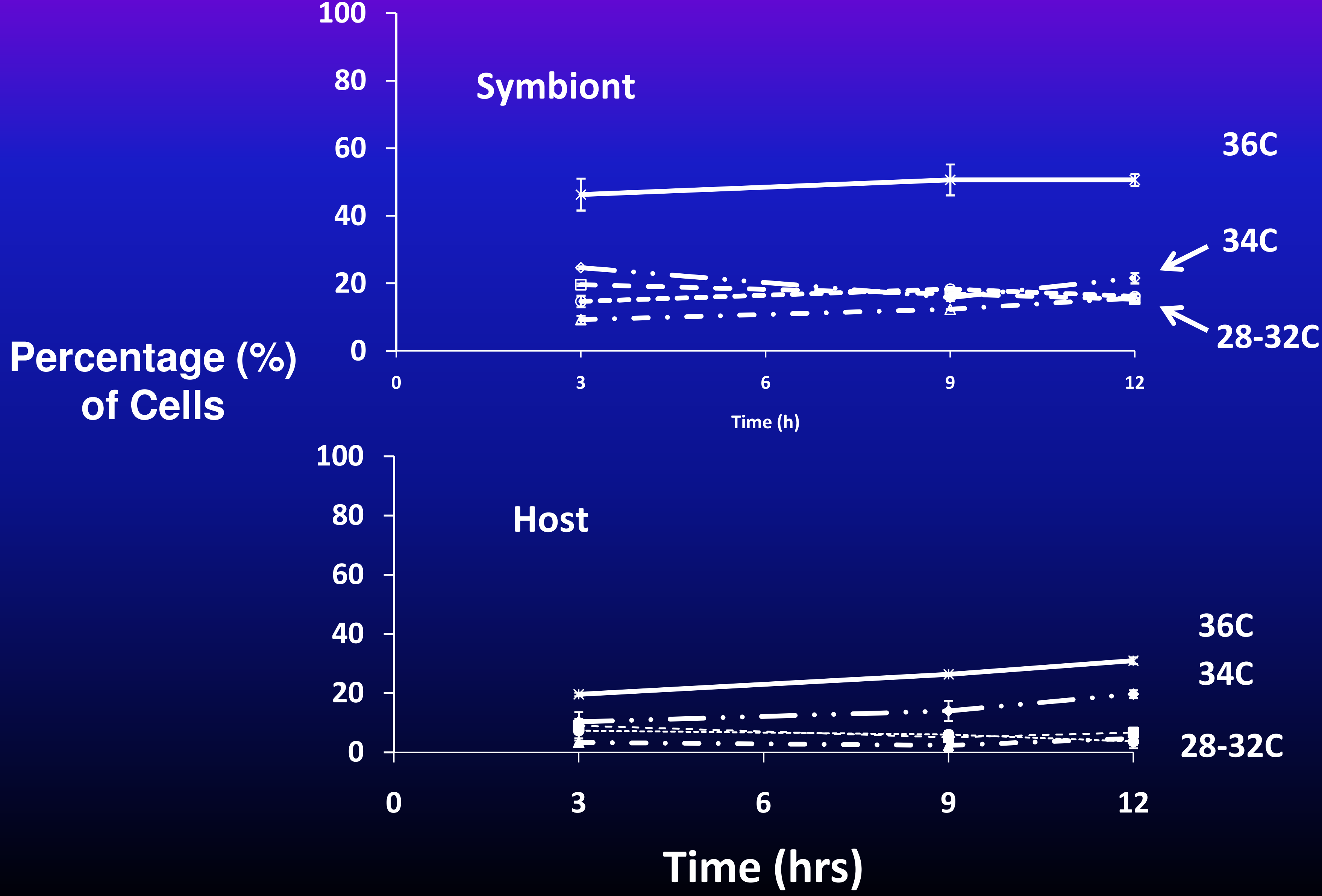
Predictions

Predictions

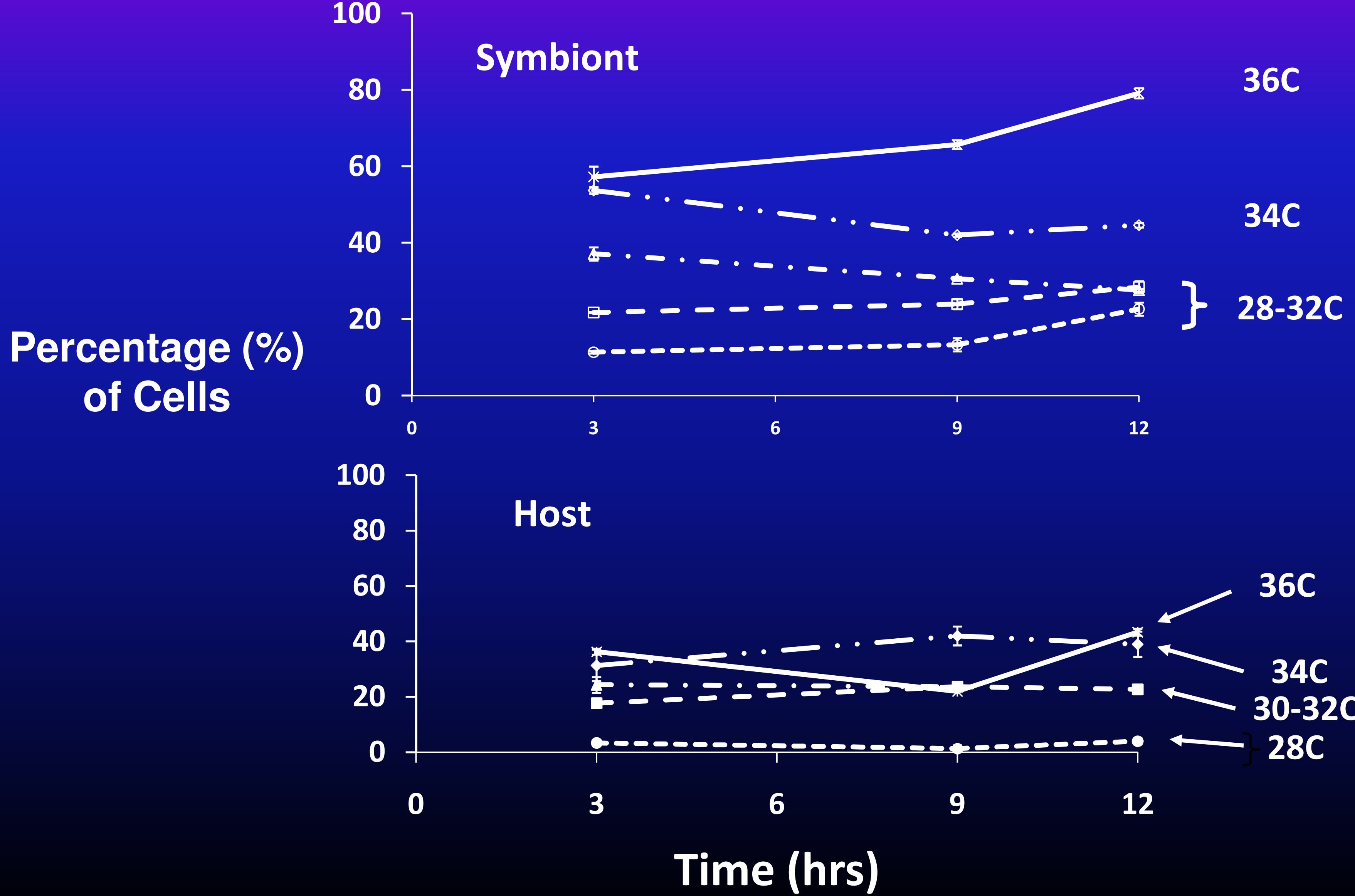
. Decreased dependence upon zooxanthellae by corals

- Revert to mutualism, commensalism, or absence
- Decrease dependence upon light
- Increase feeding rate / heterotrophy (documented)

Sinularia lochmodes
Necrotic Cells

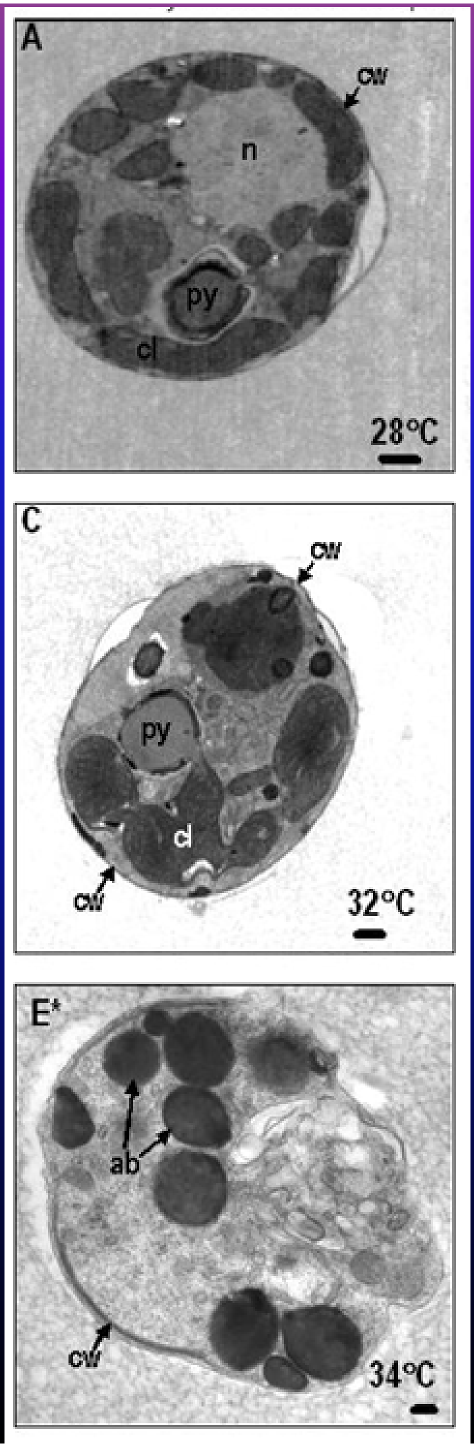


Xenia elongata
Necrotic Cells, *in situ*



Cell State
as a Function of
Time and Temperature

Frequencies



Sinularia lochmodes

Symbiodinium cells

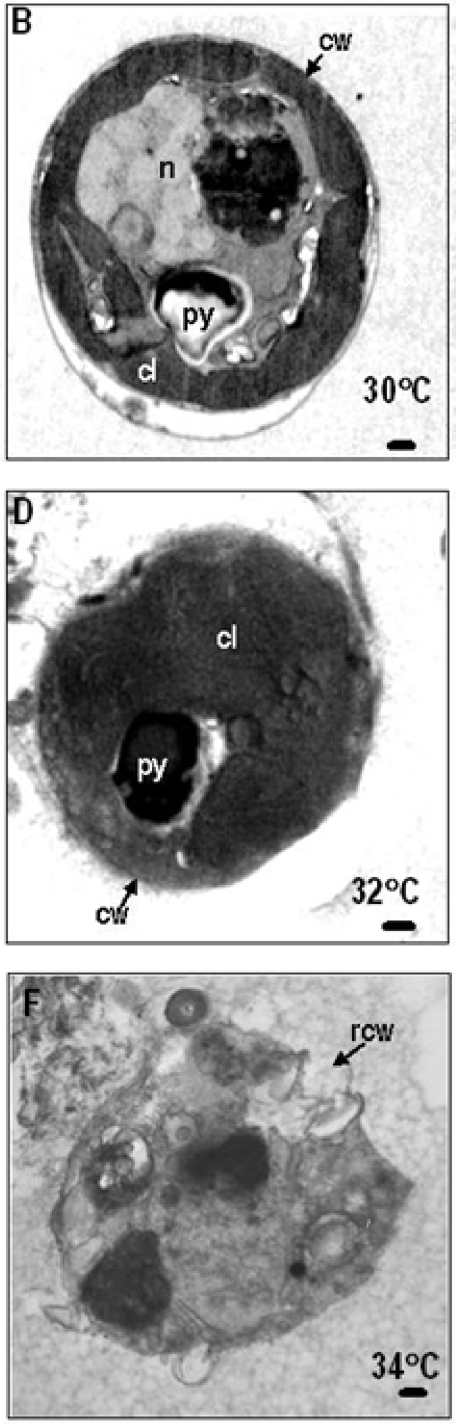
Apoptosis

28°C – Normal

32°C - Early Apoptosis - Reversible

34°C - Late Apoptosis - Irreversible

Bar = 500 μm



Sinularia lochmodes

Symbiodinium cells

Necrosis

28^{o}C – Normal

32^{o}C - Early Necrosis

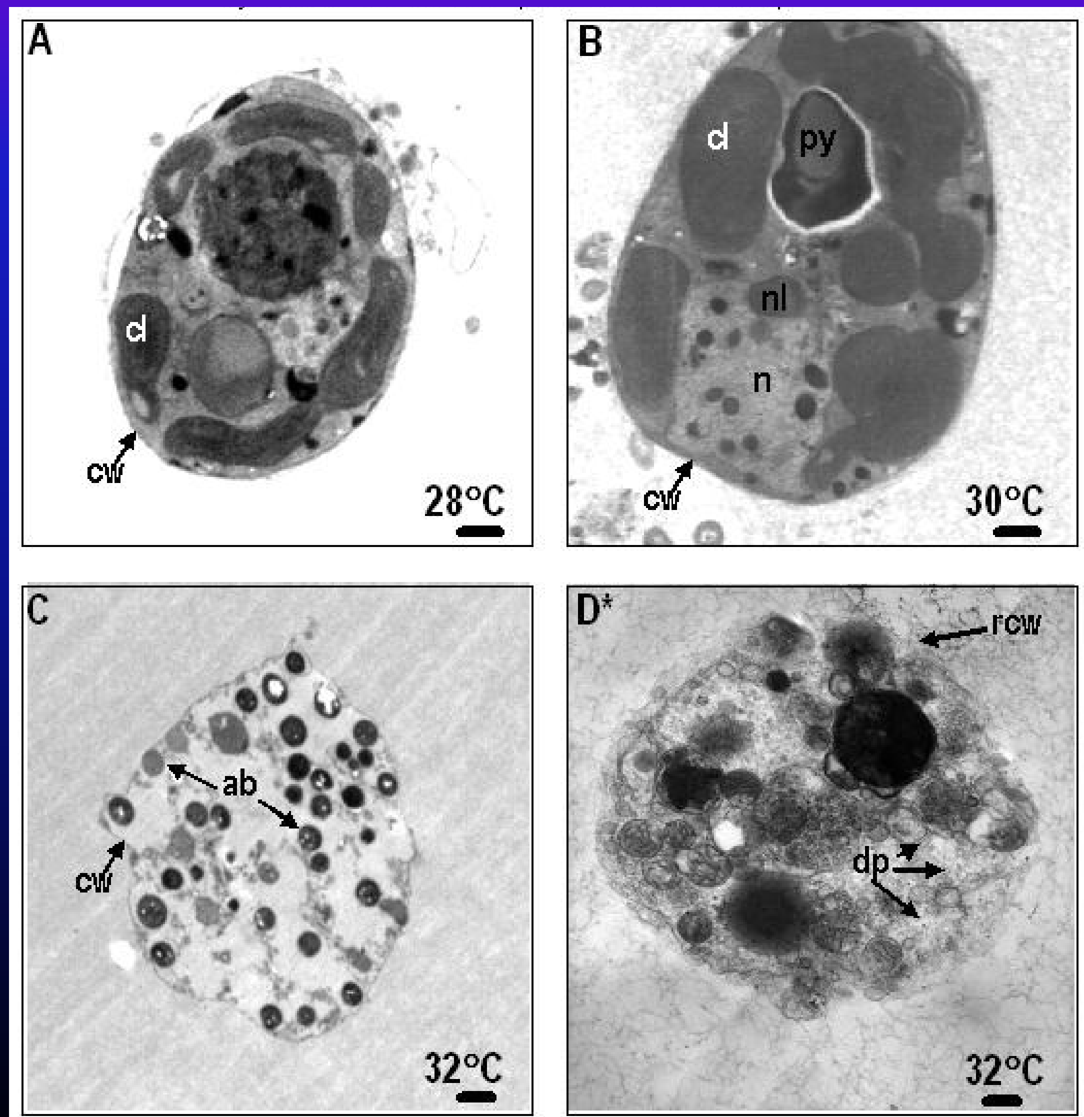
34^{o}C - Late Necrosis

Bar = 500 µm

Xenia elongata
Symbiodinium cells
Apoptosis and Necrosis

28°C
Normal

30°C
Evidence of Cell Mortality



32°C
Late stage Apoptosis, Irreversible

32°C
Late stage Necrosis, Irreversible

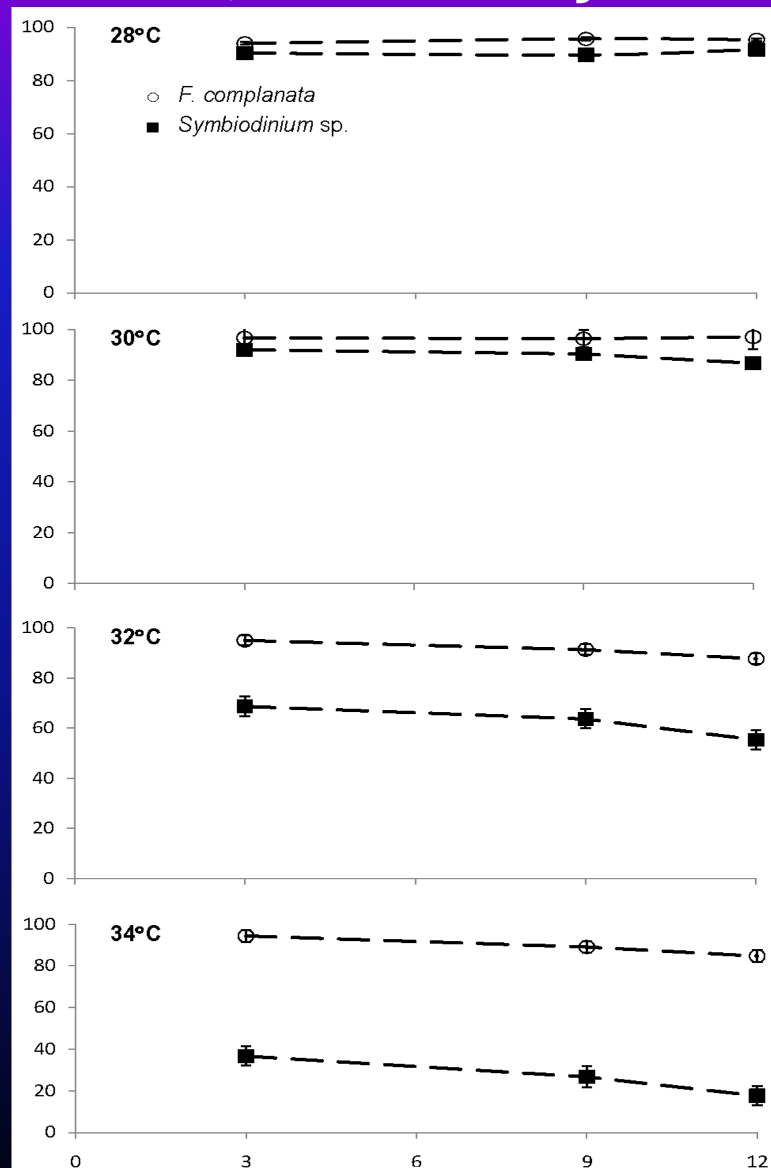
Bar = 500 µm

Cell State / Ultrastructure as a Function of Temperature

Transmission Electron Micrographs (TEMs)

Favia complanata (Faviidae)
Viable Cells, Host *vs.* Symbiont

Percentage (%) of Cells



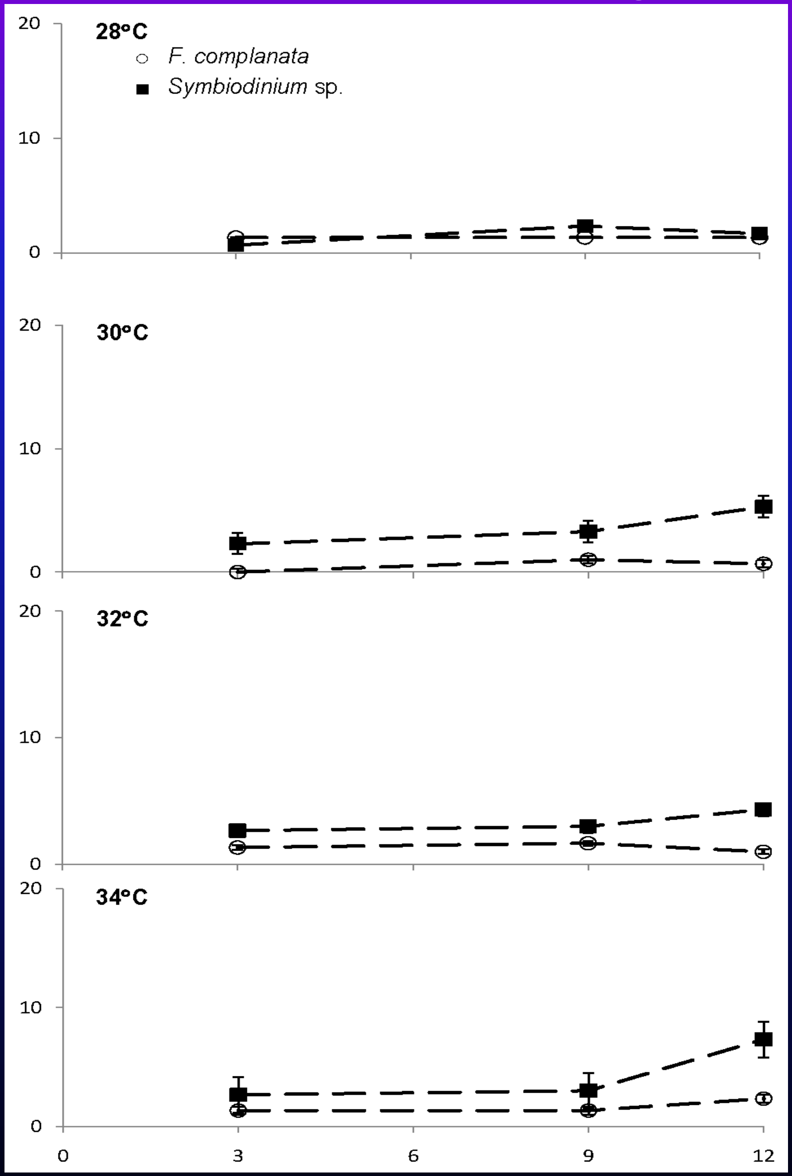
Time (hrs)

F. complanata (Faviidae - coral)

Symbiodinium sp. (symbiont)

Favia complanata
Necrotic Cells, Host *vs.* Symbiont

Percentage (%) of Cells

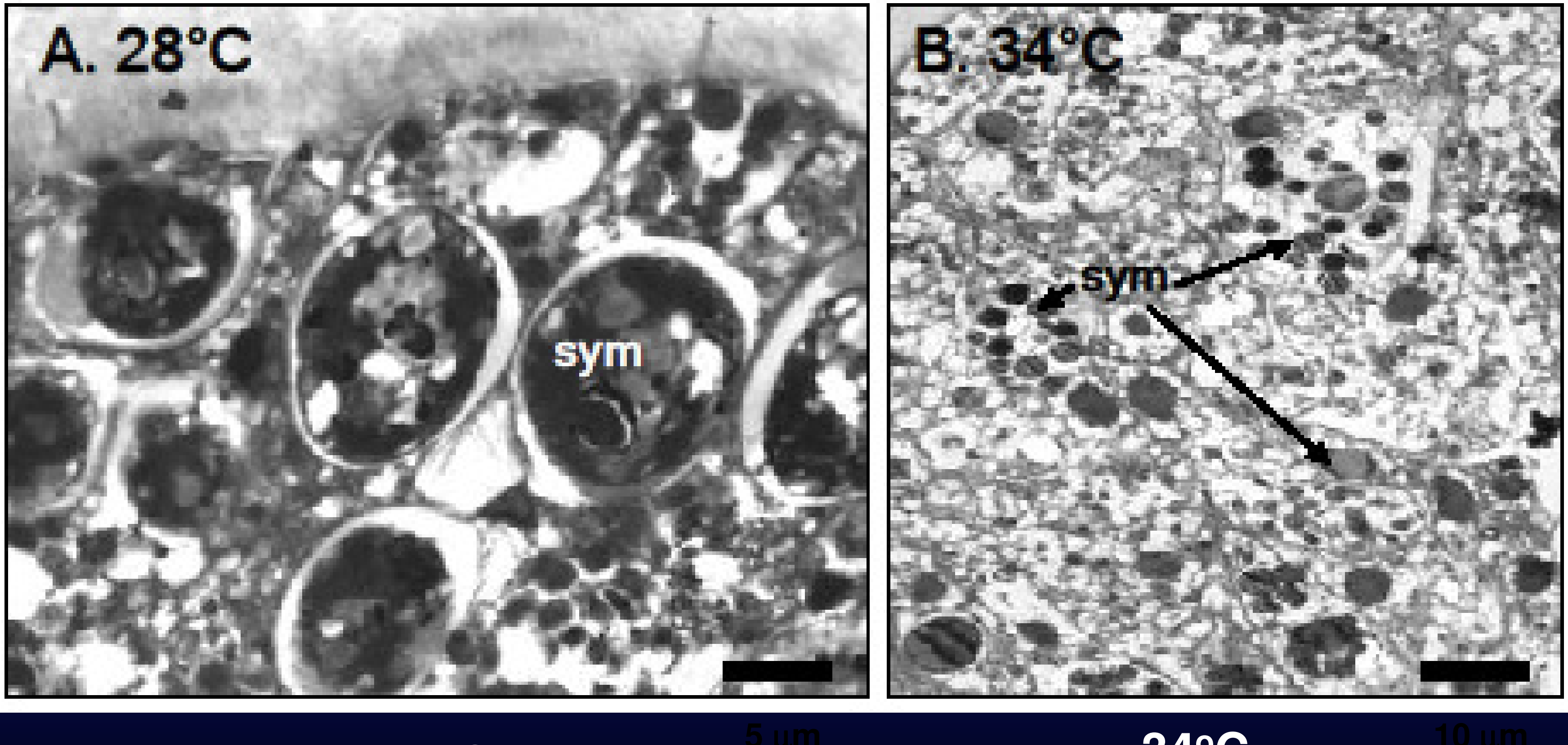


Time (hrs)

F. complanata (Faviidae - coral)

Symbiodinium sp. (symbiont)

Host *(Acropora hyacinthus)* and Symbiont *(Symbiodinium* sp.) cells *in situ*

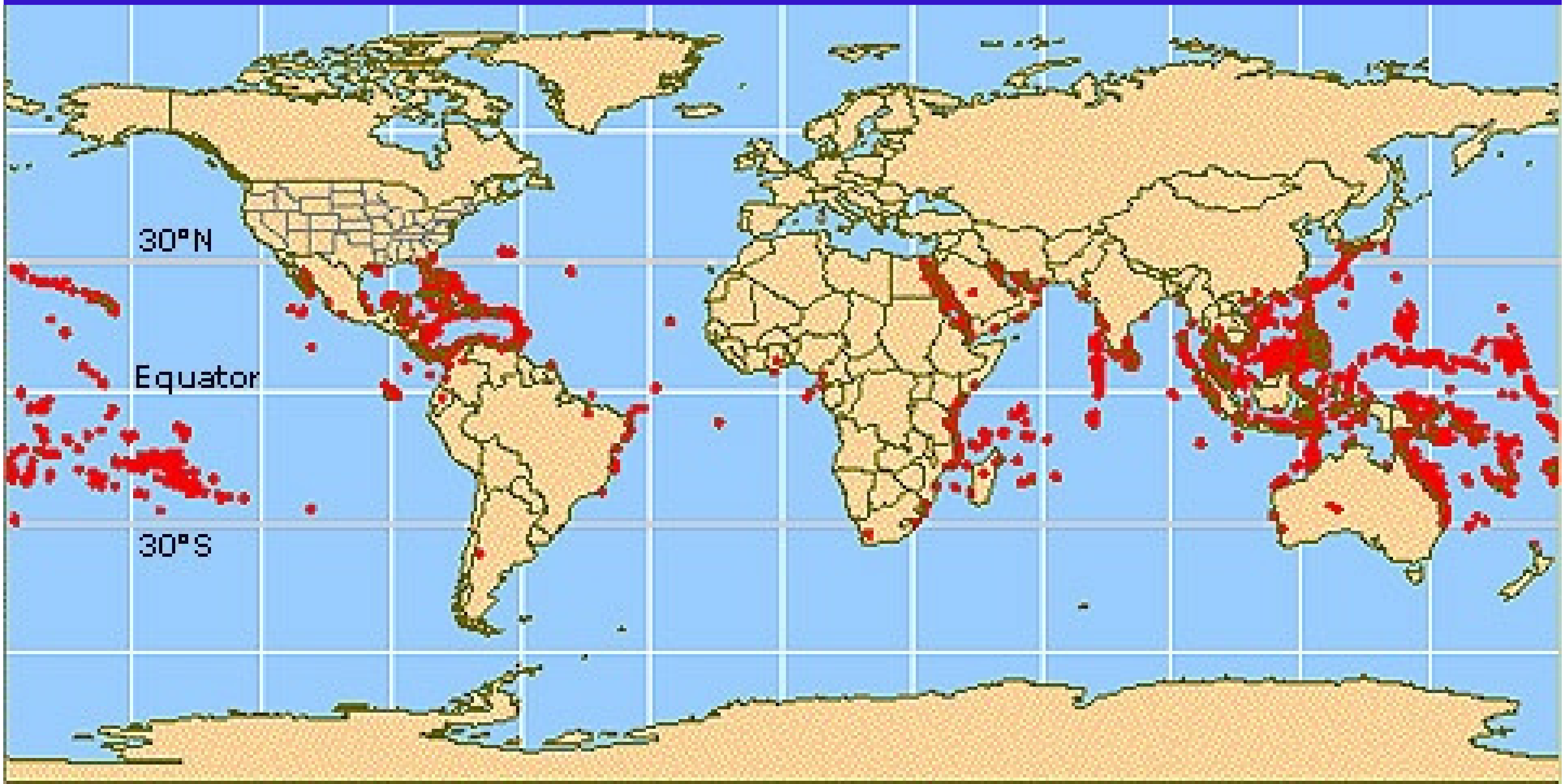


28°C
All Cells Normal

34°C
Coral Host Cells - Normal
Symbiont Cells – Apoptotic & Necrotic

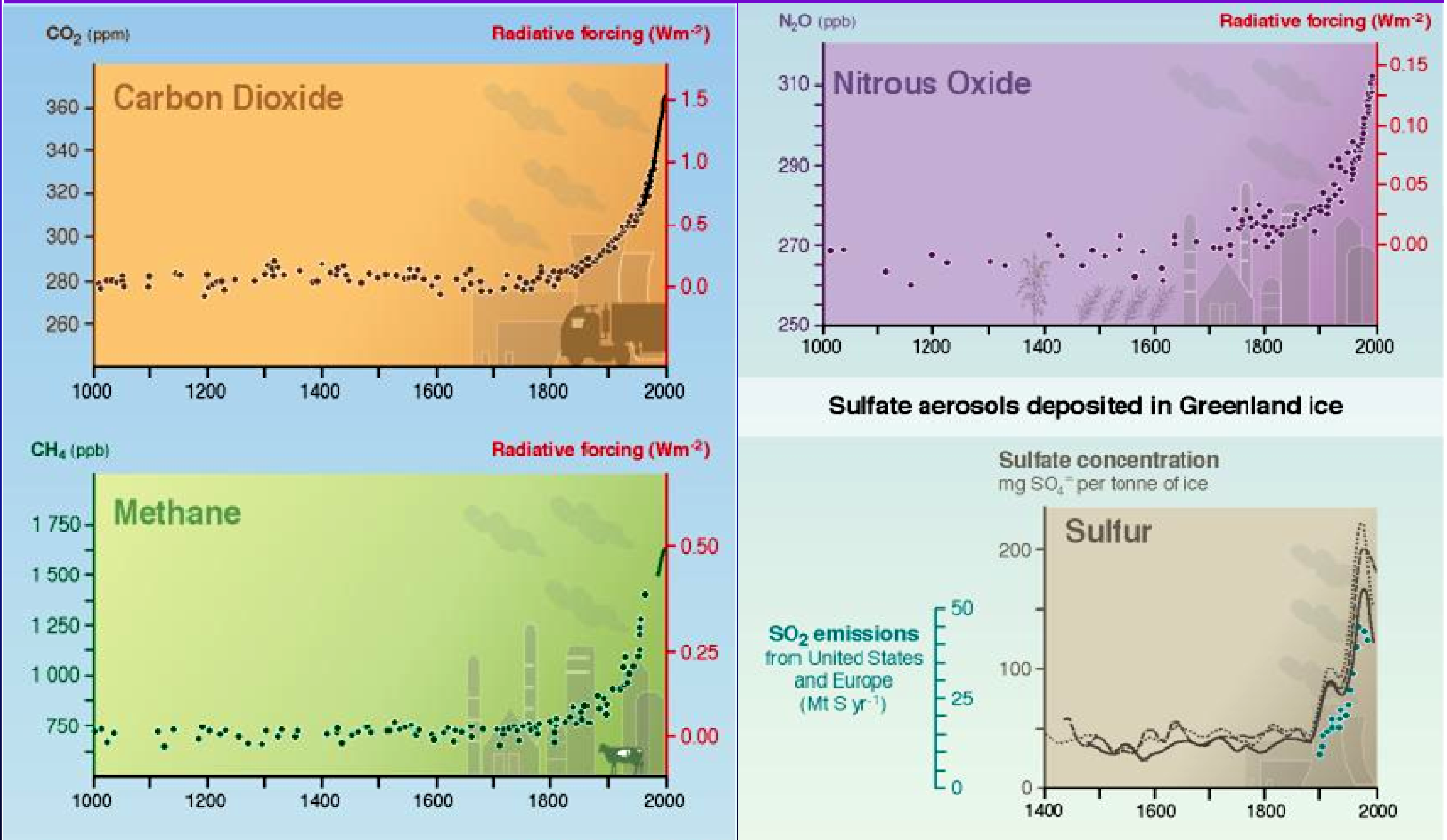
Maxwell's Corrective Map of the Earth

World Distribution of Coral Reefs

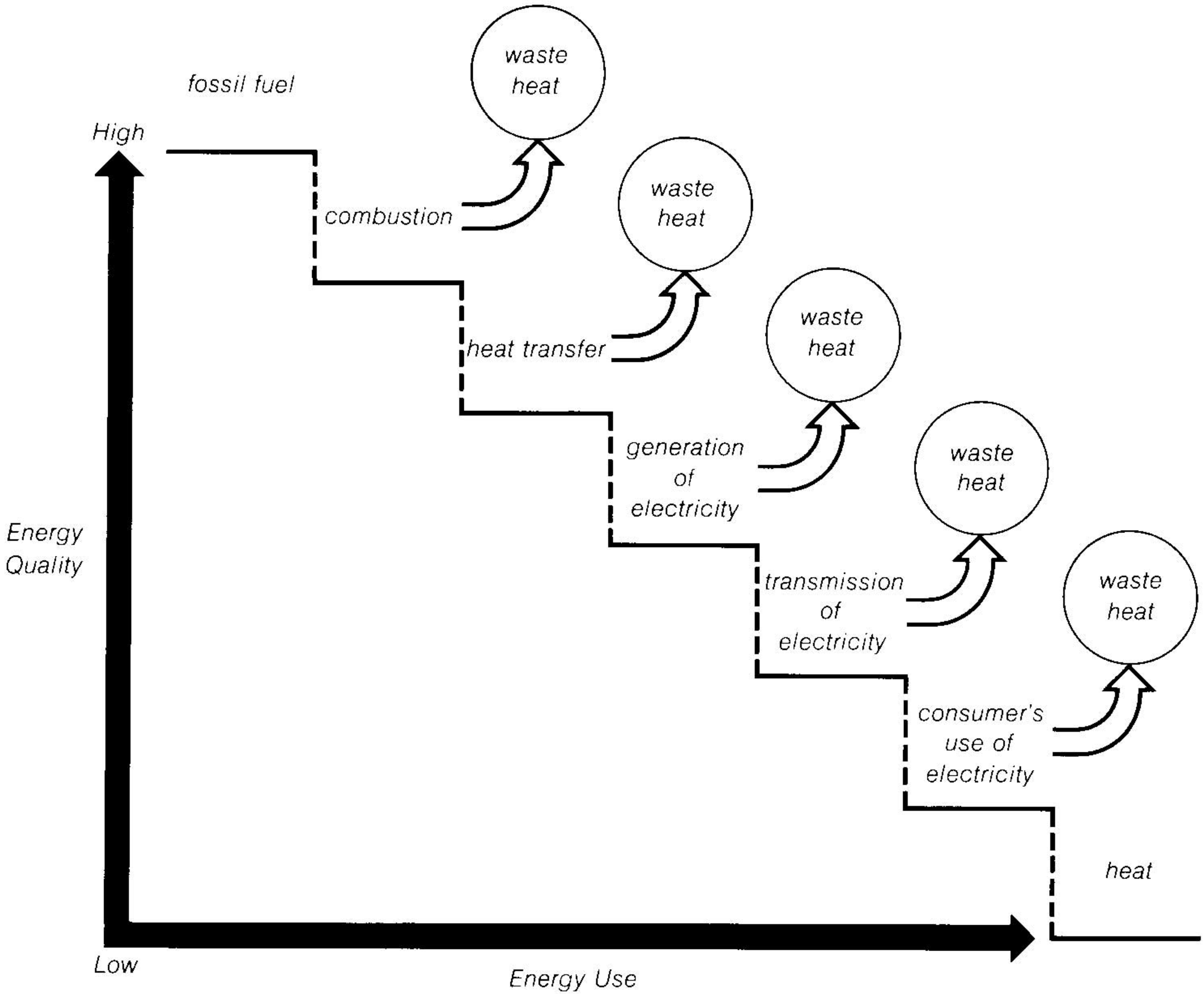


http://oceanservice.noaa.gov/education/kits/corals/media/coral05a_480.jpg

www .celsias.com/media/uploads/
admin/greenland-glacier-melt.jpg

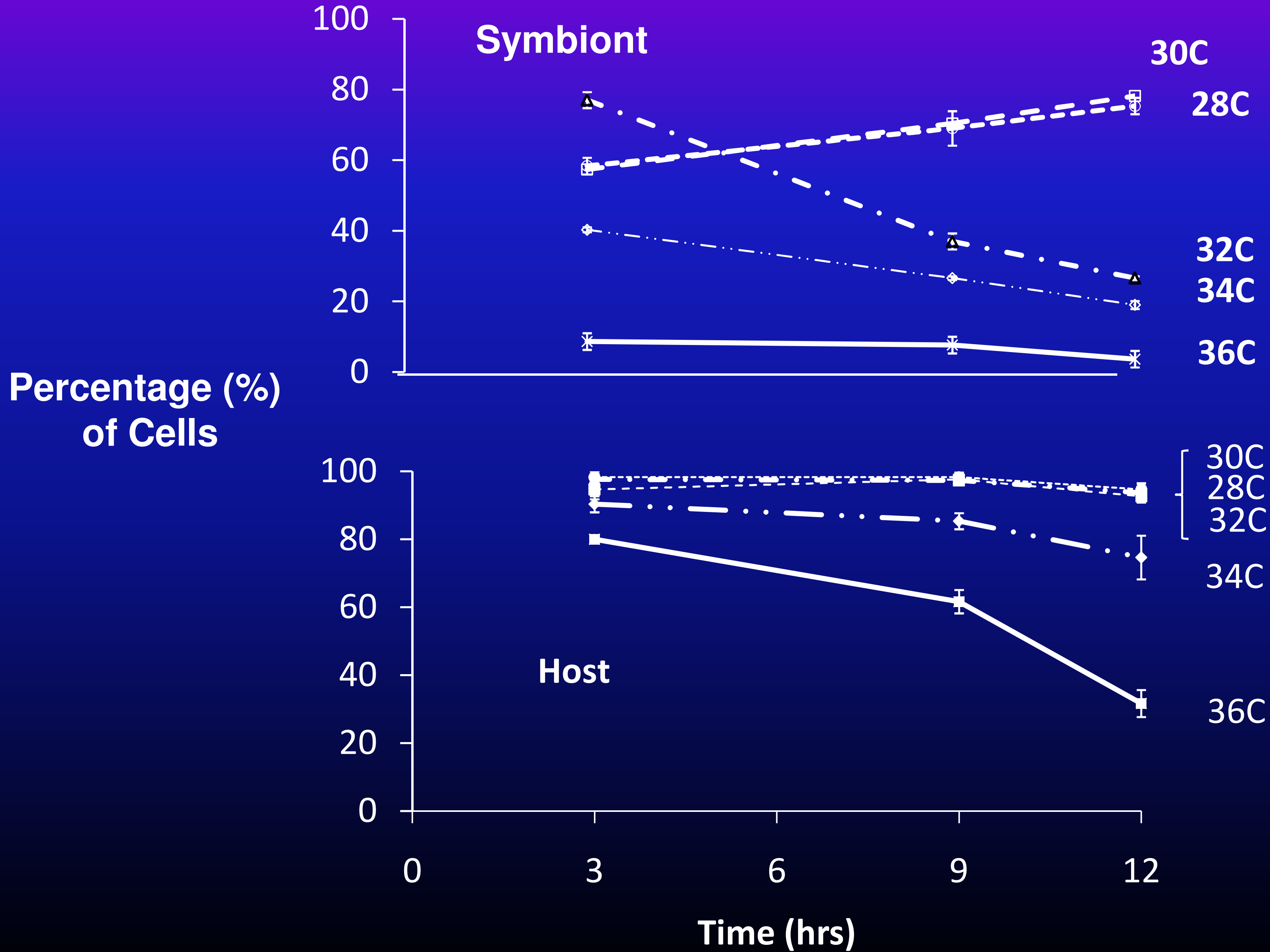


CO2 (ppm)
Radiative forcing (Wm-2)
Carbon Dioxide
360
340
320
300
280
260
1.5
1.0
0.5
0.0
1000
1200
1400
1600
1800
2000
CH4 (ppb)
Radiative forcing (Wm-2)
Methane
1 750
1 500
1 250
1 000
750
0.50
0.25
0.00
1000
1200
1400
1600
1800
2000
N2O (ppb)
Radiative forcing (Wm-2)
Nitrous Oxide
310
290
270
250
0.15
0.10
0.05
0.00
1000
1200
1400
1600
1800
2000
Sulfate aerosols deposited in Greenland ice
Sulfate concentration
mg SO4= per tonne of ice
Sulfur
200
100
0
1400
1600
1800
2000
SO2 emissions
from United States
and Europe
(Mt S yr-1)
50
25
0


fossil fuel
High
waste heat
combustion
waste heat
heat transfer
waste heat
generation of electricity
waste heat
transmission of electricity
waste heat
consumer's use of electricity
heat
Energy Quality
Low
Energy Use

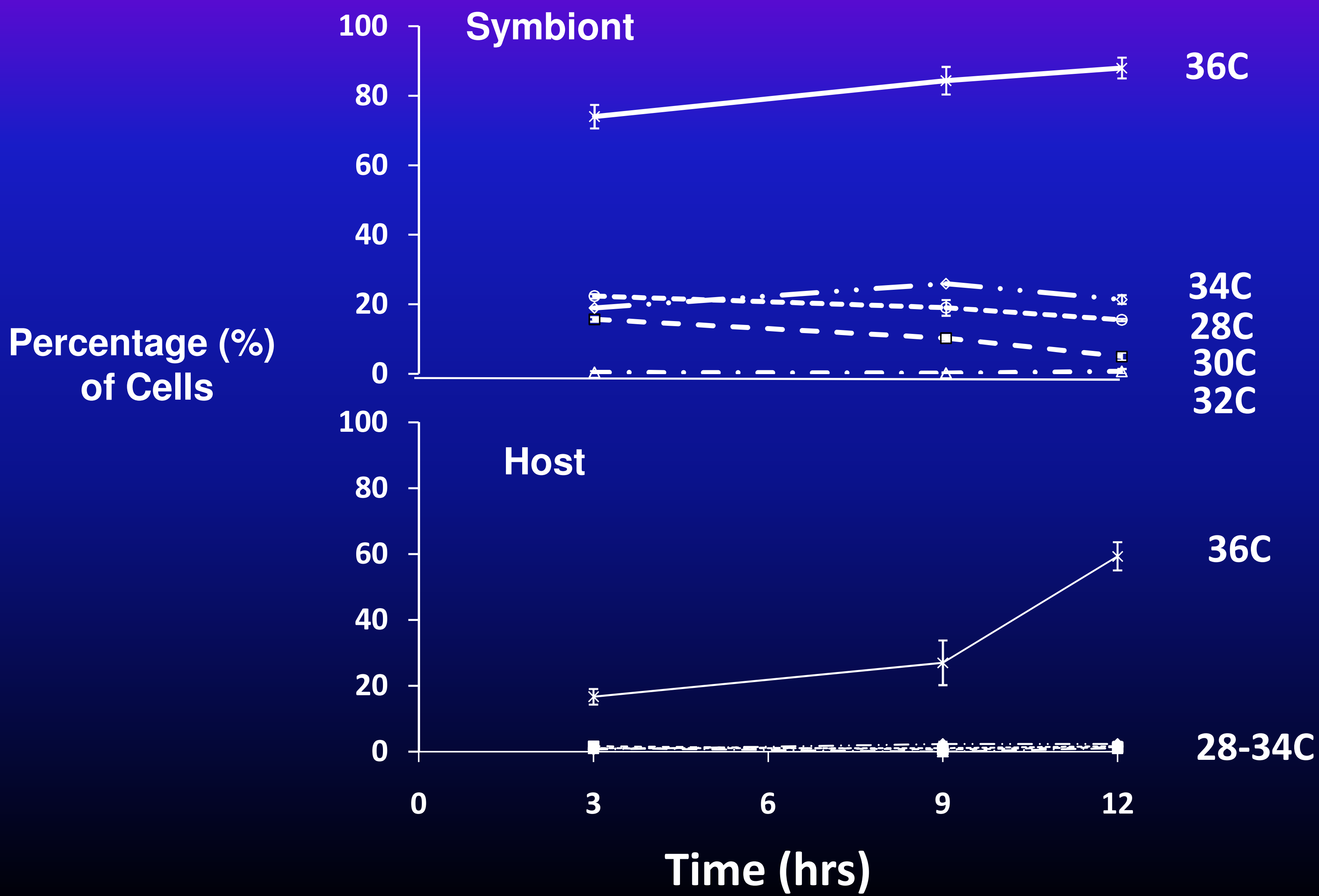
Sarcophyton ehrenbergi

Viable Cells

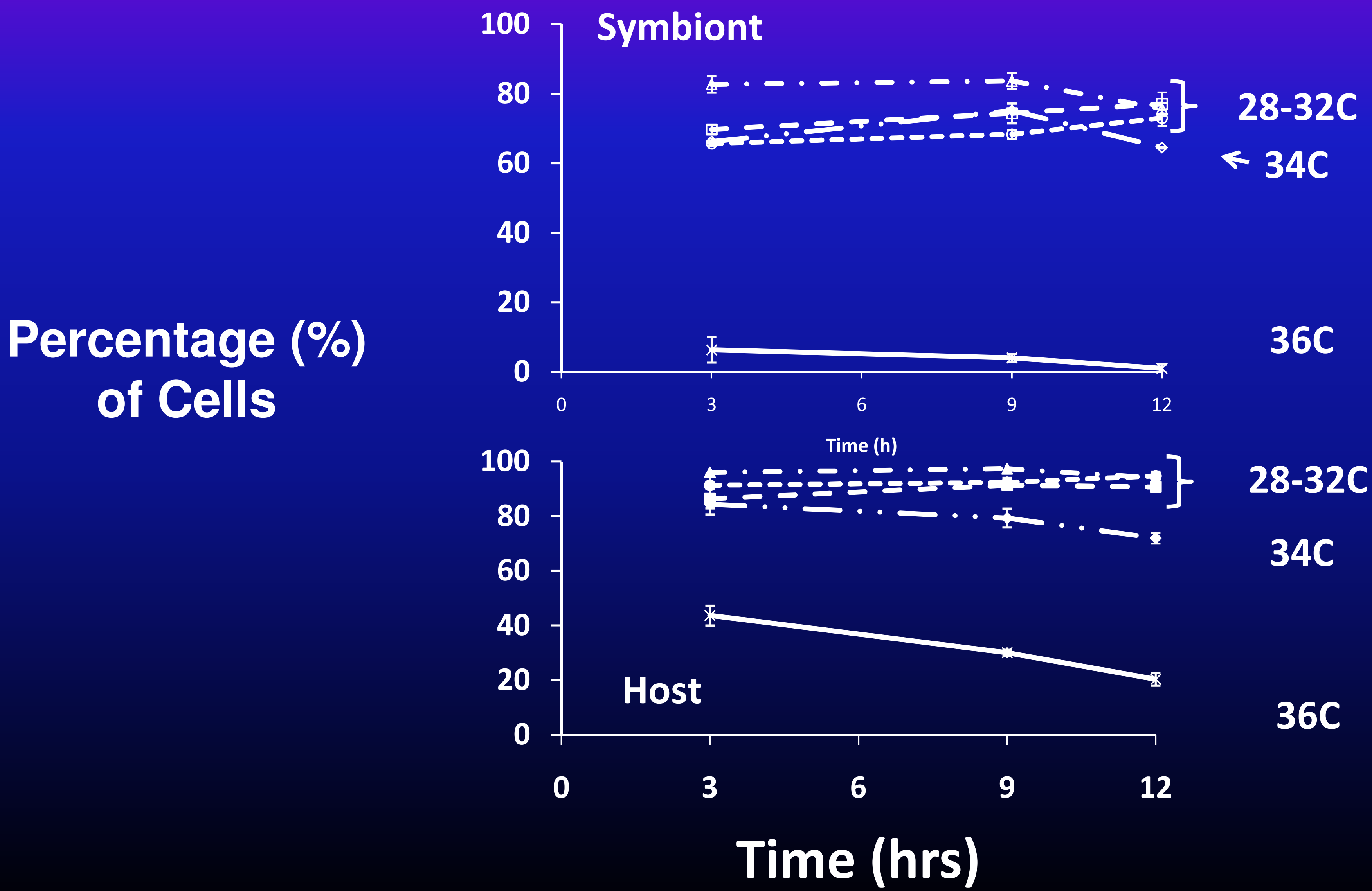


Sarcophyton ehrenbergi

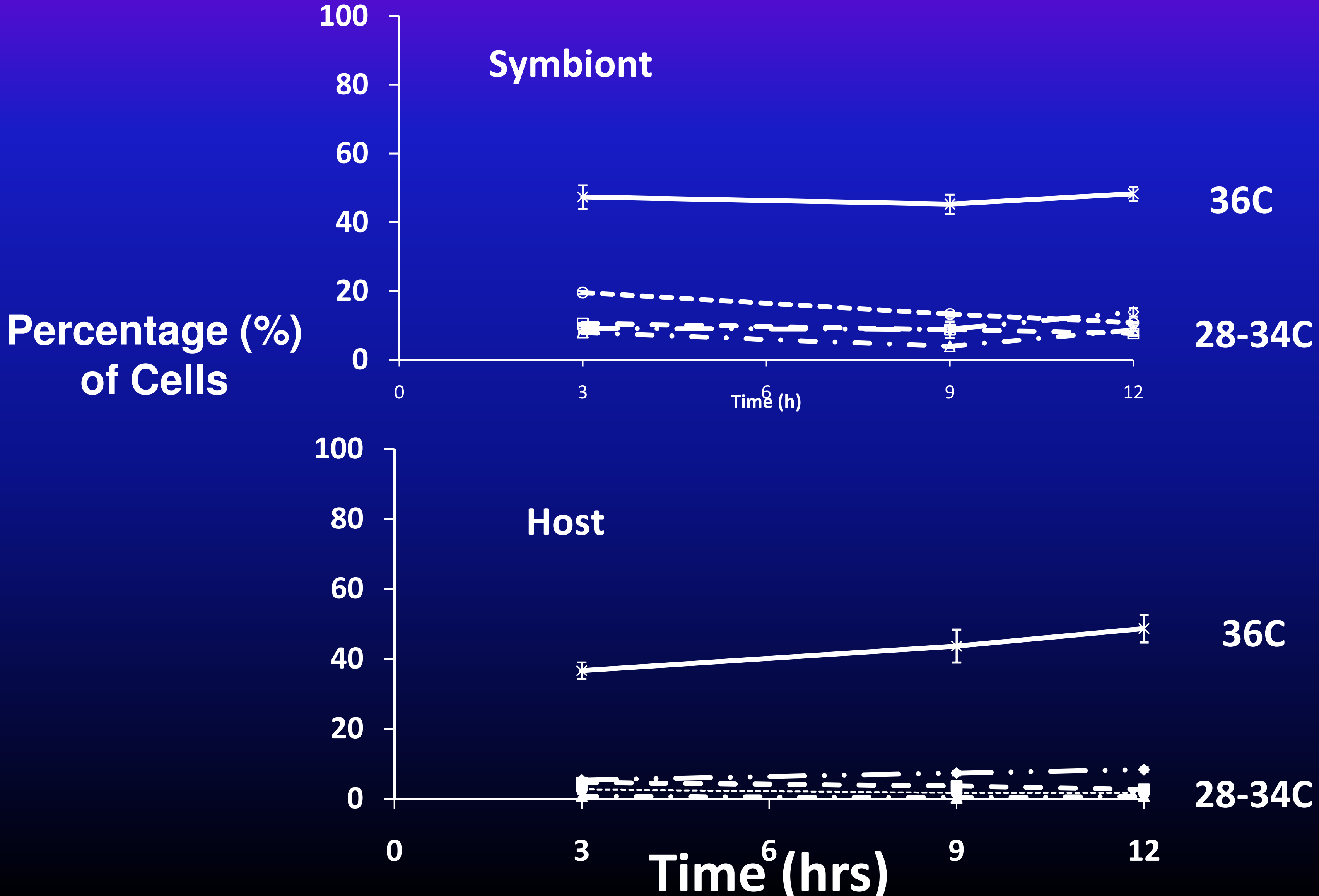
Apoptotic Cells



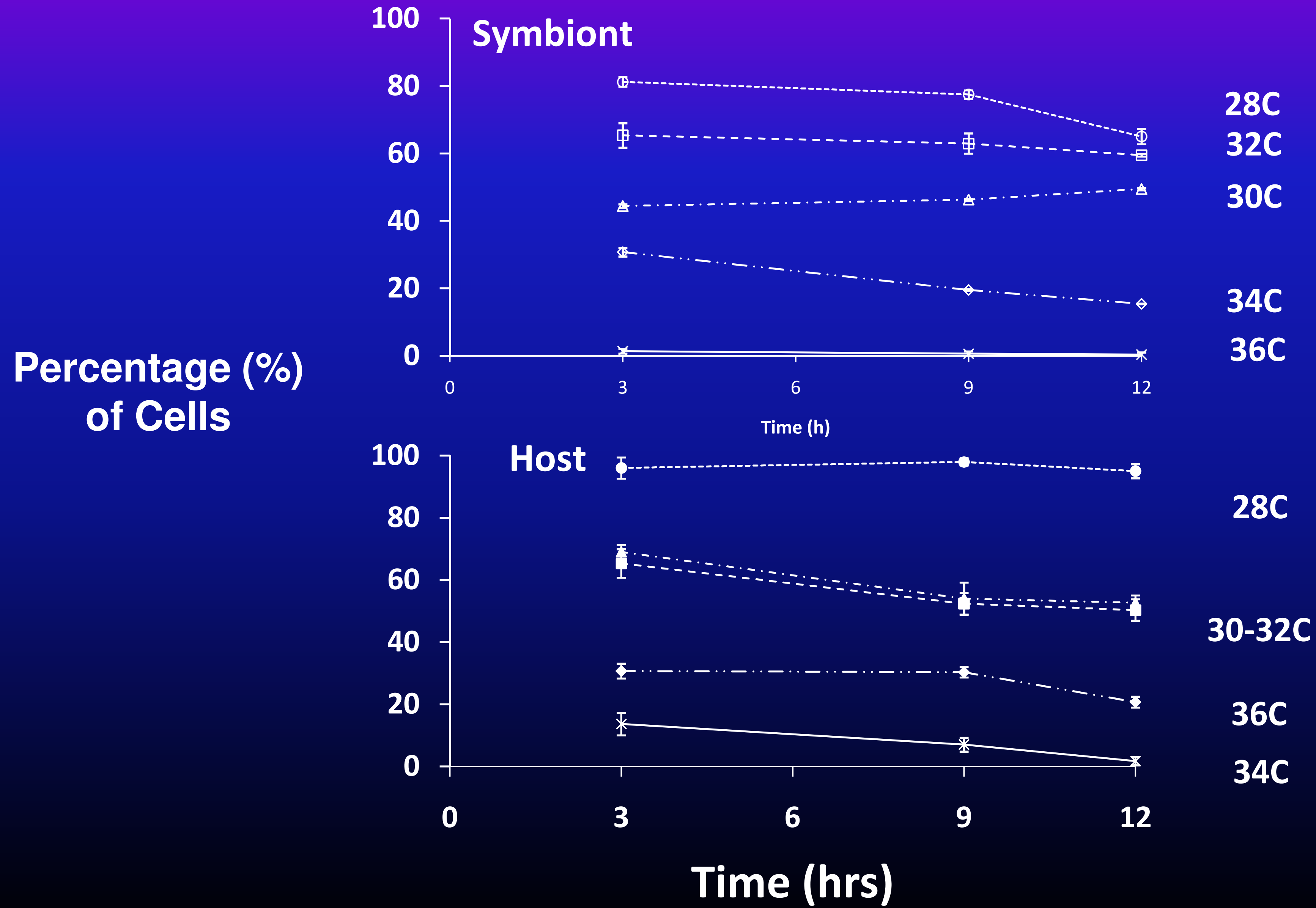
Sinularia lochmodes
Viable Cells



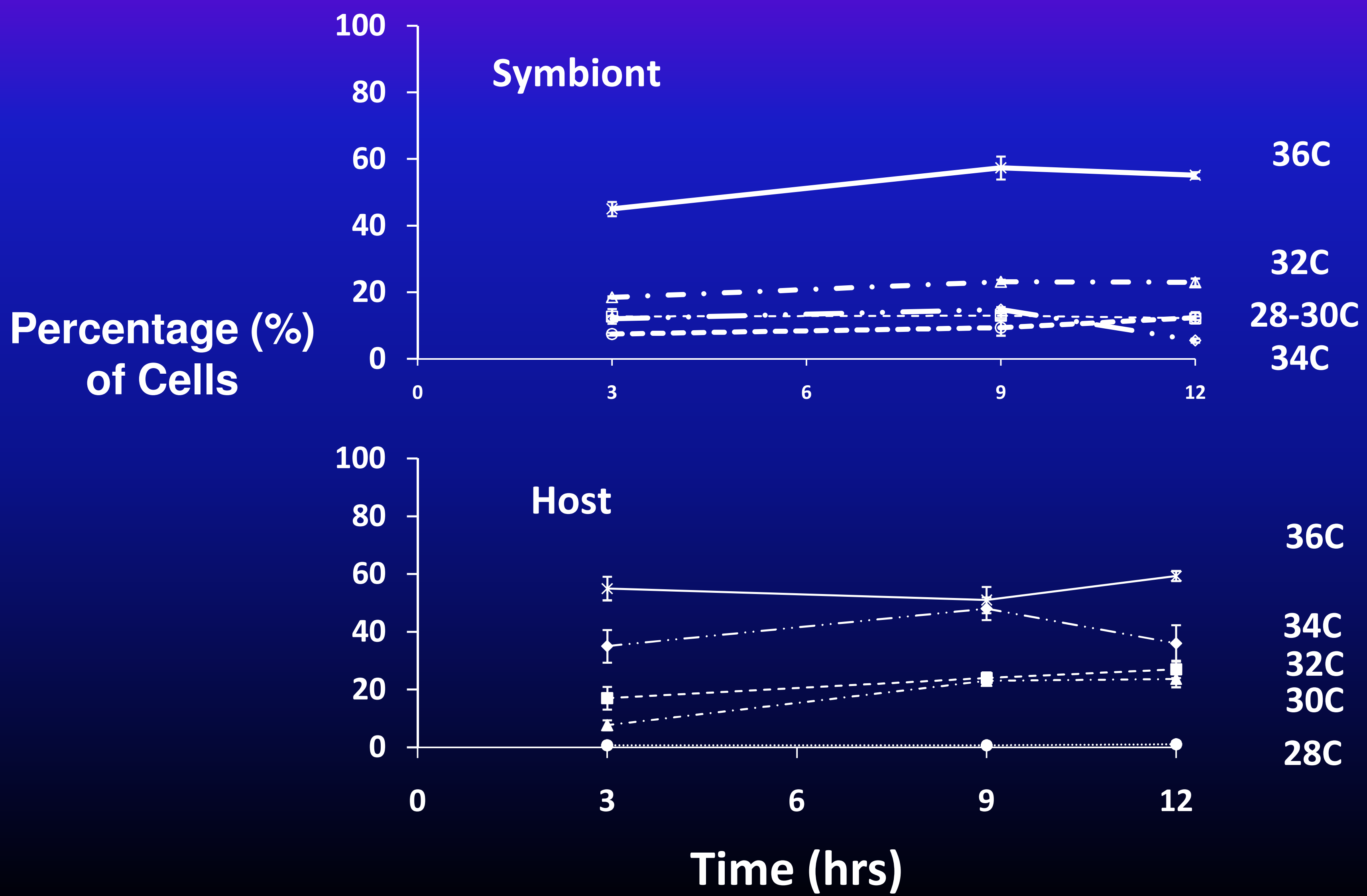
Sinularia lochmodes
Apoptotic Cells



Xenia elongata
Viable Cells, *in situ*



Xenia elongata
Apoptotic Cells, *in situ*



Adaptive Bleaching Hypothesis

. Buddemeier and Fautin (1993)

Kinzie et al. (2001)

Fautin and Buddemeier (2004)

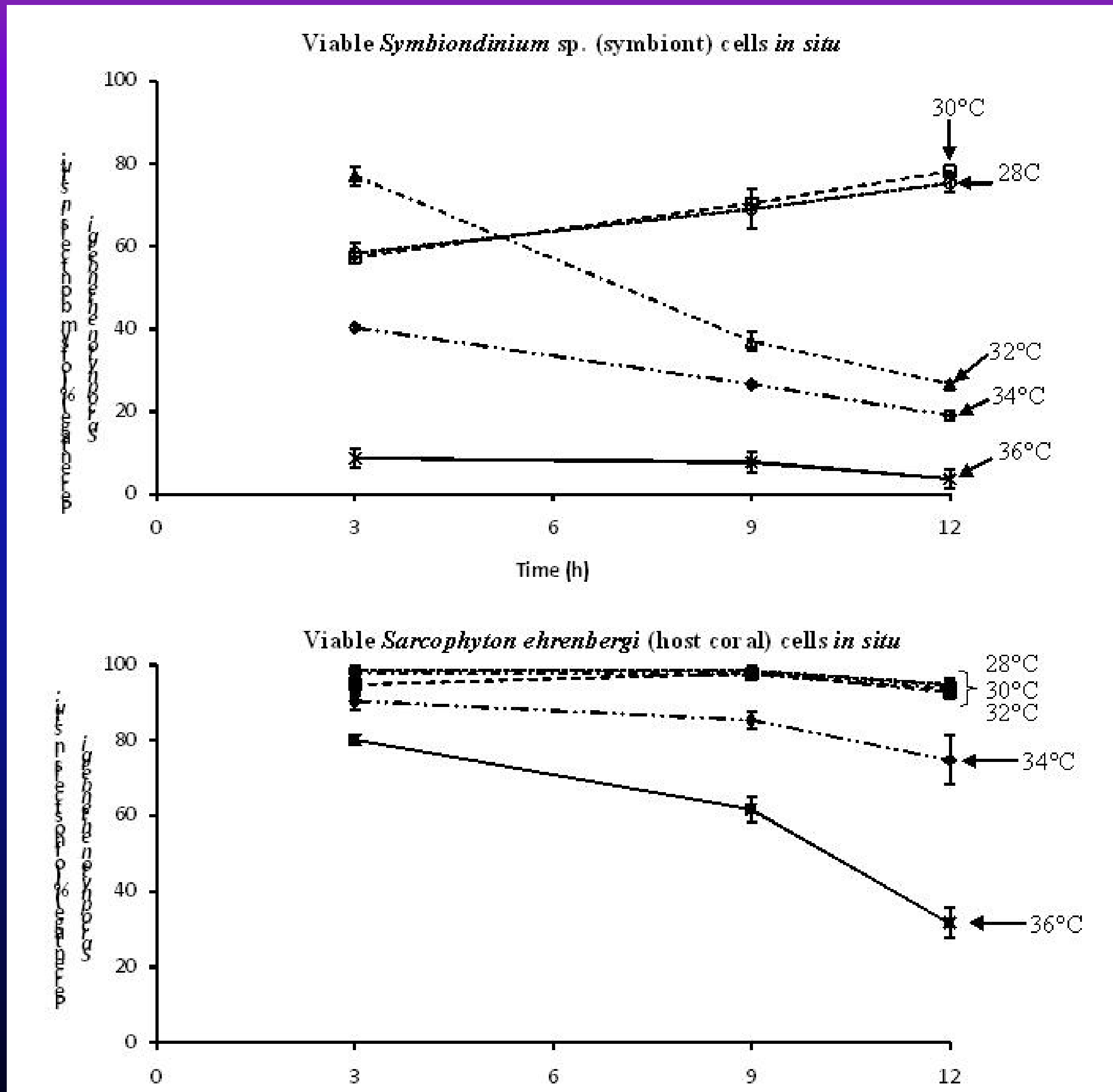
. Temperature stress causes corals to release some proportion of zoox

. Corals re-associate with zoox better-adapted to increased temperatures

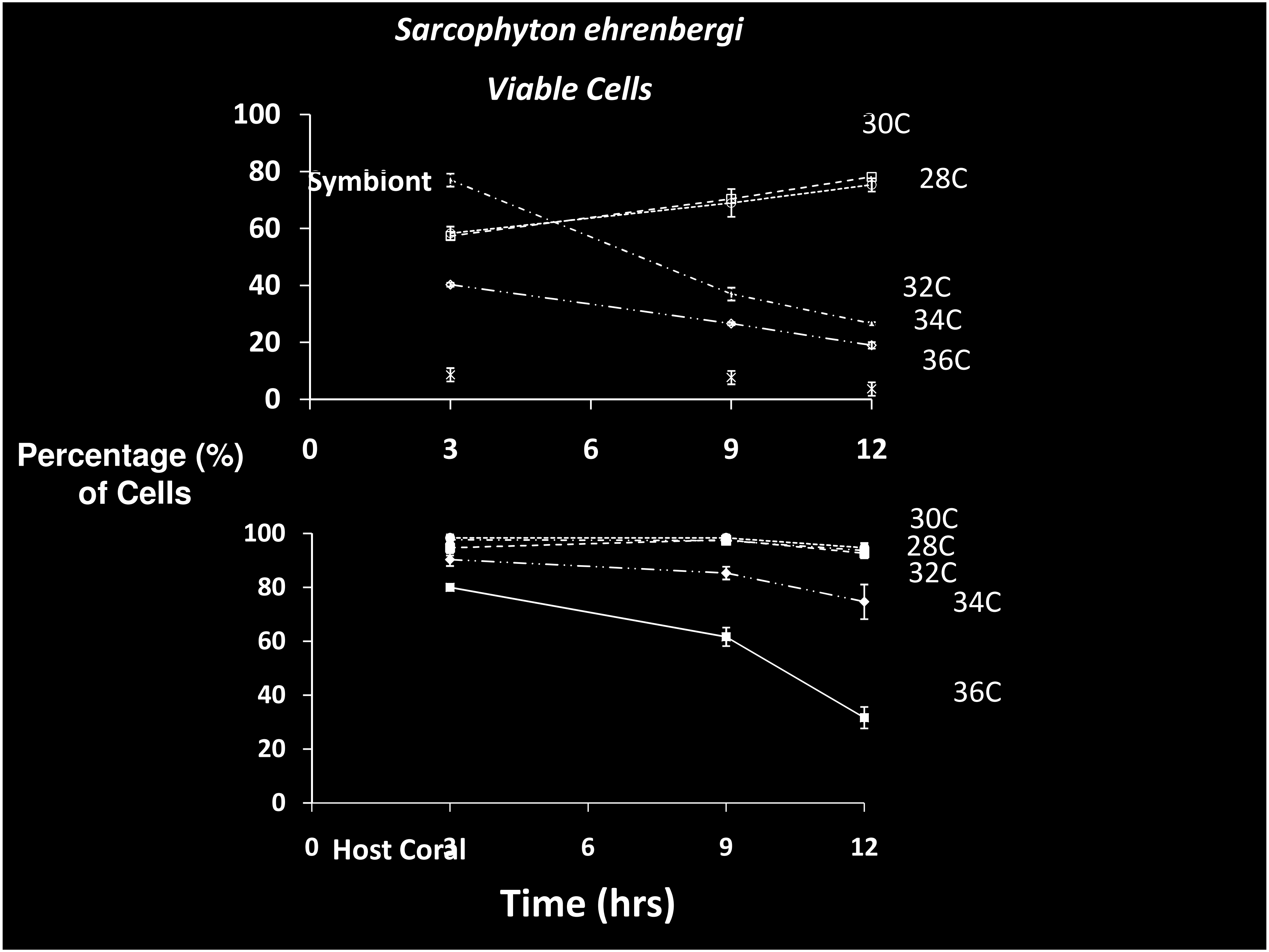
Predictions (cont.)

- Reefs to become more geographically isolated with time
  - Due to decreased dispersal capabilities
- Brooding species will become increasingly dominant
- Coral depth distributions may expand (by $\leq$10m?)
  - But negligible compared to latitudinal expansion.

Sarcophyton ehrenbergi



Time (hrs)


Sarcophyton ehrenbergi
Viable Cells
Symbiont
Host Coral
Percentage (%) of Cells
Time (hrs)
30C
28C
32C
34C
36C
100
80
60
40
20
0
3
6
9
12

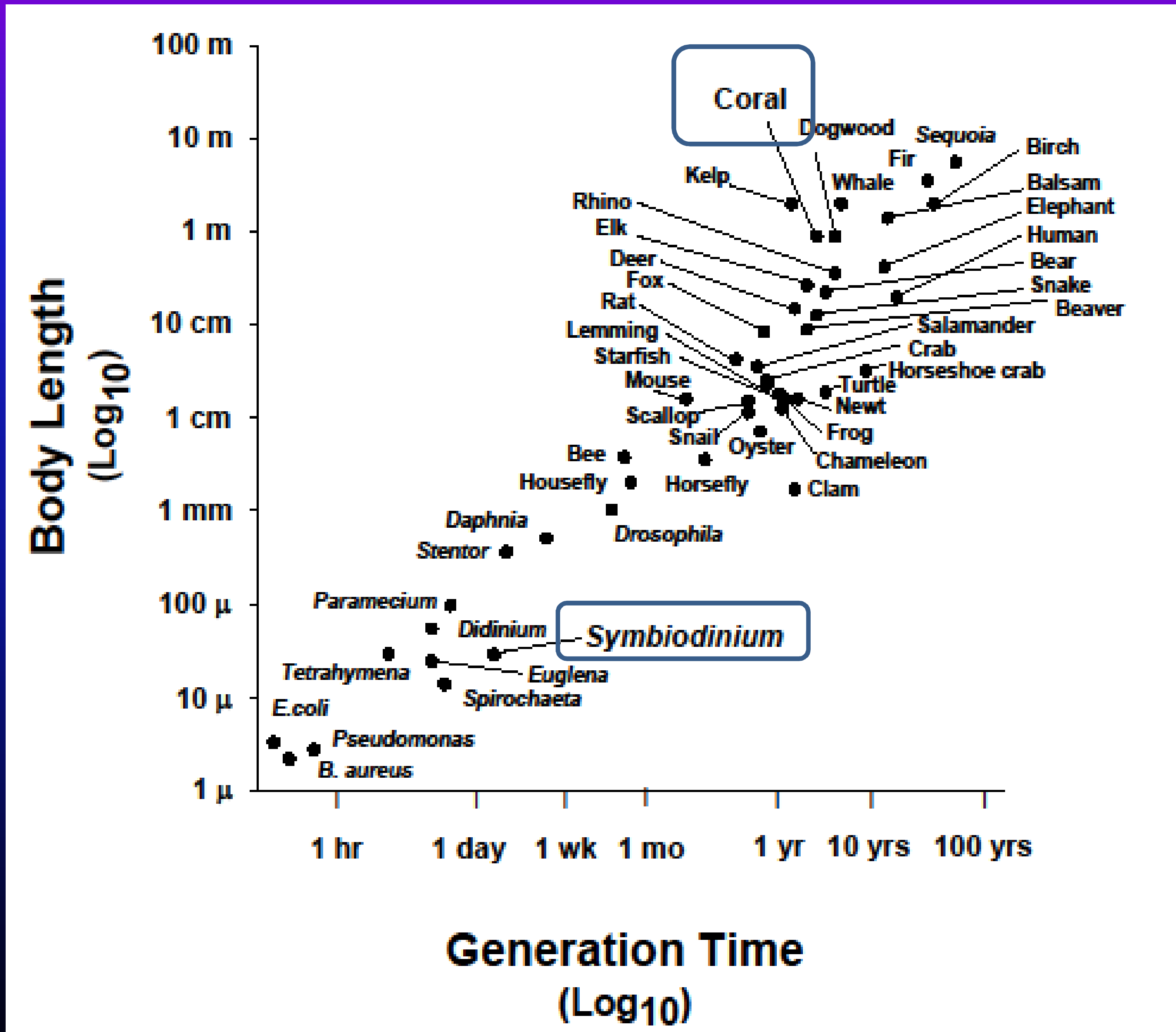
Comparative Generation Times in

the Coral Host

vs.

the Zooxanthellae

Body Length *vs.* Generation Time



(Bonner, 1964; McNaughton and Wolf, 1979)

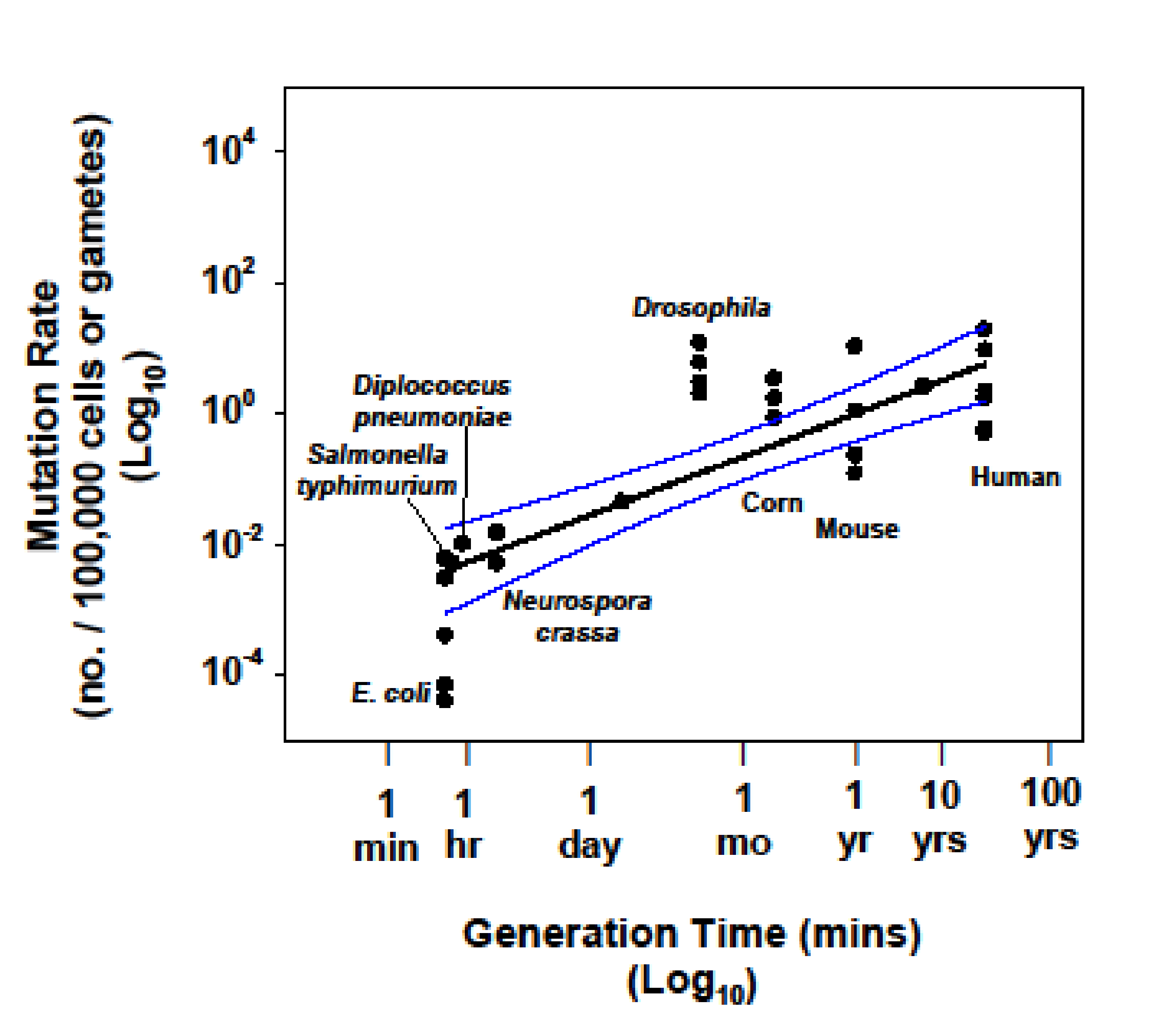
Comparative Mutation Rates in

the Coral Host

vs.

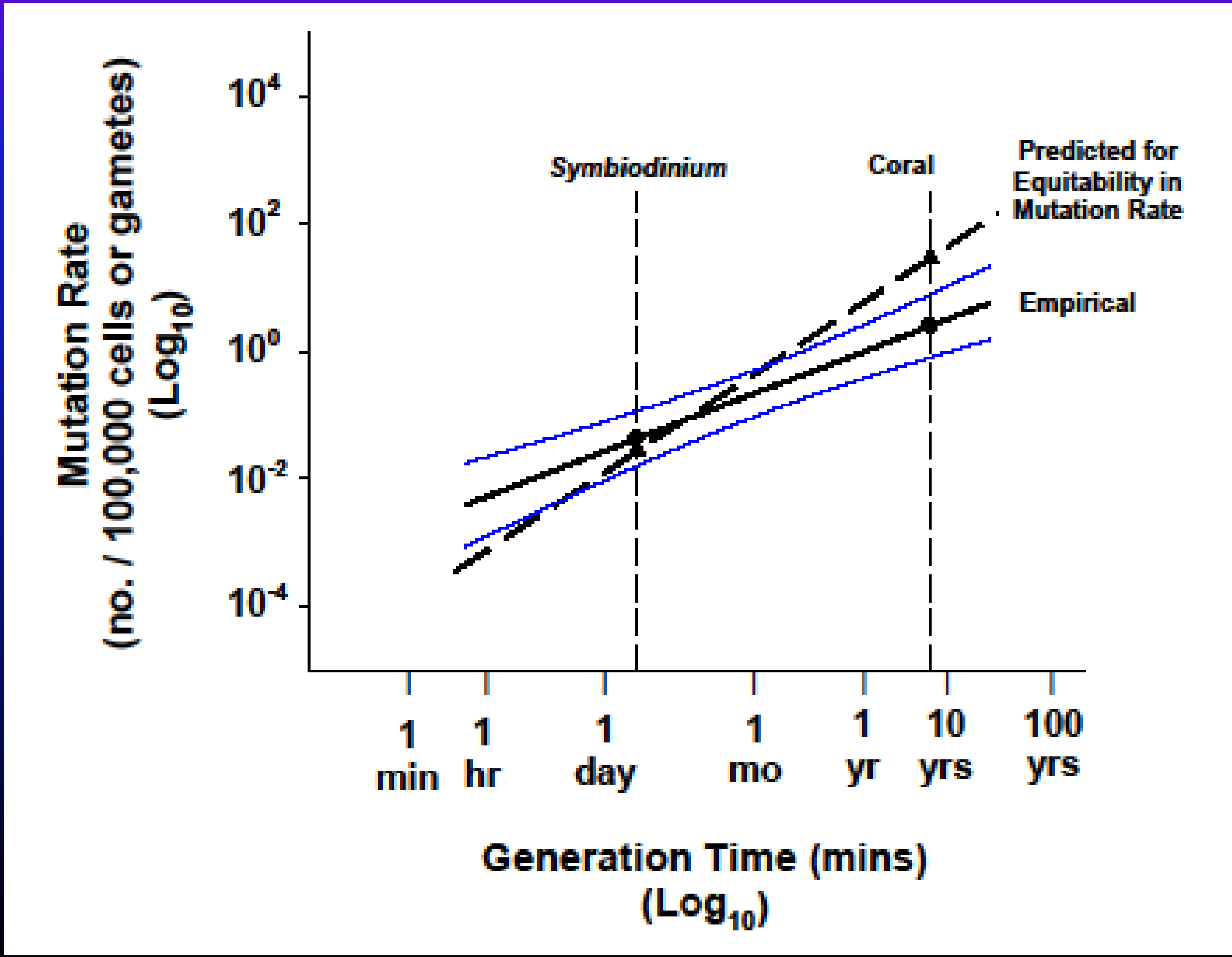
the Zooxanthellae

Generation Time *vs.* Mutation Rate (Empirical)



Derived from Strickberger, 1968; Dobzhansky, 1970; Drake, 1974; Futuyma, 1998)

Generation Time *vs.* Mutation Rate
(Empirical *vs.* Predicted)

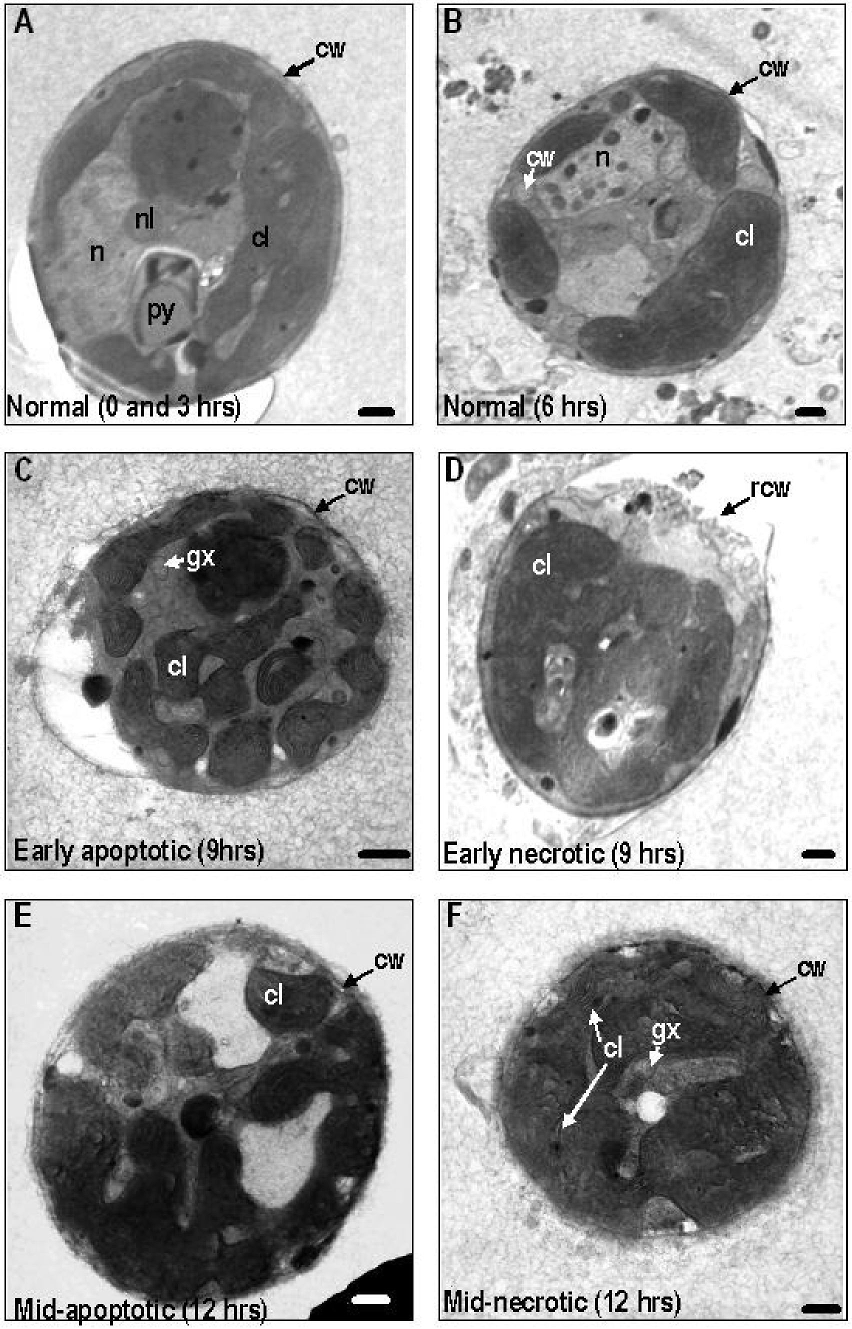


Mutation Rate vs. Generation Time

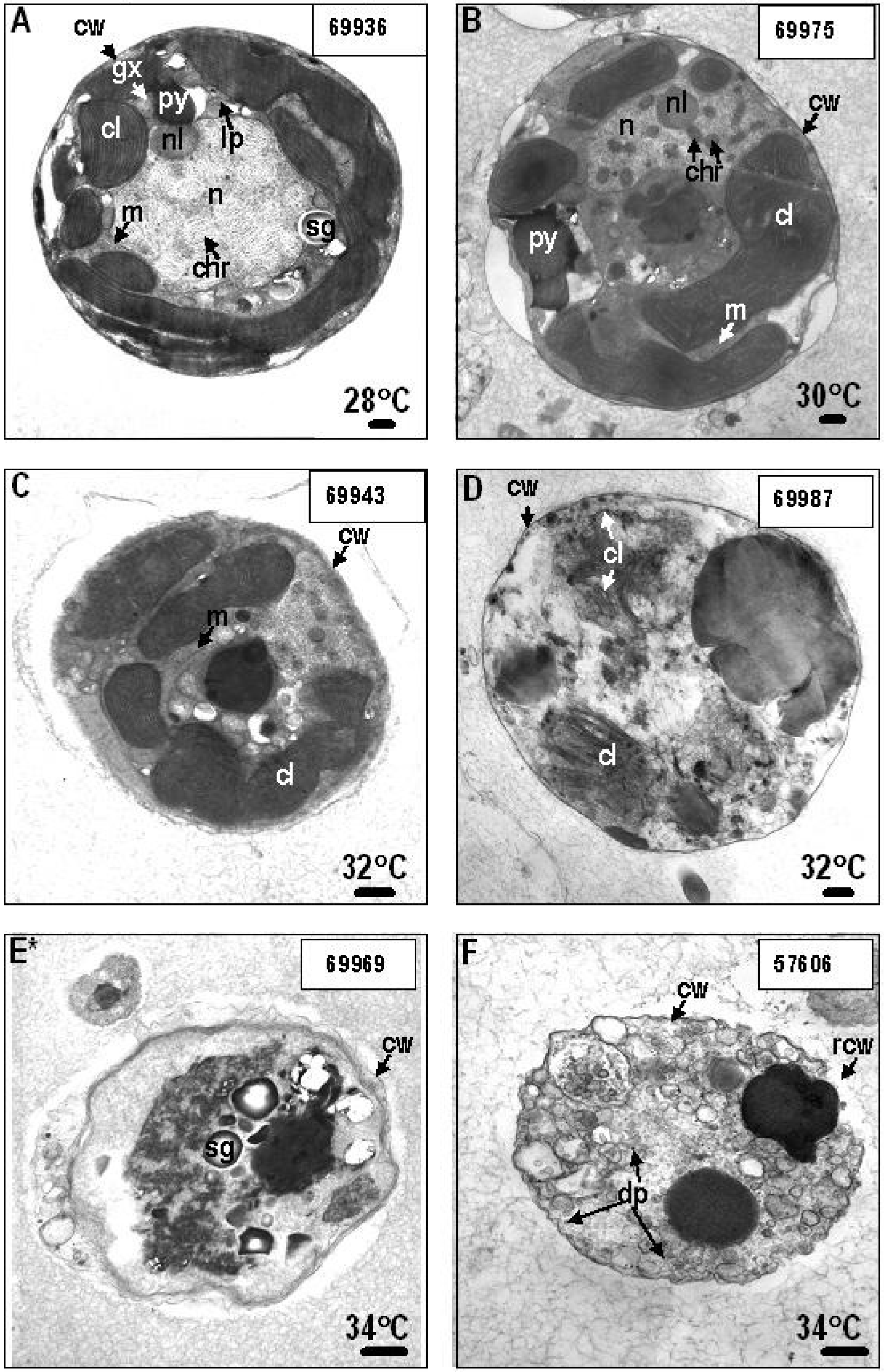
Host vs. Symbiont

- Important when selection pressure is relatively constant or changing slowly, relative to host generation time
- Moot for host when selection pressure changes at rate more rapid than host's generation time
- Moot for host when host is adapted/exapted to rapidly changing selective factor – but -
  - The mutation rate of the symbiont then becomes critical.

Symbiodinium cells expelled from *Sarcophyton ehrenbergi* sampled every 3 hrs at 34°C



Symbiodinium cells expelled from *Sarcophyton ehrenbergi*



Zooxanthellar Clades

. Increasing rate of discovery of new clades and sub-clades

- 5 clades for scleractinian corals (2009)
- 8 clades (with overlap) for other host organisms
- 77 sub-clades for scleractinian corals
- 9 species for other host organisms

. Why this increase through time?

- New strains arising via mutation plus selection?
- Greater effort expended in the search?
- Increase in our ability to detect differences due to more powerful and higher resolution technology (e.g. molecular genetics)?

Marine or Freshwater Invertebrates

with Other Algal Symbionts

Examples

Spongilla lacustris (Porifera) with *Chlorella* (Chlorophyceae)

Jim Novak
www.biolib.cz/en/image/id18059/

Lissoclinum patella (Ascidea)
with symbiotic cyanobacteria

www.eol.org/pages/65008