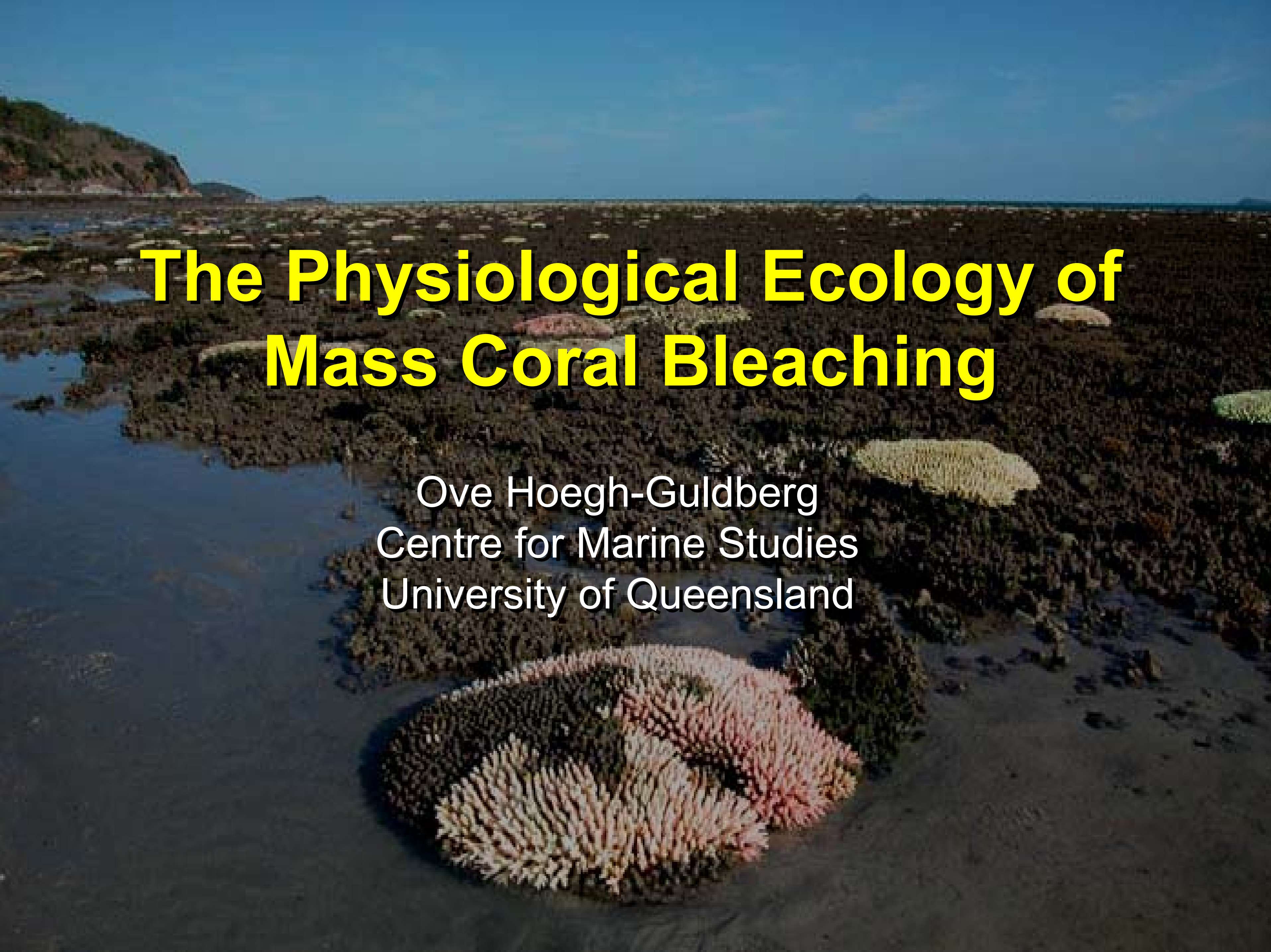
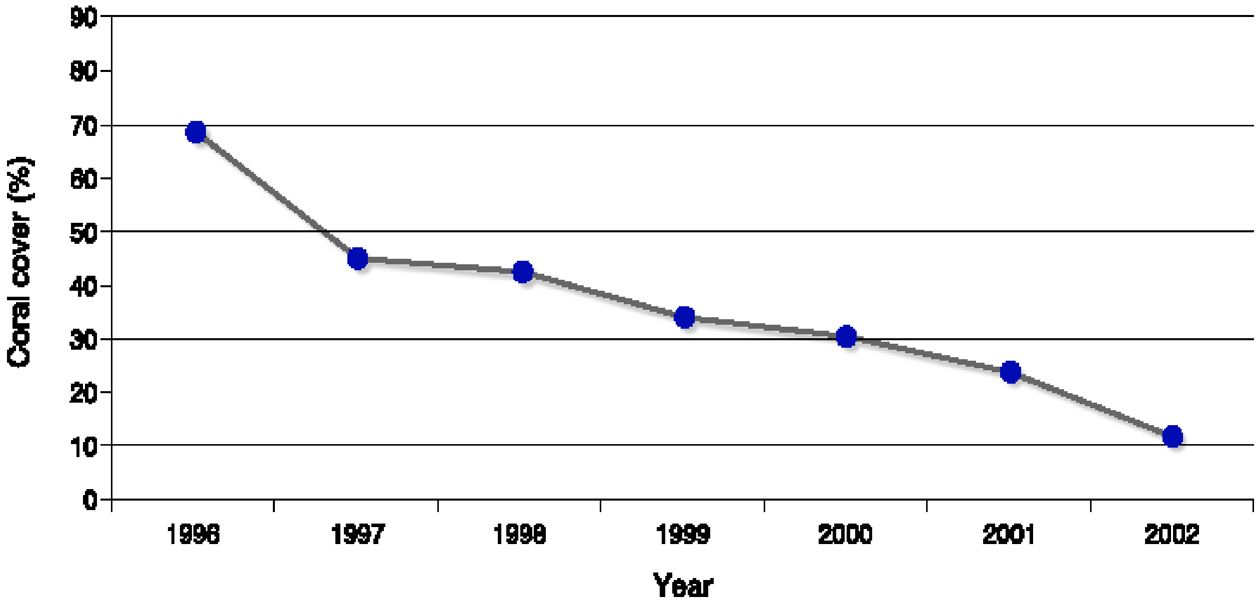


The Physiological Ecology of Mass Coral Bleaching

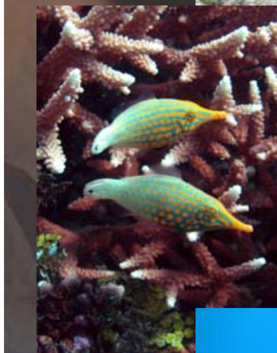
Ove Hoegh-Guldberg
Centre for Marine Studies
University of Queensland

Status of Coral Reefs of the World: 2002

Papua & New Guinea



The average coral cover on 8 reefs in Kimbe Bay, New Britain PNG, shows a serious declining trend from 70% cover to around 20% in 6 years following several bleaching events and damage from sediments from lands cleared for oil palm plantations flowing onto the reefs during floods.

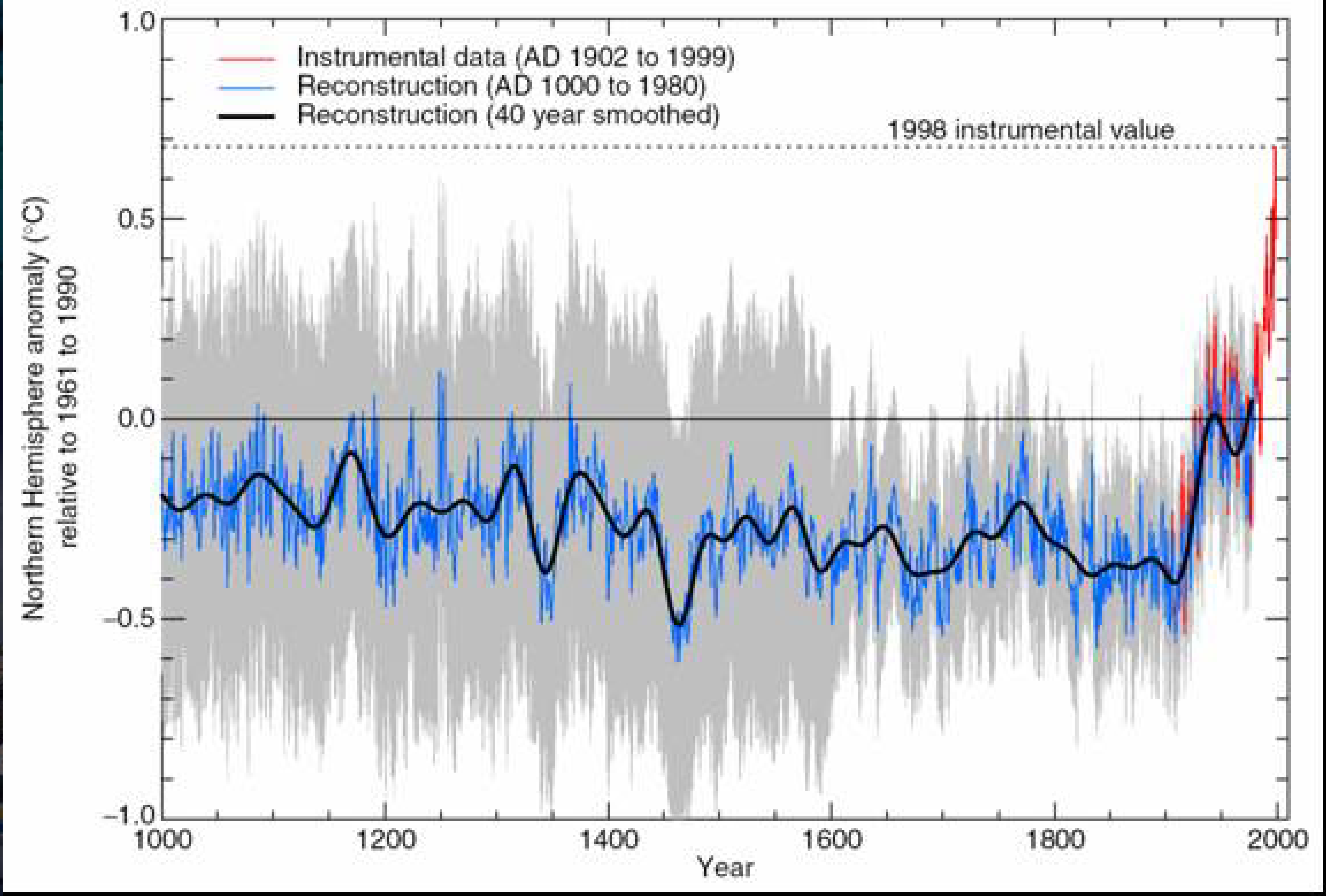


Outline

1. Patterns of change
2. Physiology of thermal stress.
3. Thresholds and global change
4. Acclimation and adaptation
5. Conclusion

1. Patterns of change

Reasons behind current change in reef health include a complex cocktail of direct and indirect factors



1. Patterns of change

Marine ecosystems are also changing rapidly

- Environmental changes
  - Increasing sea temperatures and sea levels
  - Decreasing carbonate alkalinities
  - Changing currents and global circulation
- Biotic responses abundant already
  - Warm-water fish populations have advanced poleward (Holbrook et al 1997)
  - Intertidal communities moved poleward over the past 70 years (Southward et al. 1995).
  - Krill populations in Antarctica are 10% of what they were 40 years ago – salps, more open water species, have increased 10 fold. Impacts on penguin populations reported (Barbraud and Weimerskirch 2001).
  - Mangroves have expanded and salt marsh contracted.
  - Many other examples.

1. Patterns of change

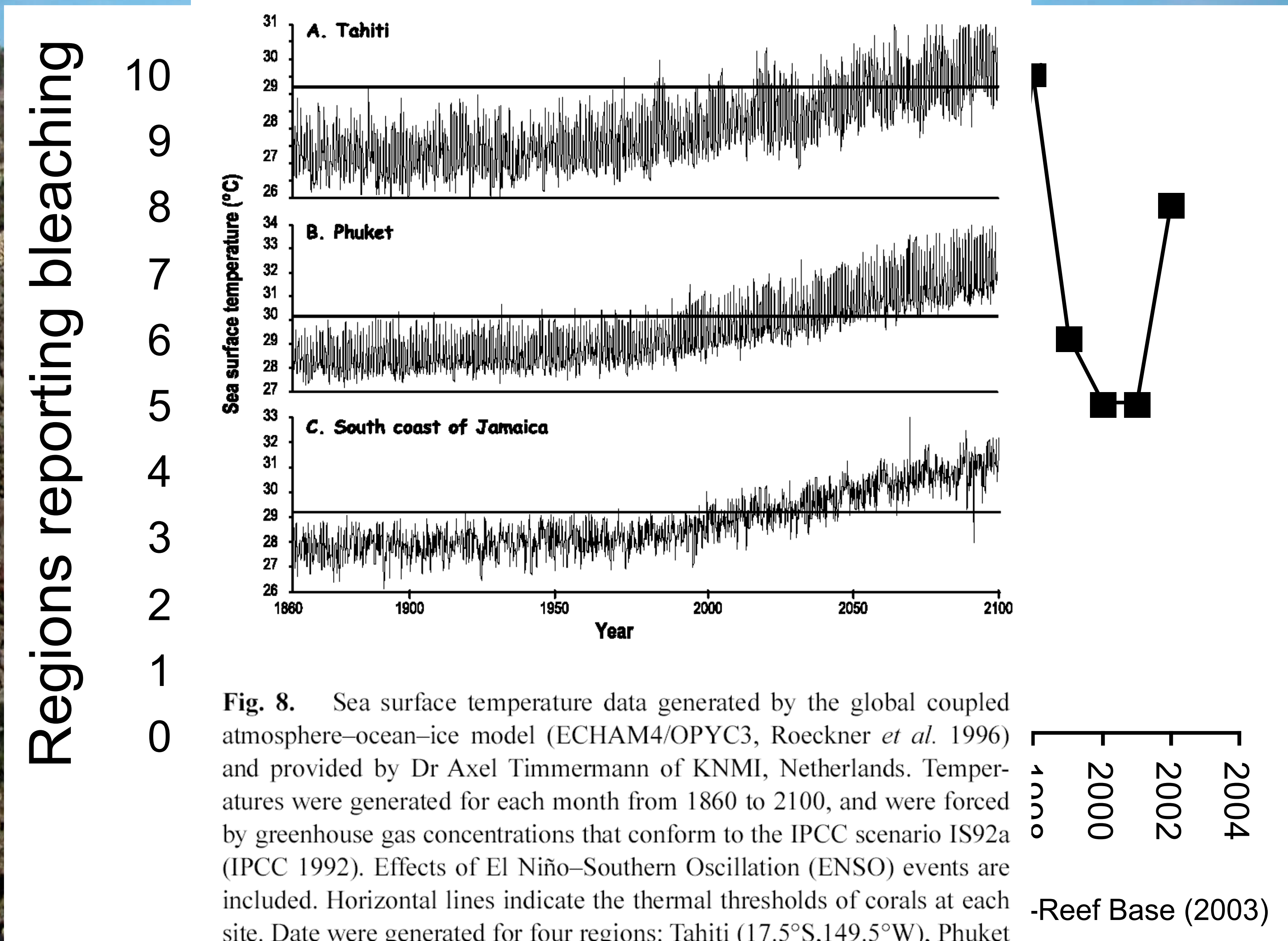
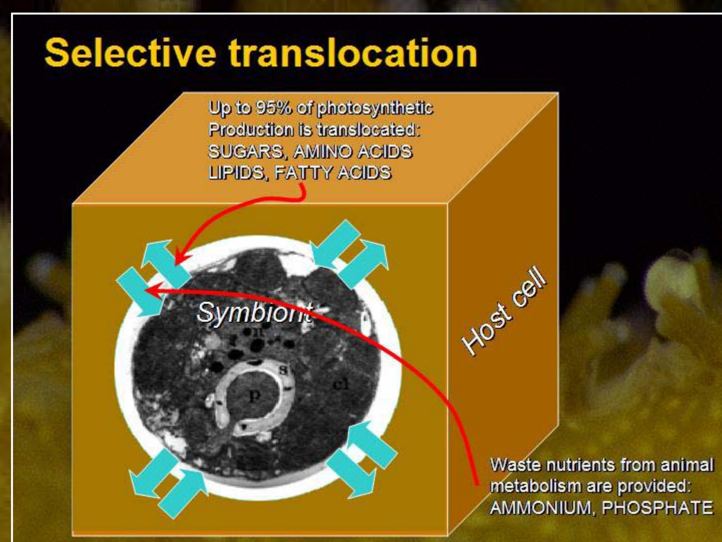


Fig. 8. Sea surface temperature data generated by the global coupled atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996) and provided by Dr Axel Timmermann of KNMI, Netherlands. Temperatures were generated for each month from 1860 to 2100, and were forced by greenhouse gas concentrations that conform to the IPCC scenario IS92a (IPCC 1992). Effects of El Niño–Southern Oscillation (ENSO) events are included. Horizontal lines indicate the thermal thresholds of corals at each site. Date were generated for four regions: Tahiti (17.5°S,149.5°W), Phuket (7.5°N,98.5°E), Jamaica (17.5°N,76.5°W), and Rarotonga (data not shown).

2. Physiology of thermal stress.

Mutualism

Thermal
sensitivity



2. Physiology of thermal stress.

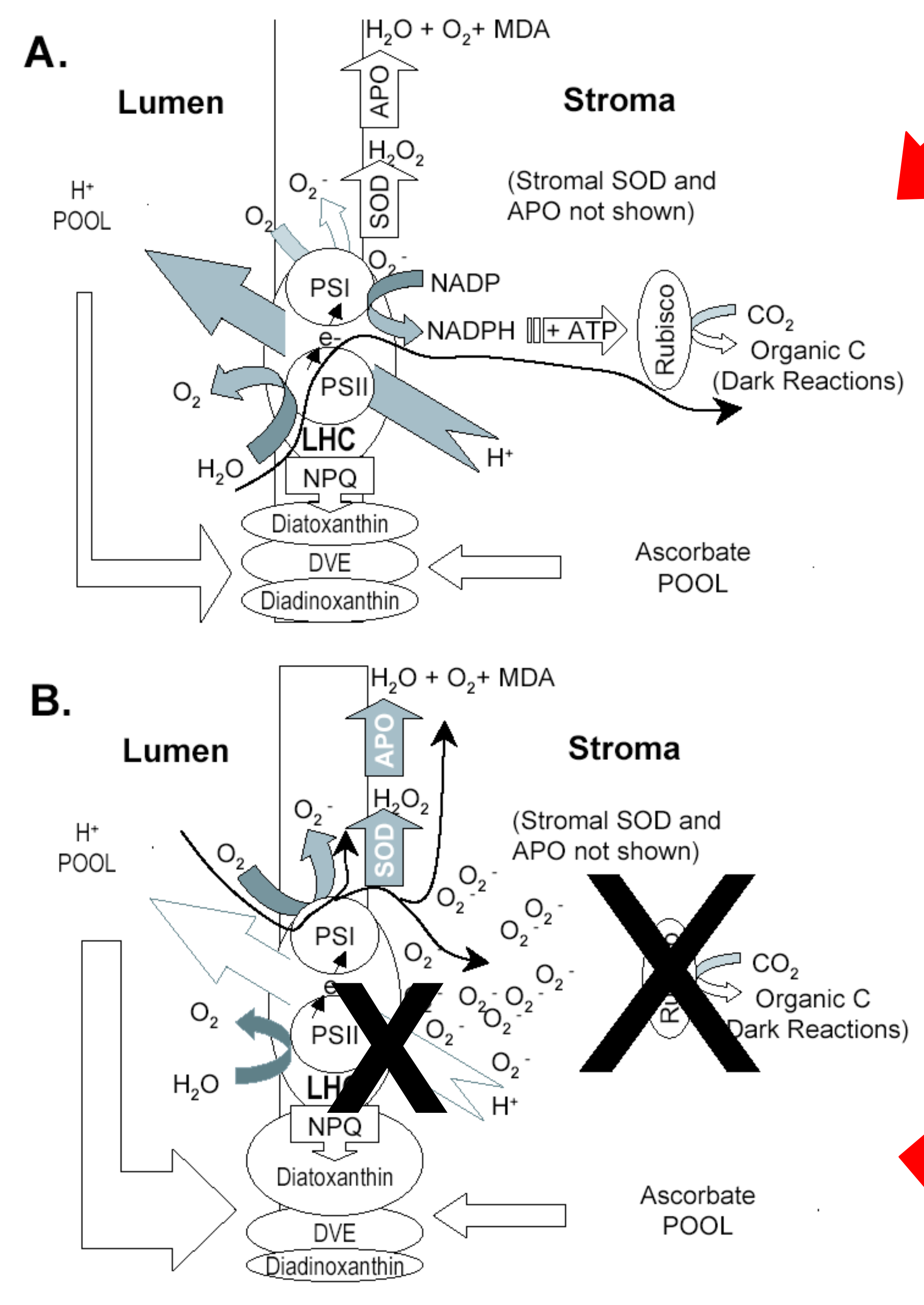
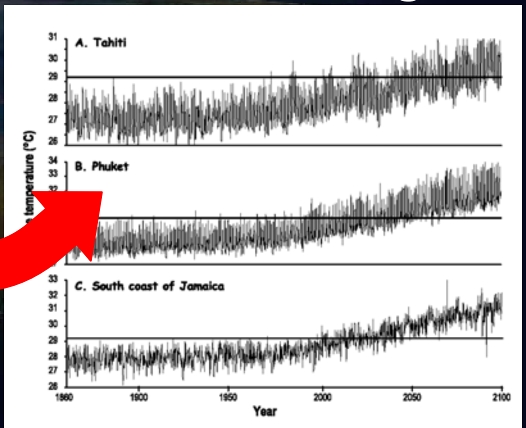


Fig. 6. Photoinhibition model of coral bleaching (Jones *et al.* 1998).

1. **Model largely correct**
2. **Explains wide array of phenomena such as light (PAR, UVR), flow effects**
3. **Explains how short-term acclimation can come about through acclimation to light**

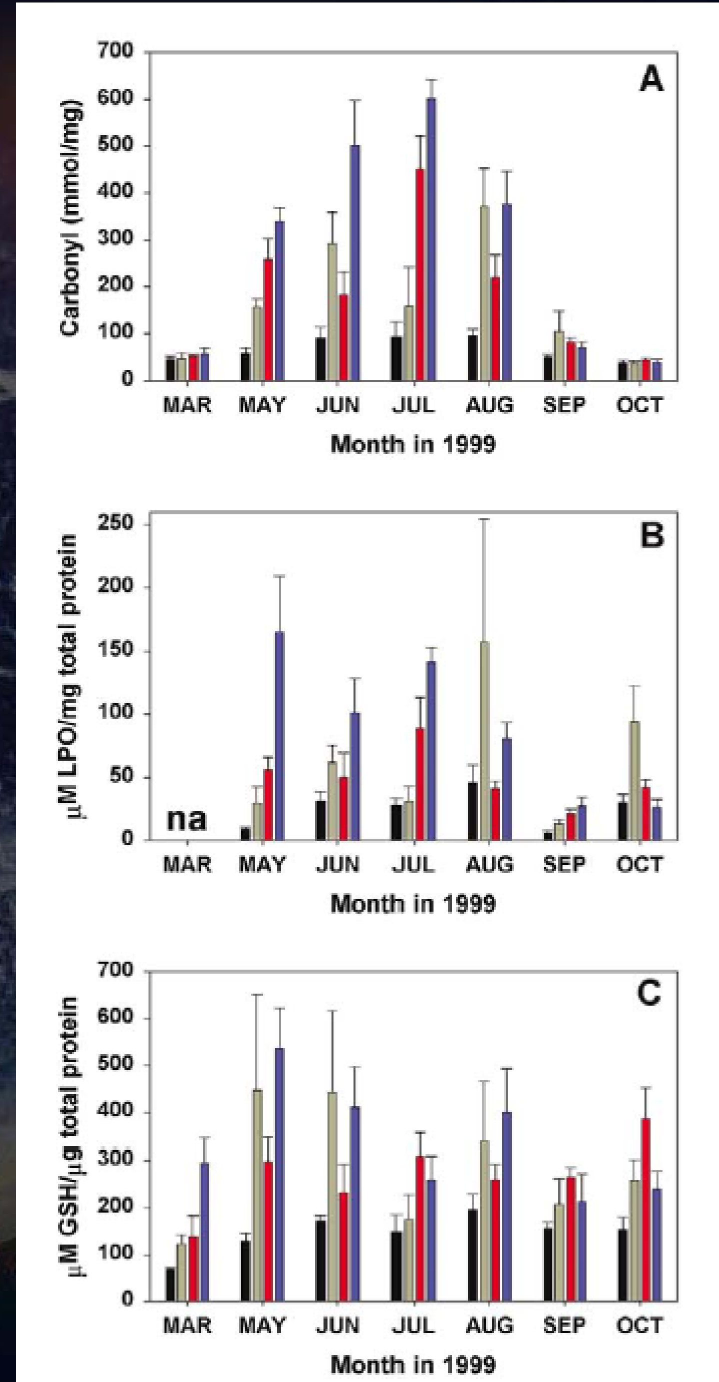


2. Physiology of thermal stress.

Downs et al (2003)

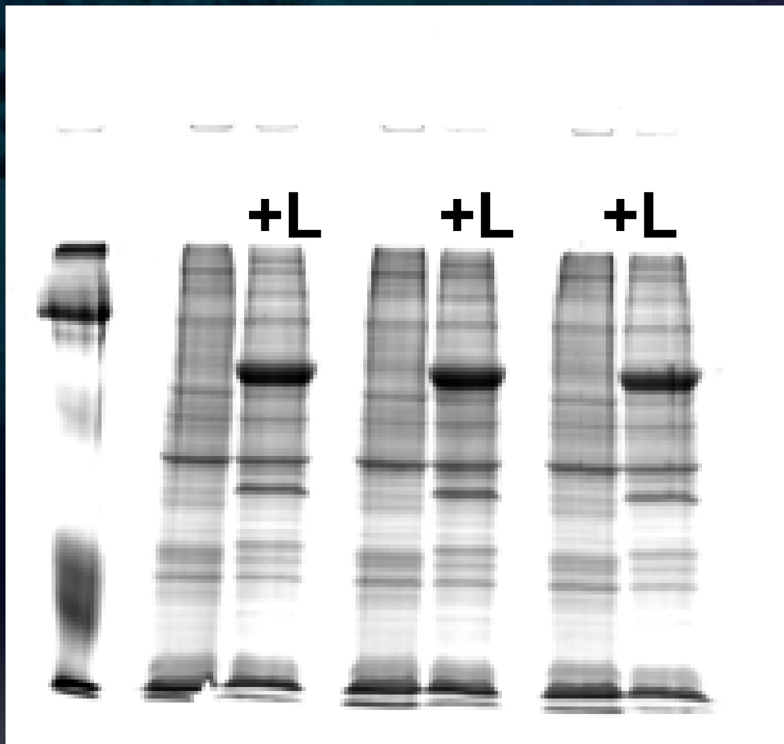
- General stress response to thermal stress in the presence of light
- Complex responses – indicating general oxidative response – ie bleached corals suffer from enormous quantities of active oxygen.

Montastraea annularis (Florida keys)



2. Physiology of thermal stress.

Carolyn Smith (in prep.)



- Irradiance is needed to get up-regulation of stress proteins
- No light , no bleaching

Mumby et al 2001 – deviation from expected impacts due to cloud.

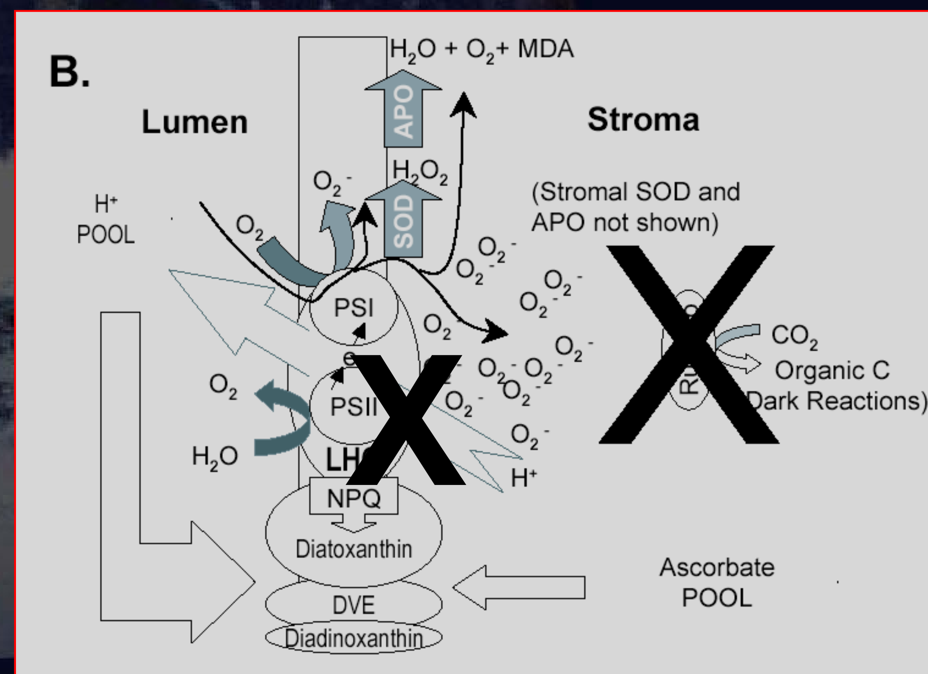
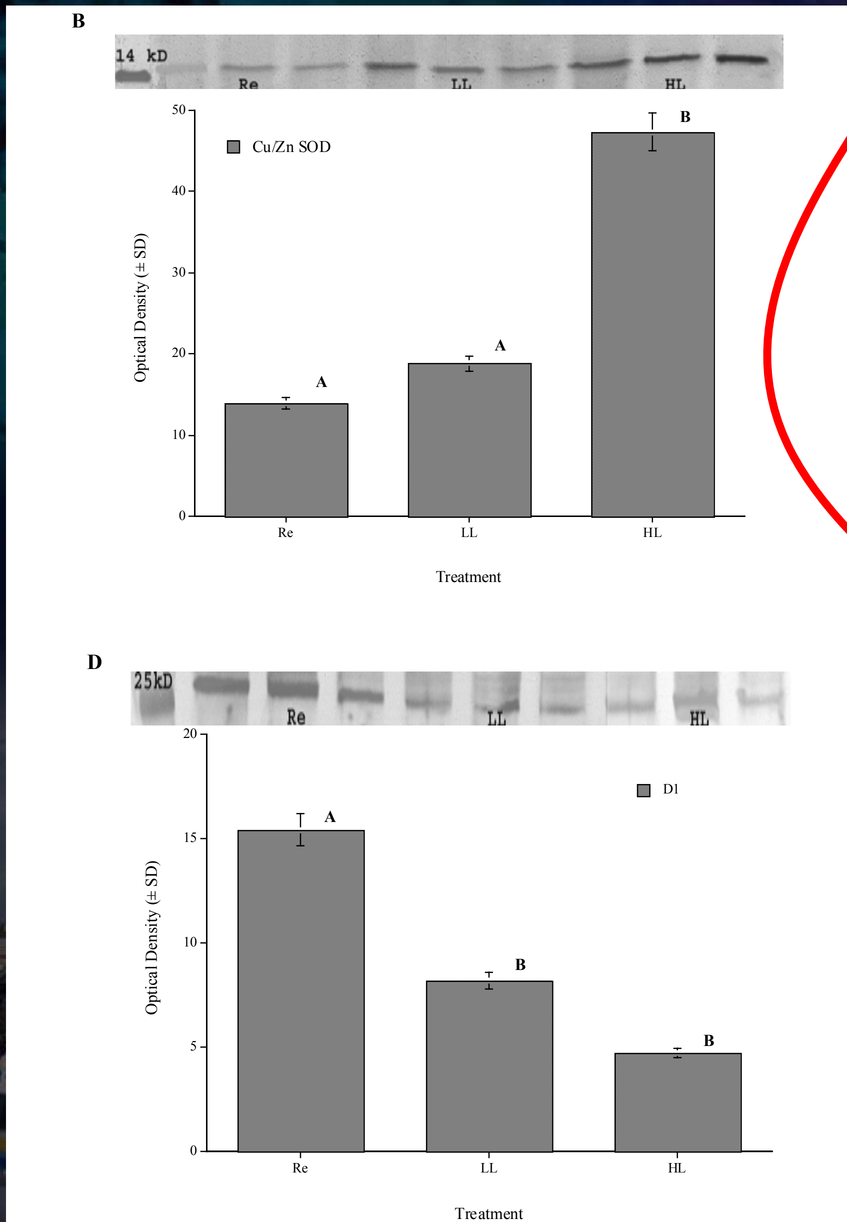


Fig. 6. Photoinhibition model of coral bleaching (Jones *et al.* 1998).

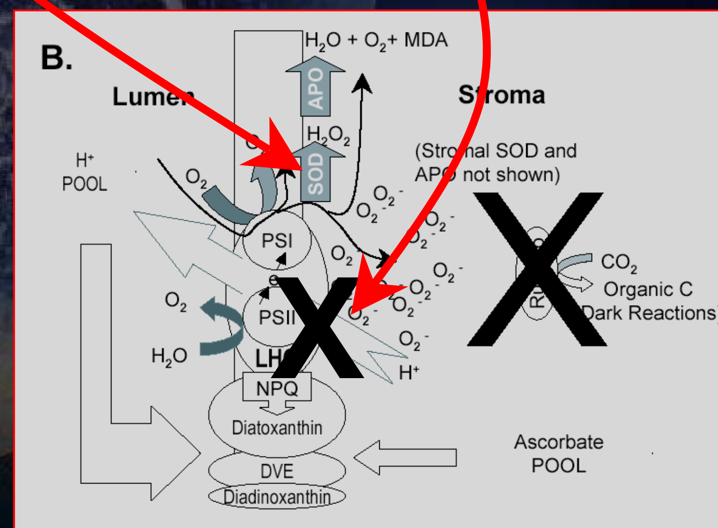
2. Physiology of thermal stress.

Michael P Lesser (in press)



Montastrea (Bemuda)

- Superoxide dismutase (SOD) is stimulated under heat and light (HL)
- Functional D1 protein (from PSII) is much lower when coral is subjected to heat and light.



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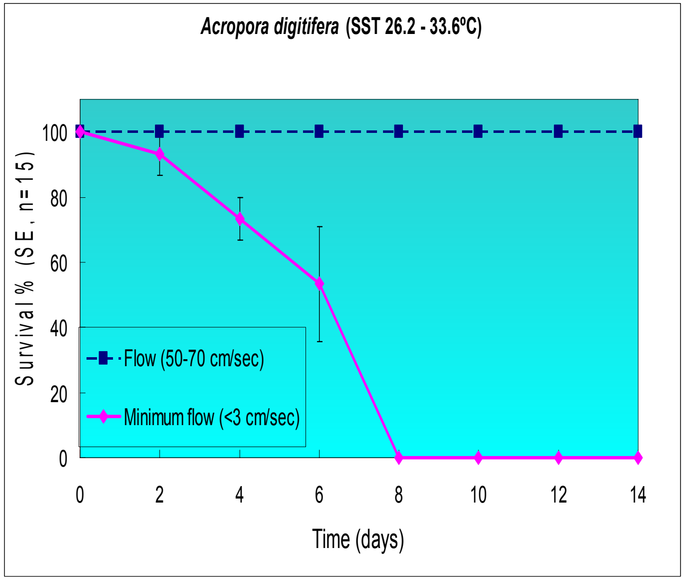
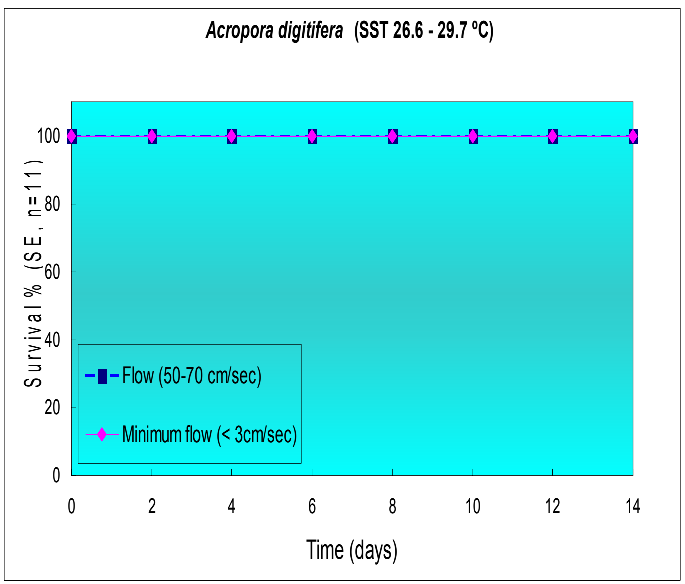
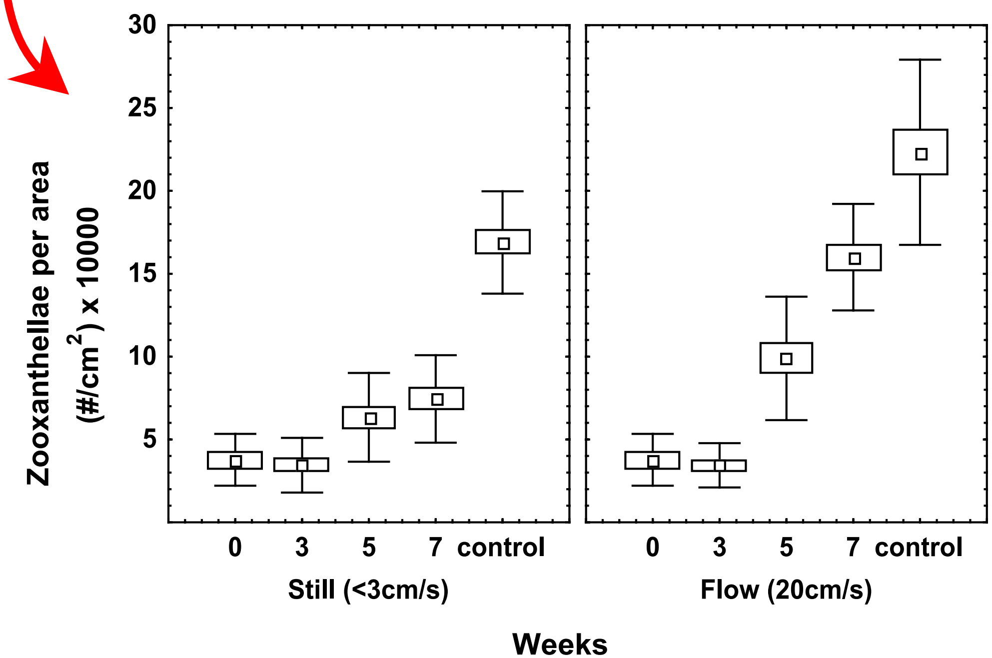




Low flow interacts to cause a greater impact of thermal stress.

High flow causes greater recovery



Nakamura, Yamasaki & Van Woesik. Mar Ecol Prog Ser (In Press)

Programmed cell death?

- PCD involves activation of ‘cell removal’ pathways.
- Many of the markers for PCD have been found in bleaching symbiotic associations
- Sequence:

Environmental stress → Photosynthetic dysfunction → Oxidative damage → Removal by PCD

Dunn et al. (2002)

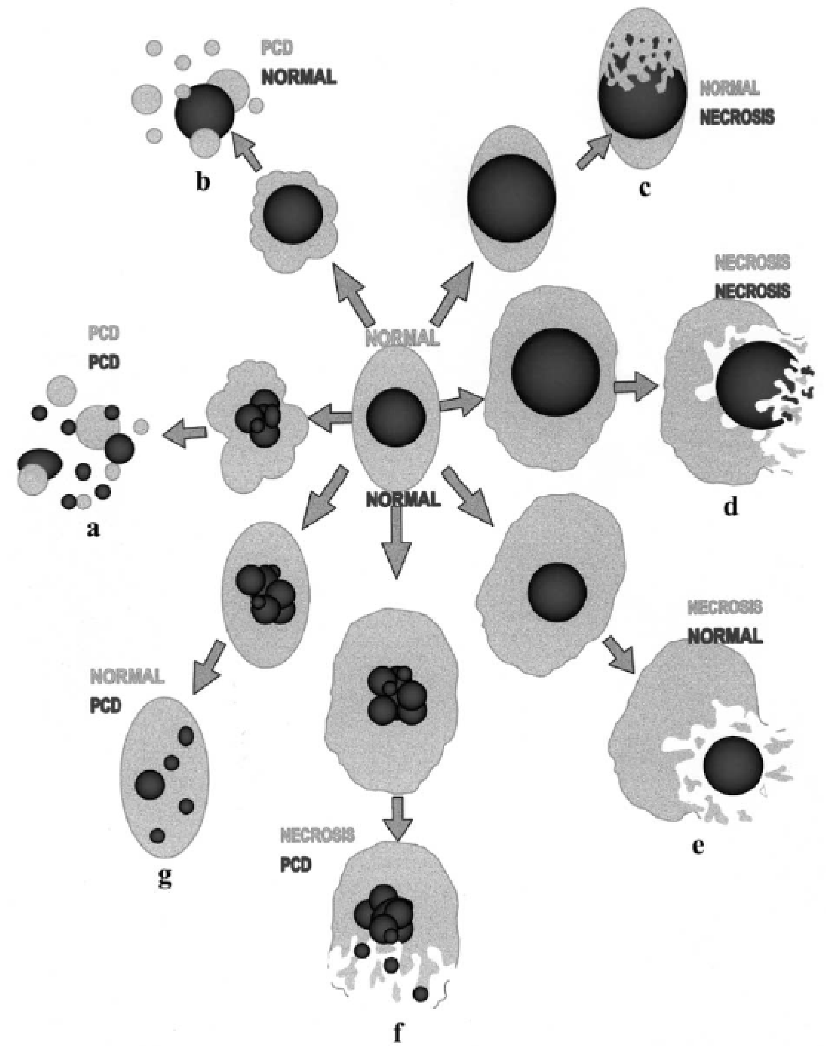


Fig. 11. Schematic diagram illustrating possible combinations of PCD and cell necrosis activity in an endosymbiotic system and can lead to zooxanthella release and in-situ degradation, which can result in bleaching. Combinations (a) and (b) were observed by Dunn et al. (2002) and combinations (d) (e) and (f) were observed during this study. Combinations (c) and (g) were not observed in this study or by Dunn et al. (2002). Key: light cells/script = animal cells, dark cells/script = zooxanthella, NORMAL = normal healthy cell, PCD = programmed cell death, and NECROSIS = cell necrosis.

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4. Acclimation and adaptation
5. Conclusion

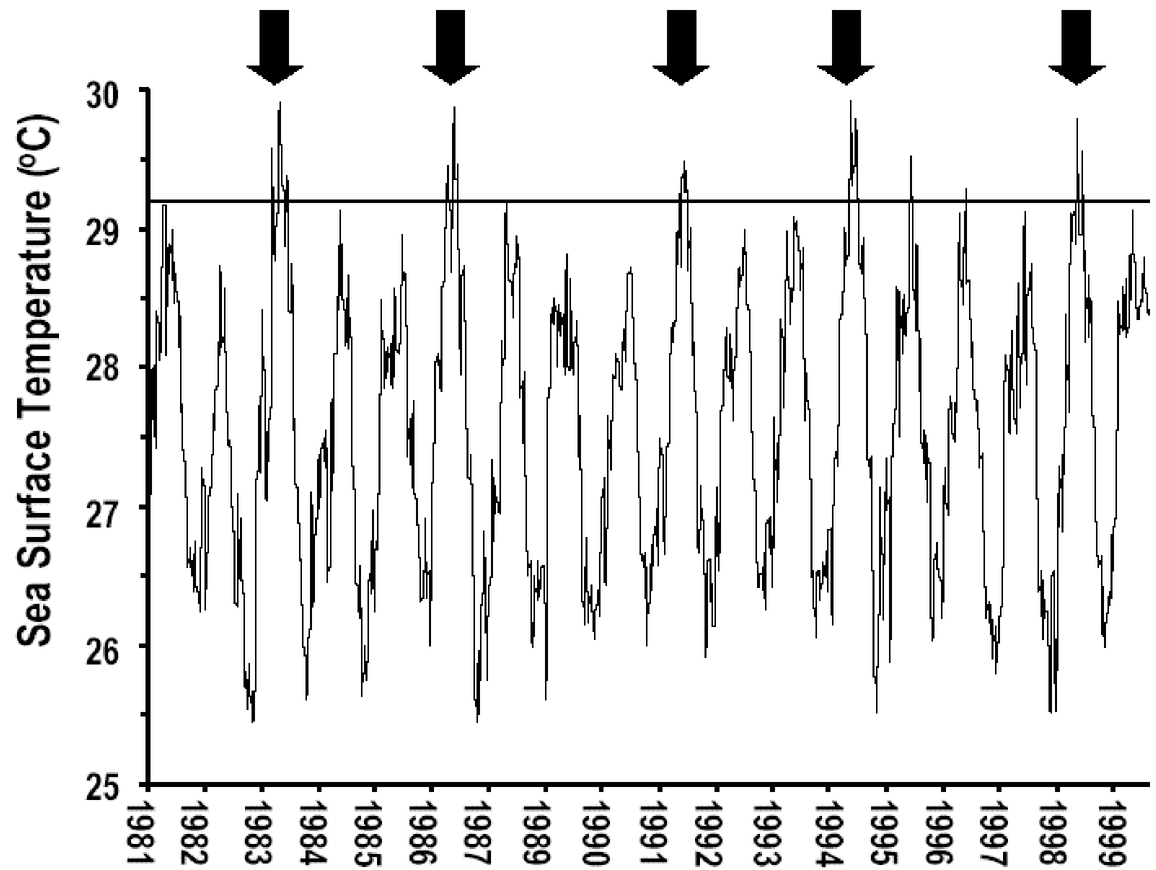
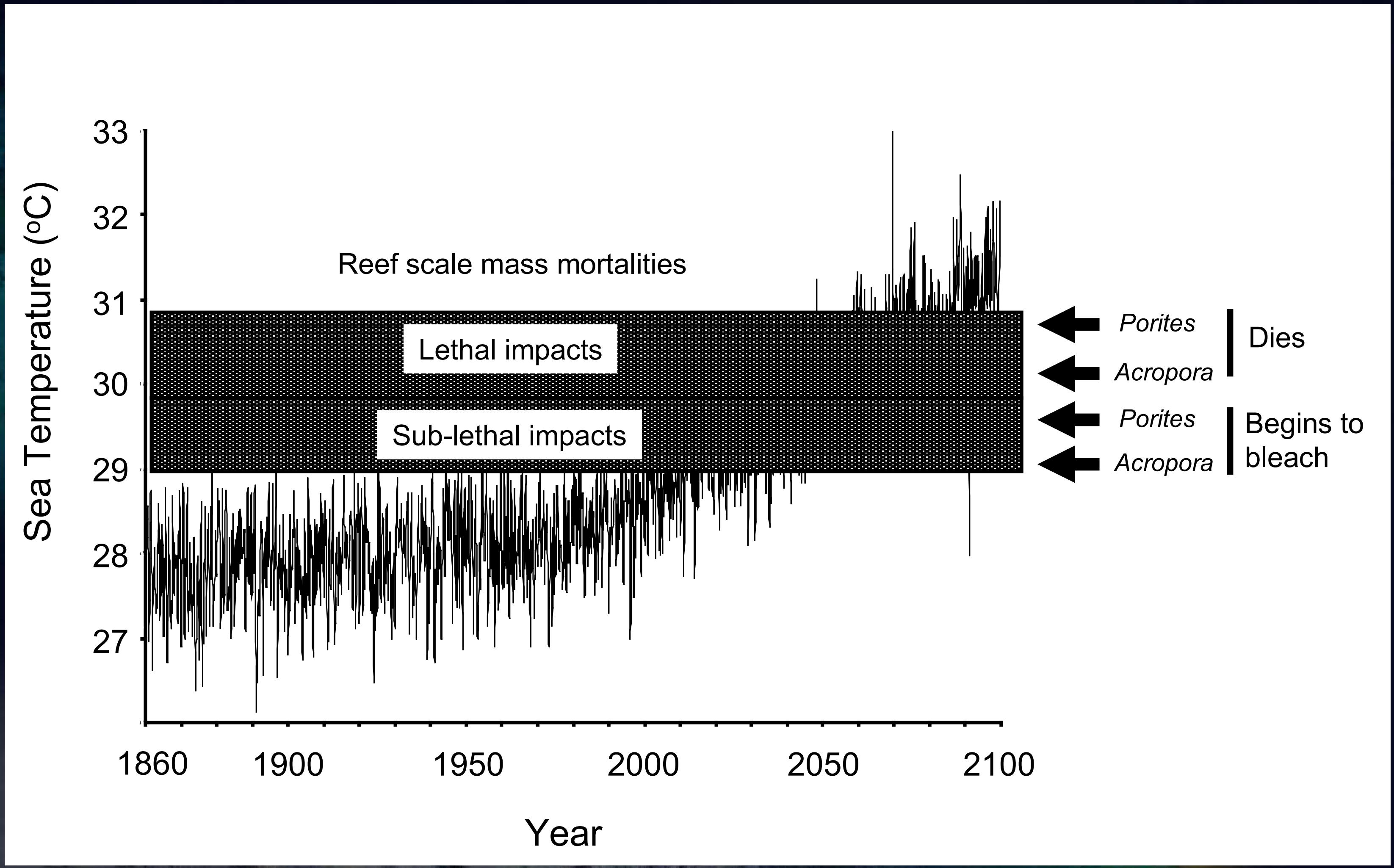


Fig. 7. Weekly sea surface temperature data for Tahiti (17.5°S,149.5°W). Arrows indicate bleaching events reported in the literature. Horizontal line indicates the minimum temperature above which bleaching events occur (threshold temperature). IGOSS-nmc blended data courtesy of the Lamont-Doherty Climate Center at Columbia University.

3. Thresholds and global change



1. While a coral colony will have a single thresholds determined by temperature and contributing factors (light, history, genetics, acclimation etc), a reef will have a band of thresholds that wil vary according to different species tolerances.
2. At the lower end of this band, community change will be seen. At the higher end, reef scale mass mortalities will eventuate.

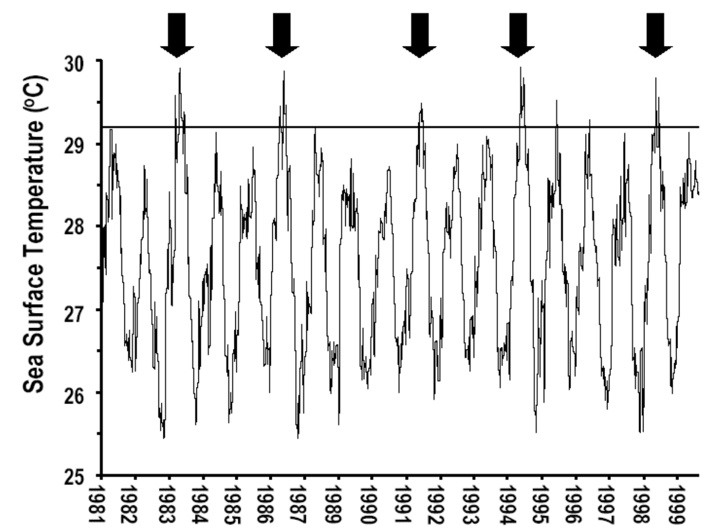
3. Thresholds and global change

Table 6. Comparison of recent Degree Heating Months and mass bleaching mortality estimates from incidents of bleaching within the 1998 mass bleaching event (adapted from Hoegh-Guldberg 2002).

Severe events (mortality > 80%)			
Location	**Degree heating months**	**Mortality**	**Source**
Palau	3.9	70-90%	J. Bruno, unpublished data
Seychelles	3.1	Up to 75%	Spencer et al. (2000)
Okinawa	3	90-95%	Loya et al. (2001)
Scott Reef	2.6	75-90%	L. Smith and A. Heyward, unpublished data
Mean ± 95% CI	3.2 ± 0.47		

Mild events (mortality < 10%)			
Location	**Degree heating months**	**Mortality**	**Source**
Southern GBR (reef crest)	1.7	10-30%	Jones et al.
Central GBR (inner reefs)	1.4	1-16%	Marshall ai
Moorea (outer reef crest)	0.9	0% mortality	Personal ol bleached)
Cook Is (Southern; reef crest)	0.4	0% mortality	Personal ol bleached)
Mean ± 95% CI	1.1 ± 0.49		

Degree Heating Months = Intensity of anomaly X time



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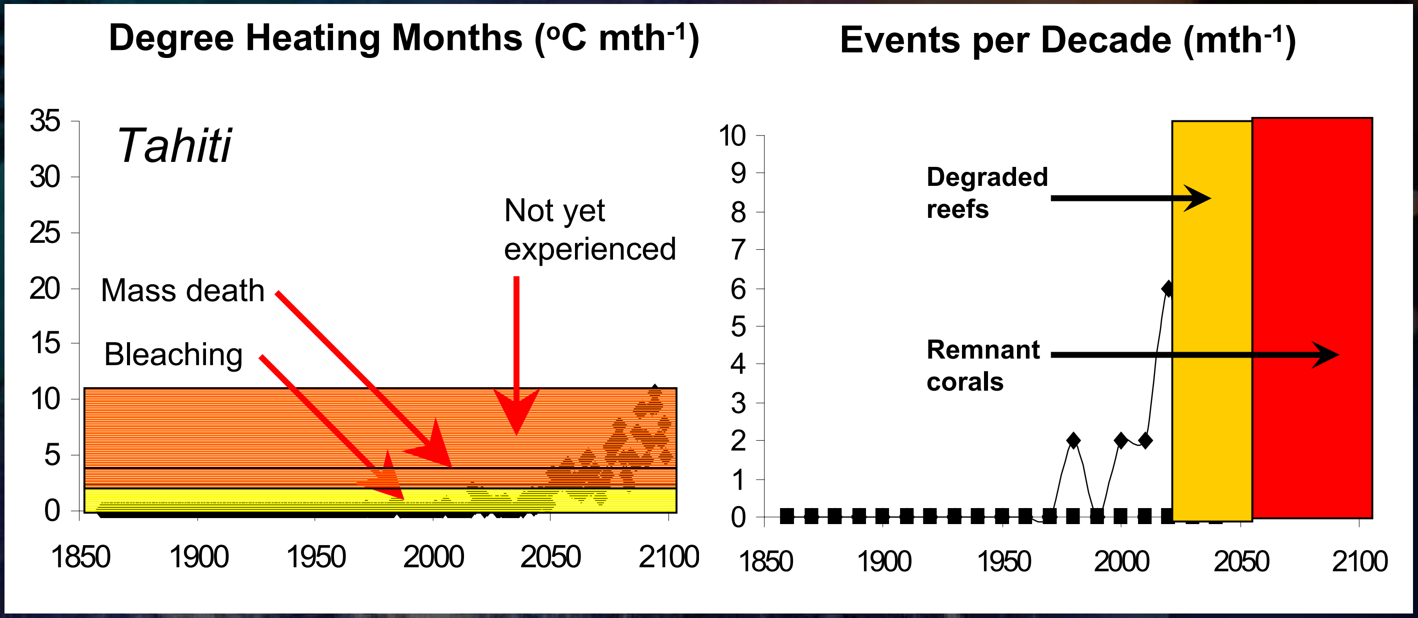
3. Thresholds and global change

DHM and the future (B2 scenario)

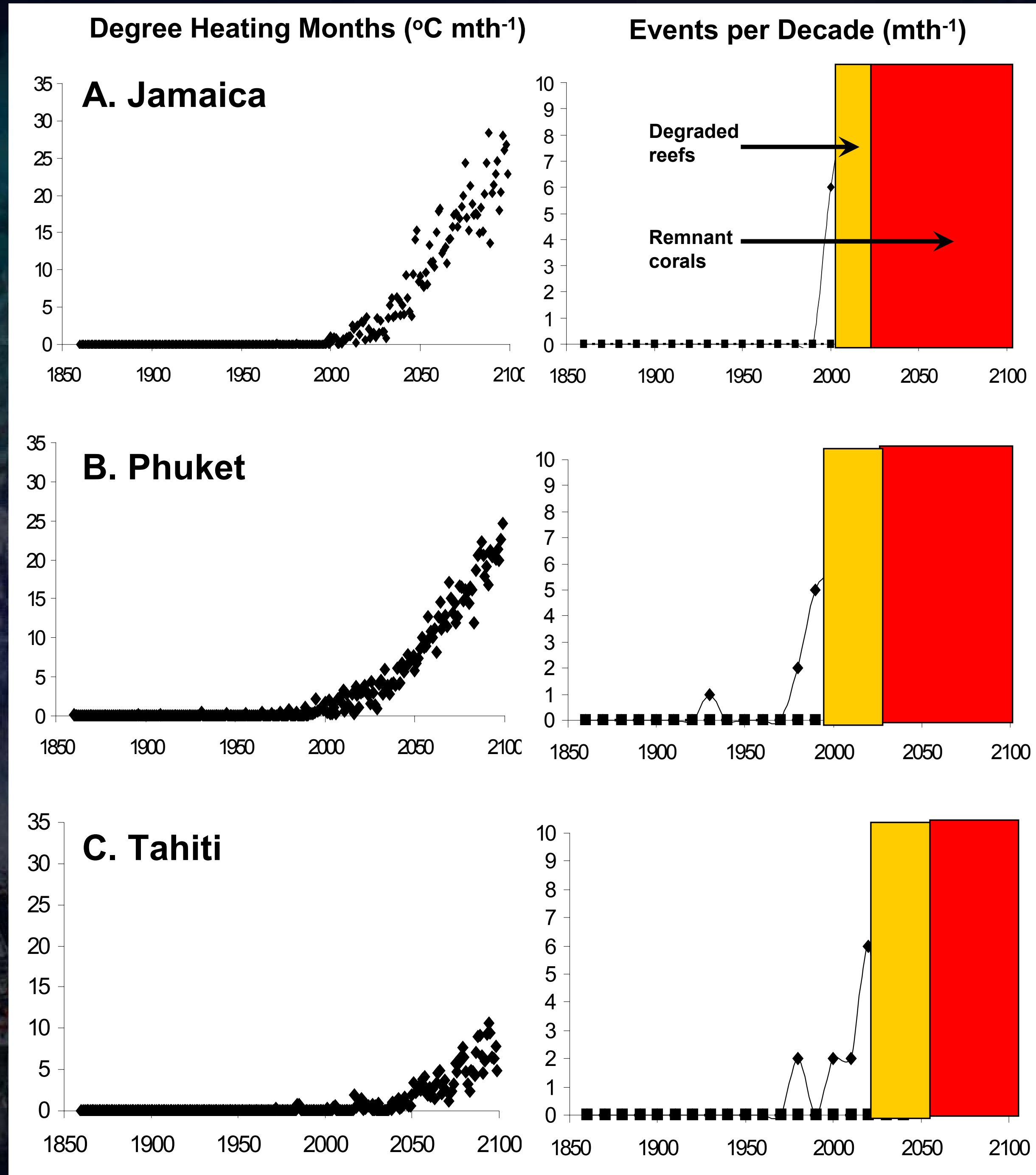


Two categories of response can be defined:

<u>Degraded Reefs</u>: Reefs that experience 0.5 Degree Heating Months (DHM) during the summer months will experience mass bleaching. They will recover if stress levels return to previous levels.

<u>Remnant coral reefs</u>: Reefs that experience near total coral mortality: Reefs that are exposed to 3.2 DHM per year or more will experience almost complete mortality of their coral populations. Logic – corals don't recruit and grow fast enough to have reefs recover within 3 years from a total mortality.

3. Thresholds and global change



Outline

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4. Acclimation and adaptation

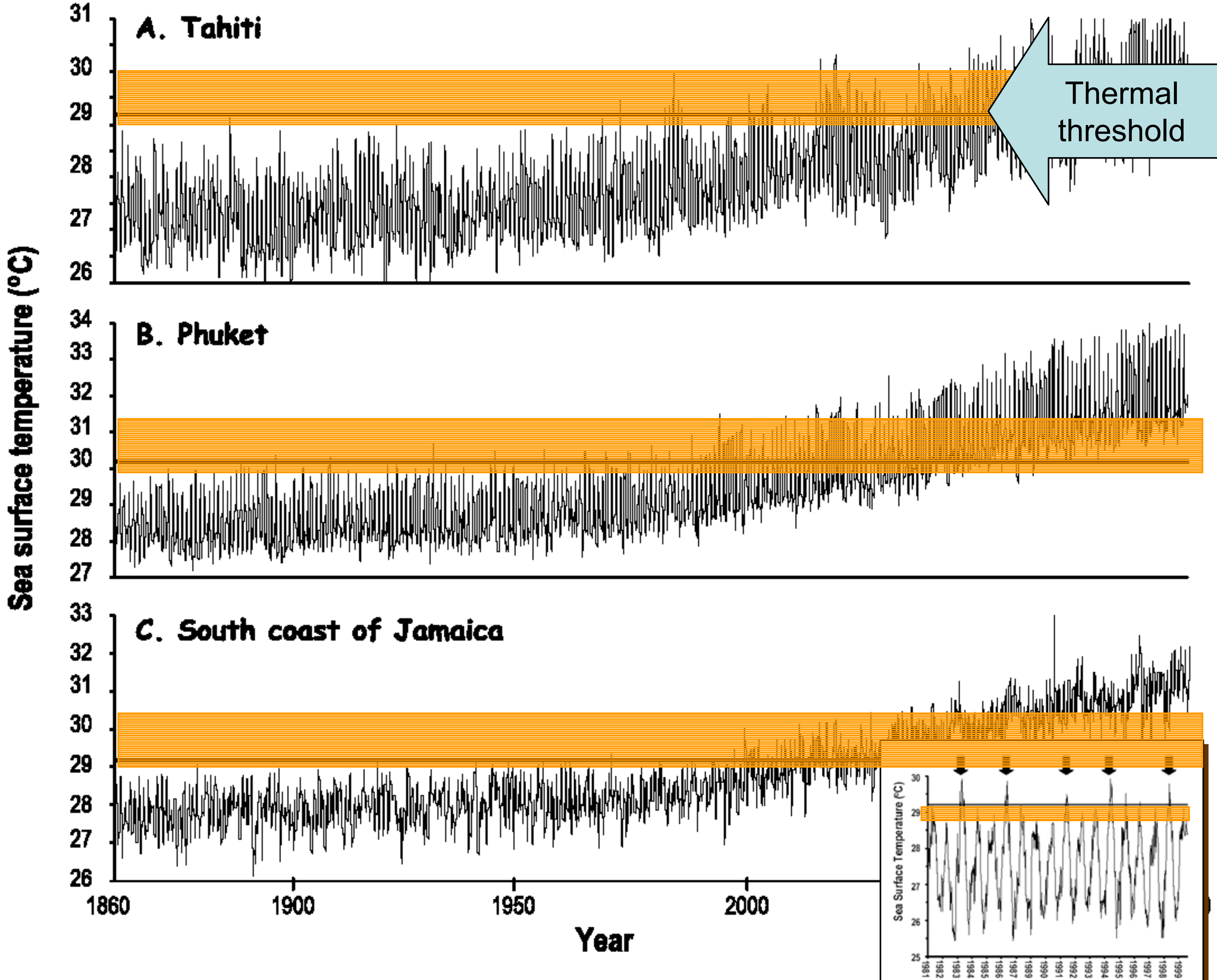

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Fig. 8. Sea surface temperature data generated by … atmosphere–ocean–ice model (ECHAM4/OPYC3, Roeckner *et al.* 1996)

4. Acclimation and adaptation

Acclimation, acclimatization and adaptation (definitions are critical) have been demonstrated in reef-building corals.

Acclimation: Short-term phenotypic change

- Reviewed extensively by Brown and others
- Habeeb and Edmunds (in press) show acclimation of corals to short-term stresses.

Acclimatization: Phenotypic change to natural environment

- Berkelmans and Willis (2000) have demonstrated seasonal acclimatization in several species.

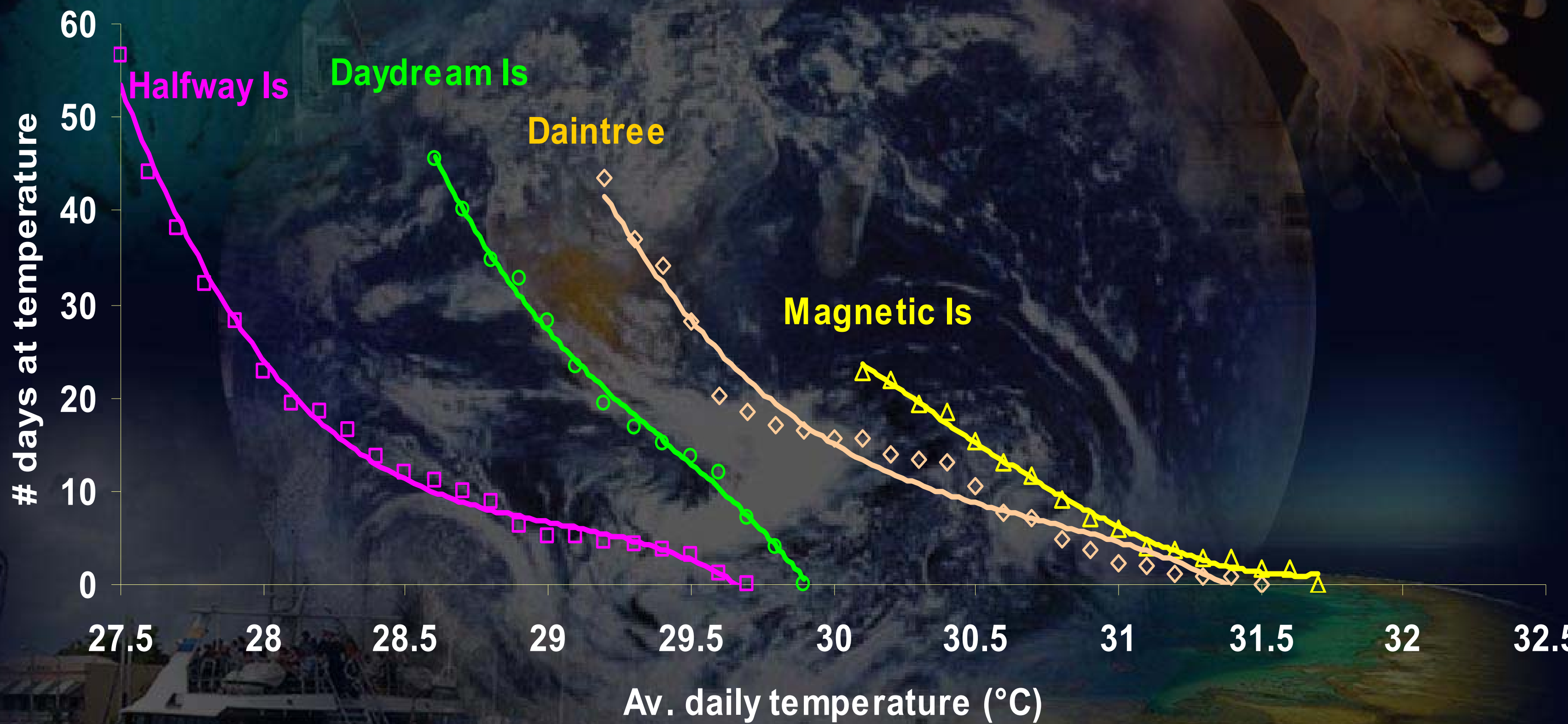
Adaptation: Genetic change in coral population

- Glynn (1983) and many others have observed that different species of corals have different thermal thresholds.
- Coles et al. (1976) and later authors have demonstrated that corals are adapted to the temperature conditions around them – corals at different latitudes have different thermal thresholds.
- Berkelmans (2002) – latitudinal variation in thresholds in a single ecosystem

Adaptation: Genetic change by swapping symbionts

- Recent reviews by Baker, LaJeunesse
- Definite switches in evolutionary time
  - Loh et al. (2002): Pocillopora damicornis has clade A in Japan, D in Indonesia and C in Australia
  - Rodriquez-Lanetty et al. (2001): Plesiastrea versipora has clade A and B in Southern Australia and C on the Great Barrier Reef
  - Among others

Evidence of adaptation to sea temperature



Berkelmans (2002)

Evidence of rapid adaptation (past 20 years)?

- Glynn et al. (2001)
  - Observed less bleaching and mortality in Eastern Pacific in 1997-98 than in 1982-83. Despite fact that temperatures may have been higher in 1997-98
- Obura (in prep)
  - Lower impacts in recent bleaching (2003) in East Africa to that seen in 1997-98. Similar speculation to Glynn et al. (2001)
- Baker (2001)
  - Possible switching of symbionts (or is this re-mixing of existing types)

Problems:

- Sample design between times?
  - E.G. site variability within locations not strictly controlled
- Low precision measurements of bleaching (bleached, non-bleached, normal)
  - Jones 1997, Fitt et al. 2001, Warner et al. (2002) all point to the fact that up to 30% of the cells can be missing before a coral will be classified as bleached.
- Environmental conditions complicated by secondary factors
  - As shown by Mumby and others – clouds can ameliorate the effect of thermal stress

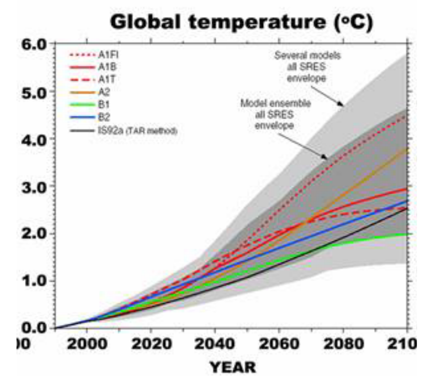
4. Acclimation and adaptation

Rate of change versus possible rate of response

Table 1. Regression slopes calculated for periods of rapid change in Antarctic (interglacial-glacial transitions) within the Vostok ice core. Also shown in table are rates of change over the last 100 years and that projected to occur from climate change over the next century.

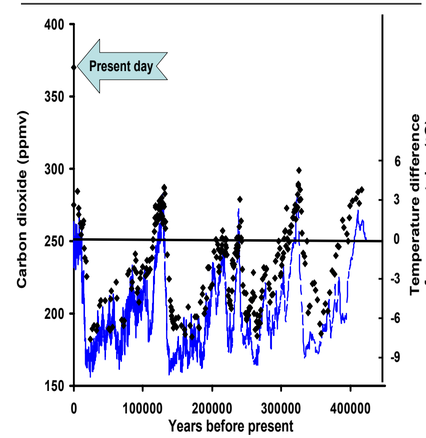
A. Maximum rates of change in carbon dioxide (using data from Barnola *et al.* 1999).

Period	ppmv per 100 yr
24,315 to 9.523 yr BP	0.52 ± 0.080
130,653 to 143,732 yr BP	0.72 ± 0.034
240,006 to 248,364 yr BP	0.96 ± 0.097
325,400 - 355,795 yr BP	0.30 ± 0.043
Recent (last 100 yrs)	100
Projected (B1) - 2002-2100	150
Projected (A1T) - 2002-2100	330
Projected (A1B) - 2002-2100	530



B. Maximum rates of change in temperature (using data from Petit et al. (1999)

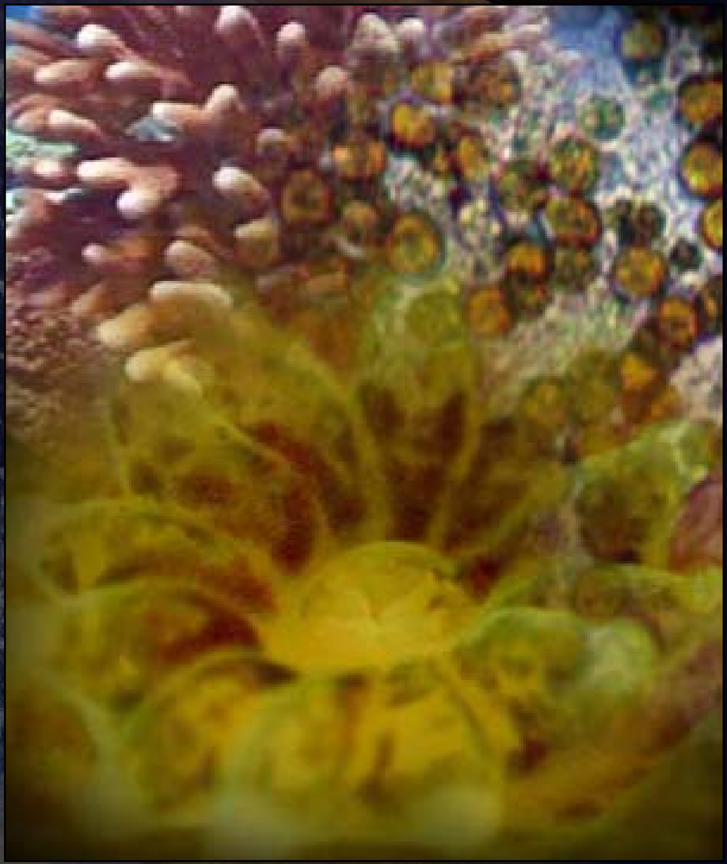
Period	°C per 100 y
11,191 - 16,808 BP	0.092 ± 0.005
130,467 - 145,006 yr BP	0.135 ± 0.003
237,866 - 241, 792 yr BP	0.227 ± 0.005
322,638 - 332,164 yr BP	0.117 ± 0.003
Recent (last 100 yrs)	0.600
Projected (B1) - 2002-2100	2.500
Projected (A1T) - 2002-2100	2.400
Projected (A1B) - 2002-2100	2.800



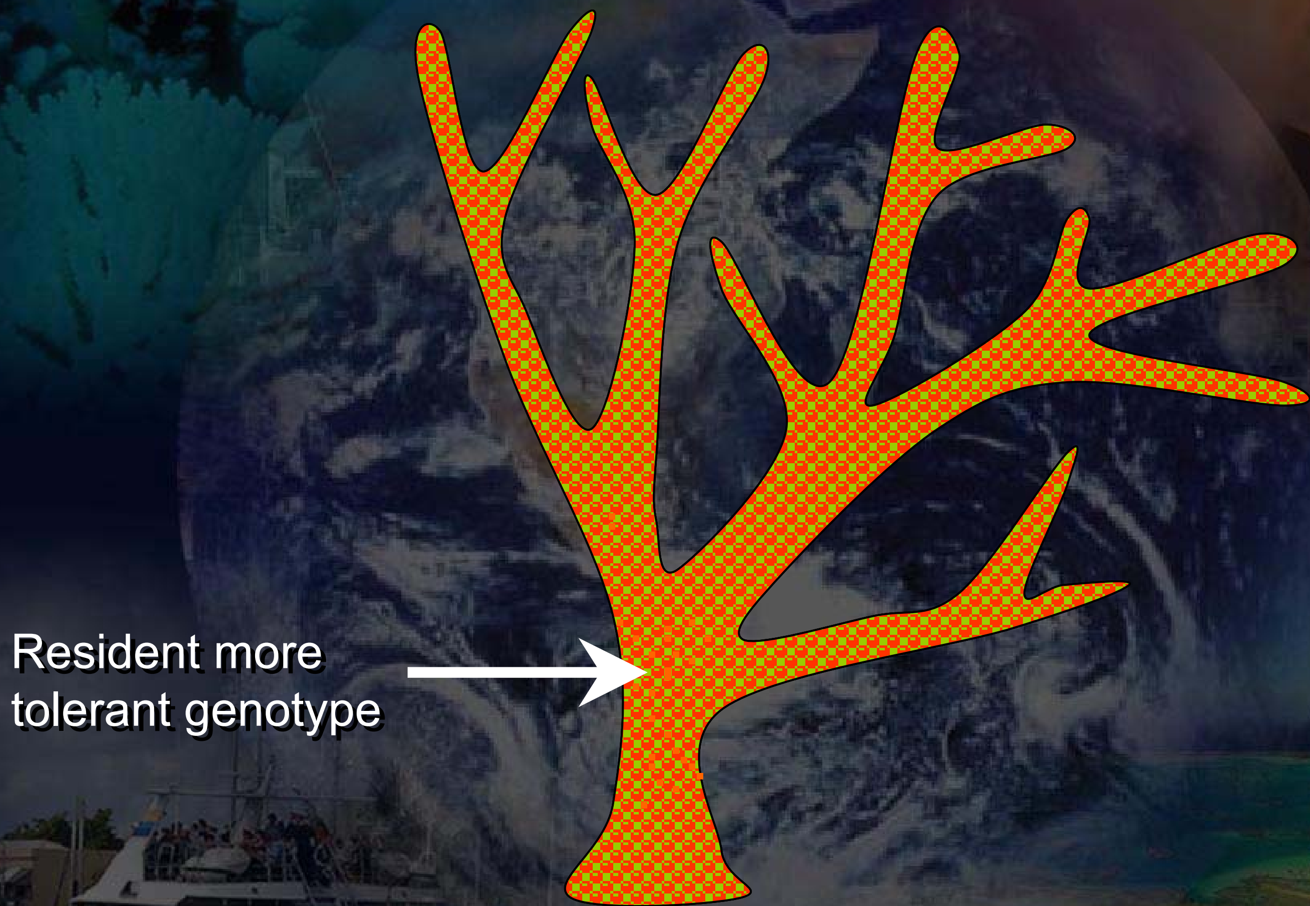
4. Acclimation and adaptation

Adaptive Bleaching Hypothesis?

- Two or more partners (genomes) not one
- Dinoflagellate contributes a major part of thermal tolerance. Perhaps changing symbiont can result in tougher holobiont (host-symbiont genotype)
- Includes de novo acquisition or remixing of symbionts
- And - perhaps - bleaching is adaptive (Buddemeier and Fautin 1993)?

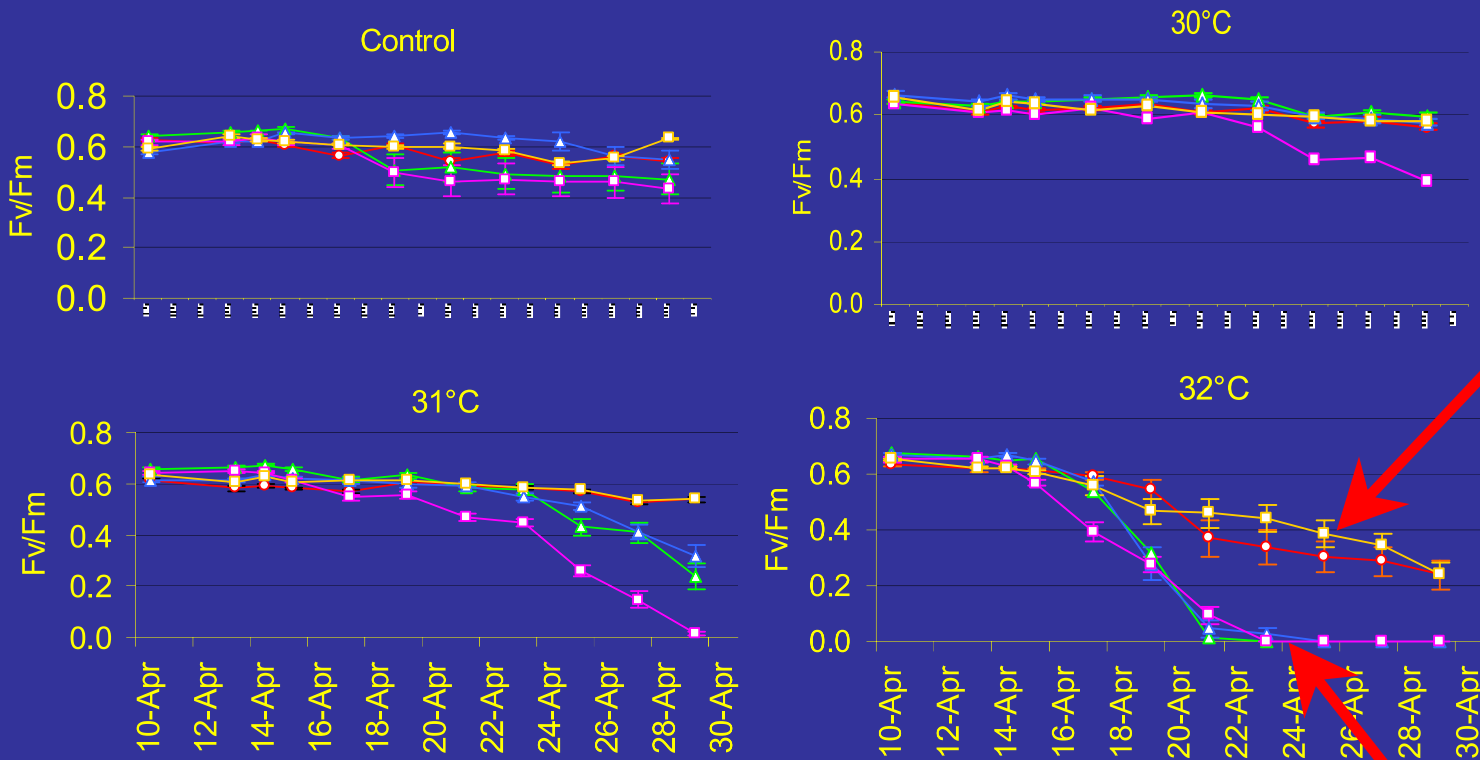


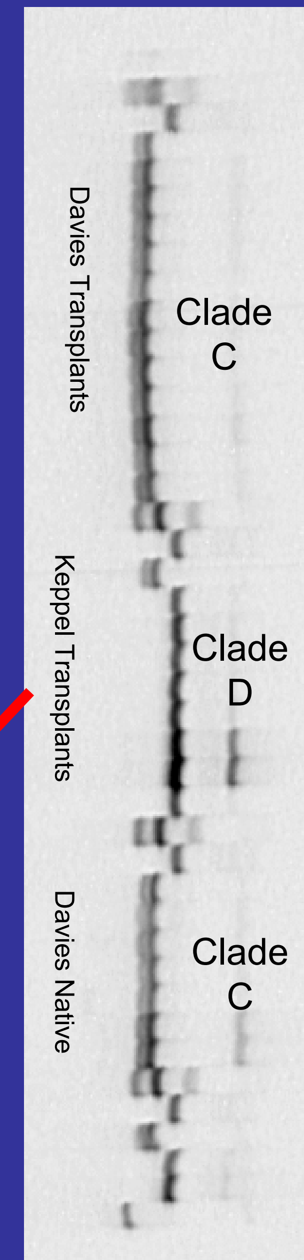
Direct acquisition of new symbionts is probably debatable. However, remixing of existing ones has been observed.



Baker (2002, Nature) shows this mechanism to operate. However, no new combination arises from this process (its phenotypic in nature)

Effect of zoox. clade on thermal tolerance *Acropora millepora*

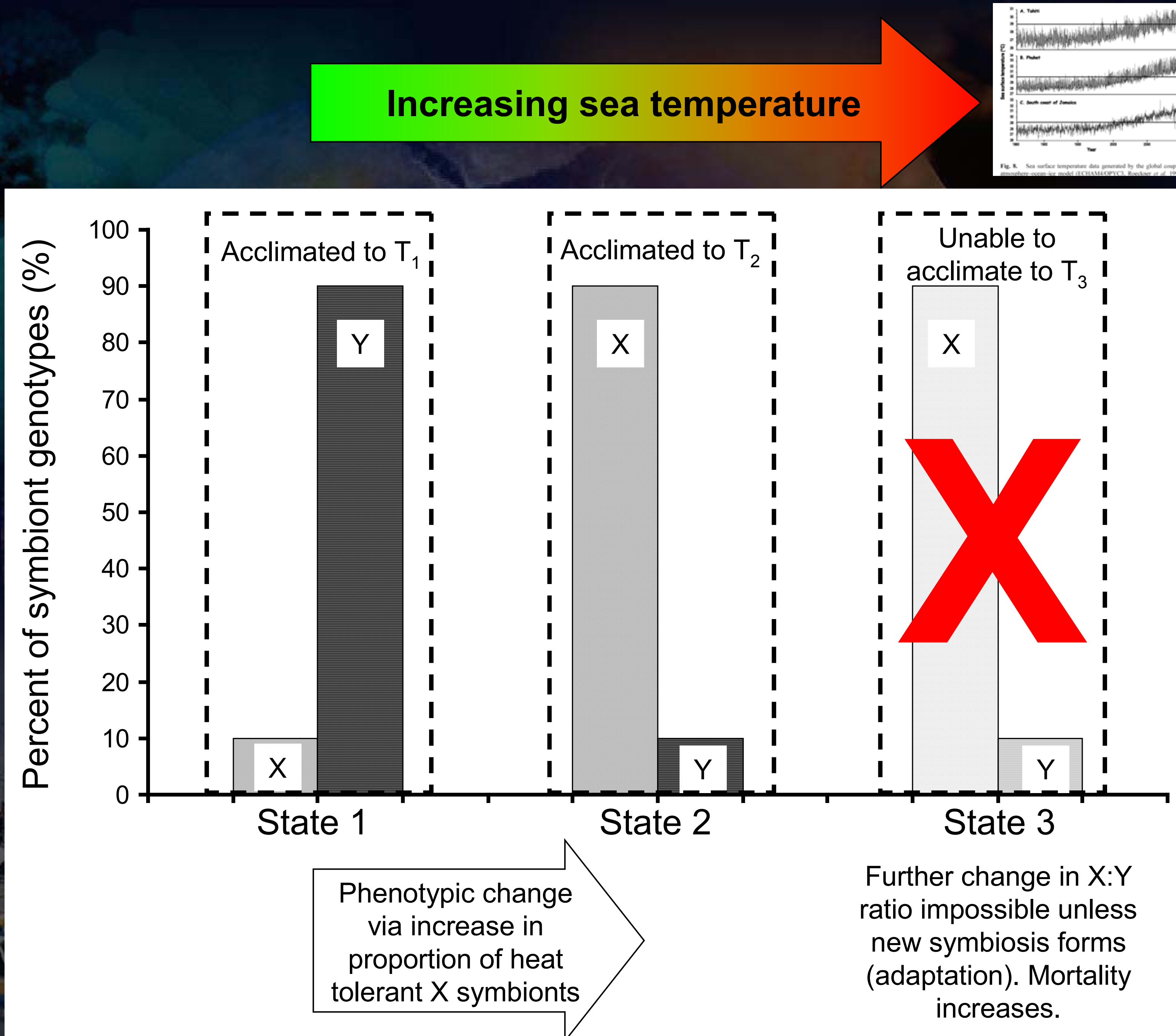




Native Keppels = Clade C

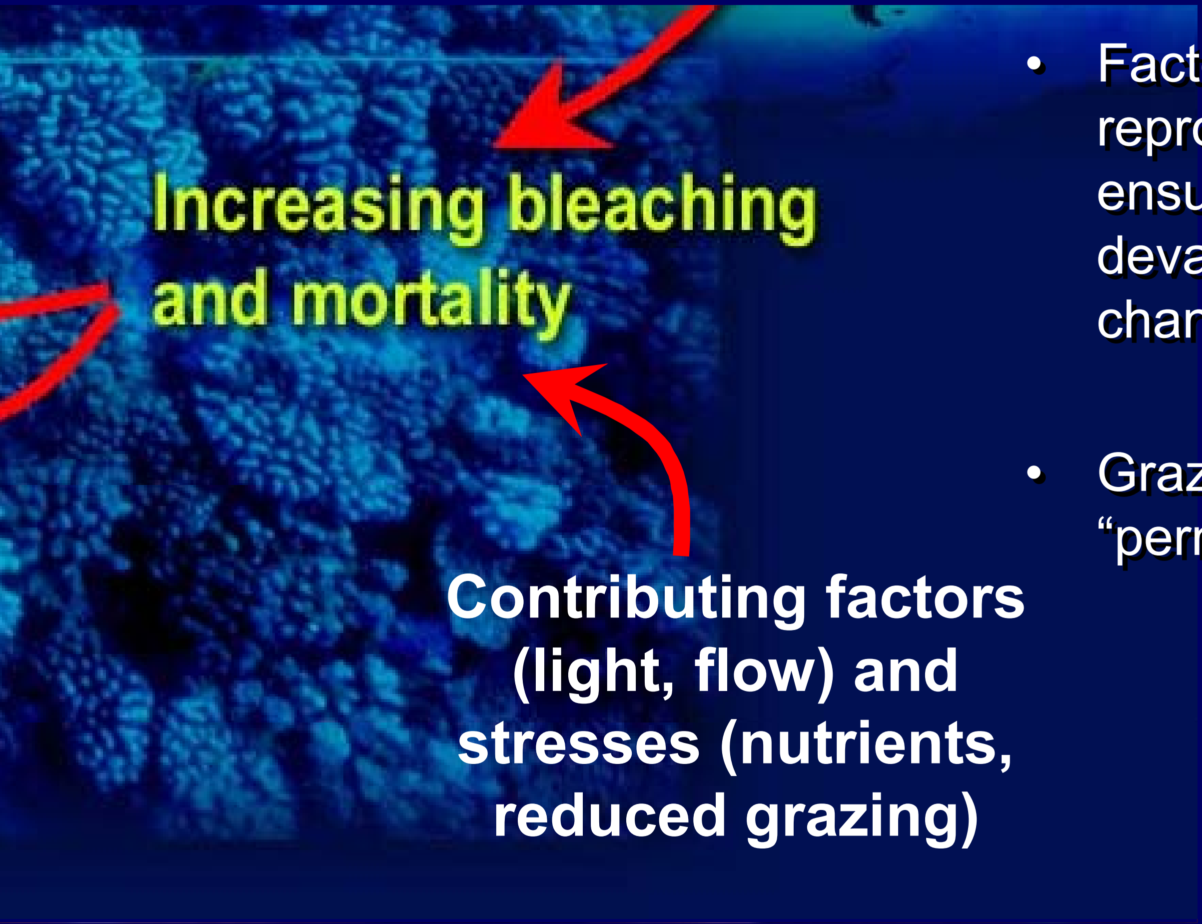
Berkelmans and van Oppen (in press.)

4. Acclimation and adaptation



Managing for ecological resilience

- Evidence that healthy reef systems recover faster from bleaching
- Factors that impact growth and reproduction of corals will ensure more immediate and devastating impacts of climate change.
- Grazers play a role in avoiding "permanent" phase shifts



5. Conclusions

PATTERNS OF CHANGE

- Climate change (of only 0.8°C) has changed the biosphere
- Projected changes (2-6°C) have major implications for all ecosystems including coral reefs

PHYSIOLOGY

- Warmer than normal sea temperatures trigger bleaching
- Thermal stress results in failure of photosynthetic apparatus, which leads to oxidative stress in host and symbiont.
- This may trigger apoptosis (programmed cell death)
- PAR, UVR and flow play important secondary roles
- The increase in disease is probably related directly or indirectly to rising stress

THRESHOLDS

- Thermal thresholds form a band of sea temperatures in which responses range from community change to mass mortality.
- Projected increases under even the mildest climate scenarios will rapidly exceed the known thermal thresholds of populations of corals
- Corals and coral reefs will experience conditions that have not seen for 400,000 years (if not at least 20 million years)
- The weight of evidence indicate serious modifications to the function of coral reef ecosystems.

ACCLIMATION AND ADAPTATION

- Acclimation is limited ultimately by genotype and therefore is not a "solution" to climate change.
- Corals and their symbionts have adapted to sea temperature in the past
- Corals have swapped their symbionts to adapt to environmental conditions in the past.
- Re-mixing existing ratios of symbionts is a phenotypic not genotypic change.
- Changes, however, have occurred in evolutionary time not the ecological timeframe of bleaching.

RESPONSES

- Reefs must be urgently managed for maximum ecological resilience
- Factors contributing to climate change must be rapidly brought under control.

1. Patterns of change

Marine ecosystems are also changing rapidly

- Environmental changes
  - Increasing sea temperatures and sea levels
  - Decreasing carbonate alkalinities
  - Changing currents and global circulation
- Biotic responses abundant already
  - Warm-water fish populations have advanced poleward (Holbrook et al 1997)
  - Intertidal communities moved poleward over the past 70 years (Southward et al. 1995).
  - Krill populations in Antarctica are 10% of what they were 40 years ago – salps, more open water species, have increased 10 fold. Impacts on penguin populations reported (Barbraud and Weimerskirch 2001).
  - Mangroves have expanded and salt marsh contracted.
  - Many other examples.

4. Acclimation and adaptation

Definitions are critical here …

Acclimation: short- term physiological changes that lead to increased tolerance.

Acclimatization: longer-term phenotypic changes in response to changes in the natural environment.

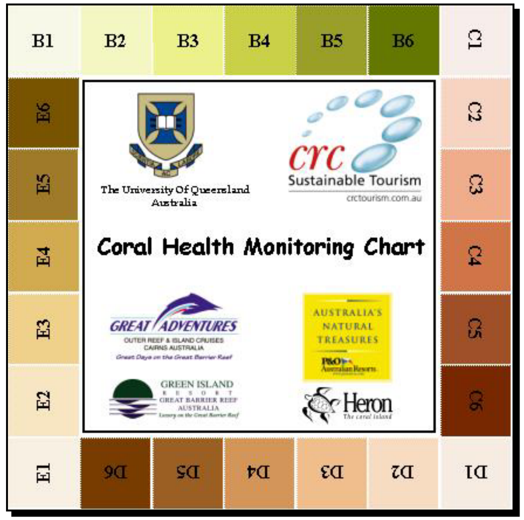
Adaptation: Changes in the genetic structure of a population a species in response to environmental changes. Usually the result or natural selection or migration.

Note – a change in community structure in response to environmental change does not fall under the definition of adaptation.

Colour chart project (to be launched in July 2003)

Siebeck, Marshall, Hoegh-Guldberg

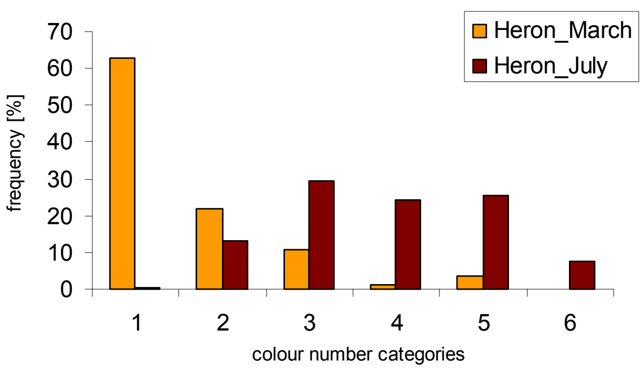
2-types of useful data collection

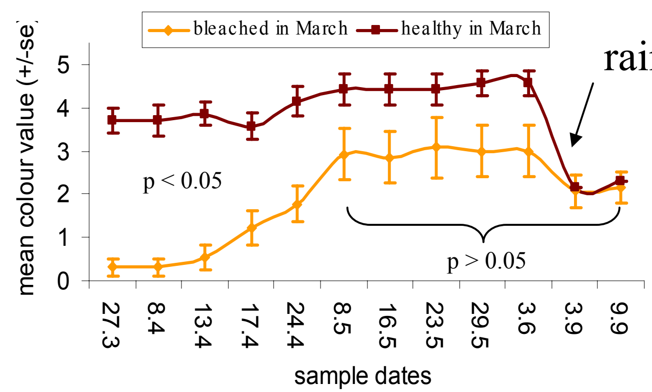


"fingerprints" of a reef at different times: Data of many random corals

Time-series of selected colonies

Heron reef flat during and after the 2002 bleaching





rainstorm

(comparison before and after rainstorm: $p < 0.05$)

Swapping genotypes

Bleaching rids coral host of one genotype which is replaced by a second more tolerant genotype.

Rainforests in Switzerland?

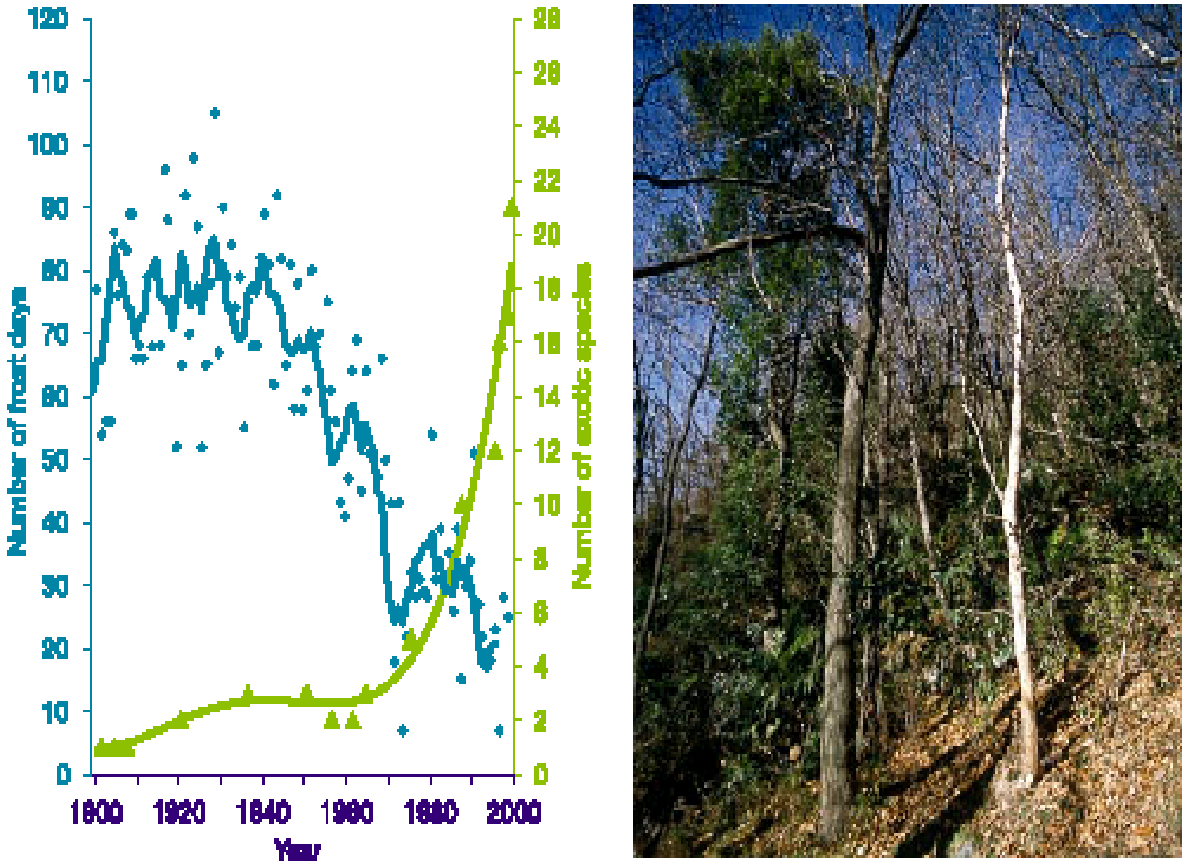
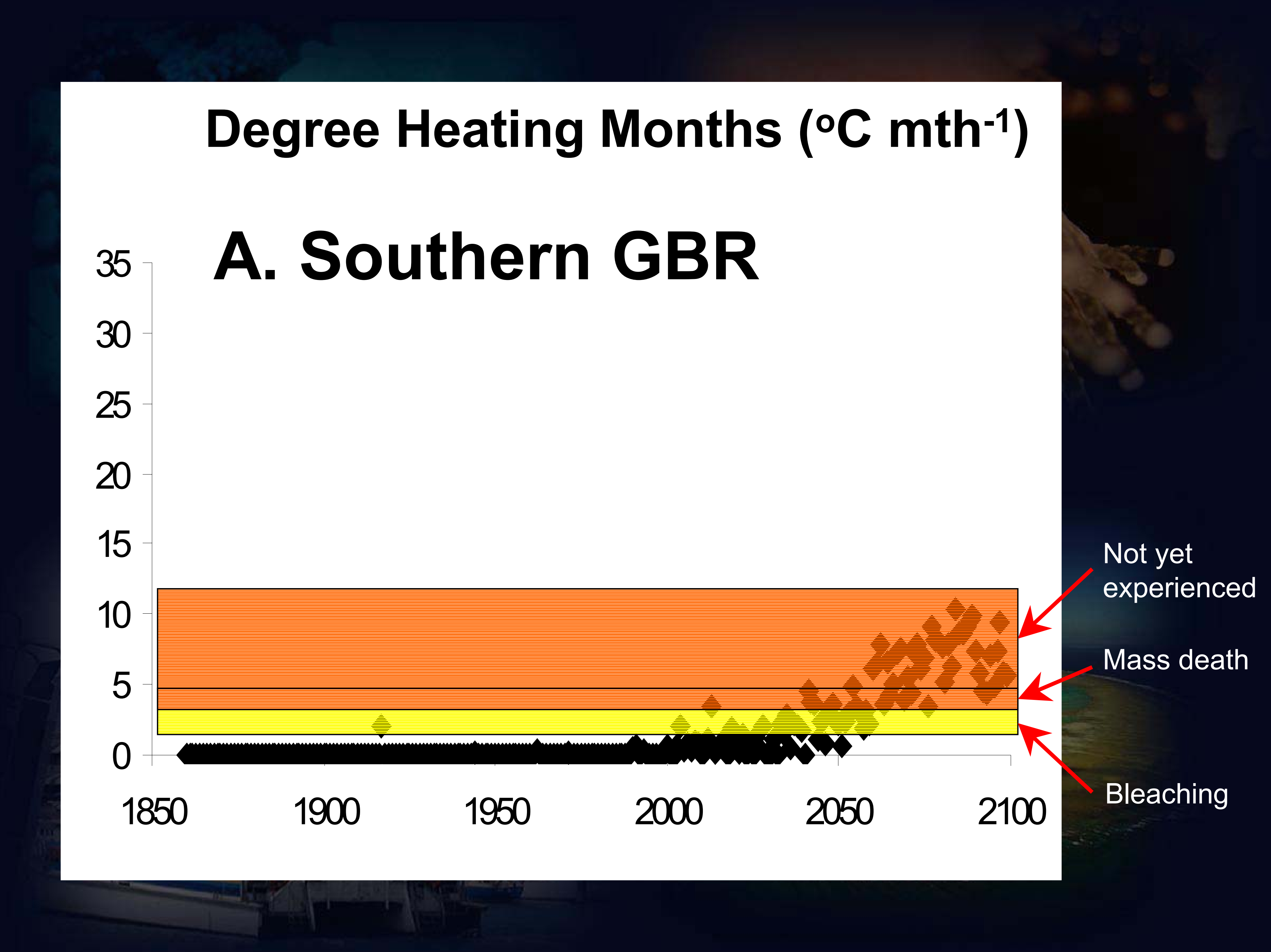


Figure 3 Vegetation shift from indigenous deciduous to exotic evergreen broad-leaved vegetation in southern Switzerland. The shrub layer is dominated by the growing number of spreading exotic evergreen broad-leaved species (see illustration) that appear to profit from milder winter conditions, indicated here by the decreasing number of days with frost per year (the smoothed curve gives five year averages for the number of frost days per year)[29].


Degree Heating Months (°C mth-1)
A. Southern GBR
35
30
25
20
15
10
5
0
1850
1900
1950
2000
2050
2100
Not yet experienced
Mass death
Bleaching

At greater time scales – corals can acquire completely new symbionts

- Loh et al. (2002)
  - *Pocillopora damicornis* has clade A in Japan, D in Indonesia and C in Australia
- Rodriquez-Lanetty et al. (2001)
  - Plesiastrea versipora has clade A and B in Southern Australia and C on the Great Barrier Reef

Evidence that swapping does occur. However, this is not evidence that this happens in the ecological time frame of a bleaching event. Given the complexity of endosymbiosis, establishing novel symbioses probably will take decades and centuries as opposed to years.