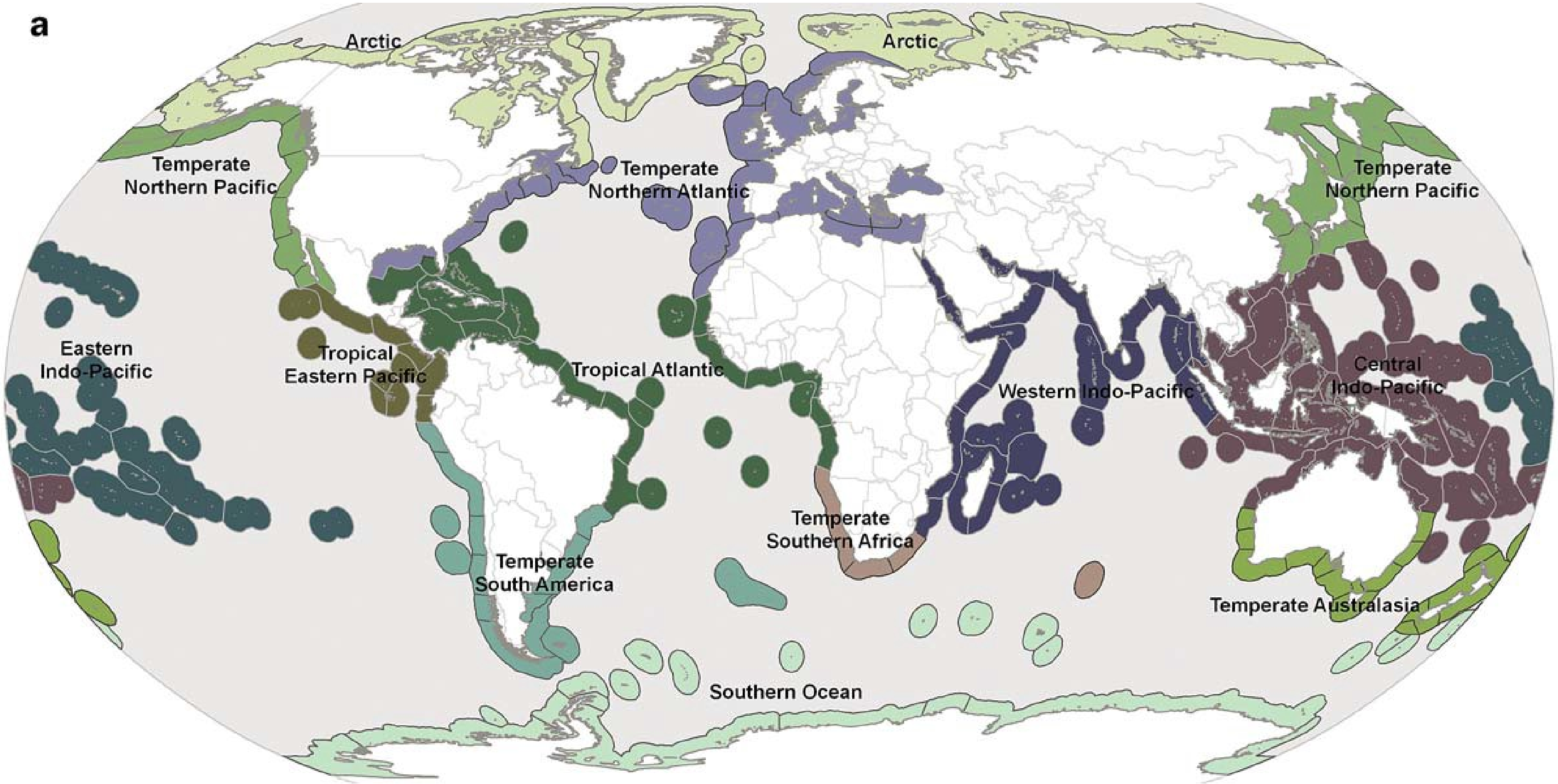
Tropical marine vegetation

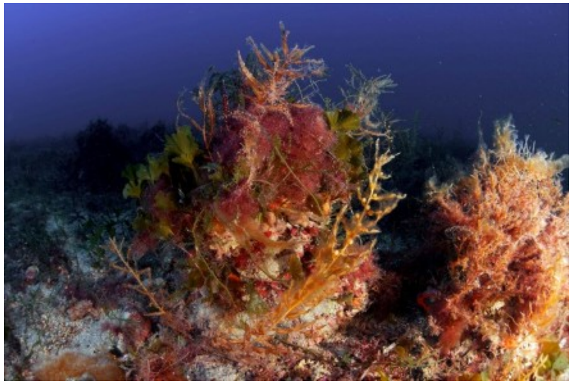


12 biotic realms (5 in the tropics) but slightly differently defined 4 phycogeographical regions (Eastern Atlantic, Western Atlantic, Indo-Western-Central Pacific, Eastern Pacific)

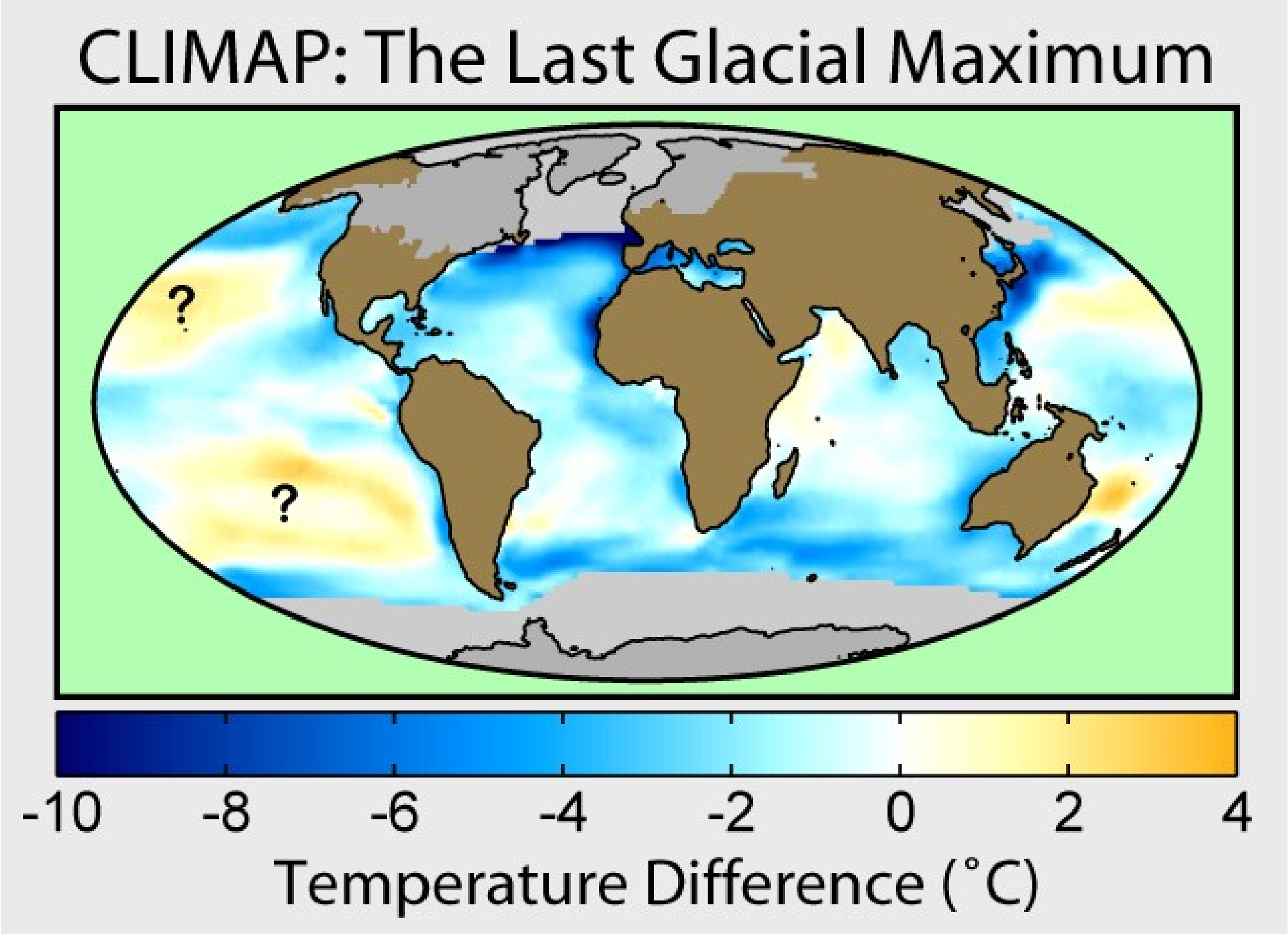
key temperature limits: > SST 20°C February minimum
(maximum levels generally over 25°C, up to 30-32°C in some areas)

Spalding et al., 2007, BioScience
Lücking, 1991, Seaweeds

very simplified three part classification of macroalgal communities



tropical marine vegetation habitats have **the oldest uninterrupted continuity** among all the others
[however, their extent was limited a during glacial periods of the Pleistocene]



maximum temperature levels might not have been higher than 35°C during all of the Phanerozoic
(virtually all the recent seaweed lineages have the upper survival limits at about 35-40°C)

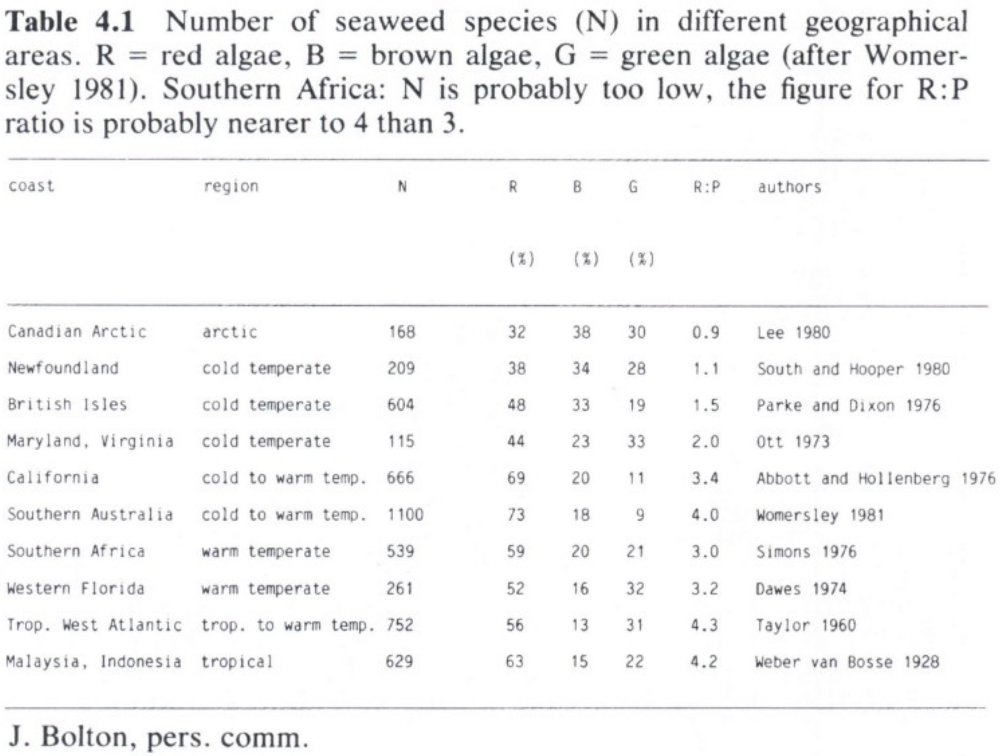


Table 4.1 Number of seaweed species (N) in different geographical areas. R = red algae, B = brown algae, G = green algae (after Womersley 1981). Southern Africa: N is probably too low, the figure for R:P ratio is probably nearer to 4 than 3.

coast	region	N	R (%)	B (%)	G (%)	R:P	authors
Canadian Arctic	arctic	168	32	38	30	0.9	Lee 1980
Newfoundland	cold temperate	209	38	34	28	1.1	South and Hooper 1980
British Isles	cold temperate	604	48	33	19	1.5	Parke and Dixon 1976
Maryland, Virginia	cold temperate	115	44	23	33	2.0	Ott 1973
California	cold to warm temp.	666	69	20	11	3.4	Abbott and Hollenberg 1976
Southern Australia	cold to warm temp.	1100	73	18	9	4.0	Womersley 1981
Southern Africa	warm temperate	539	59	20	21	3.0	Simons 1976
Western Florida	warm temperate	261	52	16	32	3.2	Dawes 1974
Trop. West Atlantic	trop. to warm temp.	752	56	13	31	4.3	Taylor 1960
Malaysia, Indonesia	tropical	629	63	15	22	4.2	Weber van Bosse 1928

J. Bolton, pers. comm.

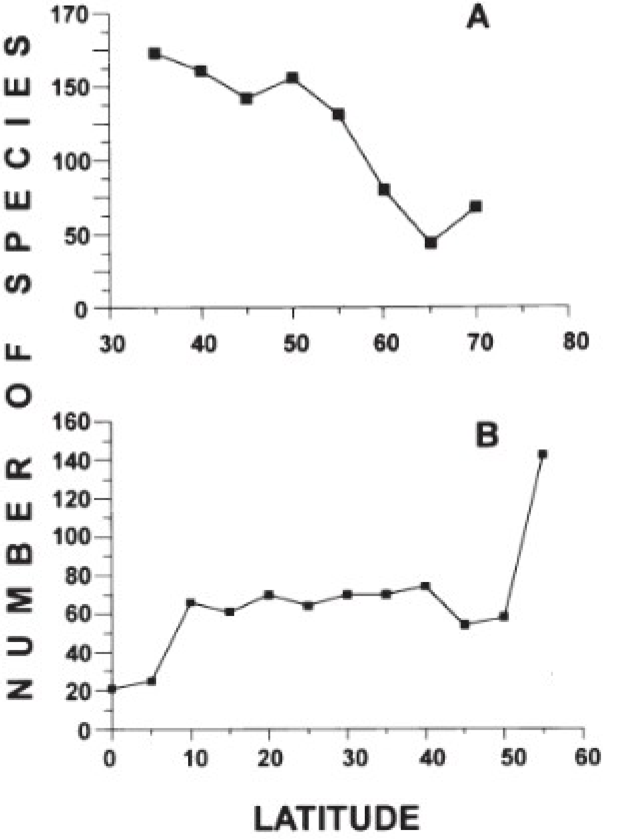
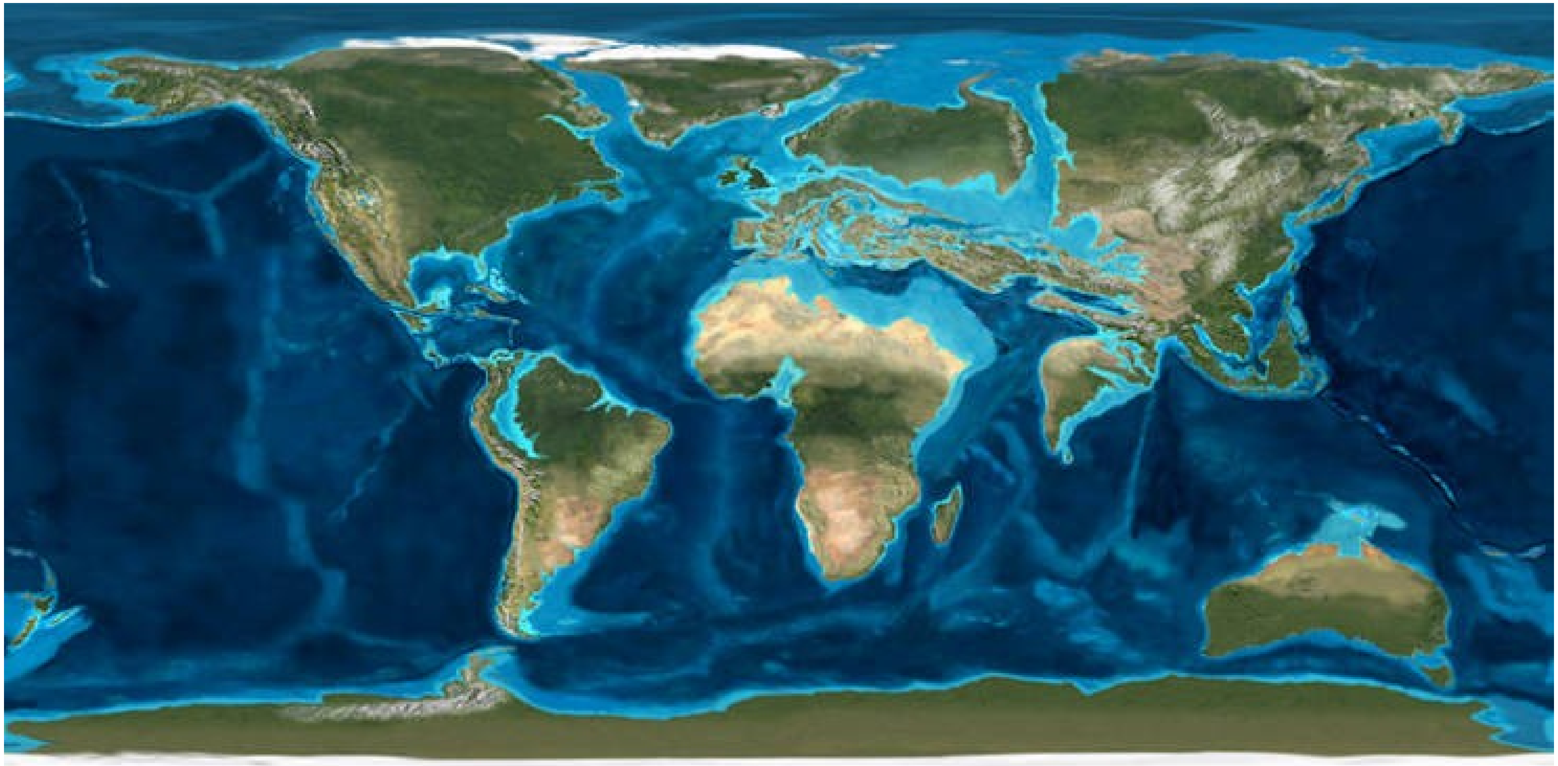


Fig. 1. Latitudinal algal species diversity gradients along the Atlantic coast of Europe (A) and the temperate Pacific coast of South America (B).

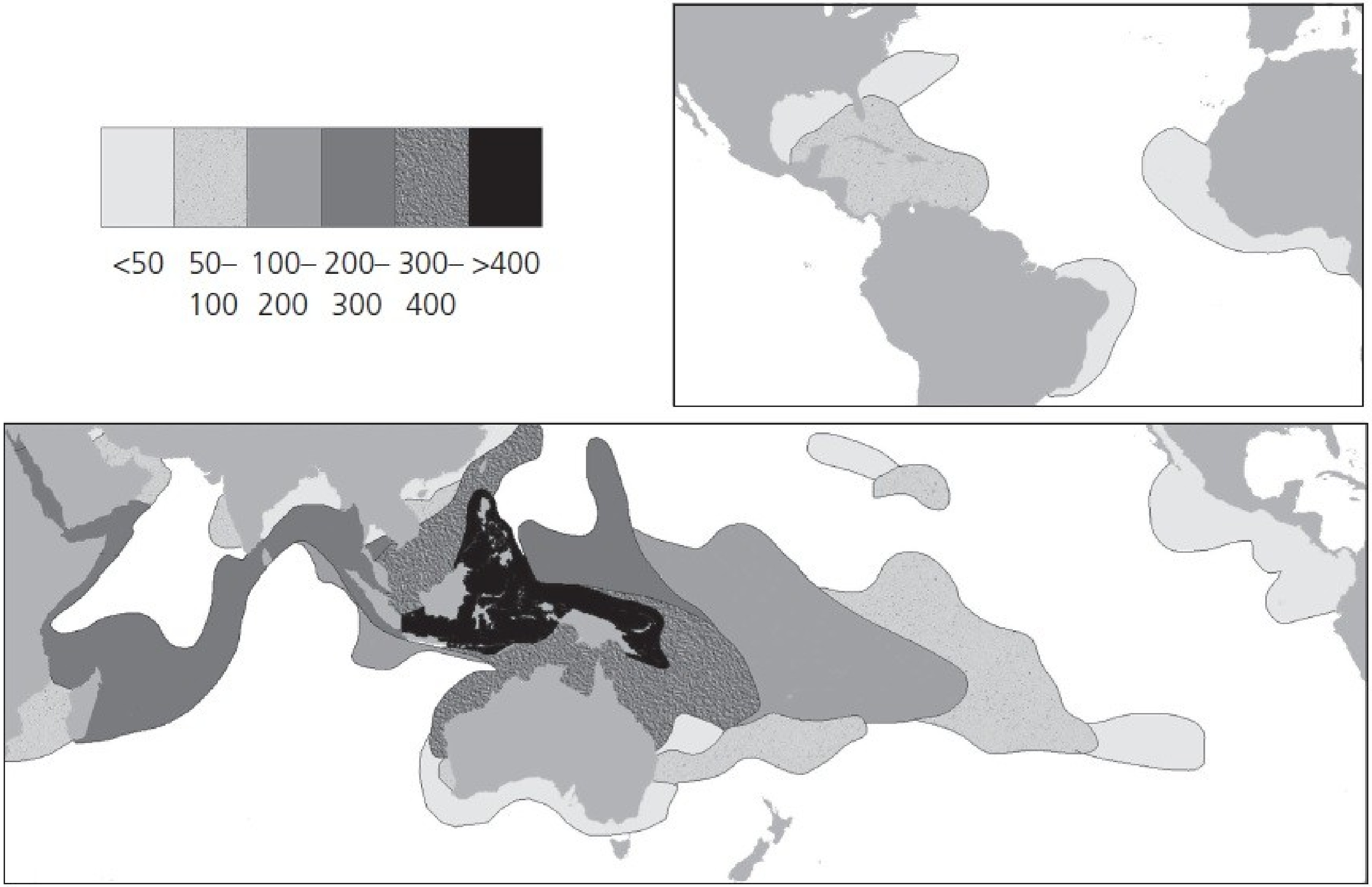
Santelices & Marquet, 1998, Divers Distrib

R:P index
latitudinal diversity gradients (high diversity regions of the Mediterranean and S Australia)
factors reducing seaweed diversity in tropics: herbivory, spatial competition of corals



relatively high connectivity of the tropical oceans in the Tertiary (the figure indicates the late Eocene) → westward circumglobal tropical current
(Panama land bridge constituting effective migration barrier: 3-4 mya; Panama canal includes freshwater barriers)

thus, there is still a high similarity of the vegetation at the level of genera and higher taxa (Sargassum, Dictyota, Padina, Turbinaria, Caulerpa, Halimeda, etc.); species are typically geographically restricted (relatively rapid speciation in the tropics) northern and southern distribution limits of tropical marine vegetation coincide with the distribution of hermatypic corals (i.e., the „coral reefs“)



Map of the distribution of coral reefs, including species diversity of reef-building corals.

coral reefs in the Atlantic - impoverished during Pleistocene, Carribean Sea even became landlocked several times

Sheppard et al., 2018, The Biology of Coral Reefs
Lücking, 1991, Seaweeds

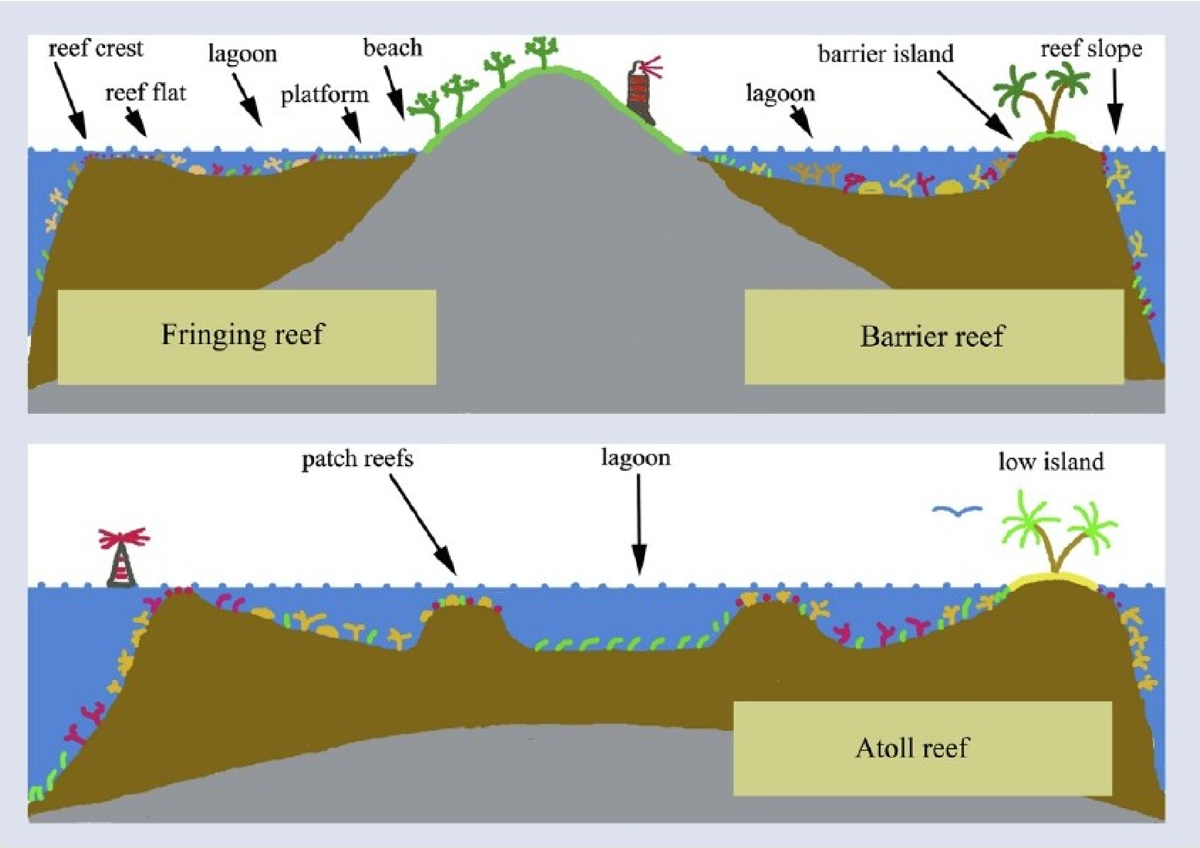
FIG. 2.9 Large colony of *Porites* cf. *lutea* near Ta'u, American Samoa. Drill cores determine it to be about 540 years old. *(Photo courtesy of Larry Basch.)*

minimum temperature limits for hermatypic coral reefs: 20-22°C, optimum 23-29°C

Sheppard et al., 2018, The Biology of Coral Reefs

Table 1.1 Areas of coral reefs in different parts of the world.

Rank	Country	Area (km^2)	Per Cent of World Total
1	Indonesia	51,020	17.95
2	Australia	48,960	17.22
3	Philippines	25,060	8.81
4	France, including territories	14,280	5.02
5	Papua New Guinea	13,840	4.87
6	Fiji	10,020	3.52
7	Maldives	8,920	3.14
8	Saudi Arabia	6,660	2.34
9	Marshall Islands	6,110	2.15
10	India	5,790	2.04
11	Solomon Islands	5,750	2.02
12	United Kingdom and territories	5,510	1.94
13	Micronesia, Federated States	4,340	1.53
14	Vanuatu	4,110	1.45
15	Egypt	3,800	1.34
16	USA and territories	3,770	1.33
17	Malaysia	3,600	1.27
18	Tanzania	3,580	1.26
19	Eritrea	3,260	1.15
20	Bahamas	3,150	1.11



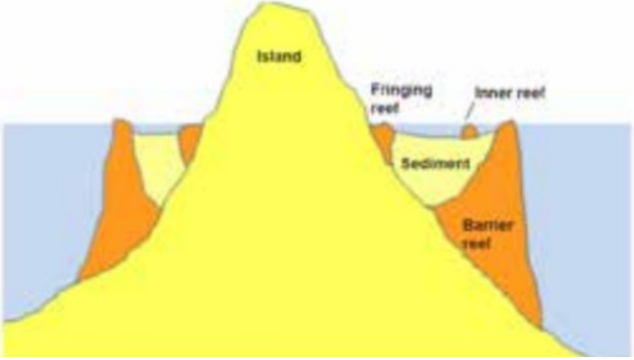


FIGURE 1.1 Architecture of coral reefs (most of the coral reefs around Hainan Island and neighboring islands are fringing reefs and patch reefs) *Modified according to Littler, M.M., Littler, D.S., 2003. South Pacific Reef Plants. A Divers' Guide to the Plant Life of South Pacific Coral Reefs. Offshore Graphics, Washington, 331 pp.*

+ „subfossil reefs“ - those that died off during rapid sea surface increase at the end of the last Glacial as they were unable to catch the rapidity of the rise and became submerged (ca in 100 m depth)

Titlyanov et al., 2017

A reef flat extending about 300 m seaward of the beach. The line of breakers marks the edge of the reef flat; seaward of that line, the reef slopes downwards steeply. Darker

Evolution of marine calcified reef ecosystems

the relation with the calcite/aragonite fluctuations

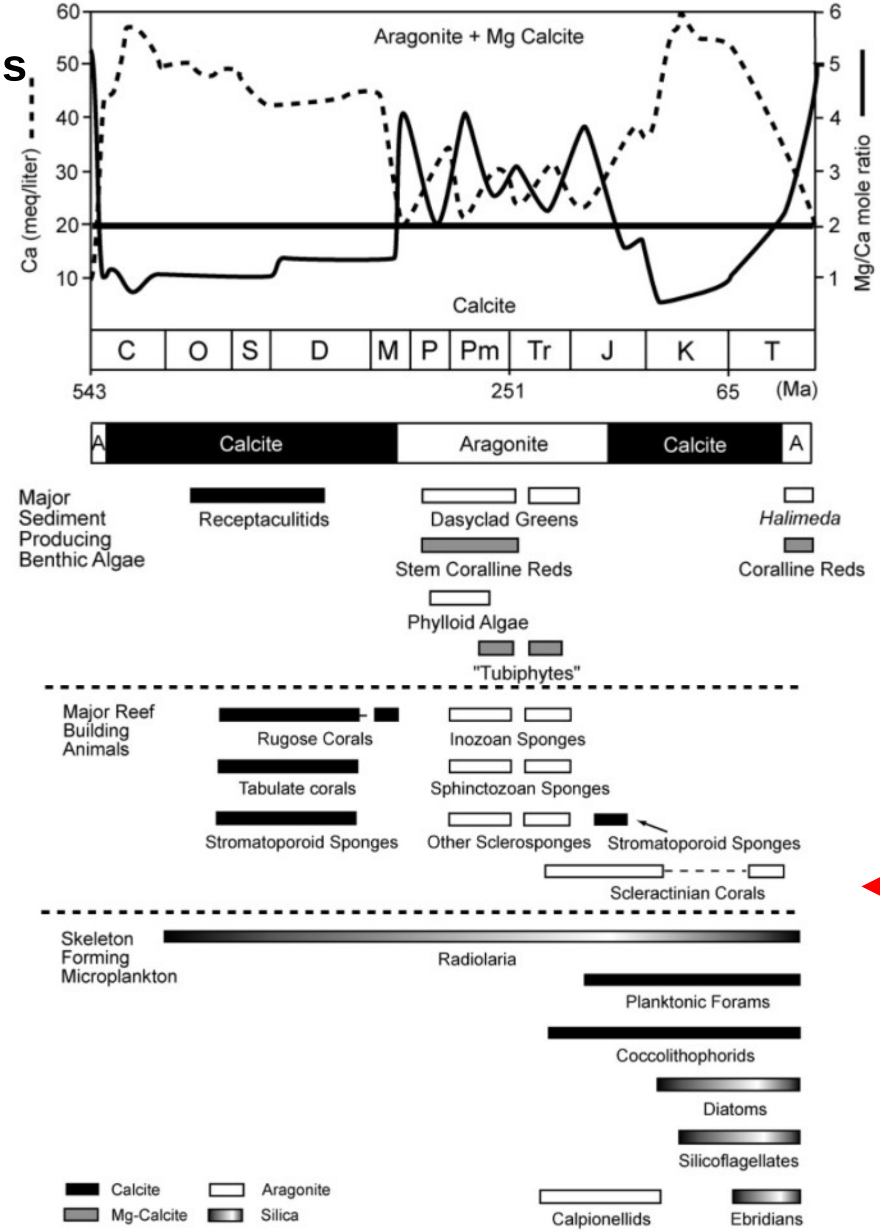
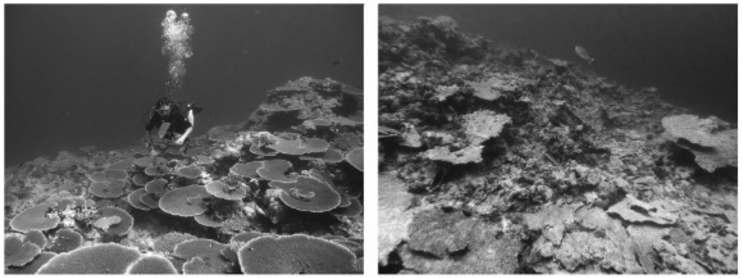


Figure 7. The stratigraphic relationship between ocean chemistry and skeletal mineralogy in major sediment producing benthic algae and animals, modified from Stanley and Hardie (1998). The figure shows Stanley and Hardie's (1998) estimates of Ca abundance and Mg/Ca in ancient oceans, as well as the principal time intervals dominated by "calcite" and "aragonite" seas. Aragonite and Mg-calcite are favored when the Mg/Ca mole ratio is above 2; calcite is favored at ratios below 2. Also shown are the time distributions of principal skeleton–forming protists; calpionellids are thought to be tintinnids with calcified tests (see text for references).

Knoll, 2003

Plate 1 The richest part of any coral reef lies below the depths where waves break, where light is abundant for photosynthesis, sedimentation is low, the salinity is near that of the open ocean (about 31–34 ppt) and the temperature is about 20–29 °C. (See Preface to 2nd edition).



The same site on the ocean-facing reefs of Salomon Atoll, Indian Ocean, at 10 m depth. Left: 2006, with very high cover of diverse corals, especially table corals. Right: 2017, showing less than 5% live coral with much broken and tumbled dead coral skeletons. *Photo:* Anne Sheppard.

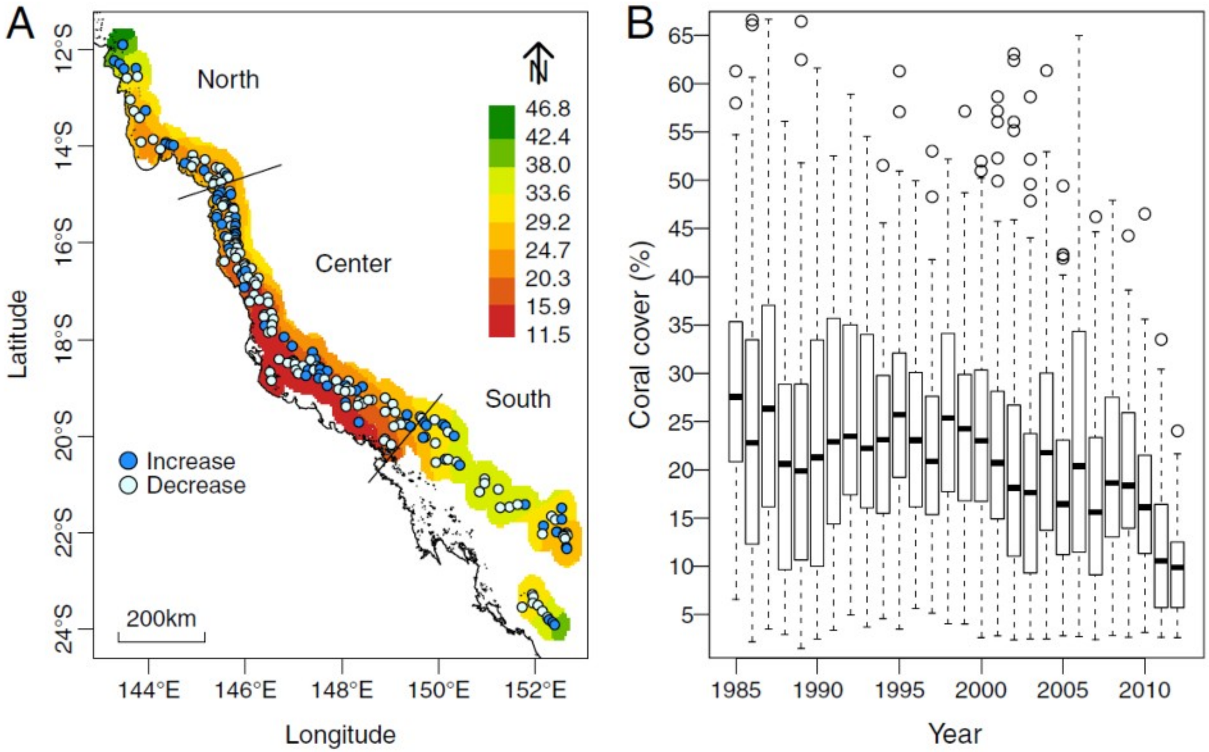
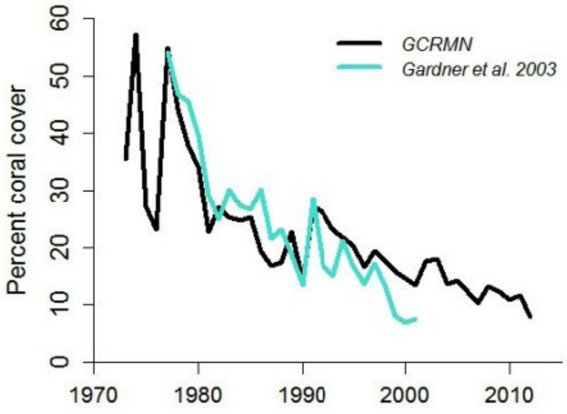


Fig. 1. Coral cover on the GBR. (*A*) Map of the GBR with color shading indicating mean coral cover averaged over 1985–2012. Points show the locations of the 214 survey reefs in the northern, central, and southern regions, and their color indicates the direction of change in cover over time. (*B*) Box plots indicate the percen ns within each year and suggest a substantial decline in coral cover over the 27 y.



decline of the Carribean reefs

De´ath et al., 2012, PNAS

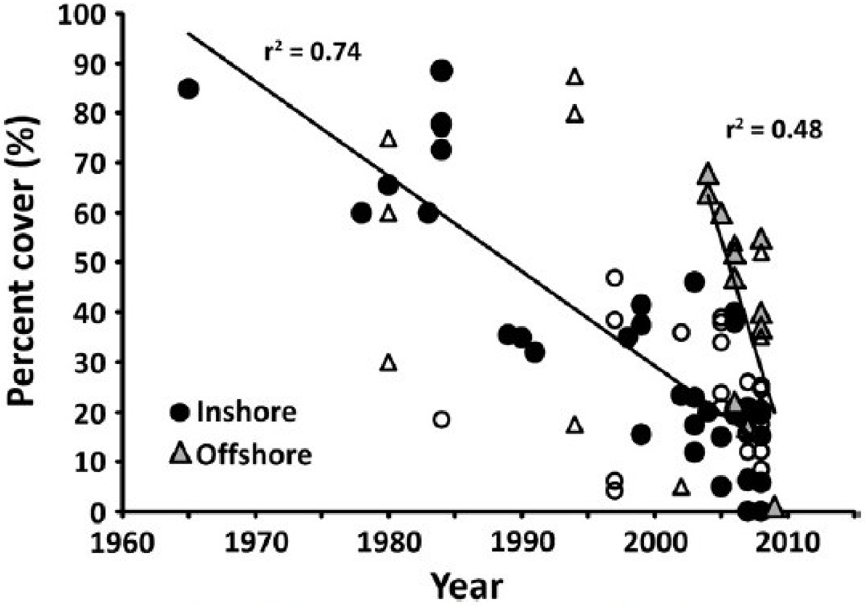
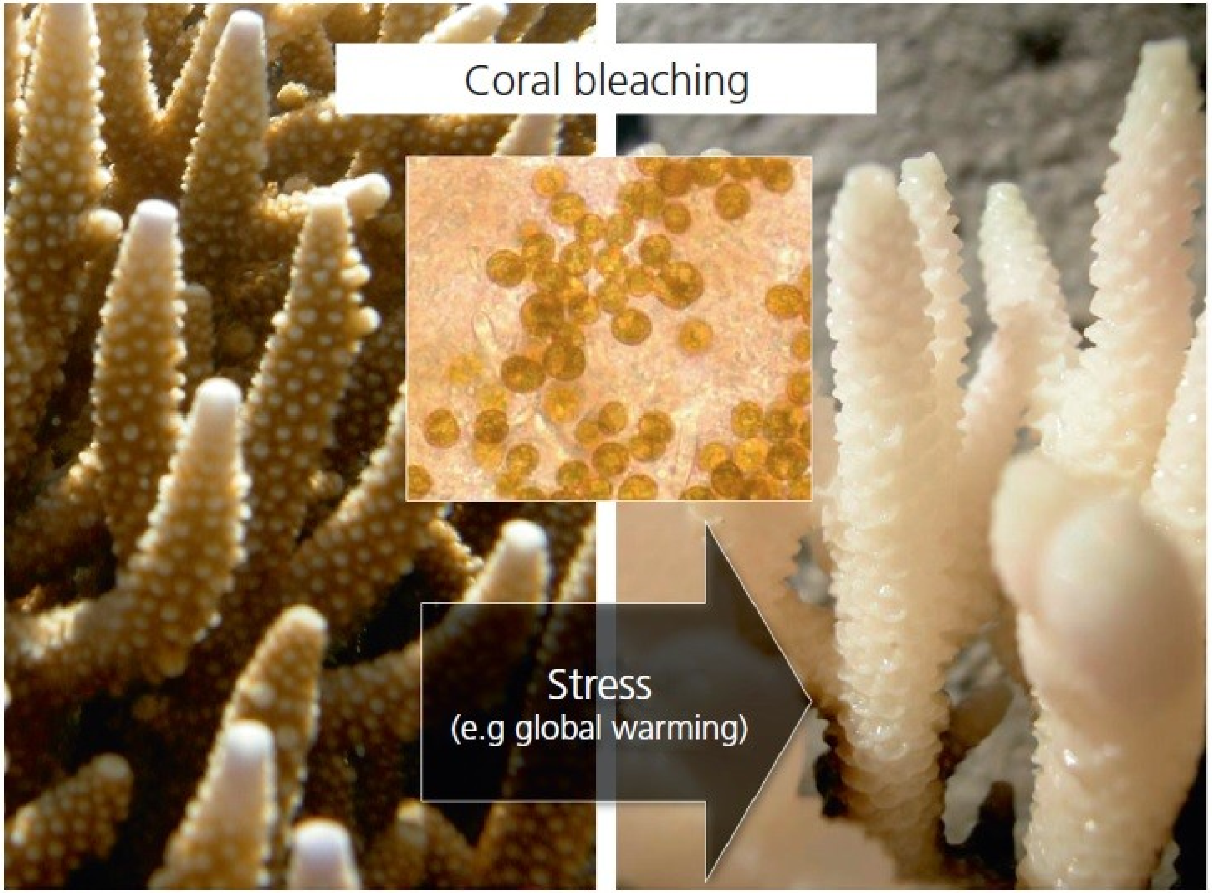


FIGURE 1.4 Percentage of coral cover over time on China's inshore and offshore reefs in the South China Sea. *According to Hughes, T.P., Huang, H., Young, M.A.L., 2013. The wicked problem of China's disappearing coral reefs. Conservation Biology 27 (2), 261–269.*

Titlyanov et al., 2017

Decline of coral reefs



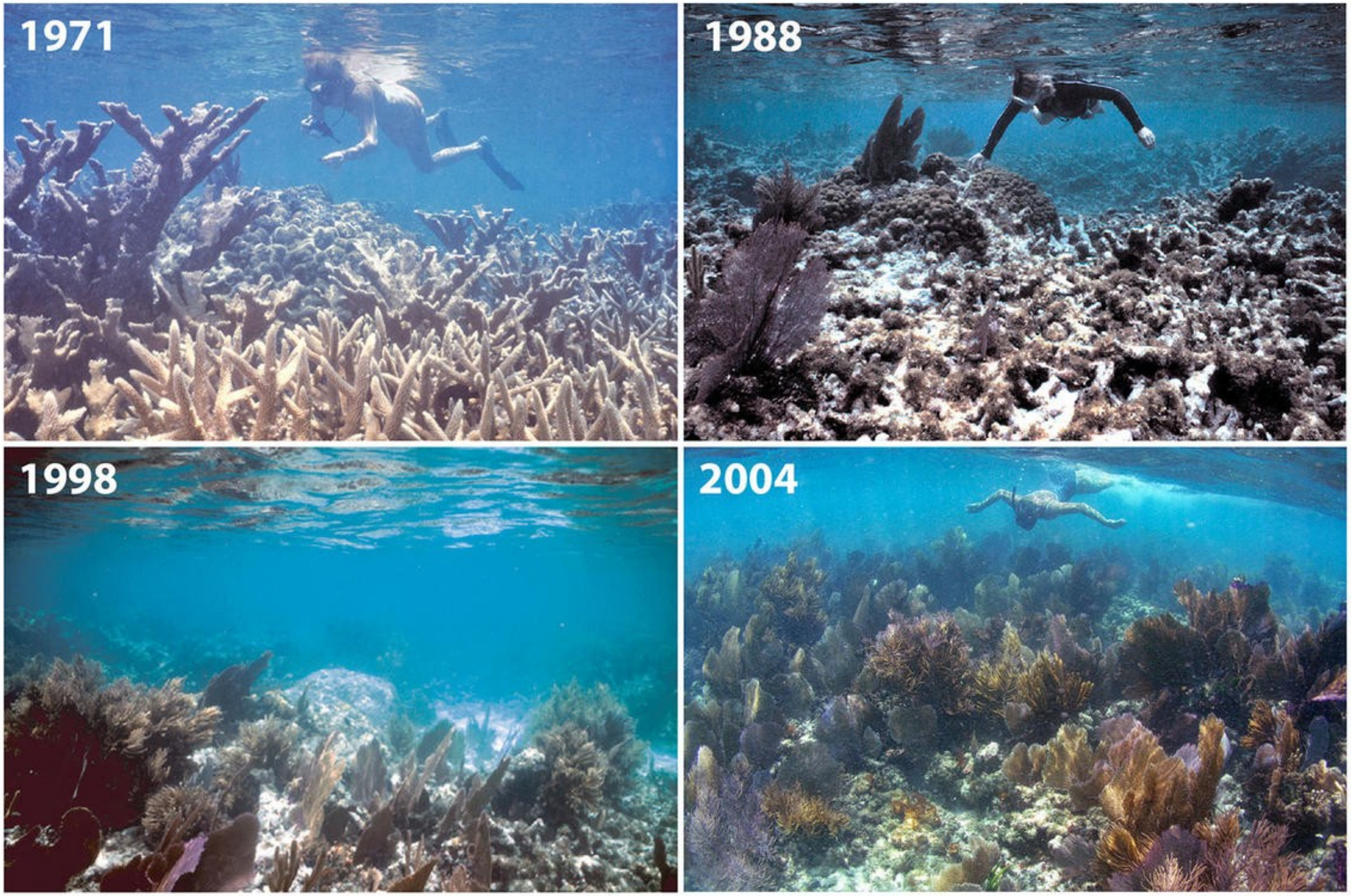
1. irreversible bleaching

2. overgrazing

Plate 11 Outbreak of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on the Great Barrier Ree in 2014 (See page 174).

3. eutrophication

The benthic filamentous cyanobacterium, *Lyngbya majuscula*. Elevated levels of usually limiting nutrients are a major cause of blooms such as the one shown here, where the cyanobacterium is overgrowing corals. This bloom was near Great Keppel Island, Queensland, Australia (See page 139).



S Florida, decline of hard corals and their substitution by non-calcified macroalgae (possibly due to the decline of herbivorous fishes)

FIGURE 2.34 Coral reef of Sesoko Island (Okinawa, Japan), 4 years after bleaching events happened in 1998, the algal coverage amounted to about 90%. Inset: same place in 1995 before bleaching, the coral coverage was up to about 95% (Titlyanov and Titlyanova, 2012b).

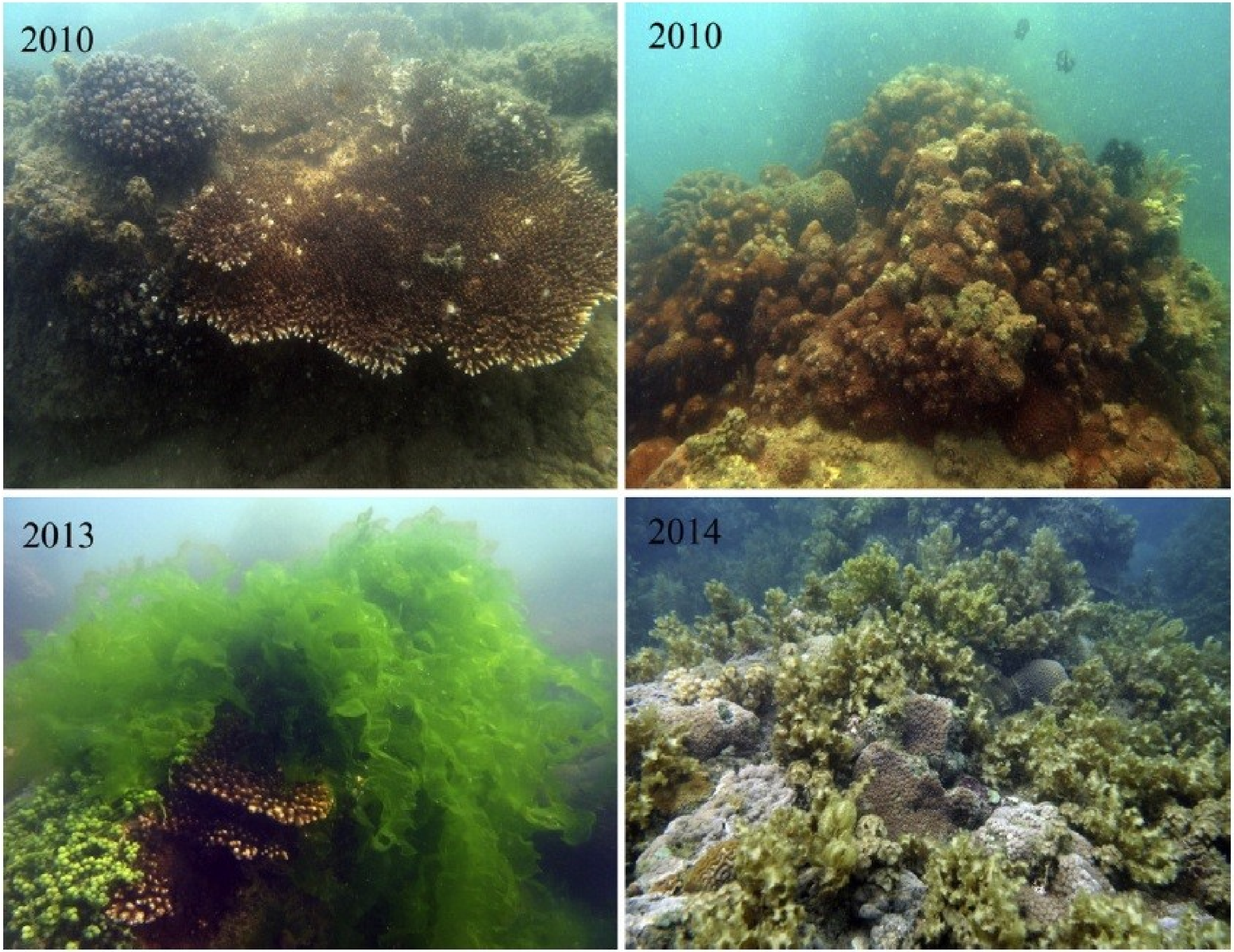
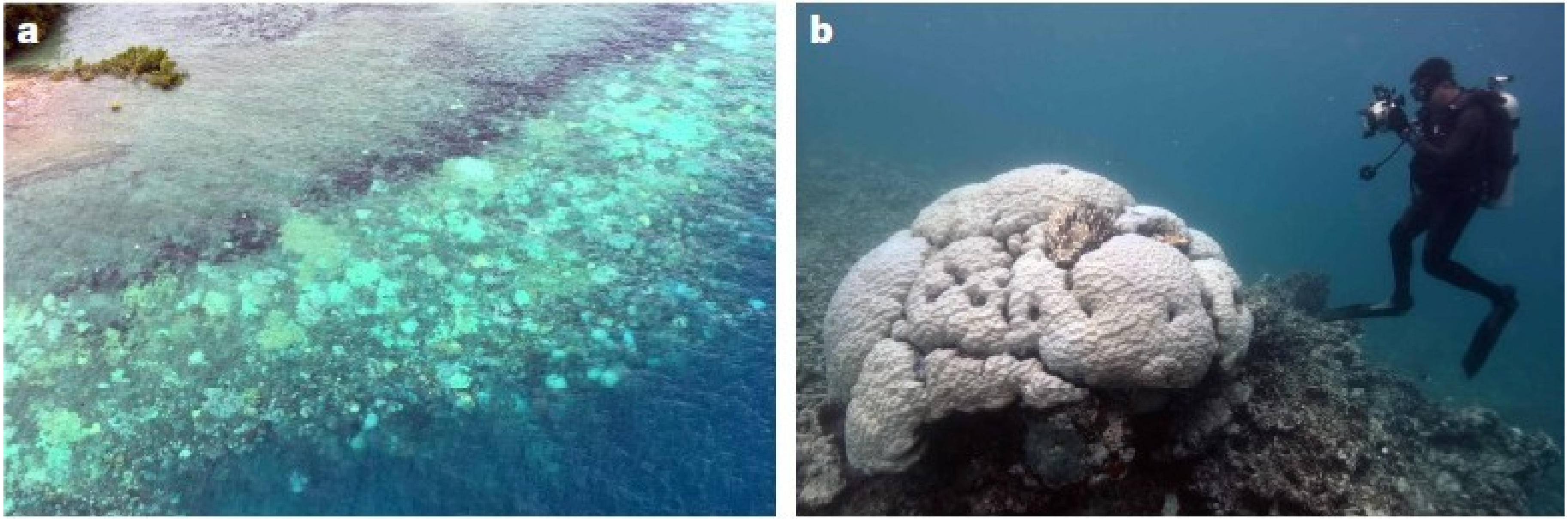


FIGURE 1.2 Coral reefs in Sanya from 2010 to 2014.

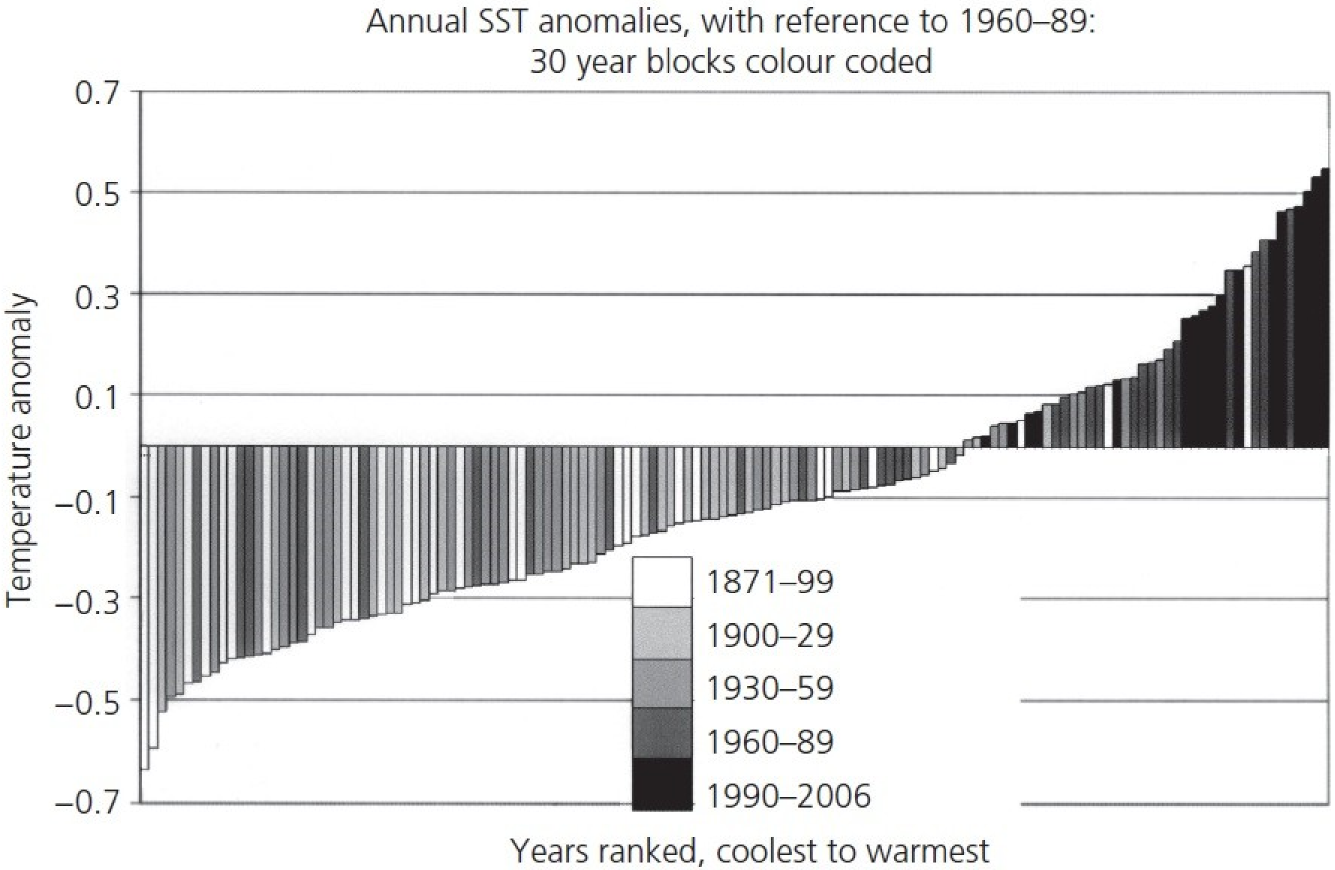
coral reefs - nutrient-poor ecosystems, nutrient are rapidly turned over (like in tropical forests)
eutrofication leads to increase in ruderal macroalgae and turf cyanobacteria (Lyngbya), turf algae (ephemerals)
[phosphates are also crystal poisons of calcification - possibly therefore no coral reefs in upwelling areas]

FIGURE 2.33 Bleached colony of *Acropora* sp. (after temperature was lowered to 10°C) during the winter season and dead colony (after bleaching) of the same species. Inset: dead coral occupied by green algae and red algae (Titlyanov and Titlyanova, 2012b).

FIG. 2.6 Bleaching of *Pocillopora* spp. in Molokini crater, Hawaiian Archipelago, October 31, 2015. *(Photo courtesy of Darla White, Maui Division of Aquatic Resources, State of Hawaii.)*

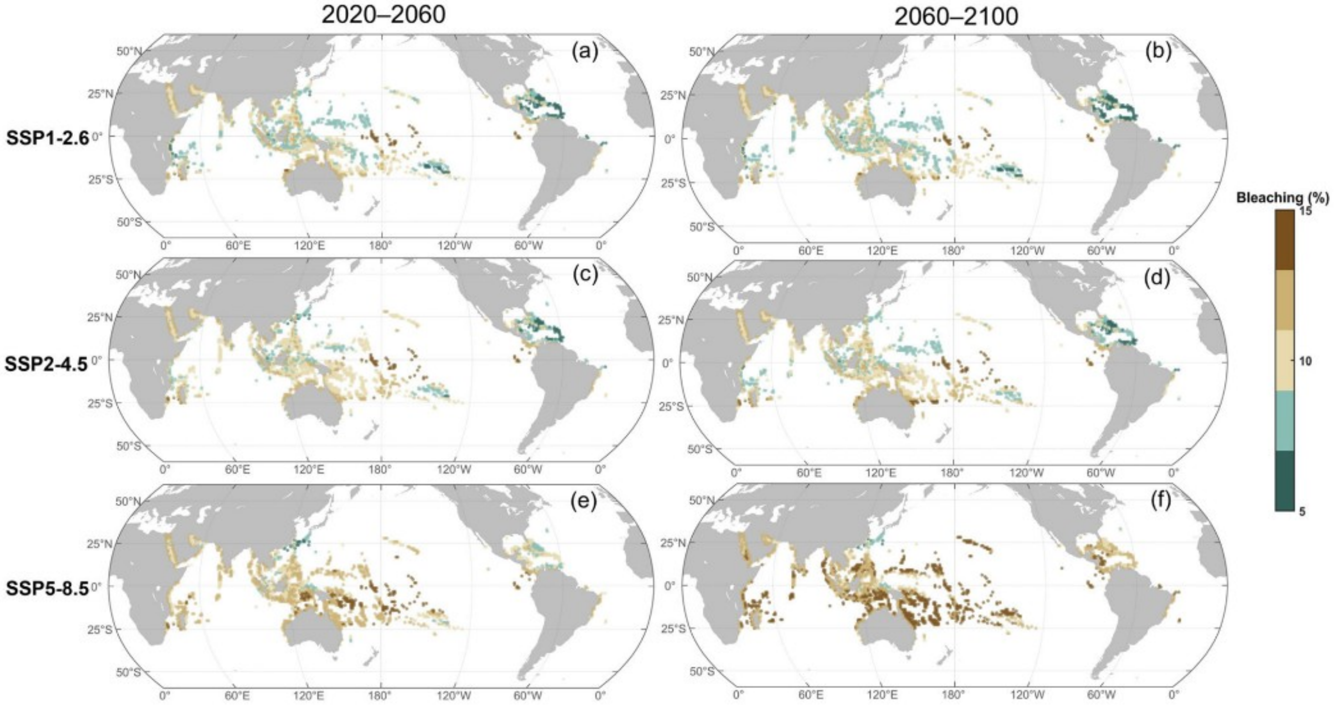


Hughes et al., 2018, Nature



10 Trend of average sea surface temperatures 1871–2006 in the Chagos Archipelago, a central Indian Ocean site. Each year's temperature is averaged, and years are ordered (left to right) from coolest to warmest. Each 30-year block has a different shade of grey (lightest = oldest; darkest = most recent), but note that the final block has fewer columns (1990–2006 only). The y-axis is not absolute temperature but its difference from the 1960–1990 average reference temperature; SST, sea surface temperature.

Sheppard et al., 2018, The Biology of Coral Reefs



ig. 4 | **Projected bleaching under future climate scenarios.** Projected mean annual coral bleaching under three climate scenarios: (**a**, **b**) low emission (SSP1-2.6), (**c**, **d**) nedium emission (SSP2-4.5), and (**e**, **f**) high emission (SSP5-8.5) during the periods 2020–2060 (**a**, **c**, **e**) and 2060–2100 (**b**, **d**, **f**).

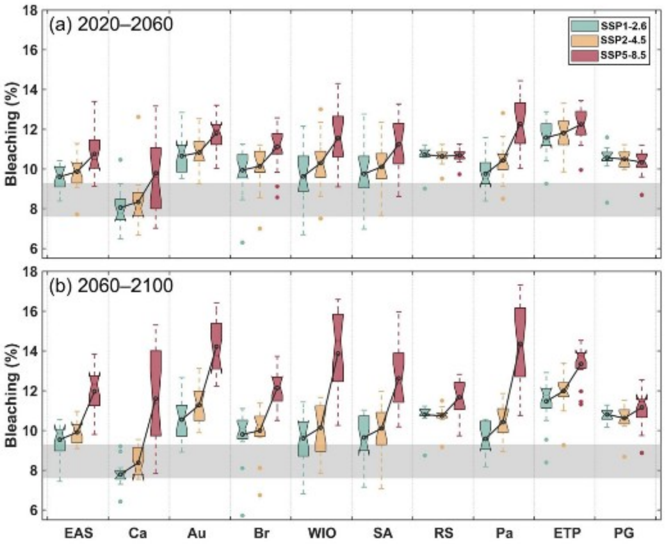


Fig. 5 | Regional bleaching projections under climate scenarios. Coral bleaching statistics in ten regions of the world for the periods 2020–2060 (a) and 2060–2100 (b) under three climate scenarios: low emission pattern SSP1-2.6 (green box), medium emission pattern SSP2-4.5 (yellow box), and high emission pattern SSP5-8.5 (red box). East Asian Seas (EAS), Caribbean (Ca), Australia (Au), Brazil (Br), West Indian Ocean (WIO), South Asia (SA), Red Sea (RS), Pacific (Pa), East Tropical Pacific (ETP), and Persian Gulf (PG). Horizontal shaded bands represent 95% confidence intervals for mean annual coral bleaching when coral decline is zero.

Zeng et al., 2025, Nature

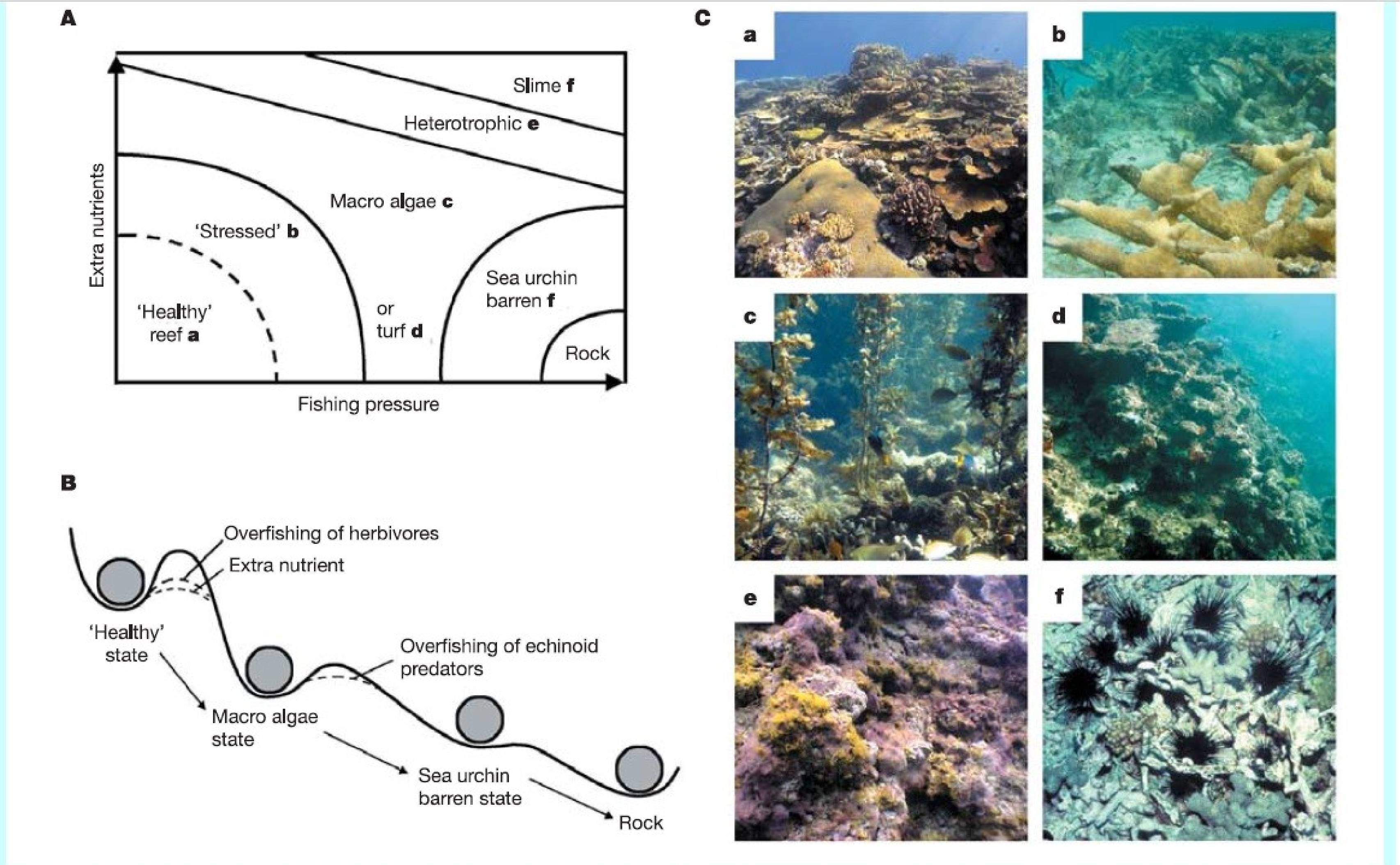
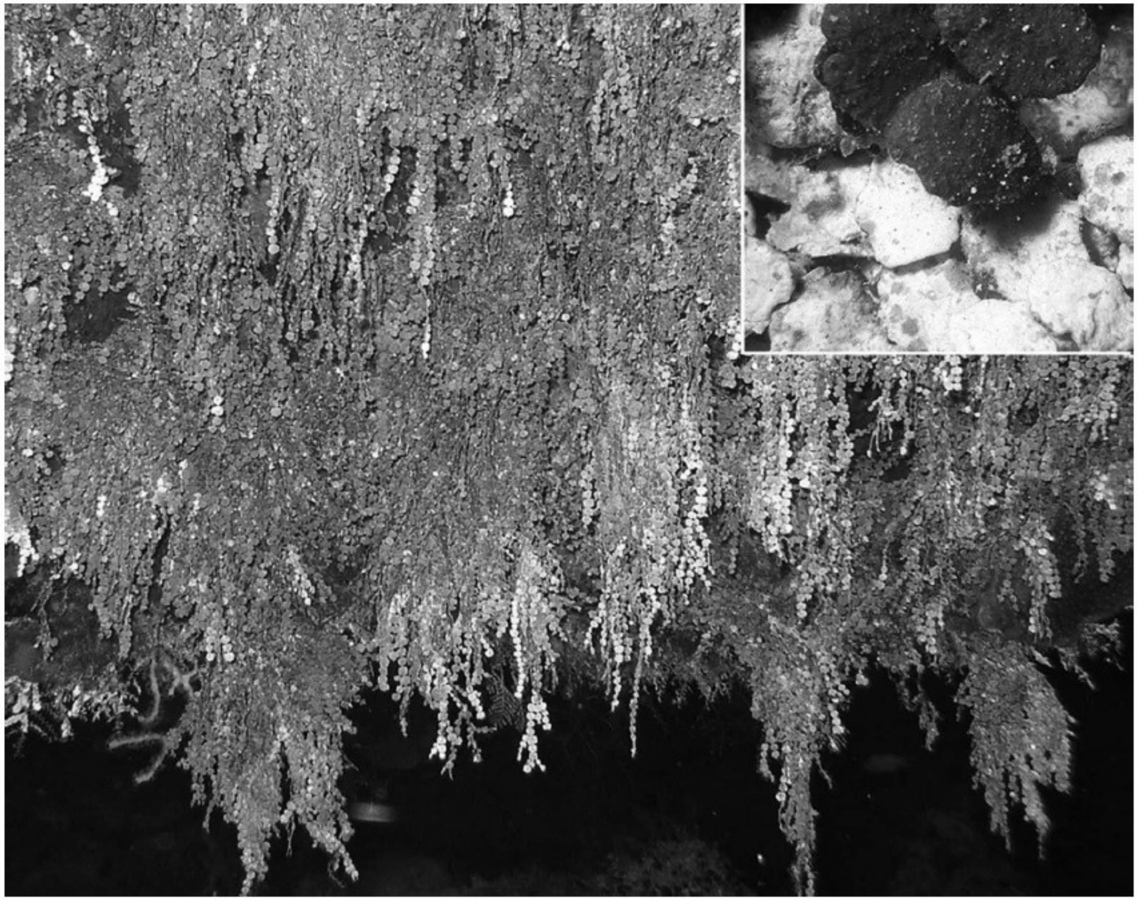


Figure 2 Alternate states in coral reef ecosystems. **A**, A conceptual model showing human-induced transitions between alternate ecosystem states based on empirical evidence of the effects from fishing and excess nutrients[15–17]. The 'stressed' state illustrates loss of resilience and increased vulnerability to phase-shifts. **B**, A graphic model depicting transitions between ecosystem states. 'Healthy' resilient coral-dominated reefs become progressively more vulnerable owing to fishing pressure, pollution, disease and coral bleaching. The dotted lines illustrate the loss of resilience that becomes evident when reefs fail to recover from disturbance and slide into less desirable states. **C**, Six characteristic reef states (as in **A**) from sites on the Great Barrier Reef (**a**, **c**, **d**, **e**) and in the Caribbean (**b**, **f**).

Bellwood et al., 2004, Nature

In marginal areas, corals live amongst macroalgae. In this case, *Acropora* in southern Oman amongst the macroalgae *Sargassum* at the top and (more kelp-like *Nizamuddinia zanardinii*, which is a regional endemic (See



In both the Indo-Pacific and the Caribbean, reef walls may be heavily festooned with the calcareous green alga *Halimeda*. Each frond is a chain of small discs, made of limestone secreted by the disc's enveloping green tissue. Each chain may produce a new disc every day in good growing conditions, producing large quantities of coarse sand. Inset: Close-up of *Halimeda* discs, with several dead discs now forming part of the sand.

non-calcified, erect macroalgae become dominant in the absence of herbivores (fish, echinodermes)
lower limits of reefs regulated by these algae (Sargassum, Udotea, Padina) - overgrowing the corals
upwelling areas - more macroalgae due to less nutrient-limitation

overall most frequent genera: Turbinaria, Sargassum, Laurencia, Caulerpa, Padina, Halymenia

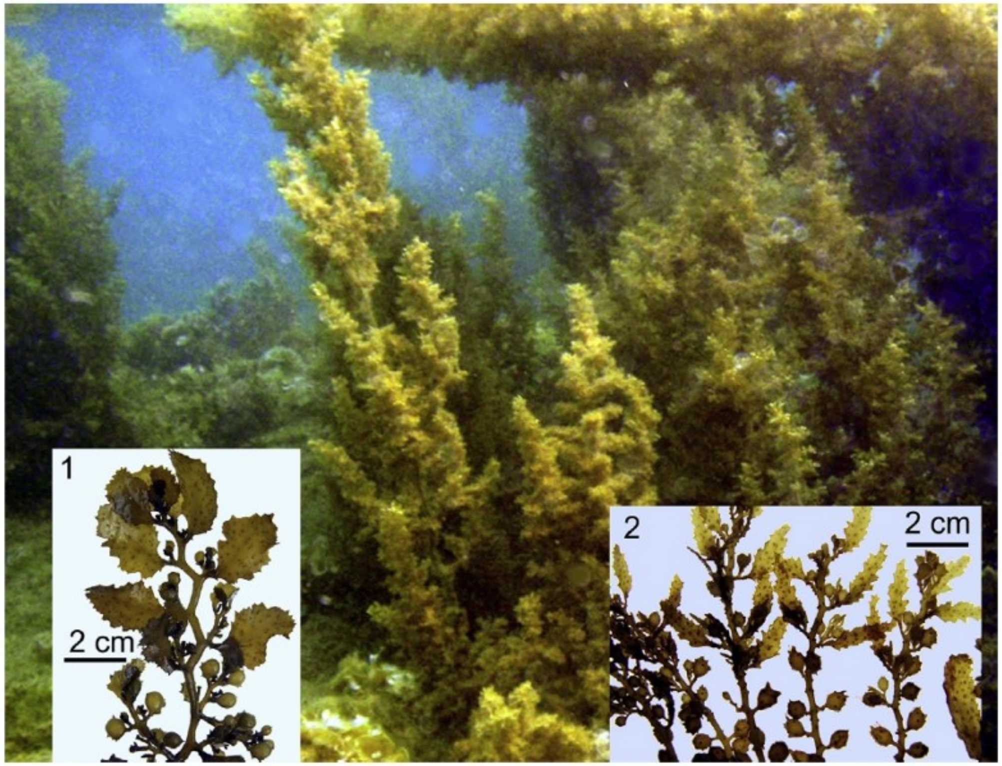


FIGURE 2.21 Thicket of brown *Sargassaceae* at the Luhuitou coral reef. April 2012 (Inset 1: *Sargassum sanyaense*; 2: *Sargassum polycystum*.).

Titlyanov et al., 2017

FIGURE 2.20 Monodominant community of the brown alga *Padina australis* at the low intertidal zone. Sanya Bay, March 2012.

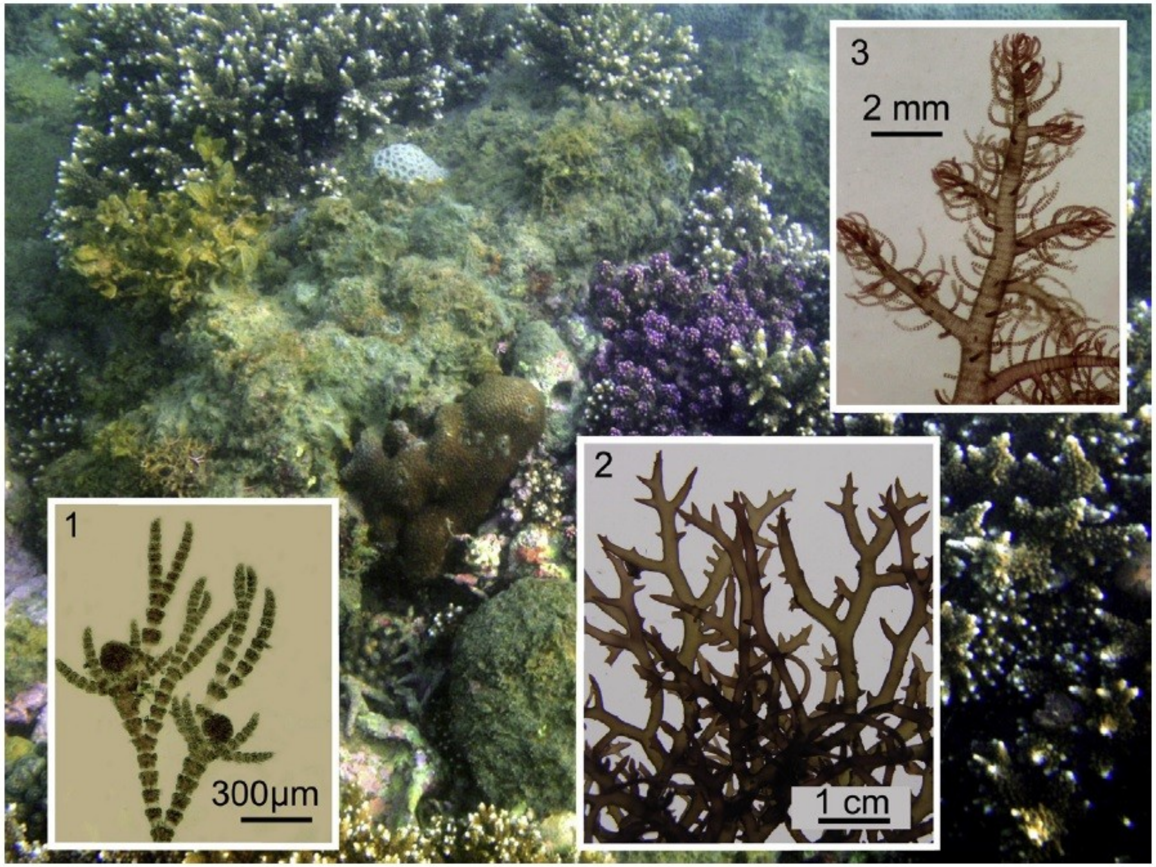
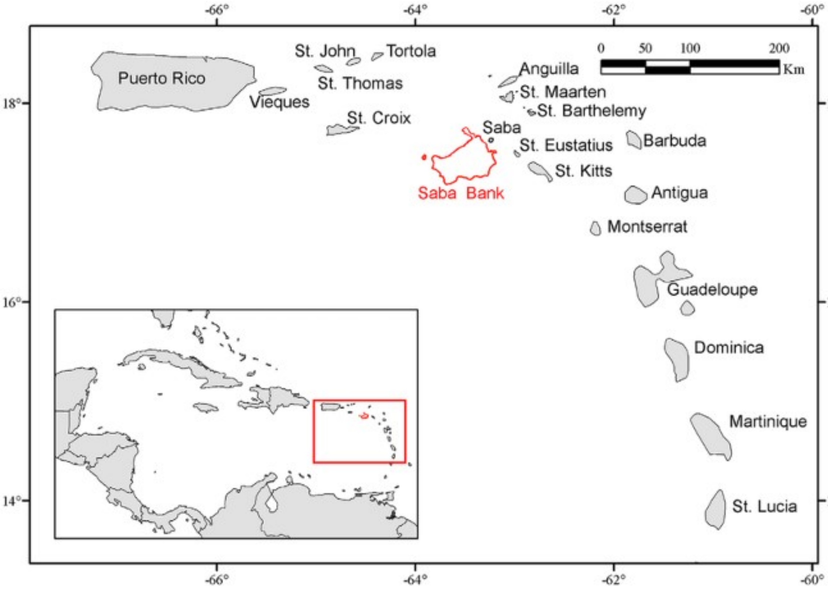


FIGURE 2.19 Polydominant community of algal turf in the upper subtidal zone. Dominant species: *Gayliella mazoyerae* (Inset 1), *Hypnea pannosa* (Inset 2), and *Spyridia filamentosa* (Inset 3). Luhuitou Peninsula, March 2012.

most algae in the tropics are grazed, most algae in cold regions are decomposed - it is due to absence of herbivorous fishes (about 20% of fish species in coral ecosystems are herbivores)

[hypothesis - kelps excluded from the tropics by herbivorous fishes]



Saba Bank, Carribean

[the largest submerged atol in the Atlantic]

Figure 5. Selected specimens from "Seaweed City". Specimens dominating the stony pavement area (30 m deep) termed "Seaweed City", dominated by red algae (Rhodophyta). Top left: *Wrightiella blodgettii*. Top right: *Hypoglossum hypoglossoides*. Middle right: *Gracilaria cylindrica*. Bottom left: *Jania capillacea*. Bottom right: *Tricleocarpa fragilis*.
doi:10.1371/journal.pone.0010677.g005

Littler et al., 2010, Plos One

Figure 4. Selected species from "Brown Town". The large region (> one hectare) of Saba Bank (depth 25 m) nicknamed "Brown Town" because of the domination by brown macroalgae (Phaeophyceae). Top left: Overview of "Brown Town" habitat with over 50% cover of *Dictyota* turf. Top right: *Dictyota hamifera*. Middle left: *Stypopodium zonale*. Middle right: mixture of *Lobophora variegata* and *Dictyota humifusa*. Bottom right: *Dictyopteris justii*. Bottom right: *Sargassum hystrix*.

Saba Bank, Carribean

Littler et al., 2010, Plos One

Figure 3. Selected species from "Field of Greens". A region (> one hectare) of Saba Bank (depth 25 m) that our group named "Field o Greens" because the vast sand plain was dominated by green algae (Chlorophyta). Top left: *Udotea occidentalis*. Top right: *Caulerpa mexicana*. Middl left: *Halimeda* cf. *tuna* forma *platydisca*. Middle right: *Caulerpa prolifera*. Bottom left: *Penicillus dumentosus*. Bottom middle: *Caulerpa cupressoides* Bottom right: *Caulerpa racemosa* f. *lamourouxii*.

doi:10.1371/journal.pone.0010677.g003

Saba Bank, Carribean

Littler et al., 2010, Plos One

Mesophotic coral ecosystems

- depth < 30 m, up to 150 m
- low light conditions, fluctuating light limitation of photosynthesis (related to turbidity)

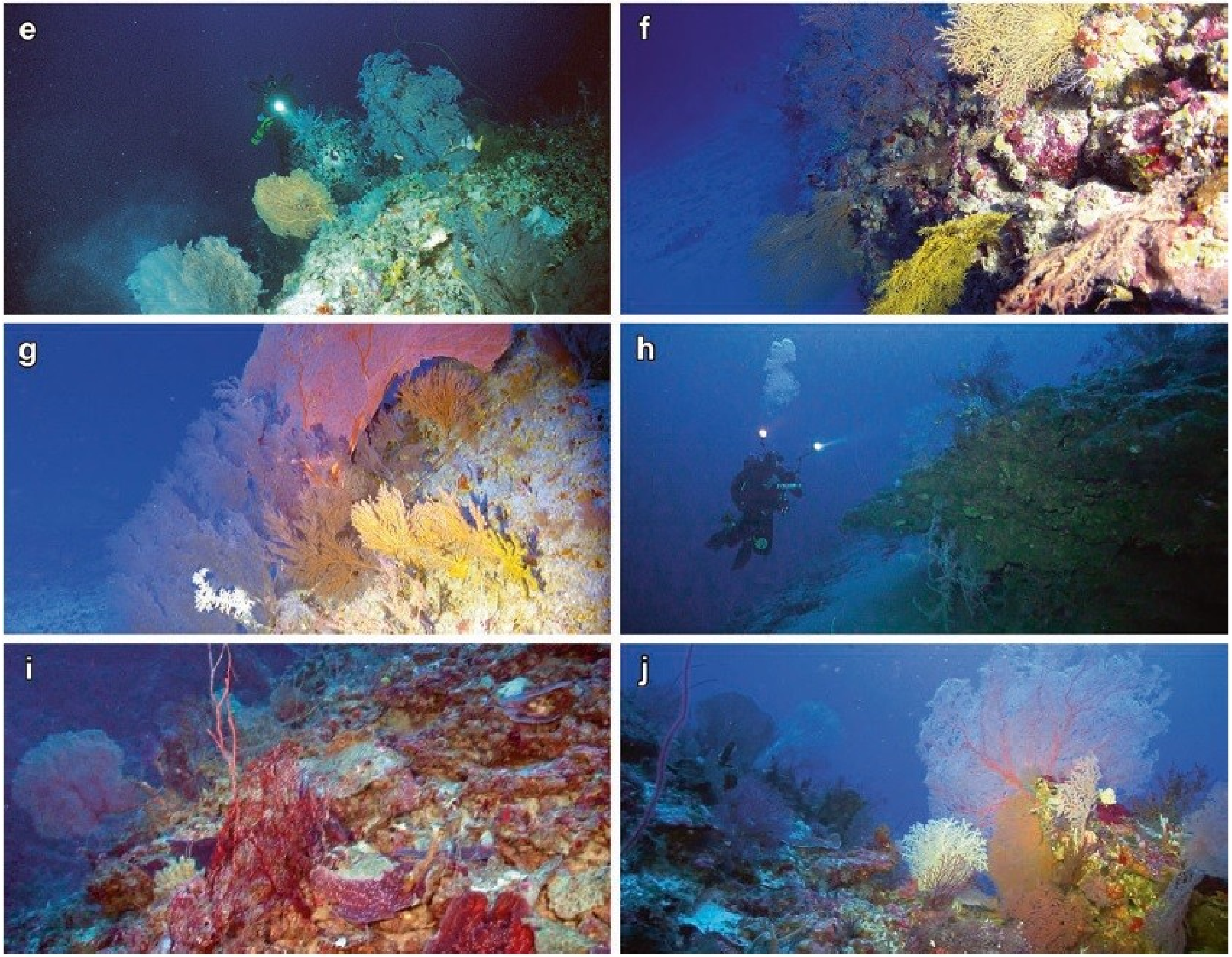


Fig. 1.2 General MCE habitat in (**a**) Indonesia, 80 m; (**b**) Pohnpei, 135 m; (**c**) Christmas Island (Line Islands), 115 m; (**d**) Cook Islands, 110 m; (**e**) Fiji, 110 m; (**f**) American Samoa, 108 m; (**g**) Okinawa, 90 m; (**h**) South Africa, 120 m, (**i**) Vanuatu, 100 m; and (**j**) Palau, 110 m. Images (**c**, **f**, **g**) have been inverted horizontally. (Photo credits: R.L. Pyle, can be reused under the CC BY license)

Loya et al., 2019,
Mesophotic Coral Ecosystems

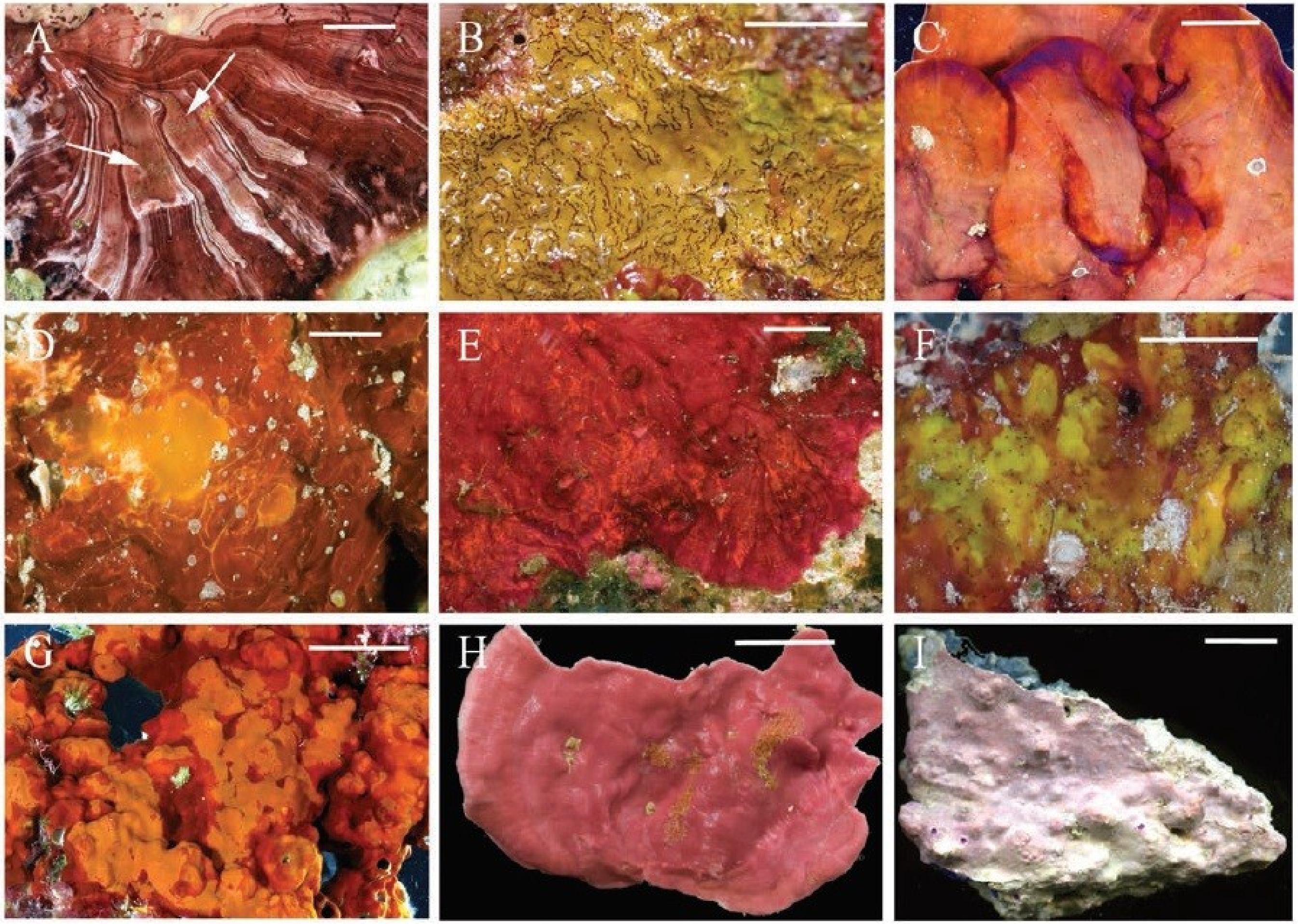


FIGURE 2. Encrusting deepwater rhodophyte species. (A) *Peyssonnelia gigaspora* (*DLB7637*); sporangial sori are denoted by arrowheads. These tetrasporangia are the largest reproductive algal spores known (scale bar = 1.0 cm). (B) *Peyssonnelia flavescens* (*DLB5883*; scale bar = 2.0 cm). (C) *Peyssonnelia iridescens* (*DLB7116*; scale bar = 1.0 cm). (D) *Peyssonnelia incomposita* (*DLB7777*; scale bar = 1.0 cm). (E) *Peyssonnelia* sp. 3 (*DLB7411*; scale bar = 5 mm). (F) *Peyssonnelia* sp. 2 (*DLB7286*; scale bar = 2.0 cm). (G) *Ethelia* sp. (*DLB6355*; scale bar = 2.0 cm). (H) *Polystrata fosliei* (*DLB7912*; scale bar = 2.0 cm). (I) *Hydrolithon abyssophila* (*Athanasiadis PR135A*; scale bar = 2.0 cm). Photos by Hector Ruiz Torres.

seaweeds adapted to low light conditions (CCA, few phaeophytes and green algae)

Ballantine et al., 2016, The Mesophotic, Coral Reef–Associated, Marine Algal Flora of Puerto Rico, Caribbean Sea

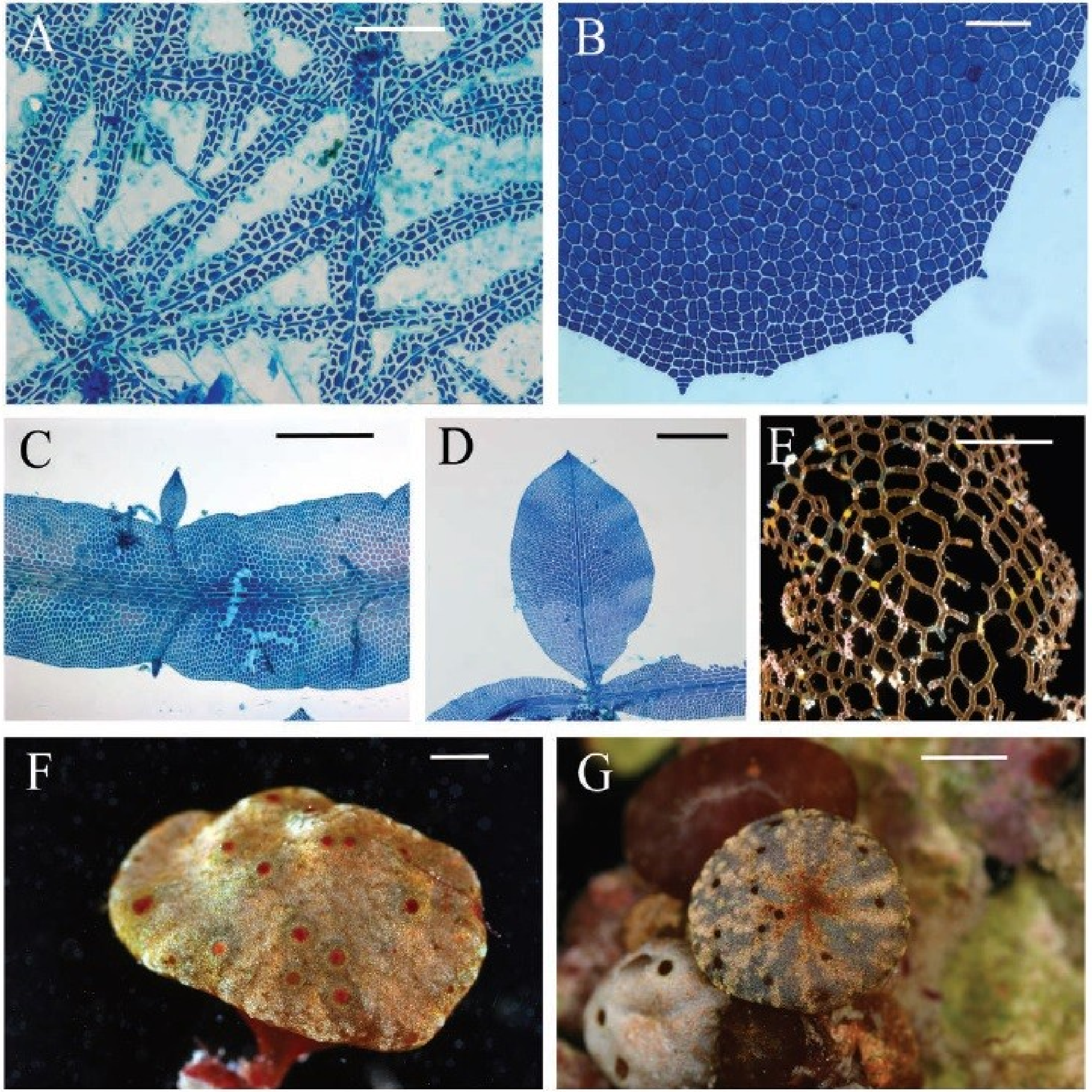


FIGURE 3. Deepwater Rhodophyta algal species. (A) *Hymenoclonium serpens* (*DLB0720*; scale bar = 100 μm). (B) *Myriogramme prostrata* (*DLB6029*; scale bar = 100 μm). (C) *Hypoglossum anomalum* (*DLB7569*; scale bar = 200 μm). (D) *Hypoglossum caloglossoides* (*DLB7569*; scale bar = 200 μm). (E) *Rhododictyon bermudense* (*DLB7527*; scale bar = 1.0 mm). (F) *Cresia opalescens* (*DLB6343*; scale bar = 1.0 mm). (G) *Botryocladia iridescens* (*DLB6307*; scale bar = 2.0 mm). Photos by Hector Ruiz Torres.

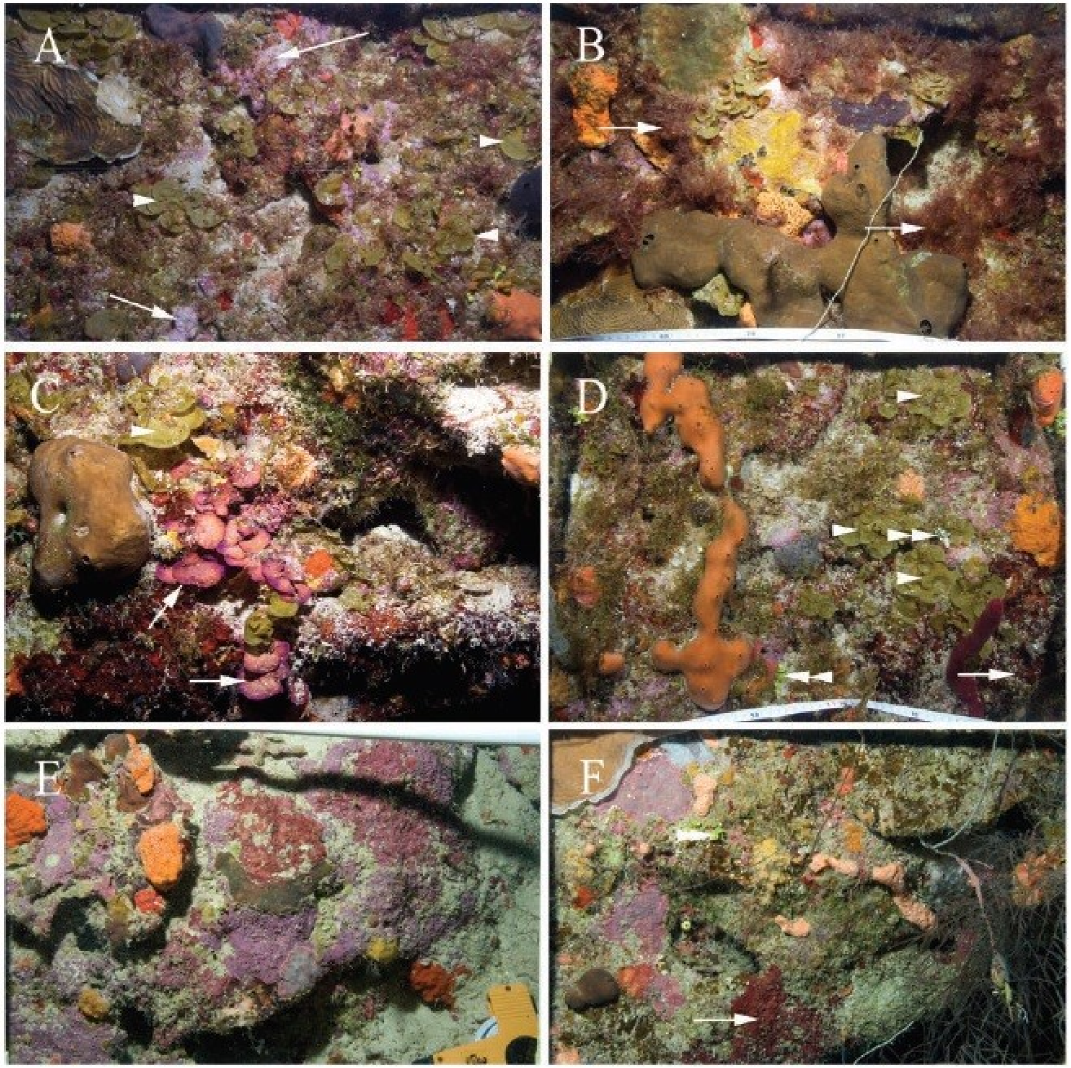


FIGURE 4. Bottom habits at edge of insular shelf south of La Parguera (all 1 m^2). (A) "Weinberg," 47 m. Pinkish background growths are Corallinales, mostly *Hydrolithon abyssophila* (arrows); also present are leafy *Lobophora* (probably *L. guadeloupensis*) (arrow heads) and several small *Halimeda* sp. in the lower right; orange growths are sponges; and at the far upper left is a colony of *Agaricia lamarcki* Milne Edwards et Haime. (B) "Hole in the wall," 47 m. The frame is dominated by a brown sponge (bottom); the large yellow incrustation at center is *Peyssonnelia flavescens*; algal turf (including *Wrangelia* spp.) is indicated by arrows; and leafy *Lobophora* (probably *L. guadeloupensis*) is shown by the arrowhead. (C) "Hole in the wall," 67 m. Nearly free blades of *Peyssonnelia iridescens* dominate the center of the frame (arrows); crustose coralline algae (some covered with sediment) appear as pink encrustations; the deep maroon encrustation at lower left is *Peyssonnelia* sp.; and leafy *Lobophora* (probably *L. guadeloupensis*) is shown by the arrowhead. (D) El Hoyo Terrace, 59 m. Coralline algae are pinkish encrustations; maroon encrustations (arrow) are *Peyssonnelia* sp.; leafy *Lobophora* (probably *L. guadeloupensis*) are shown by arrowheads; and *Halimeda cryptica* is indicated by double arrowheads. (E) "Hole in the wall," 76 m. Bottom is dominated by encrusting coralline red algae, *Peyssonnelia* sp., and sponges.

Halimeda bioherms

„carbonate factories“ of the modern biosphere

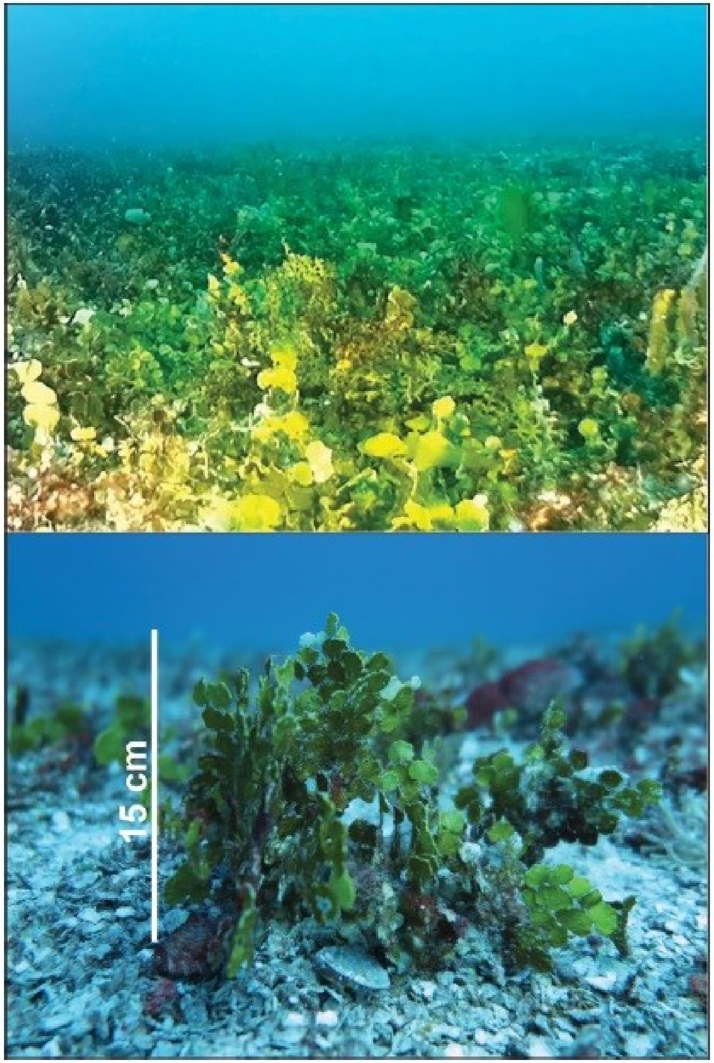


FIGURE 1 Photographs of a living *Halimeda* meadow near Lizard Island in the northern Great Barrier Reef (GBR) (see Figure 3). Photo credit (top) M. McNeil and (bottom) E. Kennedy

$CaCO_3$ production - up to 2200 g/m^2/year

McNeil et al., 2016, Coral Reefs; Mayakun et al., 2018, Phyc. Res.
Sangil et al., 2018, Botanica Marina; Ballesteros, 1991, Bot. Mar.

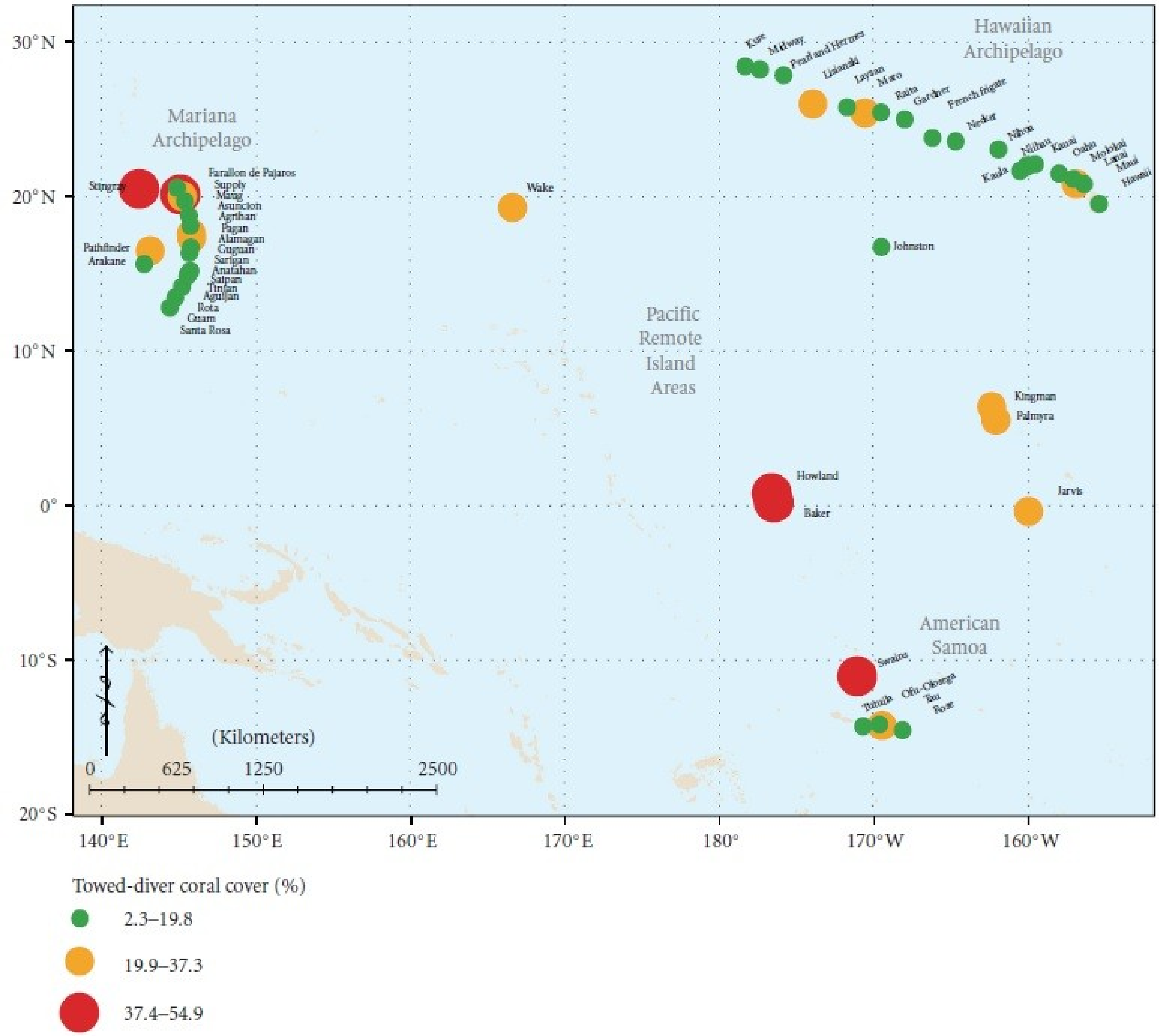
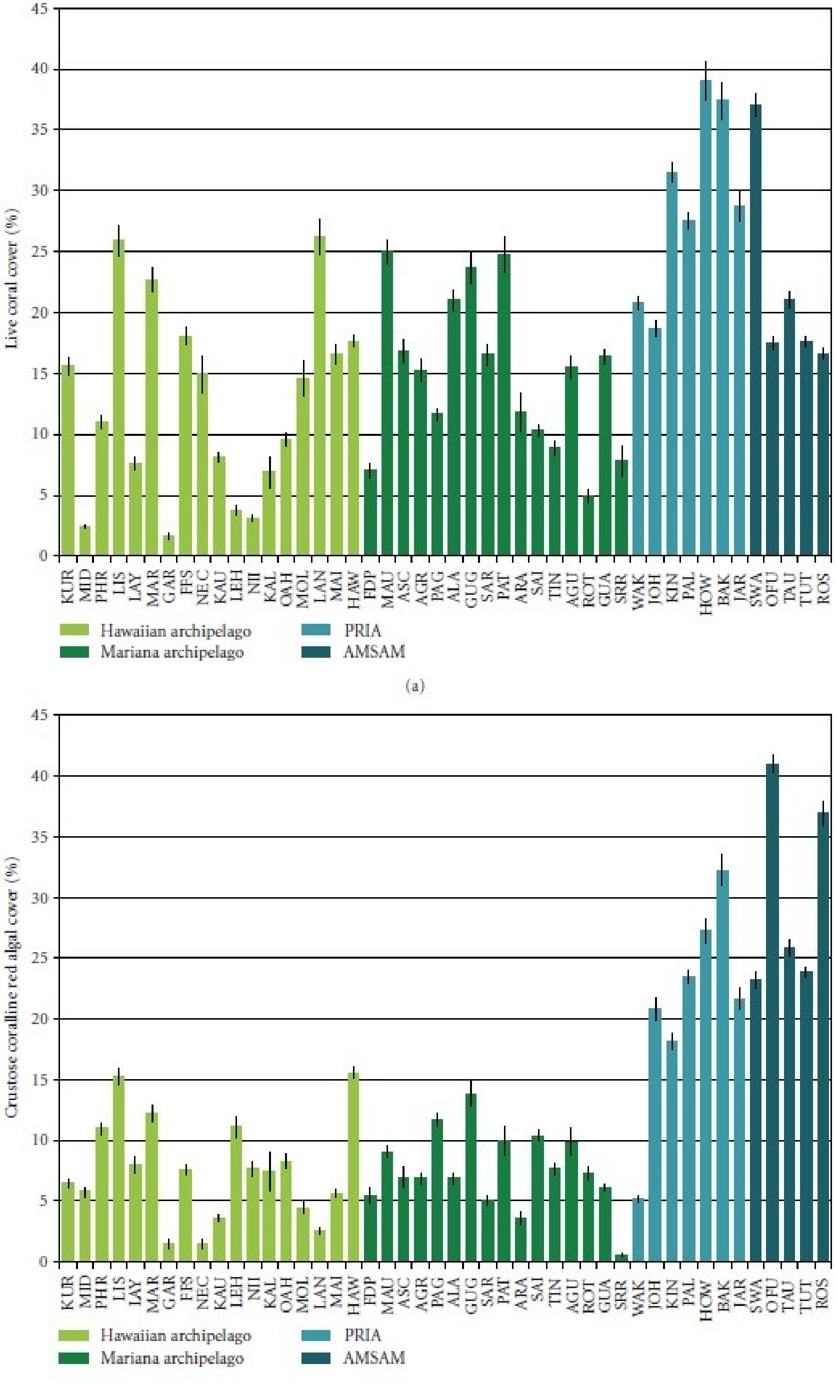


Figure 1: Average island-wide percent cover of scleractinian corals on islands under U.S. jurisdiction in the Pacific Ocean. Many of these reefs are considered to be among the least impacted tropical marine ecosystems in existence, yet average coral cover rarely exceeds 30% and is <18% at the majority of islands monitored. Percent cover data were collected via CRED towed-diver surveys [38] from 2000 through 2009 Reef Assessment and Monitoring Program research expeditions. Figure credit: Tomoko Acoba.

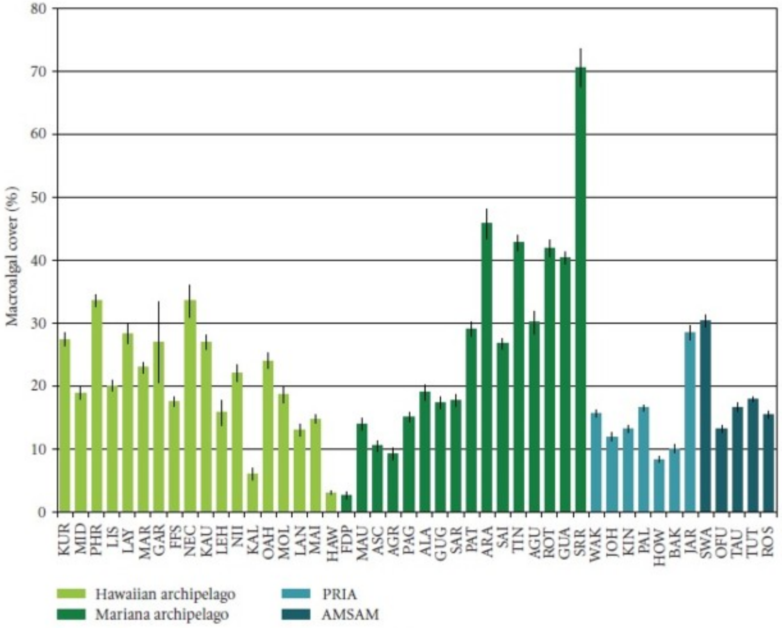
Vroom, 2011, J. Mar. Biol.

Coralgal reefs...



(a)

(b)



(c)

Figure 2: Average percent cover data of (a) live coral, (b) crustose coralline red algae, and (c) macroalgae (both calcified and noncalcified (fleshy) algae which often are attached on top of living CCA communities) collected via CRED towed-diver surveys [38] from 2000 through 2009 Reef Assessment and Monitoring Program research expeditions. Islands within each archipelagic system are arranged in geographic order from north to south (left to right), and archipelagic systems are also presented in geographic order from north to south (although latitudinal overlap between archipelagic systems is not represented; see Figure 1). Standard error bars are provided. Figure credit: Amanda Toperoff and Tomoko Acoba.

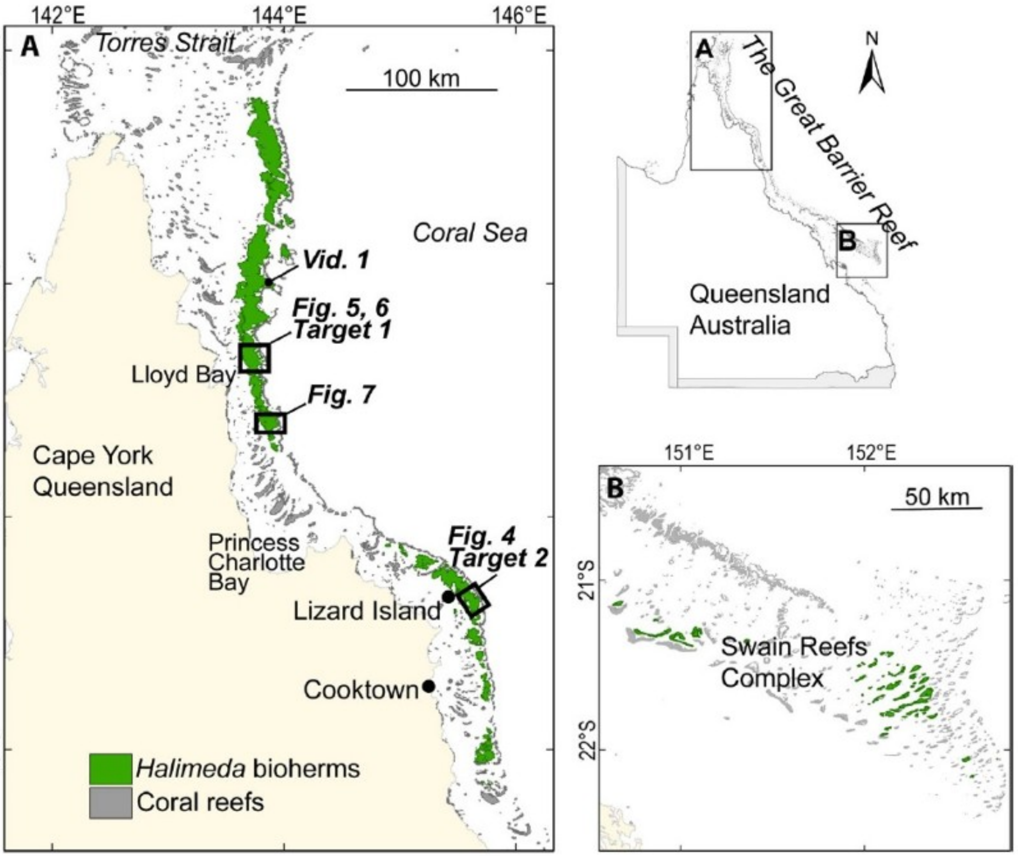
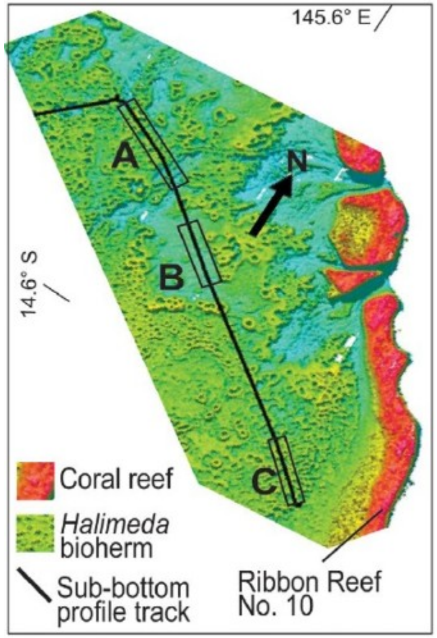
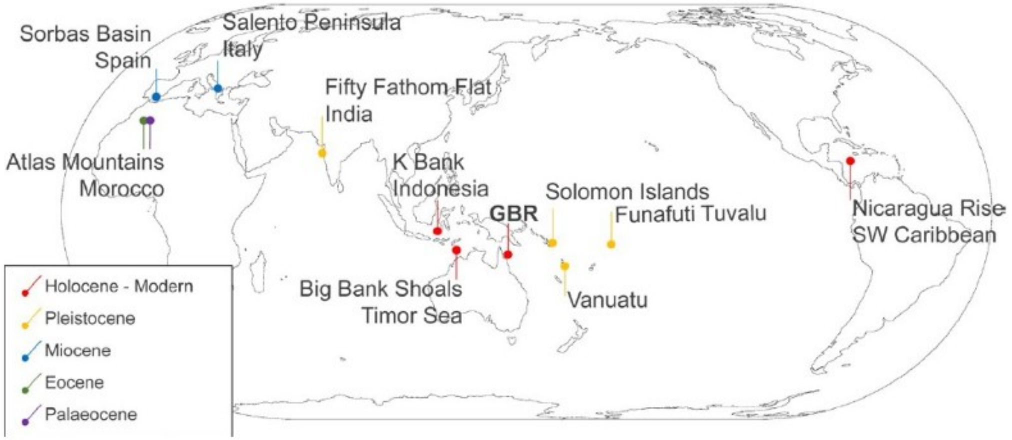


FIGURE 3 Regional map of study area. (A) Northern Great Barrier Reef *Halimeda* bioherm distribution and locations of figures referred to in this study; (B) southern Great Barrier Reef *Halimeda* bioherm distribution in the Swain Reefs. *Halimeda* bioherm distribution from McNeil *et al.* (2016)





McNeil et al., 2020, Depos. Rec.

FIGURE 2 Global distribution of known Holocene and fossil *Halimeda* bioherm locations (see Tables 1 and 2). GBR, Great Barrier Reef

Table 3.6. Forms of calcium carbonate deposited by different taxonomic groups

Group	Photosynthetic	Crystal Form of Carbonate	Ecological and Main Calcification Role
Corals	Reef forms have symbiotic algae	Aragonite	Reef builders
Soft corals	Some	Calcite spicules	Some contribute to reef building
Macroalgae (greens and browns)	Yes	Aragonite, Mg calcite and calcite	Sand production
Calcareous red algae	Yes	High-Mg calcite	Reef crest construction
Echinoderms	No	High-Mg calcite	Minor role in limestone production
Molluscs	Not usually (some clams have symbiotic algae)	Calcite and aragonite	Minor role in limestone production
Crustaceans	No	Skeleton mainly organic, but some with mineral salts especially High-Mg calcite	Negligible role in limestone production
Foraminifera	Some	Calcite	Benthic and planktonic, sand production
Pteropods	No	Aragonite	Planktonic food
Coccolithophores	Yes	Calcite	Planktonic food

Note: High-Mg calcite is commonly 3%–15% MgO.

main marine communities dominated by calcified taxa:

- coral reefs
- Halimeda meadows/bioherms
- Halimeda draperies
- CCA
- rhodoliths
- coralliths

[tropical rhodoliths - up to 200 m
very old individuals
(30 cm diameter - 500-800 years)
their fields sometimes confused with „coral reefs“]

up to 40% of Neogene carbonate sediments are due to Halimeda calcification

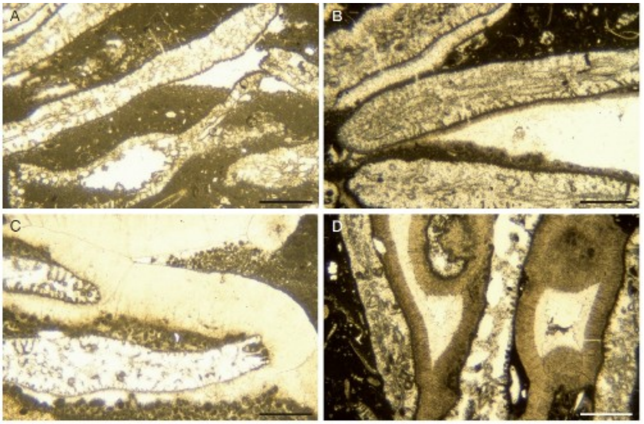


FIG. 10. — Miocene *Halimeda* facies, mostly *Halimeda* rudstones: **A**, micritic to clotted mud fills most of the intergranular space and the organic porosity; it is post-depositional for it took place by percolation; **B**, a fibrous calcitic fringe borders the shelter cavities beneath segments of *Halimeda*; **C**, a rather thick stage of botryoidal cementation is sandwished between two successive stages of post-depositional and geopetal clotted micrite; **D**, a yellowish fibrous-botryoidal cement borders the intergranular space and the rest of it is filled by a translucent drusy calcitic cement; Messinian; Sorbas, Spain. J. C. Braga Collection. Scale bars: 1 mm.

Sheppard et al., 2018, The Biology of Coral Reefs
Granier, 2012, Geodiversitas

Evolution of marine calcified reef ecosystems

the relation with the calcite/aragonite fluctuations

approximately 10% of marine macroalgae are calcified;
ca 100 genera, 85 reds, 1-2 browns

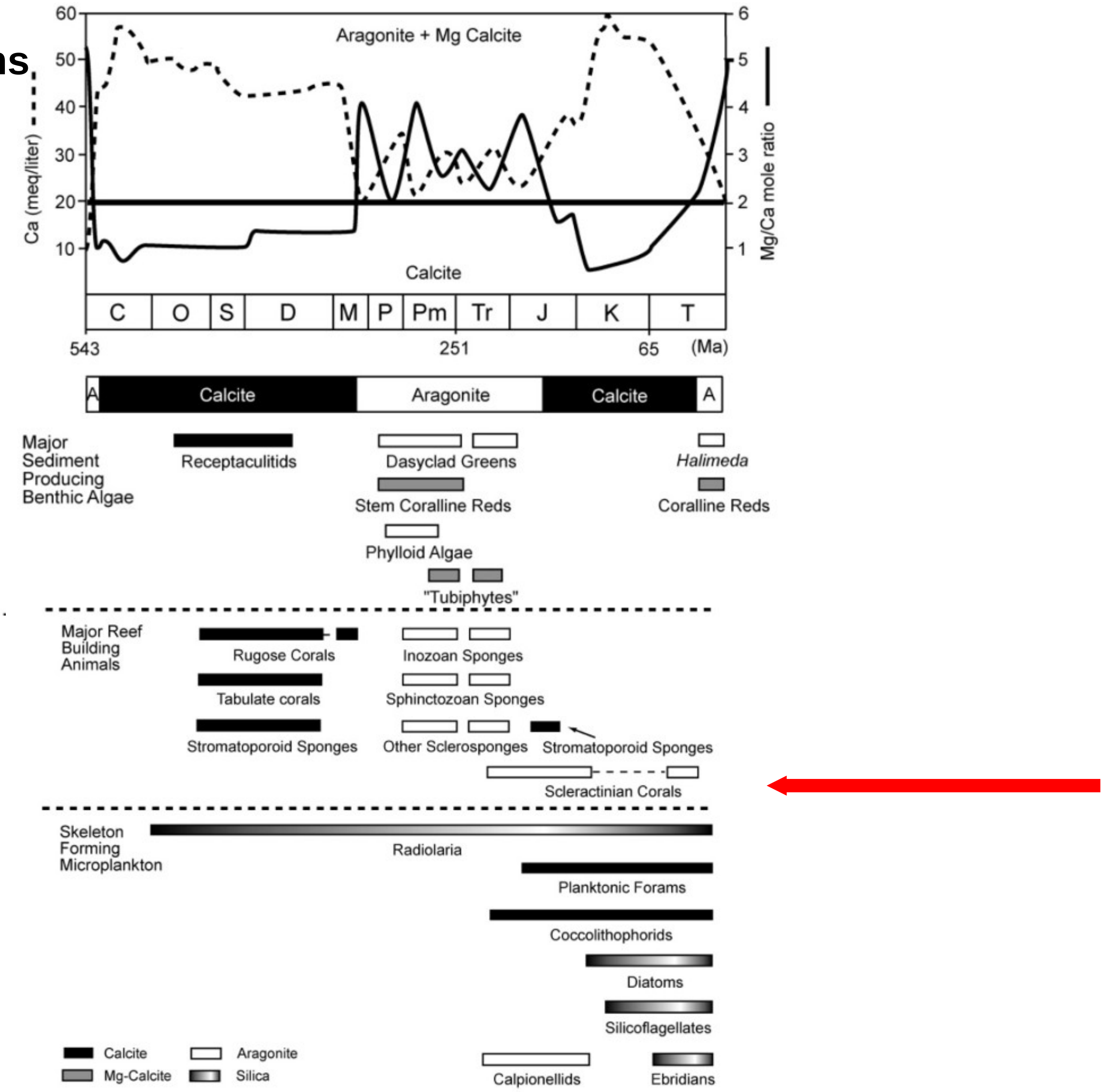
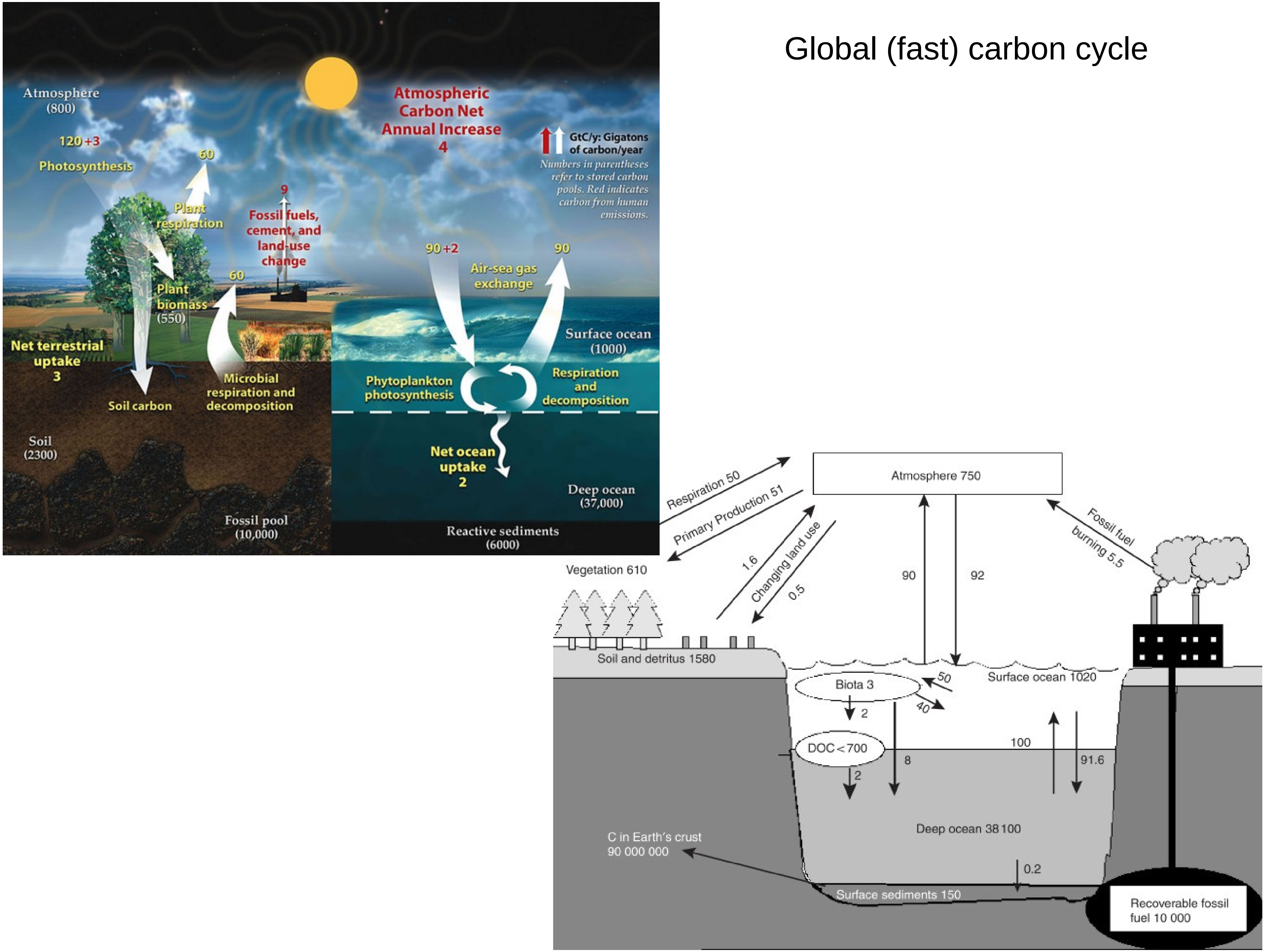


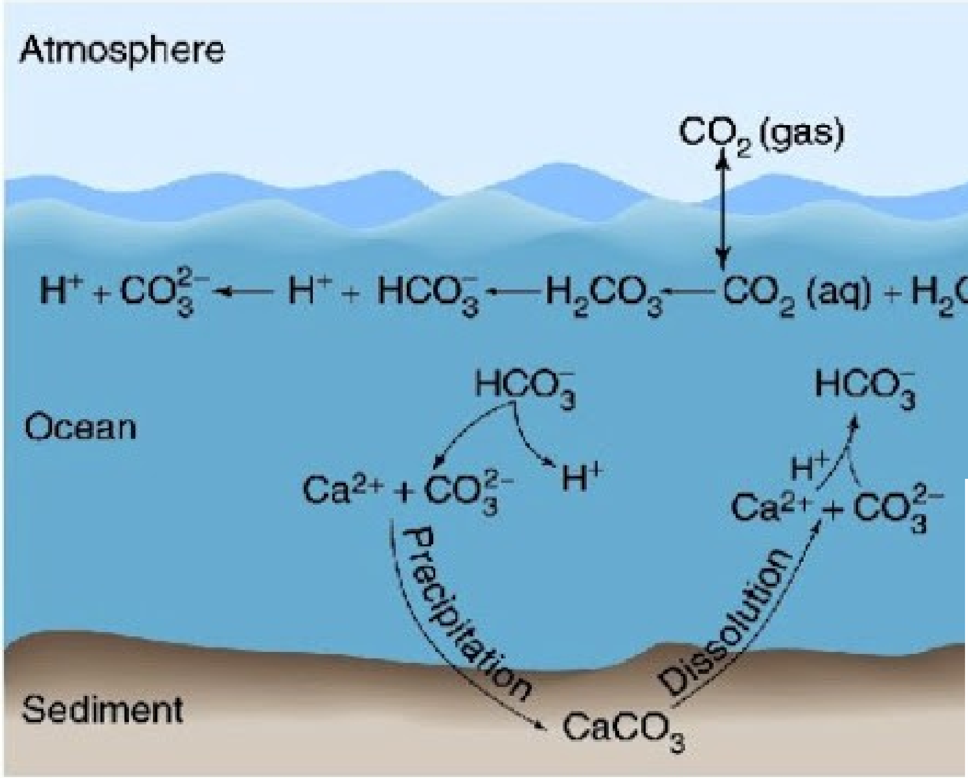
Figure 7. The stratigraphic relationship between ocean chemistry and skeletal mineralogy in major sediment producing benthic algae and animals, modified from Stanley and Hardie (1998). The figure shows Stanley and Hardie's (1998) estimates of Ca abundance and Mg/Ca in ancient oceans, as well as the principal time intervals dominated by "calcite" and "aragonite" seas. Aragonite and Mg-calcite are favored when the Mg/Ca mole ratio is above 2; calcite is favored at ratios below 2. Also shown are the time distributions of principal skeleton–forming protists; calpionellids are thought to be tintinnids with calcified tests (see text for references).

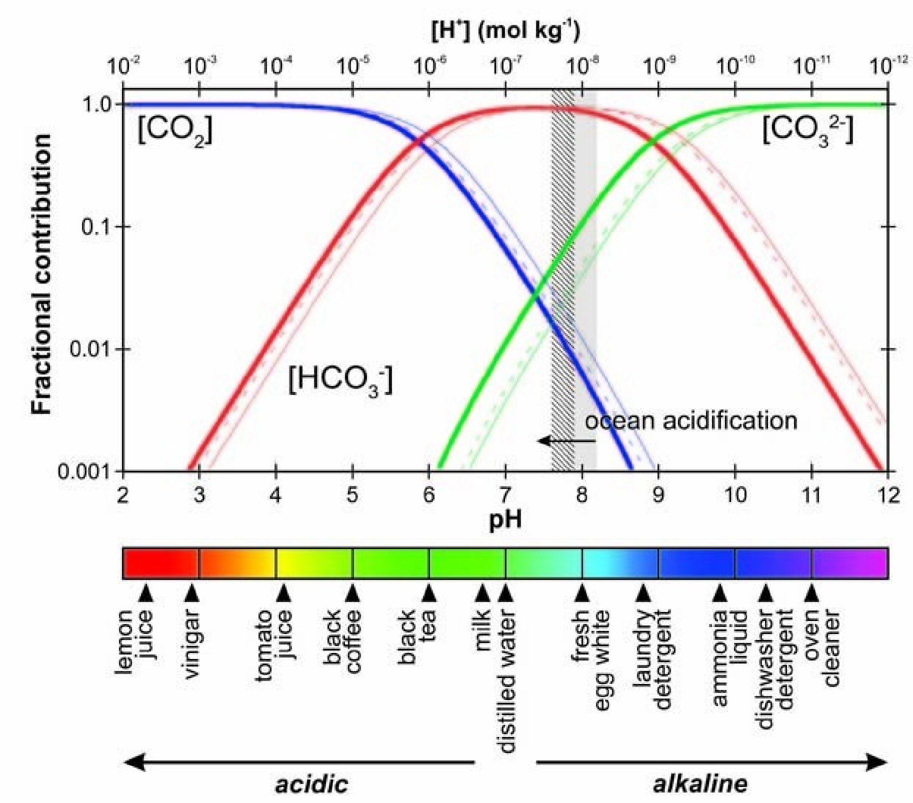
Knoll, 2003

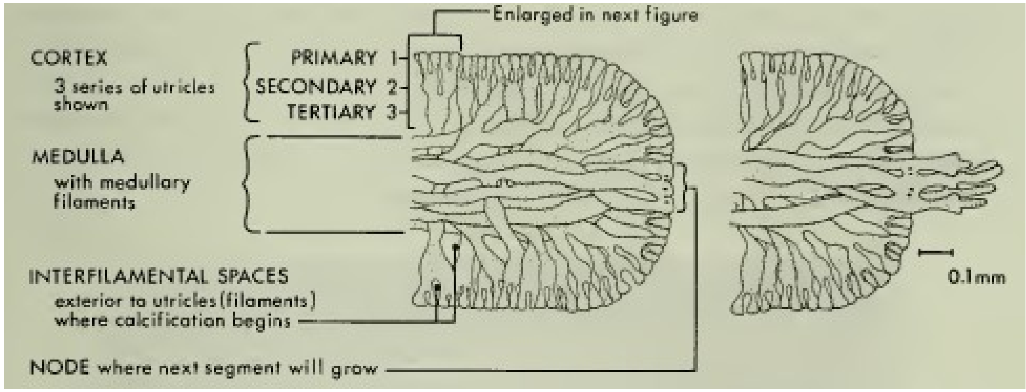
Global (fast) carbon cycle



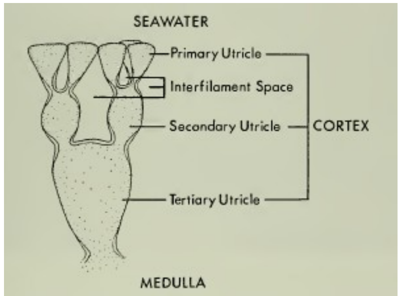
Carbonate - Bicarbonate Seawater Buffer System

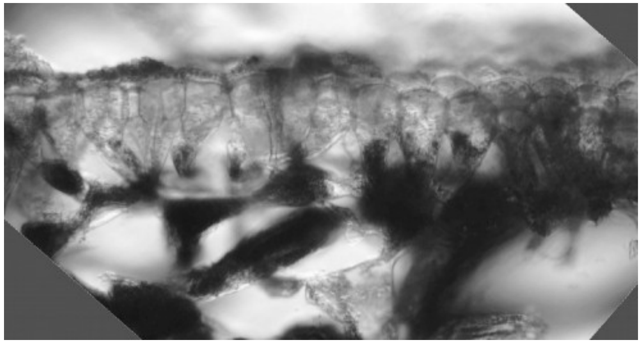


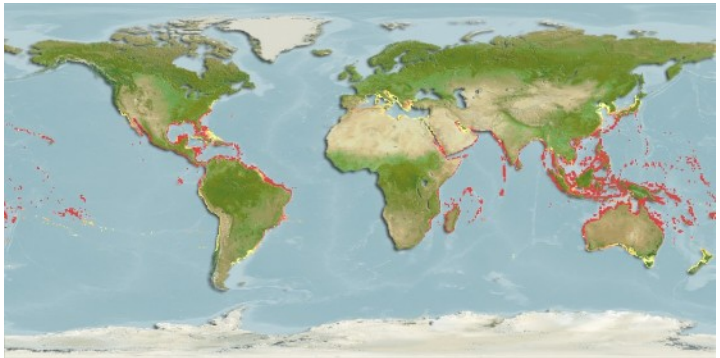


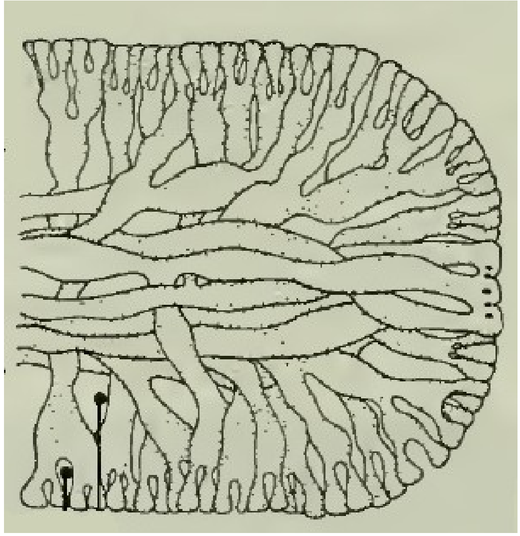


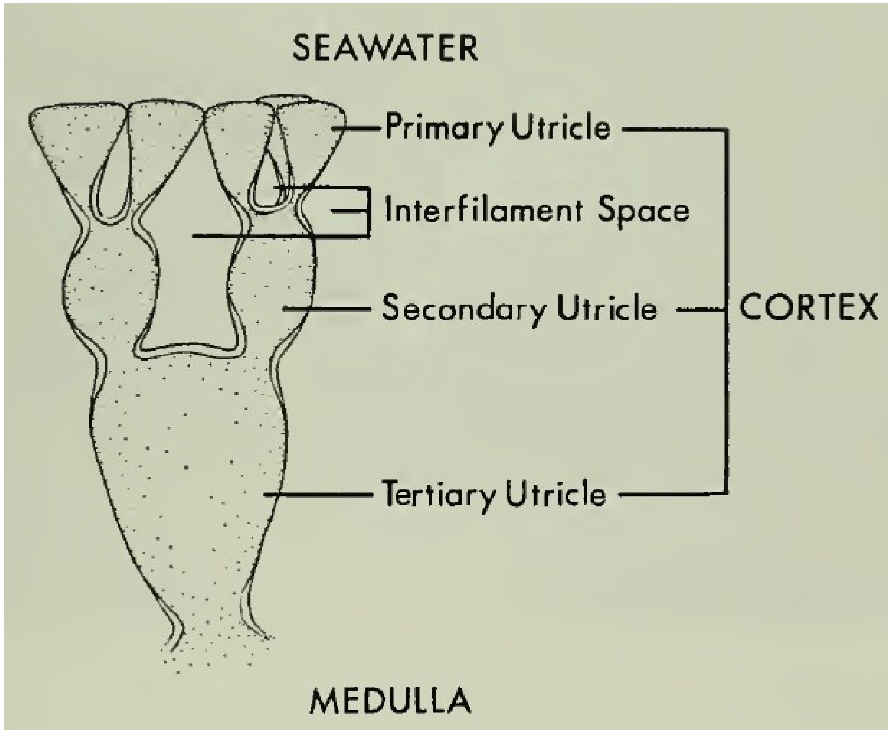
H. opuntia - up to 90% of dry weight constituted by aragonite

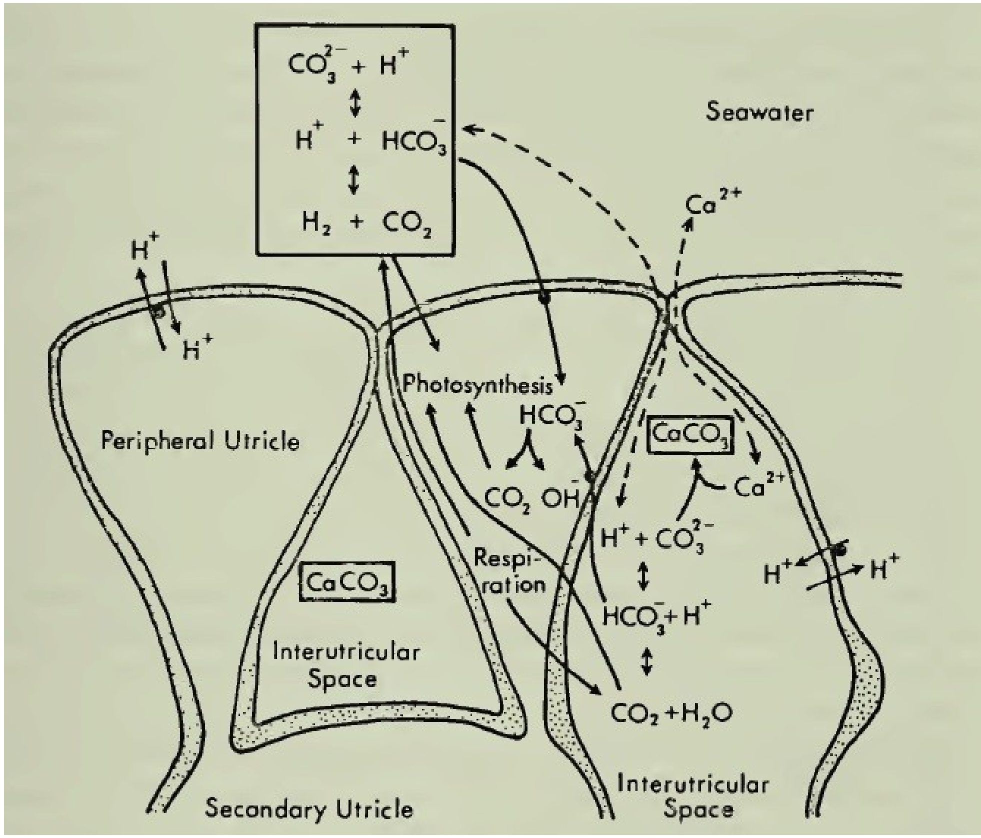


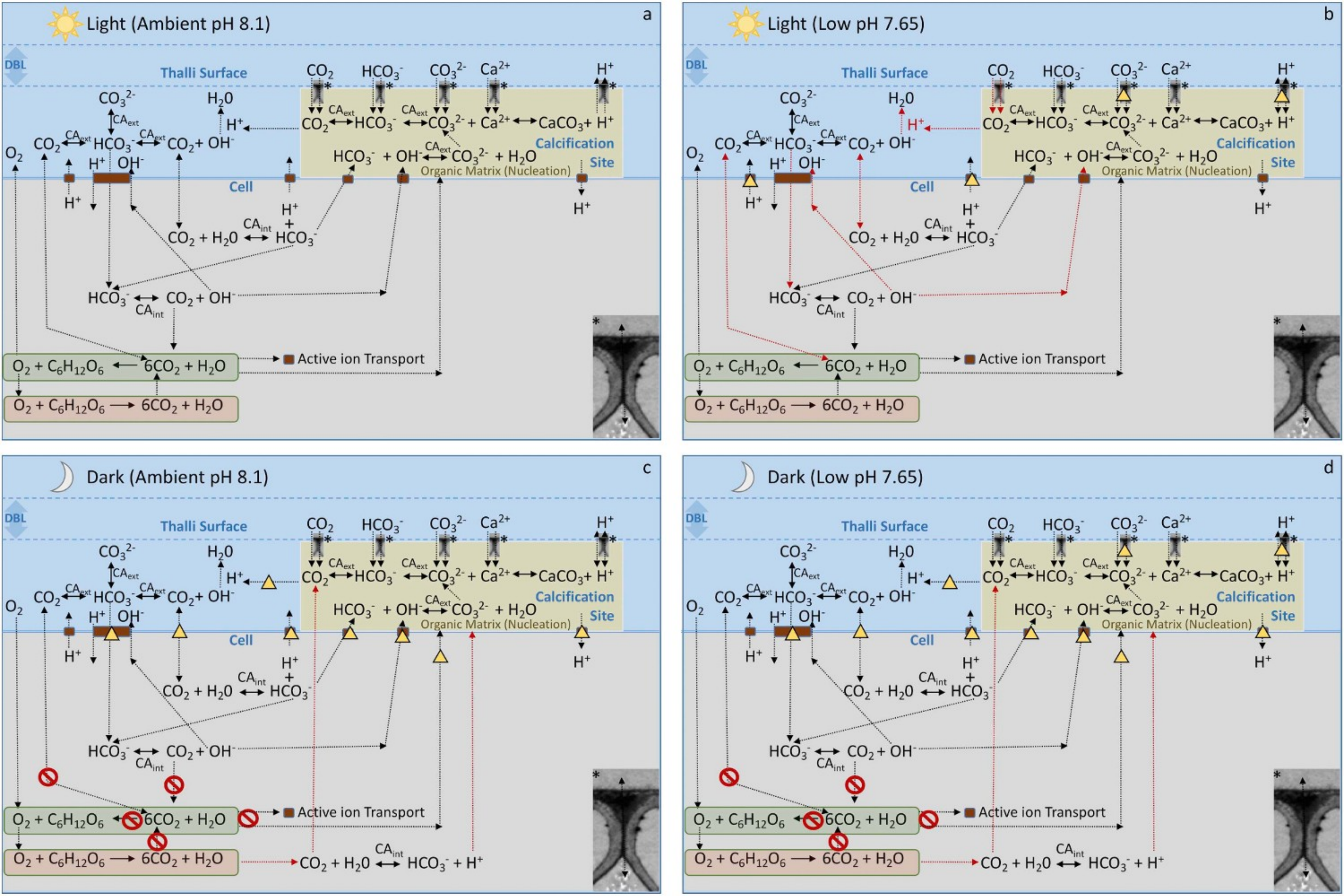







SEAWATER
Primary Utricle
Interfilament Space
Secondary Utricle
CORTEX
Tertiary Utricle
MEDULLA


$CO_3^{2-} + H^+$
$H^+ + HCO_3^-$
$H_2 + CO_2$
Seawater
Ca^{2+}
H^+
H^+
Photosynthesis
HCO_3^-
CO_2 OH^-
Peripheral Utricle
$CaCO_3$
Ca^{2+}
$H^+ + CO_3^{2-}$
H^+
H^+
$CaCO_3$
Respi-ration
$HCO_3^- + H^+$
Interutricular Space
$CO_2 + H_2O$
Secondary Utricle
Interutricular Space



a Light (Ambient pH 8.1)

b Light (Low pH 7.65)

c Dark (Ambient pH 8.1)

d Dark (Low pH 7.65)

MnNicholl et al., 2019, J Exp Mar Biol Ecol

Eastern Atlantic Region

limits: Cape Verde a Mocamedes (Angola), these limits are constituted by two cold currents;
both are then deflected westwards (towards S Am), between them - The Equatorial Countercurrent warms the coast

however, tropical character only up to 50 m, occasional upwellings may even decrease summer temperature to 19°

dominated by soft bottoms

diversity decreased for about 70% in comparison with Western Atlantic Region
important missing pantropical genera: Neomeris (Dasycladales), Turbinaria (Sargassaceae)

most species - amphiatlantic, about 25% common with the Indo-Pacific
about 7% endemic taxa (flagship species: Dictyurus fenestratus)

Caulerpa sertularioides

Dictyurus

L. ochroleuca - ends in Morocco in 30 m depth
L. pallida in S Hem evolved by L.o. crossing the equator

Cymodocea nodosa - reaches only to Senegalese coast

Halodule

vegetation dominants often also occur outside of the tropics (eurytherm taxa)
[typical genera: Caulerpa, Laurencia, Sargassum, Gelidium, Halimeda, ...]
soft bottoms dominated by Caulerpa spp. and Halodule

hermatypic corals scarce - no typical reefs (although they occured until late Pliocene
progressive diversity loss during Pleistocene (SST decrease in Heinrich events during Glacials)

Ascension Island, Saint Helena Island

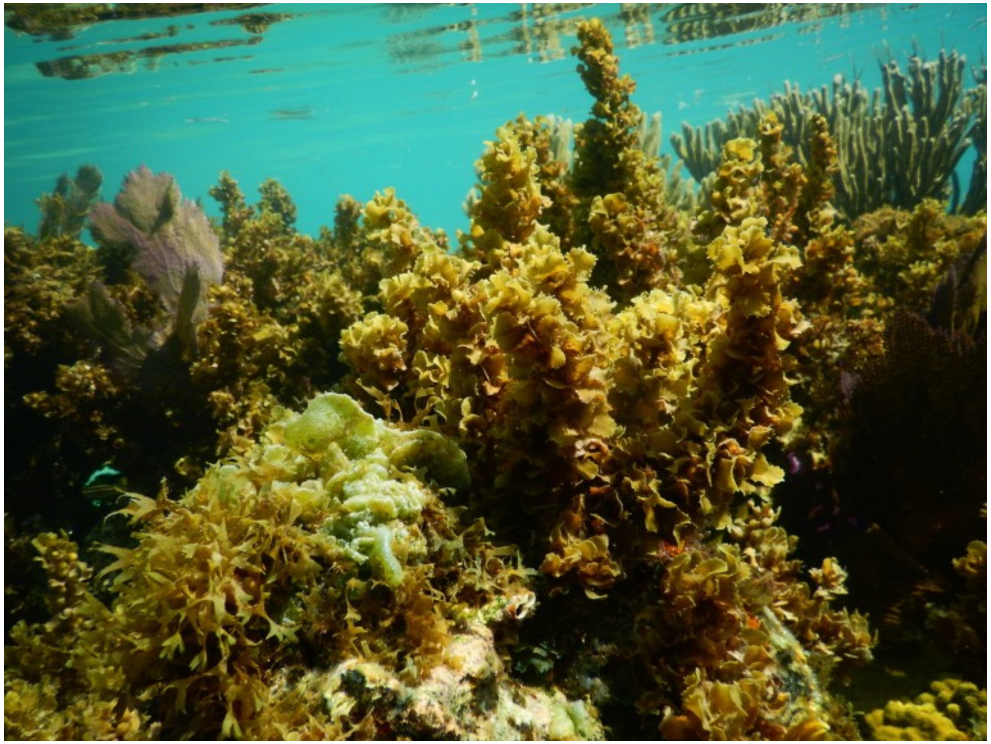
a lot of hard bottom volcanic sites
annual temperature: 22-26°C - but no coral reefs...

low diversity, mostly pantropic or „cosmopolitan taxa“ - Sargassum vulgare, Gelidium pusillum, Ulva spp.

reasons: low age of the islands, isolation effects

Western Atlantic Region

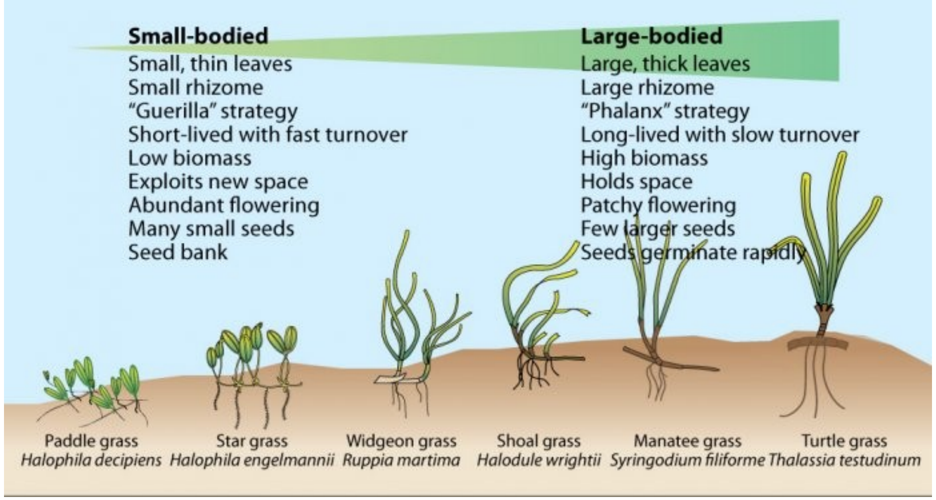
S Florida to Cape Frio (close to Rio de Janeiro)
S Equatorial Current warms the coast up to Rio (also called Brazil Current)
Nwards - Guayana Current, up to Carribean, then as Florida Current transformed into Gulf Stream warming Bermudas, drift of algal thalli sometimes up to Carolinas




(c) T.Murdoch 2008

coral reefs - most typical habitat of this region
when corals absent on hard substrates - dense Sargassum vegetation
soft substrates (N coast of S Am, Amazonas estuary); mangroves - Caulerpa, Catenella, Acanthophora, Bostrychia, seagrasses (Halophila, Halodule, Syringodium)

Seagrass meadows in the Carribean Sea



Small-bodied

- Small, thin leaves
- Small rhizome
- "Guerilla" strategy
- Short-lived with fast turnover
- Low biomass
- Exploits new space
- Abundant flowering
- Many small seeds
- Seed bank

Large-bodied

- Large, thick leaves
- Large rhizome
- "Phalanx" strategy
- Long-lived with slow turnover
- High biomass
- Holds space
- Patchy flowering
- Few larger seeds
- Seeds germinate rapidly

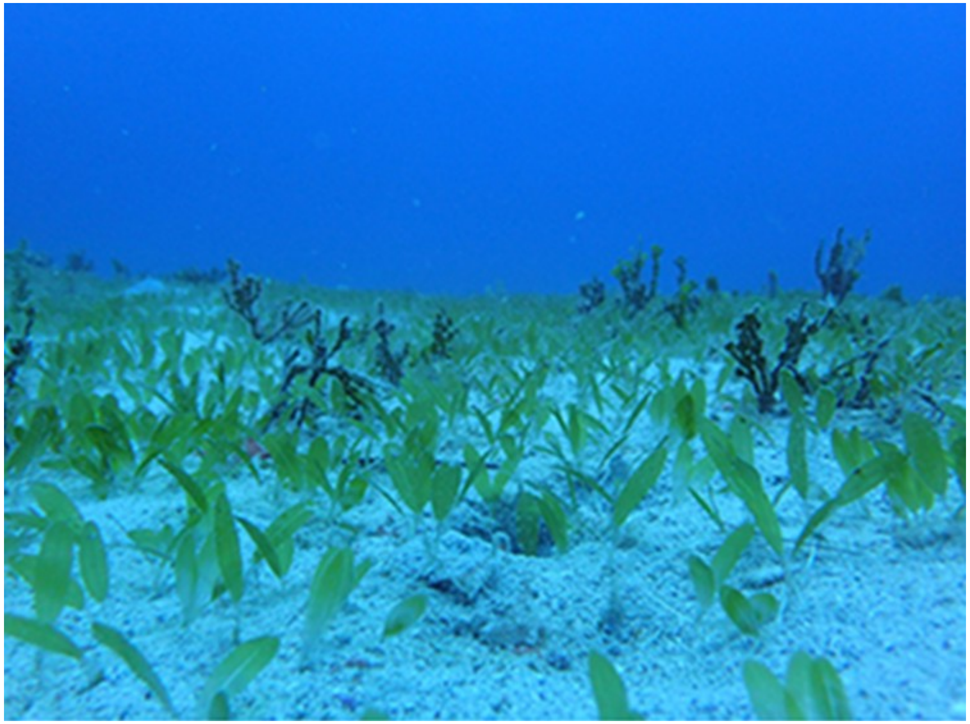
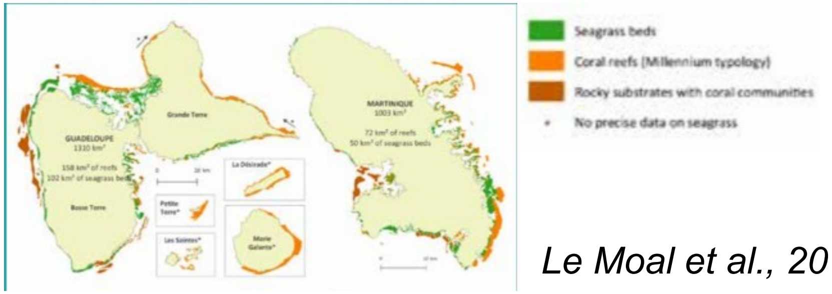


Figure 22. Algal communities observed on seagrass beds in the Caribbean. Perennial (A: *Avrainvillea* and *Halimeda*; B: *Caulerpa prolifera*, *C. ashmediea* and *Amphiroa*; C: *Dichotomaria obtusata*; D: *Galaxaura subverticillata*), seasonal (E, F: Liagoraceae) and opportunistic algae (G, H: filamentous green algae).



Le Moal et al., 2016

Lower sublittoral off the Brazilian coast

Lobophora variegata dominant down to 100 m, in addition: Stypopodium, Dictyopteris, Padina, CCA
deep water kelps: Laminaria abyssalis, L. brasiliensis

Sargasso Sea
floating (not just) Sargassum rafts

known since the end of the 15th century

S. fluitans, S. natans - originated either from Carribean or Tethys Sea ancestors
- no receptacles, no holdfasts, veget. reprod.

Tertiary origin, endemic invertebrates („dispaced benthos“)

specialized fish: Histrio histrio, Antennarius marmoratus

evolution of Sargassum rafts: early Miocene fossils of specialized fishes and typical Sargassum air bladders known from Carpathian parts of Tethys Sea and from Sicily

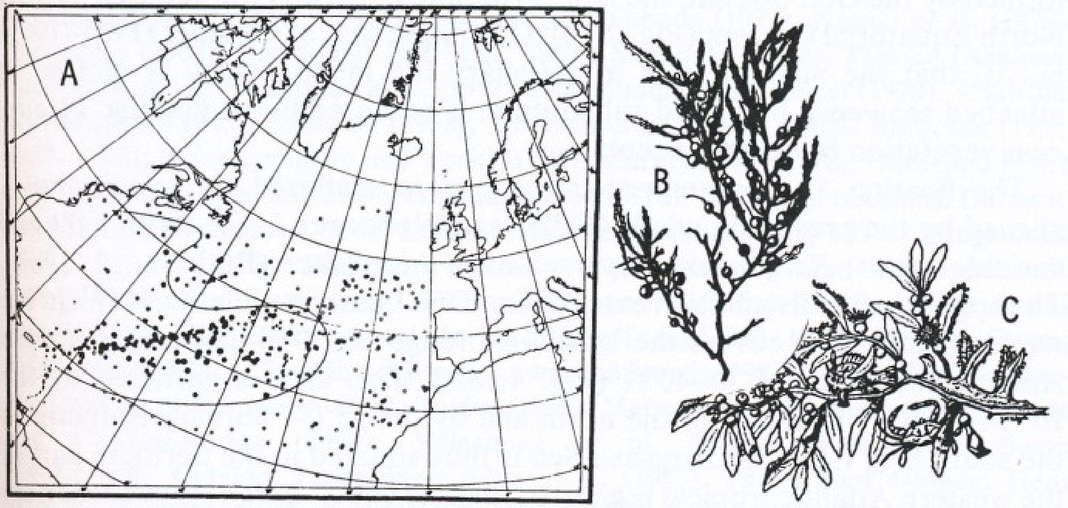


Fig. 4.16 **(A)** Boundaries of the Sargasso Sea, as determined by the *Dana* Expedition in 1920–1922. Black circles: collection sites of floating *Sargassum;* abundance increases with diameter of circles. Open circles: no *Sargassum* present. **(B)** *Sargassum natans* from the Sargasso Sea. **(C)** Invertebrate and fish fauna of floating *Sargassum* in the Gulf of Mexico. The Sargasso fish *Histrio histrio* hovers motionless among the *Sargassum* blades, then rapidly attacks and swallows a nearby animal. (A,B from Winge 1923; C after Hedgpeth 1957*a*.)

may include drifts of Asc. nodosum and F. vesiculosus in the NW margins of the distribution area

temperature limits:
20 st. Feb isotherm in the north;
25 st. Feb isotherm in the south

Lüning, 1991, Seaweeds

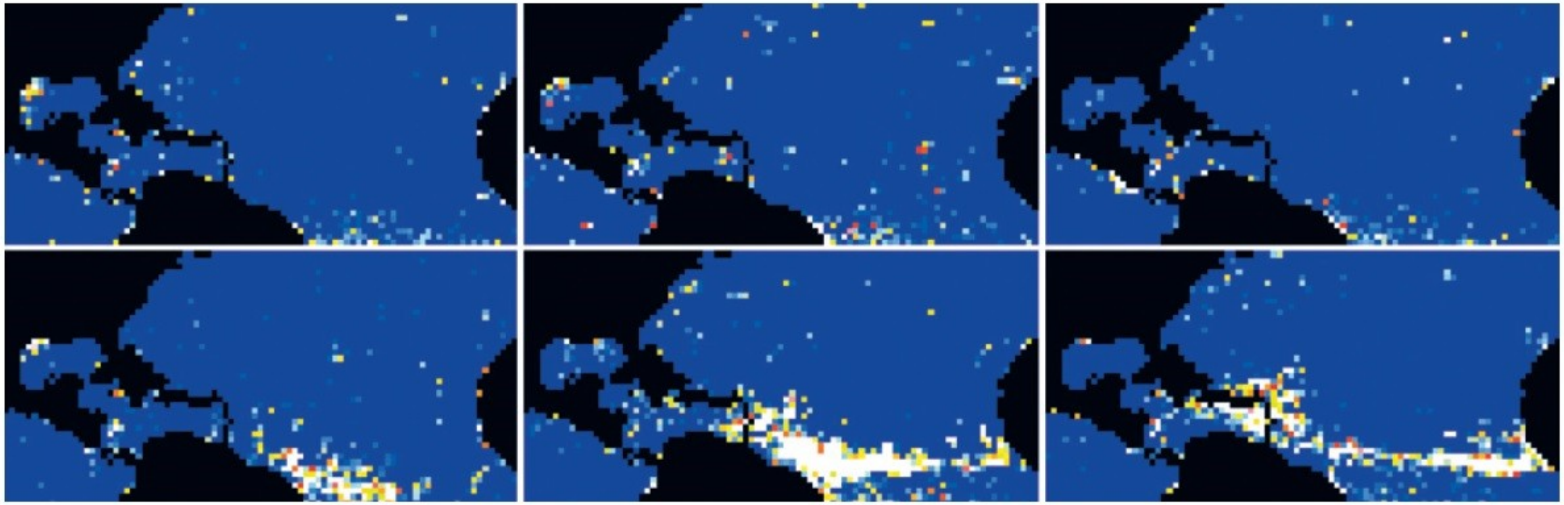
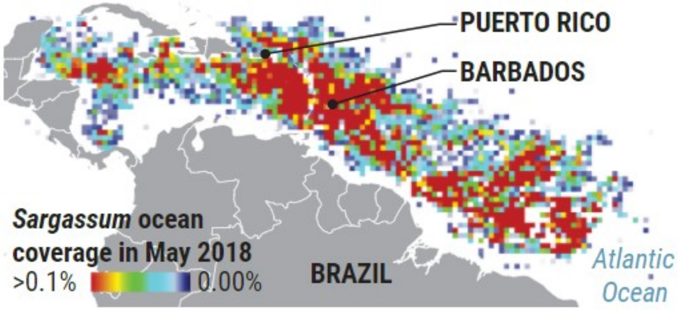


Figure 3 | Distribution of drifting *Sargassum* rafts derived from MERIS satellite images across the central Atlantic Ocean. An average year (2010, top panels) compared with the spectacular 2011 event (bottom panels). From left to right, panels show May, July and September for both years. High concentrations are shown in white and red, and low concentrations in deep blue. Note the high *Sargassum* concentrations in the north-western Gulf of Mexico in May for both years. Reprinted with permission from ref. 39.

Smetacek & Zingone, 2013, Nature

21st century Sargassum rafts in the tropical Atlantic („golden tides“)

new source areas...



Guadeloupe

Antigua, 2011

Langin, 2018, ScienceMag

Indo - Western and Central Pacific Region

the primary centre of benthic marine diversity on the planet

the highest temperature stability - among Malaya, Philip. and N.G. - the highest diversity levels

Eastern Africa - mostly soft bottom
Madagascar, Mauritius, Reunion - Sargassum spp., Cystoseira myrica, Turbinaria spp., Hormophysa triquetra (Sargassaceae)



Red Sea - isotherms up to 33 st, salinity up to 42-46 psu - one of the highest in the global ocean

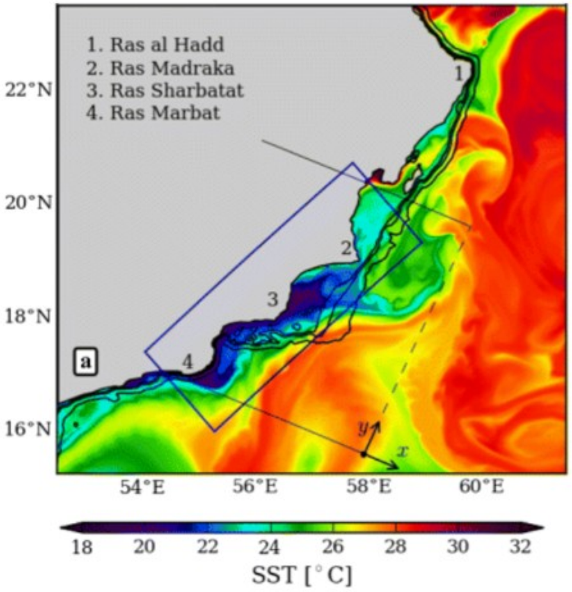
typical components - (species-poor) coral reefs, Cystoseira myrica, Caulerpa serrulata, Gelidiella acerosa, Turbinaria decurrens/elatensis, Padina pavonica, Cymodocea spp., Halimeda spp.

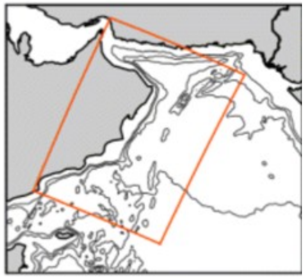


Danièle Heitz

Eastern Arabian Penninsula upwelling

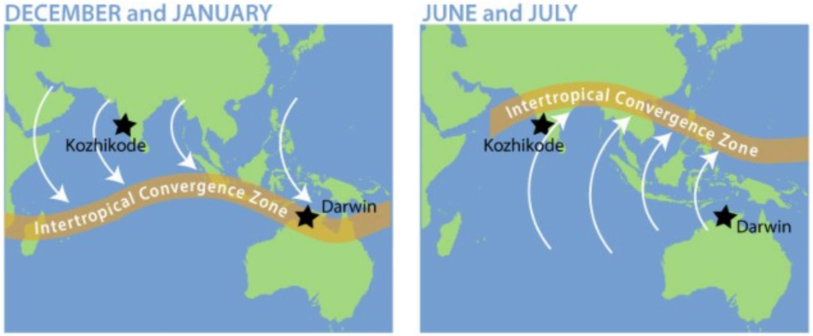
Oman upwelling (5th largest globally) - Ecklonia radiata [?] (close to those from S Australia)





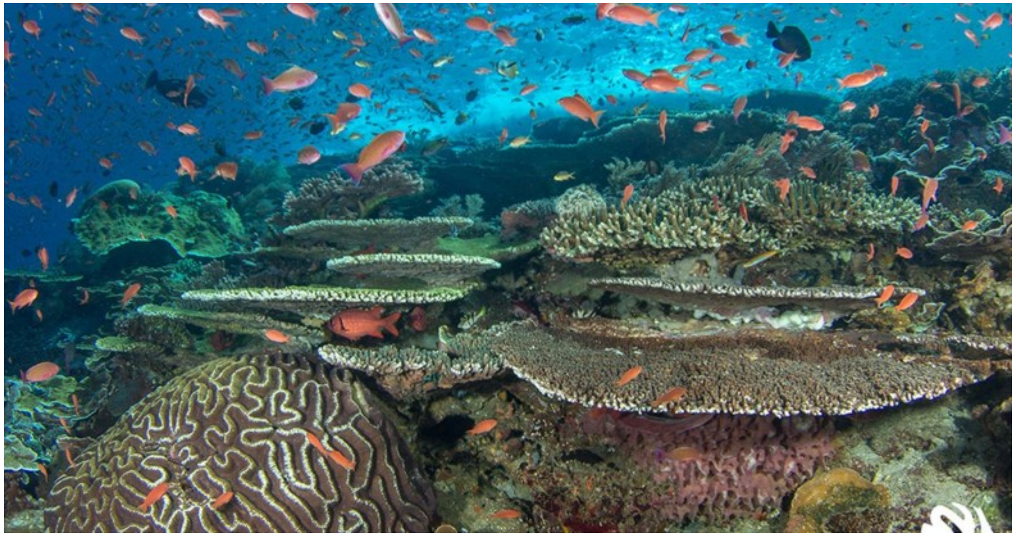
monsoon areas (India, Ceylon, W Indonesia, South China Sea)

no significant temperature fluctuations, no daylight fluctuations - but monsoons
wet monsoon brings nutrients but turbidity, algal phenological cycles - adapted to this cycles



coral reefs of the Indo-Pacific

high alpha-diversity, possibly relatively low beta-diversity (Maledives coral seaweed communities are relatively similar to those of Marshall Islands, etc.)



Euchema - a frequent component of W Indonesian seaweed communities

GBR - Halimeda bioherms (H. opuntia, other species)

additional frequent taxa: Caulerpa racemosa complex, Chlorodesmis, Boodlea, Padina, Cystoseira trinodis, Sargassum, Amphiroa, Laurencia, Thallasia, Halophila ovalis, CCA, Tydemania

Pacific Islands

decrease in diversity towards west - island isolation theory explains relatively low diversity of far-away islands (Hawai, etc.)

Easter Island - 80% widely distributed species, affinity to coral ecosystems of the Western Pacific, not Southern America, low endemism levels

eastern Pacific barrier -
vast land-less area - "Waterworld"

Eastern Pacific Tropical Region

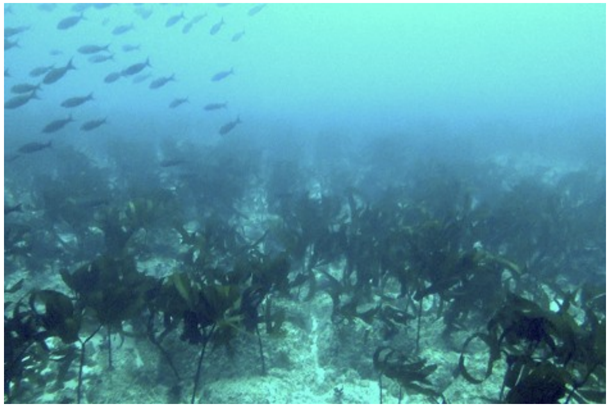
Southern Baja California to Gulf of Guayaquil
spatially restricted by cold currents
huge tidal amplitude (typically more than 6 m)
relatively high seasonal SST variation - Panama 15-32°C
(Carribean sea only 24-30°C)
only about 300 traditional species

low diversity coral reefs - fringing reefs in Panama, S Baja, etc.

in general - high similarity of macroalgae to Carribean coasts
at the genus level; species diverging for 3.5 my (Panama bridge)

Galapagos Islands

volcanic, young - only since Pliocene
species-poor coral reefs (only about 32 species of corals,
310 seaweed species)
algae more like warm temperate than tropical, kelps (!)
(Eisenia galapagensis)



Buglass, 2019,
Darwin Found.

Charpy, 2009

Clipperton

the only atol in Eastern Pacific
mostly widely distributed
pantropical species (low endemism)

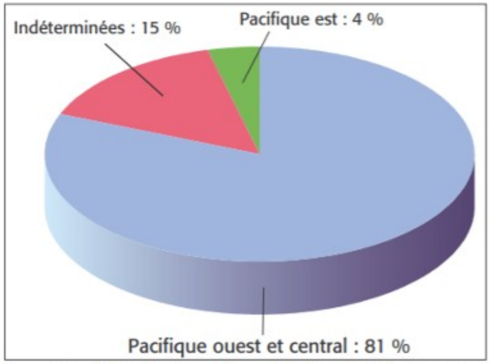


Figure 125: affinités biogéographiques de la flore algale de Clipperton.
Biogeographical affinities of the algal flora of Clipperton.

Global distribution of seagrasses

12 traditional genera, 7 originally from the Indo-Pacific,
3 in Western Atlantic; only 1 also in Eastern Atlantic (Halodule)

the genus Cymodocea - originally from the tropics
(tropical Tethyan element in the Mediterranean)

Zostera (oldest fossil records from Japan),
originally in Western Pacific, distributed into the Atlantic
by crossing the NW passage (after loosening the Bering passage)

Posidonia - Mediterranean (Tethyan) endemite