Reef Digress: Coral Oases

Chris Aslett

Vast areas of worldwide reefs have been denuded by bleaching and disease. Amongst these wastelands adorned by merely ~11 percent coral cover, surveys between 2012 to 2017 unearthed oases of comparatively pristine ecosystems with communities of stony corals covering up to and more than 40 percent (Fig. 1.; Elahi et al. 2022). By serving as diverse reservoirs of coral larvae (planulae), they have the potential to restore depleted territories, and as such, they have caught the attention of teams of international conservationists that have the power to override countrywide prerogatives (Harden-Davies & Serdy 2018) whose governance embraces and consults indigenous stakeholders and validates their prevailing rights, as reef conservation cannot be implemented by administrations or researchers in far distant lands (Cinner et al. 2016; Webster et al. 2017; Elahi et al. 2022; Shumway et al. 2024). Furthermore, by virtue of their typically-remote subregional locations, conservation initiatives must not enforce economic constraints on local people to the extent that their families starve.

Since their discovery, scientists have searched for an explanation as to why corals in these locales appear unaffected by the stressors that impact surrounding reefs. To date, survey dataset accruals and sophisticated statistical analyses have yet to identify the unique features of oases that expedite exceptional scleractinian performance, yet most are not associated with densely-populated landmasses while they occur in subregions where sea-surface temperatures (SSTs) are exceedingly variable and irradiance downwelling is significantly attenuated with depth. Equally, some are close to industrialised areas and exposed to persistent greater than average SSTs (Elahi et al. 2022). We can only state with any certainty, these pockets sustain extremely-productive diverse communities of zooxanthellate Scleractinia (hermatypic corals) which are surrounded by sparsely-populated, dysfunctional, and depleted ecosystems.

Each site was confirmed on another occasion during the six-year series of surveys; however, most likely thanks to the protracted recouperation of those that have lost pigment or tissue, and the remarkable conspicuousness of each oasis, a solitary sighting or “snapshot” was considered sufficient (NOAA Coral Program 2014; Elahi et al. 2022).

In an attempt to ascertain the conditions that underpin each site, dataset appraisals calculated the mean and coefficient of variation (CV) for each of the six chosen covariate predictors: sea-surface temperature (SST); light attenuation; calcium carbonate deposition customarily referred to as primary productivity; wave energy; the frequency and category of storms, and landmass-proximity and human population density. Each 21.2 square kilometre (km^2) grid cell was designated an oasis if its percent coral cover was equal to or exceeded 2 standard deviations above the subregional mean (Fig. 1.). 4 to 8 percent of regional grid cells contained oases, whereas anywhere from 0 to 10 percent were delineated at the subregional scale (Elahi et al. 2022).

As opposed to turbidity or cloudiness that only appraises waterborne particles, the attenuation of 490 nanometre (nm) irradiance downwelling per metre (Kd_{490} m^{-1}) was chosen insofar as it evaluates suspended particles that absorb and/or scatter light like phytoplankton and dissolved photoactive biochemicals such as phenols, as well as merely absorbative dissolved organic matter (DOM; Elahi et al. 2022). Corals gain nutrition from DOM and the building blocks of proteins called amino acids (Houlbrèque &

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Ferrier-Pagès 2009), whilst numerous useful and toxic dissolved substances form complexes with organics (Holmes-Farley 2002; Louis et al. 2009). Stony corals will capture and consume detritus, but do not let it amass.

The selection of candidate covariates ultimately determines whether a study establishes causality. Remote computation-based statistical and prediction analyses are limited insofar as they can only consider measurements that have been accrued in databases, and the precision and accuracy of each outcome relies upon a sufficiently large number of samples. Each of these kinds of studies select different covariates in the hope of unearthing a subset of conclusive critical determinants.

Tenured scientists often underestimate or discount the experience of longstanding successful aquarists, yet we are uniquely positioned to advise on the conditions that are key to coral health, because the effects of ionic depletion or enrichment and injurious substances are exaggerated ex situ, or if you prefer, in recirculating life support systems. Suitably-experienced and -qualified aquarists are also required to ensure experiments in aquaria are conducted in analogous conditions to the wild, and that the experimental design has not overlooked confounding biochemical processes. Otherwise, objectivity and worthwhile findings will remain out of reach. Hence the outcomes of numerous ex situ enquiries may only be significant in comparison to the study's experimental controls. This is unlikely to change unless the organisations that award research grants demand the team includes a consulting aquarist. Who wishes to donate hundreds of thousands to studies whose findings cannot withstand the scrutiny of laypersons.

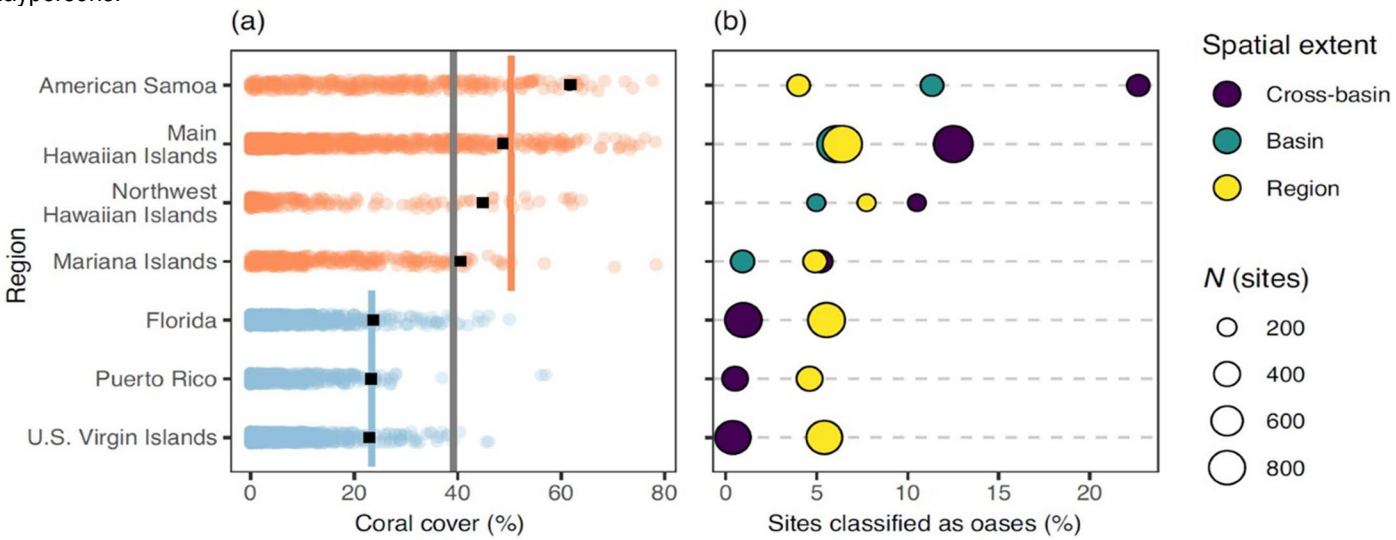


Fig. 1. Sites classified as oases according to the extent of their coral cover that far exceeded the local average from 2012 to 2017. Comparisons were calculated and expressed over four spatial extents: **cross-basin**, consisting of 3766 sites in the Pacific and western Atlantic; **basin**, comprising 1994 sites in the western Atlantic or 1772 sites in the Pacific; **region**, within each basin, and **subregion**, where blue specifies the western Atlantic while orange refers to the Pacific. (a) plots of percent coral cover where the grey line represents the cross-basin oasis threshold of 2 standard deviations above the mean, whereas the coloured lines represent the collective regional threshold, and black squares specify those of each subregion. Of note, is the comparatively low oasis threshold of the western Atlantic compared to that of the Pacific. (b) a pheatmap summarising the raw data of (a) plotting the percentage of sites classified as oases for each spatial extent. Courtesy of Elahi et al. 2022 and The Creative Commons Attribution-NonCommercial-NoDerivs License.

From this aquarist's perspective, the kinds of things that are likely to determine the occurrence of oases are temperature, solar radiation, the bioavailability of nutrients, trace elements, oxygen, and carbon dioxide as well as localised biota. Infrequent upwellings drag cooler nutrient- and ion-rich oxygen-diminished CO_2-fortified water from the seafloor (Fdez-Riverola & Corchado 2004) which provides corals with an ephemeral pulse of valuable dissolved solutes (Delbeek & Sprung 1994).

Diminished dissolved oxygen (DO) or hypoxia is exceptionally injurious in recirculating reefs, especially so, during the hours of darkness. Symptoms range from the overnight loss of fish to a total collapse of life support and expiration of livestock. As reef aquarists we are forced to use inherently hazardous natural ways of cycling nitrogen. Like wild reefs, a recirculating system's function or dysfunction is determined by the interactions of numerous interdependent processes in an often-precarious steady state known as dynamic equilibrium, but on a much smaller scale. Limitless oceanic dilution means that change is not only protracted, but its effects are negligeable or comparatively mild, whereas variation in a closed system can be brutal and profound. Modifying one parameter thus impacts numerous others.

Merely 18 of the 2500000 litres of an olympic-sized swimming pool filled with synthetic seawater can carry DO, whereas 5000 litres can be taken up by CO_2, which represents an optimal dissolution ratio of 1:282 (Aslett 2024). *Importantly*, the maximum amount of oxygen that seawater can carry is extremely low. *Safe* and *complete* denitrification occurs in microoxic environments where DO is momentarily available and is quickly used (Geomans, personal communication; Wilson, personal communication). As reef aquarists we try to nurture masses of this kind of activity in rock and sump bricks. However, even mild diminishment of waterborne DO can lead to safe denitrification transforming into anaerobic digestion (Nielsen et al. 2010) that evolves the lethal byproduct hydrogen sulphide gas (H_2S), which like hydrogen cyanide (HCN; Domingo et al. 2011), is deadly to all oxygen-respiring life, because it poisons mitochondrial cytochrome oxidase which prevents the cell from using oxygen (Jahn & Theede 1997; Soto et al. 2012; Jiang et al. 2016; Sharma et al. 2017; Appendix). These kinds of processes also occur in coral skeletons (Ricci et al. 2019) which are just as prone to descending into injurious anoxia. Preventing such environments from surfacing and releasing deadly toxins (Nielsen et al. 2010) or remaining as bearable denitrification within coral heads, relies upon a continual supply of high velocity water carrying optimal

8 milligrams per litre (mg l^{-1}) of DO (Muangkaew et al. 2002; Nielsen et al. 2010). Furthermore, vigorous water movement minimises coral boundary layers which optimises gaseous- and ionic-exchange (Riddle 2016). Sulphide-detoxifying symbionts are likely necessary for sponge survival (Lavy et al. 2018; NCBI 2019) the inefficiency of which likely contributes to their captive demise.

Redressing DO deficiencies can be a simple as uncovering the display, upregulating "in-tank" turbulence, introducing streams of cm-sized air bubbles in the rear corners, or avoiding the downregulating nighttime cycles of wavemakers. Provide rockwork grottos for oval-bodied fish and do not disturb sump bricks or deep substrate.

Zooxanthellae reside in symbiosomes within the symbiocytes of the mesoglea-associated coral endoderm (Putnam et al. 2017), where abrupt cessation of illumination and photosynthesis accompanies a profound depletion of cellular DO and plummeting pH (Kuhl et al. 1995; Laurent et al. 2013; Appendix). Coral skeletons are inhabited by anaerobic endolithic green sulphur bacteria (Bryantseva et al. 2019; Yang et al. 2019) descended from lineages of prolific H_2S synthesisers (Takashima et al. 2000). Such findings exemplify the importance of optimal DO because its diminishment is associated with rapid tissue necrosis (RTN) and the fatalities of SPS colonies (Haas et al. 2014; Aslett 2024).

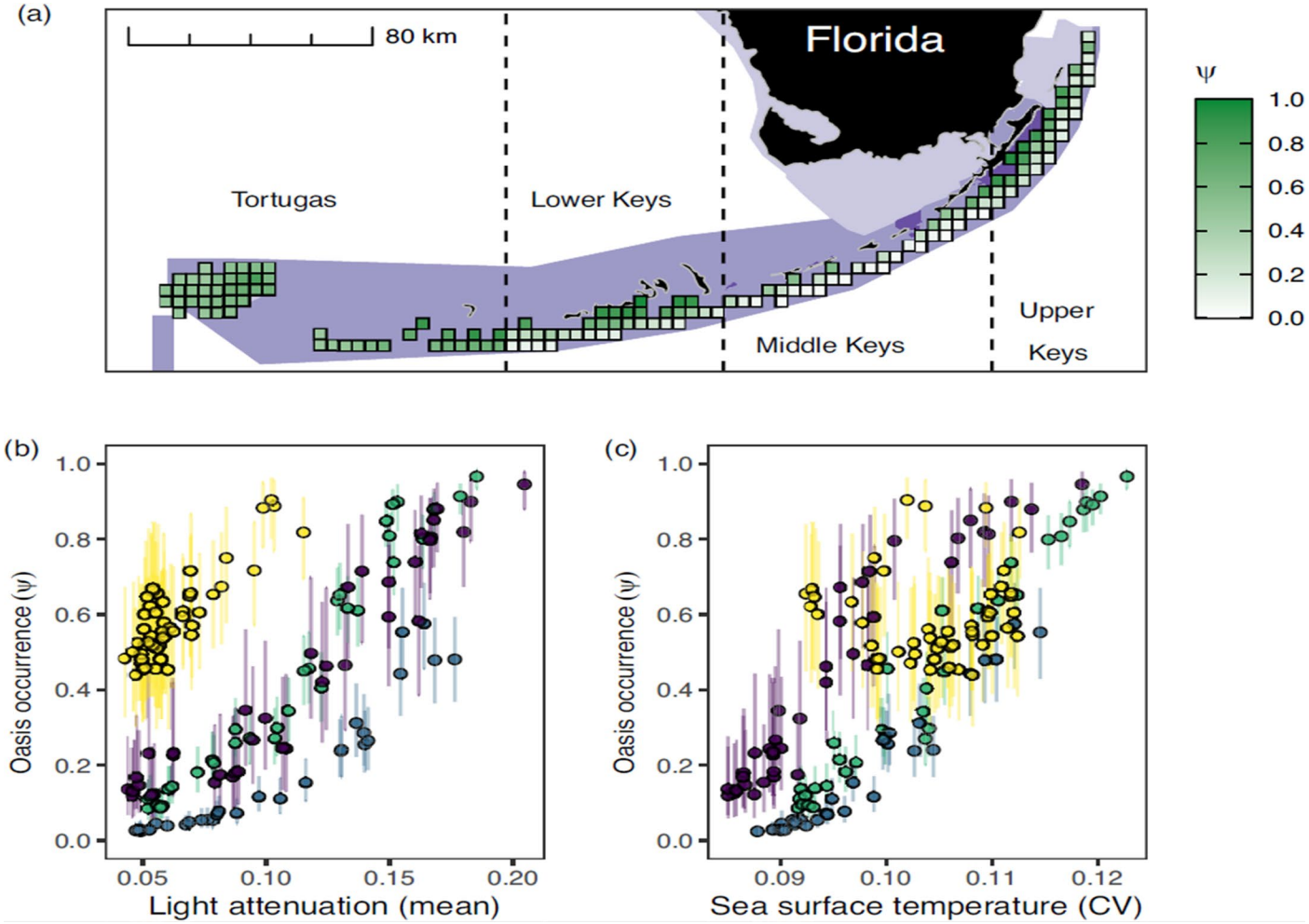


Fig. 2. (a) Elahi and collaborators' heatmap of median probability of subregional oasis occurrence (ψ) in 21.2 square kilometre (km^2) grid cells of the USA's territories: Tortugas and Florida's Lower, Middle, and Upper Keys where light-, medium-, or dark-purple shading represent the United States National Parks, the Florida Keys National Marine Sanctuary, and Florida's State Parks. (b) a graph of mean light attenuation per metre (Kd_{490} m^{-1}) versus ψ, and (c) a graph of the coefficient of variation (CV) of monthly sea surface temperature (SST) expressed in ^oC versus ψ, where cross-basin, basin, and region are specified by black, green, and yellow circles with 50 percent credible interval error bars. Analyses, heatmap, and graphs courtesy of Elahi et al. 2022 and The Creative Commons Attribution-NonCommercial-NoDerivs License.

Daytime CO_2-enriched upwellings will boost photosynthesis, calcium carbonate deposition, and promote hermatypic health. Nevertheless, by virtue of the nocturnal reversal of photosynthetic organism respiration from absorbing CO_2 and the evolution of O_2, nighttime upwellings could conceivably cause anoxic tissue and expedite the production of endolithic H_2S leading to colony demise. Such seafloor contributions are typically associated with storms that lower salinity and increase wave action, which assist aeration and likely nullify the effects of nocturnal enriched CO_2. Similarly, non-linear large amplitude internal waves (LAIWs) that occur infrequently during each tidal cycle in numerous tropical seas, dispense pulses of chilled, deep water, which can instigate almost instantaneous respective 10^oC, 0.6, and 12 percent decrements in temperature, pH, and DO, as well as respective 12-, 5-, and 20-fold increments in nitrite (NO_2^-) and/or nitrate (NO_3^-), silicate (SiO_4^{4-}), and phosphate (PO_4^{3-}; Schmidt & Richter 2013; Sawall et al. 2020). *So much for limitless oceanic dilution conferring stability*.

Off the Similan Islands situated on an archipelago off the west coast of Thailand in the Andaman Sea, LAIWs and the southwestern monsoon act synergistically to deliver sediment-laden, chilled, pH-diminished, nutrient-rich water to westward reefs which makes them significantly hostile to reef ecology, whereas their eastward shores nurture thriving communities. Despite the abrupt and acute declines in pH delivered by LAIWs, remarkable rates of scleractinian growth and calcite bioerosion were highest

within these eastward ecosystems (Schmidt & Richter 2013), insofar as a much earlier study had linked biotic calcite dissolution to strong westward water advection around the Galapagos Islands during the El Niño Southern Oscillation (ENSO) of 1982/83 (Fig. 3.; Reaka-Kudla et al. 1996). Storm magnitude and occurrence were one of the covariates considered by Elahi and allies, yet this parameter proved non-discriminating.

The day- to night-time metabolic shifts of phototrophs cause pH drifts whose maximum is around -0.17 on pristine wild reefs (Koweek et al. 2014), and no more than -0.2 (pH 8.4 to 8.2) in well-designed and run recirculating facilities operating within acceptable constraints. Remember to calibrate the pH instrumentation before each reading with freshly prepared buffers of pH 7 then 9. Ostensibly regarded as trivial, 0.2 within this range of pH represents a change of 1,403,158,820,380,000 of acidifying protons (H^+) per litre (l^{-1}; 0.264 US gallons^{-1}; $10^{-pH} = [H^+]$; Aslett 2024; Appendix).

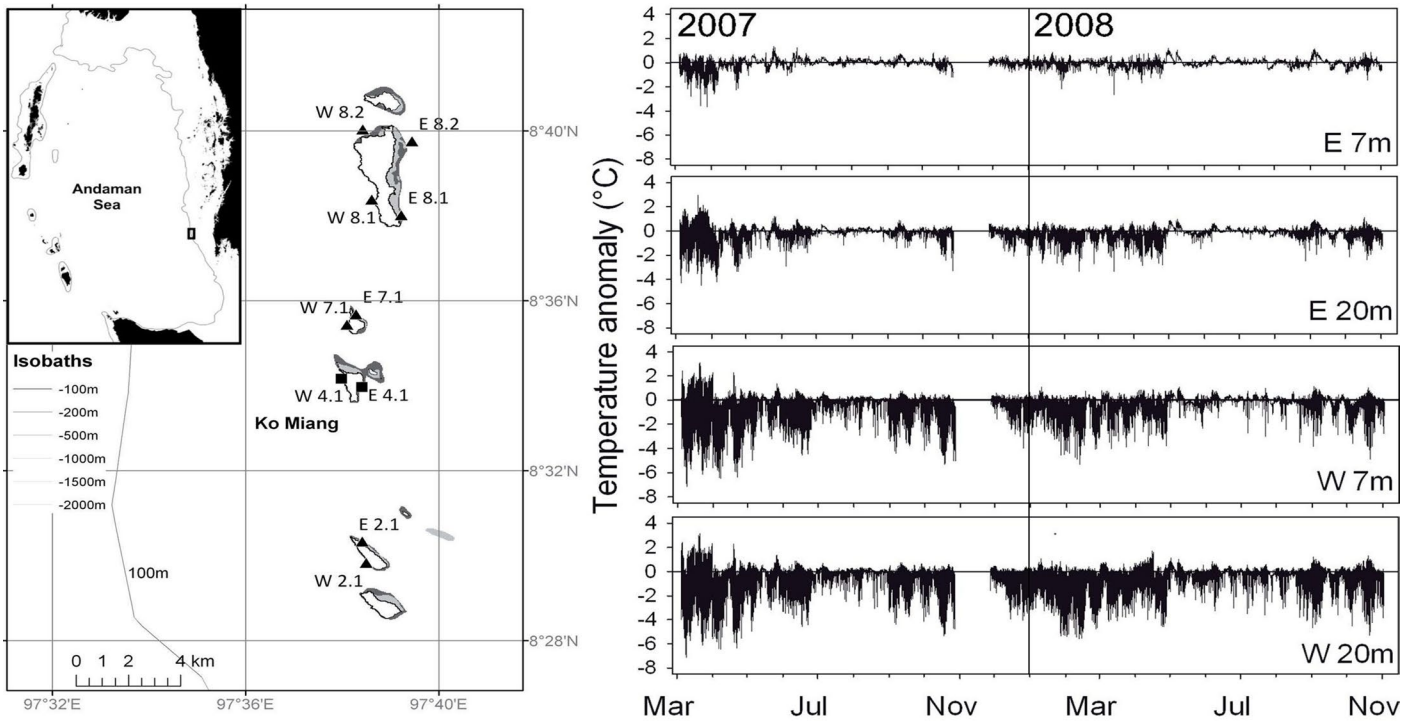


Fig. 3. Left - the geographic locations of non-linear large amplitude internal wave (LAIW) and monsoon study sites off Thailand's Similan Islands in the Andaman Sea: [▲] temperature loggers and growth rate experiments; [■] bioerosion experiments. Right - changes in sea surface temperature (SST) at 7 and 20 metres on the east [E] and west [W] coasts of Ko Miang throughout 2007 and 2008. Map inset, Buschmann, A. ©. Map and graphs courtesy of Schmidt & Richter 2013 and The Creative Commons Attribution Licence.

Numerous kinds of dissolved inorganic ions are depleted in surface waters due to phytoplanktonic sequestration. Referred to as the biological carbon pump, when waterborne phototrophs die, they descend as marine snow to accumulate on the seafloor where microorganisms biomineralize their vestiges to inorganic ions (Falkowski 2000; Zhang et al. 2018). Dissolved trace elements are also released by abyssal volcanic activity such as divergent plate tectonics (Bingman 2000), whereas convergent subduction can sequester carbon-, nitrogen-, and phosphorus-encumbered sediment into the upper mantle for thousands of years (Gattuso & Hansson 2011). Specific vitamins and minerals are used as vital cofactors or ligands in various globular proteins or as electron carriers in intracellular cascades and thus ionic depletion common to countless aquaria and surface waters, conceivably diminishes the competency of surplus irradiance-quenching protective mechanisms that ultimately forestall bleaching (Hoegh-Guldberg & Jones 1999; Frank et al. 2000; Müller-Moulé 2002; Lesser 2006; Balling et al. 2008; Reynolds et al. 2008; Smith-Keune & Dove 2008; Wallace 2014; Slavov et al. 2016). That said, supplement *judicious*ly and only after determining the prevailing concentration. The seafloor is much cooler hence upwellings provide a welcome respite from the relentless heat which now epitomise tropical summers, which helps damaged or heat-stressed corals and their "algal"-partners adjust and subsist (Takahashi et al. 2009; Palumbi et al. 2014). Furthermore, cooler water can dissolve more gases (Dickinson et al. 2002).

Researchers postulated that bleaching could be mitigated by artificial upwellings (AUs; Sawall et al. 2020; Berger, personal communication). If permanent and analogous to what often happens in nature, suboptimal DO and enriched nutrients would likely prompt an ecological meltdown. Nonetheless, during heatwaves, the DO concentration of the deep oligotrophic water from 50 to 60 metres surrounding the pseudo-atoll platform of Bermuda, increases with depth in proportion to decrements in temperature. Yet DO progressively diminishes as sensors descend, where water from the seafloor is very different. All the same, scientists understand that the physicochemical properties of the cooling water must be quasi-equivalent to that of the euphotic zone (Sawall et al. 2020). Corals remain vulnerable to acute chill, particularly when illuminated with intense irradiance, which also induces bleaching and mortality; they respond in a similar manner to those subjected to warmwater anomalies (Saxby et al. 2003; Lirman et al. 2011).

Experiments were conducted ex situ but in flowthrough systems, while depth-harvested water from 50 and 100 metres was stored in the dark without circulation at 4°C to minimise biological activity. Corals were exposed to simulated 20 or 24°C upwellings for merely 25 minutes per day, followed by seven to nine minutes of additional temperature consolidation, which brought about 3.5 to 5°C decrements that took one and a half to two hours to return to each group's predesignated temperature. Meaningful palliation of 31°C thermal stress measured by the evolution of photosynthetic oxygen as well as the concentration of tissue-bound chlorophyll

a and zooxanthellar density, became evident in *Montastrea cavernosa* and *Porites astreoides* compared to *Pseudodiploria strigosa*. De Bakker and allies had recognised that *P. strigosa* were resilient to many of the rigours of climate change in 2016, which was corroborated by the current study insofar as fragments of this species were mostly unaffected by heat stress or simulated AUs. Five fragments of *Porites* and merely one fragment of *Montastrea* and *Pseudodiploria* died during the 20-day experiments (Sawall et al. 2020) which is noteworthy because it is inferred that species of *Porites* devote significant resources to background immunity which includes thermal protection. However, coral resources are finite and thus their depletion can lead to moribundity and death (Palmer 2018; Sawall et al. 2020). Heat treatment alone caused more mortality, where all deceased corals exhibited a loss of colouration before they succumbed (Sawall et al. 2020).

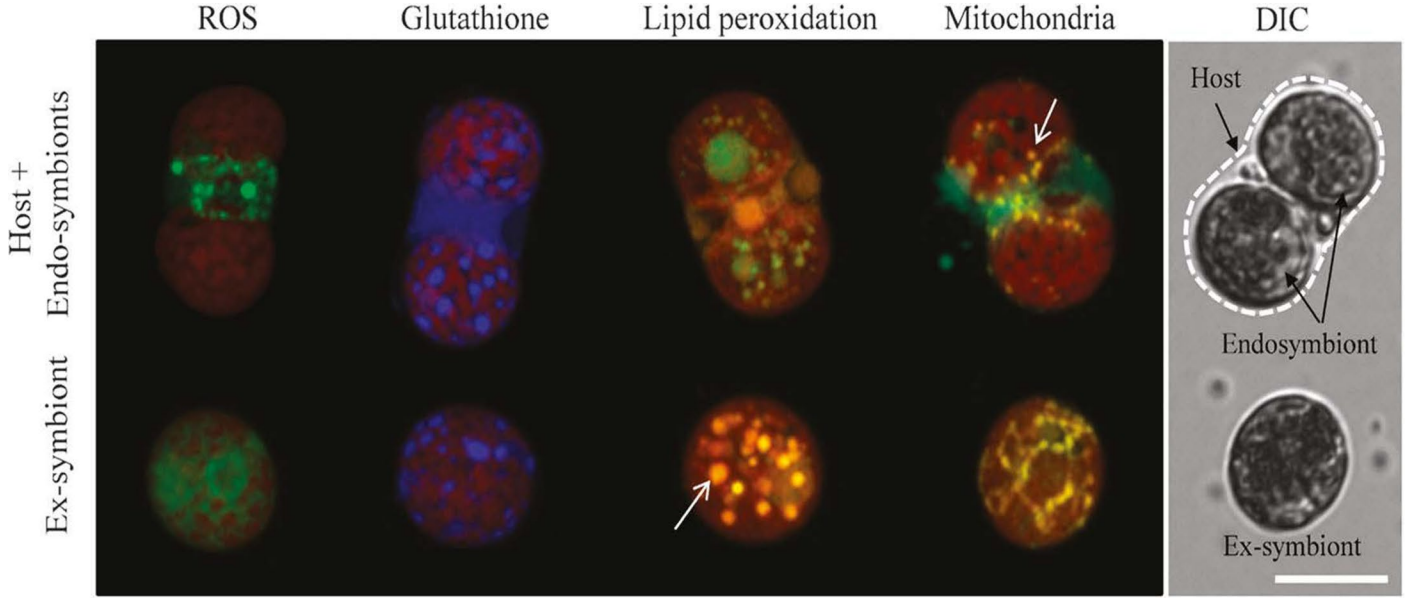


Fig. 4. Laser scanning confocal micrographs of the control group's fluorescent stained symbiocyte-resident pairs of zooxanthellae (top) and autonomous ex-symbionts (bottom), where the auto-fluorescence of chlorophyll appears red. Right - differential interference contrast (DIC) micrographs of host symbiosomes within a symbiocyte as specified by the white dotted line comprising a pair of coccoid zooxanthellae with an ex-symbiont (bottom) and a 10-micrometre (micron; μm) scale bar. [ROS] CM-H2DCFDA fluoresces green; [Glutathione] mBBr appears blue in its reduced form; [Lipid peroxidation] Image-iT is evident as a ratio of yellow to green; [Mitochondria] Rhodamin123 highlights mitochondrial activity yellow, and [DIC] Calcein AM colours esterase activity teal. White arrows indicate a mitochondrion (top) and a lipid body (bottom). Courtesy of Nielsen et al. 2018 and The Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License http://creativecommons.org/licenses/by-nc-nd/4.0/

Traces of H_2S which have significant impacts, were likely generated beneath the upper 2 inches of the 25-litre deep water storage vessels. Reducing the temperature of natural seawater by 16 to 20°C over several hours will have a sterilising effect as it will instigate dormancy or akin to the pre-hypoxic crash of eutrophication, kill much microbiota. However, bacteria acclimate rapidly, and daytime zooplankton are copiously abundant at mesophotic depth which would not survive, whilst unwholesome water with the remnants of deceased life was stored for up to 20 days. Continuously warm and aerated fresh- and salt-water reservoirs for recirculating systems must be routinely decommissioned, cleansed, and reinstated, otherwise livestock begin to suffer. Remarkably, the Bermudan euphotic zone extends beyond 100 metres and thus zooplankton will be scarce during daylight, whilst this depth's concentration of chlorophyll *a* is indicative of abundant phytoplankton from which Scleractinia derive *little* nourishment (Osinga et al. 2012). The ex situ facilities were fed with local reef water from a depth of 2 metres which would mitigate the deleterious impacts that might otherwise be felt in recirculating systems (Sawall et al. 2020).

The author found it refreshing for researchers to acknowledge the harmful effects of diminished DO and their nocturnal exacerbation (Murphy & Richmond 2016; Sawall et al. 2020), yet this parameter does not appear to have been monitored in the test groups or stored water, whereas pH was continuously estimated with instrumentation that was only calibrated every seven days (Sawall et al. 2020; Appendix). However, compared with hobbyist grade monitors and probes, authentic analytical Orion Star apparatuses manufactured by Thermo Fisher Scientific costing upwards of 1500USD will be less prone to a drift in virtual scale, but they will not eliminate inaccuracies. Be that as it may, the experimental design also accommodated the scrutiny of salinity, total alkalinity, and dissolved inorganic carbon (DIC).

Implementing infrequent in situ AUs would be at best challenging because when not in use, water in conduits must freely mix with that in the water column to forestall the production of H_2S. Exposing corals to copious amounts of water poisoned in this way would be tantamount to squirting them with sodium cyanide which bleaches and instigates mortality. This brutal and thankfully outdated practice stunned fish hiding in coral heads so they could be easily caught for the ornamental trade (Jones & Steven 1997). Fortuitously, limitless oceanic dilution *usually* averts disaster, whilst the practicalities of AUs may have been successfully overcome when prototypes were used to fertilise surface waters (Pan et al. 2016; Sawall et al. 2020).

AU was originally conceived as a means by which N-, P-, and silicon (Si)-fortified deep ocean water (DOW) could be delivered to the typically ionically-depleted euphotic zone, in order to boost photosynthetic CO_2 sequestration, and thus alleviate anthropogenic carbon by virtue of the biological carbon pump. The resultant cooling could offset deoxygenation caused by hypoxic DOW because colder water can carry more gas (Dickinson et al. 2002). Nevertheless, the biological carbon pump ensures DOW is inundated with

inorganic carbon; hence AUs could augment the discharge of CO_2 into the atmosphere. The findings of Dutreuil and collaborators' study published in 2009 suggested that AUs would increase CO_2's oceanic efflux and continuously supress DO. Furthermore, an increase of deceased phototrophs necessitates more aerobic biomineralization which will likely exacerbate deoxygenation and CO_2-laden seawater is acidic (Pan et al. 2016), which negatively impacts the calcite deposition of marine organisms (Ries et al. 2009; Reymond et al. 2013). Given that pH is suppressed by carbonic acid and dissolved H_2S and its ionic derivatives like bisulphide (HS^-; Aslett 2024), elevated nutrients increase planktonic nourishment for calcite-boring sponges and carbonate-eroding algae (Schmidt & Richter 2013), and it remains vital that reefs lie within a critical distance from the surface: accelerated calcite dissolution can cause them to drown (Perry et al. 2014; Molina-Hernández et al. 2020; Alvarez-Filip et al. 2022).

Numerous AU devices have been designed and some "successfully" implemented in the wild (Pan et al. 2016). However, in conventional engineering style, most were reliant upon extensively long tubes that descended 300 metres or more. Such water is already hypoxic, and as such, confining it in tubes that forestall oxygenation guarantees that any oxygen is quickly utilised by aerobes and thus the water becomes anoxic and exceedingly injurious. Trade windward (eastward) reefs tend to be highly productive thriving ecosystems (Schmidt & Richter 2013). However, wind-driven westward water advection can result in upwellings inundating leeward reefs with low pH, nutrient-rich, bioerosion-expediting water, which in combination with the accrual of sediment, leads to a shortage of robust reef frameworks (Riegl 2003).

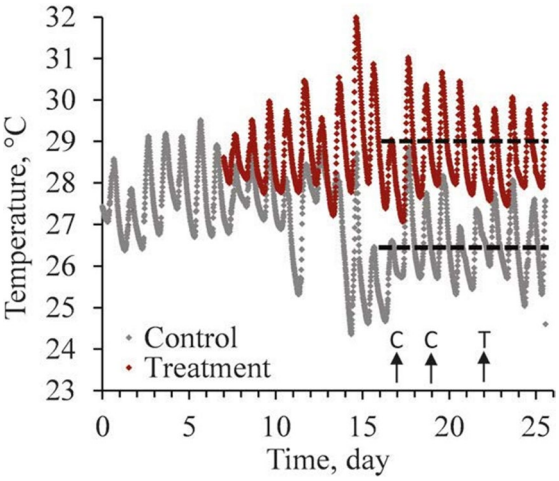


Fig. 5. Temperature throughout Nielsen and allies' thermal stress experiments where grey and red lines specify that of the control and heat treatments, which commenced on day seven. Arrows indicate the days of control analyses on days 17 and 19 which lasted three days, whereas the micrographs of heated fragments of *Pocillopora damicornis* were prepared on day 22 (Fig. 4.). Courtesy of Nielsen et al. 2018 and The Creative Commons Attribution-NonCommercial-NoDerivatives International License.

The perpetual salt fountain concept, utilised differences in the salinity and temperature of euphotic versus DOW. It required only a long pipe and a float that maintained its uprightness and buoyancy between the surface and the intermediate halocline. After the initial filling of the pipe with DOW, the process occurs naturally without a requirement for additional power (Tsubaki et al. 2007). However, as DOW rises, it equilibrates to the temperature of the surrounding water which nullifies cooling, whereas the device's slow effluent proved insufficiently nutrifying. High density DOW has a propensity to sink after discharge (Ouchi et al. 2005; Pan et al. 2016). Liang and Peng proposed an AU apparatus in 2005 that used a pump to deliver compressed air into the bottom of a long, deep pipe, which lowered the density of the mixture below that of the surrounding water, so water was drawn upwards. Model trials were redolent of significant efficiency where the volume of rising water was 100 times that of the injected air (Pan et al. 2016).

Ocean thermal energy conversion (OTEC) generates nominal electricity by exploiting disparities in temperature between sunlight-energised surface waters and the deep (Pan et al. 2016). A team at The University of Zhejiang developed a self-powered AU device based on the injection of pressurised gas into an airlift whose compression exploited renewable energy. The efficiency of upwelling increased in proportion to pipe diameter, where flow approached 40 times that of the propelled air. Its power supply was commissioned with a photoelectric array, wind turbines, a multiple-axis wave energy converter (WEC), and a conventional diesel generator (Zhang et al. 2013). Its unreliance on external energy meant it could be installed in remote regions (Fan et al. 2013). Furthermore, several kinds of diesel generator will run on vegetable or rapeseed oil, especially so in warmer climes, which would go some way to making the entire project carbon neutral. Continual air injection would also oxygenate DOW and thus lessen the risk of surfacing significant amounts of H_2S.

Field trials at Qiandao Lake and in the eastern China Sea demonstrated that 300 square metres (m^3) of water from 30 metres depth could be mixed with ~1200 m^3 of surface water each hour, whilst a nutrient-rich plume was evident at 18 metres (Fan et al. 2013; Pan et al. 2016).

Most exceedingly-productive tropical marine ecosystems require comparatively ultra-pure water, where nearshore fringing reefs or flats are invariably polluted by dense human settlements and nearby pastoral or arable farming and their land runoff and sewage discharge (Frias-Lopez et al. 2002; Aslett 2024), whereas enriched nutrients exacerbate bleaching and coral disease (Voss & Richardson 2006; Cunning & Baker 2013; Ho 2013; Vega Thurber et al. 2014). Traces of eutrophicants such as dissolved inorganic nitrogen (DIN; ammonia/ammonium; $NH_{3(gas)}/NH_4^+$; NO_2^-; NO_3^-) and phosphorus (DIP; ≡phosphate; PO_4^{3-}) are vital for "algal" symbionts and their host's wellbeing, yet their enrichment often proves deleterious. DIP in most pristine ecosystems ranges from 0.0032 to 0.0305 mg l^{-1} (0.0096 to 0.092 mg l^{-1} PO_4^{3-}); however, concentrations in polluted lagoons may attain 0.128 to 0.192 mg l^{-1} (0.38 to 0.58 ppm PO_4^{3-}; Ferrier-Pagès et al. 2016). In the late 20th century, NO_3^- and PO_4^{3-} were 0.0372 and 0.019 mg l^{-1} on 90 percent of assayed reefs (Kleypas et al. 1999) which is nutrient limited. Nevertheless, corals have evolved in oligotrophic waters nutrified by infrequent spikes from phenomena like upwellings, ammonium emanating from shoals of fish, or nocturnal heterotrophic feeding (Delbeek & Sprung 1994; Meyer & Schultz 1985; Ezzat et al. 2015).

The anabolic transformations observed throughout Ezzat and allies' co-nutrient experiments that exposed SPS nubbins to varying ratios of NH_4^+/NO_3^- and PO_4^{3-}, implied coral-"algal" symbiosis is largely constrained by nutrient-limitation in pristine oligotrophic environments (Ezzat et al. 2015). Enriched nitrate and limited phosphate lessen the inorganic carbon fixation of zooxanthellae and debilitate its translocation (Wiedenmann et al. 2013) in *Stylophora pistillata*. Intriguingly, moderate enrichment of

ammonium causes a doubling of zooxanthellae and enhances skeletal accretion as well as carbon fixation and its transference. Ammonium appears to be the preferred source of dinoflagellate nitrogen and thus its derivation from nitrate necessitates reduction, whose final step exploits nitrite reductase as well as reduced ferredoxin and six electrons from the photosynthetic transport chain. Hence photosynthesis becomes significantly less efficient in the presence of oligotrophic phosphate and elevated nitrate. Modest co-enrichment of ammonium and phosphate led to an upsurge of zooxanthellae, which like raised nitrate, caused a profound reduction in the translocation of photosynthetic in- and -organic carbon. Besides, photosynthesis per alga decreased thanks to self-shading (Ezzat et al. 2015). Coral culture within recirculating systems is thus expedited by ammonia-liberating ammoniotelic residents such as bony fish (teleosts; Aslett 2024).

Realistic domestic targets include nitrate concentrations of less than 1 and phosphate of no less than 0.065 mg l^{-1} (Aslett 2024), because limited phosphate or dissolved inorganic iron (DIFe) in the presence of significant DIN, lessen the thermal tolerance of SPS hermatypes and their "algal" partners which leads to pastel colouration and their demise (Wiedenmann et al. 2013; Angelo & Wiedenmann 2014; Ezzat et al. 2015). Teleostean diets comprise much iron (Bjørnevik & Maage 1993) because their requirements are challenging to appease, yet DIFe rapidly depletes in recirculating reefs which may require *frugal* administrations every third day. For essential guidance consult open-access Aslett 2024b.

Elevated DIN causes the over proliferation of SPS corals' zooxanthellae which become so dense that they shade one another (Byun et al. 2014; Ezzat et al. 2015; Gardner et al. 2017), whilst the conventional acquisition of dissolved inorganic carbon (DIC) attained from waterborne carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-), becomes insufficient to satisfy skeletal accretion and photosynthesis (Dennison & Barnes 1988; Dubinsky et al. 1990; Riddle 2016). Even so, recent evidence implies most skeletal-precipitating HCO_3^- is formed from CO_2 liberated from the overzealous aerobic respiration of mitochondrial-rich calicoblastic cells that overlie the sites of deposition (Tinoco et al. 2023; Appendix). Enriched DIN decelerates the growth of SPS corals (Hylkema 2014; Ezzat et al. 2015) and causes them to turn brown (Balling et al. 2008), as it is the colour of most zooxanthellae (Yu et al. 2000; Palmer et al. 2011), whereas the chronically-affected enter a degenerative dormancy (Aslett 2024).

It may seem counterintuitive that corals with a glut of "algal" symbionts are more likely to bleach (Cunning & Baker 2013; Gardner et al. 2017), yet the progressive nature of dinoflagellate loss, may be a cross-holobiont reflection of an autonomous cellular process (Nielsen et al. 2018). Lost pigment may not necessarily be directly related to a lack of zooxanthellae, insofar as bleaching may be a consequence of indiscriminate cytosolic "bale out", where the coral exocytoses its cellular contents including its shielding and colour-conferring biochemicals (Fitt & Warner 1995; Müller-Moulé 2002; Starcevic et al. 2010; Fujise et al. 2014; Aslett 2024). Notwithstanding, a "trigger" of oxidative stress together with photosystem impairment and the accumulation of cellular machinery-damaging reactive oxygen species (ROS) was the prevailing paradigm of the day (Gardner et al. 2017). However, judging by the upregulation of antioxidant pathways in both host and zooxanthellae, and despite overwhelming evidence to the contrary (de Grey 2002; Riddle 2004; Yakovleva et al. 2004; Béraud et al. 2013; Riddle 2014; Ferrier-Pagès et al. 2016; Jin et al. 2016; Gardner et al. 2017), a related team's seminal study published in the following year discovered heat-induced upsurges of zooxanthellar ROS, *do not* appear to cause physiological insult, compromise "algal" partners, or amass in concentrations that are likely to leak. And although thermal stress coincided with a loss of zooxanthellae, mean 29°C with a noon maximum of 30 to 31°C and a nocturnal low of 27 to 28°C, elicited at the very most, an almost trivial decline in photosynthetic efficiency of just 11 percent (Fig. 5.). It is improbable therefore, in the absence of photosystem damage, that ROS would induce the expulsion of zooxanthellae in *Pocillopora damicornis*. The study identified coccoid symbionts that were not confined to symbiocytes but remained in coral tissue which were referred to as ex-symbionts. It was postulated that these cells had been ousted from the endosymbiome and were awaiting expulsion from the coral. However, they differed from symbiosome residents insofar as they contained elevated concentrations of lipids (fats; Nielsen et al. 2018). Previous studies had recognised that thermal stress leads to the enrichment of intra-zooxanthellar lipids and polyunsaturated fatty acids (PUFAs; Hillyer et al. 2016) which may therefore represent an alternative "trigger". Although groundbreaking, Nielsen and collaborators' findings could not exclude the possibility that a rise in ROS may prove a significant inducer of symbiont expulsion when accompanied by photosystem overload and impairment, which was intentionally avoided in their experimental design (Fig. 4.; Nielsen et al. 2018).

If the endosymbiome was the source of ROS like hydrogen peroxide (H_2O_2), one might expect the *in hospite* dinoflagellates to mount a more powerful antioxidant response. However, the ROS-quenching pathways of *Acropora millepora* and *Stylophora pistillata* were significantly upregulated compared to those of their symbionts (Gardner et al. 2017). If therefore, ROS originate from the tissues of heat stressed hosts, why expel zooxanthellae unless bleaching is as already suggested, indiscriminate. Such dichotomy has divided scientific communities, whilst objectivity demands we present the best evidence. Differences aside, candidate "triggers" include danger-associated molecules like those indicative of cellular rupture such as heat shock proteins, uric acid, and other reactive molecules. The signals from the holobiont's putative microbe- and danger-associated molecular pattern (MAMP and DAMP) receptors may thus facilitate the judicious allocation of available resources and the modulation of an antimicrobial, regenerative, and an intentionally transitory dysbiotic response, whilst mutualists could be reimbursed for incidental harm (Palmer 2018). Even so, a sequential loss of photosynthesis and zooxanthellae appears commensurate with thermal stress which is redolent of photosystem damage followed by expulsion of the phototrophically-impaired (Sawall et al. 2020). However, heat stressed *Acropora millepora* and *Stylophora pistillata* suffered a reduction in zooxanthellae several days before a decline in photosynthetic efficiency where a deficit of 70 percent or more appeared prerequisite. Photosystem damage does not appear to induce the breakdown of the host-zooxanthellae alliance, whereas an extensive arsenal of antioxidant cascades may compensate those with less plastic communities of "algal" partners (Gardner et al. 2017). Photosynthesis increased in heat- and 20°C AU-exposed *Porites* despite a meaningful dilution of their endosymbiome (Sawall et al. 2020).

The mortality rates of Bermudan *Porites astreoides* during simulated AUs suggests that their symbionts are the least heat- and light-tolerant, whilst *Cladocopium* appear to generate twice the photosynthetic oxygen of either heat-resilient *Durusdinium* (Sorek et al. 2013; LaJeunesse et al. 2018) or *Symbiodinium* (Sorek et al. 2013; Fig. 7.). Yet the surplus irradiance-quenching mechanisms of *Cladocopium* cease photosynthetic electron transport and convert the energy to infrared (IR; heat; Slavov et al. 2016), whereas the zooxanthellae of Australia's *Porites cylindrica* may exploit the surplus excitation-quenching xanthophyll cycle that requires violaxanthin whose dawn reserve depletes during daylight, which can only be regenerated in darkness and in the presence of the potent antioxidant, vitamin C (Hoegh-Guldberg & Jones 1999; Frank et al. 2000; Müller-Moulé 2002). Nevertheless, like coral genotypes (Veron 1995, cited in Arrigoni et al. 2016; Ramirez-Portilla et al. 2022), symbiotic communities appear geographically and regionally distinct (Clerissi et al. 2018) whilst corals seem to retain a greater or lesser competency for winnowing their "algal" partners to suit the prevailing conditions (Fautin & Buddemeier 2004; Gardner et al. 2017; Munn 2019).

Do not be tempted to supplement aquaria with vitamin C as it is ascorbic acid which may injuriously supress pH in significant concentrations, whereas most is likely synthesised by holobiont microbes (Kramarsky-Winter et al. 2006; Ainsworth et al. 2015; Munn 2019) where it is conserved by extensive recycling (Hoegh-Guldberg & Jones 1999; Frank et al. 2000; Müller-Moulé 2002). Moreover, additional sources include fish diets.

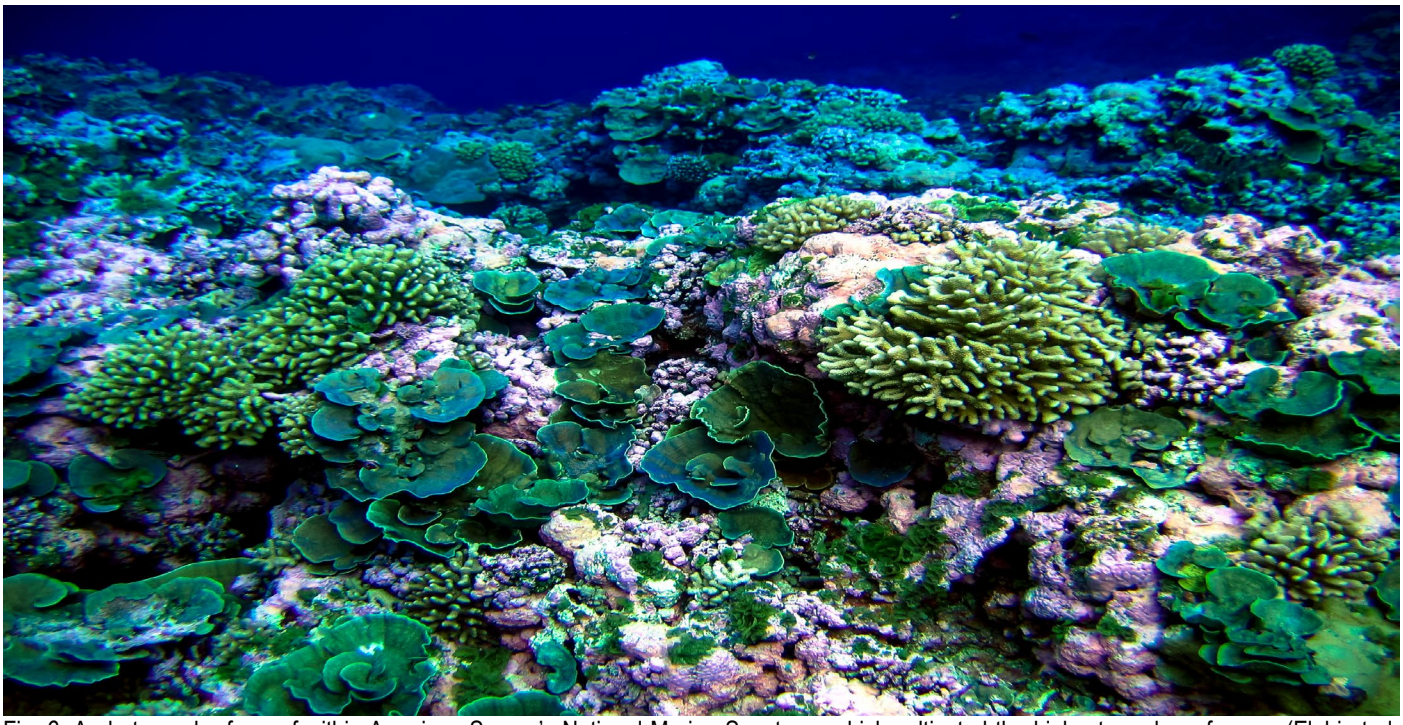


Fig. 6. A photograph of a reef within American Samoa's National Marine Sanctuary which cultivated the highest number of oases (Elahi et al. 2022) whose foreground lacks alpha diversity, insofar as merely three species of coral appear to be competing with crustose coralline algae. Yet clearly, these waters are meaningfully alkaline which supports primary productivity.

Slight fortifications of DIP expedite low-density calcite deposition in SPS hermatypes to the detriment of skeletal strength (Cruz-Piñón et al. 2003; Dunn et al. 2012; Ferrier-Pagès et al. 2016) or slow accretion and compromise aragonite's integrity (Ezzat et al. 2015). Eutrophication results in localised wildlife-decimating ecological hypoxia, while significant nutrient enrichment fuels upsurges of skeleton-invading micro- and macro-algae. Neighbouring algae can inhibit the settlement of coral planulae (Bulleri et al. 2018; Schmitt et al. 2019; Berger, personal communication) and destabilise the mucosal microbiome with allelopathic biochemicals that instigate colony demise (Smith et al. 2006; Birrell et al. 2008). Oases may be in situ analogues of exceptionally rare, anomalous, and currently inexplicable reef aquaria that somehow house healthy zooxanthellate Scleractinia in the face of ~0.1 PO_4^{3-} and >5 mg l^{-1} NO_3^-. There are so many inconsistencies in recirculating systems that it is impossible to make objective comparisons unless replicate aquaria are setup, stocked, and run in indistinguishable ways. However, regular *parsimonious* dosing of *costly* phytoplankton could partly clarify these occurrences. Nevertheless, ex situ algal blooms cannot be sustained unless phosphate concentrations attain a likely lethal 1 mg l^{-1} PO_4^{3-} (Aslett 2024). Elahi and colleagues considered land proximity and human population density as one of their oasis predictors (Elahi et al. 2022).

Subregions exposed to routine upwellings tend to support buoyant populations of phytoplankton which in turn boost zooplanktonic communities as they ascend to dine on these primary producers at night (Houlbrèque & Ferrier-Pagès 2009; Craig et al. 2011; Ferrier-Pagès et al. 2016). Euphotic-dwelling hermatypes, albeit unlikely to capture and consume vast amounts of phytoplankton (Osinga et al. 2012), supplement their nutritional requirements with particulate organic matter (POM) and zooplankton (Petersen et al. 2008; Houlbrèque & Ferrier-Pagès 2009; Osinga et al. 2011; Barton et al. 2015) together with nanoplankton consisting of mainly bacteria and minuscule diatoms (Ferrier-Pagès et al. 2016; Leblanc et al. 2018). Furthermore, such heterotrophic feeding assists recuperation from transient and inconspicuous remedial microbial purging known as dysbiosis (Egan & Gardiner 2016; Bass et al. 2019; Boilard et al. 2020), of which perceptible bleaching represents an acute instance (Boilard et al. 2020). Whereafter, the capture and consumption of prey become the only hope for aposymbiotic "algal" partner-lacking reef-forming corals (Aslett 2024). Moreover, ubiquitous toxic chemical-coated microplastics (Lamb et al. 2018) are ingested at analogous rates, which

are not purged from the gastrodermis, so polyps with congested cavities cannot feed (Hall et al. 2015). The analyses of Elahi and colleagues included the attenuation of 490 nm which in most cases will likely relate to the concentration of chlorophyll and phytoplanktonic abundance which was positively correlated to the presence of oases (Elahi et al. 2022). Conceding that most hermatypes are stressed and bleached by anomalous temperature and irradiance (Fitt & Warner 1995; Müller-Moulé 2002; Saxby et al. 2003; Starcevic et al. 2010; Lirman et al. 2011; Fujise et al. 2014; Aslett 2024), phytoplanktonic light absorption and phenolic scattering might explain why corals in oases are uncommonly well, whereas clouds can temper solar irradiance (Gardner et al. 2017) by as much as 50 percent (Crisp 1997) which accumulate around the peaks of shore-adjacent mountains. Similarly, sunlight is diminished by Hawai'i's volcanic smoke (Riddle, personal communication, cited in Neptune Systems 2019). Be that as it may, nearshore turbidity can trigger an ostensible Stokes shift from deep-penetrating 400 to 500 nm blue/green to longer wavelength 500 to 550 nm green (Austin & Petzold 1986; Aslett 2024) which features in the auxiliary carotenoid absorption spectrum and stimulates chlorophyll *a* (Kuhl et al. 1995; Roth 2014). It is possible to remotely sense Kd_{490}, yet thanks to this spectral anomaly, inshore appraisals are best measured with underwater sensors (Elahi et al. 2022). Elevated waterborne concentrations of this chlorophyll have been implicated in increased coral cover (Williams et al. 2015; Robinson et al. 2018) while most oases occur offshore or they are associated with sparsely-populated landmasses. Novel test and evolve approaches are being carried out on The Great Barrier Reef (GBR) such as localised fogging, misting, and cloud brightening (Shumway et al. 2024).

Fig. 7. *Porites astreoides* susceptible to black band disease which may be suffering from yellow band or white syndrome (Aslett 2024).

The scleractinian mucosal microbiome is the colony's first line of defence, which often, but not always (Gong et al. 2023), consists of a subpopulation of environmental microbes (Brown et al. 2023). The instability of localised microbiota has the potential to impact coral holobionts which can leave them vulnerable to bleaching and disease (Palmer et al. 2018; Voolstra & Ziegler 2020). For instance, disproportionate upsurges of DIFe instigate variable outcomes such as the proliferation of "good" as well as harmful bacteria (Holmes-Farley 2002; Wilson, personal communication; Keuter 2017), whilst local shipwrecks and iron chains were held responsible for the frenetic proliferation of endemic discosomid Corallimorpharia, *Rhodactis howesii* that smother and overgrow the reef surrounding Palmyra Atoll in the central Pacific's Line Islands (Work et al. 2018). Even so, atolls tend to be surrounded by exceedingly-decontaminating oligotrophic deep ocean and are purified by cross-channel flushing (Kraines et al. 1999), whilst the mucosal communities of ostensibly healthy hermatypes retain an inertia (Santoro et al. 2021). Soft coral- or algal-derived allelopathic biochemicals are known to perturb these microbes (Smith et al. 2006; Birrell et al. 2008). Upwellings also surface the dormant cysts of numerous harmful algal blooms (HABs) alongside germination-stimulating and population-exploding nutrients (Fdez-Riverola & Corchado 2004), which also indulge in this kind of biochemical warfare (Hallegraeff 1993; Burkholder 1998; Imai et al. 2006; Martnez et al. 2010; Shi et al. 2012; Wang et al. 2018; Hargreaves et al. 2019; Tibiriçá et al. 2019). They limit light penetration but interfere with sea-surface gaseous-exchange. Extensive blooms of multicellular diazotrophic dinoflagellates of the genus *Trichodesmium* fix dissolved and atmospheric dinitrogen (N_2) into organic molecules during which they generate the intermediate ammonium (NH_4^+) which leaks environmentally (Bergman et al. 2012; Sandh & Bergman 2012). Localised CO_2 retention and seawater acidification exacerbated by diminished DO together with enriched ammonium, are likely far from advantageous for reef-forming corals. Similarly, toxins liberated by highly motile unicellular dinoflagellates of the genus *Ostreopsis* have instigated mass extinctions of algae in the Italian Mediterranean (Ramos & Vasconcelos 2010).

Lustre-lacking duller saltwater has a lower oxidation reduction potential (ORP; Wilson, personal communication) and thus more reductants, less DO, and a suppressed pH. Be that as it may, water clarity is also impacted by gas supersaturation when ORPs remain buoyant (Aslett 2024), which causes gas bubble disease (GBD) in susceptible teleosts and invertebrates (Groham 1899; Edsall & Smith 1991; Geist et al. 2013; Aslett 2024).

The presence or absence and the extent of nutrient-rich upwellings are thus likely predictors that should be considered when trying to elucidate the origin of oases. For comprehensive clarification consult: The Complete Reef Aquarist—A Conservation Manual (https://ebay.us/m/ALPZd6).

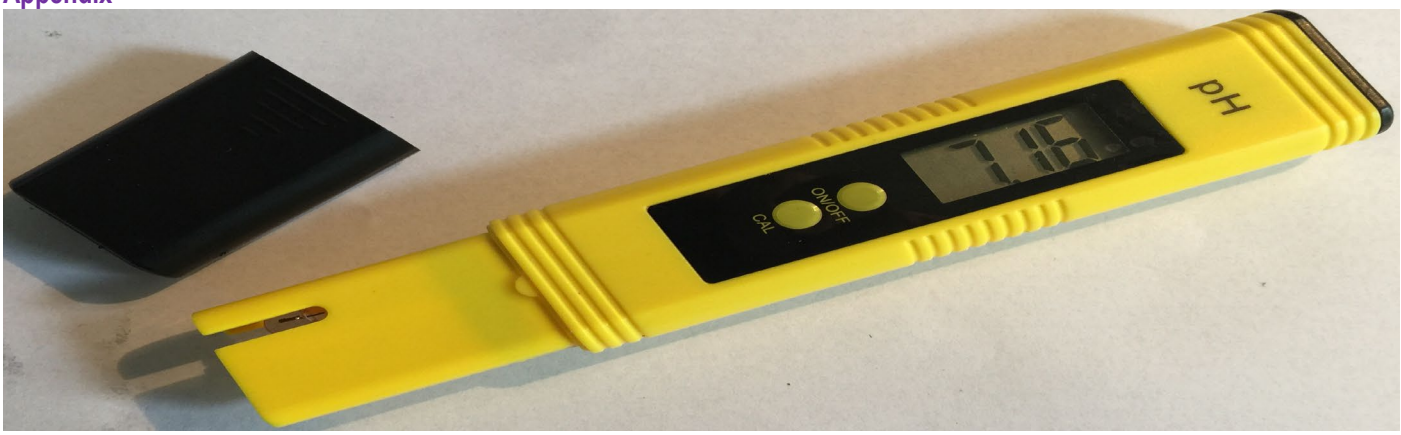
Reef interconnectivity appears a critical determinant insofar as the strong currents on GBR's southeastern rim of the continental shelf likely contribute to this region's densely-adorned diverse communities. It is easier for corals on these reefs to interbreed and share their progeny which elevates genetic heterogeneity (Figueiredo et al. 2022). Divergent populations retain a significant competency for surviving and adapting to a- and -biotic disturbances (Aitken & Whitlock 2013). Nevertheless, the findings of prediction analyses infer that global warming will diminish reef interconnectivity by as much as several kilometres (Figueiredo et al. 2022).

The topography of the underlying bedrock may prove a significantly contributing factor as features such as valleys and grooves may shelter reefs from many of the purging hydrodynamic forces common to tidal ebb and flow, whilst undulations can intensify localised turbulence which enhances nitrogen cycling by expediting advection into substratum (Delbeek & Sprung 2005; Janssen et al. 2005). Equally, numerous stony corals are vulnerable to the accumulation of sediment (Pastorok & Bilyard 1985; Ferguson et al. 2013; Work et al. 2018) which predominates on wave action-diminished backreef slopes and leeward reefs (Aslett 2024). Wave energy featured in Elahi and collaborators' prediction analyses; however, depth and seascape were excluded insofar as they vary significantly over 21.2 km^2 (Fig. 2. a). Wave action was negatively correlated with oases when considering both the Pacific and Atlantic basins, but this trend was positive at the subregional scale (Elahi et al. 2022). Genetic heterogeneity is likely rife amongst communities in subregions offering a variety of habitats (Aitken & Whitlock 2013). Quigley and van Oppen developed a prediction framework that identified 251 candidate locations from 3255 reefs that likely harboured corals that had adapted to anomalous warming on GBR (Quigley & van Oppen 2022).

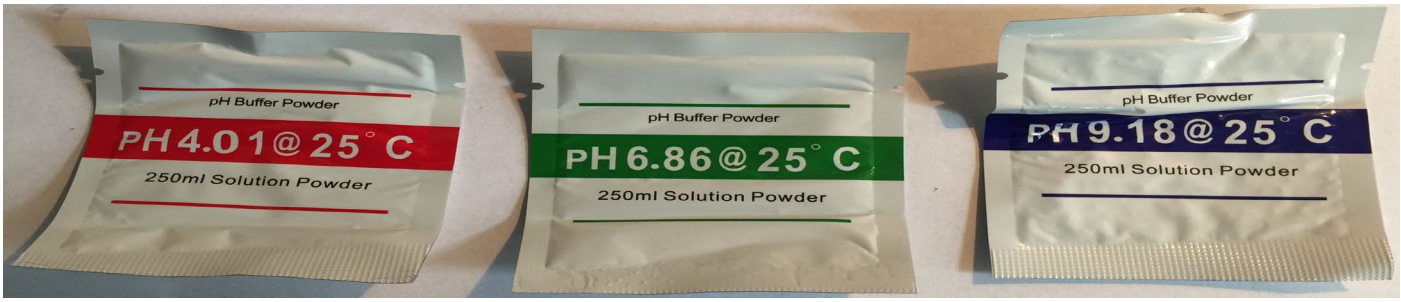
Oases and the optimism of intensive management and international reef restoration projects provide hope that the reefs will adapt and subsist in the face of an everchanging environment. Nevertheless, the Intergovernmental Panel on Climate Change (IPCC) predicts 90 percent of reefs will not survive another 1.5^{o}C of mean global warming, whereas utter extinction is likely at 2^{o}C (Shumway et al. 2024; Kler Lago et al. 2025). All the same, hermatypes and numerous other forms of life were no doubt decimated but survived a reversal of the global ocean conveyor (GOC) in the Palaeocene/Eocene some fifty-five million years ago which coincided with a 7 to 8^{o}C rise in global temperature instigated by a catastrophic elevation of greenhouse gases (Nunes & Norris 2006). For clarification see open-access Aslett 2024a.

It remains vital we continue to make small but consistent changes to our day-today activities in the hope that it will go some way to alleviating the current threats to global reef ecology (Shumway et al. 2024). For instance, mend and reuse and buy paper-packaged and glass-bottled local produce.

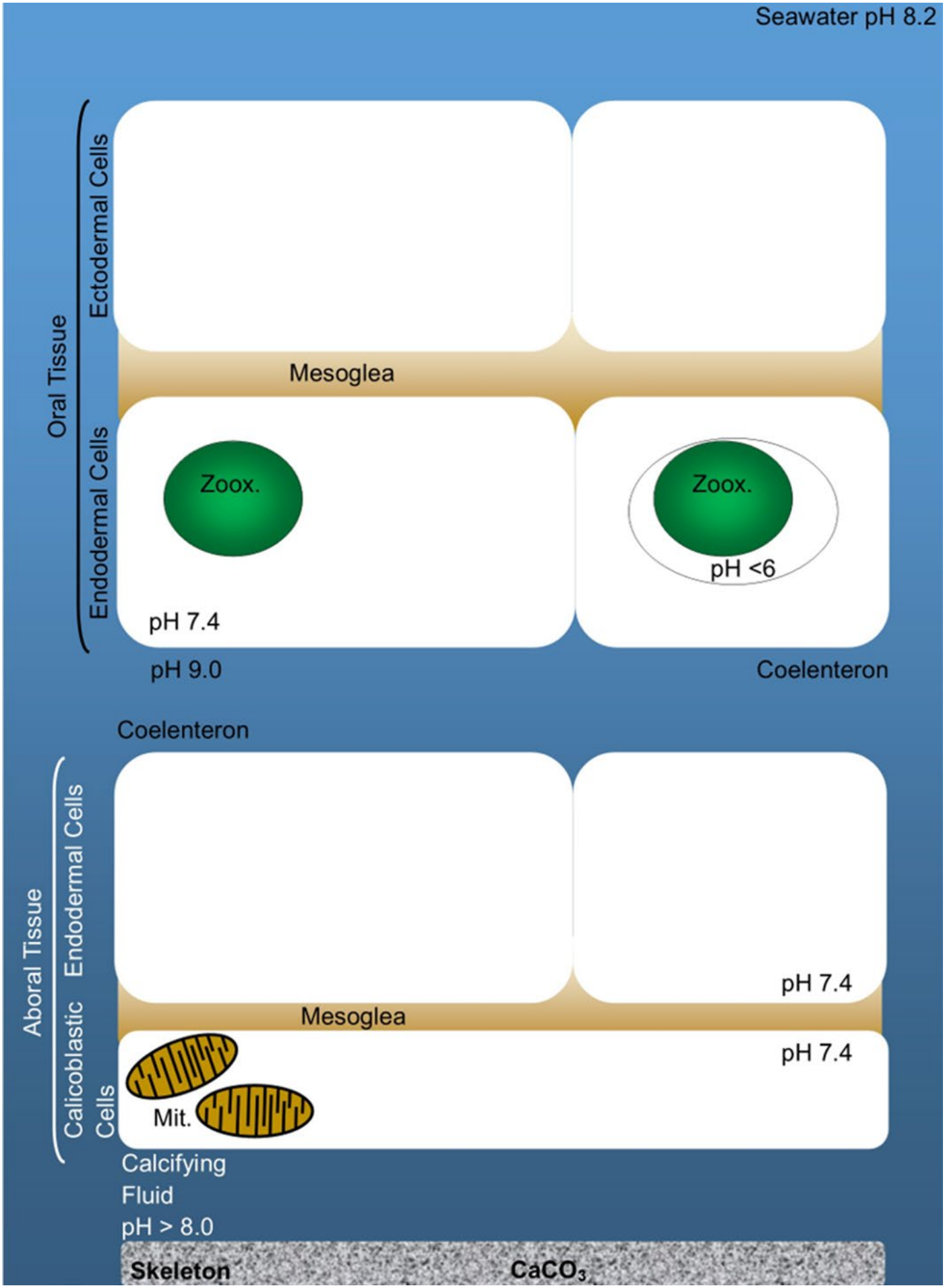
Appendix



A pH pen probe available from ~7GBP which is suitably accurate because all pH instrumentation must be calibrated immediately before each reading with freshly constituted buffers, which makes continuous monitoring, as ever, moot. Saltwater alkalinity demands these instruments are first calibrated to pH 7 and then 9, because their virtual scales must be set to read above neutral. The tip must be rinsed before transference in reverse osmosis water while the entire instrument is stored preferably in a tall, sealed jar with its bulb submerged in virtually-saturated 4 molar (M; 60 g $100ml^{-1}$ anhydrous potassium chloride; KCl).



As pH is temperature dependent, each of these sachets of low-cost buffer provide the specified pH at 25^{o}C when dissolved in 250 ml of reverse osmosis water. pH 4 and 9 are corrosive so exercise care and wear suitable personal protective equipment (PPE).



An illustration of the diploblastic cell types and compartmental pH of Scleractinia with seawater above, which features a zooxanthella (Zoox.) occupying a symbiosome to the right. Mitochondrion (Mit.)- and respiration-rich calicoblastic cells overlie the sites of skeletal deposition, which is mostly composed of solidified calcium carbonate ($CaCO_3$). Mitochondria are indispensable for the utilisation of oxygen which occur in all cells of oxygen-dependent eukaryotes. Image consistent with the observations of Zoccola et al. 2015 and Putnam et al. 2017.

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As the principal director of Reef Ranch Publishing Ltd (https://reefranch.co.uk/) and author of The Complete Reef Aquarist – A Conservation Manual (https://reefranch.co.uk/reef-aquarium-guide/), Chris has over 55 years of experience keeping aquatic animals with 47 of them nurturing marine species. His innate passion for system dynamics drove him from the laboratory to university where he gained a greater appreciation of biochemistry, biotechnology, epidemiology, genetics, histology, inorganic and organic chemistry, mariculture, molecular and microbiology, saltwater zoology, and the diagnosis and treatment of aquatic diseases. His dedicated marine livestock supplier, The Reef Ranch™, demanded he devise, streamline, and establish protocols for combined acclimation and prophylactic pest/parasite clearance, and innovate system design, optimisation, maintenance, and husbandry in the face of incessant influxes of hundreds of delicate marine animals. With exceptional, uncompromising, and likely the UK's most disease-free reef and fish-only facilities, losses were less than one resident every six months. 20 years hence, he has refined his expertise for digesting, authoring, editing, and publishing reef conservation-driven scientific literature (https://reefranch.co.uk/reef-research-and-aquarium-advice/), to an end of diminishing the impact the tropical marine ornamental industry exerts in the wild.

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