Considerations for determining warm-water coral reef tipping points.

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Abstract. Warm-water coral reefs are facing unprecedented human driven threats to their continued existence as biodiverse, functional ecosystems upon which hundreds of millions of people rely. These impacts may drive coral ecosystems past critical thresholds, beyond which the system reorganises, often abruptly and potentially irreversibly, this is what the IPCC (2022) define as a tipping point. Determining tipping point thresholds for coral reef ecosystems requires robust assessments of multiple stressors and their interactive effects. In this perspective piece we draw upon the recent Global Tipping Points Revision initiative (Lenton et al., 2023) and a literature search to identify and summarise the diverse range of interacting stressors that need to be considered for determining tipping point thresholds for warm-water coral reef ecosystems. Considering observed and projected stressor impacts we endorse the Global Tipping Points Revision conclusion of a global mean surface temperature (relative to pre-industrial) tipping point threshold of 1.2°C (range 1-1.5°C) and the long-term impacts of atmospheric CO_2 concentrations above 350 ppm, whilst acknowledging that comprehensive assessment of stressors, including ocean warming response dynamics, overshoot and cascading impacts, have yet to be sufficiently realised. These stressor considerations are likely to further lower tipping point thresholds in most cases. Uncertainties around tipping point thresholds for such crucially important ecosystems underlines the imperative of robust assessment and, in the case of knowledge gaps, employing a precautionary principle favouring lower range tipping point values.

1. Introduction

Warm-water coral reefs (tropical and subtropical) support one quarter to one third of marine biodiversity (Plaisance et al., 2011), including over 25% of marine fish species, and provide US$2.7 - 9.8 trillion per year of ecosystem services (Laffoley and Baxter, 2016; Souter et al., 2021), upon which at least 500 million people are reliant (IPBS 2019). They are also among the most sensitive ecosystems to anthropogenic driven stressors with approximately 50% of global live coral cover lost over the last 50 years (Souter et al., 2021), primarily due to ocean warming, but other factors have contributed locally such as fishing, pollution, disease, nutrient enrichment and predation by crown of thorns starfish (IPCC 2022). IPBES (2019) states that over 80% of the world's coral reefs are severely over-fished or have degraded habitats (McClanahan et al., 2015). Eddy et al., (2021) estimate coral reef ecosystem services have halved since the 1950s. Although local stressors continue to impact coral reef health, climate driven stressors have become the dominant threat to the functional viability of these ecosystems (IPBES 2019; IPCC 2022).

It is well established that coral reef ecosystems are vulnerable to multiple interacting tipping points (TPs) (Norström et al., 2016; Heinze et al., 2021; Armstrong-McKay et al., 2022; IPCC 2022). IPCC (2022) defines a TP as *"a critical threshold beyond which a system reorganises, often abruptly and/or irreversibly"*. Coral reefs are prone to TPs that can produce coral die offs and replacement by other ecological communities such as macroalgae, soft corals, or urchin barrens (Norström et al., 2016), with reductions in biodiversity and degradation of ecosystem services (IPBES 2019). Warm water coral reefs cross a threshold of ecosystem collapse (Bland et al., 2018) when they cease to have sufficient live coral cover (typically ~ 10%) necessary for supporting the wide diversity of taxa, ecological interactions and positive carbonate production state typical of a coral reef (Perry et al., 2013; Darling et al., 2019; Sheppard et al., 2020; Vercelloni et al., 2020; Armstrong-McKay et al., 2022). Coral mortality may take weeks or a few months for acute events (e.g. bleaching), or years for chronic threats (e.g. diseases), but prolonged failure to recover over a decade is necessary to qualify a coral reef as 'collapsed'.

Coral reef losses have accelerated in recent decades due to climate change and other stressors (IPBS 2019; Souter et al., 2021), with high variability among regions, but some localised recovery and resilience observed (e.g. Richards et al., 2021). Localised responses of corals to increasing scales and intensities of stressors are aggregating at scales now exceeding 1000 km and manifesting as regional die-offs (e.g. Western and Central Indian Ocean, Great Barrier Reef, Mesoamerican Reefs) (Le Nohaïc et al., 2017; Muñiz-Castillo et al., 2019; Sheppard et al., 2020; Obura et al., 2022; Amir 2022), with most regions experiencing multiple die-off events (Darling et al., 2019; Cramer et al., 2020; IPCC 2022). Coral reef bleaching TPs have already been reached in seven ocean systems (IPCC 2022).

2. Considerations for assessing coral reef TPs.

Direct and indirect local human activities are increasingly degrading coral reef ecosystems through a combination of coastal development, water quality reduction, over-harvesting, invasive species and disease spread. At the local level, these stressors have already tipped some areas from coral to macroalgae dominated ecosystems (Bruno et al., 2009; IPBES 2019; Souter et al., 2021). Local stressor impacts are increasingly exacerbated by anthropogenic climate change, for example, high abundance of macroalgae or urchins exacerbating coral loss after bleaching (Donovan et al., 2021).

It's important to consider the combined impact of multiple stressors. Doing so can significantly alter assessments of coral reef futures (Setter et al., 2022; Lenton et al., 2023). Interactions between different stressors can be antagonistic (the combined effect is less than the additive), additive (the combined effect is equal to the sum of their individual effects) or synergistic (the combined effects exceed their individual effects) (Good and Bahr 2020). Some studies find antagonistic interactions between multiple stressors (Darling et al., 2010; Johnson et al., 2022). However, a wide variety of interacting and synergistic stressors also occur (ICRS 2021; IPCC 2022; Setter et al., 2022; Lenton et al., 2023), generally lowering the thermal threshold for bleaching and/or mortality, accelerating collapse, or even surpassing thermal stress in local importance (Ban et al., 2013; Edmunds et al., 2014; Rocha et al., 2015; Anthony 2016; Darling et al., 2019; IPBS 2019; Cramer et al., 2020; Setter et al., 2022; Lenton et al., 2023). Stressor onset rate can have a major effect on significance, for example for reef fish mortality (Genin et al., 2020). Depending on onset rate and magnitude, the same interacting stressors may initially have antagonistic effects but may transition to additive or synergistic (e.g., Fisher et al., 2019).

Increasing atmospheric greenhouse gas (GHG) concentrations, especially carbon dioxide (CO_2), are disrupting Earth Energy Balance. The resultant Earth Energy Imbalance (EEI) is increasing atmospheric and ocean temperatures (IPCC 2021; Loeb et al., 2021; Von Schuckmann et al., 2023). CO_2 concentrations are the dominant driver of rate and magnitude of ocean warming and acidification (Meinshausen et al., 2020). Because of its large thermal inertia the ocean takes hundreds of years to fully respond to the atmospheric temperature increases that human driven GHG concentrations are causing (IPCC;. 2021; Abraham et al., 2022; Cheng et al.; 2022). The resultant *committed* heating and sea level rise (SLR) needs to be calculated for any given GHG/temperature level. Although both ocean heat uptake and SLR take centuries to fully respond, it takes approximately 25-50 years for the majority of committed ocean warming to be realised (Hansen et al; 2005; Abrams et al., 2023), with the upper ocean level having the shortest response time. Due to these inertia considerations, TP thresholds can be exceeded decades before the full physical impacts are observed.

Overshoot describes warming pathways that temporarily increase global mean temperature over a specific temperature target (IPCC 2022). Overshoot of multiple decades implies severe risks and irreversible impacts in many ecosystems (Meyer et al., 2022; Wunderling et al., 2022; Schleussener et al., 2024), including coral reefs from heat-related mortality and associated ecosystem transitions (high confidence) (IPCC 2022).

TP cascades describe a TP in one system triggering, or stabilising, subsequent TPs in other systems (Rocha et al., 2018; Armstrong-McKay et al., 2022; IPCC 2022; Wunderling et al., 2022). Here we summarise the most important stressors relevant to TP sensitivity for coral reefs and explore interactions between them.

3. Ocean warming and heatwaves

Warmer ocean temperatures, driven by Anthropogenic climate change, compounded by El Niño heating events, is the primary stressor of regional- and ocean-basin- scale mortality of scleractinian corals. Heat stress results from small increases in seawater temperature above the summer maxima to which corals are acclimatised, destabilising the symbiosis between host corals and their symbiotic algae, commonly referred to as coral bleaching (Hughes et al., 2017; Houk et al., 2020; UNEP 2020; IPCC 2022).

Mass bleaching occurs when sea temperatures persist at more than 1 degree above established summer maxima for 8-12 weeks (known as 8-12 Degree Heating Weeks or DHW). Although mass bleaching has resulted in significant coral morality, we note that with the loss of sensitive corals, acclimation and adaptation, the definition of DHW may require adjustment (Lenton et al., 2023).

Previous assessments have highlighted consequences of different levels of warming:
0.7°C - "In the late 1990s when global warming was around 0.7°C large-scale coral reef bleaching also became apparent … supporting the lower boundary for this transition in respect of coral reefs" (Veron et al., 2009; IPCC, 2022)
1.0°C - "temperatures of just 1°C above the long-term summer maximum … over 4–6 weeks are enough to cause mass coral bleaching … and mortality (very high confidence)" (Hoegh-Guldberg et al., 2018; Skirving et al., 2019).
1.2°C - "Warm water (tropical) coral reefs are projected to reach a very high risk of impact at 1.2°C …, with most available evidence suggesting that coral-dominated ecosystems will be non-existent at this temperature or higher (high confidence). At this point, coral abundance will be near zero at many locations and storms will contribute to 'flattening' the three-dimensional structure of reefs without recovery, as already observed for some coral reefs **(**Alvarez-Filip et al., 2009)." (Hoegh-Guldberg et al., 2018). Coral reef bleaching TPs have already been passed in seven ocean systems (IPCC 2022; Lenton et al., 2023).
1.5°C - "...coral reefs… will undergo irreversible phase shifts due to marine heatwaves with global warming levels >1.5°C and are at high risk this century even in <1.5°C scenarios that include periods of temperature overshoot beyond 1.5°C (high confidence)." (IPCC 2022). Projections predict 70-90% coral loss at 1.5°C (Hoegh-Guldberg et al., 2018; IPBS 2019; Souter et al., 2021; Armstrong McKay et al., 2022), whereas finer scale modelling projects a 95-98% loss (Kalmus et al., (2022) and suggest 99% loss (Dixon et al., 2022).
2.0°C - "literature since AR5 has provided a closer focus on the comparative levels of risk to coral reefs at 1.5°C versus 2°C of global warming … reaching 2°C will increase the frequency of mass coral bleaching and mortality to a point at which it

will result in the total loss of coral reefs from the world’s tropical and subtropical regions.” (IPCC 2018). Predictions show 99% coral loss at 2.0C (Frieler et al., 2013; Hoegh-Guldberg et al., 2018; IPBS 2019; Knowlton et al., 2021; Souter et al., 2021; Armstrong McKay et al., 2022; Wang et al., 2023). Finer scale modelling projects 100% loss at 2.0°C. (Dixon et al., 2022; Kalmus et al., 2022).

Since the first global bleaching event of 1998, up to 71% of the world’s reefs have experienced three further global mass bleaching events, with a fourth event being experienced in 2023/2024 (https://www.noaa.gov/news-release/noaa-confirms-4th-global-coral-bleaching-event).

Assessments of risk to corals from heating typically don’t consider co-occurring or interacting stressors or the delayed heating response to atmospheric greenhouse gas concentrations. Ocean warming inertia may mask the impact severity of stated greenhouse gas and temperature levels. When emissions-driven temperature overshoot is considered, lower target temperatures can have similar impacts to higher, with little difference in coral survival between an overshoot scenario that peaks at 2°C and subsequently reduces temperatures to 1.5°C versus a 2°C scenario without a subsequent reduction in temperatures (Tachiiri et al., 2019).

Tanaka and Van Houtan (2022) confirm the normalisation of extreme heating events. The frequency and duration of bleaching events are likely to increase, occurring earlier in the year and potentially overlapping with critical spawning periods (Mellin et al., 2024). The compounding heat stress of El Niño events (Claar et al., 2018; Hughes et al., 2018b; Lough et al., 2018) may increase with projected Arctic and Antarctic sea ice loss (England et al., 2020; Liu et al., 2022). Real world observations from the NOAA coral reef watch program demonstrate that coral reef damage is accelerating and underscores the threat anthropogenic climate change poses for the irreversible transformation of these essential ecosystems (Eakin et al., 2022).

Interactions of ocean warming and heatwaves with other stressors

Warming effects are so far reaching in their impacts that they can adversely impact many other coral stressors, these stressors, in turn, can increase vulnerability to thermal stress. For example, heating-induced bleaching increases disease risk and lowers calcification which increases the impact of ocean acidification (Rosenberg and Ben-Haim, 2002; Marshall and Clode, 2004; Ward et al., 2007; Eakin et al., 2008; Bak et al., 2009; Miller et al., 2009; Veron et al., 2009; Chan et al., 2019; Davis et al., 2021; Burke et al., 2023). Corals that survive bleaching can have compromised growth rates and reproduction (Rodrigues and Padilla-Gamino, 2022; Speare et al., 2022; Briggs et al., 2024). Furthermore, warming oceans and heatwaves increase storm intensity and raise sea-level through thermal expansion and cryosphere melting.

4. Stratification

Ocean stratification is the layering of water masses, based on density. Stratified water layers are a barrier to mixing, which impacts the exchange of heat, oxygen, nutrients and carbon between shallow and deep water. This impacts marine organisms in a number of significant ways, including impacting primary productivity and potentially the entire marine food chain. Stratification has increased globally by 5.3% in recent decades (Li et al., 2020).

Interactions

Stratification is strongly linked with warming oceans. Stratification magnifies the warming effect at the upper layers, thus increasing thermal stress to warm water reefs, this is a vicious circle as warming oceans further increase stratification. Additionally, stratification reduces CO_2 uptake, further exacerbating anthropogenic warming. Stratification impedes ocean mixing impacting nutrient flows. Stratification is strongly linked with deoxygenation. Stratification is also linked with melting of Antarctic ice shelves and sea-level rise (Reed and Harrison 2016; Li at al., 2020; Auger et al., 2021). Stratification is increasing which has dramatic consequences for sea temperature and CO_2 concentrations (Goreau and Hayes, 2024)

5. Ocean acidification

Ocean acidification (OA) is the process of the increasing absorption of atmospheric CO_2 by the surface seawaters of the oceans (Raven 2005), which in turn reduces the calcification rates of most scleractinian tropical and subtropical corals (Comeau et al., 2014; Kornder et al., 2018), and can alter the photo-physiology and calcification physiology of some corals (Comeau et al., 2018). OA causes a change in the speciation of dissolved inorganic carbon and an increase in protons (Caldeira and Wickett 2003; Feely et al., 2004; Sabine et al., 2004; Raven et al., 2005). This results in increased dissolution of exposed calcareous material due to decreases saturation state of $CaCO_3$, and also inhibition of calcification through increasing proton concentration with the calcifying space in corals and calcareous algae (Comeau et al., 2018; Comeau et al., 2019).

OA causes declines in coral calcification rates (Comeau et al., 2018). Early work predicted large-scale loss of coral calcification at catastrophic levels, whereby OA was projected to result in coral bleaching and in some cases net dissolution of corals (see data within Leung et al., 2022). Contemporary research demonstrates that some corals are resistant to OA (Comeau et al., 2018; Kornder et al., 2018). The most comprehensive modelling estimates are that by year 2100 coral calcification would decline by 1% under RCP2.6, 4% under RCP4.5 and 15% at RCP8.5 (Cornwall et al., 2021). When combined solely with the metabolic effects of temperature increases, this decline would be 1% (RCP2.6), 8% (RCP4.5), and 33% (RCP8.5). However, the calcification rates of susceptible coral taxa (e.g., *Acropora* spp.) would decline by much more, and resistant species (e.g., *Pocillopora* spp. or *Porites* spp. generally) could be unaffected.

The direct metabolic impacts of OA do not manifest a TP, but TPs at ecological levels are likely. Recent evidence indicates that ecological TPs within coral reefs caused solely by ocean acidification would occur around 550 ppm, roughly the same concentration of atmospheric CO_2 that would cause detectable declines in both coral and coralline algal calcification (Cornwall et al., 2024). However, ecosystem trajectories are uncertain, and much more future research is required to determine the generality of these findings.

The adverse impacts on coral and coralline algal calcification are direct negative effects, when combined with the direct positive effects on other taxa (such as opportunistic turfing algae). Susceptible species would start to give way to tolerant species over time (as generally occurs at natural analogues in the field (Fabricius et al., 2011; Comeau et al., 2022), and other non-coral taxa would start to dominate space on what once were traditional coral reefs. Species that are capable of maintaining stable internal carbonate chemistry or compensate for these changes tend to be more tolerant to OA.

Interactions

Reduced calcification increases disease risk and weakened skeletons are vulnerable to storms (Suwa et al., 2010; Anthony et al., 2011; Steffen et al., 2015; Setter et al., 2022). There is also some evidence that elevated CO_2 will exacerbate heat stress induced declines in coral calcification and physiological performance, though the strength and direction of these interactions varies widely by coral reef taxa, and even within different coral genera (Kornder et al., 2018). However, of greater immediate importance to the majority of corals will be successive marine heatwaves that will reduce the coral cover of less heat tolerant species, populations and genotypes over the majority of the oceans in the near future (van Hooidonk et al., 2014; Cornwall et al., 2021; Logan et al., 2021; Cornwall et al., 2023). Survivors of this human-driven evolutionary force will not necessarily be those that are tolerant to OA also, and thus numerous TPs in time could occur.

6. Deoxygenation

Deoxygenation on coral reefs is perhaps the least studied of the major threats directly linked to climate change such as warming and acidification (Hughes et al., 2020). However, there is sufficient evidence to say that dissolved oxygen is a critical resource on coral reefs, and that oxygen limitation (i.e. hypoxia) results in non-linearities and feedbacks that contribute to ecological tipping points (Nelson and Altieri 2019). The consequences of crossing these TPs are perhaps most dramatically evident in sudden mass mortality events, which has led to calls to accelerate the research agenda on deoxygenation on coral reefs (Altieri et al., 2017). The oxygen concentration threshold at which corals lose their ability to maintain homeostasis is 2 mg/L with lethal doses between 0.5-2 mg/L (Hughes et al., 2020; Johnson et al., 2021a).

The problem of deoxygenation on coral reefs is becoming more prevalent and severe in the Anthropocene from a combination of global climate change (Altieri and Gedan 2015; Pezner et al., 2023), as well as local pollution in the form of excess nutrient and organic matter (Diaz and Rosenberg 2008), that are magnified by local oceanographic patterns (Adelson et al., 2022). Around 13% of coral reefs are at risk of deoxygenation, and this is likely to increase with continued climate change (Altieri et al., 2017; Pezner et al., 2023).

We suggest that evidence to date for feedbacks and non-linear thresholds indicates that a TP framework should be used to guide future research on deoxygenation in coral reefs, and that hypoxia should be considered in studies of thermal stress and acidification.

Interactions

Climate-related variables of temperature and acidification are also likely to exacerbate deoxygenation by affecting the physiological responses of corals and other reef organisms. It is widely recognized that increased temperatures lead to increased metabolic demand and decreased tolerance thresholds in marine organisms including corals (Vaquer-Sunyer and Duarte, 2011; Alderdice et al., 2022; Weber et al., 2012). Given the prevalence, co-occurrence, and synergistic effects of these co-stressors with deoxygenation, a multi-stressor perspective is essential, and many of the assumed thresholds for TPs on coral reefs based on single or even double stressor treatments under laboratory experiments are likely overly conservative estimates. Coral reefs are vulnerable to a number of feedbacks that exacerbate deoxygenation events, these include: bleaching (Altieri et al., 2017; Alderdice 2021; Johnson et al., 2021a,b;), excessive dead material from mass mortality events (Simpson et al., 1993), coral disease and algal growth (Dinsdale and Rohwer, 2011), and shifts in the coral microbiome (Howard et al., 2023).

7. Storm intensity

The direct force of wind and waves, along with changes in storm direction, increase risks of physical damage and exposure to reduced water quality and sediment runoff (IPCC 2018). Storms contribute to unstable rubble substrate, compromising coral settlement (Sheppard et al., 2020). Furthermore, frequent intense storms can hinder reef recovery (Puotinen et al., 2020). Setter et al., (2022) ascribe a threshold value of storm strength category <4 with a return time of >5 years.

Interactions

Ocean warming may increase the severity of cyclones (IPCC 2021; Setter et al., 2022) and coral bleaching has likely reduced the ability of reefs to recover from cyclone damage (Laffoley and Baxter 2016). The likelihood of more intense cyclones within time frames of coral recovery by mid-century poses a global threat to coral reefs and dependent societies (Cheal et al., 2017). Storms can have an antagonistic interaction with heat stress, reducing bleaching severity, but also generate sediment resuspension (Gardner et al., 2005; Manzello et al., 2007; Carrigan and Puotinen, 2014; Puotinen et al., 2020; Setter et al., 2022). Reduced calcification increases susceptibility to storm impacts (Suwa et al., 2010; Anthony et al., 2011; Steffen et al., 2015; Setter et al., 2022).

8. Sea level rise

Sea-level rise (SLR) can cause 'reef drowning' from exceeding *Darwin Point* thresholds (Grigg 2008). Saunders et al., (2016) note that while individual corals may keep pace with SLR, likely maximum reef framework accretion rate on reef flats is only 3 mm $yr^{–1}$. Saintilan et al., (2023) estimate likely vulnerability to relative SLR at 7 mm yr^{-1} for coral reef islands. Global mean sea level between 2006 and 2018 increased to 3.7 mm yr-1 (IPCC 2021). Under SSP1-2.6, due to the risk of loss of reef structural integrity and transitioning to net erosion by mid-century the rate of sea level rise is very likely to exceed that of reef growth by 2050, absent adaptation (IPCC 2022). Depending on reef type and location suggested SLR threshold rates range from 4-9 mm yr^{-1}.

Closely connected seagrass and mangrove ecosystems (Guannel et al., 2016) are very vulnerable to projected SLR (Saunders et al., 2014; Törnqvist et al., 2021; Saintilan et al., 2023) which will further compromise coral reef resilience and functionality. In summary, SLR rate and magnitude looks increasingly likely to overwhelm the accretion ability of coral reefs which will be further challenged by increased wave energy, sedimentation, turbidity and resultant compromised light conditions for symbiont photosynthesis (Saunders et al., 2014; Woodroffe and Webster 2014; Törnqvist et al., 2021; Saintilan et al., 2023).

Interactions

Moderate rates of sea level rise may potentially provide cooling for some reefs contending with thermal stress and thus have an antagonistic effect (Baldock et al., 2014; Cinner et al., 2015; Brown et al., 2019; Zuo et al., 2021). However, SLR rate and magnitude predictions (eg. Ciraci et al., 2023; Vernimmen and Hooijer 2023) imply increasingly synergistic impacts, especially in the tropics (Spada et al., 2013; Hooiler and Vernimmen 2021; Cazenave et al., 2022). High SLR rate and magnitude can change the interactions from antagonistic to synergistic, for example: reducing light availability, increasing sedimentation and turbidity (Laffoley and Baxter, 2016; Perry et al., 2018; IPCC 2022).

9. Pollution & disruption

Here we use pollution as an all-encompassing term covering sediment, eutrophication, turbidity and chemicals, while disruption as a term covering local land use change, human population density and overfishing. Sedimentation reduces water clarity and hence solar energy supply, furthermore sediments settling on corals require greater energy to remove. It is caused mainly by land-based activities such as coastal urbanisation, with plumes in large tropical river systems travelling many km (Brodie et al., 2012). Organic pollution from sewage and agricultural run-off (e.g. fertiliser) are the main causes of eutrophication (increase in nutrient content in water), which reduce light, actively poison invertebrates, introduce pathogens and reduce resistance to disease with direct impact on corals being decreased colony sizes, growth anomalies, and reduced growth and survival (Setter at al 2022). Metals and organic chemicals can rupture cell membranes, disrupt enzyme pathways reducing corals' ability to resist other stressors. Plastics have also been identified as a major cause of coral reef stress due to light interference, toxin release, physical damage, anoxia and increasing the likelihood of pathogen disease 20-fold (Lamb et al., 2018). Land use can be used as a proxy for quantifying land-based pollution and other human stressors on coral reefs (Packet et al., 2008; Cinner et al., 2012; Setter et al., 2022). Setter et al., (2022) use human population density as the closest indicator available to quantify local human stressors, involving coral growth anomalies and disease, low biodiversity and fish biomass and reduced growth and survival. To calculate reef change threshold exceedance, Setter et al., (2022) use an ideal value of summed proportion agricultural/urban land use <0.5 in a 50 km radius around a reef. Perhaps the most direct disruptive impact is overfishing with IPBS (2019) stating that more than 80% of the world's coral reefs are severely over-fished or have degraded habitats (McClanahan et al., 2015).

Interactions

Under certain circumstances poorer water quality can mediate bleaching resilience through a shading effect. Pollution exacerbates stress and increases disease risk, both of which are exacerbated by thermal stress. Eutrophication increases deoxygenation and exacerbates crown-of-thorn-seastar (COTS) outbreaks (De'ath and Fabricius 2010; Redding et al., 2013; Laffoley and Baxter 2019; MacNeil et al., 2019). Sites with historic disturbance may recover more slowly from heat stress and storms (Walker et al., 2024). Overfishing can lead to algae overgrowth inducing disease and lowering calcification (Fabricius 2005; Packett et al., 2009; Maina et al., 2013; Kroon et al., 2014; Prouty et al., 2017).

10. Disease

Diseases are major drivers of the deterioration of coral reefs and are linked to major declines in coral abundance, reef functionality, and ecosystem services (Alvarez-Filip et al., 2022). Disease outbreaks have severe consequences for coral reef ecosystems, resulting in extensive coral mortality and endangering long-term survival. Noteworthy events include the rapid proliferation of diseases like Stony Coral Tissue Loss Disease (SCTLD), Black Band Disease, and various forms of White Syndrome (Alvarez-Filip et al., 2022). Coral diseases are driven largely by a changing environment and are contributing to whole ecosystem regime shifts (Thurber et al., 2020). Although diseases are becoming increasingly prevalent with temperature rise and pollution, these, by themselves, have had relatively little overall impact outside of the Caribbean Sea, to date. In the Caribbean SCTLD is a major present source of coral mortality, impacting more than a third of all reef-building coral species present, and potentially driving the extinction of Pillar coral *Dendrogyra cylindrus* (among others). The relative impact of diseases elsewhere is likely to change in the future, becoming more prevalent and interacting with heatwaves and other stressors (Estrada-Saldívar et al., 2021; Cavada-Blanco et al., 2022).

Interactions

Some coral diseases (but not all) have been linked to both marine heatwaves and the longer-term warming trend (Bruno et al., 2007; Randall and van Woesik, 2015). For example, viral infections of coral symbiotic dinoflagellate partners (Symbiodiniaceae) will likely increase as ocean temperatures continue to rise, potentially impacting the foundational symbiosis underpinning coral reef ecosystems (Howe-Kerr et al., 2023). Furthermore, predation scars leave corals susceptible to disease (Nicolet et al., 2018). Invasive species can directly cause or increase the risk of disease spread.

11. Invasive and other problem species

Increased native and invasive coral predators and competitors can have severe impacts on reefs. One example is the impact of COTS on the Great Barrier Reef (Uthicke et al., 2015). The coral-killing sponge, *Terpios hoshinota*, is a global invasive species which has led to a significant decline in living coral cover at various geographical locations (Thinesh et al., 2017).

Interactions

Warming is a driving factor in the increased impact of invasive and problem species. Studies on Mexican Pacific coast coral reefs confirmed that post bleached corals are increasingly vulnerable to boring sponge impacts (Carballoe et al., 2012). COTS outbreaks appear to be significantly influenced by a combination of heat stress resiliency (Byren et al., 2024) and increased larval survivorship due to higher food availability, linked with anthropogenic runoff and warmer sea temperature facilitating faster settlement of larvae (Uthicke et al., 2015). Predation scars can leave corals susceptible to disease (Nicolet et al., 2018).

12. Reef impact example

Chagos Archipelago demonstrates positive feedback (TPs).

Observations from the Chagos Archipelago, central Indian Ocean, reveal several related lessons. Coral cover collapsed 90% after heatwaves in 2015-2016. Very few adults capable of spawning survived, with new growth not observed for 3 years (Sheppard and Sheppard, 2019).

Settlement of larvae, when it occurred, was compromised by disintegrating substrates. In many shallow areas, where wave energy had already swept the substrate clear of rubble, large areas are becoming covered by the encrusting and bioeroding sponge *Cliona* spp (Sheppard et al., 2020) and almost no larvae were seen in these areas. These sponges are clearly increasing; with one reef showing over 80% *Cliona* cover preventing coral larvae settlement.

On at least one lagoon floor, the former foliaceous coral dominance was also killed with skeletons disintegrating resulting in fine sediment covering all surfaces. Both sedimented surfaces and turbid water are hostile to larval settlement, and none were seen in such areas over many hectares.

The scenario of fewer corals producing fewer larvae, more turbid water in some areas and less substrate available for settlement is a classical positive feedback or TP situation. These factors all act synergistically in a direction that inevitably leads to an ever more impoverished reef system. Recovery from this will require a prolonged period without heat stress and a gradual removal of the vast volumes of sediment and rubble left from previous bleaching events (Sheppard and Sheppard, 2019).

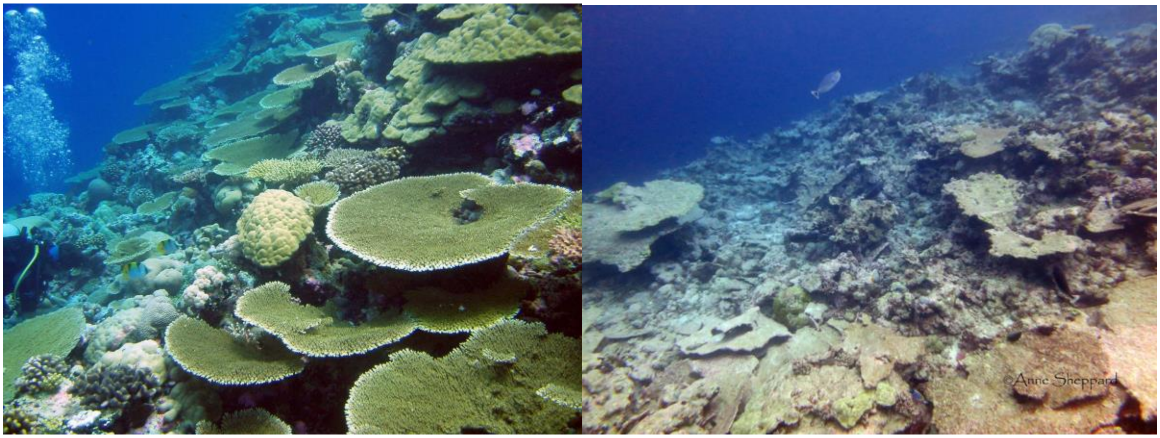

Figure 1: Reef slope on Salomon atoll, Chagos Archipelago, before and after the mass mortality caused by warming in 2015

13. Cascade effects contributing to coral reef TP threshold sensitivity

The cascading effects of well-researched TPs in other globally important systems have not been sufficiently assessed for their potential impact on coral reef systems. Accelerating West Antarctic Ice Sheet melt (Naughten et al., 2023), increasing methane emissions (Zhang et al., 2023) and Arctic sea ice decline have the potential to increase rate and magnitude of coral reef stressor impacts, including temperature and SLR. For example, Liu et al., (2022) predict that 37–48% of the increase of strong El Niño near the end of the 21st century is associated specifically with Arctic sea-ice loss. Many climate impact predictions make assumptions of the stability of the wider earth system, but this may not hold true and lead to dramatic cascading impacts, for example, Ke et al., (2024) show dramatic decline in land carbon sinks in 2023 which will have wider implications on CO_2 levels and associated stressors.

14. Resilience and adaptation

Lenton et al., (2023) state ‘The potential for coral adaptation to warming is a critical but poorly known factor, and subject to high levels of variation locally. The potential effectiveness of restoration for coral reefs at scale, and with enhanced capacity to resist future threats, are both currently poor. The effect of climate migration on coral recovery is poorly known, with potentially positive effects at higher latitude (with in-migration), but negative at lower latitudes (with out-migration, but no replacement; Herbert-Read et al., 2023).' IPCCs AR6 "Impacts and vulnerability" report states that 'impacts of climate change may overwhelm attempts at restoration/conservation, particularly when the ecosystem is already near its TP, as is the case with tropical coral reefs (Bates et al., 2019; Bruno et al., 2019).'

Mass coral mortality repeated more than twice per decade and over local, regional and ocean scale, and by aggregation to global scales, is increasingly recognized as giving insufficient time for recovery of impacted populations and ecological function (Hughes et al., 2018a,b; Obura et al., 2022; Lenton et al., 2023; Venegas et al., 2023). Ecological and biogeographical (spatial) feedback loops prevent recovery through failure of reproduction, dispersal, recruitment and growth of corals (Sheppard et al., 2020). Other stressors reduce the ability of corals to resist thermal stress thus lowering tipping thresholds. Increasing frequency and intensity of regional scale coral mortality events (1+ °C warming) are suggestive of the majority of coral reefs already having reached their bleaching TP (IPCC 2022). The potential for thermal refuges for corals under likely future scenarios is doubtful (Beyer et al., 2018; Dixon et al., 2022; Setter et al., 2022; Lenton et al., 2023) as very few or no reef areas are predicted to remain below tipping thresholds of all key stressors. The existence of putative refuges at greater depths (Bongaerts and Smith, 2019) or higher latitudes (Setter et al., 2022) are not strongly supported by recent work (Hoegh-Guldberg et al., 2017; Hoegh-Guldberg et al., 2018; Rocha et al., 2018; Montgomery et al., 2021; IPCC 2022).

There is evidence of the persistence of heat adapted genotypes but the loss of poorly adapted corals leads to a loss of diversity (Fox et al., 2021) Although potential for adaptation exists, stronger warming rates may outpace adaptive processes and limit coral persistence (Logan et al., 2021; Venegas et al., 2023). Historical and paleo evidence suggests fringe distributions are likely to be compromised by increasing frequency and intensity of extreme-weather (Toth et al., 2021). Donovan et al., (2021) show that local stressors act synergistically with climate change to kill corals. Local factors such as high abundance of macroalgae or urchins have magnified coral loss in the year after bleaching. Notably, the combined effects of increasing heat stress and macroalgae intensified coral loss, suggesting that effective local management, alongside global efforts to mitigate climate change, could aid coral survival. Agostini et al., (2021) suggest that ocean acidification will reshape coral communities around the world, selecting species that have an inherent resistance to elevated pCO_2.

Kleypas et al., (2021) provide a blueprint for coral reef survival and state that existing conservation measures such as marine protected areas and fisheries management are no longer sufficient to sustain reef ecosystems and many additional and innovative actions to increase reef resilience. Anthony et al., (2020) discuss new interventions and provide a conceptual model to guide effective strategy choices. They also state that warm-adapted coral traits may not spread fast enough in most coral species to keep up with the rate of global warming, even under strong carbon mitigation. Hughes et al., (2023) provide recommendations and a conceptual framework to guide restoration projects and state that coral restoration is likely to continue to fail unless climate change and other anthropogenic impacts are urgently reduced.

15. Conclusions

Robust inclusion of multiple, interacting stressors into vulnerability assessments will lead to a greater understanding of coral reef futures and address concerns that assessments have been too reliant on temperature thresholds (McClanahan 2022; Klein et al., 2024). Stressor onset rate, magnitude and overshoot factors are important considerations for determining stressor interactions and their significance.

Veron et al., (2009) argue that to ensure long-term viability of coral reefs, atmospheric CO_2 levels must be reduced significantly below 350 ppm. Lenton et al., (2023) recognise the long term consequences of >350 ppm as a critical TP threshold, along with a global mean surface temperature (relative to pre-industrial) threshold of 1.2°C (range 1-1.5°C), whilst acknowledging that the "combined effects of long-term warming, sea level rise, ocean acidification, deoxygenation, and other stressors, bears more investigation." The significance of both these TP thresholds is highlighted by the fact that global warming has already reached 1.2°C and CO_2 levels have exceeded 420 ppm. Considering the calculations of von Schuckmann et al., (2020) that CO_2 levels would need to be reduced to 353 ppm to realise the Paris temperature target, 350 ppm is likely to be insufficient for realising a 1.2°C TP threshold, especially as other significant greenhouse gases are still increasing.

We note that interacting stressors, ocean response dynamics, GHG emissions overshoot and cascade considerations have yet to be sufficiently evaluated. These and other uncertainties around TP sensitivities for such a crucially important ecosystem underlines the imperative of robust assessment (Aronson and Precht, 2016; Dixon, Forster and Beger, 2021; Heinze et al., 2021; Laffoley et al., 2022; Lenton et al., 2023) and, in the case of knowledge gaps and uncertainties, employing a precautionary principle (Rockström et al., 2021; OECD 2022; Deutloff et al., 2023; Lenton et al., 2023b; Ripple et al., 2023; Fletcher et al., 2024) favouring lower range threshold values. Recognising threat severity is essential if the necessary response actions are to be realised.

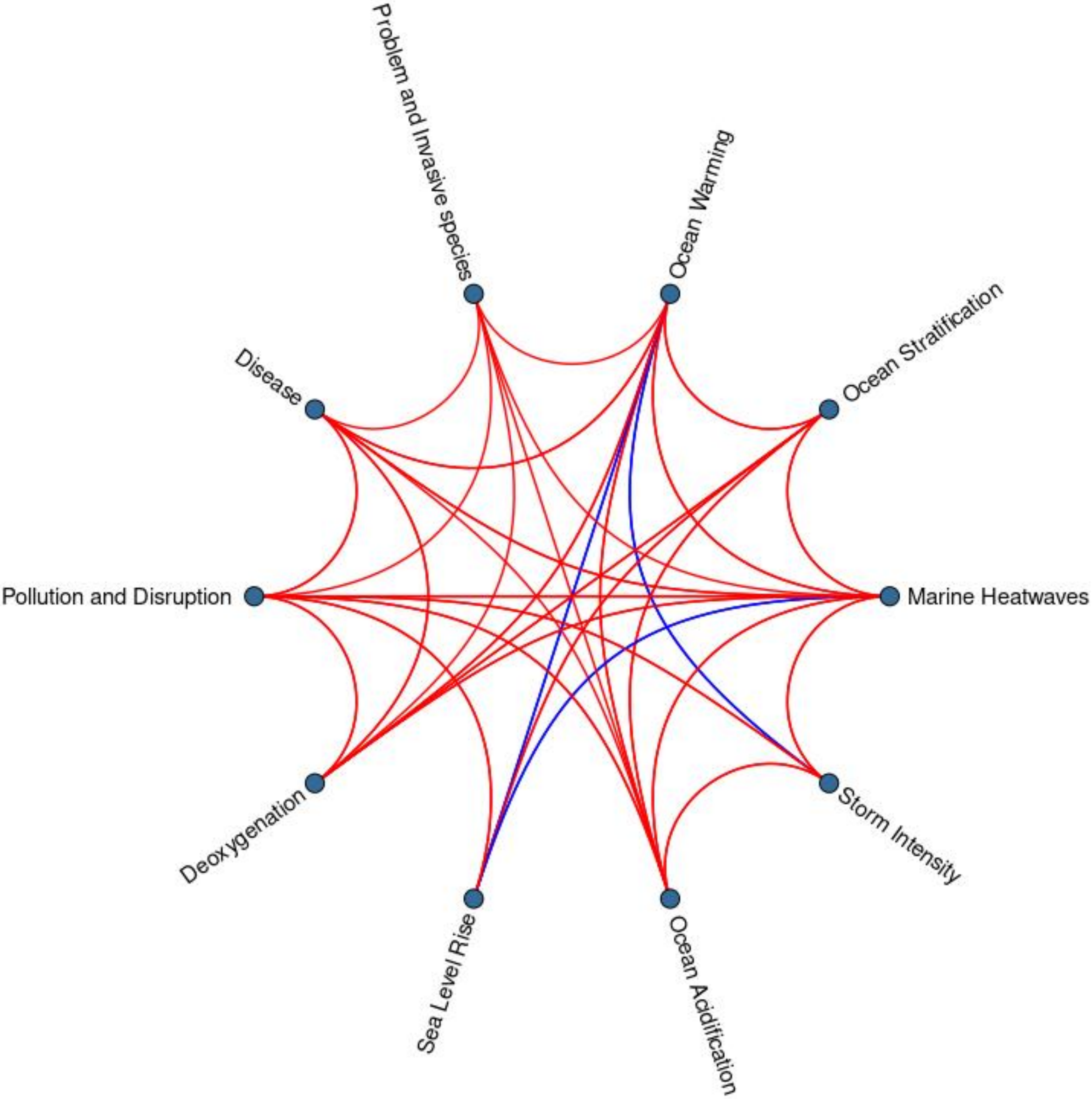

Figure 2: Visualisation of stressor interactions. Red links denote synergistic associations and blue links denote both synergistic and antagonistic associations depending on magnitude and other factors.

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Competing interests

The contact author declares that none of the authors have any competing interests.

Author contribution

All authors contributed to writing and revising the text.

Code/Data availability

No new code or data was generated for this manuscript

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