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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 Intergovernmental Panel on Climate Change (IPCC, 2022) define as a tipping point. Determining tipping point thresholds for coral reef ecosystems requires a robust assessment of multiple stressors and their interactive effects. In this perspective piece, we draw upon the recent global tipping point revision initiative (Lenton et al., 2023a) 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 point revision's 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, while acknowledging that comprehensive assessment of stressors, including ocean warming response dynamics, overshoot, and cascading impacts, have yet to be sufficiently realised. These tipping point thresholds have already been exceeded, and therefore these systems are in an overshoot state and are reliant on policy actions to bring stressor levels back within tipping point limits. A fuller assessment of interacting stressors is likely to further lower the tipping point thresholds in most cases. Uncertainties around tipping points for such crucially important ecosystems underline 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 (Laffoley and Baxter, 2016). The estimated annual economic value of coral reef ecosystem services ranges from USD 29.8 billion (Cesar et al., 2003) up to USD 2.7 trillion (Souter et al., 2021), upon which at least 500 million people are reliant (IPBES, 2019). They are also among the most sensitive ecosystems to anthropogenic-driven stressors, with approximately 50 % of global live coral cover lost and accelerated declines seen over the last 30 years (IPBES, 2019), 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) state that over 80 % of the world's coral reefs are severely overfished or have degraded habitats (McClanahan et al., 2015). Eddy et al. (2021) estimate that 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). The IPCC (2022) define 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 the 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 the sufficient live coral cover (typically ~ 10 %) necessary for supporting the wide diversity of taxa, ecological interactions, and a 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 having "collapsed".

Coral reef losses have accelerated in recent decades due to climate change and other stressors (IPBES, 2019; Souter et al., 2021), with high variability among regions, but some localised recovery and resilience have been 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, and the Mesoamerican Barrier Reef System) (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, overharvesting, 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 through, for example, a high abundance of macroalgae or urchins exacerbating coral loss after bleaching (Donovan et al., 2021).

It is 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., 2023a). 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) (see Fig. 2; Good and Bahr, 2021). Some studies find antagonistic interactions between multiple stressors (Darling et al., 2010; Johnson et al., 2022). However, a wide variety of synergistic interactions also occur (IPCC, 2022; Lenton et al., 2023a), generally lowering the thermal threshold for bleaching and/or mortality, accelerating collapse, or even surpassing thermal stress in local importance (Ban et al., 2013; Rocha et al., 2015; Anthony, 2016; Darling et al., 2019; IPBES, 2019; Cramer et al., 2020; Setter et al., 2022; Lenton et al., 2023a). The stressor onset rate can have a major effect on the significance, for example, of reef fish mortality (Genin et al., 2020). Depending on the onset rate and magnitude, the same interacting stressors may initially have antagonistic effects but may transition to additive or synergistic effects (e.g. Fisher et al., 2019).

Increasing atmospheric greenhouse gas (GHG) concentrations, especially carbon dioxide (CO_2), are disrupting Earth's 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 drivers of the 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 concentra-

tions 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 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 the global mean temperature over a specific temperature target (IPCC, 2022). An overshoot of multiple decades implies severe risks and irreversible impacts in many ecosystems (Meyer et al., 2022; Wunderling et al., 2023; Schleussener et al., 2024), including coral reefs from heat-related mortality and associated ecosystem transitions (high confidence) (IPCC, 2022). Overshoot is an urgent consideration for coral reefs because CO_2 levels and global mean surface temperature have already exceeded critical thresholds; as such, we are already in overshoot, and this problem is compounded by stressor rate and magnitude (Lenton et al., 2023a).

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., 2023). Here we summarise the most important stressors relevant to TP sensitivity for coral reefs and explore the interactions between them.

3 Ocean warming and heatwaves

Warmer ocean temperatures, driven by anthropogenic climate change and compounded by El Niño–Southern Oscillation (ENSO) heating events, are the primary stressors of regional-scale and ocean-basin-scale mortality of scleractinian corals. Heat stress, in combination with irradiance, results from small increases in the seawater temperature above the summer maxima to which corals are acclimatised, destabilising the symbiosis between host corals and their symbiotic algae and 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 °C above established summer maxima for 8–12 weeks (known as 8–12 °C heating weeks or DHWs). Although mass bleaching has resulted in significant coral mortality, we note that with the loss of sensitive corals, acclimation, and adaptation, the definition of DHWs may require adjustment (Lenton et al., 2023a).

Previous assessments have highlighted the consequences of different levels of warming, as follows:

- 0.7 °C. "In the 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" (IPCC, 2022).
- 1.0 °C. "[T]emperatures 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., 2023a).
- 1.5 °C. "[C]oral 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; IPBES, 2019; Souter et al., 2021; Armstrong-McKay et al., 2022), whereas finer-scale modelling projects a 95 %–98 % loss (Kalmus et al., 2022) and suggests a 99 % loss (Dixon et al., 2022).
- 2.0 °C. "[L]iterature 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 a 99 % coral loss at 2.0 °C (Frieler et al., 2013; Hoegh-Guldberg et al., 2018; IPBES, 2019; Knowlton et al., 2021; Souter et al., 2021; Armstrong-McKay et al., 2022; Wang et al., 2023). Finer-scale modelling projects a 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, last access: 17 January 2025).

Assessments of risk to corals from heating typically do not 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 the stated greenhouse gas and temperature levels. When emission-driven temperature overshoot is considered, lower target temperatures can have similar impacts to higher ones, with little difference in the coral survival between an overshoot scenario that peaks at 2 °C and subsequently reduces in temperature to 1.5 °C versus a 2 °C scenario without a subsequent reduction in temperature (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 programme demonstrate that coral reef damage is accelerating and underscore the threat that 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 (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 changing 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 and impacts nutrient flows. Stratification is strongly linked with deoxygenation. Stratification is also linked with the melting of Antarctic ice shelves and sea level rise (Reed and Harrison, 2016; Li et al., 2020; Auger et al., 2021). Stratification is increasing, which has dramatic consequences for sea temperatures 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 et al., 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 an increased dissolution of exposed calcareous material due to a decreased saturation state of $CaCO_3$ and also the inhibition of calcification through increasing proton concentration with the calcifying space in corals and calcareous algae (Comeau et al., 2018, 2019).

OA causes declines in coral calcification rates (Comeau et al., 2018). Early work predicted a 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 (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 the year 2100, coral calcification would decline by 1 % under RCP2.6, 4 % under RCP4.5, and 15 % under 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 toler-

ant 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 compensating for these changes, tend to be more resilient in the presence of OA.

Interactions

Reduced calcification increases disease risk, and weakened skeletons are vulnerable to storms (Suwa et al., 2010; Anthony et al., 2011; 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, 2023; Logan et al., 2021). Survivors of this human-driven evolutionary force will not necessarily be those that are resilient in the presence of OA, and thus numerous TPs 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 research on the deoxygenation on coral reefs (Altieri et al., 2017). The oxygen concentration threshold at which corals lose their ability to maintain homeostasis is $2\,mg\,L^{-1}$, with lethal doses between $0.5–2\,mg\,L^{-1}$ (Hughes et al., 2020; Johnson et al., 2021b). Previous mass extinctions have been linked to deoxygenation, indicating the potential severity of this threat (Liu et al., 2019).

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) and local pollution in the form of excess nutrients and organic matter (Diaz and Rosenberg, 2008), which 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 on 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 recognised 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). Considering the 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 to be overly conservative estimates. Coral reefs are vulnerable to a number of feedbacks that exacerbate deoxygenation events. These include bleaching (Altieri et al., 2017, 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, increases risks of physical damage and exposure to reduced water quality and sediment runoff (IPCC, 2018). Storms contribute to unstable rubble substrates, 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 suscep-

tibility to storm impacts (Suwa et al., 2010; Anthony et al., 2011; 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, the 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, without adaptation (IPCC, 2022). Depending on the 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 look 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, the SLR rate and magnitude predictions (e.g. Ciraci et al., 2023; Vernimmen and Hooijer, 2023) imply increasingly synergistic impacts, especially in the tropics (Spada et al., 2013; Hooijer and Vernimmen, 2021). High SLR rate and magnitude can change the interactions from antagonistic to synergistic, for example, reducing light availability and increasing sedimentation and turbidity (Laffoley and Baxter, 2016; Perry et al., 2018; IPCC, 2022).

9 Pollution and disruption

Here we use pollution as an all-encompassing term covering sediment, eutrophication, turbidity, and chemicals, while disruption is 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 be removed. Sedimentation is caused mainly by land-based activities such as coastal urbanisation, with plumes in large tropical river systems travelling many kilometres (Brodie et al., 2012). Organic pollution from sewage and agricultural runoff (e.g. fertiliser) are the main causes of eutrophication (increased nutrient content in water), which reduces light, poisons invertebrates, introduces pathogens, and reduces resistance to disease. This has direct impacts on corals including decreased colony sizes, growth anomalies, and reduced growth and survival (Setter et al., 2022). Metals and organic chemicals can rupture cell membranes and disrupt enzyme pathways, reducing the 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., 2009; 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, fish biomass, and reduced growth and survival. To calculate the reef change threshold exceedance, Setter et al. (2022) use an ideal value of the summed proportion of agricultural/urban land use < 0.5 in a 50 km radius around a reef. Perhaps the most direct disruptive impact is overfishing, with IPBES (2019) stating that more than 80 % of the world's coral reefs are severely overfished or have degraded habitats (McClanahan et al., 2015).

Interactions

Under certain circumstances, poor 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-thorns starfish (COTS) outbreaks (De'ath and Fabricius, 2010; Redding et al., 2013; Laffoley and Baxter, 2019; MacNeil et al., 2019), while overfishing is also linked to COTS outbreaks (Babcock et al., 2016). 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).

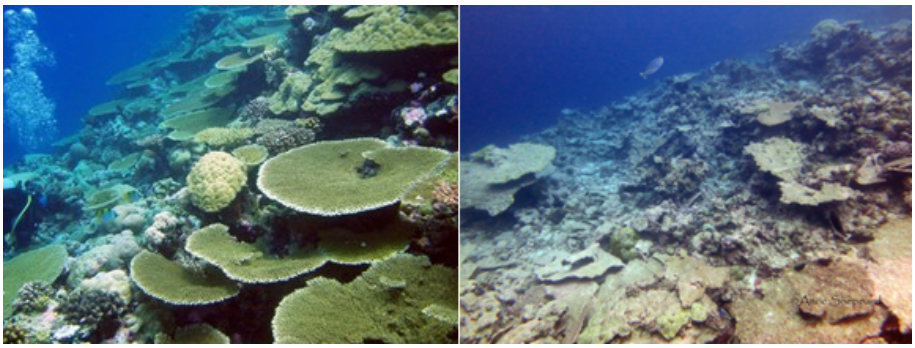

Figure 1. Reef slope on Salomon Atoll, Chagos Archipelago, before and after the mass mortality caused by the warming of 2015. Images: Charles Sheppard.

10 Disease

Diseases can be 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 increasing the extinction risk of the 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 have been linked to 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 (Byrne et al., 2023) and increased larval survivorship due to higher food availability, linked with anthropogenic runoff and warmer sea temperature facilitating the 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 by 90 % after heatwaves in 2015–2016 (Fig. 1). 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 coral settlers 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 and resulting in fine sediment covering all surfaces. Sedimented surfaces and turbid water are not preferred conditions for larval settlement, with no juvenile corals recorded 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 increasingly 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).

13 Cascade effects contributing to coral reef TP threshold sensitivity

The cascading effects of well-researched impacts 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 the 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 in strong El Niño events near the end of the 21st century is associated specifically with Arctic sea ice loss. Many climate impact predictions make assumptions about the stability of the wider Earth system, but this may not hold and lead to significant cascading impacts. For example, Ke et al. (2024) show a dramatic decline in land carbon sinks in 2023 which, if continued, will have wider implications on CO_2 levels and associated stressors.

14 Resilience, adaptation, and refugia

Lenton et al. (2023a) state that

> 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 not 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., 2022).

The IPCC AR6 Impacts, Adaptation, 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 events repeated more than twice per decade and over local, regional, and ocean scales, and by aggregation to global scales, are increasingly recognised as giving insufficient time for the recovery of impacted populations and ecological function (Hughes et al., 2018a, b; Obura et al., 2022; Lenton et al., 2023a; Venegas et al., 2023). Ecological and biogeographical (spatial) feedback loops prevent recovery through the 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 the 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., 2023a) 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) is not strongly supported by recent research (Hoegh-Guldberg et al., 2017, 2018; Rocha et al., 2018; Montgomery et al., 2021; IPCC, 2022).

There is evidence of the persistence of heat-adapted genotypes in some species, but the loss of poorly adapted corals leads to a loss of diversity (Fox et al., 2021). Although the 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 palaeoevidence suggest 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 a 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, indicating a need for 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 warming, even under strong carbon mitigation.

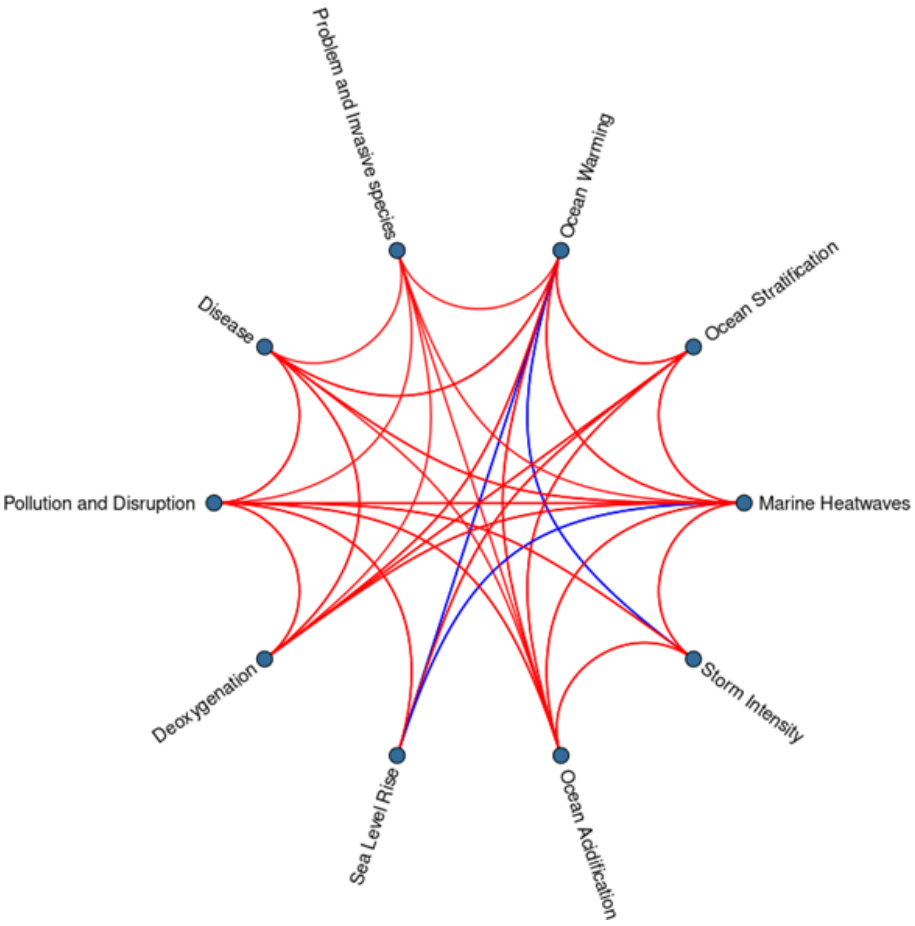

Figure 2. Visualisation of stressor interactions. Red links denote synergistic associations, and blue links denote synergistic and antagonistic associations, depending on magnitude and other factors.

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 the long-term viability of coral reefs, atmospheric CO_2 levels must be reduced significantly below 350 ppm. Lenton et al. (2023a) 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), while 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 underline the imperative of robust assessment (Aronson and Precht, 2016; Dixon et al., 2021; Heinze et al., 2021; Laffoley et al., 2022; Lenton et al., 2023a) 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.

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