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Considerations for determining warm-water coral reef tipping points.

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General comments:

The manuscript is a very useful contribution outlining the potential tipping points arising from the many faceted issues, and interactions therein, that impact and increasingly threaten coral reefs.

More information on the rationale for selection of 1.2 C and 350 ppt CO₂, as per the Veron et al. (2009) paper, would be useful. The paper could benefit from an expanded Section 13 on Chagos, to include more of the history, given it is one of the best studied, remote reef systems. The paper could also benefit from additional case-studies from Caribbean (nutrient enrichment, over-fishing, heat-waves, diseases, invasive species) and Great Barrier Reef (COTS, storms, run-off, heat waves, etc.), with summary noting differences in resilience among the three systems in respect to oceanographic connectivity and variability therein, coral population sizes, habitat heterogeneity, depth ranges etc.

The paper would benefit from a hard edit to shorten some sections that appear repetitive; and with shifting of some text that may fit better in other sections. The Interactions sections may be better combined into one section following all those dealing specifically with the various stressors. This would help to minimize repetition. Eg. Ocean acidification section also presently includes comments on heat waves – those could be covered solely in the Interactions section. I have suggested shuffling and shifting some text accordingly (see below Lines 196-210). Similarly in Disruptions section, some text seems to fit better in Pollution section.

Specific comments:

References could be improved by including more of the primary sources. Some examples are provided. Citations in text need to be standardized as per journal requirements.

Lines 39-42:

“They are also among the most sensitive ecosystems to anthropogenic driven stressors with an estimated 50% of global live coral cover having been lost over the last 50 years (Souter et al., 2021, WWF 2022), primarily due to ocean warming (and related climate change threats of ocean acidification and deoxygenation), but in some locations also due to fishing, pollution, and disease (IPCC 2022).”

LD: Loss of cover – consider noting ‘... albeit with significant temporal fluctuations, as on the Great Barrier Reef (see AIMS LTMP reports).

<https://www.aims.gov.au/monitoring-great-barrier-reef/gbr-condition-summary-2023-24>

Also, Crown-of-thorns seastar (*Acanthaster* spp., COTS) outbreaks have caused sig. loss of coral cover across the Indo-Pacific since at least the 1960s. Heat-wave driven bleaching mortalities are increasing rapidly, since 1998. However, to date, loss of significant cover from ocean acidification and deoxygenation is not well established (at least as far as I am aware),

although these are serious looming threats. Nutrient enrichment (as a specific form of pollution) has had sig. impacts in the Caribbean and in parts of the Coral Triangle (eg. Areas of Java Sea).

Line 63:

“Approximately half the live coral cover on coral reefs has been lost since the 1870s ...”

LD: presumably 1970s? Also recently estimated as dropping from 36 to 19 percent from 1997 to 2018 (Tebbett et al. 2023), with decreases most severe in the Western Atlantic and Central Pacific.

Tebbett SB, Connolly SR, Bellwood DR (2023) Benthic composition changes on coral reefs at global scales. *Nat Ecol Evol* 7: 71–81. <https://doi.org/10.1038/s41559-022-01937-2>

Lines 67-70:

“... regional die-offs (e.g. Western and Central Indian Ocean, Great Barrier Reef, Mesoamerican Reefs) (Le Nohaïc et al., 2017; Amir 2022; Muñoz-Castillo et al., 2019; Obura et al., 2022; Sheppard et al., 2020), with most reef regions having experienced multiple die-off events (Darling et al., 2019; Cramer et al., 2020; IPCC 2022). Coral reef bleaching tipping points have already been reached in seven ocean systems (IPCC 2022).”

LD: On GBR, Earth’s largest and arguably oceanographically best-connected reef system, and elsewhere, the ‘die-offs’ (coral cover losses) since the 1960s (COTS mainly) have been interspersed with recovery of cover, as has again recently happened, but prior to severe 2024 mass bleaching.

<https://www.aims.gov.au/monitoring-great-barrier-reef/gbr-condition-summary-2023-24>

This is not to downplay the seriousness of present impacts and future risk, nor the shifts in community structure (eg. See Richards ZT, Juskiewicz DJ, Hoggett A (2021) Spatio-temporal persistence of scleractinian coral species at Lizard Island, Great Barrier Reef. *Coral Reefs* 40: 1369-1378. <https://doi.org/10.1007/s00338-021-02144-4>), but to add some nuance to the statements.

Line 100:

“...is over centennial time (IPCC 2021).

Lines 104-105:

“(IPCC 2022). Overshoot of multidecadal time spans imply severe risks and irreversible impacts in many ecosystems Meyer et al. (2022), including ...

Lines 110-111:

“Increasingly warmer ocean temperatures, driven by Anthropogenic climate change, compounded by El Niño heating events, is the primary stressor of regional scale mortality of scleractinian corals..

LD: ... and ocean-basin ...

Line 113:

Primary sources would be better: Eg. Cite Barbara Brown and John Ogden, Peter Glynn, Ove Hoegh-Guldberg, among others, here.

Glynn, P.W., D’Croz, L. (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8: 181–191. <https://doi.org/10.1007/BF00265009>

Brown, B.E. and Ogden, J.C. (1993) Coral Bleaching. *Scientific American* 268 (1): 64-70. <https://doi.org/10.1038/scientificamerican0193-64>

Glynn, P.W. (1996) Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* 2 (6): 495-509. <https://doi.org/10.1111/j.1365-2486.1996.tb00063.x>

Hoegh-Guldberg, O. (1999) Climate Change, Coral Bleaching and the Future of the World’s Coral Reefs. *Marine and Freshwater Research* 50: 839-866. <http://dx.doi.org/10.1071/MF99078>

Line 143:

“Since **the first** bleaching event of 1998,...

LD: Pedantic, but this should be ‘... first global bleaching event ...’ Bleaching had been documented since at least 1960s following flooding (Tom Goreau Snr).

Line 145-146:

“With repeated events, loss of sensitive corals and acclimation and adaptation, the DHW thresholds may change (Lenton et al., 2023)

LD: Also see and cite:

van Woessik R, Kratochwill C (2022) A global coral-bleaching database, 1980–2020. *Sci Data* 9: 20. <https://www.nature.com/articles/s41597-022-01121-y>

van Woessik R, Shlesinger T, Grotto AG, et al. (2022) Coral-bleaching responses to climate change across biological scales. *Glob Chang Biol* 28: 4229-4250. <https://doi.org/10.1111/gcb.16192>

Donner SD, Rickbeil GJ, Heron SF (2017) A new, high-resolution global mass coral bleaching database. *PLoS One* 12:e0175490. <https://doi.org/10.1371/journal.pone.0175490>

LD: The time series suggested a possible increase in coral thermal tolerance – see Virgen-Urcelay and Donner 2023, Shlesinger and van Woessik 2023.

Shlesinger T, van Woessik R (2023) Oceanic differences in coral-bleaching responses to marine heatwaves. *Sci Total Environ* 871: 162113. <https://doi.org/10.1016/j.scitotenv.2023.162113>

Virgen-Urcelay A, Donner SD (2023) Increase in the extent of mass coral bleaching over the past half-century, based on an updated global database. *PLoS ONE* 18: e0281719. <https://doi.org/10.1371/journal.pone.0281719>

Lines 182-184:

The introduction to ocean acidification could benefit from a more detailed explanation of the process, or citations thereof. Many primary sources are provided in Kleypas, J.A., Yates, K.Y. (2009) Coral reefs and ocean acidification. *Oceanography* 22(4): 108-117. https://www.coris.noaa.gov/activities/oa/resources/22-4_kleypas.pdf

Lines 196-210:

LD: Suggest restructuring for clarity, as below.

“OA acts to alter the internal chemistry of corals and coralline algae, slowing calcification rates. The direct metabolic impacts of OA do not manifest a tipping point, but tipping points at ecological levels are likely. Recent evidence indicates that ecological tipping points within coral reefs caused solely by ocean acidification would occur around 550 ppm, roughly the same concentration of atmospheric CO₂ 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.

LD: The following paragraph may be better placed at end of Interactions section.

“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 tipping points in time could occur.”

Lines 218-219 and elsewhere.

LD: Greenhouse gas driven climate and ocean change poses a quintuple threat: ocean warming and heat waves, OA, deoxygenation, super-storms, and sea level rise - reefs having to ‘catch-up’ or ‘drown’, esp. on their lower slopes, and esp. if sea level rises rapidly and exceeds several metres over coming centuries. These are each mentioned in later sections of the manuscript.

Deoxygenation – consider mentioning that several of the ‘reef gaps’ in the fossil record coincide with periods of deoxygenation. Eg. See Veron, J.E.N. (2011) Mass Extinctions, Anoxic Events and Ocean Acidification. In: Hopley, D. (eds) Encyclopedia of Modern Coral Reefs. Encyclopedia of Earth Sciences Series. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-2639-2_37

Line 278:

“Moderate rates of sea level rise may potentially aid some reefs to contend with thermal stress ...”

Line 287:

“... , with plumes in large tropical river systems travelling many km from disturbance ...”

Line 306-307 seem better placed in this Section on Pollution:

“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 50km radius around a reef.”

Lines 301-309:

10. Disruption

LD: Consider a different sub-heading. The inclusion of Land use change, as a proxy for pollution, seems repetitive, as covered in section 9. Suggest focus here on Over-fishing and consider Diseases only in sub-heading 11.

Lines 320-322:

11. Diseases

“Regions such as the Great Barrier Reef, the Caribbean, the Pacific Islands, and the Indian Ocean have been particularly impacted by these outbreaks, in some places surpassing the devastating impact of bleaching events by causing even greater coral mortality. Coral diseases stand out as being driven largely by a changing environment and are contributing to whole ecosystem regime shifts (Thurber et al., (2020)....”

This statement appears too broad – perhaps ‘Some areas within the GBR ...’

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 SCTL 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 future, however, becoming more prevalent, interacting with heat waves.

Two additional, relevant references.

Cavada-Blanco F, Croquer A, Vermeij M, et al. (2022) *Dendrogyra cylindrus*. The IUCN Red List of Threatened Species 2022: e.T133124A129721366.
<https://www.iucnredlist.org/species/133124/129721366>.

Estrada-Saldívar N, Quiroga-García BA, Pérez-Cervantes E, et al. (2021) Effects of the Stony Coral Tissue Loss Disease outbreak on coral communities and the benthic composition of Cozumel reefs. *Front Mar Sci* 8: 632777. <https://doi.org/10.3389/fmars.2021.632777>

Diseases are also a major risk as ‘invasive species’, as more ornamental reef species are traded and transported, deliberately or accidentally, across and between ocean basins. For example, several Indo-Pacific species of fish and coral have been released, mainly it seems by aquarium hobbyists, into the Atlantic, and shipping ballast water also poses significant risk as a transport mechanism. This aspect could be included in an Interactions section.

13. Reef impact example

Lines 350-353: Edit for clarity

“... large areas are becoming covered by the encrusting and bioeroding sponge *Cliona* spp (Sheppard et al., 2020 skeletons formed a very abrasive layer on the substrate and, like liquid sandpaper, 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.”

This case study could be expanded to include more of the history, given it is one of the best studied remote reef systems. The paper would benefit from additional case-studies from Caribbean (nutrient enrichment, over-fishing, heat-waves, diseases, invasive species) and Great Barrier Reef (COTS, storms, run-off, heat waves, etc.), with summary noting differences in

resilience and potentially tipping points among the three systems in respect to oceanographic connectivity, coral population sizes, habitat heterogeneity etc.

15. Resilience and adaptation

Lines 390-391: Edit for clarity

“Evidence of a persistence of heat adapted genotypes at the cost of the reduction of coral diversity, i.e. the reef may survive but the biodiversity diminishes (Fox et al., (2021) Although ...”