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Earth's Future

COMMENTARY

10.1029/2024EF004879

Key Points:

- The ocean's capacity to provide viable habitats is being compromised by the combined threat of ocean warming and associated deoxygenation
- For marine organisms to survive, changes in environmental conditions should be slower than their ability to adapt
- Global warming is leading to more frequent and severe abrupt changes in ocean habitability

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Towards a Less Habitable Ocean

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Abstract Ocean warming and associated deoxygenation caused by anthropogenic global warming are impacting marine ecosystems. This article contextualizes and provides perspectives on key insights from a recently published study by Fröb et al. in *Earth's Future* (2024). The authors employ historical and high-emission scenario simulations through a state-of-the-art Earth system model to detect abrupt and persistent changes in the viability of marine habitats by leveraging an ecophysiological framework that quantifies how temperature and oxygen jointly limit the distribution of life in the ocean for a number of ecophysiotypes. A changepoint analysis is used to objectively detect shifts in decadal to multi-decadal mean states in potential marine habitats. They observe a decrease in the ocean volume capable of providing viable habitats for those ecophysiotypes with positive sensitivity to hypoxia. About half of these decreases occur abruptly, thus highlighting potential risks on the capacity of marine organisms to cope with a changing environment.

Plain Language Summary The unabated emission of atmospheric carbon dioxide from human activities threatens all ecosystems on Earth. In the ocean, marine organisms are encountering a warmer, less-oxygenated and acidified environment. While many of these changes occur gradually, allowing (in some cases) marine organisms time for adaptation, some alterations may happen abruptly, jeopardizing their ability to cope. This paper comments on the recently published study of Fröb et al., which explores the occurrence of such abrupt changes in the ability of marine ecosystems to provide viable habitats, drawing upon the well-established concept of the “metabolic index.” This index assesses whether the resting metabolic requirements of organisms are met by the availability of oxygen at a given temperature. By employing historical (1850–2014) and a high-emission scenario (2015–2100) as simulated by an Earth system model, the authors uncover that global warming has already begun to drive abrupt alterations in ocean habitability. These findings provide further evidence that ocean biodiversity is poised to undergo major changes during this century.

1. Introduction

Broadly speaking, habitability refers to an environment's ability to support life's necessities. In the case of marine ecosystems, these “needs of life” are essentially represented by the rate of dissolved oxygen supply that must exceed organisms' resting metabolic demand. With the current and projected warming of the ocean (Cheng et al., 2024), its oxygen-holding capacity is diminishing due to reduced oxygen solubility in seawater and increased vertical stratification (Breitburg et al., 2018; Helm et al., 2011; Oschlies et al., 2018). Conversely, the metabolic demands of marine organisms are anticipated to rise (Eaton et al., 2022; Gillooly et al., 2001). Consequently, a potential decline in the capacity of the ocean to support life is envisaged (Howard et al., 2020) as more energy-demanding organisms may not be able to meet their oxygen needs.

Both metabolic demand and oxygen availability are temperature dependent, giving rise to an index that gauges how ocean warming together with oxygen levels constrain the distribution of life in the ocean. Introduced back in 2015, the metabolic index (Φ ; Deutsch et al., 2015) established a framework for evaluating the extent of aerobic habitat conditions in the ocean and their alterations under global warming, by integrating the physiological responses to changing environmental conditions. Since then, this metric has found successful application in various fields, including biogeography studies (Deutsch et al., 2020), assessments of current climate change impacts (Deutsch et al., 2022; Parouffe et al., 2023), evaluation of the effects of climate overshoots (Santana-Falcón et al., 2023), and assessments of past (Penn et al., 2018; Stockey et al., 2021) and future risks (Penn & Deutsch, 2022) of mass extinctions. Writing in the present journal, Fröb et al. (2024) further demonstrate that ongoing global warming is leading to an increase in abrupt losses of ocean habitability, with potential implications for marine ecosystems.

2. Time Matters

Changing ocean conditions to which organisms are adapted have the potential to impact marine ecosystems. The so-called “deadly trio” of ocean warming, deoxygenation and acidification (Bijma et al., 2013), along with other anthropogenic stressors such as overfishing, plastics, and pollution, are indeed jeopardizing the survival of marine biota. While marine organisms may respond to these threats in various ways (Poloczanska et al., 2016), the severity of their impacts will ultimately depend on the time organisms have to develop coping strategies (Hoffmann & Sgrò, 2011; Seebacher et al., 2015).

Long term trends, such as global warming, present a progressive challenge for marine organisms to adjust to an evolving environment in order to meet their metabolic requirements. Tracking shifts in ocean temperature (Pinsky et al., 2013; Stuart-Smith et al., 2017), considered the best predictor of marine biodiversity (Lenoir et al., 2020; Tittensor et al., 2010), reveals that marine organisms are moving poleward and/or deeper (Hastings et al., 2020; Perry et al., 2005) to mitigate the risks of extinction. However, factors beyond temperature, such as food availability, changing pH levels, and species interactions, may impose constraints on the distribution shifts of threatened marine organisms (see Pinsky et al., 2020 for a review). Furthermore, seeking refuge at depth may be hindered by higher hydrostatic pressure (Thatje, 2021), changing thermal environments (Santana-Falcón & Séférian, 2022), or reduced oxygen availability, which compromises the hypoxic limits of organisms (Deutsch et al., 2015). Therefore, survival for species unable to relocate will depend on their capacity to acclimatize or adapt to “new” conditions. Acclimatization involves adjustments developed within an individual's lifetime to cope with environmental alterations, whereas adaptation entails changes occurring over many generations. Some organisms exhibit plasticity in their thermal tolerances (Seebacher et al., 2015), or undergo metabolic adjustments resulting from changes in body size (Audzijonyte et al., 2020; Deutsch et al., 2022). However, if environmental changes occur so abruptly as to overwhelm organisms' ability to migrate, acclimatize, or adapt, mass die-offs may ensue. Fröb and colleagues shine light into the occurrence of such abrupt alterations of the capacity of the ocean to provide viable habitats.

The perception of abruptness varies depending on the timescale considered. Current anthropogenic global warming, exemplified by the “hockey stick” curve (Mann et al., 1999), can be deemed abrupt when viewed in the context of global geological timescales. At the other end, short-term extreme events like marine heatwaves (Hobday et al., 2016) and compound events, where multiple extremes coincide (Gruber et al., 2021), represent another example of abrupt changes occurring from seasonal to decadal timescales that may cause acute stress to marine organisms with possible devastating outcomes (Smale et al., 2019).

In general, abrupt changes are associated with regime shifts from one state to another (Drijfhout et al., 2015; de Young et al., 2008). Therefore, it is necessary to understand the timescale of the “original state”, and its variability, to differentiate between regime shifts and natural fluctuations. Furthermore, identifying the threshold or “tipping point” that delimitates the regime shift is often challenging. In addition, the diversity of responses among organisms complicates our ability to identify risks of regime shifts in marine ecosystems. Fröb and colleagues addressed these by computing the metabolic index (Φ) for a number of constructed ecophysiotypes, assumed to include a number of marine organisms, using ocean temperature and pO_2 (partial pressure of oxygen) data simulated by an Earth system model under the historical and the high emission scenario SSP5-8.5 (Gidden et al., 2019). These extensive simulations, spanning from 1850 to 2100, enabled them to employ a changepoint analysis, as developed by Beaulieu and Killick (2018), to detect decadal to multi-decadal abrupt changes in Φ at each grid point and vertical levels up to 700 m depth.

Fröb and colleagues' analysis predicts key patterns in future occurrence of abrupt changes in marine ecosystems viability. First, they find that abrupt transitions from viable to non-viable habitats are projected to increase as we progress through the present century, with the majority occurring before 2040. This suggests that marine organisms are committed to face regime shifts in the coming decades regardless of the level of global warming. The authors focused on the SSP5-8.5 high-emission scenario, which represents the pessimistic end of scenarios considered in the last intercomparison project (i.e., CMIP6). Presumably, adopting a moderate emission scenario, such as the SSP2-4.5 which aligns more closely with the current pace of warming, would lessen the trend of the occurrence of abrupt changes; although the most significant differences between scenarios tend to occur after mid-century.

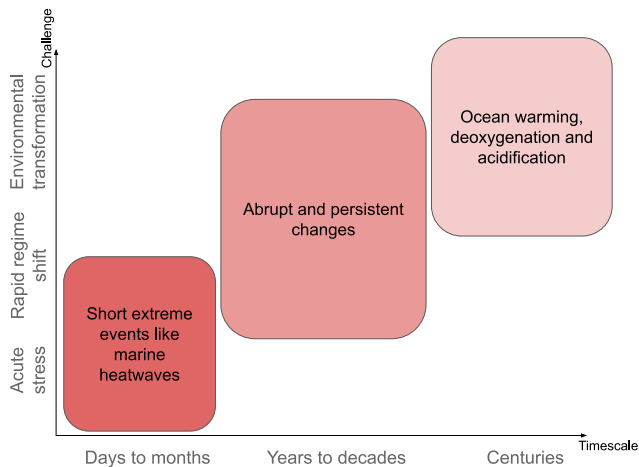


Figure 1. Schematics of ongoing threats to marine ecosystems induced by anthropogenic activities. As global warming persists, marine ecosystems will progressively encounter a warmer, less-oxygenated and acidified ocean. In addition, more frequent and severe abrupt shifts have begun to defy the capacity of marine ecosystems for adaptation. On top of those, recurrent and intense short extreme events are putting marine ecosystems beyond the limits of their resilience.

Second, while the changepoint methodology cannot identify the driver of abrupt changes, the authors decomposed Φ into its thermally and non-thermally driven components. This enabled them to discern whether changes in habitability were primarily driven by temperature or oxygen levels. They observed that most changes occur at the sea surface in response to warming, but also highlighted that abrupt losses of habitat viability below 200 m deep are driven by decreasing oxygen levels, imposing hypoxia limits.

Third, Fröb and colleagues measured the severity of the changes by the distance between Φ and the critical demand in oxygen (or Φ_{crit} , that is, the minimum metabolic requirements of an organism to carry out key physiological activities, which is a factor of Φ) at the moment at which the changepoint analysis indicates an abrupt shift. This exercise indicates an increase of the severity of the shifts, which further exacerbates the potential risks to organisms.

Alternative methodologies have recently emerged in studying abrupt changes in ocean conditions. Heinze et al. (2024), from the same research group, defined global anthropogenic forcings as background variability to examine abrupt changes in ocean warming, deoxygenation and acidification as those occurring at a faster rate. Akin to the “Time of Emergence” approach (Hawkins & Sutton, 2012), Trisos et al. (2020) introduced the concept of “Climate Horizon”, which identifies the projected time at which climate conditions (in terms of mean annual temperature) surpass the

realized niche at which a given organism lives. They considered exposure to unprecedented conditions abrupt when it affects most species in a given habitat simultaneously. Additionally, Frölicher et al. (2018) used satellite data and ESM simulations to analyze historical and future trends in marine heatwaves occurrences across the global ocean. Despite employing different methodologies and scopes, recent studies, including these, consistently indicate an increase in the frequency and intensity of abrupt changes. This convergence underscores that global warming not only steadily pushes marine organisms to their limits, but also heightens the likelihood of regime shifts, destabilizing their ability to cope with both anthropogenic and natural stressors (Figure 1).

3. Physiological Approach

The metabolic index is built upon species-specific physiological parameters representing the organism's thermal and hypoxia sensitivities. Consequently, generalizing results poses a challenge since physiological parameters have only been estimated for a few dozens of species. Apart from focusing solely on individual species (as in Parouffe et al., 2023 or Burford et al., 2022), alternative approaches have been devised to address this limitation. One workaround involves building a probability range distribution of Φ computed for species with known parameters as demonstrated in Santana-Falcón et al. (2023). Another approach is to define metabolic traits, as proposed by Deutsch et al. (2020), and then compute ecophysiotypes based on their distribution, as exemplified by Howard et al. (2022) or Stockey et al. (2021). In line with this latter approach, Fröb and colleagues constructed nine ecophysiotypes by exploring the distribution of thermal and hypoxia sensitivities for 61 species (see Deutsch et al., 2020). They assigned six values to their critical demand in oxygen (i.e., Φ_{crit}) based on previous literature. While this approach may include considerable variability, physiological parameters still fall within the range provided by a limited number of species. Considering the approach of Fröb and colleagues as valid for most marine species, they found a consistent increase in abrupt losses of viability across all ecophysiotypes that peaks around the 2030s. However, the extent to which Φ is enough to inform species responses and distributional shifts remains controversial.

Most research on biogeography has been focused on changes in ocean temperature, from which Φ , by incorporating hypoxia sensitivities to the equation, should provide a more complete picture. However, Φ is based on the fact that organisms' thermal tolerance is limited by oxygen supply, which is under debate (see Seibel & Deutsch, 2020). Indeed, projections based only on temperature tend to have similar findings,

probably because Φ assumes organisms are more sensitive to hypoxia at higher temperatures. At cold temperatures the ability of a given organism to supply oxygen to its tissues declines more than does metabolic demand, hence, Φ better describes the warm edge of a species thermal tolerance. In this sense, Endress et al. (2024) recently generalized the Φ framework suggesting oxygen limitation also constrains the distribution of species toward cold edges. On the other hand, Φ -based physiological parameters come from laboratory experiments, which may yield different estimations and not be indicative of real conditions. All in all, as beautifully explained by Seibel (2024), Φ depends upon a number of assumptions that need to be further investigated to accurately interpret its projections, especially as studies suggest major rearrangements of marine biota, including decreases in habitability and mass extinctions. As shown by Slesinger et al. (2024), the utility of Φ differs among the species considered. In addition, other factors such as physical barriers, changes in ocean currents, salinity, or prey availability, which is a key factor limiting the distribution of predators, may also play a role. In line with this, the third most relevant factor affecting marine ecosystems, ocean acidification, remains unexamined.

When CO₂ enters the ocean via the air-sea interface, it causes pH reductions and alterations of the carbon chemistry balance by forming carbonic acid in a process called ocean acidification (Caldeira & Wickett, 2003). pH has already decreased by ~0.11 units (Orr et al., 2005), and it is projected to further decrease up to ~100%–150% following the low-mitigation SSP5-8.5 (Kwiatkowski et al., 2020). Though calcifying marine organisms as corals for which ocean acidification alters the production of calcium carbonate that provides the foundation of their structure will be the most heavily impacted (Kroeker et al., 2013), other marine organisms such as fishes (e.g., Bignami et al., 2013) can be impacted while not accounted for in the metabolic index framework.

A similar approach tackling the capacity of the ocean to hold viable habitats is provided by the Aerobic Growth Index, or AGI (Clarke et al., 2021), which is also based on that temperature-dependent hypoxia sets limits to metabolically viable habitats. Analogously to Fröb and colleagues, Morée et al. (2023) found a decrease in the viable ocean volume as ocean warming persists into the present century. These studies posit that AGI may be more easily applicable to a greater number of species. However, as with Φ , AGI ultimately assumes organisms are limited by oxygen supply, and thus questions about Φ interpretation also apply to AGI.

4. Results Leveraging Ocean Risk for Concerns

Research on the impacts of ocean warming and accompanying deoxygenation to marine ecosystems is gaining attention, yet many questions remain unanswered. Fröb and colleagues dig into the occurrence of abrupt changes in temperature and oxygen jointly, defining metabolically viable marine habitats by leveraging the metabolic index framework. As a key contribution, they observe that about half of the losses of ocean viability detected occur abruptly. Changes that outpace the ability of organisms to acclimate, adapt and migrate would pose a lethal threat. Thus, abrupt shifts such as those highlighted by the authors are poised to potentially affect marine ecosystems. In addition, they found that most of these abrupt changes would occur before 2040, highlighting that the major changes the ocean is undergoing have already begun to alter the ocean's habitability. Despite issues remaining about the metabolic index interpretation, these results clearly indicate that the abruptness of the changes in temperature and oxygen is another stressor dooming marine ecosystems, especially for those organisms unable to move which are highly vulnerable. Future research, building on this work, should examine the response of marine ecosystems to abrupt changes in order to develop effective adaptation strategies to prevent an enduring ocean from becoming uninhabitable.

Data Availability Statement

Data were not used, nor created for this commentary.

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