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The role of CO_2 variability and exposure time for biological impacts of ocean acidification

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[1] Biological impacts of ocean acidification have mostly been studied using future levels of CO_2 without consideration of natural variability or how this modulates both duration and magnitude of CO_2 exposure. Here we combine results from laboratory studies on coral reef fish with diurnal in situ CO_2 data from a shallow coral reef, to demonstrate how natural variability alters exposure times for marine organisms under increasingly high-CO_2 conditions. Large in situ CO_2 variability already results in exposure of coral reef fish to short-term CO_2 levels higher than laboratory-derived critical CO_2 levels (~600 µatm). However, we suggest that the in situ exposure time is presently insufficient to induce negative effects observed in laboratory studies. Our results suggest that both exposure time and the magnitude of CO_2 levels will be important in determining the response of organisms to future ocean acidification, where both will increase markedly with future increases in CO_2. **Citation:** Shaw, E. C., P. L. Munday, and B. I. McNeil (2013), The role of CO_2 variability and exposure time for biological impacts of ocean acidification, *Geophys. Res. Lett.*, *40*, 4685–4688, doi:10.1002/grl.50883.

1. Introduction

[2] There has been a rapid expansion of ocean acidification research over the past decade since *Kleypas et al*. [1999] and *Caldeira and Wickett* [2003] published modeled predictions of how global ocean pH would change as a result of increasing CO_2 emissions. Annual ocean acidification-related publications increased tenfold from 2004 to 2010, with the majority of publications describing biological effects of changes to seawater chemistry [*Gattuso and Hansson*, 2011]. While perturbation experiments that determine the impacts of ocean acidification on organisms have expanded to include an increasingly large number of different species and life history stages [*Albright*, 2011; *Kroeker et al*., 2010], the carbonate chemistry levels used in these experiments have mostly been set at some constant future atmospheric CO_2 level [*McElhany and Busch*, 2013]. Many of the most vulnerable species to ocean acidification are found in coastal environments that exhibit large natural variability compared with that of the open ocean [*Hofmann et al*., 2011; *McElhany and Busch*, 2013]. Large natural variability in CO_2, whether diurnal or seasonal, has the potential to significantly alter the duration of time that organisms and habitats are exposed to a given CO_2 level in the future. In this study, we seek to first understand and illustrate theoretically how natural variability will modulate CO_2 exposure times for organisms and habitats. We then combine in situ carbonate chemistry data from a coral reef along with the CO_2 levels known to cause behavioral impairments of coral reef fishes, to illustrate how CO_2 exposure times and magnitudes, and the associated biological impacts, will be modulated in the future. Although the data used in this synthesis study are taken from a highly varying shallow coral reef, the implications are important for other marine habitats that have some degree of natural diurnal or seasonal variability in CO_2.

2. How Does Natural Variability Modulate CO_2 Exposure Time?

[3] Partial pressure of CO_2 (pCO_2) and pH in coastal marine systems have been found to exhibit large variability on a variety of timescales, indicating that organisms in those environments are exposed to considerable natural temporal and/or spatial variability in carbonate chemistry [*Hofmann et al*., 2011] (Figure S1 in the supporting information). There are a number of different environments that experience large natural variability. Shallow coral reefs can experience diurnal changes in carbonate chemistry that exceed the predicted end-century open ocean changes [*Santos et al*., 2011; *Shaw et al*., 2012]. This is due to high levels of benthic community metabolism, where these changes are diluted with increasing depth, such that deeper reefs do not experience the same magnitude of change [*Bates et al*., 2001]. Other shallow productive environments, such as sea grass meadows, intertidal and subtidal pools, and rocky reefs, can experience similar, and even larger, natural diurnal variability than coral reefs due to biological metabolism [*Bensoussan and Gattuso*, 2007; *Christensen et al*., 2011; *Invers et al*., 1997]. Upwelling of CO_2-rich waters can also lead to large seasonal increases in seawater pCO_2 in coastal environments [*Feely et al*., 2008; *Thomsen et al*., 2010]. In high-latitude seas, seasonal carbonate chemistry variability occurs in response to seasonal changes in upwelling, biological production, and sea ice melt [*McNeil and Matear*, 2008; *Yamamoto-Kawai et al*., 2009]. Extreme variability is also observed in estuarine and mangrove environments in response to variability in physical and biological processes [*Chen and Borges*, 2009]. Importantly, the variability in these environments is likely to increase in the future as long-term anthropogenic changes to oceanic CO_2 reduce the ability of the ocean to buffer these natural changes [*Melzner et al*., 2013; *Schulz and Riebesell*, 2013; *Shaw et al*., 2013].

Additional supporting information may be found in the online version of this article.

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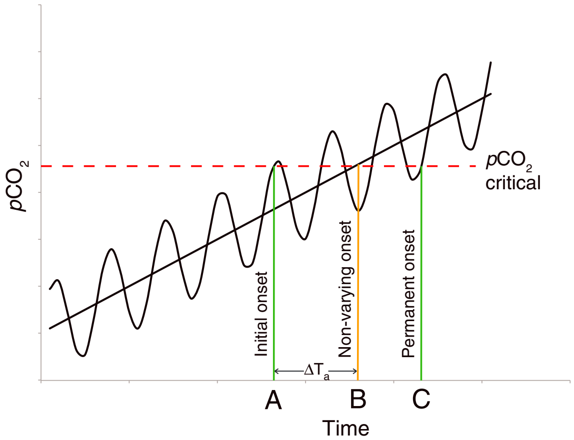

Figure 1. Conceptual diagram of how natural variability in carbonate chemistry modulates the onset of ocean acidification impacts. Black lines show an increasing atmospheric CO_2 signal, along with a periodic oceanic natural variability signal (could be diurnal or seasonal). For a given pCO_2 threshold for which impacts are observed in a species or ecosystem, then natural variability will hasten the initial crossing of this value (initial onset, green line), but delay the amount of time until this level of CO_2 is permanently crossed (permanent onset, green line), compared with the nonvarying scenario (orange line). For a diurnal signal, the daily exposure beyond a given threshold will increase from <1 h at initial onset to ~12 h at nonvarying onset, up until 24 h a day when atmospheric CO_2 levels are well beyond the pCO_2 threshold.

[4] Given the large natural variability that has been observed in many marine habitats, it is important to understand how these short-term variations will combine with the long-term average increases in atmospheric CO_2 over the coming century. Figure 1 shows an idealized marine habitat subject to both short-term natural variability and long-term average increases in atmospheric CO_2. Added is a critical pCO_2 threshold, which can be thought of as a known biological impact level for CO_2 on a species, as determined in the laboratory or elsewhere.

[5] In a naturally varying marine environment subject to long-term atmospheric CO_2 increases, the onset and exposure times of biological thresholds for pCO_2 vary significantly over a considerable time period (Figure 1). Natural variability brings forward the initial onset of a critical pCO_2 threshold by ΔT_a (Figure 1). At this time point (time A), the pCO_2 critical threshold is reached despite average pCO_2 levels being lower than the critical level. If a diurnal signal, the initial exposure time maybe an hour or two during each day; while if seasonal in nature, it could be a month or two [*McNeil and Matear*, 2008].

[6] As atmospheric CO_2 continues to increase in this variable marine environment, at some point, the average pCO_2 matches the critical pCO_2 level (i.e., time B). However, the CO_2 exposure time in the naturally variable habitat differs from a nonvarying environment, whereby for approximately half of the time pCO_2 levels will be above and half of the time below the critical pCO_2 threshold in the varying habitat. This is critically important, since the high-CO_2 levels used in most laboratory experiments are nonvarying [*McElhany and Busch*, 2013]. Exposing marine organisms to permanently high CO_2 without regard to the in situ reality that for up to half of the time, the organisms could be exposed to pCO_2 levels below the critical level could lead to misleading biological results. Eventually, with increases in atmospheric CO_2, the anthropogenic change moves beyond the magnitude of natural variability, whereby exposure time for a marine environment is permanently above the critical threshold (i.e., time C). In reality, most experimental studies have been examining the impacts of marine organisms when subject to this permanent condition, rather than a varying CO_2 exposure.

3. Real-World Example: CO_2 Exposure Times for Coral Reef Fish in a Naturally Varying Habitat

[7] To illustrate a real-world example, we use in situ carbonate chemistry data for a coral reef flat at Lady Elliot Island (LEI) in the Great Barrier Reef [*Shaw et al.*, 2012], combined with laboratory knowledge of biological pCO_2 thresholds for coral reef fish species that are known to inhabit this habitat. By combining both the chemical and biological data, we seek to demonstrate how natural variability significantly alters exposure times for these coral reef fish under high CO_2 conditions. pCO_2 levels at LEI were observed to range from 70 to 1325 µatm, driven primarily by reef metabolic processes (photosynthesis/respiration and calcification/dissolution) at shallow depth [*Shaw et al.*, 2012]. Presently, pCO_2 levels on the reef flat vary from a mean minimum daily value of ~200 µatm to a mean maximum of ~900 µatm. By end-century under higher CO_2 levels, the same metabolic processes that drive natural variability at LEI will result in a predicted daily pCO_2 range of 400–2100 µatm, with the amplification in pCO_2 range occurring as a result of the decline in seawater buffer capacity [*Shaw et al.*, 2013] (Figure 2a).

[8] Meanwhile, laboratory experiments on a number of coral reef fishes (e.g., clownfish, damselfish, and cardinal fish) have shown significant impairment of behavioral and sensory performance at pCO_2 levels of 550–950 µatm, levels within the present range of natural variability (Figure 2a). Abnormalities include increased boldness and activity [*Munday et al.*, 2010], loss of behavioral lateralization [*Domenici et al.*, 2012], altered auditory preferences [*Simpson et al.*, 2011], and impaired olfactory function [*Cripps et al.*, 2011; *Dixson et al.*, 2010; *Munday et al.*, 2009], the latter affecting predator-prey interactions, habitat selection, and homing ability [*Allan et al.*, 2013; *Cripps et al.*, 2011; *Devine et al.*, 2012; *Ferrari et al.*, 2011; *Munday et al.*, 2010].

[9] Given the known pCO_2 impact threshold for these coral reef fish (~600 µatm), how does the daily exposure times for this threshold vary as atmospheric CO_2 levels increase? The coral reef fish at the LEI reef flat are presently exposed to pCO_2 levels of ≥600 µatm for ~5 h per day, which will increase to ~21 h per day by end-century (Figure 2b). Furthermore, the magnitude of CO_2 exposure will be considerably higher by end-century (Figure 2). However, although laboratory evidence suggests that biological impacts for coral reef fish start at 600 µatm, our results from LEI show that even when atmospheric CO_2 reaches this level (year 2060), seawater CO_2 levels in this particular coral reef will be below this known biological threshold for ~12–14 h of each day (levels ranging from 290 to 600 µatm) (Figure 2b). This example demonstrates how exposure time significantly varies and evolves into the future for marine organisms living in naturally variable habitats.

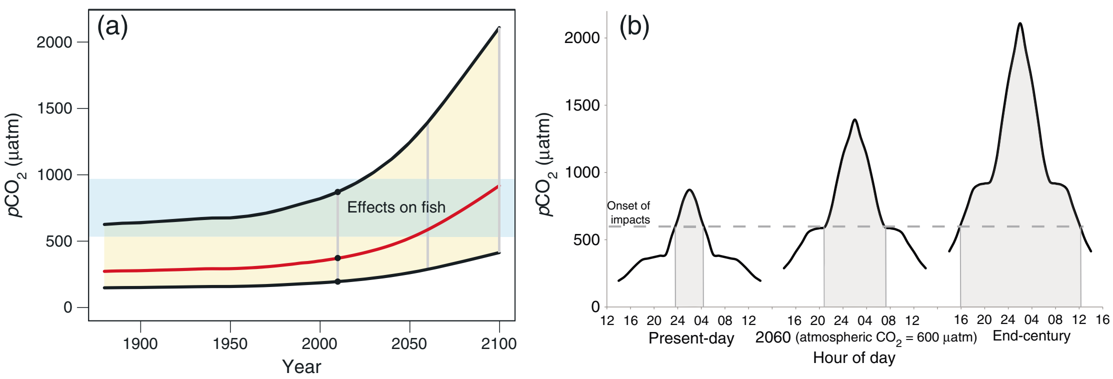

Figure 2. The pCO_2 magnitude and exposure at Lady Elliot Island (Great Barrier Reef). (a) pCO_2 natural variability measured in 2010 (black dots) and future projections [*Shaw et al.*, 2013]. Minimum and maximum reef flat projections are in black, and the mean open ocean projection is in red. Years 2010 (~present), 2060, and 2100 (end-century) are indicated with gray lines. pCO_2 levels at which negative responses in coral reef fish have been observed are indicated. (b) Diurnal variability in CO_2 exposure magnitude for a given day for present, 2060 (atmospheric CO_2 level of 600 μatm), and end-century. Shaded areas show the number of hours per day above critical CO_2 level for which impacts have been observed in coral reef fish.

4. Discussion

[10] Toxicological studies show that the response of an organism to a stressor is dependent on both the magnitude and duration of exposure. Our biological understanding of ocean acidification impacts has been focused on the semipermanent chronic changes that are unfolding in a high-CO_2 world. Due to a paucity of measurements, our understanding of the biological processes during natural short-term (diurnal to seasonal) marine CO_2 events has been lacking. However, these events can result in acute exposure to CO_2 levels that are of equal or greater magnitude and severity to those predicted from anthropogenic ocean acidification and can provide new insights into species resilience.

[11] The same species of fish that experienced impairment of behavior and sensory performance in the laboratory at pCO_2 levels of 550–950 μatm likely inhabit shallow reef flats that already have short-term CO_2 levels of up to 1300 μatm. We suggest that this is possible because the duration of exposure to high CO_2 is presently insufficient to induce the physiological changes responsible for behavioral and sensory impairment. *Munday et al*. [2010] demonstrated that behavioral effects of high CO_2 take 24–96 h to manifest for coral reef fish, depending on the CO_2 level experienced. In a recent study, *Nilsson et al*. [2012] showed that changes to ion concentrations in the tissues of fish exposed to high CO_2 are responsible for the diverse effects of high CO_2 on behavior and sensory abilities of marine fish. When exposed to high CO_2, fish regulate the concentration of acid-base relevant ions (primarily HCO_3^- and Cl^-) to maintain blood and tissue pH despite higher blood pCO_2. These changes in ion concentrations interfere with brain neurotransmitters, causing abnormal responses to sensory cues. Importantly, restoration of acid-base is usually achieved over a period of 8–48 h [*Brauner and Baker*, 2009; *Esbaugh et al*., 2012]. Therefore, the ionic changes responsible for behavioral impairment occur on a longer timescale than the short-term extremes of high CO_2 that are naturally experienced on the reef (1–6 h). This mismatch between timescales may help explain why behavioral impairment does not occur in fish currently living in shallow reef habitats. While fish likely experience some level of respiratory acidosis and alkalosis during routine short-term fluctuations in CO_2 on the reef, the duration of exposure to high CO_2 may not be currently sufficient to induce the serious neurological effects that occur as a result of longer-term exposure to high CO_2.

[12] Variable CO_2 exposure times also provide important insight into the vulnerability of marine organisms to future ocean acidification. Populations from highly variable environments may be more tolerant to future high pCO_2 than populations from less variable environments [*Melzner et al*., 2009]. However, the timescale of exposure is an important consideration; organisms may not respond to high pCO_2 on the timescale that natural variability operates (diurnal timescale in this case) but may respond with longer-term exposure to high pCO_2. We show that coral reef fish at the study site are presently exposed to pCO_2 levels of ≥600 μatm for ~5 h per day but that by end-century, this will increase to ~21 h per day (Figure 2b). Furthermore, the magnitude of CO_2 exposure will be considerably higher by end-century (Figure 2). This is important as the duration of time to the onset of a response has been shown in a number of toxicological studies to be inversely related to the magnitude of exposure [*Rozman*, 1999, and references therein]. This has already been observed with CO_2 perturbation experiments on fish, where the onset of negative impacts of CO_2 has been shown to be shorter at higher exposure concentration [*Munday et al*., 2010]. While populations of species that inhabit variable environments may be more resilient to increases in pCO_2, these populations will also experience more extreme conditions in the future via the nonlinear amplification of the maximum pCO_2 values (Figure 2) [*Shaw et al*., 2013].

5. Conclusions

[13] As ocean acidification research has evolved, it has become apparent that there is large variability in the carbonate chemistry that many organisms experience, either for part or all of their life history, and that this will influence their vulnerability to future ocean acidification. Our work seeks to show how naturally varying environments will significantly modulate the onset of certain future pCO_2 thresholds for marine organisms. By using both theoretical and in situ data, we conclude that exposure time for CO_2 could be just

as important as the magnitude of ocean acidification itself in understanding how marine species will respond to a high CO_2 world. Future work will be required to determine more quantitatively how exposure to natural variability influences resilience and to improve our understanding of the interaction between the magnitude of pCO_2 exposure and the duration, where both the exposure time to critical CO_2 levels as well as the magnitude of CO_2 exposure will increase with increasing anthropogenic CO_2 emissions.

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