Coping with Climate Change: Evaluating the Plastic Responses of Brittle Stars to Ocean Acidification and Warming

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Abstract

Beginning in the Industrial Revolution, increasing levels of carbon dioxide produced by human activity have been absorbed into the ocean, lowering its pH, in a process called ocean acidification (OA). OA has been shown to have negative effects on the growth, development, and survival rates of a multitude of marine organisms, most notably calcifiers, which are organisms that make and use calcium carbonate to form their shells or skeletons. Ocean warming (OW), the global increase in water temperature, is occurring simultaneously. Thus, it is necessary to study the combined impact that OA and OW has on marine organisms. Studies have examined the effects of OA and OW on marine species with aquacultural importance, while research on other organisms, such as echinoderms, is less prevalent. This project will explore the pre-existing abilities of brittle stars, a type of echinoderm, to plasticly respond to OA and OW on short time scales. The potential for marine organisms to acclimate to near-future water conditions will be important to consider as we work to reduce the impact of climate change on marine environments.

Introduction

The unprecedented levels of carbon dioxide (CO_2) in the atmosphere caused by human activity, primarily greenhouse gas emissions, have drastic effects on the ocean and marine environments (IPCC, 2023). As atmospheric CO_2 is absorbed by seawater, carbonic acid (H_2CO_3) forms, which then dissociates into bicarbonate (HCO_3^-) and hydrogen ions (H^+), causing the water to become more acidic (Figure 1). As a result of ocean acidification (OA), the ocean's pH, currently 8.1, has decreased by 0.1 units since the Industrial Revolution and is predicted to drop to around 7.8 by the year 2100 (Doney et al., 2009). The impact of OA on calcifying organisms is widely recognized because it leads to a lack of available carbonate ions (CO_3^{2-}), which calcifiers use to form calcium carbonate ($CaCO_3$) for certain skeletal structures (Leung et al., 2022) (Figure 1). Greenhouse gas emissions have also raised global temperatures by 1.1°C since the later half of the 19th century (IPCC, 2023). Ocean warming (OW) has been shown to negatively affect survival in marine organisms; they are able to tolerate temperatures within a certain range, though survival steadily declines outside of this range (Harvey et al., 2013). OW is occurring along with OA, so it is important to study the effects of these stressors combined in order to form realistic predictions and possible solutions for mitigating climate change's impact on marine ecosystems. Additionally, interactions between OA and OW could lead to varied effects (Harvey et al., 2013; Kroeker et al., 2013; Lang et al., 2023).

Existing research on echinoderms has shown them to be more resistant to OA compared to other groups of organisms such as mollusks, coccolithophores, calcifying algae, and corals (Dupont et al., 2010; Kroeker et al., 2013; Leung et al., 2022). Thus, they are likely already capable of acclimating to water chemistry changes in certain ways, such as increasing metabolic and calcification rates. Brittle stars, a type of echinoderm, are ecologically important. Research on brittle star skeletal composition suggests that their skeletons are particularly high in magnesium. Therefore, it is proposed that they will be especially vulnerable to dissolution caused by OA due to the increased solubility of magnesium calcite (Azcarate et al., 2024; Dubois, 2014; McClintock et al., 2011). However, research on how climate change impacts brittle stars is lacking (Kroeker et al., 2013). Brittle star populations can be found across the globe in varying habitats, including benthic ecosystems and intertidal regions. Brittle stars use their arms for movement and feeding, and they can regenerate if damaged or lost. Brittle stars, especially burrowing species, are key members in their ecosystems because of their roles in bioturbation (i.e., moving around and reworking the sediment) and biogeochemical cycling (Wood et al., 2011; Kristensen et al., 2012; Hu et al., 2014; Christensen et al., 2017). For example, burrowing brittle stars often have to ventilate their burrows, which contributes to oxygen flow in benthic ecosystems (Christensen et al., 2017).

Compared to other echinoderms, less is known about the response of brittle stars to OA or OW (Kroeker et al., 2013), despite them being vulnerable to these stressors and vital members of marine ecosystems. Therefore, this literature review will examine how brittle stars respond to OA and OW on short time scales and summarize their current physiological capacity to cope with these stressors. This work will aim to identify and explain the characteristics of brittle stars that help facilitate acclimation through analyzing how OA and OW affects them, and the differences in resiliency among populations around the world. For the literature analysis, a reference list was generated in Scopus by entering the keywords ocean acidification, global warming, ocean warming, warming climate, pH, CO_2, and brittle stars, and setting the date range to January 2013 to May 2025. These sources were supplemented with relevant articles found on Google Scholar and by backwards citation tracking (i.e., finding references in a reference list). From this research, I found that brittle stars are able to acclimate to short-term OA and OW by increasing metabolic rate and net calcification rate (Christensen et al., 2011; Christensen et al., 2017; Liao et al., 2025; Wood et al., 2008; Wood et al., 2011; Márquez-Borrás and Sewell, 2024). Observed changes in behavior such as the retraction of arms into burrows (Hu et al., 2014) and slower righting response (Márquez-Borrás and Sewell, 2024) were also observed under OA and OW conditions. However, these responses are often associated with biological and energetic costs such as muscle wastage (Márquez-Borrás and Sewell, 2024; Wood et al., 2008; Wood et al., 2011), poor burrow ventilation, and reduced feeding (Hu et al., 2014). Longer-term exposure to more severe OA conditions may even induce metabolic depression (Hu et al., 2014). Furthermore, brittle stars populations found in polar regions appear to be more vulnerable to OA and OW compared to populations in intertidal areas (Márquez-Borrás and Sewell, 2024; Peck et al., 2009; Wood et al., 2011). Knowledge of the acclimation abilities of brittle stars could be used to predict potential changes to populations in the future, and help direct efforts that address the impact of climate change on brittle stars to the species and habitats that are most vulnerable to OA and OW.

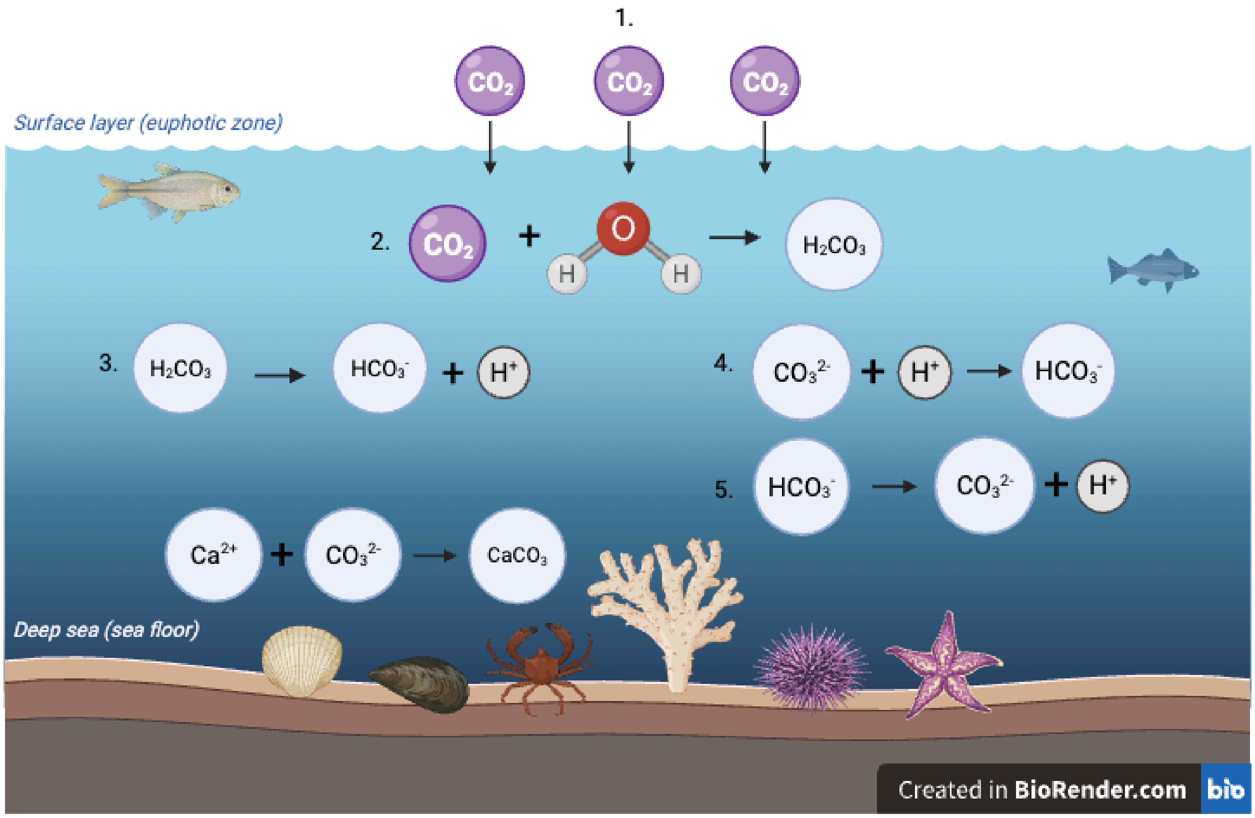


Figure 1. Chemistry of ocean acidification and its impact on calcifiers. Atmospheric carbon dioxide (CO_2) is absorbed by sea water (Step 1) and reacts to form carbonic acid (H_2CO_3) (Step 2). Carbonic acid then dissociates into bicarbonate (HCO_3^-) and hydrogen ions (H^+), and an increase in hydrogen ion concentration causes a decrease in ocean pH (Step 3). Calcium carbonate ($CaCO_3$) formation requires calcium (Ca^{2+}) and carbonate ions (CO_3^{2-}), however carbonate ions also react with hydrogen ions to form bicarbonate ions (Step 4). Bicarbonate further dissociates into carbonate and hydrogen ions (Step 5). Thus, an increase in hydrogen ion concentration makes calcium carbonate less available to calcifiers including brittle stars.

Impact of OA, OW, and combined stressors on brittle stars

Previous research on brittle star responses to OA and OW measures the impact of OA and OW on survival, growth, calcification, and metabolism. The results of the literature analysis were compiled into a table reporting neutral, positive, and negative effects that OA, OW, and the two processes combined had on brittle star species, including some findings about brittle star larvae. Experimental methods such as the type and duration of the study, as well as the pH and temperature treatments simulating OA and OW conditions, are also noted (Table 1). Bar graphs displaying the information in this table were then created for OA and OW (Figure 2). Based on the available literature, OA seems to negatively impact survival and growth of brittle stars. OA seems to have an overall neutral effect on calcification, although one study reported increased calcification rates and one study reported decreased rates. OA typically has a positive effect on metabolism, causing increased metabolic rate, although three studies found that it decreased under specific pH conditions. The literature analysis suggests that OW negatively impacts survival in brittle stars. Growth appears to have increased under elevated temperature, although one study suggested decreased growth in response to elevated temperature. Calcification seems to be neutrally or negatively affected by OW, and several studies suggest that metabolism was positively affected by it (Figure 2).

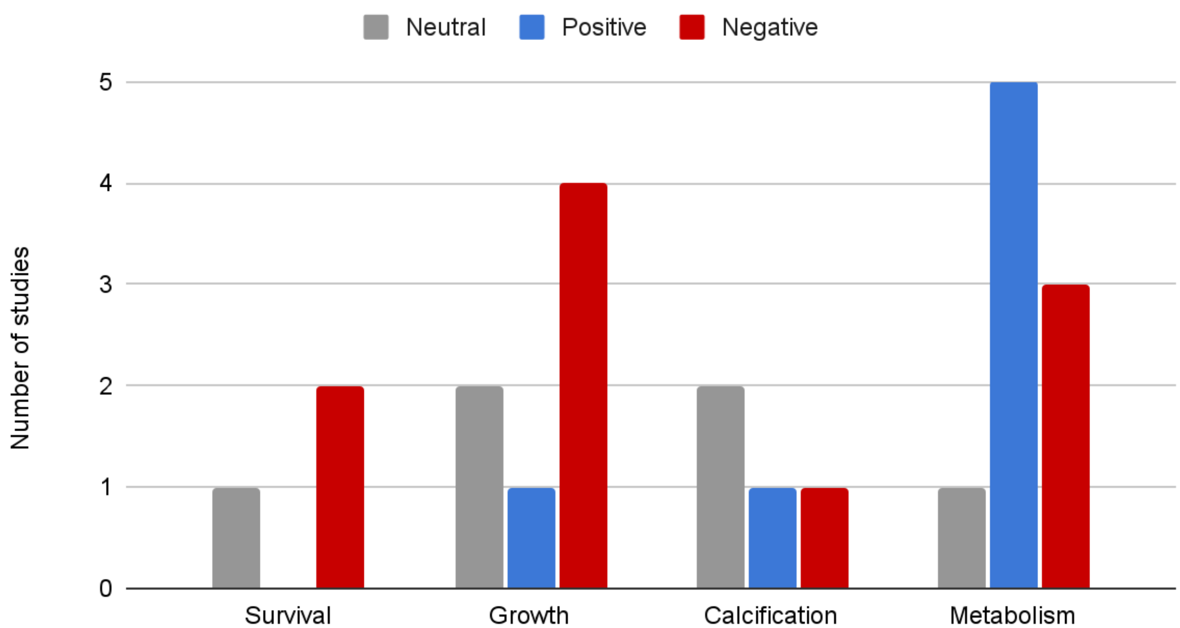
Compared to the effects of OA and OW separately, fewer studies have examined the combined effect of OA and OW on brittle stars. However, existing research suggests that in regards to OA and OW combined, calcification may be neutrally or negatively impacted while metabolism may be positively affected (Table 1). The interaction between OA and OW produces complex effects on brittle stars and lacks sufficient research (Christensen et al., 2017; Márquez-Borrás and Sewell, 2024), so it is necessary to continue studying their combined impact. Survival and growth in brittle star larvae appear to be negatively impacted by OA (Table 1), which could act as a bottleneck to brittle star populations overall (Chan et al., 2016; Dupont et al., 2008). Brittle star larvae are often displaced to neighboring populations, so a local OA event prior to displacement could impact populations within a broader region. More research on the impact of OA and OW on brittle stars during all life stages is needed in order to better understand how adult populations will truly be impacted (Dupont et al., 2008).

Table 1. Impact of ocean acidification (OA) and warming (OW) individually and when combined on survival, growth, calcification, and metabolism in brittle stars based on results of the literature review analysis. Effects on survival (S) were determined by changes in mortality rates. Changes in growth (G) were determined by body size and arm regeneration. Calcification (C) was measured by calcium content in the arms, or percent inorganic carbon or percent inorganic content. Metabolism (M) was monitored by oxygen uptake and/or respiration rates. Each effect is either neutral (0), positive (+), or negative (-), and only statistically significant results are included. Effects are based on how organisms responded under experimental conditions compared to the control groups. For laboratory-based methods, the experiment duration is included under Methods. *O. fasciata* = *Ophionereis fasciata*, *O. sericeum* = *Ophiocten sericeum*, *A. filiformis* = *Amphiura filiformis*, *H. cordifera* = *Hemipholis cordifera*, *M. gracillima* = *Microphiopholis gracillima*, *O. fragilis* = *Ophiothrix fragilis*, *O. victoriae* = *Ophionotus victoriae*, *O. schayeri* = *Ophionereis schayeri*, *O. sarsii vadicola* = *Ophiura sarsii vadicola*.

Species	Citation	Acidification				Warming				Combined				Methods	pH and Temperature
		S	G	C	M	S	G	C	M	S	G	C	M		
A. filiformis	(Hu et al., 2014)		-		- 7.0 + 7.3									Lab 4 weeks	7.0, 7.3
A. filiformis	(Wood et al., 2008)		+	+	+									Lab 40 days	6.8, 7.3, 7.7
A. filiformis larvae	(Chan et al. 2016)	-	-											Lab 7 days	7.3, 7.7
H. cordifera *M. gracillima*	(Christensen et al., 2017)		0	0	+ H. cordifera 0 M. gracilima	-	+	0	+ H. cordifera 0 M. gracillima			0	+	Lab 2 months	7.6, 7.8 25°C, 28°C, 32°C

Species	Citation	Acidification				Warming				Combined				Methods	pH and Temperature
		S	G	C	M	S	G	C	M	S	G	C	M		
O. fasciata	(Márquez-Borrás and Sewell, 2024)	0	0	-	-	-	-	-	+	0	0	-		Lab 15 weeks	7.6, 7.7 21°C, 24°C
O. fragilis larvae	(Dupont et al., 2008)	-	-											Lab 8 days	7.7, 7.9
O. sarsii vadicola	(Liao et al. 2025)					0			+					Lab 1 week, 2 months	19°C
O. schayeri	(Christensen et al. 2011)				- 7.8 + 7.4, 7.6	-			+				+	Lab 5 weeks	7.4, 7.6, 7.8 25°C
O. sericeum	(Wood et al., 2011)		-	0	+		+	0	0					Lab 20 days	7.3, 7.7 8.5°C
O. victoriae	(Peck et al. 2009)					-								Lab	2°C, 3°C

A



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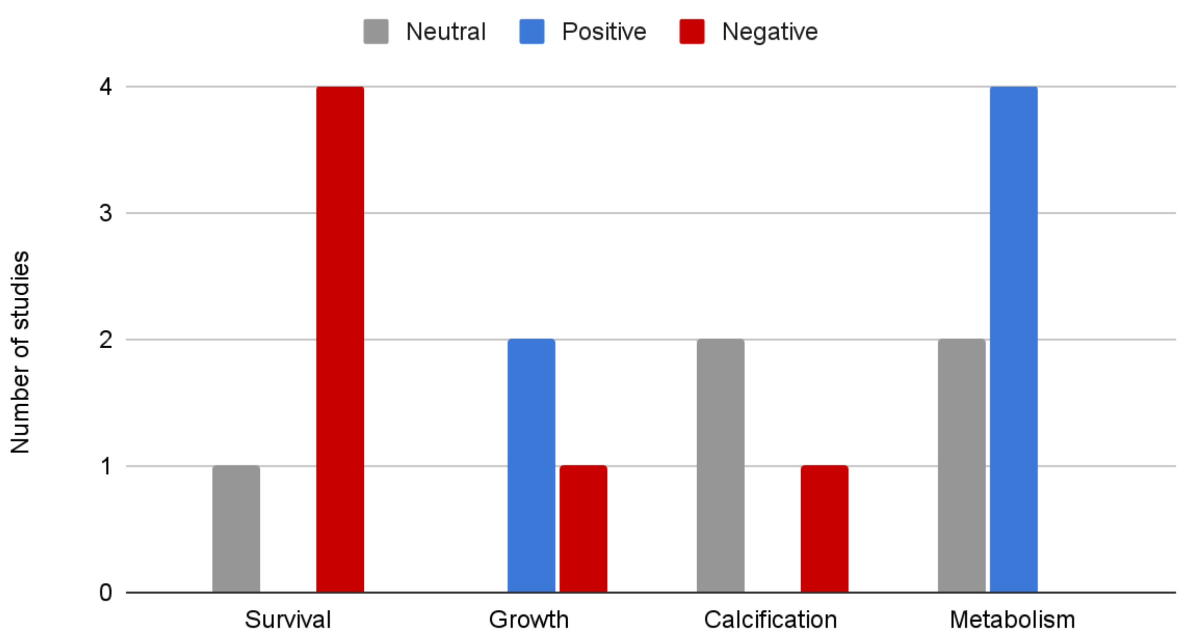

Figure 2. Number of studies from the literature review analysis reporting neutral, positive, and negative effects of ocean acidification (A) and warming (B) on survival, growth, calcification, and metabolism in brittle stars. All studies in Table 1 are included. The pH, temperature, or species dependent results are each considered separate findings.

Physiological responses to OA and OW

Recent studies have shown that metabolism and calcification in brittle stars is increased under elevated temperature and lower pH conditions. Metabolic rates in brittle stars are typically determined through measuring oxygen uptake and respiration rates. In the brittle stars *Amphiura filiformis*, *Ophiocten sericeum*, *Hemipholis cordifera*, and *Ophionereis schayeri*, increased metabolism occurred under low pH conditions (Christensen et al., 2011; Christensen et al., 2017; Hu et al., 2014; Wood et al., 2008; Wood et al., 2011). In response to elevated temperature, *Ophionereis fasciata*, *H. cordifera*, *O. schayeri,* and *Ophiura sarsii vadicola* were found to have increased metabolic rates (Christensen et al., 2011; Christensen et al., 2017; Liao et al., 2025; Márquez-Borrás and Sewell, 2024). *H. cordifera*, *Microphiopholis gracillima*, and *O. schayeri* increased metabolism when exposed to both low pH and elevated temperature (Christensen et al., 2011; Christensen et al., 2017). Additionally, *O. sarsii vadicola* underwent upregulation of protein processing and chaperone gene expression (Liao et al., 2025). In *O. schayeri*, the authors suggest that metabolism increased because of higher levels of mucus production–a response to environmental stress like OA and OW (Christensen et al., 2011). Metabolic upregulation is a response to OA and OW that demonstrates plasticity in brittle star physiology, as they are able to cope with low pH and high temperature.

Metabolic upregulation has been observed as a potential coping mechanism against OA and OW (Wood et al., 2008; Wood et al., 2011), however this physiological strategy may have physiological costs under long-term exposure (Márquez-Borrás and Sewell, 2024), At a lower pH, seawater is undersaturated with carbonate ions, which calcifying organisms use to form calcium carbonate (Wood et al., 2008). Under these conditions, brittle stars may increase metabolism and expend energy to maintain their calcium carbonate structures (Wood et al., 2008; Wood et al., 2011). This situation results in an energy deficit for the brittle stars, which may manifest as muscle wastage and loss of muscle mass in their arms. Studies of the brittle star species *O. sericeum* and *A. filiformis* both reported loss of muscle mass as evidence of muscle wastage during low pH treatments (Wood et al., 2008; Wood et al., 2011). The trade off between maintaining or enhancing calcification and muscle wastage brings up questions about the sustainability of this response for brittle stars over periods of long-term exposure to OA and OW.

The majority of studies saw negative effects or no significant effects of OA and OW on calcification (Table 1/Figure 2), but *A. filiformis* was an exception, where OA had a positive effect on net calcification (Wood et al., 2008). Calcification in brittle stars is measured based on calcium content and percent inorganic carbon in their body parts. Calcium carbonate structures, like the arms, central disk, and ossicles of brittle stars, are subject to degradation or dissolution in acidified seawater (Christensen et al., 2017; Márquez-Borrás and Sewell, 2024; Wood et al., 2008). In turn, *A. filiformis* may compensate for OA-driven dissolution by increasing calcification rates. Indeed, Christensen et al., 2017 hypothesized that an increase in net calcification rate in *A. filiformis* occurred because of its thinner arms compared to other brittle star species

(Christensen et al., 2017). Brittle star species with thinner arms may be more heavily impacted by dissolution, so changes in calcification rate due to OA and OW could be dependent on the thickness of brittle stars' arms.

Because most studies focus on short-term OA and OW, Hu et al., 2014 addresses the lack of research on how long-term exposure impacts brittle stars physiology. They found that metabolic rates increased when *A. filiformis* was exposed to OA at pH 7.3, but that stronger OA at pH 7.0 caused metabolism to decrease due to extracellular acidosis. Acidosis occurs when there is excess acid in the body of an organism. In this case, a CO_2 diffusion gradient is maintained across the epithelia of the brittle stars with a higher concentration in tissues. When the CO_2 concentration of the surrounding environment is increased during OA, the CO_2 concentration in the tissues must also increase in order to maintain this gradient. However, the brittle stars, like other echinoderms, are weak acid base regulators and cannot compensate for this change by secreting enough H^+ or gaining enough HCO_3^-. They were able to increase ammonium (NH_4^+) excretion and gain some HCO_3^-, which are both methods of acid base regulation, but could not fully compensate for the changes. Acidosis in the brittle stars led to metabolic downregulation, as the study measured lower rates of gene expression in acid base and metabolic genes in their arms. This decrease in metabolic rate also seems to be accompanied by decreased arm regeneration rate. In contrast to moderate OA over short periods, brittle stars are less resistant when faced with longer exposure to more severe OA. It may lead to metabolic depression, which has negative consequences for arm regeneration (Hu et al., 2014).

Behavioral responses to OA and OW

In addition to physiological responses, changes in brittle star behavior have been observed under OA and OW exposure. For instance, *A. filiformis* is a burrowing brittle star and usually extends its arms outside of its burrow and into the water. A behavioral response that was observed involved the brittle stars retracting their arms into their burrows when exposed to acidified water. This could be an attempt to conserve energy, because suspension feeding requires a lot of arm movement. However, retracting their arms back into their burrows could reduce the amount of food they can access and reduce burrow ventilation, since both of these processes require the use of their arms (Hu et al., 2014). Retraction of the brittle stars' arms into their burrows may be disadvantageous even though it decreases energy use.

Another observed behavioral response driven by OA and OW is the increase in righting response time of the mottled brittle star *O. fasciata*, which can be found in the intertidal and subtidal zones of New Zealand (Márquez-Borrás and Sewell, 2024). An organism's righting response is a reflex to return to normal position after they are flipped over. In response to OA and OW conditions over time and as the treatment became stronger, righting response time lengthened. The brittle stars most likely took longer to carry out a righting response in order to reduce the amount of movement and energy that they would have to use (Márquez-Borrás and

Sewell, 2024). Also, the brittle star *O. schayeri* experienced more lethargic movements in response to lower pH treatments (Christensen et al., 2011). Slower righting response and general movement could realistically make a brittle star more easily targeted by predators. Both the arm retraction and increase in righting time could be attempts to conserve energy by reducing movement, but they could result in consequences such as limited access to food, poor burrow ventilation, and vulnerability to predators.

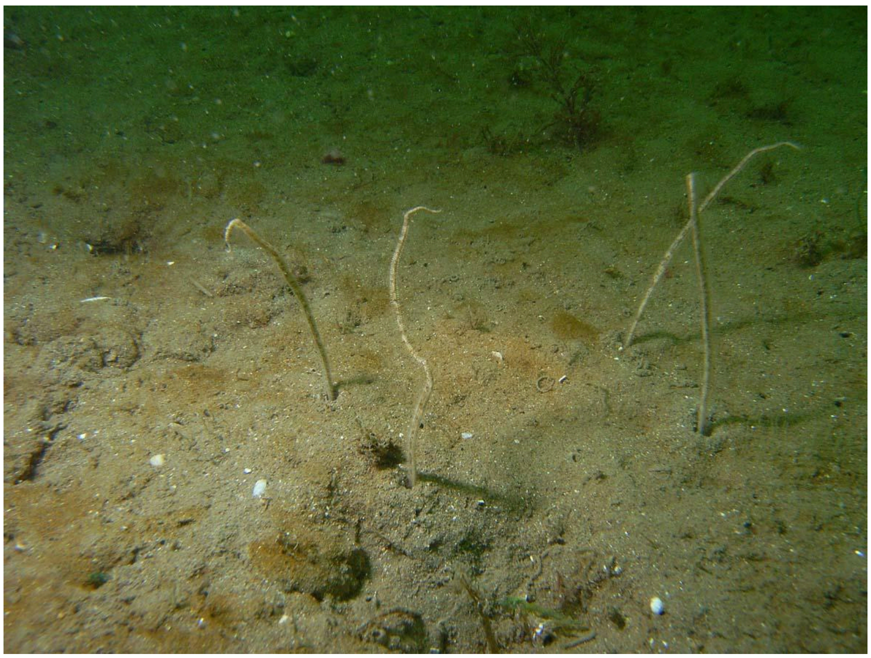

Figure 3. Close-up of *Amphiura filiformis* in Plymouth Sound near Plymouth, UK. Image: Dr Keith Hiscock MBE. Used with permission.

Vulnerability assessment of brittle star populations

Based on information from multiple studies on species of brittle stars around the globe and in different habitats, we can infer that some may be better suited to cope with OA and OW than others. Populations regularly exposed to fluctuations in temperature and pH in their natural habitats are generally more resistant to changing conditions in the laboratory. For example, the mottled brittle star *O. fasciata* experiences fluctuations of temperature and pH with the tide that resemble the predicted conditions of OA and OW in the near future (Márquez-Borrás and Sewell, 2024). Similarly, *O. schayeri*, which lives in the shallow coastal waters of Australia (Figure 4), experiences constant fluctuations with higher water temperatures during the day and lower pH levels during the night. Though, elevated temperature and low pH do not typically occur simultaneously (Christensen et al., 2011). In contrast, brittle stars that live near the poles, such as the Arctic brittle star *O. sericeum* are more vulnerable to OA and OW (Figure 4). The Arctic brittle star is adapted to surviving in extremely low temperatures, which is associated with having a smaller thermal tolerance range (Peck et al., 2009; Wood et al., 2011). Arctic waters are also predicted to be more heavily affected by future OA (Wood et al., 2011). A study by Peck et al., 2009 demonstrated the poor acclimation abilities of the Antarctic brittle star *Ophionotus victoriae* to OW. I The average survival time when experimental temperatures were raised by 2°C was 42 days, and only 24.4 days for a temperature rise of 3°C. These results indicate that *O. victoriae* could be one of the most vulnerable brittle star species to OW (Peck et al., 2009). However, it has been proposed that Arctic species might be able to cope with low carbonate concentrations caused by OA, given that they are adapted to low calcite and aragonite concentrations in their current environments (Wood et al., 2011).

Additionally, benthic burrowing brittle stars such as *A. filiformis* live in a reduced pH micro-habitat within their burrows, but near future OA could result in even lower pH conditions (Hu et al., 2014). They are especially valuable contributors to benthic ecosystems, which makes them an important concentration for research and protection efforts. Burrowing brittle stars that must ventilate their burrows, like *M. gracilima*, are more directly exposed to changes in sea water chemistry and therefore may be more severely impacted by OA and OW than a non-ventilating species such as *H. cordifera* (Christensen et al., 2017).

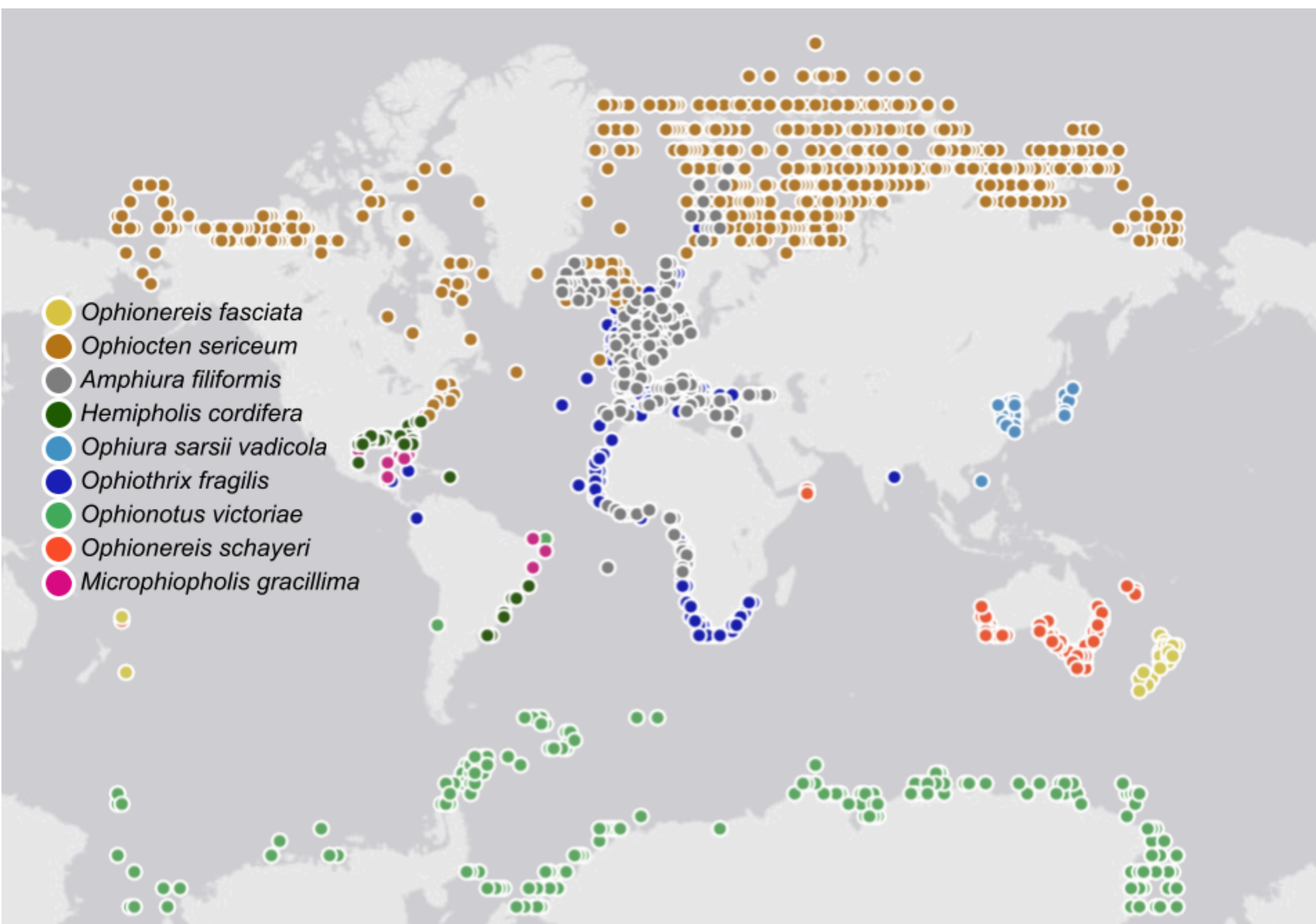

Figure 4. Map of brittle star species' geographic distributions. The nine species referenced in Table 1 are included. This map was generated through the Ocean Biodiversity Information System (OBIS) mapper by plotting OBIS observation data for each species. OBIS (2025) Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. https://obis.org.

Discussion

Most research has focused on the effects of OA and OW as separate factors and therefore information is lacking on their combined effect. However, it is important to study how OA and OW interact, as this will be more representative of marine ecosystems impacted by climate change (Harvey et al., 2013; Kroeker et al., 2013). Most studies have been performed in laboratories rather than in the field, and within relatively short time periods (Table 1). However, it has been shown that the duration of treatment impacts the responses of marine organisms (Christensen et al., 2017; Kroeker et al., 2013; Liao et al., 2025; Márquez-Borrás and Sewell, 2024). For example, Liao et al., 2025 found that short term OW activates defense responses in *O. sarsii vadicola*, whereas long term OW elicits a stronger response that focuses on energy storage and structural stabilization (Liao et al., 2025). Previous studies that used longer exposure periods have focused on the short-term responses of brittle stars to OA and OW which indicate plasticity (Dupont et al., 2010; Liao et al., 2025; Márquez-Borrás and Sewell, 2024), however it is unknown how brittle stars might evolve under future ocean conditions. The responses of brittle stars could differ depending on whether the study was performed in their natural habitat or in a laboratory, due to the potential added impact of interspecies interactions, food resources, and other ecological interactions similar to what has been observed in other marine organisms (Kroeker et al., 2013; Wood et al., 2011). OA may cause higher mortality and impaired development in brittle star larvae, acting as a potential population bottleneck (Chan et al., 2016; Dupont et al., 2008). Therefore, further research on how OA and OW impacts different brittle star life stages is needed (Dupont et al., 2008).

Brittle stars are able to acclimate to OA and OW in ways such as increasing metabolism and calcification, and adjusting behavioral responses. Some studies have shown that metabolic rate and calcification increase in order to compensate for the low availability of carbonate in the water and dissolution of calcium carbonate structures. However, these responses are not sustainable under long term exposure to OA and OW. Although upregulation of metabolism may be necessary to maintain calcium carbonate structures, it causes an energy deficit, which can result in muscle wastage (Márquez-Borrás and Sewell, 2024; Wood et al., 2008; Wood et al., 2011). Longer exposure periods to stronger OA might also cause metabolic downregulation in brittle stars (Hu et al., 2014). Behavioral responses aimed at conserving energy such as arm retraction, slower movement, and increased righting response time could have biological costs like reduced feeding and burrow ventilation, and increased vulnerability to predators (Hu et al., 2014; Márquez-Borrás and Sewell, 2024).

The impacts of OA and OW are highly varied depending on the species studied and the conditions of its natural habitat (Chan et al., 2016; Hu et al., 2014; Márquez-Borrás and Sewell, 2024; Peck et al., 2009; Wood et al., 2011). By looking at differences in the effects of OA and OW on different species of brittle stars and their responses, we can infer that brittle stars that are regularly exposed to variability in water pH and temperature in their natural habitats are likely better equipped to cope with OA and OW. These tend to be brittle stars that live in shallow, intertidal coastal areas. In contrast, polar regions, particularly burrowing brittle stars, experience extreme low temperatures in the deep ocean, a limited thermal tolerance range, and a low pH micro-habitat inside burrows (Hu et al., 2014; Peck et al., 2009; Wood et al., 2011). Future protection efforts should be directed towards Arctic and Antarctic brittle stars, which might be the most vulnerable populations to OA and OW.

Conclusion

Brittle stars plasticly respond to OA and OW by physiologically increasing metabolism and calcification, and reducing movement through behavioral changes. These responses may come with energetic and biological costs, suggesting that they might not be sustainable if brittle stars are faced with long term OA and OW. Intertidal populations exposed to pH and temperature fluctuations in their natural habitats appear to be more resistant to OA and OW, whereas polar populations tend to be more vulnerable. This literature review is limited to prior research and existing information on the impact of OA and OW on brittle stars and their plastic responses. Future studies should concentrate on the combined effect of OA and OW on brittle stars and use longer exposure periods. Research should address impacts on different brittle star life stages, and field studies should be considered in order to account for ecological factors in natural habitats. Furthermore, how brittle stars will evolve in warmer, acidified marine environments is currently unknown. Conservation and management efforts should focus on brittle star populations in Arctic and Antarctic environments, as these populations seem to be the most vulnerable to OA and OW.

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