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Ocean Acidification Research on Ecologically and Economically Important Sea Cucumbers Is Limited Globally

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Abstract

Ocean acidification (OA) caused by increasing levels of partial pressure of carbon dioxide (CO_2) and subsequent changes in seawater carbonate chemistry exerts knock-on effects on various calcifying organisms. However, little is known about the echinoderms (e.g., sea cucumbers) that are being overexploited globally for economic benefits. Most importantly, less is known about the impacts of OA on these organisms. Within this framework, the current study synthesized the available global data on the effects of OA on various sea cucumber species. Results indicate studies on OA impacts on sea cucumbers are limited to 10 species across eight countries globally, with *Apostichopus japonicus* being highly utilized under experimental conditions. Our results suggest that OA impacts reproduction, spawning events and sperm flagellar motility of sea cucumbers under low pH. This leads to the loss of energy allocations and reduction in somatic growth. Under low pH, the effects on Ca^{2+} and Mg^{2+} composition of calcareous ring and ossicles were species-specific and enzymatic activity was reduced. This study highlights the existing gaps that need to be addressed to prevent various knock-on effects of OA on sea cucumbers. This information is critical to managers and conservationists to manage the globally declining sea cucumber populations.

1 | Introduction

Ocean acidification (OA) caused by the unprecedented increase of atmospheric carbon dioxide (CO_2) levels and subsequent changes in seawater carbonate chemistry is one of the pressing environmental challenges of the 21st century (Jiang et al. 2019). OA results in decreasing the pH of seawater, leading to alterations in physiology and energy balance in marine organisms (e.g., calcifying organisms such as corals or bivalves) (Doney et al. 2020). Echinoderms such as sea urchin and sea cucumbers (class: Holothuroidea) are calcifiers and are predicted to be more sensitive than other noncalcifying organisms to the effects of OA. However, studies related to the effects of OA on the class Holothuroidea are very limited despite their high ecological and economic significance (Yuan et al. 2018; González-Durán et al. 2024; Yuan and Xie 2024).

Sea cucumbers are widespread from intertidal habitats to various depths and contribute to the ecological functioning of these habitats (Mishra et al. 2024; Woo et al. 2013). These organisms also act as the source of food to various other marine organisms such as fish and crabs; hence, they transfer animal tissue and nutrients to higher trophic levels (Purcell et al. 2016). Ecologically, sea cucumbers are deposit feeders that feed on sediment organic matter, therefore, reducing the organic matters load and redistribution of sediments. Additionally, they also excrete inorganic nitrogen and phosphorus, thereby facilitating primary productivity and nutrient cycling (MacTavish et al. 2012). Sea cucumbers help to locally buffer OA by digesting calcium carbonate ($CaCO_3$) sediments and excreting dissolved bicarbonate (HCO_3^{-}) and carbonate (CO_3^{2-}) ions (Vidal-Ramirez and Dove 2016). However, sea cucumber faces myriads of challenges apart from OA that arises mainly due to their economic significance (Gamboa-Álvarez et al. 2020; Ramírez-González et al. 2020). Sea cucumbers have been overexploited in various coastal regions (Hasan 2019; Gamboa-Álvarez et al. 2020; Ramírez-González et al. 2020), such as food, traditional medicines and cosmetics, which has led to a significant decrease of sea cucumber populations worldwide (Pasquini et al. 2021). Additionally, unregulated and unsustainable fishing practices, coupled with habitat degradation and pollution, further amplify the challenges faced by these organisms (Ramírez-González et al. 2020; Pasquini et al. 2021). Mariculture of sea cucumbers is considered as an alternative to decreasing wild populations, however, the majority of farming practices are done in marine environments making them prone to environmental changes such as OA (Grosso et al. 2021). Despite their ecological and economic importance, sea cucumbers have received less attention compared to calcifying organisms such as corals and oysters in the context of OA research (Doney et al. 2020; Garner et al. 2022) or their fellow echinoderms, sea urchins (Stumpp et al. 2013; Chan et al. 2015). Understanding the response of sea cucumber to OA is critical owing to their ecological and economical significance. In addition, alteration in sea cucumber populations may have a cascading effect on associated ecosystems, influencing nutrient stability and the loss of various ecological functions (Purcell et al. 2016; Gianasi et al. 2020; Floren et al. 2021).

It is against this background that this review seeks to collect the current available information on the physiological, behavioural and ecological responses of sea cucumbers to OA. By synthesizing the existing research findings and knowledge gaps, this study aims to highlight the future research directions to improve our understanding on the impacts of OA on sea cucumber populations. The outcomes of this study will contribute towards future research efforts and conservation strategies aimed at mitigating the impacts of OA on these ecologically important organisms.

2 | Methodology

2.1 | Literature Search, Data Acquisition and Analysis

In January 2025, we conducted a literature search using the Web of Science database (Clarivate Analytics) and SCOPUS database selecting articles published up to December 2024. These databases were chosen, as they encompass a wide range and quality of scientific publications (Gomes et al. 2023). For this study, we used the following keywords: 'Ocean acidification' OR 'Sea cucumber' OR 'Holothuroid' OR 'Holothurians' OR 'pH' OR 'Survival' OR 'Growth' OR 'Development' OR 'Feeding' OR 'Physiology'. The total articles obtained from the search strings were further screened based on the PRISMA guidelines (Moher et al. 2009). In the first stage, before the initial screening, the total list of articles was cleaned by removing duplicates followed by reading the title and abstract of each article. During this first screening, the articles that were not related to OA and sea cucumber were excluded. The remaining articles (Table S1) were checked for eligibility to be included for data extraction. For an article to be eligible, it had to meet the following two criteria: (i) it should be a peer-reviewed and original research article and not a conference abstract or review article, and (ii) must be reporting the effect of OA on any of the sea cucumber traits (e.g., growth, physiology and reproduction). Based on these criteria, the final list of eligible articles for data extraction was obtained (Table S2).

3 | Results

From the literature, we recorded 11 out of 12 studies specifying the sea cucumber species ($n = 10$) related to OA effects on sea cucumbers, with *Apostichopus japonicus* being the most studied ($n = 5/12$) sea cucumber species worldwide (Table S3). Interestingly, most of these OA studies on sea cucumbers were restricted to eight countries globally (Figure 1), and experiments of short-term durations (< 1 year) were preferred, with the longest duration of 22 weeks (Table S3).

Negative effects of OA on sea cucumber growth and reproduction were observed (Figure 2), with limited studies examining the OA effects on various stages of growth. From the limited studies, strong evidence was observed on OA altering the somatic growth of *A. japonicus* by initiating changes in energy allocations under low pH (7.41), where most energy was lost in faeces. Contrastingly, the sea cucumber larvae of *Holothuria spinifera* showed high growth rates when exposed to low pH (6.5–7.5) conditions. For sea cucumber reproduction, OA negatively affected the timely separation of Di-Acyl-Glycerol Ether (DAGE), fatty acids from Tri-Acyl-Glycerol (TAG) and delayed the translocation of these important fatty acids for successful reproduction efforts of the sea cucumber *Cucumaria frondosa*. Additionally, the number of spawning events of *C. frondosa* under low pH conditions was reduced. Consequently, the sperm flagellar motility of *A. japonicus* was reduced by more than 41% when pH was changed from 8.0 to 7.7. This reduction in sperm mobility in *A. japonicus* also reduced the post fertilization success (PFS), and the stage duration, such as the early Auricularia, was longer under low pH conditions. Moreover, there was a disparity in the gene expression in sea cucumber developmental stages (blastula, auricularia and doliolaria). Similarly, the survival of deep-sea sea cucumbers such as *Amperima robusta*, *Staurocucumis abyssorum* and *Scotoplanes globosa* was low under low pH conditions (Figure 2).

The response of sea cucumber's ossicles morphology and coelomic fluid to OA was species-specific. Under low pH, insignificant effects on the Ca^{2+} and Mg^{2+} composition of both calcareous ring and ossicles of *C. frondosa* and *Holothuria forskali* were observed (Figure 2). The coelomic fluid of *H. forskali* was not affected by pH changes, whereas the coelomic fluid pH of *Holothuria parva* and *Holothuria scabra* decreased under exposure to low pH. Interestingly, the response of different enzymatic activities to OA was enzyme-specific. For example, in *A. japonicus*, the enzymes such as lactate dehydrogenase (LDH) increased, whereas the activities of alkaline phosphates (ALP) activity significantly decreased under the influence of low pH conditions. The bioturbation potential of the sea cucumber *Stichopus herrmanni* under a low pH environment remained unaffected.

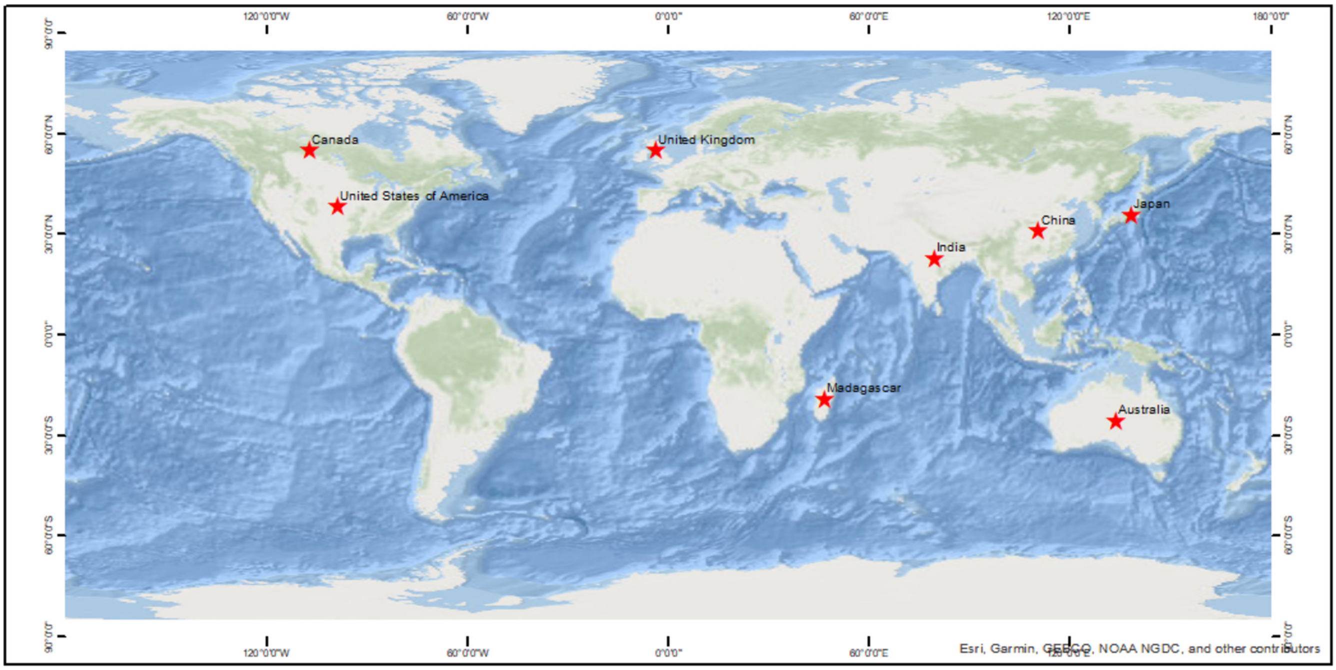

FIGURE 1 | Map showcasing the countries that have carried out ocean acidification research on sea cucumbers globally. The figure was designed by QGIS (3.42.0) software using the information of the country where the specific study was conducted (see Table S3).

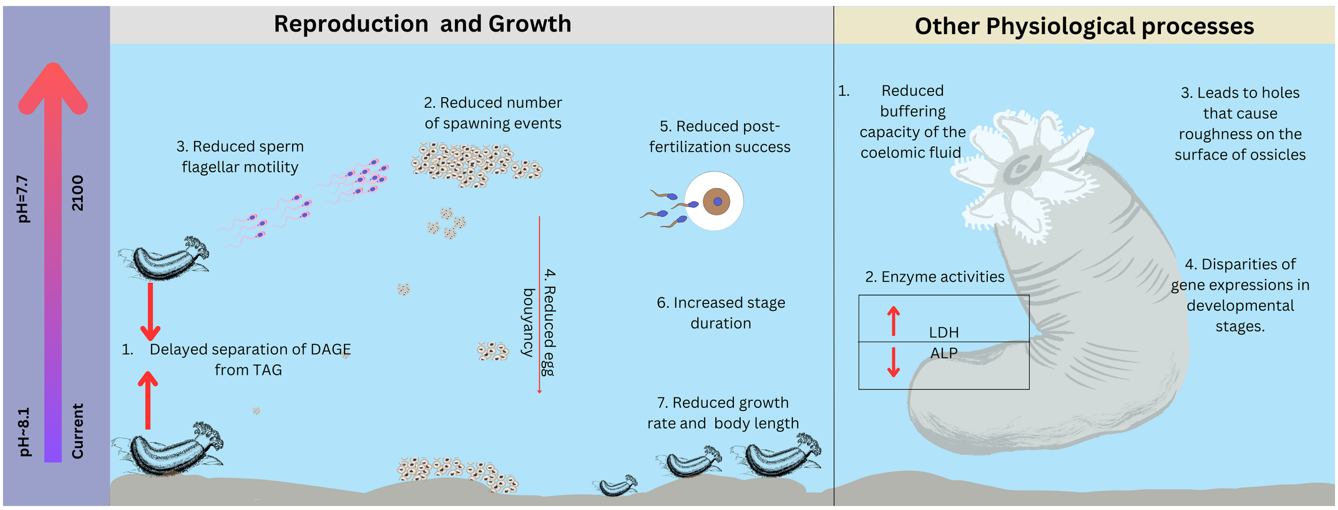

FIGURE 2 | Illustrations of the effects of ocean acidification on sea cucumbers on reproduction, growth and physiological processes derived from the literature review of this study. DAGE (Di-Acyl-Glycerol Ether), TAG (Tri-Acyl-Glycerol), LDH (Lactate Dehydrogenase) and ALP (Alkaline Phosphates).

4 | Discussion

Sea cucumbers like other marine invertebrates can reproduce both sexually and asexually, but common reproduction strategy includes sexual reproduction by external fertilization through broadcast spawning (Ramofafia et al. 2003; Lee et al. 2009; Sonnenholzner et al. 2017). The sea cucumbers release eggs into the water that are fertilized by sperm (Gianasi et al. 2020; Webb et al. 2021; Avila-Poveda et al. 2022). Being broadcast spawners, sea cucumbers are challenged by the environmental factors, such as dilutions and OA. Changes in these environmental factors result in a decrease of the number of spawning events. This leads to a reduced rate of reproduction and subsequent decline in sea cucumber population. Egg buoyancy is an important factor in the reproduction of every broadcast spawner, and lower buoyancy results in a reduced chance for egg fertilization. These low buoyant unfertilized eggs fall to the bottom of their habitat and subsequently die (Verkaik et al. 2016). Contrastingly, for successful fertilization, the sea cucumber sperms utilize their flagellar swimming movement to reach the eggs and fertilize them. The enzymes responsible for flagellar beating (i.e., Dynein ATPases) are activated when the seawater is within an optimal pH range, facilitating ion exchange and calcium (Ca) signalling. However,

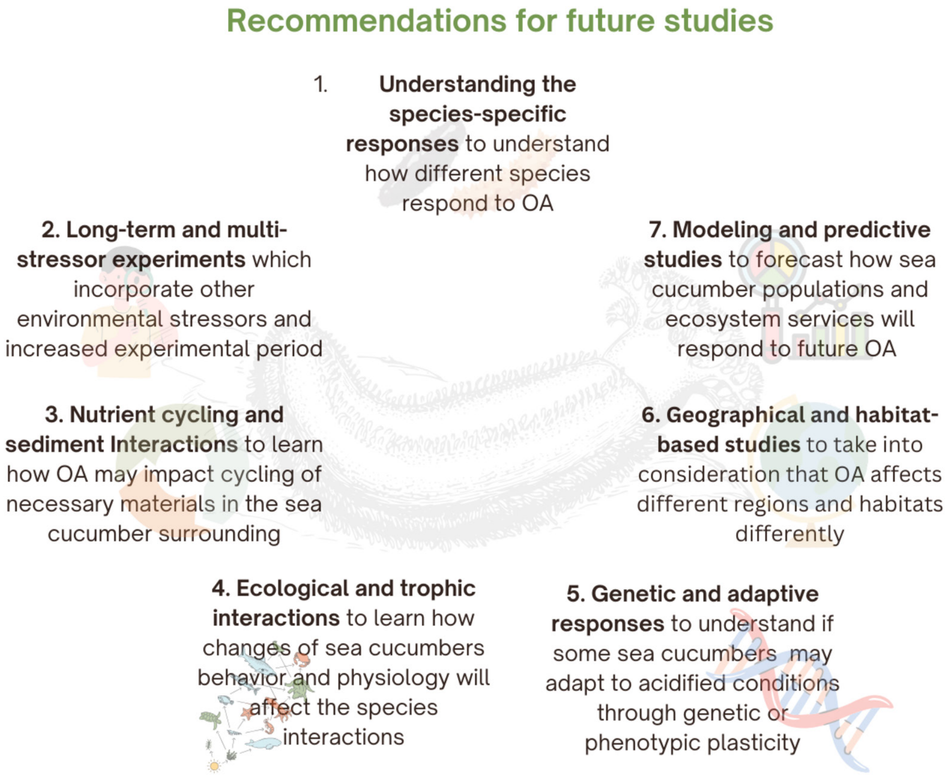

FIGURE 3 | Recommendations for future studies based on the existing knowledge gaps derived from this study.

under acidic conditions, the flagellar movement of sperms are reduced (Morita et al. 2009), resulting in low rates of egg fertilization. These low fertilization rates, when coupled with the observed low PFS (e.g., in *A. japonicus*) and reduced growth rates, may lead to decline in sea cucumber populations.

From this study, it is evident that the reproduction and growth of sea cucumbers are partly prone to OA (Figure 2). The early process and stages up to postfertilization are prone to OA, while the larval growth and development are less prone to OA. The resilience of larval stages of sea cucumbers to future OA conditions can be attributed by two possible/strategies: (i) lack of larval calcareous skeleton that when exposed to low pH dissolves, and (ii) lecithotrophic life strategy: The larvae derive their nutrition from the energy stored in the eggs (Verkaik et al. 2016). In contrast to planktotrophic larvae, sea cucumbers larvae largely rely on energy stored in their eggs, hence making them less dependent on external environments for energy acquisitions. Lecithotrophic echinoderm larvae benefit from their yolk-based energy reserves under OA, as they bypass reliance on planktonic food, which OA can impair. For instance, *Crossaster papposus* larvae exhibit increased growth rates under low pH, likely due to their ability to sustain essential processes without external input (Dupont et al. 2010). However, this strategy limits adaptability; *Meridiastra calcar* larvae showed resilience in early stages but were vulnerable to prolonged warming combined with OA due to fixed energy resources (Nguyen et al. 2012). Thus, while beneficial for short-term survival, this independence may constrain long-term resilience under future OA scenarios combined with changing environmental conditions.

Echinoderms have coelomic fluid, which is responsible for acid base and osmotic balance, transport of nutrients, immunity and helps in evisceration as a source of hydrostatic pressure (Jiang et al. 2016; Ding et al. 2021). Under OA conditions, acidosis of coelomic fluid occurs, which can lead to gamete impairment, as observed in *C. frondosa* (Verkaik et al. 2016). This acidosis also disrupts normal hormonal pathways and nutrient translocation for gamete synthesis. However, in other echinoderms such as sea urchins, the internal acidosis caused by changes in external environment (e.g., pH changes), can be buffered by the coelomic fluid (Collard et al. 2013). But in sea cucumbers, under acidosis, the coelomic fluid loses its capability to buffer external changes in seawater chemistry, which poses a serious threat to their acid-base regulation capacity. Similarly, understanding the activity of metabolic enzymes is important as they determine energy budgeting and utilization of an organism. The changes in the activity of enzymes caused by pH changes highlight OA-induced stress and may result in disturbing the anaerobic and biomineralization process of sea cucumbers. However, the observation is made for only one species (i.e., *A. japonicus*) (Shi et al. 2021) and following the species-specific response of sea cucumbers to OA, there is an urgent need to assess the effects of OA on other sea cucumber species.

The findings of this study provide valuable insights into the physiological and behavioural impacts of OA on various sea cucumber populations. However, the majority of the studies ($n=10$) focused on the effects of a single stressor on sea cucumber traits and with only two studies (Song et al. 2024; Zhao et al. 2024) focused on the effects of multiple stressors (OA and ocean warming) on sea cucumbers. Therefore, the findings from this study highlight the existing limitations of our understanding on the multifaceted interactions between different stressors (climate change + anthropogenic stressors) and sea cucumbers response that would occur under natural conditions. Furthermore, these limitations will also hinder the conservation and management of globally declining sea cucumber populations under projected future ocean scenarios where, for instance, increase in temperature, decrease in dissolved oxygen levels and pollution may interact with OA.

5 | Conclusions and Recommendations for Future Studies

This review showcases the existing knowledge in scientific research on the effects of OA on various sea cucumber populations and highlights that the documented evidence on sea cucumbers response to OA are understudied globally. The main findings of this study showcase that (i) OA affects the reproduction, growth and physiological processes of sea cucumbers, (ii) sea cucumber dependence on external fertilization and sperm mobility makes them particularly vulnerable to changes in seawater acidity and (iii) OA-induced acidosis impairs key physiological functions, such as acid-base regulation and metabolic enzyme activity, thus making the global sea cucumber populations vulnerable to future OA scenarios. The finding of this study suggests that the management initiatives intended to increase the resilience of sea cucumbers under future ocean scenarios should be location and species specific. Recommendations for future studies aiming at understanding the effects of OA on sea cucumbers are highlighted in Figure 3, which includes priority-based data generation on the following aspects:

1. Understanding species-specific responses of sea cucumbers due to differences in their physiology, feeding rates and behaviour, habitat preferences, metabolism, growth and reproductive behaviours.
2. Conducting long-term and multi-stressor experiments to assess the cumulative impacts of OA and other environmental stressors (e.g., temperature, hypoxia and pollution) across transgenerational life stages is essential.
3. Including nutrient cycling and sediment interactions studies to understand how OA affects these processes (including the process of dissolving the carbonate sediments through digestions), particularly in carbonate-dominated sediments (e.g., coral reefs) and how changes in sediment chemistry might feedback to affect sea cucumber populations.
4. Ecological and trophic interactions studies to understand how changes of sea cucumbers behaviour and physiology will affect the species interactions, predator–prey dynamics and competition within the ecosystem, as well as its impact on the food web at large.
5. Genetic and adaptive responses studies to understand if some sea cucumbers may adapt to acidified conditions through their genetic or phenotypic plasticity.
6. Geographical (e.g., tropical to temperate) and habitat-based studies on the effects of OA to local environmental factors and the presence or absence of keystone coastal ecosystems (e.g., coral reefs and seagrass beds)
7. Modelling and predictive studies to forecast how sea cucumber populations and ecosystem services will respond to future OA scenarios.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data generated for this study are available as Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.