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Review

Impact of ocean acidification on the biology of marine bivalves

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Abstract

Ocean acidification, resulting from increased atmospheric CO_2 levels, poses a significant threat to marine ecosystems, particularly to shell-forming organisms such as marine bivalves. This review synthesizes current knowledge regarding the impacts of ocean acidification on bivalves, including oysters, clams, and mussels, focusing on their physiology, development, and ecological interactions. Acidification impairs shell formation, disrupts energy metabolism, alters feeding and respiration patterns, and inhibits the growth and recruitment of larvae. These changes can destabilize bivalve populations and impair the ecosystem services they offer, such as water filtration, habitat creation, and support for fisheries and aquaculture. The report discusses potential strategies to mitigate the impacts of climate change, including the reduction of carbon emissions, selective breeding, and habitat management. This underscores the necessity of interdisciplinary research to comprehend the long-term impacts of climate change and to promote sustainable resource management that benefits the environment.

Key words: acidification, calcification, larval recruitment, ecosystem services, aquaculture resilience, metabolic stress.
Abbreviations: OA, ocean acidification.

Introduction

The oceanic process of acidification was propelled by the assimilation of surplus atmospheric carbon dioxide. This resulted in conditions such as a decrease in the pH of seawater, which increased its acidity. Carbonic acid is produced when carbon dioxide dissolves in seawater, thereby altering the ocean's chemical equilibrium (Harris et al. 2023). Marine organisms, particularly those with calcium carbonate shells like bivalve mollusks, are gravely endangered by this chemical imbalance. These conditions impede their capacity to construct and uphold their shell structures (Zhao et al. 2017; Van Colen et al. 2018; Wang et al. 2022). Ocean acidification (OA) is a significant consequence of climate change caused by human activities, and it threatens marine ecosystems, biodiversity, and the innumerable services they offer to human societies across the globe.

Carbon dioxide absorption from the atmosphere is the primary factor contributing to OA. Carbon dioxide emissions into the atmosphere, which are subsequently absorbed by the ocean surface, are at an all-time high due to anthropogenic activities such as deforestation and burning of fossil fuel (Nunes 2023). A decrease in the pH of the seawater results from the formation of carbonic acid. Local acidification may also be caused by biodegradation of organic matter and nutrient discharge (Capelle et al. 2020; Savoie et al. 2022).

Marine bivalves, including oysters, clams, and mussels, are economically and ecologically vital to the marine and human environment. Through the filtration of substantial quantities of seawater, they actively participate in the ecological preservation of water quality through the elimination of dispersed particles and excess nutrients, thus augmenting the overall health of the ecosystem (Vereycken, Aldridge 2023). Bivalves, apart from serving as critical food sources for a multitude of marine organisms, are also integral constituents of the marine food web (Jiang et al. 2023). Additionally, their activities promote biodiversity through the establishment of microhabitats in sedimentary ecosystems (van der Ouderaa et al. 2021). From an economic standpoint, bivalves play a crucial role in the worldwide seafood sector by sustaining coastal communities via aquaculture and natural harvest (Jacquet et al. 2017). The economic significance of bivalve fisheries transcends mere direct consumption, encompassing employment, trade, and cultural practices on a global scale (Wood, Filgueira 2022). Furthermore, the shellfish industry contributes to environmental preservation by facilitating mitigation of nutrient pollution through the absorption of nitrogen and phosphorus by bivalve aquaculture (Kong et al. 2023). This further emphasizes the ecological and economic importance of these organisms.

A comprehensive examination of the consequences of OA on marine bivalves is crucial in light of the growing danger presented by the alteration of ocean chemistry. A thorough awareness of the multifaceted consequences of OA on bivalves is crucial for assessing potential disruptions to their physiological mechanisms, growth, and reproductive capabilities. Given the considerable ecological and economic importance of bivalves in the contexts of aquaculture and fisheries, it is imperative to undertake an exhaustive examination in order to provide guidance for adaptive management approaches and policies that tackle the complex interplay between climate change, OA, and the long-term viability of bivalve populations and associated sectors.

Physiological responses of bivalves to ocean acidification

The calcification processes of marine bivalves are significantly influenced by OA, which poses a critical hazard to their structural integrity and overall survival. The acidification of the ocean causes a decrease in pH levels, which hinders the accessibility of carbonate ions, which are fundamental components in the construction of calcium carbonate shells in bivalves. This situation was confirmed by the outcomes of several experimental investigations. A reduction in pH level resulted in a decrease in shell length of *Astarte borealis* clams under laboratory conditions (Goethel et al. 2017). The shells of *Pinctada fucata* oysters exhibited a poorly organized nacreous microstructure, as the nacreous layer demonstrated a loss of structural integrity when exposed to water with a pH of 7.40 (Liu et al. 2017). The ongoing acidification of the ocean adversely affects the calcification physiology of the mussel *Mytilus edulis* by hindering its ability to extract dissolved inorganic carbon from seawater (Lu et al. 2018). OA impedes the capacity of bivalves to sustain and develop their protective shells, thereby increasing their vulnerability to predation and environmental stresses.

An increase in acidity has the potential to cause the dissolution of pre-existing shell material, thereby exacerbating the structural fragility of bivalves. For example, an experiment revealed breakage of the periostracum in the thick shell mussel *Mytilus coruscus* when exposed to a acidified condition, which led to dissolution of calcite crystals on external surfaces of the shells (Zhao et al. 2020). In another investigation, significantly greater dissolution rates on the shells of the razor clam *Ensis magnus* were observed in cold-acidic water under laboratory conditions (Babarro et al. 2023). The process of dissolution not only compromises the shells' protective function but also depletes energy that would be otherwise utilized for vital life processes, thereby affecting the organisms' overall fitness.

The process of OA has a substantial impact on the energy metabolism of marine bivalves, thereby presenting potentially far-reaching physiological challenges. In an effort to sustain their acid-base equilibrium amidst a progressively acidic environment, the blood clam *Tegillarca granosa* allocates a significant proportion of its metabolic energy to acid-base regulation (Zhao et al. 2017). This diversion may result in a reduced availability of energy for critical life processes. Furthermore, in marine bivalves, the heightened metabolic requirements linked to adapting to increased acidity could potentially deplete their energy reserves, thereby impeding vital processes including reproduction, growth, and immune responses (Medeiros, Souza 2023). The redirection of energy from critical life processes may undermine the overall robustness and adaptability of bivalves, thereby affecting their capacity to flourish and endure in dynamic oceanic conditions.

In addition, by perturbing the feeding behaviors of marine bivalves, OA may even have an effect on the efficacy with which they acquire energy. Ong et al. (2017) reported that in cockle *Cerastoderma edule* pH fluctuations can affect chemoreception and sensory cues that are used to identify and locate suitable food sources (Ong et al. 2017). Nutrition and energy consumption of bivalve species may be significantly impacted by alterations in feeding behavior, such as decreased feeding rates or altered food preferences (Goethel et al. 2017).

The respiration of bivalves is dependent on gill structures, and the alteration of ocean chemistry has the potential to affect this vital process. Acidified environments have the capacity to disrupt oxygen uptake and transport, which may have adverse effects on the respiratory efficacy of bivalves and consequently affect their metabolic performance. In a low pH environment, the bivalve *Abra alba* exhibited reduced respiration rates, signifying a shift from aerobic to anaerobic metabolic pathways (Vlaminck et al. 2022). A comparable reaction was noted in the surfclam *Spisula solidissima*, wherein there was a decrease in the oxygen/nitrogen (O:N) excretion ratio (Pousse et al. 2020). This finding indicates the occurrence of a metabolic strategy transition.

Impacts on bivalve larvae and early life stages

The larval stages of bivalves are exceptionally vulnerable to the effects of OA because the development of calcium carbonate shells requires the presence of carbonate ions. The reduction in carbonate accessibility presents a clear and immediate obstacle for bivalve larvae, impeding their capacity to construct and sustain protective shells. An acidified environment induced a significant incidence of deformity in the larvae of the oyster *Crassostrea angulata* (Yang et al. 2017). A comparable finding was documented regarding the larvae of congeneric species, namely *Crassostrea gigas* and *Crassostrea glomerata*, which exhibited heightened abnormalities under conditions of elevated CO_2 (Gibbs et al. 2021). Similarly, it has been reported that the biomineralization of *Spisula solidissima* larvae, a species of surfclam, was considerably reduced under 7.3 pH conditions following a 30-day incubation period (Czaja et al. 2023). When OA occurs, bivalve larvae frequently experience a decrease in calcification rates, which can impede the correct development of their shells and potentially impact their ability to settle and survive.

The recruitment and population dynamics of bivalve larvae may be significantly impacted by OA, which may have far-reaching implications for the species' overall health and sustainability. Bivalve larvae may be less capable of constructing robust shells due to the impaired calcification rates and shell development in acidic environments. Consequently, these larvae may be more vulnerable to predation and environmental stresses. The larvae of the oyster *Saccostrea cuculata* exhibited a higher mortality rate compared to *Reishia clavigera*, a predatory whelk, in a low pH environment (Campanati et al. 2018). Increased mortality in the larval stage caused by OA may have an impact on the recruitment of the former. Similarly, high mortality rates in the larvae of the bivalve *Ervilia castanea* following colonization raise concerns about the effects on the population of the species (Martins et al. 2018). The susceptibility observed in the larval stages may result in reduced rates of survival and have an adverse effect on the successful establishment of bivalves. Any disturbances to the larval recruitment process, which is an essential component of the life cycle of bivalves, can potentially result in profound implications for population dynamics.

The potential consequences of low pH levels on juvenile bivalve capacity to identify appropriate substrates for attachment and settlement include probable effects on their abundance and distribution. Changes in burrowing behavior were noted in juvenile soft-shell clams Mya arenaria, leading to a decreased number of clams penetrating sediment with low pH (Clements et al. 2016). Similarly, when the pH was decreased, the juvenile oyster *Crassostrea hongkongensis* exhibited a greater success rate in metamorphosis but a diminished ability to select the substratum (Lim et al. 2021). Acidification-induced alterations in the quality and accessibility of food sources may exert an impact on dietary behaviours, potentially leading to ramifications for growth rates and general well-being. The aforementioned effects were noted in juvenile *Arctica islandica*, where the apparent stunted development of tissues and shells can be ascribed to the limited availability of food caused by fluctuating pH conditions (Ballesta-Artero et al. 2018). The potential consequences of OA on juvenile bivalves extend beyond population dynamics and affect the fisheries and aquaculture sectors, which are dependent on the sustainability of these species within marine ecosystems. The physiological challenges mentioned have the potential to lead to reduced survival rates and impaired resilience, thereby exerting an impact on the overall viability of juvenile bivalve populations.

Ecological consequences

OA has the potential to induce detrimental consequences across marine food webs, where bivalves occupy a pivotal position in these interactions. The possible effects of OA on the physiology of bivalves include potential disruptions in their capacity to filter and process planktonic food sources, which could impede energy transfer within the food web. The scallop *Crassadoma gigantea* exhibited a higher concentration of saturated fatty acids and a decreased concentration of polyunsaturated fatty acids upon exposure to high pCO_2 (Alma et al. 2020). This observation implies that fatty acid chains underwent reorganization, potentially affecting the nutritional value of the scallop in the marine environment. This may underscore the interdependence of species and the potential for broad ecological implications when continuous environmental transformations occur.

Significant changes in the composition and structure of marine bivalve communities can be induced by OA, which has extensive consequences for the dynamics of ecosystems. Acidic conditions can lead to compromised shell integrity and reduced calcification of bivalves, which can result in potential alterations to their abundance and distribution. A model indicated that the bivalves *Argopecten irradians* and *Mercenaria mercenaria* face a high risk (> 90%) of population decline under scenarios of elevated pCO_2 (Grear et al. 2020). There may be a significant number of species that are more robust or adaptable to shifting carbonate chemistry, whereas species that rely heavily on carbonate for shell formation may experience a decline. It has been suggested that bivalves, in comparison to other invertebrates, are more susceptible to the effects of OA (Parker et al. 2013). Such fluctuations may result in changes to the relative abundance of various bivalve species within given communities.

Modifications in the composition and structure of marine bivalve communities have serious implications for the functioning of ecosystems and the species that are associated with them. Bivalves are of significant importance in processes such as nutrient cycling, habitat provision, and water filtration; changes in their population size can have an impact on the accessibility of resources and microhabitats for other organisms (Strayer et al. 2011; Jones et al. 2017; Lamine et al. 2023). Predator-prey relationships and competition dynamics in marine ecosystems may be impacted by variations in the structure of bivalve communities (Uzkiaga et al. 2022; Greatorex, Knights 2023). Moreover, economic ramifications may result from fluctuations in bivalve populations for sectors dependent on these organisms, including aquaculture and fishing (Tan, Zheng 2020).

Fig. 1 summarizes the major processes associated with OA and its multi-level biological impacts on marine bivalves.

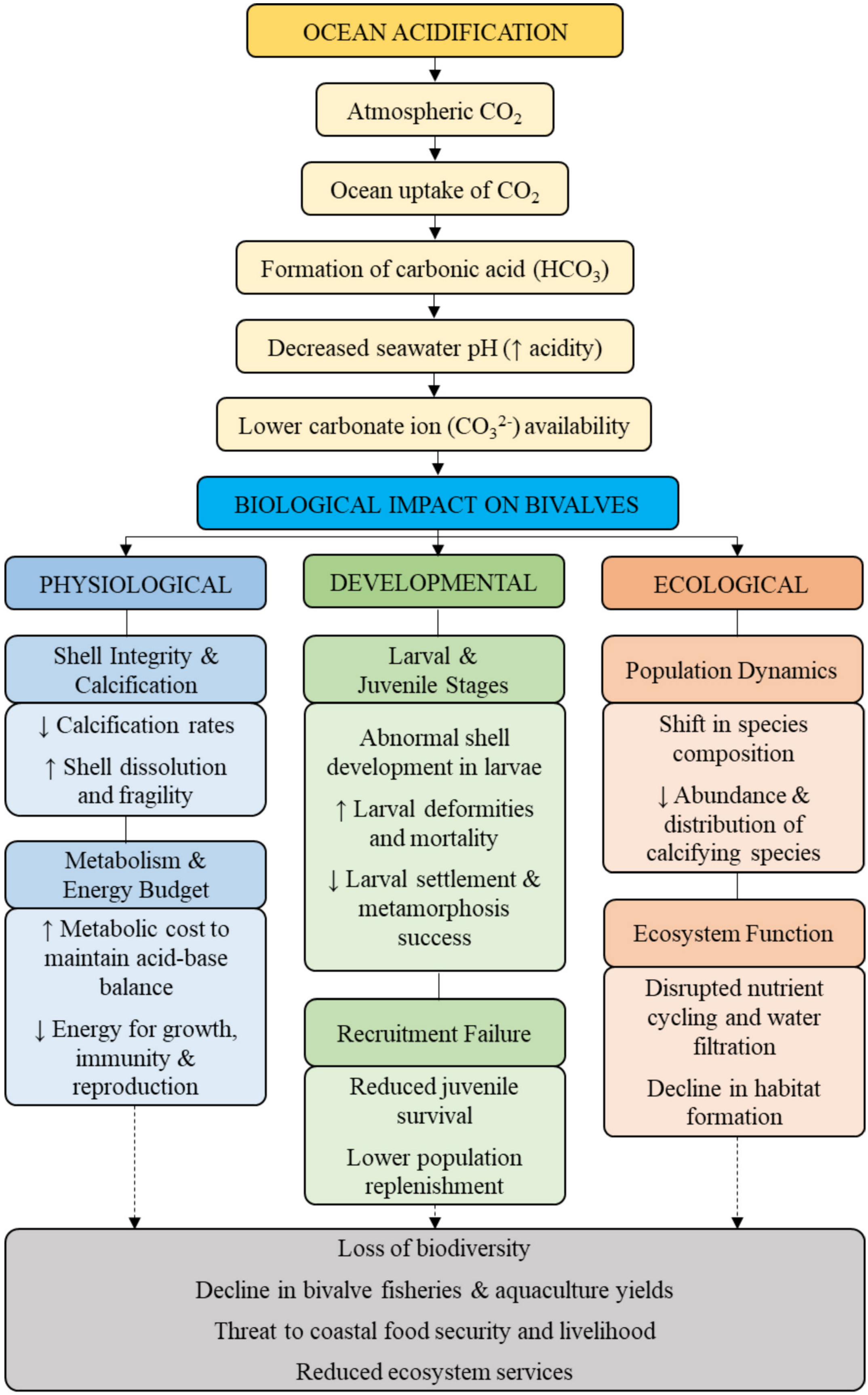

Fig. 1. Cascading effects of ocean acidification on marine bivalves across physiological, developmental, and ecological levels.

Mitigation and adaptation strategies

In order to mitigate and adapt to the effects of OA on marine bivalves, a holistic approach is necessary that addresses both the direct consequences and the underlying causes of shifting ocean chemistry. Mitigating OA requires a global effort to decrease carbon dioxide emissions via the adoption of sustainable practices and the transition to renewable energy sources (Magi, Murai 2011; Hofmann et al. 2019). Acidification in coastal regions can be further intensified by nutrient discharge, which can be mitigated through localized initiatives (Cui et al. 2021). By reducing the influx of nutrients into marine environments, sustainable land use and agricultural practices can mitigate the impact on bivalve habitats (Kelly et al. 2011).

Adaptation strategies for bivalve populations encompass aquaculture practices and targeted research. Tan and Zheng (2019) state that it is possible to increase the resilience of bivalves to shifting environmental conditions, such as increased acidity, through the implementation of selective breeding programmes. Potential strategies for mitigating the impacts of OA include the identification and breeding of individuals possessing genetic traits that confer enhanced resistance (Zhang et al. 2022). Furthermore, sustainable harvests can be maintained through the implementation of innovative bivalve aquaculture techniques, including the establishment of controlled environments and the application of selective breeding to confer resistance to acidification (Clements, Chopin 2017). Integrated management strategies, which take into account the interrelationships among bivalves and their ecosystems, can facilitate the adaptation of marine bivalve populations to a shifting ocean environment by protecting and rehabilitating critical habitats (Hilmi et al. 2021).

Future research directions

Subsequent investigations into the ramifications of OA on marine bivalves ought to delve into the intricate and reciprocal dimensions of this multifaceted phenomenon. Studies concerning the molecular and genetic processes that govern the reactions of bivalves to acidic environments may yield crucial knowledge regarding their adaptability and tendency for evolutionary transformation. In order to evaluate the cumulative effects on bivalve populations and ecosystems over prolonged durations, it is critical to conduct long-term field studies that account for various environmental stressors, including temperature fluctuations and nutrient availability. Additionally, it is imperative that scientific investigations explore the possible synergistic impacts of various stressors on bivalves, such as deoxygenation and warming waters, in order to enhance our ability to forecast the ecological ramifications as a whole. By integrating experimental manipulations, field observations, and modeling efforts, our comprehension of the ecological and physiological reactions of marine bivalves to OA will be improved. This will aid in the formulation of efficacious conservation and management strategies that safeguard the resilience of these crucial species amidst continuous environmental transformations.

Conclusions

In conclusion, OA presents a substantial risk to marine bivalves, as it affects their calcification mechanisms, energy expenditure, and general physiological reactions. The extent to which bivalve larvae and juveniles are susceptible to alterations in carbonate chemistry highlights the potential implications for the efficacy of recruitment and the dynamics of populations. Consequences that have an impact on marine food webs, community composition, and ecosystem functioning highlight the interdependence of species and the ecological repercussions that extend beyond present environmental alterations. In order to mitigate and adapt to these impacts, a holistic strategy is necessary, encompassing local tactics like sustainable land use practices and global initiatives such as carbon emission reduction that contribute to ocean acidification. Subsequent areas of investigation ought to center on elucidating the molecular and genetic processes that underlie the responses of bivalve species, delving into the potential synergistic consequences of numerous stressors, and undertaking protracted field studies that provide insights into efficacious conservation and management approaches. In light of this intensifying environmental challenge, it is critical to protect the ecological and economic functions of marine bivalves through a comprehensive and cooperative endeavor.

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