Environmental Research 248 (2024) 118238

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

Review article

Biological and physiological responses of marine crabs to ocean acidification: A review

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ARTICLE INFO

Keywords:
Marine crabs
Ocean acidification
Growth
Molting
Antioxidants
Metabolic enzymes

ABSTRACT

Marine crabs play an integral role in the food chain and scavenge the debris in the ecosystem. Gradual increases in global atmospheric carbon dioxide cause ocean acidification (OA) and global warming that leads to severe consequences for marine organisms including crabs. Also, OA combined with other stressors like temperature, hypoxia, and heavy metals causes more severe adverse effects in marine crabs. The present review was made holistic discussion of information from 111 articles, of which 37 peer-reviewed original research papers reported on the effect of OA experiments and its combination with other stressors like heavy metals, temperature, and hypoxia on growth, survival, molting, chitin quality, food indices, tissue biochemical constituents, hemocytes population, and biomarker enzymes of marine crabs. Nevertheless, the available reports are still in the infancy of marine crabs, hence, this review depicts the possible gaps and future research needs on the impact of OA on marine crabs.

1. Introduction

The ocean is a massive salt water of the earth with 138 million km^2 of the exclusive economic zone (EEZ) and an average harvestable potential of 177.8 million tons of total capture and culture fisheries for humankind (FAO, 2022). In recent years, pollution like industrial, sewage, pesticide, chemical, pharmaceutical, microplastic wastes, etc., due to anthropological activities is unfavorable to the ocean environment (Ansari and Matondkar, 2014). Likewise, ocean acidification (OA) is becoming one of the global severe issues due to the continuous emission of carbon dioxide (CO_2) (NOAA, 2021). The ocean surface absorbs approximately one-third of the carbon dioxide that has already been emitted to the atmosphere over the last 10 decades (Caldeira and Wickett, 2003), and this resulted in the increase of partial pressure of carbon dioxide (pCO_2) and increased the acidity of seawater (Denman et al., 2007). Briefly, OA is the atmospheric CO_2 combined with the seawater surface, which causes ocean pH reduction and forms carbonic acid (H_2CO_3). The H_2CO_3 releases the hydrogen (H^+) ions and form bicarbonate (HCO_3^-) ions (Figuerola et al., 2021). These changes in the seawater cause calcium carbonate ($CaCO_3$) reduction in seawater. Thus the reduction in CO_3^{2-}reducing the $CaCO_3$ saturation in seawater resulted in a negative impact on the calciferous animals (Kleypas et al., 2006).

Reports are insight that the calcification rate, survival, molting, biochemical, hypercapnia, reproduction, feeding habit, calcite, and aragonite of marine animals such as corals, Echinoidea, Gastropoda, Annelida, Foraminiferans, Coccolithophores, bivalves, and crustaceans are decreasing due to the increasing pCO_2 level in the seawater (Fabry et al., 2008; Andersson and Gledhill, 2013; Thomsen et al., 2015; Duquette et al., 2017; Verkaik et al., 2017; Guamán-Guevara et al., 2019; D'Amario et al., 2020; Muralisankar et al., 2021). Also, the survival, growth, molting, food indices, and reproduction capacity can affect marine calciferous animals by OA (Kurihara et al., 2008; Kroeker et al., 2013; Thangal et al., 2022). Marine crabs are a diverse group of crustaceans that play a significant ecological and economic role in marine ecosystems. They are found in various habitats, ranging from intertidal zones to deep-sea environments. Ecologically, marine crabs serve as important predators, prey, and scavengers, contributing to maintaining a healthy environment and balancing the marine food

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https://doi.org/10.1016/j.envres.2024.118238
Received 6 November 2023; Received in revised form 2 January 2024; Accepted 17 January 2024
Available online 21 January 2024

Abbreviations

ACP	Acid phosphatase
ALP	Alkaline phosphatase
ATP	Adenosine triphosphate
Ca	Calcium
$CaCO_3$	Calcium carbonate
$CaCO_3$	Calcium carbonate Na Sodium
CAT	Catalase
CO_2	Carbon dioxide
CO_3^{2-}	Carbonate ion
Cu	Copper
EEZ	Exclusive economic zone
Fe	Iron
GOT	Glutamic oxaloacetic transaminase
GPT	Glutamic pyruvic transaminase
GPx	Glutathione peroxidase
GST	Glutathione S-transferases
H^+	Hydrogen ions
H_2CO_3	Carbonic acid
HCO_3^-	Bicarbonate ions
K	Potassium
LPO	Lipid peroxidation
Mg	Magnesium
OA	Ocean acidification
P	Phosphorus
pCO_2	Partial pressure of carbon dioxide
ROS	Reactive oxygen species
Se	Selenium
SOD	Superoxide dismutase
Zn	Zinc

webs. They also play a crucial role in nutrient cycling and ecosystem functioning, as they help to break down organic matter and recycle nutrients (Xie et al., 2022) as they feed on decaying organic matter and help to break it down and recycle it back into the ecosystem. In addition to their ecological importance, marine crabs have significant economic value as a seafood resource.

Crab fisheries provide significant income and employment opportunities for coastal communities, especially in developing countries where they are a major source of protein for local populations. Southeast Asian nations such as Vietnam, the Philippines, and Indonesia are the major crab production countries, with an average production of 65,463, 18,100, and 15,000 tons, respectively (Yxtung, 2020). Crabs help to maintain the balance of marine ecosystems by controlling the populations of other marine organisms, such as small fish, mollusks, and other crustaceans. Despite their importance, marine crabs are threatened by various anthropogenic stressors, including overfishing, habitat destruction, and pollution (Tiansongrassamee, 2004). As such, it is important to manage these resources sustainably and protect their habitats to ensure the continued ecological and economic benefits that they provide. The effect of OA on marine crabs' survival, molting, growth, physiology, and immunology (Long et al., 2017; Meseck et al., 2016; Turra et al., 2019) has been studied earlier. Based on the information from existing reports, comprehensive reviews were performed earlier on the effect of OA on growth, survival, feeding, behavior, calcification, reproduction, development, stress response, etc., on marine organisms (Kroeker et al., 2013; Bhadury, 2015; Mostofa et al., 2016; Figuerola et al., 2021), however, a review for a specific group of organisms including marine crabs is not performed. Hence, the present review was exclusively focused on understanding the effect of OA on the biological and physiological response of marine crabs. The present review was performed with a total of 111 articles and discussed the reports from 37 research papers on the effect of OA and OA with other stressors (heavy metals, temperature, hypoxia, and salinity) on survival, growth, food indices, molting, chitin quality, biochemical elements, antioxidants, metabolic enzymes, and minerals in marine crabs. Moreover, this review has also discussed the possible research gaps and future required investigations.

2. Data collection and analysis

The effect of OA on marine organisms is studied widely, however, limited reports are available on marine crabs. This review focused on the OA experiments conducted on marine crabs at laboratory and field levels to address the impacts. The main aim of writing this review is to summarize the available information from the existing research papers, examine the depth of knowledge, identify the research gaps, and way forward for future research on the impact of OA on marine crabs. The literature search was performed for this review in October 2023 by various databases such as PubMed, Scopus, Google Scholar, and Web of Science using various keywords related to OA and marine crabs (ocean acidification, low pH, high pCO_2, hypercapnia, effect on climate change, global issues, marine crabs, elevated pCO_2, pH stress, combined effect of ocean acidification and warming, multiple stresses, etc.). A total of 37 research papers were collected for this review published from November 2010 to October 2023. All research articles were indexed in Google Scholar, followed by Web of Science, Scopus, and PubMed with indexing of 35, 24, and 22 papers respectively (Fig. 1 a). Based on the corresponding author's affiliation of each paper, it was recognized that the papers originated from seven different nations like USA, China, Germany, India, Korea, Norway, and South Africa. Among nations, the USA holds the top position with 20 research papers, followed by other countries (Fig. 1b). Furthermore, the year-wise publication analysis reveals the papers published from 2010 onwards and the maximum number of papers published during 2019–2021. However, the maximum number of citations was noticed during the years 2010–2012 and the citations gradually declined in recent years (Fig. 1 c).

3. Impact of OA on marine organisms

Change in seawater chemistry like pH, salinity, temperature, alkalinity, carbonates, etc., affects marine organisms. Among seawater properties, the elevated pCO_2 decreases seawater pH (OA), carbonates, saturation state of calcium and aragonite, and increases the dissolved inorganic carbon, and bicarbonates which leads to affects marine organisms in many ways like decreased growth, calcification, and altering biological and physiological activities. In phytoplankton, OA increases the toxic phenolic compounds that could be transferred to higher tropic-level organisms (Jin et al., 2015). Increased CO_2-charged waters can lead to a transient increase in surface pCO_2 sufficient to cause widespread physiological shock, climatic shock, or both, resulting in mass mortality of marine animals (Knoll et al., 1996). Elevated internal CO_2 concentrations also contribute to physiological mechanisms that trigger metabolic slowing or arrest. Marine invertebrates like crabs, shrimp, lobster, limpets, corals, sea urchins, etc., showed decreases in net calcification with increased pCO_2 (Ries et al., 2009; Mongin et al., 2021; Anand et al., 2021). Dissanayake and Ishimatsu (2011) and found a synergistic effect of elevated CO_2 concentrations and temperature, which can impair penaeids' breathing and swimming capacities. Organisms that produce $CaCO_3$ skeletons are particularly sensitive to hypercapnia because carbonate biomineralization requires precise control of the acid-base balance. At high partial pressure, CO_2 binds directly with respiratory pigment, decreasing its ability to carry oxygen. Studies

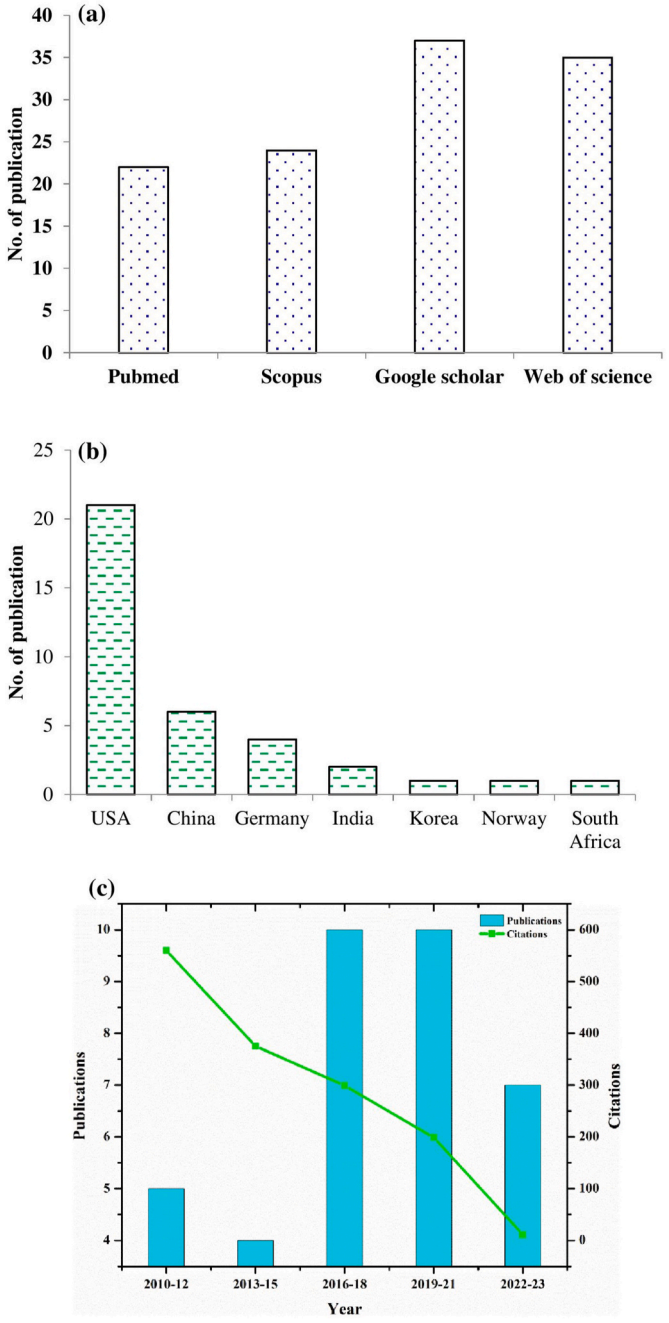

Fig. 1. (a) Indexing database of reviewed papers, (b) publication origin nations, and (c) year wise publication and citation of reviewed publications.

reported that the projected future rises of seawater pCO_2 and accompanying reductions of pH would lead to decreases in the $CaCO_3$ saturation state to the extent that several marine calcifying organisms suffer from a reduction of calcification rate and an increase in $CaCO_3$ dissolution rate (Riebesell et al., 2000; Feely et al., 2004; Orr et al., 2005; Gazeau et al., 2007). Therefore, calcifying marine organisms are the earliest organisms to be impacted by the OA due to ever-increasing atmospheric CO_2 levels (Kurihara and Shirayama, 2004; Hoegh-Guldberg et al., 2017; Lemasson et al., 2017). Species like coccolithophores, crabs, sea urchins, etc., are adversely affected by OA. OA, along with other stressors such as temperature, hypoxia, heavy metals, salinity, etc., can have harmful impacts on the survival, growth, foraging behavior, molting, etc., of marine animals, including fishes (Lopes et al., 2018), sea urchin (Zhan et al., 2020), bivalves (Shi et al., 2016), and crabs (Wu et al., 2017; Turra et al., 2019; Gravinese et al., 2022). In this context, the impact of OA on marine animals upon the level of pCO_2 and species type of marine calcifiers. OA affects the calcifiers in larval forms rather than adults, which have high tolerance (Leung et al., 2022). Among marine calcifiers marine crabs are one of the most vulnerable to OA (Tomasetti et al., 2018; Long et al., 2019; Thangal et al., 2022; McElhany et al., 2022; Algayer et al., 2023) and the possible mechanisms of the effect of OA on marine crabs are depicted in Fig. 2.

4. Methods used in OA experiments of crabs

Most of the OA experiments were performed on crabs at the laboratory level to maintain the desired pH condition. However, the experimental design like manipulation of seawater pH is the main factor in OA experiments to investigate the response of crabs to changing seawater chemistry. Bubbling pure CO_2 in seawater is an efficient method to alter the carbonate chemistry (Riebesell et al., 2011). Regarding this, the automated pH manipulation systems were performed in some crabs' experiments (Wanamaker et al., 2019; Landes and Zimmer, 2012; Baag and Mandal, 2023). The automatic pH manipulation system involves continuous monitoring of pH in each aquarium by a pH meter that is connected to an electronic controller. The desired pH is programmed in the device and the controller automatically opens the gas valves of the CO_2 cylinder to bubble through a rubber tube connected to a gas diffuser in seawater when the pH is above the desired level and closes the valve when the target pH is reached. Some studies were performed by manually releasing CO_2 to the seawater-containing aquarium to manipulate the seawater pH. This system consisted of a gas cylinder that connected with valves, rubber tubes, and a diffuser. The desired pH is maintained by the manual release of CO_2 using valves and a pH probe is always dipped in the experimental seawater to monitor the pH level (Thangal et al., 2022, 2023). Moreover, a few experiments on marine crabs were performed by preparing high CO_2-enriched seawater at pH 5.5 as stock, and the desired level of pH was manipulated by mixing this stock with the ambient seawater (Long et al., 2013, 2017, 2019; Swiney et al., 2016; Coffey et al., 2017; Dickinson et al., 2021; Algayer et al., 2023). In this context, strong acid (HCl) and base (NaOH) addition to the seawater for pH manipulation was also performed in OA experiments on crabs (Zhao et al., 2021). Among OA systems, the computerized automated feedback method does not require the regular monitoring of changing pH, which is an efficient way to manipulate the seawater pH with minimal deviation. In this context, the manual methods require regular monitoring of pH at different time intervals (2 h, 12 h, daily, weekly, etc.) and the addition of CO_2 to keep the desired pH by manpower (Appelhans et al., 2012; Lin et al., 2020; Dickinson et al., 2021; Thangal et al., 2022). Nonetheless, the deviation pH might be higher in manual OA experiments compared to automatic feedback systems. Further, experiments on OA with other stressors like temperature, hypoxia, heavy metals, salinity, etc., were also performed in marine crabs. For these synergistic stress experiments, the temperature was raised by digitally controlled thermostats, aquarium heaters, temperature-controlled water baths, titanium heaters, etc. (Paganini et al., 2014; Manríquez et al., 2021; Gravinese et al., 2022; Baag and Mandal, 2023). The hypoxia environments were created in OA experiments in marine crabs by bubbling CO_2+ N_2+ ambient air (Walther et al., 2010) and O_2+N_2+CO_2 (Wanamaker et al., 2019). In this context, OA experiments with heavy metals (metal salts) and oil were performed by direct exposure to the experimental culture water (Adeleke et al., 2020; Zhao et al., 2021; Thangal et al., 2023; Baag and Mandal, 2023) (Table 2).

Choosing the life stages and housing of crabs are other key factors in OA research. Instars and juveniles are used for OA experiments due to their greater metabolic rate than adults and higher sensitivity to the fluctuating environment (Long et al., 2013; McElhany et al., 2022; Gravinese et al., 2022; Thangal et al., 2022, 2023). Whereas, adults are

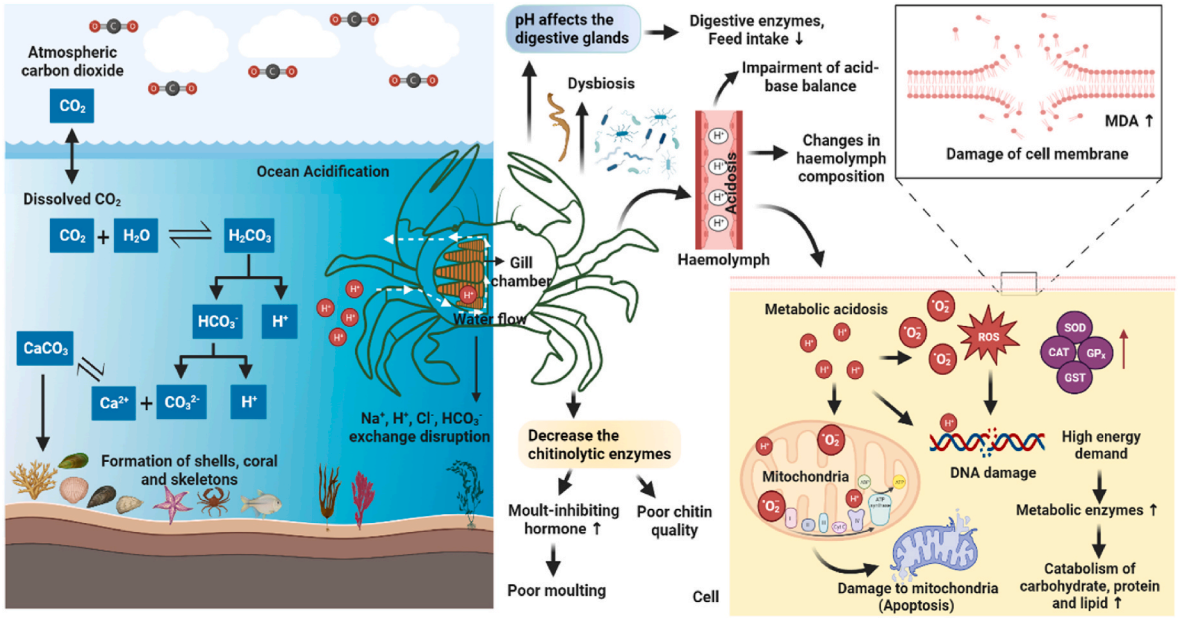

Fig. 2. The possible mechanism of ocean acidification in marine crabs.

used for studying the foraging behavior, predation behavior, feeding, ingestion, absorption, growth, exoskeletons properties, metabolic and physiological activities, etc. (Hammer et al., 2012; Wu et al., 2017; Dickinson et al., 2021; Algayer et al., 2023; Baag and Mandal, 2023). Besides, the housing of crabs in OA experiments was performed in plastics aquaria, glass tanks, jars, etc., with different stockings of 1–30 individuals per aquaria, however, the stocking densities were varied based on the life stages. Further, some studies designed the experiment with a cage system fabricated using polyvinyl chloride (PVC) pipes where the individual crabs were stocked in a cage to prevent cannibalism. (Hammer et al., 2012; Kim et al., 2016; Coffey et al., 2017; Long et al., 2017, 2019; Adeleke et al., 2020; McElhany et al., 2022; Thangal et al., 2022, 2023). In concerning to the feed for marine crabs during OA experiments, they were fed with live feeds (brine shrimp nauplii and rotifers) frozen feeds (brine shrimp, fishes, squids, shrimps, bloodworms, etc.), dried fish pellets, commercial feed, etc., at an adequate level (ad-libitum) on regular basis (Kim et al., 2016; Giltz and Taylor, 2017; Tomasetti et al., 2018; Long et al., 2019; Zhao et al., 2021; Thangal et al., 2022; Baag and Mandal, 2023).

5. Effect of OA on survival and growth of crabs

Survival and growth are essential parameters to know the physiological status of an organism because these parameters can be altered by biotic and abiotic stressors. It has been well documented that the increasing pCO_2 in seawater decreases ocean pH (OA), followed by declining the carbonate level and saturation state of calcium and aragonite in the seawater can harm the growth and survival of many marine organisms, including crabs (Shi et al., 2016; Wu et al., 2017; Turra et al., 2019; Zhan et al., 2020; Gravinese et al., 2022; Thangal et al., 2022, 2023). Crabs under acidified environments spend more energy to tolerate the acidic stress and regulate the internal pH, decreasing feeding and poor survival and growth. Moreover, OA could disrupt the sensory organs of the crabs, which can lead to a decrease in their ability to detect food particles, which leads to decreased survival and growth (Durant et al., 2023). Many studies have investigated the effect of OA on the survival and growth of marine crabs. Seawater acidification caused decreases in survival and growth of blue crab *Callinectes sapidus* in both planktonic (at pH 7.8) and juvenile (at pH 7.2, 7.3, and 7.8) stages have been noticed (Giltz and Taylor, 2017; Tomasetti et al., 2018). The significant decrease in the survival of juvenile blue king crabs (*Paralithodes platypus*) exposed to pH 7.5 for one year was studied by Long et al. (2017). Similarly, a notable reduction in the survival and growth of the mud crab *Scylla serrata* instars exposed to the CO_2-driven acidified seawater environment (pH 7.6, 7.4, 7.2, and 7.0) for sixty days was observed by Thangal et al. (2022). Long et al. (2013) recorded the cent percent mortality and reduced growth in the juvenile red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes bairdi*) exposed to the pH 7.5 on the 95th day of the 200 days experiment. The decreased larval development was recorded in the spider crab (*Hyas araneus*) exposed to the CO_2-driven acidic seawater at pH 7.81 and 7.33 (Walther et al., 2010). Most of the above studies suggest that OA can negatively affect the survival and growth of marine crabs, on the contrary, few studies indicated an insignificant and positive impact on survival in crabs despite reduced growth. The hermit crab (*Pagurus criniticornis*) exposed to a pH of 7.7 for 120 days showed an insignificant reduction in survival and a significant decrease in growth (Turra et al., 2019). At the same time, a report published by McElhany et al. (2022) stated that a higher survival rate and poor growth were observed in the juvenile Dungeness crab *Metacarcinus magister* exposed to higher CO_2 (pH 7.2) than in ambient CO_2 for 300 days (Table 1). Furthermore, the existing reports carry limited information on the detrimental effect of OA on marine crabs. Hence more studies must be focused on the different developmental stages of various crab species, including edible species. Moreover, the molecular mechanisms related to poor growth in growth gene expression can also be focused on marine crabs under OA treatments.

6. Molting and chitin quantity of crabs under OA

Molting is a critical process for crustaceans, including crabs, as it allows them to grow and regenerate lost limbs (Fujaya et al., 2020). However, studies have shown that OA can affect the molting process of crabs in several ways. One of the primary ways that OA affects crabs is by reducing the availability of calcium carbonate, which is a crucial component of the exoskeletons of crustaceans. As the pH of the ocean decreases, the concentration of carbonate ions and calcium saturation level in the seawater also decreases, making it more difficult for crabs to

Table 1
Effect of ocean acidification on marine crabs.

Sl. No.	Species	Experiment site/Method adopted for OA	pH/pCO_2	Exposure duration	Observation	Reference
1	Snow crab (*Chionoecetes opilio*)	Lab study/ CO_2 bubbling	7.58	2 years	(↓) Ca	Algayer et al. (2023)
2	Mud crab (*Scylla serrata*)	Lab study/CO_2 bubbling	7.8, 7.6, 7.4, 7.2 & 7.0	2 months	(↓) SR (pH 7.6 to 7.0) (↓) GR (pH 7.8 to 7.0) (↓) M (pH 7.8 to 7.0) (↓) CN (pH 7.4 to 7.0) (↓) FI & (↑) FCR (7.2 & 7.0) (↓) PRO, CHO & AA (pH 7.8 to 7.0) (↓) L (pH 7.4 to 7.0) (↓) Ca, Na & K (pH 7.8 to 7.0). (↑) SOD, CAT & LPO (7 pH 7.8 to 7.0) (↓) ALP (pH 7.2 & 7.0) (↑) GOT & GPT (pH 7.8 to 7.0)	Thangal et al. (2022)
3	Juvenile Dungeness crab (*Metacarcinus magister*)	Lab study/CO_2 bubbling	7.2	300 days	(↑) SR (↓) GR	McElhany et al. (2022)
4	Horseshoe crab (*Tachypleus tridentatus*)	Lab study/CO_2 bubbling	7.3	28 days	(↓) Ecdysone hormone (↓) Chitinase (↑) LPO, SOD, CAT & GPx (↑) ALP first and then (↓)	Liu et al. (2022)
5	Tanner crabs (*Chionoecetes bairdi*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.5	2 years	(↓) Claw hardness	Dickinson et al. (2021)
6	Dungeness crabs (*Metacarcinus magister*)	Field study at US West coast	7.48	1 month	(↑) Dissolution of carapace	Bednaršek et al. (2020)
7	Chines crab (*Portunus trituberculatus*)	Lab study/CO_2 bubbling	750 &1500 µatm	4 weeks	(↑) SOD & GST (750 & 1500 µatm) (↓) LIP & AMY (750 & 1500 µatm)	Lin et al. (2020)
8	Dungeness crab (*Cancer magister*)	Lab study/CO_2 bubbling	7.45	32 days	(↑) MB & L	Wanamaker et al. (2019)
9	Hermit crab (*Pagurus criniticornis*)	Lab study/CO_2 bubbling	7.7	4 months	(↔) SR (↓) GR (↓) M (↓) L	Turra et al. (2019)
10	Red king crab (*Paralithodes camtschaticus*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.5	3 week	(↓) M	Long et al. (2019)
11	Juvenile blue crab (*Callinectes sapidus*)	Lab study/CO_2 bubbling	8000 µatm	1 month	(↓) Thickness of whole cuticle & endocuticle (↑) Ca & Mg	Glandon et al. (2018)
12	Brown crab (*Cancer pagurus*)	Lab study/CO_2 bubbling	1200 & 2300 µatm	2 weeks	(↓) FCR, FB, TBP, ST, FCT & HT (1200 & 2300 µatm)	Wang et al. (2018)
13	Blue king crabs (*Paralithodes platypus*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.8 & 7.5	1 year	(↓) Microhardness of chelae (pH 7.5) (↓) Cuticle thickness (pH 7.5) (↑) Carapace Ca (pH 7.8 & 7.5) (↔) Chelae Ca (pH 7.8 & 7.5) (↔) Carapace & chelae Mg (pH 7.8 & 7.5)	Coffey et al. (2017)
14	Blue king crab (*Paralithodes platypus*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.5	1 year	(↓) SR	Long et al. (2017)
15	Blue crabs (*Callinectes sapidus*)	Lab study/CO_2 bubbling	7.2, 7.3 & 7.8	14 days	(↓) SR (pH 7.8 to 7.2) (↓) GR (pH 7.8)	Giltz and Taylor (2017)
16	Hermit crab (*Pagurus tanneri*)	Lab study/CO_2 bubbling	7.1	20 weeks	Damage to the antennular flickering (↑) FIT (↑) MR	Kim et al. (2016)
17	Snow crab (*Chionoecetes bairdi*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.5	2 years	(↓) Ca	Swiney et al. (2016)
18	Mud crab (*Panopeus herbstii*)	Lab study/CO_2 bubbling	785 & 9274 µatm	71 days	(↓) FI, FHT & PCT (785 & 9274 µatm)	Dodd et al. (2015)
19	Intertidal porcelain crab (*Petrolisthes cinctipes*)	Lab study/Direct CO_2 bubbling	7.58	6 days	(↓) MR	Carter et al. (2013)
20	Red king crab (*Paralithodes camtschaticus*) Tanner crab (*Chionoecetes bairdi*)	Lab study/CO_2 enriched seawater used as stock at pH 5.5	7.8 & 7.5	200 days	(↓) SR & GR (pH 7.5) (↓) Ca (pH 7.8 & 7.5)	Long et al. (2013)
21	Green crab (*Carcinus maenas*)	Lab study/CO_2 bubbling	7.4, 6.6 & 6.3	4 weeks	(↓) GLY & PROL (pH 6.3 to 7.4)	Hammer et al. (2012)
22	Green crab (*Carcinus maenas*)	Lab study/CO_2 bubbling	7.7	5 months	(↓) ML of chelated crusher legs (↔) Predator-prey behavior	Landes and Zimmer (2012)
23	The shore crab (*Carcinus maenas*)	Lab study/ CO_2 bubbling	1120 & 4000 µatm	10 weeks	(↓) FCR (1250 & 3000 µatm)	Appelhans et al. (2012)

Alkaline phosphatase (ALP), Amino acids (AA), Amylase (AMY), Calcium (Ca), Carbohydrate (CHO), Catalyse (CAT), Chitin (CN), Feed conversion ratio (FCR), Feed identifying time (FIT), Feed intake (FI), Food consuming time (FCT), Food handling time (FHT), Foraging behavior (FB), Glutathione peroxidase (GPx), Glutamic pyruvic transaminase (GPT), Glutamic oxaloacetic transaminase (GOT), Glutathione S-transferases (GST), Glysin (GLY), Growth (GR), Heat tolerance (HT), Lipids (L), Lipase (LIP), Lipid peroxidation (LPO), Magnesium (Mg), Metabolic rate (MR), Molting (M), Metabolites (MB), Muscle length (ML), Potassium (K), Predator capture time (PCT), Proline (PROL), Protease (PRO), Searching time (ST), Sodium (Na), Superoxide dismutase (SOD), Survival (SR), Time to break the prey (TBP).

Table 2
Impact of ocean acidification with other stressors on crabs.

Sl. No	Species	Experiment site/ Method adopted for OA	pH/pCO_2	Other stressors/Mode of administration	Exposure duration	Observation	Reference
1	Mud crab (*Scylla serrata*)	Lab study/CO_2 bubbling	7.7	Temperature (34 °C) + Diesel (5 mg L^{-1})/Digitally controlled thermostat & Direct exposure of diesel to culture water	1 month	(↓) I & A (pH 7.7 + 5 mg L^{-1}) (↑) RR & E (pH 7.7 + 34 °C) (↓) CTmax (pH 7.7 + 34 °C)	Baag and Mandal (2023)
2	Mud crab (*Scylla serrata*)	Lab study/CO_2 bubbling	7.8, 7.6, 7.4, 7.2 & 7.0	Cd (10 mg L^{-1})/Direct exposure to culture water	2 months	(↑) Accumulation of Cd in tissue (pH 7.8 to 7.0) (↓) SR (pH 7.2 & 7.0 + 10 mg L^{-1}) (↓) GR (pH 7.8 to 7.0 + 10 mg L^{-1}) (↓) M (pH 7.0 + 10 mg L^{-1}) (↓) FI (pH 7.8 to 7.0 + 10 mg L^{-1}) (↑) FCR (pH 7.8, 7.6, 7.4 + 10 mg L^{-1}) (↓) PRO, CHO, AA, L (pH 7.8 to 7.0 + 10 mg L^{-1}) (↑) SOD, CAT, LPO (pH 7.8 to 7.0 + 10 mg L^{-1}) (↑) ALP (pH 7.8 to 7.0 + 10 mg L^{-1}) (↔) GOT, GPT (pH 7.8 to 7.0 + 10 mg L^{-1}) (↓) HP (pH 7.8 to 7.0 + 10 mg L^{-1})	Thangal et al. (2023)
3	Fiddler crab (*Leptuca thayeri*)	Lab study/CO_2 bubbling	7.0 & 6.3	Temperature (20, 25, 30, 35, 40 °C) Salinity (10, 20, 30, 40, and 50 psμ)/ NM	3 days	CD (pH 7.0 + 40 °C & pH 6.3 + 40 °C) (↑) OC (pH 6.3 + 30 °C & pH 7.0 + 50 psμ) (↓) OC (pH 6.3 + 35 °C & pH 6.3 + 50 psμ) (↓) HI (pH 6.3 + 35 °C & pH 6.3 + 20 & 30 psμ)	Andrade et al. (2022)
4	Caribbean king crab (*Maguimithrax spinosissimus*)	Lab study/CO_2 bubbling	7.7	Temperature (31 °C)/Temperature probe connected with hearts		(↓) SR (pH 7.7 + 31 °C) (↓) M (pH 7.7 + 31 °C)	Gravinese et al. (2022)
5	Estuarine fiddler crab (*Leptuca thayeri*)	Lab study/CO_2 bubbling	6.2	Temperature (30 °C)/Aquarium heater	10 days	(↓) SR (pH 6.2 + 30 °C) (↓) HEV (pH 6.2 + 30 °C)	Pardo and Costa (2021)
6	Mitten crab (*Eriocheir sinensis*)	Lab study/1 mol· L^{-1} NaOH and 1 mol· L^{-1} HCL	pH 7.8, 7.3 & 6.5	Cd (1 mg L^{-1})/Direct exposure to culture water	21 days	(↑) SOD and CAT (pH 7.8 to 6.5 + Cd 1 mg L^{-1})	Zhao et al. (2021)
7	Shell-crushing crab (*Acanthocyclus hassleri*)	Lab study/CO_2 bubbling	pCO_2 (~500 & 1400 μatm)	Temperature (~15 & 20 °C)/ Temperature controlled water bath	10–16 weeks	(↓) SR, CR, AL (1400 μatm + 25 °C) (↑) FI and OC (25 °C alone) (↓) CPS (1400 μatm alone) (↓) CHO (1400 μatm + 20 °C). (↑) HSP70 level (25 °C alone)	Manríquez et al. (2021)
8	Crab (*Dotilla fenestrata*)	Lab study/CO_2 bubbling	7.2, 7.4 & 7.6	Cd (0.5, 0.75, 1.0 mg L^{-1}), Pb (6.50, 8.50, 10.50 mg L^{-1}) & Cd/Pb (4.50, 5.75, 7.00 mg L^{-1})/Direct exposure to culture water	96 h	(↑) Accumulation of Cd in pH 7.4 > 7.6 > 7.2 (↔) Pb accumulation with varying pH (↑) Accumulations in combined Cd and Pb in pH 7.2 and 4.50, and 7.0 mg L^{-1}	Adeleke et al. (2020)
9	Dungeness crab (*Cancer magister*)	Lab study/AADDFS	7.45	Dissolved oxygen (3 mg L^{-1})/MOATS (O_2+ N_2 + CO_2	32 days	(↑) MB & L (DO 3 mg L^{-1} alone) (↔) MB & L (pH 7.45+ DO 3 mg L^{-1} & DO 3 mg L^{-1})	Wanamaker et al. (2019)
10	Blue crabs (*Callinectes sapidus*)	Lab study/CO_2 bubbling	7.16 to 7.33	Dissolved oxygen (3.74–4.06 mg L^{-1})/ Bubbling of 5% CO_2+ N_2+ ambient air	14 days	(↓) SR 60% (3.74 mg L^{-1}), 49 % (pH 7.16), & 87 % (pH 7.16 + 3.74 mg L^{-1})	Tomasetti et al. (2018)
11	Juvenile blue crab (*Callinectes sapidus*)	Lab study/CO2 bubbling (pH stat system)	8000 μatm	Temperature (32 °C)/Heated & chilled seawater	1 month	(↓) Thickness of whole cuticle & endocuticle (8000 μatm + 32 °C) (↑) Ca & Mg	Glandon et al. (2018)
12	Red king crab (*Paralithodes camtschaticus*)	Lab study/CO_2 bubbling	7.8	Temperature (Ambient +2 & 4 °C)/ Aquarium heater	184 days	(↓) SR (7.8 + 4 °C) (↓) IMP (7.8 + 4 °C) (↓) GR (7.8 + 4 °C)	Swiney et al. (2017)
13	Japanese stone crab (*Charybdis japonica*)	Lab study/CO_2/ pH controller	7.3 & 8.1	Temperature (18 & 25 °C)/NM	2 days	(↑) FIT, FBT, FCT, FHT (pH 7.3 + 18 & 25 °C)	Wu et al. (2017)

(*continued on next page*)

Table 2 (*continued*)

Sl. No	Species	Experiment site/ Method adopted for OA	pH/pCO_2	Other stressors/Mode of administration	Exposure duration	Observation	Reference
						(↓) PP, PPT (pH 7.3 + 18 & 25 °C)	
14	Great spider crab (*Hyas araneus*)	Lab study/CO_2 bubbling	1120 &1960 µatm	Temperature (5 & 10 °C)/Thermostat	10 weeks	(↑) Stress response genes (1120 µatm + 10 °C) (↔) Stress response genes (1960 µatm + 10 °C) (↓) HpH (1960 µatm + 10 °C)	Harms et al. (2014)
15	Porcelain crab (*Petrolisthes cinctipes*)	Lab study/CO_2 bubbling	7.6 & 7.15	Temperature (25 & 30 °C)/Titanium heaters	2.5 weeks	(↓) RR (pH 7.15 + 30 °C) (↑) HT (pH 7.15 + 30 °C)	Paganini et al. (2014)
16	Spider crab (*Hyas araneus*)	Lab study/(Kautex bottle filled with CO_2+ O_2 in N_2	710 & 3000 ppm	Temperatures (3, 9 & 15 °C)/NM	–	(↓) Ca (710 & 3000 ppm + 9 &15 °C) (↓) LDP (3000 ppm + 15 °C)	Walther et al. (2010)

Absorption (A), Amino acid (AA), Alkaline phosphatase (ALP), Arcomere length (AL), Calcification rate (CR), Calcium (Ca), Cadmium (Cd), Carbohydrate (CHO), Catalyse (CAT), Claw pinching strength (CPS), Complete death (CD), Excretion (E), Feed breaking Time (FBT), Feed conversion ratio (FCR), Feed identifying time (FIT), Feed intake (FI), Food consuming time (FCT), Food handling time (FHT), Growth (GR), Glutamic oxaloacetic transaminase (GOT), Glutamic pyruvic transaminase (GPT), Heat shock protein 70 (HSP70), Hemolymph pH (HpH), Haemocyte population (HP), Hepatosomatic Index (HI), Heat tolerance (HT), Higher egg volume (HEV), Ingestion (I), Inter molt periods (IMP), Mobile ocean acidification treatment system (MOATS), Magnesium (Mg), Molting (M), Metabolites (MB), L (Lipids), Larval development period (LDP), Lead (Pb), Lipid peroxidation (LPO), Oxygen consumption (OC), Not mentioned (NM), Pray predation Time (PPT), Protease (PRO), Prey profitability (PP), Respiration rate (RR), Superoxide dismutase (SOD), Survival (SR), Thermal critical maxima (CTmax).

form and maintain their exoskeletons. This can lead to slower growth rates, smaller body sizes, and increased vulnerability to predation and pathogens. OA can also affect the ecdysone hormone levels of juvenile horseshoe crabs (*Tachypleus tridentatus*) at pH 7.3 after seven days of the experiment (Liu et al., 2022), which can cause regulation in molting. This disruption can lead to an abnormal molting cycle, increased disease susceptibility, and reduced overall fitness. The report showed that the red king crab *P. camtschaticus* was exposed to pH 7.5 for three weeks and showed a slower molting process than the ambient pH 8.1 (Long et al., 2019). The mud crab *S. serrata* exposed to the acidified seawater (pH 7.8, 7.6, 7.4, 7.2, 7.0) for 60 days showed an abnormal molting rate when compared to the ambient pH (Thangal et al., 2022). According to the report of Turra et al. (2019), the hermit crab (*P. criniticornis*) exposed to pH 7.7 for 120 days showed a slower molting frequency than the crabs in an ambient pH environment. Glandon et al. (2018) revealed a decrease in the whole cuticle and endocuticle thickness of juvenile blue crab (*C. sapidus*) exposed to the high pCO_2 for 30 days. Nearly 10% of carapace dissolution arose in Dungeness crabs *M. magister* over the last two decades due to OA (pH 7.48) caused by excess emission of atmospheric CO_2 along the United States West Coast (Bednaršek et al., 2020) (Table 1). These studies reveal changes in seawater chemistry by the OA process that affect the crabs' molting process, which ultimately affects their physiological activities, followed by growth and survival. Nevertheless, the specific molecular mechanism is still unclear, hence, future studies need to be focused on these aspects.

Chitin is a natural polymer widely distributed in the animal kingdom, playing a fundamental role in structural support, defense, and other biological functions (Lavall et al., 2007; Abdou et al., 2008; Hendriks et al., 2015). It is the primary constituent of the exoskeleton of crustaceans, such as crabs, lobsters, and shrimp. OA can affect the exoskeleton properties of crustaceans, however, it may vary based on the species and pCO_2 levels (Siegel et al., 2022). Chitin combined with calcium carbonate produces a stronger composite in crustaceans, hence, the decreased carbonate and saturation of calcium under acidified seawater pH may affect the chitin production. A reduction in the chitin level and quality changes in the mud crab *S. serrata* exposed to pH 7.4, 7.2, and 7.0 for two months was observed by Thangal et al. (2022). The loss of chitin in the crab species may result from the loss of chitin synthetases and chitinolytic enzymes under the acidified seawater environment (Merzendorfer and Zimoch, 2003). Liu et al. (2022) noticed a notable decrease in the chitinase enzyme in horseshoe crab *T. tridentatus* exposed to pH 7.3 for 28 days (Table 1). Nonetheless, the studies on the impact of OA on the chitin production and quality of marine crabs are fragmentary. Hence, more studies have to be focused on various crab species at different growing stages. Moreover, the molecular mechanism of OA on the crab's chitin and molting must also be focused on in future investigations.

7. Effect of OA on food indices of crabs

Feed intake of animals can affect unfavorable conditions as the stress response. OA's effect on crabs' food indices has been investigated in some studies. A study investigated the impact of OA is reduced feeding behaviors like feed intake, food handling time, and lasting predator capture time in the mud crab *Panopeus herbstii* exposed to the high pCO_2 (9274 µatm) during the 71 days experiment (Dodd et al., 2015). Another study by Manríquez et al. (2021) recorded the reduction in the feeding rates and claw pinching strength of the crab *Acanthocyclus hassleri* exposed to high pCO_2 (1400 µatm) for 10–16 weeks. This study also found that acidification reduced the amount of energy available to the crabs, which could affect their ability to reproduce and maintain their normal physiological functions. The food consumption ratio, such as decreased feed intake and increased feed conversion ratio was noticed in the mud crab *S. serrata* exposed to pH 7.2 and 7.0 (Thangal et al., 2022). The brown crab *Cancer pagurus* exposed to the high pCO_2 (1200 and 2300 µatm) for two weeks showed a negative impact on the food consumption rates, foraging behavior like time to break the prey, searching time, food consuming time, and handling time than control crabs (Wang et al., 2018). The shore crab *C. maenas* showed a 41% decrease in food consumption rates at high pCO_2 (1120 and 4000 µatm) exposed for 10 weeks (Appelhans et al., 2012). Significant damage in the antennular flicking rate and long duration to identify the food was observed in deep-sea hermit crabs *Pagurus tanner* exposed to pH 7.1 for 20 weeks (Kim et al., 2016). In this context, the predation behavior of the crab *C. maenas* was not affected in acidified (pH 7.7) conditions (Landes and Zimmer, 2012) (Table 1). The overall available literature reveals that OA can significantly affect the food indices of crabs, leading to poor growth, survival, and other physiological activities. Nonetheless, the existing reports on the effect of OA on food index parameters are very limited to crab species. Therefore, more studies are essential in various species, including edible crabs, for understanding the effect of OA on various marine crabs.

8. Biochemical constituents of crabs exposed to OA

Crabs are fascinating creatures that inhabit various aquatic environments. As with many other living organisms, crabs rely on a complex network of biochemical elements such as proteins, amino acids, carbohydrates, lipids, nucleic acids, and numerous secondary metabolites to carry out their essential biological functions. Animals under stressful conditions need more energy to overcome the stress. Under this circumstance, the available elements like protein, carbohydrates, and lipids in the body can undergo the catabolic process to produce more energy, which leads to decreases in these biochemical elements in the tissues (Michaelidis et al., 2005; Rosa et al., 2014). Few investigations have revealed the alterations in biochemical elements of crabs under an acidified environment. A study by Thangal et al. (2022) showed that OA (pH 7.8, 7.6, 7.4, 7.2, and 7.0) could affect the biochemical constituents like protein, amino acid, and carbohydrates of the crab (*S. serrata*) which can have negative consequences for their growth, development and overall physiological activities. The outcome of this study reveals that crabs under acidified environments did not accept adequate feed, followed by poor growth and survival. A stronger reduction in the carbohydrate levels in the crab *A. hassleri* reared for 16 weeks in high pCO_2 (1400 μatm) was observed earlier (Manríquez et al., 2021). Also, a reduction in intracellular osmolytes such as glycine and proline amino acids was observed in the green crab *C. maenas* maintained at pH 7.4, 6.6, and 6.3 for four weeks (Hammer et al., 2012). Further, OA can reduce lipids in the crab's tissues, leading to health consequences as lipids play a vital role in various physiological processes, including energy storage, membrane structure, and cellular signaling. A notable drop (42%) in the lipid content of hermit crab *P. criniticornis* treated at a low pH of 7.7 for a 120-day experiment was reported previously (Turra et al., 2019). A significant decrease in the lipid level was noted in mud crab *S. serrata* under the low pH (7.4, 7.2, and 7.0) for two months (Thangal et al., 2022). A study on the Dungeness crab *C. magister* exposed to a pH of 7.5 showed many metabolites and lipids, which reveal that numerous molecules respond to low pH (Wanamaker et al., 2019) (Table 1). Based on the above information, indicates the detrimental effect of OA on the biochemical elements of marine crabs. Nevertheless, the studied crab species are limited in these aspects. Furthermore, to our knowledge, no one report is available on the impact of OA on marine crabs' amino acids and fatty acids composition. Therefore, forthcoming studies are required on these gaps to know the marine crab species' physiological state and muscle meat quality. In this context, studying crabs' biochemical constituents has become an increasingly important area of research for understanding the fundamental biology of these animals. Moreover, several studies have shown that crab biochemical elements possess unique properties that make them attractive for various biomedical applications. For example, certain proteins and peptides isolated from crab hemolymph have demonstrated antimicrobial, antifungal, and anticancer activities (Shan et al., 2016; Tornesello et al., 2020; Chen et al., 2021; Yang et al., 2022). Hence, the production of secondary metabolites by marine crabs under acidic stress also needs to be studied for pharmacological activities.

9. Antioxidants and lipid peroxidation status of crabs treated under OA

The antioxidant system has a major function in the animal body to prevent cell damage caused by environmental stresses (Jia et al., 2019). Superoxide dismutase (SOD) is one of the main operative antioxidant enzymes in the cells. SOD catalyzes O_2^- free radicles and H^+ ions to O_2 and H_2O_2. Further, Catalase (CAT) decays H_2O_2 into H_2O and O_2. This way, the interactions between the SOD and CAT successively eliminate the reactive oxygen species (ROS) produced by external stress (Ighodaro and Akinloy, 2018). Lipid peroxidation (LPO) acts as a free radical-mediated chain of reaction (Hampel et al., 2016) that can lead to the oxidative breakdown of polyunsaturated fats, and cell membranes are the primary target parts of a biological system. Many studies proved that OA could alter animals' antioxidants and LPO status, including crabs (Lin et al., 2020; Thangal et al., 2022). The juvenile horseshoe crab *T. tridentatus* exposed to pH 7.3 for 28 days duration showed notable increases in the reactive oxygen species and elevation of SOD, CAT, and glutathione peroxidase (GPx) activities, and LPO level was noted in the juvenile horseshoe crab at low pH (pH 7.3), which indicate the juvenile horseshoe crab was under oxidative stress and cell membrane damage (Liu et al., 2022). A sudden substantial elevation was observed in SOD and glutathione s-transferases (GST) activities and the rapid regulation in the mRNA expression of ecCuZnSOD and cMnSOD in the hepatopancreas of the Chinese crab *Portunus trituberculatus* reared in high pCO_2 (750 and 1500 μatm) for four weeks, which indicate a significant elevation in the antioxidant capability of this crab (Lin et al., 2020). Furthermore, the mud crab *S. serrata* exposed to the acidified seawater (pH 7.8, 7.6, 7.4, 7.2, and 7.0) for 60 days showed a significant elevation in the SOD, CAT, and LPO activities observed recently by Thangal et al. (2022)(Table 1). However, the studied crab species are very limited in these biomarkers aspects. Hence, more information is required to understand the status of biomarkers in the different life stages of crab species with the expression of specific genes under OA.

10. Metabolic enzymes and digestive enzymes levels in crabs under OA experiments

Metabolic enzymes such as glutamic oxaloacetic transaminase (GOT) and glutamic pyruvic transaminase (GPT) are vital to the organism for their digestion, cell respiration, transcription, and energy storage. Alkaline phosphatase (ALP) is one of the membrane-bound metalloenzymes that have a key role in the metabolite and biomineralization process and is used as an indicator to identify the physiological situation of an animal under acidic stress (Zambonino-Infante et al., 2008; Szabo and Ferrier, 2014). ALP, a hydrolase in the innate immune system can kill extracellular attackers directly. Variations in the metabolic enzymes can indicate liver damage of animals (Sookoian and Pirola, 2015). Earlier studies noticed that marine crabs under acidified seawater showed significant changes in metabolic enzymes. A notable increase in the level of GOT and GPT enzymes was identified in mud crab *S. serrata* exposed to the acidified seawater (Thangal et al., 2022). Alteration in ALP level was observed earlier in marine invertebrates, including crustaceans such as crabs and brine shrimp due to the acidic stress (Zheng et al., 2015; Wang et al., 2020; Liu et al., 2022). A notable decrease in the level of ALP was observed in the mud crab *S. serrata* exposed to the acidified seawater at pH 7.2 and 7.0 for 60 days of experimental duration (Thangal et al., 2022). It was observed to increase first and then decrease in the activity of ALP in the juvenile horseshoe crab *T. tridentatus* exposed to pH 7.3 for 28 days, which denoted the adverse effect of OA on ALP under chronic exposure (Liu et al., 2022). Besides, a study by Kim et al. (2016) recorded significant elevations in the metabolic activities of the hermit crab *P. tanneri* exposed to acidified seawater (pH 7.1) for 20 weeks. A significant reduction in the metabolic rate of intertidal porcelain crab *Petrolisthes cinctipes* exposed to a pH of 7.58 for six days was recorded by Carter et al. (2013) (Table 1). Digestive enzyme activities are critical to nutrient digestion, overall health, and survival of crustaceans. Studies have investigated the effects of OA on the digestive enzyme activities of crabs and found a significant detrimental impact, which can affect their ability to digest food and obtain the necessary nutrients for normal physiological activities. The Chinese crab *P. trituberculatus* exposed to the elevated pCO_2 (750 and 1500 μatm) for 20 weeks showed a significant decrease in lipase and amylase activities when compared to the crabs in the ambient pH environment (Lin et al., 2020) (Table 1). The reduction in the lipase activity might be due to the switch from the lipid and protein metabolism in the hepatopancreas (Carter et al., 2013). Nonetheless, no more reports are available on the effect of OA on marine crabs' metabolic enzymes and digestive enzyme activities. Since the larval stages of marine crabs served as good sources

of exogenous enzymes in the food chain, more investigations need to be conducted to explore the state of the metabolic and digestive enzymes of different developmental stages of various crab species in acidified seawater environments.

11. Effect of OA on mineral levels of crabs

Marine crustaceans, such as shrimp, crabs, and lobsters, are excellent sources of minerals essential for human health. These minerals play important roles in numerous biological processes and contribute to the overall nutritional value of crustaceans (Truong et al., 2022). Calcium (Ca), phosphorus (P), magnesium (Mg), and potassium (K) are considered macro minerals, and iron (Fe), zinc (Zn), copper (Cu), and selenium (Se) are considered trace elements in marine crustaceans. Marine crustaceans are rich in Ca, P, Mg, and K and have crucial roles in developing and maintaining strong bones, nerve and muscle functions, and fluid balance. Also, marine crustaceans are rich in Fe, Zn, and Cu, with significant roles like oxygen transport, immune function, and antioxidant defense (Muralisankar et al., 2022). Reductions in the mineral levels affect marine crustaceans in various ways like mineralization, antioxidant defense, osmoregulation, etc. OA alters the availability of carbonate ions, disrupts mineral homeostasis, and impairs the formation and maintenance of calcified structures such as calcium carbonate dissolution, impaired shell formation, and mineral homeostasis in marine animals (Hofmann et al., 2010; Kroeker et al., 2010). Significant and insignificant alterations in minerals in marine animals under OA have been observed with different pCO_2 levels (Siegel et al., 2022), however, most of the marine crabs had shown a detrimental effect on minerals levels, when exposed to OA. In particular, seawater acidification has been found to cause a reduction in Ca, Mg, and Fe concentrations in crabs (Coffey et al., 2017). Lack of availability of essential minerals negatively affects the organism, such as hyponatremia, weakness and fatigue, and skeleton strength (Karppanen et al., 2005). The red king crab *P. camtschaticus* and tanner crab *C. bairdi* exposed to the low pH (7.8 and 7.5) seawater showed a significant decrease in the carapace Ca condition index and Ca contents (Long et al., 2013). About 38% of the reduction in the microhardness of the claw in the Tanner crabs *C. bairdi* exposed to pH 7.5 for two years was observed. It might be due to reduced pH altering the carapace's elemental contents, such as low calcium and high magnesium (Dickinson et al., 2021). Reduction in the Ca content was observed in the snow crab *C. opilio* exposed to pH 7.5 for two years (Algayer et al., 2023). The snow crab *C. bairdi* reared at pH 7.5 for two years showed a significant reduction of Ca content (Swiney et al., 2016). Thangal et al. (2022) observed a reduction in Na, K, and Ca levels in the carcass of mud crab *S. serrata* exposed to the acidified seawater (pH 7.8, 7.6, 7.4,7.2, and 7.0) for 60 days indicates the OA may inhibit the intake of the minerals from water and feed. The same studies discuss that the reduction of the content of calcium carbonate in seawater might be responsible for the poor calcification levels in crabs in an acidic environment. In this context, a significant increase in Ca characteristics of the carapace and insignificant changes in Ca level in chelae and Mg level in both chelae and carapace have been noticed in the blue crab *Paralithodes platypus* at low pH (7.8 and 7.5) exposed for one year (Coffey et al., 2017), which denotes that the effect of OA on the mineralization marine crabs is species and time-dependent (Table 1). However, information from overall reports indicates the adverse effect of OA on the mineral levels of crabs. However, the mechanism of reducing minerals content in crabs under a reduced pH environment is unclear, hence, more studies are required to understand this mechanism. Furthermore, the impact of OA on the mineral contents of marine crabs is infancy, hence, more studies need to be done on various crab species. Meanwhile, marine crabs are being used as a good source of mineral nutrition. So, more attention is needed to discover the status of essential and trace minerals of different parts of the crab's body under OA.

12. Ocean acidification with other stressors on crabs

The acidification of seawater and other stressors can harm the biology and physiology of crabs. Some investigations recorded the synergetic effect of OA with other stressors like temperature, hypoxia, heavy metals, and salinity in marine crabs (Tomasetti et al., 2018; Adeleke et al., 2020; Pardo and Costa, 2021; Andrade et al., 2022). The elevated atmospheric CO_2 leads to increased seawater temperature facilitates less oxygen carrying capacity and makes the acidic condition of seawater which raises the oxygen demand and disturbs the carbonate saturation (Venegas et al., 2023). This synergistic interaction between temperature and pH affects normal metabolic function thereby poor energy production growth, and survival (Paganini et al., 2014; Swiney et al., 2017; Gao et al., 2020). The combined treatments of OA (pH 7.3) and ocean warming (18 and 25 °C) for two days significantly affected the foraging behavior of the Japanese stone crab *Charybdis japonica*. The observations revealed prolonged durations in various foraging activities, including feed searching, breaking time, eating, and handling time of crabs. Moreover, this study showed a decrease in prey profitability and reduced the predation of food by the crabs under these combined stressors (Wu et al., 2017). The shell-crushing crab *A. hassleri* exposed to the high pCO_2 (1400 μatm) along with temperature (20–25 °C) for a period of 10–16 weeks showed a decreased survival and decrease in the carbohydrate level in claw muscles (Manríquez et al., 2021). The same study also found a decreased calcification rate at the high pCO_2 and warm temperature (1400 μatm + 25 °C). Also, the Caribbean king crab *Maguimithrax spinosissimus* showed a decreased survival and molting rate exposed to the low pH (7.7) at 31 °C (Gravinese et al., 2022). Swiney et al. (2017) revealed that the long time exposure (184 days) of the red king crab *P. camtschaticus* subjected to the low pH 7.8 along with increased 4 °C temperature from ambient temperature showed a significant reduction in survival, growth, and taking more time to complete their molt. Also, the great spider crab *H. araneus* subjected to the high pCO_2 seawater (1120 and 1960 μatm) with the alterations in seawater temperature (5 and 10 °C) showed an upregulation of metabolic and stress response-related genes at 1120 μatm + 10 °C suggests that the stimulated acid-base regulation with increased oxidative stress which leads to high metabolism, however, gene response of crabs in 1960 μatm + 10 °C close to the control indicates that the molecular responses of studied crab is based on the pCO_2 levels (Harms et al., 2014). The Porcelain crab *P. cinctipes* subjected to pH 7.6 and 7.15 with temperatures 25 and 30 °C for 2.5 weeks showed significant decreases in respiration rate and heat tolerance capacity at pH 7.15 + 30 °C (Paganini et al., 2014). Also, a significant decrease in the Ca contents of the spider crab *H. araneus* subjected to the high pCO_2 seawater (710 and 3000 ppm) along with high temperatures (9 and 15 °C) was observed previously (Walther et al., 2010). The decrease in the whole cuticle and endocuticle thickness of juvenile blue crab *C. sapidus* exposed to the high pCO_2 (8000 μatm) with temperature (32 °C) was recorded (Glandon et al., 2018). The multiple combined effects of OA along with the temperature and salinity treatment of the fiddler crab *Leptuca thayeri* showed a complete death at a high temperature (40 °C) along with pH 7.0 and 6.3 experiments were recorded earlier by Andrade et al. (2022). Further, this study noticed higher levels of oxygen consumption at pH 6.3 + 30 °C and pH 7.0 + 50 psμ salinity, and decreased oxygen consumption at pH 6.3 + 35 °C and pH 6.3 + 50 psμ salinity by crabs indicates the alterations in physiological activities of crab. Besides, notable increases in respiration and decreases in critical thermal maxima of the mud crab *S. serrata* subjected to the pH 7.7 + 34 °C were noticed. Further, the same study recorded the poor ingestion and absorption of crabs exposed to pH 7.7 + 5 mg L^{-1} diesel (Baag and Mandal, 2023) (Table 2).

The aerobic respiration of organisms that use oxygen and emit carbon dioxide at a stoichiometric point results in O_2 deficits and an acidic environment for marine life, which is related to increased ocean acidification and hypoxia (Redfield et al., 1963; Feely et al., 2018). The metabolic activity of organisms increases under acidic stress producing

more energy to tolerate the stress, which leads to the utilization of more oxygen. Hypoxia combined with OA can increase the physiological stress on shellfish, affecting their growth, development, and survival (Gobler et al., 2014; Tomasetti et al., 2018; Wang et al., 2020). The blue crab *C. sapidus* exposed to low pH (7.16) along with low dissolved oxygen (3.74 mg L^{-1}) for 14 days showed an 87% decrease in survival (Tomasetti et al., 2018). The production of numerous metabolites and lipids by the Dungeness crab *C. magister* exposed to decreased seawater pH (7.45) and dissolved oxygen (3 mg L^{-1}) was also recorded. Nonetheless, this study noticed an insignificant response by crabs exposed between OA + hypoxia and hypoxia alone experiments and suggests the physiology of *C. magister* can be driven by hypoxia. The pathway analysis of this study suggests that the crabs may respond to hypoxia by processes like downregulation and upregulation of glutathione biosynthesis and glycogen storage respectively, and crabs increased the ATP production as a low pH response (Wanamaker et al., 2019).

Heavy metals can interact synergistically with OA to worsen the negative impacts on crustaceans. These interactions can impair their physiological processes, heavy metal accumulations, and compromise their overall health (Adeleke et al., 2020; Thangal et al., 2023). The more fraction metals can be driven by poor hydroxide and carbonate ions in lower seawater pH due to the strong complex of some metals like copper, nickel, lead, etc., with carbonate ions, which affect the solubility and toxicity of heavy metals (MillerO et al., 2009; Adeleke et al., 2020). Regarding this, the impact of OA along with heavy metals in crabs was studied earlier. Zhao et al. (2021) recorded a notable elevation in the level of antioxidants like SOD and CAT of the mitten crab *Eriocheir sinensis* subjected to the low pH (7.8, 7.3, and 6.5) with heavy metal cadmium (1 mg L^{-1}) for three weeks of exposure. A 96 h study conducted by Adeleke et al. (2020) found that exposure of crab *Dotilla fenestrate* to low pH seawater (pH 7.2, 7.4, and 7.6) in combination with heavy metal Cd (0.5, 0.75, and 1.00 mg L^{-1}), Pb (6.50, 8.50, and 10.50 mg L^{-1}), and a mixture of Cd and Pb (4.50, 5.75, and 7.00 mg L^{-1} resulted in the pH-dependent accumulation of heavy metals. More recently, Thangl et al. (2023) noticed that the combined effect of Cd (10 mg L^{-1}) and ocean acidification (7.8, 7.6, 7.4, 7.2, and 7.0) showed significant elevation in tissue Cd accumulation, antioxidants (SOD and CAT), lipid peroxidation, and metabolic enzymes (GOT and GPT) in the crab *S. serrata*. Furthermore, this experiment revealed a significant decline in survival, growth, molting, feed intake, tissue biochemical elements, alkaline phosphatase activity, and hemocyte populations was observed in *S. serrata* exposed to OA and Cd treatments compared to crabs exposed to ocean acidification alone treatments (Table 2). Most studies investigated the combined effect of OA and temperature on crabs, and minimal reports are available on the combined effect of OA with other stressors like salinity, hypoxia, and heavy metals. Therefore, more research is required on the combination of the effect of OA with other stressors like microplastics, hydrocarbons, pesticides, etc.

13. Summary

The present review summarizes the information on the impact of OA on nearly 23 different species of marine crabs, including the methods adopted for experimental set-up, the housing of crabs, and the responses to OA. Based on the existing literature, seawater was acidified by bubbling of CO_2 in the aquarium either automatic computerized feedback system or manual methods, however, the automatic system is recommended for reducing the pH variation and manpower. Further, the different stages of crabs (larvae, instars, juveniles, and adults) were used as an experimental model. They were housed in various types of aquariums like plastic tanks, jars, glass tanks, etc., and some studies adopted the PVC-based cage system in the aquarium to prevent cannibalism. Moreover, crabs were fed with different types of feeds like live feeds, frozen shrimp, squid, commercial feeds, etc., based on their species and selected life stages. As a result of all experiments, most of the studies reveal the detrimental effect of OA on biological and physiological responses like foraging, pray handling, feed intake, molting, growth, survival, the thickness of cuticle, tissue biochemical elements (protein, amino acids, carbohydrate, and lipid), enzymes (amylase, lipase, chitinase, and alkaline phosphatase), ecdysone hormone, chitin quality, and minerals (Na, K, and Ca). Moreover, studies indicate the elevations biomarker enzymes like antioxidants (SOD, CAT, GST, and GPx), metabolic enzymes (GOT, GPT, and ALP), and LPO that denotes the oxidative stress and high metabolic demand under the acidic stress in carbs. Nonetheless, few studies observed the positive and or insignificant effects of OA on survival, molting, carapace Ca and Mg, production of metabolites, and insignificant changes in the predatory behavior of marine crabs (Table 1), which signifies the crabs may adapt to elevated CO_2 mediated OA (Dodd et al., 2015; Meseck et al., 2016; Long et al., 2023). Moreover, the effect of OA on marine crabs depends on species, age of crabs, exposed pH and its associated seawater properties, exposure duration, evolutionary rate, etc. Nevertheless, the consequence of OA with other stressors like heavy metals, temperature, hypoxia, salinity, and oil showed significant synergistic negative effects on feeding behavior, food indices, growth, molting, survival, oxygen consumption, biochemical constituents, antioxidants, metabolic enzymes, hemolymph pH, calcium level, etc., in marine crabs as reported by most of earlier studies. These results show that OA with other marine pollutants can produce more severe adverse effects on marine crabs than OA alone (Table 2).

14. Conclusion and future perspectives

The present review explores most of the existing literature that showed the adverse effect of OA on survival, growth, molting, chitin, food indices, tissue biochemical elements, digestive enzymes, and minerals in marine crabs. The elevations in antioxidants, metabolic enzymes, and lipid peroxidation were reported. These observations indicate that OA can negatively affect marine crabs. Whereas, few reports showed insignificant changes in survival, feeding, and molting of marine carbs at near future pH, which indicates the tolerance of marine crabs, however, the effect might depend on species, age, and pH level. Besides, stressors like temperature, hypoxia, heavy metal, and salinity combined with OA have a synergistic detrimental effect on the biological and physiological indices of the crabs. However, based on the present review, future investigations have to focus on the following perspectives to address the research gaps

1. The computerized automatic system is recommended for stimulating OA in the laboratory to reduce the pH deviation, however, the comparison experiments need to be performed on crabs between the automatic feedback system and manually releasing CO_2 to find out the problems in manual methods. Besides, the cost-effective fabrication method for automatic feedback system-driven OA should be addressed.
2. Different species of marine crabs with different life stages were undertaken for OA experiments, however, it is recommended to conduct OA experiments on various developmental stages of crabs including edible species with different exposure periods for a better understanding of their response at various life stages.
3. The existing literature discloses the adverse effect of OA and altered seawater chemistry on growth, survival, molting, and chitin in marine crabs, while, the molecular mechanisms behind the poor growth, molting, chitin quality, and altered gene expression under OA conditions remain unclear. Hence, the investigation should be prioritized on these aspects for a better understanding.
4. The available reports on food index parameters of marine crabs are very limited under OA exposures, particularly concerning edible crabs. Consequently, it is crucial to conduct further investigation on various edible crab species to understand the

effect of OA on foraging behavior, prey selection and capture, feed utilization, feed conversion, etc.

5. Reports are limited on the impact of OA on the tissue biochemical elements (protein, lipid, carbohydrate, etc.) and the composition of amino acids and fatty acids of marine crabs. Therefore, future studies should address these gaps to elucidate crabs' physiological state and muscle quality under OA environments.
6. The studies on the response of biomarkers enzymes such as antioxidants (SOD, CAT, GPx, GST, etc.) in crab species are limited. More information is required in these aspects to comprehend the biomarker status of crab species exposed to OA during different life stages with different time intervals.
7. There is a lack of reports on the effects of OA on metabolic enzymes (GOT, GPT, ALP, ACP, etc.) and digestive enzyme (protease, amylase, lipase, cellulase, etc.) activities in marine crabs. Since marine crabs serve as a valuable source of exogenous enzymes in the food chain, further investigations are necessary to explore the state of these bio-enzymes in different developmental stages of various crab species under acidified seawater environments.
8. The hemocytes are the essential component of crabs in the innate defense system due to their encapsulation, phagocytosis, and foreign cell lysis properties, however, the investigations on the susceptibility crabs to pathogens and their innate immune system (melanization, phagocytosis, encapsulation, hemolymph coagulation, phenoloxidase activation, production of antimicrobial peptides, etc.) against pathogens under OA is limited. Hence, more attention must be provided to these aspects to elucidate the health status of marine crabs under OA.
9. The information on the impact of OA in the intestinal microflora is still in infancy in marine crabs because gut microflora play a significant role in nutrient metabolism, structural maintenance of the intestine, immune modulation, and protection against pathogens in invertebrates, hence, more investigations are required on the effect of OA on intestinal microflora in crabs.
10. Current knowledge on the impact of OA on mineral contents in marine crabs is fragmentary. Considering that marine edible crabs are an important source of mineral nutrition, more attention is required to assess the status of essential minerals in crab tissues under OA.
11. Most studies have investigated the combined effects of OA and temperature on crabs. At the same time, there is limited research on the combined effects of OA with other stressors such as salinity, hypoxia, and heavy metals. Therefore, more investigations are needed to examine the combined effects of OA with other stressors, including microplastics, heavy metals, hydrocarbons, pesticides, etc., to understand the synergistic effect of OA with other marine pollutants.
12. In conflict, some studies revealed that survival, molting, carapace calcium and magnesium contents, and predator-prey behavior of certain crabs are not affected by near future pH, hence this tolerance mechanism and evolutionary adaption of these carb species needs to be clarified.

Marine crabs occupy an important place in ecological and economic sectors of the earth as an ecosystem's engineers, nutrient cyclers, essential components of the food chain, source of therapeutically viable metabolites, and delicious seafood. Nonetheless, earlier reports disclose the detrimental effect of OA on the biological and physiological aspects of marine crabs. In this context, some studies stated that the acidic tolerance and evolutionary adaptation of crabs. Hence, the present review recommended future investigations on the above-stated perspectives to address research gaps, which leads to providing clear information on the impact of OA on marine crabs for environmental biologists and policymakers.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this review.

CRediT authorship contribution statement

Said Hamid Thangal: Conceptualization, Writing – original draft. **Thirunavukkarasu Muralisankar:** Supervision, Writing – original draft, Writing – review & editing. **Kannan Mohan:** Software, Writing – review & editing. **Perumal Santhanam:** Writing – review & editing. **Balu Alagar Venmathi Maran:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgment

The first author (SHT) and second author (TM) are grateful to the Department of Science and Technology (DST), Ministry of Science and Technology, Government of India, New Delhi for the infrastructure facility to the Department of Zoology, Bharathiar University, Tamilnadu, India through the programme Fund for Improvement of Science and Technology (FIST) (SR/FST/LS-II/2017/111 (c); dt.: January 25, 2019).

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