



Effects of ocean acidification on abalone (*Haliotis* spp.) reproduction, early development, and growth: a review

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Abstract

Abalone (*Haliotis* spp.) is a highly valuable and economically relevant marine commodity worldwide, with its production and value showing significant growth over the past two decades. Additionally, abalone hold essential ecological value by serving as a grazer and providing a microhabitat for various benthic organisms. Currently, seawater is experiencing a decrease in pH due to increased carbon dioxide (CO₂) levels. It is projected that by 2100, the pH of seawater will decrease by approximately 0.3–0.4 units, with this trend continuing to 0.7–0.8 units by 2300. Abalone is particularly susceptible to ocean acidification due to its limited ability to maintain acid-base balance. Moreover, even if the effects on abalone are not lethal, world production values and ecosystem balance are likely to be impacted. This review examines the economic and ecological significance of abalone, as well as the morphological and physiological effects of ocean acidification on abalone during its early development, juvenile, and adult stages based on previous studies. In summary, the adverse effects of ocean acidification on abalone depend on several aspects, including the species, developmental stage, size, and duration of exposure.

Keywords: Abalone, Ocean acidification, Economical values, Ecological values, Impact

Introduction

The industrial revolution has led to a significant and rapid increase in the emissions of carbon dioxide into the atmosphere. This rise in carbon emissions is mostly attributed to anthropogenic activity, with fossil fuels and land use conversion, re-

spectively accounting for 90% and 10% of these CO₂ emissions (Friedlingstein et al., 2023). Prior to the industrial revolution, the level of carbon dioxide in the atmosphere was approximately 278 parts per million (Betts, 2021). Nevertheless, this level has steadily increased over the past decades. The average global atmospheric concentration of CO₂ in 2022 was 417.1 ± 0.1 ppm.

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On March 10, 2024, the concentration of atmospheric CO₂ was 421.56 ppm, representing a 51.6% increase relative to the pre-industrialization era (Global Monitoring Laboratory, 2024).

Increasingly higher levels of atmospheric CO₂ are being absorbed by the world's oceans at an accelerating rate. Since the onset of worldwide industrialization, the ocean has absorbed approximately 20%–30% of all anthropogenic carbon dioxide (CO₂) emissions (Jiang et al., 2023). Over the past few decades, the oceans have absorbed approximately 2 billion metric tons of CO₂ out of the total annual carbon emissions of 7 billion metric tons released into the atmosphere by all nations worldwide. It is projected that by 2100, the seas will absorb around 5 billion metric tons of CO₂ annually (Upton & Folger, 2013).

Ocean acidification is the process by which the pH of seawater falls due to the ocean's increasing absorption of anthropogenic CO₂ from atmosphere (Upton & Folger, 2013). Oceanic CO₂ absorption triggers a chemical reaction whereby carbon dioxide and water produce carbonic acid (H₂CO₃). In turn, carbonic acid undergoes dissociation, producing hydrogen ions (H⁺) and bicarbonate ions (HCO₃⁻). Bicarbonate ions (HCO₃⁻) then dissociate, resulting in the formation of H⁺ and CO₃²⁻ ions. This is the primary factor responsible for the decrease in oceanic pH. Crucially, hydrogen ions (H⁺) in water can also react with carbonate ions (CO₃²⁻) to produce bicarbonate ions (HCO₃⁻), leading to a reduction in the concentration of CO₃²⁻ ions, which are essential for the formation of shells and bones in marine organisms.

Since the beginning of the industrial revolution, seawater pH levels have experienced an overall reduction of pH 0.1 units (Melendez & Salisbury, 2017), with the average pH of oceanic surface waters falling from 8.2 to 8.1 (Logan, 2010). This 0.1 unit decline has resulted in a 30% increase in seawater acidity over the course of more than 200 years (Laffoley et al., 2017), and oceanic pH levels are expected to continue decreasing as atmospheric CO₂ absorption levels rise. Melendez & Salisbury (2017) have predicted a 120% increase in the acidity of seawater by the year 2060. Furthermore, Basso et al. (2015) projected that the pH of seawater will fall by approximately 0.3–0.4 units by 2100 and 0.7–0.8 units by 2300.

Ocean acidification poses a serious threat to marine organisms, particularly calcifying animals such as abalone, as they rely on calcium carbonate (CaCO₃) for shell formation (Wessel et al., 2018). Several studies have already documented the impact of pH fluctuations on various aspects of abalone biology such as hatching rate (Li et al., 2013), larval development (Tahil & Dy, 2016), larval settlement (Tahil & Dy, 2015), immunity, stress

response (Kim et al., 2023), growth, and shell thickness (Cumings et al., 2019). Abalone, a globally distributed gastropod, is a highly valuable seafood product. The high demand and price of abalone have driven the global expansion of abalone aquaculture, with this sector experiencing significant growth in recent years. However, decreased pH levels could severely undermine the sustainability of abalone aquaculture, thereby hindering the advancement of abalone production (Tahil & Dy, 2016).

This review aims to comprehensively examine the scientific literature on the impact of ocean acidification on abalone, focusing on early life stages, juvenile and adult development, shell thickness, and physiology. Understanding the impact of pH on abalone will provide a valuable basis for the development of farming procedures to reduce stress, enhance productivity, and promote abalone health and quality (Morash & Alter, 2016).

Economical Values of Abalone

Abalone (*Haliotis* spp.) is a highly valuable commodity due to its premium price, high nutritional value, and unique flavor. Abalone products can be consumed in various ways, including cooked, raw, chilled, and canned (Taridala et al., 2020). Abalone has also been shown to contain a number of bioactive compounds, including phenolic compounds, glycogen, carbohydrates, protein, amino acids (Mohammadi et al., 2022), fatty acids (Suleria et al., 2017), and minerals (Latuihamallo et al., 2019), all of which offer health-promoting effects beyond those of basic nutrition. Nutritional analyses revealed that 100 g of the edible portion of abalone contained 20 grams of high-quality protein (Shi et al., 2020). According to Mulvaney et al. (2015), 100 g of abalone also contains 94 mg of n-3 long-chain polyunsaturated fatty acids (LC PUFA), which is higher than the 70, 26, and 50 mg of PUFA found in beef, pork, and chicken, respectively. Furthermore, abalone possesses anti-microbial, anti-thrombotic, anti-cancer activities, and anti-inflammatory properties (Suleria et al., 2017).

Abalone production has steadily increased due to strong market demand over the past decade. The total abalone production from aquaculture and capture fisheries has increased significantly, from 14,599.00 tons in 2001 to 253,111.71 tons in 2021 (Fig. 1). In the past, worldwide abalone production derived mainly from fishing. However, aquaculture now makes up the overwhelming majority of global abalone production (Hernández-Casas et al., 2023). As of 2021, aquaculture accounted for more than 97% of the total global abalone produc-

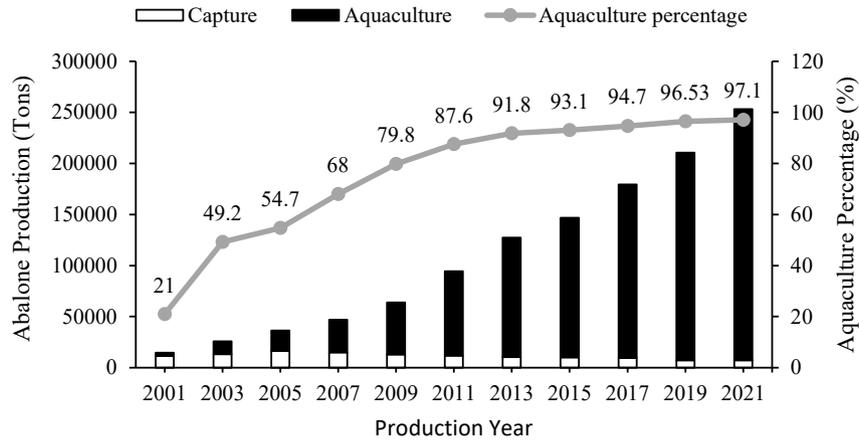


Fig. 1. Global abalone production quantity (tons live weight) from 2001 to 2021. Adapted from FAO (2024) with public domain.

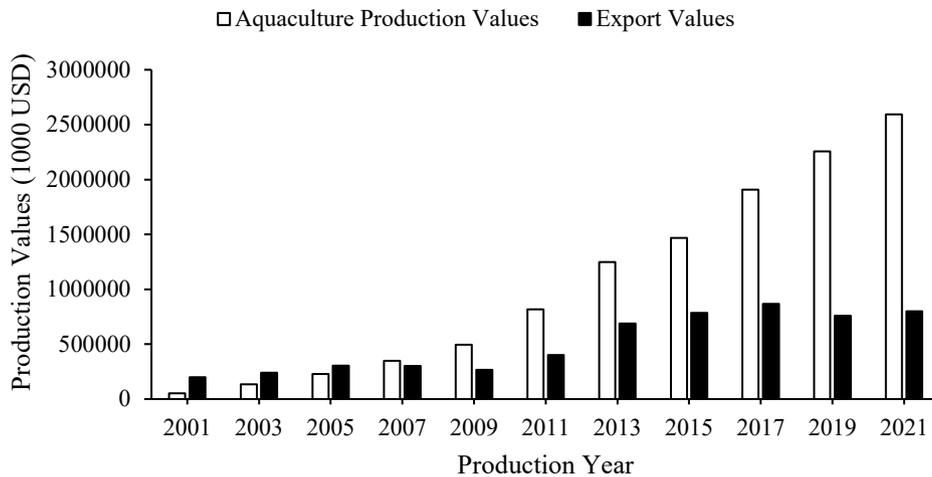


Fig. 2. Abalone production values (1,000 USD) from 2001 to 2021. Adapted from FAO (2024) with public domain.

tion, achieving a total output 245,777.34 tons (Fig. 1) and an estimated value of \$2.59 billion (Fig. 2). In contrast, production of captured abalone decreased considerably from 11,529 tons in 2001 to 7,334.37 tons (Fig. 1). The depletion of abalone populations in various Southeast Asian countries, such as Malaysia, Thailand, Indonesia, and the Philippines, suggests that the natural supplies of abalone have reached a critical threshold (Sososutiksno & Gasperz, 2017). In turn, this reduction in abalone fishing yields has been attributed to a number of factors, including the degradation of marine ecosystems, diseases, illegal fishing, overexploitation, and rising operational costs (Hernández-Casas et al., 2023).

In 2021, China dominated the abalone aquaculture industry, producing 217,831 tons valued at \$1.85 billion (FAO, 2024). Chi-

nese abalone farms are mostly located in the provinces of Fujian and Guangdong, although a significant proportion of abalone seed production takes place between the Shandong Peninsula and Dalian, in the Northern Province of Liaoning (Cook, 2023). According to FAO (2024), South Korea ranks second with a production of 23,199.49 tons valued at \$606 million (Table 1). Most of the production in Korea takes place in Wando County, located in the province of South Jeolla. Cage culture covers a total area of 3,095 hectares across 2,549 abalone farms in Korea (Cook, 2023). Chile, South Africa, New Zealand, Australia, and the United States have also engaged in abalone cultivation (FAO, 2024). However, in a few countries, including Australia, Japan, Mexico, and New Zealand, abalone capture fisheries remains the dominant source of abalone production. Among these countries,

Table 1. Abalone aquaculture production in various regions in 2021

Country	Production quantity (tons-live weight)	Production value (1,000 USD)
China	217,831	1,848,513.87
South Korea	23,199.49	606,881.21
South Africa	2,463.29	79,505.71
Chile	1,124	24,393.8
Australia	750.24	20,282.32
Taiwan	176.59	6,189.31
Unites Stated	154	6,451.06
New Zealand	45	1,527.8
Malaysia	24.74	149.28

Adapted from FAO (2024) with public domain.

Australia is the largest producer of captured abalone, with a total catch of 2,352.13 tons (FAO, 2024).

The global abalone export value has also increased, from over US\$200 million in 2001 to US\$800 million in 2021, clearly demonstrating the growing demand for abalone (Fig. 2). China ranks first in terms of abalone export value with a total value of US\$437 million (FAO, 2024), followed by Australia with a value of US\$120 million, South Africa with US\$61 million, and South Korea ranks fourth with a value of US\$54 million (Table 2; FAO, 2024). The price of abalone in different nations varies according to the species, size, location of origin, and quality of the abalone meat. Abalone with a shell size of 40 mm sells for US\$10 per kilogram in the Chinese seafood market, whereas larger abalone sells for US\$100 per kg. In 2023, the wholesale price of abalone in Korea ranged from US\$26.4 to US\$28.7 per kg, with retail buyers paying far higher costs (Cook, 2023). Future demand for abalone is expected to increase, which is likely to result in an ongoing expansion of abalone production. Therefore, it is crucial for farmers to reduce production costs and enhance production efficiency.

Ecological Values of Abalone

Abalone can significantly influence both the structure of ecological communities and the functioning of ecosystems through several means, such as their role as grazers and the provision of microhabitats for benthic organisms (Zeeman et al., 2013). Additionally, these gastropods are considered valuable environmental bioindicators (Liao et al., 2004). As herbivores, abalone play a significant role in controlling the population of algae and

Table 2. The abalone export value in various region in 2021

Country	Export quantity (tons-live weight)	Export value (1,000 USD)
China	16,099.28	437,642.71
Australia	2,203.12	120,310.61
South Africa	1,672.87	61,551.56
South Korea	2,187.64	54,458.39
New Zealand	718.36	23,561.6
China Hongkong	732.43	18,375.05
Taiwan	669.6	10,869.91
Chile	592.02	12,886.07
Philipines	446.25	4,478.47
Malaysia	326.69	3,552.82

Adapted from FAO (2024) with public domain.

other invertebrates that compete for the same food (Zeeman et al., 2012). Abalone and sea urchins are primary competitors, as they both consume kelp. Assuming that abalone populations were at their typical levels, they would effectively control the sea urchin populations and prevent them from excessively feeding on kelp. Sea urchins and abalone are the predominant herbivorous animals in the kelp forests of Australia, South Africa, and the North Pacific and they exhibit significant overlap in their food preferences and habitat utilization (Luo et al., 2023). Additionally, post-larval abalone has been shown to compete for food resources with the small Sea snail (*Homalopoma amussitatum*) (Won et al., 2011).

According to Zeeman et al. (2013), South African Abalone (*Haliotis midae*) shells serve as a microhabitat for benthic organisms, including coralline algae such as *Titanoderma polycephalum*, Melobesoid alga (*Mesophyllum engelhartii*), as well as members of the genus *Spongites*. Due to its ability to thrive in abundant numbers, its flat shell with uneven ridges, and long lifespan, this abalone species serves as a habitat for a wide range of organisms. Moreover, given the scarcity of hard surface areas in marine ecosystems, gastropod shells serve as a significant secondary substrate for colonization. Interestingly, however, the populations inhabiting the surface of abalone shells are distinct from the species residing on the neighboring rock. Hence, the excessive fishing of abalone can have a significant impact on the entire ecosystem through both top-down (e.g., predation) and bottom-up (e.g., competition) interactions. This can result in a trophic cascade within the ecosystem, potentially leading to a shift to an alternative stable state (Won et al., 2011).

An effective bioindicator should be immobile, plentiful,

long-lived, easily collectible, capable of accumulating pollutants, and providing appropriate tissue for contaminant analysis (Liao et al., 2004). Abalone fulfills all of these criteria, making them excellent bioindicators for marine environments. Previous study have reported that abalone are able to accumulate zinc (Liao et al., 2004), cadmium, copper, and iron (Skinner et al., 2004). The shell (Liao et al., 2004) and foot muscle (Skinner et al., 2004) of abalone can thus be utilized for detecting the accumulation of heavy metals. Abalone can serve as a bioindicator and effectively remove heavy metals from aquatic food webs (Liao et al., 2004).

Impact of Ocean Acidification on Abalone

Early stage development

Ocean acidification changes the saturation of calcium carbonate in aquatic environments, thereby affecting marine shelled mollusks such as abalone, as well as other organisms that require calcium carbonate to form their skeletons and other similar anatomical structure (e.g., coral spicules). Alterations in pH also leads to acidosis, which hampers several physiological functions (Kavousi et al., 2022). Mollusk larvae are often more vulnerable to pH stress compared to adult mollusks due to their lack of specialized ion-regulatory epithelia necessary for maintaining acid-base balance (Parker et al., 2013). During the early stages of development, a lower pH can decrease fertilization rates, delay embryonic development, reduce hatching rate, larval length, and shell growth rates, and increase the malformation rate (Li et al., 2013). A summary of the impacts of ocean acidification on the early development of abalone (*Haliotis* spp.) is presented in Table 3.

Fertilization rate

Kimura et al. (2011) performed two experiments to examine the effects of ocean acidification on the fertilization success of Ezo abalone (*Haliotis discus hannai*). The initial experiment involved exposing seawater to CO₂ partial pressures (pCO₂) of 450, 650, 850, and 1,050 µatm, resulting in seawater pH values of 7.96, 7.83, 7.79, and 7.73, respectively. In this first experiment, the 1,050 µatm treatment resulted in the lowest rate of fertilization. The second experiment involved setting pCO₂ levels at 500, 1,100, 1,650, and 2,150 µatm, which resulted in pH values of 7.94, 7.68, 7.54, and 7.43, respectively. In this case, a pCO₂ level of < 1,100 µatm did not have any impact on the fertilization rate of abalone. However, a pCO₂ of 1,650 µatm (pH 7.54)

resulted in the lowest fertilization rate, followed by treatment with pCO₂ of 2,150 µatm (pH 7.43). These data indicates that the optimal pCO₂ range for ezo abalone is between 1,000 and 1,600 µatm. This outcome is comparable to that of Red abalone (*Haliotis rufescens*), which exhibited a drop in fertilization rate when exposed to a pH ranging from 7.95 to 7.2. Particularly, a pH below 7.55 under 9 °C and 13 °C seawater temperatures resulted in an apparent reduction in fertilization rate (Boch et al., 2017). According to Byrne et al. (2010), the fertilization rate of Reddish-rayed abalone (*Haliotis coccoradiata*) did not vary significantly across a pH range of 8.2 to 7.6. Moreover, Boch et al. (2017) indicated that lower fertilization rates may be due to the potential impact of lower pH on sperm kinematic and/or swimming behavior. Shi et al. (2017) demonstrated that excessive CO₂ absorption notably impairs sperm motility in Blood clams (*Tegillarca granosa*). The ocean absorbs excess carbon dioxide in the atmosphere, increasing the quantity of hydrogen ions. These ions penetrate into the cells, causing intracellular acidosis and modifying intracellular pH. A decrease in intracellular pH can disrupt the sperm activation, sperm chemotactic behavior, and flagellar motility (Shi et al., 2017). Lower pH levels may diminish sperm mitochondrial membrane potential (Schlegel et al., 2015), limiting sperm flagellar motility (Shi et al., 2017), and impairing the activity of dynein ATPase, a protein involved in sperm movement (Boulais et al., 2018). Similar to acidic pH conditions, lower sperm concentrations have also been linked to reduced fertilization rates (Parker et al., 2013).

Hatching rate

Acidification also negatively impacts the hatching rate and viability of fertilized eggs. In the Donkey ear abalone (*Haliotis asinina*), decreasing the pH level by 0.19 to 0.57 units relative to normal seawater levels not only decreased hatching rates but also impaired the growth of trocophore larvae. Hatching rates exhibited a significant decline at pH 7.6, which is 0.3 units lower than the normal pH level (Tahil & Dy, 2016). Kimura et al. (2011) also observed notable decrease in hatching rate compared to the control group in *H. discus hannai* at pH levels ranging from 7.43 to 7.54. This finding aligns with the study conducted by Li et al. (2013) on the same species, which found no significant difference in hatching rate at pH 7.6 to the control group. Substantial differences were observed in the pH 7.3 treatment. These findings suggest that a pH level of 7.54 or lower has a negative impact on the hatching rate of *H. discus hannai*. However, Pratiwi et al. (2024) discovered that the pH range of

Table 3. Summary of the impact of ocean acidification on early larval development

Species	CO ₂ /pH range	Experiment duration	Measured	Findings	References
<i>Haliotis tuberculata</i>	8.2, 7.9, 7.8, and 7.6	15 min	Fertilization rate	NS	Byrne et al., 2010
<i>Haliotis coccoradiata</i>	8.2, 7.9, 7.8, and 7.6	15 min	Fertilization rate	NS	
<i>H. coccoradiata</i>	7.8 and 7.6	21 h	Shelled larvae	Decrease under low pH	Byrne et al., 2011
<i>Haliotis kamtschatkana</i>	400, 800, and 1,800 ppm (pH 8.3, 8.07, 7.81)	Total duration 8 d	Number of larvae Normal shell Shell length	Decrease under low pH	Crim et al., 2011
<i>Haliotis discus hannai</i>	450, 650, 850, and 1,050 μ atm (pH 7.96, 7.83, 7.79, 7.73)	15 h	Settlement rate	NS	Kimura et al., 2011
		75 h	Fertilization rate	NS	
			Hatching rate	Decrease at 650–1,050 μ atm	
			Mortality	NS	
<i>H. discus hannai</i>	500, 1,100, 1,650, and 2,150 μ atm (pH 7.94, 7.68, 7.54, 7.43)	15 h	Malformation rate	NS	Kimura et al., 2011
			Shell length	Decrease at 850–1,050 μ atm	
			Fertilization rate	Decrease at 1,650–2,150 μ atm	
			Hatching rate	Decrease at 1,650–2,150 μ atm	
<i>H. discus hannai</i>	500, 1,100, 1,650, and 2,150 μ atm (pH 7.94, 7.68, 7.54, 7.43)	75 h	Mortality	NS	Kimura et al., 2011
			Malformation rate	Increase at 1,100–2,150 μ atm	
			Shell length	Shorter at 1,650–2,150 μ atm	
<i>H. discus hannai</i>	8.2, 7.9, 7.6, and 7.3	15 h	Hatching time	Longer at pH 7.6–7.3	Li et al., 2013
			Hatching rate	Decrease at pH 7.3	
		60 h	Malformation rate	Increase at 7.6 and 7.3	
			48 h	Metamorphosis rate	
				Shell length	
<i>H. discus hannai</i>	400, 800, 1,500, 2,000, and 3,000 ppm (8.15, 7.94, 7.71, 7.61, 7.43)	30 min	Fertilization rate	Decrease at 3,000 ppm	Guo et al., 2015
		8 h	Hatching rate	Decrease at 1,500, 2,000, 3,000 ppm	
		24 and 48 h	Shell length	Shorter at 800 ppm	
<i>Haliotis diversicolor</i>	400, 800, 1,500, 2,000, and 3,000 ppm (8.15, 7.94, 7.71, 7.61, 7.43)	30 min	Fertilization rate	Decrease at 2,000–3,000 ppm	
		8 h	Hatching rate	Decrease at 1,500, 2,000, 3,000 ppm	
		24 and 48 h	Shell length	Shorter at 800 ppm	
<i>Haliotis asinina</i>	7.9–58.03, 7.63–7.89, 7.46–7.70, and 7.24–7.52	15 d	Settlement rate	Decrease at low pH	Tahil & Dy, 2015
<i>H. asinina</i>	7.95–7.99, 7.76–7.80, 7.58–7.62, and 7.37–7.41	6.4 h	Hatching rate Normal hatch trocophore	Decrease at pH 7.6 and 7.4	Tahil & Dy, 2016
<i>Haliotis rufescens</i>	7.1, 7.3, 7.5, 7.7, 7.9	600 s	Survival rate	Decrease under low pH	Boch et al., 2017
<i>H. asinina</i>	8.15, 7.85, and 7.65	24 h	Shell length	Decrease under low pH	Santander & Sayno, 2018
			Malformation rate	Increase at low pH	

Table 3. Continued

Species	CO ₂ /pH range	Experiment duration	Measured	Findings	References
<i>Haliotis tuberculata</i>	8.0, 7.7, and 7.6	Total duration 5 d (sampling at 20, 30, 48, 96 hpf)	Larval viability The percentage of shelled larvae Shell calcification	Decrease under low pH Lower at pH 7.6 Decrease at pH 7.6	Wessel et al., 2018
<i>Haliotis iris</i>	8.05 and 7.65		Settlement rate	NS	Espinel-Velasco et al., 2021
<i>Haliotis tuberculata</i>	8.0 and 7.7	Total duration 96 h (sampling at 24, 72, 96 hpf)	Hatching rate Swimming rate Shell formation	NS NS Decrease at low pH for 24 and 72 hpf larvae	Kavousi et al., 2022
<i>H. tuberculata</i>	8.0 and 7.7	Total duration 96 h (sampling at 24, 72, 96 hpf)	Tissue organogenesis Shell length Shell calcification	Decrease at low pH for 24 and 72 hpf larvae Shorter at low pH for 72 hpf larvae Decrease at low pH for 72 hpf larvae	Kavousi et al., 2022
<i>H. tuberculata</i>	8.0 and 7.7		Larval settlement Larval swimming behaviour	NS NS	Kavousi et al., 2022
<i>Haliotis rufescens</i>	8.0, 7.8, and 7.6	48 and 108 h	Veliger maturation	Decrease at pH 7.6	Gómez-Reyes et al., 2023
		Short term and long term	Settlement rate	Decrease under low pH for short term experiment	
<i>Haliotis discus hannai</i>	8.2, 7.9, 7.6, 7.3, and 7.0	30 hpf	Hatching rate Larvae length Malformation rate	NS Decrease at pH 7.0 Increase at pH 7.0 and 7.3	Pratiwi et al., 2024

NS, non significant.

7.0–8.2 had no significant effect on the hatching rate of *H. discus hannai*. In contrast, *H. rufescens* and Multicolored abalone (*Haliotis diversicolor*) exhibited notable variations in hatching rates at pH 7.6 (Gómez-Reyes et al., 2023) and 7.71 (Guo et al., 2015), respectively. Jiang et al. (2021) attributed these decrease in hatching rate to the weakening and loss of elasticity of the egg membrane caused by acidic conditions, resulting in the premature release of the embryo from the egg followed by death. García et al. (2024) suspect that low pH interferes with the ability to regulate acid-base homeostasis in embryos, thus slowing down embryo development and hatching time. Acidification can also induce a stress response in mollusks that enhances energy metabolism for survival, thereby suppressing growth activity (Li et al., 2013). Alternatively, acidic conditions could also decrease RNA concentrations, thereby decreasing the production of the key proteins during early development and lowering hatching rates (Franke & Clemmesen, 2011). Low pH could

impact hatching enzyme secretion, decreasing the hatching rate (García et al., 2024).

Larval development and malformation rate

In some abalone species, lower pH has been linked to deleterious effect on larval growth. Li et al. (2013) reported that *H. discus hannai* larvae grown at pH 7.6 and 7.3 developed more slowly and exhibited higher deformity rates, slower metamorphosis rates, and a shorter shell length. Pratiwi et al. (2024) also discovered that 30 hpf *H. discus hannai* larvae cultured at pH 7.0 were significantly shorter than controls. The malformation rate of 30 hpf larvae cultured at pH 7.9, 7.6, 7.3, and 7.0 increased compared to control but was only significant at pH 7.0 and 7.3 (Pratiwi et al., 2024). Similarly, European abalone (*Haliotis tuberculata*) larvae developed more slowly, had fewer shelled larvae, and were shorter when the pH was 7.7 or 7.6. These abalone larvae also exhibited lower survival and shell mineralization rate (Wessel et al., 2018).

When exposed to pH 7.85 and 7.65, the shell length of *H. asinina* (Linnaeus 1758) shrank and the number of malformations rose compare to the control animals reared under ambient pH conditions (Santander & Sayno, 2018). This decrease in shell length and calcification can occur due to decreased calcium carbonate saturation in more acidic conditions. In turn, the larvae deposit less calcium carbonate and produce a thinner shell. The earliest instance of CaCO₃ deposition in abalone occurs during the early veliger stage. During this process, amorphous calcium carbonate (ACC) is deposited and quickly converted into crystalline aragonite (Auzoux-Bordenave et al., 2010). Decreased seawater pH can lead to a lack of saturation of aragonite and calcite, which hinders the generation of new shells or skeletons by larvae (Mostofa et al., 2016). Moreover, decrease in shell size are likely a result of the inhibition of metabolism caused by hypercapnia, leading to delayed development (Brennand et al., 2010). In *H. coccoradiata*, the impact of pH on the calcification and shell formation process in abalone is further exacerbated by increasing the temperature 2°C and 4°C above normal. Byrne et al. (2011) found that only a minority of eggs developed into healthy larvae under warm temperatures (+2°C to 4°C) and low-pH conditions (pH -0.4 to 0.6 U). Smaller larval mollusks with weaker and thinner shells may require more time in their planktonic stage to accumulate sufficient energy for metamorphosis. A prolonged larval life span can potentially result in reduced survival rates and elevated mortality rates due to heightened susceptibility to predation and additional environmental stressors (Parker et al., 2013).

Settlement rate

The larval settlement process is an essential part of the life cycle of various benthic marine species, including abalone. Recent studies have indicated that future populations of abalone might be adversely affected by a decline in settlement (Espinel-Velasco et al., 2021). Studies investigating the impact of pH on settlement rate have been conducted on many species of *H.* genus, including Blackfoot paua (*Haliotis iris*) (Espinel-Velasco et al., 2021), Northern abalone (*Haliotis kamtschatkana*) (Crim et al., 2011), *H. asinina* (Tahil & Dy, 2015), European abalone (*Haliotis tuberculata*) (Kavousi et al., 2022), and *H. rufescens* (Gómez-Reyes et al., 2023). In *H. kamtschatkana*, a decrease in pH due to the administration of CO₂ did not have a significant impact on the settlement rate (Crim et al., 2011). Similarly, the settlement rate of *H. tuberculata* at pH 7.7 was not substantially different from the control. Moreover, decreasing the pH to 7.65 did not significantly affect the settlement rate of *H. iris* (Espi-

nel-Velasco et al., 2021). These result were likely because the examined pH conditions were still within an acceptable range for the species to settle. However, abalones capable of settling under low pH conditions are likely to experience shell damage. In the case of *H. kamtschatkana*, nearly all larvae that undergo settlement and metamorphosis at a concentration of 1,800 ppm exhibit anomalous shell development or lack a shell altogether. This condition could render them especially susceptible to predation by bottom-dwelling organisms in their natural habitat (Crim et al., 2011). Studies conducted on different abalone species have demonstrated that lower pH levels can negatively impact larval settlement rates. For example, a reduction in pH to 7.76, 7.57, and 7.41 significantly affects the settlement rate of *H. asinina* (Tahil & Dy, 2015). Gómez-Reyes et al. (2023) found that short-term reduction of pH had a noticeable effect on the settling rates of *H. rufescens* larvae after being incubated under pH levels of 7.8 and 7.6. The effect of pH on settlement is believed to be caused by the disturbance of abalone chemosensory signals, which hinders their ability to detect appropriate settlement sites under low pH conditions (Crim et al., 2011). Acidic conditions can also disrupt the capacity of crustose coralline algae to cover settlement plates. Tahil & Dy (2015) reported a decrease in the coverage of crustose coralline algae after 15 days of exposure to pH levels of 7.57 and 7.41 compared to the normal pH levels (Tahil & Dy, 2015).

Juvenile and adult stage

During their early life stages, abalone are more susceptible to the negative impacts of ocean acidification. Therefore, numerous studies have been conducted to characterize the effect of pH on the development of abalone larvae. However, very few studies have analyzed the impact of pH on juvenile and adult abalone. A summary of the impacts of ocean acidification on the juvenile and adult of abalone (*Haliotis* spp.) is presented in Table 4.

Survival, shell growth, and calcification

Abalone shells consist of two different types of calcium carbonate polymorphs. The outer prismatic layer may be calcite, aragonite, or a combination of both (Cummings et al., 2019), whereas the inner shell (nacre) is made of aragonite (Thompson et al., 2000). Aragonite and calcite saturation may decrease in response to an increase in atmospheric CO₂ (Feely et al., 2012), which can influence the development of abalone shells during all life phases from early development to the juvenile and adult phases. Abalone

Table 4. Summary of impact of ocean acidification on juvenile and adult of abalone

Species	CO ₂ /pH range	Experiment duration	Measured	Findings	References
<i>Haliotis laevis</i> (Juvenile)	pH 9.25, 8.45, 7.95, 7.30, 6.72, and 6.08	68 d	Oxygen consumption rate	Reduce at 9.25, 6.72, and 6.08	Harris et al., 1999
<i>H. laevis</i> (Juvenile)	pH 9.01, 8.27, 7.76, 7.46, 7.16, and 6.79	68 d	Survival rate	Reduce at 6.79	
			Food consumption	Reduce at 7.16	
<i>Haliotis rubra</i> (Juvenile)	pH 9.01, 8.27, 7.76, 7.46, 7.16, and 6.79	68 d	Survival rate	Reduce at 7.76 and 6.79	
			Food consumption	Reduce at 7.16	
<i>Haliotis iris</i> (Juvenile)	450, 1,000, and 1,600 µatm (pH 8.1, 7.8, 7.6)	100 d in autumn/winter and 100 d in spring/summer	Survival	Reduce in large juvenile in pH 7.6 during autumn/winter experiment	Cunningham et al., 2016
			Shell length	- Shorter at pH 7.6 in autumn/winter for small juveniles - Shorter at pH 7.8 and 7.6 in spring/summer for small juveniles - Shorter at pH 7.8 and 7.6 on autumn/winter for large juvenile	
			Growth (wet weight)	- Decreased for small juveniles at both seasons - NS on autumn/winter for large juvenile - Decrease on spring/summer for large juvenile	
<i>Haliotis iris</i> (Juvenile)	450, 1,000, and 1,600 µatm (pH 8.1, 7.8, 7.6)	100 d in autumn/winter and 100 d in spring/summer	Respiration	NS	Cunningham et al., 2016
<i>H. iris</i> (Juvenile)	400 and 1,000 µatm (pH 8.00 and 7.66) combine with temperature 13°C and 15°C	4 mon	Survival	NS	Cummings et al., 2019
			Shell growth	NS	
			dry flesh weigh	NS	
			Total thickness of the shells	NS	
			The prismatic layer	Thinner at low pH	
			Nacre layer	Thickened at lowered pH and higher temperature	
<i>Haliotis tuberculata</i> (Adult)	400 and 1,000 µatm pCO ₂ (pH 8.0 and 7.7)	5 mon	Survival rate	NS	Avignon et al., 2020
			Growth rate	Lower at pH 7.7	
			Haemolymph and muscle weights	NS	
			Gonad weight	Decreased weight at lower pH at the end of 4 mon	
			Phagocytosis efficiency	NS	
			Respiration rate	NS	
			Excretion rate	NS	

Table 4. Continued

Species	CO ₂ /pH range	Experiment duration	Measured	Findings	References
<i>H. tuberculata</i> (Adult)	400 and 1,000 µatm pCO ₂ (pH 8.0 and 7.7).	5 mon	Calcification related gene expression	NS	Avignon et al., 2020
			Stress related gene expression	NS	
			Shell coloration	Pale at low pH	
			Calcification rate	Decrease at low pH	
			Shell weight and thickness	NS	
			Periostracum thickness	Thinner at low pH	
			Shell fracture force	Increase at low pH	
<i>H. tuberculata</i> (Adult)	pH 7.9, 7.7, and 7.4	15 d	Survival and growth	NS	Auzoux-Bordenave et al., 2021
			Haemolymph pH _T	Decrease at pH 7.4	
			Total alkalinity (AT) in haemolymph.	Decrease at pH 7.4	
			pCO ₂ in haemolymph.	Decrease at pH 7.4 in day 10	
			HCO ₃ ⁻ haemolymph	Decrease at pH 7.4	
			Protein content in haemolymph	NS	
<i>Haliotis diversicolor</i> (Adult)	560, 880, and 1,600 µatm	1 year	Shell surface	Pale at low pH and decrease spirorbid density	Guo et al., 2023
<i>Haliotis diversicolor</i> (Adult)	560, 880, and 1,600 µatm	1 year	Shell growth	Lower in the pCO ₂ 1,600 µatm	Guo et al., 2023
			Shell thickness	NS	
			The ratio of nacre layer thickness to prismatic layer thickness	Higher in the pCO ₂ 1,600 µatm	
			Mechanical properties of the shell	Decrease in the pCO ₂ 1,600 µatm	
			The number of nano-asperities in the nacre tablet	Decrease in the pCO ₂ 1,600 µatm	
<i>Haliotis discus hannai</i> (Adult)	560, 880, and 1,600 µatm	1 year	Shell surface	Periostracum layer pale and decrease spirorbid density at high pCO ₂	Guo et al., 2023
			Shell growth	Decrease only in the pCO ₂ 880 µatm	
			Shell thickness	Lower the shell thickness	
			The ratio of nacre layer to prismatic layer thickness	NS	
<i>H. discus hannai</i> (Adult)	560, 880, and 1,600 µatm	1 year	Mechanical properties of the shell	Decrease in the pCO ₂ 1,600 µatm	Guo et al., 2023
			The number of nano-asperities in the nacre tablet	NS	
			The Na/Ca ratio in the prismatic aragonite layer	NS	

Table 4. Continued

Species	CO ₂ /pH range	Experiment duration	Measured	Findings	References
<i>H. discus hannai</i> (Adult)	pH 8.1 and 7.5 combination with 15°C, 20°C, and 25°C	5 d	Survival rate H ₂ O ₂ and MDA levels in hemolymph mRNA expression of SOD enzymes, CAT, and caspase-3 Apoptosis level in the hepatopancreas	NS H ₂ O ₂ , MDA levels and SOD, CAT, caspase-3 expression were Increased under low/high temperature and/or low pH Higher under high temperatures and low pH conditions	Kim et al., 2023
<i>Haliotis tuberculata</i> (Adult)	pH 8.01 and 7.7	3 mon	Food consumption	NS	Roussel et al., 2024

NS, non significant; MDA, malondialdehyde; SOD, superoxide dismutase; CAT, catalase.

shells provide protection from predators, noxious substances, and adverse environmental circumstances. Therefore, inhibiting abalone shell growth or reducing their mechanical strength may reduce their survival rate (Guo et al., 2022).

Several studies have examined the consequences of ocean acidification on the survival and shell growth of juvenile and adult abalone. Cunningham et al. (2016) investigated the survival and shell growth of both large and small juvenile *H. iris*. During the experiment, which lasted 100 days in autumn/winter and 100 days in spring/summer, the juveniles were grown at three pH levels (8.1, 7.8, and 7.6). Only large abalone exhibited significant variation in survival rate during the autumn/winter period between pH treatments. However, shell growth exhibited a notable deceleration at low pH levels in both small and larger abalone, regardless of the season. These findings indicate that the impact of pH on the survival rate depend on the size of the juvenile and the season, with the latter parameter being related to the sea water temperature. Particularly, the negative effects of acidification on abalone survival may be exacerbated by higher temperatures (Parker et al., 2013). However, a study conducted by Cummings et al. (2019) demonstrated that exposing juvenile *H. iris* to a reduced pH of 7.6 for a 4 months did not have any impact on their survival and growth rate. These discrepancies were likely due to difference between the carbonate saturation levels in the aforementioned studies, with the study by Cunningham et al. (2016), reporting a lower saturation, as well as disparities in feed and ambient conditions (Cummings et al., 2019).

The shell growth of juvenile *H. tuberculata* cultured for three months at four different pH levels (8.1, 7.8, 7.7, and 7.6) was also significantly slower at a lower pH (pH 7.6) compared

to the control group. However, survival rates were not markedly different between pH treatments (Auzoux-Bordenave et al., 2020). Similarly, low pH conditions significantly affected juvenile *H. discus hannai* growth but had no effect on survival rate (Li et al., 2018). In contrast, exposing adult *H. tuberculata* to three pH levels for 15 days had no significant effect on survival rates and shell growth (Auzoux-Bordenave et al., 2021). These differences were likely attributable to species-specific variations, as well as the duration of the pH treatment. According to Gazeau et al. (2013), the reaction of shelled mollusks to low seawater pH and high pCO₂ appears to be species-specific and even varied within species.

The calcification process of abalone shells is known to be negatively impacted by ocean acidification. For example, juvenile *H. discus hannai* cultivated at pH 7.7 for three months exhibited shell surface deteriorated, with large regions of shell lacking periostracum. Additionally, their brown-colored shell apex was hard to recognize. SEM analysis further confirmed the occurrence of large-scale deterioration of the nacreous layer and periostracum layer in abalone raised at pH 7.7. Calcite dissolution was also noted as exposed nacreous layer surfaces that were uneven and rough (Li et al., 2018). Similarly, adult *H. discus hannai* and *H. diversicolor* exposed to high pCO₂ conditions for a year exhibited shell periostracum deterioration and reduced resistance to crushing force (Guo et al., 2023). Periostracum alterations were also observed in juvenile *H. tuberculata* that were cultivated under a pH 7.6. Furthermore, the shell mineral layers exhibited altered texture and porosity (Auzoux-Bordenave et al., 2020). Ocean acidification profoundly affects the thinner prismatic calcite layer, leading to a more noticeable erosion of

the outer shell surface of juvenile *H. iris* at a lower pH of 7.6 (Cummings et al., 2019).

Ocean acidification has also been linked to the erosion and whitening of the periostracum layer, which is likely due to a decrease in the production of sulfated polysaccharides. These polysaccharides play a crucial role in preventing shell degradation (Cummings et al., 2019). Reduced calcification can occur due to either a direct impact on the dissolution of calcium carbonate (CaCO₃) or by indirect metabolic influences, such as the regulation of physiological and molecular processes involved in the formation of shell biominerals, including the expression of carbonic anhydrase, chitinase, tyrosinase, and other related factors. The effects of ocean acidification can also vary depending on whether aragonite or calcite are present in the shell, as aragonite is more sensitive to dissolution (Auzoux-Bordenave et al., 2020).

A further impact of thinning the abalone shell is that it can increase the vulnerability of the abalone to predation and pathogens (Barclay et al., 2020). Survival and health are also dependent on its shell because the shell is an external defense system (Muznebin, 2022). Some parasites or pathogens that attack abalone include shell-boring polychaete (*Polydora hophura*) (Winkler et al., 2024), shell-boring sponge (*Cliona* sp.) (Huchette et al., 2006), herpes-like virus (Chang et al., 2005), and spherical viruses (Wang et al., 2004). Chang et al. (2005) first identified the herpes-like virus in 2005, and it was associated with the mass mortality of *H. diversicolor* supertexta in Taiwan in 2003. Spherical viruses can also cause high mortality and be linked to crack-shell disease (Wang et al., 2004).

Physiology and metabolism

Decreases in water pH can lead changes in the immune system (Kim et al., 2023), hemolymph, respiration, and excretion rates (Avignon et al., 2020). Low pH levels, individually and in combination with high temperature stress, lead to oxidative stress in abalone, which can induce an increase in the levels of malondialdehyde (MDA), H₂O₂, catalase (CAT), superoxide dismutase (SOD), caspase-3, and apoptotic rate in *H. discus hannai* (Kim et al., 2023). SOD, a main scavenger of O₂⁻ formed during stressful situations, inhibits the production of oxygen radicals following exposure to low-pH seawater, stimulating CAT activity (Liao et al., 2019). A decrease in pH, especially when combined with high temperatures, triggers reactive oxygen species (ROS) production, which in turn stimulates the expression of SOD and CAT to stabilize ROS (Kim et al., 2023). Under excessively high ROS conditions, the secreted antioxi-

dant enzymes may not be sufficient to alleviate oxidative stress, leading to DNA damage, enzyme inactivation, and membrane lipid damage (Liao et al., 2019). In turn, increasing cell toxicity can also lead to caspase-3 upregulation, which sends apoptotic signals and leads to cell death (Kim et al., 2023). Another study reported that adult *H. tuberculata* cultured at pH 7.7 for 1 week, 2 months, and 4 months did not exhibit significant differences in phagocytosis efficiency compared to the control treatment. However, acid-base regulation, as measured by the pHT of hemolymph, was reduced at pH 7.7, leading to general internal acidosis.

Respiration and excretion rates in *H. tuberculata* also did not vary significantly between pH 8.0 and 7.7 after 4 months (Avignon et al., 2020). Presumably, the 0.3 pH unit drop in seawater pH might have posed a significant challenge for *H. tuberculata* during the first two months of exposure but the abalones began acclimate after 4 months. In this case, acidification had a greater impact on shell growth and structural integrity than on metabolism (Avignon et al., 2020). However, lowering the pH may also have a significant impact on metabolism in other abalone species. For example, Greenlip abalone (*Haliotis laevis*) experienced a decrease in oxygen consumption rate that was significantly different from the control (pH 8.27) after being incubated in seawater with extreme high and extreme low pH (9.25, 6.72, 6.08) for 68 days (Harris et al., 1999). The abalone from this experiment most likely experienced alterations in oxygen-hemocyanin affinity, which is aggravated by anaerobic metabolic products, resulting in a decrease in oxygen consumption rate (Harris et al., 1999).

Reduced seawater pH can influence abalone food consumption; however, the effect varies according to the species and age. At pH 7.16, juvenile *H. laevis* consumed considerably less food than at pH 7.76. Meanwhile, juvenile Blacklip abalone (*Haliotis rubra*) food consumption was significantly reduced at pH 7.16 when compared to pH 9.01 (Harris et al., 1999). Ocean acidification can diminish the ability of mollusks to detect food sources, resulting in a decrease in food consumption (Horwitz et al., 2020). However, there was no significant influence on food consumption of adult *H. tuberculata* between pH 8.01 and 7.7 after three months of treatment (Roussel et al., 2024).

However, cultivating abalone using formulated feed or seaweed could have negative environmental consequences. Animal waste, including feces and urine, as well as uneaten food, accounts for the majority of waste water from abalone cage farms. This increases the acidity of bottom sediment (Kang et al.,

2016), alters benthos populations, and induces eutrophication (Lee et al., 2016). Integrated multi-trophic aquaculture (IMTA) offers an alternate approach to addressing this issue and combating ocean acidification. Hamilton et al. (2022) demonstrate that integrated multitrophic aquaculture has the ability to improve growth, reduce nutrient loads, elevate system pH, and alleviate environmental conditions when compared to standard single-species culture approaches.

Conclusion

The impact of ocean acidification on abalone depends on various aspects, including the species, developmental stage, size, and duration of exposure. Moreover, the effects of pH stress can be compounded with other environmental conditions, thereby having a more pronounced influence on abalone. Therefore, future research should focus on the combined effects of several stressors (e.g., temperature) on the various life-history phases of abalone, as well as the potential for adaptation of acclimatization in certain species.

Competing interests

No potential conflict of interest relevant to this article was reported.

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Availability of data and materials

Upon reasonable request, the datasets of this study can be available from the corresponding author.

Ethics approval and consent to participate

Not applicable.

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