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Effect of Ocean Acidification on the Metabolism and Behavior of Tropical Sea Cucumbers

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Abstract In recent years, CO_2 emitted by human activities has continued to rise. The ocean absorbs these CO_2 and has caused seawater acidification. It is expected that the pH of the sea surface will drop by 0.3~0.4 by the end of this century. Tropical sea cucumbers are the "engineers" of the subsea ecosystem, promoting organic degradation and nutrient circulation through feeding disturbances. This study reviews the effects of marine acidification on the metabolism and behavior of tropical sea cucumbers. Studies have shown that under low pH conditions, sea cucumbers have increased respiratory metabolic pressure, digestive enzyme activity is reduced, and more energy is used to maintain the acid-base balance in the body, and their growth and reproduction are limited. At the same time, sea cucumber feeding rate and defense behavior are inhibited, and habitat distribution may change. These changes will have a chain effect on tropical ecosystems such as coral reefs, weaken the nutrient circulation function, and affect ecological balance. In-depth research on the impact mechanism of marine acidification on sea cucumbers will help predict the response of marine ecosystems under climate change and provide scientific basis for resource conservation and aquaculture management.

Keywords Ocean acidification; Tropical sea cucumber; Metabolism; Behavior; Ecological impact

1 Introduction

As humans emit large quantities of greenhouse gases such as CO_2, the concentration of atmospheric CO_2 continues to rise, and the ocean absorbs about 1/4 of the artificial CO_2, resulting in an increase in the acidity of seawater. The average pH of the ocean surface has dropped by about 0.1 compared with pre-industrialization, and is expected to drop by about 0.3~0.4 at the end of the 21st century under high emission scenarios (Sun, 2024). Ocean acidification has poses a threat to sensitive ecosystems such as tropical coral reefs, manifested as adverse effects such as coral calcification rate and reduced biodiversity.

Tropical sea cucumbers play an important role in marine benthic ecosystems. As a typical “ecological engineer,” sea cucumbers feed on seabed sediments and organic debris and excrete them, allowing sediments to be tilled and oxidized, promoting organic matter decomposition and nutrient circulation (Wolfe et al., 2018). Sea cucumber activities help maintain the water quality of the coral reef base and provide nutrient sources for symbiotic algae. In addition, many sea cucumber species have economic value and are an important resource for coastal fisheries and aquaculture. Therefore, studying the impact of marine acidification on sea cucumbers is not only ecologically significant, but also helps in the management and protection of tropical marine resources.

Currently, research on marine acidification on echinoderms focuses on highly calcified sea urchins and starfish, and relatively insufficient attention is paid to sea cucumbers with low calcification. There are only a small number of lime-like bone fragments in tropical sea cucumbers, which are believed to be less sensitive to acidification than calcified organisms such as reef-making corals. However, acidification may indirectly endanger its survival and ecological function by interfering with the metabolic balance and behavioral patterns of sea cucumbers. In recent years, trials have begun to focus on the physiological responses of sea cucumbers under acidified conditions, such as changes in respiration rate and feeding vitality (Sun, 2024). A deep understanding of the effects of ocean acidification on the metabolism and behavior of tropical sea cucumbers is of great significance to reveal the mechanisms of non-calcified groups to cope with climate change. This study will review the domestic and foreign research progress in recent years from the aspects of marine acidification, the physicochemical mechanism, the metabolic characteristics of sea cucumber, the impact of acidification and ecological effects, and look forward to future research directions.

2 Physical and Chemical Mechanism of Marine Acidification

2.1 The relationship between carbon dioxide emissions and the decline in seawater pH

The fundamental reason for ocean acidification is the increase in atmospheric CO_2 concentration. After excessive CO_2 is absorbed by the ocean, it reacts with water molecules to form carbonic acid, further ionization produces hydrogen ions, resulting in a drop in the pH of seawater. The average seawater pH has decreased by about 0.1 since industrialization, meaning that the hydrogen ion concentration has increased by about 30%. At first, the carbonate buffer system of the ocean can neutralize part of the acidity, but as CO_2 continues to dissolve, the buffer capacity gradually weakens. The IPCC report predicts that if high emissions are maintained, the drop in ocean surface pH will significantly exceed the natural fluctuation range of the past few million years by 2100.

2.2 Spatial differences and dynamic changes in acidification in tropical seas

The degree of ocean acidification varies in different regions. The acidification of the open ocean surface is relatively uniform, while tropical nearshore and coral reef areas show more complex pH dynamics due to local biogeochemical processes. For example, photosynthesis in the reef area during the daytime reef increases the pH of water, and the release of CO_2 at night biorespiration reduces the pH, and the fluctuation amplitude of day and night can reach more than 0.2 (Cryer et al., 2021). Some semi-enclosed sea areas may acidify faster than the global average due to seawater stagnation and high organic matter decomposition. The study found that frequent low pH extreme events occurred in the coral triangle in the Western Pacific from 2015 to 2022, with Ω_{ar} and pH drops higher than those in other sea areas. On the contrary, in tropical oceans far away from the mainland, the carbonate saturation of seawater is still relatively high, providing a certain "buffer" space for coral reefs. In addition, factors such as eutrophication and upflow will also aggravate local acidification: organic matter decomposition and freshwater input in the nearshore area of the estuary often cause a rapid decline in pH, forming an acidification "hot spot" (Isah et al., 2022).

2.3 Effect of marine acidification on carbonate system and marine buffering capacity

As the CO_2 content in seawater increases, the carbonate system changes significantly: the carbonate ion concentration decreases and the bicarbonate ion concentration increases. This leads to a decrease in saturation of calcium carbonate in seawater, weakening the biocalcification effect. Reef-making corals and shellfish are more difficult to form skeletons and shells at low pH, with significantly lower growth rates. Increased seawater acidity is also gradually weakening the ocean's chemical buffering capacity. When the pH drops, the bicarbonate/carbonate balance system moves in the direction of releasing more H^+, reducing the ability of seawater to resist foreign acids (Figure 1) (Sulpis et al., 2022). In summary, on the one hand, ocean acidification directly affects the carbonate chemical balance of seawater, and on the other hand, it also reduces the ocean's self-regulation ability of acidification, which will further amplify the potential impact on marine ecology.

3 Metabolic Characteristics of Tropical Sea Cucumbers

3.1 Basic characteristics of respiration and energy metabolism pathways

Sea cucumbers are benthic slowly moving debris animals, and their basal metabolic rate is relatively low. Sea cucumbers have a unique respiratory structure - a breathing tree at the end of the intestine, which absorbs water and expels water through the anus for gas exchange. This breathing method is not efficient, but it is enough to meet its slow lifestyle oxygen needs. In adverse environments, sea cucumbers can also actively reduce their metabolic rate to save energy. For example, when the temperature is high in summer, the prickly ginseng will enter a summer hibernation state, and the metabolic level will drop significantly, thus passing through the period of high temperature and food scarcity.

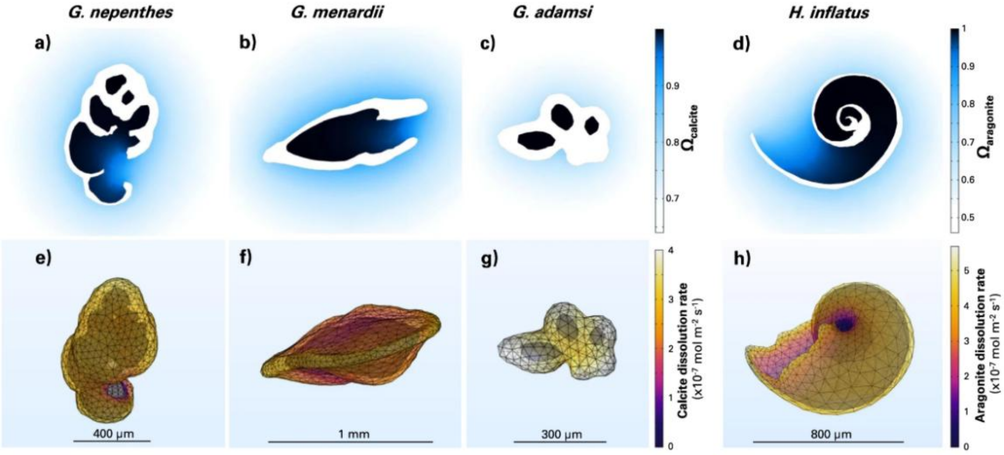

Figure 1 Dissolution of natural marine $CaCO_3$ grains after a minute in suspension in water (Adopted from Sulpis et al., 2022)

3.2 The role of protein and lipid metabolism in sea cucumber physiology

The nutrients in sea cucumbers are mainly stored in the form of protein. The body wall of sea cucumber is rich in structural proteins such as collagen, accounting for a large proportion of the dry weight; during the peak season of feeding, sea cucumbers convert the organic matter intake into body wall and muscle protein for accumulation. When faced with high energy consumption stages such as hunger or reproduction, these protein reserves can be decomposed to provide energy (Zamora and Jeffs, 2015; Asha and Muthiah, 2018). In contrast, sea cucumbers have low fat content in their bodies, but lipids provide necessary energy for developing reproductive gonads during the reproductive period. High-protein baits can promote the growth and repair of sea cucumber tissue, while appropriate lipid levels help improve reproductive performance.

3.3 Metabolic regulation mechanism for environmental stress (temperature, salinity, acidification)

Tropical sea cucumbers have evolved a series of metabolic regulatory mechanisms to deal with environmental stresses such as temperature, salinity and acidity. When the temperature is too high, sea cucumbers often reduce their activity and even enter dormant state to reduce energy consumption and oxidative damage. For example, ginseng stops eating and sleeping in summer when the water temperature is too high in summer, thereby protecting its own tissues from depletion (Li et al., 2021). When salinity changes drastically, sea cucumbers maintain body fluid balance through osmotic regulation: in a low-salt environment, their body cavity fluid Na^+-K^+-ATPase plasma pump activity is improved, and they actively ingest ions to stabilize the osmotic pressure (Jiang et al., 2024). Faced with the acidification stress of lowering seawater pH, sea cucumbers also show obvious physiological plasticity. Long-term exposure experiments show that adult sea cucumbers can adjust the ion composition of body fluids to stabilize the pH of the internal environment, and the pH of the body cavity fluid gradually returns to normal levels after the initial decrease. This shows that sea cucumbers have certain acid-base regulation capabilities and can withstand moderate environmental acidification. At the same time, research has found that increasing water temperature can offset the adverse effects of acidification on sea cucumber metabolism to a certain extent: for example, the feeding and growth rates of citrus citrus under heating conditions are higher than those of pure acidification conditions (Li et al., 2021).

4 Effects of Marine Acidification on Sea Cucumber Metabolism

4.1 Changes in respiration rate under low pH conditions

The effect of ocean acidification on sea cucumber respiratory metabolism depends on the degree of acidification and exposure time. Under moderately intense acidification conditions, sea cucumbers can maintain near-normal metabolic levels through physiological regulation. Experiments showed that in an environment with a pH reduction of about 0.3, the oxygen consumption rate of pilosula was not significantly different from that of the control group, and its energy distribution pattern did not change significantly. This shows that the basal respiratory metabolism of sea cucumbers has a certain degree of toughness to moderate acidification and will not immediately cause disorders. When the acidification level exceeds the tolerance range, sea cucumbers may initiate metabolic inhibition to reduce energy consumption. Long-term deep acidification will lead to a continuous low respiration rate of sea cucumbers, and insufficient oxygen supply will affect its vitality and other physiological functions (Wang, 2024).

4.2 Effects of acidification environment on digestive enzyme activity and nutrient absorption

Seawater acidification not only affects the respiration of sea cucumbers, but also has a negative effect on their digestive and absorption functions. Studies have found that low pH stress significantly reduces the activity of digestive enzymes such as alkaline phosphatase in the intestine of sea cucumber (Wu et al., 2013). Alkaline phosphatases are involved in the decomposition and absorption of organophosphorus, and the decrease in enzyme activity means that sea cucumbers are less efficient in obtaining nutrients from food. In addition, acidification may disrupt the balance of the intestinal flora of sea cucumbers and damage the digestive tract epithelium, further weakening its digestive capacity. Due to the decrease in food interest and inhibition of enzyme activity, the absorption rate of nutrients of sea cucumbers decreases accordingly. Long-term experiments have confirmed that the intake and growth rate of sea cucumbers under acidification conditions have significantly decreased: the specific growth rate of citrus citrus decreased by nearly 20% compared with the control when the pH decreased by about 0.3 (Yuan et al., 2016). Inadequate nutritional intake forces sea cucumbers to use their own reserves, resulting in weight loss and tissue growth restriction, ultimately endangering their health and survival.

4.3 Redistribution of energy metabolism and increase in metabolic costs

Faced with acidification stress, sea cucumbers often need to invest more energy to maintain their homeostasis, which leads to the redistribution of their energy metabolism. In order to regulate the acid-base balance of body fluids, sea cucumbers must strengthen ion transport, ammonia discharge and other processes to increase basal metabolic energy consumption. This means that the energy used for growth and reproduction is relatively reduced. Experimental evidence shows that under the combined action of acidification and other stresses (such as heating), the energy distribution of sea cucumbers has significantly changed: the digestion and absorption efficiency of citrus ginseng is reduced under acidification and heating conditions, and the proportion of feces excretion energy is significantly higher than that of the control group. This suggests that sea cucumbers use more energy intake to cope with environmental stresses and reduce the share of energy allocated to growth and reproduction (Yuan et al., 2016). In the long run, the increase in metabolic costs will lead to a decrease in weight in sea cucumbers, a decrease in reproductive investment, and may also be impaired in physiological functions such as immunity. Ocean acidification breaks the original energy distribution balance by increasing the energy expenditure of sea cucumbers to maintain life activities, and ultimately has a potential negative impact on population renewal and ecological functions.

5 The Effect of Marine Acidification on Sea Cucumber Behavior

5.1 Changes in feeding behavior

Ocean acidification usually leads to a weakening of sea cucumber feeding behavior. Experimental observations show that the feeding rate of sea cucumbers decreased, the feeding interval was prolonged, and food intake was significantly reduced. Research on ginseng found that the intake of ginseng decreased under acidification treatment, and its growth rate decreased by nearly 20% compared with normal pH. Long-term diet reduction will directly affect the nutritional acquisition of sea cucumbers and further affect their metabolism and growth through insufficient energy intake.

5.2 Changes in activity and habitat selection

In addition to feeding, the activity level and habitat of sea cucumbers are also affected by ocean acidification. Different species have different behavioral responses to acidification. For example, low pH significantly reduced the frequency of nocturnal activity of luminous snails in the same domain, but had little effect on the activity of sea cucumbers; after several days of domestication, the activity level of both returned to normal. This suggests that sea cucumbers have stronger behavioral tolerance than some invertebrates (Yuan et al., 2018). In the low-pH coral reefs formed by the CO_2 leakage in Papua New Guinea, a large number of sea cucumbers can still be observed, while many shrimps, crabs and other crustaceans are almost extinct. This shows that sea cucumbers can still live normally in a mild acidification environment (Wolfe et al., 2018). However, when the acidification is more severe, sea cucumbers may reduce their activity, hide in concealed areas to avoid adverse environments, and even escape areas with severe acidification in local areas.

5.3 The weakening of defensive behavior and environmental perception capabilities

Sea cucumbers rely on touch and chemical sensations to perceive the environment and predators, and acidification may have an impact on their sensory and defensive behavior. Studies have shown that ocean acidification interferes with sensory functions and neural processes in marine animals. For sea cucumbers, low pH may weaken their sensitivity to chemical signals and tactile stimuli. For example, some sea cucumbers will spit out their internal organs or release sticky wires for defense when encountering predators, but the threshold for triggering such reactions under acidification stress may increase and slow down the reaction rate. Under moderate acidification conditions, studies have also found that the defense behavior of sea cucumbers has not changed significantly: in the experiment, adult sea cucumbers can still shrink their bodies normally and defend against foreign enemies under stimulation, showing that their behavior has certain resilience under moderate acidification (Yuan et al., 2018). Overall, the environmental perception and defense response of sea cucumbers under moderate acidification can remain normal, but stronger acidification may weaken their sensory and neurological functions, reduce their defense efficiency, and thus increase the risk of predation.

6 Chain Effects At the Ecosystem Level

6.1 The nutrient circulation effect of sea cucumbers in marine benthic ecosystems

Sea cucumbers play an important role in the material circulation of marine benthic ecosystems through feeding and excretion. They swallow the organic matter of sediment and discharge the metabolic waste rich in nutrients, which promotes the regeneration of elements such as nitrogen and phosphorus from sediment to water. In tropical coral reef ecology, sea cucumbers are regarded as "scavengers" and "engineers" who maintain the health of the benthic environment: their feeding disturbances prevent sediments from silting, and the ammonium nitrogen in the feces can be used by algae and coral symbiotic algae to support primary production (MacTavish et al., 2012). It is worth noting that sea cucumbers also have a special contribution to the carbonate cycle - dissolving the swallowed calcium carbonate particles during digestion and releasing additional alkalinity, which can partially offset the acidification of coral reef water bodies due to biological respiration at night. Therefore, the reduction in the amount of sea parameters will weaken the above nutrient circulation and alkalinity buffering functions, which may lead to the accumulation of sedimentary organic matter and the aggravation of local hypoxia, and damage the quality of coral reef substrates (Figure 2) (Pan et al., 2024).

6.2 Effects of marine acidification on the release of heavy metals in sediment and decomposition of organic matter

Ocean acidification not only affects organisms themselves, but also affects the sediment process by changing the chemical environment. The pH drop increases the release of many heavy metals at the sediment-water interface. Experimental research found that under CO_2-driven acidification conditions, metals such as Cd, Cu, Ni, Pb, Fe, Mn in the sediment are dissolution accelerated into the overburden water, and their release rate is controlled by the acidification intensity and metal chemical morphology (He et al., 2019). After being released from sediments, heavy metals can be ingested by benthic organisms or enter the food web, increasing the risk of ecological toxicity. In addition to heavy metals, acidification can also affect the decomposition efficiency of microorganisms on organic matter. The metabolic activities of many sedimentary microorganisms are sensitive to pH changes, and the acidity of seawater may reduce the activity of decomposing bacteria, resulting in slowing down the decomposition of organic residues in the sediment. Observations near the estuary show that excessive mineralization of organic matter caused by eutrophication will aggravate local seawater acidification, and the two promote each other to form a vicious cycle. If the function of the crumbled eaters such as sea cucumbers is weakened and the sedimentary organic load is further increased, it may induce hypoxia in the base and release more reducing substances, affecting the water quality and the stability of benthic communities.

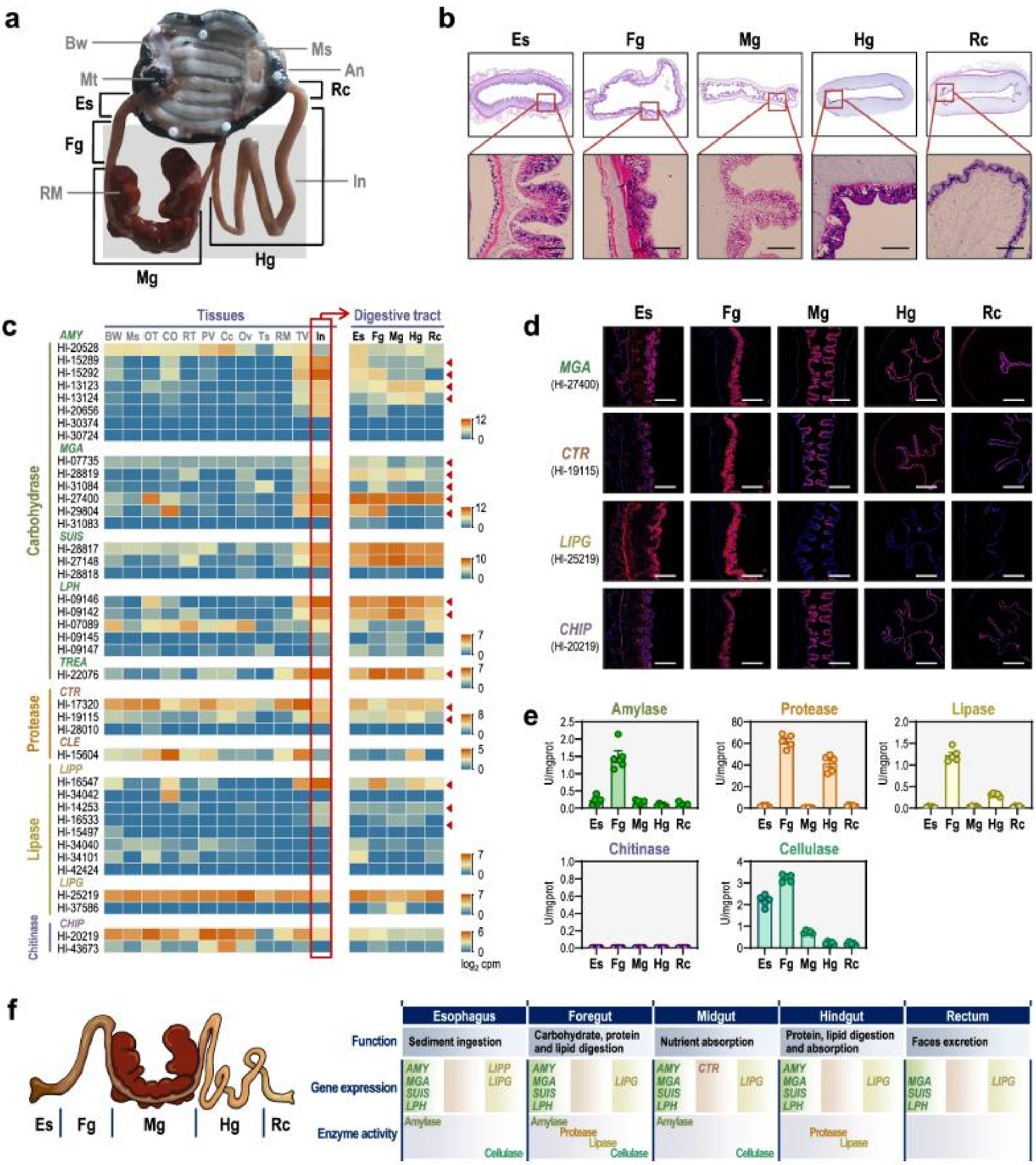

Figure 2 The structure and digestive enzyme system of the *H. leucospilota* digestive tract (Adopted from Pan et al., 2024)

6.3 Potential impact on coral reefs and tropical ocean food web

Ocean acidification and its impact on key species such as sea cucumbers will produce chain reactions at the ecosystem level. In coral reef ecosystems, changes in sea parameter quantity and behavior are transmitted to other organisms through nutrient circulation and habitat engineering effects (Wu et al., 2024). If sea cucumber feeding decreases and the amount decreases, sediment organic matter will accumulate (Clements et al., 2024), the matrix environment of coral larvae attachment deteriorates, and coral reef structural stability is impaired (Maritan et al., 2025). At the same time, the nutritional reduction of sea cucumber excretion may affect the growth of symbiotic algae and algae communities and change the primary production pattern. The decline of sea cucumbers will also affect predators that feed on them, such as certain fish and invertebrate predators, causing reorganization of energy flow in the food web (Viyakarn et al., 2020).

7 Actual Case Analysis

7.1 Papua new guinea volcanic Yongquan district: sea cucumber community under natural low pH environment

There is a natural CO_2 leak in the seabed near Dobu Island in Papua New Guinea, which has maintained the pH of the sea water in the sea for a long time at a low level of about 7.7~7.8. This environment provides a natural experimental field for studying the effects of marine acidification. According to on-site investigation, in this low-pH coral reef area, non-calcium-dependent organisms such as sea cucumbers and sea urchins still exist in large quantities, while many highly calcified species such as shrimp and crabs are almost extinct (Pichler et al., 2019). Sea cucumbers living in this area did not show obvious abnormal behavior: they still feed, move, and inhabit normally, with only slightly different population density and composition from the surrounding normal areas. It is speculated that sea cucumbers can survive in this acidification environment, thanks to their low calcification needs and strong acid-base regulation capabilities in the body. However, the ecology of the region has changed overall: coral cover and diversity decline, algae breeding and invertebrate “weed” organisms dominate (Geissler et al., 2021). As a residual functional group, sea cucumbers continue to play the role of sediment cleaning and nutrient regeneration to a certain extent, but cannot stop the tendency of coral reef decline. This case shows that sea cucumbers are relatively tolerant of acidification stress, and their ecological function is more important in the upheaval of environmental changes.

7.2 Philippine sea farming experiment: sea cucumber farming performance under acidification conditions

To evaluate the impact of marine acidification on sea cucumber farming, researchers in the Philippines conducted simulated farming experiments on tropical sea cucumber larvae. In this experiment, ginseng was exposed to water bodies that lowered 0.3 units of pH (approximately 7.8) and raised 3 °C for 5 days to observe its feeding and growth status. The results showed that the feeding vitality and nocturnal activity of sea cucumbers under low pH conditions did not show a significant decrease, while the control luminescent spiral activity decreased significantly under the same conditions. More importantly, after several days of domestication, there was no significant difference in feeding rate and growth rate between different treatment groups, whether it was sea cucumbers or luminous snails (Figure 3) (Campo et al., 2022). This shows that sea cucumbers have strong short-term acidification adaptability: their feeding and growth can be adjusted and restored in a short period of time even in seawater at pH 7.8 (Yuan et al., 2016). This experiment provides inspiration for the breeding industry: under the future marine acidification scenario, tropical sea cucumbers may still maintain a high survival rate and growth efficiency. However, the study also emphasized that corresponding measures need to be taken according to different species, such as selecting sea cucumber varieties with stronger acid resistance and optimizing aquaculture water quality to improve the risk resistance of seawater aquaculture to acidification (Campo et al., 2022).

8 Coping and Prospect

Ocean acidification has had a certain impact on the physiology and behavior of tropical sea cucumbers, but its degree and performance are complex. Sea cucumbers have strong physiological regulation capabilities and can maintain basic functions under moderate acidification, but in severe acidification situations, negative effects such as reduced feeding and increased metabolic burden may still occur. The weakening of the ecological function of sea cucumber will impact the coral reef ecosystem through nutrient circulation and other links, which requires attention.

Faced with the continuous advancement of marine acidification, it is of great significance to conduct in-depth research on the adaptability potential and population differences of tropical sea cucumbers. On the one hand, there are differences in tolerance to acidification in different sea cucumber species and developmental stages: studies have shown that adult sea cucumbers are relatively tolerant to the predicted acidification levels in the near future, but the larval stage often exhibits higher vulnerability (such as delayed development and reduced survival). Revealing the genetic and physiological mechanisms of these differences can help predict which populations are more susceptible to shocks and develop targeted protection strategies. On the other hand, in the field of aquaculture and resource management, sustainable strategies to deal with marine acidification should be actively adopted. Cultivating and breeding acid-resistant sea cucumber varieties is one direction, and the tolerance of sea cucumbers to low pH environments can be improved through manual selection. At the same time, a multi-nutrient-level integrated aquaculture model (IMTA) is developed, such as the mixing of seaweed or filter-feeding shellfish, and the use of algae photosynthesis to increase the pH of water and the dissolution of shellfish shells to provide alkalinity buffer, thereby reducing the acidification effect of aquaculture water. In addition, it is also crucial to strengthen monitoring and habitat protection of wild sea cucumber populations, and healthy and diverse ecosystems tend to have stronger acidification resistance.

Figure 3 (A) Healthy *Holothuria scabra* broodstock, each weighing more than 250 g; (B) Spawning and larval tanks at the sea cucumberhatchery of BFAR-GMFDC in Guiuan, Eastern Samar; (C) Indoor nursery rearing tanks for experimentation on various seaweed feedregimen; (D) Sea cucumber juveniles fed with *Sargassum* sp. harvested from an experiment in indoor nursery rearing tanks after 45 days (Adopted from Campo et al., 2022)

The latest research proposes that coral reefs with high carbonate stability should be included in marine protected areas planning first to use natural buffer conditions to enhance the risk resistance of the ecosystem. Future research needs to be comprehensively promoted across disciplines, including collaboration in the fields of marine chemistry, ecology, physiology and genomics. In addition to laboratory control tests, the response mechanism of sea cucumbers under long-term progressive acidification and multiple stresses (such as heating, hypoxia, etc.) should also be evaluated in combination with on-site observation and model simulation. Through the above efforts, the impact of marine acidification on tropical sea cucumbers and their ecosystems can be more comprehensively understood, providing scientific support for protecting marine biodiversity and maintaining ecosystem service functions.

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Conflict of Interest Disclosure

The authors confirm that the study was conducted without any commercial or financial relationships and could be interpreted as a potential conflict of interest.

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