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Mini-review: the utility of macroalgae in abalone diets and their role in heat resilience

Pemanfaatan makroalga pada pakan abalone dan peranannya pada ketahanan panas

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ABSTRACT

Abalone aquaculture production is predicted to continue to increase. Nutrition and health aspect are becoming two major issues that can impede the development and economic sustainability of abalone aquaculture industries. Feeding fresh macroalgae to abalone has supply inconsistency and biosecurity issues in the culture system. The utilization of commercially formulated diets could improve abalone growth rates. However, in general, the health condition of abalone which has been fed commercially formulated feeds was lower than abalone fed fresh macroalgae diets. An abalone diet should not only need to sustain a high growth rate but also promote optimal health. The use of dried macroalgae meal as a dietary ingredient in formulated diets for abalone could potentially increase growth rate, reduce feed costs and gain the health and immunity benefits of macroalgae. This review aims to improve understanding of the potential benefits of using fresh and dried marine macroalgae as feed ingredients to provide nutritional and health improvements for abalone.

Keywords: abalone, aquaculture, health, macroalgae, nutritional requirement

ABSTRAK

Produksi budidaya abalon diperkirakan terus meningkat. Aspek gizi dan kesehatan menjadi dua isu besar yang dapat menghambat perkembangan dan keberlanjutan ekonomi industri budidaya abalon. Pemberian pakan makroalga segar ke abalon memiliki permasalahan pada ketersediaan pasokan yang tidak konsisten dan biosekuriti dalam sistem budidaya. Pemanfaatan pakan komersial dapat meningkatkan laju pertumbuhan abalon. Namun secara umum, kondisi kesehatan abalon yang diberikan pakan formula komersial lebih rendah dibandingkan dengan abalone yang diberikan pakan makroalga segar. Pakan abalon sebaiknya tidak hanya perlu meningkatkan pertumbuhan tetapi juga meningkatkan kesehatan yang optimal. Penggunaan tepung makroalga kering sebagai bahan makanan dalam formulasi pakan abalon berpotensi meningkatkan laju pertumbuhan, mengurangi biaya pakan dan mendapatkan manfaat kesehatan dan kekebalan dari makroalga. Kajian ini bertujuan untuk meningkatkan pemahaman tentang potensi manfaat penggunaan makroalga laut segar dan kering sebagai bahan pakan untuk memberikan peningkatan nutrisi dan kesehatan abalon.

Kata kunci: abalon, budidaya, kebutuhan nutrisi, kesehatan, makroalga

INTRODUCTION

Abalone is one of the most valuable seafood species worldwide. Global abalone production more than tripled from 34,867 tonnes in 2006 to 162,771 tonnes in 2016 (FAO, 2017). Abalone aquaculture production is predicted to continue to increase because of the rising global demand for this species, mainly from China, Japan and other Asian countries. However, an issue related to the abalone's nutritional requirements to enhance health during critical production periods (summer mortality) can impede the development and economic sustainability of abalone aquaculture industries in the future. Generally, abalone farmers feed fresh macroalgae and formulated feeds to abalone. Due to the nutrient content and bioactive compounds in macroalgae, it can enhance immunity and act as a feeding stimulant compared to feeding formulated feeds (Dang *et al*., 2011a).

Feeding a combination of two or more fresh macroalgae may provide a better nutritional profile for abalone than only a single algal species (Kemp *et al*., 2015). On the other hand, the inconsistencies of supply on-farm and the biosecurity issues (introduction of disease, predators and competitors) in culture systems are also other weaknesses of using fresh macroalgae in abalone culture. Therefore, the use of commercially formulated diets on large-scale farms can be a more practical option because of their constant supply, and it leads to higher growth in abalone (Bansemer *et al*., 2016c). Unfortunately, this is also not an ideal option. Generally, the health condition of abalone fed commercial formulated feeds was lower than abalone fed fresh macroalgae diets.

Increasing global temperatures, as a result of climate change, are also a major threat to abalone culture. According to Vandepeer (2006), up to 50% of greenlip abalone mortalities occurred in one farm in the Port Lincoln area in 2000. Mass blacklip abalone mortalities have also been reported in Tasmania and Victoria. The prevalence of pathogenic bacteria and the virus *Vibrio harveyi* during this heat stress has emerged as a plausible key component of summer mortality syndrome (Vandepeer, 2006). A sudden increase in water temperatures is known to be a key factor of mass mortality of molluscs, including abalone during the summer months (summer mortality) (Shiel *et al*., 2018). Feed availability and quality are also generally considered to be one of the contributing factors of summer mortality in aquatic organisms (Bansemer *et al*., 2023).

The improvement of nutritional treatments could be one of the strategies that can support growth and immune system development for abalone aquaculture. High-quality abalone diets should not only increase growth rates and become economically feasible for abalone aquaculture industries but also improve health and product quality. Recently, there has been an increasing interest in incorporating dried macroalgae meal as a dietary ingredient in formulated diets for abalone to reduce feed costs and gain the health and immunity benefits of macroalgae. Numerous studies have investigated the use of marine macroalgae meals, including *Laminaria digitata* meal, *Palmaria palmata* meal, *Ulva lactuca* meal, *Ulva australis* meal, *Gracilaria cornea* meal, *Gracilaria cliftonii* meal, *Undaria pinnatifida* meal and *Sargassum horneri* meal in formulated feeds for abalone.

This suggests the potential of further improvements of formulated feeds for abalone with inclusions of dried macroalgae meal (Ansary *et al*., 2019a; Ansary *et al*., 2019b; Bansemer *et al*., 2016a; O'Mahoney *et al*., 2014; Viera *et al*., 2015). Research on the potential benefits of using marine macroalgae to improve the growth of abalone is increasing. However, there is a lack of literature review investigating the utility of macroalgae on enhancing the growth, health, and immune system of abalone. Therefore, this review covers (i) the nutritional requirements of abalone, (ii) the use of macroalgae as an abalone feed and their potential benefits, (iii) the impact of summer mortality on abalone industries and its aetiology, and (iv) the preventative strategies of summer mortality undertaken in aquaculture.

Nutritional requirements of abalone in aquaculture

Feed ingredients of abalone diets should be nutritious, digestible, palatable and cost-effective. Protein is the most expensive component of abalone feed. Therefore, it is crucial to determine protein requirements accurately to supply the right balance of essential amino acids tailored to each abalone species to ensure optimal growth (Coote *et al*., 2000; Stone *et al*., 2013). The protein requirements differ between abalone species and needs to be tailored to age and/or size and water temperature during abalone culture (Table 1). Optimal dietary protein levels across abalone species have been found to vary between 23.66 %

and 45 % (Table 1). On the table, it can be seen that higher protein levels are required at higher temperatures for *Haliotis laevigata*.

Meanwhile, optimal dietary protein levels vary with age and are inconsistent across species. Coote *et al*. (2000) stated that feed formulation based on digestible amino acids precisely meet the nutritional requirements of abalone. This could increase dietary protein utilization by abalone and also lead to better feed conversion efficiency, minimum nutrient losses and lower production cost in terms of feed cost for the abalone aquaculture industry. However, a limited database of the digestible protein and energy content of abalone feed could make abalone diet formulation slightly complicated. Alternatively, the ideal protein requirement of abalone could be determined by calculating the dietary essential amino acids for abalone (Bansemer *et al*., 2016c).

The optimal dietary energy level in formulated feeds not only depends on the animal size, water temperature and levels of protein but it is also influenced by the digestibility of ingredients, the levels of dietary carbohydrate and lipid (Britz & Hecht, 1997). In terms of the level of lipid, abalone requires low levels of dietary lipids,

Table 1. Optimal dietary protein percentage for different abalone species and their hybrids, including across size, age and water temperature of culture environment.

Species	**Age**	**Initial Weight (g)**	**Water Temperature (°C)**	**Optimal dietary protein level (%)**	**Source**
Greenlip abalone (*Haliotis laevigata*)	6 months	0.91	14 17 20	29 29 35	Bansemer *et al*. (2015)
Greenlip abalone (H. *laevigata*)	1 year	1.75	14 22	29 35	Stone *et al*. (2014a)
Greenlip abalone (H. *laevigata*)	2 years	22.93	14 22	24 34	Stone *et al*. (2014b)
Blacklip abalone (*Haliotis rubra*)	-	0.04	17	45	Dunstan (2010)
Hybrid abalone (H. *rubra* x H. *laevigata*)	9 months	0.196	13.71	23.66	Mulvaney *et al*. (2013)
Hybrid abalone (H. *rubra* x H. *laevigata*)	-	3.2	17.5	39.8	Stone *et al*. (2016)
South African abalone (H. *midae*)	6 months 20 months	0.2 7.8	18 18	34 44	Britz and Hecht (1997)
Green ormer (*Haliotis tuberculata*)	1 year	2.2	-	19.6	Roussel *et al*. (2019)
Pacific abalone (*Haliotis discus hannai*)	-	6	18 - 18.6	29.7	Ansary *et al.* (2019a)
Tropical abalone (*Haliotis asinina*)	3 months	0.48	27.8 – 30.5	32.4	Capinpin and Corre (1996)
Tropical abalone (*Haliotis squamata*)	-	3.07	-	28 - 31	Giri *et al.* (2015)
Tropical abalone (*Haliotis squamata*)	-	5.30	-	24 - 25	Giri *et al.* (2016)
Tropical abalone (*Haliotis squamata*)	-	10	-	6 - 8	Prihadi *et al.* (2018)
Tropical abalone (*Haliotis squamata*)	1 month	5	-	23 - 28	Hadijah *et al.* (2020)

and it was suggested for approximately 3.5% of crude lipid in H. *laevigata* feed (Dunstan *et al*., 2000) and 2-6% of crude lipid in *Haliotis midae* feed (Britz & Hecht, 1997). Various economic and ecologically sustainable plant-based protein sources have been widely investigated as a fish meal substitute, including soybean meal (Yu *et al*., 2022), corn gluten meal (Wu *et al*., 2022), *Spirulina* sp. (Jin *et al*., 2020), and lupin meal (Hassan *et al*., 2024). However, some of these ingredients do not provide the necessary balance of amino acids, and also contain some anti-nutrients, which can reduce abalone growth (Coote *et al*., 2000). Alternatively, given that they are herbivorous, abalone can utilise carbohydrates that are contained within macroalgae as an energy source (in place of protein) because abalone possesses high carbohydrase activity in their gastrointestinal system (Bansemer *et al*., 2016c; Lucas *et al*., 2019; O'Mahoney *et al*., 2014). The provision of highly digestible carbohydrates could satisfy the energy requirements of abalone (Dunstan, 2010).

The use of macroalgae and their benefits as abalone feed

Macroalgae, in particular, seaweeds provide several compounds including minerals, vitamins, proteins (Biris-Dorhoi *et al*., 2020), polyunsaturated fatty acids (PUFA) (Al-Adilah *et al*., 2021), sterols (Hannan *et al*., 2020), pigments (chlorophylls, carotenoids, phycobiliproteins) (Lomartire & Gonçalves, 2022), and polysaccharides which are the most abundant compounds derived from macroalgae (Stiger-Pouvreau *et al*., 2016). Carbohydrate-rich macroalgae containing both reserve and structural carbohydrates (polysaccharides) are different for each algae group (Table 2). Limited studies have investigated the differences between the digestibility of the reserve carbohydrate (i.e. starch in terrestrial plants) and structural carbohydrate (i.e. cellulose in terrestrial plants) in macroalgae. The nutritional characteristics of macroalgae are very species-specific and can vary with location, seasonality and cultivation condition (Forbord *et al*., 2020; Gaillard *et al*., 2018; Kumar *et al*., 2018; Marinho *et al*., 2015; Nunes *et al*., 2017; Zhou *et al*., 2015).

Macroalgae is also a source of valuable bioactive compounds such as phlorotannins, bromophenols, flavonoids, and phenolic acids (Cotas *et al*., 2020, Saeed *et al*., 2020). The potential of macroalgae's bioactive compounds in pharmaceutical applications has been widely explored to enhance human health as prebiotics and have antibacterial, antiviral, anti-inflammatory and antioxidant activity (Table 3). Antioxidants in macroalgae prevent or repair oxidative stress-related damage and have a significant potential for treating a variety of diseases (Liu & Sun, 2020). As a prebiotic, polysaccharides in seaweed can stimulate the secretion of endogenous digestive enzymes (amylase, protease, and lipase) and exogenous enzymes from the microbiota that live in the digestive tract (Bullon *et al*., 2023). The potency and utility of various seaweed-based abalone feeds have been broadly investigated.

Several studies have been conducted to compare the effect of macroalgal diets as compared to formulated commercial diets on abalone growth and survival (Table 4). The growth rate of abalone fed a mixture of macroalgal species can be seen to be higher than abalone fed a single macroalgal species because it provides a more balanced essential amino acid profile (Capinpin *et al*., 2015; O'Mahoney *et al*., 2014). In comparison to the formulated diets, juvenile tropical abalone (*H. asinina*) fed formulated diets demonstrated higher growth rates compared to those fed macroalgae diets at the beginning of the culture. However, the reverse condition occurred after those abalone accustomed to macroalgal diets (Capinpin & Corre, 1996). This could have been because commercially formulated diets were carefully formulated and contained highly palatable and digestible ingredients to optimize the nutritional and energy requirements for the growth of juvenile abalone.

The growth rates of hybrid abalone and red abalone fed macroalgae diets are typically higher than abalone fed formulated feeds might be because the abalone used in Mulvaney *et al*. (2013) study had not been weaned to formulated diets before the commencement of the study (Bansemer *et al*., 2016b). This is suggested by the extreme poor growth rates of hybrid abalone fed formulated diets (0.39% per day) (Mulvaney *et al*., 2013). In addition, there were no significant differences in the growth rate between Japanese abalone fed formulated and macroalgae meal diets suggesting the potential of marine macroalgae meal as a fish meal replacement in formulated diets for abalone (O'Mahoney *et al*., 2014). There are also several other potential benefits provided by feeding macroalgae to abalone. Macroalgae can act as an effective feeding stimulant (Bansemer *et al*., 2016c).

Table 2. Reserve and structural carbohydrates contained within each macroalgae group.

Macroalgae group	Reserve carbohydrates	Structural carbohydrates	Source
Green macroalgae (Chlorophyta)	Amylose, Amylopectin, Xyloglucan and Glucuronan	Cellulose, Xylans, Mannans and Ulvan	Stiger-Pouvreau *et al*. (2016)
Red macroalgae (Rhodophyta)	Floridean starch, Floridoside (soluble organic compounds)	Cellulose, Xylans, Mannans, Agar and Carrageenan	Stiger-Pouvreau *et al*. (2016)
Brown macroalgae (Phaeophyta)	Laminaran and Manitol	Cellulose, Alginic acid, Alginate and Fucoidan	Stiger-Pouvreau *et al*. (2016)

Table 3. The biological properties of macroalgae's bioactive compounds.

Seaweed	Bioactive compound	Properties	Reference
Rhodophyceae			
Gracilaria verrucosa	Alkaloid, Flavonoid, Tannin, Phenols	-Moderate antibacterial activity against *Aeromonas hydrophila, Pseudomonas aeruginosa, Pseudomonas putida* -Weak antibacterial activity against *Vibrio harveyi* and *Vibrio algynoliticus* bacteria	Maftuch *et al*. (2016)
Gracilaria verrucosa (fermented)	Phenols, terpenoids	Antibacterial activity against *Micrococcus luteus* and *Pseudomonas aeruginosa*	Fatmawati *et al.* (2022)
Porphyra sp.	Porphyran	Anti-inflammatory, antioxidant, anticancer activities	Isaka *et al*. (2015) Wang *et al*. (2017) Liu *et al*. (2019)
Phaeophyceae			
Laminaria japonica	Laminarin	Immunostimulatory	Kadam *et al*. (2015)
	Fucoxanthins	Antitumor activity on lung cancer cells	Mei *et al*. (2017)
	Fucoidans	Antimicrobial activity against *Escherichia coli* and *Staphylococcus aureus*	Liu *et al*. (2017)
Sargassum prismaticum	Fucoxanthins	Antioxidant activity and hepatoprotective ability	Atya *et al*. (2021)
Padina australis	Phenols	Antimicrobial activity against *Bacillus cereus*, *Escherichia coli*, *Pseudomonas aeruginosai*, *Staphylococcus aureus*	Chellappan *et al*. (2020)
Chlorophyceae			
Ulva lactuca	Phenols	Antiproliferative activity on MCF-7, HeLa cells, antimicrobial activity, and antifungal activity	Saeed *et al*. (2020)
	Sulphate Polysaccharides	Anticoagulant activity	Reis *et al*. (2020)
Caulerpa racemosa	Caulerpin	Anti-inflammatory activity	Lucena *et al*. (2018)

Table 4. Growth and health conditions of abalone resulting from trials comparing macroalgae and formulated commercial diets.

Species	Feed	Growth & Health condition	Source
Hybrid abalone cross (H. *rubra* and H. *laevigata*)	Formulated feed (A), formulated feed (B), *Grateloupia turuturu*, *Ulva australis* and/or *Ulva laetevirens*	• Juvenile abalone fed macroalgae diets resulted in a higher specific growth rate (SGR) than those fed two formulated feeds. • The health and condition of abalone fed macroalgae increased.	Mulvaney *et al*. (2013)
Greenlip abalone (H. *laevigata*)	Formulated feed, *Ulva lactuca*, *Spyridia filamentosa*, cyanobacteria *Arthrospira maxima*, microalgae *Dunaliella salina*.	• Pellets supplemented with *A. maxima* or *D. salina* resulted in increased abalone shell length and body weight. • Higher antiviral activity was detected in abalone fed *U. lactuca* or *S. filamentosa* compared to abalone fed pellets or pellets supplemented with *A. maxima* or *D. salina*.	Dang *et al*. (2011a)
Greenlip abalone (H. *laevigata*)	Formulated feed, grape seed extract (GSE), dried macroalgae (U. *lactuca*)	• The survival rate of abalone fed formulated feed was significantly lower than abalone fed both GSE and dried macroalgae additive diet. • No significant differences in survival rate between abalone fed fresh U. *lactuca* and abalone fed 30% of dried *U. lactuca* in commercial diet.	Lange *et al*. (2014)
Red abalone (H. *rufescens*)	Formulated diet, *Macrocystis pyrifera, Porphyra columbina* and formulated diet + *P. columbina*	• Abalone grew best when fed *P. columbina*. • No significant differences in survival rate (SR) between treatments (87%).	Hernandez *et al*. (2009)
Japanese abalone (H. *discus hannai*)	Formulated feed, a mixed-species marine algae meal (*Laminaria digitata* meal, *Palmaria palmata* meal and U. *lactuca* meal)	• No significant differences in body weight to shell length ratios and survival rate.	O'Mahoney *et al*. (2014)
Tropical abalone (H. *asinina*)	Formulated feed, Gracilariopsis heteroclada, Kappaphycus alvarezii	• Juveniles fed the artificial diet had a faster growth rate for body weight (the first 90 days) and shell length (the first 75 days) than those fed *G. heteroclada*, but abalone fed *G. heteroclada* grew faster in terms of weight (from day 105 onwards) and shell length (from day 90 onwards). • No significant differences in survival rate (SR) between treatments (93 -100%).	Capinpin and Corre (1996)
Tropical abalone (H. *asinina*)	*Hydropuntia edulis* (*Gracilaria edulis*) and a diet of mixed algae (*H. edulis, Eucheuma arnoldii*, and *Halymenia durvillaei*)	• Mixed species of red algae produced better growth in shell length and weight. • No significant differences in survival rate (SR) between treatments (100%). • No formulated diets were tested.	Capinpin *et al*. (2015)
Tropical abalone (*Haliotis squamata*)	Fresh *Gracilaria* sp., formulated diets mixed with *Ulva* sp. meal, *Gracilaria* sp meal, and *Sargassum* sp. meal	• Abalone fed fresh *Gracilaria* sp. performed the best growth rate compared to abalone fed formulated feeds. • Abalone fed formulated feed I (mixture of Gracilaria sp. meal, *Ulva* sp. meal, and fish meal) or formulated feeds II (mixture of *Gracilaria* sp. meal, *Sargassum* sp. meal and fish meal) had better growth compared to abalone fed other formulated feed combinations.	Giri *et al.* (2015)
Tropical abalone (*Haliotis squamata*)	Fresh *Gracilaria* sp., formulated diets (a mixture with different composition of *Ulva* sp. meal, *Gracilaria* sp meal, and *Sargassum* sp. meal)	• No significant differences in growth rate between treatments. • Abalone fed formulated diets had higher protein content compared to abalone fed fresh *Gracilaria* sp.	Giri *et al.* (2016)
Tropical abalone (*Haliotis squamata*)	*Gracilaria* sp., *Spinosum* sp., *Ulva* sp.	• No significant differences in growth rate between treatments.	Prihadi *et al.* (2018)
Tropical abalone (*Haliotis squamata*)	Formulated diets (a mixture of fish meal with different composition of *Gracilaria verrucosa*)	• No significant differences in growth rate between treatments.	Hadijah *et al.* (2020)

Haliotis iris displayed a feeding response when exposed to *Gracilaria* spp. compared to the commercially formulated diets by extending their cephalic tentacles and forepart of their foot and relying on chemosensory cues to detect macroalgae fragments (Allen *et al*., 2006). Feeding preferences for macroalgal species differs between abalone species. Tropical abalone, *H. asinina*, preferred red macroalgae (Capinpin *et al*. 2015) for example *Gelidium japonica* (Yu *et al*., 2014). Another tropical abalone *H. squamata*, mostly consumed red macroalgae which were *Gracilaria* sp., *Eucheuma spinosum*, *Ulva lactuca* (Yusup *et al*., 2020). Meanwhile, *H. iris, H. discus hannai* and *H. rufescens* preferred brown macroalgae species (Cornwall *et al*., 2009; Pan *et al*., 2018; Wulffson, 2020).

The product quality and marketability of abalone are determined by their texture, taste and colour. The major factors characterizing the abalone flavour were the concentration of certain amino acids like glycine and glutamate and the nucleotide adenosine-5'-monophosphate (AMP) (Brown *et al*., 2008). Meanwhile, they stated that the flesh texture of the abalone was determined by the distribution of the protein within the abalone foot. The type and concentration of long-chain polyunsaturated fatty acids also influenced the taste of abalone (Britz & Hecht, 1997; Dunstan *et al*., 1996). Feeding macroalgae can improve the flesh quality of abalone products (Bansemer *et al*., 2016c). A significant effect on the taste of abalone products occurred when abalone *Haliotis diversicolor* fed *Gracilaria* sp. (Brown *et al*., 2008). According to Hoang *et al*. (2016), fresh macroalgae and dried algae supplementation in abalone feed can change the colour of abalone H. *laevigata* foot and shell.

The shell of this abalone fed the commercial diet and fresh *Ulva* sp. was green, but abalone fed fresh *Gracilaria cliftonii* developed a brown shell. The fresh *G. cliftonii* increased shell colour purity, while fresh *Ulva* sp. increased shell brightness. Feeding abalone with either fresh *Ulva* or fresh *G. cliftonii* produced a yellowish foot. Most temperate abalone have a slow growth rate, and it takes approximately three years or more to reach a marketable size. Due to their long culture period, abalone is susceptible to health issues and immunosuppression on-farm including virus infections, high water temperatures and exposure to anaesthetics and physical damage during handling causing stress (Cardinaud *et al.*, 2015; Dang *et al*., 2011b; Vandepeer, 2006).

Therefore, their nutrition not only needs to provide sustainable growth but also maintain the optimal health of the animal. Feeding macroalgae or extracted compounds from macroalgae to abalone may provide health benefits to abalone and reduce abalone mortality by enhancing dietary antimicrobial, antiviral, anti-inflammatory and antioxidant activity (Bansemer *et al*., 2016c). Polysaccharides in seaweed (galactans, fucoidan, laminarin and alginates) are considered a potential prebiotic which stimulates the growth of gut bacteria in human (Lopez-Santamarina *et al*., 2020). Many studies have reported that polysaccharides can also act as an immunostimulant for aquatic animals (Akbary & Aminikhoei, 2018; Siddik *et al.*, 2023). Previous studies have particularly evaluated the gastropod immune activity suggesting that abalone health and condition increased, and higher antiviral activity was detected in abalone fed macroalgae including *U. lactuca* (64.2%) or *S. filamentosa* (69.51%), compared to abalone fed formulated pellets (47.42%) or pellets supplemented with *A. maxima* (46.3%) or *D. salina* (46%) (Dang *et al*., 2011a; Mulvaney *et al*., 2013).

Summer mortality on abalone industries and the main aetiology

Summer mortality is a phenomenon that leads to sudden mass mortality of molluscs during the summer period. Molluscs that can be affected include oysters (Yang *et al.*, 2021; Cowan *et al*., 2024), clams (Liu *et al*., 2023) and abalone (Bansemer *et al*., 2023; Roberts *et al*., 2019; Vandepeer, 2006). Massive mortality (up to 50%) occurred on abalone farms in southern Australia when water temperatures exceed 22ºC (Stone *et al*., 2014b). Tropical abalone (H. *asinina*) was also significantly affected by elevated temperature. According to the study conducted by Pedroso (2017), the survival rate of larvae tropical abalone reared in high temperatures (31ºC and 33ºC) was significantly lower compared to the larvae reared in ambient temperature (29ºC).

In addition, not only the early developmental stages of tropical abalone, but the survival rate of abalone breeders exposed to high temperature was also lower than those exposed to ambient temperature, and prolonged exposure to elevated temperature resulted in gonadal atrophy of adult abalone. The exact cause of this phenomenon is still unclear. A sudden increase in water temperatures which reduces the dissolved oxygen in the water is a necessary precursor. The metabolic rate and respiration levels increase as the water temperature increases.

This condition leads to oxidative stress by disrupting the oxidant-antioxidant equilibrium (Tan *et al.*, 2019). However, high temperature is insufficient to explain this severe condition. Several intrinsic and extrinsic factors are considered to be factors that can contribute to summer mortality. Based on the study conducted by Shiel *et al*. (2018), the intrinsic factors that contribute to summer mortality are the genetics, age of the animal and their reproductive stage (spawning and gametogenesis). Meanwhile, the availability and quality of feed, water quality (increased temperature, decreased dissolved oxygen, and increased salinity) and the introduction of the pathogen in the culture system are considered to be the contributing extrinsic factors.

A sudden increase in water temperatures has been suggested to be the key cause of summer mortality in molluscs. However, mass mortality in molluscs may not be directly related to high temperatures, but indirectly, through exogenous and host-related factors (pathogens). As stated in Stone *et al*. (2014b), summer mortality occurred as an interaction between abiotic and biotic environmental factors at elevated water temperatures (>22 °C), affected health, growth and contributed up to 50% mortality of larger cultured abalone (≥60 mm) in Southern Australia. Disease from bacterial infections like *Vibrio harveyi* or viruses such as herpes virus has a strong association with summer mortality in molluscs (Mortensen *et al*., 2016) including abalone populations (Cardinaud *et al.*, 2015; Cardinaud *et al.*, 2014; Stone *et al.*, 2014b).

Genetic variability has been thought to be a significant factor in the sensitivity to summer mortality (Shiel *et al*., 2018). About 45% of the variance between susceptible (S) and resilient (R) strains occurred between families with high heritability oysters (*Crassostrea gigas*) (Dégremont *et al*., 2015). Summer mortality susceptibility has also been associated with the stress of reproduction during sexual maturation, spawning and post-spawning events. During sexual maturation and spawning, abalone experience a loss of energy reserves due to the allocation of energy for gonad development and gamete production, and can contribute to the increasing pathogen susceptibility (Morash & Alter, 2015). Moreover, during summer conditions, high temperatures inducing spontaneous spawning in abalone interferes with their immune system and leads to mass mortality (Shiel *et al*., 2017). Correlations have also been found between disease susceptibility and the maturation and spawning processes of *H. tuberculata*, with increased bacterial infection demonstrated after spawning (Travers *et al*., 2008).

The preventative strategies for summer mortality

A variety of management practices have been developed to prevent summer mortality in molluscs. In China, harvesting abalone at a smaller size (20-24 individuals/kg) than in northern regions (10-14 individuals/kg) was conducted to reduce the mortality rate (Wu & Zhang, 2016). However, this method is not economically viable (Vandepeer, 2006; Wu & Zhang, 2016). In France, the most cost-effective prevention strategies of summer mortality in the oyster were conducted by determining the best site (location with temperature less than 19ºC) and/or time to introduce or stock spat to grow-out farm conditions and selecting resistant oysters after exposing large quantities of spat to the herpes virus (Azéma *et al*., 2017). In Canada, at certain farms, the useful technique for giving Pacific oysters resistance to summer mortality was by partially culturing them in the intertidal zone (Mackenzie *et al*., 2024). Meanwhile, in Australia, another strategy involved temporarily rearing oyster stock in colder conditions (<18ºC) as this may deactivate or slow down the virus (IMAS, 2020). Genetic improvement has been demonstrated to prevent mortalities in abalone and oyster culture.

These strategies are including broodstock conditioning and cryopreservation of sperm, enhancing genetic variation, use of genetic markers to assist in broodstock selection, hybridisation, single-sex production, triploids, gene manipulation and selection (Dégremont *et al*., 2015; Elliott, 2023; Shiel *et al*., 2020). Elliott (2023) mentioned that extension of the spawning period (out of season or earlier in the season) could be employed to take advantage of particular grow-out conditions. This can be conducted by controlling the broodstock conditioning or maturation and/or the use of cryopreserved sperm or ova. Crossbreeding is another alternative that has been widely used for genetic improvement in molluscs, including abalone. The survival of interspecific abalone hybrids between *Haliotis fulgens* and H. *discus* resulted in hybrid vigour for growth and survival, as well as a higher temperature tolerance which can provide resistance against summer mortality in abalone culture (You *et al*., 2015).

The production of triploid oysters can increase their commercial value because they could reach their market size earlier and their larger cell size possibly resulted in higher phagocytic capabilities which used to assess their immune status (Brianik and Allam 2023). Another strategy that has been conducted to improve the survival trait is a selective breeding program for several abalone species, including H. *discus hannai*, *Haliotis rufescens*, and *Haliotis diversicolor* (Brokordt *et al.*, 2015; Li *et al*., 2018; Liu *et al*., 2015; Yu *et al.*, 2021). Numerous studies have focused on enhancing the health and immune system by providing a high quality of feeds to alleviate the effects of excessive heat stress. The supplementation of antioxidants (vitamins, carotenoids and phenols) could improve the antioxidant capacity of abalone exposed to heat stress (Dai & Cho, 2022; Duong *et al.*, 2016; Zou *et al*., 2023). The survival rate of abalone fed dietary supplements of 0.5-2.5% green tea extract or 5% grape seed extract increased compared to abalone fed commercial diets or diets supplemented with 0.5-5% peanut extract or 1 % vitamin C (Duong *et al*., 2016).

The study focusing on the utilisation of macroalgae to improve the immune system of abalone is still limited. The improvement of health and condition of abalone was achieved by feeding macroalgae dietary treatments (*Grateloupia turuturu*, U. *australis* and/or *Ulva laetevirens*) compared to formulated diets (Mulvaney *et al*., 2013). The supplementation of U. *lactuca* and S. *filamentosa* in an abalone diet could be useful for abalone aquaculture in areas with a high risk of herpes virus infection (Dang *et al*., 2011a). The survival of larger cultured greenlip abalone (≥ 60 mm) fed live macroalgae (U. *lactuca*) was exceed 97% at high water temperature (26ºC), whereas, the survival rate of greenlip abalone fed commercial diet was significantly reduced by 50% (Stone *et al*., 2014b). Interestingly, another study suggested that there was no significant difference between the survival of abalone fed live U. *lactuca* and abalone fed 30% of dried U. *lactuca* in the commercial diet at 26ºC water temperature (Lange *et al*., 2014). These results indicated that there is a potential dietary intervention using both live and dried macroalgae to improve the growth and immunity of abalone.

CONCLUSION

This review highlighted the nutritional requirements of abalone and the potential benefits of feeding fresh and dried macroalgae supplementation in formulated diets for abalone. The variability in the nutrient content, the inconsistency of supply and the biosecurity issues in culture systems currently limit the use of fresh macroalgae in abalone culture. The inclusion of dried macroalgae meal in abalone formulated feeds can improve abalone growth, act as a feeding stimulant, improve product quality and have the potential to enhance abalone health conditions. Summer mortality is sudden mass mortality that can affect molluscs including oysters, scallops, clams and abalone during the summer period. The intrinsic factors that contributed to summer mortality are the genetics, age of the animal and reproduction.

The extrinsic factors are the availability and quality of feed, water quality (increased temperature, decreased dissolved oxygen, and increased salinity), and also the introduction of pathogens in the culture system. Dietary intervention by using macroalgae could alleviate mass mortality of abalone at elevated water temperatures. Various macroalgae species may provide bioactive compounds which have an important role as antibacterial, antiviral, anti-inflammatory, antioxidant to reduce the susceptibility of abalone to summer mortality. Macroalgae species and the ideal percentage of dried macroalgae inclusion in abalone formulated diets is species-dependent. Manufacturing processes play an important role in supplying high-quality macroalgae as a dietary ingredient for abalone feed.

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