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REVIEW ARTICLE

The role of aquafeeds in abalone nutrition and health: A comprehensive review

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Abstract

Overpopulation and the pressure on land-based resources have driven the aquaculture sector to increase its production since the 1980s. To address such demands, new aquafeed technologies have been developed relying on natural and artificial ingredients that are commercially viable. In addition, current global sustainable initiatives require feed technologies to reduce the pressure on limited wild fisheries and minimize negative environmental effects. Although there are numerous studies on abalone nutrition, most tend to focus on animal growth and nutrient utilization. A more holistic research approach to ensure a sustainable future for this industry will require the development of feeds that provide integrated nutrition and health benefits. In this review, we aim to synthesize the most recent scientific literature on the nutritional and health benefits and shortcomings of two main abalone feeding approaches (seaweed and formulated feeds) within aquaculture production practices. We also identify major research gaps and future directions for the development of sustainable abalone feeds.

KEYWORDS

abalone, aquafeeds, formulated feed, health, nutrition, seaweeds

1 | INTRODUCTION

Aquaculture is the fastest-growing food production sector in the world, currently providing around 47% of the global seafood demands and is well-positioned to supply the protein requirements of our increasing population (FAO, 2018). The exponential growth of the global aquaculture industry has fostered the development of commercial diets which are cost-effective and optimized for each species. In aquaculture, feed accounts for over 50% of the production costs (Huntington & Hasan, 2009). Fishmeal accounts for almost 73% of aquaculture feeds (Asche & Oglend, 2016; Ringø, Olsen, Vecino, Wadsworth, & Song, 2012). However, recent declines in the availability and lack of sustainability of fishmeal have prompted the search for alternative protein sources.

Abalones are a widespread group of herbivorous gastropods, from the genus *Haliotis*, inhabiting both tropical and temperate waters around the world. Approximately 90 species of abalone are found worldwide, and about 15 species are cultured in Australia, China, Japan, Korea, New Zealand, Philippines, South Africa, and Taiwan (Sales & Janssens, 2004). Although abalone production is relatively small compared to other seafood products, it is one of the most highly prized delicacies globally, especially in Asia (Cook, 2014).

Animal nutritional requirements are based on three main components: endogenous factors (e.g., animal genetics, age, sex, metabolism, physiology), environmental conditions (e.g., water temperature, oxygen, salinity) and feed properties (e.g., composition, delivery system, digestibility, solubility). Aquafeeds are composed of macronutrients, such as proteins, carbohydrates, lipids, and micronutrients including vitamins and minerals. In abalone feed formulations, protein is the most expensive component and represents 20–40% of the total ingredients. The amount of protein is crucial in abalone feeds since it is the main macronutrient used to build tissues in the animal (Fleming, Van-Barneveld, & Hone, 1996). Carbohydrates make up 50–60% of the nutritional requirements of abalone, and they are the most preferred source of energy (Lee et al., 2017). Lipids, on the other hand, represent 1–5% of the nutritional requirements, and although this percentage is relatively low compared to proteins and carbohydrates, their consumption is essential for the acquisition of polyunsaturated fatty acids (PUFAs) (Mulvaney, Jahangard, Ingram, Turchini, & Winberg, 2015), which cannot be synthesized de novo by the animal (Bautista-Teruel, Koshio, & Ishikawa, 2011). In addition, lipids supply the phospholipids needed to build cell bio-membranes (Bautista-Teruel et al., 2011).

Optimizing nutrition involves a comprehensive analysis of not just metabolic provisioning, but also the interplay between physiological traits (e.g., ingestion, digestion) (Guillaume, Kaushik, Bergot, & Metailler, 2001), biological characteristics (e.g., sex, age, species, genetics, reproduction, health) and environmental conditions (e.g., temperature, water, salinity, oxygen, pH, water quality, tank density). For instance, if the objective is growth-related, nutritional requirements should aim to provide fuel for metabolic expenses and tissue formation. On the other hand, if the priority is to enhance health during critical production periods, the feed must primarily strengthen the immune defenses to overcome season-related stressors, such as elevated temperatures and high pathogens loads, which predominate in the summer months.

Previous studies on optimization of feed formulations have focused on both, generating nutritionally balanced diets, and reducing feed costs. To this end, strategies have aimed to replace the protein component with more cost-effective ingredients (e.g., seaweed extracts, plant protein) while still achieving good growth performance (Sales, Truter, & Britz, 2003). Other approaches have focused on the addition of specific amino acids, immunostimulants, vitamins, and probiotics to the feed mixture. The success of these strategies ultimately requires careful evaluation of potential benefits in feed intake, assimilation, digestion, and metabolic efficiency (Kemp, Britz, & Aguero, 2015; Yu et al., 2014), health (Tanaka, Sugimura, Sawabe, Yoshimizu, & Ezura, 2003), and flesh composition (Bewick, Wells, & Wong, 1997).

The development of optimal abalone diets has taken two main approaches: natural (macroalgae) and formulated feeds. To date, previous studies have evaluated how these types of diets affect abalone growth (Bansemer et al., 2015; Mulvaney, Winberg, & Adams, 2013) health (Grandiosa et al., 2018; Tanaka et al., 2003) and nutritional quality (Bewick et al., 1997; Preece, 2006) among others. However, the effectiveness of these approaches has been hampered by the few studies considering a holistic analysis or integrated approach to evaluate the benefits and disadvantages of each type of diet. Such a comprehensive analysis requires a clear review of the current knowledge and identification of knowledge gaps to guide future research. To this end, the present review outlines our current knowledge on (a) abalone feed requirements, including the effect of endogenous and exogenous factors, and (b) the advantages and disadvantages of the application of seaweeds and formulated feeds in abalone aquaculture. Finally, a set of recommendations are provided to guide future research in abalone feed development aiming to enhance this important global production.

2 | ABALONE NUTRITION

Abalone naturally grazes on a range of algal species in intertidal to subtidal high-energy coastal habitats. During the early life stages (juveniles), abalone feed on microalgae usually contained within diverse biofilms on surfaces of rocks and boulders. At some stage in their development, abalone shifts to macroalgae, which provide appropriate nutrition to develop somatic and reproductive tissues (Johnston, Moltschaniwskyj, & Wells, 2005; Shepherd, Tegner, & Guzman del Proo, 1992). In the wild, abalone may encounter a range of algal species with varying nutritional compositions, which ultimately affect their growth, reproductive state, and survival. The relationship between animal and food types, as well as the environmental conditions that affect optimal nutrition, can be mimicked in controlled aquaculture settings to improve production.

2.1 | Feeding across life stages

Abalone has four major developmental stages which include larvae, post-larvae, juveniles, and adults (Hahn, 1989). After 19 hr in the water column, fertilized eggs hatch as trochophore larvae, which subsequently develop into competent veliger larvae after 46–74 hr post-fertilization, depending on the species (Balkhair, Al-Mushikhi, & Rivera, 2016; Huang et al., 2012). The lecithotrophic planktonic larvae swim for 40–118 hr (Balkhair et al., 2016; Genade, Hirst, & Smit, 1988) until they sense biological and chemical cues from suitable habitats to safely settle (Manahan, 1992; Takami, 2003). These biological cues include biofilms (Li et al., 2006), conspecific mucus trails (Gallardo & Buen, 2003) and diatoms (Kawamura, Saido, Takami, & Yamashita, 1995), while chemical inductive signals include gamma-aminobutyric acid (GABA). Indeed, GABA is an exudate component of crustose coralline algae, which is thought to play a major role in inducing settlement and metamorphosis on abalone (Shepherd et al., 1992).

After settlement, benthic post-larvae use a primitive radula with chitinised teeth (Takami & Kawamura, 2003) to feed on crustose coralline algae, benthic diatoms and the proteins and polysaccharides present in the mucus trails left by adult abalone (Takami & Kawamura, 2003). Diatoms are considered to be one of the most important sources of nutrition for post-larvae (Balkhair et al., 2016; Kawamura et al., 1995) with high levels of protein (Courtois de Viçose, Viera, Huchette, & Izquierdo, 2012) and lipids (Dunstan, Baillie, Barrett, & Volkman, 1996).

The juvenile stage starts approximately 8 weeks after settlement (Hahn, 1989). Juveniles shift from microalgae to macroalgae once the digestive system has developed a more matured digestive gland to secrete enzymes to process seaweeds (Garcia-Esquivel & Felbeck, 2006; Onitsuka, Kawamura, Ohashi, Horii, & Watanabe, 2007; Viana et al., 2007). Juvenile and adult abalone consume macroalgae as the main source of nutrition due to their high carbohydrate content, which is their main source of energy to grow (Bautista-Teruel et al., 2011).

Once abalone start to consume seaweeds, their feeding pattern becomes nocturnal, which reduces predation pressure (Shepherd & Turner, 1985) and avoids competition with other grazing animals. Abalone grazes continuously throughout the night until early morning showing high activity after sunset to a few hours after midnight (Tahil & Juinio-Menez, 1999). Their feeding behavior is opportunistic when they encounter drift seaweeds (Cornwall, Phillips, & McNaught, 2009; Tahil & Juinio-Menez, 1999; Zeeman, Branch, Peschak, & Pillay, 2012), foraging when hydrodynamic forces are favorable (Tahil & Juinio-Menez, 1999).

Adult abalone consume seaweeds at a rate close to 20–35% (wet algal weight) of their body weight per day (Tahil & Juinio-Menez, 1999) and their selection is based on three main aspects: environmental conditions (e.g., water temperature, water movement, habitat characteristics), animal characteristics (e.g., size, species, maturity) and seaweed properties, such as phenolic composition (Shepherd, 1992), drifting or attachment (Cornwall et al., 2009) and digestibility (Tahil & Juinio-Menez, 1999). For instance, colder water temperatures promote a more varied consumption of algal species in *Haliotis midae*, compared to warm waters (Barkai & Griffiths, 1986). Another example is water movement and its influence on feed intake. Water movement enhances the quantity of drifting seaweeds (Zeeman et al., 2012), and abalone species such as *Haliotis corrugata*, *H. midae* and *Haliotis fulgens* may consume certain types of seaweeds in the proportions in which these algae drift nearby (Tutschulte & Connell, 1988; Wood & Buxton, 1996), while still actively selecting from what is abundant in the surrounding habitat (Alcantara & Noro, 2005; Barkai & Griffiths, 1986). Previous studies have shown that abalone may select seaweeds based on their compositional properties that are influenced by the region where seaweeds are located. For example, the Japanese abalone *Haliotis diversicolor* and the New Zealand abalone *Haliotis iris* are more likely to consume brown seaweeds (e.g., *Ecklonia maxima*, *Ecklonia radiata*, and *Macrocystis pyrifera*) due to their better digestibility and less toughness compared to red seaweeds (Alcantara & Noro, 2005; Cornwall et al., 2009), while *Haliotis asinine* from Thailand and Philiphines prefer red seaweeds, including *Laurencia*, *Hypnea*, *Gracilaria* and *Amphiroa* (Tahil & Juinio-Menez, 1999) due to their higher digestibility (Shepherd, 1992) and lack of polyphenols compared to brown seaweeds (Fleming, 1995). In addition, the selection of seaweeds for nutritional purposes may be selected according to the needs during different developmental stages (Burtin, 2003). For example, smaller *H. midae* (<65 mm) prefer green seaweeds, while bigger *H. midae* (65–145 mm) prefer brown seaweeds (Barkai & Griffiths, 1986). *Haliotis tuberculata* with mature gonads preferentially consume seaweeds with high omega-3 fatty acids (FAs), more soluble carbohydrates, and total protein compared to immature animals (Roussel et al., 2019), and *H. diversicolor* scarcely consume green seaweeds species since they mostly have defensive compounds that deter consumption (Alcantara & Noro, 2005).

2.2 | Abalone digestive system

The digestive system in abalone is similar in all species (McLean, 1965) and consists of a mouth, which collects the food and passes it to the buccal cavity. After mixing the food with saliva and mucus, the bolus enters the esophagus that extends posterior to a large crop organ, where it is mixed with enzymes and digestive fluids and stored before entering the stomach. The digestive gland or hepatopancreas, which overlies the crop and stomach, moves the food by muscular contractions and ciliary currents. Later, undigested food is transported from the hepatopancreas to the stomach and intestine, where the rejected material is eliminated through the anus (Hughes, 1986; McLean, 1970; Venter, Loots, Vosloo, van Rensburg, & Lindeque, 2018).

Ingestion is determined by the development of the radula and its mechanical ability to graze on microalgae or macroalgae. Developmental changes in the radula occur mainly during the larval and juvenile stages. In this period, the number of teeth on the radula increases along with a change in their morphology (from pointed serrations to less pronounced serrations), indicating the shift in food from biofilms to seaweeds. Lateral teeth are more pointed and longer, which allows them to cut macroalgae when the animal is approximately 2-mm in shell length. In addition, the clearance angle, which is a measure of the function of the radular teeth, evolves from a scoop shape to a cut shape, again reducing the ability to consume small particles and increasing the ability to consume macroalgae (Takami & Kawamura, 2003).

Digestion refers to the mechanical and chemical processes that occur in the digestive system, including numerous reactions triggered by proteases, carbohydrases, and lipases (Erasmus, Cook, & Coyne, 1997). The two main digestion regions in abalone are (a) the mouth-intestine region where lipase and aminopeptidase activity are high (Picos-García, García-Carreño, & Serviere-Zaragoza, 2000) and (b) the stomach-digestive gland region where the majority of enzymatic activity occurs (Garcia-Esquivel & Felbeck, 2006) and is characterized by enzyme activity that degrades carbohydrates such as cellulase and lysozyme. Gut polysaccharide-degrading enzymes produced in the abalone digestive system include agarase, carrageenase, alginate lyase, carboxymethylcellulase and laminarinase (Erasmus et al., 1997; Tanaka et al., 2003).

Gut microbiota consists of indigenous and non-indigenous bacteria, and their profile changes according to the life stage (Tanaka et al., 2003), environmental conditions (Gobet et al., 2018) and food consumed (Antonopoulou et al., 2019; Stenberg et al., 2019). At 4 months of age—when artificial diets are usually started in an aquaculture farm—the gut microbiome is mainly composed of algal polysaccharide-degrading bacteria with mostly facultative anaerobes and non-motile fermenters, such as *Vibrio halioticoli* (Tanaka et al., 2003). Although seasons and dietary intake affect the gut microbiome, abalone possesses a core group of bacteria that remains stable (Gobet et al., 2018). For example, the core bacterial community in the digestive gland of *H. tuberculata* fed on macroalgae was found to be dominated by the Phyla Fusobacteria (e.g., *Psychrilyobacter*), Tenericutes (e.g., *Mycoplasma*) and Gammaproteobacteria (e.g., *Vibrio*), which were different from the core bacteria found in the gut of 1-year abalone, which included the Phyla Alphaproteobacteria, Firmicutes, Mollicutes, and Bacillales (Tanaka, Ootsubo, Sawabe, Ezura, & Tajima, 2004).

2.3 | Abalone metabolism

Metabolism is defined as the chemical reactions involved in the synthesis of biological macromolecules and the generation of energy for vital functions through the processes of catabolism, anabolism and amphibolism. Catabolism involves the oxidation of molecules to generate adenosine triphosphate (ATP), the main substrate of energy. Anabolism corresponds to the synthesis from precursors where ATP is used for endergonic reactions and amphibolism, which includes catabolic or anabolic processes (Garrett & Grisham, 2010).

In abalone, the energy sources (carbohydrates, proteins, and lipids) tend to be attributed to specific activities. Indeed, carbohydrates are mainly used for locomotion and respiration (Fleming et al., 1996), while proteins are prioritized for tissue building and maintenance, and lipids are utilized for cell membrane formation and gonad maturation (Dunstan et al., 1996; Uki, Sugiura, & Watanabe, 1986). When carbohydrate intake is restricted or abalone is under stress, they use protein as an alternative energy source (Lee et al., 2019). Carbohydrates are broken down into acetyl CoA or Coenzyme A, which are subsequently used as a substrate for the tricarboxylic acid cycle or opine, lactate and oxaloacetate derivatives. Coenzyme A is the base for the generation of ATP, NH_3, H_2O and CO_2 via the mitochondrial oxidative phosphorylation system (van Rensburg & Coyne, 2009). Proteins are broken down into amino acids, which then undergo a series of transformations to produce citric acid intermediates. Furthermore, triacylglycerols are broken down into FAs, which are oxidized in the mitochondria into Acetyl Co-A.

Abalones are facultative anaerobes and can make use of anaerobic metabolism (lactate and opine synthesis) for functions, such as crawling locomotion and survival during stress periods. In normal conditions, their metabolism is controlled by anabolic activity, involving the synthesis of molecules for growth and recovery (Garrett & Grisham, 2010). During stressful conditions, catabolic metabolism is activated, ensuring available energy to restore equilibrium (Venter, Loots, Mienie, et al., 2018).

The environment, diet, and animal characteristics have a great influence on abalone metabolism, thus modifying feed intake. For example, abalone food intake in warm waters is higher than in cold water due to the high energetic expenses involved in respiration (Lopez & Tyler, 2006), resulting in more algal consumption in warmer seasons. In addition, seaweeds have a lower caloric content (Allen, Marsden, Ragg, & Gieseg, 2006; Bautista-Teruel & Millamena, 1999), producing an increased feed consumption compared to formulated diets (Bansemer et al., 2015; Bautista-Teruel & Millamena, 1999; Coote, Hone, Van Barneveld, & Maguire, 2000; Mai, Mercer, & Donlon, 1995; Sales et al., 2003). The body weight of abalone also has been shown to affect feed intake. Juvenile *H. fulgens* consume 1.43–1.65% (dry weight formulated feed) of their body weight (BW) per day (Gómez-Montes et al., 2003) compared to 1% in juvenile *H. midae* (Britz, 1996). *H. fulgens* of 1–2 cm in shell length require about 1% BW per day compared to the 0.2–0.3% required by animals larger than 3 cm (Farías, García-Esquivel, & Viana, 2003).

2.4 | Abalone nutritional profile

Abalones have been considered a functional human food that improves health beyond basic nutrition (Suleria, Masci, Gobe, & Osborne, 2017). The range and quality of available nutrients from abalone products depend on whether the animal comes from the wild or farm. Abalone in aquaculture facilities, where formulated feeds are used, are exposed to higher levels of dietary protein and lipids compared to those in the wild which feed on seaweeds. Thus, the protein proportion in the flesh of wild abalone is 14–18% (Chiou, Lai, & Shiau, 2001; Hatae et al., 1995) compared to 40–56% in farmed abalone (Mai et al., 1995; Tung & Alfaro, 2011). Indeed, farmed juvenile *Haliotis laevigata* fed on higher amounts of dietary protein were shown to have 65% greater flesh protein than juveniles fed on macroalgae (Stone et al., 2013).

The protein profile of abalone is determined by the type of amino acids available in the body. Abalone meat contains all essential amino acids: Arg—arginine, His—histidine, Ile—isoleucine, Leu—leucine, Lys—lysine, Met—methionine, Phe—phenylalanine, Thr—threonine, Trp—tryptophan and Val—valine, and nonessential amino acids: Ala—alanine, Asp—aspartic acid, Cys—cystine, Glu—glutamic acid, Gly—glycine, Pro—proline, Ser—serine and Tyr—tyrosine (Fleming et al., 1996; Latuihamallo, Iriana, & Apituley, 2015). Amino acids, such as Arg, Met, Thr, Leu and Phe are considered crucial for abalone growth, and therefore, feeds for abalone should contain certain levels of these amino acids from dietary ingredients (Mai, Mercer, & Donlon, 1994; Roussel et al., 2019). From these amino acids, leucine is the most abundant in abalone meat (Shi, Hao, Chen, Ma, & Weng, 2020).

The carbohydrate proportion in abalone meat is less than the protein and includes many types of sugars. In general, the carbohydrate content varies between 0.5–7% (Shi et al., 2020) and fluctuates depending on the season, being higher in the summer and lower in the autumn (Hatae et al., 1995). Sulphate and neutral polysaccharides are the most significant sugars in abalone flesh due to their immunomodulatory (Zhu et al., 2009), anti-thrombotic and anti-fatigue effects (Liu, Jia, Li, Chen, & Fang, 2020), which also have nutraceutical applications. Other carbohydrates include ʟ-rhamnose, ᴅ-xylose, ᴅ-mannose, ᴅ-glucose, ᴅ-galactose, glucuronic acid, and fucose.

The lipid fraction in abalone is minimal and depends on the feed given (Chiou et al., 2001). Lipid levels vary from 0.2–1% in wild abalone (Hatae et al., 1995) compared to 5–7% in farmed ones (Stone et al., 2013; Thongrod, Tamtin, Chairat, & Boonyaratpalin, 2003). Abalones are a good source of omega-3 PUFAs (Su, Antonas, & Li, 2004), which have been found to be higher compared to beef, pork, and chicken (Mulvaney et al., 2015). Among these acids, eicosapentaenoic acid (EPA), docosapentaenoic acid, arachidonic acid (ARA) and α-linolenic acid (ALA) are the most commonly found in wild or farmed *Haliotis rubra* (Su et al., 2004). Sterols are another class of lipids available in abalone with an essential role in their growth and metabolism (Nelson, Leighton, Phleger, & Nichols, 2002). Cholesterol is the main component, accounting for 87–96% followed by desmosterol which accounts for 1–7.6% and phytosterols which are present in almost undetectable amounts (Dunstan et al., 1996; Zhang et al., 2009).

3 | TYPES OF FEEDS AND THEIR EFFECTS ON NUTRITION AND GROWTH

The most used indicators to measure aquaculture efficiency and productivity are animal growth, performance, and survival (Kankainen et al., 2012). External conditions, such as water quality, climatic conditions, feed quantity and quality, and tank design, as well as animal characteristics, such as sex, immune system, and age, have an impact on stock performance, ultimately affecting the profitability of production. Among these conditions, the feed has an extensive impact on animal health and growth (Guillaume et al., 2001). The type, quantity and quality of nutrients influence many aspects of the animal's performance, such as growth, immunity, and meat quality and taste. For this reason, aquaculture nutritional studies have received considerable attention in the last decade.

General growth indicators include physical measurements of body size and shape and meat to shell ratio. Nutrient utilization parameters include feed conversion ratio (FCR), nutrient deposition (ND), protein efficiency ratio (PER), and energy efficiency ratio. These parameters are calculated based on the sum and difference of the feed given, consumed, and excreted. In summary, growth performance indicates objectively how the feed is translated into weight, length, and width, and nutrient utilization parameters identify how the animal can effectively transform the feed into muscle tissue.

3.1 | Nutritional composition of seaweeds

In general, seaweeds contain between 5–27% protein, 1–5% lipids and 32–65% total carbohydrates (Bansemer, Qin, Harris, Howarth, & Stone, 2016; Viera et al., 2005, 2011). The crude protein varies according to the algal species (Lourenço, Barbarino, De-Paula, Pereira, & Marquez, 2002), habitat conditions and season (Gaillard et al., 2018). For instance, crude protein in red algae (20–31%) is higher than brown algae (6–19%) (Dawczynski, Schubert, & Jahreis, 2007; Ruperez & Saura-Calixto, 2001), and higher amounts of crude protein are often found in seaweeds during spring compared to autumn (Gaillard et al., 2018). Generally, seaweeds have all essential amino acids and high amounts of non-essential amino acids, such as glutamic acid (Glu) and aspartic acid (Asp) (Lourenço et al., 2002). However, red seaweeds tend to have higher concentrations of total amino acids than green and brown seaweeds (Gaillard et al., 2018). Other differences among the major seaweed groups include that green algae generally have lower percentages of both aspartic and glutamic acid compared to red and brown algae (Lourenço et al., 2002).

Compared to terrestrial plants, seaweeds have a relatively low content of total lipids. Total lipids in red algae vary from 1 to 2.8%, brown algae from 1 to 4.5% (Dawczynski et al., 2007) and green algae from 2 to 3% (Nelson, Phleger, & Nichols, 2002; Rodrigues et al., 2015). Seaweeds contain different lipid classes, such as FAs, sterols and triacylglycerols. Three types of FAs are present in seaweeds: saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs) and PUFAs. Among these FAs, PUFAs represent the highest proportion (31–74%) with more n-3 species (10–51%) than n-6 (Dawczynski et al., 2007; Nelson, Phleger, & Nichols, 2002). In general, linoleic acid (C18:2, n-6), α-linoleic acid (C18:3, n-3, ALA), stearidonic acid (C18:4, n-3) and ARA (C20:4, n-6, AA) are the most representative FAs, while eicosapentaenoic (C20:5, n-3, EPA) is the most abundant PUFA (10–42%) in seaweeds (Dawczynski et al., 2007). High proportions of SFAs, such as palmitic acid (C:16) and MUFAs, such as oleic acid (C18:1, n-9), are found in red, green and brown algae (Nelson, Phleger, & Nichols, 2002; Rodrigues et al., 2015). Seaweeds contain low n-6:n-3 ratios of 0.1–1.1 (Dawczynski et al., 2007; Floreto, Teshima, & Koshio, 1996) compared to the well-known high levels (0.2–0.3) found in salmon (Berge et al., 2009). Macroalgae are considered to be the most important contributors of long-chain fatty acids (n-3) (Arterburn et al., 2007), which are only synthesized de novo in photosynthetic organisms.

Sterols are another type of lipid present in seaweeds and are involved in cell structure and function (Mouritsen et al., 2017). Some sterols, such as fucosterols are dominant in brown algae (>70% of total sterols), while ergosterols are common in green algae and cholesterols and desmosterols are predominant in red algae (34–88%) (Lopes et al., 2011).

Carbohydrates are the main macronutrients in seaweeds, accounting for 60–70% of the composition and are available in two types: storage and structural polysaccharides. Non-starch polysaccharides account for 30–50% of the total carbohydrates (Dawczynski et al., 2007) placing seaweeds as a very important source of dietary fiber compared to terrestrial plants. Generally, sugars are stored as laminarian (brown algae), floridian starch (red algae) and starch (green algae), whereas the cell wall polysaccharides comprise cellulose; alginic acid and fucan in brown algae; agar, carrageenan, and xylan in red algae; and mannan and xylan in green algae (Stiger-Pouvreau, Bourgougnon, & Deslandes, 2016). Sulphated polysaccharides are other types of carbohydrates available in seaweed, which have bioactive relevance as anti-coagulant, anti-proliferative, anti-tumoral, anti-inflammatory and anti-viral (Chojnacka, Saeid, Witkowska, & Tuhy, 2012).

Vitamins (Norziah & Ching, 2000) and polyphenols are also in the nutritional profile of seaweeds. Carotenoids, such as α and β-carotene, lutein, zeaxanthin, and fucoxanthin are present in the three divisions of macroalgae (Burtin, 2003) while phlorotannins are the most abundant phenolic compounds in brown and red seaweeds (de Quirós, Frecha-Ferreiro, Vidal-Perez, & López-Hernández, 2010). Vitamin B-12 levels are higher in seaweeds than terrestrial plants (Takenaka et al., 2001) and vitamin C is high especially in brown seaweeds compared to the other seaweed groups (Matanjun, Mohamed, Mustapha, & Muhammad, 2009).

Seaweeds can absorb inorganic substances from the marine environment and store them as mineral content. This value is higher in seaweeds than in edible terrestrial plants and animal sources, accounting for 30.1–39.3% (ash content) in brown algae, such as *Fucus vesiculosus*, *Laminaria digitata*, *Undaria pinnatifida* and 20.6–21.1% in red algae, such as *Chondrus crispus* and *Porphyra tenera* (Rupérez, 2002). Additionally, previous reports have highlighted seaweeds as one of the most important vegetable sources of calcium (Ca) (Norziah & Ching, 2000; Rajapakse & Kim, 2011), sodium (Na), potassium (K), magnesium (Mg), phosphorous (P) and trace elements, such as iron (Fe), iodine (I), zinc (Zn) and cooper (Cu) (Robledo & Freile Pelegrin, 1997; Vieira et al., 2020).

3.2 | Use of seaweeds in aquaculture

In many countries, such as China, Korea, South Africa, and Chile, macroalgae are a common food source in abalone farming (Flores-Aguilar, Gutierrez, Ellwanger, & Searcy-Bernal, 2007; Robertson-Andersson et al., 2007). In these countries, seaweeds are extensively harvested or cultivated offshore to feed abalone. When seaweeds are harvested from the wild for aquaculture production, the final operation relies on seasonal availability, which can hinder abalone production. In other countries, legislation protects seaweed harvests against intense depletion. In these countries, formulated feeds are the only option to promote growth in abalone aquaculture.

The selection of seaweeds depends on what grows and/or can be cultivated locally. The species of macroalgae mostly cultivated for abalone aquaculture are *Laminaria*, *Undaria* and *Porphyra* in Japan, China, and Korea (Hwang, Baek, & Park, 2009), *Macrocystis* in Chile (Macchiavello & Bulboa, 2014), and *Ulva* and *Ecklonia* in South Africa (Robertson-Andersson et al., 2007; Troell et al., 2006). These species can be used as a single source, or in conjunction with pelletized feed.

Feeding farmed abalone on an exclusive live seaweed diet has both advantages and disadvantages. Diets based on one type of live seaweed can negatively affect the weight gain and nutrient utilization of *Haliotis* species. For example, *H. midae* fed exclusively on macroalgal diets gained less weight and showed less protein in their tissues compared to animals fed formulated diets (Britz, 1996). Similarly, *Haliotis rufescens* fed live kelp showed lower growth than animals fed formulated feeds containing 25–38% protein (Garcia-Esquivel & Felbeck, 2009). *Haliotis discus Reeve* fed *U. pinnatifida* grew 10% less than the ones fed on formulated feed, including *U. pinnatifida* meal (Ansary et al., 2019). The low growth shown in such studies suggests that an exclusive seaweed food type is not the best choice for abalone. Indeed, a single algal species may provide a limited or poor nutritional profile, and relatively low protein content compared to balanced commercial feeds (Bansemer, Qin, Harris, Duong, Hoang, et al., 2016d). Alternatively, a mixture of live seaweeds may provide a better amino acid range and overall nutritional profile for abalone. For example, Kemp et al. (2015) demonstrated that a combination of two live seaweeds (*M. pyrifera* and *Lessonia berterona*) improved the growth performance of *H. rufescens* compared to a fed regime exclusively based on formulated pellets. In that study, animals fed on those two live seaweeds increased their weight gain ratio by 20% and length by 40% when compared to formulated pellets. In addition, Bansemer, Qin, Harris, Duong, Hoang, et al. (2016d) showed that a mixture of seaweeds (*Gracilaria* sp. and *Ulva* sp.) resulted in enhanced growth and nutrient utilization (e.g., tissue protein deposition and PERs) compared to commercial feeds in *H. laevigata*.

In the last years, many attempts have been made to increase the nutritional profile of seaweeds, particularly in terms of protein, through enrichment techniques. These techniques aim to increase protein, carbohydrate, and lipid levels in seaweeds by growing them in high nitrogen content media (Viera, Courtois de Viçose, Robaina, & Izquierdo, 2015). For example, Bansemer, Qin, Harris, Duong, Hoang, et al. (2016d) found that using fishpond effluents to cultivate seaweeds resulted in increased protein levels by >33%. Another study by Viera et al. (2015) showed an increase in *Halioitis coccinea Reeve* growth rate by 10% and weight gain by 30–169% when animals were fed enriched algae compared to animals fed on formulated feeds. In that study, an enriched-live mixture of *Gracilaria cornea* and *Ulva rigida* promoted 50% more growth and led to a weight gain of more than doubled when compared to formulated feeds. Furthermore, the above-mentioned studies concluded that enriched seaweeds improve not only growth performance but also nutrient utilization.

3.3 | Composition of formulated feeds

Generally, formulated feeds are made up of a mixture of traditional and alternative sources of proteins, carbohydrates, and lipids to supply the animal's energy demands. Traditional ingredients include fishmeal and casein as protein sources, starch or cornflour as carbohydrates, and fish oil and cod liver oil as lipid sources. Alternative sources have been incorporated into aquafeeds to reduce the use of traditional ingredients, which are prioritized for human consumption or are unsustainable. These alternatives include seaweed extracts, seaweed meals, terrestrial plant meals, agriculture by-products, insect meals and oils, and microalgae extracts. In addition, supplements, such as immunostimulants can be added into the formulation to boost growth by strengthening the immune status of aquatic animals. Formulated feeds have been demonstrated to be effective in generating good growth rates and nutrient utilization parameters. The reason for their effectiveness is the high load of macronutrients, especially protein, and the synergy of the variety of ingredients in the final formulation. The high diversity of nutrients positively affects nutrient delivery and the digestibility of the whole formula which in turn impacts abalone growth (Agbidye, Ofuya, & Akindele, 2009).

Seaweeds are incorporated in aquafeeds as supplements, whether dry or wet, to increase the animal feed response. This incorporation ensures good feed intake without compromising growth, survival, and nutrient utilization. For example, Dlaza, Maneveldt, and Viljoen (2008) supplemented fishmeal-based formulated diets with fresh wild seaweeds (*Ecklonia m.* and *Ulva lactuca*) improving shell growth rates (wt%/day), daily increases in shell length and condition factor (CF) of post-weaning juvenile *H. midae* compared to diets without supplementation. Allen et al. (2006) mixed dried *Gracilaria* sp. and *Macrocystis* sp. with commercial feed, which resulted in a significant increase of weight and shell growth of 110 ± 3 μm/day with *Gracilaria* ssp. compared to 87 ± 4 μm/day in animals fed AB-Feed™. Also, Nel et al. (2017) reported that the inclusion of 0.4–5.5% dry kelp (*E. maxima*) promoted faster growth and higher biomass in *H. midae* compared to animals fed on non-supplemented feed. In addition, Ansary et al. (2019) demonstrated that abalone fed on pelletized diets containing dry seaweeds showed an improved survival rate of 92–96% compared to 86% in the ones fed on exclusive live seaweeds with a survival of 86%. Seaweed inclusion in aquafeeds not only increases feed intake but also improves nutritional markers, such as PER and digestibility. For instance, abalone fed on aquafeeds supplemented with *Macrocystis* sp. (Allen et al., 2006), *E. maxima* (Nel, Pletschke, Jones, et al., 2017) or *Ulva* sp. (Bates et al., 2017) increased their meat yield compared to animals fed on exclusive live seaweeds (Kemp et al., 2015).

Abalone diets without seaweeds also provide good growth rates and nutritional parameters. Bansemer, Qin, Harris, Duong, Currie, et al. (2016c) developed a seaweed-free diet that despite having a lower intake, produced higher protein deposition levels and protein efficiency compared to aquafeeds with dried macroalgae. The formula included three different sources of protein (non-vegetable and vegetable) that might improve ND due to a synergistic effect between different amino acid profiles. In fact, aquafeeds composed of a mixture of fish and vegetable protein sources produce better growth than feeds based on a singular source of protein (Bautista-Teruel, Fermin, &

Koshio, 2003). For instance, the inclusion of a mixture of corn gluten meal, silkworm pupae meal and soy meal along with crustacean meal has been shown to improve the growth performance of abalone by providing a good amino acid profile including lysine, arginine, methionine, threonine, and histidine (Cho, 2010).

Agricultural by-products have been included in aquafeeds with promising results for abalone. These ingredients include abalone silage (Viana, López, García-Esquivel, & Mendez, 1996), fermented fish by-products (Jung et al., 2016), feather meal (Campos, Matos, Marques, & Valente, 2017), insect meal (Henry, Gai, Enes, Peréz-Jiménez, & Gasco, 2018) and grape marc (Currie, Purvis, Harris, Stone, & Bansemer, 2019). The improved growth rate as a result of the inclusion of these ingredients is dependent on the percentage used. For instance, Guzmán and Viana (1998) showed that abalone viscera silage can entirely replace fishmeal producing comparable feed consumption rates and growth in *H. fulgens*. Similarly, Jung et al. (2016) concluded that fermented tuna by-products can be included at up to 21% in the whole formula without compromising growth and weight gains in *H. discus*. Other atypical sources, such as silkworm pupae meal, can only be included at up to 16% to produce higher growth rates in *H. discus* compared to other fishmeal-based feeds (Cho, 2010).

In addition to protein, carbohydrate and lipid proportions included in the feed, other ingredients can be added to stimulate the immune system as well as growth performance. These substances are called immunostimulants and have a direct effect on the immune response of the animal, leading to healthy animals and improved survival. Examples of immunostimulants are vitamins, minerals, nucleotides, marine-polysaccharides, prebiotics, and probiotics. Most of these compounds have been successfully included in the feed of many aquatic species, but limited research has been performed for abalone. One of the best-known immunostimulants is vitamin C. Nevertheless, in a previous study, the inclusion of this vitamin in feeds for *H. discus hannai* did not show significant differences in growth and survival compared to animals not receiving vitamin supplements (Mai, 1998). To our knowledge, the effect of other vitamins on the growth of abalone has not been studied. Other types of immunostimulants are polysaccharides, such as alginate and chitosan, which have been tested in common carp and shrimp with successful results (Gopalakannan & Arul, 2006; Wang & Chen, 2005). However, studies on abalone species are lacking. The study by Cheng and Yu (2013) is probably the only one, which reported the beneficial effect of the inclusion of alginate in abalone diets. However, the results in that study were aimed to evaluate the immune capacity rather than the growth performance of *H. diversicolor supertexta*. The most recent immunostimulants used in aquaculture are probiotics. These bioactives have been shown to have positive effects on abalone health and growth. For instance, Grandiosa et al. (2018) showed that *H. iris* fed on a diet supplemented with multi-strain probiotics improved growth by 32% and weight gain by 110% compared to 32 and 73%, respectively, in animals fed non-supplemented feeds. Similarly, Zhao, Ling, Zhang, Ke, and Hong (2018) concluded that *H. diversicolor* fed on a supplemented commercial feed with probiotics showed a 70% growth rate compared to 36% in animals fed a non-supplemented diet.

In addition to probiotics, prebiotics have been included in aquafeeds due to their gastrointestinal benefits and easy management. Ingredients, such as grape marc could provide many benefits to aquatic species due to their high levels of non-digestible carbohydrates. For example, *H. laevigata* fed on a diet with a 5–20% inclusion of grape marc showed 10–12% higher biomass and 5–6% better growth rates compared to animals fed non-grape meal feeds (Currie, Purvis, Bansemer, Harris, & Stone, 2019). In that study, animals consumed 9% less grape marc-based feed, yet the protein deposition and FCR were superior. The results from that study indicate that good nutrient utilization parameters are not necessarily linked to feed intake.

4 | USE OF FORMULATED FEEDS

Most on-land abalone farms tend to use some kind of formulated feed, which in some cases also may contain a certain amount of dried seaweed or seaweed derivatives. Formulated feeds may also contain other sources of nutrients, such as fish meal, shrimp meal or plant-based protein along with other trace and essential ingredients.

Aquafeed development is often started by designing practical diets with a single source of protein, carbohydrates, and lipids, along with minerals and vitamins premixed to enhance growth. To shorten the growth period, abalone aquafeeds may include high amounts of protein (20–50%), lipids (1–5%) and carbohydrates (30–60%) (Fleming et al., 1996). Macronutrients are usually included in high quantities in aquafeeds, which makes it possible for abalone to consume the carbohydrates and lipids for energy production. This leaves all the existing protein to be used for building muscle via the "protein-spare effect" (Lee et al., 2019). The right percentage of protein in formulated feeds is the amount that increases the current growth rate of 2–3 cm per year (achieved with natural seaweed), reducing the on-farm rearing period to less than 5 years (Hahn, 1989).

Protein is the most studied ingredient in aquafeed due to its high price and main role in abalone growth improvement. For a protein source to be adequate for aquafeeds, the amino acid profile of the source of protein must resemble that of the animal (Bautista-Teruel & Millamena, 1999). Additionally, the protein source must have a good digestibility index to promote feed consumption. Sources, such as fishmeal, casein, and defatted soybean meal are commonly used due to their excellent amino acid profiles. Other protein sources, such as cottonseed, peanut meal, and canola meal, show a high digestibility index of almost 96%, which also makes them suitable for aquafeeds. However, these sources of protein are not popular. From all these types of protein, fishmeal is the preferred ingredient due to its positive effect on animal growth, palatability, and nutritional value (Britz, 1996). Despite the excellent nutritional properties of fishmeal, it is considered an unsustainable source since it comes from wild fish. Nevertheless, almost 63% of the fishmeal produced worldwide is used for aquaculture purposes (Nugroho & Nur, 2018), making it scarce and expensive.

There is a wide range of carbohydrate sources that can be used in aquaculture feeds with a maximum inclusion of 50%. The most used are dextrin, glucose, rice starch, corn starch, α-cellulose, maltose, sucrose, cornflour, and wheat flour, which have been demonstrated to produce good growth (Lee et al., 2017). The selection of the right carbohydrate type is based on the composition, interaction with other co-ingredients, digestibility, and price (Sales & Janssens, 2004). For example, carbohydrate sources with higher degrees of polymerization are preferred for *H. discus* due to the high polysaccharidase activity common for these seaweed grazers (Garcia-Esquivel & Felbeck, 2006; Thongrod et al., 2003). Carbohydrates are included for their energy supply and binding properties that ultimately influence water stability, which facilitates nutrient delivery and feed absorption.

Lipids, as with other macronutrients, are essential due to their role in reparation and generation of new tissues in aquatic animals (Lee et al., 2019). The most used lipid sources in abalone aquafeeds are single sources or a combination of fish oil, soybean oil, and cod liver oil. Other sources, such as microalgal lipids (Sarker et al., 2016) and insect oil (Belghit et al., 2018) have also shown good results in other aquatic species. From these sources, fish oil is the most popular ingredient in aquafeeds due to its PUFA profile, which includes EPA and DHA. The lipid requirements of herbivores, such as abalone, are relatively low due to the limited lipase activity found in their digestive system (Garcia-Esquivel & Felbeck, 2006). Thus, diets high in lipid content reduced feed intake in these herbivores (Thongrod et al., 2003). The maximum level of lipid inclusion depends on the lipid source. However, it is generally considered that 5% is the maximum inclusion for abalone aquafeeds (Uki, Kemuyama, & Watanabe, 1985). Higher levels of lipids deteriorate the growth of certain species, such as *H. discus* (Lee et al., 2019) and *Haliotis asinina* (Bautista-Teruel et al., 2011). As Durazo-Beltrán, D'Abramo, Toro-Vazquez, Vasquez-Peláez, and Viana (2003) reported, *H. fulgens* grew best when diets contained 1.5% lipid, *H. asinine* grew best at a maximum of 6.1% (Bautista-Teruel et al., 2011) and *H. midae* at a maximum of 7% (Green, Jones, & Britz, 2011). Abalone feeds should contain approximately 1% of omega-3 fatty acids (Uki et al., 1986) and 0.23% cholesterol to promote optimal growth (Zhang et al., 2009).

5 | ABALONE DISEASE RESISTANCE

Blood cells or hemocytes are the main cell types involved in cell-mediated immune responses. They possess similar functions to macrophages in vertebrates (Loker, 2010). These cells are capable of chemotaxis, antigen recognition, attachment followed by agglutination, phagocytosis, and elimination of invaders by respiratory burst or exocytosis of antimicrobial factors (Loker, 2010). Other hemocyte responses include the generation of immune mediators called chemotaxins, such as Interleukin-8, Lipopolysaccharide and formyl-methionyl-leucyl-phenylalanine (Hooper, Day, Slocombe, Handlinger, & Benkendorff, 2007). The humoral immune response includes lectins, lysosomal enzymes, and antimicrobial peptides.

Most of the immune responses in abalone are centered on the hemocyte. These blood cells are involved in phagocytosis, an important process, which eliminates microorganisms or foreign particles (Bayne, 1990). During phagocytosis, several kinds of reactive oxygen intermediates (ROIs) are produced. These species include superoxide anion (O^{2-}), hydrogen peroxide (H_2O_2), singlet oxygen and hydroxy radical ($OH^{\cdot}$) (Klebanoff, 1982). The release of superoxide anion is known as respiratory burst, which plays a microbicidal role. Hemocytes release enzymes, which also have a role in the humoral immune response. Examples of these enzymes are acid phosphatase, alkaline phosphatase, superoxide dismutase (SOD), lysozyme, and phenoloxidase (Hooper et al., 2007). These enzymes are used as markers of the immune response. Generally, the most common immune measurements in abalone include total hemocyte count (THC), phagocytic rate, intracellular superoxide anion, phenoloxidase activity, respiratory burst, lysosomal membrane stability (NRR time), and antibacterial activity.

Abalone immune responses are dependent on the type of stressor and the stress duration. The prolonged presence of stressors can lead to immunosuppression, which in turn can cause early mortality. Studies have shown that stressed abalone may present a transient drop in hemocyte count (haemacytopenia) (Yang & Min, 2019), increased hemocyte apoptosis and necrosis (Yang & Min, 2019), increased phagocytic activity (Cheng, Juang, & Chen, 2004; Cheng & Yu, 2013; Hooper et al., 2014), reduced phenoloxidase activity (Cheng, Hsiao, & Chen, 2004; Hooper et al., 2014) and respiratory burst. In addition to these cell-mediated changes, there is an upsurge of antioxidant enzyme levels, such as glutathione peroxidase (GPX) and SOD under stress conditions (Vosloo, Laas, & Vosloo, 2013). The high antioxidant enzyme activity serves to prepare the animal from potential oxidative stress. SOD, converts free radicals to H_2O_2, where-after GPX and catalase reduce H_2O_2 to H_2O and O_2 (Matés & Sánchez-Jiménez, 1999).

6 | EFFECT OF FEEDS ON ABALONE DISEASE RESISTANCE

The immune markers used to evaluate the impact of environmental stressors in aquatic animals are currently used to determine the effect of aquafeeds in different animal life stages during different exposure periods. The type of nutrition affects the immune status of aquatic species as a result of the vast number of chemical feed-host interactions. Particularly, nutrition has a high impact on gastrointestinal processes, such as digestion and ingestion. Diets can provide an important proportion of the daily fiber, which stimulates the growth of gut bacteria (prebiotic) (Nayak, 2010), affect digestive endogenous/exogenous enzymatic activity, and cell-mediated and humoral immunity responses (Erasmus et al., 1997).

6.1 | Effects of seaweed

Seaweed diets have been shown to produce beneficial effects on animal health. These benefits are linked to the activity of the many bioactive compounds present in seaweed, such as sterols, polyphenols, fatty acids, polysaccharides, and sulphated polysaccharides. These bioactive molecules are responsible for the anti-microbial (García-Bueno et al., 2014), anti-viral (Dang, Benkendorff, & Speck, 2011; Kitikiew et al., 2013) and anti-inflammatory effects (Chojnacka et al., 2012) in living animals.

From these molecules, polysaccharides are highly valued due to their tested immunomodulatory effects. Seaweed polysaccharides are considered a potential prebiotic in aquatic animals (Mohan et al., 2019). These polymers improve intestinal health by stimulating the secretion of endogenous digestive enzymes, such as amylases (Erasmus et al., 1997), proteases (García-Carreño, Navarrete del Toro, & Serviere-Zaragoza, 2003), lipases, and exogenous enzymes produced by the host microbiota (Nawaz, Bakhsh Javaid, Irshad, Hoseinifar, & Xiong, 2018). The most common non-soluble polymers in seaweeds are carragenate-oligosaccharides, alginate-oligosaccharides, fucoidans, galactofucans, and laminarin (Gomez-Zavaglia, Prieto Lage, Jimenez-Lopez, Mejuto, & Simal-Gandara, 2019).

Many studies have reported the positive immunomodulatory effects of extracted polysaccharides in aquatic species, such as stellate sturgeon, sea bream and European sea bass (Akrami, Iri, Khoshbavar Rostami, & Razeghi Mansour, 2013; Guerreiro, Enes, & Oliva-Teles, 2015; Guerreiro, Oliva-Teles, & Enes, 2015). However, only one study evaluated the prebiotic effect of dietary live seaweeds on farmed abalone. The study of Dang, Li, Speck, and Benkendorff (2011) reported that *H. laevigata* fed on a combination of macroalgae (*Spyridia filamentosa* and *U. lactuca*) increased THC and improved the haemolymph anti-bacterial activity against *Vibrio anguillarum* and *Herpesvirus* compared to animals fed on commercial diets. Nevertheless, this combination did not generate significant changes in phagocytosis, superoxide anion, phenoloxidase levels, and haemolymph anti-viral activity. In the same study, an *U. lactuca* diet produced abalone extracts with the higher anti-viral activity of 64% compared to 47% in abalone fed on commercial pellets. Some studies have evaluated the effect of enriched seaweeds on the immune responses of aquatic animals, such as rainbow trout (Araújo et al., 2016) and Nile tilapia (Valente et al., 2016). However, the literature on gastropod immune activity is still limited. The only study available reported that the cell-mediated immune response in abalone fed on enriched *Ulva* sp. had a stronger antioxidant potential (ferric ion reducing antioxidant power) and higher SOD activity compared to animals fed on commercial diets (Stone et al., 2014).

6.2 | Effect of formulated feeds

There is a wide range of ingredients included in aquafeeds that can assist in promoting health and boosting growth simultaneously. Seaweed meals, seaweed extracts, microalgae extracts, probiotics, postbiotics, symbiotics, prebiotics, nucleotides, vitamins, minerals, and antioxidants are some examples of the ingredients that can supplement aquafeeds for specific purposes in farms.

Seaweed meals have been included in aquafeeds in the past as attractants. However, their inclusion has recently shown positive effects on the general welfare of abalone. One of the effects of seaweed meal inclusion is on the abalone bacterial gut environment as reported by Nel, Pletschke, and Britz (2017). In their study, the inclusion of kelp up to 3.5% in formulated diets for subadult *H. midae* promoted a more balanced gut bacterial composition than in animals fed non-supplemented feeds. The researchers found that the main components of the abalone gut microbiota were Proteobacteria and Tenericutes, which can be modified when animals are exposed to a kelp-supplemented diet. The authors claimed that kelp diets promoted a more balanced and regulated gut-bacterial environment. Based on these findings, Nel, Jones, Britz, and Landzela (2018) investigated the diversity of bacterial communities during the weaning phase of *H. midae* fed kelp and formulated feed with or without the inclusion of kelp *E. maxima*. The results showed the guts of abalone weaned onto kelp were dominated by anaerobic *Clostridium* species, where as a variety of bacterial genera from Proteobacteria, Actinobacteria, and Flavobacteria were prevalent in abalone fed formulated feed. Another effect of seaweed meal inclusion is the effect on digestive enzyme activities. The inclusion of 5% of *Ulva* sp. meal in feeds for *H. laevigata* produced higher trypsin activity levels, an indicator of improved digestion and growth, compared to animals fed non-supplemented feeds (Bansemer, Qin, Harris, Schaefer, et al., 2016).

The inclusion of probiotics and prebiotics has been widely used in aquaculture with outstanding results during the last decade (Gao et al., 2018; Grandiosa et al., 2018; Grandiosa, Young, Van Nguyen, Mérien, & Alfaro, 2020; Hadi, Gutierrez, Alfaro, & Roberts, 2014; Zhao et al., 2018). Probiotics have been included in abalone aquafeeds not only to promote growth but also to boost immunity and antioxidant capacity (Grandiosa et al., 2018; Jiang, Liu, Chang, Liu, & Wang, 2013). The mechanisms of action of probiotics can be classified as (a) modifying the host-associated or ambient microbial community, (b) improving the use of feed or enhancing its nutritional value, and (c) improving the quality of its ambient environment (Das, Ward, & Burke, 2008). As reported by Zhao et al. (2018), abalone fed on a probiotic-enriched diet showed a more diverse gut microbial environment. This diversity in the gastrointestinal environment promotes higher survival (Jiang et al., 2013), improved THC, higher hemocyte viability, higher reactive oxygen species (Grandiosa et al., 2018), lysozyme activity (Gao et al., 2018), and non-apoptotic cell levels compared to animals fed commercial feeds without probiotics.

Prebiotics have only been included in aquaculture research since the last decade (Hanley, Brown, & Carberry, 1995), and they are defined as "non-digestible food ingredients that stimulate the growth and activity of bacterial species in the host's colon improving the host's intestinal health" (Gibson & Roberfroid, 1995). Prebiotics are carbohydrates, which can be monosaccharides, oligosaccharides or polysaccharides according to their molecular size (Ringø et al., 2010). By altering the gastrointestinal microbial activity and/or composition (Dimitroglou et al., 2009), prebiotics regulate the innate immune response of the host. This regulation may positively affect the animal's growth (Li & Gatlin, 2004; Staykov, Spring, Denev, & Sweetman, 2007) and ability to fight pathogen infections (Wu, Tseng, & Nan, 2016). One of the advantages of prebiotics is their easy management and lower cost compared to probiotics, especially in large-scale applications. Common prebiotics used in fish aquaculture to date include soluble fermentable fibers such as alginate from seaweeds (Nel et al., 2018; Nel, Pletschke, & Britz, 2017), inulin, fructooligosaccharides, short-chain fructooligosaccharides, mananoligosaccharides (MOS), galactooligosaccharides, xylooligo-saccharides, arabinoxylooligosaccharides, isomaltooligosaccharides and Grobiotic™ (Ringø et al., 2010).

Prebiotics have been tested in rainbow trout (Staykov et al., 2007), hybrid striped bass (Li & Gatlin, 2004), common carp (Hoseinifar et al., 2017) and shrimp (Rungrassamee et al., 2014). However, only a couple of studies have included them in abalone feeds. Meng et al. (2019) reported that *H. discus hannai* fed on a diet containing MOS, extracted from the cell wall of *Saccharomyces cerevisiae*, showed 20 times more total antioxidant capacity and three times more total superoxide (SOD) activity than animals fed non-supplemented feeds. In that study, the inclusion of MOS caused 30% less mortality when animals were exposed to *Vibrio parahaemolyticus*. Other prebiotics included in aquafeeds are β-glucans, which can be extracted from yeast, fungi, plant, and bacterial cell walls. β-glucans have not been included as a supplement in abalone feeds, but have had success in other species, such as popano fish *Trachinotus ovatus Linnaeus* (Do Huu, Sang, & Thanh Thuy, 2016) and Nile tilapia *Oreochromis niloticus Linn* (Amphan, Unajak, Printrakoon, & Areechon, 2019). In these two species, β-glucan inclusion increased survival and resistance to bacterial infections. Although β- glucans have not been included in feeds for abalone, Wu et al. (2016) demonstrated a positive effect of the injection of β-1,3–1,6 -glucan on *H. diversicolor supertexta* immune response. The study showed an increased superoxide anion and phenoloxidase response, phagocytic index, phagocytic rate, and ROIs. Sodium alginate is another polysaccharide with prebiotic effects (Van Doan, Tapingkae, Moonmanee, & Seepai, 2016) that has been tested in some abalone species. Alginic acid, its precursor, is a polysaccharide with proven immunomodulatory activity derived from brown algae and certain bacteria. In a bacterial challenge where *H. diversicolor* was exposed to *V. parahaemolyticus*, Cheng and Yu (2013) reported that a 0,1–0,3% sodium alginate dietary supplement improved immune responses. The study found that animals with sodium alginate supplementation had higher phenoloxidase, SOD and phagocytic activity, and respiratory bursts than animals fed non-supplemented feeds.

Other types of prebiotics which have demonstrated an immunostimulant effect on aquatic species are chitin and the deacetylated product chitosan. Chitin is a natural polymer abundantly found in the exoskeletons of crustaceans and insects and fungal cell walls. To our knowledge, there are no studies of dietary chitin and chitosan in abalone. However, the effects of dietary chitin and chitosan have been tested in other species, such as rainbow trout, *Oncorhynchus mykiss* (Siwicki, Anderson, & Rumsey, 1994) and gilthead seabream, *Sparus aurata* L (Esteban, Cuesta, Ortuño, & Meseguer, 2001). These studies indicate a positive regulation between chitin/chitosan and non-specific immune responses. Although chitin or chitosan have not been included in aquafeeds for abalone, their origin sources, such as shrimp meal or insect meal, have been used. The study of Cho (2010) obtained good growth rates with the replacement of fishmeal by shrimp meal and insect meal in aquafeeds for *H. discus hannai* Ino. Unfortunately, that study only evaluated growth performance.

Certain prebiotics have been successfully commercialized for their use in aquaculture. An example is Grobiotic™, a prebiotic mixture of partially autolyzed brewer's yeast, dairy ingredient components and dried fermentation products. Although Grobiotic™ has not been included in abalone feeds, it has been included in other aquatic species, such as striped bass, *Morone chrysops* x *Morone saxatilis* (Li & Gatlin, 2004), Nile tilapia, *O. niloticus* (Zheng, Wang, Gatlin III, & Ye, 2011) and largemouth bass, *Micropterus salmoides* (Yu et al., 2019). The study performed by Li and Gatlin (2004) showed that the inclusion of 1 and 2% of Grobiotic™ in feeds for striped bass led to higher feed efficiency and growth after 7 weeks of feeding. Additionally, animals fed on diets containing Grobiotic™ showed enhanced fish survival rates of 73–90% compared to 53% in animals fed diets without Grobiotic™ when animals were challenged with *Streptococcus iniae*. Also, Yu et al. (2019) reported that the inclusion of Grobiotic™ contributed to the abundance of *Bacillus* bacteria, which promotes disease resistance in largemouth bass. Furthermore, the study by Zheng et al. (2011), reported that the inclusion of 1.2% of Grobiotic™ improved growth rates and survival of Nile tilapia infected with *Aeromonas hydrophila*.

7 | CONCLUSIONS AND FUTURE DIRECTIONS

According to the World Bank, global food demand from aquatic systems will reach 150 million tons in 2030, 27% more demand compared to 2010 (FAO, 2018). The increasing demand for aquaculture products is promoting the development of new feed technologies with the primary goal of attaining more growth in shorter time periods. However, with increasing consumption, food quality awareness, and sustainability, cost-effective productions are no longer the only considerations for the aquaculture industry. The studies highlighted in this review indicate that the recent focus of abalone feed research has been directed towards alternative nutritional sources and ingredients, as well as innovative techniques and applications to improve the efficiency and effectiveness of feeds leading to enhanced stock nutrition and health. However, the body of published literature also suggests that while a high number of studies have focused on the effects of feed composition on abalone growth and overall nutrition, few studies have looked at the effects of feeds on abalone health. With the increasing stocking densities and deteriorating environmental conditions associated with the continued growth of the aquaculture sector, it is expected that health parameters will have a more prominent role to play in feed formulation in the coming years.

There is no doubt that one of the main drivers of using alternative ingredients in aquafeeds is the reduction of fishmeal inclusion without compromising the growth performance and nutritional quality of abalone. Therefore, future studies should evaluate key essential metabolites in abalone, such as amino acids and fatty acids that can be impacted by different feeding approaches and ingredient replacements. In a similar fashion, future studies should include chemical profiling of the feed and its impact on abalone metabolites of special interest, such as free amino acids, volatile compounds, and organic acids which are indicators of flavor.

The use of molecular tools in nutritional studies can help address the specific effects of alternative ingredient inclusions in aquafeeds for abalone. Analytical platforms, such as GC–MS, LC–MS can be used to establish possible links between different feeding schemes and their effects on gut bacterial diversity, microbiome and metabolomic or enzymatic profile. In addition, histo-morphological studies can also be included in future research to provide insights into gastrointestinal responses, such as inflammation due to the exclusive use of natural or artificial feeds. These techniques can be used to improve our understanding of the relationship between healthy abalone production and feed requirements within commercial settings.

It is imperative that future nutritional studies in abalone are placed into a holistic framework that includes the environmental sustainability of alternative ingredients along with the financial profitability of the entire production. Current methodologies to determine environmental impacts, such as life cycle assessment have been used to assess the entire production of other aquatic species. However, such tools have not been used to evaluate abalone aquafeeds to date.

This review shows that many studies have already successfully extrapolated the laboratory technologies to the farm. Thanks to the knowledge generated throughout the last 10–15 years, many technological advancements have been possible in abalone aquaculture, creating a more robust industry in accordance with 21st century environmental needs. However, as presented earlier, there are many areas, which may represent a gap in the transfer of research outcomes to the industry. Thus, it is recommended that future studies clearly outline a path for research uptake from the start and that the abalone industry engages more closely with research experts and innovators in this field.

The application of aquafeeds in farm environments introduces other variables, such as the feasibility of feed production at an industrial scale, and ease of storage and handling which are critical for the sustainability of commercial operations. In summary, it is suggested that future research and development should focus on:

- Simultaneous evaluation of the effect of aquafeeds on animal health, growth, and nutritional quality.
- Development of long-term nutritional studies that evaluate the effect of aquafeeds across different seasons and life stages.
- Development of nutritional studies which include a solid economic assessment of the feed production costs for the farm and costs related to environmental impacts.
- Development of targeted nutritional studies, such as evaluating the effect of specific ingredients on the production of bioactive compounds in abalone, which may have specific human applications.
- Inclusion of histo-morphological studies to evaluate the impact of alternative ingredients and different feeds on the digestive health of abalone.
- Inclusion of molecular tools, such as metabolomic and microbiome analysis to evaluate the effect of different feeds in abalone nutritional quality and digestive health.
- Development of nutritional studies on abalone integrated multi-trophic aquaculture settings.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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REFERENCES

Agbidye, F., Ofuya, T., & Akindele, S. (2009). Marketability and nutritional qualities of some edible forest insects in Benue state, Nigeria. *Pakistan Journal of Nutrition*, *8*(7), 917–922.

Akrami, R., Iri, Y., Khoshbavar Rostami, H., & Razeghi Mansour, M. (2013). Effect of dietary supplementation of fructooligosaccharide (FOS) on growth performance, survival, lactobacillus bacterial population and hemato-immunological parameters of stellate sturgeon (*Acipenser stellatus*) juvenile. *Fish and Shellfish Immunology*, *35*(4), 1235–1239. https://doi.org/10.1016/j.fsi.2013.07.039

Alcantara, L. B., & Noro, T. (2005). Effects of macroalgal type and water temperature on macroalgal consumption rates of the abalone *Haliotis diversicolor* reeve. *Journal of Shellfish Research*, *24*(4), 1169–1178.

Allen, V. J., Marsden, I. D., Ragg, N. L. C., & Gieseg, S. (2006). The effects of tactile stimulants on feeding, growth, behaviour, and meat quality of cultured Blackfoot abalone, *Haliotis Iris*, *Aquaculture*, *257*(1–4), 294–308. https://doi.org/10.1016/j.aquaculture.2006.02.070

Amphan, S., Unajak, S., Printrakoon, C., & Areechon, N. (2019). Feeding-regimen of β-glucan to enhance innate immunity and disease resistance of Nile tilapia, *Oreochromis niloticus* Linn., against *Aeromonas hydrophila* and *Flavobacterium columnare*. *Fish & Shellfish Immunology*, *87*, 120–128. https://doi.org/10.1016/j.fsi.2018.12.062

Ansary, M. W. R., Jeong, H. S., Lee, K. W., Kim, H. S., Kim, J., Yun, A., … Kim, T.-I. (2019). The effect of substituting *Undaria pinnatifida* in formulated feeds with *Sargassum horneri* on growth and body composition of juvenile abalone (*Haliotis discus*, reeve 1846). *Journal of Applied Phycology*, *31*(3), 2125–2132. https://doi.org/10.1007/s10811-018-1672-2

Antonopoulou, E., Nikouli, E., Piccolo, G., Gasco, L., Gai, F., Chatzifotis, S., … Kormas, K. A. (2019). Reshaping gut bacterial communities after dietary *Tenebrio molitor* larvae meal supplementation in three fish species. *Aquaculture*, *503*, 628–635. https://doi.org/10.1016/j.aquaculture.2018.12.013

Araújo, M., Rema, P., Sousa-Pinto, I., Cunha, L. M., Peixoto, M. J., Pires, M. A., … Valente, L. M. (2016). Dietary inclusion of IMTA-cultivated *Gracilaria vermiculophylla* in rainbow trout (*Oncorhynchus mykiss*) diets: Effects on growth, intestinal morphology, tissue pigmentation, and immunological response. *Journal of Applied Phycology*, *28*(1), 679–689.

Arterburn, L. M., Oken, H. A., Hoffman, J. P., Bailey-Hall, E., Chung, G., Rom, D., … McCarthy, D. (2007). Bioequivalence of docosahexaenoic acid from different algal oils in capsules and in a DHA-fortified food. *Lipids*, *42*(11), 1011–1024.

Asche, F., & Oglend, A. (2016). The relationship between input-factor and output prices in commodity industries: The case of Norwegian salmon aquaculture. *Journal of Commodity Markets*, *1*(1), 35–47. https://doi.org/10.1016/j.jcomm.2015.11.001

Balkhair, M., Al-Mushikhi, A., & Rivera, R. (2016). Embryogenesis and larval development of the *Omani abalone* (*Haliotis mariae* Wood, 1828). *Journal of Shellfish Research*, *35*(3), 625–631, 627.

Bansemer, M. S., Harris, J. O., Qin, J. G., Adams, L. R., Duong, D. N., & Stone, D. A. J. (2015). Growth and feed utilisation of juvenile greenlip abalone (*Haliotis laevigata*) in response to water temperatures and increasing dietary protein levels. *Aquaculture*, *436*, 13–20. https://doi.org/10.1016/j.aquaculture.2014.10.033

Bansemer, M. S., Qin, J. G., Harris, J. O., Duong, D. N., Currie, K.-L., Howarth, G. S., & Stone, D. A. J. (2016c). Dietary inclusions of dried macroalgae meal in formulated diets improve the growth of greenlip abalone (*Haliotis laevigata*). *Journal of Applied Phycology*, *28*(6), 3645–3658. https://doi.org/10.1007/s10811-016-0829-0

Bansemer, M. S., Qin, J. G., Harris, J. O., Duong, D. N., Hoang, T. H., Howarth, G. S., & Stone, D. A. J. (2016d). Growth and feed utilisation of greenlip abalone (*Haliotis laevigata*) fed nutrient enriched macroalgae. *Aquaculture*, *452*, 62–68. https://doi.org/10.1016/j.aquaculture.2015.10.025

Bansemer, M. S., Qin, J. G., Harris, J. O., Howarth, G. S., & Stone, D. A. J. (2016). Nutritional requirements and use of macroalgae as ingredients in abalone feed. *Reviews in Aquaculture*, *8*(2), 121–135. https://doi.org/10.1111/raq.12085

Bansemer, M. S., Qin, J. G., Harris, J. O., Schaefer, E. N., Wang, H., Mercer, G. J., … Stone, D. A. J. (2016). Age-dependent response of digestive enzyme activities to dietary protein level and water temperature in greenlip abalone (*Haliotis laevigata*). *Aquaculture*, *451*, 451–456.

Barkai, R., & Griffiths, C. (1986). Diet of the south African abalone *Haliotis midae*. *South African Journal of Marine Science*, *4*(1), 37–44.

Bates, A. L., Howarth, G. S., Currie, K.-L., Purvis, M., Bansemer, M. S., & Stone, D. A. J. (2017). Growth and nutrient utilization of Greenlip abalone (*Haliotis laevigata*) fed Ulva Sp. protein extract. *Journal of Shellfish Research*, *36*(3), 757–761.

Bautista-Teruel, M. N., Fermin, A. C., & Koshio, S. S. (2003). Diet development and evaluation for juvenile abalone, *Haliotis asinina*: Animal and plant protein sources. *Aquaculture*, *219*(1–4), 645–653. https://doi.org/10.1016/S0044-8486(02)00410-6

Bautista-Teruel, M. N., Koshio, S. S., & Ishikawa, M. (2011). Diet development and evaluation for juvenile abalone, *Haliotis asinina* Linne: Lipid and essential fatty acid levels. *Aquaculture*, *312*(1–4), 172–179. https://doi.org/10.1016/j.aquaculture.2011.01.004

Bautista-Teruel, M. N., & Millamena, O. M. (1999). Diet development and evaluation for juvenile abalone, *Haliotis asinina*: Protein energy levels. *Aquaculture*, *178*(1–2), 117–126. https://doi.org/10.1016/S0044-8486(99)00121-0

Bayne, C. J. (1990). Phagocytosis and non-self recognition in invertebrates. *Bioscience*, *40*(10), 723–731.

Belghit, I., Liland, N. S., Waagbø, R., Biancarosa, I., Pelusio, N., Li, Y., … Lock, E.-J. (2018). Potential of insect-based diets for Atlantic salmon (*Salmo salar*). *Aquaculture*, *491*, 72–81. https://doi.org/10.1016/j.aquaculture.2018.03.016

Berge, G. M., Witten, P. E., Baeverfjord, G., Vegusdal, A., Wadsworth, S., & Ruyter, B. (2009). Diets with different n−6/n−3 fatty acid ratio in diets for juvenile Atlantic salmon, effects on growth, body composition, bone development and eicosanoid production. *Aquaculture*, *296*(3), 299–308. https://doi.org/10.1016/j.aquaculture.2009.08.029

Bewick, M. D., Wells, R. M. G., & Wong, R. J. (1997). Free amino acid and nucleotide concentrations in New Zealand abalone (Paua), *Haliotis iris*, fed casein-based, macroalgal, or wild diets. *Journal of Aquatic Food Product Technology*, *6*(4), 57–69. https://doi.org/10.1300/J030v06n04_05

Britz, P. J. (1996). The suitability of selected protein sources for inclusion in formulated diets for the south African abalone, *Haliotis Midae*. *Aquaculture*, *140*(1–2), 63–73. https://doi.org/10.1016/0044-8486(95)01197-8

Burtin, P. (2003). Nutritional value of seaweeds. *Electronic Journal of Environmental, Agricultural and Food Chemistry*, *2*(4), 498–503.

Campos, I., Matos, E., Marques, A., & Valente, L. M. P. (2017). Hydrolyzed feather meal as a partial fishmeal replacement in diets for European seabass (*Dicentrarchus labrax*) juveniles. *Aquaculture*, *476*, 152–159. https://doi.org/10.1016/j.aquaculture.2017.04.024

Cheng, W., Hsiao, I. S., & Chen, J.-C. (2004). Effect of ammonia on the immune response of Taiwan abalone *Haliotis diversicolor* supertexta and its susceptibility to *Vibrio parahaemolyticus*. *Fish & Shellfish Immunology*, *17*(3), 193–202. https://doi.org/10.1016/j.fsi.2004.03.004

Cheng, W., Juang, F.-M., & Chen, J.-C. (2004). The immune response of Taiwan abalone *Haliotis diversicolor* supertexta and its susceptibility to *Vibrio parahaemolyticus* at different salinity levels. *Fish & Shellfish Immunology*, *16*(3), 295–306.

Cheng, W., & Yu, J.-S. (2013). Effects of the dietary administration of sodium alginate on the immune responses and disease resistance of Taiwan abalone, *Haliotis diversicolor* supertexta. *Fish & Shellfish Immunology*, *34*(3), 902–908. https://doi.org/10.1016/j.fsi.2012.12.020

Chiou, T.-K., Lai, M.-M., & Shiau, C.-Y. (2001). Seasonal variations of chemical constituents in the muscle and viscera of small abalone fed different diets. *Fisheries Science*, *67*(1), 146–156.

Cho, S. H. (2010). Effect of fishmeal substitution with various animal and/or plant protein sources in the diet of the abalone *Haliotis discus* hannai Ino. *Aquaculture Research*, *41*(10), e587–e593. https://doi.org/10.1111/j.1365-2109.2010.02561.x

Chojnacka, K., Saeid, A., Witkowska, Z., & Tuhy, L. (2012). *Biologically active compounds in seaweed extracts-the prospects for the application*. Paper presented at Symposium Conducted at the Meeting of the the Open Conference Proceedings Journal.

Cook, P. A. (2014). The worldwide abalone industry. *Modern Economy*, *5*(13), 1181–1186.

Coote, T. A., Hone, P. W., Van Barneveld, R. J., & Maguire, G. B. (2000). Optimal protein level in a semipurified diet for juvenile greenlip abalone *Haliotis laevigata* (Vol. *6*, pp. 213–220).

Cornwall, C. E., Phillips, N. E., & McNaught, D. C. (2009). Feeding preferences of the abalone *Haliotis iris* in relation to macroalgal species, attachment, accessibility and water movement. *Journal of Shellfish Research*, *28*(3), 589–598.

Courtois de Viçose, G., Viera, M. P., Huchette, S., & Izquierdo, M. S. (2012). Improving nursery performances of *Haliotis tuberculata* coccinea: Nutritional value of four species of benthic diatoms and green macroalgae germlings. *Aquaculture*, *334-337*, 124–131. https://doi.org/10.1016/j.aquaculture.2011.12.040

Currie, K. L., Purvis, M., Bansemer, M., Harris, J. O., & Stone, D. A. J. (2019). Dietary inclusion of Acti-meal improves growth and feed utilisation of greenlip abalone (*Haliotis laevigata*). *Aquaculture*, *498*, 364–370. https://doi.org/10.1016/j.aquaculture.2018.08.074

Currie, K. L., Purvis, M., Harris, J. O., Stone, D. A. J., & Bansemer, M. (2019). Dietary inclusion of acti-meal improves growth and feed utilisation of greenlip abalone (*Haliotis laevigata*). *Aquaculture*, *498*, 364–370. https://doi.org/10.1016/j.aquaculture.2018.08.074

Dang, V. T., Benkendorff, K., & Speck, P. (2011). In vitro antiviral activity against herpes simplex virus in the abalone *Haliotis laevigata*. *Journal of General Virology*, *92*(3), 627–637.

Dang, V. T., Li, Y., Speck, P., & Benkendorff, K. (2011). Effects of micro and macroalgal diet supplementations on growth and immunity of greenlip abalone, *Haliotis Laevigata*. *Aquaculture*, *320*(1), 91–98. https://doi.org/10.1016/j.aquaculture.2011.08.009

Das, S., Ward, L. R., & Burke, C. (2008). Prospects of using marine actinobacteria as probiotics in aquaculture. *Applied Microbiology and Biotechnology*, *81*(3), 419–429.

Dawczynski, C., Schubert, R., & Jahreis, G. (2007). Amino acids, fatty acids, and dietary fibre in edible seaweed products. *Food Chemistry*, *103*(3), 891–899. https://doi.org/10.1016/j.foodchem.2006.09.041

de Quirós, A. R.-B., Frecha-Ferreiro, S., Vidal-Perez, A., & López-Hernández, J. (2010). Antioxidant compounds in edible brown seaweeds. *European Food Research and Technology*, *231*(3), 495–498.

Dimitroglou, A., Merrifield, D., Moate, R., Davies, S., Spring, P., Sweetman, J., & Bradley, G. (2009). Dietary mannan oligosaccharide supplementation modulates intestinal microbial ecology and improves gut morphology of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Animal Science*, *87*(10), 3226–3234.

Dlaza, T. S., Maneveldt, G. W., & Viljoen, C. (2008). Growth of post-weaning abalone *Haliotis midae* fed commercially available formulated feeds supplemented with fresh wild seaweed. *African Journal of Marine Science*, *30*(1), 199–203. https://doi.org/10.2989/AJMS.2008.30.1.22.472

Do Huu, H., Sang, H. M., & Thanh Thuy, N. T. (2016). Dietary β-glucan improved growth performance, vibrio counts, haematological parameters and stress resistance of pompano fish, *Trachinotus ovatus* Linnaeus, 1758. *Fish & Shellfish Immunology*, *54*, 402–410. https://doi.org/10.1016/j.fsi.2016.03.161

Dunstan, G. A., Baillie, H. J., Barrett, S. M., & Volkman, J. K. (1996). Effect of diet on the lipid composition of wild and cultured abalone. *Aquaculture*, *140*(1), 115–127. https://doi.org/10.1016/0044-8486(95)01191-9

Durazo-Beltrán, E., D'Abramo, L. R., Toro-Vazquez, J. F., Vasquez-Peláez, C., & Viana, M. A. T. (2003). Effect of triacylglycerols in formulated diets on growth and fatty acid composition in tissue of green abalone (*Haliotis fulgens*). *Aquaculture*, *224*(1–4), 257–270.

Erasmus, J. H., Cook, P. A., & Coyne, V. E. (1997). The role of bacteria in the digestion of seaweed by the abalone *Haliotis midae 155*, 377–386.

Esteban, M. A., Cuesta, A., Ortuño, J., & Meseguer, J. (2001). Immunomodulatory effects of dietary intake of chitin on gilthead seabream (*Sparus aurata* L.) innate immune system. *Fish & Shellfish Immunology*, *11*(4), 303–315. https://doi.org/10.1006/fsim.2000.0315

FAO. (2018). *The state of world fisheries and aquaculture 2018 - meeting the sustainable development goals*. *Rome*. Retrieved from http://www.fao.org/state-of-fisheries-aquaculture.

Farías, A., García-Esquivel, Z., & Viana, M. T. (2003). Physiological energetics of the green abalone, *Haliotis fulgens*, fed on a balanced diet. *Journal of Experimental Marine Biology and Ecology*, *289*(2), 263–276. https://doi.org/10.1016/S0022-0981(03)00049-2

Fleming, A. (1995). Growth, intake, feed conversion efficiency and chemosensory preference of the Australian abalone, *Haliotis rubra*. *Aquaculture*, *132*(3–4), 297–311.

Fleming, A. E., VanBarneveld, R. J., & Hone, P. W. (1996). The development of artificial diets for abalone: A review and future directions. *Aquaculture*, *140*(1–2), 5–53. https://doi.org/10.1016/0044-8486(95)01184-6

Flores-Aguilar, R. A., Gutierrez, A., Ellwanger, A., & Searcy-Bernal, R. (2007). Development and current status of abalone aquaculture in Chile. *Journal of Shellfish Research*, *26*(3), 705–711.

Floreto, E. A., Teshima, S.-I., & Koshio, S. (1996). The effects of seaweed diets on the lipid and fatty acids of the Japanese disc abalone *Haliotis discus* hannai. *Fisheries Science*, *62*(4), 582–588.

Gaillard, C., Bhatti, H. S., Novoa-Garrido, M., Lind, V., Roleda, M. Y., & Weisbjerg, M. R. (2018). Amino acid profiles of nine seaweed species and their in situ degradability in dairy cows. *Animal Feed Science and Technology*, *241*, 210–222. https://doi.org/10.1016/j.anifeedsci.2018.05.003

Gallardo, W. G., & Buen, S. M. A. (2003). Evaluation of mucus, Navicula, and mixed diatoms as larval settlement inducers for the tropical abalone *Haliotis asinina*. *Aquaculture*, *221*(1–4), 357–364.

Gao, X., Zhang, M., Li, X., Han, Y., Wu, F., & Liu, Y. (2018). The effects of feeding lactobacillus pentosus on growth, immunity, and disease resistance in *Haliotis discus* hannai Ino. *Fish & Shellfish Immunology*, *78*, 42–51. https://doi.org/10.1016/j.fsi.2018.04.010

García-Bueno, N., Decottignies, P., Turpin, V., Dumay, J., Paillard, C., Stiger-Pouvreau, V., … Fleurence, J. (2014). Seasonal antibacterial activity of two red seaweeds, *Palmaria palmata* and *Grateloupia turuturu*, on European abalone pathogen *Vibrio harveyi*. *Aquatic Living Resources*, *27*(2), 83–89.

García-Carreño, F. L., Navarrete del Toro, M. A., & Serviere-Zaragoza, E. (2003). Digestive enzymes in juvenile green abalone, *Haliotis fulgens*, fed natural food. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *134*(1), 143–150. https://doi.org/10.1016/S1096-4959(02)00221-X

Garcia-Esquivel, Z., & Felbeck, H. (2006). Activity of digestive enzymes along the gut of juvenile red abalone, *Haliotis rufescens*, fed natural and balanced diets. *Aquaculture*, *261*(2), 615–625. https://doi.org/10.1016/j.aquaculture.2006.08.022

Garcia-Esquivel, Z., & Felbeck, H. (2009). Comparative performance of juvenile red abalone, *Haliotis rufescens*, reared in laboratory with fresh kelp and balanced diets. *Aquaculture Nutrition*, *15*(2), 209–217. https://doi.org/10.1111/j.1365-2095.2008.00585.x

Garrett, R., & Grisham, C. (2010). *Biochemistry*. Boston, MA/Belmont, CA: Brooks/Cole Cengage Learning.

Genade, A., Hirst, A., & Smit, C. (1988). Observations on the spawning, development and rearing of the South African abalone *Haliotis midae* Linn. *South African Journal of Marine Science*, *6*(1), 3–12.

Gibson, G. R., & Roberfroid, M. B. (1995). Dietary modulation of the human colonic microbiota: Introducing the concept of prebiotics. *The Journal of Nutrition*, *125*(6), 1401–1412.

Gobet, A., Mest, L., Perennou, M., Dittami, S. M., Caralp, C., Coulombet, C., … Leblanc, C. (2018). Seasonal and algal diet-driven patterns of the digestive microbiota of the European abalone *Haliotis tuberculata*, a generalist marine herbivore. *Microbiome*, *6*(1), 60. https://doi.org/10.1186/s40168-018-0430-7

Gómez-Montes, L., García-Esquivel, Z., D'Abramo, L. R., Shimada, A., Vásquez-Peláez, C., & Viana, M. A. T. (2003). Effect of dietary protein:Energy ratio on intake, growth and metabolism of juvenile green abalone *Haliotis fulgens*. *Aquaculture*, *220*(1), 769–780. https://doi.org/10.1016/S0044-8486(02)00533-1

Gomez-Zavaglia, A., Prieto Lage, M. A., Jimenez-Lopez, C., Mejuto, J. C., & Simal-Gandara, J. (2019). The potential of seaweeds as a source of functional ingredients of prebiotic and antioxidant value. *Antioxidants*, *8*(9), 406.

Gopalakannan, A., & Arul, V. (2006). Immunomodulatory effects of dietary intake of chitin, chitosan and levamisole on the immune system of *Cyprinus carpio* and control of *Aeromonas hydrophila* infection in ponds. *Aquaculture*, *255*(1), 179–187. https://doi.org/10.1016/j.aquaculture.2006.01.012

Grandiosa, R., Merien, F., Young, T., Van Nguyen, T., Gutierrez, N., Kitundu, E., & Alfaro, A. C. (2018). Multi-strain probiotics enhance immune responsiveness and alters metabolic profiles in the New Zealand black-footed abalone (*Haliotis iris*). *Fish & Shellfish Immunology*, *82*, 330–338. https://doi.org/10.1016/j.fsi.2018.08.034

Grandiosa, R., Young, T., Van Nguyen, T., Mérien, F., & Alfaro, A. C. (2020). Immune response in probiotic-fed New Zealand black-footed abalone (*Haliotis iris*) under Vibrio splendidus challenge. *Fish & Shellfish Immunology*, *104*, 633–639. https://doi.org/10.1016/j.fsi.2020.06.007

Green, A. J., Jones, C. L. W., & Britz, P. J. (2011). The protein and energy requirements of farmed South African abalone *Haliotis midae* L. cultured at optimal and elevated water temperatures (Vol. *42*, pp. 1653–1663).

Guerreiro, I., Enes, P., & Oliva-Teles, A. (2015). Effects of short-chain fructooligosaccharides (scFOS) and rearing temperature on growth performance and hepatic intermediary metabolism in gilthead sea bream (*Sparus aurata*) juveniles. *Fish Physiology and Biochemistry*, *41*(5), 1333–1344.

Guerreiro, I., Oliva-Teles, A., & Enes, P. (2015). Improved glucose and lipid metabolism in European sea bass (*Dicentrarchus labrax*) fed short-chain fructooligosaccharides and xylooligosaccharides. *Aquaculture*, *441*, 57–63.

Guillaume, J., Kaushik, S., Bergot, P., & Metailler, R. (2001). *Nutrition and feeding of fish and crustaceans*. London: New York Springer.

Guzmán, J. M., & Viana, M. T. (1998). Growth of abalone *Haliotis fulgens* fed diets with and without fish meal, compared to a commercial diet. *Aquaculture*, *165*(3), 321–331. https://doi.org/10.1016/S0044-8486(98)00271-3

Hadi, J. A., Gutierrez, N., Alfaro, A. C., & Roberts, R. D. (2014). Use of probiotic bacteria to improve growth and survivability of farmed New Zealand abalone (*Haliotis iris*). *New Zealand Journal of Marine and Freshwater Research*, *48*(3), 405–415. https://doi.org/10.1080/00288330.2014.909857

Hahn, K. (1989). Biotic and abiotic factors affecting the culture of abalone. In *Handbook of culture of abalone and other marine gastropods*. (pp. 113–134). Boca Raton, FL: CRC Press.

Hanley, F., Brown, H., & Carberry, J. (1995). *First observations on the effects of mannan oligosaccharide added to the hatchery diets for warmwater Hybrid Red Tilapia*. Paper presented at Symposium conducted at the Meeting of the Nutritional Biotechnology in the Feed & Food Industries: Proceedings of Alltech's 11th Annual Symposium (Suppl. 1) (Abstracts of posters presented). Lexington, KY

Hatae, K., Nakai, H., Shimada, A., Murakami, T., Takada, K., Shirojo, Y., & Watabe, S. (1995). Abalone (*Hariltis discus*): Seasonal variations in chemical composition and textural properties. *Journal of Food Science*, *60*(1), 32–35.

Henry, M. A., Gai, F., Enes, P., Peréz-Jiménez, A., & Gasco, L. (2018). Effect of partial dietary replacement of fishmeal by yellow mealworm (*Tenebrio molitor*) larvae meal on the innate immune response and intestinal antioxidant enzymes of rainbow trout (*Oncorhynchus mykiss*). *Fish & Shellfish Immunology*, *83*, 308–313. https://doi.org/10.1016/j.fsi.2018.09.040

Hooper, C., Day, R., Slocombe, R., Benkendorff, K., Handlinger, J., & Goulias, J. (2014). Effects of severe heat stress on immune function, biochemistry and histopathology in farmed Australian abalone (hybrid *Haliotis laevigata* × *Haliotis rubra*). *Aquaculture*, *432*, 26–37. https://doi.org/10.1016/j.aquaculture.2014.03.032

Hooper, C., Day, R., Slocombe, R., Handlinger, J., & Benkendorff, K. (2007). Stress and immune responses in abalone: Limitations in current knowledge and investigative methods based on other models. *Fish & Shellfish Immunology*, *22*(4), 363–379. https://doi.org/10.1016/j.fsi.2006.06.009

Hoseinifar, S. H., Ahmadi, A., Raeisi, M., Hoseini, S. M., Khalili, M., & Behnampour, N. (2017). Comparative study on immunomodulatory and growth enhancing effects of three prebiotics (galactooligosaccharide, fructooligosaccharide and inulin) in common carp (*Cyprinus carpio*). *Aquaculture Research*, *48*(7), 3298–3307.

Huang, Z.-X., Chen, Z.-S., Ke, C.-H., Zhao, J., You, W.-W., Zhang, J., … Chen, J. (2012). Pyrosequencing of *Haliotis diversicolor* transcriptomes: Insights into early developmental molluscan gene expression. *PLoS One*, *7*(12), e51279.

Hughes, R. N. (1986). *A functional biology of marine gastropods*. Johns Hopkins University Press.

Huntington, T., & Hasan, M. R. (2009). Fish as feed inputs for aquaculture–practices, sustainability and implications: A global synthesis. *FAO Fisheries and Aquaculture Technical Paper*, *518*, 1–61.

Hwang, E. K., Baek, J. M., & Park, C. S. (2009). The mass cultivation of *Ecklonia stolonifera* Okamura as a summer feed for the abalone industry in Korea. *Journal of Applied Phycology*, *21*(5), 585–590.

Jiang, H.-F., Liu, X.-L., Chang, Y.-Q., Liu, M.-T., & Wang, G.-X. (2013). Effects of dietary supplementation of probiotic *Shewanella colwelliana* WA64, *Shewanella olleyana* WA65 on the innate immunity and disease resistance of abalone, *Haliotis discus* hannai Ino. *Fish & Shellfish Immunology*, *35*(1), 86–91.

Johnston, D., Moltschaniwskyj, N., & Wells, J. (2005). Development of the radula and digestive system of juvenile blacklip abalone (*Haliotis rubra*): Potential factors responsible for variable weaning success on artificial diets. *Aquaculture*, *250*(1), 341–355. https://doi.org/10.1016/j.aquaculture.2005.03.012

Jung, W. G., Kim, H. S., Lee, K. W., Kim, Y. E., Choi, D. K., Jang, B. I., … Joo, Y. I. (2016). Growth and body composition effects of tuna byproduct meal substituted for fish meal in the diet of juvenile abalone, *Haliotis discus*. *Journal of the World Aquaculture Society*, *47*(1), 74–81.

Kankainen, M., Setälä, J., Berrill, I. K., Ruohonen, K., Noble, C., & Schneider, O. (2012). How to measure the economic impacts of changes in growth, feed efficiency and survival in aquaculture. *Aquaculture Economics & Management*, *16*(4), 341–364.

Kawamura, T., Saido, T., Takami, H., & Yamashita, Y. (1995). Dietary value of benthic diatoms for the growth of post-larval abalone *Haliotis discus* hannai. *Journal of Experimental Marine Biology and Ecology*, *194*(2), 189–199. https://doi.org/10.1016/0022-0981(95)00099-2

Kemp, J. O. G., Britz, P. J., & Aguero, P. H. T. (2015). The effect of macroalgal, formulated and combination diets on growth, survival and feed utilisation in the red abalone *Haliotis rufescens*. *Aquaculture*, *448*, 306–314. https://doi.org/10.1016/j.aquaculture.2015.06.016

Kitikiew, S., Chen, J.-C., Putra, D. F., Lin, Y.-C., Yeh, S.-T., & Liou, C.-H. (2013). Fucoidan effectively provokes the innate immunity of white shrimp *Litopenaeus vannamei* and its resistance against experimental *Vibrio alginolyticus* infection. *Fish & Shellfish Immunology*, *34*(1), 280–290.

Klebanoff, S. J. (1982). Oxygen dependent cytotoxic mechanisms of phagocytes. *Advances Host Defense Mechanisms*, *1*, 111–162.

Latuihamallo, M., Iriana, D. A., & Apituley, D. (2015). Amino acid and fatty acid of abalone *Haliotis squamata* cultured in different aquaculture systems. *Procedia Food Science*, *3*, 174–181. https://doi.org/10.1016/j.profoo.2015.01.019

Lee, K. W., Kim, H. J., Kim, H. S., Choi, D. G., Bok, J., II, Cho, S. H., … Joo, Y. I. (2017). Effects of dietary carbohydrate sources on growth and body composition of juvenile abalone (*Haliotis discus*, reeve). *Journal of Shellfish Research*, *36*(1), 151–156. https://doi.org/10.2983/036.036.0115

Lee, K. W., Kim, H. S., Choi, D. G., Jang, B. I., Kim, H. J., Yun, A., … Han, H. S. (2017). Effects of substitution of fish meal (FM) and macroalgae (MA) with soybean meal and rice bran in a commercial juvenile abalone (*Haliotis duscus* hannai) diet on growth performance. *Turkish Journal of Fisheries and Aquatic Sciences*, *17*(3), 519–526. https://doi.org/10.4194/1303-2712-v17_3_08

Lee, K. W., Kim, H. S., Jeong, H. S., Kim, J., Yun, A. Y., & Cho, S. H. (2019). Effect of dietary carbohydrate-to-lipid ratio on growth and carcass composition of juvenile abalone, *Haliotis discus*, reeve 1846. *Journal of the World Aquaculture Society*, *50*(3), 604–613. https://doi.org/10.1111/jwas.12485

Li, H., Wei, L., Zhang, G., Cai, Z., Cai, G., Chang, Y., & Xing, K. (2006). Enhancement of larval settlement and metamorphosis through biological and chemical cues in the abalone *Haliotis diversicolor* supertexta. *Aquaculture*, *258*(1), 416–423. https://doi.org/10.1016/j.aquaculture.2006.04.013

Li, P., & Gatlin, D. M. (2004). Dietary brewers yeast and the prebiotic Grobiotic™AE influence growth performance, immune responses and resistance of hybrid striped bass (*Morone chrysops* × *M. saxatilis*) to *Streptococcus iniae* infection. *Aquaculture*, *231*(1), 445–456. https://doi.org/10.1016/j.aquaculture.2003.08.021

Liu, B., Jia, Z., Li, C., Chen, J., & Fang, T. (2020). Hypolipidemic and anti-atherogenic activities of crude polysaccharides from abalone viscera. *Food Science & Nutrition*, *8*(5), 2524–2534.

Loker, E. S. (2010). Gastropod Immunobiology. In K. Söderhäll (Ed.), *Invertebrate immunity* (pp. 17–43). Boston, MA: Springer US. https://doi.org/10.1007/978-1-4419-8059-5_2

Lopes, G., Sousa, C., Bernardo, J., Andrade, P. B., Valentão, P., Ferreres, F., & Mouga, T. (2011). Sterol profiles in 18 macroalgae of the Portuguese coast 1. *Journal of Phycology*, *47*(5), 1210–1218.

Lopez, L. M., & Tyler, P. (2006). Energy budget of cultured female abalone *Haliotis tuberculata* (L.). *Journal of Shellfish Research*, *25*(2), 385–389.

Lourenço, S. O., Barbarino, E., De-Paula, J. C., Pereira, L. O., & Marquez, U. M. L. (2002). Amino acid composition, protein content and calculation of nitrogen-to-protein conversion factors for 19 tropical seaweeds. *Phycological Research*, *50*(3), 233–241.

Macchiavello, J., & Bulboa, C. (2014). Nutrient uptake efficiency of Gracilaria chilensis and Ulva lactuca in an IMTA system with the red abalone Haliotis rufescens. *Latin American Journal of Aquatic Research*, *42*(3), 523–533.

Mai, K. (1998). Comparative studies on the nutrition of two species of abalone, *Haliotis tuberculata* L. and *Haliotis discus* hannai Ino.: VII. Effects of dietary vitamin C on survival, growth and tissue concentration of ascorbic acid. *Aquaculture*, *161*(1), 383–392. https://doi.org/10.1016/S0044-8486(97)00286-X

Mai, K., Mercer, J. P., & Donlon, J. (1994). Comparative studies on the nutrition of two species of abalone, *Haliotis tuberculata* L. and *Haliotis discus* hannai Ino: II. Amino acid composition of abalone and six species of macroalgae with an assessment of their nutritional value. *Aquaculture*, *128*(1), 115–130. https://doi.org/10.1016/0044-8486(94)90107-4

Mai, K., Mercer, J. P., & Donlon, J. (1995). Comparative studies on the nutrition of two species of abalone, *Haliotis tuberculata* L. and *Haliotis discus* hannai Ino. IV. Optimum dietary protein level for growth. *Aquaculture*, *136*(1–2), 165–180. https://doi.org/10.1016/0044-8486(95)01041-6

Manahan, D. (1992). Implications of dissolved organic material in seawater for the energetics of abalone larvae *Haliotis rufescens*: A review. *Abalone of the World: Biology, Fisheries and Culture*, 95–106.

Matanjun, P., Mohamed, S., Mustapha, N. M., & Muhammad, K. (2009). Nutrient content of tropical edible seaweeds, *Eucheuma cottonii*, *Caulerpa lentillifera* and *Sargassum polycystum*. *Journal of Applied Phycology*, *21*(1), 75–80.

Matés, J. M., & Sánchez-Jiménez, F. (1999). Antioxidant enzymes and their implications in pathophysiologic processes. *Frontiers in Bioscience*, *4*(4), D339–D345.

McLean, N. (1965). *Digestion in Haliotis rufescens Swainson*. Berkeley, Ca: University of California.

McLean, N. (1970). Digestion in *Haliotis rufescens* Swainson (Gastropoda: Prosobranchia). *Journal of Experimental Zoology*, *173*(3), 303–318.

Meng, X., Yang, X., Lin, G., Fang, Y., Ruan, Z., Liu, M., … Yang, D. (2019). Mannan oligosaccharide increases the growth performance, immunity and resistance capability against Vibro Parahemolyticus in juvenile abalone *Haliotis discus* hannai Ino. *Fish & Shellfish Immunology*, *94*, 654–660. https://doi.org/10.1016/j.fsi.2019.09.058

Mohan, K., Ravichandran, S., Muralisankar, T., Uthayakumar, V., Chandirasekar, R., Seedevi, P., & Rajan, D. K. (2019). Potential uses of fungal polysaccharides as immunostimulants in fish and shrimp aquaculture: A review. *Aquaculture*, *500*, 250–263. https://doi.org/10.1016/j.aquaculture.2018.10.023

Mouritsen, O. G., Bagatolli, L. A., Duelund, L., Garvik, O., Ipsen, J. H., & Simonsen, A. C. (2017). Effects of seaweed sterols fucosterol and desmosterol on lipid membranes. *Chemistry and Physics of Lipids*, *205*, 1–10. https://doi.org/10.1016/j.chemphyslip.2017.03.010

Mulvaney, W. J., Jahangard, S., Ingram, B. A., Turchini, G. M., & Winberg, P. C. (2015). Recovery of omega-3 profiles of cultivated abalone by dietary macroalgae supplementation. *Journal of Applied Phycology*, *27*(5), 2163–2171. https://doi.org/10.1007/s10811-015-0530-8

Mulvaney, W. J., Winberg, P. C., & Adams, L. (2013). Comparison of macroalgal (Ulva and Grateloupia spp.) and formulated terrestrial feed on the growth and condition of juvenile abalone. *Journal of Applied Phycology*, *25*(3), 815–824. https://doi.org/10.1007/s10811-013-9998-2

Nawaz, A., Bakhsh Javaid, A., Irshad, S., Hoseinifar, S. H., & Xiong, H. (2018). The functionality of prebiotics as immunostimulant: Evidences from trials on terrestrial and aquatic animals. *Fish & Shellfish Immunology*, *76*, 272–278. https://doi.org/10.1016/j.fsi.2018.03.004

Nayak, S. K. (2010). Role of gastrointestinal microbiota in fish. *Aquaculture Research*, *41*(11), 1553–1573.

Nel, A., Jones, C. L., Britz, P. J., & Landzela, S. (2018). The effect of juvenile abalone *Haliotis midae* (Linnaeus, 1758) weaning diet on gut-bacterial formation. *Journal of Shellfish Research*, *37*(1), 191–197.

Nel, A., Pletschke, B. I., & Britz, P. J. (2017). The effect of low-level kelp supplementation on digestive enzyme activity levels in cultured abalone *Haliotis midae* fed formulated feeds. *African Journal of Marine Science*, *39*(2), 175–182. https://doi.org/10.2989/1814232x.2017.1329166

Nel, A., Pletschke, B. I., Jones, C. L. W., Kemp, J., Robinson, G., & Britz, P. J. (2017). Effects of kelp *Ecklonia maxima* inclusion in formulated feed on the growth, feed utilisation and gut microbiota of South African abalone *Haliotis midae*. *African Journal of Marine Science*, *39*(2), 183–192. https://doi.org/10.2989/1814232x.2017.1338203

Nelson, M., Phleger, C., & Nichols, P. (2002). Seasonal lipid composition in macroalgae of the northeastern Pacific Ocean. *Botanica Marina*, *45*(1), 58–65.

Nelson, M. M., Leighton, D. L., Phleger, C. F., & Nichols, P. D. (2002). Comparison of growth and lipid composition in the green abalone, *Haliotis fulgens*, provided specific macroalgal diets. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *131*(4), 695–712. https://doi.org/10.1016/S1096-4959(02)00042-8

Norziah, M. H., & Ching, C. Y. (2000). Nutritional composition of edible seaweed *Gracilaria changgi*. *Food Chemistry*, *68*(1), 69–76.

Nugroho, R. A., & Nur, F. M. (2018). *Insect-based protein: Future promising protein source for fish cultured*. Paper presented at Symposium conducted at the meeting of the IOP Conference Series: Earth and Environmental Science. https://doi.org/10.1088/1755-1315/144/1/012002

Onitsuka, T., Kawamura, T., Ohashi, S., Horii, T., & Watanabe, Y. (2007). Dietary value of benthic diatoms for post-larval abalone *Haliotis diversicolor* associated with feeding transitions. *Fisheries Science*, *73*(2), 295–302. https://doi.org/10.1111/j.1444-2906.2007.01335.x

Picos-García, C., García-Carreño, F. L., & Serviere-Zaragoza, E. (2000). Digestive proteases in juvenile Mexican green abalone, *Haliotis fulgens*. *Aquaculture*, *181*(1), 157–170. https://doi.org/10.1016/S0044-8486(99)00223-9

Preece, M. A. (2006). Sensory qualities of the New Zealand abalone, *Haliotis iris*, reared in offshore structures on artificial diets.

Rajapakse, N., & Kim, S.-K. (2011). Nutritional and digestive health benefits of seaweed. In *Advances in food and nutrition research* (Vol. 64, pp. 17–28). Academic press.

Ringø, E., Olsen, R., Gifstad, T., Dalmo, R., Amlund, H., Hemre, G. I., & Bakke, A. (2010). Prebiotics in aquaculture: A review. *Aquaculture Nutrition*, *16*(2), 117–136.

Ringø, E., Olsen, R. E., Vecino, J. G., Wadsworth, S., & Song, S. (2012). Use of immunostimulants and nucleotides in aquaculture: A review. *Journal of Marine Science: Research & Development*, *1*, 104.

Robertson-Andersson, D. V., Potgieter, M., Hansen, J., Bolton, J. J., Troell, M., Anderson, R. J., Halling C Probyn, T. (2007). *Integrated seaweed cultivation on an abalone farm in South Africa*. Paper presented at Symposium conducted at the meeting of the Nineteenth International Seaweed Symposium.

Robledo, D., & Freile Pelegrin, Y. (1997). Chemical and mineral composition of six potentially edible seaweed species of Yucatan. *Botanica Marina*, *40*(4), 301–306.

Rodrigues, D., Freitas, A. C., Pereira, L., Rocha-Santos, T. A. P., Vasconcelos, M. W., Roriz, M., … Duarte, A. C. (2015). Chemical composition of red, brown and green macroalgae from Buarcos bay in central west coast of Portugal. *Food Chemistry*, *183*, 197–207. https://doi.org/10.1016/j.foodchem.2015.03.057

Roussel, S., Caralp, C., Leblanc, C., Le Grand, F., Stiger-Pouvreau, V., Coulombet, C., … Huchette, S. (2019). Impact of nine macroalgal diets on growth and initial reproductive investment in juvenile abalone Haliotis tuberculata. *Aquaculture*, *513*, 734385. https://doi.org/10.1016/j.aquaculture.2019.734385

Rungrassamee, W., Kingcha, Y., Srimarut, Y., Maibunkaew, S., Karoonuthaisiri, N., & Visessanguan, W. (2014). Mannooligosaccharides from copra meal improves survival of the Pacific white shrimp (*Litopenaeus vannamei*) after exposure to *Vibrio harveyi*. *Aquaculture*, *434*, 403–410.

Rupérez, P. (2002). Mineral content of edible marine seaweeds. *Food Chemistry*, *79*(1), 23–26. https://doi.org/10.1016/S0308-8146(02)00171-1

Ruperez, P., & Saura-Calixto, F. (2001). Dietary fibre and physicochemical properties of edible Spanish seaweeds. *European Food Research and Technology*, *212*(3), 349–354.

Sales, J., & Janssens, G. (2004). *Use of feed ingredients in artificial diets for abalone: a brief update*. Paper presented at Symposium conducted at the meeting of the Nutrition Abstracts and Reviews: Series B.

Sales, J., Truter, P. J., & Britz, P. J. (2003). Optimum dietary crude protein level for growth in South African abalone (*Haliotis midae* L.). *Aquaculture Nutrition*, *9*, 85–89.

Sarker, P. K., Kapuscinski, A. R., Lanois, A. J., Livesey, E. D., Bernhard, K. P., & Coley, M. L. (2016). Towards sustainable aquafeeds: Complete substitution of fish oil with marine microalga Schizochytrium sp. improves growth and fatty acid deposition in juvenile Nile tilapia (*Oreochromis niloticus*). *PLoS One*, *11*(6), e0156684.

Shepherd, S. (1992). Food preference of three Australian abalone species with a review of the algal food of abalone. *Abalone of the World. Biology, Fisheries and Culture*, 169–181.

Shepherd, S., & Turner, J. (1985). Studies on southern Australian abalone (genus Haliotis). VI. Habitat preference, abundance and predators of juveniles. *Journal of Experimental Marine Biology and Ecology*, *93*(3), 285–298.

Shepherd, S. A., Tegner, M. J., & Guzman del Proo, S. A. (1992). *Abalone of the world. Biology, fisheries and culture*. Paper presented at Proceedings of the 1st International Symposium on Abalone, Cambridge: Fishing News Books.

Shi, L., Hao, G., Chen, J., Ma, S., & Weng, W. (2020). Nutritional evaluation of Japanese abalone (*Haliotis discus* hannai Ino) muscle: Mineral content, amino acid profile and protein digestibility. *Food Research International*, *129*, 108876. https://doi.org/10.1016/j.foodres.2019.108876

Siwicki, A. K., Anderson, D. P., & Rumsey, G. L. (1994). Dietary intake of immunostimulants by rainbow trout affects nonspecific immunity and protection against furunculosis. *Veterinary Immunology and Immunopathology*, *41*(1), 125–139. https://doi.org/10.1016/0165-2427(94)90062-0

Staykov, Y., Spring, P., Denev, S., & Sweetman, J. (2007). Effect of a mannan oligosaccharide on the growth performance and immune status of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture International*, *15*(2), 153–161.

Stenberg, O. K., Holen, E., Piemontese, L., Liland, N. S., Lock, E.-J., Espe, M., & Belghit, I. (2019). Effect of dietary replacement of fish meal with insect meal on in vitro bacterial and viral induced gene response in Atlantic salmon (*Salmo salar*) head kidney leukocytes. *Fish & Shellfish Immunology*, *91*, 223–232. https://doi.org/10.1016/j.fsi.2019.05.042

Stiger-Pouvreau, V., Bourgougnon, N., & Deslandes, E. (2016). Carbohydrates from seaweeds. In *Seaweed in health and disease prevention* (pp. 223–274). Academic Press.

Stone, D. A. J., Bansemer, M. S., Lange, B., Schaefer, E. N., Howarth, G. S., & Harris, J. O. (2014). Dietary intervention improves the survival of cultured greenlip abalone (*Haliotis laevigata* Donovan) at high water temperature. *Aquaculture*, *430*, 230–240. https://doi.org/10.1016/j.aquaculture.2014.03.047

Stone, D. A. J., Harris, J. O., Wang, H. R., Mercer, G. J., Schaefer, E. N., & Bansemer, M. S. (2013). Dietary protein level and water temperature interactions for Greenlip abalone *Haliotis laevigata*. *Journal of Shellfish Research*, *32*(1), 119–130. https://doi.org/10.2983/035.032.0118

Su, X. Q., Antonas, K. N., & Li, D. (2004). Comparison of n-3 polyunsaturated fatty acid contents of wild and cultured Australian abalone. *International Journal of Food Sciences and Nutrition*, *55*(2), 149–154. https://doi.org/10.1080/09637480410001666469

Suleria, H., Masci, P., Gobe, G., & Osborne, S. (2017). Therapeutic potential of abalone and status of bioactive molecules: A comprehensive review. *Critical Reviews in Food Science and Nutrition*, *57*(8), 1742–1748.

Tahil, A., & Juinio-Menez, M. (1999). Natural diet, feeding periodicity and functional response to food density of the abalone,*Haliotis asinina* L., (Gastropoda). *Aquaculture Research*, *30*(2), 95–107.

Takami, H. (2003). Feeding ecology of an abalone, *Haliotis discus* hannai, in their early life stages. *Aquaculture and pathobiology of crustacean and other species*. Davis and Santa Barbara, CA, 180.

Takami, H., & Kawamura, T. (2003). Dietary changes in the abalone, *Haliotis discus* hannai, and relationship with the development of the digestive organ. *Japan Agricultural Research Quarterly*, *37*(2), 89–98.

Takenaka, S., Sugiyama, S., Ebara, S., Miyamoto, E., Abe, K., Tamura, Y., … Nakano, Y. (2001). Feeding dried purple laver (nori) to vitamin B 12-deficient rats significantly improves vitamin B 12 status. *British Journal of Nutrition*, *85*(6), 699–703.

Tanaka, R., Ootsubo, M., Sawabe, T., Ezura, Y., & Tajima, K. (2004). Biodiversity and in situ abundance of gut microflora of abalone (*Haliotis discus* hannai) determined by culture-independent techniques. *Aquaculture*, *241*(1), 453–463. https://doi.org/10.1016/j.aquaculture.2004.08.032

Tanaka, R., Sugimura, I., Sawabe, T., Yoshimizu, M., & Ezura, Y. (2003). Gut microflora of abalone *Haliotis discus* hannai in culture changes coincident with a change in diet. *Fisheries Science*, *69*(5), 951–958.

Thongrod, S., Tamtin, M., Chairat, C., & Boonyaratpalin, M. (2003). Lipid to carbohydrate ratio in donkey's ear abalone (*Haliotis asinina*, Linne) diets. *Aquaculture*, *225*(1), 165–174. https://doi.org/10.1016/S0044-8486(03)00287-4

Troell, M., Robertson-Andersson, D., Bolton, J. J., Anderson, R. J., Probyn, T., Maneveldt, G., & Halling, C. (2006). Abalone farming in South Africa: An overview with perspectives on kelp resources, abalone feed, potential for on-farm seaweed production and socio-economic importance. *Aquaculture*, *257*(1–4), 266–281. https://doi.org/10.1016/j.aquaculture.2006.02.066

Tung, C. H., & Alfaro, A. C. (2011). Effect of dietary protein and temperature on the growth and health of juvenile New Zealand black-footed abalone (*Haliotis iris*). *Aquaculture Research*, *42*(3), 366–385. https://doi.org/10.1111/j.1365-2109.2010.02631.x

Tutschulte, T. C., & Connell, J. H. (1988). Feeding behavior and algal food of three species of abalones(Haliotis) in southern California. *Marine Ecology Progress Series. Oldendorf*, *49*(1), 57–64.

Uki, N., Kemuyama, A., & Watanabe, T. (1985). Development of semipurified test diets for abalone [*Haliotis discus* hannai]. *Bulletin of the Japanese Society of Scientific Fisheries (Japan)*, *51*, 1825–1833.

Uki, N., Sugiura, M., & Watanabe, T. (1986). Requirement of essential fatty acids in the abalone. *Haliotis discus* hannai. *Bulletin of the Japanese Society of Scientific Fisheries*, *52*(6), 1013–1023.

Valente, L. M., Araújo, M., Batista, S., Peixoto, M. J., Sousa-Pinto, I., Brotas, V., … Rema, P. (2016). Carotenoid deposition, flesh quality and immunological response of *Nile tilapia* fed increasing levels of IMTA-cultivated Ulva spp. *Journal of Applied Phycology*, *28*(1), 691–701.

Van Doan, H., Tapingkae, W., Moonmanee, T., & Seepai, A. (2016). Effects of low molecular weight sodium alginate on growth performance, immunity, and disease resistance of tilapia, *Oreochromis niloticus*. *Fish & Shellfish Immunology*, *55*, 186–194. https://doi.org/10.1016/j.fsi.2016.05.034

van Rensburg, M. J., & Coyne, V. E. (2009). The role of electron transport in the defence response of the South African abalone, *Haliotis midae*. *Fish & Shellfish Immunology*, *26*(1), 171–176.

Venter, L., Loots, D. T., Mienie, L. J., Jansen van Rensburg, P. J., Mason, S., Vosloo, A., & Lindeque, J. Z. (2018). Uncovering the metabolic response of abalone (*Haliotis midae*) to environmental hypoxia through metabolomics. *Metabolomics*, *14*(4), 49. https://doi.org/10.1007/s11306-018-1346-8

Venter, L., Loots, D. T., Vosloo, A., van Rensburg, P. J., & Lindeque, J. Z. (2018). Abalone growth and associated aspects: Now from a metabolic perspective. *Reviews in Aquaculture*, *10*(2), 451–473. https://doi.org/10.1111/raq.12181

Viana, M. T., Correa, G., Lazo, J. P., Frías-Díaz, R., Durazo-Beltrán, E., & Vasquez-Pelaez, C. (2007). Digestive physiology and metabolism of green abalone *Haliotis fulgens* from postlarvae to juvenile, fed three different diatoms. *Aquaculture*, *271*(1–4), 449–460.

Viana, M. T., López, L. M., García-Esquivel, Z., & Mendez, E. (1996). The use of silage made from fish and abalone viscera as an ingredient in abalone feed. *Aquaculture*, *140*(1–2), 87–98.

Vieira, E. F., Soares, C., Machado, S., Oliva-Teles, M. T., Correia, M., João Ramalhosa, M., … Delerue-Matos, C. (2020). Development of new canned chub mackerel products incorporating edible seaweeds—Influence on the minerals and trace elements composition. *Molecules*, *25*(5), 1133.

Viera, M. P., Courtois de Viçose, G., Robaina, L., & Izquierdo, M. S. (2015). First development of various vegetable-based diets and their suitability for abalone Haliotis tuberculata coccinea reeve. *Aquaculture*, *448*, 350–358. https://doi.org/10.1016/j.aquaculture.2015.05.031

Viera, M. P., de Vicose, G. C., Gómez-Pinchetti, J. L., Bilbao, A., Fernandez-Palacios, H., & Izquierdo, M. S. (2011). Comparative performances of juvenile abalone (*Haliotis tuberculata* coccinea reeve) fed enriched vs non-enriched macroalgae: Effect on growth and body composition. *Aquaculture*, *319*(3), 423–429. https://doi.org/10.1016/j.aquaculture.2011.07.024

Viera, M. P., Gómez Pinchetti, J. L., Courtois de Vicose, G., Bilbao, A., Suárez, S., Haroun, R. J., & Izquierdo, M. S. (2005). Suitability of three red macroalgae as a feed for the abalone *Haliotis tuberculata* coccinea reeve. *Aquaculture*, *248*(1), 75–82. https://doi.org/10.1016/j.aquaculture.2005.03.002

Vosloo, A., Laas, A., & Vosloo, D. (2013). Differential responses of juvenile and adult South African abalone (*Haliotis midae* Linnaeus) to low and high oxygen levels. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *164*(1), 192–199.

Wang, S.-H., & Chen, J.-C. (2005). The protective effect of chitin and chitosan against *Vibrio alginolyticus* in white shrimp *Litopenaeus vannamei*. *Fish & Shellfish Immunology*, *19*(3), 191–204. https://doi.org/10.1016/j.fsi.2004.11.003

Wood, A., & Buxton, C. (1996). Aspects of the biology of the abalone *Haliotis midae* (Linne, 1758) on the east coast of South Africa. 1. Feeding biology. *South African Journal of Marine Science*, *17*(1), 61–68.

Wu, Y.-S., Tseng, T.-Y., & Nan, F.-H. (2016). Beta-1,3-1,6-glucan modulate the non-specific immune response to enhance the survival in the *Vibrio alginolyticus* infection of Taiwan abalone (*Haliotis diversicolor* supertexta). *Fish & Shellfish Immunology*, *54*, 556–563. https://doi.org/10.1016/j.fsi.2016.04.127

Yang, S. J., & Min, B. H. (2019). Sub-optimal or reduction in temperature and salinity decrease antioxidant activity and cellularity in the hemolymph of the Pacific abalone (*Haliotis discus* hannai). *Fish & Shellfish Immunology*, *84*, 485–490. https://doi.org/10.1016/j.fsi.2018.10.041

Yu, H. H., Liang, X. F., Chen, P., Wu, X. F., Zheng, Y. H., Luo, L., … Xue, M. (2019). Dietary supplementation of Grobiotic®-A increases short-term inflammatory responses and improves long-term growth performance and liver health in largemouth bass (*Micropterus salmoides*). *Aquaculture*, *500*, 327–337. https://doi.org/10.1016/j.aquaculture.2018.10.033

Yu, S. N., Duan, Z. L., Huang, B., Wang, Y. L., Wang, X. B., Li, Y., … Qiu, Y. (2014). Effects of different diet combinations on the growth of juvenile abalone (*Haliotis asinina* Linnaeus). *Animal Feed Science and Technology*, *194*, 106–112. https://doi.org/10.1016/j.anifeedsci.2014.04.018

Zeeman, Z., Branch, G., Peschak, T., & Pillay, D. (2012). Assessing the ecosystem effects of the abalone *Haliotis midae* from its diet and foraging behaviour. *African Journal of Marine Science*, *34*(2), 205–214.

Zhang, W., Mai, K., Yao, C., Xu, W., Wang, W., Liufu, Z., & Wang, X. (2009). Effects of dietary cholesterol on growth, survival and body composition of juvenile abalone *Haliotis discus* hannai Ino. *Aquaculture*, *295*(3), 271–274. https://doi.org/10.1016/j.aquaculture.2009.07.006

Zhao, J., Ling, Y., Zhang, R., Ke, C., & Hong, G. (2018). Effects of dietary supplementation of probiotics on growth, immune responses, and gut microbiome of the abalone *Haliotis diversicolor*. *Aquaculture*, *493*, 289–295. https://doi.org/10.1016/j.aquaculture.2018.05.011

Zheng, Z., Wang, K., Gatlin, D. M., III, & Ye, J. (2011). Evaluation of the ability of GroBiotic®-A to enhance growth, muscle composition, immune responses, and resistance against *Aeromonas hydrophila* in Nile tilapia, *Oreochromis niloticus*. *Journal of the World Aquaculture Society*, *42*(4), 549–557.

Zhu, B.-W., Zhou, D.-Y., Yang, J.-F., Li, D.-M., Yin, H.-L., & Tada, M. (2009). A neutral polysaccharide from the abalone pleopod, *Haliotis discus* hannai Ino. *European Food Research and Technology*, *228*(4), 591–595.

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