Ann. Anim. Sci., Vol. 26 (2026) 865–895 *DOI: 10.2478/aoas-2025-0092*

RED SEAWEEDS IN AQUACULTURE: IMPACTS ON GROWTH, IMMUNITY, ANTIOXIDANT STATUS, GENE EXPRESSION, AND GUT HEALTH – A REVIEW

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Abstract

Red seaweeds (*Rhodophyta*) and their polysaccharides represent promising, sustainable solutions for boosting aquaculture productivity. Rich in bioactive compounds such as carrageenan, agar, and sulfated galactans, these seaweeds have demonstrated the ability to improve growth, health, and disease resistance in various aquaculture species. This review examines the applications, benefits, and limitations of red seaweeds in aquaculture, with particular attention to their roles as feed binders, partial fishmeal replacements, feed supplements, and immunostimulants. Species such as *Gracilaria*, *Kappaphycus*, and *Porphyra* have been shown to enhance immune responses, promote gut health, and mitigate nutrient pollution in aquaculture systems. Despite these advantages, challenges remain, including high cultivation costs, variability in bioactivity, and supply chain constraints. This review highlights the growing potential of red seaweeds for sustainable aquaculture while identifying research needs related to dosage optimization, delivery strategies, and elucidating the molecular mechanisms of their effects. Supplementation with red seaweeds aligns with the United Nations' Sustainable Development Goals, offering an eco-friendly alternative to antibiotics with the potential to yield both environmental and economic benefits in aquaculture.

Key words: red seaweed, polysaccharides, aquaculture, immunostimulants, feed binders, sustainable aquaculture, disease resistance

Aquaculture is one of the fastest-growing sectors in global food production and plays a crucial role in ensuring nutritional security worldwide (FAO, 2020; Gabriel et al., 2024 a). With an estimated 109 million tons (MT) of fish projected to be produced by 2030, the demand for sustainable, affordable, and functional feed ingredients is more pressing than ever. The continued reliance on fishmeal and synthetic additives is being re-evaluated due to escalating costs, environmental concerns, and health risks associated with the overuse of antibiotics and chemotherapeutics (Allameh et al., 2016; WHO, 2006; Kamble et al., 2018; Daunde et al., 2025). Consequently, natural, and sustainable alternatives, such as red seaweeds, are gaining attention for their multifaceted roles in aquaculture, including promoting growth, enhancing immunity, supporting gut health, and contributing to environmental sustainability.

Despite these advancements, aquaculture continues to face major challenges from both infectious and non-infectious diseases (Vatsos and Rebours, 2015), substantially impact productivity and profitability. Disease outbreaks alone are estimated to cost the global aquaculture industry over US$6 billion annually (Stentiford et al., 2017). Although antibiotics and chemotherapeutics have traditionally been employed to manage these issues, their widespread use raises concerns regarding antimicrobial resistance, environmental contamination, and residue accumulation in aquatic species, posing risks to both human and ecosystem health (Allameh et al., 2016; WHO, 2006; Kamble et al., 2024 a, b, c).

These limitations have accelerated the search for eco-friendly, health-promoting alternatives. Among these, marine macroalgae, particularly red seaweeds, have emerged as promising candidates (Karnjana et al., 2019; Soowannayan et al., 2019 a, b; Yatip et al., 2018; Romero et al., 2012; Kamble et al., 2024 d, 2022; Yostawonkul et al., 2023; Trullàs et al., 2022). Globally, seaweeds are integral components of marine ecosystems, with produc-

tion reaching approximately 35.8 MT in 2023, 98% of which is concentrated in Asia (World Bank, 2023). Red seaweeds (Rhodophyta), distinguished by the pigment R-phycoerythrin, are widely used in the food, pharmaceutical, and aquaculture sectors (Hoffman and Dubinsky, 2010).

Dominant genera such as *Porphyra*, *Gelidium*, *Eucheuma*, and *Gracilaria* lead global red seaweed production, primarily serving the carrageenan and agar industries (Chopin and Tacon, 2020). In aquaculture, red seaweeds have been explored as feed binders, dietary supplements, and alternative protein sources (Valente et al., 2006; Bambaranda et al., 2024), offering benefits such as improved growth, enhanced disease resistance, stress mitigation, and nutrient recycling in intensive systems (Chen et al., 2012; Fu et al., 2007; Sirirustananun et al., 2011; Lin et al., 2011; Kanjana et al., 2011; Troell et al., 1999).

Red seaweeds are increasingly valued for their rich nutritional and biochemical composition, including high-quality proteins, essential polyunsaturated fatty acids (PUFAs) such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), vitamins, minerals, and a wide range of bioactive compounds like sulfated polysaccharides, polyphenols, and phycobiliproteins (Holdt and Kraan, 2011). These constituents are linked to diverse pharmacological properties including immunomodulatory (de Jesus Raposo et al., 2015; Hamed et al., 2015; Rudtanatip et al., 2017, 2018, 2015; Kamble et al., 2024 d), antibacterial (Karnjana et al., 2020, 2019; Kamble et al., 2022), and antioxidant properties (Díaz-Rosales et al., 2007; Li et al., 2009).

Multiple studies have demonstrated that dietary inclusion of red seaweeds improves growth performance, immune response, gut health, antioxidant status, and disease resistance in a variety of aquaculture species (Díaz-Rosales et al., 2007; Safavi et al., 2019; Mendoza Rodriguez et al., 2017; Bakky et al., 2023; Ferreira et al., 2022). Their integration into aquaculture practices not only supports animal health but also aligns with global sustainability goals, offering economic and environmental advantages.

Given their broad-spectrum benefits, red seaweeds contribute meaningfully to the United Nations Sustainable Development Goals (SDGs), including Zero Hunger (Schubel and Thompson, 2019), Good Health and Well-Being (Doumeizel and Aass, 2020), and Climate Action (Sangsayan et al., 2025; Ross et al., 2023). The review aims to provide a comprehensive evaluation of the roles and applications of red seaweeds and their derived polysaccharides as sustainable feed additives in aquaculture. It critically examines their effects on growth, immunity, oxidative balance, gut health, and disease resistance, while addressing current challenges such as bioactivity variability, cultivation costs, and regulatory constraints.

Composition of red seaweeds

Red seaweeds possess a unique and diverse biochemical composition that underpins their functional value in aquaculture. They are particularly rich in sulfated polysaccharides, such as agar, carrageenan, and agaran, which can comprise up to 50% of their dry weight. These compounds exhibit gelling, emulsifying, and immunostimulatory properties, contributing to improved gut health, immune modulation, and prebiotic activity in aquatic animals (Holdt and Kraan, 2011; Cian et al., 2015).

In terms of macronutrients, red seaweeds typically contain 10–44% protein and offer a well-balanced amino acid profile, including essential amino acids like lysine and methionine. This makes them promising alternative protein sources in aquafeeds (Fleurence et al., 2018). Additionally, they are rich in PUFAs, particularly EPA and DHA, which are vital for immune function and development in fish and shrimp (Wells et al., 2017).

Red seaweeds are also excellent sources of micronutrients, providing vitamins (A, C, E, and B-complex) and minerals such as iodine, iron, calcium, magnesium, and zinc, each critical for metabolic and physiological processes in aquatic organisms (El-Beltagi et al., 2022). Furthermore, they are abundant in antioxidant compounds like polyphenols, flavonoids, and phycobiliproteins (e.g., phycoerythrin), which help combat oxidative stress and strengthen cellular defense mechanisms in aquaculture species (Čmiková et al., 2024; Freitas et al., 2021; Hejna et al., 2024).

Significance of red seaweeds in aquaculture practices

Red seaweeds are widely utilized in aquaculture due to their unique biochemical composition, offering notable advantages over brown and green seaweeds. Species such as *Gracilaria*, *Kappaphycus*, and *Porphyra* are rich in valuable polysaccharides like agar and carrageenan, which are extensively used in both the food industry and aquaculture. These compounds function as binders and functional additives that enhance pellet quality and stability (McHugh, 2003). Additionally, they contribute to improved gut health and immunity in aquatic species, making red seaweeds particularly suitable for aquafeed formulation (Villamil et al., 2019; Van Doan et al., 2023).

Red seaweeds generally possess higher protein content than brown seaweeds, making them more nutritious feed ingredient for fish and shellfish (Fleurence et al., 2018). Their bioactive constituents, including antioxidants, vitamins, and essential fatty acids, further enhance growth performance, health, and disease resistance in aquaculture species (Holdt and Kraan, 2011).

Moreover, red seaweeds thrive in tropical and subtropical regions, ensuring their availability in many areas where aquaculture is practiced (Hafting et al., 2012). They are also well-suited for integration into multi-trophic aquaculture systems (IMTA), where they play a critical role in nutrient management by absorbing excess nitrogen and phosphorus from fish farming operations (Chopin and Tacon, 2020). In comparison, brown seaweeds are primarily valued for alginates and green seaweeds for their chlorophyll-rich biomass, but their use

is often constrained by regional preferences, processing complexities, or comparatively lower economic returns (Tiwari and Troy, 2015). Consequently, the versatility, abundance, and functional benefits of red seaweeds make them a preferred choice for enhancing both sustainability and productivity in modern aquaculture systems.

The VOSviewer network visualization (Figure 1) further illustrates the interconnected research areas surrounding red seaweed applications in aquaculture. At the center of the network is "seaweed", with specific emphasis on red algae (*Gracilaria*) and its polysaccharides, such as carrageenan and agar, linked to key concepts like aquaculture, growth rate, biomass, and photosynthesis. The green cluster highlights the associations with aquaculture systems and nutritional supplements for fish health. The red cluster connects red algae to marine environments, eutrophication, and bioremediation, indicating its role in water quality management. Meanwhile, the blue cluster explores the biological attributes of red algae, particularly their antioxidant-rich polysaccharides, reinforcing their contribution to both environmental sustainability and economic viability in aquaculture.

Growth-promoting effects of red seaweeds in aquaculture

In aquaculture, numerous studies have investigated the incorporation of feed additives to enhance the growth performance of aquatic animals. Dietary supplementation with red seaweeds and their polysaccharides has demonstrated beneficial effects across various aquatic species (Figure 2; Tables 1 and 2).

Feed binders

Feed binders are essential in aquaculture for improving feed stability, minimizing nutrient leaching, reducing water contamination, and boosting overall production efficiency (Paolucci et al., 2012). Red seaweeds such as *Gracilaria* and *Kappaphycus* are particularly effective in stabilizing feed, owing to their high polysaccharide content. Red seaweeds, once washed, dried, and ground, offer fish farmers an affordable and practical feed additive.

Gracilaria heteroclada and *Kappaphycus alvarezii* are among the most extensively studied red seaweeds for their binding properties and ability to enhance water stability in feed pellets when used at inclusion levels of 5–10%. Incorporating *G. heteroclada* and *K. alvarezii* into diets for species such as giant tiger prawn (*Penaeus monodon)* and Asian seabass (*Lates calcarifer*) has significantly improved pellet water stability, reduced pellet fragmentation, and prevented nutrient leaching, ultimately enhancing feed uptake (Peñaflorida and Golez, 1996; Shapawi et al., 2015). Notably, studies indicate that *K. alvarezii* achieves optimal results at a 5% inclusion rate without compromising the digestibility.

Despite their advantages, limitations have been observed when red seaweeds are included at high levels. For example, inclusion of *Gracilaria* sp. above 10% has been shown to impair growth performance in species such as striped snakehead (*Channa striatus*), likely due to increased nutrient leaching and reduced feed integrity (Hashim and Saat, 1992). Therefore, maintaining an optimal balance between binder effectiveness and digestibility is crucial for maximizing feed performance while controlling costs.

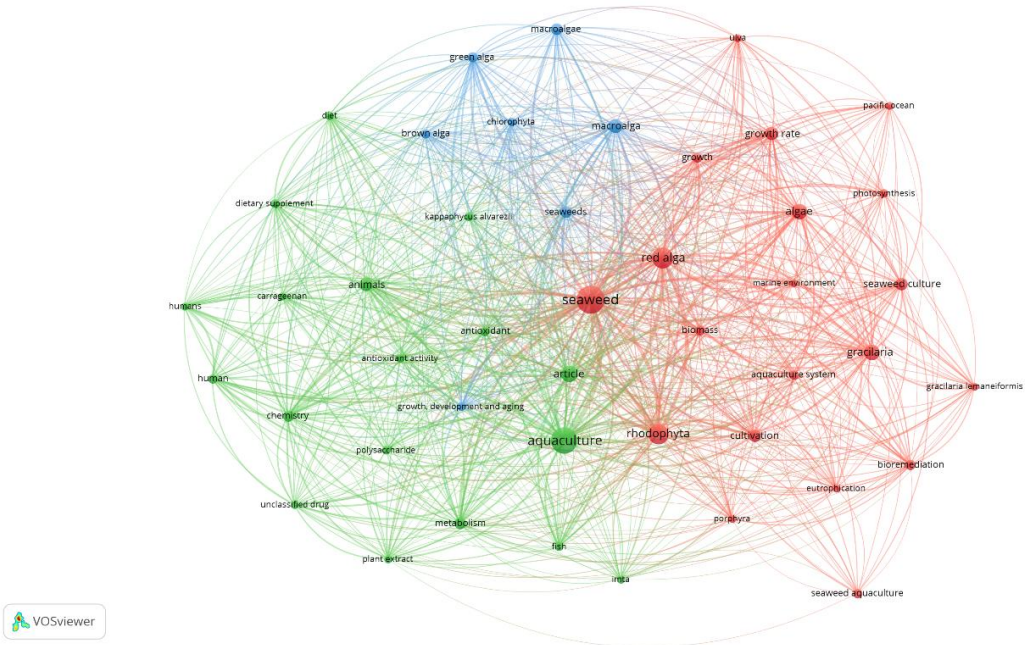


Figure 1. Bibliometric network analysis of red seaweed, polysaccharides, and their applications in aquaculture

Table 1. Application of red seaweed and their derived polysaccharide on shellfish culture: Effects on growth, immune, antioxidant status, gene expression, and intestinal health

Seaweed (form/ solvent extract)	Treatment regimen (dose/ route/duration (day (D))	Pathogen (S)	GP; BC; ADC	H; S; I; IG; A; E	IM; IE; IMB	RPS (%); OD	Application	Reference
1	2	3	4	5	6	7	8	9
Giant tiger prawn (*Penaeus monodon*)								
Asparagopsis sp. (methanol)	285, 575, 850, 1150 mg/kg/ oral/30	*V. harveyi*; *V. alginolyticus*; *V. parahaemolyticus*; *Photobacterium damselae*	Not measured	Not reported	Not measured	79.6, 74.7, 83.5, 80.9; 850 mg	Antibacterial	Manilal et al. (2012)
A. taxiformis (methanol)	850 mg/kg/oral/28	*V. alginolyticus; V. harveyi; V. parahemolyticus; V. fischeri; V. vulnificus*	Not measured	**H:** *HC* (+), *GC* (+), *THC* (+), *WBC* (+); **I:** *Pha* (+), *Agt* (+), *PO* (+)	Not measured	64, 68, 75, 87, 81; 850 mg	Antibacterial, immunostimulant	Manilal et al. (2013)
Gracilaria sp.	20 mg/mL/oral/14	*V. parahaemolyticus*	Not measured	Not measured	Not measured	86.1	Antibacterial	Lim et al. (2019)
G. fisheri (ethanol)	0.5, 1.0 mg/kg/injection/14	*V. harveyi*	Not measured	**H**: *THC* (+); **I:** *PO* (+); **A:** *SOD* (+), O^{-2} (+)	Not measured	82.6; 1 mg	Antibacterial, immunostimulant	Kanjana et al. (2011)
	50, 100 µg/mL/oral/12	*V. harveyi; V. parahaemolyticus*	Not measured	**IG:** *VopD* (-)	Not measured	83, 93.3; 100 µg	Antibiofilm	Karnjana et al. (2019)
G. fisheri (sulfated galactans)	100, 200 mg/mL/oral/7	WSSV	Not measured	**H:** *THC* (+); **I:** *PO* (+); **A:** *SOD* (+), O^{-2} (+)	Not measured	60.5; 200 mg	Antiviral, immunostimulant	Wongprasert et al. (2014)
	10, 25, 50, 100, 500, 1000 µg/mL/*in vitro*/not reported	WSSV	Not measured	Not measured	Not measured	90; 500 µg	Antiviral	Rudtanatip et al. (2014)
G. heteroclada (dried powder)	3, 5, 7, and 10%/oral/56	No pathogen	**GP:** *FW* (+), *SGR* (+), *FCR* (-)	Not measured	Not measured	10%	Feed binder	Peñaflorida and Golez (1996)
G. lichenoides (dried powder)	3, 8%/oral/56	Not measured	**GP:** *SGR* (+); **BC:** *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	**IG:** *mtMnSOD* (+), *CAT mRNA* (+), *GSH Px mRNA* (+), *Trx* (+), *Hippo* (+), *Nrf2* (+); **A:** *TAC* (+), *SOD* (+), *GSH-Px* (+), *CAT* (+), *POD* (↔), *MDA* (+), **E:** *Lip* (+)	**IE:** *Lip* (+), **IM** (+), **IMB** (+)	90; 3%	Growth promoter, antioxidant, modulated gut microbiota	Tian et al. (2024)
G. tenuistipitata	1.0, 1.5, 2.0 kg/m^3/ co-culture/30	*V. parahaemolyticus*	**GP:** *FW* (↔), *SGR* (↔)	Not measured	Not measured	82.2; 2.0 kg	Antibacterial	Anh et al. (2020)
G. verrucosa	2.0 kg/m^3/co-culture/28	No pathogen	**GP:** *FW* (+), *SGR* (+)	Not measured	Not measured	Not reported	Growth promoter	Izzati (2011)

Table 1 – contd.

1	2	3	4	5	6	7	8	9
Kappaphycus alvarezii (dried powder)	3, 5, 7, 10%/oral/56	No pathogen	**GP:** *FW* (+), *SGR* (+), *FCR* (-)	Not measured	Not measured	5%	Feed binder	Peñaflorida and Golez (1996)
K. alvarezii (ethyl acetate)	2 g/10 L/immersion/30	*V. harveyi*	Not measured	Not measured	Not measured	60.3; 2 g	Antibiofilm	Sivakumar et al. (2014)
Whiteleg shrimp (*Penaeus vannamei*)								
C. crispus (κ-carrageenan)	6 µg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (↔); **I:** *Pha* (↔), *PO* (+), *RB* (+)	Not measured	NA	Antibacterial, immunostimulant	Yeh and Chen (2008)
Eucheuma cottonii (κ-carrageenan)	6 µg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (↔); **I:** *Pha* (↔), *PO* (↔), *RB* (↔)	Not measured	NA	Immunosuppressant	Yeh and Chen (2008)
E. spinosa (ι-carrageenan)	6 µg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (↔); **I:** *Pha* (↔), *PO* (↔), *RB* (↔)	Not measured	NA	Immunosuppressant	Yeh and Chen (2008)
Gelidium amansii (hot water)	4, 6 mg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (+); **I:** *PO* (+), *RB* (+), *Pha* (+); **A:** *SOD* (+)	Not measured	55; 6 mg	Antibacterial, immunostimulant	Fu et al. (2007)
	200, 400, 600 mg/L/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (+); **I:** *PO* (+), *RB* (+), *Pha* (+); **A:** *SOD* (+)	Not measured	400 mg	Immunostimulant	Fu et al. (2007)
	0.5, 1, 2 g/kg/oral/28	*V. alginolyticus*	**GP:** *WG* (↔)	**H**: *THC* (+); **I:** *PO* (+), *RB* (+), *Pha* (+); **A:** *SOD* (+)	Not measured	80; 0.5 g	Antibacterial, immunostimulant	Fu et al. (2007)
Gigartina acicularis; *G. pistillata* (λ-carrageenan)	6 µg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (+); **I:** *Pha* (+), *PO* (+), *RB* (↔)	Not measured	NA	Antibacterial, immunostimulant	Yeh and Chen (2008)
G. birdiae (sulfated polysaccharide)	0.3%/oral/5	WSSV	Not measured	**H:** *THC* (+), *GC* (↔), *HC* (↔); **I:** *α2M* (+), *PO* (↔), *RB* (+), *Agt* (-)	Not measured	95; 0.30%	Antiviral, immunostimulant	Cantelli et al. (2019)
G. corticata	200, 400 g/m^2/co-culture/45	No pathogen	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (-)	Not measured	Not measured	400 g/m^2	Growth promoter	Fourooghifard et al. (2017)
G. fisheri (sulfated galactans)	0.5, 1, 2%/oral/7	*V. parahaemolyticus*	Not measured	**IG**: *p-NF-kB/b-actin* (+), *IMD/EF-1a* (+), *IKKb/EF-1a* (+), *IKKε/EF-1a* (+), *PEN-4* (+), *proPO-I* (+), *Cr* (+)	Not measured	47.66%; 2%	Antibacterial, immunostimulant	Rudtanatip et al. (2017)
	100 µg/*in vitro*/not reported	Not measured	Not measured	**IG:** *p-NF-kB/b-actin* (+), *IMD/EF-1a* (+), *IKKb/EF-1a* (+), *IKKε/EF-1a* (+), *PEN-4* (+), *proPO-I* (+), *Cr* (+)	Not measured	100 µg	Immunostimulant	Rudtanatip et al. (2015)

Table 1 – contd.

1	2	3	4	5	6	7	8	9
G. gracilis	2 kg/m^3/co-culture/60	No pathogen	**GP:** *SGR* (↔), *WG* (↔), *FCR* (↔)	Not measured	Not measured	-	Growth promoter	Tien et al. (2024)
G. lemaneiformis (dried powder)	1, 2, 3, 4, 5%/oral/56	Salinity stress	**GP:** *FB* (+), *WG* (+), *SGR* (+), *FCR* (-), *PER* (+); **BC**: *CP* (↔), *CL* (↔), *ASH* (↔)	**S:** *AST* (-), *ALT* (-), *TP* (↔), *TChol* (↔), *Tri* (↔); **E:** *SOD* (+)	**IM** (+)	80; 2%	Growth promoter, immunostimulant, salinity stress resistant	Yu et al. (2016)
	2%/oral/56	WSSV	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (-), *PER* (+); **BC:** *M* (-), *CP* (+), *CL* (+), *ASH* (+); **ADC**: *DM* (+), *CP* (+), *CL* (+)	**IG**: *ProPO* (+), *IkBa* (+), *TGF-b* (+), *SOD* (↔), *TNF-a* (↔), *IL1b* (↔), *IL6* (↔), *IL8* (↔)	Not measured	40; 2%	Antiviral, feed ingredient	Niu et al. (2019)
G. tenuistipitata (hot water)	400, 600 mg/L/immersion/5	WSSV	Not measured	**H:** *HC* (+), *GC* (+), *THC* (+); **I:** *PO* (+), *RB* (+), *Lyz* (+); **A:** *SOD* (+),	Not measured	62.6; 600 mg	Antiviral, immunostimulant, antioxidant	Lin et al. (2011)
	200, 400, 600 mg/L/ immersion/5	*V. alginolyticus*	Not measured	**H:** *THC* (+); **I:** *PO* (+), *RB* (+); **A:** *SOD* (-)	Not measured	65; 600 mg	Antibacterial, immunostimulant	Yeh and Chen (2009)
	0.5, 1.0, 2.0 g/kg/oral/5	*V. alginolyticus*; WSSV	Not measured	**H:** *HC* (+), *GC* (+), *THC* (+); **I:** *PO* (+), *RB* (+), *Lyz* (+); **A:** *SOD* (↔), *GPx* (↔)	Not measured	70 and 60; 2%	Antibacterial, immunostimulant	Sirirustananun et al. (2011)
	4, 6 µg/g/injection/5	*V. alginolyticus*	Not measured	**H:** *THC* (+); **I:** *PO* (+), *RB* (+), *Pha* (↔); **A:** *SOD* (↔),	Not measured	63.3; 6 µg	Antibacterial, immunostimulant	Hou and Chen (2005)
	0.5, 1.0, 2.0 g/kg/oral/5	Ammonia stress	Not measured	**H:** *HC* (+), *GC* (+), *THC* (+); **I:** *PO* (+), *Lyz* (+), *RB* (+); **A:** *SOD* (+)	Not measured	2 g	Ammonia stress resistant	Chen et al. (2012)
G. tenuistipitata	0,1.0, 1.5, 2.0 kg/m^3/ co-culture/30	*V. parahaemolyticus*	**GP:** *FW* (↔), *SGR* (↔)	Not measured	Not measured	73.3; 2.0 kg	Antibacterial	Anh et al. (2019 a)
	85, 70, 55, 40%/co-culture/ 75	No pathogen	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (-), *PER* (+); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	Not measured	Not measured	85%	Growth promoter	Anh et al. (2019 b)

Table 1 – contd.

1	2	3	4	5	6	7	8	9
	0.5, 1.5, 2.5, 3.5 g/L/ co-culture/21	No pathogen	**GP:** *FW* (↔), *SGR* (+)	Not measured	Not measured	3.5 g	Optimal biomass	Sarkar et al. (2019)
	3.5 g/L/co-culture/30	No pathogen	**GP:** *SGR* (+)	Not measured	Not measured	3.5 g	Growth promoter	Sarkar et al. (2021)
	3.5 g/L/biofloc + co-culture/ 30	No pathogen	**GP:** *SGR* (+)	Not measured	Not measured	3.5 g	Growth promoter	Sarkar et al. (2021)
G. tikvahiae	<1.5, 1.5–3.9, >4.0 kg/m^2/ co-culture/7–18	No pathogen	**GP:** *FW* (+), *SGR* (+), *FCR* (-)	Not measured	Not measured	<1.5 kg/m	Growth promoter	Samocha et al. (2015)
G. verrucosa (ethyl acetate)	0.5, 1.0, 1.5, 2.0 g/kg/ oral/14	*V. harveyi*	Not measured	**H**: *THC* (+); **I:** *Pha* (+), *PO* (+), *RB* (+)	Not measured	60; 0.5 g	Antibacterial, immunostimulant	Rudi et al. (2019)
	2, 3, 4, 5 g/kg/oral/28	WSSV	Not measured	**H:** *THC* (+); **I:** *Pha* (+), *PO* (+), *RB* (+)	Not measured	41; 4 g	Antiviral, immunostimulant	Zahra et al. (2017)
	2 g/kg/oral/42	*V. harveyi*	**GP:** *WG* (+), *SGR* (+), *FCR* (+)	Not measured	Not measured	85; 2 g	Growth promoter, antibacterial	Jasmanindar et al. (2018 a)
	1, 2, 3 g/kg/oral/42	*V. harveyi*	**GP:** *WG* (+), *SGR* (+), *FCR* (↔)	**H:** *HC* (+), *GC* (+), *THC* (+); **I:** *PO* (+), *RB* (+), *Pha* (+), *Lyz* (+); **A:** *SOD* (+)	Not measured	70; 2 g	Antibacterial, immunostimulant	Jasmanindar et al. (2018 b)
G. vermiculophylla	2, 4 g/L/co-culture/28	*V. parahaemolyticus*	**GP:** *FW* (+), *FCR* (-)	**A:** *SOD* (+); **E:** *CAT* (+)	Not measured	95; 2 g	Antibacterial, immunostimulant	Anaya-Rosas et al. (2019)
Grateloupia sp. (λ-carrageenan)	200, 400, 600 mg/L/ immersion/6	*V. alginolyticus*; WSSV	Not measured	**H:** *HC* (+), *GC* (+), *THC* (+); **I:** *PO* (+), *Lyz* (+), *RB* (+); **A:** *SOD* (+)	Not measured	60, 50; 600 mg	Antibacterial, antiviral, immunocompetence	Chen et al. (2014)
	0.5, 1.0, 2.0 g/kg/oral/21	*V. alginolyticus*; WSSV	Not measured	**H:** *HC* (↔), *GC* (↔), *THC* (↔); **I:** *PO* (↔), *Lyz* (↔), *RB* (↔); **A:** *SOD* (↔)	Not measured	Not reported	Immunocompetence	Chen et al. (2014)
Hypnea cervicornis + *Cryptonemia crenulata* (dried powder)	13, 26, 39%/oral/45	No pathogen	**GP:** *FW* (↔), *SGR* (↔), *FCR* (-)	Not measured	Not measured	26%	Partial substitution of fish meal	da Silva and Barbosa (2009)
Laurenciasnyderia (ethanol)	200, 400, 600 mg/mL/ oral/30	*V. harveyi*	**GP:** *WG* (+), *SGR* (+)	Not measured	Not measured	70; 400 mg	Growth promoter, antibacterial	Dashtiannasab and Yeganeh (2017)
K. alvarezii (water)	0.5 g/L/oral/12	*V. harveyi*	Not measured	Not measured	Not measured	94; 0.5 g	Antibacterial	Suantika et al. (2017)

Table 1 – contd.

1	2	3	4	5	6	7	8	9
Kappaphycus alvarezii (κ-carrageenan)	0.5, 1.0, 1.5, 2.0%/oral/35	WSSV	Not measured	**I:** *Agt* (+), *Po* (↔), *PC* (↔);	**IMB** (↔)	94; 1.5%	Antiviral, immunostimulant	Mariot et al. (2021)
	15, 20, 25 g/oral/60	Not measured	Not measured	**I**: *THC* (+), *Hct* (+), *PA* (+)	**IMB** (-)	20 g	Immunostimulant	Azhar et al. (2023)
	0.15, 0.30, 0.60 g/kg/oral/30	Salinity stress	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (-), *PER* (+)	Not measured	Not measured	0.30 g	Growth promoter	Jumah et al. (2020)
Porphyridium cruentum (polysaccharides)	0.5, 1.0, 1.5, 2.0%/oral/30	*V. alginolyticus*	Not measured	**I**: *PO* (↔), *THC* (↔)	Not measured	90; 1%	Antibacterial	Ozório et al. (2024)
Porphyra haitanensis (dried powder)	2%/oral/56	WSSV	Not measured	**IG**: *ProPO* (+), *IkBa* (+), *TGF-b* (+), *SOD* (↔), *TNF-a* (↔), *IL1b* (↔), *IL6* (↔), *IL8* (↔)	Not measured	40; 2%	Antiviral immunostimulant	Niu et al. (2019)
	1, 2, 3, 4, 5, 6%/oral/58	Not measured	**GP:** *SGR* (+), *FI* (+), *FCR* (-), *PER* (+); **BC:** *M* (↔), *CP* (+), *CL* (+), *ASH* (↔); **ADC**: *DM* (+), *CP* (+), *CL* (↔)	**I:** *SOD* (↔), *PO* (+), *THC* (+), *HCT* (-)	**IMB (+)**	1%	Growth promoter, gut health promoter, Feed ingredient, immunostimulant	Niu et al. (2019)
Farrer's scallop (*Chlamys farreri*)								
G. lemaneiformis	69.3, 139.1, 263.5, 347.6 g/m^3/co-culture/21	No pathogen	**GP:** *SGR* (↔)	Not measured	Not measured	139.1 g/m^3	Growth promoter, efficient nutrient uptake	Mao et al. (2009)
Smooth Australian abalone (*Haliotis laevigata*)								
Spyridia filamentosa (dried powder)	10%/oral/14	No pathogen	**GP:** *WG* (-)	**H**: *THC* (-); **I:** *PO* (↔), *Pha* (↔); **A:** *SOD* (↔)	Not measured	Not reported	Feed supplement	Dang et al. (2011)
Freshwater crab (*Paratelphusa hydrodomous*)								
Hypnae spinella (methanol)	100 µL/injection/20	WSSV	Not measured	Not measured	Not measured	100	Antiviral	Dinesh et al. (2014)
Mud crab (*Scylla paramamosain*)								
Gloiopeltis furcata (ethanol)	1, 5, 10 mg/kg/injection/8	WSSV	Not measured	**H:** *THC* (↔); **I:** *PO* (↔); **A:** *SOD* (+)	Not measured	25; 5 mg	Antiviral	Li et al. (2018)
G. lemaneiformis (ethanol)	1, 5, 10 mg/kg/injection/8	WSSV	Not measured	**H**: *THC* (+); **I:** *PO* (↔); **A:** *SOD* (↔)	Not measured	25; 5 mg	Antiviral	Li et al. (2018)
Giant river prawn (*Macrobrachium rosenbergii*)								
Gelidium pusillum (ethanol)	1 mg/mL/injection/5	*Aeromonas caviae*	Not measured	**S:** *TP* (+); **A:** *SOD* (-), *Glu* (+)	Not measured	90; 1 mg	Antibacterial, antioxidant	Agarwal et al. (2021)

Table 1 – contd.

1	2	3	4	5	6	7	8	9
G. edulis (water)	1, 3%/oral/56	WSSV	Not measured	**H:** *THC* (+), **I:** *PO* (+)	Not measured	40; 1%	Antiviral, immunostimulant	Arizo et al. (2016)
G. foliifera (polysaccharide)	10%/oral/30	*A. hydrophilla*	Not measured	**I:** *PO* (+), *SOD* (+), **S:** *TP* (+); **A:** *SOD* (+), *CAT* (+)	Not measured	78.6; 850 mg	antibacterial, Immunostimulant, antioxidant	Hindu et al. (2018)
G. tenuistipitata	1,000, 1,500, 2,000, 2,500 PL/m^3 (1.5 kg/m^3)/co-culture/30	No pathogen	**GP:** *FW* (-), *SGR* (-)	Not measured	Not measured	1.5 kg/m^3	Growth promoter	Ly et al. (2024)
Indian white shrimp (*Penaeus indicus*)								
Gracilaria tenuistipitata	1000 g/m^3/ RAS + co-culture/60	Not measured	**GP:** *SGR* (↔), *FCR* (-)	**I:** *PPO* (↔), *THC* (↔), *Lyz* (+), *TP* (+); **A:** *SOD* (↔)	Not measured	Not reported	Immunostimulant	Das et al. (2022)
	1000 g/m^3/ RAS + biofloc + co-culture/60	Not measured	**GP:** *SGR* (+), *FCR* (-)	**I:** *PPO* (+), *THC* (+), *Lyz* (+), *TP* (+); **A:** *SOD* (+)	Not measured	Not reported	Immunostimulant	
	1000 g/m^3/ biofloc + co-culture/60	Not measured	**GP:** *SGR* (+), *FCR* (-)	**I:** *PPO* (+), *THC* (+), *Lyz* (+), *TP* (+); **A:** *SOD* (+)	Not measured	Not reported	Immunostimulant	
Sea cucumber (*Apostichopus japonicus*)								
C. crispus (carrageenan)	10%/oral/84	No pathogen	**GP:** *FW* (↔), *WG* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔); **BC:** *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	Not measured	Not measured	10%	Feed binder	Won et al. (2018)
Seaweed polysaccharide	1 mg/mL/injection/6	Not measured	Not measured	**I:** *Lyz* (+); **A:** *SOD* (+)	Not measured	Not reported	Immunostimulant	Li et al. (2009)
Mussel (*Mytilus* spp.)								
C. crispus (sulfated polysaccharides)	10, 20, 50 µg/mL/ immersion/not reported	Not measured	Not measured	**H:** *THC* (+); **I:** *Lyz* (+); **IG:** *DmRNA* (+), *MmRNA* (+), *LmRNA* (+)	Not measured	50 µg	Immunostimulant	Rudtanatip et al. (2018)

A: antioxidants; **ADC**: apparent digestibility coefficients; **Agt**: agglutination titre; **ALT**: alanine aminotransferase; **ASH**: ash; **AST**: aspartate; **BC**: body composition; **CAT**: catalase; **CAT mRNA**: catalase messenger RNA; **CL**: crude lipid; **CP**: crude protein; **Cr**: crustin; **d**: days; **DM**: dry matter; **DmRNA**: defensin messenger RNA; **E**: enzymes; **FCR**: feed conversion ratio; **FW**: final weight; **GC**: granular cell; **Glu**: glucose; **GP**: growth performance; **GPx**: glutathione peroxidase; **GSH**: reduced glutathione; **GSH Px mRNA**: glutathione peroxidase messenger RNA; **GSH-Px**: glutathione peroxidase; **H**: hematological; **HC**: hyaline cell; **HCT**: hematocrit; **Hippo**: Hippo signaling pathway-related gene; **I**: immunological; **IE**: intestinal enzymes; **IG**: immune genes; **IkBa**: inhibitor of nuclear factor kappa-B alpha; **IKKb/EF-1a**: inhibitor of nuclear factor kappa-B kinase beta normalized to elongation factor 1-alpha; **IKKε/EF-1a**: inhibitor of nuclear factor kappa-B kinase epsilon normalized to elongation factor 1-alpha; **IL1b**: interleukin-1 beta; **IL6**: interleukin-6; **IL8**: interleukin-8; **IM**: intestinal morphology; **IMB**: intestinal microbiota; **IMD/EF-1a**: immune deficiency pathway gene normalized to elongation factor 1-alpha; **kg**: kilogram; **Lip**: lipase; **LmRNA**: lysozyme messenger RNA; **Lyz**: lysozyme; **M**: moisture; **MDA**: malondialdehyde; **mg**: milligram; **MmRNA**: moricin messenger RNA; **mtMnSOD**: mitochondrial manganese superoxide dismutase; **NA**: not available; **Nrf2**: nuclear factor erythroid 2–related factor 2; **O-2**: superoxide anion; **OD**: optimal dose; **PA**: peroxidase activity; **PC**: phagocytic cell; **PEN-4**: penaeidin-4; **PER**: protein efficiency ratio; **Pha**: phagocytic activity; **PO**: phenoloxidase activity; **POD**: peroxidase; **PPO**: prophenoloxidase; **ProPO**: prophenoloxidase gene; **proPO-I**: prophenoloxidase system; **RB**: respiratory burst activity; **RPS**: relative percent survival; **S**: serological; **SGR**: specific growth rate; **SOD**: superoxide dismutase; **TAC**: total antioxidant capacity; **TCho**: total cholesterol; **TGF-b**: transforming growth factor-beta; **THC**: total hemocytes count; **TNF-a**: tumor necrosis factor-alpha; **TP**: total protein; **Tri**: triglycerides; **Trx**: thioredoxin; **VopD**: Vibrio outer protein D; **WBC**: white blood cell; **WG**: weight gain; **WSSV**: white spot syndrome virus; **α2M**: alpha2-macroglobulin; **p-NF-kB/b-actin**: phosphorylated nuclear factor kappa B normalized to beta-actin; **(+)**: significant increase; **(-)**: significant decrease; **(↔)**: no significant difference.

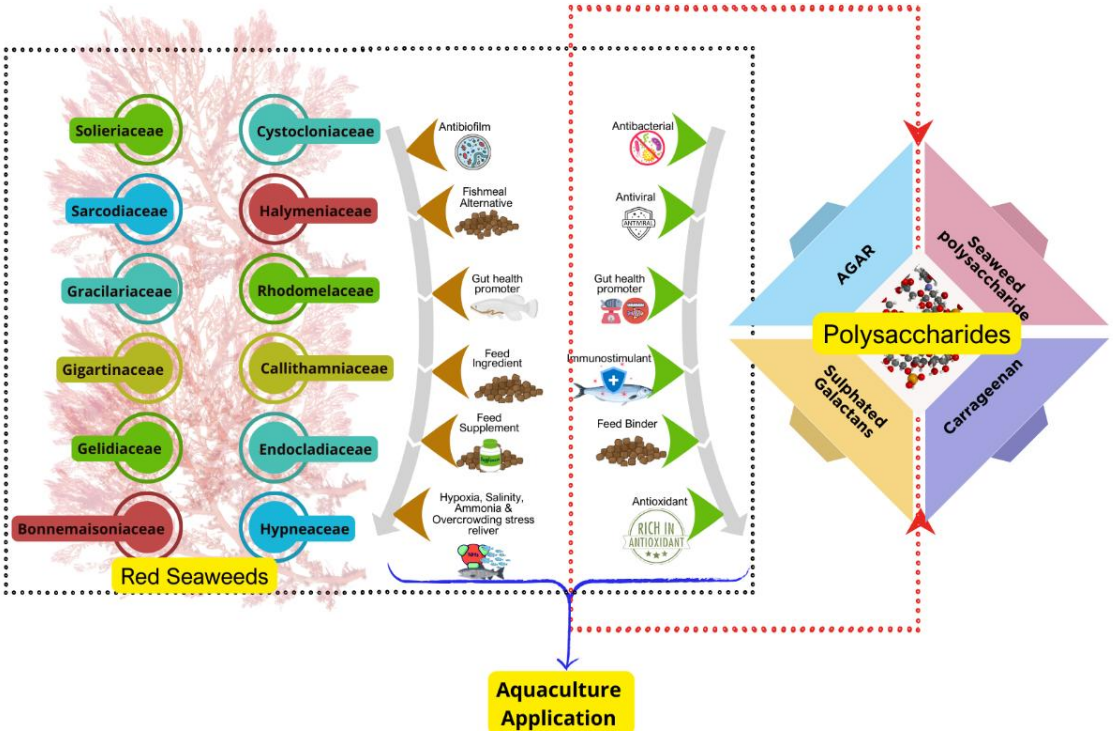


Figure 2. Applications of red seaweed and their polysaccharides in sustainable aquaculture

Polysaccharides such as carrageenan, κ-carrageenan, and sulfated galactans, extracted from red seaweeds like *Chondrus crispus* and *K. alvarezii*, play a key role in feed binding. Carrageenan enhances feed stability under the high heat and pressure typical of feed extrusion processes (Won et al., 2018; Hashim and Saat, 1992). In particular, κ-carrageenan has been shown to improve pellet quality and reduce nutrient leaching, contributing to improved growth and health in species such as sea cucumber (*Apostichopus japonicus*) and striped snakehead.

These stabilizing effects have been demonstrated using both whole dried seaweed and extract. For instance, 6% dried *K. alvarezii* inclusion in Asian seabass diets improved feed water stability without compromising growth metrics like feed conversion ratio (FCR) (Shapawi et al., 2015). Similarly, administering 5% oral carrageenan in sea cucumber and fish diets has been associated with increased pellet durability and enhanced growth. Despite the higher cost of some of these binders, their capacity to reduce fragmentation and dust during feed manufacturing significantly reduces loss, and helps maintain water quality. Looking ahead, the use of polysaccharide-rich red seaweeds, particularly *Gracilaria* and *Kappaphycus* spp., as natural feed binders is expected to grow. Their documented benefits in stabilizing feed and supporting growth and health of a wide range of aquaculture species make them a promising alternative to synthetic binders.

Feed ingredients (partial replacement of fishmeal)

Fishmeal and fish oil are primary protein and lipids sources in aquaculture diets due to their rich nutritional profiles (Teves and Ragaza, 2016; Ataguba et al., 2017; Medhe et al., 2025). However, red seaweeds present viable alternative protein sources, offering significant potential for partial fishmeal replacement, albeit with certain limitations related to amino acid profiles and anti-nutritional factors (ANFs) (Silva et al., 2015; Gabriel et al., 2024 b). Red seaweed species, such as *Gracilaria*, *Porphyra*, and *Kappaphycus*, have been evaluated in various forms, including dried seaweed and ethanol or methanol extracts, with studies showing diverse impacts on fish growth and health. The efficacy of red seaweeds depends on processing and administration techniques such as dried seaweed, lyophilized algae, and solvent-based extracts. For instance, incorporating dried *Gracilaria arcuata* at dietary levels of 10%, 20% and 30% showed no significant differences in growth performance metrics, such as specific growth rate (SGR) and FCR, in African catfish (*Clarias gariepinus*), suggesting its limited potential as a complete nutritional replacement (Al Asgah et al., 2016).

The method of administration, particularly oral feeding, plays a crucial role in determining the efficacy of red seaweed as a feed component. Dried forms of *Gracilaria* spp. and *Porphyra* spp. are often incorporated directly into diets to enhance functional benefits such as immune stimulation and improved disease resistance (Niu et al., 2019). Dosages vary widely depending on species and the intended outcomes. For example, *Porphyra haitanensis*, when included at 1–6% in the diet of whiteleg shrimp (*Penaeus vannamei*), yielded positive growth results without negatively affecting body composition or immune response, supporting its use as a feed ingredient (Niu et al., 2019). Conversely, high inclusion levels, such as 39% mixtures of *Hypnea cervicornis* and *Cryptonemia crenulate*, have been less favorable due to ANFs that reduce digestibility and growth (da Silva and Barbosa, 2009; Seyedalhosseini et al., 2024 a).

Table 2. Applications of red seaweeds and their derived polysaccharide on fish culture: Effects on growth, immune, antioxidant status, gene expression, and intestinal health

Seaweed (form/solvent extract)	Treatment regimen (dose/ route/duration (day (D))	Pathogen (S)	GP; BC; ADC	H; S; I; IG; A; E	IM; IE; IMB	RPS (%); OD	Application	Reference
1	2	3	4	5	6	7	8	9
Atlantic salmon (*Salmo salar*)								
Asparagopsis taxiformis (methanol)	0.6, 1.2%/oral/28	No pathogen	**GP:** *WG* (+), *FCR* (↔)	**I:** *RB* (↔), *PA* (↔), *Lyz* (↔)	**IMB** (+)	1.2%	Growth promoter	Thépot et al. (2022)
G. chilensis (lyophilized algae)	0.1, 1, 10%/oral/60	Infectious salmon anemia	**GP:** *SGR* (↔), *FCR* (↔)	Not measured	Not measured	46.54; 10%	Antiviral	Lozano et al. (2016)
G. chilensis (cryo concentrates)	0.1, 1, 10%/oral/60	Not measured	**GP:** *WG* (↔)	**IG:** *Mx* (+), *IL6* (-), *IFNγ* (-), *Lyz* (-), *Cli* (-)	Not measured	1%	Immunostimulant	Muñoz et al. (2019)
Pyropia columbina (lyophilized algae)	0.1, 1, 10%/oral/60	Infectious salmon anemia	**GP:** *SGR* (↔), *FCR* (↔)	Not measured	Not measured	68.02; 10%	Antiviral	Lozano et al. (2016)
P. columbina (cryo concentrates)	0.1, 1, 10%/oral/60	Not measured	**GP:** *WG* (+)	**IG:** *Mx* (-), *IL6* (-), *IFNγ* (+), *Lyz* (-), *Cli* (-)	Not measured	1%	Immunostimulant	Muñoz et al. (2019)
African catfish (*C. gariepinus*)								
G. arcuata (Dried powder)	10, 20, 30%/oral/70	No pathogen	**GP:** *FW* (↔), *WG* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔), *PPV* (↔), *K* (↔)	Not measured	Not measured	10%	Feed ingredient	Al Asgah et al. (2016)
Asian seabass (*Lates calcarifer*)								
A. taxiformis (water)	1:5, 1:10, 1:50, 1:100, 1:1,000/immersion/9	*S. iniae*	*FW* (↔)	Not measured	Not measured	57.8; 1:100	Antibacterial	Mata et al. (2013)
Gracilaria sp. (water)	3, 6, 9, 12, 15%/oral/56	Hypoxia	**GP:** *SGR* (↔), *FI* (↔)	**En:** *Cor* (-), *Glu* (-), *Lac* (-)	Not measured	100; 12%	Hypoxia stress reliever	Seyedalhosseini et al. (2023)
Gracilaria sp. (agar)	1, 2, 3 g/kg/75	*A. hydrophila*	**GP:** *SGR* (+), *FCR* (-)	**I:** *Lyz* (↔)	Not measured	65; 2 g	Growth promoter, antibacterial	Van Doan et al. (2014 b)
	2 g/kg/oral/28	*A. hydrophila*	**GP:** *SGR* (+), *FCR* (-)	**I:** *ACH* (+), *RB* (↔), *Pha* (↔), *Lyz* (↔)	Not measured	60; 2 g	growth promoter, Antibacterial, immunostimulant	Van Doan et al. (2014 b)
G. pulvinata (water)	3, 6, 9, 12, 15%/oral/56	Not measured	**GP:** *SGR* (↔), *FI* (↔)	**S:** *TP* (+), *ALP* (+) **I:** *Lyz* (+), *ACH50* (+), *Px* (+), *TIg* (+); **IG**: *IGF-1* (+), *Lyz* (+), *IL-1β* (+), *IL-8* (+); **A:** *Cat* (+), *SOD* (+), *GSH* (+)	Not measured	100; 12%	Immunostimulant, antioxidant	Seyedalhosseini et al. (2024 b)
G. pygmaea (dried powder)	3, 6, 9%/oral/42	Not measured	Not measured	**I:** *TIg* (+), *Lyz* (↔), *ACH50* (-); **IG:** *Lyz* (↔), *IGF-1* (-); **A:** *GS-t* (↔), *GR* (↔)	**IM** (↔)	6%	Partial replacement of fishmeal, immunostimulant	Tangestani et al. (2023)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
Atlantic salmon (*Salmo salar*)								
Asparagopsis taxiformis (methanol)	0.6, 1.2%/oral/28	No pathogen	**GP:** *WG* (+), *FCR* (↔)	**I:** *RB* (↔), *PA* (↔), *Lyz* (↔)	**IMB** (+)	1.2%	Growth promoter	Thépot et al. (2022)
G. chilensis (lyophilized algae)	0.1, 1, 10%/oral/60	Infectious salmon anemia	**GP:** *SGR* (↔), *FCR* (↔)	Not measured	Not measured	46.54; 10%	Antiviral	Lozano et al. (2016)
G. chilensis (cryo concentrates)	0.1, 1, 10%/oral/60	Not measured	**GP:** *WG* (↔)	**IG:** *Mx* (+), *IL6* (-), *IFNɣ* (-), *Lyz* (-), *Cli* (-)	Not measured	1%	Immunostimulant	Muñoz et al. (2019)
Pyropia columbina (lyophilized algae)	0.1, 1, 10%/oral/60	Infectious salmon anemia	**GP:** *SGR* (↔), *FCR* (↔)	Not measured	Not measured	68.02; 10%	Antiviral	Lozano et al. (2016)
P. columbina (cryo concentrates)	0.1, 1, 10%/oral/60	Not measured	**GP:** *WG* (+)	**IG:** *Mx* (-), *IL6* (-), *IFNɣ* (+), *Lyz* (-), *Cli* (-)	Not measured	1%	Immunostimulant	Muñoz et al. (2019)
African catfish (*C. gariepinus*)								
G. arcuata (Dried powder)	10, 20, 30%/oral/70	No pathogen	**GP:** *FW* (↔), *WG* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔), *PPV* (↔), *K* (↔)	Not measured	Not measured	10%	Feed ingredient	Al Asgah et al. (2016)
Asian seabass (*Lates calcarifer*)								
A. taxiformis (water)	1:5, 1:10, 1:50, 1:100, 1:1,000/immersion/9	*S. iniae*	*FW* (↔)	Not measured	Not measured	57.8; 1:100	Antibacterial	Mata et al. (2013)
Gracilaria sp. (water)	3, 6, 9, 12, 15%/oral/56	Hypoxia	**GP:** *SGR* (↔), *FI* (↔)	**En:** *Cor* (-), *Glu* (-), *Lac* (-)	Not measured	100; 12%	Hypoxia stress reliever	Seyedalhos-seini et al. (2023)
Gracilaria sp. (agar)	1, 2, 3 g/kg/75	*A. hydrophila*	**GP:** *SGR* (+), *FCR* (-)	**I:** *Lyz* (↔)	Not measured	65; 2 g	Growth promoter, antibacterial	Van Doan et al. (2014 b)
	2 g/kg/oral/28	*A. hydrophila*	**GP:** *SGR* (+), *FCR* (-)	**I:** *ACH* (+), *RB* (↔), *Pha* (↔), *Lyz* (↔)	Not measured	60; 2 g	growth promoter, Antibacterial, im-munostimulant	Van Doan et al. (2014 b)
G. pulvinata (water)	3, 6, 9, 12, 15%/oral/56	Not measured	**GP:** *SGR* (↔), *FI* (↔)	**S:** *TP* (+), *ALP* (+) **I:** *Lyz* (+), *ACH50* (+), *Px* (+), *TIg* (+); **IG**: *IGF-1* (+), *Lyz* (+), *IL-1β* (+), *IL-8* (+); **A:** *Cat* (+), *SOD* (+), *GSH* (+)	Not measured	100; 12%	Immunostimulant, antioxidant	Seyedalhos-seini et al. (2024 b)
G. pygmaea (dried powder)	3, 6, 9%/oral/42	Not measured	Not measured	**I:** *TIg* (+), *Lyz* (↔), *ACH50* (-); **IG:** *Lyz* (↔), *IGF-1* (-); **A:** *GS-t* (↔), *GR* (↔)	**IM** (↔)	6%	Partial replacement of fishmeal, immunostimulant	Tangestani et al. (2023)
K. alvarezii (dried powder)	6, 10, 14, 18, 22%/oral/70	No pathogen	**GP:** *FW* (↔), *WG* (+), *SGR* (+), *FCR* (-), *NPU* (+), *K* (↔); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔); **ADC:** *DM* (↔), *CP* (↔), *CL* (↔)	Not measured	Not measured	6%	Growth promoter, feed binder	Shapawi et al. (2015)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
K. alvarezii (polysaccharide)	50, 100 mg/kg; 0.1, 0.5%/ injection/15	*V. parahaemolyticus*	Not measured	**H:** *WBC* (+); **I:** *Lyz* (+), *RB* (+)	Not measured	80, 75; 100 mg, 0.50%	Antibacterial, immunostimulant	Sakthivel et al. (2015)
Beluga sturgeon (*Huso huso*)								
Hypnea cornua (ethanol)	5, 10, 20 g/kg/oral/56	Not measured	**GP:** *SGR* (+), *FCR* (-)	**H:** *RBC* (+), *WBC* (↔), *Hb* (+), *Hct* (+), *Lym* (↔), *Neu* (↔), *Mon* (↔), *Eos* (↔); **I:** *TP* (+), *Lyz* (+), *TIg* (↔); **IG:** *GH* (+), *IGF-1* (+); **A:** *SOD* (+), *CAT* (+), *MDA* (-), *GPx* (+)	Not measured	10 g	Growth promoter, immunostimulant, antioxidant	Ghanadi et al. (2024)
Black rabbitfish (*Siganus fuscescens*)								
Asparagopsis taxiformis (methanol)	1.5, 3, 6%/oral/28	Not measured	**GP:** *SGR* (+), *FCR* (-)	**I:** *Lyz* (↔), *ACH50* (↔), *RB* (↔)	IMB (↔)	6%	Growth promoter, immunostimulant	Thépot et al. (2021)
G. lemaneiformis	100, 200, 300, 400 g/m^3/ co-culture/40	No pathogen	**GP:** *SGR* (+), *FCR* (-)	Not measured	Not measured	Not reported	Growth promoter	Zhou et al. (2006)
	350, 550, 700, 850 g/m^3/ co-culture/30	No pathogen	**GP:** *SGR* (+), *FCR* (-)	Not measured	Not measured	Not reported	Growth promoter	Zhou et al. (2006)
Brown-marbled grouper (*Epinephelus fuscoguttatus*)								
Chondrus sp. (κ-Carrageenan)	5, 10, 20 g/kg/oral/98	*V. alginolyticus*	Not measured	**H:** *WBC* (+); **I:** *RB* (+), *Pha* (+), *PI* (+), *ACH* (+), *Lyz* (+)	Not measured	66.7; 5 g	Antibacterial, immunostimulant	Cheng et al. (2008)
Clownfish (*Amphiprion sebae*)								
Chondrococcus hornemanni (methanol)	25 mg/0.1 mL/injection/9	*V. parahaemolyticus*	Not measured	**H:** *WBC* (+); **I:** *RB* (+)	Not measured	75; 25 mg	Antibacterial, immunostimulant	Ganeshamurthy et al. (2014)
Common carp (*Cyprinus carpio*)								
C. crispus (carrageenan)	0.5 and 1%/oral/60	No pathogen	**GP:** *SGR* (+), *FCR* (+), *PER* (↔)	Not measured	Not measured	1%	Growth promoter	Murthy et al. (2017)
C. ocellatus (κ-carrageenan)	2, 3, 5 mg/100 g/ injection/14	*Edwardsiella tarda, A. hydrophila*	Not measured	Not measured	Not measured	75, 65; 2 mg	Antibacterial	Fujiki et al. (1997 a)
	0.25 mg/mL/injection/6	Not measured	Not measured	**I:** *ACH* (↔), *RB* (↔), *Pha* (↔)	Not measured	0.25 mg	Immunosuppressant	Fujiki et al. (1997 b)
G. corticata (ethanol)	0.20 mg/injection/28	*A. hydrophila*	Not measured	**H**: *RBC* (+), *WBC* (+), *Hct* (+), *Hb* (+), *MCH* (-), *MCHC* (+), *MCV* (-)	Not measured	0.20 mg	Immunostimulant	Radhika and Mohaideen (2017)
G. corticata (extract)	1 g/oral/30	Not measured	Not measured	**H:** *WBC* (+), *Mon* (↔), *Neu* (↔), *Eos* (↔), *Lym* (↔), *Thro* (↔); **I:** *NBT* (+), *Lyz* (+), *Agt* (+)	Not measured	1 g	Immunostimulant	Nasaran and Huxley (2013)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
European seabass (*Dicentrarchus labrax*)								
Gracilaria sp. (dried powder)	2.5, 7.5%/oral/84	No pathogen	**GP:** *FW* (↔), *WG* (↔), *SGR* (↔) *FCR* (↔), *PER* (↔); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *A* (↔)	**I:** *ACH* (↔), *Px* (↔) *Lyz* (↔); **A:** *LPx* (↔); *Cat* (↔); *Gst* (↔), *GSSG* (↔), *GSH* (↔), *GR* (↔), *TG* (↔); **En:** *Amy* (↔), *CTr* (↔), *Tr* (↔)	Not measured	7.50%	Feed ingredient	Peixoto et al. (2016 a)
	7.5%/oral/49	Not measured	**GP:** *WG* (↔), *SGR* (↔), *FCR* (↔)	**I:** *ACH* (-), *Px* (↔) *Lyz* (↔); **A:** *GPx* (↔), *Cat* (↔), *GSSG* (↔), *GSH* (↔), *TG* (↔); **En:** *Amy* (↔), *CTr* (↔), *Tr* (↔)	Not measured	7.50%	Immunocompetent	Peixoto et al. (2016 b)
Gracilaria sp. (water)	5%/oral/80	*P. damselae*	Not measured	**I:** *Px* (-), *Lyz* (+); **S:** *Glu* (↔), *Tri* (-); **E**: *LPx* (-), *Cat* (↔), *Gst* (+)	Not measured	85; 5%	Antibacterial, immunomodulatory, antioxidant	Peixoto et al. (2019 a)
Gracilaria sp. (methanol)	0.5%/oral/42	No pathogen	**GP:** *FW* (↔), *WG* (↔), *SGR* (↔) *FCR* (↔)	**I:** *ACH* (+), *Px* (↔), *Lyz* (↔); **En**: *LPx* (↔), *Cat* (↔); **A:** *GPx* (↔), *GR* (↔), *TG* (↔)	Not measured	0.50%	Feed ingredient	Peixoto et al. (2019 b)
G. bursa-pastoris (dried powder)	5, 10%/oral/70	No pathogen	**GP:** *FW* (↔), *WG* (↔), *DGI* (↔), *FCR* (↔), *PER* (↔), *VFI* (↔); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔); **ADC**: *DM* (↔), *CP* (↔), *CL* (↔), *A* (↔)	Not measured	Not measured	10%	Feed ingredient	Valente et al. (2006)
G. cornea (dried powder)	5, 10%/oral/70	No pathogen	**GP:** *FW* (↔), *WG* (↔), *DGI* (↔), *FCR* (↔), *PER* (↔), *VFI* (↔); **BC**: *M* (-), *CP* (-), *CL* (↔), *ASH* (↔); **ADC**: *DM* (↔), *CP* (↔), *CL* (↔), *A* (↔)	Not measured	Not measured	5%	Feed ingredient	Valente et al. (2006)
G. gracilis (ethanol)	0.35%/oral/47	Not measured	**GP:** *WG* (↔), *FCR* (↔)	**H:** *RBC* (↔), *WBC* (↔), *Hb* (↔), *Hct* (↔), *Lym* (+), *Neu* (↔), *Mono* (↔), *Eos* (↔); **S:** *ALT* (↔), *AST* (↔); **I:** *Lyz* (+), *Px* (+); **A:** *SOD* (-), *CAT* (↔), *GST* (↔), *tGSH* (+); **En:** *Trig* (↔), *Glu* (↔)	**IM (+)**	2.5%	Immunostimulant; modulated gut microbiota	Passos et al. (2021 b)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
G. gracilis (dried powder)	8%/oral/106	No pathogen	**GP:** *WG* (↔), *FCR* (↔); **BC:** *M* (+), *CP* (↔), *CL* (↔); **ADC:** *DM* (-), *CP* (-), *E* (-), *CL* (↔), *P* (↔)	**S**: *Glu* (-), *TCho* (↔), *Tri* (-), *TP* (↔), *Alb* (↔); **I:** *Lyz* (↔), *Px* (↔), *ACH50* (↔); **A:** *TAC* (↔), *GPx* (↔), *CAT* (↔); **En:** *Mal* (↔), *SI* (-), *IAP* (↔), *γGT* (↔)	**IM (↔)**	90; 8%	Partial substitution of fish meal	Batista et al. (2020)
	2.5, 5%/oral/47	Not measured	Not measured	Not measured	**IMB (+)**	2.5%	Immunostimulant; modulated gut microbiota	Gonçalves et al. (2022)
	8%/oral/106	Not measured	Not measured	Not measured	**IMB** (-)	8%	Modulated gut microbiota	Ferreira et al. (2022)
G. lemaneiformis (dried powder)	2%/oral/56	Not measured	**GP:** *SGR* (↔), *FCR* (↔); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	**IG:** *CPT1* (-), *PPAR α* (+); **A:** *SOD* (↔), *DA* (↔), *Cat* (↔),*GPx* (↔)	**IM** (+)	2%	Immunosuppressant, gut health promoter	Xie and Niu (2022)
P. haitanensis (dried powder)	2%/oral/56	Not measured	**GP:** *SGR* (+), *FCR* (-); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	**IG:** *CPT1* (+), *PPAR α* (↔); **A:** *SOD* (↔), *MDA* (↔), *Cat* (+),*GPx* (+)	**IM** (+)	2%	Immunosuppressant, gut health promoter	Xie and Niu (2022)
Japanese flounder (*Paralichthys olivaceus*)								
Eucheuma denticulatum (dried powder)	3, 6, 9%/oral/56	No pathogen	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (-), *PER* (+); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔); **ADC**: *DM* (↔), *CP* (↔), *CL* (↔), *ASH* (↔)	**H**: *Hct* (↔), *Hb* (↔); **S:** *GOT* (↔), *Tbil* (↔), *Glu* (↔), *BUN* (↔), *GPT* (↔), *TC*ho (-), *Tr* (-)	Not measured	3%	Growth promoter	Ragaza et al. (2015)
Mozambique tilapia (*Oreochromis mossambicus*)								
G. foliifera (extract)	NM/oral/15	*A. salmonicida*	Not measured	**H:** *WBC* (+), *RBC* (+); **A:** *SOD* (+),*LPx* (+)	Not measured	66	Antibacterial antioxidant	Thanigaivel et al. (2019)
Portieria hornemannii (methanol)	1 ppt/L/immersion/30	*V. parahaemolyticus*	Not measured	Not measured	Not measured	75; 1 ppt	Antibacterial	Fatima et al. (2016)
Mullet (*Mugil cephlus*)								
G. edulis (dried powder)	2, 5%/oral/28	No pathogen	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (+), *PER* (+)	Not measured	Not measured	5%	Growth promoter	Thiruna-vukkarasu et al. (2015)
K. alvarezii (dried powder)	2, 5%/oral/28	No pathogen	**GP:** *FW* (+), *WG* (+), *SGR* (+), *FCR* (+), *PER* (+)	Not measured	Not measured	2%	Growth promoter	Thiruna-vukkarasu et al. (2015)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
Nile tilapia (*Oreochromis niloticus*)								
B. occidentalis (sulfated galactans)	0.05, 0.1, 0.2 mg/g/oral/28	No pathogen	**GP:** *FW* (+), *WG* (+), *DWG* (+)	Not measured	Not measured	0.1 mg	Growth promoter	Farias et al. (2004)
H. musciformis (dried powder)	10, 20, 30%/oral/60	No pathogen	**GP:** *WG* (+), *SGR* (+), *FCR* (-)	**H**: *RBC* (+), *WBC* (+), *Hct* (+), *Hb* (+), *MCH* (+), *MCHC* (+), *MCV* (+)	Not measured	30%	Growth promoter	Nur et al. (2020)
H. musciformis (k-carrageenan)	2.5, 5, 10 g/kg/oral/30	Not measured	**GP:** *SGR* (+)	**IG**: *GH* (+), *IL-1β* (+), *Trf* (+)	Not measured	40; 5 g	Growth promoter, antibacterial, immunostimulant	Villamil et al. (2019)
Halymenia dilatata (sulfated galactan)	0.5, 1.0, 1.5, 2.0, 2.5 g/0.1 kg/oral/60	*A. hydrophila*	Not measured	**A:** *SOD* (+), *Cat* (+), *GPx* (+),	Not measured	2.0 g/0.1 kg	Antibacterial, antioxidant	Vinosha et al. (2020)
G. arcuata (dried powder)	20, 40, 60%/oral/84	No pathogen	**GP:** *FW* (-), *WG* (-), *DGR* (-), *SGR* (-), *K* (↔), *FCR* (↔), *PER* (↔); **BC**: *M* (+), *P* (+), *L* (-), *ASH* (↔)	Not measured	Not measured	20%	Partial substitution of fish meal	Younis et al. (2018)
G. vermiculophylla (dried powder)	10%/oral/84	No pathogen	**GP:** *FW* (-), *SGR* (-), *FCR* (+), *PER* (-); **BC**: *M* (↔), *P* (↔), *L* (↔), *ASH* (↔)	Not measured	Not measured	10%	Vegetal protein sources	Silva et al. (2015)
	30%/oral/36	No pathogen	**BC**: *M* (-), *CP* (-), *CL* (↔); **ADC**: *CP* (+), *CL* (+)	Not measured	Not measured	30%	Feed ingredient	Pereira et al. (2012)
G. tenuistipitata	80, 60, 40, 20% (1 kg/m^3)/co-culture/56	No pathogen	**PC:** *FW* (↔), *WG* (↔), *DGR* (↔), *SGR* (↔), *FCR* (-); **BC**: *M* (↔), *ASH* (↔), *CP* (↔), *CL* (↔)	Not measured	Not measured	80%	Reduce feed cost without affecting growth	An and Anh (2020)
Laurencia caspica (hydroethanolic)	0.5, 1, 2%/oral/50	*S. iniae* *A. hydrophila*	**GP:** *WG* (+), *FCR* (↔), *SGR* (↔), *SR* (↔)	**S:** *TP* (↔), *Alb* (↔), *Glb* (↔), *Chol* (↔); **I:** *SBA* (↔), *MBA* (+), *Lyz* (+), *TIg* (+); **En**: *Tr* (+), *α-Amy* (+)	Not measured	85, 100; 2%	Growth promoter, antibacterial, immunostimulant	Khanzadeh et al. (2024)
P. dioica (dried powder)	10%/oral/84	No pathogen	**GP:** *FW* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔); **BC:** *M* (↔), *CP* (↔), *CL* (↔), *A* (↔)	Not measured	**IM (-)**	10%	Vegetal protein sources	Silva et al. (2015)
	30%/oral/36	No pathogen	**BC**: *M* (-), *CP* (-), *CL* (-); **ADC**: *CP* (-), *CL* (-)	Not measured	Not measured	30%	Feed ingredient	Pereira et al. (2012)
Sarcodia suiae (SLE and PLE)	1, 10, 100 µg/g/injection/56	*S. agalactiae*	Not measured	**I:** *Pha* (+); **IG:** *IL-1β* (+), *IL-8* (+), *TNFα* (+), *TP2* (+), *TP3* (+), *TP4* (+), *TLR2* (+), *TLR5* (+)	Not measured	70; 10 µg	Antibacterial, immunomodulatory	Lee et al. (2020)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
Orange-spotted grouper (*Epinephelus coicoides*)								
C. crispus (*i*-carrageenan)	10, 20, 30 mg/kg/ injection/5	*V. alginolyticus*	Not measured	**I:** *ACH* (+), *Lyz* (+), *RB* (+), *PI* (+); **A:** *SOD* (+)	Not measured	80; 30 mg	Antibacterial, immunostimulant	Cheng et al. (2007)
Rabbitfish (*Siganus canaliculatus*)								
G. lemaneiformis (sulfated polysaccharide)	0.1, 0.15 g/kg/oral/56	*V. parahaemolyticus*	**GP:** *WG* (+), *FCR* (-), *FER* (+)	**S:** *ACP* (+), *ALP* (+), *AST* (-), *ALT* (↔); **I:** *Lyz* (+); **A:** *Cat* (-), *SOD* (↔), *MDA* (-), *TAC* (↔)	**IH:** VA (+); **IE:** Amy (+), Lip (+), Tr (-)	90; 0.1 g	Growth promoter, immunostimulant, antibacterial	Bakky et al. (2023)
Rainbow trout (*Oncorhynchus mykiss*)								
Galaxaura oblongata (water)	0.5, 1.0%/oral/56	Not measured	**GP:** *FW* (↔), *SGR* (↔), *FCR* (↔)	**I:** *TIg* (+), *Lyz* (+); **A:** *Cat* (+), *SOD* (+), *GPx* (+); **IG:** *GPx* (+), *SOD (↔), IL6* (↔), *TNF-a* (+);	Not measured	0.50%	Immunostimulant, antioxidant	Yazici et al. (2024)
Gracilariopsis persica (dried powder)	5, 10%/oral/83	Not measured	Not measured	**I:** *Pha* (↔), *Lyz* (+); **A:** *SOD* (+), *Px* (+), *Cat* (+); **IG:** *IL-1β* (+), *TNFα* (+), *Lyz II* (+)	Not measured	5%	Immunostimulant, antioxidant	Vazirzadeh et al. (2020)
G. persica (sulfated polysaccharide)	0.5, 1.5 g/kg/oral/56	Not measured	**GP:** *FW* (+), *WG* (+), *SGR* (↔), *FCR* (↔), *PER* (↔), *K* (↔); **BC**: *M* (-), *CP* (+), *CL* (-), *A* (↔)	**I:** *Lyz* (+), *ACH* (+); **En:** *SOD* (-), *CAT* (↔)	Not measured	1.5 g	Growth promoter, immunostimulant	Safavi et al. (2019)
G. vermiculophylla (dried powder)	30%/oral/36	No pathogen	**BC**: *M* (-), *CP* (↔), *CL* (↔); **ADC**: *CP* (+), *CL* (↔)	Not measured	Not measured	30%	Feed ingredient	Pereira et al. (2012)
	5, 10%/oral/91	WSSV	**GP:** *FW* (-), *SGR* (↔), *FCR* (↔), *PER* (↔); **BC:** *M* (↔), *P* (↔), *L* (↔), *A* (↔)	**I:** *PA* (+), *Lyz* (+), *ACH* (+)	**IM:** (↔)	5%	Immunostimulant	Araújo et al. (2016)
G. pulvinata (dried powder)	500 mg/kg/oral/60	Not measured	**GP:** *SGR* (↔), *FCR* (↔); **BC**: *M* (↔), *CP* (↔), *CL* (-), *A* (↔);	**S:** *TP* (↔), *AST* (↔), *ALT* (↔); **I:** *ACH50* (+); **A:** *SOD* (↔), *GPX* (+), *CAT* (+)	**IMB:** (↔)	500 mg	Antioxidant, gut health promoter	Yazdanpanah et al. (2021)
G. pygmaea (dried powder)	3, 6, 9, 12%/oral/49	No pathogen	**GP:** *FW* (+), *SGR* (↔), *FCR* (-); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *A* (↔); **ADC**: *CP* (+), *CL* (+)	**H:** *RBC* (↔), *WBC* (↔), *Hct* (↔), *Hb* (↔), *MCH* (↔), *MCHC* (↔), *MCV* (↔), *Lym* (-), *Neu* (↔)	Not measured	6%	Growth promoter	Sotoudeh and Jafari (2017)
Hypnea flagelliformis (dried powder)	5, 10%/oral/83	Not measured	Not measured	**I:** *Pha* (↔), *Lyz* (+); **A:** *SOD* (+), *Px* (+), *Cat* (+); **IG:** *IL-1β* (+), *TNFα* (+), *Lyz II* (+)	Not measured	10%	Immunostimulant, antioxidant	Vazirzadeh et al. (2020)
Laurencia caspica (ethyl alcohol)	0, 5, 10, 15, 20 g/kg/oral/56	*A. hydrophila*	Not measured	**I:** *ACH* (+), *Lyz* (+), *Ig* (+); **A:** *GPx* (+), *Cat* (-), *SOD* (+)	Not measured	90; 15 g	Antibacterial, immunostimulant, antioxidant	Kiadaliri et al. (2020)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
P. dioica (dried powder)	5, 10, 15%/oral/108	No pathogen	**PC:** *FW* (↔), *WG* (↔), *DGR* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔); **BC**: *M* (↔), *ASH* (↔), *CP* (+), *CL* (↔)	Not measured	Not measured	10%	Feed ingredient	Soler-Vila et al. (2009)
P. dioica (dried powder)	30%/oral/36	No pathogen	**BC**: *M* (-), *CP* (↔), *CL* (↔); **ADC**: *CP* (+), *CL* (↔)	Not measured	Not measured	30%	Feed ingredient	Pereira et al. (2012)
Red hybrid tilapia (*Oreochromis* sp.)								
G. changii	1, 3 g/L with 100 fish/m^3/ co-culture/30	No pathogen	**GP:** *SGR* (+), *FCR* (-)	Not measured	Not measured	1 g	Growth promoter	Muin et al. (2024)
Red drum (*Sciaenops ocellatus*)								
C. crispus (carrageenan)	0.5%/oral/49	Not measured	**GP:** *WG* (↔), *FE* (↔); **BC:** *M* (↔), *P* (↔), *L* (↔), *ASH* (↔)	**I:** *NBT* (↔), *Lyz* (+), *Anp* (↔), *TIg* (+), *ACP* (↔), O^{-2} (↔), *Pha* (↔); **S:** *TP* (↔)	Not measured	0.50%	Immunostimulant	Mendoza Rodriguez et al. (2017)
Rohu (*Labeo rohita*)								
E. spinosum (*i*-carrageenan)	5, 10, 20 g/kg/oral/NM	Not measured	**GP:** *FW* (+), *WG* (+), *SGR* (+)	**H:** *RBC* (+), *WBC* (+), *Hb* (+), *Thro* (+); **I:** *RB* (+), *MPx* (+); **S**: *TP* (+)	Not measured	10 g	Growth promoter, immunostimulant	Kumar et al. (2014)
Gracilaria sp. (dried powder)	10, 20, 30%/oral/45	No pathogen	**GP:** *WG* (↔), *SGR* (↔), *FCR* (↔), *PER* (↔); **BC**: *CP* (+), *CL* (+), *NFE* (+)	Not measured	Not measured	10%	Feed ingredient	Vadher et al. (2016)
Halymenia dilatata (dried powder)	25, 50, 75, 100%/oral/56	No pathogen	**GP:** *SGR* (+), *FCR* (-), *PER* (+); **BC**: *M* (↔), *CP* (+), *CL* (+), *ASH* (+)	**H:** *Hb* (↔), *Hct* (↔), *RBC* (↔), *WBC* (↔), *MCV* (↔), *MCHC* (↔), *MCHC* (↔); **A:** *SOD* (+), **En:** *Amy* (+), *Prot* (+), *GOT* (↔), *GPT* (↔)	Not measured	50%	Partial substitution of fish meal	Manikandan et al. (2022)
Small-scaled pacu (*Piaractus mesopotamicus*)								
Pyropia columbina (dried powder)	35 g/kg^{-1}/oral/90	Not measured	Not measured	**A:** *SOD* (-); *Cat* (↔); *Gst* (↔), *TBARS* (-); **En:** *Glu* (↔), *Chol* (-), *Tr* (-)	IMB (↔)	NA	Antioxidant gut health promoter	Cian et al. (2019)
	1.5 g/L, 22 g/L/oral/90	No pathogen	**GP:** FW (↔), WG (↔), SGR (↔), K (↔)	**H:** *RBC* (↔), *WBC* (-), *Hct* (↔), *Hb* (+), *MCH* (↔), *MCHC* (+), *MCV* (-), *Lym* (-), *Neu* (↔), *Eos* (↔), *Mon* (+); **A:** *SOD* (↔), *Cat* (↔), *Gst* (↔), *TBARS* (↔); **En:** *Glu* (-), *Chol* (↔), *TP* (↔), *Tr* (-)	Not measured	22 g	Overcrowding stress reliever	Bacchetta et al. (2020)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
Seabream (*Sparus aurata*)								
A. armata	0.5%/immersion/31	Not measured	**GP:** *FW* (+)	**I:** *Lyz* (↔); **En**: *Amy* (+), *Aps* (+), *Ps* (+), *AlPs* (+)	Not measured	0.50%	Immunostimulant	Castanho et al. (2017)
C. crispus (dried powder)	5%/oral/56	No pathogen	**GP:** *FW* (-), *SGR* (-), *FCR* (↔), *PER* (↔); **BC:** *M* (-), *CP* (↔), *CL* (-), *ASH* (↔)	**S:** *Chol* (↔), *Glu* (↔), *Tri* (+), *TP* (↔); **En**: *SOD* (↔), *Cat* (↔), *GPx* (↔), *GR* (↔), *LPx* (+)	Not measured	5%	Growth suppressor	Guerreiro et al. (2019)
Gracilaria sp. (ethanol)	0.5%/oral/59	No pathogen	**GP:** *SGR* (↔), *FCR* (↔)	**IG:** *Px* (↔), *Anp* (↔); **A:** *LPx* (+), *SOD* (↔), *Cat* (↔); **En:** *Cor* (↔), *Glu* (↔), *Lac* (↔)	Not measured	0.5%	Overcrowding stress reliever	Silva-Brito et al. (2020)
G. cornea (dried powder)	5, 15, 25%/oral/70	No pathogen	**GP:** *WG* (↔)	Not measured	Not measured	25%	Partial substitution of fish meal	Rico et al. (2016)
G. gracilis (ethanol)	0.15%/oral/52	*P. damselae* ssp. *piscicida*	**GP:** *WG* (↔), *FCR* (↔)	**H:** *Hct* (↔), *Thro* (↔), *Lym* (↔), *MCHC* (↔); **S:** *Tr* (↔)	Not measured	38; 0.15%	Immunocompetent	Passos et al. (2021 a)
G. gracilis (dried powder)	0.15%/oral/52	*P. damselae* ssp. *piscicida*	**GP:** *WG* (+), *FCR* (-)	**H:** *Thro* (+), *Lym* (-), *MCHC* (+); **S:** *Tr* (↔)	Not measured	52; 5%	Growth promoter	Passos et al. (2021 a)
G. gracilis	2.5% natural filtered (NF) or blue filtered (BF)/ oral/90	*Photobacterium damselae*; 5×10^5	Not measured	**H:** *Hb* (↔), *WBC* (↔), *Neu* (↔), *Mono* (↔), *Hct* (-), *RBC* (+), *MCV* (-), *MCH* (↔), *MCHC* (+); **I:** *Anp* (-), *Prot* (+), *ACH50* (↔)	Not measured	100; 2.5%	Antibacterial, immunostimulant, antioxidant	Silva-Brito et al. (2022)
G. vermiculophylla (hot water)	5%/oral/34	Acute hypoxia	**GP:** *FW* (↔), *WG* (↔), *FCR* (↔)	**H:** *Hct* (↔), *Hb* (↔), *MCHC* (↔); **A:** *LPx* (↔), *Cat* (-), *GR* (-), *GPx* (-), *Gst* (↔)	Not measured	60.7; 5%	Hypoxia stress reliever, antioxidant	Magnoni et al. (2017)
Sole (*Solea senegalensis*)								
H. cornea (water)	10, 5, 2, 1 mg/mL/ *in vitro*/1	*P. damselae* ssp. *piscicida*	Not measured	**I:** *RB* (↔)	Not measured	5 mg	Immunostimulant	Díaz-Rosales et al. (2007)
H. cornea (ethanol)	10, 5, 2, 1 mg/mL/ *in vitro*/1	*P. damselae* ssp. *piscicida;* 1×10^8	Not measured	**I:** *RB* (+)	Not measured	10 mg	Immunostimulant	Díaz-Rosales et al. (2007)
H. cornea (polysaccharide fraction)	10, 5, 2, 1 mg/mL/ *in vitro*/1	*P. damselae* ssp. *piscicida*	Not measured	**I:** *RB* (↔)	Not measured	5 mg	Immunostimulant	Díaz-Rosales et al. (2007)
Striped snakehead (*Channa striatus*)								
Gracilaria sp. (dried powder)	5%/oral/56	No pathogen	**GP:** *FW* (-), *WG* (-), *PER* (-)	Not measured	Not measured	Not reported	Partial feed binder	Hashim and Saat (1992)

Table 2 – contd.

1	2	3	4	5	6	7	8	9
C. crispus (carrageenan)	5%/oral/56	No pathogen	**GP:** *FW* (+), *WG* (-), *PER* (+)	Not measured	Not measured	Not reported	Feed binder	Hashim and Saat (1992)
Sobaity seabream (*Sparidentex hasta*)								
Gracilaria sp. (dried powder)	3, 6, 9, 12, 15%/oral/56	Not measured	**GP:** *SGR* (↔), *FI* (↔)	**I:** *Lyz* (+), *TIg* (+); **IG:** *IGF-1* (+), *Lyz* (+); **A:** *SOD* (+), *Cat* (+), *Gst* (+), *TAC* (+), *MDA* (+); **En:** *Glu* (+), *Tr* (+)	Not measured	100; 12%	Immunostimulant, antioxidant	Seyedalhos-seini et al. (2024 b)
Thick-lipped grey mullet (*Chelon labrosus*)								
P. purpurea (dried powder)	9, 18%/oral/70	No pathogen	**GP:** *FW* (-), *WG* (-), *SGR* (-), *FCR* (+), *PER* (-), *NPU* (-); **BC:** *M* (+), *CP* (↔), *CL* (-), *ASH* (↔)	Not measured	Not measured	18%	Partial substitution of fish meal	Davies et al. (1997)
White-spotted spinefoot (*Siganus canaliculatus*)								
G. lemaneiformis (dried powder)	33%/oral/56	No pathogen	**GP:** *FW* (-), *WG* (-), *SGR* (-), *FCR* (+), *PER* (-); **BC**: *M* (↔), *CP* (↔), *CL* (↔), *ASH* (↔); **ADC**: *DM* (↔), *CP* (↔)	**I**: *ACH* (+), *Lyz* (+), *SOD* (↔)	Not measured	33%	Feed ingredient	Xu et al. (2011)

A: antioxidants; **Agt**: agglutination titer; **Alb**: albumin; **ALP**: alkaline phosphatase; **ALT**: alanine aminotransferase; **Amy**: amylase; **Anp**: antiprotease; **APs**: aminopeptidase; **ASH**: ash; **AST**: aspartate aminotransferase; **BC**: body composition; **BUN**: blood urea nitrogen; **Cat**: catalase; **CL**: crude lipid; **Cli**: complement-like immune factor; **Cor**: cortisol; **CP**: crude protein; **CPT1**: carnitine palmitoyltransferase 1; **Cr**: crustin; **CTr**: chymotrypsin; **DGI**: daily growth index; **DGR**: daily growth rate; **DM**: dry matter; **E**: energy; **En**: enzymes; **Eos**: eosinophils; **FCR**: feed conversion ratio; **FE**: feed efficiency; **FI**: feed intake; **FW**: final weight; **GH**: growth hormone; **Glb**: globulin; **Glu**: glucose; **GOT**: glutamyl oxaloacetic transaminase; **GP**: growth performance; **GPx**: glutathione peroxidase; **GPT**: glutamic pyruvate transaminase; **GR**: glutathione reductase; **GSH**: reduced glutathione; **GSSG**: oxidized glutathione; **GS-t**: glutathione S-transferase; **H**: hematological; **Hb**: hemoglobin; **HC**: hyaline cell; **Hct**: hematocrit; **I**: immunological; **IAP**: intestinal alkaline phosphatase; **IE**: intestinal enzymes; **IG**: immune genes; **IGF-1**: insulin-like growth factor 1; **IH**: intestinal health; **IL-1β**: interleukin-1 beta; **IL-8**: interleukin-8; **IL6**: interleukin-6; **L**: lipid; **Lac**: lactate; **Lip**: lipase; **LPx**: lipid peroxidation; **Lym**: lymphophil; **Lyz**: lysozyme; **Lyz II**: lysozyme II; **M**: moisture; **Mal**: maltase; **MBA**: mucus bactericidal activity; **MCH**: mean corpuscular hemoglobin; **MCHC**: mean corpuscular hemoglobin concentration; **MCV**: mean corpuscular volume; **MDA**: malondialdehyde; **Mon**: monophil; **MPx**: myeloperoxidase; **Mx**: myxovirus resistance gene; **NA**: not available; **NBT**: nitroblue tetrazolium; **Neu**: neutrophil; **NFE**: nitrogen free extract; **NFα**: tumor necrosis factor-alpha; **NPU**: net protein utilization; **O-2**: superoxide anion; **OD**: optimal dose; **PA**: peroxidase activity; **Pha**: phagocytic activity; **PI**: phagocytic index; **PLE**: pressurized liquid extraction; **PPAR α**: Peroxisome proliferator-activated receptor alpha; **PPV**: protein productive value; **Prot**: protease; **Ps**: phosphatase; **Px**: peroxidase activity; **RB**: respiratory burst activity; **RBC**: red blood cell; **RPS**: relative percent survival; **S**: serological; **SBA**: serum bactericidal activity; **SGR**: specific growth rate; **SI**: sucrase-isomaltase; **SLE**: solid–liquid extraction; **SOD**: superoxide dismutase; **TAC**: total antioxidant capacity; **TBARS**: thiobarbituric acid reactive substances; **tGSH**: total glutathione; **Thro**: thrombocytes; **TIg**: total immunoglobulin; **TLR2**: toll-like receptor 2; **TLR5**: toll-like receptor 5; **TNFα**: tumor necrosis factor-alpha; **TP**: total protein; **TP2**: tilapia piscidin 2; **TP3**: tilapia piscidin 3; **TP4**: tilapia piscidin 4; **Tr**: trypsin; **Trf**: transferrin; **Trig**: triglycerides; **VA**: villus area; **VFI**: voluntary feed intake; **WBC**: white blood cell; **WG**: weight gain; **WSSV**: white spot syndrome virus; **α-Amy**: alpha-amylase; **(+)**: significant increase**; (-)**: significant decrease**; (↔)**: no significant difference.

The effectiveness of red seaweeds as feed ingredients depends largely on their amino acid and fatty acid profiles. While *Gracilaria* spp. contain essential amino acids, unfavorable ω-6 to ω-3 PUFA ratios can negatively affect growth, limiting their inclusion in aquafeeds (Pereira et al., 2012). Additionally, some species, such as *Porphyra dioica*, when included at 10% or 30% in aquafeed, have been linked to stable FCR but suppressed growth in Nile tilapia (*Oreochromis niloticus*) and rainbow trout (*Oncorhynchus mykiss*), likely due to imbalanced nutrient composition (Silva et al., 2015; Pereira et al., 2012). Combining multiple seaweed species in balanced proportions could help overcome these limitations by providing a more complete nutritional profile. ANFs – such as phlorotannins and certain polysaccharides – can further reduce digestibility at higher inclusion rates. For example, *G. arcuata* at 20–60% inclusion in Nile tilapia diets caused reduced growth performance, primarily due to these ANFs (Younis et al., 2018). Nevertheless, techniques like co-cultivation and targeted extraction can decrease ANF content, thereby improving the overall nutritional value of seaweeds as feed ingredients.

Feed supplements

Red seaweeds and their polysaccharide derivatives have been widely studied for their potential as natural growth promoters in aquaculture. Species such as *Gracilaria*, *Asparagopsis*, *Kappaphycus*, and *Gelidium*, used in dried forms, extracts, or co-culture systems, have shown improvements in growth and health when administered at optimal doses and via suitable delivery methods. Among these, oral administration of dried red seaweeds remains the most practical and widely adopted method, consistently enhancing growth performance and FCR in commercial-scale aquaculture. For example, *Gracilaria lemaneiformis*, when added at 2% of the diet in whiteleg shrimp, significantly improved SGR, FCR, and immune responses, including increased lysozyme (Lyz) activity and antioxidant enzyme levels (Niu et al., 2019). Similarly, dried *K. alvarezii* at 5–10% inclusion enhanced growth and reduced FCR across various fish species (Peñaflorida and Golez, 1996). In shrimp farming, species like *Gracilaria corticata* and *Gracilaria verrucosa* have been integrated into co-culture systems, which reduce waste emissions and improve shrimp productivity by maintaining water quality and achieving optimal biomass density (Fourooghifard et al., 2017; Izzati, 2011; Tayade et al., 2024). An optimal co-culture density of 2.0 kg/m^3 for *Gracilaria tenuistipitata* has been shown to maximize shrimp growth and survival (Anh et al., 2020). While injection of seaweed-derived polysaccharides may be effective, it is less practical for routine use and better suited to experimental conditions or high-value species. In shrimp and shellfish, immersion and injection methods have been used for extracts such as κ-carrageenan from *Eucheuma cottonii*, which improved immune responses and relative percentage survival (RPS) under bacterial challenge (Yeh and Chen, 2008).

The effects of red seaweed supplementation are dose-dependent. Lower inclusion levels typically yield positive outcomes, while higher concentrations may produce adverse effects. For example, a 2% inclusion of *G. lemaneiformis* was found optimal for whiteleg shrimp, enhancing growth, feed efficiency, and immune modulation (Yu et al., 2016; Niu et al., 2019). In contrast, inclusion rates above 10% reduced growth and nutrient digestibility in carnivorous fish like European seabass (*Dicentrarchus labrax*) and rainbow trout (Valente et al., 2006; Peixoto et al., 2019 b, 2016 a, b; Soler-Vila et al., 2009). Doses between 2 and 5% have shown to enhance immune responses, including increased serum protein levels, antioxidant enzyme activity, and immune gene expression, contributing to improved disease resistance in fish and shrimp (Rudtanatip et al., 2017, 2022; Kanjana et al., 2011; Murthy et al., 2017; Chen et al., 2014).

Polysaccharides like κ-carrageenan and sulfated galactans from red seaweeds such as *K. alvarezii* and *Gracilaria* spp., when orally administered at concentrations of 0.5–2%, have been particularly effective in improving growth, immunity, and disease resistance (Jumah et al., 2020; Villamil et al., 2019). These supplements significantly enhanced Lyz activity, phagocytic function, and antioxidant enzyme levels in various aquatic species, including shrimp, fish, and prawns (Rudtanatip et al., 2017). Notably, herbivorous and omnivorous fish species tolerate plant-derived polysaccharides more effectively than carnivorous species, which often struggle to digest higher levels of plant-based materials (Yu et al., 2016; Niu et al., 2019).

Red seaweeds as immunostimulants, antibacterials, antivirals, and gut health alternatives in aquaculture

The use of red seaweed as an immunostimulant in aquaculture has drawn significant attention due to its potential to enhance the immune system of aquatic species. Rich in bioactive compounds such as sulfated polysaccharides, phenolics, and proteins, red seaweeds have demonstrated immunomodulatory effects by enhancing innate and adaptive immunity (Figure 2 and Tables 1 and 2).

Immunostimulatory activity

Red seaweeds are applied in various forms, including dried powders, ethanolic extracts, hot-water extracts, and polysaccharide derivatives, each with different efficacies. Dried seaweed is frequently incorporated into diets due to its cost-effectiveness and convenience. For instance, a 2% dietary inclusion of *G. lemaneiformis* in golden pompano (*Trachinotus ovatus*) improved antioxidant defenses (Xie and Niu, 2022). Similarly, *Halymenia dilatata* enhanced hemoglobin, hematocrit, and white blood cell counts (WBCs) in Nile tilapia, demonstrating improved immunity (Vinosha et al., 2020). In whiteleg shrimp, *P. haitanensis* (2%) upregulated immune genes such as *prophenoloxidase* (*ProPO*) and *transforming*

growth factor-beta (*TGF-β*), while enhancing gut health (Niu et al., 2019). A dietary supplementation of 3% *Gracilaria lichenoides* enhanced both total hemocyte count (THC) and phenoloxidase (PO) activity in giant tiger prawn (Tian et al., 2024). Ethanolic extracts offer concentrated bioactive compounds suitable for administration through oral or injectable formulations. For example, ethanolic extracts of *Chondrococcus hornemanni* injected into clownfish (*Amphiprion sebae*) significantly increased WBCs and respiratory burst activity, achieving a 75% RPS against *Vibrio parahaemolyticus* (Ganeshamurthy et al., 2014). Similarly, ethanolic extracts of *Gracilaria fisheri* enhanced THC and PO activity in giant tiger prawns, resulting in an RPS of 82.6% following challenge with *Vibrio harveyi* (Kanjana et al., 2011). Polysaccharide derivatives such as sulfated galactans and carrageenans are particularly effective immunostimulants. Sulfated galactans from *G. fisheri* upregulated immune genes like *ProPO-I* and *penaeidin 4* (*PEN-4*), improving pathogen resistance in Asian seabass (Sakthivel et al., 2015). κ-Carrageenan improved Lyz activity and resulted in an RPS of 80%, whereas sulfated polysaccharides from *Gracilaria birdiae* achieved an RPS of 95% in shrimp challenged with white spot syndrome virus (WSSV) (Cantelli et al., 2019).

Oral delivery is the most common method for administering red seaweed bioactives, as it easily integrates into commercial feeds and is well-suited for enhancing long-term immunity. A 2% dietary inclusion of *G. verrucosa* improved Lyz activity, antioxidant enzyme levels, and RPS in rainbow trout (Mendoza Rodriguez et al., 2017). Similarly, *G. tenuistipitata* polysaccharides at 1.5% dietary inclusion enhanced immune gene expression (e.g., *interleukin-1β* (*IL-1β*) and *tumor necrosis factor-alpha* (*TNF-α*)) and enzymatic activity in Nile tilapia over 60 days (Vazirzadeh et al., 2020). A 0.5% dietary inclusion of sulfated polysaccharides from *G. birdiae* boosted hemocyte activity and reactive oxygen species (ROS) production, improving resistance to white spot syndrome virus (Cantelli et al., 2019). Injection delivers immunostimulants rapidly, yielding immediate immune responses, but is labor-intensive, making it suitable for high-value species or trials. Injectable κ-carrageenan (6 µg/g) in Asian seabass enhanced Lyz activity and respiratory burst, achieving 80% RPS against *V. parahaemolyticus* (Sakthivel et al., 2015). Sulfated polysaccharides from *G. fisheri* upregulated immune genes in whiteleg shrimp (Rudtanatip et al., 2017). Ethanolic extracts of *G. fisheri* improved THC and antioxidant activity in giant tiger prawns, boosting resistance to *V. harveyi* (Kanjana et al., 2011). λ-Carrageenan injections elevated immune responses in whiteleg shrimp (Chen et al., 2014). Immersion delivery is particularly effective for early developmental stages and stress mitigation, as it ensures uniform bioactive exposure. Sulfated galactans from *G. fisheri* (400–600 mg/L) enhanced antioxidant enzymes (superoxide dismutase (SOD), catalase (CAT)) and immune responses in clownfish (Ganeshamurthy et al., 2014). *G. tenuistipitata* (600 mg/L) improved innate immune markers (PO, THC) in rainbow trout (Lin et al., 2011). Polysaccharides from *Grateloupia* sp. (600 mg/L) boosted THC, PO, and ROS in shrimp, enhancing resistance to *Vibrio alginolyticus* (Chen et al., 2014). *Gracilaria amansii* (400 mg/L) improved oxidative stress resistance and immunity, reducing pathogen-induced mortality (Fu et al., 2007).

The immunostimulatory effects of red seaweed depend on dosage and duration, as both inadequate and excessive doses can reduce efficacy. Sulfated galactans from *G. fisheri* at 2% in diets improved immune responses and survival in Nile tilapia under stress (Vazirzadeh et al., 2020). Injectable λ-carrageenan (0.5 mg/kg) enhanced immune gene expression and disease resistance in Asian seabass during bacterial challenges (Sakthivel et al., 2015). A 0.3% dietary inclusion of *G. birdiae* sulfated polysaccharides boosted THC and achieved 95% RPS in whiteleg shrimp during WSSV outbreaks (Cantelli et al., 2019). Immersion treatment using polysaccharides from *Grateloupia* sp. (600 mg/L) enhanced immunity and survival of whiteleg shrimp challenged with viral and bacterial pathogens (Chen et al., 2014). Both short- and long-term immersion treatments have proven effective across multiple species, improving immune responses and disease resistance.

Mechanisms of action

Red seaweeds exert immunostimulatory effects in fish and shellfish through a range of biochemical and physiological mechanisms. These include the enhancement of hematological and serological parameters, stimulation of enzymatic and antioxidant defenses, modulation of immune-related gene expression, and improvement of both cellular and humoral immunity, ultimately leading to increased pathogen resistance.

Hematological and serological effects

Red seaweed supplementation has been shown to enhance key hematological parameters associated with immune competence. Notable improvements include elevated THC, enhanced blood protein profiles, and increased levels of red and white blood cells. For instance, ethanolic extracts of *G. fisheri* significantly increased THC in giant tiger prawns, correlating with improved immune responsiveness to *V. harveyi* infection (Kanjana et al., 2011). Similarly, dietary inclusion of *G. lichenoides* raised THC in whiteleg shrimp, demonstrating the capacity of dried red seaweed to stimulate hematological responses (Tian et al., 2024). Sulfated polysaccharides from *G. birdiae* also increased total protein (TP) in shrimp, contributing to systemic defense via enhanced immune protein production (Cantelli et al., 2019). In Nile tilapia, dietary *H. dilatata* supplementation improved red blood cell (RBC) and WBC counts, bolstering oxygen transport and immune cell circulation during pathogen challenges (Vinosha et al., 2020). These findings collectively highlight systemic benefits of red seaweed on immune readiness across multiple aquatic species.

Antioxidant enzyme activity

Red seaweeds strengthen the antioxidant defense system by increasing the activity of key enzymes such as SOD, CAT, and glutathione peroxidase (GPx). These enzymes help mitigate oxidative damage induced by immune activation or environmental stressors. For example, dietary *G. lemaneiformis* improved SOD and CAT activity in rabbitfish (*Siganus canaliculatus*), enhancing oxidative resilience (Bakky et al., 2023). Sulfated galactans from *G. fisheri* also enhanced GPx activity in shrimp, maintaining cellular integrity under oxidative stress (Rudtanatip et al., 2017). In addition, *Grateloupia* sp. polysaccharides lowered lipid peroxidation (LPx) levels, preserving membrane stability during immune responses (Chen et al., 2014). The activation of antioxidant defenses is a critical mechanism through which red seaweeds improve health and survival during immunological or environmental stress.

Modulation of immune-related gene expression

Bioactive compounds in red seaweed modulate the expression of genes involved in innate and adaptive immunity (Kamble et al., 2024 e). Polysaccharides from *G. fisheri* upregulated *ProPO-I* and *PEN-4* gene in shrimp, enhancing melanization and encapsulation mechanisms (Rudtanatip et al., 2017). Likewise, dietary *P. haitanensis* increased *ProPO* expression in whiteleg shrimp, critical for pathogen recognition and defense (Niu et al., 2019). In Nile tilapia, *H. dilatata* elevated proinflammatory cytokines such as *IL-1β* and *TNF-α* improving immune signaling (Vinosha et al., 2020). Additionally, *G. lichenoides* activated the Hippo signaling pathway and oxidative stress response genes like nuclear factor erythroid 2–related factor 2 (*Nrf2*), indicating broad systemic benefits (Tian et al., 2024). These gene-level responses reflect the molecular basis of red seaweed's immunomodulatory effects and their broad potential in aquaculture immunity.

Enhancement of cellular and humoral immunity

Red seaweed stimulates both cellular immunities, through increased hemocyte proliferation and phagocytic activity (Pha), and humoral immunity via elevated Lyz and immunoglobulin levels. For example, sulfated polysaccharides from *G. lichenoides* stimulated hemocyte activity in whiteleg shrimp (Tian et al., 2024), while κ-carrageenan elevated Lyz, and immunoglobulins in Asian seabass, reinforcing pathogen defenses (Sakthivel et al., 2015). Together, these responses illustrate red seaweed's capacity to activate both arms of the immune system, leading to better disease resistance and health outcomes.

Disease resistance

Antibacterial mechanisms

Red seaweed-derived powders, extracts, and polysaccharides have demonstrated strong antibacterial properties in aquaculture species by enhancing immune responses and improving resistance to bacterial infections. The efficacy of these seaweed products depends on factors such as the species used, concentration, route of administration (oral, injection, or immersion), dosage, and duration.

Dietary supplements including *Asparagopsis taxiformis*, *G. fisheri*, *G. verrucosa*, *Laurencia snyderia*, and *K. alvarezii*, have been shown to enhance disease resistance in whiteleg shrimp and tiger prawns against *Vibrio* infections (Manilal et al., 2013; Kanjana et al., 2011; Rudi et al., 2019; Sivakumar et al., 2014). These effects are dose-dependent, with higher concentrations leading to improved survival rates through increased Pha activity, Lyz activity, and other immune parameters. For instance, dietary enrichment with *Gracilaria* spp. enhanced immune responses in European seabass, increasing resistance to *Photobacterium damselae* (Peixoto et al., 2019 a). Optimal dosage and duration were critical, with effective conditions varying across seaweed species.

The mode of administration significantly influences efficacy. Immersion treatments using *K. alvarezii* and *Portieria hornemannii* at low concentrations over extended durations improved survival in giant tiger prawns and Mozambique tilapia (*Oreochromis mossambicus*) challenged with *V. harveyi* and *V. parahaemolyticus* (Sivakumar et al., 2014; Fatima et al., 2016). Gradual exposure to seaweed bioactives enabled optimal immune activation. In contrast, immersion with *A. taxiformis* was ineffective for Asian seabass exposed to *Streptococcus iniae*, likely due to overwhelming infection pressure (Mata et al., 2013; Rasch et al., 2004).

Injection of red seaweed extracts has shown promise for enhancing bacterial resistance. Extracts from *G. fisheri*, *G. tenuistipitata*, and *C. hornemanni* administered via injection significantly increased Pha activity and bacterial clearance in whiteleg shrimp, tiger prawn, and clownfish (Ganeshamurthy et al., 2014; Hou and Chen, 2005; Kanjana et al., 2011). This improved innate immune response underscores the potential of injected seaweed bioactivities in aquaculture disease management.

While some trials showed limited efficacy with low molecular weight agar (LMWA) and κ-carrageenan supplementation against *Aeromonas hydrophila* and *V. alginolyticus*, κ-carrageenan positively influenced fish growth and gut health by modulating intestinal microbiota (Cheng et al., 2008; Van Doan et al., 2014 a; Villamil et al., 2019). These microbiome shifts may enhance resilience to secondary infections even if primary resistance is limited (Li and Gatlin III, 2004; Villamil et al., 2019).

Furthermore, dietary supplementation with *G. lichenoides* improved growth performance, gut health, and resistance to bacterial infections. Fish fed with this seaweed exhibited significant increases in antioxidant enzyme activities, including total antioxidant capacity, CAT, and SOD, thereby reducing oxidative stress during pathogen exposure (Tian et al., 2024). These findings highlight the importance of selecting the appropriate

seaweed species, concentration, and delivery method to maximize immune benefits in aquaculture.

Antiviral mechanisms

Viral diseases such as WSSV and infectious hypodermal and hematopoietic necrosis virus (IHHNV) pose serious threats to aquaculture operations. Red seaweeds, especially those rich in sulfated polysaccharides like galactan and carrageenan, exhibit potent antiviral properties primarily by enhancing host immune responses. This immunomodulatory effect is particularly valuable, considering the high mutation rates and complex life cycles of aquatic viruses, which often complicate direct treatment approaches.

Sulfated polysaccharides derived from species such as *G. fisheri*, *K. alvarezii*, *Hypnea musciformis*, and *E. cottonii* have demonstrated strong antiviral activity against WSSV in whiteleg shrimp. When administered orally or via immersion, these compounds have been shown to elevate ProPO activity, Lyz levels, and the expression of immune-related genes such as *inhibitor of nuclear factor kappa-B kinase* (IKKβ), *crustin*, and *PEN-4*. These immune effectors are essential for recognizing viral particles, inhibiting viral replication, and activating host defense pathways (Chen et al., 2014; Wongprasert et al., 2014; Mariot et al., 2021).

Sulfated galactans from *G. fisheri* exhibit strong antiviral effects by directly binding to viral envelope proteins (VP) like VP26 and VP28, which are critical for virus-host cell attachment. This interaction impedes viral entry and reduces infection rates (Wongprasert et al., 2014; Rudtanatip et al., 2014). In addition, these polysaccharides upregulate several immune genes, including *Immune deficiency* (*IMD*), *inhibitor-κB kinase ε* (*IKKε*) , *dicer*, *PEN-4*, and *crustin*, thereby boosting antiviral defenses (Rudtanatip et al., 2015). Supplementation with *P. haitanensis* has also been shown to enhance whiteleg shrimp immunity against WSSV, increasing *proPO* activity and the expression of *inhibitor of nuclear factor kappa B alpha* (*IkBα*), and *TGF-β* (Niu et al., 2019). Elevated *proPO* activity plays a key role in melanization, a primary invertebrate defense mechanism.

Beyond shrimp, red seaweed-derived polysaccharides have proven effective in other aquatic species. Oral administration of sulfated polysaccharides from *G. birdiae* in giant tiger prawn significantly boosted THC, PO activity, and SOD levels, leading to increased RPS against WSSV (Wongprasert et al., 2014). Likewise, λ-carrageenan extracted from *Grateloupia* sp. showed dual protective effects against *V. alginolyticus* and WSSV through enhanced Lyz activity, ROS production, and immune gene expression (Chen et al., 2014). In fish species like salmon (*Salmo salar*), dietary supplementation with lyophilized *Gracilaria chilensis* or its cryoconcentrates improved immune gene expression and survival rates against infectious salmon anemia (ISA) virus. However, these effects were dose-dependent, and optimization was critical to maximize immune response without inducing stress (Muñoz et al., 2019; Lozano et al., 2016; Daunde et al., 2024).

Interestingly, antiviral effects of red seaweed can also be indirect. For example, κ-carrageenan has been shown to improve gut health and enhance antioxidant enzyme activity, which in turn supports viral resistance by promoting general physiological resilience (Yeh and Chen, 2008; Niu et al., 2019; Yu et al., 2016). These benefits are particularly important in intensive aquaculture systems, where environmental stressors often compromise immune function.

Intestinal health

The gastrointestinal tract (GIT) plays a vital role in nutrient absorption, metabolism, and immunity in aquatic species. Red seaweed has gained attention as a natural supplement that effectively promotes gut health in aquaculture. Used in various forms, such as dried powders and sulfated polysaccharides, red seaweed can influence gut structure, enzymatic activity, and microbial diversity.

The form of administration plays a key role in its effectiveness. Most studies have utilized dried seaweed. For instance, dried *G. lemaneiformis* at 1–5% for 8 weeks improved intestinal microvilli length and integrity in whiteleg shrimp, demonstrating its role in enhancing gut morphology (Yu et al., 2016). Similarly, dried *Gracilaria gracilis* at 2.5% for 47 days modulated intestinal microbiota in European seabass, suggesting prebiotic potential (Gonçalves et al., 2022). In contrast, extracts have shown varying success. Ethanol-extracted *G. gracilis* at 2.5% improved intestinal morphology in European seabass (Passos et al., 2021 b), likely due to concentrated bioactive compounds. Moreover, sulfated polysaccharides extracted from *G. lemaneiformis* (0.1 g/kg) proved more effective in enhancing enzyme activity in rabbitfish (*Siganus canaliculatus*) compared to dried seaweed forms (Bakky et al., 2023). These findings underscore the importance of bioavailability when selecting seaweed form.

Oral administration via direct feeding or incorporation into formulated diets, is the most common route and has consistently yielded positive intestinal outcomes. For example, oral supplementation of *P. haitanensis* at 1% for 58 days significantly enhanced the intestinal microbiota of whiteleg shrimp (Niu et al., 2019). Likewise, dried *G. lichenoides* at 3% for 56 days improved lipase activity and gut structure in giant tiger prawn (Tian et al., 2024). However, no studies evaluated alternative delivery methods (e.g., injection or immersion), limiting understanding of how administration routes might affect red seaweed's bioactivity and gut health impact.

Dose is another critical factor. Moderate inclusion levels (1–3%) typically yield the most promising results. *G. lemaneiformis* at 2% improved gut morphology in whiteleg shrimp (Yu et al., 2016), while *G. gracilis* at 2.5% enhanced intestinal microbiota in European seabass (Gonçalves et al., 2022). Conversely, higher doses may result in diminished or neutral effects. For instance, *P. dioica* at 10% for 84 days did not improve intestinal

morphology in Nile tilapia, suggesting a threshold beyond which efficacy declines (Silva et al., 2015). Similarly, κ-carrageenan from *K. alvarezii* fed at 15–25 g for 60 days had no effect on intestinal microbiota in whiteleg shrimp, likely due to oversaturation (Azhar et al., 2023).

Duration of supplementation also matters. Short to moderate periods (4–8 weeks) tend to show the best outcomes. For example, 2% dried *G. lemaneiformis* for 8 weeks improved gut structure in whiteleg shrimp (Yu et al., 2016) and 1% *P. haitanensis* for 58 days positively influenced microbiota (Niu et al., 2019). In contrast, prolonged feeding (over 12 weeks) may lead to neutral effects. *G. gracilis* at 8% for 106 days showed no improvements in enzyme activity or microbiota in European seabass (Ferreira et al., 2022) and *Gracilaria vermiculophylla* at 5% for 91 days had no significant impact on gut morphology in rainbow trout, possibly due to microbiota adaptation or desensitization (Araújo et al., 2016).

Practical considerations, limitations, future directions, and conclusion

The use of red seaweed and their derived polysaccharides in aquaculture offers diverse applications, including immunostimulation, growth promotion, antibacterial and antiviral effects. Various delivery methods are employed, such as oral administration, injection, immersion, and co-culture systems. Among these, oral administration is the most common and cost-effective approach, allowing the incorporation of bioactive compounds directly into commercial feed. For instance, dietary inclusion of *G. lemaneiformis* at 2% improved antioxidant defenses and gut health in fish, while *K. alvarezii* enhanced THC and PO activity in whiteleg shrimp. Injection, often reserved for high-value species or targeted immunostimulation, has shown rapid effects; for example, κ-carrageenan injections significantly increased ProPO activity and total antioxidant capacity in shrimp. Immersion is particularly effective during early developmental stages, providing uniform exposure to bioactive compounds; immersion with *Grateloupia* sp. polysaccharides (600 mg/L) significantly enhanced THC, Lyz, and SOD activities in shrimp. Co-culture systems, where red seaweeds such as *Gracilaria* spp. are cultivated alongside aquaculture species, serve dual roles as biofilters and sources of bioactives. These systems improve survival rates and growth performance while reducing the environmental impacts by minimizing waste. The efficacy of red seaweed-derived compounds varies across species. For instance, *H. dilatata* upregulated cytokines and boosted immunity, whereas *P. haitanensis* enhanced immune gene expression in whiteleg shrimp. Importantly, red seaweeds offer a natural alternative to antibiotics, aligning with sustainable aquaculture goals by reducing disease outbreaks, environmental degradation, and feed costs.

Despite their promise, several challenges hinder widespread adoption. Economic constraints are significant; cultivating and processing red seaweed into extracts or polysaccharides is resource-intensive. Large-scale feasibility assessments are needed to determine the economic viability. Regional shortages of specific high-value red seaweed species further limit consistent supply chains. Additionally, variations in species efficacy, such as the strong antiviral effects of *G. fisheri* compared to inconsistent immune responses from *K. alvarezii*, present hurdles. Experimental inconsistencies arising from differences in extraction techniques, bioactive concentrations, and dosage optimization further complicate application. Another critical limitation is the incomplete understanding of molecular mechanisms. While numerous studies report improved immunity and pathogen resistance, the exact bioactive pathways remain largely undefined. Environmental and health concerns also arise from potential bioaccumulation of heavy metals or contaminants in cultivated seaweeds, highlighting the need for stringent quality assessments before scaling up.

Red seaweeds and their polysaccharides represent a sustainable and scientifically supported alternative to synthetic additives in aquaculture, with well-documented benefits in immune enhancement, growth promotion, and disease resistance. To fully harness this potential, future research must focus on identifying specific active compounds, elucidating molecular mechanisms, and optimizing dosages and delivery systems across species. Emphasis should be placed on long-term, field-based trials, cost-benefit analyses, and their role within IMTA systems. Establishing standardized safety and efficacy protocols is also vital. Innovations such as encapsulation technologies and synergistic phytobiotic blends may further enhance functionality. In conclusion, red seaweeds hold great promise in supporting sustainable, resilient, and economically viable aquaculture practices.

Authors' contributions

Conceptualization: M.T.K.; data curation: M.T.K.; K.W.; B.R.C.; V.V.Y.D.; G.K.R.P.; S.H.T.; K.D.T.; N.N.G.; S.V.M. and N.P.; writing – original draft preparation: M.T.K.; writing – review and editing: M.T.K.; K.W.; B.R.C.; V.V.Y.D.; G.K.R.P.; S.H.T.; K.D.T.; N.N.G.; S.V.M. and N.P.; funding acquisition: N.P. All authors have read and agreed to the published version of the manuscript.

Acknowledgments

This study was supported by the Center of Excellence in Wildlife, Exotic, and Aquatic Animal Pathology (WEAP-CE), Faculty of Veterinary Science, Chulalongkorn University.

Conflicts of interest/Competing interests

There is no conflict of interest to declare.

Data availability statement

The data presented in this study are available on request from the corresponding author.

Consent for publication

All authors give consent for publication.

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Received: 25 II 2025
Accepted: 11 VIII 2025