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Seaweed as a Thermal Resilient Agent for Climate Adaptation in Aquatic Life Through Antioxidant and Heat Shock Protein Properties: A Review

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ABSTRACT

Poikilothermic aquatic organisms are vulnerable to elevating heat stress in response to climate change. Fishes and crustaceans are affected physiologically, while algae may benefit from climate change. Seaweed provides many ecosystem services including regulating, provisioning, and cultural services. One of the provisioning services of seaweed is the use of fresh seaweed in aquaculture as antioxidants may relieve the stressful conditions for cultured species. Seaweed contains antioxidative phenolic compounds such as phlorotannin, ulvans, carotenoids, and fucoxanthin to scavenge reactive oxygen species (ROS) responsible for cell damage triggered by environmental stressors including thermal stress. Antioxidant lowers the damage done by ROS due to oxidation concurrent with heat-shock protein (HSP) that increases oxidative activity when performing its defensive role. HSPs, specifically the families HSP70, HSP90, HSP60, and HSP20, function as the natural defence mechanism against stressors in all organisms. HSP upregulates under stressful conditions, returning denatured protein to its natural state via refolding. Both antioxidants and HSP function against heat stress induced by increasing ambient temperature. Coupling the synergistic effects of antioxidants and HSP through integrated multitrophic aquaculture (IMTA) of seaweed and fish stocks have potential in mitigating stress level while maximizing the output. Various research showcased positive effects and outcomes of seaweed IMTA. The antioxidants from seaweed synergizing with HSP in cultivated fishes could provide advantageous alternatives to aquaculture in adapting to climate change. This review discussed the potential of coupling the antioxidative properties and the HSP in co-culture system to alleviate heat stress caused by climate change.

INTRODUCTION

Climate change is a global issue caused by anthropogenic activities leading to the increase in average global temperature and the extremities in the weather, with more pronounced impacts as the year advances **(Shivanna, 2022)**. Climate change causes the ocean to take up 91% of the extra energy that rapidly drives the Earth's Energy Imbalance (EEI) from 2000 to 2023, which is a result of greenhouse gas (GHG) emissions caused by human activities such as deforestation, open burning, and the use of fossil fuels **(Kuhlbrodt *et al.*, 2024)**. All aquatic ecosystems are vulnerable to climate change. The metabolism and physiology of marine animals, including their growth, reproductive capability, feeding behaviour, and distribution, are affected by the increase in temperature that is expected to put them at risk of extinction, especially the coastal communities **(Assan *et al.*, 2020)**. Rising sea temperatures directly affect seawater density and can alter the rate and direction of ocean water movement.

Such subtle changes can affect the life history of coastal fishes by altering primary and secondary production in marine ecosystems **(Prakash, 2021)**. Several climate change risk factors are to be taken into consideration in aquafarming, including increasing thermal stress, increased exposure to flooding and storm surge, lowering oxygen levels, and disease vulnerability **(Engelhard *et al.*, 2022)**. Rising temperature results in poor growth and survival for cold-water species due to weakened immune system and disease prevalence, water quality deterioration, thermal stratification, and weak carbon sink capacity, while ocean acidification and changing precipitation patterns will increase the production cost in aquaculture to maintain the water level and quality parameters for culture **(Maulu *et al.*, 2021)**. This is crucial to shrimp (Penaidae) farming and cage-cultured amberjacks (*Seriola* sp.) in which these species groups are highly vulnerable to the risk factors mentioned above **(Engelhard *et al.*, 2022)**.

Climatic events caused losses of at least 79,981 tonnes of fish production, with an estimated value of at least USD 1.4 billion in Bangladesh between 2011 and 2022, with floods and cyclones being the most damaging factors to hatcheries and shrimp farms **(Islam *et al.*, 2024)**. From 2025 to 2041, the global exploitable fish mass is expected to decrease by an average of 5 to 7% under low and high CO_2 emissions, respectively **(Blanchard & Novaglio, 2024)**. Approaches to mitigate climate change in aquaculture production were focused on the reduction of GHG and CO_2 gas emission by utilizing green technologies such as solar power, feeding practices and wastewater management **(Maulu *et al.*, 2021)**. Study by **Chung *et al.*, (2013)** proposed the potential of using seaweed beds and natural seaweed ecosystems as a Coastal CO_2 Removal Belt (CCRB) to sink dissolved inorganic carbon (DIC) from the atmosphere. Integrating seaweed into the integrated multitrophic aquaculture (IMTA) could also remove harmful substances and contaminants while acting as a cooling agent to the surrounding waters **(Yadav *et al.*, 2024)**.

Seaweed communities are among the most productive habitats, providing essential ecosystem services such as coastal protection, nutrient uptake, and carbon sequestration, which help regulate climate change **(Cotas *et al.*, 2023)**. Seaweed was known to fix carbon in surrounding waters while producing a sufficient food source for animals. Polyculture of seaweed with other aquatic organisms requires minimal input for carbon storage and restoration of another coastal ecosystem such as coral reef ecosystems, while also preventing ocean deoxygenation and acidification. Besides, many seaweed species are beneficial for health and disease management, as they contain bioactive compounds with antibacterial, antiviral, and antifungal properties, as well as antioxidative properties **(Yong *et al.*, 2022)**. In 2022, seaweed accounted for 17% of total global fisheries and aquaculture production, approximately 38 million tonnes of the worldwide output **(FAO, 2025)**. Countries in Asia are the major contributors to seaweed production, with China accounting for 62% of the global output, followed by Indonesia at 25%, the Republic of Korea at 5%, and the Philippines at 4% **(FAO, 2025)**. Seaweed production tripled over 20 years, starting in 2001, reaching approximately 36.3 million tonnes globally **(FAO, 2022)**. Seaweed aquaculture production has been growing exponentially since 1950 and has steadily increased over the past 5 years (Table 1). Ten seaweed species were intensively cultured as of 2018 **(FAO, 2018)** (Table 2). Between 2005 to 2015, the total production doubled from 13.5 million tonnes to 30.4 million tonnes **(FAO,**

2018). Seaweed stock harvested from the wild was kept relatively constant, whereas seaweed harvested from aquaculture production increases by the year **(FAO, 2018)**.

Table 1. Total algae production from 2018 to 2022 and its value across the years, showing the total production from aquaculture and fishery in thousand tonnage and the total production value in USD millions

Year	*2018*	*2019*	*2020*	*2021*	*2022*
Reference	FAO, 2024	FAO, 2024	FAO, 2024	FAO, 2024	FAO, 2025
Total production (thousand tonnes) – wet weight	33,437	34,735	36,232	36,311	37,757
Production by aquaculture (thousand tonnes) – wet weight	33,433	34,587	35,080	35,172	36, 505
Production by capture (thousand tonnes) – wet weight	950	1,087	1,163	1,140	1,252
Total production value (USD millions)	13,448	14,733	15,159	15,451	16, 955

Table 2. Intensively cultivated seaweed species **(FAO, 2018)** from all three classes of seaweed in the global production of marine macroalgae

Classification	Species
Brown seaweed (Ochrophyta)	*Saccharina japonica* *Undaria pinnatifida* *Sargassum fusiforme*
Red seaweed (Rhodophyta)	*Poryphyra* spp. *Euchema* spp. *Kappaphycus alvarezii* *Gracilaria* sp.
Green seaweed (Chlorophyta)	*Enteromorpha clathrata* *Monostroma nitidium* *Caulerpa* spp.

Seaweed contains antioxidants and HSP working as a defence mechanism against hypoxia and thermal stress **(Seyedalhosseini *et al.*, 2023)**. Antioxidants are secondary metabolites synthesized by seaweeds in response to the fluctuating conditions of their environments, exposing them to biotic and abiotic stressors **(Michalak *et al.*, 2022)**. These secondary metabolites include phenols, flavonoids, carotenoids, and sterols, which are scavengers of free moving radical ions that causes oxidative damage. Unlike antioxidants, HSPs are found in most cells, acting as chaperone proteins in folding proteins or refolding denatured proteins in the cytoplasm of the cell, in response to stressors **(Khan *et al.*, 2021)**.

Among the most studied HSPs are the sHSPs, HSP70, and HSP90. As climate change poses a continuous threat to marine biodiversity, antioxidant and heat shock protein (HSP) mechanisms in seaweeds may provide alternative adaptive strategies to cope with ongoing and intensifying climate change in both natural ecosystems and aquaculture production **(Ross *et al.*, 2023)**.

The purpose of this study is to review seaweed antioxidants functioning mechanism and its relationship to HSP gene expression in aquatic organisms with main focus on fishes. It is expected that HSP genes such as HSP70 and HSP90 will be highly upregulated in events of thermal stress, but the coupling of antioxidative properties from seaweed may mitigate the damage, thus increasing survivability and physiological functioning of organisms within the ecosystem. This review may also provide an alternative for aquaculture methodology and insight for gene therapy in aquaculture live stocks to adapt to climate change.

LITERATURE REVIEW

Information relevant to the topics was gathered from previously published journal articles available in established databases (e.g., Google Scholar, ResearchGate, ScienceDirect, and other credible sources). The articles were critically analyzed and compared to provide a comprehensive discussion on the antioxidant properties of seaweed, heat-shock protein expression in fish and seaweed, and their effects on ecosystems and aquaculture.

Types and Classification of Seaweed: Red, Green, and Brown Seaweeds and Their Distribution in Aquatic Environments

Seaweeds are marine macroalgae that can be classified into three main groups according to pigmentation: brown seaweeds (Ochrophyta), red seaweeds (Rhodophyta), and green seaweeds (Chlorophyta) **(Britannica, 2025)**. Unlike macrophytes that reproduces through fertilization of the seed and possess true roots, stems, and leaves, macroalgae reproduce through spore germination or fragmentation and is lacking of true roots, stems, and leaves **(Adnan, 2024)**. The general morphology of seaweed is a thallus that consists of three parts: (1) the holdfast to allow the algae to firmly attach to substrates, (2) the stipe which connects the holdfast and blades together while providing flexibility to the plant, and (3) the blades that provide resistance to the structure and are modified according to the strength of water current **(Zhao *et al.*, 2022; Windarto *et al.*, 2025a)**. Photosynthesis occurs on the thallus, and in some macroalgae species, their blades are modified in shape (sphere, ball, cup or fan) or structure (having floats) to adapt to their natural environment **(Zhao *et al.*, 2022)**. There are approximately more than 10,000 known seaweed species, the mainly cultivated seaweeds belong to the genera *Kappaphycus*, *Euchema*, *Saccharina*, *Laminaria*, *Gracilaria*, *Undaria*, *Porphyra*, *Pyropia*, and *Sargassum* **(Chopin, 2018)**.

From the three groups of seaweeds, brown seaweeds are large in size, varying from 30-60cm for smaller species, and can reach up to 20m long for giant kelp. Brown seaweeds thrive in cold waters of around 20°C in both the Northern and the Southern hemisphere. Brown seaweeds from the genera *Laminaria*, *Undaria*, and *Hizikia* are commonly consumed as food source **(Kamleshbhai *et al.*, 2022)**. Red seaweed and green seaweed show contrast to brown seaweeds in terms of size, only ranging from few centimetres (~1 cm) to approximately 1m

long. Red seaweeds can be found in water bodies of various temperatures; in cold waters, temperate waters, and tropical waters **(Kamleshbhai *et al.*, 2022)**. Red seaweed from the genera *Gelidium* and *Gracilaria* are the source of raw material for agar extractions **(Kamleshbhai *et al.*, 2022)**. About 90% of green algae occupy freshwater around the globe **(Aina *et al.*, 2022)**. However, significant green seaweed genera like *Ulva* and *Caulerpa* thrive in marine environments **(Bambaranda *et al*, 2019; Pari *et al*, 2025)**. Chlorophyta, such as *Caulerpa*, are edible seaweeds consumed by most people in Southeast Asia and offer many health benefits **(Windarto *et al.*, 2023)**. Although seaweeds occupy a wide geographic range, they can only make habitat in shallow coastal waters from the lower intertidal zone to the shallow subtidal zones, where there is high exposure to light **(Premarathna *et al.*, 2019)**. Red seaweeds, being an exception as they have a protein complex known as phycobilisome, are responsible for light-capturing in increasing water depth where light intensity is low **(Voerman *et al.*, 2022)**.

Seaweeds are highly beneficial to both the environment and the economy by providing various ecosystem services. The ecosystem services were categorized into three categories; regulating services, provisioning services, and cultural services **(Cotas *et al.*, 2023)**. Regulating services include climate regulation, erosion regulation, water purification and treatment of waste, environmental monitoring, and the production of oxygen. Provisioning services include the fiber content in the algae and raw materials for food and medicine. Cultural services including educational values, cultural heritage values, recreation and ecotourism, and spiritual and religious services. All these ecosystem services are crucial for climate change mitigation and contribute to the livelihood for the people. Additionally, seaweeds provide habitat for marine life in the form of ecosystems known as kelp forests or seaweed beds where there is high productivity, making it a suitable nursery for fishes, mollusc and other marine life, while also contributing to nutrient cycling and the food and pharmaceutical industries **(Sreeram, 2024)**. Previous research shows that the co-culture of seaweed and filter feeders in the integrated multi-trophic aquaculture (IMTA) could support in dissolving nutrients to mitigate negative impacts of offshore aquaculture while giving an additional advantage in the economy **(Lothmann & Sewilam, 2023)**. In the system, the seaweed serves as food source to sea urchin and snails while acting as a biofilter, enhancing sea urchin's performance and improving the culture system's sustainability as a result. The green seaweed (*Ulva lactuca*) was able to assimilate 88.2% of nitrogen in the culture system. The ammonia-N was removed at a rate of 1.8g m^{-2} d^{-1} and 1.4g m^{-2} d^{-1} in the continuous aeration and intermittent aeration systems, respectively.

Antioxidant Properties of Seaweed

Global warming has caused rapid increases in water temperature beyond the optimal range for many fish species, thereby affecting their physiology, reproduction, and distribution. Not only does heat stress impede the physiological functioning of aquatic organisms but it can further affect fish by disturbing their ability to cope with additional stress (**McKenzie *et al.*, 2021**). The tolerance of seaweeds to high temperatures has an upper limit of 36°C, with extreme whitening occurring from 33°C onward. Extreme temperatures, coupled with other stressors, can easily lead to mortality (**Langford *et al.*, 2023**). However, the survival of the seaweed

Enteromorpha prolifera is not influenced by rising water temperatures in its environment, and it continues to grow abundantly (**Liu *et al.*, 2022**).

This resilience to ocean warming may also be observed in other seaweed species, highlighting the potential use of seaweed in open-system aquaculture and the restoration of degraded aquatic ecosystems. Fucoidan found in brown seaweeds (*Sargassum filipendula* and *Undaria pinnatifida*), when used as feed additives, increases the resistance of Pacific white shrimp (*Litopenaeus vannamei*) to acute thermal stress by scavenging reactive oxygen species (ROS), thereby improving shrimp survival (**Rezende *et al.*, 2022**). Farmed white seabream (*Diplodus sargus*) fed red seaweed (*Asparagopsis taxiformis*)-based aquafeeds under simulated marine heatwave conditions showed mitigation of the adverse effects of thermal stress through modulation of the antioxidant response (**Marmelo *et al.*, 2024**).

Antioxidants are chemical compounds which serves as defensive mechanism by delaying the deterioration of cells caused by oxidation **(Diplock, 1994)**. Few examples of antioxidants include the phenolic compounds, vitamin C, tocopherol, and carotenes have high chemical stability to work against oxidation **(Nirmala *et al.*, 2022)**. Oxidative activities lead to the production of radicals and ROS **(Venditti *et al.*, 2022)**. This induces oxidative stress, which is a common occurrence among aquatic lifeforms that can be caused by several factors **(Song *et al.*, 2023)**. Both external and internal factors include water temperature, dissolved oxygen (DO) level, feeding requirements, life history traits, hardness of water, and pollution from industries and agriculture, and handling processes. This will lead to the damage of cells and tissues when there is an imbalance between the production of ROS and the organisms' antioxidant defence system **(Song *et al.*, 2023)**. Antioxidants were shown to have significant role, highlighting its ability to reduce oxidative stress, to prevent and treat diseases to maintain the health of both human and animals **(Munteanu & Apetrei, 2021)**.

Seaweed contains numerous compounds against oxidative activities including carotenoids, sulphated polysaccharides (SP), phenolic compounds, and phlorotannins, in which the main antioxidative mechanism is due to phenolic compounds with multiple hydroxyl group having the ability to donate hydrogen atoms to the ROS, and stabilizing the radicals via resonance stabilization and by indirectly reducing the oxidative activities of lipid **(Hermund, 2018; Windarto *et al.*, 2024)**. Study by **Kumar *et al.* (2021)** emphasized the efficiency of four antioxidative bioactive compounds such as phlorotannin, ulvan, carotenoids and fucoxanthin. Phlorotannins were synthesized in Phaeophytes, having eight interconnected rings in its structure to actively scavenge free radicals that contributes to its therapeutic activities. Ulvan as its name suggest is derived from Chlorophytes, mainly of the genus *Ulva*, is a sulphated polysaccharide, and its activity is dependent on the concentration of the sulphated polysaccharides. Carotenoids are found in all red, brown, and green seaweeds and are used for the classification of the seaweed itself. Fucoxanthin is a secondary carotenoid containing two functional groups, the oxygenic and the carboxyl groups that is highly antioxidative in comparison to other carotenoids due to its stable binding, forming a complex structure of fucoxanthin-chlorophyll-protein.

Antioxidants can also exist in the form of polysaccharides in which fucoidan, alginates, and laminarin can be derived from phaeophytes, agar and carrageenan as the main extract from red seaweed, and ulvan from green seaweed. These antioxidants strengthen the antioxidant system internally through the upregulation of antioxidant enzymes and proteins that were gene encoded. Studies revealed that brown seaweed is capable of improving the antioxidant defence system and regulates inflammatory response through the regulation of the nuclear factor erythroid 2-related factor 2 (Nrf2) from the cytosol in the nucleus, balancing the redox reaction between the antioxidant enzymes and free radicals, while reducing apoptotic activities in the cells of the animals (**Akinyemi & Adewole, 2022; Liu *et al.*, 2022)**.

For Nrf2 to function, several processes must occur. In the normal state, Nrf2 is kept at a low level to prevent gene activation unnecessarily. Keap1 is adapted to Cul3-E3 ubiquitin ligase, forming a complex (Keap1-Cul3 E3 ligase) that constantly targets Nrf2, sending the Nrf2 to the 26S proteasome for degradation. When induced by stressors, modifications to the Keap1 complex stabilize its conformation, leading to the release of Nrf2, which subsequently translocates to the nucleus. Nrf2 forms a complex with the small Maf (sMaf) protein in the nucleus and binds to a specific DNA sequence called the antioxidant response element (ARE). This triggers the production of detoxifying enzymes and antioxidants and expresses the genes involved **(Johnson *et al.*, 2008; Ulasov *et al.*, 2022)** (Fig. 1). Although several studies have reported Nrf2-mediated antioxidant responses in farmed aquatic organisms, direct evidence linking heat stress to Nrf2 activation remains limited. Notably, **Wang *et al.*, (2018)** demonstrated that captivity-bred Chinese giant salamander exhibited upregulation of antioxidant pathway genes mediated by Nrf2 following heat stress exposure. These findings provide positive indications for fishes, as Nrf2 proteins in *A. davidianus* show high structural and functional similarity to those of other vertebrates, including teleost fishes.

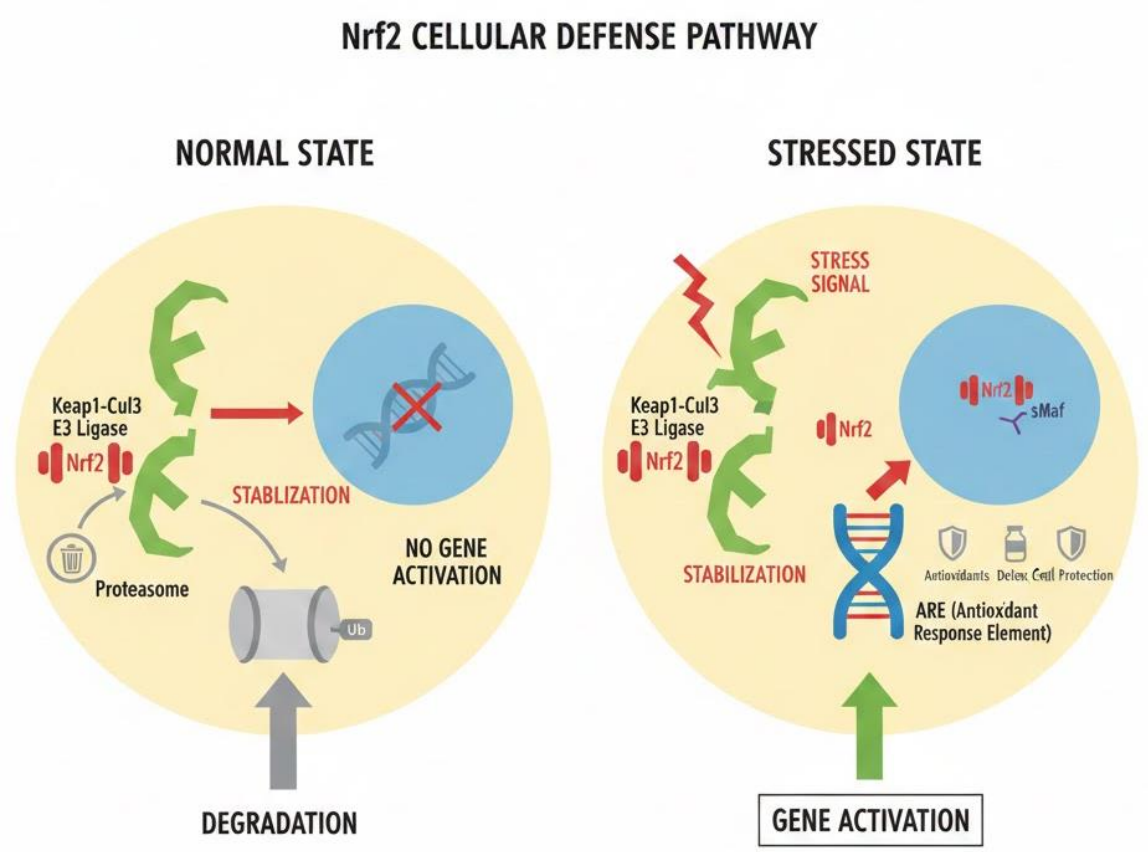

Fig. 1. Nrf2 functioning mechanism. Left: Keap1-Cul3 E3 ligase complex formed to send Nrf2 to proteasome for degradation. Right: Nrf2 forms a complex with sMaf to bind with ARE in the nucleus

Interestingly, seaweed is the only group of organisms capable of producing sulphated SP in large quantity compared to other organisms **(Presa *et al.*, 2018)**. This shows the potential of seaweed to curb oxidative damage in various organisms, coinciding with the ongoing issues of oceanic pollution caused by anthropogenic activities such as agriculture, aquaculture, the discharge of waste materials and the use of artificial or undesirable products containing heavy metals **(Li *et al.*, 2022)**. SPs from green seaweed (*Udotea flabellum*) are capable of negating oxidative damage induced by Fe^{2+} and Cu^{2+} by reducing the activity of caspase responsible for cell death, where it depends on the concentration of the SP **(Presa *et al.*, 2018)**.

Heat Shock Protein (HSP) Genes in Aquatic Organisms and Macroalgae Associated with Stress Response

Heat shock proteins (HSPs) are chaperone proteins that aid in preventing irreversible denaturation of cellular proteins in response to environmental stressors that can further be divided into biotic and abiotic stressors **(Zhang *et al.*, 2024)**. Biotic stressors include the pursuit of predators and infections from pathogen such as bacterial, viral, fungal, or parasitic. Abiotic factors that vary the survival rate of aquatic organisms including temperature, salinity, DO and pH level. These environmental stressors trigger the synthesis of HSP as a coping mechanism, especially for the poikilotherms that are vulnerable to fluctuating water temperature.

Inhabitants of warmer water environments with fluctuating parameters tend to express HSP70 and Heat Shock Cognate 70 (HSC70) on a higher level, regardless of genera **(Madeira *et al.*, 2012)**. The HSP from the HSP70 and HSP90 families are the significant HSP used by aquatic organisms including the teleost fishes, crustaceans, and mollusc to combat heat stress through upregulation when ambient temperature increases or decreases over the optimum temperature for the fish, which can also serve as indicator to their habitat's condition **(Mohanty *et al.*, 2018)**. HSP expression is crucial for invertebrates lacking true adaptive immunity. The HSP70 family is significant for the physiological development in molluscs, especially during morphogenesis **(Jeyachandran *et al.*, 2023)**, whereas the exposure of HSP to decapods (artificially induced) showed enhancement in their enzymes and immunoresponses **(Mengal *et al.*, 2023)**. Immune response can occur through homeostasis by the upregulation of various enzymes including astakines, transglutaminase, prophenoloxidase. These enzymes inhibit microbial activity by increasing the expression of antimicrobial peptides (crustin and lysosome) to work against bacteria and virus when hemocytes (through activation by HSP) melanize in the presence of Ca^{2+} to kill pathogens **(Kumar *et al.*, 2022)**.

Marine macroalgae exhibit HSP expression through small HSP (sHSP), HSP40, HSP70, and HSP90 for enhancing tolerance against heat stress, regulated by heat transcription factors (HSF) **(Lin *et al.*, 2025)**. Results showed that four families of HSP are involved in managing heat stress including HSP20, HSP40, HSP70, and HSP90 through upregulation. HSP70 genes of the red seaweed *Pyropia yezoensis* with the gene coded as *PyyHSP70* have a positive relationship between dehydration stress level and the gene expression level as a protective mechanism to intertidal seaweed that experience rapid change in physical environment, protecting the rhodophyte against desiccation damage. This may serve as a tool for monitoring change in coastal environments and to evaluate the seaweeds' tolerance to stressors **(Yu *et al.*, 2021)**. Another HSP gene, HSP20 is also involved in the regulation of abiotic stressors, such as dehydration and rehydration in seaweed and biotic factors like the red rot disease. *PyyHSP20*, an HSP gene from *P. yezoensis* downregulates significantly under dehydration and upregulates under rehydration. In addition, HSP20 plays a role in the development of red algae where all *PyyHSP20* were expressed spatially and temporarily during both the sporophyte stage of the algae and most of it expressed in its gametophyte stage **(Gao *et al.*, 2022)**.

Denatured protein caused by thermal stress undergoes refolding via the expression of HSPs. The HSP70 is an ATP-dependent primary chaperone protein with three domains, the N-terminal with a nucleotide-binding domain (NTD) bonded to a substrate-binding domain (SBD) as its middle domain (MD), and connected to a C-terminal domain (CTD). The respective functions of each domain are for binding ATP, binding substrate, and for capping the structure by enclosing the unfolded protein within the structure. HSP70 rotates upon the nucleotides exchange factors (NEFs) converting ADP to ATP. The unfolded protein substrate enters the arc-shaped HSP70 chaperone, which then the HSP40 (also known as DNA J) will act as a co-chaperone for the refolding of the protein substrate by coupling with HSP70, forming a HSP70-HSP40 complex in which HSP40 is responsible for regulating ATPase folding activity. The HSP70-HSP40 complex raises the HSP70 ATPase and the folding activity to facilitate substrate-binding while preventing the formation of aggregates. ATP will be hydrolysed into ADP and the folded substrate will be released and could potentially rebind

with HSP70 to undergo multiple cycles of the refolding process until it returns to its original folded pattern **(Hu *et al.*, 2022; Zhang *et al.*, 2024)** (Fig. 2).

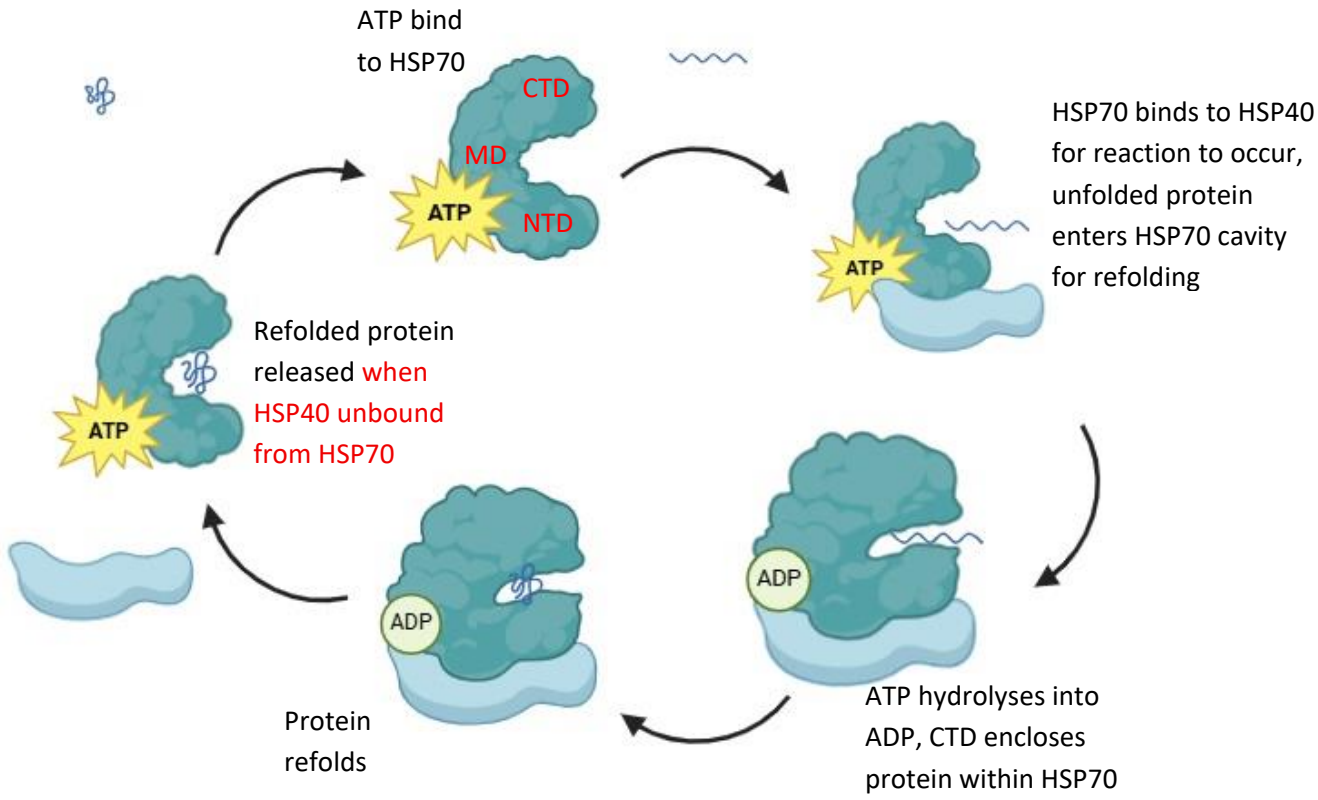

Fig. 2. The working mechanism of HSP70, where HSP40 chaperone protein aids HSP70 in the refolding of proteins when the domains of the HSP interacts with the denatured protein and ATP

HSP60 (also known as Chaperonin 60) plays a crucial role in the polypeptide assembling, translocation of protein across membranes, and the acceleration of protein folding and unfolding. The HSP60-HSP10 chaperonin complex in eukaryotes (known as GroEL-GroES in prokaryotes) functions in similar process with a slight difference, in which HSP60 functions to refold or to fix proteins that are folded in the incorrect pattern. HSP60 exist as a heptameric ring and when bound to HSP10, it forms a spherical complex with numerous heptamers. The misfolded protein enters the hydrophobic cavity of the HSP60-HSP10 structure, shaped as a cylinder folding cage. When the chaperonin complex binds with ATP, the HSP10 encapsulates the substrate for refolding. The ATP hydrolyses, it binds with another HSP60, prompting the release of ADP, HSP10, and the refolded substrate **(Hu *et al.*, 2022; Zhang *et al.*, 2024)**. The HSP60 gene was expressed when brown seaweed (*Saccharina latissimi*) experiences both low and high photosynthetically active radiation at 2°C **(Heinrich *et al.*, 2012)**.

HSP90 shares similar structure to HSP70 having NTD, MD, and CTD and all HSP90 shares elements common to its structure. The difference between HSP70 and HSP90 is that

HSP90 forms a homodimer pair with its structure with CTD joining as a homodimer, leaving the NTD as an open conformation without nucleotide bound until folding occurs. Upon the entering of the unfolded client protein, ATP binding causes the MD of HSP90 to bond chemically. The ATP hydrolyses, driving the HSP90 to twist and close in its conformation. Repeating cycles of the process folds and releases the client protein to its rightful conformation **(Hu *et al.*, 2022)**. The green seaweed (*Ulva pertusa*) expressed the HSP90 gene when stressed with heavy metal and thermal treatment **(Tominaga *et al.*, 2012)**.

The HSP20 family is the main HSP responsible for the regulation in response to increasing temperature by the inhibition of denaturing protein aggregation that is irreversible in plants and plant-like eukaryotes. The HSP20 is an ATP-independent molecular chaperone that forms oligometric protein complexes having a molecular weight of 200-800 kDa with 9-50 subunits. It forms a conserved structure consisting of a variable N-terminal, a conserved C-terminal (also known as alpha-crystaline domain or ACD), and an extended region C-terminal. The ACD with two conserve regions interact with substrates, the N-terminal region is included in the process of binding substrates and regulating oligomerization, and the C-terminal undergoes homo-oligomerization. Overexpression of the HSP20 genes increase peroxidase activity and protects the photosystem II to improve tolerance to thermal stress and oxidative stress **(Zhao *et al.*, 2018; Qi *et al.*, 2022)**.

Cross-Talk Between Antioxidants and HSPs: Synergistic Effects in Stress Mitigation

Thermal stress increases cellular reactive oxygen species (ROS) levels, triggering mitochondrial protein denaturation and leading to necrosis and apoptosis when mitochondria fail to regulate oxidative damage and protein repair (**Slimen *et al.*, 2014; Habashy *et al.*, 2019**). The expression of heat shock proteins (HSPs) and antioxidants occurs concurrently in response to heat stress: HSPs prevent protein denaturation, whereas antioxidants scavenge free radicals responsible for cellular damage. However, the induction of HSPs and antioxidant systems is highly energy-demanding, requiring substantial ATP production by the organism (**Staikou *et al.*, 2024**). Thus, co-cultivated aquatic organisms may benefit from the external antioxidant properties of seaweed, conserving metabolic energy for physiological processes that maximize growth, reproduction, and survival.

Antioxidants play a crucial role in mitigating cellular damage through the regulation of oxidative stress (**Espinosa-Diez *et al.*, 2015**). Thermal stress is associated with increasing ambient temperature. Water temperature and dissolved oxygen (DO) levels exhibit a negative relationship, whereby rising water temperatures reduce oxygen availability and induce oxidative stress in aquatic organisms under hypoxic conditions (**Lushchak & Bagnyukova, 2007; Lazem & Resen, 2010**). Conversely, low water temperatures can also enhance the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GSH-Px), which are highly reactive to ROS (**Lv *et al.*, 2021**). These antioxidant enzymes neutralize ROS by donating electrons and stabilizing reactive molecules.

Under non-stress conditions, HSP gene expression remains low, whereas antioxidants continue to function in the presence of basal ROS levels. Antioxidant deficiency resulting from excessive free radical production under hypoxic exposure activates heat shock factors (HSFs), which stimulate HSP synthesis to maintain cellular homeostasis when ROS levels increase (**Szyller & Bil-Lula, 2021**). HSP60 is associated with signaling apoptosis, whereas HSP70 and HSP90 inhibit apoptotic processes and reduce oxidative damage (**Oksala *et al.*, 2014**). However, excessive overexpression of HSPs may inhibit programmed cell death and suppress autophagy, potentially allowing harmful ROS to accumulate at elevated levels. HSP expression depends on HSF activation triggered by various stressors.

Enhancing antioxidative capacity through the co-cultivation of fish with seaweed, combined with endogenous HSP production in fish, may provide a dual defense mechanism against heat stress. This synergistic protection is expected to result in significantly lower cortisol levels and improved physiological resilience in cultured organisms.

Seaweed as a Climate Change Adaptation Tool for Aquatic Life Mitigating Thermal Stress in Aquatic Ecosystems

Seaweed's role in buffering temperature fluctuations and mitigating the effects of heatwave through carbon intake

Cumulative emission of GHG released from anthropogenic activities resulted in surplus heat in the climate system causing positive EEI in which radiative energy trapped by GHG in the atmosphere is absorbed by the ocean surface. The hydrological system is disrupted when the rate of evaporation increases and the atmosphere moisturizes when precipitation releases latent heat. A net zero CO_2 emission on the ocean surface will continuously transport heat energy into deeper regions of the ocean and the EEI will remain positive until the CO_2 uptake from land and the ocean is drastically reduced in the atmosphere **(Cheng *et al.*, 2022)**.

Tropical blue carbon ecosystems consist of coastal ecosystems like the mangrove ecosystem, seagrass ecosystem, and the seaweed ecosystem play crucial roles in carbon sequestration and storage, while providing various other ecosystem services such as the stabilizing of sediments, coastal protection by mitigating shoreline erosion, water purification, and habitats to shelter fishes and crustaceans **(Raihan, 2023)**. Seaweed has a net primary production comparable to the Amazon forest, acting as nearshore and offshore carbon sink, able to fixate 50% of the global CO_2 in oceans for photosynthesis in which was observed that seaweed cultivation sinks organic carbons into the sediment layer below the seaweed farms, while 90% of wild seaweed exports carbon into the deep sea **(Ross *et al.*, 2023)**. Approximately, 50 Gt of CO_2 is captured on an annual basis and converted to biomass by seaweed and sedimented as decaying seaweeds sink to the bottom, trapping carbon in sediment layers. Study reported that, although varying with seasons in temperate countries, it was demonstrated that *Pyropia* seaweed aquaculture beds are able to uptake carbon at a rate of 13 to 24 times than natural seaweed ecosystem, equivalent to the annual absorption of pine forest with an area of 2487 km^2 or to the emission of 449,713 automobiles, at 743 kt C yr^{-1} **(Kim *et al.*, 2024)**. Incorporating seaweed into the diet of ruminants can potentially reduce the release of methane, another carbonic gas compound that makes GHG **(De Bhowmick & Hayes, 2023)**.

These carbonic GHG can be affected by the antioxidative property of seaweeds and the inhibition of methanogenesis by key enzymes from functioning via a halogenic compound found in seaweed known as bromoform **(De Bhowmick & Hayes, 2023)**. When bromoform outcompetes the substrates of coenzyme M transferase and methyl coenzyme M reductase, CoM-SH is unable to form due to methyl not being transferred from methyl-H4MPT to release methane from the reduced methyl-conenzyme M **(De Bhowmick & Hayes, 2023)**.

Climate change impacts the water quality, as temperature increase induces flood and drought which was known to increase the concentration of nutrients in the water **(Delpla *et al.*, 2009)**. Kelp cultivation was able to improve the transparency of water by reducing turbulence and the velocity of water current caused by flood **(Jiang *et al.*, 2020)**. Macroalgae uptake dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP), decreasing the nutrient content in the water that could potentially lead to eutrophication while increasing the pH level and the DO of the water, providing a remedy for drought **(Jiang *et al.*, 2020)**.

Integrating seaweed into climate adaptation strategies for aquatic ecosystems

Macroalgae are autotrophic organisms that are able to generate organic compounds from abiotic energy sources through the process of photosynthesis. Through this function, they become one of the primary producers of coastal ecosystem to play a significance in the aquatic food web. Seaweed habitats including both kelp forests and seaweed beds are the most widely distributed and productive coastal ecosystems providing food sources to aquatic organisms, shelter and protection for various creatures, supplying oxygen, and the cycling of nutrients in the environment. Around 34 % of seaweed production is consumed by grazers, while 50-80% of Earth's oxygen is supplied by aquatic autrotrophs including seaweed. In addition, seaweed provides support to aquatic lifeforms in terms of shelter and habitat. Macroalgae form mutualistic relationships with various organisms, in which sea otters (*Enhydra lutris*) were known to obtain food source and shelter from kelp forests while the kelp forest was regulated by the consumption of otters on the sea urchin communities, with damselfish and chiton performing similar roles to the seaweed community by reducing grazing damage from the damaging feeding habit of other aquatic organisms **(Hay *et al.*, 2004)**. This mutualistic relationship has been detected when the defensive mechanism of hydroids that were co-habiting with kelp reduces the consumption of the holdfast by herbivorous snails **(González-Duarte *et al.*, 2020)**. The holdfast of marine algae also provides anchoring site to seahorses which are poor swimmers due to the lack of caudal fin as effective swim appendage **(Garrick-Maidment *et al.*, 2012)**.

Fish diet supplemented with seaweed was shown to enhance the physiology, growth performance, immune response, and stress responses, as *Saccharina latissimi* used as feed additive can improve fish resistance against oxidative stress while increasing the fish yield in aquaculture. Whereas, *Ulva* sp. was associated with an increase in the protein content of meat yield and enhancement of immune response **(Farghali *et al.*, 2023)**. Additionally, seaweed enriched- treatments enhance tolerance against abiotic stressors, as observed in red seaweed (*Hypnea musciformes* and *Gracilaria conferta*) and green seaweed (*Ulva rigida*) **(Ashkenazi *et al.*, 2022)**. The seaweeds enriched with wastewater from Seabream (*Sparus aurata*) tanks containing higher levels of nitrogen and phosphorus compound have shown elevated protein level; when cultivated in salinity above the optimum range (45-55 ppt), the starch content in

the seaweed increased **(Ashkenazi *et al.,* 2022)**. The inclusion of optimum level of starch into the fish diet reserves an additional energy for the growth of the fishes and reduces excretion of nitrogenous waste, while increasing profit to the aquaculture sector **(Nafees *et al.,* 2022)**. Inclusion of algae (macroalgae and microalgae) into the cultivated fishes' diet is species specific but generally improves the physiology of the fish: the function of the liver, response to stress, and tolerance to starvation **(Norambuena *et al.,* 2015)**. It was demonstrated that, the inclusion of algae derived products, Verdemin and Rosamin (derived from *Ulva ohnoi* and *Entomoneis* spp. respectively), increases the omega-3 long-chain polyunsaturated fatty acids (n-3 LC PUFA) content in the entire body of the fish **(Norambuena *et al.,* 2015)**. The Malaysian Mahseer (*Tor tambroides*) larvae fed with *Artermia* sp. and *Moina* sp. livefeed, enriched with microalgae, *Chorella vulgaris*, led to higher growth rate and weight gain than the controlled group fed with unenriched *Artemia* sp. and *Moina* sp. **(Joshua *et al.,* 2024)**. Eicosapentanoic acid (EPA), an omega-3 PUFA was also reported to be higher in the fish larvae fed with enriched *Artemia*, enhancing its growth and survival. The benefits mentioned shows that integrating seaweed into open systems under environmental stress serve as a viable strategy for adaptation in the changing climate.

Seaweed can be integrated into a diverse selection of cultivated fish stocks showing positive outcomes in IMTA. An IMTA of abalone (*Haliotis asinine*), seaweed (*Gracilariopsis bailinae*), and sea cucumber (*Holothuria scabra*) shows a high survival rate of abalone well surpassing 90%, and high growth rate of sea cucumber at length of 2- 3cm per day and weight of 0.2g per day **(Federico *et al.,* 2019)**. The white shrimp (*Litopenaeus vannamei*) cultured with *C. lentillifera* showed the survival rate of 96% and contained EPA 7.95% **(Herawati *et al.,* 2023)**. Another study shows that the IMTA of white shrimp (*L. vannamei*), rabbit fish (*Siganus doliatus*), and seaweed (*Euchema cottonii*) was recorded with a better performance than monoculture indicating increased weight, growth rate, and production when stocked at appropriate density **(Verdian *et al.,* 2020)**. Moreover, the culture of barrel shrimp (*Phronima pacifica*) with *C. lentillifera* showed that *P. pacifica* had SGR of 4.76%/day with population density of 53.81 ind/L **(Herawati *et al.,* 2021)**. Seaweed gains advantage from the nitrogenous compound release from co-cultured fish stocks in the form of NO_{3-} and NH^{4+} as nutrients. Red seaweed *Gracilaria conferta* and *Hypnea musciformes* doubled in biomass yield when integrated into mariculture system, whereas green seaweed *Ulva* with high nitrogen uptake quadrupled in biomass yield compared to seaweed samples in nutrient controlled condition, and all showing higher protein level **(Ashkenazi *et al.,* 2019)**. This could provide a solution to aquaculture where climate change causes vulnerability to both the fishes and seaweed to the change in abiotic factors, thereby affecting their physiology that results in high mortality and stunted growth.

Seaweed-bivalve IMTA contributes to the mitigation of ocean acidification and hypoxia, which originated from the disruption of carbon cycle by anthropogenic activities when inorganic extractive macroalgae species including those from the genera *Gracilaria*, *Ulva*, *Euchema*, and *Chaetomorpha*, to supply oxygen through photosynthesis while absorbing excess nitrogen, carbon and phosphorus in the environment, thus creating healthier fish stock not limited to bivalve but fish and shrimps altogether. The co-culturing of seaweed provides a perpetual supply of herbivory diet to the fishes in the same culture system. The availability of

seaweed in an integrated culture system can potentially relieve heat stress in the fishes, while producing higher quality of fish stock. Previous study demonstrated by adding brown seaweed (*Laminaria* sp.) rich in bioactive compounds as supplement into the feed for Atlantic salmon (*Salmo salar*) in which the phenolic compounds found in the seaweed can potentially reduce the production of ROS, altering the antioxidant defence system of fishes, allowing them to withstand acute temperature rise in the face of the worsening global warming phenomena **(Kamunde *et al.*, 2019)**. In addition, most marine algae are susceptible to increasing ocean surface temperature, which prolonged exposure will hinder the growth and photosynthesis, as shown in *Kappaphycus alvarezii* tested at a temperature range of 28-40°C by intervals of 4°C. Stressed seaweeds exposed to temperature of 33°C and above have slower growth and photosynthetic rates due to damaged cells and pigmentation that are essential for the process **(Kumar *et al.*, 2020; Zhang *et al.*, 2023)**. However, the utilization of genetic breeding or the use of heat tolerant seaweed species or strain itself, potentially from the genus *Gracilaria* may help in overcoming climate change issues in aquafarming for the future due to their ability to adapt to environment of high temperature in addition to its various advantages including its high commercial value, its strength in bioremediation, and its fast growth **(Liu *et al.*, 2021; Zhang *et al.*, 2023)**.

CONCLUSION

Future Prespectives

Antioxidants and heat shock proteins (HSPs) play crucial roles in regulating oxidative damage induced by thermal stress. The antioxidant compounds present in seaweeds mitigate oxidative damage by neutralizing free-moving reactive oxygen species (ROS) generated by environmental stressors. This capacity enables seaweeds to adapt to environments characterized by fluctuating conditions.

Integrating seaweed into integrated multi-trophic aquaculture (IMTA) systems offers both ecological and economic benefits, largely due to the antioxidative properties of seaweed in synergy with the endogenous HSP responses of marine organisms. Such integration provides a practical and sustainable strategy for the aquaculture sector, particularly as environmental and industrial challenges continue to intensify.

Based on this review, seaweed emerges as a sustainable candidate for the preservation of marine biodiversity, given its role in bioremediation and ecosystem restoration. Increased seaweed production may also enhance the uptake of greenhouse gas (GHG) compounds, thereby contributing to climate change mitigation.

Nevertheless, continued research is necessary to further elucidate the antioxidative properties of seaweed and the interaction between seaweed-derived compounds and HSP responses in aquatic livestock. A deeper understanding of these protective mechanisms will clarify their role in enhancing resilience to thermal stress and support the development of climate-adaptive aquaculture practices.

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