Optimising nutrient and light regimes for hatchery cultivation of the kelp *Ecklonia radiata*

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Abstract

Seaweed is a versatile and renewable resource with applications ranging from food and medicine to biodegradable materials and beyond. While land crops have long been domesticated, ocean farming of macroalgae like *Ecklonia radiata* has only recently developed. This common New Zealand brown seaweed holds commercial promise, but localised species-specific cultivation methods are essential for success. This study aimed to optimise hatchery conditions for *Ecklonia radiata* by testing nutrient and light regimes. Two laboratory experiments assessed full-strength (20 mL PES L^{-1}) and double-strength treatments showed no significant differences, while the quarter-strength nutrients resulted in poor growth. High-intensity hatchery lighting (exceeding 100 µmol photons m^{-2} s^{-1} for extended periods) reduced sporophyte length and density, whereas 70% outplanting shade level yielded the best early growth. Based on these findings, it is recommended to use full-strength nutrient dosing (20 mL PES L^{-1}; 18.85 mg N L^{-1}, 0.81 mg P L^{-1}) once weekly, combined with gradually increasing light from 30 to 100 µmol photons m^{-2} s^{-1}. During outplanting, light stress should be minimised, with deployment at 2-3 m depth during autumn months to promote establishment. These findings reinforce current hatchery protocols and support the scalable integration of *Ecklonia radiata* into New Zealand's emerging seaweed industry.

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1. Introduction

1.1. Global status of seaweed industry

Seaweed aquaculture is a rapidly growing industry, valued for its sustainability and diverse applications in food, pharmaceuticals, biofuels, and compostable packaging (Nakhate & van der Meer, 2021). It is the fastest-growing sector in marine aquaculture, with global production tripling from 11.8 million wet tonnes in 2000 to 38 million wet tonnes in 2022 (Figure 1.1, *The State of World Fisheries and Aquaculture*, 2024), generating over USD 13 billion annually (Moreira et al., 2022). As demand for sustainable products rises, seaweed farming is increasingly viewed as a viable method for producing renewable resources while reducing pressure on terrestrial agriculture and wild fisheries (Kim et al., 2019).

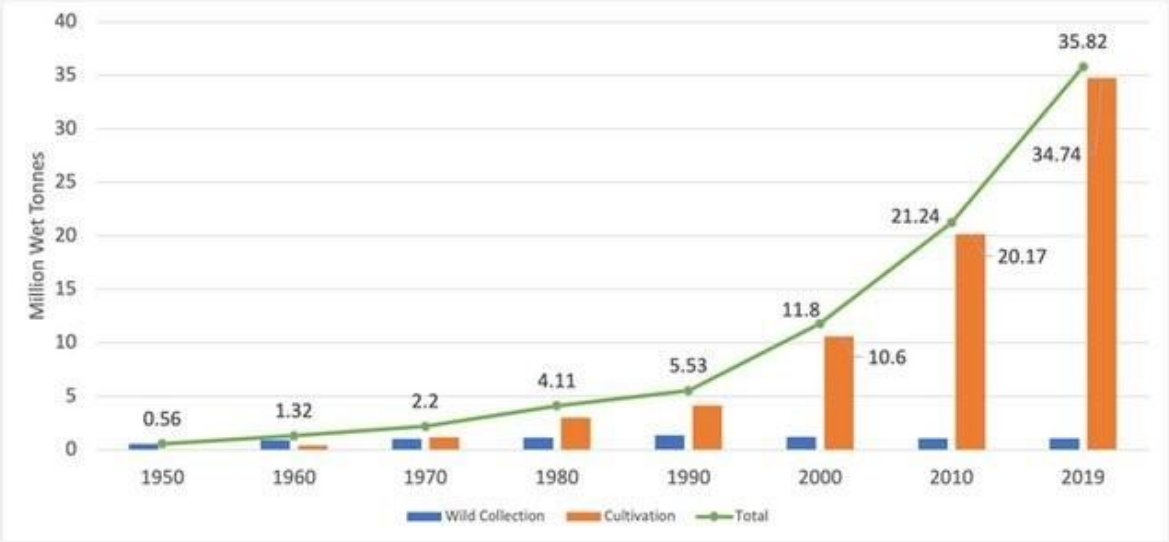

Figure 1.1. Estimated global wet weight of macroalgal resources from 1950 to 2019. Orange bars represent cultivated macroalgae, blue bars represent wild-collected macroalgae, and the green line indicates the total wet weight (combined cultivated and wild harvest). Figure sourced from (The State of World Fisheries and Aquaculture, 2024).

Currently, Asia accounts for 97% of global seaweed production, with China contributing the largest share at 60%, followed by Indonesia (25%), the Republic of Korea (5%), and the Philippines (4%) (The State of World Fisheries and Aquaculture 2024, 2024). Tropical regions primarily cultivate red algae species, such as *Kappaphycus* and *Eucheuma* (Hurtado et al., 2019). Red algae dominate global cultivation, representing 56% of total seaweed production by wet weight, followed by brown algae (44%) and green algae (0.1%) (The State of World

Fisheries and Aquaculture 2024, 2024). Asia's dominance in the market is further supported by its advanced processing infrastructure, which facilitates the production of versatile products like carrageenan and agar (Hurtado et al., 2019).

While seaweed farming is technically feasible in most coastal waters, success depends on regulatory support, economic viability, and societal acceptance (Grebe et al., 2019). Seaweed cultivation is expanding to North and South America, Europe, and East Africa (Alemañ et al., 2019; van den Burg et al., 2021), with temperate regions focusing on brown algae, particularly kelps, due to their rapid growth and bioremediation potential (Kim et al., 2019). Western countries, lacking Asia's long-established seaweed farming industry, require significant time and investment to develop infrastructure, deep-sea cultivation machinery, and advanced processing techniques (Stévant et al., 2017). In Europe, leading countries suitable for large-scale seaweed cultivation of cold and intermediate species include Norway, Ireland, Scotland, France, and Sweden (Stévant et al., 2017; Toth et al., 2025) with supportive policies, well-developed markets, and strong local engagement leading to faster industry growth (Billing et al., 2021).

1.2. New Zealand seaweed industry

New Zealand is uniquely positioned to benefit from the expanding global seaweed industry, thanks to its marine environment which is highly suitable for seaweed aquaculture (Figure 1.2., Froehlich et al., 2019). However, the country's seaweed industry has remained small-scale, primarily due to restrictive permitting regulations designed to protect the environment and uphold Māori traditions, and the inability of locally harvested or cultivated seaweed to compete financially in international markets (Zemke-White et al., 1999). As a result, commercial activity has largely been limited to the collection of beach-cast seaweed for biostimulant production, aquaculture feeds, and agar extraction (White & White, 2020). Despite these limitations, there is growing interest in New Zealand in the production of high-value products for both domestic and international markets (Hafting et al., 2015). Several small-scale initiatives, including those led by GreenWave Aotearoa and independent entrepreneurs, are actively working to establish commercial cultivation practices to meet the increasing demand for biostimulants and other products (Wheeler et al., 2021). But while interest in seaweed aquaculture is expanding, the industry remains in its early stages, facing significant barriers of limited cultivation expertise, underdeveloped processing

infrastructure, inadequate research and development funding, regulatory hurdles, and a lack of coordinated leadership (Bradly et al., 2021).

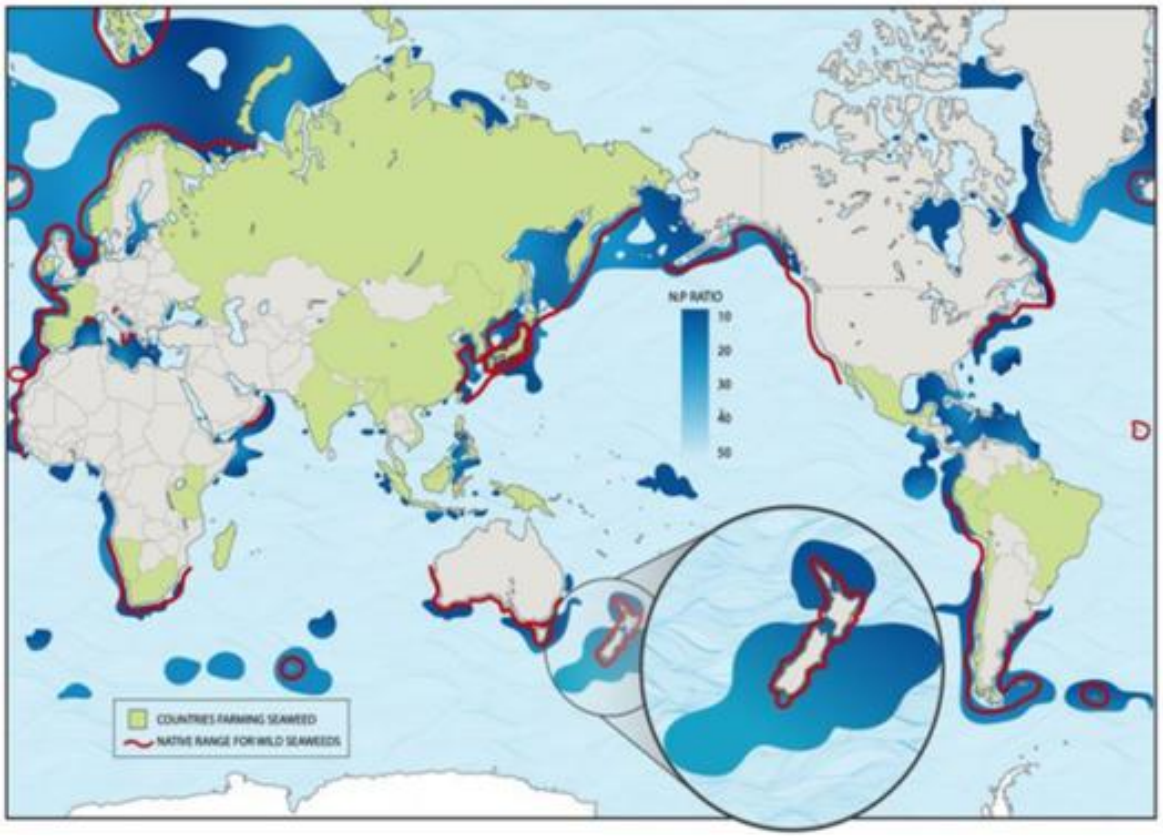

Figure 1.1. Ecological suitability map for seaweed aquaculture, illustrating ideal nutrient ratios (blue gradient) and native distribution of dominant seaweed genera (in red) in New Zealand. Adapted from Froehlich et al, 2019.

An estimated 750 native seaweed species are found in New Zealand (Hurd et al., 2004), yet only a few are utilized to produce essential phycocolloids such as agar, alginate, fucoidan, and carrageenan, which are vital in biotechnology, food production, and pharmaceuticals (Lomartire et al., 2021, 2022). Of these few species, most commercial seaweed companies rely on wild harvesting, sourcing seaweed primarily from beach-cast material and growth along mussel lines (Bradly et al., 2021). While commercial harvesting has been practiced since the 1940s, wild seaweed collection has deeper roots in traditional Māori practices (V. J. Chapman & Chapman, 1980; Colenso, 1880). This dependence on wild harvest highlights the early stage of seaweed aquaculture development in New Zealand and underscores the need for sustainable cultivation methods as wild seaweed harvests can impact marine ecosystems by removing habitat-forming species that provide shelter, food, and attachment

sites for various marine organisms, potentially leading to declines in associated species and broader ecosystem effects (Edgar et al., 2004; Tait & Schiel, 2011). Expanding cultivation techniques to include a broader range of native seaweeds could enhance our botanical understanding while unlocking their ecological and commercial potential (Luxton & Courtney, 1987).

1.3. *Ecklonia radiata*

Ecklonia radiata, a large brown alga in the order Laminariales, is a geographically widespread species found in the cool waters of southeastern Africa and Australasia where it is known as golden or common kelp (Kirkman, 1981). Ecologically, it plays a vital role as a foundational species, often forming monospecific forests in a range of habitat types (e.g. sheltered/exposed rocky reefs) (Wernberg et al., 2019) which provide shelter and food for higher trophic levels (Williams et al., 2020). It is a genetically diverse species, with regionally distinct sub-populations (Coleman et al., 2009; Nepper-Davidsen et al., 2021) and a high growth rate during the spring season, with individual plants accumulating 0.12 to 0.98 g dry weight per day (Fairhead & Cheshire, 2004).

Beyond its ecological importance, *E. radiata* holds substantial commercial value through its diverse applications across multiple industries (Bradly et al., 2021). The species contains a range of bioactive compounds with biopharmaceutical potential, contributing to the production of functional foods (Charoensiddhi et al., 2018), neurological health supplements (Alghazwi et al., 2020; Saini et al., 2021), beauty products (Lorbeer et al., 2015), and agricultural biostimulants (Fisheries New Zealand, 2023). The combination of valuable biomass, widespread distribution across New Zealand, relatively high growth rates, and adaptability to a range of habitats means that *E. radiata* is a promising candidate for developing a sustainable seaweed industry in New Zealand.

1.3.1. Ecklonia radiata life cycle

The life cycle of *E. radiata* follows the typical pattern of kelps in the order Laminariales, characterised by generations that alternate between a macroscopic diploid sporophyte and a microscopic haploid gametophyte (Figure 1.3, Wernberg et al., 2019). This heteromorphic life cycle plays a fundamental role in both natural population dynamics and aquaculture cultivation processes. The dominant phase of *E. radiata* is the diploid sporophyte, which

forms the large, leathery kelp blades commonly seen in subtidal forests (Kirkman, 1981). Sporophytes produce reproductive structures called sori (singular: sorus) on their blades, where meiosis occurs to generate haploid zoospores (Bartsch et al., 2008) which are released into the water column and dispersed by currents. Following settlement, zoospores germinate into microscopic male or female gametophytes (Figure 1.3c.). Successful gametophyte recruitment increases in temperatures around 16 – 20 °C (Mohring et al., 2013) and dim lighting commonly found beneath an *E. radiata* canopy (below 40-60 µmol photons m^{-2} s^{-1}) (Tatsumi & Wright, 2016; Wernberg et al., 2019). In low light conditions, spores will germinate, develop male or female reproductive structures, and grow vegetatively as gametophytes for extended periods (Tatsumi & Wright, 2016; Xu et al., 2005). An increase in light intensity, often following natural disturbances that remove the upper *E. radiata* canopy, can stimulate the male gametophytes to produce and release motile sperm that swim toward the oogonia of female gametophytes, where successful fertilisation results in a diploid zygote (Kirkman, 1981). With sufficient nutrients (notably nitrogen and phosphorus), appropriate temperatures, lighting, and aeration, the zygote develops into the juvenile sporophyte stage and is usually visible (approx. 500µm) 30-35 days after fertilisation (Wernberg et al., 2019). The surviving sporophytes are typically perennial, sometimes living up to ten years (Novaczek, 1981) developing reproductive sorus tissue to begin the life cycle anew.

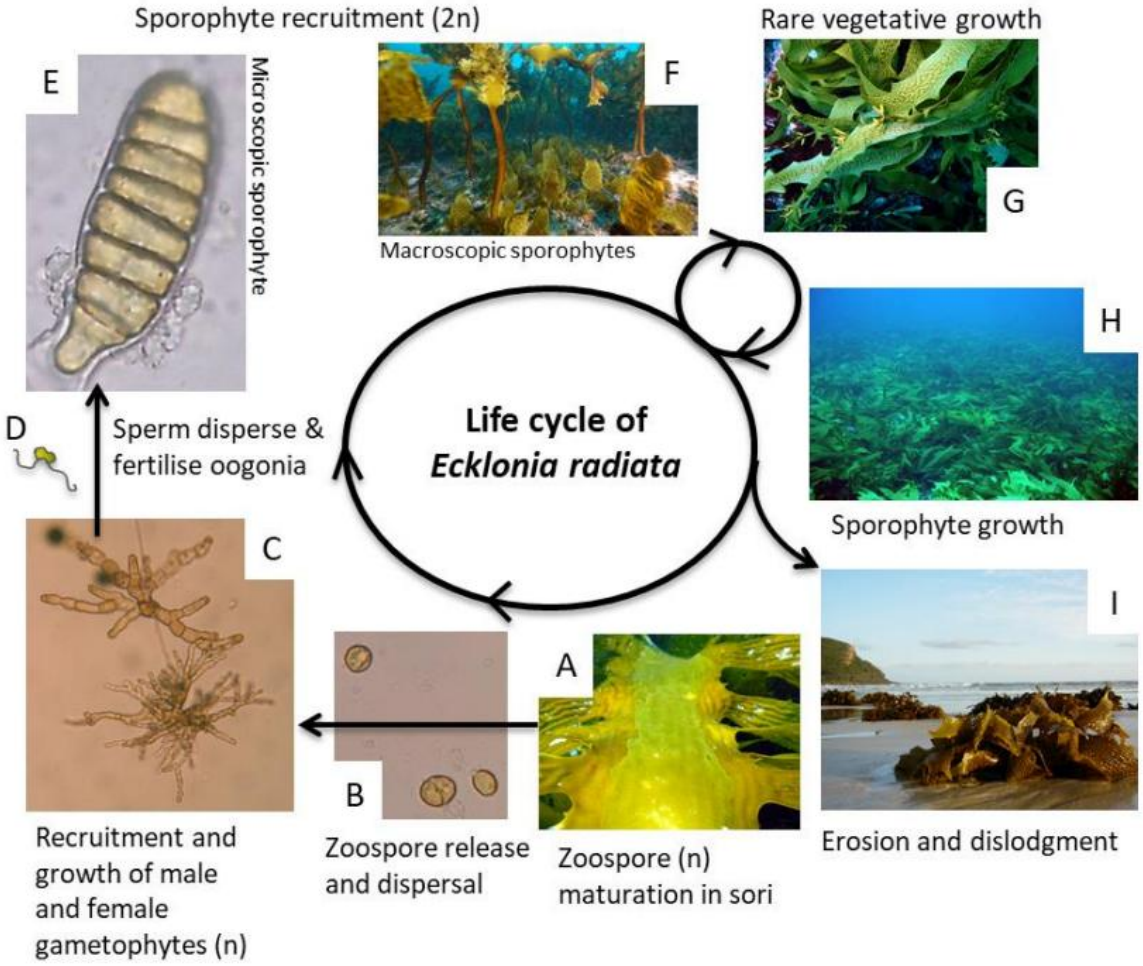

Figure 1.3. Life cycle of *Ecklonia radiata* illustrating the alternation of generations between the haploid gametophyte and diploid sporophyte stages. The different letters (A–I) indicate key stages in the life cycle, including zoospore release, gametophyte development, fertilisation, and sporophyte growth. Image sourced from Wernberg et al., 2019.

1.4. Kelp cultivation

Kelp cultivation involves two distinct phases: an indoor hatchery phase and an at-sea grow-out phase. The hatchery phase focuses on cultivation of early life cycle stages under controlled conditions to optimise the production of juvenile sporophytes, while the grow-out phase involves transferring these juveniles to marine environments for further growth until a harvestable size is reached (Mcelligott et al., 2022). During the hatchery phase, cultivation begins with the collection of mature sporophytes bearing sorus tissue to induce a spore release (Suebsanguan et al., 2021). Zoospores are either settled directly onto substrates (e.g., seeding twine wrapped around a spool) for immediate cultivation or

allowed to develop into gametophytes which are then held in suspension as a reference seedstock (Xu et al., 2005). Fertility in gametophytes can be indefinitely suppressed by continuous culturing under low intensity red light (600–700 nm), allowing cultures to remain in a vegetative state for years (referred to as multi-annual delayed gametophytes, Ebbing et al., 2021) until required for cultivation. When needed, reproduction in gametophytes can be induced by exposing cultures to white or blue light (400–500 nm) (Choi et al., 2005; Xu et al., 2005). Gametophytes can either be seeded onto substrates such as twine before inducing reproduction, allowing fertilization and sporophyte development to occur directly on the substrate under hatchery conditions, or reproduction can first be induced in culture and the resulting biomass (containing a mixture of gametophytes and microscopic sporophytes) can then be seeded onto substrates. Once attached, development continues under controlled aeration, nutrient supply, and temperature, with incremental increases in light intensity to promote further growth of juvenile sporophytes (Praeger et al., 2022).

During the grow-out phase, juvenile sporophytes are transferred to ocean farms (from here on referred to as “outplanting”), where they grow using natural sunlight and nutrients. A common outplanting method involves wrapping seeded twine around larger diameter grow ropes suspended in the water column. Light intensity decreases with increasing depth from the surface (Rohde et al., 2008), and different line configurations are used to accommodate different species and environmental conditions, such as exposed offshore sites or sheltered inshore areas (Moscicki et al., 2024; Nguyen et al., 2024). For *E. radiata* specifically, vertical dropper lines produced higher survival and growth rates in northern New Zealand (Nepper-Davidsen et al., 2023). Outplanting typically occurs in autumn and winter to take advantage of cooler temperatures and nutrient-rich conditions, with harvest occurring in spring at peak biomass before summer biofouling becomes an issue (Forbord et al., 2019).

Emerging technologies aim to improve efficiency of the entire cultivation process through direct seeding methods called binder-seeding (Kerrison et al., 2020). This approach induces gametophytes to transition to sporophytes which are then maintained in free-floating cultures until large enough for outplanting (~1 – 2 mm length). The sporophytes are then applied directly to the grow ropes shortly before outplanting (within 24 hours) using binders to effectively glue the sporophytes to the rope until they can form their own attachment (Kerrison et al., 2020). While this approach still requires more development, successful

application will reduce hatchery duration and handling requirements, offering potential cost and labour savings for large-scale operations in comparison with spore-seeded lines (Visch et al., 2023; Wilding et al., 2025).

1.5. Importance of abiotic conditions for hatchery cultivation

Nutrients, temperature and light are the key abiotic factors that influence growth and reproduction in seaweeds (de Bettignies et al., 2018; Roleda & Hurd, 2019). Hatcheries are designed to maintain tight control over these factors to enable crucial life cycle transitions and maximise growth rates (Mihaila et al., 2023). Optimising temperature, light and nutrients can enhance sporophyte development, improve outplanting stress tolerance, and support the ecological and economic sustainability of seaweed farming (X. Liu et al., 2017)

1.5.1. Nutrients

Nutrients are essential for supporting the cellular processes that underpin photosynthesis, metabolism, and biomass production in seaweeds (Tymoshuk et al., 2025). Nitrogen (N) and phosphorus (P) are the primary macronutrients required for growth (Fairchild et al., 1985). Nitrogen is a critical component of amino acids, nucleic acids, and chlorophyll (Larned, 1998), while phosphorus is integral to nucleic acids, ATP (energy transfer), and membrane structure (Cembella et al., 1982).

In natural environments, nutrient levels are highly variable and influenced by ocean currents, seasonal upwelling, terrestrial runoff, and anthropogenic inputs such as agricultural and urban wastewater discharge (Howard et al., 2014; Pitcher et al., 2010), with nutrient availability dependent upon dynamic biological, chemical and physical processes (Hamilton et al., 2022; Moore et al., 2013). Seaweeds take up these nutrients primarily in their inorganic forms such as nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}), which are more bioavailable than organic forms like urea or amino acids (Berman, 1999; Calatrava et al., 2019). Uptake occurs across the thallus surface via active transport and diffusion, with uptake rates depending on nutrient availability and environmental conditions like water flow, temperature, and pH (Smit, 2002; Wallentinus, 1984). In seawater, nitrate is more abundant than ammonium (Brandes et al., 2007). However, nitrate must be actively transported across the cell membrane, whereas ammonium, the preferred nitrogen source for many seaweed species, can be absorbed more readily through passive or facilitated

diffusion (Harrison & Hurd, 2001; Herrero et al., 2025). Once inside the cell, nitrate is enzymatically reduced to ammonium and incorporated into amino acids, the building blocks of proteins (Calatrava et al., 2019; Chapman et al., 1978). Protein synthesis drives overall biomass accumulation, while chlorophyll production supports energy generation and further nutrient uptake (Yu et al., 2022).

When nutrient concentrations are low, seaweeds experience nutrient limitations, which can restrict growth, reduce photosynthetic efficiency, impair reproductive development, and limit pigment production (Larned, 1998; Zhou et al., 2022). Nitrogen is often the primary limiting nutrient, with deficiency leading to reduced chlorophyll content, lower biomass yields, and delayed reproductive stages (Goldman, 1976). The most efficient growth rates are achieved when both nitrogen and phosphorus are steadily supplied in bioavailable forms and in a balanced N:P ratio (Sheppard et al., 2023). The optimal N:P ratio varies largely among algal species, and suboptimal ratios can affect growth rates and biomass composition (Mayers et al., 2014). For example, in the green microalgae *Nannochloropsis oculata* and *Tisochrysis lutea,* lower N:P ratios (20:1) improved growth and protein production, while higher ratios (120:1) reduced growth but promoted lipid accumulation (Rasdi & Qin, 2015). Seaweeds typically exhibit higher C:N and C:P ratios than phytoplankton, reflecting their greater capacity to store carbon relative to nutrient availability (Sheppard et al., 2023).

In hatchery settings, nutrient concentrations can be precisely controlled to support growth and biomass composition (Visch et al., 2023). Synthetic nutrient media, such as Provasoli's Enriched Seawater (PES), are commonly used to supply nitrogen and phosphorus in readily bioavailable forms (Tymoshuk et al., 2025), as organic N sources such as degassed manure and mussel excreted ammonium are suboptimal for hatchery performance (Boderskov et al., 2022). Most hatcheries use batch cultivation systems where seaweed is grown in the same water for short periods (usually one week) with regularly added nutrients (Vindy et al., 2021). Alternatively, flow-through systems supply a constant stream of seawater, providing a higher nutrient flux and ensuring that the total amount of nutrients available to cultures is sufficient, even if the incoming water is not particularly nutrient-rich (Rolin et al., 2016). In integrated multi-tropic recirculating aquaculture systems (IMTRAS), nutrients for algal growth are primarily supplied by effluent water from fish, mussel, and/or sea cucumber

cultivation (Huo et al., 2024). Adequate nutrient supply is critical to support the development of early life history stages, particularly during periods of rapid growth (Beck et al., 2017) and reproduction (Carney & Edwards, 2010; Kinlan et al., 2003). However, excessive nutrients can inhibit gametophyte reproduction at higher ammonium-nitrogen concentrations (100 µM) (Yarish et al., 1990) and promote opportunistic epiphytic growth. Therefore, tailoring nutrient concentration and delivery is critical to ensure fast growth, healthy thalli, and successful life-stage transition levels.

1.5.2. Temperature

Temperature plays a critical role in the life cycle transitions of *E. radiata*, and affects metabolic rates, enzymatic activities, and overall growth (Alsuwaiyan et al., 2019; Gonzalez et al., 2024; Purcell et al., 2024). Exposure to excessively warm conditions can impair gametophyte reproduction (gametogenesis), decrease photosynthetic activity and chlorophyll concentration, and increase oxidative stress, ultimately leading to reduced viability and eventual cell death (Wernberg et al., 2016). In the natural environment, thermal optimums in *E. radiata* vary geographically, reflecting regional biogeographical adaptations to local environmental conditions (Bearham et al., 2013). Gametophyte populations from warmer regions of the kelp's distribution exhibit higher thermal tolerance compared to those from colder regions, and this thermal tolerance is suggested to arise from plasticity and heritable genetic variation (Mohring et al., 2014). In controlled hatchery experiments, optimal gametophyte growth is observed at temperatures warmer than those typically experienced in corresponding natural habitats, with one study finding the growth optimum occurring ~3°C higher than the survival optimum (Schwoerbel et al., 2024). These thermal optima likely reflect local adaptation to tolerate climate extremes, such as marine heatwaves, rather than reliance on historically semi-consistent cooler water temperatures (Mohring et al., 2014). Different physiological mechanisms respond to increasing temperatures at different rates. For example, both photosynthesis and respiration rates increase with increasing temperature, however, respiration accelerates more rapidly and peaks at a higher temperature (Wernberg et al., 2019). These differences in response mean that while growth may increase at higher temperatures, overall survivability and functionality can decline beyond a critical threshold (Mabin et al., 2013).

Therefore, hatchery conditions typically aim for cooler temperatures closer to the thermal optimum for survival, balancing growth rates with long-term viability and reproductive success. For example, while *E. radiata* gametophyte growth can occur across a relatively broad thermal range (5–25°C), successful gametogenesis and sporophyte development are restricted to a narrower window of 10–20°C (Schwoerbel et al., 2024), indicating that reproductive processes are more sensitive to temperature extremes than vegetative growth. This sensitivity is especially pronounced in young sporophytes, which are highly vulnerable to thermal stress in hatchery settings (Alsuwaiyan et al., 2021). Elevated temperatures can impair their development by disrupting photosynthesis, reducing growth, and increasing susceptibility to disease. As such, careful temperature management not only maximises biomass production and healthy blade formation but also enhances outplanting success. Moreover, tailoring cultivation practices to local environmental conditions, such as seasonal temperature fluctuations, can help reduce transplant shock and improve sporophyte establishment in the field (Kim et al., 2019; Y. Liu et al., 2023).

1.5.3. Light

Light is essential for driving photosynthesis in seaweed, providing the energy needed for carbon fixation and growth (Augyte et al., 2019; Mackinder et al., 2017). Photosynthetic rates generally increase with light intensity until reaching a saturation point, beyond which further increases cause photoinhibition, damaging Photosystem II (PSII) and reducing photosynthetic efficiency (Bruhn & Gerard, 1996; Desmond et al., 2017; Endo et al., 2023). Different macroalgal species have varying light requirements, largely due to differences in pigment composition. The three major macroalgal groups (Phylum Chlorophyta, Phylum Rhodophyta, and Phylum Phaeophyta), possess distinct combinations of chlorophylls, carotenoids, and phycobiliproteins, which absorb specific wavelengths of light (Desmond et al., 2017; Encyclopædia Britannica, 2024, Figure 1.4). For example, brown algae such as *E. radiata* primarily use chlorophyll a, chlorophyll c, and fucoxanthin, enabling efficient light harvesting in deeper or low-light environments (Barrett & Anderson, 1977). In addition to its role in photosynthesis, light also regulates reproductive processes in seaweed. Blue and green wavelengths have been shown to trigger egg formation (Luning & Dring, 1975) and stimulate the release of motile reproductive cells such as gametes and zoospores (Hiyama & Yoshikawa, 2025). These reproductive responses are driven by light exposure duration and

circadian rhythms, rather than direct photosynthetic activity, suggesting that specific light cues act as environmental signals regulating reproduction (Hiyama & Yoshikawa, 2025).

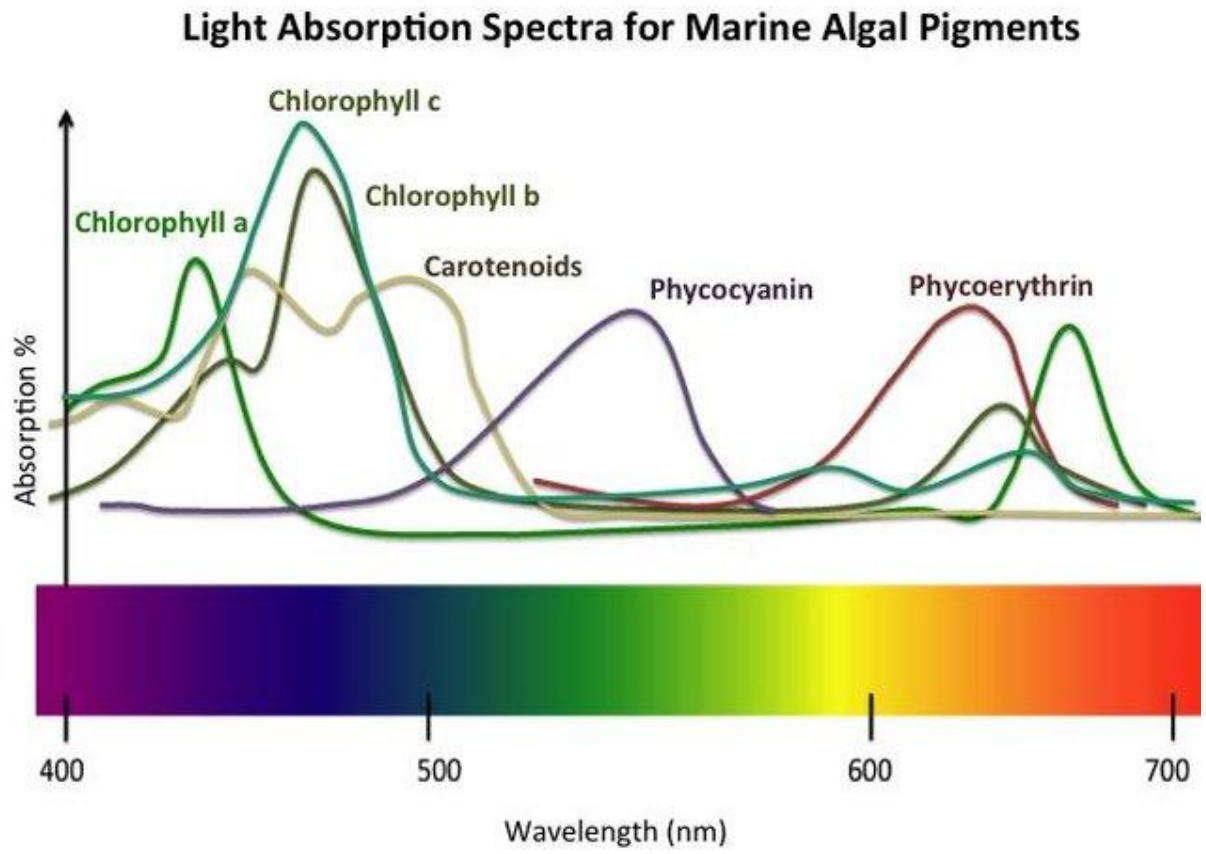

Figure 1.2. Light absorption profiles of photosynthetic pigments (Sourced from Yarish et al., 2012).

In natural ecosystems, low light levels limit both microscopic and macroscopic sporophyte recruitment under dense understory algal cover (Tatsumi & Wright, 2016). Following canopy disturbances, however, these young light-sensitive stages can shift from dormancy to rapid growth to exploit newly available light and space (Tatsumi & Wright, 2016). Early sporophyte stages of *E. radiata* are particularly sensitive to high light intensities, with optimal growth occurring under lower light levels (30 µmol photons m^{-2} s^{-1}) of Photosynthetically Active Radiation (PAR) than adult sporophytes (Roleda et al., 2007; Visch et al., 2023). While appropriate levels of PAR support sporophyte development, exposure to ultraviolet (UV) radiation can cause tissue damage, pigment degradation, reduced growth, and lower survivorship (Wood, 1987). Notably, over longer timescales of low light availability, *E. radiata* can photoacclimate through morphological and physiological adjustments. For example, *E. radiata* populations growing in shaded environments in

Milford Sound exhibit similar maximum photosynthetic rates (P_{max}) to populations in high-light areas, achieved through the development of larger, thinner blades, increased pigment concentrations, and reduced respiration rates (Miller et al., 2006; Wernberg et al., 2019).

In hatchery settings, light quality (i.e. spectrum or colour), intensity, and photoperiod must be carefully regulated to support healthy development across different life stages. Light intensity is typically increased progressively throughout the hatchery period as cultures advance through their life stages and grow larger (Visch et al., 2024). Typically, PAR wavelengths between 400–700 nm are supplied using LED lighting systems, with specific intensities adjusted according to species and developmental stage (Visch et al., 2024). Initially, low light levels are maintained to prevent photoinhibition as early-stage gametophytes are sensitive to high light intensities (e.g. above 3.6 mol m^{-2} d^{-1}) (Dring et al., 1996; Novaczek, 1984). For example, growth rates in *E. radiata* gametophytes have been shown to increase with increasing light intensities up to approximately 0.4mol photons m^{-2} d^{-1} but further increases in intensity past this point trigger gametogenesis and the relative growth constant declines as energy shifts from vegetative growth to reproduction and sporophyte formation (Novaczek, 1984). Following fertilisation, light intensity is gradually increased to support higher rates of photosynthesis and biomass accumulation as microscopic sporophytes establish, and juvenile sporophytes grow in size (Redmond et al., 2014).

An in depth understanding of light-regulated triggers of kelp reproduction has led to the development of techniques to maintain gametophyte cultures in a vegetative state for extended periods of time (>1 year), referred to as multi-annual delayed gametophytes (Ebbing et al., 2021). This method gives hatchery operators greater flexibility in cultivation scheduling, ensuring gametophyte biomass is ready when conditions are optimal. Light-based control strategies are critical for synchronising reproduction with operational demands, improving efficiency and flexibility to supply seaweed farming systems, while optimising light conditions at each developmental stage maximises growth, minimises energy wastage, and ensures reliable life cycle transitions.

1.6. Knowledge gaps

While the influence of abiotic factors on seaweed growth and reproduction has been widely studied, important knowledge gaps still exist in the context of hatchery cultivation. Nitrogen sources and concentrations have been shown to strongly influence growth rates, tissue composition, and reproductive processes across a variety of seaweed species (Jevne et al., 2020; Van Alstyne, 2018). However, despite the recognised importance of nitrogen, there are no direct studies that systematically assess the effects of varying nitrogen concentrations on the growth and development of *E. radiata* under hatchery conditions. In general, nutrient enrichment has been shown to enhance *E. radiata* growth under low-light conditions (Blain & Shears, 2020), however high nutrient concentrations can negatively affect algal development through physiological mechanisms. For example, *Saccharina latissima* exhibited optimal growth at nitrogen concentrations between 50–100 µM, while elevated ammonium concentrations (>150 µM) impaired gametogenesis (Boderskov et al., 2022). High nutrient concentrations can also lead to excess nutrient supply, which is associated with higher risk of contamination in algal cultures as it can promote the growth of nuisance algae or microbes (Nelson, 2017), but remains an area with limited empirical research, particularly for kelp hatcheries. Identifying appropriate nutrient levels that maximise growth without causing adverse effects on culture health or development is critical for efficient and successful hatchery cultivation. To date, specific nutrient concentration thresholds that optimise early sporophyte development and performance have not been established for *E. radiata*.

In addition to nutrient concentration, the frequency of nutrient delivery is another important factor potentially influencing hatchery performance. Although a periodic single large dose (e.g., once per week) may provide sufficient nutrients initially, concentrations decline as nutrients are gradually absorbed or lost from the system, potentially limiting growth before the next nutrient dose is given. Multiple smaller doses spread throughout a cultivation period could help maintain more consistent nutrient levels, potentially improving uptake efficiency and reducing the risk of nutrient depletion or wastage. While ocean nutrient levels fluctuate (Holligan et al., 1985), frequent dosing in hatchery settings should be an improvement over natural nutrient dynamics to support healthier tissue development. However, despite its potential importance for hatchery performance, the

effect of nutrient dosing frequency on the growth of *E. radiata* or any other species of kelp has not been well studied and is a critical knowledge gap.

In hatchery settings, optimising light conditions can accelerate culture growth and may even improve the resilience of sporophytes during the critical outplanting stage (Desmond et al., 2017). Controlled laboratory studies have demonstrated that consistent moderate light and temperature conditions support early development of *E. radiata* gametophytes and sporophytes (Praeger et al., 2022). However, optimal abiotic conditions can vary significantly between cultivation systems. These earlier experiments were conducted on small scales and in simplified setups (e.g., static petri dishes), which differ from practical hatchery systems using seeded spools for outplanting. As a result, the light levels identified in such studies cannot be directly applied to large-scale hatchery cultivation, highlighting the need for further research into light optimisation under hatchery-relevant conditions.

A further consideration for hatchery cultivation is the effect of hatchery light regimes on subsequent sporophyte survival and growth during and after outplanting. While environmental stressors such as temperature and wave exposure have received attention in the context of outplanting (Hayes et al., 2024; Matsson et al., 2021), the role of light stress remains comparatively understudied. Sporophytes may be exposed to sudden increases in irradiance during the outplanting process (i.e. when they are handled on boats under full sun) and after deployment in the field, depending on depth, season, and water clarity. Natural sunlight in surface waters can reach photon flux densities of ~2,000 µmol photons m^{-2} s^{-1} on clear days (Apogee Instruments, 2024), far exceeding the lower, more controlled levels typically used in hatcheries (~100 µmol photons m^{-2} s^{-1}). This abrupt shift in light conditions could contribute to stress and reduced performance post-outplanting. Although direct studies investigating light shock during outplanting are limited, previous research has shown that other aspects of pre-outplanting development can influence survivability. For example, *Saccharina latissima* sporophytes outplanted as juveniles exhibited better growth and survival compared to earlier developmental stages, likely due to their larger size and more developed holdfasts (Kerrison et al., 2018). This suggests that the physiological condition of sporophytes at the time of outplanting plays a critical role in field performance. Cultivating *E. radiata* under moderately elevated light conditions in the final weeks of hatchery production may function as a form of light "priming" or "exposure therapy,"

potentially increasing their tolerance to high irradiance. However, it remains unclear whether adjusting hatchery light regimes can effectively mitigate light stress during and/or after outplanting, representing a key knowledge gap with practical implications for improving survival and growth.

1.7. Aims and objectives

The overall aim of this thesis is to optimise nutrient and light regimes for hatchery cultivation of *Ecklonia radiata*. Specifically, it investigated how different nitrate concentrations and dosing frequencies affect growth, tissue nitrogen content, nutrient uptake, and culture health; examine the influence of varying light regimes on sporophyte density and growth during hatchery cultivation; assess whether hatchery light conditions affect tolerance to light stress during outplanting; and evaluate the effects of hatchery light regimes on initial survival and growth under different light conditions after outplanting. The findings are expected to improve hatchery cultivation protocols, enhance sporophyte resilience to environmental stress, and support sustainable seaweed aquaculture in New Zealand.

2. Methods

2.1. Nutrient regime experiment

2.1.1. Sporophyte collection, spore release, and seeding

Adult sporophytes of *E. radiata* were collected in July 2024 from Pilot Bay, Tauranga, Aotearoa New Zealand (-37.636546, 176.169012) at 1-2 m depth (MPI collection permit SP742-3). The sporophytes were transported in an insulated container to the University of Waikato's Facility for Aquaculture Research of Macroalgae (FARM), an outdoor recirculating aquaculture system within a greenhouse, in Tauranga, Aotearoa New Zealand, within one hour of collection. Sporophytes were placed into 1000 L tanks filled with nutrient enriched (Cell-Hi F2P, Varicon Aqua Solutions UK, 0.01 g L^{-1}, 12.3 mg nitrate-N L^{-1} and 1.1 mg P L^{-1}) filtered seawater maintained at approximately 15 °C, with natural light and dark cycles (approx. 10 h light: 14 h dark) and covered with 50% shaded mesh. Two days later, fronds with patches of sorus tissue were transferred to aerated 10-liter buckets filled with UV filtered (0.35 µm) seawater (UVFSW) in a temperature-controlled room (17 °C) under

indirect light (12 h light: 12 h dark, 30 µmol photons m^{-2} sec^{-1}). Sorus tissue was excised prfrom fronds four days later, and spore release was initiated following *Praeger et al. (2022),* in which the tissue was disinfected in a 200 ppm NaOCl solution, desiccated at ambient temperature, immersed in autoclaved filtered seawater with gentle stirring, and then filtered and adjusted for density using a haemocytometer. The spore solution was adjusted to a density of 4,000 spores per mL (equivalent to approximately 350 spores per linear meter of seeding twine) with nutrient enriched (full strength Provasoli enriched seawater (PES), Redmond et al., 2014) autoclaved UV treated and filtered (0.35 µm) seawater (AUVFSW) and seeded in the dark onto pre-cleaned (soaked in 2% sodium bicarbonate solution for 24 hours) 0.9 mm polyester twine wrapped around 180 mm (⌀ 80 mm) PVC pipe (referred to as "spools") (Lawton & Magnusson, 2024).

2.1.2. Hatchery cultivation

Spools were transferred into individual 2L plastic containers provided with a gentle stream of filtered (Whatman™ Uniflo syringe filters, 0.22µm) air through inlets at the base of the container forty-eight hours after seeding. Each container was filled with UVFSW and PES was added at three concentrations: double strength (40 mL L^{-1}, providing 37.69 mg N L^{-1} and 1.62 mg P L^{-1}), full strength (20 mL L^{-1}, providing 18.85 mg N L^{-1} and 0.81 mg P L^{-1}), and quarter strength (5 mL L^{-1}, providing 4.71 mg N L^{-1} and 0.20 mg P L^{-1}), with dosing frequencies of either once or three times per week (Table 2.1). For the three-times-per-week dosing frequency, one-third of the full volume of PES required to achieve the target treatment strength was added on each dosing occasion, ensuring that the same total amount of nutrients was provided per week for each nutrient concentration treatment regardless of dosing frequency. This experimental design provided a total of six treatments, and five replicate spools were seeded for each treatment (N=5).

Table 2.1. Treatments used in nutrient regime experiment with PES at three concentrations (double, full, or quarter strength) and two dosing frequencies (once or three times per week).

Nutrient strength	Doses per week	mL PES L^{-1} per dose	Total mL PES L^{-1} per week	mg N L^{-1} per dose	mg P L^{-1} per dose
Double	1	40	40	37.7	1.62
Full	1	20	20	18.9	0.81

Quarter	1	5	5	4.7	0.20
Double	3	13.3	40	12.6	0.54
Full	3	6.7	20	6.3	0.27
Quarter	3	1.7	5	1.6	0.07

Containers were placed in a temperature-controlled room at 17 °C on shelves equipped with overhead LED lights (Type A J-Series Cyanosis bulb, cool white light, 18 W, Ecopoint Ltd) programmed to a 12-hour light: 12-hour dark cycle. An initial light intensity of 30 µmol photons m^{-2} s^{-1} was achieved using shade screens and 5 cm platforms to increase spool proximity to the light source. This was increased to 50 µmol photons m^{-2} s^{-1} 18 days after seeding and to 100 µmol photons m^{-2} s^{-1} 32 days after seeding. A randomized block design was used to position containers on shelves, with each block containing one replicate container from every treatment. To distribute lighting equally to all sides of the containers, replicates were rotated 120° three times per week. Culture water was replaced by transferring spools into pre-cleaned containers (soaked for 24 hours in a 10 % bleach solution) filled with fresh UVFSW and supplemented with nutrients according to treatment requirements. This transfer occurred weekly, at which point spools were flipped vertically to ensure even exposure to light, and container positions within each block were rotated weekly to reduce potential positional effects.

2.1.3. Hatchery measurements

The overall quality of each spool was assessed using the Greenwave Hatchery Rating System at 9 and 12 weeks after seeding. This system assigns a numerical score to each spool based on sporophyte coverage, growth evenness, coloration, and contamination (Lawton & Magnusson, 2024). In addition, the length and density of sporophytes on each spool were measured 9 and 12 weeks after seeding by scraping all sporophytes off from the twine using a spatula in a 13 mm diameter circular area in the center of each spool (Figure 2.1). The removed seedlings were transferred to a ø 50 mm petri dish filled with 10 mL of filtered seawater and gently agitated to ensure even distribution and minimise overlap. A photograph of the dish was taken from a standardised distance of 20cm, and sporophyte length was determined by measuring the 10 longest individuals in the photograph. Sporophyte density was quantified by converting the photographs to black and white and

calculating the percentage of the petri dish surface covered by sporophytes (Lawton & Magnusson, 2024). All analyses were conducted using Photoshop and ImageJ2 software (Rueden et al., 2017).

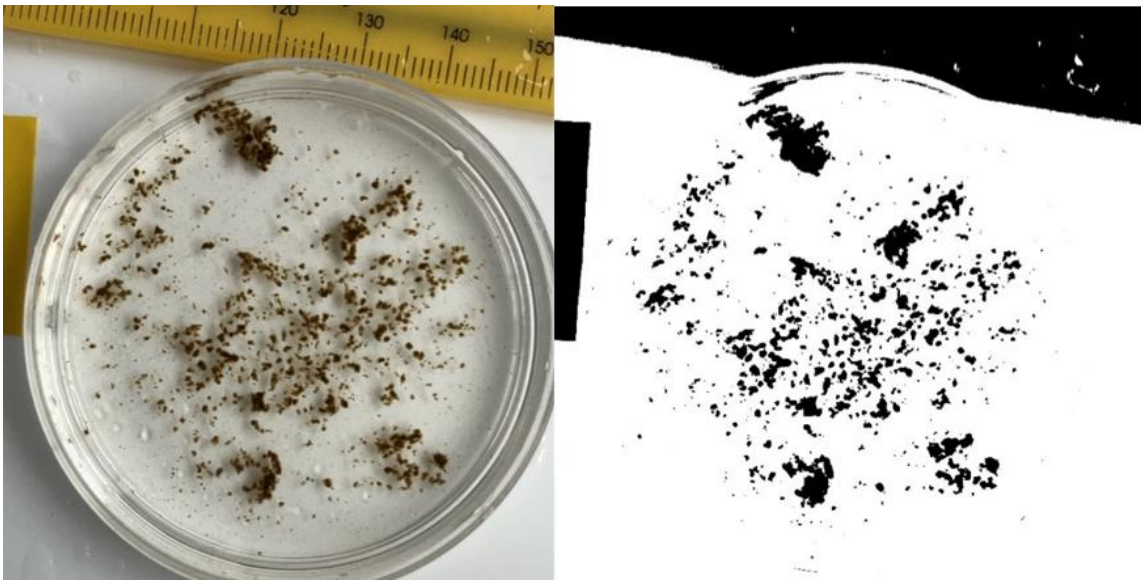

Figure 2.1. Petri dish filled with 10 ml filtered seawater and sporophytes scraped off from 13 mm diameter area of twine from spool (left image). Photograph of petri dish and scraped sporophytes converted to black and white for density measurement (right).

Assumed nitrate uptake was estimated by measuring the total nitrate concentration in the culture water in each replicate at the beginning and end of each week at 6, 9, and 12 weeks after seeding. Water samples were collected immediately after the weekly water change and immediately before the next water change one week later for all treatments. Approximately 25 mL of culture water was filtered (Minisart Syringe Filters, 0.45µm) into sterile 50 mL clear plastic test tubes (Labserv) and immediately frozen. Samples were thawed and nitrate concentrations were quantified within 15 weeks of sample collection using a HACH 900 spectrophotometer (HACH, USA) following the cadmium reduction method (Method 8039). For treatments receiving nutrients three times per week, the initial nitrate concentration was multiplied by three to account for cumulative dosing. The assumed nitrate uptake for each replicate was calculated as the difference between the initial (adjusted) and final nitrate concentrations.

Biomass tissue nitrogen content for each replicate was determined by carefully scraping the wet biomass off from each spool 12 weeks after seeding. The biomass was oven-dried at 60°C for 72 hours to ensure complete moisture removal and then ground to fine particles (<

0.5 mm) using a mortar and pestle. The content of carbon (C) and nitrogen (N) in the ground biomass was analyzed commercially by OEA Laboratories Limited (Okehampton, UK) using percentage elemental analysis (EA). In this process, milligram amounts of the samples were combusted or pyrolyzed and the resulting gases (i.e. CO_2, H_2O, N_2) were separated using gas chromatography and quantified against certified reference standards via a thermal conductivity detector.

2.2. Light Regime Experiment

2.2.1. Sporophyte collection and gametophyte culture establishment

In January and February of 2024, adult *E. radiata* sporophytes were collected from two sites in the Hauraki Gulf, Aotearoa New Zealand (Wilson Bay, -36.886517, 175.422597; and Esk Point, -36.807126, 175.440656) and transported to the University of Waikato's FARM, where they were placed in 1000 L holding tanks and maintained as described above for the nutrient regime experiment. Spore release was induced in sorus bearing fronds 4-5 months later (June 2024) following methods described above. The resultant spore solution (approx. 100 mL, 30,000 spores mL^{-1}) was added to a 2 L plastic container supplied with gentle aeration and diluted with autoclaved, UV- treated and filtered seawater (UVFSW) enriched with half-strength PES nutrients (10 mL L^{-1}). The container was placed into a plant growth cabinet (Panasonic MLR-352) maintained at 17 °C, under red light (15 µmol photons m^{-2} s^{-1}) with a 12-hour light:12-hour dark cycle and water changes every 2-4 weeks. After germination into gametophytes, the cultures were grown vegetatively under the same conditions for ten months before the start of the experiment.

2.2.2. Hatchery Cultivation

In early April 2025, gametophytes were dewatered by pouring through a 100 µm mesh sieve and fragmented to an average length of 412 µm (± 108 S.D.) using a blender (Kenwood Hand Blender model HDP109WG). The biomass was individually seeded onto 15 replicate spools at a rate of 0.238 mg dry weight (7.22% fresh weight) per meter of seeding twine by mixing it with a 0.7% w/v xanthum gum binder. This binder was prepared by adding 2.625 g xanthum gum to 200mL AFSW, and then 22mL of the binder+biomass solution was evenly applied to each individual spool with gloved hands. After seeding, the spools were placed into individual 2 L AFSW- filled containers enriched with 20 mL L^{-1} PES without aeration to

promote initial attachment of biomass to the twine. Containers were arranged on shelves in a temperature-controlled room maintained at 17 °C and provided with either 30 or 50 µmol photons m^{-2} s^{-1}, depending on the assigned light treatment as described below. After three days, gentle aeration was introduced and spools were maintained for the remainder of the experiment under identical conditions as described above with the exception of the differing light treatments. The results from the nutrient experiment led to nutrients being applied only once per week at full-strength PES (20 mL L^{-1}) after water changes.

Spools were maintained under one of three hatchery light regimes: Standard, Standard+Primer, and Higher Intensity, with five replicate spools per treatment (Figure 2.2). The Standard treatment served as the control, in which light intensity was initially set to 30 µmol photons m^{-2} s^{-1}, increased to 50 µmol photons m^{-2} s^{-1} on day 7, and to 100 µmol photons m^{-2} s^{-1} on day 14 and was maintained at this intensity until outplanting on day 35 (5 weeks after seeding). The Standard+Primer treatment followed the same light regime as the Standard treatment for the first four weeks, but light was further increased to 120 µmol photons m^{-2} s^{-1} during the final week (from day 28 onwards) as a "primer" treatment. This treatment aimed to determine whether a short-term exposure to high intensity light prior to outplanting could enhance sporophyte tolerance to light stress and improve post-outplanting performance. The Higher Intensity treatment maintained elevated light intensity throughout cultivation compared to the Standard Treatment, starting at 50 µmol photons m^{-2} s^{-1}, increased to 100 µmol photons m^{-2} s^{-1} on day 7, and then to 120 µmol photons m^{-2} s^{-1} on day 14 until outplanting. This treatment tested whether sustained high light intensity would accelerate sporophyte growth and reduce the time required for sporophytes to reach outplanting size. Light intensity was measured using a light meter (Apogee Instruments microCache, S/N: 1666), and treatment differences were achieved by varying shade screen opacity and quantity of LED lights. Light intensities in this experiment were increased earlier compared to the nutrient experiment. This adjustment was made because spools were seeded with gametophytes rather than spores, which develop into visible sporophytes more quickly. As a result, the overall hatchery duration in this experiment was shorter than the nutrient experiment. Shade screens and lighting were adjusted on days 7, 14, and 28 after seeding to accommodate the faster development timeline, with simulated outplanting occurring on day 35.

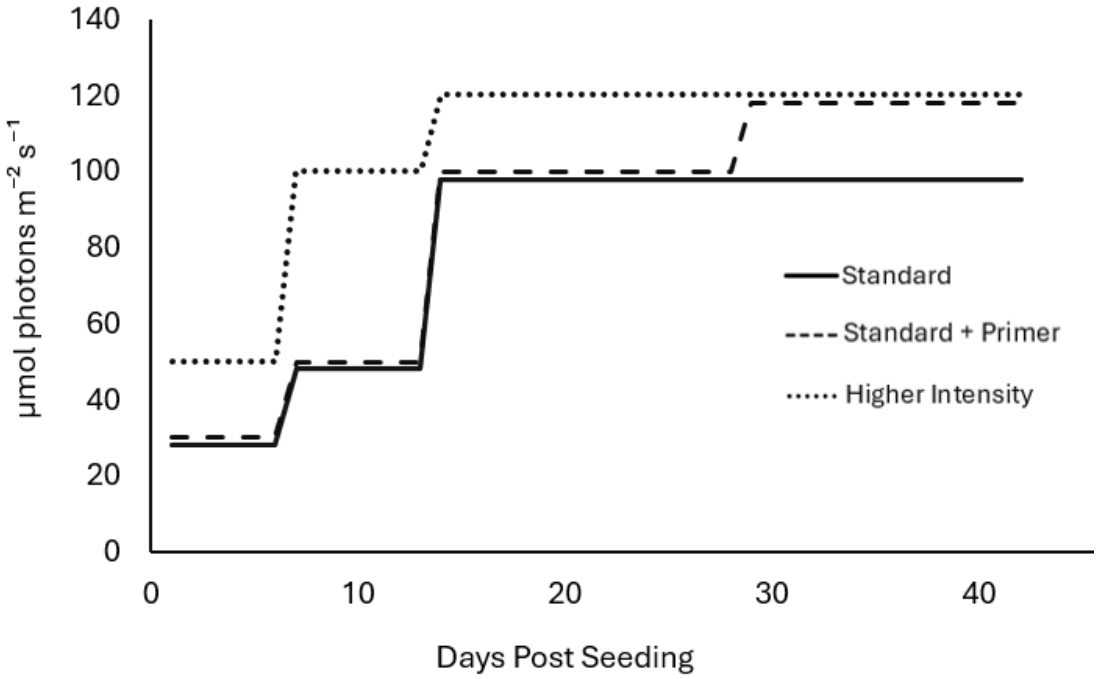

Figure 2.2. Light intensity (µmol photons m^{-2} s^{-1}) received by cultures over time (days post seeding) in the hatchery for each of the treatments (Standard, Standard+Primer, Higher Intensity) in the light regime experiment. Light intensity incrementally increased 7, 14, and 28 days after seeding.

Overall spool quality, sporophyte length, and sporophyte density were determined for each spool 5 weeks after seeding. Overall spool quality was determined following the Greenwave Rating system described above. Sporophyte length was assessed by measuring the 10 longest individuals within a randomly selected 10 mm section of twine under a stereo microscope (Olympus SZX2-ILLTQ) using the Olympus CellSens Entry Software (Version 2.3). Sporophyte density was quantified by counting the total number of sporophytes and the number of sporophytes larger than 1 mm within each 10 mm section of twine.

2.2.3. Simulated outplanting

Five weeks after seeding, twine from the spools was transferred to a raceway tank at the University of Waikato's FARM facility to simulate outplanting and investigate the effects of hatchery light regimes on post-outplanting performance. A full factorial design was used, with three hatchery light treatments, two outplanting exposure treatments, and three outplanting shade levels, with three replicates of each treatment combination (54 experimental units total, Figure 2.3).

Twine sections (50 cm) from the three replicate spools with the highest sporophyte density in each hatchery light treatment were wrapped around pre-wetted 50 cm lengths of ø 1 cm twisted polyester rope, and transferred to a 4,000 L outdoor raceway tank (Figure 2.4). The tank was filled with nutrient enriched (2 g Varicon Aqua Cell-Hi F2P) UV-filtered (0.35 µm) seawater maintained at 17 °C that was continuously circulated around the tank by a paddlewheel at a speed of 1.5 m s^{-1}. Ropes were secured to PVC pipe frames placed along the straight section of the tank to keep them submerged under 20 cm of water. To simulate light stress during the outplanting process, half of all replicates were subjected to an exposure treatment upon transfer to the raceway tank. During this exposure treatment, 27 rope samples (3 hatchery light treatments × 3 shade levels × 3 replicates) were exposed to overcast sunlight for 10 minutes at an average light intensity of 500 µmol photons m^{-2} s^{-1} before being placed in the raceway tank. To prevent desiccation, salt water was sprayed onto the ropes approximately every 30 seconds. In addition to the 10 minutes of direct light exposure, the exposure treatment samples received an additional hour of indirect natural light (averaging 200 µmol photons m^{-2} s^{-1}) compared to the control samples during experimental setup in which they were submerged but not shaded while the non-exposure replicates were planted alongside. To simulate different light conditions following outplanting, the surface of the tank was covered with three levels of shade cloth: 50% (low shade), 70% (medium shade), and 90% (high shade), with 3 replicates of each hatchery light treatment and exposure treatment combination under each shade treatment. Sporophyte length, sporophyte density, and the percentage of sporophytes >1mm were measured at one- and two-weeks post- “outplanting” by removing 15 cm sections of twine from each replicate rope and quantifying these metrics for the best 8.5 cm section of the twine under a microscope as described above. Water in the raceway tank was replaced weekly and nutrients (2 g Varicon Aqua Cell-Hi F2P) were added every 2-3 days.

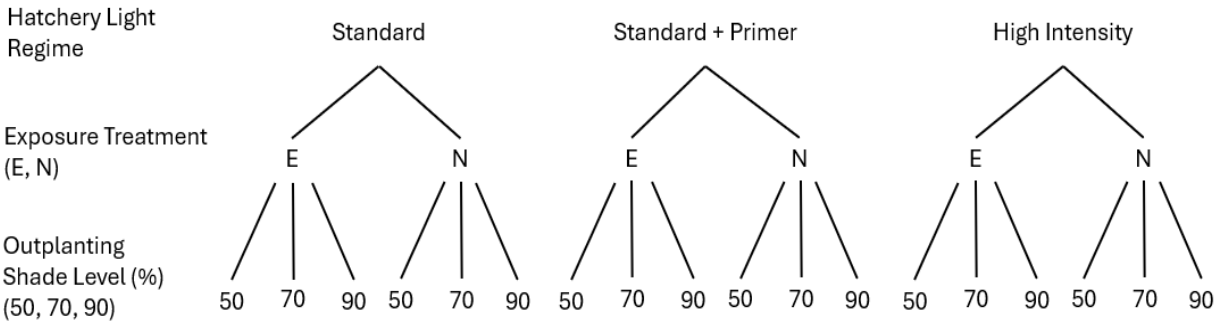

Figure 2.3. Design of the factorial experiment examining the effects of hatchery light regime, post-outplant light exposure, and outplant shading on *E. radiata* sporophyte development. Sporophytes were reared under one of three hatchery light regimes (Standard, Standard + Primer, or High Intensity), then either Exposed (E) or Not-Exposed (N) to high light for 10 minutes during simulated "outplanting." Sporophytes were subsequently placed under one of three shade treatments (50%, 70%, or 90% shade), resulting in 18 unique treatment combinations with 3 replicates each.

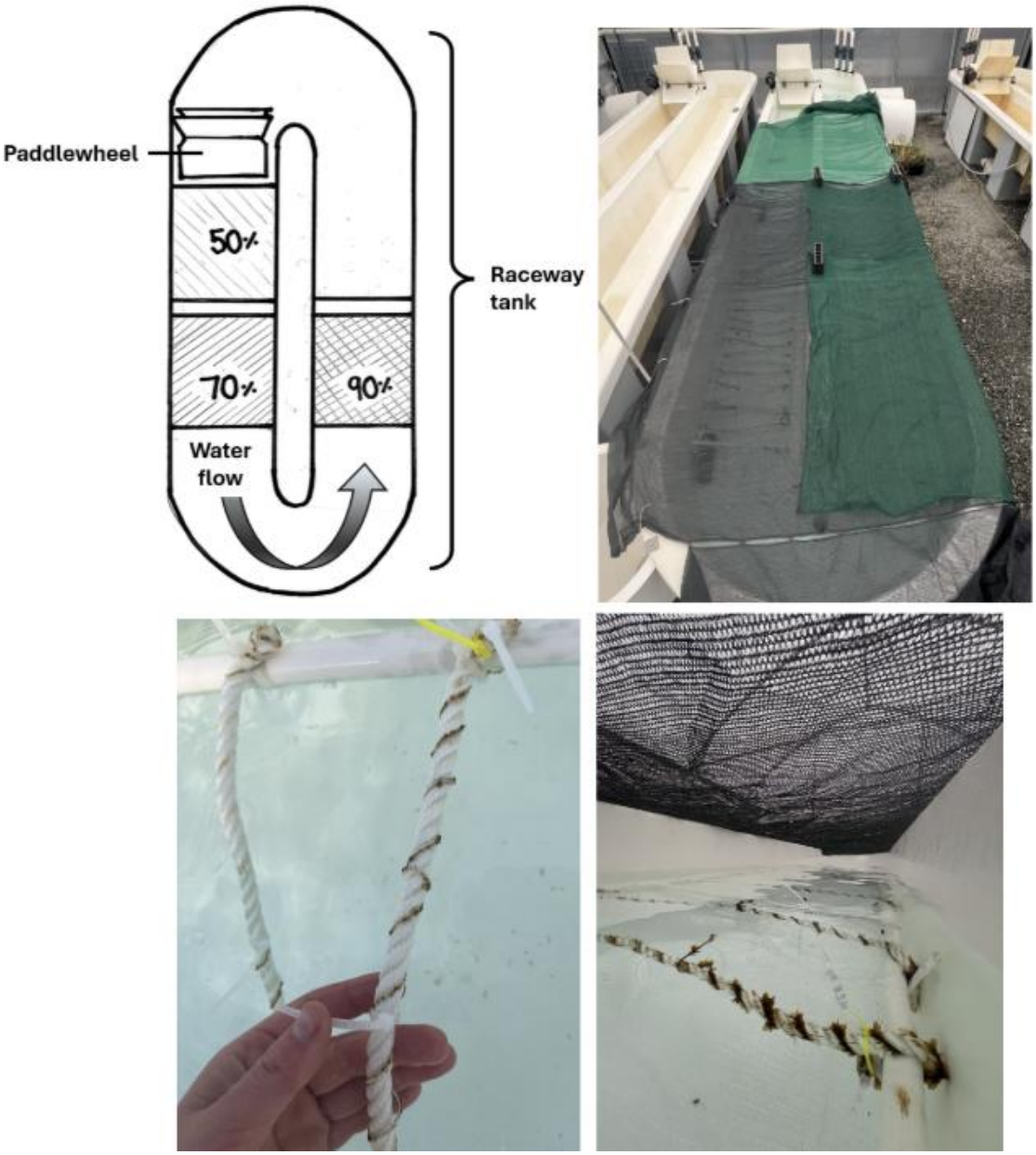

Figure 2.4. Overview of the experimental setup for simulated outplanting. Top left: Schematic diagram showing the layout of the three shade treatments (50%, 70%, 90% shade) and paddlewheel in the raceway tank. Top right: Overhead photo of the raceway tank. Top right: Overhead photo of the raceway tank covered with shade cloth. Bottom left: Close-up of the twine wrapped around the cultivation rope on the first day of simulated outplanting. Bottom right: View under the shade cloth of twine-covered ropes attached to submerged PVC frame submerged in the water.

2.3. Statistical Analyses

In the nutrient regime experiment, separate three-way analyses of variance (ANOVA) were conducted to examine the effects of nutrient concentration, nutrient dosage, and week (all

fixed factors) on spool quality scores, sporophyte length, sporophyte density, and assumed nitrate uptake. Additionally, a two-way ANOVA was conducted to assess the effects of nutrient concentration and dosing frequency on *E. radiata* nitrogen content and tissue C:N ratios. In the light regime experiment, a one-way ANOVA was conducted to assess the effects of hatchery light regime (fixed factor) on sporophyte length, sporophyte density, and overall spool quality at the end of the hatchery period (week 5). Separate three-way ANOVAs were conducted to examine the effects of hatchery light regime, outplanting light exposure, and outplanting shade level (all fixed factors) on sporophyte length after exposure treatments and simulated outplanting. Data collected at 1 week and 2 weeks after outplanting were analysed separately. Prior to conducting ANOVAs, all data were assessed for normality and homogeneity of variance to ensure assumptions were met. Post hoc Tukey's Honest Significant Difference (HSD) tests were performed for pairwise comparisons where significant interactions were detected. All statistical analyses were conducted in RStudio (version 2022.07.1+554) and data are presented as means ± standard error (SE).

3. Results

3.1. Nutrient regime experiment

There was a significant difference in spool quality rating scores among nutrient concentrations, and weeks (three-way ANOVA, concentration: $F_{2,40} = 55.4$, $P < 0.001$; week: F2,40 = 8.6, P = 0.005; Figure 3.1) but not dosage frequencies. Across both weeks, spool quality rating scores for the double- and full- strength nutrient treatments (9.7 ± 0.2 S.E. and 9.1 ± 0.3 S.E, respectively) were significantly higher (69.1 % and 58.9 % higher, respectively; post hoc, $P < 0.001$) than scores in the quarter-strength treatment (5.7 ± 0.5 S.E.). In general, week 12 scores were higher than week 9 scores (post hoc, P = 0.005) for each nutrient concentration.

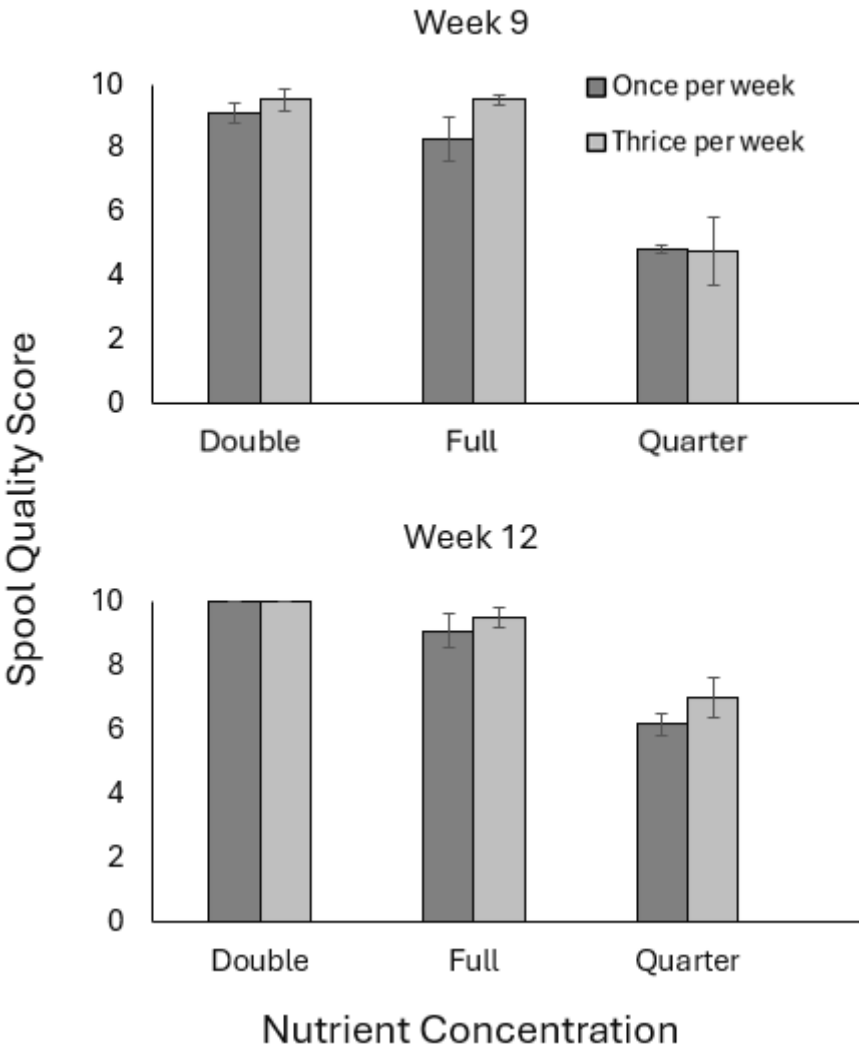

Figure 3.1. Mean (± S.E.) spool quality rating score of *E. radiata* sporophytes grown under three nutrient concentrations (double-strength, full-strength, and quarter-strength) and two dosing regimes (one per week, thrice per week) after 9 weeks (upper panel) and 12 weeks (lower panel) cultivation in a hatchery. N=5.

Mean sporophyte length varied significantly among nutrient concentrations, but effects were not consistent between weeks (three-way ANOVA, Concentration × Week, $F_{2,40} = 11.2$, $P < 0.001$, Figure 3.2). At week 9, sporophyte lengths were generally low across all treatments (< 3.3 mm), with minimal growth observed in the quarter-strength treatment (< 1 mm). By week 12, sporophyte lengths increased substantially in the double- and full-strength treatments (> 9.8 and 8.4 mm respectively), but remained very small in the quarter-strength treatment (< 2.3 mm), often not exceeding the minimum measurable size threshold of 1 mm.

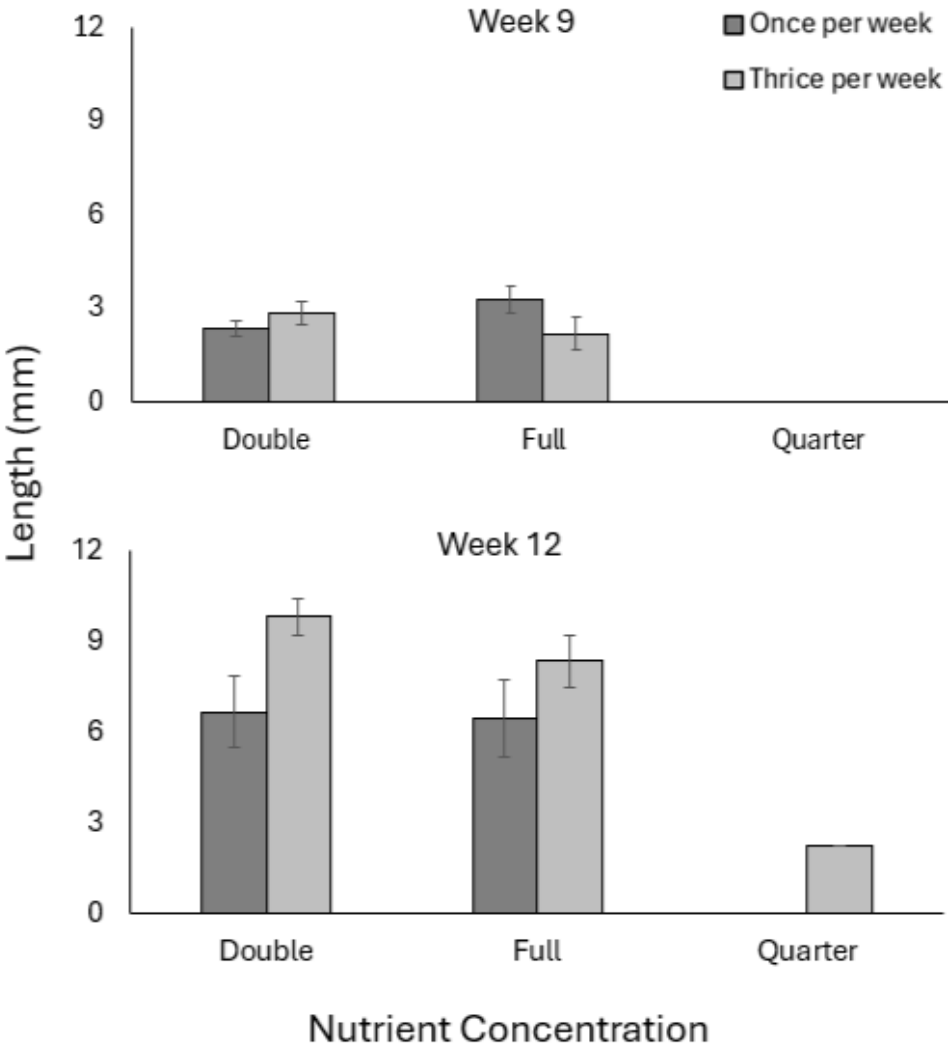

Figure 3.2. Mean (± S.E.) length (mm) of *E. radiata* sporophytes grown under three nutrient concentrations (double-strength, full-strength, and quarter-strength) and two dosing regimes (one per week, thrice per week) after 9 weeks (upper panel) and 12-weeks (lower panel) cultivation in a hatchery. N=5.

Data for week 9 quarter-strength treatment are not displayed as sporophytes were below the minimum measurable size threshold of 1 mm. Sporophyte density differed significantly among nutrient concentrations (Three-way ANOVA, $F_{2,40} = 60.5$, $P < 0.001$, Figure 3.3). When averaged across both dosing frequencies and time points, sporophyte density in the double-strength and full-strength nutrient treatments (40.7 % ± 15.1 and 50.3 % ± 9.9, respectively) was over four times higher than density in the quarter-strength treatment (8.1 % ± 4.2).

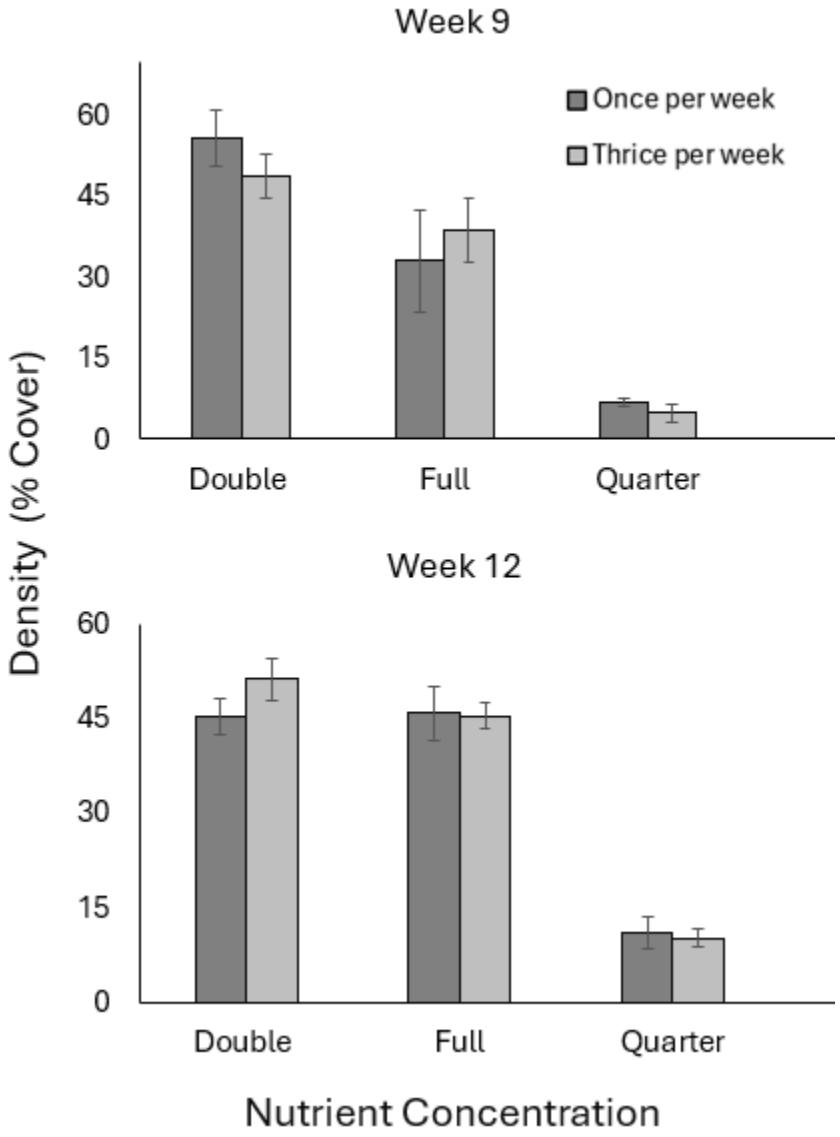

Figure 3.3. Mean (± S.E.) density (% cover of detached seedlings) of *E. radiata* sporophytes grown under three nutrient concentrations (double-strength, full-strength, and quarter-strength) and two dosing regimes (one per week, thrice per week) after 9 weeks (upper panel) and 12 weeks (lower panel) cultivation in a hatchery. N=5.

The tissue nitrogen content of sporophytes after 12 weeks of hatchery cultivation varied significantly among nutrient concentrations (two-way ANOVA, $F_{3,20}$ = 16.7, P = < 0.001) and in general, increased with increasing nutrient concentration (Figure 3.4). Tissue nitrogen content of sporophytes in the double-strength treatment (2.5 % ± 0.1 S.E.) was 64 % and 75 % higher than the full-strength (1.5% ± 0.15 S.E.) and quarter-strength (1.4% ± 0.2 S.E.) treatments, respectively. Nutrient concentrations also had a significant effect on C:N ratio (two-way ANOVA, $F_{3,20}$ = 57.7, P = < 0.001, Figure 3.4), with all concentration treatments

differing significantly from one another (post-hoc, P < 0.05). C:N ratios were highest in the quarter strength nutrient treatment (17.3 +/- 0.86 S.E), and lowest in the double strength treatment (8.4 +/- 0.28 S.E).

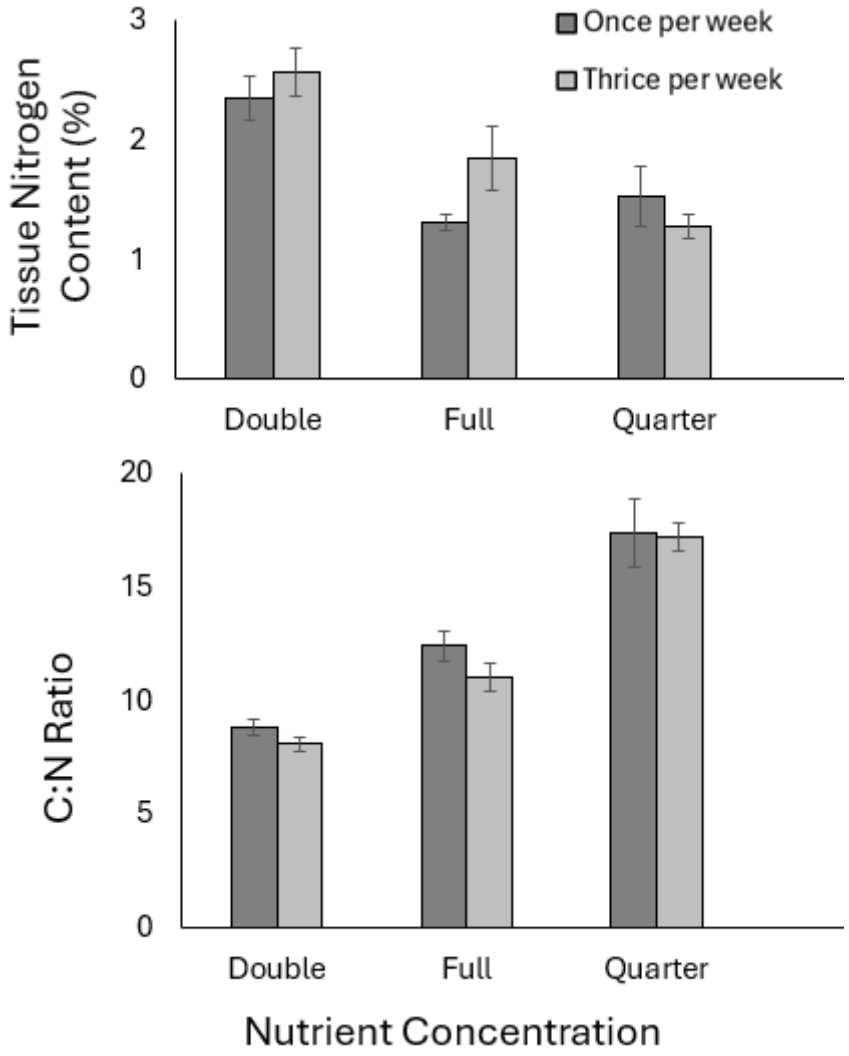

Figure 3.4. Mean (± S.E.) tissue nitrogen content (%, upper panel) and C:N ratio (lower panel) of *E. radiata* sporophytes grown under three nutrient concentrations (double-strength, full-strength, and quarter-strength) and two dosing regimes (one per week, thrice per week) after 12 weeks of hatchery cultivation. N=5.

There was a significant difference in assumed nitrate uptake amongst dosing frequencies and nutrient concentrations (Three-way ANOVA, dosing frequency: $F_{1,34}$ = 28.9, P = < 0.001, nutrient concentration: $F_{2, 34}$ = 32.0, P = <0.001; Figure 3.5). Assumed nitrate uptake, averaged across weeks, was at least 49% higher in the three-times weekly dosing treatment (8.5–21.4 mg L^{-1}) compared to the once-weekly dosing treatment (2.0–14.4 mg L^{-1}; post-hoc,

P < 0.001). In general, higher nutrient concentrations resulted in higher assumed nitrate uptake. When averaged across both nutrient dosing frequencies and sampling weeks, mean uptake increased from 5.7 mg L^{-1} (± 3.9 S.E.) in the quarter-strength treatment, to 13.7 mg L^{-1} (± 7.5 S.E.) in the full-strength treatment and to 17.9 mg L^{-1} (± 5.4 S.E.) in the double-strength treatment. No significant differences in nitrate uptake were detected between sampling weeks ($F_{2,34}$ = 1.13, p = 0.336).

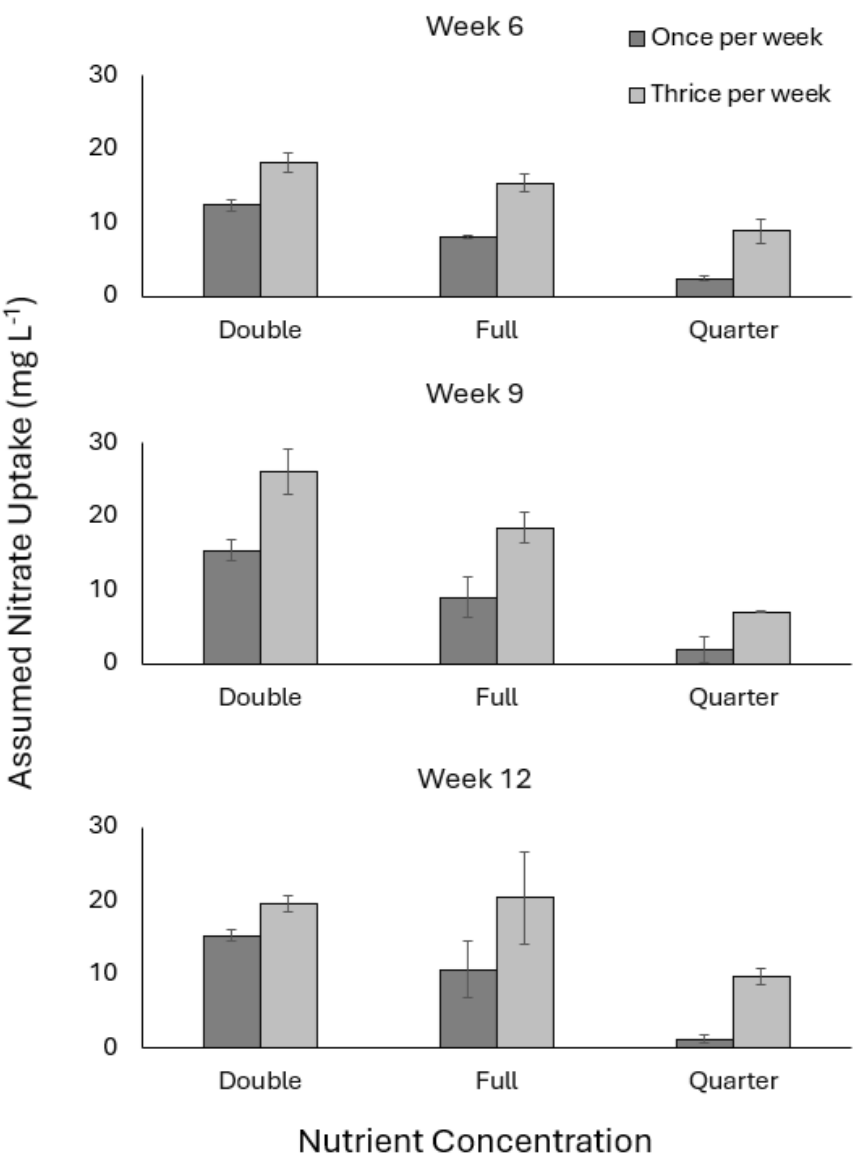

Figure 3.5. Mean (± S.E.) assumed nitrate uptake (mg L-1) of *E. radiata* cultivated in a hatchery for 6 weeks (upper panel), 9 weeks (middle panel) and 12 weeks (lower panel)

under three nutrient concentrations (double-strength, full-strength, and quarter-strength) and two dosing regimes (one per week, thrice per week). N=5.

3.2. Lighting Regime Experiment

3.2.1. Hatchery Cultivation

Prior to simulated outplanting, there were no significant differences (one-way ANOVA; all $P > 0.05$; Figure 3.6) among hatchery light regimes (Standard, Standard+Primer, High Intensity) in overall spool quality (range: 3 - 6.5), sporophyte length (0.39mm - 0.037mm), sporophyte density (range: 1.5 - 10.8 sporophytes per cm), or the percentage of sporophytes longer than one millimetre (range: 0 - 12.5%).

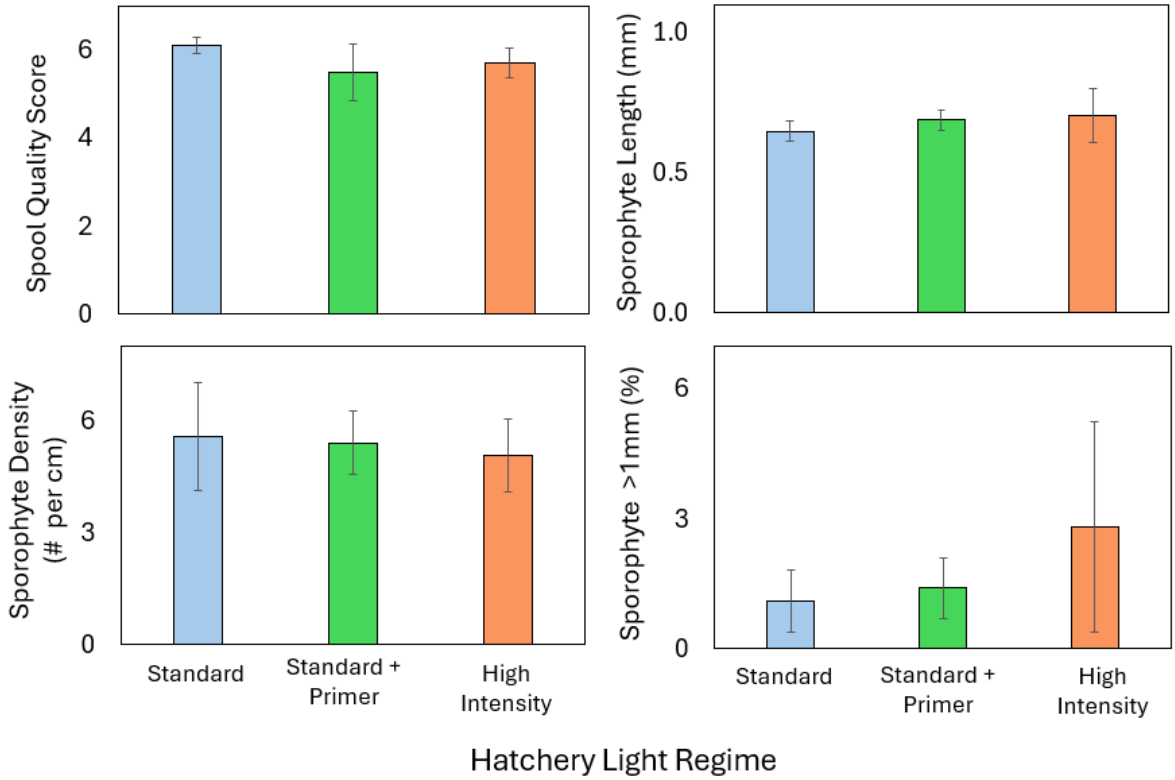

Figure 3.6. Mean (± S.E.) measurements of *E. radiata* sporophytes cultivated for five weeks under three hatchery light regimes: Standard, Standard+Primer, and High Intensity. Panels show spool quality scores (top left), sporophyte density (number per cm, bottom left), sporophyte length (mm, top right), and the percentage of sporophytes longer than 1 mm (%, bottom right). N = 5.

3.2.2. Exposure and Simulated Outplanting

Exposure treatment had a significant effect on sporophyte length one week after simulated outplanting, but hatchery light regime or outplanting shade level did not (three-way ANOVA, Exposure: $F_{1,36} = 6.8$, $P = 0.013$; Figure 3.7). Unexposed sporophytes (2.1mm ± 0.18mm) were over 16% longer than exposed sporophytes (1.8mm ± 0.26mm). Two weeks after simulated outplanting, this difference increased so unexposed sporophytes (5.0mm ± 0.8mm) were 25% longer than exposed (4.0mm ± 0.5mm) sporophytes (three-way ANOVA, Exposure: $F_{1,36} = 20.1$, $P < 0.001$). However, in week 2 there were also significant differences in sporophyte lengths among hatchery light treatments (three-way ANOVA, Hatchery regime: $F_{2,36} = 4.1$, $P = 0.025$; Figure 3.7), with sporophytes being nearly 19% longer in the Standard treatment (4.92mm ± 0.3mm) compared to the High Intensity treatment (4.14mm ± 0.6mm) (post hoc: $P = 0.048$).

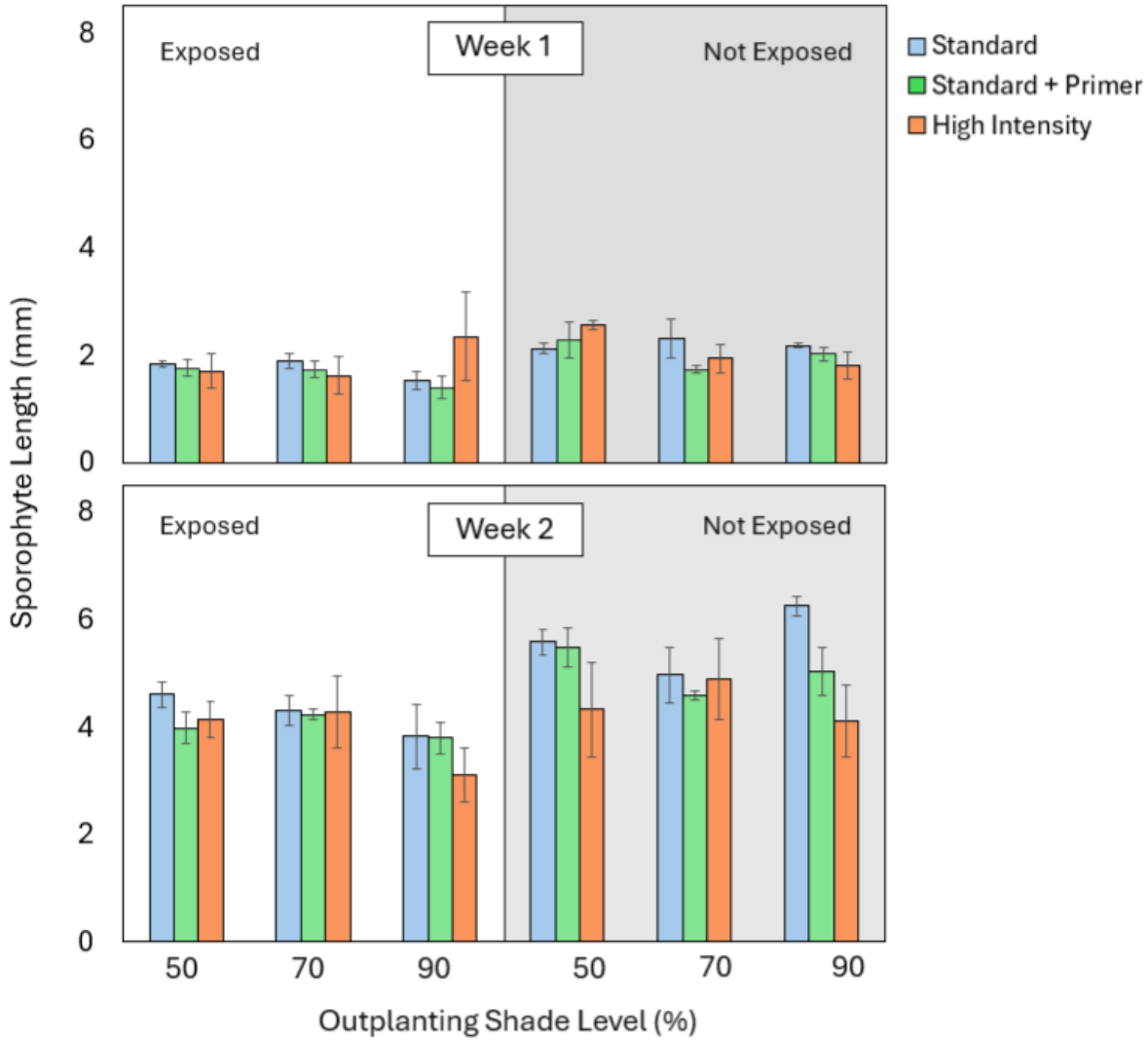

Figure 3.7. Mean (± S.E.) length (mm) of *E. radiata* sporophytes maintained under three hatchery light regimes (Standard, Standard+Primer, and High Intensity), subjected to an outplanting light exposure treatment (0 min, 10 min), and then grown under three shade levels (50, 70, 90%) after 1 week (upper panel) and 2 weeks (lower panel) of simulated outplanting in a raceway tank. N = 3.

One week after simulated outplanting, sporophyte density per cm of twine differed significantly among hatchery light treatments and outplanting light exposure treatments (three-way ANOVA: Hatchery, $F_{2,36} = 5.2$, P = 0.0103; Exposure, $F_{1,36} = 4.7$, P = 0.0361; Figure 3.8). Sporophyte densities were significantly higher in the Standard+Primer hatchery light treatment (4.54 ±± 0.55 S.E.) compared to the High Intensity (3.77 ± 0.53 S.E.) and Standard (3.38 ± 0.32 S.E.) treatments (post-hoc, P = 0.035 and P = 0.015, respectively). Similarly, two weeks after simulated outplanting, sporophyte density remained significantly influenced by hatchery treatment (three-way ANOVA: Hatchery, $F_{2,36} = 7.5$, P = 0.002*J* but was additionally

affected by shade level *(*three-way ANOVA: Shade, $F_{2,36} = 6.1$, $P = 0.005$). The Standard+Primer treatment continued to show significantly higher densities than the Standard treatment (post-hoc, $P = 0.002$), while sporophyte densities in the 70% shade treatment were significantly higher than densities in the 50% or 90% shade treatments (post-hoc, $P = 0.023$).

The proportion of sporophytes exceeding 1 mm in length 1 week after simulated outplanting was significantly influenced by both hatchery light regime and outplanting light exposure (three-way ANOVA: Hatchery; $F_{2,36} = 3.7$, $P = 0.035$; Exposure $F_{1,36} = 4.7$, $P = 0.036$; Figure 3.8). However, post hoc tests only detected a significant effect of exposure, with non-exposed samples (66.2% ± 6.9% S.E.) having a 16.8% higher proportion of large sporophytes than exposed samples (56.7% ± 10.2% S.E.). By week 2, significant differences in the proportion of sporophytes exceeding 1 mm in length among hatchery light regimes emerged (three-way ANOVA: Hatchery, $F_{2,36} = 9.8$, $P < 0.001$). The proportion of large (>1 mm) sporophytes was more than 10% lower in the High Intensity treatment (82% ± 2.83% S.E.) compared to both the Standard+Primer (94% ± 1.65% S.E.; $P < 0.001$) and Standard (94% ± 1.42% S.E.; $P = 0.0003$) treatments.

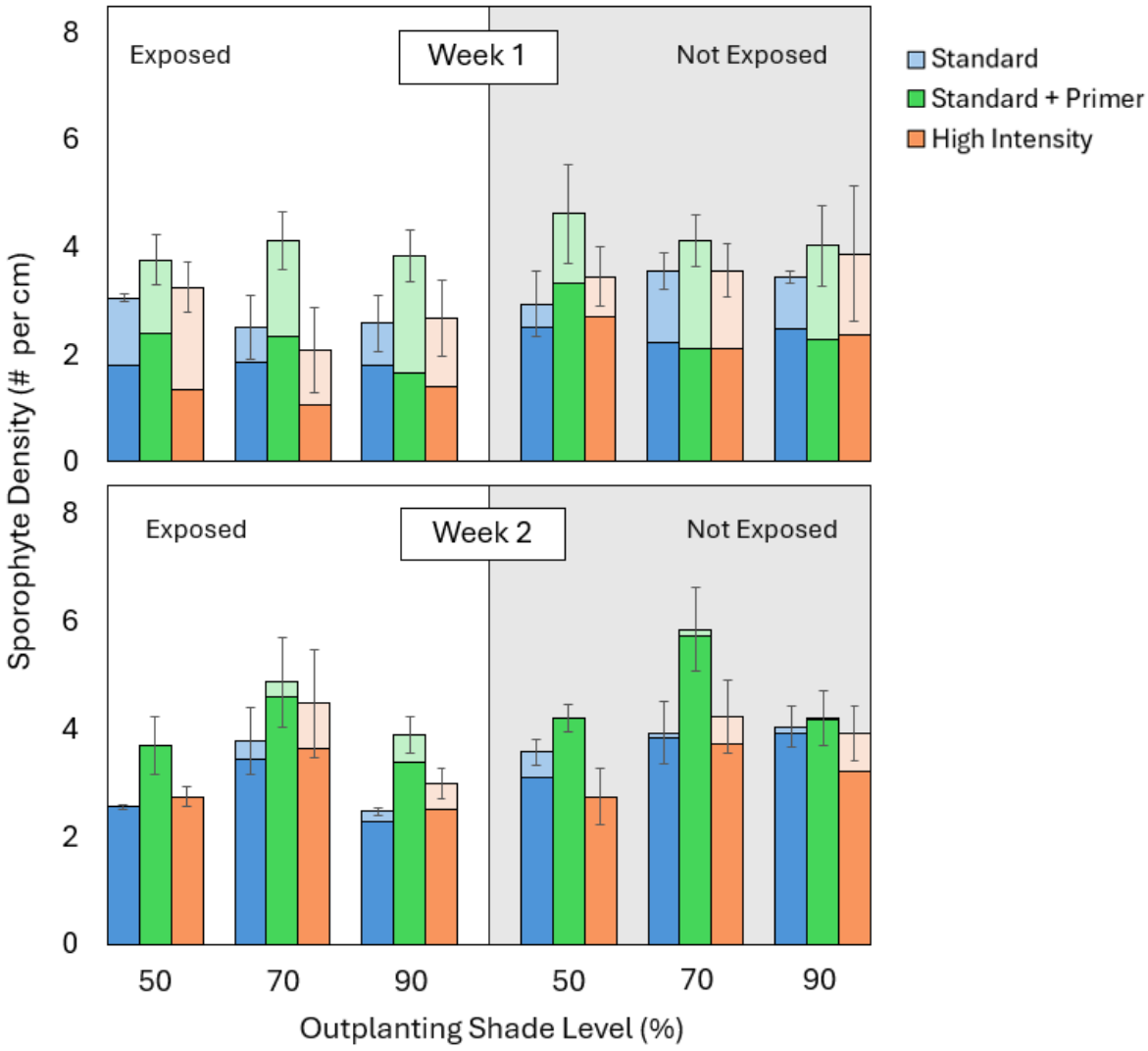

Figure 3.8. Mean (± S.E.) density (number per cm) of *E. radiata* sporophytes maintained under three hatchery light regimes (Standard, Standard+Primer, and High Intensity), subjected to an outplanting light exposure treatment (0 min, 10 min), and then grown under three shade levels (50, 70, 90%) after 1 week (upper panel) and 2 weeks (lower panel) of simulated outplanting in a raceway tank. Shading of individual bars denotes sporophyte size class: darker shaded lower segment represents the density of sporophytes >1 mm, the lighter shaded upper segment represents sporophytes <1 mm. N = 3.

4. Discussion

The global seaweed industry is gaining momentum for its potential to produce sustainable materials and support climate change mitigation (Yong et al., 2024). A critical step in scaling this industry, especially in Aotearoa New Zealand, is the efficient production of fast-growing, resilient seedstock (Liu et al., 2022). To support both environmental and economic

sustainability, hatchery protocols must optimise growth while minimising energy use and waste from lighting, water circulation, refrigeration, and fertiliser inputs (Seghetta & Goglio, 2020). Additionally, as different species have unique requirements, species-specific optimisation is essential (Jiksing et al., 2022). This study demonstrated that *E. radiata* can be successfully cultivated under standard hatchery conditions, using either spores or gametophytes, provided sufficient nutrients are supplied (at least 20 mL PES L^{-1}) and light levels are moderate (30 – 120 µmol photons m^{-2} s^{-1}).

4.1. Nutrient Experiment

Previous studies investigating the effects of PES concentration in seaweed hatcheries have primarily focused on lower nutrient levels than those tested here. *Lawton and Praeger (2025)* evaluated PES concentrations ranging from full-strength (20 mL L^{-1}) to 1/20th strength (1 mL L^{-1}) in *E. radiata. Poza et al. (2022)* tested quarter- to full-strength PES (5–20 mL L^{-1}) in the brown alga *Asperococcus ensiformis*, and *Boderskov et al. (2023)* used nutrient media equivalent to approximately 1/16th to 1/6th strength PES (50–150 µM N) in experiments on *Saccharina latissima*. In contrast, the present study tested nutrient concentrations ranging from quarter- to double-strength PES (40 mL L^{-1}). These higher nutrient levels address a critical knowledge gap: whether sporophyte development in the hatchery is constrained by nutrient limitation, and therefore whether hatchery performance can be improved through increased nutrient supply. The present experiment showed clear performance improvements at higher nutrient concentrations, with sporophytes in the quarter-strength treatment consistently underperforming across all metrics. *Lawton and Praeger (2025)* similarly found that decreasing PES concentration reduced sporophyte formation and length in *E. radiata*. In *S. latissima*, *Boderskov et al. (2022)* showed that concentrations from 50 to 100 µM N (full range testing from 10 - 150 µM N) led to higher sporophyte densities. In contrast, *Poza et al. (2022)* found that *A. ensiformis* sporophytes were longest in the quarter-strength treatment. These differing responses may reflect fundamental differences in nutrient requirements between taxonomic groups as both *E. radiata* and *S. latissima* are laminarians, while *A. ensiformis* belong to the order Ectocarpales (Fraser, 2012). This idea is supported by *Narvarte et al. (2024)*, who demonstrated that three species of eucheumatoid seaweeds had different optimal phosphate levels for ammonium uptake. Such variability reinforces the importance of

tailoring hatchery nutrient regimes to the specific species or group being cultivated. The nutrient concentration experiment showed that quarter-strength PES was insufficient for optimal *E. radiata* sporophyte development and growth. Although C:N ratios were below 20 in all treatments, below the global average of 27.5 reported for brown seaweeds (Sheppard et al., 2023), and thus suggestive of adequate nitrogen availability, the significantly lower growth and density observed in the quarter-strength treatment compared to the full- and double-strength treatments indicate that it did not provide sufficient nutrients to support maximal development and growth. An interesting result from this experiment was that sampling week had no significant effect on assumed nitrate uptake. However, because biomass in all treatments was lower in earlier weeks compared to later weeks, uptake per gram of biomass was likely higher during early development. This suggests active nitrogen acquisition even in the absence of visible growth differences. Given that the experiment began from spores, the high per-gram uptake may reflect increased nutrient demand during gametogenesis and the transition to the sporophyte stage, a period shown by *Lawton & Praeger (2025)* to be nutrient-sensitive and potentially limited by nutrient availability in *E. radiata*. The poor performance of the quarter-strength treatment may thus reflect not only reduced growth but also reduced success in sporophyte establishment. It should be noted, however, that no control for nitrogen offgassing was included in the experimental setup. This may have led to underestimation of actual nitrate availability, particularly in higher-concentration treatments where nitrogen losses to the atmosphere may have been greater compared to lower-nitrogen concentration treatments in these non-axenic cultures. These findings nonetheless highlight the importance of maintaining adequate nutrient availability during the initial hatchery period, even when biomass is low.

A key finding from the nutrient experiment was that full- and double-strength treatments produced no significant differences in growth or density, suggesting that the additional nutrients in the double-strength treatment provided no added benefits. However, assumed nitrate uptake rates were 301% higher in the double-strength treatment compared to the full-strength treatment and tissue nitrogen content in the double-strength treatment was 64% higher than the full-strength treatment. In combination, these results suggest luxury uptake of nitrogen not required for growth was occurring in the double-strength treatment. This strategy of luxury uptake and internal storage is common in macroalgae and may offer

a post-outplanting advantage in nutrient-variable ocean conditions (Michel et al., 2010). These findings suggest that full-strength PES is sufficient to meet the nutrient demands of *E. radiata* throughout hatchery cultivation. However, the data also raises the possibility that nutrient requirements change over time. Lower concentrations or dosing frequencies may be adequate during the early hatchery period when sporophyte biomass is minimal, while higher nutrient inputs may become more beneficial as the sporophytes grow and demand increases. Tailoring nutrient supply to match biomass development could optimise resource use and reduce costs, though this would require careful monitoring.

This study is the first to investigate how nutrient dosing regimes affect hatchery performance in a kelp species. Nutrient uptake was higher in the thrice per week dosing treatment compared to the once per week treatment, suggesting reduced nutrient loss and improved nitrogen utilisation and indicating that more frequent dosing provides a more efficient delivery of nutrients. As there was no significant interaction between dosing frequency and nutrient concentration, the benefits of more frequent dosing appear to be consistent across concentrations. This raises the possibility that lower concentrations, delivered more frequently, could achieve similar or improved outcomes compared to higher concentrations delivered less often. For example, dosing at half strength three times per week might yield comparable growth to full strength dosed once per week, with the added benefit of reducing excess nutrient buildup. However, more frequent dosing would increase labour and logistical demands, and implementing automation would likely be necessary for this approach to be cost-effective at scale. Taking all findings into account, we recommend applying full-strength nutrients (20 mL PES L^{-1}; 18.85 mg N L^{-1}, 0.81 mg P L^{-1}) once weekly as the most effective and practical dosing strategy for individual container hatchery systems of *E. radiata.*

High nutrient levels are often associated with increased contamination risk (Ylivainio et al., 2017). However, this was not supported by our findings. Only one replicate in the experiment (from the thrice-weekly full-strength treatment) was excluded due to visible contamination. This suggests that under the specific hatchery conditions used in this study, with spools maintained in individual containers under stable temperatures and regularly cleaned, nutrient concentration alone was not a strong driver of contamination. Other abiotic factors, such as temperature, may have a stronger influence as *Visch et al. (2023)*

identified temperature as a primary driver of contamination risk when testing three brown seaweed cultures (*E. radiata, Lessonia corrugata, and Macrocystis pyrifera*), highlighting the need to consider multiple environmental variables when managing hatchery hygiene.

An area worth further investigation is whether short-term exposure to high-concentration nutrient baths can meet the nutritional demands of juvenile *E. radiata*. This strategy could reduce overall nutrient use by leveraging kelp's capacity for rapid nitrogen uptake and internal storage, offering an alternative to continuous or weekly dosing. The nutrient experiment initially included such a treatment, consisting of a 5-hour weekly bath at quadruple-strength PES (470.4 µM nitrate). However, this high concentration nutrient bath treatment was ultimately discontinued due to poor performance. Water sampling showed minimal nutrient uptake, and the sporophytes remained visibly underdeveloped. This outcome was likely due to a combination of stress from high nutrient concentrations and subsequent nutrient deprivation over the remainder of the week. While nitrate toxicity is unlikely at the levels provided in this treatment (Nederlof et al., 2022), research suggests that excessive nutrient concentrations can induce physiological stress, particularly in early developmental stages with limited storage capacity (Harrison & Druehl, 1982; Worm & Sommer, 2000). The poor uptake and growth in our high concentration nutrient bath trial suggest that short nutrient pulses may only be viable once sporophytes reach a more advanced size. Additionally, high nutrient pulses can have unintended ecosystem effects. For instance, *Worm & Sommer (2000)* found that a single 5-hour nutrient pulse significantly increased epiphyte load on *Fucus vesiculosus*, which indirectly suppressed macroalgal growth. Future research could explore whether more frequent, lower-intensity nutrient bath treatments or size-targeted treatments improve outcomes, while also weighing practical constraints like labour, contamination, and nutrient wastage.

There is growing interest in using organic fertilisers, such as seaweed-based products, compost, and blood and bone meal, as nutrient sources in marine aquaculture (Nasmia et al., 2021; Pramita et al., 2022). This interest is partly driven by the potential for organic certification, which is increasingly important for accessing premium markets. Currently, the use of synthetic nutrients in hatchery phases disqualifies seaweed from being certified as organic, so replacing these with approved organic alternatives could support more sustainable and marketable production systems (Robson, 2020). Organic fertilisers typically

contain nitrogen in organic forms, as dissolved organic nitrogen (DON), which must first be converted into dissolved inorganic nitrogen (DIN) to be taken up by kelp as kelp primarily utilises DIN for growth (Boderskov et al., 2022). However, this microbial conversion process does not readily occur in the clean, controlled conditions of a hatchery, where microbial activity is minimal (Tarquinio et al., 2018). This presents a major knowledge gap regarding the suitability of organic nutrient sources in kelp hatchery systems, particularly during the early sporophyte stages that are highly dependent on DIN. To explore this, an experiment comparing synthetic and organic nutrient sources was conducted during the study. The organic treatments performed poorly, likely due to limited DIN availability, and were further compromised by contamination from unwanted algal growth, leading to the early termination of the trial. In addition, calculated nitrogen contents based on manufacturer specifications of the organic fertilisers used in the trial proved to be inaccurate, resulting in unequal total nitrogen supply between fertiliser types and limiting the ability to make meaningful comparisons across treatments. Future research could investigate methods to pre-process organic materials to release DIN or explore microbial inoculation strategies to enhance conversion from DON to DIN. Until such approaches are validated, inorganic nutrient sources remain the more reliable option for early-stage kelp cultivation.

4.2. Lighting experiment

Light is an important driver of early sporophyte formation and growth in kelps (Wernberg et al., 2021). However, light regime treatments had no significant effects on sporophyte growth or density after 5 weeks of hatchery cultivation in the light experiment. This result agrees with *Praeger et al. (2022)*, who found that light intensities of 35 - 55 µmol photons m^{-2} s^{-1} under photoperiods of 8:16, 12:12, and 16:8 light:dark had no significant effect on the transition from gametophyte to sporophyte or sporophyte length in *E. radiata* after 30 days of cultivation in petri dishes. In contrast, *Schwoerbel et al. (2023)* found that *E. radiata* sporophytes cultivated on spools under hatchery conditions similar to those used in the current experiment were longer under a light intensity of 30 µmol photons m^{-2} s^{-1} compared to 60 µmol photons m^{-2} s^{-1}, but there were no differences in sporophyte density between treatments. Notably, the lack of a significant effect of light intensity on initial sporophyte growth or density in the current study was despite testing an extended range of light intensities (30–120 µmol photons m^{-2} s^{-1}) compared to previous works (<60 µmol

photons m^{-2} s^{-1}). This finding shows that *E. radiata* can develop and grow successfully across a broad range of light intensities (30 – 120 µmol photons m^{-2} s^{-1}). Moreover, the lack of differences among hatchery light regimes suggests that all treatments fell within an optimal range of irradiance; high enough to avoid light limitation but not so high as to cause photoinhibition. However, it is also possible that a longer experimental duration than that tested here (5 weeks) is required to detect more subtle or cumulative effects of light exposure on early sporophyte development. It is also possible that there was less variation between light regimes treatments in the amount of light received by individual sporophytes on the spools due to the upright cultivation system and overhead placement of the lights that was used, which meant that only the upper part of each spool was directly illuminated (Figure A1). Rotating spool systems, recently proposed as an alternative hatchery method (Nardelli et al., 2024), expose the full surface of the spool to the same light conditions evenly and may enhance sporophyte growth by improving overall light delivery. Future experiments using rotating spools and a wider range of light intensities may help determine whether light can be optimised further to improve hatchery performance of *E. radiata*. Given that *E. radiata* sporophytes typically reach photosynthetic saturation between 100–150 µmol photons m^{-2} s^{-1} (Fairhead & Cheshire, 2004), it is unlikely that the High Intensity treatment exceeded this threshold. However, since this treatment conferred no advantage in either hatchery performance or post-outplanting results, testing even higher irradiance levels appears unnecessary. Instead, lower hatchery light levels are recommended, as they provide comparable outcomes with reduced energy costs.

Exposure to high light during outplanting significantly reduced sporophyte performance, with exposed treatments producing shorter individuals and fewer sporophytes exceeding 1 mm after two weeks of cultivation in simulated outplanting conditions. Laboratory experiments by *Wood (1987)* suggest this photoinhibition was likely caused by UV damage as *E. radiata* exposed to natural sunlight in outdoor tanks showed significantly better tissue health and pigment retention when protected with UV-opaque screens, even under similar PAR levels. An important finding from our experiment was that hatchery light regimes significantly influenced sporophyte growth and density during simulated outplanting phase following the high light exposure. The Standard hatchery light regime treatment produced the longest sporophytes by week 2, the Standard+Primer treatment consistently supported

higher sporophyte densities, while the High Intensity hatchery light regime had the lowest sporophyte length and density. There was no evidence that elevated light in the hatchery improved tolerance to high light stress during outplanting, and instead may have reduced tolerance, suggesting that a gradual increase in light exposure may improve tolerance to environmental shifts by priming the sporophytes before transfer. There was also no evidence that light intensity following outplanting could mitigate the negative effects of earlier high light exposure. Sporophytes in the exposed treatments showed consistently lower growth across all outplanting shade levels compared to their non-exposed counterparts, indicating that early light stress had lasting impacts on performance. Together, these findings suggest that moderate hatchery lighting, such as the Standard regime (with a maximum of 100 µmol photons m^{-2} s^{-1}), combined with the prevention of intense light exposure during outplanting, is likely to maximise early sporophyte growth and survival after outplanting.

While light is relatively simple to control in hatchery settings, its availability at sea varies with season, weather conditions, depth, light attenuation, and biotic interactions such as epiphytic growth. Although *E. radiata* can photoacclimate to varying light levels (Fairhead & Cheshire, 2004), both insufficient and excessive light can be detrimental, with light levels after outplanting strongly affect survival and growth (Nepper-Davidsen et al., 2023). Therefore, understanding how light conditions interact with developmental stage and seasonal timing is essential for optimising deployment strategies. In this experiment, shade levels following outplanting significantly affected sporophyte density but not blade length. This result was unexpected as previous studies have generally shown that increased light increases sporophyte growth (Schwoerbel et al., 2023; Tatsumi et al., 2021). Sporophyte densities were highest under the 70% shade treatment, suggesting this intermediate light level was optimal for early survivorship, while lower densities in the 50% and 90% shade treatments may have been due to light stress, through either photoinhibition or light limitation, respectively (Adams III et al., 2008). The slower initial growth observed under 50% shade during the two-week outplant simulation may reflect a delay in photoacclimation due to the early development stage of sporophytes. However, post-experiment observations of faster growth in the 50% shade treatment compared to the 70% and 90% shade levels suggest successful photoacclimation over time, aligning with

photophysiological responses found by (Blain et al., 2020), in which *E. radiata* was found to allocate energy toward development of photosynthetically active tissue under suboptimal light conditions. Based on light intensities at varying depths in nearshore northern New Zealand waters (Nepper-Davidsen et al., 2023), the 70% shade cloth used in this experiment corresponds approximately to light conditions at 2.5–3 m depth, while 50% and 90% shade approximate conditions at 1.4 m and 6.1 m depths, respectively. In the present study, the 70% shade treatment supported the highest sporophyte densities and was identified as the optimal light level for early outplanting. This differs from the findings of *Nepper-Davidsen et al. (2023),* where survival and growth of *E. radiata* increased with depth, up to 6 m. However, their study used substantially larger individuals (10–15 cm at deployment), whereas the sporophytes in this experiment were <10 mm, which may explain the differing light responses across developmental stages.

Overall, these findings suggest that optimal outplanting conditions for *E. radiata* sporophytes depend not only on light level but also on seasonal timing, developmental stage, and environmental variability. Since outplanting typically occurs in autumn, depths of 2–3 m in northern nearshore New Zealand waters (equivalent to ~70% shade, Nepper-Davidsen et al., 2023) may offer the best balance of light for survival and initial growth during the first few weeks post-outplanting. However, it is important to acknowledge that the outplanting phase in this study was limited to two weeks, and thus recommendations about optimal depth are specific to this early establishment period. As sporophytes grow and environmental conditions shift, optimal light levels may change (Jing et al., 2020). For instance, as light and temperature decline through late autumn and winter, shallower deployment may help maintain sufficient irradiance for continued growth. In contrast, during early spring, when light and temperature increase, deeper outplanting or the use of shading may be necessary to avoid photoinhibition or premature degradation (Caley et al., 2024). These seasonal dynamics highlight the importance of adapting outplanting depth in response to both long-term seasonal trends and short-term weather variability. Emerging technologies may allow growers to adjust the depth of cultivation lines after deployment, such as infrastructure developed by Arctic Seaweed in Norway, which offer promising tools for managing light exposure dynamically (Arctic Seaweed, n.d.). With such innovations, it may become possible to extend the outplanting window from autumn into winter and even

early spring, provided sporophytes are sufficiently developed and biofouling is minimised (Xu et al., 2024). Ultimately, carefully aligning depth and timing with the sporophytes' changing physiological needs could improve survival, growth, and harvest outcomes, though further research is needed to determine how these needs evolve beyond the initial post-outplanting period.

This experiment was conducted in a controlled environment, but at sea, cultivation is subject to a wide range of dynamic variables. Seasonal shifts in temperature, light intensity (as a combination of depth and light attenuation), photoperiod, wave exposure, nutrient levels, and biotic interactions all influence performance. For successful cultivation, hatchery and outplanting methods must be tailored to the biology of the species, the season, and local environmental conditions. In *E. radiata*, photosynthetic traits such as saturation point, photosynthetic efficiency, and respiration rate shift seasonally, enabling the species to make better use of low light during autumn and winter before light levels increase again in spring (Fairhead & Cheshire, 2004). This acclimation supports traditional timing of cultivation, where sporophytes are raised in the hatchery in autumn with outplanting in late autumn or early winter, allowing sporophytes to take advantage of increasing light and temperatures in spring. As seaweeds enter their growing season, self-shading and shading from neighbouring individuals become more significant, raising the light level required for optimal growth (Xiao et al., 2019). Future research should investigate how hatchery light conditions influence long-term seaweed performance after outplanting. While this study identified significant short-term effects of hatchery light regimes during early outplanting simulation, it remains unclear whether these initial differences persist under natural conditions and affect final yield, survival, or product quality. A valuable next step would be to conduct extended grow-out trials, tracking sporophytes reared under varying hatchery light regimes throughout a full cultivation cycle at sea. Such research would clarify whether the benefits of intermediate hatchery light levels (e.g. Standard or Standard+Primer regimes ranging 30–120 µmol photons m^{-2} s^{-1}) translate into improved growth, light tolerance, or harvest quality in commercial settings. Further, exploring whether optimal hatchery light conditions vary with seasonal timing or environmental factors such as turbidity and temperature could provide practical insights for aligning hatchery protocols with site-specific conditions. These

studies will be essential for determining whether hatchery lighting can serve as a reliable and adaptable lever to enhance consistency and yield in seaweed farming operations.

5. Conclusion

This study examined how hatchery nutrient regimes, light levels, and simulated outplanting conditions influence the early development of *E. radiata* sporophytes. We recommend using full-strength PES nutrients dosed once per week, as this treatment supported strong performance in sporophyte length, density, and overall spool quality with minimal contamination and reduced labour requirements. For hatchery lighting, more extreme light levels, such as those used in the High Intensity regime, should be avoided, as this treatment consistently resulted in the lowest sporophyte lengths and densities upon simulated outplanting. Simulated outplanting results suggest that intermediate light levels (e.g. 70% shade, equivalent to 2 – 3 m depth in nearshore New Zealand waters) are optimal for initial survival and growth, particularly when outplanting occurs in mid-autumn. Intense light exposure during the outplanting process should be avoided where possible to minimise light stress. As environmental conditions shift seasonally, adjusting outplanting depth may be necessary to maintain adequate irradiance while avoiding high light and temperature stress. While these findings provide valuable insights for optimising early cultivation stages, field-based trials are needed to determine whether hatchery conditions have lasting effects on performance and yield at sea. Future research should assess long-term outcomes over a full grow-out cycle under natural conditions and investigate whether optimal hatchery light regimes vary with seasonal timing and farm location. Such studies will be essential for developing adaptable, regionally informed hatchery and deployment strategies for commercial kelp cultivation.

References

Arctic Seaweed. (n.d.). *Enabling a Global Sustainable Seaweed Industry*. https://aseaweed.com/

Alemañ, A. E., Robledo, D., & Hayashi, L. (2019). Development of seaweed cultivation in Latin America: current trends and future prospects. *Phycologia*, *58*(5), 462–471. https://doi.org/10.1080/00318884.2019.1640996

Alghazwi, M., Charoensiddhi, S., Smid, S., & Zhang, W. (2020). Impact of *Ecklonia radiata* extracts on the neuroprotective activities against amyloid beta (Aβ1-42) toxicity and aggregation. *Journal of Functional Foods*, *68*. https://doi.org/10.1016/j.jff.2020.103893

Alsuwaiyan, N. A., Mohring, M. B., Cambridge, M., Coleman, M. A., Kendrick, G. A., & Wernberg, T. (2019). A review of protocols for the experimental release of kelp (Laminariales) zoospores. *Ecology and Evolution*, *9*(14), 8387–8398. https://doi.org/10.1002/ece3.5389

Alsuwaiyan, N., Vranken, S., Filbee-Dexter, K., Cambridge, M., Coleman, M., & Wernberg, T. (2021). Genotypic variation in response to extreme events may facilitate kelp adaptation under future climates. *Marine Ecology Progress Series*, *672*, 111–121. https://doi.org/10.3354/meps13802

Augyte, S., Yarish, C., & Neefus, C. D. (2019). Thermal and light impacts on the early growth stages of the kelp *Saccharina angustissima* (Laminariales, Phaeophyceae). *ALGAE*, *34*(2), 153–162. https://doi.org/10.4490/algae.2019.34.5.12

Barrett, J., & Anderson, J. M. (1977). Thylakoid membrane fragments with different chlorophyll A, chlorophyll C and fucoxanthin compositions isolated from the brown seaweed *Ecklonia radiata*. *Plant Science Letters*, *9*(3), 275–283. https://doi.org/10.1016/0304-4211(77)90037-2

Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C. M., Buck, B. H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S., Karez, R., Karsten, U., Molis, M., Roleda, M. Y., Schubert, H., Schumann, R., Valentin, K., Weinberger, F., & Wiese, J. (2008). The genus *Laminaria* sensu lato: Recent insights and developments. *European Journal of Phycology*, *43*(1), 1–86. https://doi.org/10.1080/09670260701711376

Bearham, D., Vanderklift, M. A., & Gunson, J. R. (2013). Temperature and light explain spatial variation in growth and productivity of the *kelp Ecklonia radiata*. *Marine Ecology Progress Series*, *476*, 59–70. https://doi.org/10.3354/meps10148

Beck, W. S., Rugenski, A. T., & Poff, N. L. (2017). Influence of experimental, environmental, and geographic factors on nutrient-diffusing substrate experiments in running waters. *Freshwater Biology*, *62*(10), 1667–1680. https://doi.org/10.1111/fwb.12989

Billing, S. L., Rostan, J., Tett, P., & Macleod, A. (2021). Is social license to operate relevant for seaweed cultivation in Europe? *Aquaculture*, *534*, 736203. https://doi.org/10.1016/J.AQUACULTURE.2020.736203

Blain, C. O., & Shears, N. T. (2020). Nutrient enrichment offsets the effects of low light on growth of the kelp *Ecklonia radiata*. *Limnology and Oceanography*, *65*(9), 2220–2235. https://doi.org/10.1002/lno.11449

Boderskov, T., Rasmussen, M. B., Cassard, C. H., Svensgaard, J., Enevoldsen, L. N., & Bruhn, A. (2022). Comparing effects of nutrient sources approved for organic seaweed production on hatchery stage development of sugar kelp*, Saccharina latissima*. *Algal Research*, *61*. https://doi.org/10.1016/j.algal.2021.102602

Bradly, N., Syddall, V., Ingram, C., Clarkson, R., Elliot, A., & Adams, S. (2021). Stocktake and characterisation of Aotearoa New Zealand's seaweed sector: market and regulatory focus. www.sustainableseaschallenge.co.nz

Brandes, J. A., Devol, A. H., & Deutsch, C. (2007). New Developments in the Marine Nitrogen Cycle. *Chemical Reviews*, *107* (2), 577–589. https://doi.org/10.1021/cr050377t

Bruhn, J., & Gerard, V. A. (1996). Photoinhibition and recovery of the kelp *Laminaria saccharina* at optimal and superoptimal temperatures. *Marine Biology*, *125*(4), 639–648. https://doi.org/10.1007/BF00349245

Calatrava, V., Hom, E. F. Y., Llamas, Á., Fernández, E., & Galván, A. (2019). Nitrogen scavenging from amino acids and peptides in the model alga *Chlamydomonas reinhardtii*. The role of extracellular L-amino oxidase. *Algal Research*, *38*. https://doi.org/10.1016/j.algal.2018.101395

Caley, A., Marzinelli, E. M., Byrne, M., & Mayer-Pinto, M. (2024). Antagonistic Effects of Light Pollution and Warming on Habitat-Forming Seaweeds. *Ecology and Evolution, 14*(10). https://doi.org/10.1002/ece3.70420

Carney, L. T., & Edwards, M. S. (2010). Role of nutrient fluctuations and delayed development in gametophyte reproduction by *Macrocystis pyrifera* (Phaeophyceae) in southern California. *Journal of Phycology*, *46*(5), 987–996. https://doi.org/10.1111/j.1529-8817.2010.00882.x

Cembella, A. D., Antia, N. J., & Harrison, P. J. (1982). The Utilization of Inorganic and Organic Phosphorous Compounds as Nutrients by Eukaryotic Microalgae: A Multidisciplinary Perspective: Part I. *CRC Critical Reviews in Microbiology*, *10*(4), 317–391. https://doi.org/10.3109/10408418209113567

Chapman, A. R. O., Markham, J. W., & Lüning, K. (1978). Effects of nitrate concentration on the growth and physiology of *Laminaria saccharina* (Phaeophyta) in culture. *Journal of Phycology*, *14*(2), 195–198. https://doi.org/10.1111/j.1529-8817.1978.tb02448.x

Chapman, V. J., & Chapman, D. J. (1980). *Seaweeds and their Uses*. Springer Netherlands. https://doi.org/10.1007/978-94-009-5806-7

Charoensiddhi, S., Lorbeer, A. J., Franco, C. M. M., Su, P., Conlon, M. A., & Zhang, W. (2018). Process and economic feasibility for the production of functional food from the brown alga *Ecklonia radiata*. *Algal Research*, *29*, 80–91. https://doi.org/10.1016/j.algal.2017.11.022

Choi, H. G., Kim, Y. S., Lee, S. J., Park, E. J., & Nam, K. W. (2005). Effects of daylength, irradiance and settlement density on the growth and reproduction of *Undaria pinnatifida* gametophytes. *Journal of Applied Phycology*, *17*(5), 423–430. https://doi.org/10.1007/s10811-005-0432-2

Coleman, M. A., Gillanders, B. M., & Connell, S. D. (2009). Dispersal and gene flow in the habitat-forming kelp, *Ecklonia radiata*: relative degrees of isolation across an east - west coastline. *Marine and Freshwater Research*, *60*(8), 802. https://doi.org/10.1071/MF08268

Colenso, W. (1880). Art. I.—On the Vegetable Food of the Ancient New Zealanders before Cook's Visit. *Transactions and Proceedings of the Royal Society of New Zealand*, *13*.

de Bettignies, T., Wernberg, T., & Gurgel, C. F. D. (2018). Exploring the Influence of Temperature on Aspects of the Reproductive Phenology of Temperate Seaweeds. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00218

Desmond, M. J., Pritchard, D. W., & Hepburn, C. D. (2017). Light dose versus rate of delivery: implications for macroalgal productivity. *Photosynthesis Research*, *132*(3), 257–264. https://doi.org/10.1007/s11120-017-0381-z

Dring, M. J., Makarov, V., Schoschina, E., Lorenz, M., & Lüning, K. (1996). Influence of ultraviolet-radiation on chlorophyll fluorescence and growth in different life-history stages of three species of *Laminaria* (phaeophyta). *Marine Biology*, *126*(2), 183–191. https://doi.org/10.1007/BF00347443

Ebbing, A. P. J., Pierik, R., Fivash, G. S., van de Loosdrecht, N. C. J., Bouma, T. J., Kromkamp, J. C., & Timmermans, K. (2021). The role of seasonality in reproduction of multiannual delayed gametophytes of Saccharina latissima. *Journal of Phycology*, *57*(5), 1580–1589. https://doi.org/10.1111/jpy.13191

Edgar, G. J., Barrett, N. S., Morton, A. J., & Samson, C. R. (2004). Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. *Journal of Experimental Marine Biology and Ecology*, *312*(1), 67–87. https://doi.org/10.1016/j.jembe.2004.06.005

Encyclopædia Britannica. (2024). Algae: Photosynthesis and light-absorbing pigments. In R. Anderson & R. Lewin (Eds.), *Encyclopædia Britannica: https://www.britannica.com/science/algae/Photosynthesis-and-light-absorbing-pigments*.

Endo, H., Moriyama, H., & Okumura, Y. (2023). Photoinhibition and Photoprotective Responses of a Brown Marine Macroalga Acclimated to Different Light and Nutrient Regimes. *Antioxidants*, *12*(2), 357. https://doi.org/10.3390/antiox12020357

Fairchild, G. W., Lowe, R. L., & Richardson, W. B. (1985). Algal Periphyton Growth on Nutrient-Diffusing Substrates: An in situ Bioassay. *Ecology*, *66*(2), 465–472. https://doi.org/10.2307/1940395

Fairhead, V. A., & Cheshire, A. C. (2004). Rates of primary productivity and growth in Ecklonia radiata measured at different depths, over an annual cycle, at West Island, South Australia. *Marine Biology*, *145*(1). https://doi.org/10.1007/s00227-004-1308-8

Fisheries New Zealand. (2023). *Seaweed farming in New Zealand: Fact sheet*. Ministry for Primary Industries. https://www.mpi.govt.nz/dmsdocument/58012-Seaweed-farming-in-New-Zealand-fact-sheet

Forbord, S., Steinhovden, K. B., Solvang, T., Handå, A., & Skjermo, J. (2019). Effect of seeding methods and hatchery periods on sea cultivation of *Saccharina latissima* (Phaeophyceae): a Norwegian case study. https://doi.org/10.1007/s10811-019-01936-0/Published

Fraser, C. (2012). Is bull-kelp kelp? The role of common names in science. *New Zealand Journal of Marine and Freshwater Research, 46*(2), 279–284. https://doi.org/10.1080/00288330.2011.621130

Froehlich, H. E., Afflerbach, J. C., Frazier, M., & Halpern, B. S. (2019). Blue Growth Potential to Mitigate Climate Change through Seaweed Offsetting. *Current Biology*, *29*(18), 3087-3093.e3. https://doi.org/10.1016/j.cub.2019.07.041

Grebe, G. S., Byron, C. J., Gelais, A. S., Kotowicz, D. M., & Olson, T. K. (2019). An ecosystem approach to kelp aquaculture in the Americas and Europe. In *Aquaculture Reports* (Vol. 15). Elsevier B.V. https://doi.org/10.1016/j.aqrep.2019.100215

Hafting, J. T., Craigie, J. S., Stengel, D. B., Loureiro, R. R., Buschmann, A. H., Yarish, C., Edwards, M. D., & Critchley, A. T. (2015). Prospects and challenges for industrial production of seaweed bioactives. In *Journal of Phycology* (Vol. 51, Issue 5, pp. 821–837). https://doi.org/10.1111/jpy.12326

Hamilton, D. S., Perron, M. M. G., Bond, T. C., Bowie, A. R., Buchholz, R. R., Guieu, C., Ito, A., Maenhaut, W., Myriokefalitakis, S., Olgun, N., Rathod, S. D., Schepanski, K., Tagliabue, A., Wagner, R., & Mahowald, N. M. (2022). Earth, Wind, Fire, and Pollution: Aerosol Nutrient Sources and Impacts on Ocean Biogeochemistry. *Annual Review of Marine Science*, *14*(1), 303–330. https://doi.org/10.1146/annurev-marine-031921-013612

Harrison, P. J., & Druehl, L. D. (1982). Nutrient Uptake and Growth in the Laminariales and other Macrophytes: A Consideration of Methods. In L. M. Srivastava (Ed.), *Synthetic and*

Degradative Processes in Marine Macrophytes (pp. 99–120). De Gruyter. https://doi.org/10.1515/9783110837988-009

Harrison, P. J., & Hurd, C. L. (2001). Nutrient physiology of seaweeds: Application of concepts to aquaculture. In *Cah. Biol. Mar* (Vol. 42).

Hayes, L., Lukić, I., Moy, S. R., Fagerli, C. W., Rinde, E., Christie, H., & Bekkby, T. (2024). Effects of wave exposure and habitat fragmentation on growth and grazing of rocky shore seaweeds: a mesocosm experiment. *Marine Biology*, *171*(7), 145. https://doi.org/10.1007/s00227-024-04456-9

Herrero, J. J., Alexandre, A., Silva, J., & Santos, R. (2025). Urea as a key nitrogen source for the invasion of the southern coast of Portugal by the brown seaweed *Rugulopteryx okamurae* (Dictyotales, Phaeophyceae). *Journal of Phycology*, *61*(1), 108–118. https://doi.org/10.1111/jpy.13534

Hiyama, T., & Yoshikawa, S. (2025). Blue and green light-induced release of swarmers in *Petalonia fascia* (Ectocarpales, Phaeophyceae). *Phycological Research*. https://doi.org/10.1111/pre.12580

Holligan, P. M., Pingree, R. D., & Mardell, G. T. (1985). Oceanic solitons, nutrient pulses and phytoplankton growth. *Nature*, *314*(6009), 348–350. https://doi.org/10.1038/314348a0

Howard, M. D. A., Sutula, M., Caron, D. A., Chao, Y., Farrara, J. D., Frenzel, H., Jones, B., Robertson, G., McLaughlin, K., & Sengupta, A. (2014). Anthropogenic nutrient sources rival natural sources on small scales in the coastal waters of the Southern California Bight. *Limnology and Oceanography*, *59*(1), 285–297. https://doi.org/10.4319/lo.2014.59.1.0285

Huo, Y., Stuart, K., Rotman, F., Ernst, D., & Drawbridge, M. (2024). The culture of fish, mussels, sea cucumbers and macroalgae in a modular integrated multi-tropic recirculating aquaculture system (IMTRAS): Performance and waste removal efficiencies. *Aquaculture*, *585*, 740720. https://doi.org/10.1016/j.aquaculture.2024.740720

Hurd, C. L., Harrison, P. J., Bischof, K., & Lobban, C. S. (2014). *Seaweed Ecology and Physiology*. Cambridge University Press. https://doi.org/10.1017/CBO9781139192637

Hurtado, A. Q., Neish, I. C., & Critchley, A. T. (2019). Phyconomy: the extensive cultivation of seaweeds, their sustainability and economic value, with particular reference to important lessons to be learned and transferred from the practice of eucheumatoid farming. *Phycologia*, *58*(5), 472–483. https://doi.org/10.1080/00318884.2019.1625632

Jevne, L. S., Forbord, S., & Olsen, Y. (2020). The Effect of Nutrient Availability and Light Conditions on the Growth and Intracellular Nitrogen Components of Land-Based Cultivated *Saccharina latissima* (Phaeophyta). *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.557460

Jiksing, C., Ongkudon, M. M., Thien, V. Y., Rodrigues, K. F., & Yong, W. T. L. (2022). Recent advances in seaweed seedling production: A review of eucheumatoids and other valuable seaweeds. *Algae, 37*(2), 105–121. https://doi.org/10.4490/algae.2022.37.5.11

Jing, M., Bao, M., Xu, T., Zhou, H., Zhang, T., Li, Z., Gao, G., Li, X., & Xu, J. (2020). Response of the red algae *Pyropia yezoensis* grown at different light intensities to CO_2-induced seawater acidification at different life cycle stages. *Algal Research, 49*, 101950. https://doi.org/10.1016/j.algal.2020.101950

Kerrison, P. D., Innes, M., Macleod, A., McCormick, E., Elbourne, P. D., Stanley, M. S., Hughes, A. D., & Kelly, M. S. (2020). Comparing the effectiveness of twine- and binder-seeding in the Laminariales species *Alaria esculenta* and *Saccharina latissima. Journal of Applied Phycology*, *32*(4), 2173–2181. https://doi.org/10.1007/s10811-020-02069-5

Kerrison, P. D., Stanley, M. S., & Hughes, A. D. (2018). Textile substrate seeding of *Saccharina latissima* sporophytes using a binder: An effective method for the aquaculture of kelp. *Algal Research*, *33*, 352–357. https://doi.org/10.1016/j.algal.2018.06.005

Kim, J. K., Stekoll, M., & Yarish, C. (2019). Opportunities, challenges and future directions of open-water seaweed aquaculture in the United States. *Phycologia*, *58*(5), 446–461. https://doi.org/10.1080/00318884.2019.1625611

Kinlan, B. P., Graham, M. H., Sala, E., & Dayton, P. K. (2003). Arrested development of giant kelp (*Macrocystis pyrifera*, Phaeophyceae) embryonic sporophytes: A mechanism for delayed recruitment in perennial kelps? *Journal of Phycology*, *39*(1), 47–57. https://doi.org/10.1046/j.1529-8817.2003.02087.x

Kirkman, H. (1981). The first year in the life history and the survival of the juvenile marine macrophyte, *Ecklonia radiata* (Turn.) J. Agardh. *Journal of Experimental Marine Biology and Ecology*, *55*(2–3), 243–254. https://doi.org/10.1016/0022-0981(81)90115-5

Larned, S. T. (1998). Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology*, *132*(3), 409–421. https://doi.org/10.1007/s002270050407

Lawton, R. J., & Magnusson, M. (2024). Effects of seeding twine type and seeding density on hatchery performance and initial at-sea cultivation performance of the kelp *Ecklonia radiata*. *Algal Research*, *84*, 103777. https://doi.org/10.1016/j.algal.2024.103777

Lawton, R. J., & Praeger, C. (2025). Effects of nutrient concentration, germanium dioxide and seeding density on sporophyte production in the kelp *Ecklonia radiata*. *Journal of Applied Phycology, 37*(2), 1189–1199. https://doi.org/10.1007/s10811-025-03451-x

Zemke-White, W., Bremner, G., & Hurd, C. L. (1999). The status of commercial algal utilization in New Zealand. In *Hydrobiologia* (Vol. 398).

Liu, J. J., Dickson, R., Niaz, H., Van Hal, J. W., Dijkstra, J. W., & Fasahati, P. (2022). Production of fuels and chemicals from macroalgal biomass: Current status, potentials, challenges, and prospects. *Renewable and Sustainable Energy Reviews, 169*, 112954. https://doi.org/10.1016/j.rser.2022.112954

Liu, X., Bogaert, K., Engelen, A. H., Leliaert, F., Roleda, M. Y., & De Clerck, O. (2017). Seaweed reproductive biology: Environmental and genetic controls. In *Botanica Marina* (Vol. 60, Issue 2, pp. 89–108). Walter de Gruyter GmbH. https://doi.org/10.1515/bot-2016-0091

Liu, Y., Cao, H., Du, C., Zhang, Z., Zhou, X., Yao, C., Sun, W., Xiao, X., Zhang, Y., Zhao, Z., Sun, Z., & Wang, Z. (2023). Novel water-saving cultivation system maintains crop yield while reducing environmental costs in North China Plain. *Resources, Conservation and Recycling*, *197*, 107111. https://doi.org/10.1016/j.resconrec.2023.107111

Lorbeer, A. J., Lahnstein, J., Bulone, V., Nguyen, T., & Zhang, W. (2015). Multiple-response optimization of the acidic treatment of the brown alga *Ecklonia radiata* for the sequential extraction of fucoidan and alginate. *Bioresource Technology*, *197*, 302–309. https://doi.org/10.1016/j.biortech.2015.08.103

Luning, K., & Dring, M. J. (1975). Reproduction, growth and photosynthesis of gametophytes of Laminaria saccharina grown in blue and red light. *Marine Biology*, *29*(3), 195–200. https://doi.org/10.1007/BF00391846

Luxton, D. M., & Courtney, W. J. (1987). New developments in the seaweed industry of New Zealand. *Hydrobiologia*, *151–152*(1), 291–293. https://doi.org/10.1007/BF00046143

Mabin, C. J. T., Gribben, P. E., Fischer, A., & Wright, J. T. (2013). Variation in the morphology, reproduction and development of the habitat-forming kelp *Ecklonia radiata* with changing temperature and nutrients. *Marine Ecology Progress Series*, *483*, 117–131. https://doi.org/10.3354/meps10261

Mackinder, L. C. M., Chen, C., Leib, R. D., Patena, W., Blum, S. R., Rodman, M., Ramundo, S., Adams, C. M., & Jonikas, M. C. (2017). A Spatial Interactome Reveals the Protein Organization of the Algal CO2-Concentrating Mechanism. *Cell*, *171*(1), 133-147.e14. https://doi.org/10.1016/j.cell.2017.08.044

Matsson, S., Metaxas, A., Forbord, S., Kristiansen, S., Handå, A., & Bluhm, B. A. (2021). Effects of outplanting time on growth, shedding and quality of *Saccharina latissima* (Phaeophyceae) in its northern distribution range. *Journal of Applied Phycology*, *33*(4), 2415–2431. https://doi.org/10.1007/s10811-021-02441-z

Mayers, J. J., Flynn, K. J., & Shields, R. J. (2014). Influence of the N:P supply ratio on biomass productivity and time-resolved changes in elemental and bulk biochemical composition of *Nannochloropsis* sp. *Bioresource Technology*, *169*, 588–595. https://doi.org/10.1016/j.biortech.2014.07.048

Mcelligott, D., Mackey, M., & Maguire, J. (2022). Technical report on Seaweed Hatchery and Sea Grow-Out Site Design.

Michel, G., Tonon, T., Scornet, D., Cock, J. M., & Kloareg, B. (2010). Central and storage carbon metabolism of the brown alga *Ectocarpus siliculosus*: Insights into the origin and evolution of storage carbohydrates in Eukaryotes. *New Phytologist, 188*(1), 67–81. https://doi.org/10.1111/j.1469-8137.2010.03345.x

Mihaila, A. A., Lawton, R. J., Glasson, C. R. K., & Magnusson, M. (2023). Early hatchery protocols for tetrasporogenesis of the antimethanogenic *seaweed Asparagopsis armata*.

Journal of Applied Phycology, *35*(5), 2323–2335. https://doi.org/10.1007/s10811-023-03029-5

Miller, S. M., Wing, S. R., & Hurd, C. L. (2006). Photoacclimation of *Ecklonia radiata* (Laminariales, Heterokontophyta) in Doubtful Sound, Fiordland, southern New Zealand. *Phycologia*, *45*(1), 44–52. https://doi.org/10.2216/04-98.1

Mohring, M. B., Wernberg, T., Kendrick, G. A., & Rule, M. J. (2013). Reproductive synchrony in a habitat-forming kelp and its relationship with environmental conditions. *Marine Biology*, *160*(1), 119–126. https://doi.org/10.1007/s00227-012-2068-5

Mohring, M., Wernberg, T., Wright, J., Connell, S., & Russell, B. (2014). Biogeographic variation in temperature drives performance of kelp gametophytes during warming. *Marine Ecology Progress Series*, *513*, 85–96. https://doi.org/10.3354/meps10916

Moore, C. M., Mills, M. M., Arrigo, K. R., Berman-Frank, I., Bopp, L., Boyd, P. W., Galbraith, E. D., Geider, R. J., Guieu, C., Jaccard, S. L., Jickells, T. D., La Roche, J., Lenton, T. M., Mahowald, N. M., Marañón, E., Marinov, I., Moore, J. K., Nakatsuka, T., Oschlies, A., … Ulloa, O. (2013). Processes and patterns of oceanic nutrient limitation. *Nature Geoscience*, *6*(9), 701–710. https://doi.org/10.1038/ngeo1765

Moreira, A., Cruz, S., Marques, R., & Cartaxana, P. (2022). The underexplored potential of green macroalgae in aquaculture. In *Reviews in Aquaculture* (Vol. 14, Issue 1, pp. 5–26). John Wiley and Sons Inc. https://doi.org/10.1111/raq.12580

Moscicki, Z., Swift, M. R., Dewhurst, T., MacNicoll, M., Chambers, M., Tsukrov, I., Fredriksson, D. W., Lynn, P., Landon, M. E., Zotter, B., & MacAdam, N. (2024). Design, deployment, and operation of an experimental offshore seaweed cultivation structure. *Aquacultural Engineering*, *105*, 102413. https://doi.org/10.1016/j.aquaeng.2024.102413

Nardelli, A. E., Visch, W., Farrington, G., Sanderson, J. C., Bellgrove, A., Wright, J. T., MacLeod, C., & Hurd, C. L. (2024). A new nursery approach enhances at-sea performance in the kelp *Lessonia corrugata*. *Journal of Applied Phycology, 36*(2), 591–603. https://doi.org/10.1007/s10811-023-03061-5

Narvarte, B. C. V., Hinaloc, L. A. R., Gonzaga, S. M. C., & Roleda, M. Y. (2024). Impacts of aquaculture nutrient sources: Ammonium uptake of commercially important

eucheumatoids depends on phosphate levels. *Journal of Applied Phycology, 36*(2), 557–565. https://doi.org/10.1007/s10811-023-03073-1

Nasmia, Rosyida, E., Masyahoro, A., Putera, F. H. A., & Natsir, S. (2021). The utilization of seaweed-based liquid organic fertilizer to stimulate *Gracilaria verrucosa* growth and quality. *International Journal of Environmental Science and Technology, 18*(6), 1637–1644. https://doi.org/10.1007/s13762-020-02921-8

Nederlof, M. A. J., Neori, A., Verdegem, M. C. J., Smaal, A. C., & Jansen, H. M. (2022). *Ulva* spp. performance and biomitigation potential under high nutrient concentrations: Implications for recirculating IMTA systems. *Journal of Applied Phycology, 34*(4), 2157–2171. https://doi.org/10.1007/s10811-022-02751-w

Nelson, W. G. (2017). Development of an epiphyte indicator of nutrient enrichment: A critical evaluation of observational and experimental studies. *Ecological Indicators*, *79*, 207–227. https://doi.org/10.1016/j.ecolind.2017.04.034

Nepper-Davidsen, J., Magnusson, M., Glasson, C. R. K., & Lawton, R. J. (2023). Line configuration and farming depth markedly affect survival and growth in the kelp *Ecklonia radiata. New Zealand Journal of Marine and Freshwater Research*. https://doi.org/10.1080/00288330.2023.2256685

Nepper-Davidsen, J., Magnusson, M., Glasson, C. R. K., Ross, P. M., & Lawton, R. J. (2021). Implications of Genetic Structure for Aquaculture and Cultivar Translocation of the Kelp *Ecklonia radiata* in Northern New Zealand. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.749154

Nguyen, H. P., Wang, C. M., von Herzen, B., & Huang, C. (2024, June 9). Hydroelastic Responses of Submersible Seaweed Cultivation Platforms with Single-Point Mooring Systems. *Volume 9: Philip Liu Honoring Symposium on Water Wave Mechanics and Hydrodynamics; Blue Economy Symposium*. https://doi.org/10.1115/OMAE2024-124766

Novaczek, I. (1981). Stipe growth rings in *Ecklonia radiata* (C. Ag.) J. Ag. (Laminariales). *British Phycological Journal*, *16*(4), 363–371. https://doi.org/10.1080/00071618100650411

Novaczek, I. (1984). Response of gametophytes of *Ecklonia radiata* (Laminariales) to temperature in saturating light. *Marine Biology*, *82*(3), 241–245. https://doi.org/10.1007/BF00392405

Poza, A. M., Fernández, C., Latour, E. A., Raffo, M. P., Dellatorre, F. G., Parodi, E. R., & Gauna, M. C. (2022). Optimization of the rope seeding method and biochemical characterization of the brown seaweed *Asperococcus ensiformis*. *Algal Research, 64*, 102668. https://doi.org/10.1016/j.algal.2022.102668

Pitcher, G. C., Figueiras, F. G., Hickey, B. M., & Moita, M. T. (2010). The physical oceanography of upwelling systems and the development of harmful algal blooms. *Progress in Oceanography*, *85*(1–2), 5–32. https://doi.org/10.1016/j.pocean.2010.02.002

Praeger, C., Magnusson, M., & Lawton, R. (2022). Optimising the zoospore release, germination, development of gametophytes and formation of sporophytes of *Ecklonia radiata*. *Journal of Applied Phycology*, *34*(5), 2535–2549. https://doi.org/10.1007/s10811-022-02806-y

Pramita, S., Erniati, E., Zulpikar, Z., Khalil, M., & Muliani, M. (2022). Cultivation of seaweed *Caulerpa racemosa* on a laboratory scale using liquid organic fertilizer. *Acta Aquatica: Aquatic Sciences Journal, 9*(1), 26. https://doi.org/10.29103/aa.v9i1.5502

Purcell, D., Wheeler, T. T., Hayes, M., & Packer, M. A. (2024). Effect of photoperiod and temperature on bioproduct production from juvenile sporophytes of *Macrocystis pyrifera*. *Frontiers in Marine Science*, *11*. https://doi.org/10.3389/fmars.2024.1410877

Rasdi, N. W., & Qin, J. G. (2015). Effect of N:P ratio on growth and chemical composition of Nannochloropsis oculata and Tisochrysis lutea. *Journal of Applied Phycology*, *27*(6), 2221–2230. https://doi.org/10.1007/s10811-014-0495-z

Redmond, S., Green, L., Yarish, C., Kim, J., & Neefus, C. (2014). *New England Seaweed Culture Handbook*. http://digitalcommons.uconn.edu/seagrant_weedculthttp://digitalcommons.uconn.edu/seagrant_weedcult/1

Robson, A. (2020). *AsureQuality Organic Standard version 8*. https://www.asurequality.com/assets/Organic-Files/Organics-Standards/AQ-Organics-Standard_2020-v8.pdf

Roleda, M. Y., & Hurd, C. L. (2019). Seaweed nutrient physiology: application of concepts to aquaculture and bioremediation. *Phycologia*, *58*(5), 552–562. https://doi.org/10.1080/00318884.2019.1622920

Roleda, M. Y., Wiencke, C., Hanelt, D., & Bischof, K. (2007). Sensitivity of the Early Life Stages of Macroalgae from the Northern Hemisphere to Ultraviolet Radiation†. *Photochemistry and Photobiology*, *83*(4), 851–862. https://doi.org/10.1562/2006-08-17-IR-1005

Rolin, C., Inkster, R., Laing, J., Hedges, J., & Mcevoy, L. (2016). *Seaweed cultivation manual: Shetland Seaweed Growers Project 2014–16*.

Rueden, C. T., Schindelin, J., Hiner, M. C., DeZonia, B. E., Walter, A. E., Arena, E. T., & Eliceiri, K. W. (2017). ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics*, *18*(1), 529. https://doi.org/10.1186/s12859-017-1934-z

Saini, R. K., Mahomoodally, M. F., Sadeer, N. B., Keum, Y.-S., & RR Rengasamy, K. (2021). Characterization of nutritionally important lipophilic constituents from brown kelp *Ecklonia radiata* (C. Ag.) J. Agardh. *Food Chemistry*, *340*, 127897. https://doi.org/10.1016/j.foodchem.2020.127897

Schwoerbel, J., Visch, W., Wright, J. T., Bellgrove, A., Sanderson, J. C., & Hurd, C. L. (2024). Thermal performance curves identify seasonal and site-specific variation in the development of *Ecklonia radiata* (Phaeophyceae) gametophytes and sporophytes. *Journal of Phycology*, *60*(1), 83–101. https://doi.org/10.1111/jpy.13406

Seghetta, M., & Goglio, P. (2020). Life Cycle Assessment of Seaweed Cultivation Systems. In *Methods in Molecular Biology* (Vol. 1980, pp. 103–119). Humana Press Inc. https://doi.org/10.1007/7651_2018_203

Sheppard, E. J., Hurd, C. L., Britton, D. D., Reed, D. C., & Bach, L. T. (2023). Seaweed biogeochemistry: Global assessment of C:N and C:P ratios and implications for ocean afforestation. *Journal of Phycology*, *59*(5), 879–892. https://doi.org/10.1111/jpy.13381

Smit, A. J. (2002). Nitrogen Uptake by *Gracilaria gracilis* (Rhodophyta): Adaptations to a Temporally Variable Nitrogen Environment. *Botanica Marina*, *45*(2). https://doi.org/10.1515/BOT.2002.019

Stévant, P., Rebours, C., & Chapman, A. (2017). Seaweed aquaculture in Norway: recent industrial developments and future perspectives. In *Aquaculture International* (Vol. 25, Issue 4, pp. 1373–1390). Springer International Publishing. https://doi.org/10.1007/s10499-017-0120-7

Suebsanguan, S., Strain, E. M. A., Morris, R. L., & Swearer, S. E. (2021). Optimizing the initial cultivation stages of kelp *Ecklonia radiata* for restoration. *Restoration Ecology*, *29*(5). https://doi.org/10.1111/rec.13388

Tait, L. W., & Schiel, D. R. (2011). Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. *PLoS ONE*, *6*(10). https://doi.org/10.1371/journal.pone.0026986

Tarquinio, F., Bourgoure, J., Koenders, A., Laverock, B., Säwström, C., & Hyndes, G. A. (2018). Microorganisms facilitate uptake of dissolved organic nitrogen by seagrass leaves. *The ISME Journal, 12*(11), 2796–2800. https://doi.org/10.1038/s41396-018-0218-6

Tatsumi, M., Layton, C., Cameron, M. J., Shelamoff, V., Johnson, C. R., & Wright, J. T. (2021). Interactive effects of canopy-driven changes in light, scour and water flow on microscopic recruits in kelp. *Marine Environmental Research, 171*, 105450. https://doi.org/10.1016/j.marenvres.2021.105450

Tatsumi, M., & Wright, J. (2016). Understory algae and low light reduce recruitment of the habitat-forming kelp Ecklonia radiata. *Marine Ecology Progress Series*, *552*, 131–143. https://doi.org/10.3354/meps11743

The State of World Fisheries and Aquaculture - Blue Transformation in action. (2024). Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/cd0683en

Toth, G. B., Hargrave, M., Stedt, K., Steinhagen, S., Visch, W., & Pavia, H. (2025). Advances in Swedish Seaweed Aquaculture: Enhancing Biomass Production and Quality. *Reviews in Aquaculture*, *17*(3). https://doi.org/10.1111/raq.70031

Tymoshuk, K., Schaeffer, T., Mitchell, L., Day, S., & Buchwald, C. (2025). Optimizing nutrient concentration and sterilization techniques for the sugar kelp (*Saccharina latissima*) hatchery phase. *Journal of Applied Phycology*. https://doi.org/10.1007/s10811-024-03416-6

Gonzalez, vadillo, Hurd, C. L., Britton, D., Bennett, E., Steinberg, P. D., & Marzinelli, E. M. (2024). Effects of temperature and microbial disruption on juvenile kelp *Ecklonia radiata* and its associated bacterial community. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1332501

Van Alstyne, K. L. (2018). Seawater nitrogen concentration and light independently alter performance, growth, and resource allocation in the bloom-forming seaweeds Ulva lactuca and Ulvaria obscura (Chlorophyta). *Harmful Algae*, *78*, 27–35. https://doi.org/10.1016/j.hal.2018.07.005

van den Burg, S., Selnes, T., Alves, L., Giesbers, E., & Daniel, A. (2021). Prospects for upgrading by the European kelp sector. *Journal of Applied Phycology*, *33*(1), 557–566. https://doi.org/10.1007/s10811-020-02320-z

Vindy, A. B., Agustono, & Alamsjah, M. A. (2021). The Influence of PES (Provassoli's Enriched Seawater) media and modification of Vitamin B12on technical culture for the growth of *Sargassum* sp. *IOP Conference Series: Earth and Environmental Science*, *718*(1). https://doi.org/10.1088/1755-1315/718/1/012011

Visch, W., Biancacci, C., Farrington, G., Sanderson, J. C., Nardelli, A., Schwoerbel, J., Lamb, P., Evans, B., Hurd, C. L., Bellgrove, A., & Macleod, C. (2024). Aquaculture Production of Australian Laminarian Kelps: A manual and research recommendations for *Ecklonia radiata, Lessonia corrugata,* and *Macrocystis pyrifera*.

Visch, W., Lush, H., Schwoerbel, J., & Hurd, C. L. (2023). Nursery optimization for kelp aquaculture in the Southern Hemisphere: the interactive effects of temperature and light on growth and contaminants. *Applied Phycology*, *4*(1), 44–53. https://doi.org/10.1080/26388081.2023.2174903

Wallentinus, I. (1984). Comparisons of nutrient uptake rates for Baltic macroalgae with different thallus morphologies. *Marine Biology*, *80*(2), 215–225. https://doi.org/10.1007/BF02180189

Wernberg, T., Coleman, M. A., Babcock, R. C., Bell, S. Y., Bolton, J. J., Connell, S. D., Hurd, C. L., Johnson, C. R., Marzinelli, E. M., Shears, N. T., Steinberg, P. D., Thomsen, M. S., Vanderklift, M. A., Vergés, A., & Wright, J. T. (2019). Biology and ecology of the globally significant kelp *Ecklonia radiata*. In *An Annual Review* (Vol. 57).

Wernberg, T., Li, K., Pan, Y., Yu, Y., Huang, S., de Bettignies, T., Wu, J., Zhou, C., Huang, Z., & Xiao, X. (2021). Artificial light source selection in seaweed production: Growth of seaweed and biosynthesis of photosynthetic pigments and soluble protein. *PeerJ, 9*, e11351. https://doi.org/10.7717/peerj.11351

Wheeler T, Romanazzi D, & Adams S. (2021). *Stocktake and characterisation of New Zealand's seaweed sector: Species characteristics and Te Tiriti o Waitangi considerations*. www.sustainableseaschallenge.co.nz/our-research/building-a-seaweed-economy

White, L. N., & White, W. L. (2020). Seaweed utilisation in New Zealand. In *Botanica Marina* (Vol. 63, Issue 4, pp. 303–313). De Gruyter Open Ltd. https://doi.org/10.1515/bot-2019-0089

Wilding, C. M., Smith, K. E., Daniels, C. L., Knoop, J., & Smale, D. A. (2025). The influence of seeding method and water depth on the morphology and biomass yield of farmed sugar kelp (*Saccharina latissima*) at a small-scale cultivation site in the northeast Atlantic. *Journal of Applied Phycology*, *37*(1), 459–470. https://doi.org/10.1007/s10811-024-03394-9

Williams, J., Coleman, M. A., & Jordan, A. (2020). Depth, nutrients and urchins explain variability in *Ecklonia radiata* (laminariales) distribution and cover across ten degrees of latitude. *Aquatic Botany*, *166*, 103274. https://doi.org/10.1016/J.AQUABOT.2020.103274

Wood, W. F. (1987). Effect of solar ultra-violet radiation on the kelp *Ecklonia radiata*. *Marine Biology*, *96*(1), 143–150. https://doi.org/10.1007/BF00394848

Worm, B., & Sommer, U. (2000). Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system. *Marine Ecology Progress Series, 202*, 283–288. https://doi.org/10.3354/meps202283

Xu, L., Culliton, D., Fahad, S., Ali, Z., & Kang, E.-T. (2024). Nature-inspired anti-fouling strategies for combating marine biofouling. *Progress in Organic Coatings, 189*, 108349. https://doi.org/10.1016/j.porgcoat.2024.108349

Xu, Z., Dapeng, L., Hanhua, H., & Tianwei, T. (2005). Growth Promotion of Vegetative Gametophytes of *Undaria pinnatifida* by Blue Light. *Biotechnology Letters*, *27*(19), 1467–1475. https://doi.org/10.1007/s10529-005-1313-0

Yarish, C., Penniman, C. A., & Egan, B. (1990). Growth and reproductive responses of *Laminaria longicruris* (Laminariales, Phaeophyta) to nutrient enrichment. *Hydrobiologia*, *204–205*(1), 505–511. https://doi.org/10.1007/BF00040278

Ylivainio, K., Albihn, A., Elving, J., Hermann, L., Lehmann, L., Sarvi, M., Schaaf, T., Schick, J., & Turtola, E. (2017). Contamination of organic nutrient sources with potentially toxic elements, antibiotics and pathogen microorganisms in relation to P fertiliser potential and treatment options for the production of sustainable fertilisers: A review. *Science of The Total Environment, 607–608*, 225–242. https://doi.org/10.1016/j.scitotenv.2017.06.274

Yong, W. T. L., Thien, V. Y., Misson, M., Chin, G. J. W. L., Said Hussin, S. N. I., Chong, H. L. H., Yusof, N. A., Ma, N. L., & Rodrigues, K. F. (2024). Seaweed: A bioindustrial game-changer for the green revolution. *Biomass and Bioenergy, 183*, 107122. https://doi.org/10.1016/j.biombioe.2024.107122

Yu, D., Yin, J., Wang, Y., Lu, A., He, Y., & Shen, S. (2022). Nitrogen assimilation-associated enzymes and nitrogen use efficiency *of Pyropia yezoensis* (Rhodophyta) in nitrate-sufficient conditions. *Algal Research*, *64*. https://doi.org/10.1016/j.algal.2022.102682

Zhou, W., Wu, H., Huang, J., Wang, J., Zhen, W., Wang, J., Ni, J., & Xu, J. (2022). Elevated-CO2 and nutrient limitation synergistically reduce the growth and photosynthetic performances of a commercial macroalga *Gracilariopsis lemaneiformis*. *Aquaculture*, *550*, 737878. https://doi.org/10.1016/j.aquaculture.2021.737878

Appendix

Figure A1. Left: Aerated containers with spools in hatchery with LED lighting from above. Right: Labeled containers with spools at beginning of experiment.