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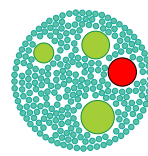
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# Reviewing laboratory culturing of laminarian kelp: *Laminaria hyperborea*, *L. digitata*, and *Saccharina latissima* and their use in ecotoxicology

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## ABSTRACT

Despite underpinning entire polar and temperate coastal ecosystems, kelp is rarely examined in standard ecotoxicology test batteries, and no universally accepted testing guidelines exist despite the growing regulatory interest in macroalgal tests. Declines in kelp populations, linked increasingly to pollution and other anthropogenic stressors, reinforce an urgent need to quantify contaminant effects on kelp health and survival. Reliable and consistent kelp cultivation protocols are therefore essential for generating ecotoxicological data that both addresses critical gaps in environmental risk assessment and provides alternatives to vertebrate testing in toxicology. The microscopic kelp life stages present a particular opportunity for reproducible assays at recognized bottlenecks in the life cycle, where kelp is often most sensitive to environmental stressors. This review consolidates laboratory cultivation techniques for three key species: *Laminaria hyperborea*, *L. digitata*, and *Saccharina latissima*, drawing on published literature and practitioner interviews. Protocols are outlined for spores, gametophytes, juvenile sporophytes, and mature sporophytes, with an emphasis on managing life stage transitions. Key parameters include temperature (5–15°C), nutrient enrichment (F2P), and precise control of light intensity, wavelength, and photoperiod. Strategies to address challenges such as contamination, genetic drift, and long-term culture maintenance are identified, alongside a discussion of emerging efforts to standardize kelp bioassays. The synthesis supports a broader and more robust use of kelp-based assays, which will strengthen our capacity to assess and understand pollution risks to kelp forests, and advance conservation and sustainable management of coastal ecosystems.

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## Introduction

Kelp is a collective term for brown marine macrophytes, usually of the order Laminariales, that underpin temperate and polar coastal ecosystems (Steneck et al., 2002). These canopy-forming algae are primary producers and ecosystem engineers, providing a range of important ecosystem services (Carranza et al., 2024; Shelamoff et al., 2022; Smale et al., 2013; Steneck et al., 2002; Teagle et al., 2017). Kelp contributes to the productivity of fisheries by providing nurseries, feeding grounds, and protection for economically important species (Bertocci et al., 2015). In addition, kelp-derived carbon can be exported to deep sediments or offshore sinks, with retention times varying by species and habitats, giving kelp a potential (but debated) role in long-term carbon sequestration (Duarte et al., 2022; Filbee-Dexter et al., 2022; Fujita et al., 2023; Krause-Jensen et al., 2018). Kelp is known to modify abiotic conditions positively by reducing water flow, sedimentation, and irradiance (Layton et al., 2019; Shelamoff et al., 2022), with their structural influence within coastal ecosystems often more significant than their role as a food source (Denny, 2021; Miller et al., 2018). However, kelp degradation can impair their ecosystem engineering capabilities, potentially leading to reduced resilience and stability (Layton et al., 2019).

Kelp is also sensitive to environmental stress and is recognized as a bioindicator of coastal water quality (Areej et al., 2012; Bryan, 1969, 1980; Chalkley et al., 2019). Changes in abundance, vigor, and morphology can signal issues with the underlying health of kelp populations. For example, bleaching, growth abnormalities, and population declines can signal pollution or broader stressors in the field (Edwards, 2022; Wear et al., 2023). At the tissue level, kelp readily takes up and concentrates

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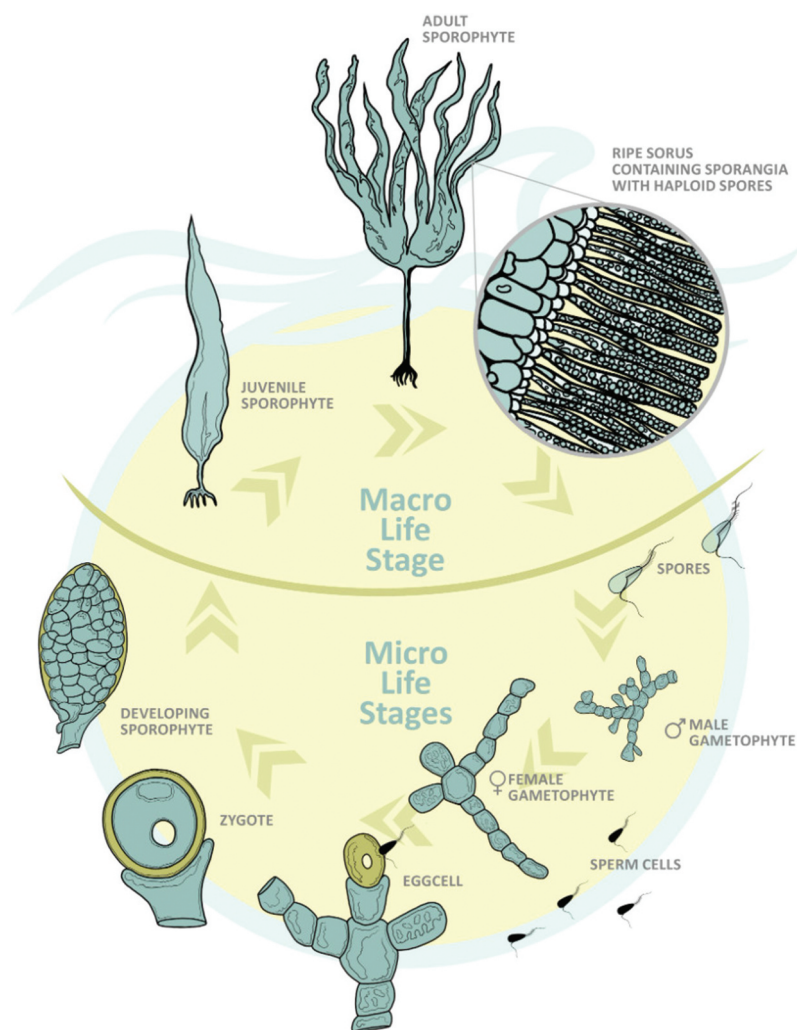
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pollutants, often mirroring ambient concentrations or, in some cases, showing bioaccumulation (Bryan, 1969, 1980; Burger et al., 2007). This sensitivity underpins its formal use in regulatory monitoring. For instance, the U.S. Environmental Protection Agency (EPA) developed a reproduction test for *Saccharina latissima*, later replaced in West Coast effluent toxicity assessments by the more locally relevant *Macrocystis pyrifera* (Chapman, 1990). The resulting 48-hour spore germination and growth inhibition test is now formally recognized in West Coast water quality regulations (Andersen, 2005). In Norway, *L. hyperborea* is used routinely to monitor short-term exposure to organic and inorganic pollutants (Ervik, 2019). Despite such local examples, no single, unifying global standard exists, such as an International Organisation for Standardization (ISO) or an Organization for Economic Co-operation and Development (OECD) method, and kelp remains absent from most routine ecotoxicological batteries, which focus instead on vertebrates, invertebrates, or microalgae (Burridge & Bidwell, 2002).

Despite their ecological importance, kelp forests worldwide are in decline, driven by climate change, localized pollution, and habitat degradation (Krumhansl et al., 2016; Steneck et al., 2002). These losses compromise ecosystem services and reduce biodiversity, prompting conservation practitioners to explore active restoration initiatives (Eger et al., 2022). Kelp cultivation methods, already a mainstay in commercial seaweed production, have become increasingly relevant to conservation, providing an approach for the propagation of kelp in controlled settings for use in restoration out-planting (Eger et al., 2022; Fredriksen et al., 2020). In addition, a clearer and more robust understanding of how pollutants affect kelp at various life stages is also critical (Bartsch et al., 2008; Burridge & Bidwell, 2002; Hughes et al., 2005). Pollution may play a role in significant, acute and chronic kelp decline, yet there is limited standardization in the ecotoxicological testing protocols for these algae to enable us to quantify the impact (Burridge & Bidwell, 2002; Eklund & Kautsky, 2003). As interest grows in using kelp for ecotoxicology, motivated by both regulatory concerns and the shift away from vertebrate testing, robust and reproducible cultivation methods are needed urgently to meet research demands and strengthen marine ecotoxicological test batteries. Bridging these gaps requires a concerted effort to review, synthesize, and standardize cultivation methodologies. Doing so would also advance ecotoxicological research on kelp by ensuring robust, reliable data that can inform regulatory guidelines and conservation strategies. Standardized protocols could also help illuminate the relative importance of pollution, both generally and specifically, as a driver of kelp decline, thereby guiding restoration and management approaches.

This review focuses on three kelp species of ecological, restoration and economic relevance to Southeast England: *Laminaria hyperborea*, *L. digitata*, and *Saccharina latissima*. These species were selected for their prevalence in UK waters, their alignment with local restoration priorities, and their contrasting life history traits, which offer insights relevant to kelp forest recovery and management in other temperate regions. *L. hyperborea* is currently the dominant kelp in UK waters, while *L. digitata* dominates the historical record for Southeast England (Natural History Museum, n.d.). Both *Laminaria* species are long-lived perennials (4–20 years) that form the structural foundation of marine kelp forests (Fletcher, 2024). By contrast, *S. latissima* is a short-lived (1–3 years), fast-growing pioneer that rapidly colonizes disturbed substrates where other kelp species are limited or absent (Fletcher, 2024). All three species are also of commercial significance. *S. latissima* is widely cultivated commercially in the Northern Hemisphere (Sæther et al., 2024). *L. hyperborea* is harvested from wild populations in Scandinavia, although it is not yet cultivated in laboratory-based systems (Vea & Ask, 2011), and *L. digitata* is being explored for its aquaculture potential (Purcell-Meyerink et al., 2021). The three targeted species are all subtidal brown phaeophyte macroalgae. Their life cycle is biphasic, alternating between a large diploid sporophyte (0.2–2.0 m) with blades, stipe, and holdfast, characterized by fucoxanthin pigmentation, producing microscopic haploid flagellated motile spores by mitosis from ripe sorus tissue (Bartsch et al., 2008; Kain, 1979). The spores develop into haploid gametophytes by mitosis. The gametophytes differentiate into flagellated motile sperm cells or non-motile egg cells. A sperm cell fertilizes the egg cell to produce a diploid zygote, which develops by mitosis into a juvenile sporophyte (Fig. 1). The timing and duration of the different stages for each species are plastic, showing variation across the geographic range of the species, and with the development stage being triggered by a range of stimuli rather than always exhibiting a simple circannual rhythm (Bartsch et al., 2008; Bolton & Lüning, 1982).

Commercial growers have developed cultivation techniques to meet industrial demands for seeded spore cultures (Edwards & Watson, 2015; Flavin et al., 2013; Rolin et al., 2016). There is also a substantial body of



**Fig. 1.** Life cycle for Laminariales: *Laminaria hyperborea*, *L. digitata* and *Saccharina latissima*.

growth and single-substance toxicology studies that, although not codified into formal guidelines, have effectively operationalized the cultivation of *L. digitata*, *L. hyperborea*, and *S. latissima* in controlled laboratory environments (Eklund & Kautsky, 2003). Standardized cultivation methods not only support aquaculture but also provide reproducible, controlled life stage material for ecotoxicological tests, ensuring results are comparable across laboratories (Andersen, 2005; Bartsch, 2018; Charrier et al., 2018; Forbord et al., 2018). Despite these developments, no internationally standardized bioassay currently exists (Eklund & Kautsky, 2003; Environment Agency, 2025; European Environment Agency, 2025; U.S. Environment Protection Agency, n.d.). This review aims to consolidate laboratory cultivation protocols for the three kelp species included —*L. hyperborea*, *L. digitata*, and *S. latissima*—and evaluate their application in ecotoxicological studies. First, it details cultivation methodologies across each life stage, analyzing challenges and proposing solutions drawn from published literature and interviews with expert practitioners. It then discusses the application of these methodologies to ecotoxicological bioassays and concludes with recommendations for standardization.

## Method

### Integrative literature review

We carried out an integrative literature review of cultivation protocols for *L. hyperborea*, *L. digitata*, and *S. latissima* during the winter of 2023 (Callahan, 2010; Snyder, 2019; Torraco, 2005, 2016). Searches were run in SCOPUS, Web of Science, and with the University of Sussex Library, using keywords covering

culture methods, life stage descriptors, species names (past and present), and collective nouns likely to capture cultivation studies (Supplementary table S1, Supplementary table S2; Clarivate, [n.d.](#); Elsevier, [n.d.](#); University of Sussex Library, [n.d.](#)). Searches were completed in November 2022, and publication alerts were set up to capture new articles published up to manuscript submission. All species names were updated to the current taxonomy (Bartsch et al., 2008). We tabulated results across common themes and emphasized findings supported by multiple peer-reviewed publications (Johnson et al., 2020; Newing et al., 2011). Studies reporting conflicting or isolated findings were still included but given less weight when shaping overall recommendations.

### ***Semi-structured interviews***

To complement the literature review, we conducted 12 qualitative interviews with practitioners in laboratory-based kelp cultivation in academia, restoration, and commercial kelp production (Flick et al., 2004). The aim was to capture current practices and practical insights that may not appear in published sources, including perspectives from practitioners who may not publish in English (Johnson et al., 2020; Newing et al., 2011). Semi-structured interviews were conducted between March and May 2023, each lasting between 45 and 120 minutes, and followed a topic guide focused on critical steps in propagation and cultivation (Supplementary table S3). Participants represented work conducted on four continents: Europe (including the UK), North America, South America, and Australasia. The group included three commercial growers producing 'seeded' kelp lines, six restoration practitioners, and three academic researchers.

## **Results**

The keywords and criteria searches identified 274 publications consisting of 13 books, 235 journal articles, one dissertation/thesis, and 25 lay publications. Academic journal articles provided the primary material of the findings, while commercial kelp growing instructions offered valuable practical details on the specifics of each step or stage. Practitioner interviews were invaluable in specifying and describing the degree of variability with how these methods and guidelines are applied in practice, what results were achieved, and how they adapted and introduced methods for their specific circumstances and strategies. The integrative literature review and practitioner interviews revealed robust and consistent cultivation practices for each kelp life stage. However, considerable variability also existed, reflecting diverse research objectives and potential geographic adaptations. This variability highlights and reinforces the critical need for standardization to ensure reliable comparability of ecotoxicological data across different studies.

### ***Cultivation protocols by life stage***

These life stages, from spore release to gametophyte maintenance and sporophyte growth, directly align with ecotoxicological endpoints, such as spore germination success, gametophyte growth rate, and juvenile sporophyte size, which can be measured to assess sub-lethal stress responses. Light intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is expressed in photon flux density, the standard unit used in plant and algal physiology to describe photosynthetically active radiation (PAR).

### ***Sorus collection***

Mature sporophytes with fertile sorus tissue are the starting point for laboratory kelp cultures. All studies used the collection of wild sorus tissue from mature individuals. This reproductive tissue is situated on kelp blades with the more mature sorus at the distal ends. The sorus tissue is identified by darker areas of blade tissue, which is in raised patches. In many protocols, spores from multiple individuals are pooled; to avoid dominance by a single genotype in such cases, collections are made from at least 5–10 individuals (ideally 20+). In some experimental contexts, such as intra-population variation studies, spores or gametophytes from individual sporophytes are kept separate to preserve genotype identity. Maintaining genetic diversity is important in ecotoxicology, as it supports representative responses and reduces the risk of including artefacts from unusually sensitive or tolerant genotypes. Sorus tissue is generally sourced with each phase of study from the same range of population



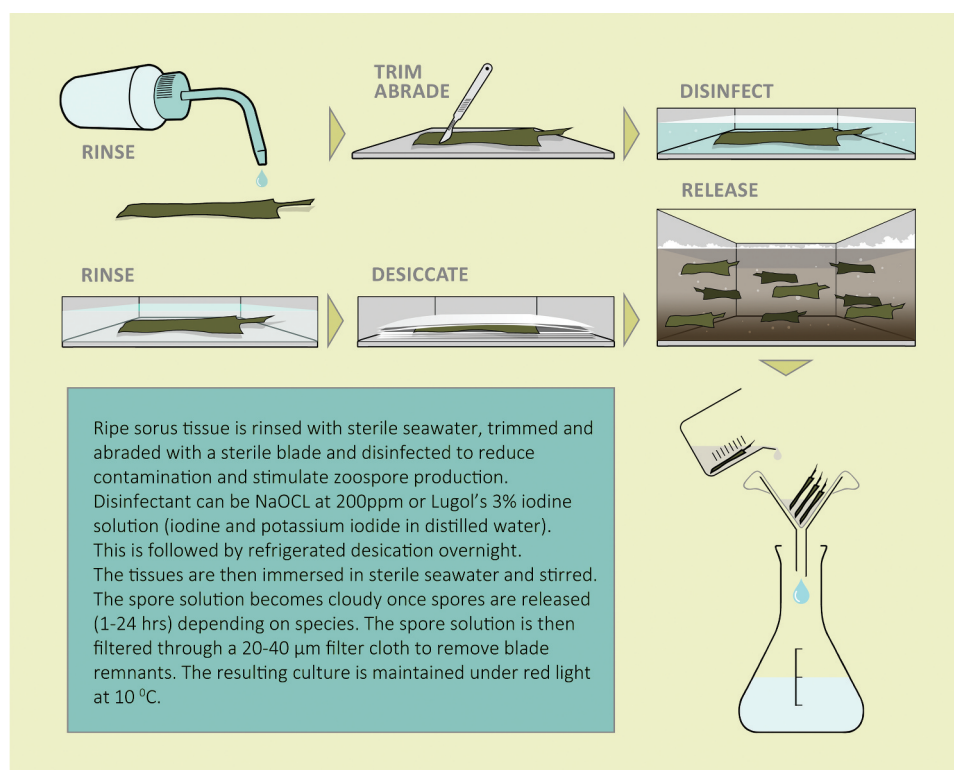
sources to preserve its genetic identity and associated physiological traits. This also helps limit the risks of inbreeding depression (loss of fitness from breeding between closely related individuals) and outbreeding depression (loss of local adaptation from genetic mixing between distinct populations). Inbreeding depression is well documented in *Macrocystis pyrifera*, where sibling crosses significantly reduce female fecundity and fertility (Camus et al., 2021). While direct demonstrations for Laminariales are lacking, population genetic studies in *L. digitata* and *S. latissima* indicate reduced genetic diversity in small or isolated populations, suggesting a potential risk (Billot et al., 2003; Guzinski et al., 2020; Møller Nielsen et al., 2016).

Increasingly, local regulations govern the approach for sorus sampling. For example, Alaska's 50:50 Rule requires tissue from at least 50 unrelated individuals and restricts replanting to within 50 km of the source site, while in the UK, the Sussex IFCA Hand Gathering (Restrictions and Permitting) Byelaw requires application for a permit (Gruenthal & Habicht, 2022; Sussex IFCA, 2021). Best practice guidelines, including the ASC-MSC seaweed (algae) standard (Aquaculture Stewardship Council, & Marine Stewardship Council, 2018) and the Guidelines for the ecolabelling of fish and fishery products from marine capture fisheries: Revision 1 (Food and Agriculture Organization of the United Nations, 2009), recommend sourcing locally to maintain population integrity but do not set universal thresholds for distances or sample sizes. Where wild stocks are limited, sustainable sampling should be designed, defined, quantified, and prioritized. For example, rather than removing entire fertile blades or whole sporophytes, small discs or strips of fertile sorus can be collected, allowing adequate sorus collection while leaving the donor sporophytes intact and able to reproduce (Bartsch, 2018). This approach minimizes ecological impact and should be encouraged as standard practice in research and restoration.

The timing and duration of sorus development vary widely in kelp life cycles. Some authors propose an underlying endogenous and circannual rhythm, while others suggest external drivers such as temperature and nutrient availability (Dring, 1992; Ebbing, Pierik, et al., 2021; Martins et al., 2017; Roleda, 2009; Schaffelke & Lüning, 1994; Stekoll et al., 2021; Yarish et al., 1990). The relative influence of these factors is likely to differ by site and years, with interactions between photoperiod, temperature, and nutrient conditions determining the onset and duration of sorus production. *L. hyperborea*, *L. digitata*, and *S. latissima* sorus tissue can be sampled throughout the year, but not for all locations. Typically, practitioners report greater peaks in autumn/winter and spring (Bartsch et al., 2008; Boderskov, 2021; Dring, 1992; Lee & Brinkhuis, 1988; Yarish et al., 1990), though some populations of *L. digitata* in Helgoland (Martins et al., 2017) and Arctic regions (Roleda, 2009; Zacher et al., 2019) show peak production in summer.

### Spore release

Laboratory cultures are typically initiated by triggering spore release through the cleaning, desiccation, and submersion of fertile sori, often using temperature and osmotic stress (see Fig. 3 and Supplementary tables S4 and S5). Variation in induction methods, drying duration, temperature, or rehydration protocol suggests that the process is relatively insensitive, indicating phenotypic plasticity in local variants. Sorus segments are typically cleaned to remove epiphytes by scraping and rinsing, often with freshwater or diluted iodine/bleach solutions (Alsuwaiyan et al., 2019; Bartsch, 2018; Charrier et al., 2018; Kain & Jones, 1964). Two main approaches are then used to induce spore release. The more common method involves desiccating cleaned sori overnight at ~4°C to trigger maturation, followed by rehydration in sterile, filtered seawater, enriched with nutrients, which stimulates mass spore release over 1–24 hours depending on species (Alsuwaiyan et al., 2019; Boderskov et al., 2022; Forbord et al., 2018; Fig. 2). The alternative method, described by Bartsch (2018), avoids prolonged air exposure; cleaned sori are placed in humid conditions in covered petri dishes, allowing only ripe, mature sporangia to release spores. Spores can be motile for days to weeks, depending on blue light exposure (Bartsch, 2018; Bartsch et al., 2008). If immediate culture is not possible, dried sorus tissue is refrigerated for short periods from days to weeks with some retention of spore viability. A more long-term approach is to germinate spores into gametophytes and maintain these rather than storing spores (see Gametophyte Culture Initiation and Maintenance).



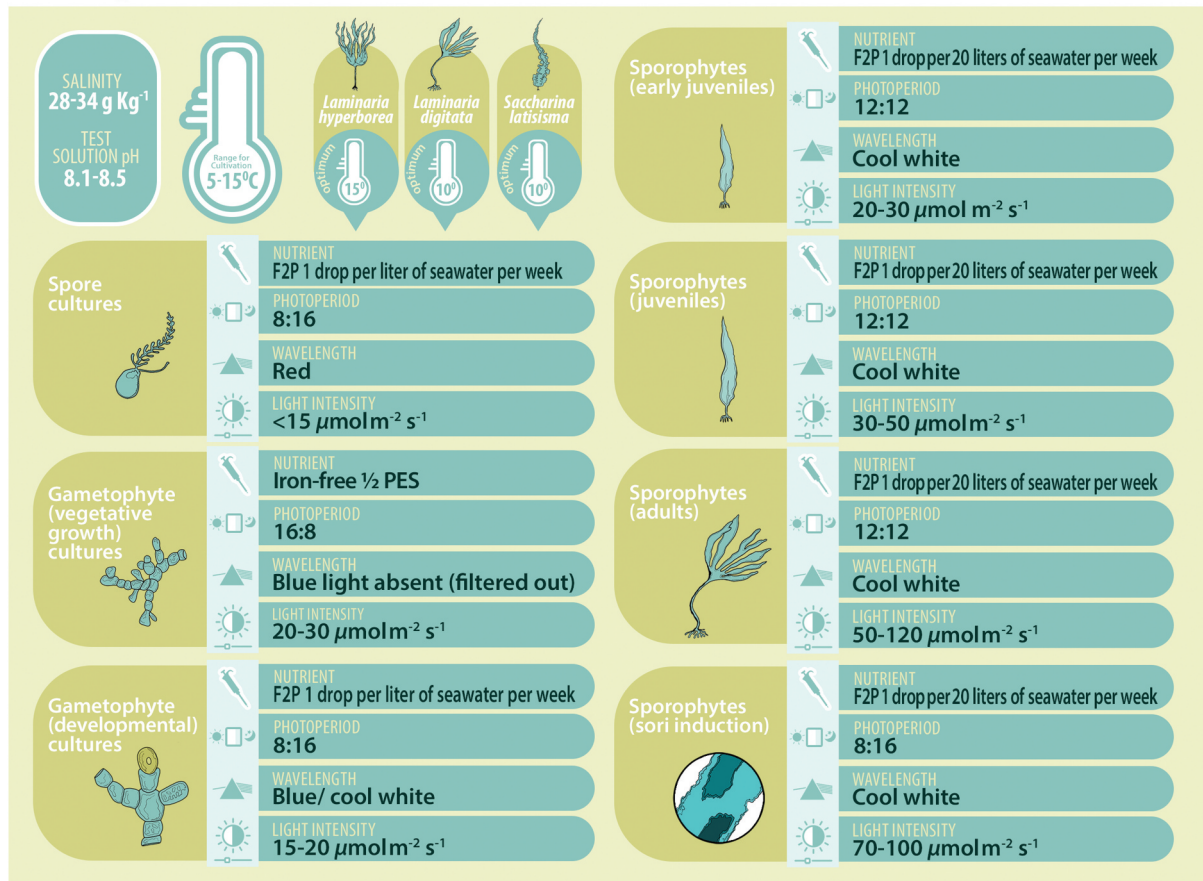
**Fig. 2.** Sorus tissue preparation for spore release.

### **Gametophyte culture initiation and maintenance**

Under favorable conditions, spores settle quickly and germinate into male and female gametophytes, usually within 1–2 days. Each spore's internal reserves support initial development, but culture media should be enriched to sustain further growth after germination (Forbord et al., 2018). While various enrichment formulations have been used, nutrient-enriched seawater is used most frequently and can improve germination and early gametophyte growth. The preferred formulation from this review is F2P, which has been widely adopted in laboratory kelp culture development (see Fig. 3, see Nutrients). The F2P medium is defined as Guillard's *f/2* medium supplemented with Provasoli's vitamin mix, combining the macronutrients and trace metals of *f/2* with the vitamin profile of PES (Guillard, 1975; Guillard & Ryther, 1962; Provasoli, 1968). Optimal germination and gametophyte growth for cold-water kelp occurs at 10–15°C (Bolton & Lüning, 1982; Flavin et al., 2013; Forbord et al., 2012; Lee & Brinkhuis, 1988; Redmond et al., 2014). Conditions for germination are highly temperature-sensitive; *S. latissima* spores show close to zero germination at 20°C, whereas they germinate readily at 0–15°C (Lee & Brinkhuis, 1988). Light is kept low during gametophyte initiation (10–30  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  of white light) to prevent photo-inhibition and excessive heating (Bartsch, 2018; Redmond et al., 2014). Gametophytes start as tiny filaments or clumps of cells; these vegetative gametophytes can be grown in liquid suspension cultures or on surfaces. Martins et al. (2017) reported improved gametogenesis in *L. digitata* under long-day regimes when nutrient levels were enhanced (see Fig. 3).

Long-term maintenance requires adjusting to favor vegetative growth rather than reproduction. This is achieved by providing moderate nutrients and limiting the light quality to red wavelengths or low intensities, since blue light and high irradiance induce gametogenesis (Lüning, 1991). The removal of iron from the nutrient solution, combined with the application of relatively high but sub-lethal temperatures, has also been reported to promote gametophyte vegetative growth (Lewis et al., 2016; Nielsen et al., 2003; Stekoll et al., 2021; Zhang et al., 2015). Gametophyte stock cultures are often held under dim red light or in a 12:12 light:dark cycle at 8–15°C, which allows them to proliferate mitotically without forming gametes (Anderson et al., 2004; Charrier et al., 2018; Forbord et al., 2012; Lüning, 1991). Under such conditions, kelp gametophytes can be sustained for many months or even years through regular subculturing. Nutrient-enriched seawater media should be changed weekly (Bartsch, 2018). Extended storage is possible using multi-annual delayed (MAD) gametophyte culture methods

# Kelp Cultivation



**Fig. 3.** Summary of cultivation parameters by life stage. Photoperiod is in hours light:dark.

that combine light and nutrient control to maintain vegetative growth for up to several years, with reproduction suppressed until required (Ebbing, Fivash, et al., 2021, 2021; Ebbing et al., 2025; see Sorus Collection). Periodic dilution or fragmentation of gametophyte cultures is performed to prevent over-density and nutrient depletion. These vegetative cultures can then be induced to reproduce for sporophyte production or be maintained as genetic stock for later seeding applications (Andersen, 2005). Cryopreservation techniques are also being explored for kelp gametophytes (Andersen, 2005; Visch et al., 2019); if perfected, this would allow laboratories to store a library of diverse strains and revive them as needed, ensuring a sustainable supply of genetically diverse material. *S. latissima* gametophyte germplasm banks in aquaculture have been successfully established via cryopreservation and could potentially be similarly helpful for research cultures (Visch et al., 2019).

## Sporophyte development and substrate attachment

To produce sporophytes from vegetative gametophyte cultures, reproduction is induced by changing culture conditions. This involves increasing light intensity (providing blue-rich light) and, in the case of *S. latissima*, shifting to a short-day photoperiod (8:16 light:dark; Lüning, 1988). Blue light is a well-established cue for kelp gametogenesis in *L. hyperborea*, *L. digitata* and *S. latissima* (Bartsch, 2018; Hsiao & Druehl, 1973; Lüning, 1980, 1991; Lüning & Dring, 1975). Standard practice is to transfer vegetative gametophyte cultures from red light to white or blue light ( $20\text{--}30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), ensuring both sexes are present. A 1:1 to 2:1 male-to-female ratio maximizes fertilization success. Within days, fertilization occurs, and juvenile sporophytes typically appear as tiny blades ( $\sim 0.5\text{--}1$  mm after 1–2 weeks, depending on species) attached to the substrate the gametophyte occupies (Bartsch, 2018; Forbord et al., 2018).

In hatchery and research practice, sporophytes can be initiated in two main ways. In spore seeding, fertile sori are induced to release motile spores, which then settle directly onto the target substrate. Spores adhere



strongly because they secrete adhesives upon contact with the substrate. This method also preserves high genetic diversity, since each spore represents a unique meiotic product from multiple source sporophytes (Kerrison et al., 2016). In gametophyte seeding, vegetative or fertilized gametophytes are maintained under controlled conditions and then applied to substrates. This allows greater genetic control, often from a small number of parental lines, but typically results in lower attachment success due to weaker adhesion (Augyte et al., 2017; Forbord et al., 2012). Hatchery practice generally matches the method to production goals: spore seeding is favored for broad genetic representation and rapid colonization, whereas gametophyte seeding is preferred for propagation of selected genotypes.

Substrate properties strongly influence settlement. Roughened or fabric surfaces, such as polyester strings, nylon meshes, and textured slides, often yield better attachment success than smooth surfaces (Kerrison et al., 2016). In hatcheries, gametophytes are commonly seeded onto spools of twine or tape to provide an attachment medium for developing sporophytes. In research studies, microscope slides or Petri dishes are used as settlement surfaces for spores (Kerrison et al., 2016). Substrates are pre-cleaned and may be conditioned with a thin coating of organic compounds such as poly-L-lysine, D-glucose or yeast extract to enhance spore adhesion (Kerrison et al., 2016). Once attached, sporophytes derive nutrients from the culture medium and can either remain in place or be transferred by moving the colonized substrates. Growth and nutrient availability must be monitored to avoid overcrowding and nutrient limitation, with thinning or transfers as needed. *L. hyperborea* sporophytes grow more slowly than *S. latissima*, so time frames to reach a given size can vary by species. Gentle water motion and adequate nutrition remain critical to producing robust juveniles.

While most laboratory culture work focuses on early life stages, it is possible to complete the life cycle to sorus production under controlled conditions. Sporophytes are grown to maturity in outdoor or large flow-through tanks, then sporogenesis is induced by trimming distal blade sections (5–15 cm) and maintaining them at ~10°C under cool white light at moderate irradiance (70–100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for 4–12 weeks (Boderskov, 2021; Buchholz & Lüning, 1999; Forbord et al., 2012). A short-day photoperiod (8:16 h, light: dark) is commonly included in these protocols (Bartsch, 2018; Boderskov, 2021; Boderskov et al., 2022; Forbord et al., 2018; Lüning, 1988), but its role in sorus production appears species-specific. An effect of daylength has only been demonstrated in *S. latissima* (Boderskov, 2021; Boderskov et al., 2022). It appears unnecessary in *L. digitata* (Buchholz & Lüning, 1999) and has not been reported for *L. hyperborea*.

### Optimal environmental parameters for kelp culture

Successful laboratory cultivation of kelp demands specific, controlled environmental conditions. Each life stage has particular optimum ranges, often reflecting the cool, nutrient-rich habitats these species inhabit. Key parameters include temperature, light (intensity, photoperiod, and wavelength), nutrient media, seawater source, and water movement (see Fig. 3).

#### Temperature

All three kelp species are cold-temperate algae that have adapted to relatively low temperatures (Fig. 3; Supplementary table S6). Early life stages of all three species are cold-tolerant, surviving to –1.5°C (Dieck, 1993). For example, Arctic *S. latissima* spores germinate at 0°C with 100% success (Diehl et al., 2023). Spore and gametophyte stages generally tolerate temperatures of 5–15°C, with germination and vegetative growth being optimal near 10°C for many populations (Bartsch, 2018; Bolton & Lüning, 1982; Edwards & Watson, 2015). *L. digitata* growth is optimal at 10°C (Bartsch et al., 2013), showing poor survival and fertility at temperatures  $\geq 20^\circ\text{C}$ , with high temperatures blocking the gametophyte-to-sporophyte transition (Lee & Brinkhuis, 1988). *S. latissima* gametophytes grow best at 10–15°C, with declines outside this range depending on thermal history (Bass et al., 2023; Diehl et al., 2023; Edwards & Watson, 2015). Juvenile growth is inhibited at  $\geq 17^\circ\text{C}$ , it fails to produce sporophytes at 20°C, and Arctic strains fail to survive at 20°C (Diehl et al., 2023; Lee & Brinkhuis, 1988). *L. hyperborea* shows optimal growth at 15°C (Bolton & Lüning, 1982) but has a lower heat tolerance than the other two species, with gametophytes and juveniles exhibiting stress when sustained above 16–17°C, and upper survival limits of 20–21°C for sporophytes and gametophytes (Bolton & Lüning, 1982; Dieck, 1993). At its southern range limit in Portugal, *L. hyperborea* has declined markedly, linked to summer sea temperatures exceeding its tolerance and reduced coastal

upwelling (Casado-Amezúa et al., 2019; Monteiro et al., 2022; Pinho et al., 2016). In culture,  $\sim 10^{\circ}\text{C}$  is used as a practical optimum for multi-species cultivation (Bartsch, 2018; Flavin et al., 2013; Lee & Brinkhuis, 1988). Thermal history can shift tolerance limits; *L. digitata* can acclimate seasonally to warmer conditions by a few degrees (Bass et al., 2023; Bolton & Lüning, 1982; Lüning, 1984) but long-term culture development near the upper tolerance is not recommended (Bolton & Lüning, 1982).

### Light intensity and photoperiod

Light is important for kelp culture management, both providing energy for photosynthesis as well as acting as a developmental signal (see Fig. 3; Supplementary table S7).

**Intensity.** Kelp gametophytes and young sporophytes are shade-adapted and grow under relatively low light (Han & Kain (Jones), 1996). Gametophytes are maintained under  $20\text{--}30\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ , depending on photoperiod and species, following gametogenesis at  $15\text{--}20\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  (Edwards et al., 2016). Juvenile sporophytes grow initially under  $20\text{--}30\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ , increasing to  $30\text{--}50\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  after the first week, and then from 50 to  $120\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$  as adult sporophytes develop (Edwards & Watson, 2015; Lüning, 1988). High light intensity can cause kelp photo-stress, such as bleaching or DNA damage, particularly if combined with elevated temperatures. It is, therefore, typical practice to use moderate fluorescent or LED lighting and to avoid direct sunlight.

**Photoperiod.** Daylength influences kelp physiology (Lüning, 1991). For general growth, a 12:12 light:dark cycle is widely used (Forbord et al., 2018). For vegetative growth of gametophyte cultures, a long day regime is recommended with a 16:8 light:dark (Bartsch, 2018). To delay reproduction, practitioners keep gametophytes under red light. To induce reproduction, short-day regimes (8:16 h, light:dark) are combined with blue-enriched light (Lüning, 1988). For sorus production of mature blade sections, short-day (8:16 light:dark) is established until sorus ripens (Boderskov, 2021).

**Light quality.** Wavelength has a strong influence on development (see Fig. 3). Blue light (434–452 nm) reliably triggers gametogenesis in brown algae (Lüning, 1991), whereas gametophytes remain vegetative when blue light is absent. This absence is achieved in culture by using red light ( $\sim 660\ \text{nm}$ ) or filters that block blue wavelengths. Practitioners use this to their advantage; fertility is suppressed under red LEDs or blue-blocking filters and promoted with cool white or blue-enriched lighting. This is why the spectrum profile of the light source should always be checked against the study aims (Bartsch, 2018). Both LED and fluorescent lighting are widely used. Many laboratories use broad-spectrum ‘cool white’ lights containing red and blue components (Bolton & Lüning, 1982). For routine growth, low-to-moderate light intensity, a 12:12 h light:dark photoperiod, and cool white spectra are optimal. To induce reproduction, cultures are shifted to higher intensities, shorter photoperiods and blue-enriched spectra. Practical considerations also matter; energy efficiency and low heat output reduce refrigeration loads. While one restoration practitioner perceived daylight as superior, most cultivation relies on artificial lighting. Unlike horticulture, kelp culture management has not yet adopted crop-specific spectral recipes (Sipos et al., 2020).

### Nutrients

Kelp are large algae and require a full complement of macro- and micronutrients for sustained growth in the laboratory (Grobbelaar & Bornman, 2004). In natural seawater, nitrates and phosphate levels fluctuate seasonally; in culture, growth media is enriched to avoid limitation. PES and Guillard f/2 medium (f/2), initially developed for microalgae, are widely used media for kelp cultures (see Supplementary table S8; Andersen, 2005; Forbord et al., 2012; Kerrison et al., 2016; Provasoli, 1968; Provasoli et al., 1957; Ratcliff et al., 2017; Redmond et al., 2014; Rolin et al., 2016). These provide nitrogen (as nitrate or ammonia), phosphorus (as phosphate), vitamins (e.g. B12, thiamine), and trace metals (iron, zinc, manganese) in standardized concentrations (Alsuwaiyan et al., 2019; Kerrison et al., 2016). Typical target concentrations are nitrate at  $\sim 0.1\text{--}0.5\ \text{mM}$  and phosphate at  $\sim 0.01\text{--}0.03\ \text{mM}$ . For example, f/2 provides  $\sim 0.088\ \text{mM NO}_3^-$  and  $0.0036\ \text{mM PO}_4^{3-}$ , sufficient to support algal growth without excessive bacterial growth (Andersen, 2005). Iron is critical for kelp photosynthesis, respiration, and energy metabolism, and nutrient media usually include chelated iron (such as Fe-EDTA) in the order of  $10^{-6}\ \text{M}$  unless actively excluded to prevent

gametophyte development (Andersen, 2005; Lewis et al., 2013). Trace metals, such as zinc, cobalt, molybdenum, and manganese, are added in micromolar or nanomolar amounts according to PES/F/2 recipes (Andersen, 2005). Vitamins (B12, B1, biotin) are also included for optimal growth, energy metabolism, and proper cellular function.

Overall, this review suggests that F2P, Guillard's F/2 medium supplemented with the Provasoli vitamin mix, is the most successful nutrient mix, as it provides both the macro- and micronutrients of F/2 and the vitamin profile of PES (Guillard, 1975; Guillard & Ryther, 1962; Provasoli, 1968).

### Media

Media should be sterilized to avoid contamination. For batch cultures, complete media changes every 1–2 weeks are standard; for continuous or semi-continuous cultures, fresh media may be added continuously, along with periodic dilution (Alsuwaiyan et al., 2019; Anderson et al., 2004).

### Seawater source (natural vs. artificial)

Natural seawater provides the ionic composition, trace elements, and dissolved organic compounds that kelp is adapted to. It should be filtered or sterilized (via autoclaving or UV/Tyndallization) to remove microorganisms (Alsuwaiyan et al., 2019). Many kelp researchers and practitioners use filtered natural seawater enriched with nutrients, as it replicates seawater chemistry (Alsuwaiyan et al., 2019). Artificial seawater, made from reagent-grade salts, offers both quantified consistency and purity, valuable for toxicology assays to eliminate unknown background pollutants. However, artificial mixes may lack influential trace components or organic matter. Both sources can produce good results, provided they are adequately supplemented. In a review of kelp culture studies, 72% used filtered natural seawater (often nutrient-enriched), and 14% used Provasoli-enriched seawater directly (Alsuwaiyan et al., 2019). Only 2% used artificial seawater without enrichment (Alsuwaiyan et al., 2019).

### Salinity

Kelp grows best at salinities close to natural seawater. *L. digitata* tolerates 20–35 g kg<sup>-1</sup>; while *S. latissima* is reported across slightly narrower ranges, 28–34 g kg<sup>-1</sup> and 24–35 g kg<sup>-1</sup> in different studies (Davison & Reed, 1985; Flavin et al., 2013; Kerrison et al., 2016; Redmond et al., 2014; Reed et al., 1985). Low salinity causes physiological stress and reduces growth. We recommend maintaining a salinity level of 28–34 g kg<sup>-1</sup>.

### pH

Reported pH ranges for healthy kelp culture are 8.1–8.5 (Fox & Swanson, 2007; Kerrison et al., 2016) to 7.0–9.0 (Flavin et al., 2013). pH should be monitored and stabilized with buffers (such as bicarbonate or Tris), especially in static cultures where photosynthesis can raise pH (Andersen, 2005). This study suggests that pH be maintained at 8.1–8.5.

### Aeration and water movement

Kelp benefits from gentle water movement which enhances nutrient and gas exchange, supplies CO<sub>2</sub> for photosynthesis, prevents clumping of sporophytes, and dilutes inhibitory exudates (Charrier et al., 2018; Edwards & Watson, 2015). Aeration also helps maintain uniform light exposure and temperature, while reducing the risk of surface films or anoxia in dense cultures (Andersen, 2005).

During delicate stages such as spore settlement or early gametophyte growth, aeration is kept minimal; water is typically static or only lightly bubbled for the first 24–48 hours. Once attachment is secure, gentle bubbling can be introduced (1–2 bubbles s<sup>-1</sup> in 100–500 ml flasks; Edwards & Watson, 2015). In larger tanks, air stones are commonly used to circulate water without dislodging juveniles (Andersen, 2005). Care must be taken to avoid excessive aeration, which can cause shear stress or detachment, even in species with robust hapters such as *L. hyperborea* and *L. digitata*. In large flow-through tanks, orbital shakers or low-flow recirculating pumps can provide water motion, but inlets should be screened to protect small sporophytes (Andersen, 2005).

## Ecotoxicological sensitivity

Ecotoxicological assays have generated valuable but disparate insights into the sensitivity of *L. hyperborea*, *L. digitata*, and *S. latissima* to pollutants (Supplementary table S10). A synthesis of published data highlights that early life stages are more sensitive to stressors, reflecting the bottleneck role these play in the kelp life cycle (Bartsch et al., 2013; Edwards, 2022). Fig. 4 summarizes the lowest observed effect concentration (LOEC) and, where available, lethal doses, reported for these species across major pollutant classes, including metals, herbicides, pesticides, and detergents.

These comparisons suggest apparent differences in sensitivity across species and pollutant classes. For example, *L. hyperborea* shows a reported sensitivity of LOEC  $0.05 \mu\text{g l}^{-1}$  atrazine (herbicide A), whereas *S. latissima* was inhibited at  $72.2 \mu\text{g l}^{-1}$  (Hopkin & Kain, 1978; Thursby & Tagliabue, 1990). Copper thresholds span LOECs ranging from  $0.025 \mu\text{g l}^{-1}$  in *L. hyperborea* to  $50 \mu\text{g l}^{-1}$  in *L. digitata* and  $10 \mu\text{g l}^{-1}$  in *S. latissima* (Chapman, 1990; Chung & Brinkhuis, 1986; Gledhill et al., 1997; Hopkin & Kain, 1978). Similarly, mercury has been reported at concentrations as low as  $0.001 \mu\text{g l}^{-1}$  in *L. hyperborea* compared to  $0.5\text{--}5 \mu\text{g l}^{-1}$  in *S. latissima* (Hopkin & Kain, 1978; Thompson & Burrows, 1984). Detergents also show inhibitory effects at sub- $\mu\text{g l}^{-1}$  levels in some cases. On first examination, these results imply significant differences in species sensitivity. However, in reality, they largely reflect variation in study design, including the exposure concentration tested, the life stage examined, and the response metric used. Environmental parameters further complicate interpretation. Temperature, salinity, and light regime also influence the timing and magnitude of kelp responses (Eklund & Kautsky, 2003), making it challenging to separate pollutant effects from background variability without standardized conditions. This underscores the need for harmonized protocols and shared endpoints to allow meaningful comparisons of sensitivity across species, pollutants and studies.

Eklund & Kautsky (2003, p. 171) emphasized that ‘many [kelp] stages are more sensitive than other aquatic organisms’, and argued that macroalgal assays should be incorporated into coastal monitoring programs. Although some Laminariales are endemic, their shared habitat requirements and parallel life stages provide a strong basis for comparative testing. Standardized protocols would not only improve reproducibility but also enable results from different species to be interpreted within a broader ecological framework.

## Response metrics

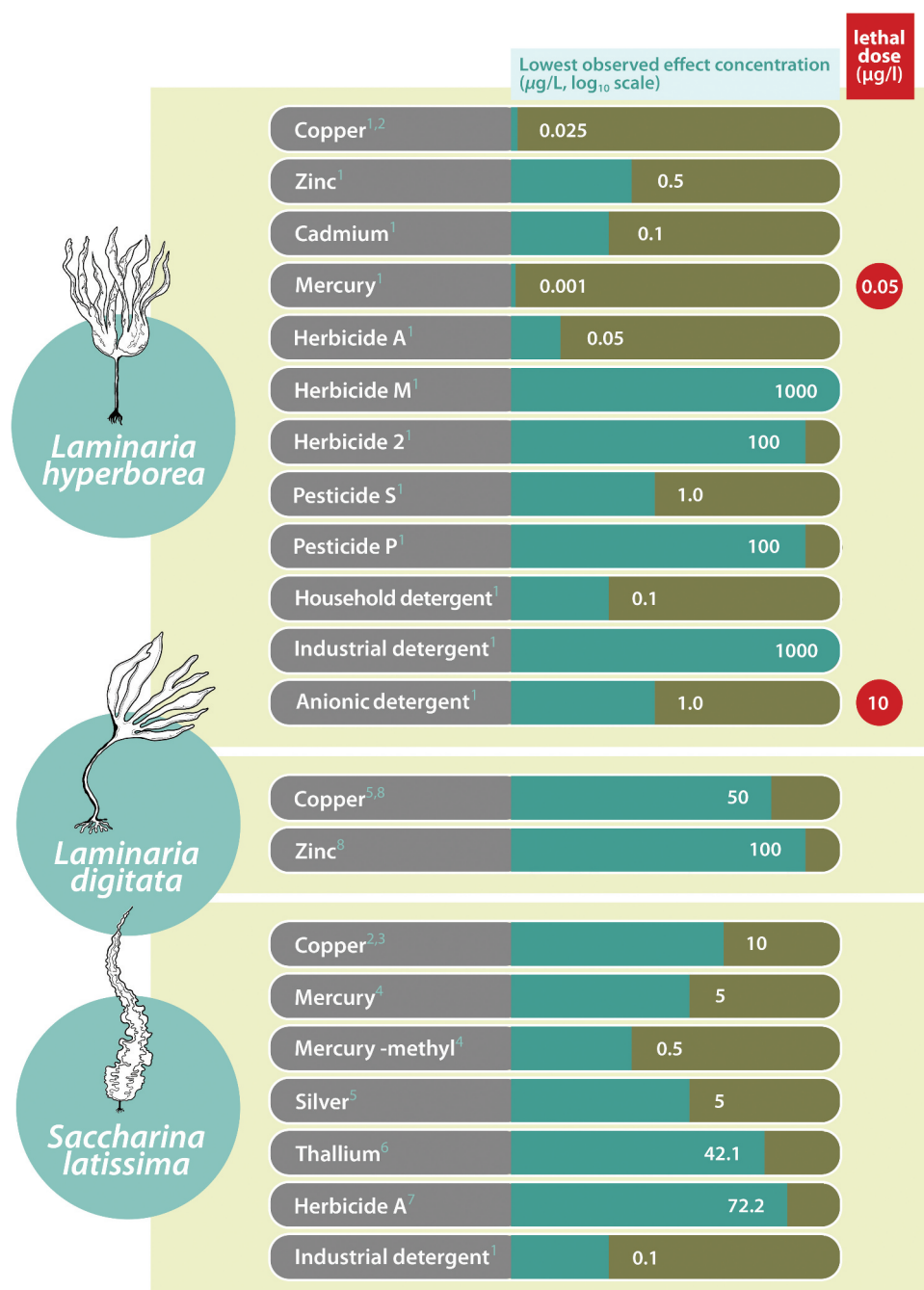
A range of response metrics have been used in ecotoxicology studies on kelps. Here we outline the most consistently applied endpoints, along with some emerging approaches.

**Spore germination percentage.** Microscopic assessment determines the proportion of spores that have germinated, produced a germ tube, or undergone first cell division versus those that remained ungerminated (Anderson et al., 2004). Typically, ~100 spores per replicate are scored.

**Germ tube length, gametophyte dimensions, sporophyte growth.** Early growth can be quantified by measuring germ tube length or gametophyte diameter of young gametophytes after a defined exposure period, with often 48 and 96 hours used as the preferred timescale. A reduction in length relative to the control indicates growth inhibition (Anderson et al., 2004; Hopkin & Kain, 1978; Thompson & Burrows, 1984). For sporophytes, blade length is the most widely used endpoint reported.

**Developmental stage.** For longer tests (>96 hours), developmental progress can be tracked, with progress defined as the percentage of gametophytes that have transitioned to a two-celled stage or the percentage forming sporophytes after a defined number of days. Toxicants may delay or prevent these life stage transitions (Chapman, 1990; Chung & Brinkhuis, 1986; Gledhill et al., 1997; Hopkin & Kain, 1978; Thompson & Burrows, 1984; Thursby & Steele, 1988; Thursby & Tagliabue, 1990).





**Fig. 4.** Summary of lowest observable effect concentrations and lethal doses reported across studies for *Laminaria hyperborea*, *L. digitata*, and *Saccharina latissima*. Key to test substances: herbicide A - Atrazine; herbicide M - methyl chlorophenoxy acetic acid (MCPA); herbicide 2 - 2,4-dichlorophenoxyacetic acid (2,4-D); pesticide S - Sodium pentachlorophenate; pesticide P - Phenol pentachlorophenate; household detergent - fairy Liquid; industrial detergent - Blusyl; anionic detergent - sodium lauryl ether sulphate. Key to sources (1) Hopkin & Kain (1978); (2) Gledhill et al. (1997); (3) Chung & Brinkhuis (1986); (4) Thompson & Burrows (1984); (5) Chapman (1990); (6) Thursby & Steele (1988); (7) Thursby & Tagliabue (1990); (8) Bryan (1969).

**Survival.** In chronic exposures, the survival of gametophytes or juvenile sporophytes can be monitored directly. For short spore tests, mortality is often inferred from a failure to germinate (Garman et al., 1994; Hopkin & Kain, 1978).

**Physiological indices.** Measures include chlorophyll content and photosynthetic efficiency measured by pulse amplitude modulated (PAM) fluorometry or continuous excitation fluorimetry, respiration rates, and nutrient

uptake. Respiration can be measured indirectly through changes in oxygen concentrations in the culture medium. However, this endpoint can be confounded by simultaneous photosynthetic activity, so specific control of light:dark cycles and replication is required to distinguish the two processes. A drop in the ratio of variable fluorescence (Fv) to maximum fluorescence (Fm) indicates the maximum quantum yield of photosystem II in algae. In sporophytes, it can indicate sublethal stress from a pollutant affecting photosynthesis (Gera et al., 2012; Gledhill et al., 1997; Mayer-Pinto et al., 2020). In other macroalgae, simple visual inspection of thallus color has been tested as a bioassay endpoint, though this has not yet been applied to kelps (Han et al., 2007).

**Reproductive success.** Multi-week exposures can test whether gametophytes previously exposed to a pollutant retain the ability to produce sporophytes, based on how reduced sporophyte formation relative to controls affects fertility or fertilization (Oyarzo-Miranda et al., 2020; Wear et al., 2023).

**Bioaccumulation.** This approach uses tissue analyses with ecotoxicological bioassays and offers potential use in both environmental monitoring and regulatory decision-making. To illustrate how kelp can be a bioaccumulator, Burger et al. (2007) examined mercury concentrations in different parts of a 5 m-long kelp blade. The study found that environmental mercury levels correlated negatively with kelp blade length. However, levels within kelp tissues differed substantially between the stipe and blade tissue, underscoring the importance of standardized sampling protocols, as each tissue can harbor distinct contaminant loads. In the case of heavy metals or organics, measuring the concentration of a pollutant in kelp tissue quantifies uptake. Although this is not a direct effect endpoint, it helps correlate internal dose with observed effects and can act as a ‘bioindicator for short-term exposure’ (Ervik, 2019, p. 4). By analyzing these tissue-specific burdens, researchers can identify hotspots of metal accumulation and track pollution gradients in coastal ecosystems.

Kelp species, through bioassays, can be reliable bioindicators of environmental pollution. There is a range of possible endpoints for models of impacts, from metals to organics, that could be applied to pollutants. The micro-life stages provide a bottleneck in the development, growth, and establishment of kelp and represent a valuable metric for viability in the wild (Coelho et al., 2000; Underwood & Fairweather, 1989).

### **Genetic diversity and sustainability of cultures**

Maintaining genetic diversity in laboratory cultures is a key challenge for ensuring ecologically meaningful results. When cultures are initiated from a single sporophyte or a small number of parent plants, the gametophyte stocks may have limited genetic variation (Robuchon et al., 2014). Over time, repeated sub-culturing of these lines can lead to clonal propagation and potential inbreeding effects, increasing the risk that responses to stressors will reflect narrow genetic traits rather than those of natural populations. Diversity can be further reduced by parthenogenesis, in which female gametophytes form sporophytes without fertilization, creating homozygous offspring (Oppliger et al., 2024). To counter these risks, optimized sampling strategies (see Spore Collection), including maintaining multiple gametophyte lines that can be intercrossed and supplementing cultures with new wild collected material on an annual or seasonal basis, can help offset genetic drift and sustain representative diversity.

### **Contamination by microalgae and microbes**

Contamination is a persistent challenge in kelp culture management. Kelp spores and gametophytes are small and grow relatively slowly, making them vulnerable to being overgrown by faster-growing organisms such as microalgae, diatoms, fungi, and bacteria. Diatoms are the most common contaminants, often introduced via sorus surfaces or airborne spores, and can bloom in nutrient-rich seawater. A thick film of diatoms can smother kelp gametophytes and prevent sporophyte attachment. To reduce the risk, protocols include thorough surface sterilization of sorus tissue before spore release and the use of selective inhibitors. The most widely applied is germanium dioxide (GeO<sub>2</sub>), which disrupts silica uptake in diatoms. It has been applied to kelp culture media at a rate of 0.045–0.1 mg l<sup>-1</sup> during the first week after spore settlement (see Supplementary table S9; Charrier et al., 2018; Kerrison et al., 2016; Markham & Hagmeier, 1982; Shea &

Chopin, 2007). However, prolonged or high-dose use can affect kelp development negatively (Andersen, 2005; McLachlan et al., 1971; Thomas et al., 2022). For this reason, some practitioners apply  $\text{GeO}_2$  only briefly while others avoid it entirely, relying instead on frequent media changes or careful culture density management to prevent microalgal overgrowth.

Bacterial contamination is another concern. Bacteria can proliferate in nutrient media and sometimes form films on developing gametophytes or sporophytes, potentially causing disease or altering growth. An initial sorus pretreatment with iodine or dilute bleach is partly aimed at reducing bacterial load (Alsuwaiyan et al., 2019). Antibiotics can be used when axenic cultures are required, such as a mix of penicillin-streptomycin in the medium, though they may also slow algal growth (Tatewaki, 1989). Most laboratories focus on minimizing bacterial introductions by using filtered, autoclaved seawater, sterile handling techniques and maintaining moderate culture densities.

Fungal endophytes can be another source of contamination, with Laminariales hosting filamentous fungi in their tissues (Vallet et al., 2020). While some may function as mutualists (Bonthond et al., 2022), they can complicate culture work. Cleaning and disinfection of collected tissue, sterile media and dedicated incubators are the most utilized methods for reducing risk.

## Discussion

This review investigates both the opportunities offered by kelp in ecotoxicological assays and the challenges we face in turning opportunity into reality. Laboratory protocols increasingly enable reliable and controlled cultivation across life stages. Building on this foundation and integrating this learning into ecotoxicology assays requires a greater understanding of methodological stress, biological variability, the route to standardization, and reproducibility to support development within regulatory frameworks.

### *Impact of stress-induction methods on spore viability and ecotoxicological relevance*

Laboratory stress-induction methods, including osmotic shock, desiccation, and mechanical scraping, are routinely employed to trigger spore release from sorus tissue. However, these procedures could introduce unintended physiological stress, potentially affecting spore viability, developmental trajectories, and subsequent greater sensitivity to environmental pollutants. Studies have shown variability in spore performance post-stress, including delayed germination, reduced motility and reduced growth rates in response to changes in temperature and salinity (Bartsch, 2018; Fernández et al., 2021; Lind et al., 2017). Comparable effects from mechanical, osmotic, or desiccation stress have not been well quantified. Further work to assess their potential influence would help ensure that laboratory ecotoxicology results remain ecologically relevant, consistent and credible.

### *Ecological context: plasticity and local adaptation*

Kelp responses to environmental conditions reflect both short-term plasticity and longer-term genetic adaptation. Bolton & Lüning (1982) observed plasticity, the capacity of an organism to adjust its physiology or development in response to environmental variation without requiring genetic change. In *L. digitata* and *S. latissima*, they found plasticity to be more influential than fixed local strain adaptation. This plasticity could explain why some studies report a wide range of responses to similar cultivation or pollutant conditions. For ecotoxicology, distinguishing plasticity from genetic adaptation is critical. Plastic responses may buffer kelp against pollutants in the short term, but they also complicate comparisons between studies if culture history or environmental conditioning is not reported. Conversely, low genetic diversity (from limited culture sources) may mask the potential range of responses. Recognizing these dynamics is essential for designing assays that yield results relevant for natural populations.

### *Standardization and reproducibility*

Variability in kelp cultivation methods remains a key barrier to consistency and reproducibility in ecotoxicology. Protocols differ widely in desiccation times, media composition, and induction conditions,

even with the same species (Alsuwaiyan et al., 2019). Such inconsistencies make it difficult to compare results across laboratories and risk confounding pollutant effects with methodological artefacts. Best-practice guidelines from cultivation handbooks (Edwards et al., 2016; Redmond et al., 2014) recommend defined media, controlled temperatures, and standard light regimes. For ecotoxicology, early-life stage endpoints are more reproducible across laboratories than sporophyte assays, which are more sensitive to cultivation idiosyncrasies. Wider adoption of standard protocols outlined by Bartsch (2018) and Forbord et al. (2018), coupled with transparent reporting, will help generate comparable toxicity thresholds. Encouragingly, the *M. pyrifera* spore germination test has already been standardized for regulatory use on the U.S. West Coast (Anderson et al., 2004), and adaptations for *Laminaria* and *Saccharina* species show promising reproducibility (Han et al., 2011). Progress will depend on interlaboratory comparison studies and the inclusion of reference toxicants to calibrate test sensitivity (Eklund & Kautsky, 2003; Okumura et al., 2018). These steps are essential precursors for international standardization.

### Regulatory outlook

For kelp bioassays to gain regulatory traction, they must be validated and incorporated into guideline frameworks. Progress has begun with the *M. pyrifera* spore test incorporated as part of Whole Effluent Toxicity (WET) testing (Anderson et al., 2004; Hunt et al., 1991; Thursby et al., 1993), and similar approaches have been applied in Australia for local kelp such as *Ecklonia* in antifouling assessments (Gunns Ltd, 2007). Despite these precedents, macroalgae remain absent from international test batteries. Including kelp would fill a critical gap by representing benthic primary producers, particularly for pollutants that disproportionately affect macroalgae. The next step is to develop and propose standardized methods through organizations such as ISO or OECD. This process will require interlaboratory ring tests, reference toxicant validation, and clear evidence that kelp assays are both robust and broadly applicable. A pragmatic approach may be to standardize a generic Laminariales spore germination and growth inhibition test, with species selected regionally, such as *L. hyperborea*, *L. digitata*, or *S. latissima* in the Eastern North Atlantic, and *M. pyrifera* in the Pacific. Such a framework would mirror existing flexibility in fish or invertebrate tests. By formalizing kelp assays within regulatory structures, ecotoxicology would gain a tool that not only complements existing models but also strengthens the protection of the ecosystems that kelp forests underpin.

### Conclusion

Kelp is a critical primary producer and ecosystem engineer, yet remains underrepresented in standard ecotoxicology test batteries. Declining kelp populations, increasingly linked to pollutants and other anthropogenic stressors, highlight the urgent need for kelp-based assays. The microscopic life stages – spores, gametophytes, and early sporophytes – are especially valuable for ecotoxicology: they are readily reproducible in culture, sensitive to stress, and represent natural bottlenecks in the kelp life cycle in which population success or failure is determined.

Reliable cultivation protocols now exist to sustain kelp year-round. Maintaining near-optimal temperatures (5–15°C), enriching seawater with F2P nutrients, controlling light intensity and wavelength to regulate reproduction, and managing contamination all make it possible to generate consistent test material. These practices also reduce reliance on wild harvest, especially when combined with laboratory sorus ripening and long-term gametophyte banks. The next step is wider standardization. At present, laboratory methods vary, creating challenges for reproducibility and comparability across studies. The *M. pyrifera* spore test in California demonstrates that kelp assays can be formalized into regulatory frameworks. Adapting similar protocols for *L. hyperborea*, *L. digitata*, and *S. latissima* would extend this approach to European waters, ensuring that kelp is included alongside microalgal and animal tests in ecotoxicological assessments.

Integrating kelp bioassays into formal guidelines would provide regulators and researchers with a more complete picture of coastal ecosystem risk. By refining culture techniques, aligning methodologies, and validating endpoints such as spore germination, gametophyte growth, and sporophyte development, kelp tests can move from specialist applications into standardized practice. Doing so will strengthen our capacity to detect and manage pollutant impacts, while supporting the conservation, restoration, and sustainable



management of kelp forests – ecosystems that anchor biodiversity, fisheries, and carbon cycling in temperate and polar coasts worldwide.

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## Author contributions

**M. Glascott:** Conceptualization, Investigation, Writing – original draft, Data curation, Formal analysis, Visualization, Validation, Writing – review and editing, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software; **W. Hughes:** Supervision, Writing – review and editing; **M. Peck:** Conceptualization, Supervision, Writing – review and editing; **T. Cane:** Writing – review & editing; **C. Yesson:** Conceptualization, Supervision, Writing – review and editing.

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## Data availability statement

Interviews were conducted confidentially to encourage openness and protect the commercial sensitivity and intellectual property of academic researchers, restoration professionals, and commercial growers. Therefore, interview recordings and verbatim transcripts are not publicly available.

## Human research ethics application

Ethics Application ER/MG611/1: A Critical Review of UK Kelp Cultures in Ecotoxicology Studies was submitted 12 January 2023, and approved by the Sciences & Technology C-REC, University of Sussex.

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