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SCIENCE ADVICE FOR GENETIC EFFECTS FROM MACROALGAE AQUACULTURE IN SOUTHERN CALIFORNIA AND THE GULF OF AMERICA

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Science Advice for Genetic Effects from Macroalgae Aquaculture in Southern California and the Gulf of America

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Executive Summary

The purpose of this report is the present a synthesis of knowledge about aquaculture of macroalgaes in the context of potential culture-wild interactions and subsequent genetic effects on wild populations. The scope of effects from aquaculture in this report is focused on genetic effects related to culture-wild interactions and loss of genetic diversity due to escaped/dispersed culture-origin material surviving in the wild. This report does not specifically address potential ecological effects such as competition of invasive species with native species, disease, or other factors, although information provided in this report may inform evaluations of ecological risk.

Candidate species for marine aquaculture were selected by NOAA based on known industry interest, potential for significant industry development, environmental suitability in each respective region, and environmental and technical feasibility for farming offshore in federal waters. Species included here do not represent an exhaustive list of potential species that could be cultivated in federal waters, nor an explicit endorsement by NOAA of these species for cultivation.

Based on a synthesis of each of the candidate species (presented in Chapters 2 and 3), an assessment of the influence of species and population dynamics on the genetic risk level was determined for each species as a qualitative assessment of potential for genetic effects to wild populations from commercial culture of macroalgae. A summary of findings related to genetic risk for each of the species in the Southern California and Gulf of America regions are shown in the tables below. More detailed factors contributing to these findings are tabulated in Chapter 4.

The genetic risk level is based on specific risk factors that would influence genetic effects to wild populations from aquaculture, based on species and population characteristics. The risk factors are: potential for maturity in culture (e.g. harvest after maturity age would present greater genetic risk), dispersal capacity (ability of spores to disperse over a large area presents a greater risk; potential for vegetative fragmentation and rafting presents a greater risk), current thinking on wild population abundance (low abundance of the local population would mean greater demographic contribution from cultured gametes, with potential for greater genetic risk), biological characteristics in cultured strains that may differ from wild populations, and knowledge on genetic structure and population structure of the species on a region level.

The evaluation of uncertainty in the risk level is based on available data to support findings on wild population status and genetic diversity. The Low/Moderate/High assessment for the genetic risk level and uncertainty presented in the tables is based on a broad review of the available research and scientific literature regarding wild population dynamics and characteristics for each species. The risk levels do not account for culture production levels, escape rates or other operational factors. As such the genetic risk levels in the table can be considered for factors that influence risk but should not be construed as a full assessment of genetic risk from aquaculture.

Southern California Candidate Macroalgae Species: Summary of Risk Factors, Uncertainty in assessment, and Priorities to Minimize Genetic Effects from Aquaculture of Macroalgae

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Alaria marginata	Ribbon kelp	Low; limited dispersal ability, physical separation between suitable habitat and offshore culture, some settlement preferences, and most cultured material harvested prior to maturation. Dispersal of fertile/nearly fertile dislodged fronds may enable long distance dispersal, but without floatation mechanism, likely to be rare.	Moderate; better understanding of the fine scale population structure and current patterns will improve prediction of potential genetic impacts.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultured lines; harvesting ahead of sexual maturation; lowering long lines during high energy events to reduce breakage on plants, if permitting/user conflicts allow
Fucus distichus	Bladderwrack	High; significant dispersal capability due to gas-filled bladders, capacity for self-fertilization, ability to vegetatively reproduce. Genetic evidence, based on patterns of spatial genetic structure, suggest dispersal could occur at distances greater than anticipated distances between offshore aquaculture locations and coastal habitat.	Moderate; uncertainty is based on unresolved local population genetic structure scale, which will be important to understanding local connectivity patterns based on current dispersal patterns among wild populations.	Utilizing genetically diverse seedstock/fragements representative of local populations; and consider propagation approach (vegetative versus seed); maintain genetic diversity in cultivated populations, particularly when using vegetative propagation approaches.
Gracilaria andersonii	Sea Spaghetti	Moderate; action of harvesting *Gracilaria* species is known to release spores and fragments, high potential to colonize due to broad tolerance of environmental factors and suitability for various habitats. However, presence of spatial genetic structure from other, less invasive *Gracilaria* spp indicate successful dispersal and colonization may not be frequent.	Moderate; no population genetic studies for this species. Understanding water current patterns will also be important to predicting impacts from dispersed cultured material.	Utilizing genetically diverse seedstock representative of local populations; using culture approaches to reduce breakage of plants (e.g., adjusting line depth during high energy events, reducing epiphyte loads, etc.); maintain genetic diversity in cultivated populations, particularly when using vegetative propagation approaches; harvesting ahead of sexual maturation. Completely collecting all biomass at end of grow-out period.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Hedophyllum sessile (formerly *Saccharina sessilis*)	Sea Cabbage	Low; limited dispersal of spores and gametes, physical separation between suitable habitat and offshore culture, majority of kelp harvested prior to maturation. Dispersal of fertile/nearly fertile dislodged fronds may enable long distance dispersal, but without floatation mechanism, likely to be rare.	High; there is a substantial amount of information is currently unavailable, including population abundance, population genetic studies, cultivation approaches, which hinders our ability to evaluate the potential genetic impacts resulting from cultivating *H. sessile*.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; harvesting ahead of sexual maturation; using culture practices to reduce breakage of plants (e.g., expose new plants to wave energy or currents to increase holdfast strength).
Laminaria setchellii	So. Stiff Stiped Kelp	Low; late maturation of plants would likely exceed grow-out period if similar to wild plants (2-3 yrs), although fragments of related spp. are frequently found in multi-species kelp drifts, fragments would likely break down before sori develop. Long-lived natural populations may provide genetic resistance to infrequent introgression, but experience long-lasting consequences if more frequent.	Moderate to high; the genetic population structure and overall abundance of *L. setchellii* populations across their range, as well as the methodology for offshore cultivation of this species, represent significant gaps in the understanding of genetic risks from cultivation of this kelp.	Unknown with current state of information; general priorities include harvesting material ahead of sexual maturation, utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; harvesting ahead of sexual maturation; lowering lines during high energy events to minimize breakage and dislodgement of plants if permitting/user conflicts allow.
Macrocystis pyrifera	Giant Kelp	Moderate to high; dislodged kelp is capable of dispersing over great distances. Some kelp will mature prior to harvest, and dispersal of blades or spores from early maturing individuals, or growth of sporophylls on rafting kelp, remain a risk. Genetic structure among populations in Southern California leads to greater risk in disrupting genetic patterns among locations.	Moderate; to evaluate risk to natural populations, knowledge of farm locations and prevailing oceanographic patterns will be important to ascertaining risk.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations.; synthesizing oceanographic information to predict impact patterns from dispersed material; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting ahead of sexual maturation.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Mastocarpus spp.	Turkish Washcloth	Low to moderate; limited dispersal capabilities of propagules, more limited suitable settlement habitat for dispersed propagules. However, fertile vegetative fragments, in addition to asexual reproduction without the need for fertilization, poses greater genetic risk from cultivated material. Little information available on extent of rafting, and duration for which fragments remain fertile.	High; great deal of missing information including knowledge of which species would be cultivated, absence of population genetic studies. Would need to determine which life-history variants exist in populations expected to be in impacted by the farm (different genetic consequences). Lack of developed cultivation approaches. These together hinder a more thorough assessment of the genetic risks associated with farming these spp.	Difficult to predict based on available information; general priorities include sourcing seed material from nearby populations, maintaining genetic diversity in cultivated populations, using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting ahead of sexual maturation.
Nereocystis luetkeana	Bull kelp	Low; most dispersal occurs at scales under 10 m, although longer distance dispersal is possible, especially through rafting; majority of plants harvested prior to sexual maturation. Studies indicate that rebuilding of wild populations have been limited by low settlement and recruitment, dispersed cultured propagules may face same limitations for successful settlement and recruitment.	Low to moderate, the only population genetic study may have lacked power in analyses to detect finer-scale structure.	Utilizing genetically diverse seedstock representative of local populations (although this may be challenging south of Pt. Conception due to rarity of occurrence), and maintaining genetic diversity in cultivated populations; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation.
Postelsia palmaeformis	Sea Palm	Low; limited dispersal ability, low likelihood of dispersed spore settlement in suitable habitat, slightly higher potential for dislodged plants / fronds to drift into suitable habitats, but colonization success from this type of dispersal is rare even in natural populations. However, wild populations are small, and would be more susceptible to genetic impacts from cultivated material.	High; cultivation approaches have not yet been developed and no knowledge of population abundance.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations, using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Pyropia spp.	Nori, black seaweed	Low to moderate, characteristics of spores and the fragility of thalli decrease likelihood of dispersal, however some potential exists for rare long-distance dispersal events (possibly occurring during conchocelis phase on transported shells/barnacles). Rapid harvest cycle for these spp. Intricate life-cycles of this genus, and specific settlement requirements lower success for propagule spread, unless in close proximity to shellfish farms or fouling shellfish on equipment/boats).	Moderate; species of interest for commercial cultivation has not been determined, and population genetic structure is lacking. However, general considerations for this genus are similar among species.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation; making sure farm equipment/service boats are free from biofouling (e.g., barnacles) that may transport conchocelis away from farm site.
Saccharina latissima	Sugar kelp	Low to moderate; studies in other regions for *S. japonica* and *L. hyperborea* have demonstrated transport distances for kelp particulates (which could include spores) can extend from 100s of m up to 200 km away from farm site, but distances depend on farm location. Majority of kelp would be harvested prior to maturation, but early maturing plants are possible. If fertile tissue or spores are dispersed, a moderate level of settlement requirements (combination of factors) may reduce successful recruitment into natural populations.	Moderate; need to determine the scale of regional connectivity among populations, and better information on status / abundance of populations at southern end of their range in California to provide better risk assessment.	Using culture approaches to minimize breakage (e.g., allowing sufficient time for holdfasts to firmly attach to lines, subjecting young sporophytes to current velocities to strengthen holdfasts, and not overcrowding lines to give individual holdfasts space for attachment), harvesting prior to sexual maturation. Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations. This is particularly important until a population genetic study can shed light on the scale of genetic structure in the region.

Gulf of America Candidate Macroalgae Species: Summary of Risk Factors, Uncertainty in assessment, and Priorities to Minimize Genetic Effects from Aquaculture of Macroalgae

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Codium spp.	Dead Man's Fingers / Oyster Thief	High; if native species possess characteristics similar to those observed in *C. fragile*, dispersal is likely, vegetative propagation may result in low genetic diversity in cultured material which may impact natural populations directly (introgression) or indirectly (displacement). However, native *Codium spp*. may not present a risk level equivalent to *C. fragile*, and lack of information makes it challenging to assess potential genetic risk from *Codium spp*. in Gulf.	High; little available information regarding these species in the Gulf, including details on abundance, population structure, and ease of spread and establishment. This missing information leads to a high degree of uncertainty in risk assessment of genetic impacts from culturing *Codium*.	Utilizing *Codium* species native to the Gulf, preferably sourced close to farm, employing techniques such as environmental DNA (eDNA) to ensure that *C. fragile* is not inadvertently propagated at farm sites, removing or increasing distances between artificial structures to minimize dispersal, in addition to regularly treating, cleaning, or replacing aquaculture equipment to remove *Codium* present due to fouling. Using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow).
Eucheuma spp.	Eucheumatoids	Moderate to high; cultured material will likely disperse to native populations. Vegetatively propagated cultured plants will likely have reduced genetic diversity compared to wild populations. Although they may not genetically introgress into wild populations (limitations of vegetative fragmentation), they have a demonstrated ability to displace native populations, potentially leading to loss of genetic diversity indirectly through population decline.	Moderate; population structure is unknown in Gulf; genus has demonstrated ability to disperse and colonize locations.	Culturing native species, sourced from local populations, maintaining genetic diversity in asexually propagated lines, genetically characterizing cultured and wild strains or populations. Using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow).

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Gracilaria spp.	Sea Spaghetti	Moderate; relatively high capacity for dispersal, plants easily establish in natural settings. Genetic impact on wild populations will depend on whether dispersed fragments reproduce sexually. Cultured material spreading through genetic introgression or vegetative growth displacing wild plants may genetically impact natural populations.	Low to moderate; need to understand whether cultured dispersed vegetative fragments will become fertile if settled in natural habitat; this will determine if genetic introgression occurs. If it does occur, genetic risk outcomes will depend on the genetic diversity and degree of domestication in cultured lines.	Utilizing culture approaches to minimize breakage, for example, conditioning hardy thalli and holdfasts through water current exposure; Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations, with extra attention paid to minimize transfer between the distinctive eastern and western Gulf populations.
Sargassum spp.	Sargassum	Moderate; high capacity for dispersal due to buoyant vesicles, ease of settlement in variety of habitats / conditions, ability for vegetative fragmentation. However, if natural populations are abundant, and the population is structured over broad scales (currently unknown in Gulf, but reasonable assumption based on information from other *Sargassum* spp. until more information is available), genetic impact may be minimal if locally representative genetic diversity can be maintained in cultured material.	Moderate; a better understanding of population dynamics is needed to evaluate genetic risk from culture of this species. Population abundance and genetic connectivity among populations in the Gulf will be key to determining genetic risk to natural populations.	Using culture approaches to minimize breakage, for example, lowering long lines during grow out to 3 m to delay reproductive development and reduce epiphyte growth; utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations.
Ulva spp.	Sea lettuce	Moderate to high; high dispersal propensity, rapid reproductive maturation in culture, easy settling parameters and/or ability to grow unattached. Given number of spp. found in Gulf, need to determine which are native vs. introduced, and which would be cultivated. If species chosen for cultivation has/have been previously introduced into Gulf, then perhaps impacts on naturalized populations are less of a concern, however, potential risk would still remain for displacement of native populations.	Moderate; need information on the targeted species for culture, and population genetic structure. Given that dispersal to wild populations is likely, the impact will depend on the species, connectivity among populations in the Gulf, and oceanographic processes in region of the farm.	Utilizing culture approaches to minimize breakage, for example, extending the time in the nursery to provide greater degree of attachment and culturing *Ulva* at depths several meters below surface to reduce wave energy. Using shorter grow out periods to decrease biomass loss from tissue degradation and release of fertile material; utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; developing sterile strains.

1.0 How Cultured Organisms Escape and Consequences of Escape

The purpose of this report is to present a synthesis of knowledge about aquaculture of macroalgaes in the context of potential culture-wild interactions and subsequent genetic effects on wild populations. The scope of effects from aquaculture in this report is focused on genetic effects related to culture-wild interactions and loss of genetic diversity due to escaped/dispersed culture-origin material surviving in the wild.

Candidate species for marine aquaculture were selected by NOAA based on known industry interest, potential for significant industry development, environmental suitability in each respective region, and environmental and technical feasibility for farming offshore in federal waters. Species included here do not represent an exhaustive list of potential species that could be cultivated in federal waters, nor an explicit endorsement by NOAA of these species for cultivation.

In considering risk, Kaplan (1981) advise defining and addressing three questions: (1) what can go wrong; (2) what is the likelihood of that happening; and (3) what are the consequences? With that guidance in mind, the following sections describe how and the likelihood that cultured organisms may escape (Section 1.1, *Escape Background and* Categories) and the consequences of escaped cultured organisms (Section 1.2, *Consequences of Escape*).

1.1 Escape Background and Categories

In this section, we address the first of Kaplan's (1981) definitions of risk, 'what can go wrong', or in this context, how cultured organisms escape or disperse away from grow-out sites.

Dispersal of propagules

Propagule dispersal involves the dispersal of spores, gametes, zygotes, and microscopic germlings originating from cultivated material that attains fertility either during the grow-out phase at the farm-site or following breakage or detachment (explained below) from the farm-site. Dispersal of propagules is thought to result in the most significant opportunity for genetic interaction between wild populations and cultured material (Stévant et al. 2017). Macroalgae exhibit a wide range of life-history strategies, influencing the number and types of propagules they disperse. The general life-history traits of brown, green, and red macroalgae are summarized below, though variations exist within each group. More detailed information will be provided in the individual species summaries.

Brown macroalgae have an alternation of generations life cycle, where the visible diploid sporophytes produce haploid spores via meiosis. These spores develop into typically microscopic gametophytes, which produce male and female gametes that fuse to form diploid sporophytes (Bringloe et al. 2020). Most brown algae reproduce sexually, though some species (e.g., *Lessonia nigrescens*) may also reproduce via parthenogenesis from unfused female gametes (Oppliger et al. 2007).

Green macroalgae also alternate between a diploid sporophyte stage that generates motile zoospores through meiosis, and a haploid gametophyte stage, which produces motile gametes (Moreira et al. 2022). Unlike brown algae, where one stage (typically the gametophyte) is microscopic, some green macroalgae, such as *Ulva*, look similar in both stages, though this varies by species. Green algae can also reproduce parthenogenetically from unfused gametes (e.g., *Ulva*) or propagate vegetatively through fragmentation (e.g., *Codium*) (Moreira et al. 2022).

In contrast to brown and green macroalgae, red macroalgae have a triphasic life cycle (Searles 1980). Diploid tetrasporophytes produce haploid tetraspores through meiosis, which develop into male and female gametophytes. Male gametes fertilize female gametes, which remain on the female gametophyte, forming a diploid carposporophyte. This carposporophyte produces diploid carpospores that grow into tetrasporophytes (Searles 1980; Borg et al. 2023). Some red algae also reproduce parthenogenetically (e.g., *Mastocarpus* species; Krueger-Hadfield 2019) or vegetatively (e.g., *Gracilaria* species; Redmond et al. 2014).

The duration of the grow-out period plays a pivotal role in determining the likelihood of a macroalgal species becoming fertile before harvest or achieving fertility on dislodged or broken macroalgae from the farm-site. A species' life-history, as it pertains to the timing of reproductive maturity, will also largely determine the degree of genetic risk posed by dispersed propagules. This timing varies widely among macroalgal species, with some, like *Laminaria setchelli*, becoming reproductive after 2 to 3 years (Klinger 1985), while others, such as *Ulva* spp., exhibit reproductive capabilities only 2 to 3 weeks after thallus development (Hiraoka 2021)

The dispersal tendency of propagules varies among macroalgal species and is likely to be positively associated with the duration spent in the water column (Macaya et al. 2005). Each organism's specific life cycle determines whether it has one or multiple types of propagules. Spores serve as the primary mode of dispersal for most macroalgal species, with dispersal periods ranging from hours to days and distances spanning from meters to hundreds of kilometers (Springer et al. 2010, Alberto et al. 2011). The dispersal patterns of spores are predominantly influenced by their release height, as well as the intensity of turbulence (e.g., waves), and prevailing water currents in the release area (Alberto et al. 2011, Schoenrock et al. 2021).

Certain macroalgal species may exhibit spore motility (e.g., *Ulva* and *Codium* species) and/or respond to environmental factors like light, chemicals, and nutrients (e.g., *Ulva* species, *Mutimo cylindricus, Macrocystis pyrifera, Pterygophora californica*), potentially extending their time in the water column (Churchill and Moeller 1972, Amsler and Neushul 1989, Reed et al. 1999, Carl et al. 2014, Kinoshita-Terauchi et al. 2019). For instance, species demonstrating positive phototaxis tend to remain higher in the water column, experiencing more significant passive transport by currents compared to species lacking this trait (Reed et al. 1999). Some spores possess photosynthetic capabilities, further prolonging both their viability and potential dispersal range (Reed et al. 1988, Reed et al. 1992). Additionally, certain spores can maintain viability through dormancy periods, germinating only when environmental conditions are conducive to growth (Dieck 1993, Schiel and Foster 2006).

While gametes also disperse, this effectively occurs over much smaller distances (<1 m) to enable fertilization or fusion of the gametes (Springer et al. 2010). However, there are species of macroalgae where parthenogenetic development of haploid gametes is known to occur (e.g., *Codium* and *Ulva* species) (Churchill and Moeller 1972, Chang et al. 2003, Wichard et al. 2015, Hiraoka 2021), which increases the dispersal risk from gametes in those species as only a single gamete is needed for development.

Breakage of portions of, or the dislodgement of the entire sporophyte

Another means of 'escape' from macroalgal farming involves the breakage of a segment of the macroalgae or the complete detachment of the entire macrophyte during the offshore cultivation phase. High wave energy stands out as a primary factor in the offshore environment contributing to both breakage and detachment (Milligan and DeWreede 2000). Particularly, storm-driven removal of biomass can be significant (Dawes 1974), with macroalgae detachment peaking during the winter months compared to other seasons (Hobday 2000a, Milligan and DeWreede 2000). The levels of breakage and detachment may also be influenced by cultivation practices, such as seeding density, which may or may not allow sufficient space for the development of secure holdfasts, conditioning of young sporophytes before outplanting to promote strong holdfast attachments, and the physical arrangement of cultivation systems and line positioning to minimize drag on the macrophytes during the cultivation period (Buck and Buchholz 2005), and the approaches used to secure the macroalgae to the lines where breakage may be higher for macroalgal species tied onto culturing lines because they do not adhere to the substrate (e.g., *Gracilaria*) (A. Concepcion, personal communication). Herbivore grazing, fouling by other seaweeds/epiphytes, and diseases that weaken the thalli of species can further contribute to breakage and detachment during the cultivation phase (Dawes 1974, Ask and Azanza 2002, Ask et al. 2003), with some of these factors potentially influenced by the duration of the cultivation period.

The biological characteristics of each macroalgal species are crucial in assessing the risk associated with this form of 'escape'. Certain species, for instance, exhibit pronounced brittleness and a propensity for fragmentation (e.g., *Eucheuma* and *Gracilaria* spp.; Dawes, 1974, Albright 2021). Additionally, some macroalgal species possess morphological features that facilitate long-distance dispersal, such as air bladders or pneumatocysts (e.g., *Macrocystis*, *Sargassum*, *Fucus spp*.; Mayaca et al. 2005, Hernández-Carmona et al. 2006, Hatchett et al. 2022). For these species, broken or dislodged material may travel hundreds of kilometers and remain adrift for over 100 days (unless washed ashore earlier) (Hobday et al. 2000b, Hernández-Carmona et al. 2006). The disintegration rates of rafting algae are influenced by various abiotic factors (e.g., temperature, sunlight damage, nutrient levels) and biotic factors (e.g., epibiont growth, grazing, thickness of the thalli) (Macaya et al. 2005).

Dispersed material may have the potential to propagate via vegetative fragmentation, with certain species capable of vegetative growth from fragments of any size, for example, *Eucheuma*, *Codium*, *Gracilaria*, *Fucus*, and *Sargassum* species (Dawes, 1974, Chang et al. 2003, Redmond et al. 2014, Albright 2021, Hatchett et al. 2022). Even species unable to propagate vegetatively may still transport spore-bearing tissue through drifting fragments or sporophytes (e.g., *Macrocystis pyrifera*, *Postelsia palmaeformis*, *Nereocystis luetkeana*; Hernández-Carmona et al. 2006, Kusumo et al. 2006, Springer et al. 2010, Gjerke 2019). There are a large number of macroalgal species where reproductive structures have been reported on floating or drifting specimens, with these reported sightings varying from ‘common’ to ‘occasional’ occurrences (see Macaya et al. 2005 for an extensive referenced list of these species). Rafting can be particularly effective for the dispersal of hermaphroditic species, where colonization can be achieved with a single fertile individual (Whitaker et al. 2017, Hatchett et al. 2022).

There has been debate regarding whether drifting algae contributes significantly to local recruitment, as the dispersal of macroalgae typically decreases with distance from the source (Alberto et al. 2011). Nevertheless, long-distance dispersal is believed to play a role in re-establishing macroalgae beds that have experienced local extirpations, enhancing genetic diversity within populations, and diminishing genetic structure among populations (Reed et al. 1988). Many species capable of long-distance dispersal exhibit minimal population genetic structure, even among locations separated by hundreds of kilometers (Valero et al. 2011).

Small- to medium-scale loss of infrastructure

Another form of 'escape' situation for macroalgae involves the small- to medium-scale loss of farm infrastructure containing macroalgae during the grow-out period. This loss may entail the loss of a long line(s), cage(s), basket(s), or the partial or complete loss of seeded lines (smaller lines with young macrophytes wrapped around a long-line). Such incidents might occur sporadically at the farm-site, yet the grow-out cycle would typically continue to harvest. However, this loss of infrastructure could result in significant breakage, dislodgement, or propagule release on or from the lost equipment, depending on when during the grow-out cycle the loss occurred, and where (if known) the equipment was deposited. Some types of infrastructure may be recoverable, potentially allowing for the retrieval of a portion of the biomass. However, the extent of biomass loss would likely vary depending on the duration of detachment from the array and the turbulence encountered during that period. While a range of outcomes is possible, the impact is likely constrained by the relatively smaller scale of this type of infrastructure loss, similar to episodic losses observed in finfish escape scenarios.

Large-scale loss of infrastructure

This final scenario of escape involves the large-scale loss of farm infrastructure due to catastrophic events. Similar to fish aquaculture, such losses may occur as a result of extreme storms, adverse weather conditions, or disasters like collisions, tsunamis, or fires that disrupt the mooring system. However, unlike fish aquaculture, if the infrastructure is retrieved, a portion of the macroalgal biomass may also be salvaged, although the catastrophic event itself, recovery efforts, and/or the duration of detachment after the array loss may increase the likelihood of breakage and dislodgement of the macroalgae. Furthermore, unlike fish aquaculture, there are numerous potential outcomes from this type of loss. The array may remain unrecovered, sinking to depths where the macroalgae are no longer biologically relevant from a genetic dispersal perspective. Alternatively, it may not be recovered but drift into a natural macroalgal bed, or it may be retrieved but with significant biomass loss, or with minimal biomass loss. The scale of the operation will determine the extent of the impact, but unlike with fish, there are more opportunities to mitigate risks through biomass recovery in certain circumstances.

1.2 Escape Risk Factors

In the following section, we now address the second component of risk (Kaplan et al. 1981), how likely is the risk to occur, and specifically in the context of escaped/dispersed organisms, what are the factors that contribute to the likelihood of their interacting with wild populations.

Interactions: Survival

Propagule Survival

The viability of propagules largely hinges on their ability to remain viable over time and whether they possess the capacity for dormancy or suspended growth. It remains challenging to ascertain the persistence of microscopic macroalgal stages in the natural environment (Reed et al. 1988). For many species, spores settle within a few days of release and decrease in density as they move away from the parental macrophytes (Reed et al. 1999, CDFW 2021). Some species have spores that remain viable for only a couple of days (e.g., *Mastocarpus* spp.; Engel et al. 2004, Al-Marayati 2019). However, the spores of other species, such as *Codium* spp. (Churchill and Moeller 1972, Watanabe et al. 2009), and *Ulva* spp. (Shories 1995, Romero 2018), are known to remain viable for extended periods (e.g., from weeks up to 10 months in darkness for these species, respectively). *Gracilaria* spp. not only demonstrate prolonged survival of both haploid and diploid spores but the spores can also endure days of desiccation while remaining viable (Kain and Destombe 1995).

In certain macroalgal species, gametophytes, spores, and sporelings can collectively serve as a 'seed bank' (Dieck 1993, Ladah and Zertucke-González 2007, Bartsch et al. 2008, Springer et al. 2010, Klinkenberg 2020), enabling these species to endure adverse conditions and regrow once conditions improve (Romero 2018). In a study by Dieck (1993) involving 47 Laminarian species, many were capable of surviving for up to 16 months in darkness, with a few enduring 18 months. As reported by Miller (2023), gametophytes of *Laminaria setchelli* may persist for over 18 months in complete darkness. Similar periods of 'dormancy' or suspended growth have been observed in other kelp species (Ladah and Zertucke-González 2007), *Fucus distichus* (Ang 1991), and *Ulva* spp. (Romero 2018). These periods of suspended growth can enhance the survival of macroalgal species by providing additional time and opportunities (e.g., resuspension due to storm activity followed by settling in suitable habitat) for interactions with the natural population.

Fragmented or dislodged macrophyte longevity

The timeframe for fragmented or dislodged material to degrade is crucial in evaluating the potential scale of dispersal and the likelihood of encountering natural populations (Broch et al. 2022). Certain species of macroalgae may persist for extended periods after detachment (Macaya et al. 2005). For instance, kelp have demonstrated the ability to remain afloat for up to three months or even longer after becoming detached (CDFW 2021). However, there are other species characterized by fragile blades or thalli that are prone to tearing and fragmentation (Milligan and DeWreede 2000, Lindstrom et al. 2015, Hiraoka 2021), suggesting that fragments and macrophytes of these species would likely degrade more rapidly upon detachment.

Importantly, if a species can grow or re-establish itself through vegetative propagation, it enhances the opportunity for prolonged persistence in the environment or expansion into areas where populations of the same species exist, consequently increasing the likelihood of encounters (Dawes 1974, Hatchett et al. 2022). For instance, *Gracilaria* species not only propagate vegetatively but also produce free-floating thalli that can develop into extensive beds (Guillemin et al. 2008). In species capable of vegetative growth, the survival of these fragments depends not only on their ability to drift to other locations (as described below) but also on their viability in areas where they may be deposited. For example, *Eucheuma* species are brittle and frequently fragment; however, they thrive at shallow depths up to 3 meters in regions with high visibility (Dawes 1974). The survival rate of fragments from an offshore farm may be lower for this species compared to *Sargassum filipendula*, which can grow at depths of up to 40 meters (Dawes and Tomasko 1988).

Interactions: Probability of Encounter

Dispersal characteristics of macroalgal propagules

The dispersal characteristics of macroalgal propagules vary widely and significantly impact the likelihood of encountering wild populations. For certain macroalgal species, propagules may be released in a manner that promotes retention near the parental macrophytes through mechanisms like the timing of propagule release (Blanchette 1996), mucus on the spores (Fierst et al. 2010), and negative buoyancy (Coleman and Brawley 2005). For instance, in *Fucus distichus*, spores are negatively buoyant and release a sticky substance to adhere to the substrate upon settling (Coleman and Brawley 2005, Hatchett et al. 2022). In some species, these mechanisms can limit dispersal to distances as short as under 2 meters from the parental macrophyte (Paine et al. 2017). Similarly, other species possess mechanisms that enhance the likelihood of propagule dispersal, including motility (Coleman and Brawley 2005), buoyancy (Sahoo and Yarish 2002), and photosynthetic and chemotactic capabilities (Amsler and Neushul 1989). For instance, propagules (swarmer cells) of green algae (e.g., *Ulva* and *Codium* spp.) are motile for a period (minutes to hours) after release, and even after this motility ceases, their extremely small size (4 µm to 37 µm), even in comparison to other macroalgal species, and low sinking rate, facilitates the distribution of these propagules at distances up to 10s of km from the point of release (Churchill and Moeller 1972, Coleman and Brawley 2005, Watanabe 2009, Romero 2018).

Dispersal capacity of fragments or dislodged macroalgae

The capacity of a species to float or raft significantly enhances the likelihood that cultured material may encounter natural conspecific beds. Many macroalgal species may disperse over long distances only infrequently, potentially with reproductive propagules on the released fragments; these sporadic events often coincide with high wave energy events such as storms (Kusumo and Druehl 2000, Wootton and Pfister 2013, Gjerke 2019). Conversely, for other species, rafting may occur more regularly due to physical adaptations that enable frequent long-distance dispersal, such as air-filled structures if a storm, high wave energy, or other physical disturbance dislodges the algae (Macaya et al. 2005, Cheang et al. 2010, Schoenrock et al. 2021).

Accessibility of wild population habitat

The likelihood of encountering the natural population is also influenced by the accessibility of the habitat occupied by the wild population. Certain macroalgal species inhabit a broad range of habitat types (Dawes and Tomasko 1988, Neill et al. 2006), while others occupy more specific and less accessible habitats (Barner et al. 2011, Lindstrom et al. 2015), or habitats with limited available space, as seen in rocky intertidal systems (Kusumo et al. 2006, Paine et al. 2017). For instance, the sea palm (*Postelsia palmaeformis*) inhabits patches in the mid- to upper-rocky intertidal zone where there is intense competition for space from mussels (*Mytilus californianus*) (Kusumo et al. 2006). In contrast, *Codium* species can be found in sheltered bays, estuaries, and semi-exposed coastal areas in both intertidal and subtidal zones, attaching to a diverse array of hard substrates (Neill et al. 2006). Consequently, there is a greater opportunity for conspecific cultured material (e.g., propagules, fragmented or dislodged material) to encounter wild *Codium* across its habitat range compared to encountering wild *Postelsia* with its more restricted and less accessible habitat (i.e., upper intertidal). Furthermore, the likelihood of encounter with the natural population may vary over time as wild beds undergo local extinctions and repopulation due to various environmental (e.g., El Niño-Southern Oscillation (ENSO) cycles) and ecological factors (e.g., sea urchin barrens) (Reed et al. 1988).

Prevailing ocean currents

For macroalgal species, ocean currents play a significant role in determining the encounter rate between cultured material and wild populations. Along coastlines, currents can reinforce biological breaks or facilitate transport between distant locations (Andersen 2013). In the case of *Macrocystis pyrifera* ocean currents are considered the primary influence on genetic connectivity among populations (Alberto et al. 2011). Alberto et al. (2011) emphasized that current-mediated transport between locations is inherently asymmetric and may vary depending on the time of year. Currents between the farm site and the coastline can either push propagules or fragmented/dislodged material towards or away from wild macroalgal beds or lead to encounters with specific populations more frequently than others. These currents may also exhibit seasonal variations. Understanding current patterns concerning the grow-out site(s) and natural populations is crucial for comprehending the encounter rate and predicting the genetic risk posed by cultured material to wild populations.

Interactions: Requirements for Successful Recruitment

When evaluating the likelihood of cultured macroalgae interacting with wild conspecific populations, it is important to consider what is necessary for a species to undergo successful recruitment. Most macroalgal species display complex alternation of generation life-histories, involving both microscopic and macroscopic developmental and reproductive stages before reaching the recognizable or targeted macrophyte stage (McConnico and Foster 2005). For some species, there may exist a strict set of biotic and/or abiotic parameters that must be met for life-cycles to progress towards successful recruitment, while in other species, a broader range of parameters may suffice, enabling easier opportunistic recruitment (Mooney et al. 2018).

Macroalgal recruitment is characterized by high mortality at the spore and early post-settlement phases, though successful completion of the life cycle requires high densities of settled spores

(Reed et al. 1988, Dobkowski et al. 2019). This recruitment may be further limited by stringent requirements in some macroalgal species, leading to successful recruitment only occurring during windows where these conditions are met (Reed et al. 1988). For instance, in *N. luetkeana*, gametophytes could only grow within a narrow temperature window, between 10 and 18°C and sporophytes could only be produced between 10 and 14°C (Weigel et al. 2023). In addition to abiotic parameters, some species may require the presence of other species or specific habitats to complete their life cycle. For instance, in *Pyropia* species, the zygotospores need to settle on shellfish shells, barnacle casings, or calcareous stone (Green and Neefus 2015), and *Hedophyllum sessile* may more successfully recruit on articulated corallines (Barner et al. 2016). These factors likely decrease the likelihood of successful recruitment of dispersed cultured material from offshore aquaculture sites. Furthermore, there are other species where delayed maturity, lower fecundity, or competition for space would further restrict the success of recruitment from conspecific offshore macroalgal culture (Klinger 1985, Barner et al. 2011).

In contrast, other species such as *Codium* and *Sargassum* demonstrate the ability to recruit to a wide range of habitats and exhibit broad tolerance to various abiotic factors (Robledo et al. 2003, Neill et al. 2006, Li et al. 2017), thereby enhancing the likelihood of successful recruitment from the culture of these species. Moreover, certain macroalgae may complete a portion of their life cycle on parental macrophytes and release ready-to-settle sporelings that have already progressed through some stages of the recruitment process (e.g., *S. filipendula*; Redmond et al. 2014). This mechanism may further increase the chances of successful recruitment from dispersed material. As mentioned earlier, some macroalgal species can develop parthenogenic gametes or easily develop and reattach from vegetative fragments (Tano et al. 2015, Tan et al. 2022). In such cases, these species may further enhance their odds of successfully recruiting into conspecific habitats.

Summary of risk factors for macroalgal species

The potential for interaction, and consequently the risk of gene flow from cultured material to conspecific populations, varies among macroalgal species. Although the components contributing to interactions are challenging to quantify, the genetic population structure among natural populations of a given macroalga can provide valuable insights into propagule duration, dispersal mechanisms, and the distance over which effective dispersal occurs (Kelly and Palumbi 2010, Gjerke et al. 2023). Understanding the distance over which gene flow occurs in a species is crucial for comprehending the extent of genetic risk posed by macroalgal cultivation to conspecific populations (Mooney et al. 2018). Furthermore, certain species have been identified as particularly invasive in novel habitats (e.g., *Codium* and *Gracilaria* species; Muha et al. 2019, Lipinska et al. 2023). Even within their native range, cultured versions of these species likely possess a combination of traits that increase the probability of gene flow or interactions with conspecific populations.

1.3 Consequences of Escaped Organisms

The previous sections described the first and second aspects of risk assessment (Kaplan et al. 1981): 1) things that can go wrong, or in this context, the different ways cultured organisms 'escape', and 2) the aspects that contribute to the likelihood of escaped/dispersed organisms interacting with wild populations. The third component of assessing risk from escaped cultured organisms revolves around the potential consequences from those escapes/dispersals.

Genetic Consequences - Macroalgae

While extensive research has focused on the genetic impacts of fish aquaculture on wild populations, there is notably less attention given to assessing the effects of seaweed cultivation on the genetics of wild macroalgal populations (Mooney-McAuley et al. 2016). Particularly lacking are studies addressing the extent of gene flow between cultivated and wild populations and the genetic repercussions of such interactions (Loureiro et al. 2015, Campbell et al. 2019). Many existing studies primarily examine the consequences of introducing non-native species and the role of aquaculture, both directly (via macroalgal cultivation) and indirectly (through cultivation of other species), in facilitating these introductions. The adverse effects of such introductions have prompted a shift towards prioritizing the cultivation of native species in numerous regions globally. However, the dispersal and colonization of introduced species underscore the potential for macroalgae to 'escape' and establish themselves in habitats distant from farm sites (William and Smith 2007). Consequently, it is widely acknowledged that offshore macroalgal cultivation may lead to genetic mixing between cultivated and wild populations (Mooney et al. 2018).

Patterns of gene flow are likely to exhibit variability across species and locations. For instance, reports indicate genetic introgression of cultivated *Undaria pinnatifida* into wild populations in France (where this species was introduced decades ago and has since become established in many European regions) and East Asia, (Grulois et al. 2011, Shan et al. 2018). However, in certain areas such as the English Channel near France, minimal gene flow was observed between cultivated and wild populations of *U. pinnatifida* (Grulois et al. 2011).

Genetic impacts on wild populations stemming from cultivated material may occur without actual genetic introgression. Tano et al. (2015) found that non-native cultivated strains of *Eucheuma* have become established in wild beds surrounding *Eucheuma* farms in Tanzania. Southeast Asian genotypes, cultivated in these farms, now dominate previously wild-type beds in many evaluated sites, resulting in a corresponding decline in genetic diversity of native East African genotypes in the most affected areas. Interestingly, genetic introgression between cultivated and wild *Eucheuma denticulatum* strains was not detected, and this loss of diversity likely occurred due to displacement and/or decline of the wild strains (Tano et al. 2015).

Although there is still much to be understood about the mechanisms of gene flow between cultivated and wild macroalgal populations, and the extent to which it may occur, it is evident that this genetic risk does exist and should be expected in macroalgal culture (Thomson 2021). Gaining a better understanding of the farmed-to-wild gene flow, and the impacts on the genetic diversity, effective population size, and genetic fitness on the wild populations from the cultivated material will be important to determining how to most effectively mitigate negative consequences.

Consequences of dispersed macroalgae on genetic diversity, effective population size and fitness of wild populations

The gene flow from cultivated to wild populations is expected to present similar genetic risks and potential impacts on natural populations, whether it involves fish, shellfish, or macroalgae. Despite the limited documentation regarding the extent of gene flow from macroalgal cultivation into native populations (Valero et al. 2017), it is anticipated that this gene flow will lead to a decrease in local genetic diversity within natural populations (Cottier-Cook et al. 2016, Valero et al. 2017, Hasselström et al. 2018, Grebe 2019, Wilding et al. 2021), potentially undermining locally adapted genetic variation among populations (Grebe 2019). However, existing genetic baselines or studies on genetic population structure in macroalgal species often lack the resolution needed to predict, measure, or mitigate potential impacts on wild populations (Wilding et al. 2021).

Macroalgae exhibit distinct characteristics compared to fish and shellfish, owing to their diverse array of propagation techniques available for cultivating a particular species. Cultivation methods may involve collecting reproductive material from the wild (such as sorus collection), utilizing gametophyte cultures, or propagating through vegetative fragmentation. The level of genetic risk from farm to wild populations will largely depend on the cultivation strategies adopted within the industry (Grebe 2019). Similar to breeding programs in fish culture, propagation strategies employed in macroalgal culture can also potentially reduce the effective population size (N_e) within cultivated lines, thereby potentially diminishing N_e within wild populations following gene flow from farms to the wild (Wilding et al. 2021).

Despite the expectation of large effective population sizes in macroalgae (Thomson 2021), Coyer et al. (2008) reported surprisingly low values (N_e ranging from 73 to 386 and a N_e/N ratio of 10^{-3} to 10^{-4}) for *Fucus serratus* in Norway. This metric of population size is less well understood in macroalgae than in fish. However, comprehending the relationship between effective and census population sizes of macroalgal species will be crucial for predicting the impacts of and recovery from gene flow originating from cultivated material interacting with wild populations.

As macroalgal aquaculture continues to expand, processes such as domestication, selective breeding, or genetic enhancement of cultivated macroalgal lines are expected to emerge to enhance commercially relevant traits and bolster economic returns (Thomson 2021). There are some regions already growing selected strains of macroalgae, for example, *Porphyra spp*. in Japan (Niwa et al. 2010), and *S. japonica* and *Undaria pinnatifida* in China (Li et al. 2007, 2008, Hu et al. 2024), and there is interest in implementing selective breeding in other areas (e.g., *S. latissima* in the northeastern U.S.; Huang et al. 2022). However, the effects of these cultivars on natural populations remain poorly understood, though they could potentially be significant (Campbell et al. 2019), leading to phenomena such as gene swamping, genetic contamination, and maladaptation in affected wild populations (Stévant et al. 2017, Hasselström et al. 2018, Thomson 2021, Wilding et al. 2021).

Losses in genetic diversity and reductions in effective population sizes have the potential to diminish the resilience of wild populations against various environmental shifts, whether biotic or abiotic in nature (Grebe 2019). Similarly, the spread of cultivated genotypes into wild populations may contribute to the genetic erosion of those natural populations (Valero et al. 2017). In a review of the environmental risks linked to macroalgal culture, Campbell et al.

(2019) identified genetic depression of wild populations as one of the few high-risk consequences associated with this form of aquaculture, particularly underscoring it as a potential widespread negative outcome of large-scale seaweed cultivation. It will become increasingly important to develop strategies to predict and mitigate these genetic consequences on wild populations as the industry progresses.

Potential for Mitigation

The impact of gene flow from cultivated to wild populations will vary based on factors such as the scale of the operation, the extent of cultivation activities in a given area, environmental conditions at the farm site and between the farm site and wild populations, and the species being cultured (Campbell et al. 2019). Nevertheless, there are overarching mitigation strategies that can help reduce the genetic risk to wild populations. Among the most crucial strategies is understanding the spatial scale over which cultivated material disperses (Thomson 2021). Mitigation efforts to address this issue may include research aimed at establishing a genetic structure baseline for a macroalgal species lacking such information, developing biophysical models to estimate dispersal distances for spores and fragmented/dislodged material from farm sites, and identifying factors that influence this dispersal (Eggertsen and Halling 2021, Wilding et al. 2021).

Another important mitigation strategy involves sourcing reproductive material from species native to a region and from local populations near the farm site (Mooney-McAuley et al. 2016). This practice is already observed in parts of the U.S. (Kim et al. 2019) and Sweden (Hasselström et al. 2018), among other regions. However, the definition of 'local' requires clarification, and for certain species, determining what constitutes local may not rely on empirical evidence or biological data, such as genetic population structure or dispersal distances (Thomson 2021).

In addition to sourcing material locally, it is recommended that material be collected from multiple locations and individuals near the farm site to maximize genetic diversity in cultured populations. It is advisable not to use farmed sources unless specifically part of a selective breeding program (Campbell et al. 2019, Wilding et al. 2021). Utilizing reproductive material from a larger number of individuals helps increase the effective size of the cultured population and mitigate genetic impacts on wild populations resulting from gene flow with cultivated material (Wilding et al. 2021). For example, although it is not a substantial number of individuals, the Alaska Department of Fish and Game does require that farmers and hatchery managers collect spores from 50 individuals within a 50 km radius of the farm operation.

Long-term storage of cryopreserved macroalgal strains has been suggested as another potential mitigation strategy (Campbell et al. 2019). This method can be employed for cultivated strains to supply commercial seed farms, develop selected lines, and serve as a backup for selected lines in case of contamination or other failures (Loureiro et al. 2015, Wilding et al. 2021). Importantly, it may also be utilized to help conserve the genetic diversity found among wild strains and reduce dependence on wild sources (Valero et al. 2017, Grebe 2019, Wilding et al. 2021).

Sterilization technologies or the cultivation of naturally sterile lines are regarded as highly effective mitigation strategies to limit genetic risks on wild populations, and they are of interest for macroalgal culture (Loureiro et al. 2015, Stévant et al. 2017), including with ongoing research aimed at producing infertile strains of *S. latissima* (S. Nuzhdin, personal communication, 2023; https://dornsife.usc.edu/nlab/grants/). The development of sterile cultivars would mark a significant advancement in mitigating genetic risks associated with macroalgal culture (Campbell et al. 2019).

Culturing and grow-out site practices offer opportunities to implement various mitigation measures. Nursery procedures, such as conditioning (e.g., for *Saccharina latissima*) or acclimatization (e.g., for *Mastocarpus papillatus*), have been shown to decrease incidents of dislodgement and breakage post-outplanting (Buck and Buchholz 2005, Kitzes and Denny 2005). Opting for infrastructure materials less prone to degradation in the marine environment can also lower the frequency of equipment loss (Campbell et al. 2019). However, Campbell et al. (2019) found that with responsible management of cultivation practices and maintenance of gear, accidental losses of infrastructure should be minimal in this type of aquaculture. Removing harvest lines and any remaining cultivation biomass at the end of each season is also important for several reasons, which could both directly and indirectly impact genetic risk to natural populations (Thomson 2021). Removal of gear may be necessary to comply with siting regulations, but it importantly has the added benefit of easier access to lines for routine maintenance. However, in the removal and storage process, it is important to sanitize and properly store the gear to prevent degradation of the materials, which could lead to break down when deployed in subsequent seasons (A. Concepcion, personal comm.).

Harvesting the crop before the onset of reproductive maturity can significantly minimize gene flow from farmed to wild populations (Wilding et al. 2021), although the effectiveness of this strategy will vary among species. For instance, it may be practical to harvest *Alaria marginata* before a significant portion of their biomass becomes fertile, but much less feasible for other species like *Ulva*, which can reach fertility within a matter of weeks. For other species, such as *S. latissimi*, success of such an approach will vary by region, and by when sorus tissues begin to form in those different geographic regions.

Monitoring and research efforts should also be prioritized as proactive measures to detect and quantify the impacts of cultivated material on the genetic diversity and fitness of wild populations (Campbell et al. 2019), including exploring the distance over which these impacts extend. This information will be vital for future permitting and expansion of the industry, as well as for reducing uncertainty in evaluating the risks associated with macroalgal culture (Campbell et al. 2019).

Lastly, while more of a risk avoidance measure than a direct mitigation strategy, the siting of the program is also a crucial consideration in determining the genetic consequences on wild populations. Both abiotic factors (e.g., high wave energy locations that increase the frequency of breakage or dislodgement) and biotic factors (e.g., biogeographic breaks where aquaculture could act as a stepping-stone bridge) at various sites may lead to different levels of genetic risk to wild populations.

2.0 Southern California Candidate Species for Marine Aquaculture

2.1 Geographic range

The north, central north, south, and central south portions of the Southern California bight were considered in these evaluations.

2.2 Macroalgae Candidate Species for Marine Aquaculture

2.2.1 Sugar kelp (Saccharina latissima)

2.2.1.1 Range/Description

S. latissima, commonly known as sugar kelp, is a cold-water kelp species with a wide distribution spanning polar to temperate regions across the northern hemisphere. Its habitat includes the North Atlantic, North Sea, and both sides of the Pacific, from Korea and Japan in the west, to the Bering Sea in the east extending southward from the Aleutian Islands in Alaska to California (https://www.centralcoastbiodiversity.org/sugar-kelp-bull-saccharina-latissima.html; accessed on 10-21-23). In these regions, sugar kelp is typically found along rocky shorelines, growing in the intertidal and upper subtidal zones to depths of 15-30 meters (Bekkby and Moy 2011).

Belonging to the Laminariales (kelp) family, sugar kelp shares common characteristics with other kelp species. It features a branched holdfast that attaches to a stipe, which, in turn, gives rise to a single blade (Klinkenberg 2020). Mature sugar kelp plants may reach an overall size of 4 meters (White and Marshall 2007), with stipes that can grow up to 50 cm in length, and blades that may reach dimensions of up to 3.5 meters in length and 18 cm in width (Klinkenberg 2020). The blades have an elongated shape without a midrib but may display wavy surfaces and edges. In areas with greater wave exposure, the blades tend to be narrower (Diehl et al. 2023).

While populations of *S. latissima* generally exhibit adaptation to local temperature ranges, warmer temperatures exceeding 19°C at the southern end of their range may have adverse effects on growth and reproduction. Warmer conditions might also favor the production of male individuals over females (Klinkenberg 2020). This species is also sensitive to environmental pollutants, where for example, petroleum has been shown to inhibit spore release (Klinkenberg 2020).

Species within the Laminariales family are extensively cultivated worldwide, with China, Korea, and Japan serving as the primary producers of these seaweeds (Purcell-Meyerink et al. 2021). *S. japonica* is a popular food item in Asia, and sugar kelp (*S. latissima*) is gaining traction in the U.S. as an increasingly integral part of the edible seaweed market. Sugar kelp is valued for its fiber content, mineral composition, and vitamin content (Heidkamp et al. 2022). It also finds application in food processing as a source of mannitol, a natural sweetener that gives sugar kelp its name (Diehl et al. 2023). Additionally, it, along with other brown seaweeds serve as versatile industrial thickeners and gelling agents due to their polysaccharide content (i.e., alginate, laminarin, and fucoidan components) (Souto-Prieto et al. 2024), which has found utility in cosmetics production (Purcell-Meyerink et al. 2021). According to Heidkamp et al. (2022), sugar kelp stands out as one of the most promising species for domestic cultivation in the U.S. Currently, both commercial and experimental cultivation of this species are underway in the U.S., particularly in regions like Maine and Alaska (Heidkamp et al. 2022).

Although *Saccharina latissima* is not explicitly listed by the California Department of Fish and Wildlife, the department oversees the commercial harvesting and regulation of all edible and agar-bearing marine algae in California.

2.2.1.2 Biological Characteristics

While sugar kelp is generally considered a perennial species, it can behave as an annual kelp depending on its location within the shoreline habitat. In subtidal regions, it reaches maturity within 15 to 20 months and can have a lifespan of 3 to 5 years (Lee and Brinkhuis 1988, Peteiro and Freire 2013). The maximum size is typically achieved in the second year of growth (Diehl et al. 2023). In contrast, in the harsher intertidal zone, this species often functions as an annual kelp (Lee and Brinkhuis 1988).

Sugar kelp exhibits a heteromorphic life-cycle, characterized by the production of haploid zoospores through meiotic division in sporangia located on the sporophyte blades in patches known as sori (Klinkenberg 2020). These spores are then released from the sori and settle on the substrate. These spores typically tend to settle near the parent sporophytes (Schiel and Foster 2006). These settled spores develop into microscopic benthic haploid male and female gametophytes, which grow vegetatively and eventually start producing gametes. The antheridia produce sperm, while the oogonia produce eggs. Upon fertilization of the egg on the female gametophyte, the zygote begins development and matures into the macroscopic sporophyte (Visch et al. 2019).

The typical dispersal range for spores and gametes is believed to be within a few meters of the parent plants (Schiel and Foster 2006). However, under specific conditions, dispersal events may extend over several kilometers (Mooney et al. 2018). As outlined in White and Marshall (2007), this species has a known ability to swiftly colonize cleared habitats and can become prevalent in those areas within a span of 6 months. Similarly, Andersen (2013) also suggested that large-scale oceanographic processes increased connectivity among *S. latissima* populations, which was again supported by recolonization and colonization patterns in this species. In a different

Laminarian species, *Laminaria hyperborea*, effective propagule dispersal was estimated to reach up to 200 km (Mooney et al. 2018), suggesting the potential for longer-distance dispersal at the propagule stage. Additionally, individual plants may possess the capability to survive and re-establish in suitable habitats if dislodged (White and Marshall 2007).

Plants are believed to become fertile when their blades reach a length of 1 to 2 meters, and under optimal laboratory conditions, this size was reached in 8 months (White and Marshall 2007). The percentage of plants becoming fertile likely peaks at varying times, depending on the location. However, in some regions, *S. latissima* may produce sori year-round (Boderskov et al. 2021). In British Columbia, on the west coast of North America, the formation of spores was observed to peak in the spring and again in the early fall, although it is important to note that individuals forming spores in the fall are descendants of individuals from the previous fall, not offspring of spores released months earlier in the spring (Klinkenberg 2020).

The periods of maximum growth for *S. latissima* can vary with latitude, resulting in delayed growth at higher latitudes compared to more southerly locations (Klinkenberg 2020). Generally, this species grows fastest from late winter to spring (White and Marshall 2007). During phases of rapid growth, sporophytes may grow at a rate of 1.1 cm per day (or higher) and can add up to 1.6 meters in length within four months (White and Marshall 2007). Growth is hindered by lower light levels in the fall, leading to seasonal dieback of the blades during the late fall and winter, often leaving only the holdfast and stipe in perennial individuals. These plants regenerate their blades in the spring (Klinkenberg 2020).

2.2.1.3 Population Structure

While no specific studies on the population genetic structure of *S. latissima* in the eastern Pacific were identified, it is still possible to make inferences about levels of connectivity based on research conducted in other regions. Generally, existing studies reveal a hierarchical structuring of genetic differentiation, with some variation among different regions. However, these patterns may be substantially influenced by environmental factors that either facilitate or limit gene flow between regions or sites. For instance, Breton et al. (2018) identified fine-scale genetic structure among populations along the eastern Maine coastline. Nevertheless, they also discovered no significant differentiation among locations that were twice as distant as those where genetic structure was detected (Breton et al. 2018). In the same region, Mao et al. (2020) detected a biogeographic barrier at Cape Cod, resulting in deeper levels of genetic differentiation that separated populations within the Gulf of Maine from those in Southern New England. A similar trend was observed by Mooney et al. (2018) who identified fairly extensive gene flow among populations in the Irish and Inner Seas on a scale of less than a few tens of kilometers, driven by connectivity from local currents. However, on larger scales, oceanographic conditions such as strong currents or freshwater efflux may act as a barrier to spore dispersal and survival (Mooney et al. 2018). The hydrodynamic modeling conducted by Mooney et al. (2018) demonstrated patterns of spore dispersal that generally aligned with genetic connectivity patterns. Thomson (2021) utilized genome-wide SNP panels (over 12,000 and 9,000 markers) in a seascape genomic approach to investigate genetic connectivity patterns on the west coasts of Scotland and

Sweden. Similar to the other studies, they identified hierarchical structuring patterns with more pronounced barriers to dispersal among certain locations. As with Mooney et al. (2018), when hydrographic dispersal modeling was applied, oceanographic processes were found to significantly influence genetic differentiation at both local and regional scales (Thomson 2021).

Genetic diversity within populations was found to be variable among locations (Guzinski et al. 2016, Luttikhuizen et al. 2018, Guizinski et al. 2020, Thomson 2021), and in some regions, this diversity may be sufficiently low to raise concerns (Diehl et al. 2023). Future genetic studies in this species are poised to benefit from recently developed genomic resources reviewed in Diehl et al. (2023), including a mitochondrial genome assembly (Wang et al. 2016), and the ongoing progress in creating a de novo nuclear genome assembly (https://phaeoexplorer.sb-roscoff.fr/home/).

2.2.1.4 Aquaculture

The cultivation techniques for the Laminariales genera are generally similar, and Purcell-Meyerink et al. (2021) outlined the approach for *L. digitata*, which closely resembles the method used for *S. latissima*. Sori are collected from wild-sourced tissue and then prepared in the lab to facilitate the release of zoospores (achieved through cycles of cold and darkness, or periods of dessication) (Purcell-Meyerink et al. 2021) (a.k.a., the "paper towel" method; J. Hollarsmith, pers. comm.). The spores settle onto a seed string and grow in the hatchery under controlled light, temperature, and nutrient conditions, which allows them to develop into microscopic male and female gametophytes, which subsequently develop and produce gametes that then fuse into zygotes and grow into macroscopic sporophytes on the seed line. Once the sporophytes reach a size of ≥1mm, a processs that takes about 5 weeks, the seed lines are outplanted by wrapping the seed strings around pipes or larger ropes that are anchored on longlines in the ocean environment (Kerrison et al. 2018, J. Hollarsmith, pers. comm.).

Other culturing approaches have been explored, although they remain primarily experimental at this point. One such technique involves applying gametophytes or budding sporophyte stages, instead of spores, to the seed lines (Le François et al. 2023). Cultures containing gametophytes are grown for 3-5 months to achieve the biomass required for seeding the lines, however, following the line seeding, time to outplanting is estimated to take between 30 and 45 days, which is 2 to 3 weeks shorter than approaches seeding spores (Purcell-Meyerink et al. 2021).

Outplanted lines are regularly monitored, with checks every two months, and harvest occus after 5–6 months, typically in April–May (northern hemisphere spring) (Purcell-Meyerink et al. 2021). The timing of the harvest is intentionally set to occur before the water temperature rises, preventing the seaweed from becoming infested with epiphytes. *L. digitata* experiences a longer growing season, with growth slowing in September, whereas in *S. latissima*, this occurs in July (Purcell-Meyerink et al. 2021).

Seeding lines with either spores or gametophyte cultures has its own advantages and disadvantages (Boderskov et al. 2021). In spore seeding, hatchery procedures are generally less demanding, however, this approach does rely on obtaining sori/spores during times when the populations are naturally fertile, which may or may not align with seeding periods (Boderskov et al. 2021). On the other hand, using gametophyte cultures for seeding allows the collection of spores when populations are naturally fertile, and the culture can be prepared for seeding at any time. However, this approach requires the ongoing maintenance of gametophyte cultures, which is time-consuming and carries a risk of contamination (Boderskov et al. 2021).

While there have been notable achievements in controlling the reproductive cycle of *S. latissima* at various laboratory stages (Yarish et al. 2017), ongoing research aims to further refine hatchery and grow-out methods. As outlined in Yarish et al. (2017), there is a keen interest in optimizing the maintenance of long-term vegetative gametophyte cultures spanning multiple years. Additionally, there is a focus on developing techniques for cultures of delayed gametophytes and implementing cryopreservation methods to establish genetic diversity reservoirs for *S. latissima*. Further efforts are being directed towards enhancing methods for rapidly accelerating vegetative growth of gametophyte cultures to attain sufficient seeding biomass (Yarish et al. 2017).

Boderskov et al. (2021) explored the direct seeding of juvenile sporophytes on textile ribbons. Their findings indicated that this approach yielded comparable results to traditional seeding methods on twine when applied in exposed sites in Norway, though outcomes were less favorable in sheltered sites. Kerrison et al. (2018) investigated the use of binders to thicken and prevent suspensions of gametophytes and sporophytes, which were sprayed onto culture lines at a later stage, from being washed off seed lines before they can attach. If successful, this method could save both time and hatchery space. However, as reported in Le François et al. (2023), this method produced mixed results, although it performed better for sporophytes compared to gametophytes.

Preliminary investigations have delved into the feasibility of breeding programs centered on genomic selection. Huang et al. (2023) utilized modeling to demonstrate that genomic prediction, employing a mixed-ploidy additive relationship matrix, holds significant potential for achieving genetic improvement. The biphasic life cycle of kelp provides an advantage, as selection can be applied to both sporophytes and gametophytes. However, this approach faces certain challenges, including the duration required to complete a breeding cycle, limitations on the number of maintainable gametophytes in the laboratory, and the feasibility of executing positive selection on farm-tested sporophytes. Its effectiveness hinges on whether clonal vegetative growth of selected gametophytes can yield sufficient biomass for crosses in the subsequent season (Huang et al. 2022).

Buck and Buchholz (2005) conducted a study on the influence of drag forces on the breakage of cultivated *L. saccharina* (now *S. latissima*) by observing the growth patterns of sugar kelp blades across its life cycle. During the initial grow-out phase, the species exhibited morphological adaptability, producing narrower, streamlined blades in areas with high current velocities. In the subsequent phase, which took place in calmer summer ocean conditions, the blades displayed a greater range of length-to-width ratios. Finally, in late summer, the blades widened, possibly in preparation for sorus development in the fall (Buck and Buchholz 2005).

To mitigate kelp breakage in high-energy environments, Buck and Buchholz (2005) recommended several measures. These included allowing sufficient time for holdfasts to firmly attach to lines, early transplantation of young sporophytes into the sea or subjecting them to current velocities to strengthen holdfasts and stipes, and to promote the development of streamlined blades. It was also advised to ensure that lines are not overcrowded to allow individual holdfasts enough space for attachment. Furthermore, certain culturing systems, such as floating ring systems, may create an artificial canopy, a phenomenon observed in natural kelp canopies, which has been shown to reduce drag on algae positioned more centrally. However, this approach may also reduce growth in centrally positioned plants due to reduced nutrient and gas exchange (J. Hollarsmith, pers. comm.). There are also concerns that a ring system would create shading in the benthic environment, and prohibit the production of other organisms (A. Concepcion, pers. comm.).

2.2.1.5 Considerations on genetic risk to wild conspecifics

The typical range for spore and gamete dispersal from *S. latissima* is believed to be within a few meters of the parent plants (Diehl et al. 2023). Nevertheless, under specific conditions, dispersal events may extend over several kilometers (Mooney et al. 2018). Andersen (2013) proposed that large-scale oceanographic processes contribute to increased connectivity among *S. latissima* populations, a notion supported by recolonization and colonization patterns observed in this species (e.g., White and Marshall 2007). A different Laminarian species, *Laminaria hyperborea,* exhibits effective propagule dispersal estimated to reach up to 200 km (Mooney et al. 2018), suggesting the potential for longer-distance dispersal at the propagule stage.

As reviewed in Broch et al. (2022), throughout the grow-out phase, macroalgal tissue fragments are susceptible to shredding, and entire plants may become dislodged. In offshore cultivation settings, macroalgae face the challenge of coping with violent currents and high waves (Buck and Buchholz 2005). Fragmentation of *S. latissima* is influenced by a combination of factors related to frond size, current velocity, and wave acceleration. Studies by Buck and Buchholz (2005) highlight that drag forces vary depending on these variables, impacting dislodgement and stipe breakage in Laminarians. For macroalgae, such as *S. latissima*, if grown in environments devoid of significant currents, these individuals are more susceptible to dislodgement and breaking stresses compared to algae acclimated to currents (Buck and Buchholz 2005). Their modeling suggests that algae, which have been acclimated to currents at early stages, can exhibit tolerance to these forces, even in storm conditions (Buck and Buchholz 2005). In particular, *S. latissima*, with its flexible stipe, is able to rapidly reorient itself to become more streamlined and reduce drag on the plant (Buck and Buchholz 2005).

Blade erosion is another significant factor in kelp dispersal. The tips of blades commonly experience erosion, resulting in the release of particulate organic matter (POM) into the water column, which may include sori. As reviewed in Broch et al. (2022), as much as 50% of net primary production may be released as POM due to erosion, and reports from cultivated *S. japonica* in China have shown erosion percentages as high as 61% of the cultivated net primary production. In contrast, Norway has observed lower erosion percentages, ranging from 8% to

13% of net primary production when kelp is harvested earlier in the spring, compared to 49% if harvested in the summer (Broch et al. 2022). Although these studies are examining POM, specifically, these findings suggest it could be important to consider blade erosion as a factor in kelp dispersal away from cultured sites.

Broch et al. (2022) conducted simulations revealing a broad spectrum of potential transport distances for kelp particulate matter at cultivated sites, ranging from hundreds of meters to as far as a hundred kilometers away from the release site. The specific distances were contingent on sinking rates, release timing, and location of the farm. The sheltered site exhibited the least dispersion, whereas the offshore location displayed the highest level of dispersion. Specifically, around 80% of the sedimented particulate organic matter (POM) released from the sheltered site traveled less than 1 kilometer from the center of the release site. In contrast, from the offshore site, only 60% of the POM was transported at least 2 kilometers from the center, and approximately 20% was carried as far as 16 kilometers away. These findings underscore the importance of site-specific characteristics in shaping the dispersal of kelp fragments (Broch et al. 2022). Although Broch et al. (2022) used data from *L. hyperborea* for their modeling, the sinking rates of *S. latissima* blade fragments remain to be established. It is speculated that the sinking speeds for sugar kelp may be lower. The duration it takes for kelp fragments to degrade plays a pivotal role in dictating the scale of their dispersal (Broch et al. 2022).

In China, studies have revealed varying degrees of gene flow from spontaneous volunteer populations of *S. japonica* located on cultivation rafts adjacent to growing lines, however, in natural populations further from the culture site (approximately 500 meters away), populations exhibited fewer signs of gene flow from farms to the wild populations (as described in Thomson 2021). This pattern is generally supported by the few genetic studies identified in related species, where gene flow occurs at a smaller scale, but is controlled by oceanographic processes at larger scales, creating in some circumstances strong patterns of differentiation across regions of limited gene flow. As discussed in Mooney et al. (2018), it is important for cultured sites to not act as 'stepping stones' around naturally occurring biogeographic breaks.

These aspects of *S. latissima* taken together suggest that genetic impacts from cultivated-to-wild introgression likely represent at least a moderate level of risk. The lack of information on genetic population structure makes it difficult to determine the scale of regional connectivity among populations. And although more information is needed on the duration of reproductive capabilities in fragmented sugar kelp, oceanographic processes and other biological factors may limit successful reproduction and colonization of dispersed propagules/fragments that hinge on meeting a set of stringent criteria. These criteria include having sufficient male and female gametes for fertilization (although not relevant for spore dispersal), suitable substrate for settlement, low grazing pressure, appropriate temperature and light levels, ample nutrients, and the right current and wave exposure (Mooney et al. 2018). From offshore sites, achieving this combination of factors is less likely for dispersed propagules, with greater potential observed closer to shore (Mooney et al. 2018). Importantly, mitigation steps in culturing approaches may greatly reduce potential for genetic risk to wild populations. As suggested by Stévant et al. (2017) and Mao et al. (2020), locally sourcing seed stock may help preserve natural patterns of genetic structure and diversity. Other approaches, such as earlier harvests of kelp may help to reduce the amount of fragmentation on fronds due to erosion and reduce the percentage of reproductive kelp on the site.

2.2.1.6 References

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2.2.2 *Ribbon kelp (Alaria marginata)*

2.2.2.1 Range/Description

The intertidal kelp species, *Alaria marginata*, is distributed from the Western Aleutian Islands in Alaska to Point Conception in California. This brown algal species can form densely concentrated patches (approximately several hundred individuals/m^2) in the mid- to low rocky intertidal zones, and in some parts of its distribution, such as the Big Sur coastline in California, it is the dominant macroalga in that portion of the intertidal zone (McConnico and Foster 2005).

A. marginata, commercially branded as Wakame due to some similarities to true Wakame (*Undaria pinnatifida*), is gaining increasing commercial culture interest (e.g., https://seaweedmermaid.com/2022/01/06/wakame-the-womens-seaweed/, Stekoll 2019). This species has been cultivated in British Columbia, Canada, and Alaska (Blasco 2012, Stekoll et al. 2017), and has been demonstrated as a successful commercial species in Alaska (Kim et al. 2019). The consumer market for this edible species includes both fresh and dried products, and other uses include feed for molluscan aquaculture, and alginate production for commercial purposes (e.g., cosmetics) (Kraan and Guiry 2000, Garza 2012, Kim et al. 2019).


Image from NOAA

In California, the species is managed by the California Department of Fish and Wildlife (https://wildlife.ca.gov/Conservation/Marine/Kelp; accessed on 10-16-2023). While no specific stock concerns were identified, this species may be susceptible to stress from warming water temperatures (Farrugia Drakard et al. 2023); it is not known whether southern populations may exhibit local adaptation that helps to buffer from effects of thermal stress.

2.2.2.2 Biological Characteristics

A. marginata is an annual macroalgal species that exhibits an alternation of generation life-history with morphologically distinct stages. Macroscopic sporophytes emerge in late winter/early spring and grow rapidly in early spring before reaching a maximum length in August, whereafter blade tips start eroding more quickly than the plant can grow (McConnico and Foster 2005). This species becomes fertile and releases spores in summer with peak spore release occurring in the fall. It is possible that spore release is triggered by increased wave action which may act as a mechanism to increase dispersal of the 10^8 to 10^9 spores each individual sporophyte is capable of releasing during this period (McConnico and Foster 2005). Although not directly observed, timing suggests that the microscopic stages develop and reproduce during fall and winter. Very few sporophytes survive to the following year, largely due to losses over the winter from wave activity displacing individual plants (McConnico and Foster 2005). This species does persist in the same location from year to year, partly because most dispersal is close to the parent plants (McConnico and Foster 2005).

2.2.2.3 Population Structure

In the northeastern Pacific, there has been debate regarding the number of officially recognized *Alaria* species as opposed to a broader *A. marginata* species complex. Nevertheless, complete reproductive isolation has not been achieved for certain members of these species, thus allowing the possibility of hybridization in certain crosses (Lane et al. 2007, Grant and Bringloe 2020). Despite the several phylogenetic studies attempting to address questions of speciation in *Alaria*, only one study has explored population genetic structure in *A. marginata*. Kusumo and Druehl (2000) used AFLPs (amplified fragment length polymorphisms) to examine sporophytes sampled at varying scales (<1m to >100 km apart). Generally, patterns followed an isolation by distance pattern, with genetic similarity decreasing with distance. However, local scale (patch and within-stand) heterogeneity was discovered, while some samples exhibited larger scale (between-stands) homogeneity (Kusumo and Druehl 2000). Temporal genetic signals were also variable in one sampled location, but not the other. Prevailing ocean currents and exposure of sites to wave action are thought to have influenced these genetic patterns (Kusumo and Druehl 2000). While no population genetic studies for *A. marginata* have been publish recently, whole genome sequencing by Bringloe et al. (2021) provided genomic resources that could be used for a more in-depth genomic evaluation of population connectivity in this species in the future.

2.2.2.4 Aquaculture

Cultivation of *A. marginata* involves collecting wild reproductive fronds to obtain sori for meiospore production (Blasco 2012, Raymond and Stekoll 2021). The predictable annual cycle of fertile wild sporophytes would reliably supply brood stock for commercial production (Raymond 2020). These meiospores are then seeded onto lines, where the microscopic male and female gametophytes develop and produce gametes that then form zygotes. These zygotes grow into macroscopic sporophytes, which are subsequently out-planted by wrapping the seed lines around longlines in the ocean-based operation once they reach 2-3mm in size. Raymond and Stekoll (2021) have investigated methods to prolong the life of seeded lines in culture, gaining an additional 36 days by storing the lines at 4°C without compromising subsequent grow-out of *A. marginata*.

The timing of out-planting and harvest varies by region. In Alaska, optimal results were seen when seeded lines were out-planted in October or November and harvested in April (Stekoll et al. 2017), although some operators wait longer to take advantage of longer day lengths for increased biomass (Umanzor and Stephens 2022). Daily growth rates can reach up to 5 percent during peak grow-out (Stekoll et al. 2017), and related species (e.g., *Alaria esculenta*) can grow up to 10 cm per day during peak growth (Kraan and Guiry 2000). However, growth decreases and blades deteriorate in late spring and early summer (Garza 2012, Stekoll et al. 2017). Along California's Big Sur coastline, reproductive sori form from March to April, with the highest sorus surface area occurring from August to October (McConnico and Foster 2005). While winter upwelling provides nutrients for growth, commercial harvest may occur earlier in California than in Alaska due to warmer water temperatures.

While there are no published reports of selective breeding in *A. marginata*, in hybrid offspring of related species, blade width phenotypes may be sex-linked to male gametophytes. With little-to-no genetic research required, if validated, this trait may be of interest for selective breeding across commercially cultivated *Alaria* species (Kraan and Guiry 2000).

2.2.2.5 Considerations on genetic risk to wild conspecifics

As *A. marginata* is an intertidal kelp, there is physical separation in distribution between potential offshore culture locations and this species' natural habitat. Reviewed in Norton (1992), the dispersal range of spores in a closely related species (*A. esculenta*) is limited to about 10 meters from the parent plant. This suggests that propagules from offshore cultivation are unlikely to significantly impact coastal beds. However, a genetic study conducted by Kusumo and Druehl (2000) indicates that longer distance dispersal does occur, although its frequency remains uncertain. This dispersal is believed to happen as propagules get caught in prevailing coastal currents or though breakage and transport of reproductive fronds. Despite lacking a flotation mechanism, broken fronds may still drift over shorter distances.

In Alaska, where commercial cultivation of *A. marginata* occurs, natural populations enter their reproductive phase in summer, yet most cultivated ribbon kelp is harvested in April. This suggests that commercial harvest occurs before the majority of the kelp becomes reproductive, minimizing the chance of spore release from offshore operations. While timeframes may vary in California, a similar harvest schedule is anticipated. However, there remains a possibility of spore dispersion from early maturing sporophytes or from reproductively-capable sori on drifting broken fronds as seen with other species of kelps (i.e., *S. lattissima*).

If propagules from offshore aquaculture operations do manage to disperse and successfully recruit in the intertidal zone, the potential genetic impact remains uncertain. Kusumo and Druehl (2000) discovered genetic patchiness at smaller scales, but also noted some degree of genetic similarity over larger distances. Nevertheless, they observed an overall pattern of isolation by distance. Considering this pattern, and without additional genetic information to further refine patterns of connectivity, obtaining broodstock or sori from nearby populations may be an important mitigation step.

Considering these factors, the risk posed by offshore *A. marginata* aquaculture to natural populations appears likely to be minimal, although occasional successful introductions of cultivated individuals into natural habitats may occur. However, the current health or stock abundance of natural populations was not discerned in literature searches. This remains a crucial aspect that needs clarification for a more accurate assessment of potential risk from dispersed cultured propagules. In addition, substantial advancements in population genetic methodologies warrant a new examination of population connectivity in this species, building on the Kusumo and Druehl (2000) study.

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2.2.3 Giant Kelp (Macrocystis pyrifera)

2.2.3.1 Range/Description

The brown alga *Macrocystis pyrifera* (giant kelp) is the world's largest alga, with sporophytes reaching over 45 meters in length (Johansson et al. 2015). As a key habitat-forming species, *M. pyrifera* supports kelp forests, offering critical ecosystem services to numerous marine species (Rosenthal et al. 1974). This macroalgae grows in temperate and sub-polar waters with rocky substrates, and most abundantly in wave-sheltered areas at depths up to 30 meters (Graham et al. 2007 and references therein, CDFW 2021, Le 2022). In the northeast Pacific, *M. pyrifera* ranges from Baja California to Kodiak Island, Alaska, with the highest abundance along the California coast south of San Francisco (Johansson 2015, Carr and Reid 2016). Kelp surveys are conducted annually by the California Department of Fish and Wildlife (CDFW) and MBC Aquatic Sciences (CDFW 2021).


Image from the California Department of Fish and Wildlife

The species' distribution is highly sensitive to environmental conditions. Events such as El Niño-Southern Oscillations (ENSO), which bring warm water, low nutrients, and high wave energy, can drastically reduce *M. pyrifera* populations over large areas, particularly in Baja California and Southern California (Edwards and Estes 2006). Recovery from such events can take years, resulting in highly dynamic regional biomass estimates (Cavanaugh et al. 2011, Edwards 2019, Leichter et al. 2023). Climate models suggest that southern parts of its range, including Southern California, may become unsuitable *for M. pyrifera* within the next 75 years due to ongoing climate change (Beas-Luna et al. 2020, Gonzalez-Aragon et al. 2024).

In California, *M. pyrifera* is managed spatially in Administrative Kelp Beds, and harvest limitations are administered by the California Department of Fish and Wildlife (CDFW) (https://marinespecies.wildlife.ca.gov/kelp/management/; accessed 10-15-2024). Kelp restoration projects have been done for several decades in southern California and this approach is currently being considered as a strategy for incorporation in kelp management (CDFW 2021).

2.2.3.2 Biological Characteristics

M. pyrifera undergoes an alternation of generations life cycle, with large diploid sporophytes (the visible kelp) producing sporophylls—modified fronds near the holdfast—that release biflagellated zoospores (Rosenthal et al. 1974). These zoospores develop into microscopic male and female gametophytes, which release gametes that fuse to form new sporophytes (Rosenthal et al. 1974). The number of sporophylls produced varies from a few to over 100, depending on factors such as kelp bed density, grazing pressure, and wave activity (Reed 1987). While Brandt (1923) suggested it may take up to nine months for zoospore release, it may happen sooner when plants reach approximately 150 cm in length (Schiel and Foster 2015). Under optimal photosynthesis conditions, *M. pyrifera* can continuously produce sporophylls and sori (Neushul 1963).

Zoospores are typically released near the seafloor and settle within a few meters in slow currents (Reed et al. 1988, Gaylord et al. 2006). In faster currents, spores can disperse over several kilometers (Reed 2004, Gaylord et al. 2006, Le 2022). Despite the dilution effect over distance, successful recruitment has been observed, potentially due to synchronized spore release (Reed 2004). Zoospores settle and germinate within a few days, developing into male or female gametophytes. Because the gametophyte stage is microscopic, successful fertilization requires a high spore density, ideally less than one spore per square millimeter (Reed et al. 1991).

M. pyrifera grows rapidly, with blades extending up to 50 cm per day (Neushul and Haxo 1963, Graham et al. 2007). Sporophytes develop holdfasts that anchor the plant to hard substrates, from which several stipes with blade-bearing fronds grow (Neushul and Haxo 1963). Air-filled pneumatocysts at the base of each blade provide buoyancy, enabling efficient photosynthesis (Rosenthal et al. 1974). While giant kelp can live up to seven years, typical lifespans range from one to four years depending on environmental conditions (Rosenthal et al. 1974, Graham et al. 2007).

2.2.3.3 Population Structure

A recent study by Assis et al. (2023) examined the population genetic structure of *M. pyrifera* along the eastern Pacific coastline (and other locations) using six highly polymorphic microsatellite markers (with 15 to 39 alleles per locus). The study identified distinct genetic clusters in the northeast Pacific, roughly corresponding to: 1) Alaska, Canada, and Monterey, 2) Santa Cruz to Port San Luis, 3) Point Conception, and 4) Channel Islands to Mexico. The Channel Islands and San Mateo Point (near San Clemente) had the highest allelic richness, with the Channel Islands also containing the most private alleles. While the genetic patterns observed in this study may partly reflect range contractions and expansions during and after the last glacial maximum (Assis et al. 2023), the findings also highlight that genetic structuring exists within California. Notably, Southern California appears to be an important source of genetic diversity for *M. pyrifera*.

An earlier study by Johansson et al. (2015), using seven microsatellite markers reveled similar genetic structuring in the northeast Pacific with clusters corresponding to: 1) Alaska and Canada, 2) central California, 3) continental Santa Barbara, 4) Channel Islands, and 5) mainland Southern California and Baja California. While many of patterns were similar between the studies, the focused sampling range in Johansson et al. (2015) identified the Channel Islands as a distinct genetic cluster. As with Assis et al. (2023), allelic richness was also greater in the southerly sampled locations in Johansson et al. (2015).

Importantly, results by Hollarsmith et al. (2020) strongly suggest that populations of *M. pyrifera* in the lower-latitude versus high-latitude California locations exhibit patterns of local adaptation to temperature and pH gradients. Given this species' vulnerability to environmental stressors, such as the severe reductions or depletions in biomass following strong ENSO events (Edwards and Estes 2006, Cavanaugh et al. 2011), preserving the genetic diversity in Southern California is crucial. This diversity may play a critical role in supporting local adaptation and buffering against the anticipated range contractions driven by climate change (Beas-Luna et al. 2020, Gonzalez-Aragon et al. 2024).

2.2.3.4 Aquaculture


Image from the NOAA Monterey Bay National Marine Sanctuary

Giant kelp for commercial use has historically been harvested from wild populations (Le 2022). Since 1916, both giant kelp and bull kelp were harvested at rates of tens of thousands of wet tons per year, but large-scale commercial operations ended in 2006. Currently, small-scale wild harvesting, primarily from surface canopies, yields less than 4,000 wet tons annually, mostly used as feed for abalone farms (CDFW 2021). Large-scale cultivation of giant kelp has been explored globally using longlines and other methods, but environmental requirements for successful growth differ by region, indicating possible localized adaptations (Kopczak 1991). As a result, no universal farming conditions exist, and site-specific environmental and seasonal factors must be considered. General approaches and key considerations for *M. pyrifera* cultivation are outlined below.

Approaches to the commercial cultivation of *M. pyrifera* include sourcing wild-collected sori, which are desiccated to trigger sporulation, or using gametophyte material from vegetative cultures maintained in closed culture systems. Once spores or gametophyte solutions reach suitable concentrations, they are seeded onto lines for further growth (Le et al. 2022). These seed lines are then transferred to nurseries, where juvenile sporophytes grow until they are ready for out-planting into the natural environment. Under optimal culture conditions, juvenile sporophytes can grow to 4–5 mm within 45 days of spore release (Camus and Buschmann 2017). Grow-out methods include shallow-water grid arrays (in sites less than 30 meters deep) and offshore deep-water suspension lines. However, site selection is critical, regardless of the grow-out structure, to minimize warm temperature spikes, wave energy, and the presence of grazers and fouling organisms, while maximizing access to nutrients and light (Camus et al. 2018, Le et al. 2022).

A challenge in *M. pyrifera* grow-out is managing culture lines throughout the growth period. While the first two months are stable, the development of pneumatocysts can abruptly alter buoyancy, and later, blade loss can cause high sinking biomass, potentially collapsing the system. Therefore, continuous adjustments using weights or buoys are required (Camus et al. 2018). Another consideration is that due to the species' susceptibility to environmental stressors, such as ENSO events and temperature anomalies, it will likely be important for commercial operations to maintain a steady supply of seeding material that does not rely solely upon wild populations. This can be achieved through vegetative cultures for short-term needs or through long-term strategies like germplasm banking or cryopreservation to preserve genetic diversity (Le et al. 2022).

2.2.3.5 Considerations on genetic risk to wild conspecifics

Since sori maturation on *M. pyrifera* sporophylls occurs year-round in wild populations, cultivated giant kelp in offshore operations will likely produce and release spores. Spore dispersal generally declines with distance from source plants, with a significant reduction observed within just 3 meters (Reed et al. 1988). Due to low zoospore settlement and high post-settlement mortality, kelp species exhibit high temporal variability in recruitment (Reed et al. 1988). Consequently, recruitment success from released spores is expected to be limited. Furthermore, if cultivation occurs at depths exceeding the species' maximum growth depth (30 meters) (Graham et al. 2007, CDFW 2021), the chances of successful recruitment in natural habitats decrease further. However, turbulent events, such as storms, can resuspend and disperse spores over greater distances (Reed et al. 1988). Since peak *M. pyrifera* cultivation coincides with winter and spring—seasons with frequent storms and high-energy events (Visch et al. 2023)—greater spore dispersal could occur under these conditions. Additionally, dispersal would likely be influenced asymmetrically by prevailing ocean currents, rather than uniformly in all directions (Alberto et al. 2011).

In offshore locations, higher energy levels are expected year-round compared to inshore areas, potentially leading to breakage of kelp plants or even infrastructure failure in extreme cases (Visch et al. 2023). Buoyant kelp species like *M. pyrifera* are known to form floating rafts, which can drift up to 7 km per day and persist for 65 to 109 days, depending on the aging method used (Hobday 2000a, Hernández-Carmona et al. 2006). These rafts result from the breakage or dislodgment of parent plants, with breakage rates higher in winter (23%) and lower in fall (8%) (Hobday 2000b). Along the California coast, kelp rafts typically drift northward from July to January and southward from January to August, with Point Conception serving as a dispersal boundary, allowing some cross-boundary movement from October to January (Hobday 2000b). Studies in Chile and Monterey, California, suggest that while sori and zoospore production may decline after detachment, spores from drifting *M. pyrifera* remain viable and capable of reproduction (Macaya et al. 2005, Hernández-Carmona et al. 2006). However, research indicates that drifting rafts of giant kelp contribute minimally to recruitment or population connectivity (Reed et al. 1988, Reed et al. 2004, Alberto et al. 2011). Therefore, recruitment impacts and genetic flow from drifting kelp are likely limited.

The proximity of a kelp culture site to existing wild kelp beds is critical in assessing the likelihood of interactions between cultured and wild populations. In Southern California, *M. pyrifera* biomass fluctuates significantly due to environmental conditions. Despite periods of decline and gradual recovery, kelp beds along the mainland coast and around the Channel Islands maintain higher genetic diversity compared to northern populations (Klingbeil 2022). This may be due to both high genetic diversity within local populations and the oceanographic transport of dislodged living sporophytes via rafting (Johansson 2015). Southern and Central California also exhibit significant genetic structure, with at least three distinct genetic clusters. Therefore, kelp farms in specific locations could impact one or more of these populations, and seed stock selection should consider oceanographic patterns to anticipate which populations may be most impacted by dislodged material (Alberto et al. 2011).

In cases where gene flow occurs from cultivated to wild kelp populations, the genetic risk is largely dependent on the seed production methods used by the industry (Grebe 2019). Mitigation strategies, such as those recommended by the Alaska Department of Fish and Game, involve sourcing spores from a moderate number of individuals near the operation, which can help reduce potential impacts on locally adapted populations and preserve genetic diversity. For a species whose distribution may already be, or soon be, impacted by warming water temperatures, it is especially important to protect genetic diversity in the southern part of the range for *M. pyrifera*.

The cultivation of *M. pyrifera* likely presents a moderate to high risk of genetic impacts natural populations through the dispersal of cultured material. The extent of this risk is closely tied to the location of the culture site and prevailing oceanographic patterns. To mitigate genetic impacts, one crucial step would be to develop a genetically diverse seed stock that reflects the population most likely to interact with the farmed kelp. This would help preserve genetic integrity and reduce the potential for maladaptation in wild populations. Additionally, advancements like selective breeding of sterile strains, which have drawn industry interest (S. Nuzhdin pers. comm.), offer substantial promise in minimizing genetic risks associated with cultivation.

Several uncertainties remain in cultivating *M. pyrifera*, particularly around farm location and its suitability for growth and containment. Site-specific oceanographic investigations are essential to optimize conditions such as water depth and current patterns that influence growth. Offshore programs need to set longlines at appropriate depths, which could promote optimal growth while minimizing risks related to spore release and dispersal (Bak 2020). Given that *M. pyrifera* releases spores year-round, farm siting should also consider whether spore fertilization can be controlled by manipulating substrate type or water depth. Cultivating in deep waters may reduce the chances of spore fertilization between cultured and wild populations, potentially offering a method to further mitigate risks.

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2.2.4 Bull kelp (Nereocystis luetkeana)

2.2.4.1 Range/Description

Bull kelp, *Nereocystis luetkeana*, establishes extensive macroalgal beds in rocky habitats along the Pacific west coast. While sporophytes of this species can reach up to 40 meters in height, this species is typically found growing at depths under 30 meters (Springer et al. 2010, CDFW 2021). The most common depth range for bull kelp is from the lowest low-tide to 18 meters, as indicated by Carney et al. (2005) and CDFW (2021). The distribution of this brown alga, which is in the order Laminariales, spans from Point Conception, California (southern portion of the range), to Unimak Island, Alaska (northern portion of the range), as outlined by Springer et al. (2010, and references therein). Bull kelp is characterized as an annual species with a typical life-span of one year, occasionally surviving into a second year (CDFW 2021).

Commercial markets for bull kelp are primarily based on human consumption and feed for other aquaculture species (e.g., abalone). Within California, commercial harvest is now exclusively for human harvest (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commercial-Harvest#sonoma-mendocino; accessed 9-18-23). Harvest approaches, which are usually restricted to the upper 2 m of the canopy, are more detrimental to bull kelp, as all fronds (photosynthetic and reproductive tissues) and pneumatocyst (buoyancy mechanism) are located at the top of the individual sporophyte, and plants are likely to sink and die following harvest (Springer et al. 2010).

While historical surveys often failed to differentiate bull kelp from *M. pyrifera* (Springer et al. 2010), recent reports indicate significant declines in this species within certain parts of its range. Notably, Rogers-Bennett and Catton (2019) highlight a drastic reduction, exceeding 90%, in bull kelp canopy since 2014 along a 350 km stretch of the northern California coastline. This decline is attributed to factors such as thermal stress and other ecological stressors, including the impact of sea urchins. Gjerke (2019) describes similar declines in Puget Sound, Washington, and Oregon. The notable reduction in bull kelp populations has prompted increased attention on the species, as evidenced by the Giant Kelp and Bull Kelp Enhanced Status Report (CDFW 2021). In response to these declines, regulatory measures such as harvest quotas and moratoriums on bull kelp have been implemented in specific regions along the California coast (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commercial-Harvest#humboldt-delnorte; accessed 9-18-23). Additionally, a petition was submitted in 2022 for the listing of bull kelp under the Endangered Species Act (ESA), but the listing was ultimately rejected in July 2023 following review.

2.2.4.2 Biological Characteristics

The annual bull kelp fronds generate sori throughout late spring, summer, and fall across their range, with this process typically occurring from late summer through early fall in California (Carney et al. 2005, CDFW 2021). A study by Amsler and Neushul (1989), that surveyed bull kelp from three sites in central California, found that approximately 80% of mature sori detach from frond tissue between 2 hours before and 4 hours after sunrise, a timing believed to optimize sunlight exposure for spores (Amsler and Neushul 1989). Sori on individual plants abscise in synchronous intervals of 2 to 4 days (Amsler and Neushul 1989).

Experimental studies indicate that over 50% of spores are released within the first hour post-abscission, with approximately 94% released within 4 hours. This mechanism is thought to enhance spore distribution across the water column, facilitating both dispersal and local retention (Amsler and Neuschul 1989). Sporophytes produce vast quantities of spores, estimated at 2.3 x 105 spores/cm2 of sori per minute during initial release (Amsler and Neushul 1989). While bull kelp spores are believed to have limited movement, typically spanning tens of meters, this is contingent on water currents and storm activity (Springer et al. 2010). Due to the buoyant pneumatocyst characteristic, there is also potential for the rafting of fronds with mature or maturing sori, potentially dispersing spores much farther than would otherwise be possible (Macaya et al. 2005, Hernández-Carmona et al. 2006).

Once settled onto hard substrates, spores develop into microscopic male or female gametophytes. The duration for which bull kelp gametophytes persist in natural settings remains unknown (Reed et al. 1988), but it is likely that environmental cues such as light and nutrients are necessary for gamete production (Weigel et al. 2023). Some suggest that gametophytes serve as a 'seed bank' for this annual species (Dieck 1993, Springer et al. 2010).


Image from NOAA Fisheries

Under non-optimal conditions, gametophytes do not undergo growth or become fertile (Dieck 1993, Korabik et al. 2023). However, once fertility is achieved, sexual pheromones produced by eggs play a role in attracting sperm, though this process operates on a relatively small spatial scale. In the case of *M. pyrifera* successful recruitment requires spore density to be greater than 1-10 spores/mm, and similar densities are likely necessary for bull kelp recruitment (Springer et al. 2010 and references therein). Following fertilization on female gametophytes, the fertilized eggs develop into sporophytes (CDFW 2021). Observations of juvenile sporophytes in the wild have been documented from late February to early March in the Pacific Northwest, although the timing may vary by region (Carney et al. 2005, Springer et al. 2010).

2.2.4.3 Population Structure

In California, the California Department of Fish and Wildlife (CDFW) oversees all commercial and recreational harvesting activities related to kelp and marine algae, with bull kelp falling under the management of this comprehensive kelp fishery (Springer et al. 2010, CDFW 2021). The management of these species involves spatial regulation across 87 Administrative Kelp Beds distributed along the California coast (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commercial-Harvest; accessed 9-19-23). Each of these beds is subjected to unique harvest limits, leasing options, licenses, closures, and other restrictions (CDFW 2021).

Specifically for bull kelp, additional regulations were recently implemented in 2023 to alleviate harvest pressure on this species. These measures encompassed closures to both commercial and recreational harvesting, along with reduced allowable harvest levels in several Administrative Kelp Bed areas where bull kelp is found (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commercial-Harvest; accessed 9-19-23). It is important to note that the delineation of these Administrative Kelp Beds, extending from the shoreline (mean high tide mark) to the state water boundaries, does not align with any genetic population/stock structure or distinct distribution of kelp beds (CDFW 2021).

Unfortunately, there is limited information available regarding the genetic population structure in *N. luetkeana*, other than a recently published study by Gjerke et al. (2023). The study by Gjerke et al. (2023) involved sampling bull kelp across the species' range at 53 sites spanning from Herring, Alaska, to Cambria, Bay California in 2016 and 2017. Utilizing seven microsatellites for genetic analysis, the study revealed genetic differentiation among the sampled locations, resulting in four "co-ancestry groups" that did not adhere to an isolation-by-distance pattern (Gjerke et al. 2023).

While no genetic differentiation was identified among the sampled sites within California in Gjerke et al.'s study (2023), it is worth noting that the study's ability to detect more subtle genetic structure may have been constrained by the number of genetic markers and samples used in this project. Intriguingly, the highest levels of genetic diversity, as estimated by mean allelic richness, were observed at the northern and southern limits of the bull kelp's range, with central California exhibiting the highest genetic diversity (Gjerke et al. 2023). This was observed despite recent population declines in that region (Rogers-Bennett and Catton 2019). Gjerke et al. (2023) note that similar patterns of maximum genetic diversity in the southern reaches of a species' range have been documented in other seaweed species, such as *Fucus serratus* and *Macrocystis pyifera*, which may be linked to glacial expansion and contraction patterns during the last glaciation period.

2.2.4.4 Aquaculture

Similar to many other kelp species at the present time, bull kelp sori are harvested from wild fronds and then subjected to stressors, such as desiccation and temperature, in a laboratory setting to induce spore release (CDFW 2021). While sori from just a few individual plants can produce enough spores to seed a commercial farm, best practices, as required by agencies like the Alaska Department of Fish and Game (ADFG), involve collecting spores from 50 to 60 individuals within 50 km of the grow-out operation. This approach aims to mitigate potential impacts on population structure across regions and prevent a loss in genetic diversity (https://www.adfg.alaska.gov/index.cfm?adfg=wildlifenews.view_article&articles_id=949; accessed 9-18-23).

The ability to vegetatively propagate kelp gametophytes facilitates the relatively straightforward generation of cultivars, providing reproducible lines for selective breeding and hybridization efforts (Visch et al. 2023). Consequently, selective breeding for specific traits, such as disease resistance, heat tolerance, and seasonal duration, has been initiated for some commercially cultured macroalgal species (Le et al. 2022 and references therein). However, no reports were found describing domestication or selection efforts in bull kelp.

Spores settle onto small diameter twine, where haploid gametophytes develop, produce gametes that combine to form diploid embryos, and subsequently develop into juvenile sporophytes; this entire process spans between 1 and 2 months (CDFW 2021). The seedlines are then out-planted by wrapping the twine around "backbone" ropes on larger longline arrays (Visch et al. 2023). In Alaska, out-planting of the seed lines typically takes place from September through January, with the harvest occurring in May (https://www.adfg.alaska.gov/index.cfm?adfg=wildlifenews.view_article&articles_id=949; accessed 9-18-23). The duration of the seasonal growth for this species depends on nutrient availability. Therefore, while there may be variations in the timing of out-planting and harvest in California and elsewhere along its distribution, a grow-out period of approximately 3 to 7 months is anticipated prior to harvest (Hollarsmith pers comm., https://www.adfg.alaska.gov/index.cfm?adfg=wildlifenews.view_article&articles_id=949; accessed 9-18-23). Given that bull kelp sori mature in late spring (Carney et al. 2005, CDFW 2021), there is potential for spore release from culture operations.

2.2.4.5 Considerations on genetic risk to conspecifics

Considering that sori maturation in the wild population typically begins in late spring (Carney et al. 2005, CDFW 2021), it is plausible that a portion of cultivated bull kelp in offshore operations will produce and release spores. Although data on spore dispersal for bull kelp are limited (Springer et al. 2010), more comprehensive studies have been conducted on other kelp species. Generally, spore dispersal diminishes with increasing distance from source plants, with a significant decline observed within just 3 meters from parent plants (Reed et al. 1988). The distinctive abscission and subsequent sinking of sori in bull kelp may further constrain spore dispersal. Kelp species, including bull kelp, exhibit high temporal variability in zoospore recruitment due to low zoospore settlement and elevated early post-settlement mortality (Reed et al. 1988); low recruit survival has been similarly noted in bull kelp (Dobkowski et al. 2019). Given this information, one can anticipate restricted successful recruitment from released spores. Additionally, if offshore operations occur at depths beyond the maximum growth depth for bull kelp (30m) (Springer et al. 2010, CDFW 2021), the likelihood of successful recruitment in natural settings may be further diminished.

Nonetheless, sporadic occurrences such as turbulent events in the water column (e.g., storms) have the potential to resuspend and/or disperse spores across greater distances (Reed et al. 1988). Given that bull kelp cultivation takes place during the winter and spring months, a period associated with increased storms and high energy events (e.g., waves and wind) (Visch et al. 2023), it is plausible that greater dispersal from operations might occur during these conditions. This effect is likely mitigated in operations situated in deeper waters or locations with elevated sedimentation levels, known to have adverse effects on gametophyte and early sporophyte stages (Carney et al. 2005). Dispersal away from the operation would also not be uniform in all directions but would be influenced asymmetrically by prevailing ocean currents (Alberto et al. 2011).

In offshore locations, elevated energy levels are anticipated throughout the year compared to inshore areas, potentially resulting in breakage of kelp plants or the kelp line infrastructure in extreme cases (Visch et al. 2023). Buoyant kelp species, including bull kelp, are known to form floating rafts that can drift up to 7 km per day and persist for 65 to 109 days, contingent on the aging method applied to the kelp (Hobday 2000a, Hernández-Carmona et al. 2006). These rafts originate from the breakage or dislodgment of parent plants, with studies on the closely related *Macrocystis* species indicating higher loss from breakage in winter (23%) and lower in fall (8%) (Hobday 2000b), a trend that may be mirrored in bull kelp. Kelp rafts along the California coast generally exhibit northward dispersal from July to January and southward from January to August, with Point Conception acting as a seasonal dispersal boundary, allowing some movement across it from October through January (Hobday 2000b). Studies on rafting giant kelp in Chile and Monterey, California, found that while sori and zoospore production may decrease after detachment, the spores remain fertile and functionally reproductive in *Macrocystis* (Macaya et al. 2005, Hernández-Carmona et al. 2006). Although these studies are based on *Macrocystis*, the impact of sorus abscission and spore fertility in bull kelp after detachment remains uncertain. For *Macrocystis*, evidence suggests that drifting rafts contribute minimally to recruit density or population connectivity (Reed et al. 1988, Reed et al. 2004, Alberto et al. 2011); thus, it is reasonable to infer that recruitment impacts and genetic flow from drifting bull kelp would likely be limited.

In the event of gene flow from cultivated kelp to wild populations, the level of genetic risk is closely tied to the seed production strategies employed by the industry (Grebe 2019) and the patterns of dispersal influencing gene flow away from the cultured site (Alberto et al. 2011). Mitigation measures, akin to those outlined by the Alaska Department of Fish and Game, involving the collection of spores from a diverse array of individuals in close proximity to the operation, can effectively reduce potential impacts on locally-adapted populations and genetic diversity. Although not extensively characterized, a single study analyzing the genetics of bull kelp across its Californian range identified individuals belonging to a single co-ancestral group (Gjerke et al. 2023). If corroborated by additional research, this finding may allow for sourcing sori from a broader area around the operation without jeopardizing locally-adapted populations, however, it is also important to consider that California locations exhibit greater genetic diversity than other regions within the species range, underscoring the importance of prioritizing the preservation of this diversity, particularly in a species that has already faced considerable population declines. It is also important to note that cultivating bull kelp in the Southern California Bight would constitute a range expansion for this species. Technological advancements, such as sterile strains, which have garnered interest from the industry (S. Nuzhdin pers comm.), hold significant promise in substantially mitigating concerns related to genetic risk.

There is a notable data gap for bull kelp, particularly in the absence of published genetic or genomic studies comprehensively addressing population structure across its range. The sole identified genetic study to date (Gjerke et al. 2023) utilized a limited number of markers, potentially lacking the power needed to discern fine-scale population signals (e.g., Jeffrey et al. 2018 vs. Bradbury et al. 2018). To establish robust seed sourcing guidelines, future research should include obtaining more detailed genetic or genomic information for bull kelp, especially in the southern part of its range. Assessing the temporal stability of any identified population structure signals and thoroughly characterizing genetic diversity throughout the California range of bull kelp are also imperative.

Another data gap pertains to the fact that most studies on the significance of rafting kelp have focused on Macrocystis. Understanding the impact of rafting on bull kelp, given its unique sorus abscission, becomes crucial for an industry seeking grow-out during periods when breakage is most likely to occur. Finally, similar to most passively distributed organisms, a comprehensive understanding of ocean currents at and around the operational site is vital for predicting regions that may be impacted, or disproportionately impacted, by the gene flow of cultured kelp into wild populations.

Based on the information summarized above for bull kelp, dispersal of cultivated material away from offshore operations is likely to have a low to moderate impact on natural populations. While this species is capable of rafting, sori abscission and the rapidity at which spores are released are an important consideration. In addition, while the gametophyte stages may be vegetatively cultured in vitro, this type of clonal propagation does not appear to be common for this species in vivo. Colonization, even in areas previously occupied by this species, appears to be slow. Based on the only genetic study available, all of California appears to belong to one co-ancestry group, although genetic surveys over a finer scale with higher genetic resolution are strongly recommended. While these factors may point towards a low impact on natural populations, the diminished populations of bull kelp beds in California, and the high level of genetic diversity in the Central California region, do warrant extra protection of these populations and genetic resources, and also makes them more susceptible to impacts from introgression of cultured genetic material.

The information summarized above on bull kelp suggests that the dispersal of cultivated material from offshore operations has the potential for a low to moderate impact on natural populations. Despite the ability of this species to form floating rafts, the abscission of mature sori and the speed at which spores are released, may limit their ability to disperse to new areas. In addition, while the gametophyte stages can be cultured vegetatively *in vitro*, this form of clonal propagation appears to be uncommon in kelp species *in vivo*, which further limits the colonization potential for this species. The colonization rate, even in previously occupied areas, appears to be slow, and may reflect similar limitations to colonization from cultured material. While these factors point towards a lower potential impact of cultured material on natural populations, the diminished bull kelp biomass in California, coupled with the high genetic diversity in this region, indicate the need for additional care and protection of these populations and genetic resources. Furthermore, these aspects make the populations more vulnerable to potential impacts from the introgression of cultured genetic material, and as a result, warrant the "low to moderate" potential impact. A genetic survey conducted over a finer scale with higher genetic marker resolution will be very important for this species if commercial culture is planned in this region.

2.2.4.6 References

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2.2.5 Bladderwrack (Fucus distichus)

2.2.5.1 Range/Description

Fucus distichus, previously known as *F. gardneri*, is a prevalent brown alga inhabiting the high- and mid-intertidal zones along the temperate Pacific North American coastline. This perennial alga, which may live for 2 to 3 years (Ang 1991b), has a distribution that spans from Santa Barbara, California to Alaska (Wright et al. 2004, Miller 2023). Rising temperatures may lead to an expansion of this species' northern range (Jueterbock et al. 2016). The species features bilaterally flattened fronds with a central midrib extending from the thallus, which is anchored to the substrate by a discoid holdfast (Hatchet et al. 2022). While individuals commonly attain heights of 25 to 30 cm, the morphology of this species displays considerable variability depending on the level of wave exposure. Specifically, plants in wave-exposed areas tend to be shorter with narrower blades and receptacles, while those in protected sites have larger thalli with wider blades and receptacles (Hatchett et al. 2022). Recent research suggests that these morphological distinctions arise from the tattering of plants of varying sizes by wave forces, rather than being due to phenotypic plasticity resulting from genotypic variation (Hatchett et al. 2022). Additionally, the growth, reproduction, and survivorship of this species exhibit variability across its range, during different times of the year, and at various locations within the intertidal zone (Wright et al. 2004).


Image from NOAA Fisheries

Fucus species may serve various purposes, including as food sources, ingredients in food supplements, and additives in livestock and pet feed (FAO and WHO 2022). They are also employed as fertilizers in coastal areas (Hatchett et al. 2022). The *Fucus* genus, renowned for its high polysaccharide and alginate content, offers potential for the extraction of these valuable compounds (Knoop et al. 2022). Moreover, *Fucus* species contain compounds like phlorotannins and fucoxanthin, which are utilized for specialized cosmetics and as biostimulants (Meichssner et al. 2021). Notably, *F. distichus* has demonstrated significant chemical antioxidant activity and a remarkable ability to scavenge reactive oxygen species (ROS), which is also of commercial interest (Kellog and Lila 2013).

In California, the management and harvest of *F. distichus*, like other algal and kelp species, are overseen by the California Department of Fish and Wildlife (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commonly-Harvested-Marine-Algae; accessed 10-20-2023). This particular species ranks as the 6th most frequently harvested kelp species in California (Kübler et al. 2021).

While generally abundant, factors like eutrophication and environmental contaminants have been associated with population stress and declining abundance in *Fucus* species (Whitaker et al. 2017, Meichssner et al. 2021, Knoop et al. 2022).

2.2.5.2 Biological Characteristics

The monoecious *Fucus distichus* undergoes reproduction in specialized structures called conceptacles, located at the tips of its thalli (Ang 1991). Fertile plants can be found year-round, and individual thalli may maintain their reproductive capacity throughout the entire year (Ang 1991). Within the conceptacles, eggs and sperm are formed in structures called oogonia and antheridia, respectively, and these gametes are then released onto the surface of the receptacles (Ang 1991). Rates of fertilization are high for this species, ranging from 90% to 100%, with settlement occurring in laboratory settings within 4 to 6 hours after fertilization (Coleman and Brawley 2005, Wright et al. 2004).

On a single plant, branches reach reproductive maturity at different times, and plants may reproduce over several successive years (Ang 1991b). Mature plants develop distinctive air bladders at their apices as a sign of reproductive readiness (Hatchett et al. 2022). In *F. distichus*, size (greater than 9.5 cm) has proven to be a more accurate indicator of reproductive capacity compared to age alone (Ang 1991). Ang (1991) reported reproductive peak times occurring in the fall and winter of each year, though these peak periods vary by location. The potential egg production, determined by the number of eggs produced per conceptacle and the number of conceptacles per unit area of receptacle, is size-dependent (Ang 1991). Receptacle formation and embryonic development are primarily regulated by photoperiod rather than temperature (Jueterbock et al. 2016), although warmer temperatures and higher saline environments have been associated with increased output and fertilization success in receptacles (Wood 2023).

Dispersal of gametes in *Fucus* species is relatively restricted. Sperm have a short lifespan, and are primarily attracted to eggs within millimeter distances, leading to limited dispersal potential (Coleman and Brawley 2005). Propagules are released within a meter from the substratum, and zygotes, which are negatively buoyant, secrete a sticky substance to adhere to the substrate (Coleman and Brawley 2005, Hatchett et al. 2022). Eggs and larvae experience high mortality rates during dispersal, and their survival rates vary considerably both in space and time (Ang 1991). The survival and emergence patterns of macrorecruits (visible after 3 to 4 months) may be distinct from those of microrecruits or may not align with the prevailing reproductive patterns at earlier stages (Ang 1991). Additionally, sporelings of *Fucus distichus* can exhibit prolonged growth, potentially remaining in an embryonic stage for 5 to 6 months (Ang 1991).

Fucus species are known for their capacity for both sexual and asexual reproduction, with asexual reproduction through fragmentation being particularly common in populations located at the periphery of their habitat range (Hatchett et al. 2022). For instance, populations of *F. radicans* in the northern Baltic region can range from entirely sexual to over 90% monoclonal (Hatchett et al. 2022). In the Baltic Sea*,* *F. vesiculosus* has been observed to engage in vegetative propagation more frequently in wave-exposed sites (22%) compared to sheltered sites (4%) (Malm and Kautsky 2004). Although this mode of reproduction may lead to a reduction in genetic diversity, it does not necessarily lead to a reduction in fitness (Preston et al. 2022). Interestingly, in certain locations, *F. vesiculosus* can exist in either an attached form, which primarily undergoes sexual reproduction, or a free-floating asexual form (Hatchett et al. 2022). Furthermore, detached branches have the ability to reattach to a substrate via rhizoids which can then develop into male and female thalli; this phenomenon can give rise to extensive clones (e.g., a female clone in the Baltic was documented to be over 550 kilometers long) (as reviewed in Hatchett et al. 2022).

Long-distance dispersal, facilitated by the rafting of fertile *Fucus*, likely increases connectivity among populations, especially for species equipped with air bladders, such as *F. distichus* (Hatchett et al. 2022). Floating algae that share a similar morphological structure and reproductive phenology with *F. vesiculosus* have demonstrated high floating persistence (Rothäusler et al. 2020). Genetic analyses have provided evidence for successful rafting in hermaphroditic *Fucus* species (Coleman and Brawley 2005) and through detached branches (asexual reproduction) (Hatchett et al. 2022). Rafting may play a particularly important role in the dispersal of hermaphroditic species, as successful colonization can be achieved with just one fertile individual, allowing for stepping-stone dispersal across longer distances (Hatchett et al. 2022). As documented in Whitaker et al. (2017), genetic analyses have supported the occurrence of selfing in *F. distichus*, which is a hermaphroditic species.

2.2.5.3 Population Structure

Several genetic studies have explored connectivity among populations of various *Fucus* species. For example, in *F. ceranoides*, Neiva et al. (2012) observed diverse levels of divergence and population structure across spatial scales. It was noted that migration alone was insufficient to counteract differentiation due to drift or the colonization of new sites (Neiva et al. 2012). In a separate study focused on *F. spiralis* in Maine, Coleman and Brawley (2005) detected low levels of genetic differentiation among sites, even ones separated by distances of up to 500 km. Interestingly, genetic structure did not exhibit a correlation with distance. Coleman and Brawley (2005) also suggested the occurrence of selfing and/or inbreeding in this species. They theorized that sporadic recruitment or colonization events contribute to the low levels of genetic structure, while the presence of drifting algal rafts increases gene flow between locations on a broader scale. These findings imply that gene flow in this species occurs across extensive spatial ranges, hindering the development of strong spatial genetic structure (Coleman and Brawley 2005). To further complicate genetic structure patterns in this genus, the results from Malm and Kautsky (2004) suggest that a substantial proportion of holdfasts comprise more than one genetic individual, likely due to fragmentation and reattachment. This phenomenon poses challenges for calculations of population structure and other estimations of population dynamics, such as effective population size (Malm and Kautsky 2004).

For *F. distichus* specifically, Coleman and Brawley (2005) reported genetic structure at smaller spatial scales, ranging from centimeters to meters. However, in a study conducted by Whitaker et al. (2017), based on microsatellite analyses of *F. distichus* samples collected from 11 sites across the central and eastern regions of San Francisco Bay, a different pattern was detected. Their findings indicated that populations exhibited low genetic diversity and limited levels of geographic population structure. Similar to *F. spiralis*, Whitaker et al. (2017) found a higher-than-expected frequency of homozygotes which suggested a high degree of inbreeding in *F. distichus*.

While these studies indicate that discerning patterns of connectivity in *F. distichus* and other *Fucus* species may be challenging, forthcoming genetic studies on *F. distichus* may benefit from newly developed genomic resources including a reference genome and transcriptome for this species (Hatchett et al. 2021; https://phaeoexplorer.sb-roscoff.fr/home).

2.2.5.4 Aquaculture

While interest in the cultivation of this species is growing (Roleda and Hurd 2019, Meichssner et al. 2021, Knoop et al. 2022), there is currently limited information available on commercial cultivation practices for this species. However, some experimental *Fucus* aquaculture was established in the Kiel Fjord in 2015, focusing on two species, *F. vesiculosus* and *F. serratus*, and this initiative provides some insights into feasible practices and challenges in culturing these species (Meichssner et al. 2021).

There are two potential mechanisms for the culturing of *Fucus* species: asexual vegetative propagation and sexual seed production. In vegetative propagation, small vegetative apices are cut from fronds and allowed to grow unattached in drifting baskets or net cages. At harvest, vegetative apices are cut from the cultivated fronds and used as seedlings for the next growing period, eliminating the need for more intensive lab culture (Meichssner et al. 2021). However, when vegetative pieces were collected from formerly attached forms of *Fucus*, fertility (i.e., receptacle formation) became problematic, as this terminated growth and degraded the tissue after gamete release (Meichssner et al. 2021b). This led to minimal overall growth or even biomass loss for these two species. Despite being cultured vegetatively for 2 years, fertility did not decrease. In contrast, using a naturally unattached population, which is largely infertile in the wild, resulted in almost entirely vegetative production (with only 2 to 3% fertile apices). Ongoing experimentation is being conducted in this regard (Meichssner et al. 2021b).

Cultivating *Fucus* species using sexual production would involve the production of gametes and fertilization of zygotes followed by seeding the zygotes onto cultivation ropes, a technique similar to what is used for the cultivation of kelp (order Laminariales) species. Well-established protocols for the production of *Fucus* zygotes, as referenced by Meichssner et al. (2021), indicate that this approach is indeed feasible for *Fucus* species. While the potential loss of genetic diversity is a concern in any cultivation program, sexual seed production would facilitate easier introduction of genetic variation into the breeding program. It is worth noting an important distinction in seed line production between *Fucus* species and other species like *Laminaria*. In other species, spores actively swim towards a submerged seed line. However, for *Fucus* species, non-mobile fertilized zygotes must be capable of sinking onto and attaching to the seed lines (Meichssner et al. 2021).

Regardless of the chosen method, Meichssner et al. (2021) recommend using local populations to prevent the introduction of non-native *Fucus* genotypes.

2.2.5.5 Considerations on genetic risk to wild conspecifics

Fucus species present intriguing aspects to consider when assessing genetic risks to wild populations from cultured sources. While considered abundant along portions of its coastal range, sensitivity to eutrophication in certain regions was noted (e.g., Whitaker et al. 2017). Reproductive individuals can be found year-round, and reproductive capacity is determined by size rather than age (Ang 1991). Alongside sexual reproduction, including selfing, these species are also capable of asexual vegetative reproduction (Hatchett et al. 2022). Although spore and gamete dispersal are limited in *F. distichus* and other *Fucus* species, rafting of fragments, including fertile thalli, is considered a key dispersal mechanism (Coleman and Brawley 2005). Gas-filled bladders in mature apices in several *Fucus* species, including *F. distichus*, are believed to enable long-distance dispersal. Studies have indicated that the floating time of *F. vesiculosus* ranges from 3 weeks to 3 months in the Baltic Sea during spring and summer (Rothäusler et al. 2020). Transport modeling suggests that floating times of 20 days could transport fragments distances of about 50 km, whereas 100 days could extend that range to over 200 km (Rothäusler et al. 2015). However, *Fucus* thalli with reproductive receptacles are more likely to disintegrate and sink, potentially indicating a tradeoff between fertilization success and dispersal distance (Rothäusler et al. 2020). Even if fertilization occurs, post-settlement survivorship in *F. distichus* embryos is notably low, ranging from 0 to 16.7% after one month (Wright et al. 2004).

Genetic analyses support the likelihood of fairly frequent long-distance dispersal in *Fucus* species. Most individuals of *F. spiralis* examined at each site in a study were migrants from another population (Coleman and Brawley 2005). Genetic studies also provided evidence for inbreeding and selfing within populations (Whitaker et al. 2017). Patterns of population connectivity in *F. distichus*, and other *Fucus* species, show low levels of smaller-scale genetic structure, with limited increase in genetic structure over larger spatial scales, likely due to dispersal of fragments or plants.

In summary, successful dispersal of *F. distichus* from offshore aquaculture into wild populations is likely based on its rafting ability which is enhanced by gas-filled bladders, its capacity for self-fertilization, and its ability to vegetatively reproduce. Genetic evidence supports that dispersal over distances greater than those considered for offshore aquaculture occurs frequently enough to prevent genetic structure over those scales. For this species, considering source populations for seed/fragment material, and the method of culturing (vegetative versus seed), are crucial aspects to be considered, with attention to potential impacts on genetic diversity in wild populations when dispersal occurs.

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2.2.6 Southern Stiff Stiped Kelp (Laminaria setchelli):

2.2.6.1 Range/Description

Laminaria setchellii, commonly referred to as southern stiff-stiped kelp is a perennial brown kelp inhabiting the coastal regions of the northeast Pacific. Its distribution spans from the Aleutian Islands in the north to Baja California, Mexico, in the south (Garza 2005, Klinkenberg 2020). Occupying a habitat characterized by strong wave action, this species resides on rocky substrate within the intertidal and subtidal zones, where it may form dense stands (Klinger 1985). The thickness of its blades is believed to contribute to its resilience in this high-energy setting (McLean 1962, Bartsch et al. 2008, Starko et al. 2018), and plants of a similar age from more exposed sites had longer and thicker stipes than plants in protected sites (Bartsch et al. 2008).

Image from California Dept. of Fish and Wildlife

L. setchellii is distinguished by its rigid stipe and a single blade supported by a basal meristem, which it retains throughout the year (Starko et al. 2018). The species undergoes a distinctive growth pattern, experiencing rapid growth in late winter and early spring, followed by a period of slow growth and blade erosion from late summer to early winter (Klinger 1985, tom Dieck 1991, Bartsch et al. 2008, Starko et al. 2018). This growth pattern often results in the discernible presence of a constriction between the old and new blade (Miller 2023). The seasonal growth of *L. setchellii* is closely tied to the availability of environmental nutrients (Starko et al. 2018).

Starko et al. (2018) have found that variations in carbohydrate content and composition play a pivotal role in the cell wall thickening and mechanical reinforcement observed in the overwintering tissues of *L. setchellii*. Cross sections of the stipe exhibit visible annual growth rings, attesting to the potential longevity of individual plants, which can live for 18 to 20 years (DeWreede and Klinger 1988). This extended lifespan contributes to the species' relatively slow response to environmental changes, both in positive and negative directions (Watson 2014).

In terms of physical dimensions, stipes can extend up to 2.7 feet in length with corresponding blades reaching lengths of up to 31 inches and widths of 10 inches (Klinkenberg 2020). In deeper waters, stipes may grow even larger to 5 feet in length, and the blade area may cover 6 square feet (McLean 1962). Blades frequently division into narrow straps originating from a common base (Garza 2005).

Laminaria species play a significant role in the global seaweed production sector (Purcell-Meyerink et al. 2021). The market for their carbohydrate extracts, including fucoidan and alginate, is primarily directed towards applications in food or feed additives (Starko et al. 2018, Purcell-Meyerink et al. 2021).

In California, similar to other kelp species, the management and harvest of *L. setchellii* fall under the jurisdiction of the California Department of Fish and Wildlife (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commonly-Harvested-Marine-Algae; accessed 10-20-2023).

2.2.6.2 Biological Characteristics

L. setchellii, like other kelp species, undergoes an alternation of heteromorphic generations. It begins with macroscopic diploid sporophytes that release male and female zoospores. These zoospores then mature into haploid gametophytes, which in turn generate gametes which when fertilized to form a zygote. This zygote ultimately develops into a new sporophyte, thereby completing the life cycle (Klinkenberg 2020).

In *L. setchellii*, which is a perennial and iteroparous species, certain life-history characteristics have been observed. These include lower annual fecundities, delayed maturity, and an increase in reproductive effort with age (Klinger 1985). Typically, *L. setchellii* becomes reproductive in the second or third year, although a few individuals may develop sori in the first year (De Wreede and Klinger 1988). Klinger (1985) found a correlation between age and the likelihood of sorus production in a given season, but not between age and sori productivity. As sori develop, the growth rates of the sporophytes decrease temporarily but then increase again after sporangia develop (tom Dieck 1991).

Reproduction in *L. setchellii* is primarily regulated by photoperiod, with the transition from longer to shorter daily photoperiods triggering the formation of sori approximately 6 to 14 weeks after the shift (tom Dieck, 1991, Bartsch et al. 2008). While sorus production is more pronounced during the summer and fall months, it can occur year-round (Klinger 1985). These sori develop as dark, irregular patches directly on the vegetative blades, either on new blades after growth cessation, or on older, non-growing second-year blades (Klinger 1985, De Wreede and Klinger 1988, tom Dieck 1991, Klinkenberg 2020).

In laboratory-grown sporophytes of *L. setchellii*, there was an 11 to 14-week period between the appearance of sori and their release (tom Dieck 1991). Bartsch et al. (2008) noted that sorus allocation, defined as the proportion of vegetative blade transformed into sori, ranges from 1 to 37% in *L. setchellii*. This aligns with Klinger's (1985) estimate, which found an upper mean of approximately 30% of blade surface area devoted to sorus production. As reported by Bartsch et al. (2008), each individual annually produces approximately 3.6–3.8×10^8 meiospores.

As Miller (2023) reports, gametophytes may persist for over 18 months in complete darkness. This suggests that an *in vivo* seed bank may exist for this species, which could provide resilience to adverse conditions, such as warm water periods, where water temperatures exceeding 63°F inhibit egg production (Bartsch et al. 2008, Klinkenberg 2020).

2.2.6.3 Population Structure

At present, there are no published population genetic studies focused on *L. setchellii*. Nonetheless, the longevity of this species will likely impact genetic connectivity patterns along the coast. Klinger (1985) demonstrated varied age structures within *L. setchellii* populations, ranging from sites dominated by 12-year-old plants to others dominated by 2- and 3-year-old plants. Aside from instances of rapid colonization following physical disturbances, the species' longevity, with numerous reproductive seasons, is likely to contribute to genetic homogenization among neighboring beds. However, genetic signals from strong recruitment years may be disproportionately represented in populations, and could be further perpetuated through subsequent age-classes. This possible dynamic does not preclude the possibility of a gradual increase in genetic differentiation over distance, although settlement from rafting fertile tissue may modify this pattern.

2.2.6.4 Aquaculture

While there is no published culture information for *L. setchillii*, parallels may exist with the cultivation of other *Laminaria* species. Purcell-Meyerink et al. (2021) describe the cultivation of *L. digitata*, which relies on harvesting wild-sourced sori tissue, which is then brought back to the laboratory for zoospore release and gametophyte cultivation. These gametophytes, along with developing sporophytes, are then sprayed onto seed lines, where juvenile sporophytes mature. This process takes approximately 3 to 5 months (Purcell-Meyerink et al. 2021).

As reported in Purcell-Meyerink et al. (2021), deployment involves wrapping the seed lines around larger anchored and floated longlines. Out-planting for the related *L. digitata* occurs between October and December, with harvesting typically taking place 5 to 6 months later in spring. The timing of this harvest is designed to occur before temperatures rise, and before the corresponding increase in epiphytes (Purcell-Meyerink et al. 2021). While the specific adaptations for *L. setchillii* remain uncertain, culture time-lines targeting the rapid growth periods in winter and spring may be similar.

2.2.6.5 Considerations on genetic risk to wild conspecifics

The genetic population structure and overall health of *L. setchellii* populations across their range, as well as the methodology for offshore cultivation of this species, represent significant gaps in the understanding of this kelp. These aspects are essential for assessing the potential effects of interactions between cultured material and wild populations.

Like for other kelp species, dislodgement and breakage of plants during offshore cultivation of *L. setchellii* are important considerations. This kelp is characterized by its robust, stiff stipe that maintains its upright position in the water. However, in offshore conditions, where drag forces are determined by blade length and surface area (Buck and Buchholz 2005), these stipes may impede reconfiguration and amplify drag forces experienced by the holdfast or stipe (Starko and Martone 2016). Consequently, this could increase the likelihood of dislodgement and breakage during offshore cultivation of this kelp.

Dayton et al. (1984) frequently found fertile fragments of various kelp species (including *Laminaria spp*., *Macrocystis*, *Eisenia*, and *Pterygophora*) within kelp drifts. This pattern persisted even when drift traps were positioned over 2 km away from the nearest kelp beds. However, for successful fertilization and colonization, a substantial number of spores must settle in a confined area, necessitating the retention of drift material over one place for some period of time. They observed that herbivorous creatures, such as urchins, might enhance recruitment by anchoring the material in place while consuming it (Dayton et al. 1984). Although it is believed that *L. setchellii* may not be as heavily grazed upon as other species, such as *Macrocystis* (Dayton et al. 1984), the risk of genetic impact from breakage and dislodgement remains a key consideration.

An important aspect in assessing the genetic risk associated with breakage and dislodgement from culture sites is the delayed maturation of *L. setchellii*. If standard culture practices involve harvesting materials within 5 to 6 months of out-planting, in line with other *Laminaria* species, the likelihood of sori development within that time frame is significantly reduced. As mentioned earlier, the majority of plants do not produce sori until their second or third year of growth, though a few may do so in the first year. However, with a grow-out period of only half a year, the chances of sori developing before harvesting are further diminished. Even in the event of dislodgement or frond breakage, there is a higher likelihood that the material will break down before reaching a fertile state.

If cultured propagules do manage to establish themselves within wild *L. setchellii* populations, the degree of impact will hinge on the frequency at which this occurs. The long lifespan of this species may provide some genetic resistance to occasional introgression. However, if cultured material more regularly introgresses into local populations, the impacts are likely to persist over a prolonged period, influenced by the species' longevity. This could potentially affect a larger number of neighboring populations, given the increased reproductive opportunities afforded by the species' extended lifespan.

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2.2.7 Sea Palm (Postelsia palmaeformis)

2.2.7.1 Range/Description

Sea palm, *Postelsia palmaeformis*, is a brown alga found in the North Pacific coastal region spanning from central California to Vancouver Island, British Columbia (Dayton 1973; Blanchette 1996; Paine et al. 2017). This species occupies the high-energy, wave-exposed areas of the mid to upper rocky intertidal shores (Barner et al. 2011 and Blanchette 1996). This annual kelp species undergoes a heteromorphic life cycle, transitioning between a haploid gametophyte stage in winter and a diploid macroscopic sporophyte stage (associated with the sea palm morphology) in summer (Blanchette 1996; Kusumo et al. 2006; Paine et al. 2017). This species of kelp does not have a resting period. Its local survival, without a 'seed bank', hinges on successful reproduction each year (Barner et al. 2011). While this species can grow in dense stands (Kusumo et al. 2006), it often competes with *Mytilus californianus* beds for intertidal space (Dayton 1973). In cases where waves or other factors clear away mussels, sea palms tend to colonize those areas (Paine et al. 2017).

The sea palm and its commercial harvest are managed by the California Department of Fish and Wildlife as part of a broader macroalgal management approach (https://wildlife.ca.gov/Conservation/Marine/Kelp; accessed 9-28-23); recreational harvest of this species is illegal. From a commercial standpoint, this species is of interest for its fronds which are consumed raw, pickled, steam, or dried (Thompson et al. 2010).

2.2.7.2 Biological Characteristics

P. palmaeformis sporophytes become reproductive in late spring to early summer (Dayton 1973, Blanchette 1996). The exact time span between spore production and the transition to the gametophyte and sporophyte stages is not well understood (Barner et al. 2011), however, small sporophytes reappear in the winter (Blanchette 1996) and early spring (Dayton 1973, Barner et al. 2011).

In *P. palmaeformis*, sori develop on the grooved blades near the stipe, when the plant is exposed during low tide, released spores drip down the blades and fall in the immediate vicinity of the parent plants (Dayton 1973, Blanchette 1996). While spores of brown algae are mobile, the duration of this mobility prior to germination remains unknown (Blanchette 1996). Dayton (1973) suggested that the effective distance for sporophyte colonization was approximately 3 meters from the edge of an existing *Postelsia* stand. Paine et al. (2017) found that mean dispersal distance ranged only from 0.16 to 0.50 meters from the spore source across sites, and that 95% of the recruits were within 0.38 to 1.32 meters of the plant. Genetic indexes of inbreeding (F_{IS}) were high for *P. palmaeformis*, which may be associated with restricted dispersal of propagules, and indicates that selfing likely occurs at least occasionally in this species (Kusumo et al. 2006).


Image from NOAA Fisheries

While most recruitment occurs in the immediate vicinity of parent plants, longer distance colonization events likely result from displaced fertile *Postelsia* plants that have been found to float and drift onto upper intertidal habitats (Dayton 1973). However, this mechanism of colonization is likely a rare occurrence (Wootton and Pfister 2013). Paine et al. (2017) conducted a long-term (>27 year) study on *Postelsia* dispersal and found only five colonization events that occurred greater than 10 m from the source population in a total of 136 site-years (number of years in the observation period multiplied by the number of sites monitored over that time). However, Paine et al. (2017) noted that rare dispersal events are required to explain populations that are separated by more than a km over this species' 2000-km coastal range. In addition, Blanchette (1996) proposed another dispersal mechanism where algal propagules (e.g., spores, gametes, gametophytes, and sporophytes) may be transported by animal vectors, but again, there is likely a low frequency of this occurring.

2.2.7.3 Population Structure

As mentioned above, Barner et al. (2011) identified evidence of selfing in all *Postelsia* populations they investigated, with frequencies ranging from 0.333 to 1.000; these rates were as high as, or higher than, those of outcrossing. Despite a reduction in heterozygosity, the study detected few fitness costs, suggesting that deleterious recessive alleles may have already been purged from this species—a phenomenon observed in other plant species where selfing occurs (Barner et al. 2011). Selfing is believed to serve as a means to ensure reproductive success for a short-lived species with very limited dispersal (Barner et al. 2011). Kusumo et al. (2006) discovered significant genetic differentiation among sporophyte clusters over small scales (e.g., 5 meters apart), and even greater genetic structure in populations separated by up to 23 meters. The F_{ST} values were high ($F_{ST} = 0.470$) for populations separated by greater distances (up to 11 kilometers), consistent with the theory of infrequent reproductive dispersal via drifting rafts of sporophytes (Kusumo et al. 2006). Collectively, these studies indicate that local recruitment is the primary driver of the persistence of *P. palmaeformis* stands over extended periods (Kusumo et al. 2006, Barner et al. 2011).

2.2.7.4 Aquaculture

P. palmaeformis is gaining commercial interest in California, ranking as the state's third most harvested algal species (Kübler et al. 2021). It constitutes a substantial portion, up to 45%, of the total commercial collection of edible seaweed in the region and is particularly sought after in health food stores and Asian markets, where prices can range from $24 to $30 per pound (Kübler et al. 2021). Currently, this species is sourced from wild populations, however, increased frond collection may affect the reproductive potential of individual stands, depending on the number and timing of the frond collection (Thompson et al. 2010). Although specific culturing information for this species has not been identified in literature searches, it is possible that aspects may be similar to other algal species, with sporophyte out-planting in the fall and harvest in the spring prior to spore production (Thompson et al. 2010). However, cultivation techiques are unique to each species, and much remains to be learned about *P. palmaeformis* culture.

2.2.7.5 Considerations on genetic risk to wild conspecifics

Given the absence of detailed information on the culturing techniques for this species, we can utilize the available life-history data for *P. palmaeformis* to generate considerations regarding the potential genetic impact on natural populations resulting from potential aquaculture operations for this species.

Due to its restricted dispersal ability, the likelihood of spores being released from offshore aquaculture operations and successfully settling and recruiting in suitable habitat is quite low. While there is a slightly higher potential for fronds or entire macrophytes to break or become dislodged and drift towards suitable intertidal habitats, successful colonization from this type of dispersal is exceedingly rare, occurring in fewer than 5 events over 136 site-years at distances greater than 10 m (Paine et al. 2017). Using operational approaches to harvest this species before reproductive sori form on fronds will further diminish this likelihood.

In the event that reproductive fronds drift into suitable habitat already inhabited by naturally occurring sea palms, the density of spores, gametophytes, and/or juvenile sporophytes from wild individuals may overwhelm any potential reproductive capacity from cultured fronds. While colonization events might occur in disturbed areas devoid of wild sporophytes (e.g., in locations where mussels have recently been removed), dispersal away from regions colonized by cultured organisms is likely to be as restricted and sporadic as it is for natural populations. These factors should facilitate straightforward monitoring and effective implementation of mitigation strategies if cultured sporophytes are identified in the intertidal habitat.

Although the recruitment of *Postelsia* from offshore culture into natural populations may be unlikely, it is important to note that natural populations could be more vulnerable to negative consequences if such recruitment were to occur. This is especially relevant in regions where commercial harvesting of wild populations is taking place. Thompson et al. (2010) summarized several biological characteristics of *P. palmaeformis* that make this species particularly susceptible to overexploitation. These include small natural populations due to limited habitat availability and restricted dispersal, a negative correlation between population size and extinction risk, variability in population sizes from year to year, targeting of reproductive fronds by commercial collectors, and collection techniques (e.g., cutting at the stipe) that can be lethal to the entire sporophyte. Exploited populations may already exhibit reduced genetic diversity due to genetic drift (Kusumo et al. 2006), and further stress from the introgression of cultured genotypes (e.g., through non-adapted or limited-genotype diversity) may reduce the population's fitness to a point where recovery is not possible. However, given some of the same considerations mentioned above, mitigation efforts for site restoration, if needed, may be more successful compared to other algal species.

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2.2.8 Sea Cabbage or sweet kombu (Hedophyllum sessile formerly Saccharina sessilis)

2.2.8.1 Range/Description

Hedophyllum sessile, commonly referred to as sea cabbage, is a distinctive kelp species distinguished by its unusual lack of a stipe in the macroscopic sporophyte stage, which is the structure typically found between the holdfast and blades (Fales 2023). In the absence of a stipe, the blades emerge directly from the holdfast, which positions the blades close to the substrate. Its blades can grow quite thick and reach lengths of up to 1.5 meters, however, as blades age they become prone to tearing (Milligan and DeWreede 2000, Fales 2023).

Formerly classified as *Saccharina sessilis*, the native range of *Hedophyllum sessile* on the Northeast Pacific coast stretches from the Aleutian Islands in Alaska down to Point Sur in Monterey County, California (Hoos and Harley 2021). This perennial kelp species predominantly thrives in the rocky substrates of the mid-intertidal to shallow subtidal regions. Its resilience allows it to endure a range of habitats, from semi-protected to semi-exposed environments, and this species may be exposed to terrestrial conditions for hours during low tides (https://wildlife.ca.gov/Conservation/Marine/Kelp/Commonly-Harvested-Marine-Algae; accessed 10-1-23; Fales 2023).

H. sessile displays a few unique dynamics not observed in all kelp species. In locations where *H. sessile* kelp beds have low density or smaller sporophytes, sporophytes in these areas may be more vulnerable to environmental stressors, including heat tolerance during exposed periods at low tide (Hoos and Harley 2021, Fales 2023). Winter storms can result in significant biomass loss for this species through blade breakage or displacement of entire plants. Research by Milligan and DeWreede (2000) highlights a seasonal influence on holdfast attachment strength that increases with storm activity. They also note that if fronds are torn from the plant but the basal meristem and holdfast remain intact, new blades can regenerate (Milligan and DeWreede 2000).

2.2.8.2 Biological Characteristics

H. sessile, like other kelps, undergoes an alternation of generations, comprising a biphasic life-history (Hoos and Harley 2021). Macroscopic sporophytes persist year-round, with reproductive sori appearing in the fall and winter, while microscopic gametophytes develop from released zoospores throughout the reproductive period (Hoos and Harley 2021). Fox and Swanson (2007) found that *H. sessile* produces larger zoospores, which exhibit limited dispersal and survival ability compared to spores of other kelp species, such as *Nereocystis leutkeana*. The microscopic life stages may endure for several months until environmental conditions become optimal (Fox and Swanson 2007). It is believed that the distribution of putative microscopic life stages of *H. sessile* is spatially confined, mirroring the general distribution of macroscopic sporophytes, primarily along the mid-intertidal coastline (Fox and Swanson 2007).

Recruitment of *H. sessile* sporophytes primarily takes place from late winter through spring, and the success of this recruitment process varies depending on the type of substrata (Milligan and DeWreede 2000), and on the presence of algal species (Hollarsmith et al. 2022). The recruitment of *H. sessile* juveniles is the greatest near the midpoint of the species' vertical distribution and decreases towards the upper and lower distributional limits (Hoos and Harley 2021). In late spring and early summer, macroscopic juvenile sporophytes gradually emerge (Hoos and Harley 2021), and these juveniles are frequently observed beneath the adult canopy, particularly on articulated corallines (Barner et al., 2016). Unlike mature sporophytes, juveniles are characterized by the presence of a holdfast, stipe, and blade (Milligan and DeWreede 2000).

Image from California Dept. of Fish and Wildlife

2.2.8.3 Population Structure

Extensive literature searches yielded no population genetic structure studies for either *Saccharina sessilis* (former classification) or *Hedophyllum sessile*.

2.2.8.4 Aquaculture

At present, no specific information is available regarding the commercial or restorative culture of *H. sessile*. However, it is anticipated that methodologies will mirror those employed for other macroalgal species. This could encompass the collection of wild sori from reproductive blades, followed by the seeding and subsequent out-planting of seeded lines onto larger longlines within an offshore aquaculture operation. Additionally, there is potential for the integration of cultivation techniques into Integrated Multi-Trophic Aquaculture (IMTA) infrastructure (Hwang et al. 2022), which employs the culture of species at various trophic levels (e.g., fish, shellfish/sea urchins/abalone, and kelps/seaweeds) to increase productivity and reduce waste from the system as a whole. These approaches have been successfully employed in the commercial culture of *Saccharina* species sharing similar morphologies (Hwang et al. 2022). While the exact timing of harvest remains uncertain, it is likely that the offshore growth duration will align with winter upwelling periods, allowing for a springtime or early summer harvest to preempt biofouling or potential biomass losses associated with biofouling or the development of reproductive sori on the blades in fall and winter.

2.2.8.5 Considerations on genetic risk to wild conspecifics

Based on the available information for this perennial species, if seed lines are out-planted in the fall (a timing similar to other kelp species), the sporophytes may not reach maturity to produce reproductive sori in the same fall and winter period when the natural population undergoes reproduction. If harvest takes place before most blades develop sori, and considering the limited dispersal of spores and microscopic stages as noted by Fox and Swanson in their 2007 study, coupled with the distance between natural *H. sessile* habitat and potential offshore operations, the likelihood of dispersed propagules impacting natural populations is lower. Blade breakage or displacement of cultivated plants could potentially lead to extended propagule dispersal if reproductive sori form on the dislodged fragments. However, given reports of blades being easily torn by wave activity (Milligan and DeWreede, 2000), and the absence of a flotation mechanism, this is unlikely to serve as a significant dispersal mechanism for this species. As outlined by Milligan and DeWreede (2000), sporophytes exposed to higher wave activity demonstrate increased holdfast strength. Ideally, in an offshore location, this response may reduce the frequency of sporophyte displacement from the cultivation structure.

In the event that propagules effectively disperse and settle in habitats conducive to this species, the restricted dispersal capacity of *H. sessile* is likely to generate genetic structure at smaller scales. Such genetic structure could be more readily influenced by an influx of cultivated individuals. As such, until genetic population connectivity has been studied, collection of broodstock material should be sourced close to the planned aquaculture operation. Furthermore, there may be a prospect for this species to recruit in regions previously uninhabited by *H. sessile*, owing to its demonstrated capability to outcompete other algae in the intertidal range (Edwards and Connell 2012).

While we provide a summary of the available knowledge on this species, it is important to note that there is a substantial amount of information currently unavailable. This absence of data hinders our ability to evaluate the potential genetic impacts resulting from dispersed cultivated *H. sessile* propagules on natural populations. Specifically, no information was found pertaining to the health or abundance of *H. sessile* beds or populations along the northeast Pacific coast, population genetic studies, or aquaculture practices. It is important that these knowledge gaps be addressed in order to more accurately assess the potential for genetic impacts.

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2.2.9 Nori (Pyropia species):

2.2.9.1 Range/Description

Pyropia species, previously classified under the genus *Porphyra,* are annual red algae that are found along temperate coastlines worldwide, including the Pacific coast of North America (Levine and Sahoo 2010, Kim et al. 2019). Recent advancements in molecular studies have prompted a global reclassification of *Porphyra*/*Pyropia* species, and this ongoing research has led to the identification of many formerly cryptic species (Lindstrom 2009, Lindstrom et al. 2015, Harden et al. 2016). Collectively, these algae have extensive ranges along the eastern Pacific coast, spanning from the Bering Sea in Alaska to Baja California in Mexico. They predominantly inhabit the mid- to upper-intertidal zones, where they are attached to rocks (Lindstrom et al. 2015, https://wildlife.ca.gov/Conservation/Marine/Kelp/Commonly-Harvested-Marine-Algae; accessed 10-30-23).

Key characteristics of *Pyropia* species include their lanceolate-shaped thalli, which are monostromatic meaning the thalli are composed of a single layer of cells, and the majority of *Pyropia* species are dioecious, with separate male and female individuals (Lindstrom et al. 2015). Given their distribution in the more exposed portions of the intertidal zone, these algae exhibit a high tolerance to desiccation. During periods of emersion, where they are exposed to air during low tide, *Pyropia perforata* can lose up to 90% of its wet weight (Romero 2009). Furthermore*, P. perforata*, along with other *Pyropia* species, demonstrate adaptability to a wide range of salinity levels and eutrophic conditions (Romero 2009).


Image from California Dept. of Fish and Wildlife

Pyropia species, commonly known as nori, hold significant economic value as a staple ingredient in sushi and various culinary dishes (Lindstrom 2009, Levine and Sahoo, 2010, Ladner et al. 2018). The cultivation of nori has been a key component of the mariculture industry in Japan for over a century, and it remains the largest mariculture industry in Japan, Korea, and China (Ladner et al. 2018). Among *Pyropia spp*., *P. yezoenisis* and *P. tenera*, are the most economically valuable, accounting for the majority of global production (as detailed in Ladner et al. 2018).

While attempts have been made to establish offshore *Pyropia* farming in various locations across the United States, including Washington, Maine, and Alaska, several challenges have impeded the growth of this industry. In Washington, cultivation endeavors involved the importation of seven strains from Japan (*P. yezoensis*) and four local *Pyropia* strains (Kim et al. 2019). The introduction of non-native strains was chosen because of extensive knowledge of their culture and because those species were considered to pose minimal risk in terms of invasiveness (Kim et al. 2019). Despite seemingly favorable conditions in Puget Sound, only three out of the seven Japanese strains exhibited successful growth, whereas all local strains thrived (Kim et al. 2019). However, culture efforts for *Pyropia spp.* in Washington ceased due primarily to political and social resistance (Kim et al. 2019).

Similar initiatives were undertaken in Maine, focusing on the cultivation of Japanese strains. However, challenges emerged related to the physiological traits of the strains and the specific culturing conditions in the Gulf of Maine. Those attempts at culturing *Pyropia spp.* were ultimately unsuccessful (Kim et al. 2019). In Alaska, initial efforts concentrated on assessing the suitability of various *Pyropia* species, with *P. torta* emerging as a promising candidate for commercial cultivation. Nonetheless, significant hurdles remain in the production of conchospores, development of offshore cultivation techniques, and the availability of genetic population data for informed seed stock selection (Kim et al. 2019). Despite these challenges, offshore *Pyropia* farming in the United States remains of interest due to high market demand and value (Ladner et al. 2018).

Although there are numerous *Pyropia* species, only a select few are viable candidates for commercial cultivation as not all may be amenable to culture or are palatable (Levine and Sahoo 2010). *P. perforata*, which ranges from the Aleutian Islands in Alaska to Baja California, Mexico (Lindstrom 2009), is a primary species of interest for potential commercial cultivation, particularly in California (Ladner et al. 2018). However, other species may be explored as potential candidates for cultivation, including those newly classified species found along the California coast, such as *P. conwayae*, *P. montereyensis*, *P. columbiensis*, *P. lanceolata*, *P. pseudolancelota*, and *P. protolancelolata* (Lindstrom et al. 2015), and *P. nitida* (Harden et al. 2016). Wild populations of *P. perforata* are most abundant from mid-spring to early fall (Romero 2009), although seasonal variation may vary across species, population dynamics are influenced by a combination of factors including temperature, light availability, and nutrient levels (Pacheco-Ruiz et al. 2005).

As with other kelp species in California, the management and harvesting of *Pyropia* species are regulated by the California Department of Fish and Wildlife (https://wildlife.ca.gov/Conservation/Marine/Kelp; accessed 10-30-23).

2.2.9.2 Biological Characteristics

Pyropia species undergo a heteromorphic alternation of generations, as reviewed by Sahoo and Yarish (2002). In this life cycle, male gametes develop within the spermatium, located on the male section of the blade in monoecious species, or on the male blade in dioecious species.

These male gametes then fertilize the egg within the female carpogonia. Subsequently, a zygotospore is formed, released, and settles on appropriate substrates like shells from various shellfish, barnacle casings, or calcareous stone—a distinctive trait of this genus (Green and Neefus 2015). These zygotospores mature into filamentous sporophytes referred to as conchocelis. These sporophytes bore into the shells and undergo vegetative growth. When specific environmental conditions are met, the conchocelis develop filaments where meiosis takes place, giving rise to haploid conchospores. Once released, these conchospores settle on suitable substrates like rocks (or nets in a cultured environment), and develop into macroscopic haploid male or female gametophyte thalli (i.e., blades) (Sahoo and Yarish 2002, Green and Neefus 2015, Romero 2009).

All three types of microscopic propagules in *Pyropia* (e.g., gametes, carpospores, and conchospores) lack motility, relying entirely on water movement for processes like resuspension, settlement, and mate location (Amsler et al. 1992). While the rapidly growing haploid gametophytes are only present during specific seasons, the conchocelis persist throughout the year, consistently generating monospores (i.e., Archeospores) that give rise to more conchocelis (Romero 2009). These conchocelis have the ability to endure unfavorable conditions and may function as a seed bank for *Pyropia* populations. However, they only produce conchospores for the formation of macrothalli when conditions become favorable once again (Sahoo and Yarish 2002, Romero 2009). In the case of *P. perforata,* these conducive conditions have included prolonged photoperiods exceeding 12 hours and low water temperatures, conditions which usually occur during upwelling periods in the summer months (Pacheco-Ruiz et al. 2005). A study conducted by Romero et al. (2009) suggested that conchospores may possess some potential to directly serve as seed banks, as evidenced by the presence of gametophytic thalli in sites where the necessary environmental conditions for conchospore release by conchocelis had not been met for months prior to gametophyte recruitment. However, the extent of this phenomenon remains uncertain.

Asexual reproduction is a prevalent occurrence in nori species, and various spore types contribute to this mode of reproduction. During the gametophyte phase, neutral spores, endospores, or archeospores are generated within the carpogonium through mitosis, and subsequently develop into the gametophytic blade phase (Redmond et al. 2014). Endospores are characterized by uneven and irregularly shaped spores, while neutral spores are evenly size with a regular shape; the quantity of these types of spores produced varies among species (Redmond et al. 2014). In contrast, archeospores are comparatively large spores, with only one produced per female cell. This type of spore can be generated within the gametophytic thalli, giving rise to new thalli, or by the conchocelis, leading to the formation of new conchocelis (Sahoo and Yarish 2002, Redmond et al. 2014). Interestingly, in the case of *P. umbilicalis*, a species in the Northwest Atlantic, reproduction exclusively relies on neutral spores, and sexual reproduction has not yet been observed in this species (Redmond et al. 2014).

Propagule dispersal is likely a significant mechanism for *Pyropia* recruiting into newly available clearings throughout the year. The success of recruitment may fluctuate seasonally; for example, *P. perforata* recruits more often in spring months (Romero 2009), where peak occurrence of wild gametophytes occurs in March through September, and the majority of the reproductive period is from summer to fall (Ladner et al. 2018). While the upper intertidal habitat of this species primarily supports short-range dispersal, the presence of turbulent tidal and wave conditions can potentially transport propagules offshore. This phenomenon may enhance the colonization success of *P. perforata*, as well as other *Pyropia* species, onto adjacent rocky substrates (Romero 2009).

2.2.9.3 Population Structure

Despite recent taxonomic revisions in *Pyropia* species and the identification of previously cryptic species through molecular studies (Lindstrom et al. 2015), there are few studies examining population genetic structure along the North American Pacific coast. In an early genetic study, Lindstrom (1993) utilized starch gel electrophoresis to analyze 17 proteins, and aimed to characterize genetic variation within and among populations of 20 *Porphyra* (now *Pyropia*) species in British Columbia and the surrounding areas. The results indicated an overall low level of genetic variation, which was lower than levels found in Japanese species. In some instances, species exhibited no within-species variation over distances exceeding 1000 kilometers. However, with the advancement of newer sequencing techniques, the resolution for assessing genetic diversity within and between populations and species has greatly improved, as demonstrated by the recent identification of new species in Lindstrom et al. (2015). Understanding the patterns of population genetic structure and measures of connectivity among sites remains a high priority for North American *Pyropia* species, particularly in light of the potential for commercial-scale offshore production.

2.2.9.4 Aquaculture

Cultivating *Pyropia* species presents unique challenges due to their complex heteromorphic life-history. Successful cultivation requires precise management of hatchery operations to control the various life-stages and the specific environmental conditions needed at each stage (Levine and Sahoo 2010, Piña et al. 2023). Some species have established commercial protocols used to manipulate their life-cycles, enabling the mass production of conchospores for seeding commercial nets (Sahoo and Yarish 2002). However, there is considerable intra- and interspecific variability among strains and species, along with variations in environmental conditions at different sites, which makes it more challenging to adapt cultivation techniques to other species (Stekoll et al. 1999). As Stekoll et al. (1999) discovered in Alaska, over a dozen species are potential candidates for nori culture. Even when adapting culturing technology developed for some of these species from other regions, a deeper understanding of local conditions and their effects on each species' growth stages is essential to effectively modify and control the life-cycle of the target species (Stekoll et al. 1999).

Redmond et al. (2014) detail the cultivation process for the two key species in Asian nori culture, *P. yezoensis* and *P. haitanensis*. Cultivation begins in spring with the seeding of spores onto sterile or artificial mollusk shells using fertile *Pyropia* blades sourced from seed stock or wild populations. These blades undergo a stress-inducing process involving desiccation and reimmersion to release zygotospores (Redmond et al. 2014). Due to the nonmotile nature of red algal spores, they quickly settle in tanks containing shells. In large-scale commercial operations, which may require one to two million shells, this phase requires substantial space and labor (Sahoo and Yarish 2002). Once settled, the conchocelis grow throughout the summer under low light conditions (Sahoo and Yarish 2002). Conchospore release is triggered in the fall by reducing water temperatures and agitating the water through stirring or aeration (Redmond et al. 2014). Despite being nonmotile, the positively buoyant conchospores can be effectively seeded onto grow-out nets by rotating the nets through the tank or by directly spraying nets with a spore mixture (Sahoo and Yarish 2002). Nets are placed in nursery tanks to facilitate thalli development; this process often involves lifting the nets out of the water to minimize fouling. Once the blades reach approximately 23 mm, they are transferred to grow-out farms, where they are attached to floating rafts or fixed line poles, depending on the water depth (Redmond et al. 2014).

Nori can undergo multiple harvests within a single season. The initial grow-out phase spans approximately 40 to 50 days, during which blades attain lengths of 15 to 30 cm (Redmond et al. 2014). Subsequent harvests occur at shorter intervals, typically every 15 to 30 days (Sahoo and Yarish 2002; Redmond et al. 2014). Overall, Levine and Sahoo (2010) propose an average harvest duration of 37.5 days. Ladner et al. (2018) also suggest that nori harvests be timed to avoid diverting metabolic energy towards reproduction. However, success in conducting the harvest prior to gametophyte sexual maturity likely hinges on the specific species and/or domestication efforts for traits such as delayed maturity.

While the culture cycles may differ depending on the species and geographical location, in the case of *P. perforata* cultivation in California, Ladner et al. (2018) outlined a cultivation cycle that encompasses lab-based hatchery phases from May to December, followed by offshore cultivation from December to May.

Ongoing research is dedicated to refining the cultivation techniques for this highly valuable industry. There is a great interest in creating free-living conchocelis variants that can be maintained as a continuous vegetative culture, a development that is anticipated to significantly reduce the costs associated with *Pyropia* cultivation (Sahoo and Yarish 2002, Piña et al. 2023). Although, if successfully developed, these free-living conchocelis variants would greatly increase the likelihood for successful dispersal if they end up in a natural setting. Additionally, efforts have been focused on exploring the use of asexual spores for seeding nets, potentially bypassing the conchocelis stage entirely, as described in Ladner et al. (2018). Other areas of research interest include trait selection, techniques for frozen gametophyte storage, and methods for artificial seed stimulation (Piña et al. 2023).

2.2.9.5 Considerations on genetic risk to wild conspecifics

While limited studies have explored the population genetic structure of northeastern Pacific *Pyropia* species, the existing research on *Pyropia* species in other parts of the world generally reveals spatial genetic patterns among populations, although the scale of spatial structure varies by species (Bi et al. 2014, Cid Alda et al. 2023). Ladner et al. (2018) mentioned *P. perforata's* potential susceptibility to fragmentation on nets, but the role of rafting of fragmented or dislodged plants as a potential dispersal mechanism for *Pyropia* has received minimal attention (e.g., Brooks 2020). The extent to which vegetative fragments can establish themselves and the longevity of reproductive cells on free floating fragments remain unclear. However, it is reasonable to assume that thalli consisting of a single cell layer may rapidly degrade if dislodged or fragmented.

Dispersal of conchocelis may transpire through the transportation of shells or barnacles to new locations by animal vectors, such as sea otters, or through human-mediated processes like shellfish collection, and operational equipment or boat fouling. In cases where such transport occurs, the potential for subsequent sexual and asexual spore release arises. An example of this mode of dispersal was provided by Lindstrom (2018) who describes the identification of a putative Japanese *Pyropia* species on the central coast of British Columbia in 2015, believed to have been facilitated by marine debris from the 2011 Japanese tsunami. Lindstrom (2018) also summarized other suspected instances of inadvertent long-distance *Pyropia* transport via seagoing vessels. Although such transport mechanisms can operate at intercontinental scales, more frequent regional dispersal is likely mediated by the dispersal of spores.

Despite *Pyropia* spores being non-motile, their buoyant nature enables them to be transported to adjacent areas by wave action and driven by coastal currents. Given that one or more types of *Pyropia* spores may be produced by various life stages throughout the year, multiple opportunities for this form of dispersal are conceivable. For dispersing spores to establish themselves successfully, they must settle within suitable intertidal habitats and develop into reproductive thalli or conchospores. The presence of asexual modes of reproduction in these species improves the odds of colonization success.

Research indicates that cultured strains generally exhibit lower genetic diversity compared to their wild counterparts in the same region (e.g., Jia et al. 2022), and this loss of diversity can be particularly pronounced in certain cultured-wild population comparisons (Cao et al. 2018). Based on this information, if cultured *Pyropia* strains introgress into wild populations, potential exists for loss of genetic diversity. However, it is important to note that based on the existing body of literature, there is currently limited evidence demonstrating genetic impacts arising from cultivated strains on wild populations that result in a loss of genetic diversity or spatial structure (e.g., Jia et al. 2022).

Apart from a potential for rare long-distance dispersal events, the cultivation of *Pyropia* species is associated with a moderate to low level of genetic risk to wild populations of the same species. This assessment takes into account factors such as the swift harvest cycle, the intricate life-cycle of the genus, its habitat in the upper intertidal zone, as well as the characteristics of spores and thalli. Additionally, existing spatial patterns observed in other *Pyropia* species suggest an overall limited dispersal capacity for these organisms. However, it is worth noting that if *Pyropia* cultivation is conducted in multitrophic operations involving shellfish species, there could be an elevated risk. This is due to the potential for shellfish shells to serve as suitable substrates for the successful settlement and development of conchocelis. Subsequent harvesting of shellfish from the operation could lead to a widespread dispersal of cultivated individuals away from the operation site.

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2.2.10 Sea spaghetti (Gracilaria andersonii)

2.2.10.1 Range/Description

The Gracilariaceae family encompasses a diverse group of red algae, featuring species that can exist in both benthic and free-living forms (Gurgel et al. 2004). Notably, the genus *Gracilaria* holds global significance, as highlighted by Lipinska et al. (2023), as representing some of the most economically significant agarophytes (Abreau et al. 2009). These species support a thriving agar industry that encompasses both cultivated and wild plants, an industry outlined by Lopez-Bautista and Kapraun (1995). As a result, commercial cultivation of *Gracilaria* has been established in regions like Chile since the 1980s (Abreu et al. 2009). The algae's properties extend to antiviral, anti-inflammatory, and anti-hypertensive attributes, along with other uses in pharmaceutical and industrial sectors (Gurgel et al. 2004, Iha et al. 2018, van Ginneken and de Vries 2018, Lipinska et al. 2023). *Gracilaria* species also hold potential in waste recycling, particularly within multi-trophic aquaculture systems (Halling et al. 2013, Samocha et al. 2015). Beyond their industrial applications, *Gracilaria* species hold culinary value and find a place in dishes such as salads (Klinkenberg 2020).

Because of their commercial uses, some *Gracilaria* species have encountered population declines in their natural habitats due to excessive harvesting (Pereira and Yarish 2008), however, other species have exhibited remarkable success as invasive species (Lipinska et al. 2023). These species possess an inherent ability to swiftly colonize new environments, likely due to their resilience to various stressors, including fluctuations in nutrient levels, salinity, and temperature (van Ginneken and de Vries 2018, Lipinska et al. 2023). This adaptability to a wide array of conditions significantly contributes to their invasive potential, as described by van Ginneken and de Vries (2018).

With their warm-water growing seasons, ease of propagation, rapid growth rates, and high tolerance to diverse environmental conditions, *Gracilaria* species emerge as ideal candidates for aquaculture endeavors, as emphasized by Gurgel et al. (2004).

Gracilariopsis andersonii, is a red alga, is native to the Pacific Coast of North America, with a distribution from Vancouver, Canada, down to San Diego, California (Wehrenberg 2011). This species typically attains lengths of up to 2 meters, although smaller variants, around 1 meter, are more commonly observed (Wehrenberg 2011). Its coloration varies from yellowish-brown to reddish-purple, featuring numerous axial branches that anchor it to the substrate through a discoid holdfast (Wehrenberg 2011). This adaptable species is found in diverse habitats, including on exposed rock along the intertidal coasts or subtidal regions, where it may be found at depths up to 18 meters (Klinkenberg 2020). *G. andersonii* may also grow partially buried in soft sediments in estuaries and bays or grow as unattached mats (Wehrenberg 2011). Despite being a perennial species, populations along rocky coasts, less able to withstand burial, may assume a more annual lifestyle as they respond to seasonal shifts in environmental conditions (Wehrenberg 2011).

The resilience of *Gracilaria* species, particularly within California, includes their capacity to endure physical extremes in salinity and desiccation levels (Wehrenberg 2011). These species are dominant algal types within California estuaries and the sandy channels of the rocky intertidal zone (Wehrenberg 2011). Although the species, *Gracilaria andersonii,* has been recently distinguished, these species remain in a state of taxonomic flux, as outlined by Wehrenberg (2011).

2.2.10.2 Biological Characteristics

Members of the red algal family Gracilariaceae, known as Gracilaroids, feature a triphasic life history characterized by isomorphic diplohaplonty. This term implies that the gametophyte and tetrasporophyte phases share identical appearances, as erect branched thalli growing from a perennial holdfast (Guillemin et al. 2008). Visual differentiation between these phases is impossible to the naked eye, with the exception of fertilized female gametophytes bearing cystocarps (the carposporophyte phase) which can be distinguished (Wehrenberg 2011, Valero et al. 2017). These two phases often spatially and temporally overlap, seemingly occupying similar biological niches (Wehrenberg 2011).

In the triphasic life cycle of *Gracilaria*, as described by Guillemin et al. (2008), meiosis occurs on the reproductive diploid tetrasporophytes, giving rise to haploid tetrapores. After release, these tetrapores attach to the substrate, forming perennial holdfasts and developing into haploid male and female gametophytes. Male gametes, lacking flagella in red algae, are released from male gametophytes into the water, and seek eggs on the female gametophyte thallus (Wehrenberg 2011). Fertilization takes place on the female gametophyte, leading to the development of a cystocarp—a third stage that grows directly on the female gametophyte thallus as small bumps (Klinkenberg 2020). Through mitotic division, thousands of diploid carpospores are produced in this stage. Upon release, these carpospores attach to the substrate, developing into perennial holdfasts and eventually growing into tetrasporophytes (Guillemin et al. 2008). Reproduction in these species peaks in late summer at high latitudes, whereas in the tropics, it may be high throughout the year. In temperate regions, the fastest growth rate and highest biomass occur in late summer, while in the tropics, peak biomass occurs most often in winter (Kain and Destombe 1995).

Gracilaria species can also propagate through vegetative fragmentation, occurring when thalli of either the diploid tetrasporophytes or haploid gametophytes break (Guillemin et al. 2008, Valero et al. 2017). Fragments of any size and at various locations along the thallus have the potential to grow into new thalli, and the process of fragmentation may stimulate further growth and branching in the parent plant (Wehrenberg 2011). In sediment habitats, underground thalli may enable the species to over-winter during harsh periods, and studies have shown the resumption of growth after burial for up to four months (as reviewed in Wehrenberg 2011). Another mode of propagation for these species involves free-floating thalli, where plants detached from the holdfast can grow and propagate vegetatively indefinitely, and potentially form extensive beds (Guillemin et al. 2008).

The Gracilaroid life-cycle results in three propagation mechanisms for these species: sexual reproduction via carpospores, asexual reproduction through the release of tetraspores, and vegetative fragmentation from either the diploid or haploid phase (Guillemin et al. 2008, Wehrenberg 2011). The utilization and frequency of each method are influenced by factors such as water velocity, plant density, geographic location, available substrate, and fragmentation frequency (Wehrenberg 2011). For instance, in a study in California, *G. andersonii* exhibited year-round sexual fertilization at one site, while at another site, vegetative fragmentation was the primary method of reproduction; the author suggested that substrate type was the factor that likely influences the different reproductive modes in these populations (Wehrenberg 2011).

Limited information is available regarding spore dispersal in *Gracilaria* species, with both tetraspores and carpospores considered significant dispersal mechanisms (Destombe et al. 1992). While it has been suggested that haploid spores may have longer dispersal capabilities compared to diploid spores, both spore types can survive for weeks and endure days of desiccation. Seasonal changes may influence the germination rate of these spores (Kain and Destombe 1995). In terms of gamete dispersal, non-motile male gametes are estimated to have a lifespan of 6 hours, with dispersal limited to within a few meters of the male gametophytes (Destombe et al. 1992, Kain and Destombe 1995). Despite their short lifespan, fertilization in *G. verrucosa* was documented over a distance of 80 m (as reviewed in Kain and Destombe 1995).

The dispersal of *Gracilaria* species is also influenced by their tendency to fragment. Albright (2021) discovered that *G. andersonii*, within the San Francisco estuary, was more prone to fragmentation compared to other species in the same region. Albright also observed that the tensile strength of thalli may vary based on the reproductive method employed by the population and the type of habitat it occupies (rocky substrate vs sediment). In the San Francisco estuary, the population relies on vegetative fragmentation as its primary mode of reproduction, and its lower tensile strength may contribute to more frequent fragmentation and subsequent population growth (Albright 2021).

2.2.10.3 Population Genetics

There are few population genetic studies of *Gracilaria* species, and literature searches did not yield any identified population genetic studies for *G. andersonii* along the U.S. Pacific coast.

Most genetic research has been primarily dedicated to resolving the taxonomic identification of *Gracilaria* species worldwide. Because of the intriguing life-cycle of these species, capable of both sexual and asexual reproduction, the *Gracilaria* genus holds interest as an evolutionary and ecological model species (Lipinska et al. 2023). As an example, Wehrenberg's (2011) genetic study revealed that populations displaying persistent differences in reproductive modes could still be classified as the same species. While these findings are fascinating from an evolutionary perspective, determining genetic population structure among populations with varying life-cycle phases and modes of reproduction may not be straightforward.

For any forthcoming genetic research, there are available genomic resources, including genome assemblies (with differing levels of completeness) for *Gracilaria chilensis*, *G. gracilis*, *G. caudata*, and *G. vermiculophylla*, accessible at https://rhodoexplorer.sb-roscoff.fr (Lipinska et al. 2023). Moreover, sequences of chloroplasts and mitochondrial genomes are accessible for numerous *Gracilaria* species (Iha et al. 2018).

A population genetics study utilizing two microsatellites revealed that sexually reproducing *G. gracilis* populations displayed only weak, but significant structuring, with a low degree of inbreeding observed in locations separated by 2.5 to 12 km. However, substantial genetic differentiation was detected among locations separated by 500 m to 1,200 km. The study suggested an overarching pattern of isolation by distance at distances greater than a 1 km, while gene flow prevented strong genetic differentiation over shorter distances (Engel et al. 1997). The researchers concluded that *G. gracilis* populations had the potential for local adaptation within ranges of a few hundred meters to several kilometers. Within a given site, there may be genetic heterogeneity among individuals across the habitat. However, wave action and other fine-scale processes result in more frequent gene flow overall at that level (Engel et al. 1997).

In macroalgal species with both sexual and asexual reproduction, the genetic effects of selection differ between these reproductive modes. During sexual reproduction, selection targets specific genomic regions. Over generations, genetic diversity in these regions, as well as neighboring regions linked physically to the selected targets, is reduced. In contrast, asexual clonal reproduction mimics complete physical linkage across the entire genome, leading to more rapid fixation of single genotypes and loss of genetic diversity. The decrease in genetic diversity not only limits the available genetic pool for trait improvement but also hinders a population's ability to adapt to new environmental challenges or conditions (Guillemin et al., 2008). Guillemin et al. (2008) found that cultivated *G. chilensis* populations had reduced genetic diversity due to clonal propagation practices compared to wild populations. However, asexual fragmentation preserved heterozygosity due to the lack of segregation in this mode of reproduction (Guillemin et al. 2008). Guillemin et al. (2008) also observed that cultivated genotypes had spread into wild populations.

2.2.10.4 Aquaculture

The predominant and straightforward cultivation method for *Gracilaria* species involves asexual propagation, wherein growers use thallus tips to clonally generate new plants (Pereira and Yarish

2008). Observations at farm sites suggest that the selection for vegetative propagation may favor sterility (Wehrenberg 2011). Guillemin et al. (2008) noted that 40% of cultivated *G. chilensis* produced reproductive structures, but sexual reproduction was rare, indicating an incomplete life cycle under culture conditions. Domestic cultivation through asexual fragmentation may also unintentionally select for diploidy, possibly due to heterosis in heterozygotes, leading to an excess of heterozygotes in asexually propagated populations (Guillemin et al. 2008, Valero et al. 2017). Debate exists regarding whether the observed heterozygote excess indicates selection for heterozygous diploids or if clonal propagation itself leads to the accumulation of mutations, resulting in a heterozygote excess. Mutational models for clonally reproduced organisms predict the accumulation of a large number of mutations over many generations. However, the extensive production of clonally reproduced individuals for commercial purposes may also contribute to a substantial number of mutations (Guillemin et al. 2008).

Clonal reproduction offers benefits such as consistent production due to genetically identical individuals (Redmond et al. 2014), ease of selection and maintenance of desired phenotypes without the risk of loss from recombination in sexual reproduction (Valero et al. 2017), potentially higher growth and survival rates (Guillemin et al. 2014), and prevention of recombination of cultivated strains with wild conspecifics (Valero et al. 2017). However, drawbacks include reduced genetic diversity in the propagated populations compared to wild populations (Halling et al. 2013, Hurtado et al. 2015). Guillemin et al. (2008) found that cultivated populations of *G. chilensis* contained a third of the genetic diversity as nearby wild populations, potentially diminishing resilience to novel challenges (Valero et al. 2017). Higher rates of sterility in these populations may also limit opportunities for breeding improvements (Valero et al. 2017).

Spore seeding provides an alternative method for *Gracilaria* propagation, involving the seeding of spores from mature carposporophytes (life stage that produces diploid carpospores) or tetrasporophytes (life stage that produces haploid tetraspores) onto a substratum (Redmond et al. 2014). This process allows the spores to develop into juvenile plants, which are then placed into the farm site. As described by Redmond et al. (2014), the spores are released over the desired substrata, such as seed lines, by placing spore-bearing thalli on a screen suspended in water. After a 24-hour period at 20°C, the spores settle undisturbed for 24 to 42 hours in dim light. The seeded lines are maintained at 20°C under low light for 2 months until visible juvenile plants develop. These juveniles are then out-planted to the culture site.

The seeding method offers the convenience of plants attached to lines, eliminating the need to tie individual plants. Additionally, a significant advantage is the minimal volume of material required to establish a commercial farm; only 30 to 40 kg of cystocarpic plants may serve as spore stock, compared to the 10,000 kg needed for a 1 ha farm using the tying method (Alveal et al. 1997). Another notable benefit is the introduction of recombination through sexual reproduction, aiding in the maintenance of genetic diversity crucial for population adaptation to novel challenges and the development of high-quality cultivated lines over the long term (Halling et al. 2005, Redmond et al. 2014). However, drawbacks include a two-month incubation period in the nursery before out-planting, and higher levels of phenotypic variation in cultivated individuals (Redmond et al. 2014).

Gracilaria cultivation can utilize a suspended rope system, where a floating longline is anchored in place with buoys. *Gracilaria* plants are attached to the line by tying with smaller twine and are allowed to grow further once out-planted. As described by Redmond et al. (2014), in New England, out-planting occurs when temperatures are above 15°C, but this likely varies by location and species This approach can also be used for seeding, where lines are out-planted when plants are approximately 13 cm in height, as mentioned above. Harvesting methods vary, with options including trimming outer growth every 2 to 4 weeks or harvesting the entire plant (Redmond et al. 2014). This longline approach has been successfully adopted in the Republic of Korea and India (Mantri et al. 2023). Other cultivation systems, such as net tubes or floating cages stocked with unattached fronds, are also possible (Redmond et al. 2014). In warmer climates, bottom culture is a popular technique, involving seeding plants onto rocks spread on the bottom in shallow areas or attaching plants to lines suspended just above the bottom, similar to suspended line culture but less flexible for depth adjustment (Redmond et al. 2014).

Common challenges in *Gracilaria* cultivation include grazing, fouling, and environmental stress, especially in warmer regions. Effective control measures involve managing the depth of grow-out lines (deeper leads to less settlement), optimizing stocking density (higher is preferable), and strategically timing out-planting and harvest, particularly in regions with seasonal shifts in water temperatures and other conditions (more critical in temperate climates than in tropical regions) (Redmond et al. 2014). While *Gracilaria* species are relatively stress-tolerant, variations in light, salinity, and temperature can impact growth (Redmond et al. 2014). As summarized in Redmond et al. (2014), mitigating risks from extreme weather events is important, and protective measures include bringing lines into storage tanks during storms or adjusting the depth of lines to avoid damage from extreme wave action or runoff events. However, line depth adjustments may be limited by user conflicts and/or increased risk of entanglements of other marine species (A. Concepcion, pers. comm.).

Improvement of *Gracilaria* strains, where it is utilized, has predominantly centered on enhancing agar production. The initiative to correlate enhanced agar production with genomic profiles was initiated in the 1990s (Lopez-Bautista and Kapraun 1995).

In central California, *G. andersonii* emerged as one of the top candidates for red algae cultivation, following research that achieved successful vegetative and sexual propagation for *G. andersonii* and several other regional algal species (Graham 2008). Cultivation experiments conducted in Monterey Harbor revealed that this species exhibited better growth at a depth of 3 m than at the surface, which was attributed to epiphytism by algae and animals. Optimal harvesting frequency was determined to be every 4 weeks, and growth and biomass were highest during periods of high-water quality. Unfortunately, the occurrence of red tides, a known phenomenon along the California coastline, led to the rapid deterioration and death of all out-planted species at all depths (Graham 2008).

2.2.10.5 Considerations on genetic risk to wild conspecifics

In certain regions worldwide, natural populations of *Gracilaria* are facing a decline due to overharvest (Pereira and Yarish 2008). Simultaneously, introduced *Gracilaria* exhibit a high degree of invasiveness (Lipinska et al. 2023). The same characteristics that make these species appealing for cultivation, such as easy propagation from spores and vegetative fragments and high tolerance to environmental stresses like salinity and temperature, also heighten their risk as invasive species (Gurgel et al. 2004; van Ginneken and de Vries 2018). This invasiveness has already been demonstrated on the east coast of the U.S., where the invasive *G. vermicuphylla* has spread along large portions of the U.S. Atlantic coastline and is displacing the native *G. tikvahaie* in the north east regions (Nettleton et al. 2013).

In the context of offshore aquaculture, careful consideration must be given to the dispersal and subsequent growth of propagules (gametes and spores) and vegetative fragments for *Gracilaria* species. There is potential for reproductive structures to develop during the growout phase, especially with year-round reproduction in warmer regions or during summer months in temperate areas. Spore dispersal appears to be more significant than gamete dispersal, with documented spore survival over weeks (Kain and Destombe 1995). While gametes have limited duration and dispersal, documented fertilization over a distance of 80 m suggests a non-negligible impact (as reviewed in Kain and Destombe 1995). Both gametes and spores, being non-motile, disperse according to prevailing currents. Consideration of fragmented thalli is also critical for assessing dispersal propensity in these species, as vegetative growth is possible from any size fragment, and these displaced thalli may float and propagate indefinitely (Guillemin et al. 2008). As noted by van Ginneken and de Vries (2018), the act of harvesting *Gracilaria* species releases spores and fragments. Harvesting methods vary, with some involving the trimming of outer growth every 2 to 4 weeks, while others opt for harvesting the entire plant (Redmond et al. 2014); repeated harvesting likely increases the total amount of cultivated material dispersed from the operation each harvest season.

Population genetic studies of *Gracilaria* species are limited, but Engel et al. (1997) found low yet significant levels of genetic structure between locations separated by 2.5 to 12 km. In contrast, large genetic differentiation was observed between locations separated by hundreds to thousands of kilometers, suggesting a general pattern of isolation by distance at distances greater than one kilometer. Gene flow, facilitated by the dispersal of propagules and fragmented thalli, prevented genetic differentiation over shorter distances (Engel et al. 1997). The patterns of genetic connectivity over distances greater than a kilometer are likely influenced by oceanographic currents throughout the year. The risk of dispersal and the dispersal shadow from an aquaculture operation will also be influenced by current patterns in the region during the growout period, potentially extending over kilometers from the offshore operation.

If propagules or vegetative thalli successfully reach the coastline, their potential to colonize is high due to their broad tolerance of environmental factors and suitability for various habitats. The cultivation method, whether through sexual spore production or asexual fragmentation, presents different risks to natural populations. While the impact on wild populations from asexually propagated cultivated populations is uncertain, Guillemin et al. (2008) found that cultivated genotypes successfully spread into wild populations. Asexual fragmentation, as observed by Guillemin et al. (2008), rapidly reduces genetic diversity in the cultured population. However, clonally produced populations are generally less fertile than sexually reproducing ones and may pose a lower risk of genetic introgression with natural populations, though fertility assessments are necessary for each cultured population. Nonetheless, they may still spread and propagate asexually in areas overlapping with wild beds. Sexually propagated populations may be more successful at genetically introgressing into wild populations; however, compared to asexual cultivated populations, they may retain more of the genetic diversity present in wild populations.

Considering the information above, the cultivation of *Gracilaria* species in Southern California is likely to pose a moderate risk to natural populations, with the degree of risk dependent on current patterns between the operation and coastal populations. Along the U.S. west coast, there is limited information indicating population decline, and in some areas, such as bays and estuaries, *G. andersonii* is increasing in abundance, potentially impacting other species in the ecosystem (Huntington et al. 2008). Although there are no population genetic studies for this species, it is crucial to source material from populations close to the planned operation. While dispersal over kilometers is possible, the available population structure information suggests that colonization at this scale is not a common occurrence (Engel et al. 1997).

Mitigation approaches to decrease the propensity for fragmentation and thallus biomass loss from *Gracilaria* culture may include exposing juveniles in the nursery stage to strong currents to increase tensile strength, controlling the depth of grow-out lines, and lowering them by several meters to reduce wave energy, grazing, and fouling, all of which can contribute to thalli breakage (Graham 2008, Redmond et al. 2014). Additionally, to minimize dispersal, it is recommended not to leave any biomass at the grow-out site at the end of the harvest schedule (van Ginneken and de Vries 2018).

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2.2.11 Turkish Washcloth (Mastocarpus spp.):

2.2.11.1 Range/Description

Mastocarpus is a genus of red algae which are distributed worldwide along coastlines in temperate regions, primarily occupying rocky intertidal and shallow subtidal habitats (Ludington et al. 2004). Specifically, along the Pacific coast of the United States, *Mastocarpus papillatus* was thought to range from Baja California (~29°N) to the Gulf of Alaska (~60°N) (Polanshek and West 1977, Fierst et al. 2010). However, recent investigations have suggested that specimens collected within the purported range of *M. papillatus* may actually constitute five distinct species or clades (Lindstrom 2008, Lindstrom et al. 2011). Furthermore, there remains uncertainty regarding the specific classification of species in the southern portion of the range in California, as both *M. papillatus* and *M. intermedius* may occur in this region.

This species exhibits disparate macroscopic physical forms, that alternates between a diploid crustose sporophyte form, that cover rock substrates (often informally referred to as "tar spot algae") to the haploid foliose gametophyte form that is characterized by fleshy short blades (Ludington t al. 2004, Fierst et al. 2010). Only relatively recently were these dissimilar life-stages discovered to belong to a single species (West 1972).

The management of the Turkish washcloth algae, along with its harvesting activities, falls under the jurisdiction of the California Department of Fish and Wildlife, as part of a comprehensive strategy for the management of macroalgae (https://wildlife.ca.gov/Conservation/Marine/Kelp; accessed 9-28-23). From a commercial perspective, this species holds potential interest due to its carrageenan content, which finds applications in various industries as a thickening agent or emulsifier (Pereira et al. 2015).

2.2.11.2 Biological Characteristics

In all *Mastocarpus* species, two distinct life cycles are present, a sexual life cycle and an asexual life cycle (as reviewed in Ludington et al. 2004, Lindstrom 2008). The sexual life cycle incorporates the heteromorphic alternation of generations which includes the diploid crustose stage (tetrasporophyte) that meiotically produces haploid spores. The spores develop into haploid foliose gametophytes; male fronds release male gametes which fertilize ova that are retained on female fronds. The fertilized diploid zygote remains on the female frond and develops into a carposporophyte. The carposporophyte releases diploid spores that develop into crustose tetrasporophytes, completing the sexual life-cycle (West 1972, Ludington et al. 2004, Lindstrom 2008). In the asexual life cycle, upright diploid female fronds, which are visually indistinguishable from sexual female gametophytes, produce only female diploid gametophyte offspring through carpospore production without fertilization (Lindstrom 2008). It is not known how easy, if at all possible, switching between the sexual and asexual life cycles may be, as it has not been observed in culture, but interestingly, geographic and spatial partitioning between sexual and asexual variants has been observed (Fierst et al. 2010).

While understanding the underlying factors governing the partitioning of life-cycle variants within and among locations is challenging (Krueger-Hadfield et al. 2013), discernible patterns have emerged. In *M. papillatus,* the prevalence of sexual fronds is more pronounced south of Point Conception, whereas asexual variants tend to predominate in the northern stretches of its coastal range. Within central California (spanning from Point Conception to San Francisco), both variants coexist. In sites where these variants overlap, the sexual variant was typically found in lower intertidal zones, exhibiting reproductive activity during specific periods of the year. Conversely, the asexual variant occupied a broader range of intertidal habitats and demonstrated year-round reproductive capabilities (Fierst et al. 2010). However, the timing of sexual variant spawning exhibited variability, occurring either in the fall-winter or the spring-summer period, contingent upon the extent of overlap with asexual fronds (Fierst et al. 2010).


Image from California Department of Fish and Wildlife

The distinctive textured appearance of the Turkish washcloth algae, and hence its common name, arises from the presence of reproductive papillae on both sexual and asexual fronds. These papillae release both carpospores and tetraspores in a gelatinous matrix (Fierst et al. 2010). Generally, *Mastocarpus* species are thought to possess limited dispersal capabilities. Notably, all propagules, including male gametes, carpospores, and tetraspores, lack flagella or cilia, and remain viable for less than two days (Engel et al. 2004, Al-Marayati 2019). Consequently, reproductive dispersal is constrained within close proximity to the parent plants. This phenomenon has been proposed as a key factor influencing the observed geographic patterns in life cycle variants along coastal regions, thought to be strongly influenced by shoreline topography (Fierst et al. 2010). As noted in Al-Marayati (2019), asexual reproduction may be favored during colonization events to overcome infrequent reproductive opportunities in new habitats. Given the transient lifespan of propagules, the release of carpospores from asexual fronds (without the necessity for male gametes) may prove more successful in sparser environments.

2.2.11.3 Population Structure

While genetic tools have been applied to resolve taxonomic questions among Pacific *Mastocarpus* populations (e.g., AFLPs in Ludington et al. 2004 and nuclear and organellar sequencing in Lindstrom 2008), population genetic studies are limited in *Mastocarpus* species. In a study on a related species, *M. stellatus*, in Maine, England, and France, significant genetic structure was identified among sampled sites. Notably, this variation did not align with geographic distance, suggesting that habitat differences, particularly in relation to tidal positions (i.e., upper and lower intertidal zones), may play a more prominent role (Al-Marayati 2019). This complexity is further compounded by distinct modes of reproduction observed across different locations. For example, patterns of genetic connectivity differed between populations exhibiting obligate asexual reproduction and populations with sexual gametophyte and tetrasporophyte stages (Al-Marayati 2019). Al-Marayati (2019) proposed that the differing degrees of genetic differentiation observed among life-history variants may be attributed to varying selective pressures.

Similar to the Atlantic sites, regions along the Pacific coast varied in the dominance of life-history variants. As mentioned above, sexual variants were more prevalent in southern populations, while asexual variants are more abundant in northern populations (Krueger-Hadfield et al. 2013). Over a 300 km stretch of the Central California coastline, sites displayed a mixture of both variants with additional partitioning based on position in the intertidal zone (Krueger-Hadfield et al. 2013). In the absence of specific studies pertaining to the population genetics of this species, it is reasonable to consider the potential parallels with *M. stellatus*. The population connectivity of *M. papillatus* may be influenced more by life-history variants and habitat similarity, rather than adhering to an isolation by distance pattern.

2.2.11.4 Aquaculture

Limited information is currently available regarding the aquaculture of *Mastocarpus* species, particularly *M. papillatus*, despite their capacity to yield moderate quantities of commercially valuable carrageenan (Pereira et al., 2015). Pereira et al. (2015) have suggested that commercial cultivation is likely to target the female gametophyte life-cycle stage. Similar to *Mastocarpus*, other red algae, such as *Gracilaria* and *Gracilariopsis*, can be cultivated both asexually and sexually. These species are amenable to open water rope cultivation, relying on seedstock generation through vegetative propagation (Garcia-Poza et al. 2020). This method may also be applicable to *M. papillatus*, although cultivation techniques could vary widely between different species. However, it is important to acknowledge that prolonged reliance on asexual variant propagation may lead to a reduction in genetic diversity, which could have adverse repercussions on both the cultured population and any wild population influenced by genetic exchange with cultivated sources (Garcia-Poza et al., 2020; Tanoeiro et al., 2023). Owing to the paucity of available information, determining the optimal timing for out-planting and harvest remains a challenge; nevertheless, Periera et al (2015) suggest potential for a summer harvest, aligning with practices observed in other macroalgal species.

2.2.11.5 Considerations on genetic risk to wild conspecifics

Several pieces of information are currently missing, which hinder a more thorough assessment of the genetic risks that cultured *Mastocarpus* may pose to conspecific wild populations. First, there is uncertainty surrounding which *Mastocarpus* species would be cultivated in different regions in California, as both *M. papillatus* and *M. intermedius* may co-occur in central and southern California. It is important that the species selected for cultivation match with the naturally occurring species in the region, as it remains unclear whether inter-species hybridization may occur. Additional data gaps include absence of population genetic studies for either of these species. For *Mastocarpus*, such studies should also encompass an understanding of the prevailing life-history variant(s) in populations near the aquaculture operation. This information will also prove useful in understanding the reproductive periods within wild populations for sexual and asexual variants.

Given the limited dispersal capabilities of propagules in this species (Engel et al. 2004, Al-Marayati 2019), it is improbable that propagules dispersed from offshore operations would successfully reach and settle in suitable intertidal habitats. The primary concern lies in the potential breakage of vegetative fragments or dislodged thalli that retain reproductive capacity and may subsequently disperse and establish in other locations (Carrington 1990). Fragment dispersal could occur via drift on ocean currents or through alternative means such as transportation on ships or equipment (Mayaca et al. 2013). If culture operations employ vegetative propagation, there may be an increased risk of fragment detachment and subsequent colonization elsewhere. Al-Marayati (2019) observed that colonization might be more successful through asexual modes of reproduction, and once established, asexual populations may exhibit higher growth rates (Fierst et al. 2010).

Kitzes and Denny (2005) found an increase in wave tolerance in *M. papillatus* in more exposed locations. It may be possible, following acclimatization to the offshore environment, for breakage incidents to become less frequent. However, grow-out techniques, which have not been developed for this species, will likely be the largest determinant of breakage in the grow-out setting.

Given the above information, the offshore culture of Mastocarpus species likely represents a low-to-moderate genetic risk to wild populations based on the limited dispersal capabilities of propagules, and the specificity of settlement habitat required for dispersed propagules. However, fertile vegetative fragments, and the capacity for asexual reproduction (without the need for fertilization), poses greater genetic risk from cultivated material. More information is needed on the grow-out techniques for this species in an offshore setting, and on the extent of rafting and the duration for which dislodged fragments remain fertile.

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3.0 Gulf of America Candidate Species for Marine Aquaculture

3.1 Geographic Range

Regions considered in this analysis were in the west, central, east, and southeast of the Gulf of America (hereafter, 'Gulf').

3.2 Macroalgae Candidate Species for Marine Aquaculture

3.2.1 Sargassum Species

3.2.1.1 Range/Description

Sargassum, the predominant brown macroalgae found in temperate, tropical, and subtropical waters globally (Jacobucci et al. 2009), encompasses over 360 identified species with diverse environmental distributions (Guiry and Guiry 2022). Despite variations, many *Sargassum* species share common features such as long branches with leaf-like blades and air bladders (Racine et al. 2021, Guiry and Guiry 2022). These species can be generally classified as either benthic or pelagic. Pelagic *Sargassum* growing vegetatively and reproducing asexually through division, forms extensive pelagic beds in the Gulf and Atlantic Ocean basin (Phillips and Fredericq 2000, Marx et al. 2021). While these floating beds contribute to diverse and complex pelagic ecosystems, they become problematic during rapid growth episodes driven by warmer temperatures and increased nutrient discharges, resulting in massive *Sargassum* beaching events that negatively impact economies and ecosystems (Marx et al. 2021, Racine et al. 2021). In contrast, benthic species create extensive *Sargassum* beds, also serving as crucial habitats and nursery grounds for various marine organisms, without encountering the challenges associated with pelagic species (Redmond et al. 2014).

Sargassum species exhibit distinct growth and reproductive cycles, with varying optimal environmental conditions; however, the majority demonstrate peak growth rates between 24-30°C, experiencing reduced growth outside this temperature range (Redmond et al. 2014). Benthic species generally exhibit a broader salinity tolerance compared to pelagic species (Redmond et al. 2014).

In the Gulf, both pelagic species (*Sargassum natans* and *S. fluitans*) and benthic species (S. *filipendula* and *S. pteropleuron*) have been identified (Redmond et al. 2014). For these two benthic species, *S. filipendula* is observed more often in shallow coastal waters at rocky outcroppings in the subtidal regions, at river mouths, and even into nearly fresh water (Dawes 1987, Redmond et al. 2014). *S. pteropleuron*, on the other hand is found at deeper offshore rocky outcroppings and at more exposed sites (Dawes 1987). The distribution of *S. filipendula* extends from just south of Cape Cod, Massachusetts, to southern Florida, reaching into the Gulf and further south to Brazil (Simons 1906, Redmond et al. 2014). Recognized for its extensive range and rapid growth, *S. filipendula* has been identified as a promising candidate for macroalgal culture in Florida and likely across the Gulf (Redmond et al. 2014). This species is prevalent in the Gulf, thriving in estuarine bays, the subtidal zone, and at depths up to 40 m (Dawes and Tomasko 1988). Distinguished from some other macroalgal species, it predominantly remains submerged and is not exposed to air (Simons 1906). *S. filipendula* forms small holdfasts that attach to rocks or shells, it also features long cylindrical branches extending from the stipe, from which leaf-like blades with serrated edges and berry-like air floats extend (Simons 1906, Guiry and Guiry 2022). While it can reach a height of 60 cm, it is commonly shorter in stature (Simons 1906).


Image from NOAA AOML

Several *Sargassum* species are presently cultivated in China and Korea, with these seaweeds being marketed in various forms for human consumption such as dried, salted, or fresh, and incorporated into diverse dishes and seasonings (Redmond et al. 2014, Racine et al. 2021). These species are also commercially appealing due to their distinctive bioactive compounds, including fucoidans, alginate, diterpenes, and phenolic phlorotannins. Fucoidans, for their purported anti-tumor, anti-coagulant, antioxidant, anti-viral, and anti-bacterial properties, are of primary interest (Redmond et al. 2014). Alginate, valued for its gelling, thickening, and stabilizing properties in food and industrial processing, is another significant component. Depending on its cultivation location, *S. filipendula* can contain up to 26% and 45% dry weights of fucoidan and alginate, respectively (Redmond et al. 2014).

Despite the growing interest in expanding aquaculture industries among Gulf states, the development of macroalgal culture has been relatively slow (Racine et al. 2021). However, two macroalgal pilot projects, funded by the Department of Energy, are underway off the coasts of Texas and Florida. *Sargassum*, alongside *Eucheuma spp*. and *Gracilaria tikvahiae*, stands out as one of the three native species targeted for macroalgal cultivation in this region (Racine et al. 2021).

3.2.1.2 Biological Characteristics

Sargassum species undergo a relatively uncomplicated life history phase. Mature fronds generate reproductive receptacles containing conceptacles where male and female organs produce motile sperm and large non-motile eggs. While *S. filipendula* is monoecious, possessing mature receptacles with bisexual and unisexual conceptacles, both monoecious and dioecious *Sargassum* species exist (Simons 1906). Antheridia release sperm, and oogonia release a single egg (Simons 1906). The sperm, once released in the water, swim to nearby eggs which are encased in mucus, this mucus adheres the egg to the surface of the reproductive branch. This mucus attachment persists through fertilization and early sporeling stages (Simons 1906). As the zygote develops, it elongates and forms a holdfast to attach itself to the substrate once it has settled (Simons 1906). Upon settling onto suitable substrate, juvenile sporophytes grow into mature plants (Redmond et al. 2014).

The benthic *Sargassum* species in the Gulf exhibit seasonal growth and reproduction patterns. New growth emerges in spring from perennial holdfasts, a phenomenon observed by Dawes (1987), who noted this occurs by the end of March. The period of most rapid growth spans from spring to early summer (March through June), reaching peak biomass in the summer months (Redmond et al. 2014). Plants attain maturity in late summer and enter the reproductive phase in the fall, specifically from September through early November. By late October, both benthic species have populations that are 100% reproductive (Dawes 1987). These algae experience dieback in December through January, with only the perennial bases and vegetative stipes remaining into March (Dawes 1987). In more temperate regions, such as the Northeast, the reproductive phase occurs in summer, followed by a dormant period extending from November to March (Redmond et al. 2014). Maximal growth for these species is observed at temperatures ranging from 18 to 30°C, with growth decreasing above and below these temperature points (Redmond et al. 2014).

The two pelagic *Sargassum* species in the Gulf exclusively reproduce through asexual vegetative fragmentation (Redmond et al. 2014). This process of fragmentation results in considerable variation in the size of mature pelagic plants (Marx et al. 2021).

3.2.1.3 Population Structure

The differentiation of species within the *Sargassum* genus has proven systematically complex (Phillips and Fredericq 2000). Genetic investigations within this genus have primarily focused on identifying species in specific regions and distinguishing morphotypes and subspecies within particular species (e.g., Dibner et al. 2022). For the few studies that have been conducted on population genetics for these species, results have shown considerable variability in patterns of genetic structure. For instance, Cheang et al. (2010) conducted genetic analyses on *S. muticum*, a benthic species, and found homogeneity (based on analyses of genetic variation in ITS-2 and RUBSICO regions) across its native ranges in Asia and introduced ranges in Europe and North America. This species has successfully established itself globally, likely facilitated by the transport of Pacific oysters for aquaculture development (Cheang et al. 2010).

In an extensive population genetics study focusing on *S. thunbergii* in the northwest Pacific, Li et al. (2017) analyzed sequences from nuclear ITS-2 and mitochondrial cox3 regions in over 800 specimens. Contrary to expectations, the study revealed no correlation between geographic distances and pairwise genetic differentiation among populations. The analyses did reveal high levels of asymmetric gene flow, with the number of estimated migrants into populations aligning with oceanic current systems. Within each of the Japan, Korea, and China coastlines, ranges of F_{ST} estimates among sampled populations varied widely; this indicated that ocean currents in each of these regions primarily influenced dispersal patterns in *S. thunbergii* and acted to either homogenize or maintain genetic structure among these populations (Li et al. 2017). Similarly, in a study by Hu et al. (2013), a deep genetic break was identified among *S. fusiforme* populations from the Yellow-Bohai Sea, East China Sea, and South China Sea. The authors attributed these genetic patterns to a combination of post-glacial colonization pattern driven by ocean currents and contemporary asymmetric gene flow along adjacent sea margins. As reviewed in Hu et al. (2013), several *Sargassum* species exhibit low-to-moderate genetic variability among regions, and these patterns likely reflect historical climatic oscillations, such as expansions and retractions during ice age periods, and contemporary oceanic current patterns.

Although there are no identified population genetic studies for *Sargassum* species in the Gulf, it is reasonable to anticipate that similar patterns would emerge. The genetic connectivity among benthic species and populations will likely be predominantly influenced by currents within the Gulf. Despite the limited dispersal range of sporelings (approximately 1 m, Kendrick and Walker 1995), the dislodgement or breakage of parent plants can transport sporelings or gametes over longer distances due to their floating capabilities. In pelagic species within these regions, even less population structure is anticipated.

3.2.1.4 Aquaculture

Most commercial *Sargassum* cultivation approaches utilize juvenile plants generated through sexual reproduction, as this has proven important to optimizing biomass yields (reviewed in Racine et al. 2021). As such, only the cultivation process for sexually produced *Sargassum* species will be described here. As described by Redmond et al. (2014), reproduction in mature plants is induced by manipulating temperature and day-length, simulating local reproductive periods (e.g., late spring/summer). Nurseries can obtain seed stock either through collection of mature plants from the wild or by maintaining immature thalli in tanks until maturation and gamete release are triggered. Under optimal conditions, gamete release typically occurs within a week.

After fertilization, several seeding methods may be utilized to move sporelings that are attached by mucus to the parent plants onto seed lines. Horizontally situated frames with seed line wrapped around them may be situated beneath suspended reproductive thalli to allow embryos to drop onto the lines, or by collecting shed embryos (up to 24 hrs after fertilization) and pouring the solution over these seed frames. Alternatively, embryos can be seeded by brushing them onto the string. This involves removing embryos from parent thalli by rubbing them against a fine mesh, concentrating the embryos, and using the sticky mucus to adhere the brushed zygotes onto the seed lines. For all methods, once settled onto the lines, rhizoid development takes another 24 hrs before frames can be hung vertically for nursery cultivation. Nursery duration varies widely, ranging from one to two months (if subsequently moved into a protected offshore nursery) to 3 to 5 months if moved directly onto the final longline array. In either approach, juveniles are transferred to open water farms when they reach 2–5 cm in height (Redmond et al. 2014).

During grow-out, long lines are positioned at depths of 1 to 2 m, with increasing depth possibly reducing biofouling rates (Redmond et al. 2014). Due to the perennial nature of these species, seeded lines can be reused for up to 4 years, although diminishing harvests in subsequent years have been reported (reviewed in Redmond et al. 2014). The duration of grow-out depends on the operation's location and should be timed to optimize biomass production while balancing losses from grazing, biofouling, and reproduction. Largo et al. (2020) found that maximum growth in *S. siliquiosum* in the Philippines was achieved after a 6-month period. Downstream use of the harvested material should also be considered in culture durations as Dawes (1987) found protein levels were highest in young growing plants.

3.2.1.5 Considerations on genetic risk to wild conspecifics

Sargassum propagules exhibit limited short-distance dispersal, with approximately 98% found within 1 meter from the source (Kendrick and Walker 1985). However, considerable dispersal occurs from dislodged plants or broken thalli, facilitated by their buoyant vesicles (Komatsu et al. 2014). These buoyant fronds can be transported potentially over hundreds of kilometers by ocean currents (Li et al. 2017). Detached *Sargassum* not only may continue to produce gametes but may also retain germlings on drifting parental thalli (Cheang et al. 2010). This rafting of fertile plants or fragments creates a wide range of potential dispersal distances for *Sargassum* species (Schoenrock et al. 2021).

Moreover, the broad temperature and salinity tolerances of *Sargassum* species make them resilient to challenges that limit the survival or growth of many other species in different environments (Li et al. 2017). These characteristics, combined with rapid growth rates, contribute to the success of *Sargassum* species in dispersing and colonizing new regions. Notably, species like *S. muticum* have been remarkably successful as invasive species, significantly impacting marine ecosystems and regional algal assemblages in their introduced range. Colonization is attributed to the surface drifting of fertile, floating plant material, material caught in vessel steering gear, or transport by the commercial Pacific oyster aquaculture industry (Cheang et al. 2010).

When considering dispersal from cultured *Sargassum* in the Gulf, similar concerns come into play. The potential for broken or dislodged thalli to drift over distances long enough to encounter natural populations, depends largely on prevailing surface currents. However, an important factor to note is the pronounced seasonality in reproductive cycles for this species. Although there is little information available on offshore grow-out periods for *Sargassum* in the Gulf, growout may extend from early spring to mid-summer, concluding with harvest before most cultured material reaches reproductive stages. It's important to acknowledge that if cultured material is dislodged late in the grow-out period, it may become reproductive while drifting.

In the event that cultured propagules encounter wild populations, they must compete and survive at rates comparable to natural *Sargassum* propagules. A study by Kendrick and Walker (1985) highlighted the high mortality rates in early settled *Sargassum* stages, with only 0.0045% surviving to develop into visible recruits and a mere 0.0001% surviving for 12 months.

The population genetic structure of *Sargassum* species within the Gulf remains undocumented, leaving uncertainty about the potential disruption of genetic differentiation patterns through the introgression of cultured material. Drawing insights from studies in other regions, the patterns are likely to be influenced by smaller, localized surface currents, as well as broader oceanographic patterns in the Gulf. Understanding the surface current patterns around the farm site becomes crucial in identifying the region within the Gulf from which seed stock should be sourced.

Based on the information presented, there is a moderate likelihood of cultivated *Sargassum* introgressing into natural populations. The impact on natural populations will hinge on the genetic connectivity among impacted populations and the genetic diversity within the cultured population. To minimize genetic impacts from dispersed cultured material, a couple of mitigation approaches could be implemented. Addressing epiphytes and grazers, which are significant challenges in *Sargassum* culture, not only enhances biomass but also reduces thallus breakage by lowering drag and minimizing damage to thallus tissue (Jacobucci et al., 2009). Efforts to decrease these factors can contribute to both increased biomass and reduced dispersal of thalli away from the farm site. Additionally, lowering culture lines (e.g., by several meters in some locations) during the latter part of the grow-out period may delay the development of reproductive receptacles and decrease fouling of the biomass (Hwang et al. 2007). Although the permissibility of lowering lines will depend on the existence of user-conflicts in a particular location.

3.2.1.6 References

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3.2.2 *Ulva* Species (Sea Lettuce)

3.2.2.1 Range/Description


Image from California Sea Grant

Ulva species, recognized as among the most abundant seaweeds globally, are widespread in tropical and temperate coastal regions (Hiraoka 2021, Simon et al. 2022). Their extensive global distribution is facilitated by rapid proliferation, high growth rates, and tolerance to diverse environmental conditions, including temperature, salinity, and eutrophication (Simon et al. 2022, Steinhagen et al. 2019). Notably, these species can even thrive in freshwater habitats (Melton III and Lopez-Bautista 2021). This annual green alga exhibits two main types of growth: benthically attached to substrates like rocks, mollusks, wood, and other algae in intertidal and subtidal areas, or unattached as free-floating thalli in intertidal to mesophotic zones (Melton III and Lopez-Bautista 2021).

The thallus of various *Ulva* species exhibits two primary morphologies: either uniform foliose distromatic sheets consisting of two cell layers, or a tubular, monostromatic blade form (Hiraoka 2021, Simon et al. 2022). Certain species, such as *U. compressa*, may display both forms (Simon et al. 2022). The foliose sheet form is commonly known as 'sea lettuce,' while the tubular form is referred to as 'gut weed' (Melton III and Lopez-Bautista 2021). These distinct forms arise not only from genetic variability but also from morphological plasticity influenced by environmental conditions and the associated microbiome (Simon et al. 2022).

Many free-floating *Ulva* species have caused 'green tides,' leading to nuisances in coastal regions with significant environmental and economic consequences (Fort et al. 2021, Melton III and Lopez-Bautista 2021). The ability of these species to float allows them to quickly boost their biomass by enlarging their thalli, reaching new areas with fresh nutrient supplies, and avoiding competition and grazers faced by benthic species (Hiraoka 2021).

The *Ulva* genus comprises over 400 described species, with only 129 currently accepted and approximately 40 taxonomically recognized using genetic information (Melton III and Lopez-Bautista 2021; Simon et al. 2022). In their study, Melton III and Lopez-Bautista (2021) found several *Ulva* species present throughout the U.S. East Coast and the Gulf (*U. aragoensis*, *U. compressa*, and *U. torta*), while other species were only present in the Gulf (e.g., *U. californica*, *U. flexuosa subsp. paradoxa*, *U. lactuca*, *U. meridionalis*, *U. ohnoi*, *U. tepida*, and *Ulva sp. 1* and *2*). *Ulva sp. 2* was only found off Port Aransas, Texas. *U. compressa* and *U. ohnoi* were observed forming significant blooms in the Gulf and southern Florida, respectively. Introduced species in the region include *U. ohnoi*, *U. compressa*, *U. lactuca*, and *U. torta*, while *U. tepida* may be native to the Gulf. The origins of the remaining species are yet to be resolved (Melton III and Lopez-Bautista 2021).

Despite constituting a small fraction of total seaweed biomass production (less than 0.1%), there is a growing interest in cultivating *Ulva* due to its high productivity and environmental resilience (Steinhagen et al. 2019). *Ulva* holds potential applications in the food, pharmaceutical, nutraceutical, and cosmetic industries, as well as in biofuels and bioremediation (Simon et al. 2022, Steinhagen et al. 2022). Additionally, these species can be used in their fresh form for culinary purposes, such as in seaweed salads and soups (Ladner et al. 2018).

3.2.2.2 Biological Characteristics

Ulva are heterothallic and isogamous species, that display an alternation of generations with a diploid sporophyte stage and a haploid gametophyte stage. Both stages are macroscopic and morphologically indistinguishable (Smith 1947, Wichard et al. 2015). As described by Wichard et al. (2015), haploid gametophytes, either male or female, are generated from recombinant haploid zoospores (i.e., zoids) produced by sporophytes, or clonally from parthenogenic biflagellate gametes, and occasionally from zoids of parthenosporophytes. Gametes produced by gametophytes are biflagellate, positively phototactic, and can engage in sexual reproduction with a gamete of the opposite mating type. In the absence of an opposite mating type, they may also undergo parthenogenic development (developing into a gametophyte, as mentioned above). Zoospores originating from sporophytes, are quadriflagellate and negatively phototactic. Equal numbers of zoospores of both mating types are released, and these develop into male and female gametophytes. The generation time of *Ulva* is short, and species may start producing spores in just 2 to 3 weeks once the thallus has grown (Hiraoka 2021).

In most foliose *Ulva* species, fertile tissue develops along the thallus edges (Hiraoka 2021), and after the development of these reproductive tissues, the color changes to yellowish and then to brownish along the edges of the thallus (Smith 1947, Wichard et al. 2015). Laboratory cultures indicate that male gametes remain motile for less than 24 hours, while female gametes may last a few additional hours. Zoospore swarming typically lasts 4 to 5 hours, occasionally extending to 24 hours after release (Smith 1947). However, these spores may last for months, and in temperate regions, they may help the species 'overwinter,' and tolerate periods of being buried in sediment (Romero 2018). For example, viable spores may be found up to a depth of 5 cm in sediment after release (Romero 2018). The small size and high motility of *Ulva* propagules contribute to a significant dispersal range, with documented colonization occurring at distances of 24 to 35 km from the nearest populations (reviewed in Coleman and Brawley 2005 and Romero 2018). Reproduction may vary depending on the location, occurring during warmer seasons or potentially year-round (Romero 2018). For temperate species, seasonal fluctuations lead to a pattern of increasing biomass from winter to spring, followed by declines during high temperatures from summer to autumn (Hiraoka 2021).

3.2.2.3 Population Structure

Inter- and intra-specific genetic diversity in *Ulva* species, particularly foliose ones, is poorly characterized (Fort et al. 2021). In a study by Fort et al. (2021), next-generation sequencing of 110 strains of foliose *Ulva* from locations across Europe and the UK revealed high inter-specific genetic variation but low intra-specific genetic diversity. However, *U. linza*, as discussed in Coleman and Brawley (2005), displayed highly differentiated populations over small spatial scales, possibly due to local adaptations to salinity and intertidal positions. Patterns of population connectivity likely vary by species, especially between benthic and free-floating species. Additionally, understanding the interactions between genetics and responses to environmental conditions is crucial for *Ulva* aquaculture development and strain selection (Melton III and Lopez-Bautista 2021, Simon et al. 2022). Genetic variation, as highlighted in Melton III and Lopez-Bautista (2021), can lead to a fivefold difference in the levels of major compounds in cultured *Ulva*.

Given the diversity of *Ulva* species, a regional focus is crucial, particularly in areas targeted for aquaculture development, to confirm relevant species and investigate population genetic structures. In the Gulf, some sequencing has been done on *U. ohnoi* and *U. lactuca* for taxonomic purposes (Melton III and Lopez-Bautista 2021). However, there is a lack of population genetic studies in this region based on literature searches. Genetic sequencing, besides clarifying taxonomic identities, can aid in identifying species with a higher risk of overgrowth or bloom development in aquaculture-targeted regions. For instance, Melton III et al. (2014) identified *U. ohnoi* in the Gulf and along the Atlantic coast of Florida as a species prone to overgrowth.

3.2.2.4 Aquaculture

The feasibility of large-scale *Ulva* cultivation in an offshore farm using rope cultivation on longlines was demonstrated in Sweden (Steinhagen et al. 2021). While some *Ulva* species can be propagated vegetatively in an unattached form (e.g., in tank culture), when grow-out occurs offshore, spores are seeded onto nets or seed lines in a hatchery (Ladner et al. 2018). To achieve appropriate seeding concentrations, methods involving fragmentation and a culturing protocol to induce sporulation from thallus tissues independent of seasonal reproduction patterns may be employed (Hiraoka 2021, Steinhagen et al. 2021). Steinhagen et al. (2022) found that high seeding densities (10,000 gametes per mL) increased mean biomass yield by almost 84% compared to low seeding densities (500 gametes per mL). Solutions of 'swarmers' (gametes and spores) are applied to spools, and after propagules are allowed to settle, the spools are kept in the hatchery for 6 weeks to allow growth. Steinhagen et al. (2022) reported that increased contact time in the nursery period was found to minimize detachment and seedling loss caused by wave forces due to more vigorous rhizoidal attachment prior to out-planting.

Juvenile plants are gradually acclimatized to natural conditions and can then be deployed to an offshore farm (Steinhagen et al. 2021). In the Steinhagen et al. (2021) study, the grow-out duration was 6 months. Zollman et al. (2023) reported that cultivation at depths of 3 to 10 m (in their study - 5 m) has been shown to be better than depths of 1 m, due to lower growth rates caused by mechanical stress from surface waves. In Sweden, the highest biomass yields were observed in late spring, but beyond this point, the number and size of holes in the thalli, as well as the amount of fertile and fouled tissue, increased, leading to decreased biomass yields and quality (Steinhagen et al. 2022b). The timing and seasonality for grow-out and harvest will vary by location, and for warmer regions like the Gulf, the most appropriate months for grow-out and harvest will likely be different.

Additional considerations include reports of the recombinant gametophyte having faster ontogenetic development and higher growth rates compared to clonally produced gametophytes in *U. fenestrata*, indicating that the selection of the life-history phase may be crucial in developing cultivation approaches for *Ulva* species (Steinhagen et al. 2022). The authors also emphasized the importance of molecular species identification to disentangle the effects of genetic or environmental factors on biomass yield and biochemical composition, enabling site-specific selections of suitable *Ulva* species and strains. Development of sterile strains is also of interest for *Ulva* species that exhibit unpredictable fertility intervals; these species may synchronously develop reproductive tissue, and significant biomass losses can result due to the reduced quality of thallus tissue following reproduction (Steinhagen et al. 2022b). This occurrence has limited the commercial potential for large-scale cultivation in *Ulva* species where this occurs.

3.2.2.5 Considerations on genetic risk to wild conspecifics

Ulva species are abundant and widespread (Hiraoka 2021, Simon et al. 2022), and numerous species have been identified in the Gulf. These species include both introduced and native types, although not all species in this region have been classified as either yet (Melton III and Lopez-Bautista 2021). Assessing the potential genetic risk to natural populations from interactions with cultured *Ulva* reveals that the traits making these species valuable from an aquaculture perspective (e.g., rapid proliferation, high growth rates, broad environmental tolerance; Simon et al. 2022, Steinhagen et al. 2019) also elevate the risk to wild *Ulva* populations and the potential to develop into nuisance species.

Some *Ulva* species exhibit seasonality in reproduction, while others reproduce year-round (Romero 2018). Moreover, thallus tissue in *Ulva* species was observed to become reproductive in as little as two to three weeks (Hiraoka 2021). Considering an offshore grow-out period, likely lasting months (e.g., 6 months in a Swedish study; Steinhagen et al. 2021), it is probable that cultured *Ulva* in the Gulf will become reproductive during the grow-out period. Given that spores from *Ulva* species have been documented to disperse and colonize at distances of 24 to 35 km from the nearest populations (Amsler and Searles 1980), it is reasonable to assume that cultured propagules could disperse to natural populations at similar distances.

Therefore, it will be crucial to employ genetic sequencing approaches to identify the species intended for culture, understand their distribution in the Gulf, and assess the connectivity of populations across their range in the Gulf. The high dispersal potential of these species and their adaptability to a broad range of habitats increase the likelihood of their dispersion from offshore operations, settling into existing populations, or colonizing new locations. Given this risk, it is advisable to refrain from using *U. ohnoi* and *U. lactuca* as aquaculture species, considering their demonstrated ability to become nuisance species within the Gulf (Melton III and Lopez-Bautista 2021).

Considering these aspects collectively, the cultivation of *Ulva* species poses a moderate to high level of risk to natural *Ulva* populations, ***if*** native populations (and not introduced populations) exist within the region of interest in the Gulf. As mentioned above, at present, native and introduced species cannot be distinguished. If an already introduced species is chosen for aquaculture production, additional considerations regarding the importance of preserving genetic fitness and diversity of this species in the region, as well as the potential ecological impacts of increasing the potential spread of a non-native species, would need to be considered. Mitigation measures to minimize risk include extending the time in the nursery to minimize detachment, cultivating *Ulva* at depths several meters below the surface to reduce thallus breakage due to wave energy in an open environment. However, these measures will not completely eliminate the risk. Shorter grow-out durations can also help decrease thallus tissue lost to degradation and fertilization (Wichard et al. 2015). The development of sterile strains will significantly enhance the cultivability of these species (Steinhagen et al. 2022b) while also substantially reducing the potential genetic risk to natural populations.

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3.2.3 Dead Man's Fingers (Codium spp.)

3.2.3.1 Range/Description

The *Codium* genus comprises a collection of siphonous green algae encompassing over 80 species that are distributed across tropical to temperate regions (Trowbridge 1996, Chang et al. 2003, Kang et al. 2008). Within the Gulf, a couple of *Codium* species have been identified. Specifically, *C. isthmocladum* has been recognized off the Yucatan coast (Robledo et al. 2003), while *C. taylorii* has been discovered along the coast of Texas in the lower Laguna Madre, East Flower Garden Coral Bank in the northwestern Gulf, and Veracruz, Mexico (DeYoe and Hockaday 2001).

Codium species can be found in sheltered bays, estuaries, and semi-exposed coastal areas within the intertidal and subtidal zones, extending to depths of 15 meters. Some species, however, are capable of thriving at even greater depths, ranging from 42 to 53 meters (Robledo et al. 2003, Neill et al. 2006). These algae attach themselves to a diverse array of hard substrates, including rocks, shells, and artificial structures such as ropes and plastic, particularly in habitats characterized by sandy or muddy bottoms (Neill et al. 2006). Notably, *Codium* species exhibit a high tolerance to various abiotic factors, including temperature, salinity, light, and nutrients. As a consequence of this adaptability, *Codium* thrives in areas influenced by anthropogenic activities, or in areas containing artificial marine structures and/or aquaculture equipment (Neill et al. 2006).

Codium can grow up to 30 cm and exhibits two distinct thallus forms—spongy and filamentous. The filamentous forms consist of finely branched filaments which are formed initially, while the spongy form (preferred for cultivation) develops from the filamentous form under optimal conditions, including higher water movement and irradiance levels (Silva 1955, Trowbridge 1996).

While green macroalgae constitute a relatively small portion of the global seaweed biomass production, there is a growing interest in these species, including *Codium* species (Moreira et al. 2022). Despite the cultivation of *C. fragile* in Korea since the 1980s through small-scale practices, the global production is currently only around 4000 tonnes in fresh weight, with an approximate value of $2 million USD (Moreira et al. 2022). *Codium* is primarily consumed in Korea, China, Japan, and the Philippines in various forms such as fresh, dried, or salt-cured, and commonly used in dishes like kimchi (Trowbridge 1996, Hwang and Park 2020, Moreira et al. 2022). The pharmacological interest in *Codium* species revolves around their potential anti-inflammatory and anti-tumor properties, while there is also a growing interest with their application in bioremediation, particularly in Integrated Multi-Trophic Aquaculture (IMTA) systems (Moreira et al. 2022; Kang et al. 2021).


Image from Hwang and Park 2020

Certain *Codium* species exhibit invasiveness in marine ecosystems globally (Muha et al. 2019). For instance, *C. fragile* has invaded various regions worldwide, including U.S. coastal areas along the Pacific and Atlantic coasts, Europe, the Mediterranean, Australia, New Zealand, and Chile (Neill et al. 2006). The repercussions of these invasions have spanned from minor alterations in native species abundance to significant shifts in community structure, leading to adverse effects on aquaculture operations (Neill et al. 2006).

3.2.3.2 Biological Characteristics

In comparison to numerous other macroalgal species, *Codium spp*. tend to thrive during seasons characterized by the warmest water temperatures (Neill et al. 2006). These species are perennial, with spores and thalli capable of surviving winter temperatures and reinitiating growth in the spring. The most rapid growth occurs during the summer and early fall (Hanisak 1979, Neill et al. 2006). Reproductive development is believed to be predominantly influenced by temperature (Churchill and Moeller 1972), leading to the emergence of reproductive fronds in the summer and early fall (Hanisak 1979, Benson et al. 1983, Kang et al. 2008). Plant abundance declines during winter and early spring (Churchill and Moeller 1972). It is important to note that these patterns may vary by location (Chang et al. 2003).

The sexual reproduction process in *Codium* species is relatively straightforward, involving the production of gametes on gametangia found on mature thalli. Similar to other green algae, these gametes possess two flagella and undergo fusion to form a zygote. This zygote then goes through a siphonous filament phase before developing into the fleshy thalli characteristic of these species, contingent upon specific environmental conditions being met, such as water current and irradiance levels (Churchill and Moeller 1972).

Additionally, asexual reproduction has been documented in these species, including the parthenogenic development of haploid gametes, vegetative fragmentation, development of propagation buds, and the formation and growth of filamentous thalli from isolated utricles with medullary filaments (Churchill and Moeller 1972, Chang et al. 2003).

While the gametes have flagella and are motile upon release, this motility ceases approximately 30 minutes later (Churchill and Moeller 1972). Nonetheless, these gametes may remain viable and, notably, have the potential for parthenogenic development in the absence of other gametes (Churchill and Moeller 1972). The dispersal of *C. fragile* can also occur through the drifting of entire plants or plant fragments. These fragments have the capacity for vegetative growth and may also release gametes if fertile (Churchill and Moeller 1972).

3.2.3.3 Population Structure

There is a lack of information regarding the population structure of *Codium* species in the Gulf, and in general, information for the entire genus is scarce. Genetic studies have predominantly concentrated on taxonomic identification (e.g., Schneider et al. 2020). Additionally, efforts have been directed towards employing environmental DNA (eDNA) approaches for the early detection and monitoring of *C. fragile*, as highlighted by Muha et al. (2019).

The population genetic studies on *Codium* species have predominantly centered around *C. fragile*. Provan et al. (2005) discovered very low levels of genetic variation in populations of *Codium fragile ssp. Tomentosoides*. In the species' native range in Japan, only four haplotypes were identified, with introduced populations in other countries displaying only two of these haplotypes. Likewise, Kyu et al. (2006) observed low genetic diversity among populations of *C. fragile* in Korea. Provan et al. (2005) and Kyu et al. (2006) suggested that factors associated with colonization processes played a role, but they also proposed that the low fecundity of the plants and asexual modes of reproduction might contribute to this phenomenon (Kyu et al. 2006). However, it is important to note that this pattern was not observed in other *Codium* species (Provan et al. 2005).

3.2.3.4 Aquaculture

Since 1987, small-scale cultivation from natural blooming zygotes has been undertaken in Korea, using the settlement of wild zygotes (Hwang and Park 2020). However, production has been subject to variations based on recruitment success. Conversely, cultivation methods employing vegetative propagation were developed for *C. fragile*, proving successful in achieving higher production levels (Moriera et al. 2022). Hwang et al. (2005) pioneered cultivation techniques for generating seed stock, as later detailed in Hwang et al. (2009). This method includes blending vegetative thalli and seeding lines with the mixture; utricles and medullary filaments remain on these lines, and seed frames are placed in a nursery tank for a month to grow. Afterward, the seed frames are transferred to the sea, where, aided by natural water currents, medullary filaments grow and begin to form fleshy thalli after 40 days. Subsequently, seed lines are removed from the frames and wound around long lines. The thalli undergo approximately 7 months of growth before reaching the harvest stage (Hwang et al. 2009). This cultivation approach has significantly enhanced production, increasing from less than 1 kg-fresh weight to 7 kg-fresh weight per 1 m culture rope (Hwang and Park 2020).

While vegetative fragmentation is simpler due to the absence of manipulation in the sexual life cycle, it carries a higher risk of adverse effects related to the loss of genetic diversity. This may result in increased vulnerability to diseases and reduced overall production (Moriera et al. 2022).

3.2.3.5 Considerations on genetic risk to wild conspecifics

Nyberg and Wallentinus (2005) conducted a comparison of traits among 113 introduced macroalgal species in Europe, and *C. fragile ssp. Tomentosoides* emerged as the riskiest macroalgae due to its dispersal capability, likelihood of establishment, and ecological impact on the receiving community. The introduction of *C. fragile* has also led to economic losses, particularly in the aquaculture industry (Neill et al. 2006). However, other native *Codium* species from different regions do not seem to present similar issues. Unfortunately, there is a lack of information regarding these species in the Gulf, including details on abundance, population structure, and ease of spread and establishment. Knowledge of these factors is crucial for assessing the risks associated with the cultivation of *Codium* in the Gulf.

Based on the available information, the culture of *Codium* species may pose a high risk to natural populations, *if* native species possess characteristics similar to those observed in *C. fragile*. Dispersal to wild populations is likely, and vegetative propagation may result in low genetic diversity in cultured material, which may impact natural populations directly (introgression) or indirectly (displacement). However, native *Codium spp*. may not present a risk level equivalent to *C. fragile*, and lack of information makes it challenging to assess potential genetic risk from *Codium spp*.

Nevertheless, there are general recommendations to mitigate risk, including the utilization of *Codium* species native to the Gulf, preferably those specific to the region of the farm operation within the Gulf. Additionally, employing techniques such as environmental DNA (eDNA) may be important to ensure that *C. fragile* is not inadvertently propagated at farm sites. This is important because *C. fragile* has the potential to outcompete and displace native species, either in cultivation or natural populations, and early detection is key to controlling its spread (Muha et al. 2019). Instances in Chile and the North Adriatic Sea suggest that artificial substrata have served as stepping stones for the dispersal of this invasive species, as discussed in Neill et al. (2006). It is important to identify the most critical propagules for the colonization of new sites (spores or drifting plants), as they have different dispersal capacities. Mitigation strategies should involve the removal or increased distancing of artificial structures to minimize dispersal, in addition to regular treatment, cleaning, or replacement of aquaculture equipment. Such measures have been recommended to mitigate spread in Chile (Neill et al. 2006).

While native *Codium* species likely do not present an equivalent risk as *C. fragile*, the lack of additional information on these native species makes it difficult to assess the level of potential risk. If these species possess characteristics similar to those observed in *C. fragile*, then cultivation of *Codium* species likely carries a high risk of impacting natural populations. However, the degree of uncertainty remains high due to the insufficient information available for the species in the Gulf.

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3.2.4 Gracilaria species

3.2.4.1 Range/Description

The Gracilariaceae family encompasses a diverse group of red algae, featuring species that can exist in both benthic and free-living forms (Gurgel et al. 2004). Notably, the genus *Gracilaria* holds global significance, as highlighted by Lipinska et al. (2023), as representing some of the most economically significant agarophytes (Abreau et al. 2009). These species support a thriving agar industry that encompasses both cultivated and wild plants, as outlined by Lopez-Bautista and Kapraun (1995). As a result, commercial cultivation of *Gracilaria* has been established in regions like Chile since the 1980s (Abreu et al. 2009). The algae's properties extend to antiviral, anti-inflammatory, and anti-hypertensive attributes, along with other uses in pharmaceutical and industrial sectors (Gurgel et al. 2004, Iha et al. 2018, van Ginneken and de Vries 2018, Lipinska et al. 2023). *Gracilaria* species also hold potential in waste recycling, particularly within multi-trophic aquaculture systems (Halling et al. 2013, Samocha et al. 2015). Beyond their industrial applications, *Gracilaria* species have culinary value and find a place in dishes such as salads (Klinkenberg 2020).

Because of their commercial uses, some *Gracilaria* species have encountered population declines in their natural habitats due to excessive harvesting (Pereira and Yarish 2008), however, other species have exhibited remarkable success as invasive species (Lipinska et al. 2023). These species possess an inherent ability to swiftly colonize new environments, likely due to their resilience to various stressors, including fluctuations in nutrient levels, salinity, and temperature (van Ginneken and de Vries 2018, Lipinska et al. 2023). This adaptability to a wide array of conditions significantly contributes to their invasive potential, as described by van Ginneken and de Vries (2018).

With their warm-water growing seasons, ease of propagation, rapid growth rates, and high tolerance to diverse environmental conditions, *Gracilaria* species emerge as ideal candidates for aquaculture endeavors, as emphasized by Gurgel et al. (2004).

Gracilaria tikvahiae has been identified as one of the most prevalent benthic species of *Gracilaria* in the Gulf. It exhibits a wide-ranging distribution within this region, thriving in diverse habitats such as bays, inlets, and estuarine environments (Gurgel et al. 2004). This species holds economic significance for its role in agar production, though agar content may vary based on specific culture conditions, as noted by Samocha et al. (2015). Notably, this species displays remarkable adaptability to environmental parameters, including temperature and salinity. It demonstrates the capacity to withstand a broad salinity range, roughly between 10-40 ppt, with its prime growth observed in the 25-33 ppt range (Gurgel et al. 2004) Moreover, it exhibits a remarkable temperature tolerance, existing in conditions ranging from 0-35°C, with an optimal range between 20-28°C (Gurgel et al. 2004). This temperature range, in particular, continues to raise questions as to whether individuals found under ice sheets in the northeast are the same species thriving in tropical waters in the Gulf and further south (Gurgel et al. 2004).

This complexity, particularly concerning its southernmost limit, remains an area of ongoing investigation, as described by Gurgel et al. (2004).

Image from Redmond et al. 2012

G. tikvahiae are morphologically variable, contingent on the specific strain and prevailing growing conditions. This seaweed assumes a bushy, branching form, characterized by rounded branches that irregularly extend, and thalli may be cylindrical or flat (Gurgel et al. 2004). The coloration of its blades typically ranges from red to brownish, green, or nearly black based on light exposure and nutrient availability (Gurgel et al. 2004). The blades originate from a flattened disc, serving as the holdfast for attached species, and growth is driven by an apical meristem, located at the tip of each branch (Gurgel et al. 2004).

3.2.4.2 Biological Characteristics

Members of the red algal family Gracilariaceae feature a triphasic life history characterized by isomorphic diplohaplonty. This term implies that the gametophyte and tetrasporophyte phases share identical appearances, as erect branched thalli growing from a perennial holdfast (Guillemin et al. 2008). Visual differentiation between these phases is impossible to the naked eye, with the exception of fertilized female gametophyte bearing cystocarps (the carposporophyte phase) which can be distinguished (Wehrenberg 2011, Valero et al. 2017). These two phases often spatially and temporally overlap, and appear to occupy similar biological niches (Wehrenberg 2011).

In the triphasic life cycle of *Gracilaria*, as described by Guillemin et al. (2008), meiosis occurs on the reproductive diploid tetrasporophytes, giving rise to haploid tetraspores. After release, these tetraspores attach to the substrate, forming perennial holdfasts and developing into haploid male and female gametophytes. Male gametes, lacking flagella in red algae, are released from male gametophytes into the water, and seek eggs on the female gametophyte thallus (Wehrenberg 2011). Fertilization takes place on the female gametophyte, leading to the development of a cystocarp—a third stage that grows directly on the female gametophyte thallus as small bumps (Klinkenberg 2020). Through mitotic division, thousands of diploid carpospores are produced in this stage. Upon release, these carpospores attach to the substrate, and then develop into perennial holdfasts and eventually grow into tetrasporophytes (Guillemin et al. 2008). Reproduction in these species peaks in late summer at high latitudes, whereas in the tropics, it may be high throughout the year. In temperate regions, the fastest growth rate and highest biomass occur in late summer, while in the tropics, peak biomass occurs most often in winter (Kain and Destombe 1995).

Gracilaria species can also propagate through vegetative fragmentation, occurring when thalli of either the diploid tetrasporophytes or haploid gametophytes break (Guillemin et al. 2008, Valero et al. 2017). Fragments of any size and at various locations along the thallus have the potential to grow into new thalli, and the process of fragmentation may stimulate further growth and branching in the parent plant (Wehrenberg 2011). In sediment habitats, underground thalli may enable the species to over-winter during harsh periods, and studies have shown the resumption of growth after burial for up to four months (as reviewed in Wehrenberg 2011). Another mode of propagation for these species involves free-floating thalli, where plants detached from the holdfast can grow and propagate vegetatively indefinitely, and potentially form extensive beds (Guillemin et al. 2008).

The *Gracilaria* life-cycle results in three propagation mechanisms for these species: sexual reproduction based on carpospores, asexual reproduction through the release of tetraspores, and vegetative fragmentation from either the diploid or haploid phases (Guillemin et al. 2008, Wehrenberg 2011). The utilization and frequency of each method are influenced by factors such as water velocity, plant density, geographic location, available substrate, and fragmentation frequency (Wehrenberg 2011). For instance, in a study in California, *G. andersonii* exhibited year-round sexual fertilization at one site, while at another site, vegetative fragmentation was the primary method reproduction; the author suggested that substrate type was the factor that likely influences the different reproductive modes in these populations (Wehrenberg 2011).

Limited information is available regarding spore dispersal in *Gracilaria* species, with both tetraspores and carpospores considered significant dispersal mechanisms (Destombe et al. 1992). Research on *G. verrucosa* by Destombe et al. (1992) revealed a relatively short dispersal phase, and spores were not dispersed far from parent plants. While it has been suggested that haploid spores may have longer dispersal capabilities compared to diploid spores, both spore types can survive for weeks and endure days of desiccation. Seasonal changes may influence the germination rate of these spores (Kain and Destombe 1995). In terms of gamete dispersal, non-motile male gametes are estimated to have a lifespan of 6 hours, with dispersal limited to within a few meters of the male gametophytes (Destombe et al. 1992, Kain and Destombe 1995). Despite their short lifespan, fertilization in *G. verrucosa* was documented over a distance of 80 m (as reviewed in Kain and Destombe 1995).

The dispersal of *Gracilaria* species is also influenced by their tendency to fragment. Albright (2021) discovered that *G. andersonii*, within the San Francisco estuary, was more prone to fragmentation compared to other species in the same region. Albright observed that the tensile strength of thalli may vary based on the reproductive method employed by the population and the type of habitat it occupies (rocky substrate vs sediment). In the San Francisco estuary, the population relies on vegetative fragmentation as its primary mode of reproduction, and its lower tensile strength may contribute to more frequent fragmentation and subsequent population growth (Albright 2021).

3.2.4.3 Population Genetics

There are few population genetic studies of *Gracilaria* species. Most genetic research has been primarily dedicated to resolving the taxonomic identification of *Gracilaria* species worldwide. Because of the intriguing life-cycle of these species, capable of both sexual and asexual reproduction, the *Gracilaria* genus holds interest as an evolutionary and ecological model species (Lipinska et al. 2023). As an example, Wehrenberg's (2011) genetic study revealed that populations displaying persistent differences in reproductive modes could still be classified as the same species. While these findings are fascinating from an evolutionary perspective, determining genetic population structure among populations with varying life-cycle phases and modes of reproduction may not be straightforward.

A population genetics study utilizing two microsatellites revealed that sexually reproducing *G. gracilis* populations displayed only weak, but significant structuring, with a low degree of inbreeding observed in locations separated by 2.5 to 12 km. However, substantial genetic differentiation was detected among locations separated by 500 m to 1,200 km. The study suggested an overarching pattern of isolation by distance at distances greater than a 1 km, while gene flow prevented strong genetic differentiation over shorter distances (Engel et al. 1997). The researchers concluded that *G. gracilis* populations had the potential for local adaptation within ranges of a few hundred meters to several kilometers. Within a given site, there may be genetic heterogeneity among individuals across the habitat. However, wave action and other fine-scale processes result in more frequent gene flow overall at that level (Engel et al. 1997).

In macroalgal species with both sexual and asexual reproduction, the genetic effects of selection differ between these reproductive modes. During sexual reproduction, selection targets specific genomic regions. Over generations, genetic diversity in these regions, as well as neighboring regions linked physically to the selected targets, is reduced. In contrast, asexual clonal reproduction mimics complete physical linkage across the entire genome, leading to more rapid fixation of single genotypes and loss of genetic diversity. The decrease in genetic diversity not only limits the available genetic pool for trait improvement but also hinders a population's ability to adapt to new environmental challenges or conditions (Guillemin et al., 2008). Guillemin et al. (2008) found that cultivated *G. chilensis* populations had reduced genetic diversity due to clonal propagation practices compared to wild populations. However, asexual fragmentation preserved heterozygosity due to the lack of segregation in this mode of reproduction (Guillemin et al. 2008). Guillemin et al. (2008) also observed that cultivated genotypes had spread into wild populations.

Gurgel et al. (2004) conducted a study on *G. tikvahiae*, examining its genetic variability from Canada/NE U.S. through the western Gulf. The study used sequencing of the chloroplast-encoded rbcL and the nuclear internal transcribed spacer (ITS) region to infer taxonomic and phylogenetic relationships. The results, primarily based on the rbcL phylogeny, identified four lineages corresponding to distinct regions. These include the Canadian/north east U.S., south east Florida, eastern Gulf, and the Western Gulf lineages. However, the study could not precisely determine the geographic location in the northern Gulf that separates the western and eastern

Gulf lineages due to limited sampling. The authors suggest that potential genetic differentiation may occur near the mouth of the Mississippi River and/or the Chenier Plain, which is a marsh/estuarine system characterized by shallow muddy substrata extending from southeastern Louisiana to northeastern Texas (Gurgel et al. 2004).

Although no population genetic studies were found for *Gracilaria* species in the Gulf at a finer scale, the identified distinct lineages in the above study suggest the presence of dispersal barriers among some populations in the region. Future genetic research should strive to pinpoint the specific location of this lineage break and determine if there is finer-scale genetic structuring among populations within both the western and eastern portions of the Gulf. For any forthcoming genetic research, there are now genomic resources that may be utilized to enhance resolutions in those studies, including genome assemblies (with differing levels of completeness) for *Gracilaria chilensis*, *G. gracilis*, *G. caudata*, and *G. vermiculophylla*, accessible at https://rhodoexplorer.sb-roscoff.fr (Lipinska et al. 2023). Moreover, sequences of chloroplasts and mitochondrial genomes are accessible for numerous *Gracilari*a species (Iha et al. 2018).

3.2.4.4 Aquaculture

The predominant and straightforward cultivation method for *Gracilaria* species involves asexual propagation, wherein growers use thallus tips to clonally generate new plants (Pereira and Yarish 2008). Observations at farm sites suggest that the selection for vegetative propagation may favor sterility (Wehrenberg 2011). Guillemin et al. (2008) noted that 40% of cultivated *G. chilensis* produced reproductive structures, but sexual reproduction was rare, indicating an incomplete life cycle under culture conditions. Domestic cultivation through asexual fragmentation may also unintentionally select for diploidy, possibly due to heterosis in heterozygotes, leading to an excess of heterozygotes in asexually propagated populations (Guillemin et al. 2008, Valero et al. 2017). Debate exists regarding whether the observed heterozygote excess indicates selection for heterozygous diploids or if clonal propagation itself leads to the accumulation of mutations, resulting in a heterozygote excess. Mutational models for clonally reproduced organisms predict the accumulation of a large number of mutations over many generations. However, the extensive production of clonally reproduced individuals for commercial purposes may also contribute to a substantial number of mutations (Guillemin et al. 2008).

Clonal reproduction offers benefits such as consistent production due to genetically identical individuals (Redmond et al. 2014), ease of selection and maintenance of desired phenotypes without the risk of loss from recombination in sexual reproduction (Valero et al. 2017), potentially higher growth and survival rates (Guillemin et al. 2014, Valero et al. 2017), and prevention of recombination of cultivated strains with wild conspecifics (Valero et al. 2017). However, drawbacks include reduced genetic diversity in the propagated populations compared to wild populations (Halling et al. 2013, Hurtado et al. 2015). Guillemin et al. (2008) found that cultivated populations of *G. chilensis* contained a third of the genetic diversity as nearby wild populations, potentially diminishing resilience to novel challenges (Valero et al. 2017). Higher rates of sterility in these populations may also limit opportunities for breeding improvements (Valero et al. 2017).

Spore seeding provides an alternative method for *Gracilaria* propagation, involving the seeding of spores from mature carposporophytes (stage producing diploid carpospores) or tetrasporophytes (stage producing haploid tetraspores) onto a substratum (Redmond et al. 2014). This process allows the spores to develop into juvenile plants, which are then placed out at the farm site. As described by Redmond et al. (2014), the spores are released over the desired substrata, such as seed lines, by placing spore-bearing thalli on a screen suspended in water. After a 24-hour period at 20°C, the spores settle undisturbed for 24 to 42 hours in dim light. The seeded lines are maintained at 20°C under low light for 2 months until visible juvenile plants develop. These juveniles are then out-planted to the culture site.

The seeding method offers the convenience of plants attached to lines, eliminating the need to tie individual plants. Additionally, a significant advantage is the minimal volume of material required to establish a commercial farm; only 30 to 40 kg of cystocarpic plants may serve as spore stock, compared to the 10,000 kg needed for a 1 ha farm using the tying method (Alveal et al. 1997). Another notable benefit is the introduction of recombination through sexual reproduction, aiding in the maintenance of genetic diversity crucial for population adaptation to new challenges and the development of high-quality cultivated lines over the long term (Halling et al. 2005, Redmond et al. 2014). However, drawbacks include a two-month incubation period in the nursery before out-planting, and higher levels of phenotypic variation in cultivated individuals (Redmond et al. 2014).

Gracilaria cultivation can utilize a suspended rope system, where a floating longline is anchored in place with buoys. *Gracilaria* plants are attached to the line by tying with smaller twine and are allowed to grow further once outplanted. Out-planting occurs when temperatures are above 15°C. This approach can also be used for seeding, where lines are outplanted when plants are approximately 13 cm in height, as mentioned above. Harvesting methods vary, with options including trimming outer growth every 2 to 4 weeks or harvesting the entire plant (Redmond et al. 2014). This longline approach has been successfully adopted in the Republic of Korea and India (Mantri et al. 2023). Other cultivation systems, such as net tubes or floating cages stocked with unattached fronds, are also possible (Redmond et al. 2014). In warmer climates, bottom culture is a popular technique, involving seeding plants onto rocks spread on the bottom in shallow areas or attaching plants to lines suspended just above the bottom, similar to suspended line culture but less flexible for depth adjustment (Redmond et al. 2014).

Common challenges in *Gracilaria* cultivation include grazing, fouling, and environmental stress, especially in warmer regions. Effective control measures involve managing the depth of grow-out lines (deeper leads to less settlement), optimizing stocking density (higher is preferable), and strategically timing out-planting and harvest, particularly in regions with seasonal shifts in water temperatures and other conditions (more critical in temperate climates than in tropical regions) (Redmond et al. 2014). While *Gracilaria* is relatively stress-tolerant, variations in light, salinity, and temperature can impact growth (Redmond et al. 2014). As summarized in Redmond et al. (2014), mitigating risks from extreme weather events is crucial, and protective measures include bringing lines into storage tanks during storms or adjusting the depth of lines, as permits allow, to avoid damage from extreme wave action or runoff events.

Improvement of *Gracilaria* strains, where it is utilized, has predominantly centered on enhancing agar production. The initiative to correlate enhanced agar production with genomic profiles was initiated in the 1990s (Lopez-Bautista and Kapraun 1995).

3.2.4.5 Considerations on genetic risk to wild conspecifics

In certain regions worldwide, natural populations of *Gracilaria* are facing a decline due to overharvest (Pereira and Yarish 2008). Simultaneously, introduced *Gracilaria species* exhibit a high degree of invasiveness (Lipinska et al. 2023). The same characteristics that make these species appealing for cultivation, such as easy propagation from spores and vegetative fragments and high tolerance to environmental stresses like salinity and temperature, also heighten their risk as invasive species (Gurgel et al. 2004; van Ginneken and de Vries 2018). This invasiveness has already been demonstrated on the east coast of the U.S., where the invasive *G. vermicuphylla* has spread along large portions of the U.S. Atlantic coastline and is displacing the native *G. tikvahaie* in the north east regions (Nettleton et al. 2013).

In the context of offshore aquaculture, careful consideration must be given to the dispersal and subsequent growth of propagules (gametes and spores) and vegetative fragments for *Gracilaria* species. There is potential for reproductive structures to develop during the growout phase, especially with year-round reproduction in warmer regions or during summer months in temperate areas. Spore dispersal appears to be more significant than gamete dispersal, with documented spore survival over weeks (Kain and Destombe 1995). While gametes have limited duration and dispersal, documented fertilization over a distance of 80 m suggests a non-negligible impact (as reviewed in Kain and Destombe 1995). Both gametes and spores, being non-motile, disperse according to prevailing currents. Consideration of fragmented thalli is also critical for assessing dispersal propensity in these species, as vegetative growth is possible from any size fragment, and these displaced thalli may float and propagate indefinitely (Guillemin et al. 2008). As noted by van Ginneken and de Vries (2018), the act of harvesting *Gracilaria* species releases spores and fragments. Harvesting methods vary, with some involving the trimming of outer growth every 2 to 4 weeks, while others opt for harvesting the entire plant (Redmond et al. 2014); repeated harvesting likely increases the total amount of cultivated material dispersed from the operation each harvest season.

Population genetic studies of *Gracilaria* species are limited, but Engel et al. (1997) found low yet significant levels of genetic structure between locations separated by 2.5 to 12 km. In contrast, large genetic differentiation was observed between locations separated by hundreds to thousands of kilometers, suggesting a general pattern of isolation by distance at distances greater than one kilometer. Gene flow, facilitated by the dispersal of propagules and fragmented thalli, prevented genetic differentiation over shorter distances (Engel et al. 1997). The patterns of genetic connectivity over distances greater than a kilometer are likely influenced by oceanographic currents throughout the year. The risk of dispersal and the dispersal shadow from an aquaculture operation will also be influenced by current patterns in the region during the growout period, potentially extending over kilometers from the offshore operation.

If propagules or vegetative thalli successfully reach the coastline, their potential to colonize is high due to their broad tolerance of environmental factors and suitability for various habitats. The cultivation method, whether through sexual spore production or asexual fragmentation, presents different risks to natural populations. While the impact on wild populations from asexually propagated cultivated populations is uncertain, Guillemin et al. (2008) found that cultivated genotypes successfully spread into wild populations. Asexual fragmentation, as observed by Guillemin et al. (2008), rapidly reduces genetic diversity in the cultured population. However, clonally produced populations are generally less fertile than sexually reproducing ones and may pose a lower risk of genetic introgression with natural populations, though fertility assessments are necessary for each cultured population. Nonetheless, they may still spread and propagate asexually in areas overlapping with wild beds. Sexually propagated populations may be more successful at genetically introgressing into wild populations; however, compared to asexual cultivated populations, they may retain more of the genetic diversity present in wild populations.

In the Gulf, the predominant *Gracilaria* species, *G. tikvahiae*, is widespread in the western and eastern Gulf, but its distribution in the northern Gulf is considered patchy and ephemeral. A genetic break exists in the northern Gulf, with distinct lineages in the western and eastern Gulf, and the exact location of this break, possibly across the mouth of the Mississippi River or the Chenier Plain, remains uncertain (Gurgel et al. 2004). As aquaculture operations can serve as stepping stones for species dispersal across biogeographic breaks, aquaculture in the northern Gulf should be limited for *G. tikvahiae* until finer-scale population genetic studies clarify the location of the break and the degree of genetic structuring within the two regions.

Given the above information, cultivating *Gracilaria* species in the Gulf likely presents a moderate risk to natural populations. For *G. tikvahiae* specifically, the level of risk depends, in part, on the potential for dispersal across the distinct lineage break in the northern Gulf, influenced by current patterns between the operation and coastal populations.

Mitigation strategies to reduce the risk of fragmentation and thallus biomass loss from *Gracilaroid* culture may include exposing juveniles in the nursery stage to strong currents to increase tensile strength, controlling the depth of grow-out lines, and lowering them by several meters to minimize wave energy, grazing, and fouling, all of which contribute to thalli breakage (Graham 2008, Redmond et al. 2014). Additionally, to further minimize dispersal, it is recommended not to leave any biomass at the grow-out site at the end of the harvest schedule (van Ginneken and de Vries 2018).

3.2.4.6 References

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3.2.5 *Eucheuma* Species

3.2.5.1 Range/Description

Eucheuma is a genus of pantropical marine red algae that thrive in sandy and rocky substrates with moderate to strong water currents (Dawes 1974, Zemke-White and Smith 2006). These algae can have thalli ranging from 35 to 75 cm in length, with main branches extending 7 to 9 cm. The plants exhibit color variation, such as green, brown, or red, and display differences in branch flexibility, ranging from brittle to cartilaginous (Freile-Pelegrin and Robledo 2008, Azanza 2023).

The macroalgal species collectively known as eucheumatoids are recognized for their production of commercially valuable carrageenan. Recent taxonomic reclassifications have categorized all kappa-carrageenan producing species under the genus *Kappaphycus*, iota-carrageenan producing species under the genus *Eucheuma*, and beta-carrageenan producing species under *Betaphycus* (Azanza 2023). Each genus encompasses species with distinct morphological characteristics, contributing to the diversity within this group (Azanza 2023).

Among the 30 known *Eucheuma* species, only two are extensively cultivated for commercial purposes: *Eucheuma isiforme* and *E. denticulatum*. While *E. denticulatum* is native to the Indian and Western Pacific Oceans, E. *isiforme* is indigenous to the Caribbean and Gulf (Zemke-White and Smith 2006, Kim et al. 2017). *E. isiforme* is distributed in the intertidal to subtidal zones in the Caribbean and Gulf, particularly in the Northeastern, Southeastern, and Southwestern regions of the Gulf (Fredericq et al. 2009). Notably, the Gulf, off the coast of Florida, is home to various *Eucheuma* species, including *E. gelidium*, *E. acanthocladum*, and *E. nudum*, although *E. isiforme* stands out as the most promising candidate for mariculture due to its abundance, accessibility, stable life history, perennial life cycle, and the highest yield of iota-carrageenan (Dawes 1974, Hayashi et al. 2017).

In the Yucatan peninsula, the largest standing stock of *E. isiforme* is observed during colder months (November–December), with peak growth occurring from October through April, and a period during the summer in which there is no growth, and plant density remains generally low during this time (Robledo and Freile-Pelegrin 2011). In the Gulf near the Florida Keys, *E. isiforme* thrives in exposed marine waters with tidal currents of up to 0.5 knots and at sites with a continuous limestone substrate. Typically found at depths ranging from 0.5 to 3 m during low tide in areas with high water visibility, this species favors an optimal temperature range between 20 and 31°C (Dawes 1974). High-density areas may exhibit 10 plants per square meter (Dawes 1974). Natural populations in the Gulf follow a seasonal pattern, with the highest growth rates observed in the spring, summer, and early fall months (Dawes 1974), in contrast with observations from Yucatan peninsula.

The genera *Kappaphycus* and *Eucheuma* collectively contribute to over 80% of global carrageenan production, with *Eucheuma* species specifically known for producing iota carrageenan (Neish et al. 2017). Cultivation of these species is primarily concentrated in Southeast Asia, including countries such as Indonesia, the Philippines, Malaysia, China, and Vietnam (Kim et al. 2017, Tan et al. 2022). Additionally, cultivation occurs in other regions such as Belize, Antigua and Barbuda, Brazil, and Tanzania (Freile-Pelegrin and Robledo 2008, Kim et al. 2017, Eggertsen and Halling 2021). *Eucheuma*, in particular, has drawn interest for cultivation in the Gulf in the U.S. (Racine et al. 2021). However, application of aquaculture for this species has been limited due to the lack of processing facilites also needed to extract carrageenan from the raw biomass (A. Concepcion, pers. comm.). Extensive studies on the cultivation and carrageenan production of *Eucheuma* species have been conducted across its global range, including in Mexico around the Yucatan Peninsula, Belize, and the Caribbean (Robledo and Freile-Pelegrin 2011, Hayashi et al. 2017). Freile-Pelegrin and Robledo (2008) observed variations in carrageenan content, properties, and biochemical composition among populations from these different regions.

Carrageenan finds extensive applications in both the food and pharmaceutical industries, along with other derivatives derived from seaweeds. In the realm of food, it serves various purposes, such as direct consumption as a food or vegetable, and as a carrageenan source employed for thickening, stabilizing, or emulsifying purposes in dairy products like chocolate milk and ice cream, as well as in reprocessed meats, toothpaste, and a diverse array of food items like puddings, salad dressings, and more (Azanza 2023). Additionally, carrageenan is utilized in animal feed, pet food, fertilizer, and various industrial products and processes, spanning applications like air fresheners, cosmetic product binders, horticulture laboratory culture mediums, soil conditioners, insect repellents, and cough medicines (Trono and Valdestamon 1994, Azanza 2023).

Due to their significant market value for carrageenan extraction, these species are vulnerable to exploitation and depletion of natural populations, as evidenced in Florida, for instance (Dawes 1974). Moreover, in numerous locations, the abundance of these plants is seasonal, and storms can exacerbate the reduction in the density of natural populations (Dawes 1974). Similar dynamics elsewhere in the world have prompted the introduction of non-native species in various regions when local species' biomass production proved insufficient (Hayashi et al. 2017).

3.2.5.2 Biological Characteristics

Similar to other red algal species, *Eucheuma* demonstrates a triphasic alternation of generations life cycle. This species is isomorphic, meaning that the tetrasporophyte and gametophyte stages are morphologically similar. The diploid tetrasporophytes generate haploid tetraspores through meiosis, which, upon settling, develop into haploid male and female gametophytes. Sperm are produced on the male gametophytes, and eggs are produced on the female gametophytes. The released sperm fertilize the egg on the female gametophyte's carpogonial branches. The fertilized embryo matures into a diploid carposporophyte, residing on the thallus of the female gametophyte. The carposporophyte produces diploid carpospores, which upon release then develop into diploid tetrasporophytes (Dawes 1974, Zemke-White and Smith 2006). Dawes (1974) observed that during certain periods of the year, few male or female gametophytes are present, and specifically in the fall and winter months, vegetatively-produced plants or tetrasporophytes (constituting up to 60% of the plants) are more prevalent.

The thallus of *Eucheuma* species is brittle, and when fragmented, these pieces can regenerate vegetatively. However, due to their weight, these thalli have a tendency to settle quickly (Dawes 1974). Azanza-Corrales et al. (1992) discovered that through vegetative regeneration, the same life-cycle phase of the plants persists. Consequently, sites may differ in their proportions of male/female gametophytes and tetrasporophytes, depending on the original introduction or colonization in a given location.

3.2.5.3 Population Structure

While few studies have delved into the population genetic structure of eucheumatoid species, there has been progress in developing genetic markers for the reliable identification of color and morphological variants (Neish et al. 2017). This is particularly crucial as the plastic morphology of these species poses challenges in characterizing both inter- and intraspecific variability (Tan et al. 2022). Recognizing the importance of genetic resources for sustained carrageenan production, recent emphasis has been placed on genetic characterization of these species. This not only serves the purpose of identifying threats to wild stocks but also informs the development of conservation policies (Tan et al. 2022).

As sites near or associated with the cultivation of eucheumatoids often originate from a few individuals or broken thalli of farmed cultivars, they are genetically nearly identical (Neish et al. 2017). Consequently, the genetic diversity within these species has been underestimated, highlighting the need for sampling efforts that accurately assess diversity or aim to identify new cultivars (Neish et al. 2017). In Malaysia, where cultivation has been ongoing for the past five decades, Tan et al. (2022) identified four species across the Eastern Sabah region, with up to three species coexisting in single sites. The sequencing of the cox2-3 spacer and cox1 revealed 17 novel haplotypes across these species, indicating high genetic diversity in the wild sampled regions (Tan et al. 2022). However, the authors also observed farmed haplotypes in wild populations, suggesting a potential competition with indigenous eucheumatoid populations in East Malaysia (Tan et al. 2022). The study further highlighted that documenting the displacement of native populations by cultivated eucheumatoids may take decades. Consequently, the authors recommended periodic sampling of wild beds and cautioned against culturing non-native species, which could overgrow and displace local strains and species, disrupting the local ecosystem (Tan et al. 2022).

3.2.5.4 Aquaculture

The cultivation of *Eucheuma* relies on vegetative propagation, where 'seedlings' are essentially cuttings obtained from the best mature plants during harvest, serving as seedling material for subsequent crops (Ask et al. 2003). Despite variations in color and branching morphology observed in cultivars developed over decades (Ask and Azanza 2002), the farmed material is consistently generated through clonal propagation, a practice unchanged as the industry has expanded (Hayashi et al. 2017, Neish et al. 2017). Dawes et al. (1993) explored micropropagation in eucheumatoids and discovered that even fragments as small as 0.5 cm exhibited almost 100% new branch production. While controlling the sexual reproductive cycle in these species poses significant challenges, as discussed in Tan et al. (2022), Ask and Azanza (2002) note successful development of *in vitro* cystocarp formation, carpospore release, and germination in eucheumatoids. Utilizing sexual reproductive cycles could potentially offer greater flexibility in breeding manipulations.

Despite its time-intensive and laborious nature, the predominant method for cultivating *Eucheuma*, known as the "tie-tie" method, involves securing 50 to 100 cuttings with soft plastic materials at intervals of 20 to 25 cm to monofilament lines submerged in the sea (Dawes et al. 1993). With *Eucheuma* thalli having diameters exceeding 2cm, the tying process to monofilament lines is relatively straightforward, and the fragments are loosely tied to permit movement and orientation with the water current (Ask and Azanza 2002). Various cultivation parameters such as stocking density, propagule or 'seedling' size, line spacing, maintenance frequency, and planting depth are all site- and season-specific factors that must be determined for each farm location (Ask and Azanza 2002, Azanza and Ask 2017).

These lines are deployed as either shallow or deep set and connected to fixed-off bottom rigs, floating rafts, long lines, and more intricate rafting arrays and long-line configurations (Hayashi et al. 2017). In its simplest form, wooden stakes are used to anchor the ends of cultivation lines into the substrate (Hayashi et al. 2017). This off-bottom culture method is employed in East Africa, where eucheumatoids are cultivated on monolines suspended between wooden pegs in the intertidal zone (Eggertsen and Halling 2021). Some regions utilize basket cultivation methods to mitigate herbivore grazing, although the labor required for biofouling cleaning and clearance is higher with this approach (Hayashi et al. 2017). Regardless of the method used, these species can be cultured at depths ranging from 0.5 to 3 m, ensuring exposure to at least 20% of light penetration, and water movement remains a crucial factor for successful cultivation of these species (Dawes 1974). Generally, crops are ready for harvest within 6 to 8 weeks (Dawes et al. 1993).

The "tie-tie" method is gradually being replaced by tubular netting cultivation, which has demonstrated increased productivity due to simplified planting and harvesting periods. Some producers opt for large nylon netting supported by stainless steel rings with a diameter of 1 m (Hayashi et al. 2017), and farmers have the option to simply detach the tubular nets and transport them to drying facilities for further processing (e.g., a process currently used in Brazil) (Hayashi et al. 2017). Efforts are underway to develop mechanized harvesting methods, to alleviate the labor-intensive processes associated with farming these species, although even including lower-tech solutions like line strippers can help to reduce some of this effort (Ask et al. 2003, Neish et al. 2017). Despite the potential advantages of alternative methods, the industry has been slow to adopt them due to reported slower growth, higher capital investment, or increased incidences of pest species associated with newer approaches (Ask and Azanza 2002).

Selective breeding has been conducted on cultivars in various locations, targeting phenotypes linked to growth rates and carrageenan content (Dawes et al. 1993). While breeding experiments using tetraspores have been conducted, they are not yet regularly employed by the commercial industry (Ask and Azanza 2002).

Common challenges in eucheumatoid culture include herbivore grazing, storm-induced biomass removal, and fouling by other seaweeds (Dawes 1974). Given the brittleness of these species, they are susceptible to damage and breakage from various environmental stressors (Dawes 1974). The removal of epiphytes is a time- and labor-intensive process, often requiring multiple interventions each week (Hurtado et al. 2006). However, neglecting to address epiphyte growth can increase drag on lines and plants, resulting in breakages and plant loss (Ask et al. 2003). Another significant concern for eucheumatoid farmers is the outbreak of a disease known as "ice-ice," leading to pigment loss in thalli tissue (hence the name) and the breaking off of branches (Ask and Azanza 2002). Unfortunately, the vector of this disease remains unknown (Kim et al. 2017).

An additional concern in echeumatoid culture is the limited genetic diversity observed in current cultivars. In certain regions, seedlings have begun to exhibit signs of diminished strain vigor and reduced production due to continuous clonal vegetative propagation (Hayashi et al. 2017). For instance, Tan et al. (2021) noted low genetic diversity in Malaysian cultivars spanning the years 2010-2020. This loss of diversity could potentially impede the cultivars' capacity for environmental adaptation and disease resistance, rendering them more susceptible to outbreaks of "ice-ice" or epiphyte infestations. The authors emphasized the necessity for local biobanks, where farmers can access seedlings and genetically distinct germplasm from both cultivars and natural populations, ensuring a sustainable seedstock supply. Incorporating sexual reproduction to introduce new genotypes may also aid in identifying thermally tolerant and disease-resistant cultivars, addressing industry concerns (Kim et al. 2017).

3.2.5.5 Considerations on genetic risk to wild conspecifics

For eucheumatoids, cultivated haplotypes have dispersed beyond farms and are now detectable in natural habitats (Tano et al. 2015, Eggertsen and Halling 2021, Tan et al. 2022). For example, in Tanzanian waters, two Southeast Asian strains of *E. denticulatum,* introduced in 1989 in Zanzibar*,* have been identified in natural populations such as Zanzibari reefs and macroalgal habitats (Tano et al. 2015). According to the findings of Tano et al. (2015), these nonindigenous haplotypes were present at all sampled sites in their study, even in locations not in proximity to farming sites. Additionally, there has been a significant reduction in the prevalence of East African haplotypes across these sites (Tano et al. 2015). For instance, in locations near farm sites where *E. denticulatum* covers more than 5% of the substrate, 75 to 95% of the samples collected were comprised of introduced haplotypes (Tano et al. 2015). Remarkably, even in locations where cultivation has never taken place, 50% of the sampled specimens had the introduced Southeast Asian haplotypes utilized in farm sites. This is despite these sites being situated 3 to 6 kilometers away from the nearest farming locations, positioned offshore, and separated from the primary culturing region by deep water channels (Tano et al. 2015).

The reason behind the transition from native to introduced haplotypes remains unclear, with uncertainty surrounding whether this shift resulted from the overharvest and decline of East African plants from the 1950s through the late 1970s, subsequently leading to opportunistic colonization by the introduced strain, or if the introduced strain outcompeted the native strains, or a combination of both factors (Tano et al. 2015). Likewise, in Malaysia, Tan et al. (2022) discovered that a cultivated strain escaped and established itself within the natural population. The dispersion and establishment of other cultured eucheumatoids away from farm sites has been documented in various global regions, including Hawaii, India, and Venezuela (as reviewed in Tano et al. 2015). However, it is important to note that this list may not be exhaustive, as surveys have not been conducted in numerous other regions (Ask et al. 2003).

Under specific conditions, rafting over distances is believed to be possible for this species. However, as mentioned earlier, the fragments are heavy and have a tendency to settle rapidly. It is hypothesized that during periods of strong wind and water movements, broken plant pieces may aggregate into larger drifting rafts, possibly consisting of multiple macroalgal species or driftwood, and travel to more distant sites. Once there, the fragments can easily reattach and grow in suitable substrate (Tano et al. 2015, Tan et al. 2022).

Notably, Tano et al. (2015) reported finding very few reproductive structures in natural populations, and these were observed only in native types and not in introduced strains. Therefore, the extent to which hybridization occurs between these different strains remains uncertain (Eggertsen and Halling 2021). Similarly, based on available genetic data in Malaysia, Tan et al. (2022) did not detect any signs of hybridization or introgression between wild and dispersed cultivated strains, but emphasized that much remains uncertain about these interactions. In the case of Tanzanian populations, the combined effect of the loss of native biomass and little sexual reproduction may result in very low effective population sizes in native wild populations, posing concerns for the fitness and longer-term adaptability of the remaining East African populations (Tano et al. 2015).

Limited information exists regarding the genetic structure of *Eucheuma* species, particularly *E. isoforme* in the Gulf, to provide guidance for seedstock selection or to infer the risk from dispersed cultured material on natural populations. Drawing from insights gained for *E. denticulatum*, Tano et al. (2015) and Eggertsen and Halling (2021) strongly recommend the use and cultivation of strains derived from local populations near the farming site. Tan et al. (2022) similarly emphasize exercising caution when cultivating non-native eucheumatoid species to mitigate the risks of bioinvasion.

Despite the seeming limitation of dispersal from offshore locations for this species, as suggested by their preference for shallow/upper water growth conditions and the weight of their fragments, documented instances of dispersal and colonization occurring kilometers away from farmed sites underscore the existence of dispersal potential for these species. This raises particular concerns in regions like the Gulf, where other frequently occurring species capable of floating (e.g., *Sargassum*) may contribute to rafting assemblages. Moreover, evidence from around the world indicates the ease with which strains can establish themselves in natural populations or new habitats.

For offshore cultivation of *Eucheuma* species in the Gulf, it is likely that cultivated fragments will find their way into natural populations. Based on the available information, the culture of *Eucheuma* species in the Gulf is likely to pose a moderate-to-high risk to wild populations in this region. The potential impacts of this scenario will depend on the use of endemic species and local populations, and on the scale of population structure detected within the region, which needs to be surveyed. However, impacts may be mitigated through activities such as preserving genetic diversity identified in natural populations, as well as maintaining genetic diversity in cultivars used for generating seedling material.

3.2.5.6 References

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4.0 Genetic Risk Factors and Management Measures

Culture candidate species for Southern California and Gulf, discussed in Chapters 2 and 3, are summarized in the below tables, with an emphasis on risk factors that could potentially contribute to genetic effects to wild populations. Risk factors are specifically related to reproduction and the potential for culture-wild interactions, and subsequent reduced population fitness and decline in genetic diversity.

The assessment of influence of species and population dynamics on the genetic risk level is based on specific risk factors that would influence genetic effects to wild populations from aquaculture based on species and population characteristics. The risk factors are: potential for maturity in culture (e.g. harvest after maturity age would present greater genetic risk), dispersal capacity (ability of spores to disperse over a large area presents a greater risk; potential for vegetative fragmentation and rafting presents a greater risk), current thinking on wild population abundance (low abundance of the local population would mean greater demographic contribution from cultured gametes, with potential for greater genetic risk), biological characteristics in cultured strains that may differ from wild populations, and knowledge on genetic structure and population structure of the species on a region level.

The evaluation of uncertainty in the risk level is based on available data to support findings on wild population status and genetic diversity. The Low/Moderate/High assessment for the genetic risk level and uncertainty presented in the tables is based on a broad review of the available research and scientific literature regarding wild population dynamics and characteristics for each species. The risk levels do not account for culture production levels, escape rates or other operational factors. As such the genetic risk levels in the table can be considered for factors that influence risk but should not be construed as a full assessment of genetic risk from aquaculture.

4.1 Southern California Aquaculture Candidate Species – Summary of Genetic Risk Factors

Table 4.1. Macroalgae Genetic Risk Factors – Southern California

Part A: Reproductive characteristics

Species Name	Common Name	Spawning Types	Spawning Season	Propagate from vegetative fragmentation (VF)	Spore Stages	Gamete Stages	Potential for Gamete Release in Culture
Alaria marginata	Ribbon kelp	Sexual reproduction	Fall spore release, gamete release in winter and spring.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs retained on female gametophytes.	Low to moderate; likely harvest prior to reproductive maturation, but possible from early maturing plants.
Fucus distichus	Bladderwrack	Sexual reproduction and asexual fragmentation; plants are monoecious and may also self-breed.	Year-round reproduction on plants that live 2-3 years.	Yes, entire wild populations may be generated from asexual fragmentation and grow attached (may reattach) or grow free-floating.	None	Gametes released from parent plants, with zygotes settling within 4-6 hrs (in lab setting).	High for sexual strains; low if vegetative fragmentation uses unattached strains.
Gracilaria andersonii	Sea Spaghetti	Sexual and asexual reproduction and vegetative fragmentation; frequency varies due to environmental factors.	Late summer.	Yes, from thalli fragments. Detached plants can grow and propagate vegetatively indefinitely.	Yes, tetrapores and carpospores.	Yes, male gametes released, eggs retained on female gametophytes and develop into carposporophytes.	High, reproductive structures may develop during grow-out, however, plants may be sterile if generated through vegetative fragmentation.

Species Name	**Common Name**	**Spawning Types**	**Spawning Season**	**Propagate from vegetative fragmentation (VF)**	**Spore Stages**	**Gamete Stages**	**Potential for Gamete Release in Culture**
Hedophyllum sessile (formerly Saccharina sessilis)	Sea Cabbage	Sexual reproduction.	Fall and winter.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs retained on female gametophytes.	Unknown; sporophytes may not reach maturity in grow out.
Laminaria setchellii	Southern Stiff Stiped Kelp	Sexual reproduction after 2-3 years in long-lived plants, low annual fecundity that increases with age.	Summer and fall months, but may occur year-round.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs retained on female gametophytes.	Unknown but likely low; majority of kelp does not produce sori until their second or third year of growth.
Macrocystis pyrifera	Giant Kelp	Sexual reproduction.	Year-round.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs often retained on female gametophytes.	High; kelp become reproductive at 150 cm in length, potential for maturation prior to harvest.
Mastocarpus spp.	Turkish Washcloth	Sexual reproductionand asexual development from carpospores.	Variable; dependant on whether sexual and asexual variants overlap in a site.	Not mentioned in reviewed studies, however, VF is common in other red algal species.	Yes, tetrapores and carpospores.	Yes, male gametes released, eggs retained on female gametophytes and develop into carposporophytes	Unknown.

Species Name	Common Name	Spawning Types	Spawning Season	Propagate from vegetative fragmentation (VF)	Spore Stages	Gamete Stages	Potential for Gamete Release in Culture
Nereocystis luetkeana	Bull kelp	Sexual reproduction.	Late summer and early fall, but may begin as early as spring.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs retained on female gametophytes.	Low to moderate; the majority of kelp may be harvested prior to sexual maturation, but some early maturation is possible.
Postelsia palmaeformis	Sea Palm	Sexual reproduction and selfing of gametes from same plant.	Late spring to early summer.	Not mentioned for wild populations; based on other kelp species, gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, zoospores.	Yes, male gametes released, eggs retained on female gametophytes.	Unknown; if similar to other brown algae, harvest will occur prior to sexual maturation for most individuals.
Pyropia spp.	Nori	Sexual and asexual reproduction; different species utilize both methods to varying degrees.	Summer to fall for Py. perforata.	Yes, filamentous sporophytes referred to as conchocelis undergo vegetative growth once they bore into shells (e.g., oyster shells).	Yes; zygotospores, monospores, conchospores, neutral spores, endospores, or archeospores	Yes, male gametes released, eggs retained on female gametophytes and develop into carposporophytes	High; reproductive structures develop quickly; frequent harvesting may reduce extent.
Saccharina latissima	Sugar kelp	Sexual reproduction.	Varies by location; may be year-round, some locations peaks in spring and again in fall.	Not mentioned for wild populations; gametophytes may be maintained in culture settings and propagated vegetatively for seeding purposes.	Yes, male gametes released, eggs retained on female gametophytes.	Yes, zoospores.	High; most kelp harvested prior to maturation, but early maturing individuals are possible.

Part B: Population dynamics

Species name	Common name	Native to region	Population health, if native	Ease of settlement	Population structure characterized
Alaria marginata	Ribbon kelp	Not found in So. Cal.; Pt. Conception is southern limit.	Not well characterized; populations may be stressed by warming water temperatures.	Moderate; occupy mid- to low-rocky intertidal zones in patches.	Isolation by distance, although some heterogeneity within sites. Possibly able to hybridize with related species.
Fucus distichus	Bladderwrack	Not found in So. Cal.; Pt. Conception is southern limit.	Generally abundant; although eutrophication and environmental pollutants may stress populations.	High; the species is capable of reattaching itself after fragmentation and may also grow unattached if attachments are unsuitable.	Not well characterized; one study found population genetic structure at scale of meters, while another study found low genetic structure across broader scales. Complicated by inbreeding and modes of reproduction.
Gracilaria andersonii	Sea Spaghetti	Yes.	Overharvesting in some species, although *G. andersonii* reported as abundant.	High; found in diverse habitats, including on exposed rock along the intertidal coasts or subtidal regions (up to 18 m), partially buried in soft sediments in estuaries and bays, and as unattached mats.	No population genetic studies published on *G. andersonii*, however in other *Gracilaria spp*. an overarching pattern of isolation by distance at distances greater than a 1 km was found with potential for local adaptation within ranges of a few hundred meters to several kilometers.
Hedophyllum sessile (formerly *Saccharina sessilis*)	Sea Cabbage	Not found in So. Cal.; Pt. Conception is southern limit.	No information was found pertaining to the health or abundance of *H. sessile* beds or populations along the northeast Pacific coast.	Moderate; recruits on rocky substrates of the mid-intertidal to shallow subtidal regions in semi-protected to semi-exposed environments.	No population genetic studies were identified.

Species name	Common name	Native to region	Population health, if native	Ease of settlement	Population structure characterized
Laminaria setchellii	Southern stiff stiped kelp	Yes.	No information was found pertaining to the health or abundance of *L. setchelli* beds or populations along the northeast Pacific coast.	Moderate; subtidal and intertidal rocky substrate with high wave energy.	No published studies; longevity of plants may contribute to genetic homogenization of populations across smaller scales; but structure across larger scales will likely depend on prevailing water currents to determine direction of dispersal from rafting fertile tissue. Strong recruitment years may be disproportionately represented in populations, and in subsequent age-classes.
Macrocystis pyrifera	Giant Kelp	Yes.	Southern population abundances are highly variable and prone to extensive die-back during warm water events; evidence for range contraction at southern extent of distribution, and predicted future declines in So Cal.	Moderate; attach to rocky substrate, need semi-exposed shoreline near upwelling.	Yes, genetic differentiation between Channel Islands, mainland central California and mainland Southern/Baja California, suggesting isolation due to ocean currents and local adaptation among these regions despite close geographic proximity between populations.
Mastocarpus spp.	Turkish Washcloth	Yes.	Not well characterized; specimens collected within the purported range of *M. papillatus* may actually constitute five species or clades, and classification of species in the southern portion of the range in California is uncertain, as both *M. papillatus* and *M. intermedius* may occur in this region.	Moderate to high; the species occupies rocky intertidal and shallow subtidal habitats.	No studies on *M. papillatus,* and limited for genus. In other *Mastocarpus spp.*, significant genetic structure was identified among sampled sites but did not align with geographic distance; patterns were further complicated by differing patterns of genetic connectivity in populations exhibiting obligate apomixis and those with sexual gametophyte and tetrasporophyte stages.

Species name	Common name	Native to region	Population health, if native	Ease of settlement	Population structure characterized
Nereocystis luetkeana	Bull kelp	Extremely uncommon in So Cal.; rarely found south of Pt. Conception.	Significant population declines in N. CA due to thermal stress and overgrazing, significant declines in Puget Sound, WA due to to thermal and nutrient stress.	Moderate to low; variability in successful recruitment, but not closely linked to spore density; several factors may trigger development.	No genetic structure detected in California; however, genetic diversity is higher in CA than in other portions of range. Need finer scale study with greater power to detect genetic structure patterns.
Postelsia palmaeformis	Sea Palm	Not found in So. Cal.; San Louis Obispo area is southern limit.	Unknown, but populations may be more ephemeral and dependent on year-to-year recruitment success.	Moderate; settles in high-energy, wave-exposed areas of the mid to upper rocky intertidal shores.	Yes; evidence of selfing in all *Postelsia* populations which likely helps ensure reproductive success for a short-lived species with very limited dispersal. Significant genetic differentiation among sporophyte clusters over small scales (e.g., 5 meters apart), and even greater genetic structure in populations separated by up to 23 meters.
Pyropia spp.	Nori	Yes, although these spp. have not been vetted for commercial cultivation. These include, *Py. Perforata* (the candidate most likely for cultivation), Py. *conwayae*, *Py. montereyensis*, *Py. columbiensis*, *Py. lanceolata*, *Py. pseudolancelota*, *Py. protolancelolata*, and *Py. Nitida*.	Unknown; many candidate species recently identified as distinct species.	Low; spores produced from thallus tissue must settle on shellfish shells or on one of a small number of suitable substrates to complete life-cycle, and conchocelis (life-stage on shells) will only produce conchospores if suitable environmental conditions are present.	Not well characterized for listed species; most genetic studies have focused on taxonomic revisions. Higher resolution genetic studies are needed to examine population connectivity, but generally spatial structure at varying scales noted in other species.

Species name	Common name	Native to region	Population health, if native	Ease of settlement	Population structure characterized
Saccharina latissima	Sugar kelp	Yes.	Unknown in this region.	Moderate; species recruit to rocky shorelines, growing in the intertidal and upper subtidal zones to depths of 15-30 meters.	No studies on the eastern Pacific; based on pattens in other regions, oceanographic processes were found to significantly influence genetic differentiation at both local and regional scales.

Part C: Culture information

Species name	Common name	Culture propagation	Culture grow-out	Dispersal Capacity	Current aquaculture Status	Priorities for study
Alaria marginata	Ribbon kelp	Collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines.	Seed lines wrapped around long lines.	Low; related species show most dispersal is within 10 m of parent plants, no buoyancy mechanisms. Frequency unknown of rarer long-distance dispersal.	Cultured in British Columbia, Canada and Alaska.	Population genetic structure in region, water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Fucus distichus	Bladderwrack	Asexual vegetative propagation (unattached strains more successful) and sexual seed production onto seed lines.	For vegetative propagation, drifting net cages or baskets; for sexual reproduction, long lines.	High; air filled bladders help fertile/non-fertile vegetative fragments disperse over 10s to 100s of kms.	Very little culture for this species, some experimental culture in Germany.	Population genetic structure in region, water particle dispersal studies to predict directions propagules/dispersed material will travel.
Gracilaria andersonii	Sea Spaghetti	Asexual propagation (most common), sexual spore seeding methods (using carposporophytes or tetrasporophytes) becoming more common.	Longlines, net tubes, and floating cages have been used.	Moderate to high; male gametes have dispersal of a few meters (rare occurrences of fertilization over 10s of m in other *Gracilaria spp.).* Spores may survive for weeks and endure days of desiccation and disperse more broadly. Vegetative fragmentation may enable dispersal over long distances.	Cultured in many areas of the world including Chile, Korea, and India.	Population genetic studies, and water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Species name	Common name	Culture propagation	Culture grow-out	Dispersal Capacity	Current aquaculture Status	Priorities for study
Hedophyllum sessile (formerly *Saccharina sessilis*)	Sea Cabbage	Not available; may rely on collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines based on other kelp species.	Not available; may rely on seed lines grown out on longline arrays.	Low; zoospores and gametes exhibit limited dispersal and survival ability. No buoyancy mechanisms; although dislodged or broken fragments may transport reproductive blades to other location on multi-species kelp rafts.	Not yet developed.	Development of cultivation and grow out approaches; fine scale population genetic studies in region of planned farm operation, assessment of population health/abundance.
Laminaria setchellii	So. stiff stiped kelp	Not available; may rely on collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines based on other kelp species.	Not available; may rely on seed lines grown out on longline arrays.	Low to moderate; fertile fragments commonly found within kelp drifts, even across distances of 2 km from nearest source. Risk lessened because a substantial number of spores must settle in a confined area for successful settlement/colonization, which reduces risk.	None for this species; information available for different Laminarian species.	Population health and abundance, population genetic studies, culture methods - particularly growout duration as it relates to the timing of sexual maturation.
Macrocystis pyrifera	Giant Kelp	Collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines.	Seed lines wrapped around long lines.	High; buoyant pneumatocysts may keep dislodged kelp floating for extended periods and long distances. Spore dispersal can occur over kms in some conditions; gamete dispersal is under a meter.	Cultured in many regions worldwide (e.g., China, Chile, Tasmania, U.S.).	Water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Species name	Common name	Culture propagation	Culture grow-out	Dispersal Capacity	Current aquaculture Status	Priorities for study
Mastocarpus spp.	Turkish Washcloth	Not available; one study suggests targeting the female gametophyte life-cycle stage (i.e., sexual reproduction). Cultivation of other red algal species use both sexual and asexual approaches.	Not available; other red algal species are amenable to long line cultitvation following seeding of seed lines.	Low; limited dispersal capabilities. Carpospores and tetraspores contained in a gelatinous matrix, and all propagules, including male gametes, carpospores, and tetraspores, lack flagella or cilia, and remain viable for less than two days. Dislodged fronds may enable long distance dispersal, particularly for asexual spores.	Not yet developed.	Cultivation approaches; population surveys to examine connectivity among sites, species present, and life-history variant(s) present; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Nereocystis luetkeana	Bull kelp	Collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines.	Seed lines wrapped around long lines.	Moderate to high; spore dispersal occurs at scales of 10s of m (or less); rafting of reproductive fronds/plants with buoyant penumatocysts may enable long distance dispersal.	Cultured in Alaska and Washington.	Conduct higher resolution population genetic structure studies; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Postelsia palmaeformis	Sea Palm	Not available; may rely on collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines based on other kelp species.	Not available; may rely on seed lines grown out on longline arrays.	Low; 95% of dispersal < 1.4 m from parent plants, and nearly always under 3m. Rare long-distance dispersal possible for dislodged fertile *Postelsia* plants (e.g., fewer than 5 colonization events recorded in 136 survey years).	Not yet developed.	Development of cultivation and grow out approaches; fine scale population genetic studies in region of planned farm operation; water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Species name	Common name	Culture propagation	Culture grow-out	Dispersal Capacity	Current aquaculture Status	Priorities for study
Pyropia spp.	Nori	Complicated multistep process based on sexual reproduction using wild-sourced sori or seed stock (see details in species section).	Grown on nets or lines; multiple harvests in a season possible.	Moderate; potential to transport positively buoyant spores greater distances, which is suspected mechanism of colonization success in natural populations	Commercial cultivation well established in Japan, Korea, and China, but not yet established in U.S.	Determining candidate species to purse for commercial cultivation, fine-scale population structure of the candidate species; and development of cultivation approaches; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Saccharina latissima	Sugar kelp	Collection of wild reproductive fronds (sporophylls) to induce sporulation and produce seed lines; or lines are seeded through lab-based cultures of gametophytes.	Seed lines wrapped around long lines.	Moderate; dispersal of spores and gametes often within a few meters of parent plants, but may occasionally extend over several kilometers. Dislodged plants may disperse and re-establish in suitable habitats.	Cultured in many regions worldwide (e.g., U.K., Norway, Canada, Denmark, U.S.).	Higher resolution population genetic structure studies; better information on health /abundance of populations at southern end of their range; water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Part D: Assessment of risk and uncertainty

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Alaria marginata	Ribbon kelp	Low; limited dispersal ability, physical separation between suitable habitat and offshore culture, some settlement preferences, and most cultured material harvested prior to maturation. Dispersal of fertile/nearly fertile dislodged fronds may enable long distance dispersal, but without floatation mechanism, likely to be rare.	Moderate; better understanding of the fine scale population structure and current patterns will improve prediction of potential genetic impacts.	Utilizing genetically diverse seedstock representative of local populations, maintaining genetic diversity in cultured lines; harvesting ahead of sexual maturation; lowering long lines during high energy events to reduce breakage on plants if permitting/user conflicts allow.
Fucus distichus	Bladderwrack	High; significant dispersal capability due to enhanced by gas-filled bladders, capacity for self-fertilization, ability to vegetatively reproduce. Genetic evidence, based on patterns of spatial genetic structure, suggest dispersal could occur at distances greater than anticipated distances between offshore aquaculture locations and coastal habitat.	Moderate; uncertainty is based on unresolved local population genetic structure scale, which will be important to understanding local connectivity patterns based on current dispersal patterns among wild populations.	Utilizing genetically diverse seedstock/fragements representative of local populations; and consider propagation approach (vegetative versus seed); maintain genetic diversity in cultivated populations, particularly when using vegetative propagation approaches.
Gracilaria andersonii	Sea Spaghetti	Moderate; action of harvesting *Gracilaria* species is known to release spores and fragments, high potential to colonize due to broad tolerance of environmental factors and suitability for various habitats. However, presence of spatial genetic structure from other, less invasive *Gracilaria* spp indicate successful dispersal and colonization may not be frequent.	Moderate; no population genetic studies for this species. Understanding water current patterns will also be important to predicting impacts from dispersed cultured material.	Utilizing genetically diverse seedstock representative of local populations; using culture approaches to reduce breakage of plants (e.g., adjusting line depth during high energy events, reducing epiphyte loads, etc.); maintain genetic diversity in cultivated populations, particularly when using vegetative propagation approaches; harvesting ahead of sexual maturation. Completely collecting all biomass at end of grow-out period.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Hedophyllum sessile (formerly *Saccharina sessilis*)	Sea Cabbage	Low; limited dispersal of spores and gametes, physical separation between suitable habitat and offshore culture, majority of kelp harvested prior to maturation. Dispersal of fertile/nearly fertile dislodged fronds may enable long distance dispersal, but without floatation mechanism, likely to be rare.	High; there is a substantial amount of information is currently unavailable, including population health/abundance, population genetic studies, cultivation approaches, which hinders our ability to evaluate the potential genetic impacts resulting from cultivating *H. sessile*.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; harvesting ahead of sexual maturation; lowering lines during high energy events to minimize breakage and dislodgement of plants if permitting/user conflicts allow.
Laminaria setchellii	So. stiff stiped kelp	Low; late maturation of plants would likely exceed grow-out period if similar to wild plants (2-3 yrs), although fragments of related spp. are frequently found in multi-species kelp drifts, fragments would likely break down before sori develop. Long-lived natural populations may provide genetic resistance to infrequent introgression, but experience long-lasting consequences if more frequent.	Moderate to high; the genetic population structure and overall abundance of *L. setchellii* populations across their range, as well as the methodology for offshore cultivation of this species, represent significant gaps in the understanding of genetic risks from cultivation of this kelp.	Unknown with current state of information; general priorities include harvesting material ahead of sexual maturation, utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; harvesting ahead of sexual maturation; lowering lines during high energy events to minimize breakage and dislodgement of plants if permitting/user conflicts allow.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Macrocystis pyrifera	Giant Kelp	Moderate to high; dislodged kelp is capable of dispersing over great distances. Some kelp will mature prior to harvest, and dispersal of blades or spores from early maturing individuals, or growth of sporophylls on rafting kelp, remain a risk. Genetic structure among populations in Southern California leads to greater risk in disrupting genetic patterns among locations.	Moderate; to evaluate risk to natural populations, knowledge of farm locations and prevailing oceanographic patterns will be important to ascertaining risk.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations.; synthesizing oceanographic information to predict impact patterns from dispersed material; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting ahead of sexual maturation.
Mastocarpus spp.	Turkish Washcloth	Low to moderate; limited dispersal capabilities of propagules, more limited suitable settlement habitat for dispersed propagules. However, fertile vegetative fragments, in addition to asexual reproduction without the need for fertilization, poses greater genetic risk from cultivated material. Little information available on extent of rafting, and duration for which fragments remain fertile.	High; great deal of missing information including knowledge of which species would be cultivated, absence of population genetic studies. Would need to determine which life-history variants exist in populations expected to be in impacted by the farm (different genetic consequences). Lack of developed cultivation approaches. These together hinder a more thorough assessment of the genetic risks associated with farming these spp.	Difficult to predict based on available information; general priorities include sourcing seed material from nearby populations, maintaining genetic diversity in cultivated populations, using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting ahead of sexual maturation.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Nereocystis luetkeana	Bull kelp	Low; most dispersal occurs at scales under 10 m, although longer distance dispersal is possible, especially through rafting; majority of plants harvested prior to sexual maturation. Studies indicate that rebuilding of wild populations have been limited by low settlement and recruitment, dispersed cultured propagules may face same limitations for successful settlement and recruitment.	Low to moderate, the only population genetic study may have lacked power in analyses to detect finer-scale structure.	Utilizing genetically diverse seedstock representative of local populations (although this may be challenging south of Pt. Conception due to rarity of occurrence), and maintaining genetic diversity in cultivated populations; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation.
Postelsia palmaeformis	Sea Palm	Low; limited dispersal ability, low likelihood of dispersed spore settlement in suitable habitat, slightly higher potential for dislodged plants / fronds to drift into suitable habitats, but colonization success from this type of dispersal is rare even in natural populations. However, wild populations are small, and would be more susceptible to genetic impacts from cultivated material.	High; cultivation approaches have not yet been developed and no knowledge of population abundance.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations, using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation.
Pyropia spp.	Nori	Low to moderate, characteristics of spores and the fragility of thalli decrease likelihood of dispersal, however some potential exists for rare long-distance dispersal events (possibly occurring during conchocelis phase on transported shells/barnacles). Rapid harvest cycle for these spp. Intricate life-cycles of this genus, and specific settlement requirements lower success for propagule spread, unless in close proximity to shellfish farms or fouling shellfish on equipment/boats).	Moderate; species of interest for commercial cultivation has not been determined, and population genetic structure is lacking. However, general considerations for this genus are similar among species.	Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow), harvesting prior to sexual maturation; making sure farm equipment/service boats are free from biofouling (e.g., barnacles) that may transport conchocelis away from farm site.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Saccharina latissima	Sugar kelp	Low to moderate; studies in other regions for *S. japonica* and *L. hyperborea* have demonstrated transport distances for kelp particulates (which could include spores) can extend from 100s of m up to 200 km away from farm site, but distances depend on farm location. Majority of kelp would be harvested prior to maturation, but early maturing plants are possible. If fertile tissue or spores are dispersed, a moderate level of settlement requirements (combination of factors) may reduce successful recruitment into natural populations.	Moderate; need to determine the scale of regional connectivity among populations, and better information on status / abundance of populations at southern end of their range in California to provide better risk assessment.	Using culture approaches to minimize breakage (e.g., allowing sufficient time for holdfasts to firmly attach to lines, subjecting young sporophytes to current velocities to strengthen holdfasts, and not overcrowding lines to give individual holdfasts space for attachment), harvesting prior to sexual maturation. Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations. This is particularly important until a population genetic study can shed light on the scale of genetic structure in the region.

4.2 Gulf of America Aquaculture Candidate Species – Summary of Genetic Risk Factors

Table 4.2. Macroalgae Genetic Risk Factors – Gulf of America

Part A: Reproductive characteristics

Species Name	Common Name	Spawning Types	Spawning Season	Propagate from vegetative fragmentation (VF)	Spore Stages	Gamete Stages	Potential for Gamete Release in Culture
Codium spp.	Dead Man's Fingers / Oyster Thief	Sexual reproduction and asexual reproduction through parthenogenesis and fragmentation.	Summer and fall.	Yes, vegetative growth from thalli and utricles.	None.	Release of motile male and female gametes.	Unknown (little information available), but likely.
Eucheuma spp.	Eucheuma toids	Sexual and vegetative reproduction; cultured types established in wild utilize asexual VF.	Spring and summer.	Yes, high propensity for VF due to brittle thalli.	Yes, carpospores and tetraspores.	Yes, male gametes released, eggs retained on female gametophytes and develop into carposporophytes.	Low; vegetatively produced plants do not appear to revert to sexual life-cycle.
Gracilaria spp.	Sea Spaghetti	Both sexual and asexual reproduction in wild populations; differs by habitat.	Dependent on location. Late summer or year-round in tropical areas.	Yes, high propensity for VF.	Yes, carpospores and tetraspores.	Yes, male gametes released, eggs retained on female gametophytes and develop into carposporophytes.	Low to moderate; little sexual reproduction reported on cultured plants.
Sargassum spp.	Sargassum	In benthic species, almost entirely sexual reproduction; in pelagic species almost entirely asexual VF.	Fall.	Yes, more common in pelagic species.	None.	Yes, sperm are released, but eggs remain on parent plant; after fertilization remain attached by mucus;	Moderate; reproductive structures form on benthic species; release may come from early maturing individuals or during longer grow-out.

Species Name	Common Name	Spawning Types	Spawning Season	Propagate from vegetative fragmentation (VF)	Spore Stages	Gamete Stages	Potential for Gamete Release in Culture
						release as sporelings with holdfasts.	
Ulva spp.	Sea lettuce	Sexual and asexual reproduction; parthenogenic development from unfused gametes.	During warmer months and possibly year-round in some locations.	Yes, VF most common in unattached forms.	Yes, mobile zoospores that are negatively phototactic. Mobile for 4-24 hrs, viable for many months.	Yes, motile male and female gametes are released; they are positively phototactic.	High; rapid sexual maturation once thallus tissue is formed (2 - 3 weeks).

Part B: Population dynamics

Species Name	Common Name	Native to region	Population health, if native	Ease of settlement	Population structure characterized
Codium spp.	Dead Man's Fingers / Oyster Thief	Yes; some spp. native to Gulf including *C. taylorii*, *C. isthmocladum*. *C. fragile* is invasive.	Unknown for native species.	High; broad tolerance to abiotic parameters, able to settle in variety of habitats, and settle on natural and artificial structures.	No information available for Gulf species.
Eucheuma spp.	Eucheumatoids	Yes, *Eucheuma isiforme* is commercial species native to the Gulf; other species include *E. gelidium, E. acanthocladum*, and *E. nudum*.	Some depletion of populations observed in 1970s (carrageenan exploitation), current status was not found.	High; demonstrated ability to attach and grow from VF in most habitats and noted for invasiveness; spore settlement less defined.	No, but concern over loss of genetic diversity in other regions.
Gracilaria spp.	Sea Spaghetti	Yes, *Gracilaria tikvahiae* and other *Gracilaria spp* have been identified in Gulf.	Not well characterized; *G. tikvahiae* most abundant *Gracilaria spp*. in Gulf; some species declining, others thriving invasively.	High; adaptable to broad sets of environmental parameters.	Genetic structure between eastern and western Gulf; break uncertain but Mississippi river or Chenier plain suggested.
Sargassum spp.	Sargassum	Yes, both benthic (*S. filipendula* and *S. pteropleuron*) and pelagic (*Sargassum natans* and *S. fluitans*) species.	Thriving populations.	High; broad range of thermal and environmental tolerance; successful colonization documented for the genus.	No genetic structure studies within Gulf; genetic structure in other species occurs over broad scales and have asymmetric patterns dependent on prevailing ocean currents.
Ulva spp.	Sea lettuce	Yes, ~11 spp. in Gulf, *U. tepida* among other spp. may be native to region.	No information specifically within the Gulf, but generally these species are among most abundant seaweeds globally.	High; species grow abundantly and may grow unattached to substrate.	No genetic structure studies in Gulf. Species in other regions vary in scale of population genetic structure, with some showing fine scale structure potentially linked to local adaptation.

Part C: Culture information

Species Name	Common Name	Culture propagation	Culture grow-out	Dispersal Capacity	Current Aquaculture Status	Priorities for Study
Codium spp.	Dead Man's Fingers / Oyster Thief	Vegetative fragmentation.	Seed lines wrapped around long lines.	High; primary concern is dislodged/broken thalli that may grow vegetatively or reproduce asexually. Species also has motile propagules.	Cultivated in Korea, Portugal (RAS).	Identification, distribution, life-history, and abundance of species in the Gulf; population structure; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Eucheuma spp	Eucheumatoids	Clonally produced seedstock through vegetative fragmentation.	Seedlings tied to suspended lines; tubular nets, floating baskets.	High; dispersal from vegetative fragments. Evidence from multiple regions indicated colonization over 1km from farm site.	Cultured in tropical and subtropical waters globally (e.g., Philippines, Tanzania, Malaysia, Zanzibar), often from introduced strains from Southwest Asia.	Population genetics of potential spp in Gulf, characterization and preservation of wild variation; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Gracilaria spp.	Sea Spaghetti	Clonally produced seedstock through vegetative fragmentation, or through seeding of lines with cystocarpic spores.	Seedlings tied to suspended lines; tubular nets, floating baskets.	High; spores may survive for weeks, and have high dispersal propensity; vegetative fragments have high dispersal propensity.	Cultured in many regions worldwide (e.g., China, Chile, South Africa, Namibia, U.S.).	Fine scale genetic structure of Gulf to identify location of genetic break and other more subtle genetic structure patterns; water particle dispersal studies to predict directions propagules/ dispersed material will travel.
Sargassum spp.	Sargassum	Sexual production of sporelings through wild collection of wild mature plants or development of immature thalli in lab.	Seed lines wrapped around long lines.	High; very high dispersal potential over 100s kms from broken or dislodged plants due to buoyant vesicles.	Predominately cultured in China and Korea.	Population genetic study in the Gulf for candidate species; water dispersal modeling to predict direction(s) of most impact; water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Species Name	Common Name	Culture propagation	Culture grow-out	Dispersal Capacity	Current Aquaculture Status	Priorities for Study
Ulva spp.	Sea lettuce	Induce sporulation of gametes and spores which are then seeded onto lines. Vegetative fragmentation is also used, but cannot generate seeded lines this way, instead used in free-floating culture (RAS).	Seed lines wraped around long lines; unattached forms typically grown in RAS.	High; genus noted for small and easily distributed propagules; documented colonization at 24 and 35 km from source.	Make up a small amount of macroalgae cultured, but gaining interest in Japan, Mexico, Sweden, and U.S.	Determine which species are of interest for culture in Gulf, and whether they are native or introduced; examine genetic structure and population connectivity patterns in species of interest; water particle dispersal studies to predict directions propagules/ dispersed material will travel.

Part D: Assessment of risk and uncertainty

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Codium spp.	Dead Man's Fingers / Oyster Thief	High; if native species possess characteristics similar to those observed in *C. fragile*, dispersal is likely, vegetative propagation may result in low genetic diversity in cultured material which may impact natural populations directly (introgression) or indirectly (displacement). However, native *Codium spp*. may not present a risk level equivalent to *C. fragile*, and lack of information makes it challenging to assess potential genetic risk from *Codium spp*. in Gulf.	High; little available information regarding these species in the Gulf, including details on abundance, population structure, and ease of spread and establishment. This missing information leads to a high degree of uncertainty in risk assessment of genetic impacts from culturing *Codium*.	Utilizing *Codium* species native to the Gulf, preferably sourced close to farm, employing techniques such as environmental DNA (eDNA) to ensure that *C. fragile* is not inadvertently propagated at farm sites, removing or increasing distances between artificial structures to minimize dispersal, in addition to regularly treating, cleaning, or replacing aquaculture equipment to remove *Codium* present due to fouling. Using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow).
Eucheuma spp.	Eucheumatoids	Moderate to high; cultured material will likely disperse to native populations. Vegetatively propagated cultured plants will likely have reduced genetic diversity compared to wild populations. Although they may not genetically introgress into wild populations (limitations of vegetative fragmentation), they have a demonstrated ability to displace native populations, potentially leading to loss of genetic diversity indirectly through population decline.	Moderate; population structure is unknown in Gulf; genus has demonstrated ability to disperse and colonize locations.	Culturing native species, sourced from local populations, maintaining genetic diversity in asexually propagated lines, genetically characterizing cultured and wild strains or populations. Using culture approaches to reduce breakage (e.g., lowering lines during high energy events if permitting/user conflicts allow).
Gracilaria spp.	Sea Spaghetti	Moderate to high; relatively high capacity for dispersal, plants easily establish in natural settings. Genetic impact on wild populations will depend on whether dispersed fragments reproduce sexually. Cultured material spreading through genetic introgression or vegetative growth displacing wild plants may genetically impact natural populations.	Low to moderate; need to understand whether cultured dispersed vegetative fragments will become fertile if settled in natural habitat; this will determine if genetic introgression occurs. If it does occur, genetic risk outcomes will depend on the genetic diversity and degree of domestication in cultured lines.	Utilizing culture approaches to minimize breakage, for example, conditioning hardy thalli and holdfasts through water current exposure; Utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations, with extra attention paid to minimize transfer between the distinctive eastern and western Gulf populations.

Species name	Common name	Probable genetic risk level	Uncertainty in risk assessment	Management priorities to minimize genetic effects
Sargassum spp.	Sargassum	Moderate; high capacity for dispersal due to buoyant vesicles, ease of settlement in variety of habitats / conditions, ability for vegetative fragmentation. However, if natural populations are abundant, and the population is structured over broad scales (currently unknown in Gulf, but reasonable assumption based on information from other *Sargassum* spp. until more information is available), genetic impact may be minimal if locally representative genetic diversity can be maintained in cultured material.	Moderate; a better understanding of population dynamics is needed to evaluate genetic risk from culture of this species. Population abundance and genetic connectivity among populations in the Gulf will be key to determining genetic risk to natural populations.	Utilizing culture approaches to minimize breakage, for example, lowering long lines during grow out to 3 m to delay reproductive development and reduce epiphyte growth (if permitting/user conflicts allow); utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations.
Ulva spp.	Sea lettuce	Moderate to high; high dispersal propensity, rapid reproductive maturation in culture, easy settling parameters and/or ability to grow unattached. Given number of spp. found in Gulf, need to determine which are native vs. introduced, and which would be cultivated. If species chosen for cultivation has/have been previously introduced into Gulf, then perhaps impacts on naturalized populations are less of a concern, however, potential risk would still remain for displacement of native populations.	Moderate; need information on the targeted species for culture, and population genetic structure. Given that dispersal to wild populations is likely, the impact will depend on the species, connectivity among populations in the Gulf, and oceanographic processes in region of the farm.	Utilizing culture approaches to minimize breakage, for example, extending the time in the nursery to provide greater degree of attachment and culturing *Ulva* at depths several meters below surface to reduce wave energy. Using shorter grow out periods to decrease biomass loss from tissue degradation and release of fertile material; utilizing genetically diverse seedstock representative of local populations, and maintaining genetic diversity in cultivated populations; developing sterile strains.

4.3 Escape Prevention Measures and Best Management Practices

Standard measures and Action measures are procedures implemented to minimize or prevent escapes (e.g., dispersal through spore release or vegetative propagation) and operational losses (e.g., gear breakage or loss), which could result in gene flow from cultured genetic material into wild populations, potentially causing cultured-wild genetic interactions. While the implementation of one or a combination of these measures would not provide an absolute guarantee against unintended gene flow from the macroalgal culture program (hereafter referred to as the program), these measures are designed to effectively minimize the risk of this kind of escape.

The measures are grouped into a set of standard measures that apply to all macroalgae culture programs. Following standard measures, action-level measures are listed for situations where response to a medium-level or large-scale escape event is required.

4.3.1 Standard Measures

Standard measures can be applied to various programs and are primarily the aquaculture operator's responsibility. Standard measures are to be implemented wherever feasible and reasonable, and not all measures may be practical in every situation.

Measure Macroalgae-1 Onshore Procedures

Harvest starter spores from local sources and maintain genetic diversity

Spores used for reproduction in the nursery are harvested from the wild within the local region. If the program were to employ domestication or strain selection, additional steps would be needed to understand the risk that implementation of intentional selection would have on natural populations, and additional steps may be needed to minimize the risk of maladapted traits passing from cultured strains to wild macroalgae. However, mitigation steps may include developing selected strains with reduced or delayed development of fertile tissues, and/or developing sterile lines.

An example of implementation of this measure is a policy by Alaska Department of Fish and Game that requires that spore material to be used in the nursery be taken from at least 50 different plants within 50 kilometers of the aquaculture site each year. As another example, in Connecticut, the endemic kelp (*S. latissima)* must be obtained from Long Island Sound or a Connecticut hatchery that is producing native kelp spores originating from Long Island Sound source tissue (https://seagrant.uconn.edu/wp-content/uploads/sites/1985/2019/09/8-14_Permit-guide.pdf; accessed September 14, 2024). Similarly, seaweed grown in Maine must also be sourced within Maine (https://www.maine.gov/dmr/aquaculture/).

Use native seed from macroalgae seed banks

Seed banks are designed to preserve genetic diversity of vulnerable macroalgae populations through cryopreservation of gametophytes. The use of preserved seed may be an option in areas where local populations are vulnerable or lacking in genetic diversity. Seed banking is done through programs such as the Conservation Genomics and Gametophyte Banking of Bull Kelp in

California program (California Sea Grant 2023) and the Puget Sound Restoration Fund conservation hatchery (Puget Sound Restoration Fund 2024).

Implement cryopreservation of seed strains and cultivars

Macroalgae culturists can implement this measure toward ensuring genetic diversity of cultivated species by developing a seed bank for preservation of gametophytes grown from wild seed, or participating in an established seed banking program.

Development of Sterile Lines

Ongoing research for development of sterilization techniques for macroalgae make use of naturally occurring mutations in many species of kelp that can result in sterile individuals. These mutations can be identified and propagated to produce male and female gametophytes and sporophytes that produce no viable spores. In contrast to genome editing techniques to create sterile finfish lines, this is a naturally occurring mutation and production of sterile individuals which may be targeted through selective breeding. This mutation is present in many species of kelp but not in other red or brown algae species.

Measure Macroalgae-2 Program siting

Locate program to minimize loading from wave action, wind and marine currents

Macroalgae are susceptible to breakage from forces in the marine environment. Culture programs should be sited, depending on site availability based on other user conflicts, in such a way that forces from wave action, wind and marine currents can be minimized, to the extent feasible. Engineering constraints of program seed lines and mooring will be factored into site selection. Where possible siting will take advantage of land features to reduce marine forces acting on the aquaculture system. Minimizing damage to macroalgae stock from weather events will reduce the potential for line loss, raft formations of cultured material and long-distance propagation.

In locations where severe storms are common, such as in the Gulf, submersible features of the seed line system to an adequate depth should be engineered into the system to minimize potential for damage to the system or inventory.

Measure Macroalgae-3 Aquaculture System Design

Engineer seed line system to minimize risk of failure

Seed lines should have a strength rating to withstand tensioning and marine forces, including forces acting on attached harvest-size sporophytes. Lines should be tensioned to minimize risk of marine mammal entanglements, which could be another force acting on the aquaculture system. As such, an adequate factor of safety is needed to prevent line failure when in operation (e.g., worst-case conditions over a specified time horizon, such as 100 years). The seed lines should be designed to resist fouling to maintain adequate strength in a marine environment. Materials and engineering of the system should conform to ISO standards.

Causes of potential aquaculture losses include:

- Failure of seed lines due to forces in the marine environment
- Biofouling of seed lines, leading to line failure
- Line damage by large animals
- Vessel or propeller strike
- Operational errors during inspection or harvest

Measure Macroalgae-4 Aquaculture Operations Management

Frequent inspections should be implemented to ensure security of the system.

Surveillance of Aquaculture System Condition

The culture site should be monitored on a periodic basis at a high enough frequency to ensure security of the program. Training of staff should be implemented to respond to various issues, including:

- Loss of tension in lines
- Seed line breakage
- Mooring damage
- Presence of grazers, epiphytes, disease

Embed tracking devices on aquaculture system components

Seed and anchoring lines should be embedded with tracking devices at strategic locations so that system lines can be monitored for movement and enable rapid response in the event of movement past thresholds indicative of excessive strain or damage. Although, it is acknowledged that this technology would increase the cost of production.

Best practices for inventorying

A detailed inventory should be maintained of seed lines, including condition of sporophytes and estimated time to sorus development and maturity. The inventory should include an ongoing record of the condition of the grow-out system to be submitted through applicable regulatory agencies.

Prevent spore propagation from the aquaculture system

If feasible to harvest before maturity and still attain market size, minimize the potential for culture spore release by harvesting sporophytes before they develop reproductive tissue (e.g. sorus). This will substantially reduce the potential for culture-wild interactions from the aquaculture system.

Measure Macroalgae-5 Implement damage prevention measures

Limit access surrounding the facility using markers, buoys, lights or other methods

The boundary of the aquaculture system should be clearly marked with signage identifying restrictions, purpose of the site and lease information. Markers should be designed to be clearly visible to vessel operators. Lighting may be incorporated into site marking where appropriate, and where lighting would not cause a visual disturbance.

Use warning measures to restrict vessels from the area

Reactive measures such as audible sources and lights may be installed to warn vessels operating near the aquaculture boundary.

Use deterrent measures to keep large animals from entering the aquaculture area

Reactive measures such as audible sources and lights may be used to repel or deter large animals from damaging seed lines or opportunistically feeding at the aquaculture site. Air bubble generators or exclusion nets can also be effective animal deterrents, if feasible.

Implement submersible systems for severe weather events

For offshore installations, and if it is in compliance with permitting regulations and/or does not lead to user conflicts or entanglements, aquaculture systems can implement submersible designs so they can be lowered below sea level in the event of severe weather. These systems should be designed to be raised and lowered as necessary to suspend maintenance during submerged periods and resume normal operation during moderate conditions.

Plan for removal of ancillary equipment during severe weather events

A rapid response plan should be implemented to allow for removal or protection of surface level infrastructure to minimize potential for container system damage and loss of maintenance capabilities.

Implement a recovery plan to ensure rapid response to damage and equipment losses

A recovery plan should be developed to respond to damage and equipment losses within the aquaculture system. Some states (e.g., Connecticut) already require this to be submitted with the permit application. Possible components of the plan include an alarm system, staffing and required equipment for gear recovery, repair and reinstallation methods and restoration of inventory losses.

Measure Macroalgae-6 Harvest procedures

Minimize opportunities for harvest losses from seed line to harvest vessel

Harvest practices should use procedures to minimize strain or damage to seed lines or loss of inventory through breakage or fragmentation. Best practices should be reviewed periodically to optimize harvest techniques.

Minimize opportunities for harvest losses from harvest vessel to processor

Safe handling methods should be used when transferring harvest from the harvest vessel to minimize any potential for losses.

Measure Macroalgae-7 Advance Science of Aquaculture Genetic and Ecological Interactions

Ongoing monitoring and research of wild macroalgae populations and the environment should inform sustainable carrying capacities of macroalgae culture in each region, as well as risk thresholds for additional action.

Address data gaps of wild populations

Areas of further research for individual macroalgae species are described in Chapter 3 and Chapter 4. Some items for research include surveys of genetic structure, population structure, life history, reproductive behavior, population demographics, and effective population size.

Environmental monitoring

Monitor the genetic status of wild populations through genetic sampling of individuals from surrounding wild populations. Genetic markers should be utilized to identify trait values that can be traced to aquaculture origin.

1.1.1 Action Level Measures

Action level mitigation measures are implemented in the event of an escape event deemed to pose a genetic or ecological risk. These measures are conducted by the aquaculture operator with oversight of applicable regulatory agencies.

Action Macroalgae-1 Reporting of escape event in terms of size of line and volume of harvestable material lost

This action is related to Measure Macroalgae-4 Aquaculture Operations Management. Inventory reporting should include an ongoing record of any damage to the offshore container system, including a record of escape loss and response and recovery measures taken, to be issued through applicable regulatory agencies.

Action Macroalgae-2 Recapture of broken lines or detached sporophytes

This action is related to Measure Macroalgae-5, Implement damage prevention measures. This action would require recovery of lost gear to reduce potential for culture-wild interactions and generation of marine debris.

Action Macroalgae-3 Reducing program inventory

Program inventory would be reduced where a program is following operating requirements but operating above a sustainable level from a gene flow perspective. Modifications to operations can be evaluated along with reducing inventory to a level that reduces program risks to a sustainable level.

Action Macroalgae-4 Temporary or permanent cessation of operations

Cessation of operations may be required for programs not in compliance with operating requirements, or for situations where the program is linked to substantial ecological degradation from culture gene flow into local waters. This type of requirement is already in place in Connecticut, where any violation of federal permits (U.S. Army Corps of Engineers) will result in immediate cessation of the operation.

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