How does macroalgae cultivation affect marine ecosystems?

Dag Gjetø[1], Alexander Jüterbock[1], David Aldridge[2] Henning Reiss[1]

Cultivated *Saccharina latissima* (Photo: David Aldridge)

[1] Faculty of Biosciences and Aquaculture, Nord University, Universitetsalléen 11, 8026 Bodø, Norway

[2] Seaweed Solutions AS, Bynesveien 50 C, 7018 Trondheim, Norway

Contents

Introduction

In recent years the farming of macroalgae for commercial purposes has gained increasing attention and interest. It has been proposed as a possible solution to mitigating pollution from fish farms and agricultural runoffs, it has been suggested as an option for carbon sequestration, and as a way to meet a growing demand for algae for industrial and commercial use, such as pharmaceuticals, cosmetics, fish feed, and human consumption. This review aims to explore the environmental impacts of algal cultivation, and how it affects ecosystems. The review also questions the necessity of cultivating when contrasted to harvesting wild macroalgae (trawling), and will attempt to reflect the state of knowledge per 2022.

With the increasing demand for algae-derived products such as alginate, Norway's strategy has been the harvesting of seaweeds by means of trawling, which has been the most popular solution going back several decades. Over the decades, the utilization of macroalgae, especially kelp (*Laminaria hyperborea)* has become a part of the Norwegian aquaculture industry. Norway harvests its kelp forests by removing about 130 000 – 180 000t of biomass every year (Christie et al., 1998; Vea & Ask, 2011; Stevant et al., 2017), and to this end has developed and refined a harvesting scheme. (Vea & Ask, 2011) Although development of this scheme has occurred mostly within the industry, scientific research on the question of trawling suggests that with the proper regime, current kelp harvesting practices may be sustainable with regards to regrowth of the kelp forests (Vea & Ask, 2011).

However, there have been worrying findings of reduced understory recruits after several subsequent trawling sessions (Christie et al., 1998; Steen et al., 2016), which may suggest a gradual reduction of individuals in the kelp forest. This is thought to be due to the initial quick growth of the first generation of understory recruits which are too small to be harvested by trawling, developing a lush canopy which then shades the subsequent generation of recruits (Steen et al., 2016). The problem then arises when the regrown kelp forest is subsequently harvested, with fewer recruits in the understory to regrow the forest once more, which may lead to a gradual depletion of the kelp forests.

There is also a pattern of longer recovery times depending on latitude, with forests in more northern latitudes requiring a longer time to recover (Christie et al., 1998), making trawling less of an optimal choice further north. Sjøtun et al. (1993) also found lower biomass production in northerly regions than in southerly regions. The reason for this is worth going into for trawling as well as cultivation considerations: The colder waters in the north affects the physiology of the kelp, impacting photosynthesis, respiration, and development (Lüning, 1980, 1986); however, the longer hours of light during the growth season helps the kelp build up greater stocks of carbohydrates, beneficial for future growth (Lüning, 1971), and may possibly counteract the negative effects cold has on growth. Surveys from Norway showed that northern regions (70-71°N) experienced longer periods of cold water (<5°C) during the period of rapid growth (Jan-June), while the mid- (latitude 60-62°N) and southern regions (latitude 58-60°N) were warmer (Aure & Østensen, 1993; Rinde & Sjøtun 2005). Consequently, kelp was found to grow faster in southern- and mid-Norway, and have shorter lifespans (maximum lifespans were reported to be 13 years in southern Norway, 16 years in mid-Norway, and 21 years

Chapter 1 - Species and cultivation

The wild flora and fauna already present must be considered before introducing any new species so as to avoid the introduction of invasive species, risking the release of gametes into a non-native biome. Negative consequences which could contribute to the collapse of the (perhaps already damaged) ecosystem may include: the introduction of species outcompeting the native ones, the rise of hybrid species, and/or the introduction of diseases or epiphytes which could damage the local sea weeds.

In Norway, about 200 000 tons of macroalgae are harvested every year (Norwegian Directorate of Fisheries, 2022), the primary algae harvested being *Laminaria hyperborea* (forest kelp/northern kelp) and *Ascophyllum nodosum* (knotted wrack). In terms of cultivation, efforts are mostly focused on kelps, with *Saccharina latissima* being the most popular due to biomass and nutritional content (Stevant et al., 2017).

Fauna associated with common kelp sampled at four sites covering 1000km coastline. Species samples were mobile macrofauna. 238 different species were found on 56 kelps sampled. Average density of 8000 indiviuals per kelp. Amphipods and gastropods were most diverse and abundant. Composition differed between lamina, stipe, and holdfast. Highest abundance on the stipe in summer, but large variations between site and season; although not in diversity.

Cultivation period

S. latissima is usually fertile during late autumn/early winter when the days are short, and temperatures are low (Parke, 1948). Outside of this period fertility can be induced artificially by removing the meristem and controlling light conditions (Lüning, 1988). This enable*s* spores to be reliably obtained throughout the year for seeding or setting up vegetative gametophyte cultures (for upscaling and seeding at a later point in time). For cultivation at sea, deployment of seeded lines has to occur in the autumn/winter to maximise growth during the spring when nutrients and light are non-limiting. Nutrient limitation, following rapid uptake during the spring phytoplankton bloom, is thought to be main limiting factor for growth in most Norwegian fjords during summer (eg. Paasche, 1988, Forbord et al., 2012).

One problem with S*accharina latissima* cultivation is the appearance on the blades of epiphytic invertebrates (especially bryozoans) during summer months (reviewed by Stévant et al., 2017). This leads to a reduction in the quality of the seaweed, and ultimately loss of biomass. For this reason, harvesting of the crop must be timed carefully and is a compromise between maximising biomass while minimising biofouling. The exact timing varies based on latitude, and is frequently between April (southern Norway) and August (Northern Norway). From the point of view of IMTA, the requirement to harvest kelp before the onset of biofouling creates a suboptimal mismatch between the kelp growing season and the period of highest nutrient discharge from salmon farms (Fossberg et al., 2018).

Possible new species

Below we discuss some species that are highly in demand, but where there still exists large potential for developing protocols for large-scale production.

Palmaria palmata (also known as Dulse) is a red seaweed that is commonly found on rocky shores in the Northern Hemisphere. It has been eaten for many centuries all over the world. Recently, it has become very popular due to its high nutritional value (including high protein content) in addition to its favourable flavour; It is sometimes even marketed as "vegan bacon". There are several companies producing this species using tank cultivation, where biomass growths vegetatively when supplied with nutrients and sunlight (Pang & Lüning, 2004). However, this method requires land area and is also labour intensive, as well as requiring a large intake of seawater, high construction costs and high power inputs. All of these factors reduce the economic feasibility. Cultivation at sea has the potential to produce high biomass volumes more economically, but the methods for developing large-scale hatchery protocols are still in their infancy (Schmedes et al. 2021).

Asparagopsis is a genus of red algae that is widely distributed in temperate, sub-tropical and tropical oceans. There is currently a lot of interest in cultivation of Asapragopsis due to its potential to reduce methane emissions in ruminants by up to 98% when included as part of their diet (Zhu et al. 2021). Attempts to cultivate Asparagogpis date back to the 80s, with methods developed in France and Ireland in the 90s culminating in 14km of cultivation ropes being tested in Brittany (France) in 2004. However, truly large-scale cultivation is currently held back by an inability of researchers to gain full control over the environmental conditions required to close the life-cycle from the tetrasporophyte to gametophyte phase (Zhu et al. 2021).

The green seaweed ***Ulva***, commonly known as sea lettuce, has a lot of favourable traits as a species for cultivation: widely distributed, environmental tolerance, high growth rates, combined with many favourable nutritional characteristics that make it highly desirable not just in food and feed, but also for cosmetics, neutraceuticals and pharmaceuticals. *Ulva*, like *Palmaria*, has been successfully cultivated in Europe using tank cultivation, and also in near shore environments on nets and in cages. Competing with terrestrial crops, however, requires the cost savings that are made possible by large-scale cultivation at sea. Recent research in Sweden has demonstarted hatchery methods for seeding of twine for sea cultivation of Ulva fenestrata, concluding that it "is a suitable crop for large-scale off-shore cultivation in the northern European hemisphere and that it copes very well with the prevailing, often harsh (storms, heavy precipitation, strong wave action) winter conditions." (Steinhagen et al. 2021)

Associated fauna

Compared to natural kelp forests, kelp farms are short-lived habitats that do not exist in the environment longer than one year due to annual harvests of biomass. They are also habitats that grow suspended in the water column, whereas natural kelp forests grow on the seabed. For these reasons there can be some doubts about how comparable "artificial kelp forests" are with their natural counterparts. It is perhaps not surprising then that one study in Norway has shown that at kelp farms there are fewer individual species together with lower species biodiversity (Torstensen, 2020). However, the same study did show similarities between artificial and natural forests, with amphipods and snails being the dominant organisms in common across both locations. Other invertebrates that were common at the kelp farm (though not in natural kelp beds) were decapods, polychaetes and bivalve mussels.

Cultivation sites

In comparison to Asia, the seaweed cultivation industry in Europe is very much in its infancy, although it is growing rapidly. In Norway the cultivation of macroalgae, which mostly focuses on *Saccharina latissima* and *Alaria esculenta*, was initiated over 10 years ago with small-scale experiments. Cultivation is still in an early phase in Norway, but there is strong commercial interest: there were 475 permits for macroalgal cultivation distributed over 97 locations and 16 companies in 2020 (Directorate of Fisheries 2020, see fig. 1 for current permits). Production in Norway is also growing rapidly. In 2015, total production (cultivation) of macroalgae (*S. latissima* and *A. esculenta*) was 51 tonnes, increasing to over 300 tonnes in 2020 (Directorate of Fisheries 2020); in 2022 it is estimated that production will exceed 500 tonnes (Norwegian Seaweed Association, *Personal communication*).

Both *S. latissima* and *A. esculenta* are widespread in Europe, preferring cold water below 20°C (Druehl 1967, Munda and Lüning 1977). Approximately half of the natural kelp beds of *S. latissima* are found along the coast of Norway (Moy et al. 2006), demonstrating the suitability of Norway for kelp cultivation. Theoretically the whole of the Norwegian coastline can be used for kelp cultivation, with a 2-month lag in the growing season when comparing northern to southern latitudes (Forbord et al., 2020). Currently, cultivation is focused in areas that are sheltered and semi-sheltered, as this reduces logistical and engineering problems and costs that would be associated with fully offshore production. As production scales, however, offshore locations are likely to become more common and are likely to offer a number of benefits, including reduced biofouling, increased nutrient concentrations and longer growing season.

Figure 1 Cultivation sites for macroalgae along the Norwegian coast. Note that these are sites where permissions have been granted, not necessarily active cultivation sites (map from Fiskeridirektoratet 2021).

Chapter 2 - Environmental impacts of macroalgae cultivation

Norway has ambitions to massively increase its production of macroalgae towards 2050, from about 200 000 tons today (mostly harvested from wild populations), to 20 million tons by 2050 (Olafsen et al., 2012). Achieving this goal is unfeasible, as the current *production* of macroalgae is around 300-500 tons, which would necessitate a massive increase in production capabilities if this target is to be reached (Hancke *et al.*, 2021). The algae can be used for the production of oils, proteins, and biochemicals, and is therefore a potential source of revenue for industry. Norway has the natural conditions to cultivate with many upwelling areas and rivers feeding its coasts, vast ocean territory to grow in, and aquaculture and offshore technology necessary to scale it up. Norway is also in a good position to benefit from developments in IMTA in conjunction with its many fish farms.

The human introduction and cultivation of any organism in an ecosystem may shift the existing balance of the system, and even more so in cases where the cultivation is large-scale. In Norway, the cultivation of macroalgae is currently small-scale, but with goals to substantially increase the cultivated biomass by 2050, an investigation into the effects this increase will have on the environment is necessary. The impacts may be beneficial rather than harmful, which is an important factor to keep in mind when investigating the topic. The overarching question is therefore whether expanding the macroalgae cultivation industry is harmful, benign or beneficial. In the attempt to provide an answer to this question, the main subjects of investigation are:

- Carbon sequestration
- Biomass deposition
- Light limitation
- Nutrient absorption
- Pollution
- Macroalgae as artificial habitats
- Gene flow
- Vector of diseases

Carbon sequestration and release

The research on marine carbon sequestration is limited, but the concept is understood. The exact mechanics of long-term (that is, in the deep sea) storage of biomass is, however, not well understood, and we need more knowledge about how the volume of algae becomes deposited, the distribution of the biomass, and the physical and biological requirements for the algae to be successfully stored, rather than recirculated.

In nature, as well as from kelp cultivation sites, macroalgae release carbon in the form of detritus, and the volumes of particulate organic matter (POM) released from cultivation sites as well as its dispersion is a source of concern. The concern is namely that large volumes of algae will be deposited on the sea floor, and thus be a danger to benthic life forms by increased microbial activity, creating an anoxic environment, or through the production of sulfides, as has been the case for fish aquaculture (Pearson & Rosenberg, 1978) although the problem has largely been circumvented with deeper cultivation locations and changes in mooring (Kutti et al., 2007).

Kelp cultivation sites release dissolved and particulate organic material into the water by erosion and fragmentation of the plant, or by whole plants tearing away. As the kelp grows and the season progresses, more particles are released which will either be deposited for long-term storage, or be recycled into the food web (Renaud et al., 2015).

Kelp serves as an important form of connectivity between shallow, productive areas and deeper areas, affecting regional productivity and spatial organization of marine ecosystems. Exported kelp detritus can provide a significant resource subsidy and enhance secondary production in downstream communities ranging from tens of meters to hundreds of kilometers (Krumhansl & Scheibling 2012).

Through the first months of growth, less than 5% of biomass is lost, steadily increasing to about 8-13% by the time of harvesting (typically April-June, depending on latitude). If the kelp is left unharvested, as much as 50% may be lost to the environment in the late summer, until eventually, everything will have eroded away (Hancke et al., 2021). If the amount of organic material deposited onto the sea floor is too high, this can be harmful to the organisms living there as conditions of anoxia as well as leaks of sulfides that may occur as the material is broken down (Kutti et al., 2008).

However, exported kelp detritus does not tend to accumulate to any great degree. Research near Frøya in Trøndelag found that kelp detritus tends to spread thinly over large areas, depending on conditions around the cultivation site, such as topography, currents, and sediment type. It was found that under normal operating conditions, the detritus was deposited from right below the cultivation site to several kilometers out, with 90% being deposited within 4 km. The density of deposited carbon was found to be 25g C/m^2 directly below the cultivation site, to 1g C/m^2 a few kilometers out; the pattern of dispersion was found to be independent of production volume (Hancke et al., 2021).

Results from “worst-case-scenario”-simulations where fresh biomass of kelp was purposefully deposited in a 10cm thick layer directly on the sea floor (>8kg/m^2), simulating a situation that could arise in case of total collapse of the site, showed that the biodiversity fell drastically due to the affected area growing anoxic and toxic, with only a few tolerant species surviving and thriving. This was a short-lived consequence, though, as after only two weeks 50% of the deposited biomass was gone, and after 3 months more than 90% had disappeared and conditions normalized, although this process is slowed in colder waters. There was also a notable difference in the species deposited, with *S. latissima* having a shorter degradation period than other species such as *Alaria esculenta* (Hancke et al., 2021).

Organic material that is not broken down, eroded or consumed will contribute to long-term storage and sequestering of carbon, meaning a net reduction of carbon in the water column. Macroalgae in the wild do not typically grow in habitats where large amounts of it may accumulate for storage (which would happen in deeper waters), but its presence in deep water has been reported, suggesting it may be stored there (Krause-Jensen & Duarte, 2016)

The role and importance of kelp as an allocator of resources down trophic levels in an ecosystem is not fully understood. Findings indicate kelp is an important source of nutrition for recipient communities in the deep (Filbee-Dexter et al., 2018), and a benign-to-beneficial source of food for the benthic community in close proximity to the cultivation site (Walls et al., 2017).

One final point that need to be considered is that macroalgae, via photosynthesis, can remove CO_2 from seawater in the vicinity of kelp farms. When these waters are exported offshore via currents, tides, etc., they can potentially lower CO_2 concentrations in offshore surface waters, thereby enhancing CO_2 uptake (Watanabe et al., 2020).

Light limitation

Cultivated macroalgae grow close to the sea surface, down to about 30m depth, and will therefore absorb most of the sunlight, possibly shading the waters below. A valid concern may thus be that the shading might reduce the ability of phytoplankton in the area to perform photosynthesis, reducing primary production and in turn zooplankton, larvae and other organisms dependent on primary producers, therefore undermining the basis for local food webs. In addition to this, the structures and biomass of the cultivation site could dampen the wave action and in- and outflow of water to the area, reducing nutrient availability and the transport of planktonic organisms (Hancke et al., 2018). However, phytoplankton will likely not remain below the cultivation site, and the bigger threat is therefore to sedentary marine plants and -algae growing below a cultivation site. Results from Zanzibar outline the negative effects shading from macroalgae cultivation had on wild seagrass populations, although damage was also from trampling, as well as being in very shallow waters making it difficult to determine the impact of shading (Moreira-Saporiti et al., 2021). Field experiments performed in Ireland, although not specifically focused on the effects on shading, suggested that effects of macroalgae cultivation in shallow (6-20m) waters had little to no impact on the benthic community, including seagrass *Zostera marina* (Walls et al., 2017).

Literature dedicated to the effects of shading is lacking, although one can to some degree extrapolate from research dedicated to other effects of macroalgae cultivation on the surrounding ecosystem. It can, however, be counted as logical that the effects of shading on life below the cultivation site will decrease the deeper the location is. Further studies on effects of shading on the benthic community is needed, but for wild macroalgae populations, certain assumptions can be made based on related research on the antagonistic relationship between microalgae blooms and intertidal kelp, showing that shading has a negative effect on benthic primary producers in the intertidal (Kavanaugh et al., 2009). At present, it seems effects of shading is limited in terms of negative impacts, and is worse in very shallow waters. It is also logical that the problems of shading will scale as European kelp farms increase in size and coverage.

Nutrients and pollution

When it comes to nutrient absorption, there are two sides; on the one hand, it is believed macroalgae may help reduce eutrophication resulting from runoffs from e.g. agriculture or fish farming, but a concern may also be that macroalgae may deplete nutrients in "healthy" waters so that the natural populations of macro- and microalgae may be impacted, which in turn has consequences cascading up the food web (Hancke et al., 2018).

Seaweeds extract dissolved nutrients, assimilating dissolved inorganic nitrogen and phosphorous, which in many ecosystems in in northern Norway) (Rinde & Sjøtun, 2005).

If then - keeping in mind that trawling in the north may be unsustainable - kelp demand should increase, this would have a greater impact on southern regions. Considering a reduced ability to produce understory recruits for future generations, an increased harvesting of wild kelp forests might tax them to the point where they can no longer regrow. If the demand for kelp is to increase, cultivation may be an attractive and more sustainable option to meet demands. But to what extent are we able to cultivate kelp? What other species of marine flora may be of interest for cultivation? And what would be the impacts of macroalgae cultivation on an industrial scale?

The possibility of implementing macroalgae cultivation in conjunction with traditional aquaculture is also an alternative, though not one considered in any depth in this review. The practice is called integrated multi-trophic aquaculture (IMTA), and is an interesting approach to aquaculture.

IMTA has been proposed as a cultivation method to mitigate aquaculture waste release, and is believed to hold potential in reducing a cultivation site's ecological footprint, provide extra streams of revenue, and contributing to increasing social acceptance of finfish cultivation systems (Troell et al., 2009). The practice of IMTA combines the cultivation of fed aquaculture species (such as finfish), inorganic extractive organisms (such as seaweeds), and organic particulate feeders (suspension- and deposit feeders such as mussels). The aim of IMTA is to increase both sustainability and profit by recapturing energy and nutrients which are lost in intensive fish farming, and turn it into more crops with commercial value. Results from Canada indicates that IMTA is effective in increasing both biomass and growth rate of kelps (Chopin et al., 2004), and biomass of mussels, without any apparent cost in terms of accumulation of toxic products or even taste (Lander et al., 2004), but current IMTA operations are relatively small-scale, and extrapolation for larger scale operations is not feasible due to three main factors: 1) Biomitigation efficiency of extractive species cannot be well established when their biomass remains small in comparison to biomass of fed species; 2) biomass production potential cannot be accurately predicted, and 3) economic costs and benefits are also difficult to extrapolate from small, experimental systems. The capacity of seaweeds to remove nutrients in an open-water system is hard to measure, due to the fluctuating nutrient concentration in the water depending on current, depth, time of year, time of day, and other variables. Such variability has led to divergent conclusions about the effectiveness of IMTA in terms of reduction of nutrient concentration in the water column (Troell et al., 2009).

Norway originate from terrestrial runoffs or fish farming activities. Also assimilated is dissolved carbon (via CO_2 uptake) during photosynthesis.

Organic carbon transfers from seaweeds and kelp forests to other ecosystems are key processes in nature, increasing food availability to otherwise nutrient-poor environments. However, on the flip side: large-scale seaweed cultivations may also cause high material deposits on the seafloor which could have adverse consequences on benthic ecosystems and biodiversity through decomposition processes and associated oxygen depletion. In addition, physical shading of both pelagic and benthic ecosystems may affect primary production in the case of shallow in-shore areas, although this has not yet been studied.

Microalgae have a more effective uptake of nutrients than macroalgae, being able to absorb nitrate at very low concentrations (1µM) (Eppley et al., 1969). As an example, even at much higher concentrations (20µM nitrate, twice the level found in the sea surface during winter), *Saccharina latissima* sporophytes showed no evidence of having saturated their uptake rates of nitrate (Forbord et al., 2021).

Recent research has illustrated that microalgae can have a half-saturation constant 40x lower than that of kelp. Nutrient concentrations in Frohavet during summer were found to be 0.5µM, supporting only 1-2% of the maximum growth rate for kelp, whereas microalgae could grow at close to their maximum rate (Hancke et al., 2021).

The conclusion then is that in terms of nutrient availability, kelp are unlikely to negatively impact microalgae via direct competition, a conclusion which is independent of production volume.

However, as cultivated algae and the wild microalgae absorb nutrients from the water, this may reduce the availability of nutrients and thus impact wild macroalgae growing in the area, not able to take up nutrients as efficiently as microalgae. This same process can also occur within kelp farms, reducing growth internally (Hancke et al., 2018). This competitive situation may negatively affect wild macroalgae populations, which in turn might have negative consequences on the food web.

The uptake of nutrients is not necessarily negative, as it may have a positive effect in reducing eutrophication resulting from runoffs from agriculture, rivers, and fish farms. The higher level of nutrients in the water is then readily available to all primary producers, limiting growth only when the system is no longer eutrophic. In this way, cultivated kelp may positively impact the surrounding ecosystems and help towards restoring and bringing balance to ecosystems surrounding the cultivation site (Hancke et al., 2018).

The "nutrient-negative" footprint of algae cultivation sites is often believed to be synonymous with pollution-free, or put differently, a site which removes excess nutrients from the environment, is by definition part of the cleanup rather than a source of pollution; however, the framework needed to be able to grow the algae may be a source of microplastics or other pollutants.

Macroalgae as artificial habitats

Seaweed cultivation sites create temporary habitats for both invertebrates and fishes, possibly functioning as artificial reefs, and contributing to ecological interactions within nearby ecosystems. Their role as habitats has not yet been systematically investigated to a great degree, but the role as improvised habitats has been observed (Stevant et al., 2017). These artificial habitats differ from natural kelp forests in that they are exclusively monocultural, as well as growing close to the surface on artificial structures or ropes, all of which are removed upon harvesting (Hancke et al., 2021). These features lead to concerns, among which are the possibility of artificially sustaining an unnaturally large population which will be taxing on the surrounding ecosystem upon harvesting of the cultivated macroalgae, or allowing non-native species to establish a foothold they would not otherwise have been able to gain.

Macroalgae serve as both a food source as well as a habitat, and especially nurseries. The removal of habitat forming species leads to a collapse of the ecosystem; however, in naturally occurring vegetation beds both overgrazing and overgrowth is uncommon, suggesting that self-regulation is the rule in healthy systems. This is vulnerable to a range of factors such as large grazing events by migrating sea urchin, overfishing of predators, trawling and other extraordinary events (Christie et al., 2009). In the context of cultivation, a site for cultivating macroalgae might provide temporary habitats increasing both biodiversity and abundance, which is vulnerable to collapse after harvesting. The most pressing concern then is whether this will result in an overload and subsequent collapses in surrounding ecosystems, or simply be part of a natural flux in increase and reduction in associated populations, or even a beneficial addition leading to a healthier ecosystem in general. The answer to these questions is still unknown.

A multi-year, government-backed research project (KELPRO, see Hancke et al., 2021) investigating the effects of kelp cultivation on the ecosystem indicates that cultivation sites provide habitats with a species composition mimicking that of natural kelp forests in the immediate vicinity, establishing an ecosystem in connection with the cultivation site, which would not otherwise have existed (Hancke et al., 2021).

In addition to this, any anthropogenic disturbance to an ecosystem, such as the supporting structure of a cultivation site, may allow for foreign invasion of the ecosystem if the disturbance is outside of the magnitude, duration or frequency of natural disturbances (Tyrrell & Byers, 2007). This principle is corroborated in the case of kelp cultivation sites by KELPROs findings that the empty (harvested) cultivation sites had great abundances of the invasive species Japanese skeleton shrimp, *Caprella mutica*, which is designated as a "(especially) high risk" on the Norwegian black list of invasive species. The skeleton shrimp were only present when the cultivation site was empty, and had also spread to other structures such as buoys, ropes, floating docks and other artificial structures in the area. The invasive skeleton shrimp were however only observed when the cultivation site was empty, and when the macroalgae were growing only native species of skeleton shrimp were observed. The problem seems to be contained to artificial structures, as there were no observations of the invasive skeleton shrimp in surrounding kelp forests at any point (Hancke et al., 2021). The findings are limited to a time frame of less than a year, and only in one locality; the effects of multiple, large-scale cultivation sites operating simultaneously is unknown. This observation is in line with other findings indicating that non-native species are more abundant on artificial structures than natural habitats, and conversely that native species are more abundant on natural reefs (Airoldi et al., 2015).

Genetic interchange and algae as vectors of diseases

The immediate caveat to make with regards to gene flow, is to completely bar the introduction of non-native species, as that may have catastrophic effects on the existing ecosystems as has been observed time and time again in our world's oceans, examples being *Caulerpa taxifolia* in the Mediterranean, *Undaria pinnatifada* and *Sargassum muticum* in Western Europe (Fredriksen & Sjøtun, 2015; Stevant et al., 2017), and is one of the major threats to biodiversity (Schaffelke et al., 2006).

Gene flow between cultivated and wild populations is generally limited by distance and current strength, and high levels of genetic isolation between populations has been found from 0-50km (Durant et al., 2014). Spores of most kelp posess flagella and are thus capable of some autonomous movement, but this is very limited (Fredriksen & Sjøtun, 2015).

Research on the spore dispersal of *L. hyperborea* indicates that it ranges is around 200m at a minimum, depending on current and depth, but that the spore dispersal varies extremely from species to species with examples such as *Alaria esculenta* being limited to dispersal within 10m of adult colony (Fredriksen et al., 1995).

It has been found that genetic exchange between wild and cultivated species seemingly do not result in much of a negative consequence for the ecosystem (Guillemin et al., 2008). It seems that the real danger comes from introducing generalist species able to thrive better than native species, which could then outcompete the native species and drastically change the ecosystem, which could spell disaster for a wide range for other organisms (Schaffelke et al., 2006).

Beyond this, it has also been found that there are local genetic adaptions within the same species, which varies with latitude (Hancke et al., 2021). These differences, albeit minor ones, *may* be important, but a case can equally be made that areas laid barren due to overgrazing by sea urchins could benefit from a reintroduction of species that were once established in the area, and which may gradually regrow through natural migration from adjacent areas in any case.

Knowledge about disease spread and gene flow in macroalgae is lacking, although there is concern around the introduction of non-native species and risks associated with genetic interchange between wild and farmed populations of the same species based on experience from animal aquaculture as well as agriculture, where crop-to-wild gene flow has been shown to result in the impoverishment of genetic resources available for selection (Loureiro et al, 2015).

Infamous examples of disease spread as a result of human cultivation of aquatic species include the crayfish plague, where a pathogen was carried by American crayfish into Europe (Strayer, 2010), or cultivated salmon acting as reservoirs for the indigenous sea lice, a copepod parasite, spreading to wild populations and enhancing mortality (Costello, 2009).

Although research on the topic is lacking, examples from Asia shed some light on disease in cultivated algae crops: The red algae *Porphyra yezoensis* is an important commercial foodcrop which has seen an explosive increase in cultivation in recent decades, is under attack by the parasitic oomycetes *Pythium porphyrae* and *Olpidiopsis sp*, responsible for "red rot", and cythrid blight, respectively (Ding & Ma, 2005). The disease causes cell death and biomass loss, and as a result farmers routinely see losses of 10% of yield on average, even as high as 30% localized (Gachon et al, 2010). The diseases were found to occur more frequently when grown in higher densities and more intensively (Ding & Ma, 2005; Gachon et al, 2010). Treatment effectivity is lacking, and severe methods such as the complete removal of seedlings, or the acid washing with resulting discoloration of the product is often necessary to get rid of the disease (Loureiro et al, 2015)

Knowledge about crop-to-wild geneflow among seaweeds is practically unmeasured, and models of algal parasite effect on the foodweb are imprecise due to a lack of basic understanding of algal pathogen biology (Loureiro et al, 2015).

References

Airoldi, L., Turon, X., Perkol-Finkel, S., Rius, M. (2015). Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, *21*(7), 755–768. https://doi.org/10.1111/DDI.12301

Aure, J., & Østensen, Ø. (1993). Hydrografiske normaler og langtidsvariasjoner i norske kystfarvann mellom 1936 og 1992 (Hydrographical normals and long - term variations in Norwegian coastal waters from 1936 to 1992). *Fisken og Havet*, NR. 6 - 1993. 67s.

Campbell, I., Macleod, A., Sahlmann, C., Neves, L., Funderud, J., Øverland, M., … Stanley, M. (2019). The environmental risks associated with the development of seaweed farming in Europe - prioritizing key knowledge gaps. *Frontiers in Marine Science*, *6*(MAR), 107. https://doi.org/10.3389/FMARS.2019.00107/BIBTEX

Chopin, Thierry & Robinson, Shawn & Bastarache, S. & Belyea, E. & Shea, R. & Armstrong, W. & Fitzgerald, P.. (2004). The AquaNet integrated multi-trophic aquaculture project: Rationale of the project and development of kelp cultivation as the inorganic extractive component of the system. *Bulletin of the Aquaculture Association of Canada. 104*. 11-18.

Christie, H., Fredriksen, S., & Rinde, E. (1998). Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. *Hydrobiologia 1998 375:0*, *375*(0), 49–58. https://doi.org/10.1023/A:1017021325189

Christie, H., Jørgensen, N. M., Norderhaug, K. M., & Waage-Nielsen, E. (2003). Species distribution and habitat exploitation of fauna associated with kelp (Laminaria Hyperborea) along the Norwegian Coast. *Journal of the Marine Biological Association of the United Kingdom*, *83*(4), 687–699. https://doi.org/10.1017/S0025315403007653H

Christie, H., Norderhaug, K. M., & Fredriksen, S. (2009). Macrophytes as habitat for fauna. *Marine Ecology Progress Series*, *396*, 221–233. https://doi.org/10.3354/MEPS08351

Costello, M. J. (2009). How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1672), 3385–3394. https://doi.org/10.1098/RSPB.2009.0771

Ding, H., & Ma, J. (2005). Simultaneous infection by red rot and chytrid diseases in Porphyra yezoensis Ueda. *Journal of Applied Phycology*, *17*(1), 51–56. https://doi.org/10.1007/S10811-005-5523-6

Directorate of Fisheries (2020) Akvakulturstatistikk (tidsserier)-Alger (*in Norwegian*). http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Akvakulturstatistikk tidsserier/Alger. Accessed 30.01.2020

Directorate of Fisheries (2022) Tarehøsting (*in Norwegian)*. https://www.fiskeridir.no/Yrkesfiske/Havmiljoe/Tarehoesting, accessed 17.09.2022

Druehl, L.D. (1967) Distribution of two species of *Laminaria* as related to some environmental factors. Journal of Phycology 3 (2):103-108

Eppley RW, Rogers JN, McCarthy JJ (1969) Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnol. Oceanogr. 14: 912-920.

Filbee-Dexter, K., Wernberg, T., Norderhaug, K.M., Ramirez-Llodra, E.., & Pedersen, M.F. (2018). Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia*, *187*(1), 291–304. https://doi.org/10.1007/S00442-018-4121-7

Fiskeridirektoratet (2021). Aquaculture map: https://portal.fiskeridir.no/portal/apps/webappviewer/index.html?id=87d862c458774397a8466b148e3dd147. Accessed June 2021

Forbord S., Etter S.A., Broch O., Dahlen V.R., Olsen Y. (2021) Initial short-term nitrate uptake in juvenile cultivated Saccharina latissima (Phaeophyceae) of variable nutritional state. Aquat. Bot. 168: 103306

Forbord, S., Skjermo, J., Arff, J., Handå, A., Reitan, K. I., Bjerregaard, R., & Lüning, K. (2012). Development of Saccharina latissima (Phaeophyceae) kelp hatcheries with year-round production of zoospores and juvenile sporophytes on culture ropes for kelp aquaculture. *Journal of Applied Phycology*, *24*(3), 393–399. https://doi.org/10.1007/s10811-011-9784-y

Fossberg, J., Forbord, S., Broch, O. J., Malzahn, A. M., Jansen, H., Handå, A., et al. (2018). The potential for upscaling kelp (*Saccharina latissima*) cultivation in salmon-driven integrated multi-trophic aquaculture (IMTA). *Front. Mar. Sci.* 5:418. doi: 10.3389/fmars.2018.00418

Fredriksen S. & Sjøtun K. (2015). Risikovurdering ved utsetting av ikke–stedegen tare. Report from Norwegian Environment Agency, M-299 (in Norwegian).

Fredriksen, S., Sjøtun, K., Lein, T. E., & Rueness, J. (1995). Spore dispersal in laminaria hyperborea (laminariales, phaeophyceae). *Sarsia*, *80*(1), 47–54. https://doi.org/10.1080/00364827.1995.10413579

Gachon, C. M. M., Sime-Ngando, T., Strittmatter, M., Chambouvet, A., & Kim, G. H. (2010). Algal diseases: spotlight on a black box. *Trends in Plant Science*, *15*(11), 633–640. https://doi.org/10.1016/J.TPLANTS.2010.08.005

Guillemin, M. L., Faugeron, S., Destombe, C., Viard, F., Correa, J. A., & Valero, M. (2008). Genetic variation in wild and cultivated populations of the haploid- diploid red alga Gracilaria chilensis: How farming practices favor asexual reproduction and heterozygosity. *Evolution*, *62*(6), 1500–1519. https://doi.org/10.1111/j.1558-5646.2008.00373.x

Hancke K., Broch, O.J., Olsen, Y., Bekkby, T., Hansen, P.K., Fieler, R., Attard, K., Borgersen, G., Christie, H. (2021). Miljøpåvirkninger av taredyrking og forslag til utvikling av overvåkningsprogram. NIVA rapport ISSN 1894-7948, ISBN 978-82-577-7325-0

Hancke, K., Bekkby, T., Gilstad, M., Chapman, A., Christie, H. (2018). Taredyrking – mulige miljøeffekter, synergier og konflikter med andre interesser i kystsonen. NIVA-rapport 7265-2018, ISBN 978-82-577-7000-6

Kavanaugh, M. T., Nielsen, K. J., Chan, F. T., Menge, B. A., Letelier, R. M., & Goodrich, L. M. (2009). Experimental assessment of the effects of shade on an intertidal kelp: Do phytoplankton blooms inhibit growth of open coast macroalgae? *Limnology and Oceanography*, *54*(1), 276–288. https://doi.org/10.4319/LO.2009.54.1.0276

Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat. Geosci. 9: 737-42

Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., & Duarte, C. M. (2018). Sequestration of macroalgal carbon: the elephant in the Blue Carbon room. *Biology Letters*, *14*(6), 23955–26900. https://doi.org/10.1098/RSBL.2018.0236

Krumhansl, K. A., & Scheibling, R. E. (2012). Production and fate of kelp detritus. *Marine Ecology Progress Series*, *467*, 281–302. https://doi.org/10.3354/MEPS09940

Kutti, T., Hansen, P. K., Ervik, A., Høisæter, T., & Johannessen, P. (2007). Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. *Aquaculture*, *2–4*(262), 355–366. https://doi.org/10.1016/J.AQUACULTURE.2006.10.008

Lander, T., Barrington, K., Robinson, S., MacDonald, B., Martin, J. (2004). Dynamics of the blue mussel as an extractive organism in an Integrated Multi-trophic Aquaculture system. *Bulletin of the Aquaculture Association of Canada 104*, 19-28

Loureiro, R., Gachon, C. M. M., & Rebours, C. (2015). Seaweed cultivation: potential and challenges of crop domestication at an unprecedented pace. *New Phytologist*, *206*(2), 489–492. https://doi.org/10.1111/NPH.13278

Lüning, K. (1971). Seasonal growth of Laminaria hyperborea under recorded underwater light conditions near Helgoland. Proc. Eur. Mar. Biol. Symp.. 4. 347-361.

Lüning, K. (1980). Critical levels of light and temperature regulating the gametogenesis of three laminaria species (Phaephyceae). *Journal of Phycology*, *16*(1), 1–15. https://doi.org/10.1111/J.1529-8817.1980.TB02992.X

Lüning, K. (1986). New frond formation in Laminaria hyperborea (Phaeophyta): a photoperiodic response. *Http://Dx.Doi.Org/10.1080/00071618600650311*, *21*(3), 269–273. https://doi.org/10.1080/00071618600650311

Lüning K. (1988). Photoperiodic control of sorus formation in the brown alga Laminaria saccharina. *Mar Ecol Progr Ser* 45:137–144.

Matsson, S., Christie, H., & Fieler, R. (2019). Variation in biomass and biofouling of kelp, Saccharina latissima, cultivated in the Arctic, Norway. *Aquaculture*, *506*, 445–452. https://doi.org/10.1016/J.AQUACULTURE.2019.03.068

Moreira-Saporiti, A., Hoeijmakers, D., Msuya, F. E., Reuter, H., & Teichberg, M. (2021). Seaweed farming pressure affects seagrass and benthic macroalgae dynamics in Chwaka Bay (Zanzibar, Tanzania). *Regional Environmental Change*, *21*(1), 1–12. https://doi.org/10.1007/S10113-020-01742-2/TABLES/2

Moy F., Alve E., Bogen, J., Christie, H., Green, N., Helland, A., Steen, H., Skarbøvik, E., Stålnacke, P. (2006) Sugar Kelp Project: Status Report No. 1. Norsk Institutt for Vannforskning –NIVA, Oslo, Norway.

Munda, I. M., Luning, K. (1977). Growth Performance of Alana esculents off Helgoland. Helgolander wiss. Meeresunters. 29: 311-314

Olafsen, T., Winther, U., Olsen, Y., Skjermo, J. (2012) Verdiskapning basert på produktive hav i 2050. Rapport fra arbeidsgruppe oppnevnt av Det Kongelige Norske Videnskabers Selskap (DKNVS) og Norges Tekniske Vitenskapsakademi (NTVA). ISBN 978-82-7719-074-3

Paasche, E., Erga, S.R. (1988) Phosphorus and nitrogen limitation of phytoplankton in the inner Oslofjord (Norway). Sarsia 73:229–243.

Pang S, Lüning K. Tank cultivation of the red alga Palmaria palmata: effects of intermittent light on growth rate, yield and growth kinetics. Journal of Applied Phycology, 2004, 16, 93-99.

Parke M (1948) Studies on the British Laminariaceae. I. Growth in Laminaria saccharina (L.) Lamour. J Mar Biol Ass UK 27:651–709

Pearson, T.H. and Rosenberg, R. (1978) Macrobenthic Succession in Relation to Organic Enrichment and Pollution of the Marine Environment. Oceanography and Marine Biology—An Annual Review, 16, 229-311.

Ramirez-Llodra, E., Rinde, E., Gundersen, H., Christie, H., Fagerli, C. W., Fredriksen, S., … Norderhaug, K. M. (2016). A snap shot of the short-term response of crustaceans to macrophyte detritus in the deep Oslofjord. *Scientific Reports 2016 6:1*, *6*(1), 1–5. https://doi.org/10.1038/srep23800

Renaud, P. E., Løkken, T. S., Jørgensen, L. L., Berge, J., & Johnson, B. J. (2015). Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science 2*, 31. https://doi.org/10.3389/FMARS.2015.00031

Rinde, E., & Sjøtun, K. (2005). Demographic variation in the kelp Laminaria hyperborea along a latitudinal gradient. *Marine Biology*, *146*(6), 1051–1062. https://doi.org/10.1007/S00227-004-1513-5

Schaffelke, B., Smith, J. E., & Hewitt, C. L. (2006). Introduced Macroalgae – a Growing Concern. *Journal of Applied Phycology 2006 18:3*, *18*(3), 529–541. https://doi.org/10.1007/S10811-006-9074-2

Schmedes, P. S., Nielsen, M. M., Reitan, K. I., Andersen, K. L., & Petersen, J. K. (2021). Updated hatchery and cultivation methods for the Atlantic rhodophyte Palmaria palmata. Abstract from 7th Conference of the International Society for Applied Phycology , Tsukuba, Ibaraki, Japan.

Sjøtun, K., Fredriksen, S., Lein, T. E., Rueness, J., & Sivertsen, K. (1993). Population studies of Laminaria hyperborea from its northern range of distribution in Norway. *Hydrobiologia 1993 260:1*, *260*(1), 215–221. https://doi.org/10.1007/BF00049022

Steen, H., Moy, F. E., Bodvin, T., & Husa, V. (2016). Regrowth after kelp harvesting in Nord-Trøndelag, Norway. *ICES Journal of Marine Science*, *73*(10), 2708–2720. https://doi.org/10.1093/ICESJMS/FSW130

Steinhagen, S.; Enge, S.; Larsson, K.; Olsson, J.; Nylund, G.M.; Albers, E.; Pavia, H.; Undeland, I.; Toth, G.B. Sustainable Large-Scale Aquaculture of the Northern Hemisphere Sea Lettuce, Ulva fenestrata, in an Off-Shore Seafarm. J. Mar. Sci. Eng. 2021, 9, 615. https:// doi.org/10.3390/jmse9060615

Stévant, P., Rebours, C., & Chapman, A. (2017). Seaweed aquaculture in Norway: recent industrial developments and future perspectives. *Aquaculture International 2017 25:4*, *25*(4), 1373–1390. https://doi.org/10.1007/S10499-017-0120-7

Strayer, D. L. (2010). Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*(SUPPL. 1), 152–174. https://doi.org/10.1111/J.1365-2427.2009.02380.X

Torstensen, R.R.G., 2020. Miljøeffekter ved dyrking av sukkertare *(Saccharina latissima)* Et taredyrkingsanleggs rolle som kunstig habitat. Master thesis, University of Oslo, Norway; 97 pp.

Troell, M., Joyce, A., Chopin, T., Neori, A., Buschmann, A. H., & Fang, J. G. (2009). Ecological engineering in aquaculture — Potential for integrated multi-trophic aquaculture (IMTA) in marine offshore systems. *Aquaculture*, *297*(1–4), 1–9. https://doi.org/10.1016/J.AQUACULTURE.2009.09.010

Tyrrell, M. C., & Byers, J. E. (2007). Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology*, *342*(1), 54–60. https://doi.org/10.1016/J.JEMBE.2006.10.014

Vea, J., & Ask, E. (2011). Creating a sustainable commercial harvest of Laminaria hyperborea, in Norway. *Journal of Applied Phycology 2010 23:3*, *23*(3), 489–494. https://doi.org/10.1007/S10811-010-9610-Y

Walls, A. M., Kennedy, R., Edwards, M. D., & Johnson, M. P. (2017). Impact of kelp cultivation on the Ecological Status of benthic habitats and Zostera marina seagrass biomass. *Marine Pollution Bulletin*, *123*(1–2), 19–27. https://doi.org/10.1016/J.MARPOLBUL.2017.07.048

Watanabe, K., Yoshida, G., Hori, M., Umezawa, Y., Moki, H., and Kuwae, T. (2020). Macroalgal metabolism and lateral carbon flows can create significant carbon sinks. *Biogeosciences* 17, 2425–2440. doi: 10.5194/bg-17-2425-2020

Zhu, P., Li, D., Yang, Q., Su, P., Wang, H., Heimann, K., & Zhang, W. (2021). Commercial cultivation, industrial application, and potential halocarbon biosynthesis pathway of Asparagopsis sp. Algal Research, 56, 102319. https://doi.org/10.1016/j.algal.2021.102319