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Genetic heterogeneity among two bioeconomically important kelp species along the Norwegian coast

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Abstract

Knowledge of genetic diversity among wild populations is becoming increasingly important as more species are recognized for their bioeconomic value. Industrialization of natural resources, such as kelp in the marine shallow sublittoral zone through cultivation and wild-harvesting, may lead to extensive translocation and local population decimation. Without adequate resilience in the form of genetic diversity within and across populations and given the potential introduction of deleterious alleles from translocations, such anthropogenically pressured populations may not be able to sufficiently respond to future climate and other stressors. Here we provide an assessment of the genetic heterogeneity of two bioeconomically important kelp species, *Laminaria hyperborea* and *Saccharina latissima*, across the Norwegian coastal region from South (57°N) to North (78°N), by applying microsatellite genotyping. Isolation by distance was found for both kelp species when comparing genetic distance to geographic distance. *L. hyperborea* clustered into four distinct genetic groups corresponding to distinct geographical ecoregions, whereas *S. latissima* did not show equally strong geographical structuring but separated into three geographical clusters along the Norwegian coast. No genetic differentiation was found within the Norwegian Skagerrak region, corroborating previous findings. The identified genetic clustering of both kelp species supports the retention of established management regions along the Norwegian coast and argues for the continuation of a regional focused management plan for kelp resources.

Further, the results demonstrate that care should be taken to prevent translocation of kelp between ecoregions in the ongoing industrialization of kelp cultivation, to maintain a healthy coastal ecosystem and sound natural population genetic diversity.

Introduction

Anthropogenic pressure on coastal zones has contributed to dramatic habitat loss of submerged aquatic macrophytes on a global scale (Waycott et al. 2009, Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018). The loss of 'foundation species' (corals, kelp, seagrass, etc.) is especially problematic due to their key role in ecosystem functioning, threatening abundance and biodiversity of associated species (Kelp: Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018; Seagrass: Orth et al. 2006, Waycott et al. 2009; Coral: Pandolfi et al. 2003). Among these foundation species, kelp forests are highly productive marine coastal ecosystems creating three-dimensional forest-like habitats for multitudes of species, including juvenile fish important to commercial fisheries (Norderhaug et al. 2005; Christie et al. 2009). Due to their emerging role in bioeconomy, kelp species are being harvested and cultivated for their alginates and attractive nutritional content (Vásquez 2009; Kerrison et al. 2016). This industrialization of kelp in Europe has led to increased growth in harvesting of wild populations and in cultivation of selected species along the coasts of Ireland, France, and Norway for production of a number of consumer goods (Draget et al. 2005; Broch et al. 2013; Kerrison et al. 2016).

Along the Norwegian coast, natural kelp forests cover more than 8000 km^2 (Gundersen et al. 2011), dominated by the species *Laminaria hyperborea* (Gunnerus) Foslie, and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl, and G.W. Saunders. Since the 1970s, the Norwegian kelp forests have suffered large-scale loss of biomass and severe spatial diminishing, likely due to increased sea urchin population size and failed recovery (Sivertsen 1997; Norderhaug and Christie 2009). However, this trend has partially reversed during the last ten years, as sea urchin abundance and recruitment decreased as a consequence of increasing water temperatures, facilitating kelp forests' recolonization and regrowth in Mid-Norway (Norderhaug and Christie 2009; Fagerli et al. 2013; Rinde et al. 2014). The fast-growing *S. latissima* has particularly been shown to efficiently recolonize barren areas, in contrast to the slower-growing *L. hyperborea* (Leinaas and Christie 1996), potentially influencing the distribution of genetic diversity within and between these kelp species. Since the early 2000s, *S. latissima* kelp forests in Norway and globally have experienced degradation and potentially also a decline in genetic variation seemingly due to overgrowth of fine filamentous algae (turf algae), as reviewed by Filbee-Dexter and Wernberg (2018).

The changes in kelp forest distribution come at a time when science is just beginning to understand the population genetic dynamics of kelp forests (Nielsen et al. 2016; Wenberg et al. 2018; Luttikhuizen et al. 2018). Marine coastal ecosystems are generally assumed to be structured following isolation by distance (IBD), with increasing genetic differentiation between sites as a function of distance (Wright 1943; Guo 2012). However, this is not always supported by real systems due to potential long-range dispersal and the overall stochastic nature of coastal marine currents (Siegel et al. 2008; White et al. 2010). At a global scale, genetic patterns of kelp are structured by morphology (Valero et al. 2011), ocean currents (Billot et al. 1998; Tellier et al. 2009), distance (Alberto et al. 2010; Robuchon et al. 2014; Luttikhuizen et al. 2018) and occasional floating rafts

(Fraser et al. 2010; Neiva et al. 2012). Moreover, in the northern hemisphere, diversity is expected to be highest at low latitudes as a result of glacial refugia in southern regions (Hewitt 2000; Maneiro et al. 2011; Neiva et al. 2012), whereas leading edge populations are expected to have less genetic diversity, as a consequence of founder effect (Hampe and Petit 2005). Whereas several studies have investigated population genetic patterns of the smaller brown seaweeds along the Norwegian coastline (Hoarau et al. 2007; Olsen et al. 2010; Coyer et al. 2011), only a few have studied the population genetics of large kelp species in this geographic area (Guzinski et al. 2016; Nielsen et al. 2016; Luttikhuizen et al. 2018).

Kelp populations with sufficient genetic variation are considered more resilient to climatic stress compared to populations with low genetic variation (Wernberg et al. 2018). Identifying and mapping local as well as regional genetic variation is therefore of great importance to generate baseline information, which will enable efficient monitoring and sustainable use of wild kelp populations. This becomes increasingly important due to commercial interests in wild species, resulting in potential extensive translocations of organisms, and with that, the introduction of deleterious alleles hampering local adaptation. Along the Norwegian coast, extensive translocations of organisms are occurring for example as a biological measure to remove salmon lice from farmed Atlantic salmon (*Salmo salar*) by introducing fishes from the family of wrasses (Labridae) (Skiftesvik et al. 2014; Halvorsen et al. 2017a,b) and the lumpfish (*Cyclopterus lumpus*) (Powell et al. 2018) into affected areas. Translocations of organisms have proven to result in introgression of foreign genotypes into resident local wild populations (Glover et al. 2012; Jansson et al. 2017; Faust et al. 2018), which becomes even more problematic with increasing levels of genetic differentiation between the source and the resident population, possibly disrupting local adaptation if selection is not sufficiently strong to maintain locally beneficial alleles (Haldane 1930). Therefore, both the assessment of genetic diversity on a local and regional population level and the corresponding levels of genetic differentiation are needed before such translocations should occur for instance related to wide-spread industrial-scaled farming of kelp species.

This study provides documentation of genetic heterogeneity among populations and across ecoregions of the two most dominant and commercially important kelp species along the Norwegian coast, i.e. *S. latissima* and *L. hyperborea*. The study covers the entire Norwegian coast, from southern Norway to Svalbard, and encompasses six ecoregions based on climatic conditions and biogeographic patterns, with the aim to advise an ecosystem-based management of marine resources. Results are discussed in the context of current management plans and commercial exploitation of the species, and to help management preserve genetic diversity among Norwegian kelp populations, thereby securing ecological/genetic resilience against future climatic and anthropogenic pressures. The assessment of the level of genetic heterogeneity among Norwegian kelp together with the regional genetic diversity estimates provides a baseline for further studies on the genetic makeup of changing kelp populations. The results will assist the implementation of both a genetic database and a management tool for the safekeeping of healthy and sustainable kelp communities, both wild and farmed populations.

Materials and Methods

Sample collection and preparation

As part of a national environmental monitoring program, a total of 106 *S. latissima* and 98. *L. hyperborea* were sampled across 16 locations in five of the six ecoregions along the Norwegian coast, including Svalbard (Table 1, Fig. 1). Emphasis was on the most densely populated regions, thus giving a good spatial representation of the Norwegian kelp forest. No samples were collected from the 'Norwegian Sea North' region as kelp forest is very sparsely present in this region due to over grazing by green sea urchins (Norderhaug and Christi 2009). As the samples for this study were collected alongside a monitoring program prioritizing a geographically wide sample collection over intensive local sample collection, sample sizes for some of the locations did not conform to recommendations for coverage of allele frequencies within a population (Hale et al. 2012; Fung and Keenan 2014).

Tissue samples of individual sporophytes of *S. latissima* and *L. hyperborea* collected from 4 to 23 individuals per location were preserved and stored in silica gel at room temperature or stored in ethanol and freeze-dried prior to extraction. Samples used to initially test microsatellites were extracted with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) with modifications from Snirc et al. (2010). Genomic DNA from all other samples was extracted from 2 to 10 mg of dried tissue with the cetyltrimethyl ammonium bromide (CTAB) protocol developed for plants (Murray and Thompson 1980), with modifications for brown algae (Hoarau et al. 2007, Coyer et al. 2009), and eluted in 100 µl AE buffer (Qiagen).

Microsatellite genotyping

Genotyping was done for eight and nine microsatellite markers, for *L. hyperborea* and *S. latissima* respectively (Table 2). Markers were selected from Robuchon et al. (2014) and Guzinski et al. (2016), in addition to four markers originally developed for other closely related species (CS34, CS12, CS13: Wang et al. 2011; SSR 261: Zhang et al. 2015). Additional methodology and results for cross amplification tests are available in the supplementary material (Table S1).

Laminaria hyperborea: Final amplification volume was 5 µl, containing 2.5 µl 2x Multiplex Master Mix (Qiagen) with HotStarTaq DNA Polymerase, 0.08 µl forward primer (5 µM) with M13 tail, 0.33 µl fluorescent-labelled M13 tail (5 µM, FAM, PET, VIC, or NED), 0.33 µl reverse primer (5 µM), 0.76 µl Milli-Q water and 1 µl 10x diluted template DNA. PCR conditions included an initial denaturation step at 95 °C for 15 min and two rounds of cycles: 30 cycles of denaturation at 94 °C for 30 s, annealing at 50 or 55 °C for 45 s (Table 2) and extension at 72 °C for 45 s, followed by seven cycles of denaturation at 95 °C for 30 s, annealing at 53 °C for 45 s, and extension at 73 °C for 45 s. The cycles were followed by an extension at 72 °C for 20 min and a 10 °C hold.

Saccharina latissima: Final amplification volume was 10 µl, containing 5 µl 2x Multiplex Master Mix (Qiagen) with HotStarTaq DNA Polymerase, 0.4 µl fluorescent-labelled forward primer (5 µM, FAM, YaYe, 565, or VIC), 0.4 µl reverse primer (5 µM), 3.2 µl Milli-Q water and 1 µl 10x diluted template DNA. PCR conditions included an initial denaturation step at 95 °C for 15 min, 10 cycles of touchdown with denaturation at 94 °C for 30 s, annealing at 65 °C (-1 °C for each cycle) for 30 s and extension at 72 °C for 30 s, followed by 30 cycles of

denaturation at 94 °C for 30 s, annealing at 50 or 55 °C for 30 s (Table 2), and extension at 72 °C for 30 s. The cycles were followed by an extension at 72 °C for 10 min and a 10 °C hold.

All PCR amplifications were run on a Mastercycler nexus (Eppendorf, Germany) thermal cycler with PCR conditions as specified above. DNA fragments from both species were separated by capillary electrophoresis using an ABI-3130 sequencer (Applied Biosystems, USA). PCR products were pooled according to Table 2 and 1 µl was mixed with 10.5 µl of HiDi formamide (Life Technologies, USA) and 0.5 µl of GeneScan 500 LIZ (for *L. hyperborea*) and GeneScan 600 LIZ (for *S. latissima*) size standard (ABI). Peaks were scored manually using GENEMAPPER 4.0 (ABI).

Data analyses

MicroChecker v2.2.3 (Van Oosterhout et al. 2004) was used to analyze the genotyped microsatellites for null alleles and scoring errors. The number of alleles genotyped at each locus and for each sampling location was calculated with HP-RARE (Kalinowski 2005), using the rarefaction with eight genes for *L. hyperborea* and six genes for *S. latissima*. The rarefaction was thereby run based on the smallest representation of genes in the samples being four and three, respectively, due to missing data in some of the loci. Observed and expected heterozygosity, and departure from Hardy–Weinberg equilibrium (HWE) were calculated using ARLEQUIN v3.5 (Excoffier et al. 2005). Linkage disequilibrium (LD) was tested in GENEPOP v4.0 (Raymond and Rousset 1995; Rousset 2008). The power of the set of microsatellites to detect genetic differentiation (both χ^2 and Fisher's exact tests) among all samples, for both species independently, was estimated in POWSIM v4.1 (Ryman and Palm 2006) running 1 000 simulations using empirical sample sizes and allele frequencies, and loci numbers. Global and pairwise F_{ST} (Θ_{ST}; Weir and Cockerham 1984), with statistical significance tested by 10 000 permutations, was calculated using MSA v4.05 (Dieringer and Schlötterer 2003). This program was also used to calculate genetic distances between population pairs by computing Cavalli-Sforza and Edwards (1967) genetic chord distances (D_{CE}), and bootstrapping 2 000 times (Hedges 1992). These genetic distances were used to construct a Neighbor-Joining (NJ) tree (Takezaki and Nei 1996) with the PHYLIP software package (Felsenstein 2005) and visualized in SPLITSTREE v4.14.4 (Huson and Bryant 2006). All tests of statistical significance were adjusted for multiple tests by the false discovery rate (FDR) correction (Benjamini and Yekutieli 2001). Genetic relationship among individuals and sampling locations was assessed by applying a discriminant analysis of principal components (DAPC) using the adegenet v.2.0.1 (Jombart 2008) package in R v3.3.2 (R Development Core Team 2010). IBD in a northward direction along the coastline, using sampling location 1 of both kelp species as the starting point, was calculated in two ways: i) comparing either genetic distance (D_{CE}) or $F_{ST}/(1-F_{ST})$ using the ape v2.3-1 package against geographic distance and ii) testing for statistical significance in a Mantel test run in R (R Development Core Team 2010). Genetic clustering of sampled individuals was assessed using STRUCTURE v3.4.2 (Pritchard et al. 2000; Pritchard et al. 2007; Hubisz et al. 2009) performing 100 000 burn ins and 300 000 iterations with 20 replicates per K for K 1 – 10 assuming an admixture model and correlated allele frequencies (Falush et al. 2003). The best representation of each dataset was evaluated using both Ln P(K) (Falush et al. 2003) and Delta K (Evanno et al. 2005) calculated using STRUCTURE HARVESTER (Earl and vonHoldt 2012). To explore the potential presence of subpopulation structure, additional STRUCTURE runs were conducted for each K-cluster in a hierarchical

manner. To maximize the accuracy of the twenty independent runs, the program CLUMPP v1.1.2 (Jakobsson and Rosenberg 2007), using the greedy function, was used and finally the results were visualized using DISTRUCT v1.1 (Rosenberg 2004). Final evaluation of K was compared with significant bootstrapping [i.e. >70% (Hillis and Bull 1993)] in the NJ tree, population clustering in the DAPC, and positioning of the sampling locations in the IBD plots, as STRUCTURE should not stand alone (Anderson and Dunham 2008; Thaulow et al. 2013).

Results

Four microsatellite markers (CS34, CS12, CS13, SSR261) were successfully cross-amplified from other closely related species (Table 2). For all markers, a total of 34 alleles were genotyped in *L. hyperborea* ranging from 22 (sample 6) to 12 (samples 1 and 3) among sampling locations, and 59 for *S. latissima* ranging from 31 (sample 2) to 17 (sample 5) (Table 1). The rarefaction allele count showed an increasing number (decimal numbers) from the southern samples and northward for *L. hyperborea*. For *S. latissima*, rarefaction allele count was variable but with an indication of more alleles with increasing latitude (Table 1). For *L. hyperborea*, expected heterozygosity ranged from 0.000 to 0.822 with a population average range of 0.103 to 0.489 and observed heterozygosity ranged from 0.000 to 0.730 with a population average range of 0.093 to 0.340 (Table S2). For *S. latissima*, expected heterozygosity ranged from 0.000 to 0.867 with a population average range of 0.308 to 0.570 and observed heterozygosity ranged from 0.000 to 0.889 with a population average range of 0.265 to 0.343 (Table S3). None of the microsatellites, for either species, contained null alleles or LD between the same pair of loci, in any of the sampled locations. Departure from HWE was not pronounced for any loci in *L. hyperborea*, whereas locus Sacl90 in *S. latissima* showed significant departure in five of the eight sampling locations. Poor tissue preservation or extraction may have been responsible for the 6% and 2% failed microsatellite genotyping in the *L. hyperborea* and *S. latissima* data sets, respectively (Table 1). The power of the two data sets to detect true population differentiation at an F_{ST} value of 0.030 was supported by a 99% probability by Fisher's exact test and the χ^2 test of 100% for both species (Fig. 2). Since the smallest F_{ST} value for each species was above 0.030 (Table 3), these are well within the supported detection limit.

STRUCTURE clustering of the locations of *L. hyperborea* showed a clear separation into four K-clusters (Fig. S1) in accordance with ecoregions (Fig. 1 and 3). All three Skagerrak sampling locations showed over 95% genetic identity to the first cluster (Fig. 1). The two North Sea sampling locations assigned mainly to the second cluster, which was represented by 89% and 66%, respectively. The two Norwegian Sea sampling locations showed 95% and 75% identity, respectively, to the third cluster. Cluster four was the most dominant cluster in the Barents Sea sample with 89% representation. The clustering into four groups corresponding to sampling locations and ecoregions is well corroborated by the bootstrap values in the NJ tree analysis and by the DAPC, which showed a clear visual separation of the Barents Sea from the remaining *L. hyperborea* samples along the second eigenvalue axis (Fig. 3).

K=3 was the most likely clustering pattern for the *S. latissima* samples after visual inspection despite Delta K indicating K=2 (Fig. S2). STRUCTURE showed a genetic clustering of samples in relative accordance with geographic positioning (Fig. 3). However, the *S. latissima* samples did not cluster at an equally structured scale

as the *L. hyperborea* samples (Fig. 3). The two Skagerrak samples shared the same cluster with the North Sea South sample, whereas the North Sea North sample clustered together with the most southern of the Norwegian Sea samples. The two northernmost samples from the Barents Sea were assigned to the third cluster (Fig. 1). The most northern of the Norwegian Sea samples (7) showed a mixed assignment with equal representation from the two southern clusters (≈43%) and only 14.4% from the northern cluster (Fig. 1). Also, the NJ tree and DAPC (Fig. 3) grouped the Skagerrak sampling locations closely together at one end of the latitudinal gradient and the two Barents Sea sampling locations at the other end. The North Sea and Norwegian Sea samples, however, were not separated according to ecoregions, but rather as a mix between the northern and southern samples (Fig. 3).

The genetic relationship among sampling locations as a function of geographic distance (i.e. isolation by distance, IBD) was identified to be statistically significant (Mantel test) and with good data representation, calculated based on both genetic distance (p-value <0.0001, R^2=0.72, Fig. 4a) and F_{ST} (p-value= 0.0050, R^2=0.59, Fig. 4b) for the *L. hyperborea* samples in a northward direction. Significant IBD was also identified among the *S. latissima* sampling locations when calculated based on genetic distance (p-value<0.0050, R^2=0.63, Fig. 4c), however, not when using F_{ST} (p-value=0.0590, R^2=0.04, Fig. 4d).

Discussion

The present study provides the first screening of genetic diversity, geographical heterogeneity and genetic differentiation among the two most dominant and commercially important kelp species along the Norwegian coast, i.e. *S. latissima* and *L. hyperborea*. Both species demonstrated genetic heterogeneity along the Norwegian coast and clustered into three (*S. latissima*) and four (*L. hyperborea*) different genetic groups in accordance with defined ecoregions and with geographic distance from South to North, i.e. showing IBD.

Geographical heterogeneity and genetic diversity

The Norwegian coastal ecosystem is divided into six ecoregions (Fig. 1) for management purposes based on climatic conditions, ocean currents and biogeographic patterns of biologically important species and other biological quality elements (Gundersen et al. 2017). The ecoregions are defined to fulfil the requirements of the Norwegian Water Management Regulation (Water Regulation, 2016) and the European Water Framework Directive (Jncc.defra.gov.uk, 2010), which aim to ensure comprehensive ecosystem-based management of marine resources. The ecoregions are also used to determine restrictions related to aquaculture and kelp farming.

Both species of kelp showed strong signatures of IBD when using Cords distance D_{CE} compared to the more traditional regression of $F_{ST}/(1- F_{ST})$ (Fig. 4), in accordance with a recent study by Séré et al. (2017). IBD based on $F_{ST}/(1- F_{ST})$ has been found for *L. hyperborea* along the coast of France (Robuchon et al. 2014) and for *S. latissima* in the Irish Sea (Mooney et al. 2018). In contrast, larger studies of *S. latissima* across Europe have not found IBD based on $F_{ST}/(1- F_{ST})$ (Guzinski et al. 2016), which is also true for smaller scale studies along the coast of Maine, USA (Breton et al. 2018). Different genetic distance estimates for the calculation of IBD should therefore in each case be evaluated. The relatively strong differentiation among ecoregions in Norway, designated to IBD (Fig. 4) and genetic clustering (Fig. 1), indicates limited range dispersal of zoospores or

colonization success by both species. Sea urchin populations along the Norwegian coast show a weaker pattern of IBD compared to kelp (Norderhaug et al. 2016), which could be explained by the higher duration and dispersal potential of the sea urchin pelagic larval stage compared to the kelp spores (see Fredriksen et al. 1995, Sogn Andersen 2013). Despite being weaker, the genetic patterns found for kelp are consistent with ocean current larval dispersal in a northward fashion as seen for sea urchins. This indicates that the dispersal possibility also exists for kelp, but that other ecological barriers probably limit the dispersal and mixing rate, especially for *L. hyperborea*.

Overall, genetic diversity of *S. latissima* along the coast of Norway was similar if not slightly higher than reported for populations in Maine, USA (Breton et al. 2018) and lower than genetic diversity for populations within Europe, including one sample from Greenland (Nielson et al. 2016), Paulino et al. 2016). Genetic diversity of *L. hyperborea* was lower for most Norwegian populations in comparison to populations along the French coast (Robuchon et al. 2014). In the southern ecoregion of Norway, *L. hyperborea* displayed even lower genetic diversity and strong differentiation towards the remaining sampling locations in northern Norway. This finding indicates that the Skagerrak ecoregion seems to be isolated (Höglund 2009) with respect to *L. hyperborea*, a pattern that was also observed for *L. hyperborea* in a disconnected region on the French coast (Robuchon et al. 2014). Such low genetic diversity may be the consequence of more fragmented and lower density sites compared to what has been found for *S. latissima* (Norderhaug et al. 2011), for which genetic mixing with close-by populations is limited. Exchange of gametes may be further limited by slower growth in sheltered areas compared to exposed areas (Sjøtun et al. 1993) whereby spore production has been shown to be delayed (Kain and Jones 1975) and thereby reducing overall fitness.

Some differences in the regional patterns of genetic structure and connectivity between the two kelp species exist and can most likely be explained by differences in dispersal abilities. Spore dispersal of *L. hyperborea* has been found to be distance-limited (Fredriksen et al. 1995, see also Nielsen et al. 2016) while spores of *S. latissima* stay longer in the water masses (Sogn Andersen 2013) and therefore also travel farther (Kain and Jones 1975). This is reflected in the more opportunistic life strategy of the short-lived *S. latissima* (Moy and Christie 2012), and can be observed in the sea urchin removal experiment of Leinaas and Christie (1996). In this experiment, when sea urchins were removed from a small isolated island far from any known kelp beds, *S. latissima* appeared as dense beds within the first year while *L. hyperborea* took at least four years to settle. Similarly, *S. latissima* is the first to recolonize more recent sea urchin depleted areas (own unpublished observations). The dispersal ability of *S. latissima* may also explain differences in connectivity between the two species in the Skagerrak and North Sea region, given that a long coastline of sand (Jæren) divides these regions of rocky shores available for kelps, as also pointed out by Luttikhuizen et al. (2018) discussing dispersal barriers.

Ecological trends

We found, that the genetic diversity of *S. latissima* in the Skagerrak oceanic region was comparable to other regions in Norway (Table 1). This trend is surprising given the fact that the region has experienced large declines in *S. latissima* biomass, in the order of 51% to 80%, during the last fifteen years (Bekkby and Moy

2011; Moy and Christie 2012). Most of the decline has occurred in sheltered areas, at shallow depths, due to anthropogenic stressors (e.g. increased land run-off and nutrient loads from rivers) and elevated water temperatures. Warmer temperatures, in conjunction with increased shading by epibionts and decreased water transparency, have been identified as the main drivers for this substantial kelp forest loss (Sogn Andersen et al. 2011; Moy and Christie 2012; Sogn Andersen 2013). This large-scale disappearance was observed in 2002, and the severe reduction in biomass (demographic bottleneck) may have resulted in reduced allelic richness. A bottleneck analysis showed, however, no indication thereof (data not shown). The consequences of a demographic bottleneck are expected to be reduced, if connectivity among habitat patches was high (Jangjoo et al. 2016).

Due to the ability of *S. latissima* zoospores to survive for several days in ocean currents (Kain and Jones 1975), high interbreeding within the Skagerrak oceanic region is a possibility. Further, Moy and Christie (2012) indicated that *S. latissima* is a species with more opportunistic traits and dispersal abilities than other kelps, leading to shorter term disappearance and reappearance and thus higher connectivity within the region. Connectivity along the southern coastline of Norway could potentially be explained by long-range dispersal of zoospores, as indicated by genetic clustering of the southern sampling location in the North Sea region with the Skagerrak samples and single individuals from other northern populations. Indeed, no genetic differentiation was observed between a Norwegian and a Swedish population collected close to the Norwegian boarder, within the Skagerrak basin (Nielsen et al. 2016). Other causes than geographical distance exist explaining the genetic differentiation among *S. latissima* populations (Mooney et al. 2018). Evidence for connectivity therefore seems to reside with water currents within and across regions, counteracted by dispersal barriers in the form of unfavourable bottom substrate, freshwater efflux and open water (Breton et al. 2018; Luttikhuizen et al. 2018; Mooney et al. 2018).

Once the kelp species disappear, filamentous algae and sediment become dominant and may inhibit recolonization of kelps as shown by seaweed species in several regions (Gorman and Connell 2009; Sogn Andersen et al. 2011; Sogn Andersen et al. 2013). Efforts to minimize nutrient and sediment fluxes seem to be of great importance for the preservation of kelp in the region. Genetic resilience was indeed proven to play a significant role in a marine heat wave extirpation of a kelp species (Wernberg et al. 2018). In the present recovery process of the Norwegian kelp forests, after sea urchin depletion, it is important to gain knowledge on the baseline population structures, genetic diversity, and other stressors before a large-scale reforestation takes place.

Genetic diversity within and differentiation among sampling locations of *L. hyperborea* was higher in the northern regions compared to the Skagerrak locations. This could indicate more abundant and relatively isolated (sub)populations with minimal, yet sufficient, genetic exchange to cluster together, compared to what was found in the south of Norway. The extensive areas grazed by sea urchins (Sivertsen 1997; Norderhaug and Christie 2009) have created longer distances between kelp sub-populations. The possibility of genetic input from un-sampled 'ghost' populations within the regions could be feasible yet hard to document, since kelp populations have been decimated for more than 45 years. However, range expansion of the crustaceans *Cancer pagurus* and

Carcinus maenas crabs (Fagerli et al. 2013) and warming ocean temperatures (Fagerli et al. 2014) have in recent years led to collapse and northward retraction of sea urchins. In the north, these are also experiencing population decimation due to increases in king crab, *Paralithodes camtschaticus*, leading to kelp recovery on both the Russian and Norwegian coasts (Gudimov et al. 2003; Christie and Gundersen 2014). Despite their limited current scope, future populations of *L. hyperborea* and *S. latissima* might experience even higher genetic diversity within the region due to recolonization from multiple founder populations, as suggested for the brown seaweed, *Fucus distichus*, recolonizing an area after an oil spill (Coyer et al. 2011). Founder populations exist within the region harbouring in exposed habitats (Rinde et al. 2014) not utilized by sea urchins.

Recommendations for management and Outlook

Marine management must strive to preserve genetic heterogeneity among wild populations and a rich local and regional genetic diversity within species to ensure healthy kelp forests that can withstand natural and anthropogenic pressures. Genetic diversity and the integrity of differentiated populations are needed to preserve robust ecosystems and maintain natural resilience properties despite human harvesting and cultivation efforts. The results from this study are intended to serve as a baseline for follow-up studies in order to unravel the important genetic structure of wild kelp forests and the currently recovering population of kelp along the Norwegian coast. Assessment of population genetics will be particularly relevant to management agencies in the case of large-scale kelp reforestation in areas previously dominated by sea urchins. Also a detailed understanding of kelp genetic heterogeneity across ecoregions is important due to the currently high interest in large-scale cultivation of kelp, particularly of *S. latissima,* all along the Norwegian coast. The results presented here will serve as a valuable supplement to the sparse data available on kelp genetic structure and assist formulation of knowledge-based guidelines to secure a sustainable wild-harvesting and large-scale cultivation of kelp. Guidelines should include recommendations to exclusively cultivate kelp strains of local origin to preserve local genetic structure and diversity. Thus, the present study supports the continuation of the precautionary principle strategy recommended for kelp cultivation; that only local ecotypes of kelp should be cultivated and that kelp strains should not be transported between fjords and across ecoregions for cultivation (Fredriksen and Sjøtun, 2015).

Despite the rather low numbers of samples from some of the locations, the power analysis showed sufficient strength and significance to support the degree of genetic differentiation and heterogeneity (Fig. 2). Overall genetic variance among the Norwegian samples presented here are in accordance with a recent study comprising multiple regions within Europe and North America (Luttikhuizen et al. 2018; but see Neiva et al. 2018). However, to fully investigate the transition zones between genetic clusters additional samples should be collected and analysed with higher genome coverage than were available to this study. This should be done to identify areas of special concern for anticipated kelp and seaweed cultivation establishment, avoiding unintended introgression from cultured conspecifics into wild populations, as observed in the salmon farming industry (Glover et al. 2012; Faust et al. 2018). Additionally, a more intensive sampling program including higher sample density is needed to obtain a full understanding of the genetic diversity of kelp along the Norwegian coast and to draft appropriate management strategies for future large-scale seaweed and kelp cultivation.

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Literature

Alberto F, Raimondi PT, Reed DC, Coelho NC, Leblois R, Whitmer A, Serrão EA (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology 91:49–56

Anderson EC, Dunham KK (2008) The influence of family groups on inferences made with the program Structure. Mol Ecol Resour 8:1219–1229

Bekkby T, Moy FE (2011) Developing spatial models of sugar kelp (*Saccharina latissima*) potential distribution under natural conditions and areas of its disappearance in Skagerrak. Estuar Coast Shelf Sci 95:477–483

Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. Ann Stat 29:1165–1188

Billot C, Rousvoal S, Estoup A, Epplen JT, Saumitou-Laprade P, Valero M, Kloareg B (1998) Isolation and characterization of microsatellite markers in the nuclear genome of the brown alga *Laminaria digitata* (Phaeophyceae). Mol Ecol 7:1778–1780

Breton TS, Nettleton JC, O'Connell B, Bertocci M (2018) Fine-scale population genetic structure of sugar kelp, *Saccharina latissima* (Laminariales, Pheophyceae), in eastern Maine, USA. Phycologia 57:32–40

Broch OJ, Ellingsen IH, Forbord S, Wang X, Volent Z, Alver MO, Hand A, Andresen K, Slagstad D, Reitan KI, Olsen Y, Skjermo J (2013) Modelling the cultivation and bioremediation potential of the kelp *Saccharina latissima* in close proximity to an exposed salmon farm in Norway. Aquac Environ Interact 4:187–206

Cavalli-Sforza LL, Edwards AWF (1967) Phylogenetic analysis: models and estimation procedures. Evolution 21:550–570

Christie H, Gundersen H (2014) From sea urchin deserts to rich kelp forests: crabs and climate as drivers of ecosystem shifts in southern Nordland and eastern Finnmark. FRAM, Print version: ISSN 1893–5532, Online version: ISSN 8193-5540

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–233

Coyer JA, Hoarau G, Beszteri B, Pearson G, Olsen JL (2009) Expressed sequence tag-derived polymorphic SSR markers for *Fucus serratus* and amplification in other species of *Fucus*. Mol Ecol Resour 9:168–170

437 Coyer JA, Hoarau G, Van Schaik J, Luijckx P, Olsen JL (2011) Trans-Pacific and trans-Arctic pathways of the
438 intertidal macroalga *Fucus distichus* L. reveal multiple glacial refugia and colonizations from the North
439 Pacific to the North Atlantic. J Biogeogr 38:756–771
440 Dieringer D, Schlötterer C (2003) MICROSATELLITE ANALYSER (MSA): a platform independent analysis
441 tool for large microsatellite data sets. Mol Ecol Notes 3:167–169
442 Draget KI, Smidsrød O, Skjåk-Bræk G (2005) Alginates from Algae. Biopolymers Online. Wiley-VCH Verlag
443 GmbH & Co. KGaA. DOI: 10.1002/3527600035.bpol6008.
444 Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing
445 STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361
446 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software
447 STRUCTURE: a simulation study. Mol Ecol 14:2611–2620
448 Excoffier L, Laval G, Schneider S (2005) Arlequin (version 3.0): an integrated software package for population
449 genetics data analysis. Evol Bioinform 1:47–50
450 Fagerli CW, Norderhaug KM, Christie HC (2013) Lack of sea urchin settlement may explain kelp forest
451 recovery in overgrazed areas in Norway. Mar Ecol Prog Ser 488:119–132
452 Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data:
453 linked loci and correlated allele frequencies. Genetics 164:1567–1587
454 Faust E, Halvorsen KT, Andersen P, Knutsen H, André C (2018) Cleaner fish escape salmon farms and
455 hybridize with local wrasse populations. R Soc open sci 5:171752
456 Felsenstein J (2005) PHYLIP (Phylogeny Inference Package), version 3.6. Distributed by the author.
457 Department of Genome Sciences, University of Washington, Seattle, Washington.
458 Filbee-Dexter K, Wernberg T (2018) Rise of turfs: A new battlefront for globally declining kelp forests.
459 BioScience 68:64–76
460 Fraser CI, Thiel M, Spencer HG, Waters JM (2010) Contemporary habitat discontinuity and historic glacial ice
461 drive genetic divergence in Chilean kelp. BMC Evol Biol 10:203
462 Fredriksen S, Sjøtun K, Lein TE, Rueness J (1995) Spore dispersal in *Laminaria hyperborea* (Laminariales,
463 Phaeophyceae). Sarsia 80:47–53
464 Fredriksen S, Sjøtun K (2015) Risk assessment of introducing non-indigenous kelp. Report from Norwegian
465 Environment Agency. M-299. (in Norwegian)
466 Fung T, Keenan K (2014) Confidence intervals for population allele frequencies: The general case of sampling
467 from a finite diploid population of any size. PLoS ONE 9:e85925
468 Glover KA, Quintela M, Wennevik V, Besnier F, Sørvik AGE, Skaala Ø (2012) Three decades of farmed
469 escapees in the wild: a spatio-temporal analysis of Atlantic salmon population genetic structure
470 throughout Norway. PLoS ONE 7:e43129
471 Gorman D, Connell SD (2009) Recovering subtidal forests in human-dominated landscapes. J Appl Ecol
472 46:1258–1265
473 Gudimov AV, Gudimova EN, Pavlova LV (2003) Effect of the Red King Crab *Paralithodes camtschaticus* on
474 the Murmansk coastal macrobenthos: The first estimates using sea urchins of the genus
475 *Strongylocentrotus* as an example. Doklady Biol Sci 393:539–541

476 Gundersen H, Christie H, de Wit H, Norderhaug KM, Bekkby T, Walday M (2011), CO2 uptake in marine
477 habitats - an investigation, NIVA report no. 6070-2010. ISBN 987-82-577-5805-9. 25 pp
478 Gundersen H, Bryan T, Chen W, Moy F (2017), Ecosystem Services: In the Coastal Zone of the Nordic
479 Countries. TemaNord report 2016:552 by Nordisk Ministerråd. Copenhagen. DOI: 10.6027/TN2016-
480 552.
481 Guo Q (2012) Incorporating latitudinal and central–marginal trends in assessing genetic variation across species
482 ranges. Mol Ecol 21:5396–5403
483 Guzinski J, Mauger S, Cock JM, Valero M (2016) Characterization of newly developed expressed sequence tag-
484 derived microsatellite markers revealed low genetic diversity within and low connectivity between
485 European *Saccharina latissima* populations. J Appl Phycol 28:3057–3070
486 Haldane JBS (1930) A mathematical theory of natural and artificial selection. Proc Camb Philos Soc 26:220–
487 230
488 Hale ML, Burg TM, Steeves TE (2012) Sampling for microsatellite-based population genetic studies: 25 to 30
489 individuals per population is enough to accurately estimate allele frequencies. PLoS ONE 7:e45170
490 Halvorsen KT, Larsen T, Sørdalen TK, Vøllestad LA, Knutsen H, Olsen EM (2017a) Impact of harvesting
491 cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas. Mar Biol
492 Res 13:359–369
493 Halvorsen KT, Sørdalen TK, Vøllestad LA, Skiftesvik AB, Espeland SH, Olsen EM (2017b) Sex- and size-
494 selective harvesting of corkwing wrasse (*Symphodus melops*)—a cleaner fish used in salmonid
495 aquaculture. ICES J Mar Sci 74:660–669
496 Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett
497 8:461–467
498 Hedges SB (1992) The number of replications needed for accurate estimation of the bootstrap p value in
499 phylogenetic studies. Mol Biol Evol 9:366–369
500 Hewitt G (2000) The genetic legacy of the Quaternary ice ages. Nature 405:907
501 Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in
502 phylogenetic analysis. Syst Biol 42:182–192
503 Hoarau G, Coyer JA, Veldsink JH, Stam WT, Olsen JL (2007) Glacial refugia and recolonization pathways in
504 the brown seaweed *Fucus serratus*. Mol Ecol 16:3606–3616
505 Höglund J (2009) Evolutionary Conservation Genetics. Oxford University Press Inc., New York
506 Huson DH, Bryant D (2006) Application of phylogenetic networks in evolutionary studies. Mol Biol Evol
507 23:254–267
508 Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with
509 label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806
510 Jangjoo M, Matter SF, Roland J, Keyghobadi N (2016) Connectivity rescues genetic diversity after a
511 demographic bottleneck in a butterfly population network. Proc Natl Acad Sci USA 113:10914–10919
512 Jansson E, Quintela M, Dahle G, Albretsen J, Knutsen H, André C, Strand Å, Mortensen S, Taggart JB,
513 Karlsbakk E, Kvamme BO, Glover KA (2017) Genetic analysis of goldsinny wrasse reveals
514 evolutionary insights into population connectivity and potential evidence of inadvertent translocation
515 via aquaculture. ICES J Mar Sci 74:2135–2147

516 Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics
517 24:1403–1405
518 Kain JM, Jones NS (1975) The biology of *Laminaria hyperborea* VII. Reproduction of the sporophyte.
519 J Mar Biol Assoc UK 55:567–582
520 Kalinowski ST (2005) HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic
521 richness. Mol Ecol Notes 5:187–189
522 Kerrison PD, Stanley MS, Kelly M, MacLeod A, Black KD, Hughes AD (2016) Optimising the settlement and
523 hatchery culture of *Saccharina latissima* (Phaeophyta) by manipulation of growth medium and
524 substrate surface condition. J Appl Phycol 28:1181–1191
525 Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR,
526 Konar B, Ling SD, Micheli F, Norderhaug KM, Pérez-Matus A, Sousa-Pinto I, Reed DC, Salomon AK,
527 Shears NT, Wernberg T, Anderson RJ, Barrett NS, Buschmann AH, Carr MH, Caselle JE, Derrien-
528 Courtel S, Edgar GJ, Edwards M, Estes JA, Goodwin C, Kenner MC, Kushner DJ, Moy FE, Nunn J,
529 Steneck RS, Vásquez J, Watson J, Witman JD, Byrnes JEK (2016) Global patterns of kelp forest
530 change over the past half-century. Proc Natl Acad Sci USA 113:13785–13790
531 Leinaas HP, Christie H (1996) Effects of Removing Sea Urchins (*Strongylocentrotus droebachiensis*): Stability
532 of the Barren State and Succession of Kelp Forest Recovery in the East Atlantic. Oecologia 105:524–
533 536
534 Luttikhuizen PC, van den Heuvel FHM, Rebours C, Witte HJ, van Bleijswijk JDL, Timmermans K (2018)
535 Strong population structure but no equilibrium yet: Genetic connectivity and phylogeography in the
536 kelp *Saccharina latissima* (Laminariales, Phaeophyta). Ecol Evol 8:4265–4277
537 Maneiro I, Couceiro L, Bárbara I, Cremades J, Ruiz JM, Barreiro R (2011) Low genetic variation and isolation
538 of northern peripheral populations of a red seaweed (*Grateloupia lanceola*). Aquat Conserv Mar
539 Freshw Ecosyst 21:590–600
540 Mooney KM, Beatty GE, Elsäßer B, Follis ES, Kregting L, O'Connor NE, Riddell GE, Provan J (2018)
541 Hierarchical structuring of genetic variation at differing geographic scales in the cultivated sugar kelp
542 *Saccharina latissima*. Mar Environ Res 142, 108–115
543 Moy FE, Christie H (2012) Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along
544 the south and west coast of Norway. Mar Biol Res 8:309–321
545 Murray MG, Thompson WF (1980) Rapid isolation of high molecular weight plant DNA. Nucleic Acids Res
546 8:4321–4326
547 Neiva J, Pearson GA, Valero M, Serrão EA (2012) Drifting fronds and drifting alleles: range dynamics, local
548 dispersal and habitat isolation shape the population structure of the estuarine seaweed *Fucus*
549 *ceranoides*. J Biogeogr 39:1167–1178
550 Neiva J, Paulino C, Nielsen MM, Krause-Jensen D, Saunders GW, Assis J, Bárbara I, Tamigneaux É, Gouveia
551 L, Aires T, Marbà N, Bruhn A, Pearson GA, Serrão EA (2018) Glacial vicariance drives
552 phylogeographic diversification in the amphi-boreal kelp *Saccharina latissima*. Scientific Reports
553 8:1112

554 Nielsen MM, Paulino C, Neiva J, Krause-Jensen D, Bruhn A, Serrão EA (2016) Genetic diversity of *Saccharina*
555 *latissima* (Phaeophyceae) along a salinity gradient in the North Sea–Baltic Sea transition zone. J Phycol
556 52:523–531
557 Norderhaug KM, Anglès d'Auriac MB, Fagerli CW, Gundersen H, Christie H, Dahl K, Hobæk A (2016)
558 Genetic diversity of the NE Atlantic sea urchin *Strongylocentrotus droebachiensis* unveils chaotic
559 genetic patchiness possibly linked to local selective pressure. Mar Biol 163:36
560 Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar Biol
561 Res 5:515–528
562 Norderhaug K, Christie H, Fosså J, Fredriksen S (2005) fish–macrofauna interactions in a kelp (*Laminaria*
563 *hyperborea*) forest. J Mar Biol Assoc U K 85:1279–1286
564 Norderhaug KM, Nautsvoll L, Ledang AB, Bjerkeng B, Gitmark JK (2011) Sugar kelp monitoring in the coastal
565 regions of Norway. Report for 2009 and 2010. Norwegian Institute for Water Research, NIVA. ISBN
566 978-82-577-5870-7
567 Olsen JL, Zechman FW, Hoarau G, Coyer JA, Stam WT, Valero M, Åberg P (2010) The phylogeographic
568 architecture of the fucoid seaweed *Ascophyllum nodosum*: an intertidal 'marine tree' and survivor of
569 more than one glacial–interglacial cycle. J Biogeogr 37:842–856
570 Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA,
571 Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass
572 ecosystems. BioScience 56:987–996
573 Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L,
574 Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term
575 decline of coral reef ecosystems. Science 301:955–958
576 Powell A, Treasurer JW, Pooley CL, Keay AJ, Lloyd R, Imsland AK, Garcia de Leaniz C (2018) Use of
577 lumpfish for sea-lice control in salmon farming: challenges and opportunities. Rev Aquacult 10:683–
578 702
579 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data.
580 Genetics 155:945–959
581 R Development Core Team (2010) R: A language and environment for statistical computing. Vienna Austria: R
582 Foundation for Statistical Computing. Retrieved from http//www.R-project.org.
583 Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and
584 ecumenicism. J Hered 86:248–249
585 Rinde E, Christie H, Fagerli CW, Bekkby T, Gundersen H, Norderhaug KM, Hjermann DØ (2014) The
586 influence of physical factors on kelp and sea urchin distribution in previously and still grazed areas in
587 the NE Atlantic. PLOS ONE 9:e100222.
588 Robuchon M, Le Gall L, Mauger S, Valero M (2014) Contrasting genetic diversity patterns in two sister kelp
589 species co-distributed along the coast of Brittany, France. Mol Ecol 23:2669–2685
590 Rosenberg NA (2004) DISTRUCT: a program for the graphical display of population structure. Mol Ecol Notes
591 4:137–138
592 Rousset F (2008) GENEPOP '007: a complete re-implementation of the GENEPOP software for Windows and
593 Linux. Mol Ecol Resour 8:103–106

Ryman N, Palm S (2006) POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. Mol Ecol Notes 6:600–602

Séré M, Thevenon S, Belem AMG, De Meeus T (2017) Comparison of different genetic distances to test isolation by distance between populations. Heredity 119:55-63

Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proc Natl Acad Sci USA 105:8974–8979

Sivertsen K (1997) Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. Can J Fish Aquat Sci 54:2872–2887

Sjøtun K, Fredriksen S, Lein TE, Rueness J, Sivertsen K (1993) Population studies of *Laminaria hyperborea* from its northern range of distribution in Norway. Hydrobiologia 260:215–221

Skiftesvik AB, Blom G, Agnalt A-L, Durif CMF, Browman HI, Bjelland RM, Harkestad LS, Farestveit E, Paulsen OI, Fauske M, Havelin T, Johnsen K, Mortensen S (2014) Wrasse (Labridae) as cleaner fish in salmonid aquaculture – The Hardangerfjord as a case study. Mar Biol Res 10:289–300

Snirc A, Silberfeld T, Bonnet J, Tillier A, Tuffet S, Sun JS (2010) Optimization of DNA extraction from brown algae (Phaeophyceae) based on a commercial kit. J Phycol 46:616–621

Sogn Andersen G (2013) Patterns of *Saccharina latissima* recruitment. PLoS ONE 8:e81092

Sogn Andersen G, Steen H, Christie H, Fredriksen S, Moy FE (2011) Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: Implications for forest recovery. J Mar Biol 2011:690375

Sundt RC, Jørstad KE (2003) Genetic population of goldsinny wrasse, *Cetnolabrus rupestris* (L.), in Norway: implications for future management of parasite cleaners in the salmon farming industry. Fish Manag Ecol 5:291–302

Tellier F, Meynard AP, Correa JA, Faugeron S, Valero M (2009) Phylogeographic analyses of the 30°S south-east Pacific biogeographic transition zone establish the occurrence of a sharp genetic discontinuity in the kelp *Lessonia nigrescens*: Vicariance or parapatry? Mol Phylogenetics Evol 53:679–693

Thaulow J, Borgstrøm R, Heun M (2013) Brown trout population structure highly affected by multiple stocking and river diversion in a high mountain national park. Conserv Genet 14:145–158

Valero M, Destombe C, Mauger S, Ribout C, Engel CR, Daguin-Thiébaut C, Tellier F (2011) Using genetic tools for sustainable management of kelps: a literature review and the example of *Laminaria digitata*. Cah Biol Mar 52:467–483

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Vásquez JA (2009) Production, use and fate of Chilean brown seaweeds: re-sources for a sustainable fishery. In:Borowitzka MA, Critchley AT, Kraan S, Peters A, Sjøtun K, Notoya M (eds) Nineteenth International Seaweed Symposium: Proceedings of the 19th International Seaweed Symposium, held in Kobe, Japan, 26-31 March, 2007. Springer Netherlands, Dordrecht. pp. 7–17

Wang G, Tan X, Shen J, Li J, Zhang L, Sun J, Wang B, Weng M, Liu T (2011) Development of EST-SSR primers and their practicability test for *Laminaria*. Acta Oceanologica Sinica 30: 112–11

Water Regulation (2016) Norwegian Water Management Regulation of 15 December 2006 No.1446 on the framework for Water Regulation

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Wernberg T, Coleman MA, Bennett S, Thomsen MS, Tuya F, Kelaher BP (2018) Genetic diversity and kelp forest vulnerability to climatic stress. Sci Rep 8:1851

White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help explain population genetic structure. Proc Royal Soc B 277:1685–1694

Wright S (1943) Isolation by distance. Genetics 28:114–138

Zhang N, Zhang L, Tao Y, Guo L, Sun J, Li X, Zhao N, Peng J, Li X, Zeng L, Chen J, Yang G (2015) Construction of a high density SNP linkage map of kelp (*Saccharina japonica*) by sequencing *Taq* I site associated DNA and mapping of sex determining locus. BMC Genom16:189–200

Figure legends

Fig. 1 Sampling maps covering Norwegian coastal territories with indications of ecoregions and sample positions (black dots) for the two studied kelp species *Laminaria hyperborea* (left) and *Saccharina latissima* (right). Pie carts indicate percentage proportions of a defined number of genetic clusters to represent the genetic differentiation within and among ecoregions. For *L. hyperborea* and *S. latissima* four and three genetic clusters represent these, respectively. For precise sampling location positioning please see table 1.

Fig. 2 Power analysis of the genotyped microsatellites to predict true F_{ST} values based on the empirical data and evaluated by Fisher's exact test and χ^2 test, for both *Laminaria hyperborea* (LH) and *Saccharina latissima* (SL).

Fig. 3 Wild populations of both *Laminaria hyperborea* and *Saccharina latissima* significantly separated into distinct ecoregions along the Norwegian coast. STRUCTURE, Neighbor-Joining tree (with significance from 2000 bootstraps), and DAPC analyses of *L. hyperborea* (left) and *S. latissima* (right) individuals from nine sampling locations along the Norwegian coast line, including Svalbard. Numbering of sampling locations correlate to Table 1. Colours in the three different analyses correspond to ecoregions as specified for the *L. hyperborea* STRUCTURE results. However, in the *S. latissima* STRUCTURE results, the clustering of the North Sea South and the Norwegian Sea South sampling locations does not conform as consistent as *L. hyperborea*, since only three clusters were identified.

Fig. 4 Genetic differentiation of *Laminaria hyperborea* and *Saccharina latissima* as a function of geographical distance from the sampling location closest to Sweden and in a northward fashion, calculated based on genetic distance (a, c) or F_{ST} (b, d). Sample numbering is explained in table 1.