Literature Review for Implementation of the 50-50 Rule for Cultivation of Seaweeds and other Aquatic Plants in Alaska

by

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and

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Symbols and Abbreviations

The following symbols and abbreviations, and others approved for the Système International d'Unités (SI), are used without definition in the following reports by the Divisions of Sport Fish and of Commercial Fisheries: Fishery Manuscripts, Fishery Data Series Reports, Fishery Management Reports, and Special Publications. All others, including deviations from definitions listed below, are noted in the text at first mention, as well as in the titles or footnotes of tables, and in figure or figure captions.

Weights and measures (metric)

centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
milliliter	mL
millimeter	mm

Weights and measures (English)

cubic feet per second	ft³/s
foot	ft
gallon	gal
inch	in
mile	mi
nautical mile	nmi
ounce	oz
pound	lb
quart	qt
yard	yd

Time and temperature

day	d
degrees Celsius	°C
degrees Fahrenheit	°F
degrees kelvin	K
hour	h
minute	min
second	s

Physics and chemistry

all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity (negative log of)	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General

Alaska Administrative Code	AAC
all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.
all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.
at	@
compass directions:	
east	E
north	N
south	S
west	W
copyright	©
corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
District of Columbia	D.C.
et alii (and others)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.
Federal Information Code	FIC
id est (that is)	i.e.
latitude or longitude	lat or long
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S.C.	United States Code
U.S. state	use two-letter abbreviations (e.g., AK, WA)

Mathematics, statistics

all standard mathematical signs, symbols and abbreviations

alternate hypothesis	H_A
base of natural logarithm	e
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	(F, t, χ^2, etc.)
confidence interval	CI
correlation coefficient (multiple)	R
correlation coefficient (simple)	r
covariance	cov
degree (angular)	°
degrees of freedom	df
expected value	E
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	$\log_2$, etc.
minute (angular)	'
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	"
standard deviation	SD
standard error	SE
variance	
population	Var
sample	var

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LITERATURE REVIEW FOR IMPLEMENTATION OF THE 50-50 RULE FOR CULTIVATION OF SEAWEEDS AND OTHER AQUATIC PLANTS IN ALASKA

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ABSTRACT

What is colloquially known as the "50-50 Rule" is 2 of 3 separate guidelines for cultivating seaweeds and aquatic plants in Alaska waters that cover minimizing disease transmission, protecting genetic fitness in the wild, and maintaining genetic diversity within cultured broodstocks. The 50-50 Rule encompasses the latter two guidelines, including 1) limiting the distance from the site of collection to location of out planting to 50 km by water and 2) setting the minimum number of wild broodstock for each species, area, and year to 50 unrelated individuals. The original genetic guidelines were developed approximately five years ago in the absence of population genetic data for Alaska seaweeds and aquatic plants and assuming complete replacement of broodstock with new wild plants each year. These guidelines were not, and still aren't, codified in any Alaska statute or regulation. However, their language is incorporated into relevant permits, including aquatic farm operation permits, stock acquisition permits (for collection of wild stock to populate a farm or hatchery), and stock transport permits (from a hatchery/farm to another farm).

Here, we cover in detail the rationale behind the two genetic guidelines covering the 50-50 Rule; including a summarization of the original supporting literature and information published (and in preparation) since its development. In summary, the spatial/distance guideline was based on information gathered during a thorough literature review in 2016. Although a significant amount of new information covering seaweed (particularly kelp) population genetic structure has been published since that time, including in Alaska, this guideline remains relatively well-supported and no data thus far appears to warrant relaxation of the recommendations in this guideline. The second guideline regarding maintenance of minimum broodstock census size was based on the number of breeding individuals required to combat loss of genetic variation and reduce the rate of inbreeding. This also represented a pragmatic decision given farm operational capacities. As this guideline is largely based on accepted population genetic theory, and represents a compromise between management and industry, it is generally well-accepted and there are no known challenges to the recommendation at this time.

Keywords: kelp, seaweed, regulation, policies, guidelines, genetics, genomics, aquaculture, hatchery

INTRODUCTION

The State of Alaska Constitution, Alaska Statutes (AS), and Alaska Administrative Code (AAC), contain provisions to protect the wild stock resources of the state, while providing opportunities to develop resources in the best interest of the people of Alaska (see Appendix A). In 2016, based on these provisions and on increasing interest in mariculture of aquatic plants (especially kelps), the Department of Fish and Game Division of Commercial Fisheries' Statewide Aquaculture Planning and Permitting Section Chief, Fisheries Scientists, and the Director's office wrote permitting guidelines with specific criteria designed to protect wild populations from genetic and disease concerns associated with mariculture operations. Three separate guidelines were developed that address disease transmission and maintenance of genetic diversity across and within geographic areas. What is colloquially known as the "50-50 Rule" is a subset comprised of the latter two guidelines, which provide genetic recommendations.

The three guidelines for the permitting of seaweed and aquatic plant culture in Alaska are as follows:

1. To minimize the risk of disease transmission, any macroalga approved as a species to be cultured at the hatchery can be transported only to their natal drift zone, which is defined as the broad general area where the parental plants were collected. The permit holder may request a waiver from this requirement by providing evidence (plant pathology inspection) that macroalgal diseases are not a concern. The stipulation for transport back to the natal drift zone areas based on disease concerns could be removed, and the distribution broadened after 5 years, provided no disease issues have occurred with previous transports during plant production and no disease issues have been reported to the department by permitted producers and growers.

2. To maintain genetic fitness of wild populations, any macroalga cultured at the hatchery can be released only within their natal drift zone, which is defined as the broad general area where the broodstock plants were collected. The size of a natal drift zone is likely to differ amongst species because of differences in life-history characteristics, and within specific areas, because of differences in coastal current patterns. Until additional information becomes available about propagule dispersal patterns, or the genetic population structures of a particular species, the distance from the site of collection to the location of out planting will be limited to 50 km by water. The permit holder can request a waiver from this requirement by providing specific evidence that macroalgal genetic fitness is not a concern.

3. To maintain genetic diversity within cultured broodstocks, offspring must be derived from not less than 50 wild broodstock individuals if offspring are destined for out planting. Although the mechanics of culture will largely dictate broodstock size, a broodstock of at least 50 unrelated individuals will retard the short-term loss of diversity. Parental plants should be collected from dispersed locations along a shoreline to reduce the potential of sampling plants from the same families.

Although all three guidelines are listed, we will focus throughout the remainder of the report on the second and third guidelines making up the 50-50 Rule. We will discuss the rationale and references used in the development of the genetic guidelines, and review the current literature for new information that might inform adjustments to these guidelines.

BACKGROUND

Kelps are primary producers and foundation species in coastal ecosystems, providing a number of goods and services both directly and indirectly to humans (Christie et al. 2009; Steneck et al. 2002; Teagle 2017). Genetic variation within and among these kelp beds provides the raw materials necessary for their adaptation and resilience to change in local environmental conditions (e.g. substrate, temperature, salinity, turbidity), diseases (King and Lively 2012), and predators (see Hutchings and Fraser (2008) for a review of effects in finfish:). Concurrently, farm-to-wild gene flow has the potential to cause changes in, or loss of, genetic diversity among and within populations, reduced fitness, and declines in ecosystem resilience (Hutchings and Fraser 2008; Schindler et al. 2010; Waples et al. 2012). The primary objective of the latter two guidelines of the 50-50 Rule is to therefore protect the among- and within-population variation of wild populations of kelp and other aquatic plants from the effects of mariculture operations.

These guidelines were developed with the understanding that mariculture of kelp, in particular, is conducted in open conditions where cultured kelp may interact with wild kelp. Under current culture practices, sori are collected from the blades of wild sporophytes. Spores are then released in the hatchery to produce microscopic gametophytes, which are settled onto seed lines where fertilization occurs. Fertilized female gametophyte eggs become macroscopic sporophytes, completing the cycle (Flavin et al. 2013). The seed lines are wrapped onto grow lines and outplanted to farm sites located in nearshore open water areas (uncontained). Although cultured kelp are scheduled for harvest prior to reproductive maturity, once outplanted, they may

genetically interact (interbreed) with wild kelp through escape. Escape events may occur as a consequence of dislodgement or through unanticipated delays in harvest or inability to harvest prior to maturation (e.g. due to storm events or other disturbances; Shan et al. 2019; Uwai et al. 2006).

Protecting the genetic diversity of wild populations of kelp has even received recent international attention. Under the Convention on Biological Diversity (CBD 2010) Aichi Biodiversity Targets, Strategic Goal B seeks to "Reduce the direct pressures on biodiversity and promote sustainable use." To conserve biodiversity, ecosystem-based approaches were recommended for legal and sustainable management and harvest of aquatic plants, and sustainable management of agriculture, aquaculture, and forestry programs was encouraged. An ecosystem approach that "protect[s] the health and genetic diversity of wild kelp beds" was also touted by Grebe et al. (2019), wherein the authors outline a socioeconomic and environmental conceptual model for kelp aquaculture across the U.S. and Europe.

Risk management measures designed to avoid or reduce interaction between farmed and wild kelp, which in turn helps mitigate or minimize genetic concerns, are therefore recommended. Such measures are common to the permitting of finfish and shellfish aquaculture and may include methodologies like the use of sterile kelp strains (Loureiro et al. 2015; e.g., proposed future efforts in Umanzor et al. 2021), using adequate numbers of individuals for broodstock (Grebe 2019), and restricting broodstock collection to local populations (Yarish et al. 2017).

Below, we cover in more detail the literature behind each genetic guideline comprising the 50-50 Rule, including summarization of the original literature as well as salient information published and in preparation since guideline development. Should permitted kelp farming practices change to allow a more segregated approach, given the imperative in aquaculture for application of genetic improvement methodologies like selective breeding, then the applicability and construction of these guidelines will require re-evaluation. Re-evaluation will need to incorporate management goals at that time and full consideration of the best available science.

LITERATURE SUPPORTING COLLECTION OF BROODSTOCK WITHIN 50 KILOMETERS OF THE GROW-OUT SITE

To maintain genetic fitness of wild populations, any macroalga cultured at the hatchery can be released to only within their natal drift zone, which is defined as the broad general area where the broodstock plants were collected. The size of a natal drift zone is likely to differ among species, because of differences in life-history characteristics, and among areas, because of differences in coastal current patterns. Until additional information becomes available about propagule dispersal patterns, or about the genetic population structures of a particular species, the distance from the site of collection to location of out planting will be limited to 50 km by water. The permit holder can request a waiver from this requirement by providing specific evidence that macroalgal genetic fitness is not a concern.

If mariculture operations outplant kelp with the potential to become reproductively viable into uncontained (i.e., open water) areas on the farm site for grow out, there is a possibility that the cultivated kelp may genetically interact with local wild kelp. To minimize the risk of genetic

impact on wild populations, broodstock for F_1 outplanting must be sourced from local wild populations. In cases where F_2+ outplanting is permitted, outplanted progeny must have a local wild population ancestral source. Yarish et al. (2017), for example, proposed that as a first step towards bioregional seedstock guidelines in New England, seaweed nurseries could commit to only using genetic strains and reproductive material collected from the same bioregion as the farm site. To objectify these statements for Alaska, broodstock must be collected from the wild, and the distance between a broodstock source and the grow-out site was restricted to a maximum of 50 kilometers (31 miles). In other words, hatchery-cultivated macroalgae can only be transported for outplanting within 50 km by water of the broodstock collection site. ADF&G recognizes, however, that life history characteristics and natural dispersal patterns may be significantly different among species and areas. Therefore, ADF&G does consider requests to broaden the 50 km out planting zone on a case-by-case and species-by-species basis, if information based on the best-available science is sufficient to indicate that disease and genetic concerns are acceptable.

The spatial/distance guideline language was developed based on information gathered during a thorough review of the literature (Grant unpublished). The intent of this research was to determine an over-water "neighborhood size," with the farm site as the focus, within which to restrict collection of broodstock. In general, on the larger spatial scales (e.g., ≥100km between sampled populations) on which the bulk of available research has been conducted, chaotic patchiness mediated by post-glacial dynamics, large-scale oceanographic patterns, and climate change is commonly documented. Much of this work has also been conducted on species in the order Laminariales, and specifically, in the genus *Saccharina* (see Appendix B for common and scientific names for species referenced in this document), a taxon with myriad uses in food preparation and the medical, cosmetic, and biofuel industries. Over shorter spatial scales, there has been some indication of isolation-by-distance (IBD) in certain species and regions as well as smaller-scale patchiness. Small-scale signals are on the order of ten to tens of kms and are strongly mediated by localized current patterns and suitable habitat distribution. Few studies report any indication of panmixia (informally, lack of population structure).

PRE-2016 LITERATURE BASIS

The development of kelp and seaweed farming in Alaska requires an understanding of the geographical sizes of population units. Do all the kelp of a particular species within a certain area belong to the same interbreeding population or are they composed of multiple populations? Of fundamental concern was that local adaptation and population genetic variation might be compromised by mixing populations from different areas. This was the rationale behind development of Alaska's Genetic Policy for protecting population units of Pacific salmon. However, while numerous studies of North Atlantic *Saccharina latissima* have shown that variability in growth and production traits in populations are associated with environmental variables, including salinity, sea surface temperature, nutrient availability, and turbidity (e.g., Gerard 1997; Heinrich et al. 2012; Nielsen et al. 2014), there was little to no information about adaptive genetic variation or selectively neutral population structure within and among kelp populations in Alaska in 2016 when this guideline was developed.

A small amount of biogeographic work indicated that a *Palmaria mollis*, showed frequency differences between inner- and outer-coastal populations along Alaska and British Columbia and among populations near Ketchikan, Sitka, Juneau, and Prince William Sound (Lindstrom et al. 1997). Otherwise, in *Macrocystis pyrifera*, Johansson et al. (2015) primarily focused on

populations in the southern part of the species range (especially southern California), although the authors also included two collections from Southeast Alaska (SEAK) in Sitka and Craig. The SEAK and British Columbia samples clustered together and away from the more southerly populations, smaller-scale structure was found among southern California groups, particularly between offshore islands and the mainland, distances among some of which are <50 km. Similar to other studies, smaller scale population structure was found to be mediated through environmental mechanisms (e.g., light penetration, local current patterns). Some additional genetic work that had been published for populations of *M. pyrifera* in California that revealed genetic differences among populations along an ~50 km section of coastline (Alberto et al. 2010). The authors measured 'oceanographic' distance between populations and found genetic isolation along environmental gradients on this geographical scale.

Meanwhile, a study of *S. japonica*, which has an ecology similar to *S. latissima* in Alaska, showed mtDNA haplotype frequency differences over distances of 50 to 200 km (Zhang et al. 2015). The authors surmised that the phylogeographic patterning they witnessed was due to a combination of human-mediated impacts (marine transportation and aquaculture) and post-glacial population expansion. A second study on *S. japonica* also found significant genetic differentiation among populations widely spaced across Japan, China, the Korean peninsula, and Russia (Shan et al. 2016). However, Asia has thus far not proven to be the best model for Alaska because cultivation coupled with extensive selection and inbreeding has been conducted in the region for generations. Artificial selection is a main factor causing significant genetic differentiation between wild and cultivated *S. japonica*, and leakage from cultivated populations appears common (Liu et al. 2012; Shan et al. 2016).

At least two studies were conducted on *Durvillaea antarctica*, a species that requires a rocky substrate for growth. Fraser et al. (2009) looked at the effects of sea ice scour during glaciation and report single widespread organellar haplotypes present throughout much of the southern circumpolar region (~10,000 km scales), while population structuring further north was on the order of 10-100 km across much of New Zealand and Chile. Subsequently, Fraser et al. (2010) found contrasting latitudinal patterns along the coast of Chile. Central Chilean populations exhibited genetic structure coincident with habitat discontinuities due to sandy beach breaks, whereas the southern coast of Patagonia was genetically homogenous, evidencing the capability of the species for long-distance dispersal. On those broader spatial scales, Macaya and Zuccarello (2010) used mtDNA and SSCP analyses on *M. pyrifera* and found a significant, but common, genetic break at 42°S latitude associated with the splitting of the Antarctic Circumpolar Current where it hits the coast as well as a previously unknown break at 33°S that had not been detected in other marine species. Reduced levels of diversity found above and below these breaks were theorized to be associated with contemporary ENSO events in the north and historical glaciation to the south.

Another factor influencing the decision to limit broodstock collection to 50 km was that limited spore dispersal was documented for kelps, which can result in small neighborhood sizes and genetic patchiness (Grant 2016). Dispersal distances of only a few meters from parental sporophyte plants and little dispersal of gametes produced by the microscopic gametophytic stage were not uncommon (Dayton 1985; Gaylord et al. 2002, 2004, 2006). Moreover, the oogonium in the female gametophyte is not released but fertilized in situ by male gametophytes, which have a life span of only a few hours. Long distance rafting of fertile sporophytic plants is possible for kelps (e.g., *Enteromorpha* spp. and others) but not definitively documented (Amsler and Searles 1980;

Zechman and Mathieson 1985; Reed et al. 2004; Hernández-Carmona et al. 2006; Brennan et al. 2014; Saunders 2014). In fact, despite evidence of long-distance dispersal through rafting for *M. pyrifera* (Macaya et al. 2005; Thiel & Haye, 2006), Macaya and Zuccarello (2010) showed strong genetic differentiation among kelp beds separated by less than 50 km in Chile.

In *Laminaria digitata*, Billot et al. (2013) documented IBD and found that limited gamete and spore dispersal was responsible for genetic differentiation among neighborhoods that were separated by only 10 km in an unfragmented kelp forest in the English Channel and with no evidence for environmental boundaries. Meanwhile, Faugeron et al. (2005) used a hierarchical sampling design in the intertidal *Lessonia nigriscens* to cover different geographic distances. In each of two stands separated by 42 km of coastline, three sites spanning 35 km and 40 km, respectively, were sampled. The authors found strong genetic structure at all spatial scales (F_{ST} from 0.15 to 0.29) using RAPD, suggesting most spore settlement and gametophyte fertilization may occur within only a few meters of the parent.

STATE OF THE LITERATURE IN 2021

Since 2016, numerous genetic studies of kelps show genetic differences between kelp populations separated by 10s to 100s of kilometers, and a host of studies have now been conducted on species in Alaska. Despite new information, the original guideline remains well-supported.

Alaska

In Alaska, recent population structure studies have focused on *S. latissima*, *Alaria* spp.*,* and *Hedophyllum nigripes*. The results for three kelp species/genera show chaotic genetic population structures, arguing a need for protection at geographic scales smaller than that of a drift zone (RaLonde 1993; see Appendix C for delineation of "larval" drift zones in Alaska). All of the genetic data also point to the need for ecological and physiological studies to understand local adaptation. Grant & Chenoweth (2021) report that, on small scales in the Gulf of Alaska, microsatellite allele-frequency similarity between more-or-less neighboring paired populations of *S. latissima* indicated genetic neighborhoods of 10s to 100s of km, although sharing of low-frequency organellar (concatenated rbcL-COI) haplotypes between some neighboring locations may reflect some connectivity. On larger scales, chaotic distribution of haplotypes pointed to complex interglacial colonization and extinction events, and association between genetic and geographical distance weakened between populations separated by >300 km indicating population history may play a greater role at these scales.

Grant and Bringloe (2020) performed a similar study on *Alaria marginata* and found similar results. In sum, five major organellar DNA lineages do not entirely correspond to historical species' delineations, chaotic distribution of haplotypes on large spatial scales points to complex interglacial colonization/extinction events, and on smaller scales, populations separated by 10 to 10s of km could be fixed for divergent lineages, indicating the importance of local environmental conditions. Meanwhile, nuclear DNA variation points to adequate levels of gene flow to prevent speciation but not enough to homogenize populations within drift zones. A recent follow-up headed by Bringloe et al. (2021) used whole genome sequencing, which provided significantly greater resolution among lineages; some lineages occur just a few kilometers apart but do not appear to mix or hybridize.

Grant et al. (2020) then focused on the Gulf of Alaska for *H. nigripes* but also covered the Canadian Arctic and across the North Atlantic. The study used organellar DNA and found that nearly all

populations sampled in the Gulf of Alaska were genetically unique. The only other work with an Alaskan component comprises a master's thesis on *Nereocystis luetkeana* by Gierke (2019). The author used seven microsatellites to genotype 59 sites from Herring Island, AK, to Cambria Bay, CA, and including the Salish Sea. Gierke (2019) found four large-scale genetic co-ancestry groups that were geographically coherent, apart from isolation of the Salish Sea. These groupings are generally supportive of drift zone delineation, but smaller-scale information was unavailable in this study.

New England

In New England, recent population structure studies have focused on *S. latissima*. A study of 12 microsatellite loci in populations along the coast of Maine detected allele-frequency differences on spatial scales of 10s of km, with an overall lack of evidence for significant IBD (Breton et al. 2018). The authors point toward spatiotemporally limited meiospore dispersal as well as habitat discontinuity and local ocean currents as potential drivers. On a larger geographical scale along the coast of New England, Mao et al. (2020) genotyped ~4,900 SNPs and found differences among populations over 10s to 100s of km. Regional variation was high and consistent with a break between northern and southern populations at Cape Cod, although there was some evidence of shared ancestry. IBD was present in both regions.

South America

In South America, recent population structure studies have focused on *M. pyrifera, Lessonia spicata*, and *L. nigrescens*. A study by Camus et al. (2018) employing both microsatellites and morphological traits in *M. pyrifera* confirmed that major environmental discontinuities were responsible for latitudinal structuring in the species, supporting the results of Fraser et al. (2010) and Macaya and Zuccarello (2010). Work on kelp in the genus *Lessonia* similarly documented significant genetic differentiation among populations. González and Santelices (2017) found F_{ST} values of 0.15 to 0.28 among three populations of *L. spicata* spread across only 330 km of the species range, and Faugeron et al. (2005) detailed genetic structure over short distances (a few kms) in *L. nigrescens*, even in the absence of the anthropogenic disruption.

Europe

In Europe, recent population structure studies have focused on *S. latissima* and *Laminaria digitata*. For *S. latissima*, 12 microsatellites used in a low-density sample scheme from France to Sweden showed strong differences between populations (Guzinski et al. 2016), and a follow-up study using ~4,000 SNPs confirmed genetic heterogeneity on this geographic scale (300km; Guzinski et al. 2020). Within-population diversity generally decreased from north to south, except near Denmark, and while the lowest differentiation was found intra-Brittany between two neighboring populations (50km apart), all populations were still found to be significantly diverged from one another. Another study of nine microsatellite markers among populations along the entire coast of Norway showed genetic differences between populations separated by 100s of km (Evankow et al. 2019). Finally, work using six microsatellite markers in 14 samples along the Northern Irish coast detected genetic differences over 10s of km (Mooney et al. 2018). In support of earlier studies of North Atlantic *S. latissima,* where variability in growth and production traits have been linked with salinity, sea surface temperature, nutrient availability, and turbidity, recent genomic and transcriptomic surveys have also shown association with several environmental variables (Heinrich et al. 2016; Nielsen et al. 2016; Mooney et al. 2018; Montiero et al. 2019; Guzinski et al. 2020; Li et al. 2020).

Leisner et al. (2020) studied *L. digitata* across France, Germany, and Norway and found moderate local differentiation across the sampled range. Using microsatellite data, Neiva et al. (2020) found three main genetic groups matching Brittany, northern Europe, and the NW Atlantic, with finer-scale sub-structuring within each European cluster. In Brittany, for example, minimum distances between contiguously sampled populations from different clusters were of the order of 200 km, consistent with previous findings in populations sampled at smaller scales (Billot et al. 2003; Robuchon et al. 2014). In contrast, populations separated by less than 20 km in Northern Ireland exhibited a signal of IBD (Brennan et al. 2014). Finally, King et al. (2019) found differences in gene flow among southern and northern kelp beds (populations), reduced within-bed variation in southern beds, and confirmation that southern populations have evolved adaptations for resistance to heat stress.

LITERATURE SUPPORTING COLLECTION OF 50 OR MORE UNRELATED INDIVIDUALS FOR BROODSTOCK

To maintain genetic diversity within cultured broodstocks, offspring must be derived from not less than 50 wild broodstock individuals if offspring are destined for out planting. Although the mechanics of culture will largely dictate broodstock size, a broodstock of at least 50 unrelated individuals will retard the short-term loss of diversity. Parental plants should be collected from dispersed locations along a shoreline to reduce the potential of sampling plants from the same families.

Conserving genetic diversity helps to conserve adaptive potential. To minimize loss of diversity within populations, and thereby adaptive potential, offspring destined for outplanting must be derived from broodstock comprised of ≥ 50 unrelated wild-collected individuals. To help ensure unrelated individuals are obtained, parental plants should ideally be collected from dispersed locations along a shoreline. This guideline protects both wild kelp by reducing the potential for negative genetic impacts resulting from interbreeding with escaped cultured kelp (e.g. through the Ryman-Laikre effect; Ryman and Laikre 1991) and cultured kelp by reducing the potential for inbreeding and ensuring a variety of genetic backgrounds are available such that outplants can respond to variable environmental conditions (e.g. parasites and pathogens, epiphytes, water temperature and chemistry, turbidity).

The minimum broodstock census size (N_c) guideline was based on the number of breeding individuals required to combat loss of genetic variation and reduce the rate of inbreeding in the F_1 (offspring, or outplant) generation. It provided a pragmatic solution for the farms, given operational capacities. This guideline is largely based on accepted population genetic theory and represents a compromise between management and industry. Based on a selection of the conservation literature, it was originally determined by ADF&G that the broodstock N_c should be at least 100 individuals. Populations with an inbreeding effective size < 50 are at immediate risk of extinction, whereas at least 500 individuals are recommended for short-term maintenance of a captive population to combat genetic drift (i.e. the 50/500 rule, Franklin 1980). On the other end of the scale however, Lande (1995) suggested that 5,000 individuals would be preferable for long-term propagation, maintaining adaptive genetic variation, and reducing extinction risk. After

discussions with kelp farmers in the state on operational capacity, the broodstock N_c requirement was ultimately reduced from 100 to 50, the lowest effective size determined by Franklin (1980) as acceptable to avoid inbreeding depression in the short-term. Although this number is an absolute minimum, ADF&G also considered that current farming practices dictate complete broodstock replacement with new wild individuals each year. The overall genetic diversity at a particular farm site is thus increased year-over-year. If creating hatchery stocks was permissible, N_c would probably be required to be significantly higher than 50.

Alternatively, we may consider a farm's ability to annually sample for broodstock a suitable range of the genetic diversity available in wild populations. In terms of sample size determination, Hale et al. (2012) points out that, "…it is important that the sampled allele frequencies are representative of the true population allele frequencies. Increasing sample size will always increase the accuracy of the allele frequency estimate, but the rate of increase will not be linear. […] Therefore, the question researchers are really asking is: *at which sample size is the increase in accuracy of allele frequencies too small to warrant the extra cost of sampling more individuals?*" According to Chakraborty et al. (1992) that minimum sample size may be reached relatively quickly; even at a sample size of 50, alleles with a frequency ≥5% should be represented in the sample. Nevertheless, at the time of collection, it is generally unknown how well the broodstock population represents the wild population from which it was obtained.

It is also important to note that these minimum sample size stipulations are based on fundamental assumptions about the broodstock population and the contribution of these broodstocks to progeny. Violation of these assumptions may drastically reduce the effect a minimum broodstock N_c has in combating loss of adaptive potential (Kliman et al. 2008). The term "effective population size" (N_e) is often used to conceptually describe the number of individuals contributing offspring to a subsequent generation. In reality, N_e is a theoretical concept that describes the size of an ideal population that experiences the same amount of random genetic drift as a real population (Wright 1931). The concept carries with it several assumptions, including 1) equal numbers of reproductively mature males and females; 2) all individuals are equally likely to produce offspring, and the number of offspring each individual produces varies no more than expected by chance; 3) mating is random; and 4) population size is constant. Because real populations are seldom ideal, it is probable that violations to these assumptions occur. For example, during artificial breeding, mating is neither random nor can we assume each brood individual contributes equally to the progeny. Broodstock N_e is thus most likely less than broodstock N_c, although the degree to which N_e is reduced relative to N_c is unknown. A related concept not covered here is the breeding effective size (N_b), which is often used in conservation monitoring and breeding programs for animal taxa and approximated as N_e divided by the generation length (Waples 2002; Gautschi et al. 2003; Nomura 2008; Ruzzante et al. 2016). Full replacement of broodstock on an annual basis at the farm site means in essence $N_b = N_e$.

CONCLUSIONS

The 50-50 Rule for cultivating of seaweeds and aquatic plants in Alaska waters encompasses two guidelines, with a focus on genetics, including restrictions on spatial collection of broodstock and cultivation of progeny and recommendations for a minimum broodstock N_c. These guidelines were developed in 2016 as suggestions for management in the absence of population genetic data for Alaska seaweeds and aquatic plants. Since that time, a host of new genetic and genomic research has been performed on various species of seaweeds in Alaska and around the world. Few to none

of these new studies have provided information that would prompt resource managers in Alaska that there is a need to relax the recommendations in the state's seaweed genetic guidelines.

Large-scale significant among-population structuring occurs on the order of a few hundred to thousands of km and is apparent circum-globally. Patterns may be described as chaotic genetic patchiness and have been associated with movement of large-scale water masses, latitudinal climate variability, and the inference of glacial refugia coupled with post-glacial recolonization. More and more researchers have been exploring seaweed population structuring on smaller scales, however. Neighborhood sizes have been found to range from as low as 10 to 10s of km to 100+ km, with limited dispersal capabilities, IBD, habitat availability, local current patterns, and other hydrographic characteristics all variably influencing spatiotemporal population differentiation, depending on species and location.

In Alaska, three kelp species have shown chaotic genetic population structures, indicating the need for management on smaller, sub-drift zone spatial scales. The amount of variation found among sites in Alaska (and elsewhere) still supports the 50 km broodstock collection and outplanting restriction set forth in the 50-50 Rule guidelines as an appropriate limitation. However, in each study, only 5–16 locations per species were sampled over a distance of about 2,800 km. This level of spatial resolution is insufficient to formulate species- or location- specific management strategies on small geographical scales. A greater amount of finer-scale sampling across the state, particularly in areas targeted for kelp aquaculture (e.g. Kodiak Island and Southeast Alaska), coupled with enhanced resolution provided by contemporary genomic technologies, is recommended for future research, as has been done for genetic management of the five species of salmon and certain socioeconomically important invertebrates native to the state.

In terms of the second guideline covering broodstock N_c, the scope of which is defined by the spatial recommendation laid out in the first guideline, the recommendation for collecting 50 unrelated individuals for breeding is already at the low end. Moreover, the actual contribution of the broodstock as measured by N_e is likely some fraction of N_c. Farm-specific research, likely involving genetic assignment of parentage, is recommended in order to understand metrics, such as on-site genetic diversity, N_e within and among years, and realized N_e.

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APPENDICES

Excerpts from the State of Alaska Constitution, Alaska Statutes (AS), and Alaska Administrative Code (AAC) that contain provisions to protect wild stock resources of the state while providing opportunities to develop resources in the best interest of the people of Alaska.

State of Alaska Constitution

Article 8 Natural Resources,

Section 2 General Authority:

The legislature shall provide for the **utilization, development, and conservation** of all natural resources belonging to the State, including land and waters, for the maximum benefit of its people.

Section 4 Sustained Yield

Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall **be utilized, developed, and maintained** on the **sustained yield principle**, subject to preferences among beneficial uses.

Merriam-Webster definition of sustained yield: *production of a biological resource (such as timber or fish) under management procedures which ensure replacement of the part harvested by regrowth or reproduction before another harvest occurs*

Alaska Statutes (AS) Title 16. Fish and Game.

Chapter 05. Fish and Game Code and Definitions.

AS **16.05.020**. The functions of the commissioner of ADF&G are to:

(2) **manage, protect, maintain, improve, and extend** the fish, game, and aquatic plant resources of the state in the **interest of the economy and general well-being of the state**.

Chapter 40. Commercial Use of Fish and Game

AS **16.40.100**. Aquatic farm and hatchery permits.

(c) The commissioner may attach **conditions to a permit** issued under this section that are necessary to **protect natural fish and wildlife resources**.

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AS **16.40.105** Criteria for Issuance of Permits

3. the proposed farm or hatchery may **not significantly affect fisheries**, wildlife, or their habitats in an adverse manner;

Sec. **16.40.120**. Aquatic stock acquisition permits.

(c) The commissioner **shall specify** the expiration date of an **acquisition permit** and may attach conditions to an acquisition permit, including conditions relating to the time, **place,** and manner of harvest.

(f) Except as provided in (d) of this section or in a regulation adopted under (e) of this section, the commissioner shall issue a permit if

(4) wild stock is needed to **maintain the gene pool** of a hatchery or aquatic farm.

Alaska administrative Code (AAC): Title 5 Fish and Game.

Part 1. Commercial and Subsistence Fishing and Private Nonprofit Salmon Hatcheries. (5 AAC 1 - 5 AAC 41)

Chapter 41 Collection, Transportation, Possession, Propagation, or Release of Aquatic Organisms; Aquatic Farming

Article 2 Permit System Established

5 AAC **41.050**. Permit conditions

The commissioner may prescribe conditions on a fish transport or aquatic resource permit to control the occurrence of disease, **genetic change**, or other disturbances of biological origin affecting native, wild, or enhanced stocks, or to minimize effects on fisheries or other uses of aquatic resources, including research, management, monitoring, or enforcement activities. These conditions may include: designation of broodstock and release locations; methods of collection, transport, holding, or release; quarantine and depuration requirements and procedures; disease inspections; disposal of wastes and effluents; timing of transportation and release; reporting requirements; and other measures necessary to achieve the purposes of this chapter.

Article 4 Aquatic Farming

5 AAC **41.250**. Permit conditions

    (a) The commissioner will attach conditions to an aquatic farm or hatchery operation permit, including requirements that a permit holder

        (6) conduct aquatic farm and hatchery operations in a manner that **avoids significantly affecting fish, wildlife, and their habitats in an adverse manner**

5 AAC **41.290**. Aquatic stock acquisition from outside an aquatic farm site

    (e) In addition to the conditions in AS 16.40.120, and as the commissioner determines necessary to protect natural fish and wildlife resources and their habitat, the commissioner may attach conditions to an aquatic stock acquisition and transport permit.

Appendix B.– Scientific and common and names along with Families and Orders and common names for Classes for kelp species referenced in this document.

Scientific Name	Common Name	Family	Order (common Class name)
Alaria sp.	winged/ribbon kelp	Alariaceae	Laminariales (brown)
Durvillaea antarctica	southern bull kelp	Durvillaeaceae	Fucales (brown)
Enteromorpha (now Ulva) intestinalis	sea lettuce, green nori	Ulvaceae	Ulvales (green)
Hedophyllum nigripes	split kelp	Laminariaceae	Laminariales (brown)
Laminaria digitata	oar weed	Laminariaceae	Laminariales (brown)
Lessonia nigriscens	intertidal grey weed	Lessoniaceae	Laminariales (brown)
Lessonia spicata	huiro negro	Lessoniaceae	Laminariales (brown)
Macrocystis pyrifera	giant kelp	Laminariaceae	Laminariales (brown)
Nereocystis luetkeana	bull kelp (northern form)	Laminariaceae	Laminariales (brown)
Palmaria palmata	red seaweed (dulse)	Palmariaceae	Palmariales (red)
Saccharina japonica	Japanese kelp	Laminariaceae	Laminariales (brown)
Saccharina latissima	sugar kelp	Laminariaceae	Laminariales (brown)

Larval drift zones 1-6 are defined in Alaska Administrative Code Section 5 AAC 41.295 (f). Larval drift zone 7 is newly defined because of recent increases in the abundances of several marine plants and invertebrates which may be due to warming ocean conditions.

1. Southeastern Alaska, from the Canadian border north to Cape St. Elias;

2. Prince William Sound and Cook Inlet, from Cape St. Elias west and south to Cape Igvak, including Kodiak Island;

3. Chignik and the Alaska Peninsula-Aleutian Islands, from Cape Igvak west to the tip of Unimak Island;

4. the Aleutian Islands, including all islands west of Unimak Pass;

5. the southeast Bering Sea and north Alaska Peninsula, from the westernmost tip of Unimak Island north to the Kuskokwim River, including the Pribilof Islands; and

6. the northeast Bering Sea, including all coastal islands north of the Kuskokwim River.

7. Chukchi and Beaufort Seas: Cape Prince of Wales