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APPLIED STUDIES

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Comparative analysis of morphometric traits of farmed sugar kelp and skinny kelp, *Saccharina* spp., strains from the Northwest Atlantic

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Abstract

Our team has initiated a selective breeding program for regional strains of sugar kelp, *Saccharina latissima*, to improve the competitiveness of kelp farming in the United States. Within our breeding program, we also include an endemic putative species, *Saccharina angustissima*, locally referred to as skinny kelp. We crossed uniclonal gametophyte cultures derived from 37 wild-collected blades representing five sugar kelp strains and one skinny kelp strain to produce 104 unique crosses. Each cross was outplanted on a near-shore research farm located in the Gulf of Maine (GOM). After the first farming season, our results indicated that sugar kelp and skinny kelp were interfertile, and produced mature and reproductively viable sporophytes. Morphological traits of individual blades varied depending on the parental contribution (sugar vs. skinny), with significant differences found in progeny blade length, width, thickness, and in stipe length and diameter. Despite these differences, wet weight and blade density per plot showed no statistical differences regardless of the cross. Given their published genetic similarity and their interfertility shown here, *S. angustissima* and *S. latissima* may not be different species,

and may each contribute genetic diversity to breeding programs aimed at meeting ocean farming and market needs.

KEYWORDS
morphometrics, phenotyping, *Saccharina angustissima*, *Saccharina latissima*, seaweed aquaculture, selective breeding

1 | INTRODUCTION

Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, commonly referred to as sugar kelp, is currently being cultivated on both east and west coasts of the United States, as well as in Canada and Europe (Troell et al., 2009; Azevedo, Marinho, Silva, & Sousa-Pinto, 2016; Bak, Mols-Mortensen, & Gregersen, 2018; Kerrison, Stanley, & Hughes, 2018; Yarish, Kim, Lindell, & Kite-Powell, 2017; Kim, Stekoll, & Yarish, 2019) at research and commercial scales. Currently, sugar kelp is primarily grown for human consumption (Bak et al., 2018; Freitas, Salinas Morrondo, & Cremades Ugarte, 2016), although other applications such as raw material for animal feed, cosmetics, and biofuels are emerging rapidly (Kim et al., 2019; Peteiro, Sánchez, Dueñas-Liaño, & Martinez, 2014; Rajauria, 2015; Yarish et al., 2017). Sugar kelp aquaculture must overcome various challenges to continue its expansion. Some of these challenges include reliably producing a sustainably and economically high-yielding crop that can resist disease, fouling, and highly dynamic environments including rising sea surface temperatures (Kim et al., 2019; Kim, Yarish, Hwang, Park, & Kim, 2017; Park, Shin, Do, Yarish, & Kim, 2018). In light of these challenges, we have started a selective breeding program for *S. latissima* with the long-term goal of improving kelp productivity per unit area for future use as biofuels (MARINER, 2017).

This breeding program is exploring individual morphometric traits, as well as plot-level traits, associated with strains of *S. latissima* including a unique strain or putative species, *Saccharina angustissima* (Collins) Augyte, Yarish, and Neefus, also known as "skinny kelp" (Augyte, Yarish, Redmond, & Kim, 2017). Skinny kelp holds culinary and commercial interest due to its uniform morphology and high yield in rope-grown culture (Augyte et al., 2017). Skinny kelp is endemic to low intertidal and wave-exposed headlands and islands in the Gulf of Maine (GOM) and is named such due to its strap-like blade appearance (Augyte et al., 2017; Augyte, Lewis, Lin, Neefus, & Yarish, 2018). Although sugar kelp and skinny kelp have recently been considered two different species, a more recent study used genome-wide high-density markers to analyze the genetic difference between them, and found no clear separation. The differences between the two were similar to that between several different populations of *S. latissima* sampled within the GOM. Moreover, F_{ST} values between skinny and sugar kelp were no greater than those within sugar kelp populations for the same region and within populations (Mao et al., 2020). Given the lack of genetic differences between the two "species" and their compatibility to interbreed and produce fertile offspring, *S. angustissima* was included in the breeding program as another strain.

The overall priority of this breeding program is to implement genetic tools for advancing kelp domestication and to accelerate breeding efficiencies through genomic prediction methodologies. Thus far, the program has produced baseline information about the population genetics of sugar kelp sporophytes in the GOM and Southern New England regions (Mao et al., 2020), which lays an important foundation for future monitoring and management of wild and farmed kelp populations. Our major traits of interest for breeding include yield, compositional quality, thermal tolerance, and resistance to fouling. In this contribution, we report on the morphometric performance of blade and stipe traits of progeny derived from pure sugar kelp, pure skinny kelp, and mixed crosses (i.e., one sugar kelp and one skinny kelp parent) grown in farm conditions for our first outplanting season. We provide insights on how the contribution of skinny kelp influenced morphometric traits of progeny within plots, and examined potential maternal versus paternal skinny kelp contributions to the morphology of progeny when crossed with sugar kelp. These results serve as the basis for future recommendations for improving kelp traits in the breeding program and provide a first look into the performance of crosses grown in relatively high-density plots in a "common garden."

TABLE 1 Mean ± *SD* for six morphological traits measured on the parental sporophytes of *Saccharina latissima* collected from the Gulf of Maine

Sampling location (No. of samples measured)	Blade length (cm)	Blade width at 10 cm (cm)	Blade max width (cm)	Blade thickness (mm)	Stipe length (cm)	Stipe diameter (mm)
Casco Bay (6)[a]	195.7 ± 49.0	3.3 ± 0.4	7.3 ± 1.6	1.56 ± 0.21	4.3 ± 1.0	2.80 ± 0.34
Lubec (9)	188.1 ± 30.9	17.9 ± 5.0	33.1 ± 5.6	2.00 ± 0.46	85.1 ± 46.81	13.30 ± 3.73
Nubble Light (7)	149.6 ± 29.1	13.8 ± 4.3	21.4 ± 1.8	1.62 ± 0 .15	9.9 ± 3.2	5.52 ± 1.19
Orr's Island (12)	197.2 ± 28.4	17.9 ± 4.4	41.4 ± 7.9	1.38 ± 0. 17	23.4 ± 17.1	8.06 ± 2.57
Sullivan Falls (5)	202.4 ± 24.9	10.12 ± 3.5	36.9 ± 3.9	1.77 ± 0.19	133.2 ± 41.3	15.49 ± 1.04

[a]Only location with sporophytes of the skinny kelp strain collected.

2 | MATERIALS AND METHODS

2.1 | Parental sporophyte sample collection and initial phenotyping

Between April and June of 2018, 37 reproductive individual sporophytes were collected at six locations (hereafter referred to as strains) within the GOM, Northwest Atlantic. Wild collections were selected based on accessibility to kelp beds stretching from northern to southern Maine (Figure S1). Casco Bay, Maine, was the only collection that originated from farmed samples of *S. angustissima* (skinny kelp strain) previously generated from wild seedstock. All individuals were measured for blade length, maximum blade width, blade width 10 cm above the junction of the stipe and blade (hereafter blade width at 10), blade thickness, stipe length, and stipe diameter (Figure S2; Table 1).

2.2 | Spore release, isolation, and culture of gametophyte biomass

Sorus tissue samples were processed individually for every parental sporophyte. Tissue fragments with sporangia were cut out of mature sporophytes, cleaned thoroughly by wiping with iodine solution, and then washed with sterile seawater (Redmond, Green, Yarish, Kim, & Neefus, 2014). The clean tissue was wrapped in paper towels and kept in the dark for 12 hours at 10°C. Individual fragments were then submerged in filtered and sterilized seawater to release meiospores. Meiospores were either allowed to adhere to the bottom of a Petri dish until germination or sorted automatically (N = 96 isolations per parental tissue) using a flow cytometer (Augyte et al., 2020). After meiospore germination, gametophytes were sexed and isolated to individual Petri dishes containing half-strength Provasoli's enriched solution, PES (Provasoli, 1968) plus 6 mg L^{-1} germanium dioxide, GeO_2 (Lewin, 1966). Female uniclonal cultures (N = 3 per sporophyte) were maintained under red LED light at 13°C and 16:8 hr light–dark cycle photoperiod with a photon fluence that was gradually adjusted from 20 to 60 μmol photons m^{-2} s^{-1} over a 12-day period. Male uniclonal cultures (N = 3 per sporophyte) were maintained under white light at the same temperature, photon fluence, and photoperiod conditions. Gametophyte biomass was fragmented every 30 days over 6 months by disrupting each culture into 80–400 μm long filaments using either dissecting needles, microcentrifuge tubes and pestles, or mini blender cups with blades.

2.3 | Crosses, breeding design, and farm outplant

Each cross consisted of mixing cultures of a uniclonal male with a uniclonal female gametophyte to generate many genetically uniform sporophytes. Gametophytes with sufficient biomass were selected, and crosses were designed

to maximize the diversity of our germplasm (see Table S1 for the number and distribution of female and male gametophytes crossed and analyzed). All crosses (104) were generated using approximately 10 mg of female and 5 mg of male gametophyte biomass (2:1 ratio). Crosses were maintained in suspension for 14 days in 125 mL Erlenmeyer flasks at 15°C and irradiance of 80 ± 10 μmol photons m^{-2} s^{-1} in a 12:12 hr light–dark cycle. Subsequently, each cross was individually attached directly onto 1-m segments of 2-mm Kuralon twine (seedstring) wrapped around PVC tubes (10 cm in length, 5.1 cm in diameter).

Attachment was facilitated using AtSea as a binding agent (AtSeaNova, Ronse, Belgium). Crosses were mixed with 0.5% AtSea and the mixture was then painted onto the twine using a 13-mm plastic paintbrush. Once attached, crosses were transferred to clear 300 mL polycarbonate boxes (bioWORLD, Dublin, OH) containing half-strength PES plus 6 mg L^{-1} GeO_2, where they remained for 8 weeks until deployment. Media changes were conducted every 14 days and aeration was maintained throughout the hatchery period to avoid nutrient limitation. Photon fluence and photoperiod during the nursery remained as described earlier. Immediately prior to field planting, all crosses were photographed to obtain a relative measure of sporophyte size and density per meter, and temperature was gradually (8-day period) adjusted from 15 to 5°C to match that at the farm site. Crosses were outplanted side by side at 1-m intervals in a "common garden" deployed at sea in New Castle, New Hampshire, on January 26, 2019, and maintained at a 2.4-m depth for approximately 4 months until harvest. The outplanting season was at least 2 months shorter than the usual regional kelp farming season due to permitting delays.

2.4 | Offspring phenotyping

Sporophytes were harvested and transported in 1800 L insulated vats with ice on May 28, 2019, to the research processing facility (Environmental Systems Laboratory, Woods Hole Oceanographic Institution, MA). Upon arrival, vats were supplied with flowing seawater (10°C). Processing occurred over the next 72 hr (May 29–31, 2019). Each 1-m plot (representing one cross) was photographed and weighed (wet weight). Fifteen blades per plot were randomly selected to measure the same six morphometric traits described for the parental sporophytes. Blade density per plot was estimated by detaching and counting all blades within five randomly predetermined 1-cm line sections per 1-m plot.

2.5 | Analysis of morphometric traits

Correlation matrices were constructed to summarize measurements conducted on kelp crosses and to examine the contribution of skinny kelp to the morphometric traits of progeny grown in farm conditions. These matrices were also used to examine the correlation between individual morphometric traits and plot estimated density and wet weight. Histograms were constructed to visually compare the distribution of morphometric measurements of wild parental sporophytes versus their cultivated offspring with and without skinny kelp contributions. We also constructed boxplots to visually compare the performance of morphometric traits in offspring with and without skinny kelp contributions. Analyses were conducted using R 3.6.3 (R Core Team, 2013).

3 | RESULTS

3.1 | Correlation between individual-level and plot-level traits

Maximum blade width and blade width at 10 were positively and highly correlated in all progeny, regardless of their paternal and maternal origin (sugar kelp or skinny kelp). A similar trend in all progeny was observed for stipe traits including length and diameter (Figure 1a,b).

At a plot level, the correlation of individual blade traits with the overall wet weight of plots depended on whether progeny were derived from pure sugar kelp (Figure 1a) or from crosses between sugar kelp and skinny kelp (Figure 1b). For pure sugar kelp plots, individual blade thickness appears to be significantly correlated to plot wet weight (Figure 1a). This trend was not observed in plots with a skinny kelp parent. Instead, blade length and blade width were positively and negatively correlated, respectively, with plot wet weight, (Figure 1b). Blade density and plot wet weight were positively and significantly correlated in all crosses, regardless of the origin of the parents. In all crosses, individual characteristics of the stipe showed the highest correlations with plot wet weight, with relatively longer and thicker stipes within the two types of crosses resulting in plots with greater wet weight (Figures 1a,b).

3.2 | Comparison between pure skinny kelp progeny and progeny with at least one skinny kelp parent

Morphometric traits at the individual progeny level differ significantly as a function of parental origin (Figure 2 and Figure S3). Within our common garden, crosses derived from pure sugar kelp showed shorter, wider, and thinner blades than crosses with at least one skinny parent. Stipe traits were also different, with pure sugar kelp progeny showing slightly thicker and longer stipes than crosses with skinny kelp contribution. Despite the differences in morphology, no significant differences were found in plot wet weight and the estimated blade density between the pure sugar kelp and mixed progeny. The maximum plot wet weight recorded (7.62 kg/m) derived from a skinny kelp paternalal line and a sugar kelp maternal line.

3.3 | Distribution of plot wet weight and estimated plot density

Wet weight and estimated blade density per plot showed a wide distribution within the farm (Figure 3). The average plot wet weight was 2.5 kg per meter (Figure 3a), with no significant difference between sugar kelp progeny and progeny with

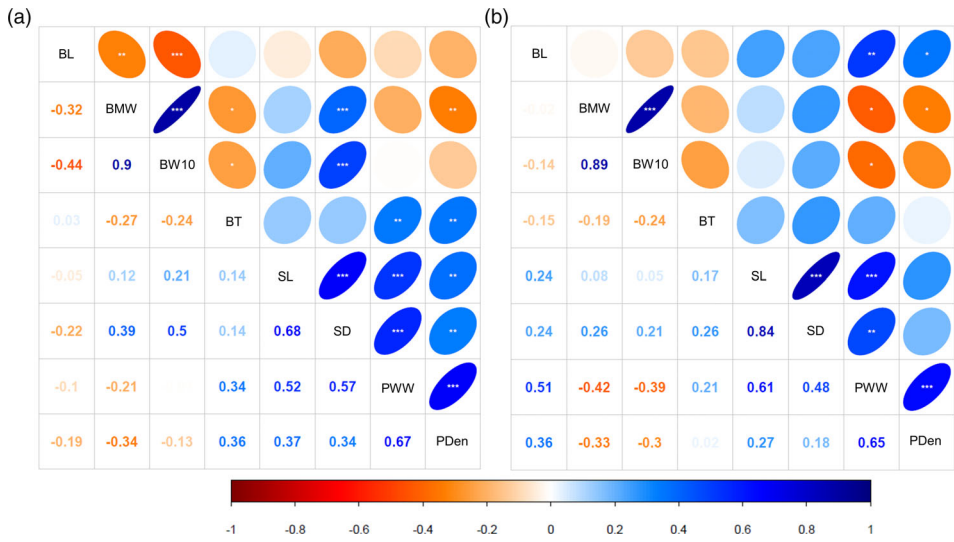

FIGURE 1 Correlation matrices showing *r* values with warm tones shifting toward −1 and cold tones toward 1, direction (positive or negative), magnitude (thinner vs. wider oval, showing a higher or lower correlation, respectively), and significance (*p* value *<.05, **<.01, or ***<.01) between morphometric traits across crossbred offspring derived from pure sugar kelp (a) and sugar kelp with either maternal or paternal skinny kelp contribution (b). BL, blade length; BMW, blade maximum width; BT, blade thickness; BW10, blade width at 10; PDen, estimated plot density; PWW, plot wet weight; and SD, stipe diameter; SL, stipe length

skinny kelp origins (Figure 3b). From the 104 plots analyzed, 49 plots had a wet weight between 2.5 and 5 kg per meter, and 9 plots weighed 5 kg or greater per meter of which 5 were skinny kelp related crosses (Figure 3b).

Most plots measured showed an estimated blade density ranging between 180 and 400 blades per meter. The estimated counts from our sampling ranged from a plot with 1 blade and a plot with 660 blades per meter (Figure 3c,d). The average blade density of crosses derived from pure sugar kelp versus those from skinny kelp was similar, with both types of crosses averaging 297 blades per meter (Figure 3c,d).

3.4 | Comparison of morphometric traits within skinny kelp-related crosses

Thirty-nine of the 104 plots had at least one skinny kelp parent from which two were pure skinny kelp crosses, 3 had a skinny kelp maternal line, and 34 had a skinny kelp paternal line (Table S1). The analyses made to assess the individual contribution of maternal and paternal lines to morphometric traits of the progeny showed no significant difference in their contribution (Figure 4). Differences in the contribution of different lines were only evident when comparing pure skinny kelp with pure sugar kelp crosses, particularly in traits associated with blade width (Figure 4).

4 | DISCUSSION

Our results showcase the first results of wild-strain performance that may form the basis for a sugar kelp breeding program. We have expanded the collection described here and characterized genetically diverse germplasm that will

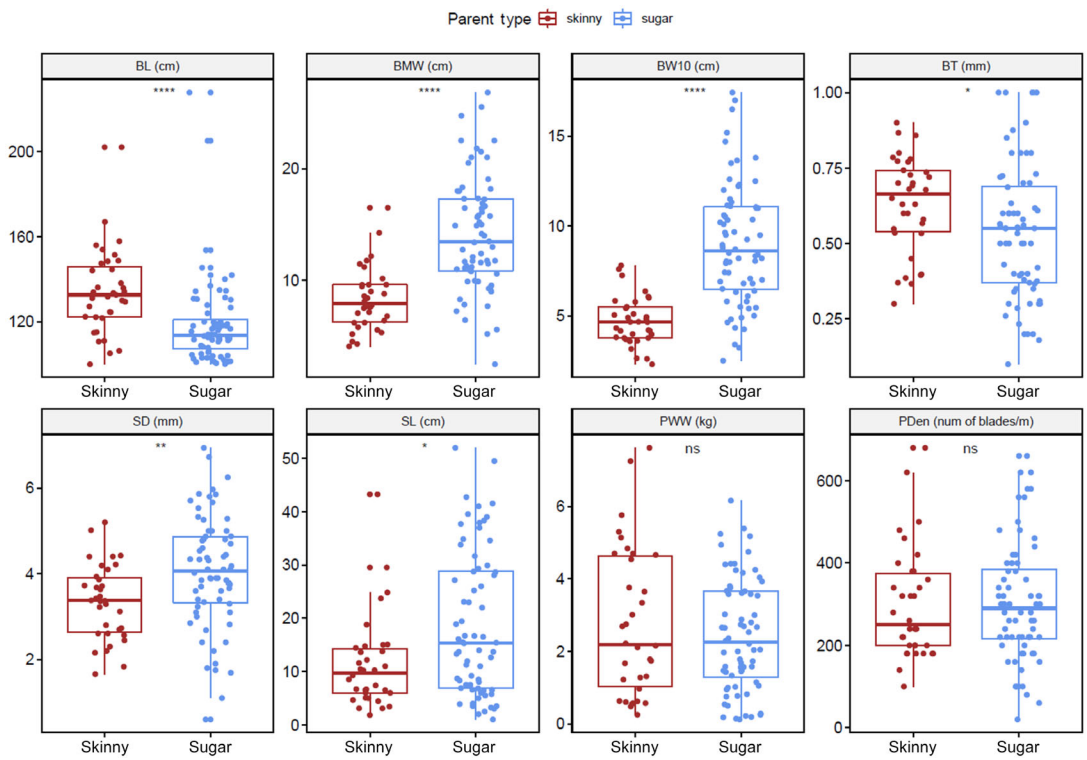

FIGURE 2 One-way analysis of variance comparison assessing the differences in morphometric traits between pure sugar kelp crosses and crosses with either a maternal or paternal skinny kelp parent. *p* value *<.05, **<.01, ***<.001, or ns = not significant. BL, BMW, BW10, and SL (cm); SD and BT (mm); PDen (number of blades per meter); PWW (kg per meter)

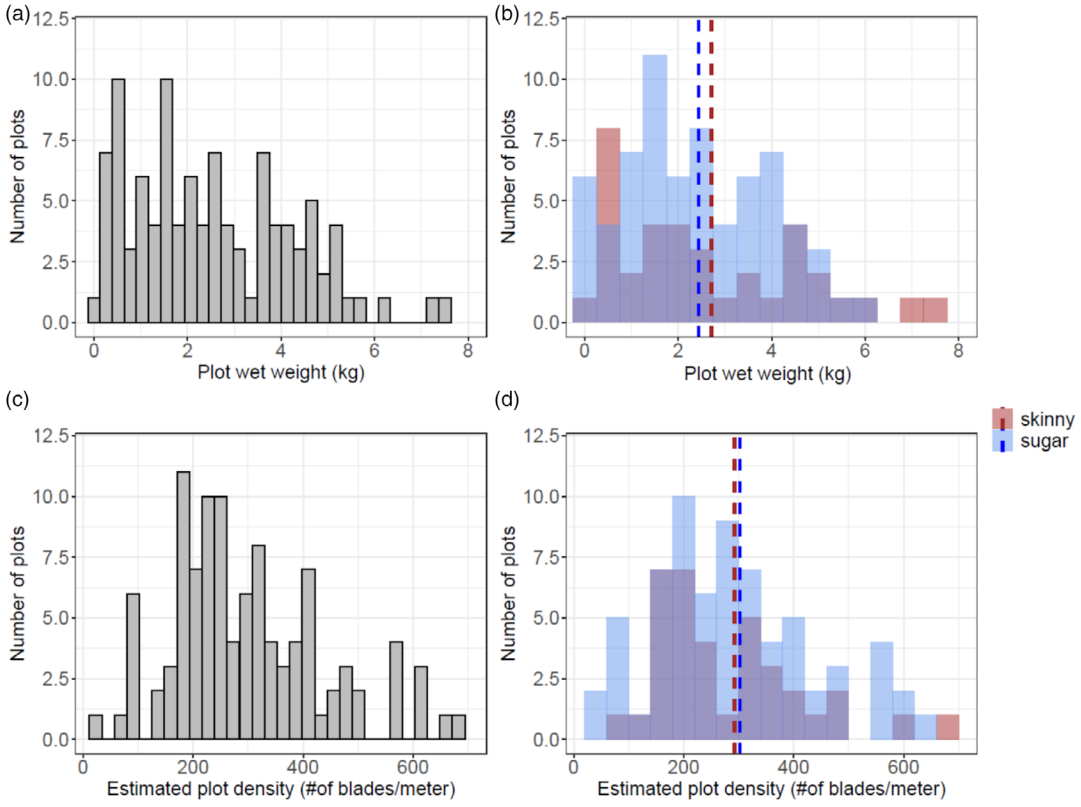

FIGURE 3 (a) Distribution of overall plot wet weight and (b) wet weight of sugar kelp progeny (avg. 2.44 kg) versus progeny with skinny kelp contribution (2.71 kg). (c) Distribution of overall estimated blade density per 1-m plots and (d) blade density of sugar kelp progeny (avg. 302.35) versus progeny with skinny kelp contribution plots with pure sugar kelp crosses versus crosses with skinny kelp distribution (avg. 292.22)

provide safeguards and diversity to meet future breeding needs (Mao et al., 2020). Starting with and maintaining sufficient genetic diversity is fundamentally important to a domestication program (Goecke, Klemetsdal, & Ergon, 2020; Valero et al., 2017). Our F1 progeny were not subjected to any systematic selection, and therefore, were expected to have a high degree of variability, as shown by our boxplot analyses per trait. Our results show that sugar kelp and skinny kelp can produce interfertile progeny, confirming their relatedness and recent divergence (Augyte et al., 2018).

Progeny derived from pure skinny kelp retained their slender morphology, confirming the phenotypic stability described for individuals of the strain while grown in farm conditions (Augyte et al., 2017). Our breeding program goal is to produce high-yield kelp cultivars. We did not find that the contribution of skinny kelp to the crosses affected plot wet weight nor the estimated blade density per meter. Crosses including one skinny and one sugar kelp parent displayed morphometric attributes similar to skinny kelp without potentially affecting yield. Further research is required to understand the individual contribution of female and male gametophytes of skinny kelp to their progeny. The relatively few crosses involving female gametophytes of skinny kelp precluded conclusive analysis.

It is critical to generate reliable phenotypic data to reach our goal of accelerating genetic gain and breeding efficiency utilizing genomic prediction tools. For now, this study describes our early understanding of the variability of morphometric traits within and between crosses of strains of skinny kelp and sugar kelp grown in a common garden in the Northwest Atlantic. All the morphological information gathered, in addition to genotypic data associated with progeny and parental sporophytes, is being used to build genomic prediction models. Our models depend on

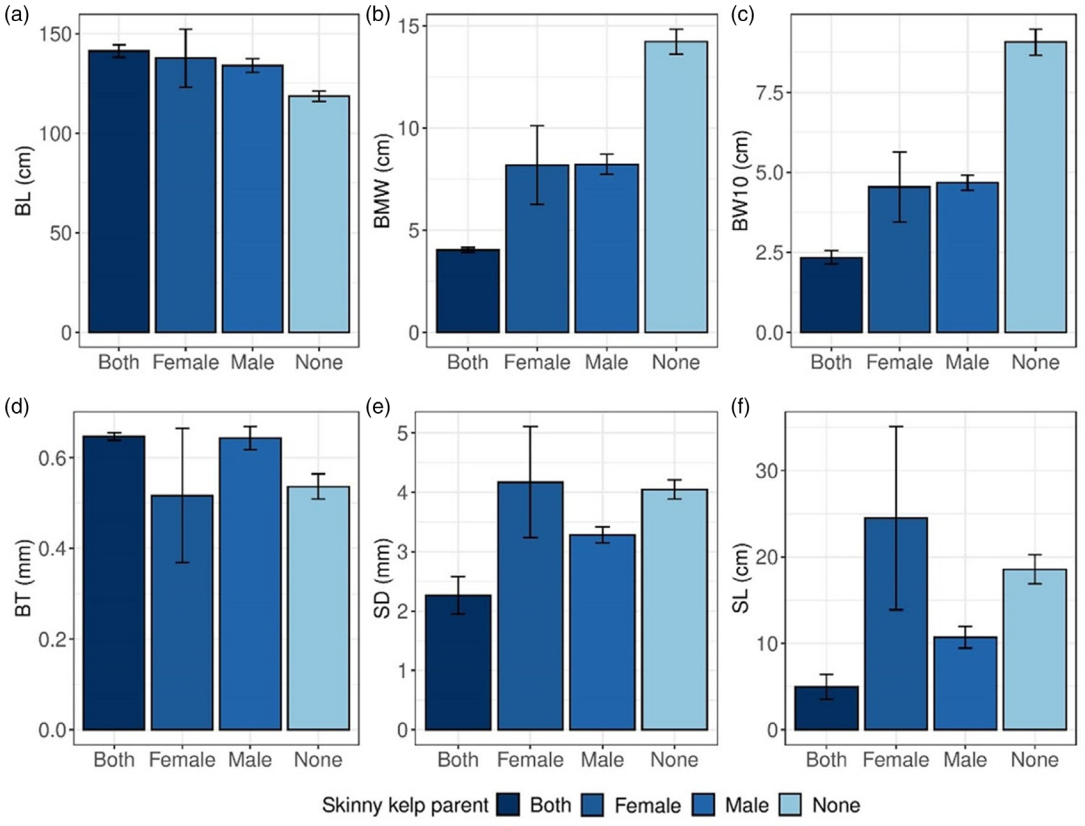

FIGURE 4 Comparisons of the morphometrics of progeny derived from skinny kelp parents only (both, $n = 2$), skinny kelp female crossed with sugar kelp male (female, $n = 3$) and reciprocal cross (Male, $n = 36$), and sugar kelp parents only (none, $n = 63$). BL, blade length; BMW, blade maximum width, BW10, blade width at 10, BT, blade thickness; SD, stipe diameter; SL, stipe length

predicting breeding values of parental gametophytes as well as obtaining gametophytes from the best performing sporophyte progeny to create new generations of improved sporophytes.

In the future, we expect to seed farms from gametophytes selected via genome prediction models to foster higher yields. We also expect that our gametophyte germplasm library will facilitate repeated cross-breeding and allow stable and predictable kelp production to be upscaled (Shan, Pang, Li, & Gao, 2016; Hwang, Yotsukura, Pang, Su, & Shan, 2019; Wade et al., 2020). We intend to develop genetic markers in our breeding program that could enable consistent production of infertile sporophytes and eliminate potential gene flow between farmed and natural populations of wild kelp. The continued evaluation of kelp phenotypes and genotypes is important for maintaining a useful level of genetic diversity in our breeding program (Shan, Pang, Zhang, Yakovleva, & Skriptsova, 2011; Hwang, Choi, Yoon, & Park, 2020; Wade et al., 2020).

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REFERENCES

Augyte, S., Lewis, L., Lin, S., Neefus, C. D., & Yarish, C. (2018). Speciation in the exposed intertidal zone: the case of *Saccharina angustissima* comb. nov. & stat. nov. (Laminariales, Phaeophyceae). *Phycologia*, *57*, 100–112. https://doi.org/10.2216/17-40.1

Augyte, S., Wikfors, G. H., Pitchford, S., Marty-Rivera, M., Umanzor, S., Lindell, S., … Yarish, C. (2020). The application of flow cytometry for kelp meiospore isolation. *Algal Research*, *46*, 101810. https://doi.org/10.1016/j.algal.2020.101810

Augyte, S., Yarish, C., Redmond, S., & Kim, J. K. (2017). Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma *angustissima*, from coastal Maine, USA, with implications for ecosystem services. *Journal of Applied Phycology*, *29*, 1967–1976. https://doi.org/10.1007/s10811-017-1102-x

Azevedo, I. C., Marinho, G. S., Silva, D. M., & Sousa-Pinto, I. (2016). Pilot scale land-based cultivation of *Saccharina latissima* Linnaeus at southern European climate conditions: Growth and nutrient uptake at high temperatures. *Aquaculture*, *459*, 166–172. https://doi.org/10.1016/j.aquaculture.2016.03.038

Bak, U. G., Mols-Mortensen, A., & Gregersen, O. (2018). Production method and cost of commercial-scale offshore cultivation of kelp in the Faroe Islands using multiple partial harvesting. *Algal Research*, *33*, 36–47. https://doi.org/10.1016/j.algal.2018.05.001

Freitas, J. R. C., Salinas Morrondo, J. M., & Cremades Ugarte, J. (2016). *Saccharina latissima* (Laminariales, Ochrophyta) farming in an industrial IMTA system in Galicia (Spain). *Journal of Applied Phycology*, *28*, 377–385. https://doi.org/10.1007/s10811-015-0526-4

Goecke, F., Klemetsdal, G., & Ergon, Å. (2020). Cultivar development of kelps for commercial cultivation—Past lessons and future prospects. *Frontiers in Marine Science*, *8*, 110. https://doi.org/10.3389/fmars.2020.00110

Hwang, E. K., Choi, J. W., Yoon, H. S., & Park, C. S. (2020). Morphological and genetic differences between Korean Sugwawon No. 301 and Chinese Huangguan No. 1 strains of *Saccharina japonica* (Phaeophyceae) in a Korean aquaculture farm. *Journal of Applied Phycology*, *32*, 2245–2252. https://doi.org/10.1007/s10811-019-02029-8

Hwang, E. K., Yotsukura, N., Pang, S. J., Su, L., & Shan, T. F. (2019). Seaweed breeding programs and progress in eastern Asian countries. *Phycologia*, *58*, 484–495. https://doi.org/10.1080/00318884.2019.1639436

Kerrison, P. D., Stanley, M. S., & Hughes, A. D. (2018). Textile substrate seeding of *Saccharina latissima* sporophytes using a binder: An effective method for the aquaculture of kelp. *Algal Research*, *33*, 352–357. https://doi.org/10.1016/j.algal.2018.06.005

Kim, J. K., Stekoll, M., & Yarish, C. (2019). Opportunities, challenges and future directions of open water seaweed aquaculture in the United States. *Phycologia*, *58*(5), 446–461. https://doi.org/10.1080/00318884.2019.1625611

Kim, J. K., Yarish, C., Hwang, E. K., Park, M., & Kim, Y. (2017). Seaweed aquaculture: Cultivation technologies, challenges and its ecosystem services. *Algae*, *32*, 1–13. https://doi.org/10.4490/algae.2017.32.3.3

Lewin, J. (1966). Silicon metabolism in diatoms. V. Germanium dioxide, a specific inhibitor of diatom growth. *Phycologia*, *6*, 112–112. https://doi.org/10.2216/i0031-8884-6-1-1.1

Mao, X., Augyte, S., Huang, M., Hare, M. P., Bailey, D., Umanzor, S., … Jannink, J.-L. (2020). Population genetics of sugar kelp throughout the Northeastern United States using genome-wide markers. *Frontiers in Marine Science*, *7*, 694. https://doi.org/10.3389/fmars.2020.00694

MARINER. (2017). Macroalgae Research Inspiring Novel Energy Resources. Retrieved from https://www.arpa-e.energy.gov/technologies/programs/mariner

Park, M., Shin, S. K., Do, Y. H., Yarish, C., & Kim, J. K. (2018). Application of open water integrated multi-trophic aquaculture to intensive monoculture: A review of the current status and challenges in Korea. *Aquaculture*, *497*, 174–183. https://doi.org/10.1016/j.aquaculture.2018.07.051

Peteiro, C., Sánchez, N., Dueñas-Liaño, C., & Martinez, B. (2014). Open-sea cultivation by transplanting young fronds of the kelp *Saccharina latissima*. *Journal of Applied Phycology*, *26*, 519–528. https://doi.org/10.1007/s10811-013-0096-2

Provasoli, L. (1968). Media and Prospects for the Cultivation of Marine Algae. In Proceedings of the US–Japan Conference, Hakone, Japan, 12–15 September 1966 (pp. 63–75)

R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing. http://www.R-project.org/

Rajauria, G. (2015). Chapter 15—Seaweeds: a sustainable feed source for livestock and aquaculture. In B. K. Tiwari & D. J. Troy (Eds.), *Seaweed Sustainability* (pp. 389–420). London: Academic Press.

Redmond, S., Green, L., Yarish, C., Kim, J., & Neefus, C. (2014). New England seaweed culture handbook-nursery systems. Connecticut Sea Grant, 93 pp. Retrieved from https://seagrant.uconn.edu/2014/01/01/new-england-seaweed-culture-handbook-nursery-systems/

Shan, T. F., Pang, S. J., Li, J., & Gao, S. Q. (2016). Breeding of an elite cultivar Haibao No. 1 of *Undaria pinnatifida* (Phaeophyceae) through gametophyte clone crossing and consecutive selection. *Journal of Applied Phycology*, *28*, 2419–2426. https://doi.org/10.1007/s10811-015-0748-5

Shan, T. F., Pang, S. J., Zhang, Y. R., Yakovleva, I. M., & Skriptsova, A. V. (2011). An AFLP-based survey of genetic diversity and relationships of major farmed cultivars and geographically isolated wild populations of *Saccharina japonica* (Phaeophyta) along the northwest coasts of the Pacific. *Journal of Applied Phycology*, *23*, 35–45. https://doi.org/10.1007/s10811-010-9530-x

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

Valero, M., Guillemin, M.-L., Destombe, C., Jacquemin, B., Gachon, C. M. M., Badis, Y., … Faugeron, S. (2017). Perspectives on domestication research for sustainable seaweed aquaculture. *Perspectives in Phycology*, *4*(1), 33–46. https://doi.org/10.1127/pip/2017/0066

Wade, R., Augyte, S., Harden, M., Nuzhdin, S., Yarish, C., & Alberto, F. (2020). Macroalgal germplasm banking for conservation, food security, and industry. *PLoS Biol*, *18*(2), e3000641. https://dx.doi.org/10.1371/journal.pbio.3000641.

Yarish, C., Kim, J.K., Lindell, S., & Kite-Powell, H. (2017). Developing an environmentally and economically sustainable sugar kelp aquaculture industry in southern New England: from seed to market. USDA/National Institute of Food and Agriculture (NIFA) Project Award # 2014–70007-225460. http://opencommons.uconn.edu/marine_sci/4.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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