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Article in *Journal of Applied Phycology* · August 2017

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Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma *angustissima*, from coastal Maine, USA, with implications for ecosystem services

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Received: 12 July 2016 / Revised and accepted: 19 February 2017
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Abstract Consumer interest and demand for North Atlantic sourced sea vegetables drives opportunities for aquaculture development in the northeast USA. The unique morphology and desirable culinary traits of the wild narrow-bladed kelp, *Saccharina latissima* forma *angustissima*, were successfully translated into a cultivated crop on two geographically distinct open-water farms in Maine, USA. Environmental conditions, growth, and tissue analysis were quantified. Peak meristematic growth rates for blade length occurred from March through April at 2.85 (± 0.34) cm day⁻¹. The kelp was harvested from May through June with yields of up to 17 (± 4.4) kg m⁻¹ of line and plant density of 330 plants m⁻¹ of line at the Bristol farm and yields of 13.3 (± 6.2) kg wet weight m⁻¹ line and a plant density of 400 plants m⁻¹ of line at the Sorrento farm. Second season yields at Sorrento were on average 24.1 (± 6.3) kg m⁻¹ of line. Both farms grew significantly narrower blades of f. *angustissima* than of the sugar kelp, *S. latissima*. Common garden experiments with the two morphotypes identified trait stability for length and width, while blade ruffles and thickness varied with the environment. Calculations estimating the nutrient bioextraction capability of the cultivated f. *angustissima* kelp harvested in June reveal N removal of 88.7 kg ha⁻¹ and C removal of 1666.7 kg ha⁻¹ (combined

farm site averages). Overall, this unique kelp form has the potential as a new aquaculture crop for the Gulf of Maine while providing several coastal ecosystem services.

Keywords Domestication · Kelp aquaculture · Maine · *Saccharina latissima* forma *angustissima* · Nutrient bioextraction

Introduction

Global seaweed aquaculture (24% of world marine aquaculture production by weight) has grown rapidly in recent decades to an annual value of US\$5.6 billion year⁻¹ (FAO 2016). About 28.5 million tonnes of seaweed is harvested annually worldwide with China and Indonesia as the top mariculture producers (FAO 2016). The demand for seaweed in Western markets is expected to increase rapidly because of growing consumer demand for human health benefits from seaweed consumption, new protein sources, fertilizers, biofuels and applications as nutraceuticals, medicine, cosmeceuticals, pharmaceuticals and food additives, as well as important ecosystem service providers (Cornish and Garbary 2010; Holdt and Kraan 2011; Mouritsen 2013; Kim et al. 2014; Hafting et al. 2015).

The USA domestic seaweed industry consists of a traditional wild harvest industry, largely based in Maine (Maine Seaweed Council 2014). The recent development of sea vegetable aquaculture in the northeast USA represents a potential opportunity to provide economic and ecological benefits while producing high value, sustainable sea vegetables (Kim et al. 2014; Redmond et al. 2014). Growing macroalgae in the cold temperate waters in the northeast USA is both feasible and practical. High productivities have been recorded in various locations at small-scale operations (Yarish et al. 2013;

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Kim et al. 2014, 2015). Commercial sea vegetable cultivation has been ongoing in Maine since 2010, with sugar kelp, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, being the first commercial kelp crop to be grown in the USA. The mild flavor and nutritional value (Maine Coast Sea Vegetables 2016) of the kelp species in Maine make them attractive as new domestic aquaculture crops.

Seaweed aquaculture produces not only an edible commodity for both animals and humans but also additional ecosystem services to coastal marine ecosystems thereby providing increased economic incentives for the local aquaculture industry (Chopin et al. 2001; Chopin 2014; Kim et al. 2014, 2015). Coastal eutrophication from point and non-point sources into coastal waterways from sewage effluent, agricultural runoff, and atmospheric deposition has been a major concern to coastal resource managers (NRC 2000; Latimer et al. 2014). The addition of large influxes of nutrients is problematic because it often leads to algal blooms, hypoxia, shading of native vegetation, loss of important habitat, fish die-offs, and changes in marine biodiversity (Rose et al. 2015). The US Clean Water Act requires states to first identify and then work to attain water quality standards for designated uses (Stephenson and Shabman 2015). Aquatic vegetation, or seaweeds, can act like renewable biological nutrient scrubbers and are excellent candidates to take up the excess inorganic nutrients in marine coastal areas (Chopin et al. 2001). The concept of nutrient bioextraction translates into the cultivation of extractive species including shellfish and/or seaweeds in order to remove excess nutrients from urbanized coastal waters (Kim et al. 2015; Rose et al. 2015).

Unique kelp The endemic intertidal kelp, *Saccharina latissima* forma *angustissima* (F.S. Collins) A. Mathieson (Laminariales, Heterokontophyta), has a restricted southern Maine distribution spanning 8 nautical miles of islands, ledges, and peninsulas exposed to heavy ocean surf (Mathieson et al. 2008). The common sugar kelp, *Saccharina latissima*, has a vast coastal range throughout much of the Northern Hemisphere including from the high Arctic to the Iberian Peninsula and a deep water population off the coast of New Jersey in the North Atlantic, and Korea to Central California in the North Pacific (Egan and Yarish 1988; Lüning 1990; Paulino et al. 2016). *Saccharina latissima* usually inhabits the wave-protected sublittoral, at depths below the low tide (Lüning 1990; Bartsch et al. 2008). The unique narrow-bladed (NB) phenotype, on the other hand, only grows in the vicinity of high ocean swells, in the low intertidal where it is further exposed to emersion stress during spring tides. Emersion has an effect on seaweed growth via changes in photosynthetic and nutrient uptake rates (Schagerl and Möstl 2011; Kim et al. 2013; Hurd et al. 2014). Furthermore, macroalgae growing subtidally usually experience water

velocities lower than those of the full-force breaking waves in the intertidal (Hurd 2000). The *f. angustissima* blade morphology is uncommon in the western North Atlantic as it is very strap-like and long, as much as 10–20 times narrower than *S. latissima* (Philibert 1990; Mathieson et al. 2008). Ecological and laboratory culture studies show that kelp morphological variation may be attributed to phenotypic plasticity allowing the form to adapt to local conditions, such as differing wave exposure gradients (Gerard and Mann 1979; Johnson and Koehl 1994; Miller et al. 2000; Roberson and Coyer 2004). Thin, broad, undulate blades may be induced to become strap-like when subjected to hydrodynamic forces and mechanical stress imposed by breaking waves and strong currents (Fowler-Walker et al. 2006; Koehl et al. 2008). For example, Gerard and Mann (1979) found that the average thickness of the center of the blade of *S. latissima* (formerly “*Laminaria longicuris*”) was on average 0.73 mm at protected sites compared to 2.35 mm at exposed sites. However, according to Philibert (1990), when grown in culture tanks for 13 weeks, the narrow-blade kelp (*S. latissima* forma *angustissima*) retained its strap-like morphology. These findings suggested that the form maintains its unique morphology over differing environmental gradients, which may indicate an ecotype, or a genetically fixed population. This debate over species vs. ecotype has been going on for a long time in the Laminariales and is complicated by the fact that many members of the order are interfertile (Kain 1979; Bartsch et al. 2008).

Cultivation techniques for the NB kelp, *f. angustissima*, were non-existent, and it was unclear how the kelp would perform when cultivated at open-water farm sites and if the unique features would be preserved. Therefore, the main objective of the present study was to investigate growth rates and yield of the NB kelp at two open-water farm sites on a submerged longline system in the Gulf of Maine, USA. Furthermore, to better understand if phenotypic plasticity alone was driving the selection of kelp morphology in the hydrodynamically stressed environment or if genotypic variation is involved in the persistence of this unique kelp, we cultivated the NB kelp and the common *S. latissima* side by side in a common garden experiment on longlines. Finally, we measured the nutrient bioextraction capabilities of this kelp as another form of ecosystem service to the local coastal environment.

Materials and methods

Cultivation sites

The Bristol, Maine, site (43°55'43" N, 69°34'23" W) is located in Clark's Cove on the seaward end of the Damariscotta River estuary watershed in Lincoln County, a full salinity and

tidally influenced lease area of 5 ha. This is a protected site, with less than 1.6 km fetch in any direction, and is relatively shallow at 9–12 m mean low water (MLW) with a mud/silt bottom. The kelp longlines were located adjacent to a suspended mussel raft on the lease. The Sorrento, Maine, site (44°27'32" N, 68°10'37" W) is located in the northern portion of Frenchman's Bay in Hancock County. The site is sheltered from open ocean swells but exposed to a southwest fetch of approximately 7 km, experiencing storm generated swells of 1.0–2.5 m, making it a relatively exposed site. This site is deeper than the Bristol site, at 21–24 m, with a mud/silt bottom.

Production of seedstring

Initial narrow-bladed kelp sorus tissue was collected from a densely populated intertidal kelp bed on a horizontal platform, Bailey's Island, Maine, USA (43°43.32' N, 69°59.46' W) in Harpswell, Maine, 8 October 2014, and processed at the University of Connecticut (UCONN) Stamford Seaweed Biotechnology Lab. Specimens were kept cool on ice for transport to the lab where the kelp sorus tissue was excised and cleaned, following protocols by Redmond et al. (2014). The voucher specimens were pressed onto acid-free herbarium paper and deposited into The George Safford Torrey Herbarium, UCONN, Storrs, Connecticut (accession numbers: 273,813, 273,814). A final cleaning using a 4% iodine wash remove associated protozoans. The sorus tissue was wrapped in paper towels dampened with seawater and placed in the dark overnight at 10 °C. The next morning, the sorus tissue was placed into 2-L beakers filled with sterile 10 °C seawater for zoospore release, where meiospore density was quantified using a hemocytometer. Meiospores were added at 5000 (\pm 1000) spores mL⁻¹ of seawater into 2700 mL containers holding PVC tubes (seedspools) wrapped with 80 m of 2 mm seedstring (Korean type string: Guraron 24, 2 mm) and were allowed to settle onto the seedstring overnight in complete dark in 10 °C. After 24 h, seedspools were placed into 75-L aquarium tanks with sterile seawater at 10 °C, nutrient additions of PES/2, and light aeration (Redmond et al. 2014). Culture media were changed weekly. Photon fluence rate was provided at 20 μ mol photons m⁻² s⁻¹ the first week and increasing 20 μ mol photons m⁻² s⁻¹ using a *Li-Cor* LI-1000 (Li-Cor, Inc., USA) photometer every week thereafter to a maximum of 100 μ mol photons m⁻² s⁻¹ by regulating bulb distance to tanks in conditions of 12:12 light:dark. After 1.5 months of growth in the nursery, the gametophyte stages produced juvenile kelp sporophytes of 1–2 mm in length. The seedstring was outplanted on 23–24 November 2014 by unwinding and wrapping the seedstring onto 2.54-cm thick longlines at two open-water farm sites (Fig. 1). At Bristol, Maine (Maine Fresh Sea Farms, ~150 m of longline), the longlines were deployed horizontally at two depths of 0.9 and 1.5 m

below the surface. At Sorrento, Maine (Maine Coast Sea Vegetables, ~260 m of longline), the longlines were deployed at 1.4 and 1.8 m depths. The planting depths differed at the two farms because of the slight variation in kelp farm set-up, specifically the minor difference in the placement of buoys. Kelp plants from the same seeded parental populations were grown at both of the farm sites. Over the growing season, and especially after storm events, the kelp lines were monitored to prevent tangling.

Morphometric measurements

We took monthly measurements of total NB kelp length, blade width at the widest part of the blade and stipe length over the growing season (randomly selected plants, $N = 30$) at both farms. Blade thickness was taken for blades from the Bristol farm site only by using a razor blade to cut at 10 cm above the stipe to blade interface and at the widest part of the blade ($N = 16$) and was measured under a compound microscope.

Plant density measurements were taken before harvest by counting the number of stipes on 10 cm of longline at every 1-m interval over 30 m. Meristematic growth rates were recorded only at the Bristol farm by taking hole punch measurements ($N = 30$) at 10 cm above the stipe blade interface and recording growth with subsequent visits as outlined by Egan and Yarish (1990). The initial hole punches were made in mid-March 2015 when cultivated plants were 3.5 months old, and the length of blade (stipe not included) was on average 51.5 (\pm 26.74) cm. The plants were flagged with yellow tape at the base of the stipe for easy identification for subsequent hole punches at 4.5 and 5.5 months and the final measurement at 6 months. Percent growth rate was calculated following the formula by Stephens and Hepburn (2016) taking into account initial and final blade lengths over time.

Harvest

The longline cultivated NB kelp was ready for harvest in May through June of 2015 prior to the reduction in growth caused by fouling, reduction in nutrients and the observance of any reproductive material. At final harvest, NB kelp productivity was estimated by measuring the fresh weight biomass of kelp per longline (e.g., kilograms FW per meter) for samples ($N = 30$) at each farm site (Kim et al. 2015). Additionally, individual kelp plants ($N = 30$) were weighed while wet and subsequently after drying in the drying oven at 55 °C to get the wet to dry ratio.

Second growing season

Some funding was available to support the cultivation operation for a second growing season (2015–2016) of NB kelp at the Bristol and Sorrento farms. The parental plant material for

seeding was collected at Harpswell, Maine, on 15 October 2015 and grown on seedstring in the nursery. The longlines were outplanted on 18 November 2015. The depths of the longlines were at 1.5 m. Yield (kilogram FW per meter) and plant density were observed at harvest started in mid-May and was completed at the beginning of June 2016.

Nutrient analyses and environmental parameters

Water samples for nutrient analysis were taken monthly starting in January 2014 running through the end of May 2015. Samples were from 1-m depth collected with handmade device of two bottles attached at the end of a measured stick. One of the bottles would fill with seawater, while the other had a plastic end that would be released by pulling a string to fill up at that particular depth. A total of three samples per site were collected with pre-cleaned, acid washed containers and frozen at -20°C that same day. With 1 month, samples were filtered through $0.45\text{-}\mu\text{m}$ filter and transferred into sterile scintillation (Fisherbrand, 20 mL HDPE) vials and re-frozen. These were stored at -20°C and thawed prior to analysis. Samples were analyzed by SmartChem discrete nutrient auto-analyzer (Unity Scientific, USA) for total inorganic nitrogen.

Over the first growing season, when conditions permitted and after the kelp plants were large enough to harvest (>10 cm in length), kelp plants were collected monthly ($N = 30$), processed, and analyzed for tissue carbon and nitrogen. During the second growing season, plants were only collected at harvest ($N = 10$). After measuring fresh weight, the plants were placed in a drying oven for 1 week at 55°C . Once dry, tissues were ground up into a fine powder using a tissue grinder (Model MM200 Grinder, Retsch, Haan, Germany). Tissue amounts of 2 ± 0.5 mg were weighed and nitrogen (N) and carbon (C) percentages were determined using a CHN analyzer (Series II, CHNS/O 2400 Analyzer, Perkin Elmer, USA). To measure the N and C removal capabilities of the kelp farm, we used values of dry biomass yield per meter of longline combined with tissue N and C content following the equation by Kim et al. (2014, 2015).

Monthly environmental parameters were measured at both farms. These included salinity and Secchi disk measurements. Additionally, at the Bristol farm, light measurements used a Li-Cor LI-185A PAR meter (USA). Temperature sensors (HOBO data logger 64K, UA-002-64) were attached to the longlines at a 1.5-m depth in Bristol and at 1.4-m depth at Sorrento. We measured salinity using a refractometer (no. 13104190, Reichert Technologies, USA) at surface.

Common garden

To identify plasticity or a genetic basis for the unique morphology of the NB kelp, and to compare the morphologies of

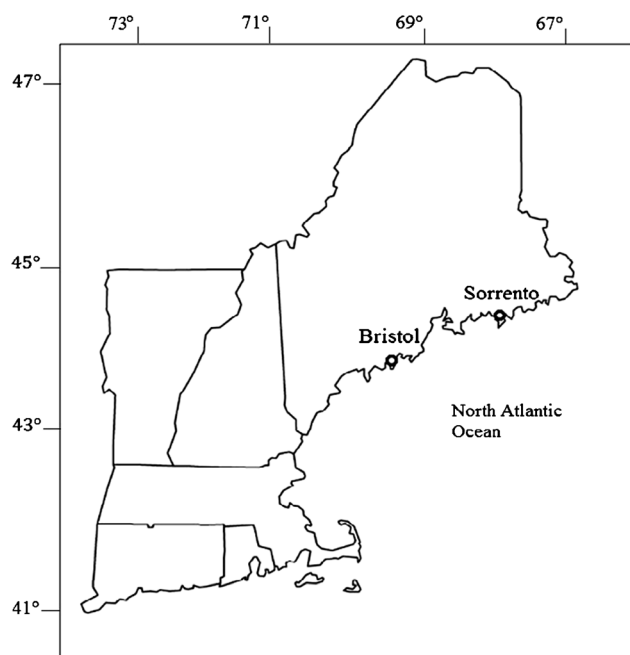


Fig. 1 Map of New England showing locations of open-water farm sites in Maine, indicated in circles

the cultivated NB kelp with *S. latissima*, we ran a common garden experiment by growing both types side by side on longlines. By keeping the environmental variables of the farm sites constant, specifically the relatively calm wave and current conditions, we wanted to observe a genetic basis as a driver for the strap-shaped morphology.

At Bristol, the sugar kelp seedspools were seeded from two parental populations: the first one from Casco Bay, Maine, outplanted on 14 October and the second one from Hancock, Maine, outplanted on 27 December 2014. At the Sorrento farm, all the seedstring was from the Hancock, Maine, population and was seeded on 22 December 2014. The nursery production of seedstring followed the same protocols as that of the NB kelp. A comparison between the two morphologies was made at the time of harvest, May through June 2015 at both sites, based upon measurements of the mean of blade length and width.

Statistical analysis

Data analysis was performed using the “R” (v 3.0.0) software and was checked for homogeneity of variance prior to running ANOVA. We evaluated differences between kelp productivity, meristematic growth rates, and tissue chemistry over the growing season (January through June) at two farm sites using a two-way ANOVA. We then performed an analysis to understand how factors such as site and parental population explained variation in adult kelp morphology in the common garden experiment. Finally, a two-way factorial design was

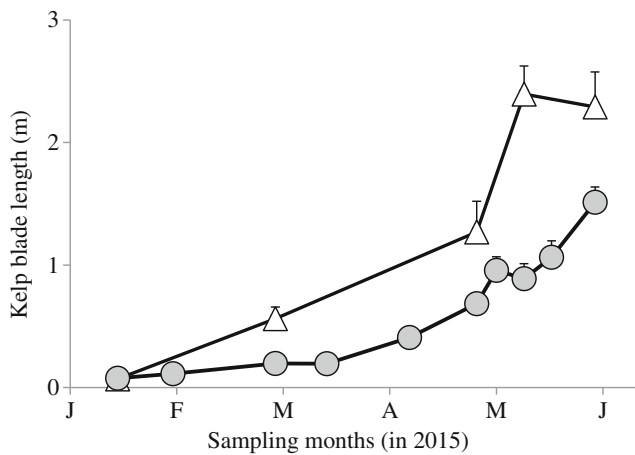


Fig. 2 Narrow-bladed kelp length, stipe included, (means, \pm CI, cm, $N = 30$) over the 2014–2015 cultivation season. Kelp was outplanted at the end of November of 2014. *Triangles* are Bristol and *circles* are Sorrento farm

used to test the differences in water chemistry at both sites over the growing season.

Results

Growing season 2014–2015—comparison of sites

Total NB kelp length (blade and stipe) was significantly different throughout the growing season ($p < 0.001$) and at the two sites ($p < 0.001$, Fig. 2). At harvest, lengths were higher at the Bristol farm at $229 (\pm 28.56)$ cm compared to Sorrento at $151 (\pm 12.5)$ cm. Kelp blade width was also significantly different throughout the growing season ($p < 0.001$) at the two sites ($p = 0.024$). At harvest, blade widths at Bristol were on average of $4.67 (\pm 0.98)$ cm compared to Sorrento at $2.76 (\pm 0.21)$ cm (Fig. 3). Similarly, stipe lengths were significantly longer ($p < 0.001$) at Bristol at $8.59 (\pm 1.46)$ cm than at Sorrento at $3.57 (\pm 0.22)$ cm throughout the growing season ($p < 0.001$, Fig. 4). At the Bristol farm, at harvest, blade thickness was $0.12 (\pm 0.02)$ mm at the stipe/blade interface and $0.11 (\pm 0.01)$ mm for the widest part of the blade. It was observed that the cultivated blades were less strap-like and had formed blade ruffles.

Meristematic growth rate measurements of the NB kelp taken over the growing season at the Bristol farm revealed highest growth rates from mid-March to mid-April of on average $2.85 (\pm 0.34)$ cm day⁻¹ with a daily growth rate of $2.00 (\pm 0.18)\%$ ($p < 0.001$, Fig. 5). From mid-April to mid-May, the kelp had slightly lower rates of growth at $2.59 (\pm 0.31)$ cm day⁻¹ at $1.16 (\pm 0.18)\%$. Later in the season, from mid-May through the end of May, the kelp only grew $1.16 (\pm 0.11)$ cm day⁻¹ at a growth rate of $0.55 (\pm 0.09)\%$.

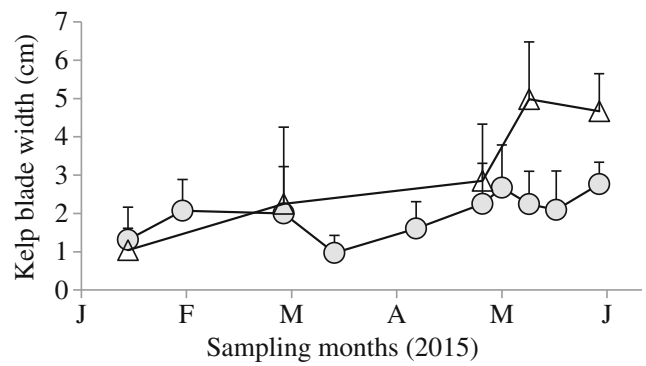


Fig. 3 Narrow-bladed kelp blade width (means, \pm CI, cm, $N = 30$) over the 2014–2015 cultivation season. *Triangles* are Bristol and *circles* are Sorrento farm

Yields

Overall, final yield was higher at the Bristol farm during the first season. The wet weight of the harvested biomass at Bristol was on average $17 (\pm 4.4)$ kg m⁻¹ of line and plant density was 330 plants m⁻¹ of line. At Sorrento, yield was $13.3 (\pm 6.2)$ kg wet weight m⁻¹ line and a plant density of 400 plants m⁻¹ of line. The average dry to wet weight ratio for kelp plants was $11.1 (\pm 2.6)\%$ with no difference observed between sites. During the second growing season (fall 2015 through spring of 2016), the average yields at the Sorrento farm site were $24.1 (\pm 6.3)$ kg m⁻¹ of line and a plant density of 1100 plants m⁻¹.

Nutrient analyses

Results from both farms show that tissue nitrogen content was highest in late January at $2.95 (\pm 0.65)\%$ dry weight (DW) in Bristol and $2.57 (\pm 0.01)\%$ DW in Sorrento and decreased over the growing season $1.30 (\pm 0.11)\%$ DW in Bristol and $1.79 (\pm 0.02)\%$ DW in Sorrento in June (Fig. 6). At harvest, during the second growing season, Bristol had tissue nitrogen content values of $1.04 (\pm 0.12)\%$ DW and Sorrento at $1.40 (\pm 0.44)\%$ DW. The tissue carbon content increased over the first growing season for the Bristol farm (from $22.48 (\pm 5.31)$ to 28.38

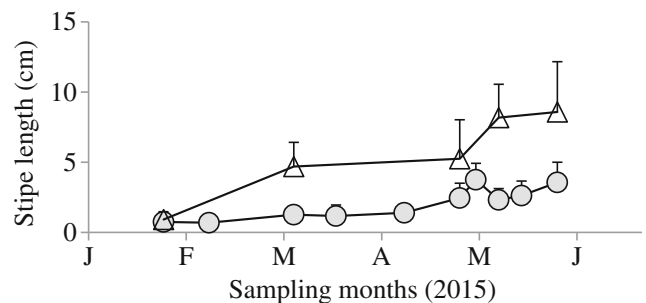


Fig. 4 Narrow-bladed kelp stipe lengths (means, \pm CI, cm, $N = 30$) over the 2014–2015 cultivation season. *Triangles* are Bristol and *circles* are Sorrento farm

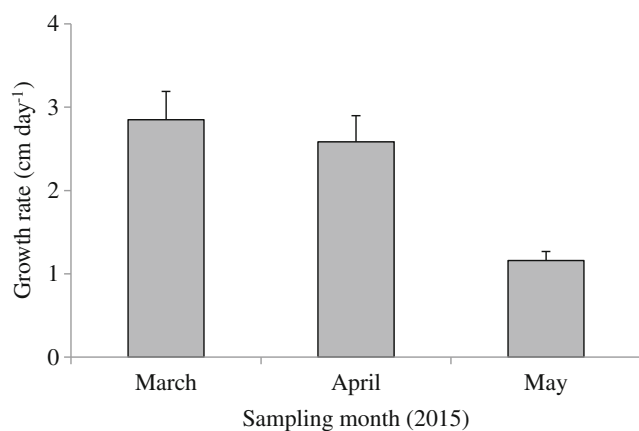


Fig. 5 Narrow-bladed kelp meristematic growth rates (means \pm 95% CI, cm day^{-1} , $N = 30$) over 3-month time in 2015 at the Bristol farm. For exact dates, refer to results section

(± 2.29)% DW), but decreased for Sorrento (from 36.22 (± 0.22) to 29.35 (± 0.23)% DW), and site was found to be statistically significant ($p = 0.027$) but not month ($p = 0.275$). At harvest, during the second season of cultivation, Bristol and Sorrento sites, respectively, had the following tissue carbon content: 30.87 (± 1.26)% DW and 25.46 (± 5.02)% DW. The carbon to nitrogen ratio increased over the first growing season at both sites and was significantly different for the months and sites tested (both variables $p < 0.001$). In February, the C to N ratio for Bristol was 7.63 and Sorrento was 14.1, while in Bristol was at 21.9 and Sorrento was at 14.4 going up to 29.5 in July (we do not have a measurement for July at Bristol).

Calculations for kelp harvested in the month of June 2015 provide the estimated N removal for Bristol and Sorrento, respectively, at 96.9 and 102.4 kg ha^{-1} for the first season and 6.8 and 148.8 kg ha^{-1} for the second growth season. The C removal for Bristol was 2309.1 kg ha^{-1} and for Sorrento, it was 1456.3 kg ha^{-1} for the first season. The second season C removal for Bristol was much lower at 203.8 kg ha^{-1} and Sorrento was at 2697.2 kg ha^{-1} .

Environmental parameters

At the time of outplanting the kelp lines in late November 2014, the water temperature at planting depth was at 7.9 °C in Bristol and 8.7 °C in Sorrento (Fig. 7). In early February through mid-March, the water temperature dropped to below freezing (maximum low was -1 °C) and coupled with several winter storms, the farms were inaccessible for over 1 month. Additionally, ice scour had damaged some of the seeded kelp and longlines and moved buoys out of place. At harvest in May through June, the water temperatures were around 11 °C. We combined results of the water analysis for nitrate, including nitrite and ammonium, and found total nitrogen to be highest in January at 30.4 and 25.3 μM and

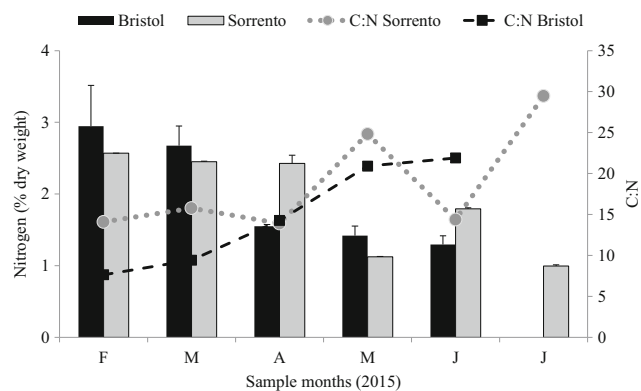


Fig. 6 Tissue nitrogen (means \pm 95% CI, % dry weight, $N = 5$) and carbon to nitrogen ratio on secondary axis for two Maine farms, Bristol and Sorrento, for the season of 2015

dropping significantly over the growing season to 11.2 and 7.3 μM at Bristol and Sorrento, respectively (Fig. 8). This pattern was consistent with the results of tissue nitrogen uptake seen over the growing season.

The Secchi disk readings showed that water clarity was around 4–5 m at both farms and then decreased to 2–3 m in Bristol starting in mid-April to late May. The Sorrento farm had a peak value of 8 m in depth in April and dropped down to 5 m in early May (graph not shown). These results revealed that water turbidity was low early in the growing season and over time slightly increased. From refractometer readings taken January through May, the average monthly salinity was 31 (± 1) ppt at the Bristol and 33 (± 1) ppt at the Sorrento farms.

Sugar kelp vs. narrow-bladed kelp

For the total lengths of *S. latissima*, Bristol had averages of 72.21 (± 18.02) cm compared to the Sorrento farm at 92.95 (± 10.1) cm (Fig. 9a). Sugar kelp widths at the Bristol and Sorrento farms were 8.72 (± 2.4) and 7.38 (± 0.83) cm, respectively (Fig. 9b). The lengths of the sugar kelp stipe were 15.29 (± 2.98) and 21.52 (± 2.66) cm at the Bristol and Sorrento farms, respectively (Fig. 9c). Comparisons of sugar kelp and NB kelp made at harvest at both farms revealed no intraspecific variation or differences of each phenotype between the farm sites in terms of their length, width, and stipe lengths

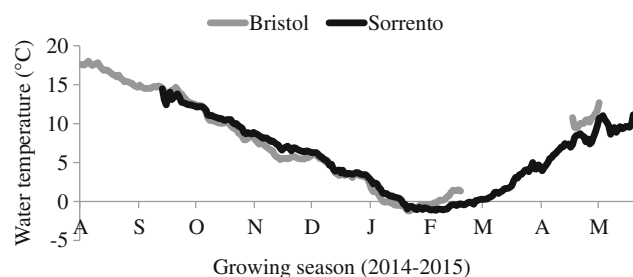


Fig. 7 Temperature data from HOBO devices deployed on the kelp longlines at each of the two farm sites

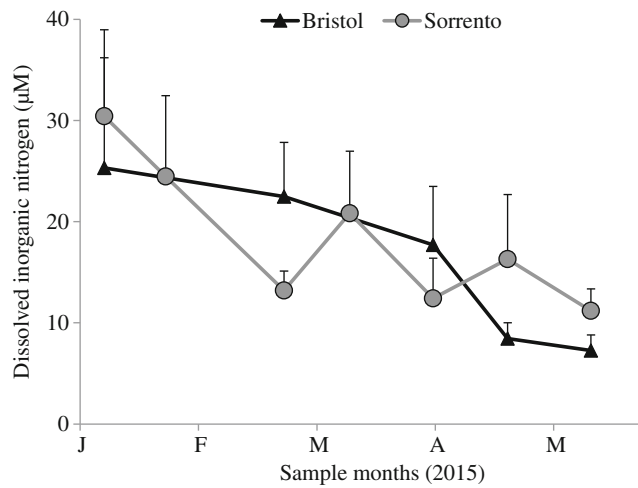


Fig. 8 Seasonal variation for total dissolved inorganic nitrogen (means ± 95% CI, µM) from water samples collected as triplicates at 1 m below surface

($p = 0.136, 0.073, \text{ and } 0.968$, respectively, Figs. 9a–c and 10a, b). However, interspecific variation was observed; the two morphologies differed in averages of total length, width, and stipe lengths (all three variables $p < 0.001$). Cultivated sugar kelp plants were wider than cultivated NB plants by 5.67 and 4.62 cm in Bristol and Sorrento, respectively. Likewise, significant differences were found between the averages of the two morphologies in their ratios of length to width ($p < 0.001$) but not across the two sites ($p = 0.179$, Fig. 11). The L:W ratio for the NB kelp was 85.89 (± 20.23) and 56.14 (± 5.02) cm, while for the sugar kelp, it was 9.54 (± 2.24) and 12.9 (± 1.10) cm for Bristol and Sorrento, respectively.

Discussion

The NB kelp, *Saccharina latissima* forma *angustissima*, was successfully cultivated at two open-water farm sites in Maine over two seasons, 2014–2015 and 2015–2016. During the first season, yields were higher at Bristol with 17 (± 4.4) kg m⁻¹ of line than in Sorrento, at 13.3 (± 6.2) kg wet weight m⁻¹ line. During the second season, yields at Sorrento were 24.1 (± 6.3) kg m⁻¹ of line. These yields are similar to other studies such as those done in Long Island Sound reporting 18 kg m⁻¹ of line in 2011–2012 and 9.3 kg m⁻¹ of line in 2012–2013 (Kim et al. 2015). In Spain, Peteiro and Freire (2013) measured *S. latissima* yields of 12–16 kg m⁻¹ of line depending on exposure of site, and in northwest Scotland, Sanderson et al. (2012) report *S. latissima* yields of 20–28 kg m⁻¹ of lines grown adjacent to fish farm cages. At harvest, blade widths at Bristol were on average of 4.67 (± 0.98) cm compared to Sorrento at 2.76 (± 0.21) cm. Several factors could be driving the difference seen in mean blade widths at Bristol. One possible explanation is the spacing of the plants on the longlines;

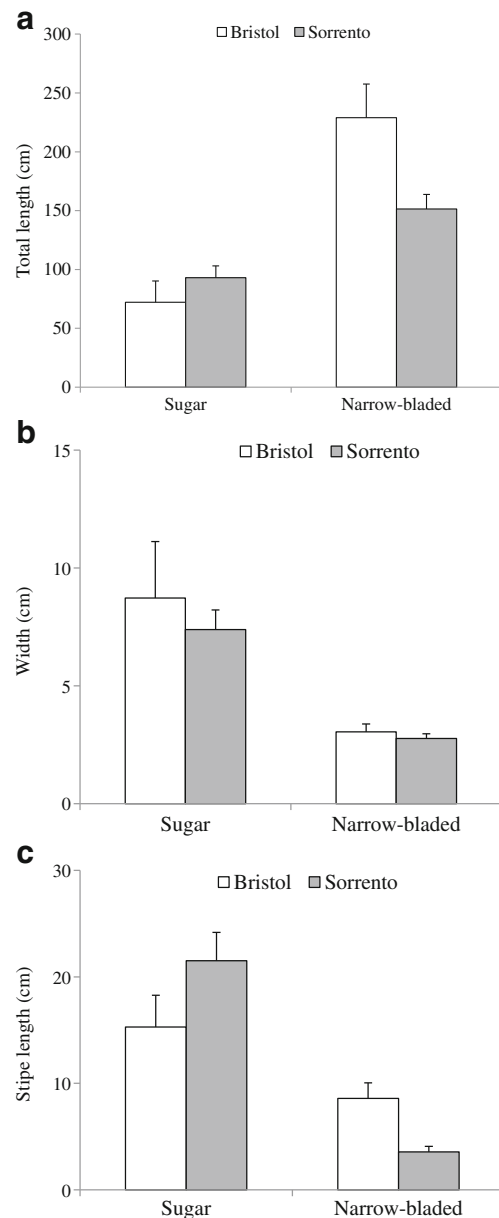
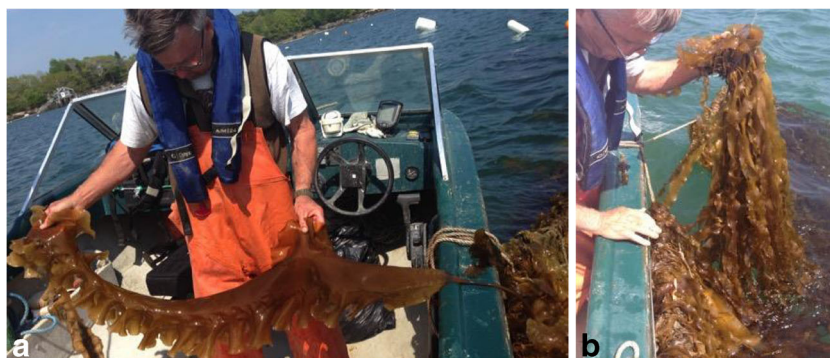


Fig. 9 a–c The lengths and widths of sugar and narrow-bladed kelps grown at the two farms at the time of harvest (means, ±95% CI, $N = 30$)

at Bristol, there were only 330 plants m⁻¹ compared to 400 plants m⁻¹ at Sorrento.

Numerous studies have shown that algal thallus morphology changes with the hydrodynamic environment where they are found (Gerard and Mann 1979; Klinger and DeWreede 1988; Johnson and Koehl 1994). As seaweeds are sessile, they are unable to move and must adapt to change their morphology and biological structure to persist on wave-swept shores (Demes et al. 2013a; Starko et al. 2015). In the present study, two kelp morphologies from different parental populations were grown in similar conditions at the two open-water farms protected from high ocean swells and currents. During the

Fig. 10 a, b Seaweed farmer, Seth Barker, holding the sugar kelp (a) and the narrow-bladed kelp (b) at the time of harvest



season and particularly at harvest, it became evident that some characteristics of the unique strap-like morphology, initially adapted to withstand high impact wave bashing, were preserved in the length to width blade ratios of the plants. These results suggest the NB kelp morphology is somewhat genetically fixed and agree with the work of Philibert (1990). Although his work was inconclusive, Philibert (1990) found that *S. latissima* f. *angustissima* retained its morphology in laboratory culture. In this study, some other adaptations seen in the wild populations, including the linearity of the blades, were lost. Previous studies show that when water flow is low, macroalgal thalli grow thin and wide forming undulations, or ruffles, on the blade margins to enhance the flux on nutrients across the diffuse boundary layer (Hurd 2000). These bullations may also enhance light capture (Hurd et al. 2014). In comparison, kelp thalli grown in areas of high turbulence grow much thicker and narrower, with few to no bullations (Hurd 2000; Roberson and Coyer 2004; Koehl et al. 2008). This intraspecific tissue variation was observed in algae growing in mechanically stressful environment and may be a critical acclimation to reduce the drag forces imposed by breaking waves (Denny et al. 1985; Gaylord et al. 2008; Demes et al.

2013b). This was consistent with the findings and comparisons of this study. Preliminary field measurements in 2013 (pers. observation) revealed that parental NB kelp blade thickness was on average 1.28 (± 0.21) mm as compared to the cultivated NB blade thickness of 0.12 (± 0.02) mm. Furthermore, unlike in the parental population, blade ruffles were induced in the NB kelp sporophytes at both the farm sites.

Sugar kelp is a perennial species with a period of maximum growth in the early part of the year followed by a period of reduced growth during the summer (Lüning 1993; Bartsch et al. 2008; Handå et al. 2013). This was highlighted in the seasonal variation of meristematic growth data that showed highest growth rates in mid-March into early May. Growth rates started decreasing in May to the end of the month. Nitrogen in the water column was highest in the winter and became limiting later in the growing season. This coincides with high nitrogen tissue accumulation during the peak times compared to those of late spring. Other studies showed that when light and temperature availability were adequate, *S. latissima* seasonal growth patterns were dependent upon nitrogen availability (Chapman et al. 1978; Egan and Yarish 1990; Gevaert et al. 2001). Early in the growth season, a lower C:N ratio (Lee and Brinkhuis 1988) coincided with high nitrogen availability in the water, and the kelp cells were actively growing. In the spring, as total dissolved inorganic nitrogen decreases substantially, the kelp used its previously stored tissue nitrogen reserves (Gevaert et al. 2001; Kim et al. 2015). Chlorophyll *a* data from the Darling Marine Center situated close to the Bristol farm site revealed that there were three peaks in phytoplankton growth, two in the spring, and the third one in the fall months. The initial bloom in the spring was from March to April and a second larger one occurred in May through June. Phytoplankton are likely outcompeting kelps for nutrient availability (Lüning 1993; Kim et al. 2015), as indicated in the decrease in nitrogen availability both in the water column and in the measured kelp tissue.



Fig. 11 Sugar and narrow-bladed kelp length to width ratio at the time of harvest at the two farms, Bristol and Sorrento (means, $\pm 95\%$ CI, $N = 30$)

Ecosystem services and beyond

Studies have shown that *Saccharina latissima* is an excellent candidate for the bioextraction of nutrients from coastal waterways in both urbanized estuaries (Kim et al. 2015) and near fish farms (Sanderson et al. 2012). To get an estimation of nutrient bioextraction capabilities for the NB kelp, we pose a hypothetical seaweed farm situation following Sanderson et al. (2012) where per hectare, there are 40 100-m longlines spaced 2.5 m apart. With this scenario, in the present study, the averages over the 2 years at both farm sites for kelp harvested in June has N removal capacity at 88.7 kg ha⁻¹ and C removal at 1666.7 kg ha⁻¹. The N and C removal rates are similar to previously published studies; Kim et al. (2015) found rates of 38–139 kg ha⁻¹ removal of N and 1100–1800 kg ha⁻¹ removal of C. To make a significant impact in a heavily N-rich water body such as Long Island Sound (LIS), Kim et al. (2015) estimated that approximately 1.5% of the whole LIS would have to be cultivated with both *S. latissima* and *Gracilaria* sp. in an area of 5100 ha. This would remove roughly 1.6–2.2 million kg N year⁻¹ or 10% of the LIS target Total Maximum Daily Load (Rose et al. 2015).

Conclusion

The results presented here suggest that *Saccharina latissima* forma *angustissima*, a morphologically unique kelp, can be domesticated and produce a high yielding product of up to 24 kg m⁻¹ of line. The morphological characteristics that make the NB kelp unique were preserved on the open-water farm. These adaptations were useful in the turbulent wave-swept intertidal environment for the reduction of drag forces and prevention of dislodgement and were retained at the open-water farm site in calm and sheltered conditions. Seaweed aquaculture is gaining popularity in the northeast USA and is becoming one of the fastest growing industries (Rose et al. 2015). Results from this study should provide opportunities for a new crop of kelp for Gulf of Maine sea farmers with culinary and ecosystem service applications.

Acknowledgements We would like to thank the Seaweed Biotechnology Laboratory interns and the Maine farmers including S. Barker, P. Fischer, P. Arnold, S. Erhart, and M. Moretti. Funding was provided by The Maine Aquaculture Innovation Center (Project No. 15-11), USDA-National Institute of Food and Agriculture (Project Award # 2014-70007-22546), The Francis Rice Trainer Endowment Fund to the Dept. of Ecology and Evolutionary Biology and the Connecticut Museum of Natural History, The Ronald Bamford Fund to the Dept. of Ecology and Evolutionary Biology, and The University of Connecticut Graduate School Doctoral Dissertation Fellowship, Sigma Xi Grants-in-Aid of Research and the Woman's Seamen's Friend Society of Connecticut.

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