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FEATURE ARTICLE

Wasted effort: recruitment and persistence of kelp on algal turf

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ABSTRACT: Declines in kelp abundance over the past 3 decades have resulted in a shift from luxuriant kelp beds to extensive mats of turf-forming algae in Nova Scotia, Canada. With the reduced availability of open rocky substrate, kelps are increasingly recruiting to turf algae. At 3 sites near Halifax, we found that turf-attached kelp *Saccharina latissima* was generally restricted to smaller size classes (<50 cm length) than rock-attached kelp at 12 m depth. Turf-attached kelp allocated a greater proportion of biomass to the holdfast (anchoring structure), which differed morphologically from that of rock-attached kelp and had lower attachment strength. To assess how these differences affect survival, we monitored kelp in 2 m diameter plots at 11 m depth over 40 wk at 1 site. Smaller kelps were predominantly turf-attached and larger ones rock-attached in late summer and autumn, but there was near-complete loss of both turf- and rock-attached kelp over winter when wave action was greatest. In a concurrent manipulative experiment at 5 m depth at another site, we transplanted small boulders with turf- or rock-attached kelp to a wave-exposed or protected location. Survival was greater for rock-attached transplants at both locations after 12 wk, with a complete loss of turf-attached kelp in the wave-exposed treatment. Classification based on holdfast morphology showed that 76% of drift kelp within a depositional area at this site was once turf-attached. Low survival of kelps that recruit to turf algae, likely due to wave dislodgement, may represent an important feedback that increases resilience of a turf-dominated state and prevents reestablishment of kelp.

KEY WORDS: Kelp · Turf-forming algae · Holdfast · Attachment strength · Recruitment · Feedback

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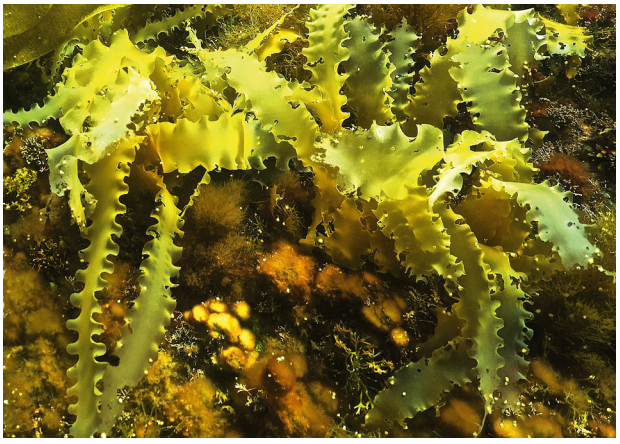

Recruits of the canopy-forming kelp *Saccharina latissima* on turf algae at 4 m depth off the coast of Nova Scotia.

Photo: Robert Scheibling

INTRODUCTION

Kelp beds (or forests) span about a quarter of the world's temperate and polar coastlines (Filbee-Dexter & Scheibling 2014) and are among the most productive, structurally complex, and diverse marine ecosystems, providing habitat and food for numerous ecologically and economically important fish and invertebrates (Dayton 1985, Steneck et al. 2002). However, widespread shifts from assemblages dominated by kelps and other habitat-forming brown seaweeds to those dominated by opportunistic turf algae have occurred in areas where environmental conditions have been altered by human activities

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(Eriksson et al. 2002, Connell et al. 2008, Perkol-Finkel & Airoldi 2010). Turf-algal assemblages vary significantly in morphology (filamentous, coarsely branched, articulated corallines) and species composition, but usually consist of a low-lying, dense matrix of algal branches and filaments (Connell et al. 2014). This type of regime shift has been documented worldwide (Filbee-Dexter & Wernberg 2018), including the coasts of South Australia (Connell et al. 2008), Norway (Moy & Christie 2012), Sweden (Eriksson et al. 2002), and eastern Canada (Filbee-Dexter et al. 2016).

Although turf algae are generally ephemeral, multiple stressors favour their growth directly by releasing them from resource limitation or indirectly by reducing abundance of kelp and other large macroalgae. Increasing ocean temperature may drive losses of kelp canopy by limiting reproduction (Bartsch et al. 2013) and growth (Bolton & Lüning 1982, Simonson et al. 2015, Gao et al. 2016) or through tissue degradation that increases fragmentation or mortality (Lüning 1984, Wernberg et al. 2013, Simonson et al. 2015). Proliferation of turf algae following canopy removal is intensified by factors that directly stimulate turf growth, including increases in ocean temperatures (Connell & Russell 2010). Also, when exposed to eutrophic conditions (Gorman et al. 2009) and predicted future levels of CO_2 (Connell & Russell 2010), species of turf algae can absorb available nutrients and increase growth rate (Hein et al. 1995), whereas some kelp store nutrients and maintain a relatively constant growth rate (Lobban & Harrison 1994). Turf algae also tolerate increased sedimentation that can decrease the diversity and distribution of kelp species (Airoldi 1998, Eriksson et al. 2002, Moy & Christie 2012). Under such conditions, turf algae can rapidly occupy space and persist by inhibiting the recruitment of kelp.

On the Atlantic coast of Nova Scotia, Canada, there has been a marked decline in the historical biomass of kelp in recent decades and a shift from a kelp bed ecosystem to one dominated by mats of turf algae (Filbee-Dexter et al. 2016). In particular, the abundance of the dominant perennial kelps *Saccharina latissima* and *Laminaria digitata* has been greatly reduced by the combined effects of large-scale biotic and abiotic factors. Repeated defoliation of the kelp canopy followed the introduction of an invasive epiphytic bryozoan *Membranipora membranacea* in the early 1990s (Scheibling et al. 1999, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). During population outbreaks of *M. membranacea*, kelp blades are heavily encrusted, resulting in increased erosion and fragmentation and massive loss of canopy cover (Saunders & Metaxas 2008, Krumhansl et al. 2011). A steady rise in ocean temperature along this coast in the past 4 decades (Scheibling et al. 2013), which has favoured recruitment and growth of the bryozoan (Saunders & Metaxas 2009, Scheibling & Gagnon 2009) and reduced kelp tissue strength (Simonson et al. 2015), has compounded the impact of this invasion on native kelps.

Kelps such as *S. latissima* exhibit a biphasic life cycle, typical of brown algae in the order Laminariales, with 2 morphologically distinct stages. In Nova Scotia, sporangia on the blade of the macroscopic sporophyte release microscopic haploid spores in autumn (Chapman 1984). The spores settle onto the substrate and develop into haploid male and female gametophytes that are subsequently fertilized and germinate to form small macroscopic diploid sporophytes in winter and spring. The sporophyte attaches to the rocky substrate via a holdfast, an anchoring structure with numerous branching extensions (haptera) that resists dislodgement by wave forces. Turf algae that have replaced kelp accumulate large quantities of inorganic sediment (Filbee-Dexter et al. 2016) that can prevent attachment of kelp spores (Devinny & Volse 1978, Deiman et al. 2012), creating a physical barrier to settlement (Gorman & Connell 2009). However, *S. latissima* has been reported anecdotally to recruit on turf in the northeastern USA (Brady-Campbell et al. 1984). The attachment strength of large brown seaweeds can be significantly weaker on so-called 'soft substrates' (e.g. barnacles, limestone) compared to harder granite, with implications for individual survival and population size structure (Barnes & Topinka 1969, Malm et al. 2003, Thomsen et al. 2004). For turf-attached kelps, the lack of stable substrate may render the sporophyte more susceptible to dislodgement by wave-forces, potentially limiting kelp population growth and recovery and perpetuating the turf-algal state.

In this study we examine the extent of recruitment and survival of kelp (mainly *S. latissima*) when attached to turf algae. To quantify the distribution of kelp on turf vs. rocky substrate, and whether this varied with thallus size, we conducted diving surveys at 3 sites near Halifax in 2016. We predicted that there would be more turf-attached than rock-attached kelp because the primary substrate was predominantly covered by turf algae in these areas. We also predicted that turf-attached kelp would be smaller than rock-attached kelp, as a solid and stable attachment surface is necessary to counteract hydrodynamic forces that can dislodge a larger thallus. To

determine the effect of substrate on holdfast morphology and allocation of biomass, we made morphological measurements from kelp collected at 5 sites. We predicted that holdfasts of turf-attached kelp would have a more elongated gross morphology, greater structural complexity, and increased allocation of biomass when compared to rock-attached kelp, as the holdfast continues to grow towards the rocky substrate when attached to turf. We also measured attachment strength of turf-attached kelp at these sites, and predicted that it would be lower than that of rock-attached kelp measured in previous studies. Finally, we experimentally examined the survival of kelp on turf vs. rock substrates by (1) transplanting individual kelps attached to turf or rock on small boulders to areas of different wave-exposure at one site for 4 mo and (2) monitoring changes in kelp size and abundance within fixed plots in relation to seasonal environmental changes (temperature and wave height) at another site over 9 mo. We predicted that turf-attached kelp had a greater probability of dislodgement than rock-attached kelp in areas or at times of increased wave action (due to a difference in attachment strength), and that the probability of dislodgement and loss of kelp would increase with blade area and attendant increases in drag and lift forces.

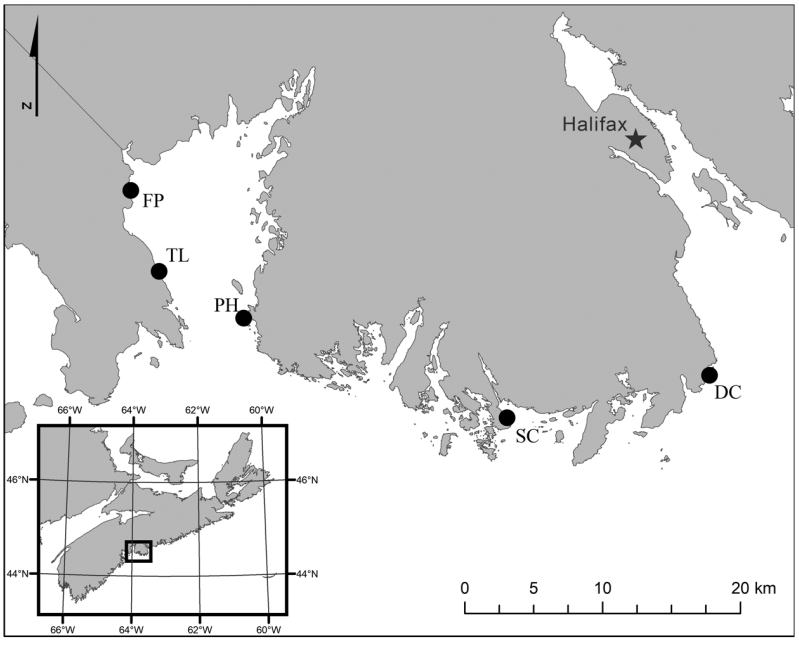

Fig. 1. Study sites on the Atlantic coast of Nova Scotia, Canada: Fox Point (FP), The Lodge (TL), Paddy's Head (PH) in St. Margarets Bay; Sandy Cove (SC) and Duncan's Cove (DC) on the Chebucto Peninsula

MATERIALS AND METHODS

Study sites

We quantified patterns of recruitment of *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum* on turf algae vs. bare or coralline-encrusted rock and examined factors that may influence subsequent survival of *S. latissima*—the predominant kelp on these substrates—between June 2016 and April 2017 at 5 rocky reefs between the western shore of St. Margaret's Bay and the western head of Halifax Harbour (Fig. 1): The Lodge (TL; 44° 33.491′ N, 64° 01.493′ W), Paddy's Head (PH; 44° 31.624′ N, 63° 57.080′ W), Fox Point (FP; 44° 36.346′ N, 64° 03.210′ W), Sandy Cove (SC; 44° 27.493′ N, 63° 42.365′ W), and Duncan's Cove (DC; 44° 29.541′ N, 63° 31.540′ W).

TL and FP on the western shore of St. Margaret's Bay are sites characterized by small boulders and sand with low kelp canopy cover. PH on the eastern shore of St. Margaret's Bay and 6.8 km from TL has an underwater landscape of ledges and medium to large boulders that also support a low canopy cover of kelp. SC on the headland between St. Margaret's Bay and Halifax Harbour supports moderate to high densities of *S. latissima* and *L. digitata* on sloping bedrock and rocky outcrops. DC at the western head of Halifax Harbour includes an exposed area at the mouth of the cove and a protected inlet ~0.25 km inland, with low to moderate kelp cover on small and medium-sized boulders. The rocky substrate at each site had a near complete cover of low-lying filamentous, foliose, coarsely branched or articulated coralline red algae that formed a dense turf from the low intertidal zone to 8–12 m depth, except at DC where turf extended to 4–7 m depth, the lower limit of rocky substrate at this site.

We calculated a wave exposure index for each site using the average fetch (m) measured at 10° intervals using Google Earth within the directional range over which ocean swells enter St. Margaret's Bay (140–210°), Duncan's Cove (52–162°) or Sandy Cove (127–197°), and bounded by 2000 km, the distance over which storm-generated waves in the North Atlantic propagate to the coast of Nova Scotia (Hart &

Evans 2001). Sites were ranked from low to high exposure as follows: (1) FP, (2) TL, (3) DC, (4) SC, (5) PH. This method of using fetch-based indices to measure the exposure of a particular site along a coastline has been shown to be a viable option for approximating wave exposure (Hill et al. 2010).

Daily mean significant wave height (SWH, m) and mean sea surface temperature (SST, °C) from 1 July 2016 to 24 April 2017 were obtained from a meteorological buoy at the mouth of Halifax Harbour (Station 44258, 44° 30′ N, 63° 24′ W), within 10–50 km of the study sites (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m600p003_supp.pdf). During the same period, daily mean sea temperatures (°C) were measured at TL with HOBO® Pendant Data Loggers at 12 m depth (Fig. S1).

Substrate composition and kelp size distribution by substrate

To determine the percent cover of turf algae and rocky substrate (including bare and coralline-encrusted boulders and bedrock) and the size frequency distribution of kelps, divers conducted surveys at TL (June 28, July 6), FP (July 13), and PH (July 13, September 13). For these, 6 to 9 quadrats (1 m^2) were placed systematically at 5 m intervals along a transect line following the 12 m depth contour. For each quadrat, divers recorded thallus length of each kelp species (*S. latissima*, *L. digitata*, *A. clathratum*), binned into 6 classes (<10, 10–30, 30–50, 50–100, 100–200, >200 cm; except at TL where kelps >50 cm were binned in a single class) and the substrate to which the holdfast was attached (haptera loosely tangled among turf algae vs. fixed to rock). Large kelps were then removed to give an unobstructed view of the substrate cover and a photograph was taken. Percent cover of the substrate was measured using image analysis software (ImageJ) by superimposing 100 uniformly distributed dots on a quadrat image and recording the substrate type (turf or rock) under each dot.

Kelp collection and morphological analysis

To examine potential morphological differences between turf- and rock-attached sporophytes of *S. latissima*, we collected specimens between 8 and 12 m depth (5 and 7 m depth at DC) throughout the study period: TL (June 28; July 6, 20; August 9), PH (July 13, 27), SC (August 2; September 12), DC (July 29; August 3, 24), and FP (July 13). Divers haphazardly sampled turf- and rock-attached kelp on encounter, carefully removing them to avoid breakage of haptera. On rare occasions, apparently turf-attached individuals had a small number of haptera extending through the turf to the rocky substrate below. These individuals were excluded from this analysis. Thalli were placed in separate fine-mesh bags for each substrate type from which they were removed. At DC, drift kelp with intact holdfasts was haphazardly collected from a depositional area to compare their holdfast morphology (Fig. S2) to that of thalli for which the attachment substrate was known. Kelp samples were transported to the laboratory in closed coolers and placed in flow-through seawater holding tanks until morphological measurements were made.

We manually cleaned each turf-attached holdfast of remnants of turf, which we collectively placed in a tray and photographed. These samples were then transferred to individually labelled plastic bags and frozen for subsequent identification of algal species. We visually estimated the abundance of 4 morphological/functional groups of turf algae in each sample photograph: (1) filamentous or delicately branched (e.g. *Ceramium virgatum, Euthora cristata, Rhodomela confervoides, Bonnemaisonia hamifera, Chaetomorpha linum*), (2) foliose (e.g. *Porphyra umbilicalis, Membranoptera alata*), (3) coarsely branched (e.g. *Phyllophora pseudoceranoides, Coccotylus truncatus, Chondrus crispus*), and (4) articulated coralline (*Corallina officinalis*). All were red algae except *Chaetomorpha linum*, a green alga. The rank abundance of each algal group in each sample photograph was scored as 0, 1, 2, or 3 if they represented 0, <20, 20–50, or >50% of the sample, respectively. To compare holdfast morphology between turf- and rock-attached kelps, we separated the holdfast from the rest of the thallus and measured the gross morphology and structural complexity of the holdfast, and the relative allocation of biomass to the holdfast, for samples collected from each substrate type. Gross morphology was measured as the length-to-width ratio of holdfasts, where width (cm) was estimated by averaging the minimum and maximum diameter at the base of the holdfast, and length (cm) was measured from the base of the stipe to the end of the longest hapteron. Structural complexity was measured by counting the number of bifurcations along the branching path of each primary hapteron (first offshoot of the stipe) and averaging these counts across all primary haptera. Allocation of biomass to the holdfast was measured as ratio of holdfast-to-

total biomass by separately blotting and weighing (0.001 g precision) the holdfast and the stipe plus blade. All holdfasts were manually cleaned of attached fragments of encrusting or turf algae and small invertebrates (primarily mussels) before weighing. We excluded thalli of total biomass >200 g (2.75% of kelp sampled) to constrain comparisons between turf- and rock-attached kelp to a similar size range.

Attachment strength

Attachment strength of *S. latissima* on turf algae was measured by divers at the sampling depths described above at TL (July 20), PH (July 13, 27), SC (August 2, September 12), and DC (July 29; August 3, 24). Turf-attached kelps were haphazardly sampled and a cable-tie was threaded through the holdfast to form a loop. A calibrated 2000 g spring scale (10 g precision) was hooked onto the cable-tie and slowly pulled vertically with a steadily increasing force until it dislodged. If the force necessary to detach the holdfast exceeded the 2000 g limit of the scale, a 5000 g (100 g precision) spring scale was substituted. The force at dislodgement was recorded in gram-force and converted to Newtons as a measure of attachment strength. This measure of attachment strength most often involved dislodgement of the holdfast from the turf algae with some breakage of the turf, but could also involve dislodgement of turf algae from the rock substrate. In a few cases, the stipe broke before dislodgement when it became evident some haptera were contacting rock and the sample was discarded. Divers collected the dislodged thallus in a mesh bag to measure the holdfast, blade and stipe as described above. Blotted fresh weight of the whole thallus was measured (0.001 precision) as well as blade surface area. Blades were carefully placed between 2 Plexiglas® sheets and photographed, and surface area (cm^2) was measured using ImageJ. Attachment strength of rock-attached *S. latissima* was not measured as the force required to dislodge these holdfasts far exceeded the range of the spring scales, and in our experience, other parts of the thallus typically break before the holdfast can be dislodged.

Manipulative experiment

To test the effect of attachment substrate (turf vs. rock) and degree of wave exposure (exposed vs. sheltered) on the rate of dislodgement of *S. latissima*, we conducted a 2 × 2 factorial experiment at Duncan's Cove over 16 wk (August 24 to December 6). For the attachment substrate treatment, divers collected small boulders with individual kelp thalli attached to either turf algae or rock from a wave-protected site inside the cove at 6–7 m depth. For the wave exposure treatment, divers haphazardly chose and transported boulders with either turf- or rock-attached kelp (10 replicates of each attachment treatment) to a wave-swept channel at the mouth of the cove or to a protected site approximately 250 m inside the cove and 2–3 m shoreward from the site of collection. At each location, 10 replicates of each attachment treatment were randomly assigned to 20 numbered positions, spaced at 1–3 m within a linear array at approximately 5 m depth and affixed to the rock substrate (cleared of turf algae) with marine epoxy (Z-spar A-788 Splash Zone Compound®). Blade surface area of each kelp transplant was measured to relate survival to thallus size across all treatment combinations. The blade was carefully sandwiched between a clear and a blue plastic (Plexiglas®) sheet with 10 cm gradations to provide contrast and scale, and a photograph was taken. Blade surface area was measured using ImageJ. This measurement was repeated at approximately 40 d intervals (August 24; October 5; November 5) and survival of kelp transplants was measured at 2–4 wk intervals (August 24; September 7, 21; October 5, 27; November 15; December 6). The cause of kelp mortality was recorded *in situ* as holdfast dislodgement, breakage at the stipe, or erosion of the kelp blade to below the basal meristem. To relate patterns of survival with the timing of large wave events, we integrated daily average SWH for each interval over the course of the experiment where daily average SWH exceeded 2 m on 1 or more consecutive days (i.e. a wave integral measured in metre-days).

Mensurative experiment

To examine how thallus length and attachment substrate (turf algae vs. rock) affect seasonal losses of kelp (summer through to winter), a 40 wk mensurative experiment was conducted at TL (July 21 to April 24). Kelps were sampled at monthly intervals from July to December 2016 and then in April 2017 from 10 circular plots (2 m diameter) spaced at 5 m intervals (between plot centres) along the 11 m depth contour and delineated by a central eyebolt affixed to the rocky bottom with marine epoxy. Within each plot, divers recorded thallus length of *S. latissima*,

L. digitata, and *A. clathratum* (binned into the 6 size classes as above) and the substrate on which each was attached (turf algae vs. rock). In the last 3 sampling intervals (November 3; December 7; April 24), divers also recorded the number of kelp stipes (without blades) and their attachment substrate.

Statistical analyses

Analyses were performed using R (version 3.3.2) and IBM SPSS Statistics (version 23.0). A 2-way ANOVA was used to test effects of attachment substrate (turf, rock) and site (DC, PH, TL, SC, FP) on holdfast morphological characteristics (holdfast length-to-width ratio, average number of bifurcations per primary hapteron, holdfast-to-total biomass ratio). Both site and substrate were treated as fixed factors. Since the designs were unbalanced due to unequal sampling, we calculated Type III sums of squares. Data on holdfast length-to-width ratio and average number of bifurcations per primary hapteron met the assumptions of normality (Shapiro-Wilk test, $p > 0.05$) and homogeneity of variance (Levene's test, $p > 0.05$). Data on holdfast-to-total biomass ratio were log-transformed to meet the assumption of homogeneity of variance (Levene's test, $p > 0.05$). Where significant main effects were detected, pair-wise comparisons were made using Tukey's HSD tests. Significant interactions were explored by examining simple main effects.

We tested for differences in attachment strength of turf-attached kelps between sites (fixed factor; PH, TL, DC, SC) accounting for the effect of thallus fresh weight (g), a continuous covariate, using ANCOVA. As with morphological measurements, we excluded the few individuals larger than 200 g. Consequently, the values of the covariate were not significantly different between sites (ANOVA: $F_{3,87} = 2.46$, $p = 0.068$). Residual plots indicated adherence to assumptions of normality and homogeneity of variance. Due to a significant interaction between site and thallus fresh weight, indicating non-homogeneous slopes among sites, a straightforward interpretation of adjusted group means was not possible. We opted to proceed with separate comparisons of site means using simple ANOVA within 2 intervals of the covariate range divided by individuals smaller and larger than 40 g, respectively. This grouping roughly corresponds to recruits, juveniles, and small adults (~50 cm or less) and larger adults, respectively. We used a Bonferroni adjustment ($\alpha = 0.025$) to account for multiple testing.

Using the morphological data for kelp thalli collected at DC, we performed a discriminant function analysis with the lda function in the MASS package in R to determine a linear combination of 6 holdfast characteristics of *S. latissima* (holdfast length, average holdfast width, number of primary haptera, average number of bifurcations per primary hapteron, holdfast-to-total biomass ratio, fresh weight of holdfast) that maximized the probability of correctly assigning holdfasts to their known attachment substrate (turf or rock). We classified each holdfast to a substrate based on their characteristics using leave-one-out cross-validation. The misclassification rate was acceptably low for both turf-attached (7.01%) and rock-attached kelp (2.34%). We then used the classification functions (Table S1) to classify drift kelp collected from DC to their likely attachment substrate prior to dislodgement. Assumptions of multivariate normality (based on a multivariate QQ plot), homogeneity of covariance (Box's M, $p > 0.05$), univariate normality (Shapiro-Wilks test, $p > 0.05$), and homogeneity of variance (Levene's test, $p > 0.05$) were met. There was no strong collinearity between the characteristics used as predictors (variance inflation factor < 5).

We fit a Cox proportional hazards regression model, using the coxph function in the Survival package in R, to assess treatment effects on survival of kelp transplants in the manipulative experiment at DC. A model was fit with the main effects of attachment substrate (turf vs. rock), site (wave-exposed vs. wave-protected), and initial blade surface area (as a covariate), along with their interactions as independent variables. A step-down model selection procedure was then used to compare nested models with likelihood ratio tests.

To test whether the interaction between attachment substrate and size class was consistent between sampling times in the mensurative experiment at TL, we fit a generalized linear model (GLM) with Poisson errors and a log link to kelp counts pooled over all plots using the glm function in the MASS package in R. We tested the significance of the 3-way interaction between substrate, size class, and time by comparing the model to a nested model that did not include the interaction term. To test the significance of the kelp substrate and size interaction throughout the experiment (i.e. for non-independence of these categorical variables), we fit separate GLMs for counts at each approximately 2 to 3 mo interval to capture seasonal changes throughout the experiment (summer, autumn, winter). Exceedingly low kelp counts across all size classes and substrate types at the end of the

experiment (April 24, 2017) precluded us from fitting a GLM to those data corresponding to a spring sampling period.

RESULTS

Substrate composition and kelp size distribution by substrate

During June and July, turf algae represented the dominant substrate cover, averaging 97.6% (±1.4% SD) across the 3 sites sampled in St. Margaret's Bay (PH, TL, and FP). *Saccharina latissima* was the predominant kelp species, accounting for 90, 85, and 72% of kelp thalli at PH, TL, and FP, respectively (Table S2 in the Supplement). Fragments of turf algae attached to holdfasts of *S. latissima* sampled at TL, PH, and FP were predominantly coarsely branched and/or filamentous/delicately branched forms; articulated coralline algae were also prominent in samples at DC and SC (Fig. S3). Turf-attached *S. latissima* was predominant in the smaller size classes (<30 cm at PH, <50 cm at FP and TL) with the greatest percentage occurrence (93–100%) in the smallest size class (<10 cm) across all sites (Fig. 2). The percentage of turf-attached *S. latissima* decreased as size increased. Rock-attached kelp was predominant in the larger size classes (>30 cm at PH, >50 cm at FP and TL), and the largest kelps (>100 cm) were exclusively attached to rock (Fig. 2). *S. latissima* sampled at PH were comprised largely of the smallest size class (<10 cm), representing 46.6% of all individuals, while kelp sampled at FP and TL were predominately within the medium size class (50–100 cm), representing 27.8% and 44.3% of individuals, respectively (Fig. 2).

Laminaria digitata was rare or absent at TL and FP and occurred at low density primarily attached to rock at PH (Table S2); only 5 small individuals (median size class, 10–30 cm) were observed on turf. The median size class of *L. digitata* on rock ranged from 10–30 (PH) to 50–100 cm (FP). *Agarum clathratum* occurred at moderate to low densities at all 3 sites, and was also primarily attached to rock (Table S2). All individuals (TL and PH combined) attached to turf were in the smallest size class (<10 cm). The median size class of *A. clathratum* on rock ranged from 10–30 (PH) to 50–100 cm (FP).

Morphological analyses

Holdfasts for turf- and rock-attached *S. latissima* differed in gross morphology, structural complexity, and allocation of biomass (Fig. S4). Holdfast length-

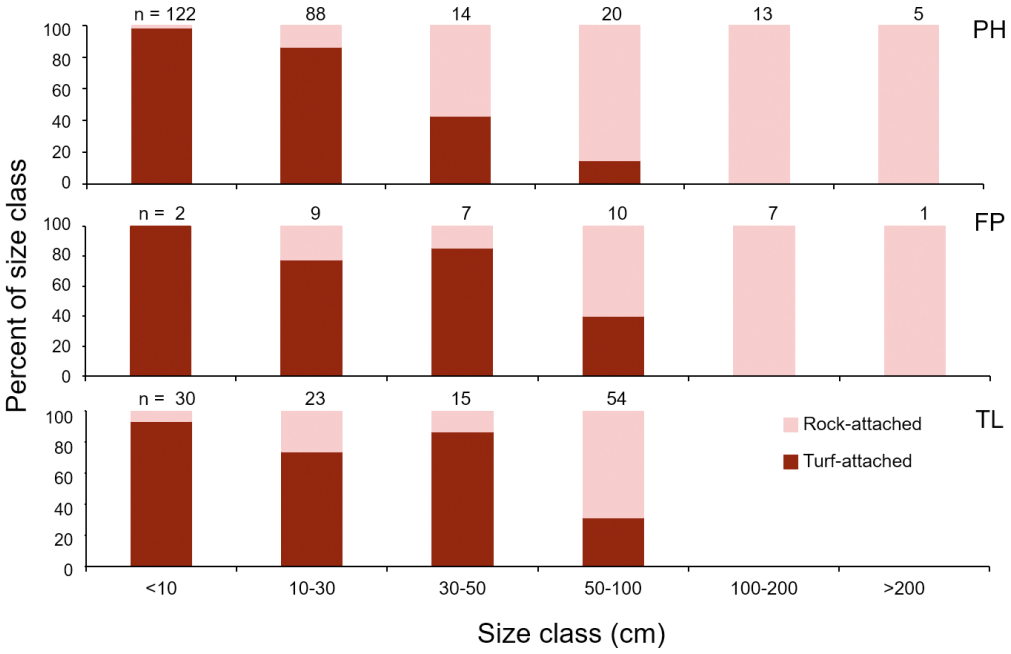

Fig. 2. Occurrence of turf- and rock-attached kelp *Saccharina latissima* in binned size classes (total length: <10, 10–30, 30–50, 50–100, 100–200, >200 cm) from 3 sites (PH, Paddy's Head; FP, Fox Point; TL, The Lodge) in June and July 2016. At time of sampling TL, measurements of kelp >50 cm were placed into a single category. Data are percent of each size class composed of turf- or rock-attached thalli, with the total number of kelp thalli (n) in each size class denoted above the bars

Table 1. ANOVA of effects of attachment substrate (turf vs. rock) and site on kelp (*Saccharina latissima*) holdfast gross morphology, structural complexity, and allocation of biomass at 5 sites (Paddy's Head, Fox Point, Sandy Cove, The Lodge, Duncan's Cove) from June to September 2016. p-values in **bold** are statistically significant

Factor	df	MS	*F*	p
Gross morphology				
Site	4	0.163	0.254	0.907
Substrate	1	49.9	77.9	**<0.001**
Site × Substrate	4	0.211	0.330	0.858
Residual	203	0.641		
Structural complexity				
Site	4	3.33	2.03	0.092
Substrate	1	13.2	8.05	**0.005**
Site × Substrate	4	5.46	3.33	**0.012**
Residual	203	1.64		
Allocation of biomass				
Site	4	6.69	19.4	**<0.001**
Substrate	1	18.9	54.9	**<0.001**
Site × Substrate	4	0.773	2.24	0.066
Residual	203	0.344		

to-width ratio was significantly greater for turf-attached than rock-attached kelp, but the effect of site and the interaction of attachment substrate and site were not significant (Table 1, Fig. 3A). There was a trend for greater holdfast structural complexity (number of bifurcations per primary hapteron) for turf-attached compared to rock-attached kelp (Fig. 3B), but there was a significant interaction between site and substrate (Table 1). Examining the simple effect of substrate at each site indicated that there was a significantly greater average number of bifurcations per primary hapteron on turf-attached compared to rock-attached *S. latissima* at TL, but not at the other sites (TL: $F_{1,203}$ = 12.2, p = 0.001; SC: $F_{1,203}$ = 0.870, p = 0.352; PH: $F_{1,203}$ = 2.32, p = 0.130; FP: $F_{1,203}$ = 0.570, p = 0.451; DC: $F_{1,203}$ = 1.29, p = 0.258). Holdfast-to-total biomass ratio was significantly greater for turf-attached than rock-attached kelp and differed significantly among sites (Fig. 3C; Tukey's HSD test: DC, PH, SC > FP, TL), but the interaction of attachment substrate and site was not significant (Table 1).

Discriminant function analysis based on 6 holdfast morphological characteristics (holdfast length, average holdfast width, number of primary haptera, fresh weight of holdfast, holdfast-to-total biomass ratio, average number of bifurcations per primary hapteron) showed that 16 out of 21 drift kelp samples (76.2%) from DC were likely turf-attached prior to dislodgement.

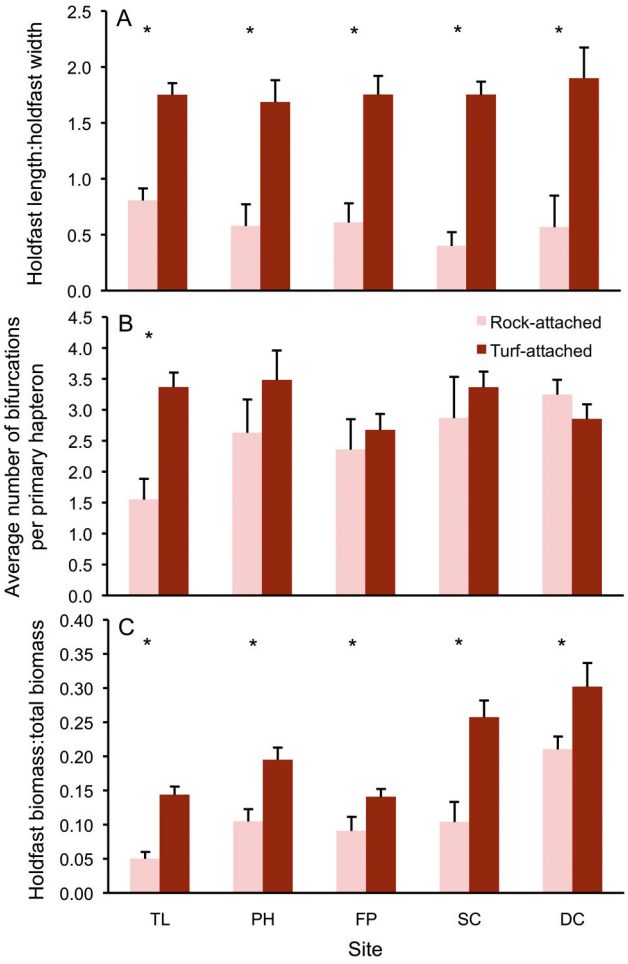

Fig. 3. Holdfast characteristics of turf-attached (n = 140) and rock-attached (n = 73) kelp *Saccharina latissima* collected from 5 sites (TL, The Lodge; PH, Paddy's Head; FP, Fox Point; SC, Sandy Cove; DC, Duncan's Cove) from June to September 2016. (A) Holdfast length-to-width ratio, (B) average number of bifurcations per hapteron, (C) holdfast-to-total biomass ratio. Data are mean + SE. *Significant difference between substrates (Tukey's HSD, α = 0.05)

Attachment strength

The mean (±SD) attachment strength of turf-attached *S. latissima* pooled across the 4 sites sampled (PH, TL, DC, SC) was 10.1 N (±6.4 N; n = 91); 75% of kelp detached at a force ≤14 N. There was a positive but weak relationship between pooled attachment strength and thallus fresh weight (R^2 = 0.06, p = 0.025). However, the slope of this relationship varied between sites (Fig. 4A). While ANCOVA indicated significant differences in attachment strength among sites ($F_{3,83}$ = 11.7, p < 0.001), the significant interaction between site and thallus fresh weight ($F_{3,83}$ = 2.77, p = 0.046) and heterogenous slopes resulted in specific pairwise differences varying along the range of

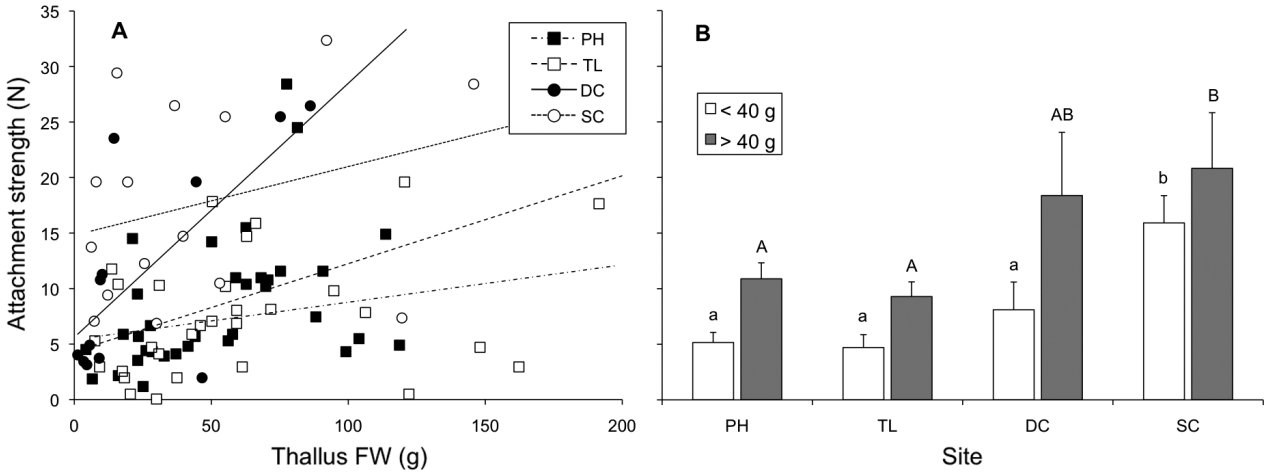

Fig. 4. Attachment strength (N) of turf-attached kelp *Saccharina latissima* collected from 4 sites (PH, Paddy's Head, n = 34; TL, The Lodge, n = 30; DC, Duncan's Cove, n = 12; SC, Sandy Cove, n = 15) from July to August 2016. (A) Plotted against thallus fresh weight (FW, g). (B) Site averages (mean + SE) grouped by individuals <40 and >40 g. Identical letters above bars indicate site means that are not significantly different (Tukey's HSD, α = 0.05). Lower and upper letter cases indicate separate comparisons

thallus weight (Fig. 4). For kelps <40 g, mean attachment strength differed significantly among sites (ANOVA: $F_{3,40} = 9.50$, $p < 0.001$) and was significantly greater at SC (Tukey's HSD: $p < 0.05$) than the other 3 sites (Fig. 4B). For kelps >40 g, mean attachment strength also differed significantly among sites (ANOVA: $F_{3,43} = 4.60$, $p < 0.01$) and was significantly greater at SC (Tukey's HSD: $p < 0.05$) than at TL and PH (Fig. 4B). Attachment strength at DC was intermediate between these groups and did not differ significantly (Tukey's HSD: $p > 0.05$) from the other sites (Fig. 4B). There was no concordance between attachment strength of kelps in each size category and exposure index among these sites.

Manipulative experiment

Turf-attached *S. latissima* in the wave-exposed location at DC experienced some mortality during early autumn following a small peak (2.3 m) in SWH (Figs. S1 & 5). After SWH increased to a higher peak (4 m) in mid-October (Figs. S1 & 5A), survival of rock-attached and turf-attached kelp decreased to 75% and 40%, respectively, in both wave-exposure treatments (Fig. 5B). At the end of the experiment, survival of turf-attached kelp was lower than rock-attached kelp, with a complete loss of turf-attached kelp in the wave-exposed treatment (Fig. 5B). Across locations, mortality for turf-attached kelp was predominately from holdfast dislodgement (56.3%) followed by stipe breakage (37.5%) and erosion of the meristem (6.2%). For rock-attached kelp, mortality was highest for stipe breakage (77.8%), followed by erosion of the meristem and holdfast dislodgement (both at 11.1%). Blade area decreased throughout the experiment in all treatment combinations (Fig. S5). The 2-way ANOVA indicated no significant difference in blade area across all combinations of attachment substrate and location at the beginning (August 24), middle (October 5), or end (November 15) of the experiment (Table S3, Fig. S5).

The Cox proportional hazards model showed a significant effect of attachment substrate on survival of kelp transplants, but no significant effect of location or initial blade surface area or the interactions between substrate type, location, and initial blade surface area (Table 2). The hazard ratio showed the risk of mortality for turf-attached kelp was over 3-fold greater than for rock-attached kelp (hazard ratio = 3.22, $z = 2.418$, $p = 0.016$).

Mensurative experiment

S. latissima represented 90% and *A. clathratum* 10% of the total kelp at TL at the start of our experiment in July 2016. We focused our analysis on *S. latissima* because it was the dominant species and recruited more frequently to turf than *A. clathratum* (Table S2). There was no significant 3-way interaction between substrate, size and time on counts of *S. latissima* in permanently marked plots at TL ($G^2 = 6.17$, df = 10, $p = 0.801$) across seasons in 2016, but the interaction between substrate and size was consistently significant in summer (July 21; $G^2 = 84.2$,

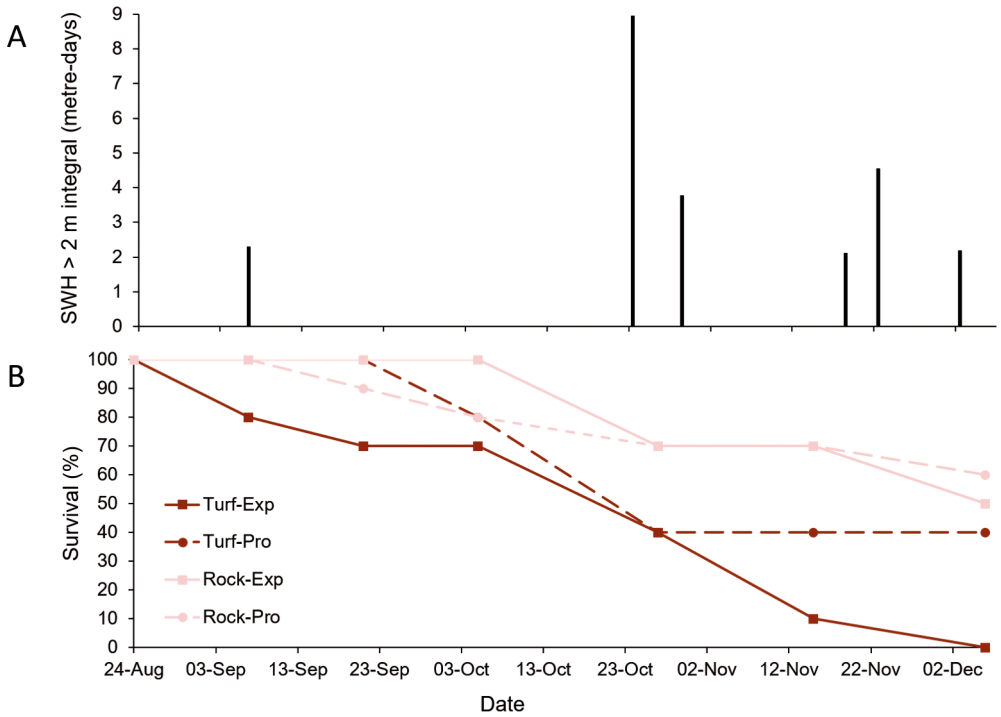

Fig. 5. (A) Integral of significant wave height (SWH) events (metre-days) for records of SWH > 2 m (<9 % of all records), and (B) survival (%) of turf- or rock-attached transplants of *Saccharina latissima* in a wave-protected (Pro) or wave-exposed (Exp) location at Duncan's Cove from August 24 to December 6, 2016

df = 5, $p < 0.001$), autumn (October 4; $G^2 = 65.5$, df = 5, $p < 0.001$), and winter (December 7; $G^2 = 11.8$, df = 5, $p = 0.038$; Fig. 6). During the first 6 wk of the experiment at TL (July 21 to September 9), there was a greater number of turf-attached *S. latissima* in the small to intermediate size classes (<100 cm) and larger kelps were mainly rock-attached (Fig. 6). Kelp density on each substrate type was fairly constant within size classes over this period, indicating minimal loss during summer 2016 when daily mean SWH was relatively low (0.5–1.4 m; Figs. S1 & 6). After periods of heavy swell (3–4 m) in late October, there was a near complete loss of large (>100 cm) rock- and turf-attached kelp by November 3 (Figs. S1 & 6). By December 7, there was a greater loss of turf-attached kelp in the intermediate (50–100 cm) size class compared to rock-attached kelp (Fig. 6). From December 7 to April 24, 2017, daily mean SWH ranged from 0.4–6 m (Fig. S1). Kelp densities were minimal across all size classes and substrate types at the end of the experiment (April 24; Fig. 6). The average number of stipes per plot, indicating breakage that would cul-

Table 2. Step-down variable selection procedure comparing hierarchical Cox proportional hazards models of survival of rock- or turf-attached kelp *Saccharina latissima* with different initial blade surface areas transplanted to wave-protected and wave-exposed locations at Duncan's Cove. Parameters include attachment substrate (A), initial blade surface area (B), location (L), and their interactions. Columns are the specific model comparisons, likelihood ratio (LR) statistics, degrees of freedom, significance, and outcome of the likelihood ratio tests

Comparison	LR	df	p	Result
B + A + L + BA + BL + AL + BAL vs. B + A + L + BA + BL + AL	0.099	1	0.726	Drop BAL
B + A + L + BA + BL + AL vs. B + A + L + BL + AL	0.014	1	0.905	Drop BA
B + A + L + BL + AL vs. B + A + L + AL	0.845	1	0.358	Drop BL
B + A + L + AL vs. B + A + L	2.613	1	0.106	Drop AL
B + A + L vs. A + L	2.015	1	0.156	Drop B
A + L vs. A	1.788	1	0.181	Drop L
A vs. null	6.238	1	0.013	Retain A

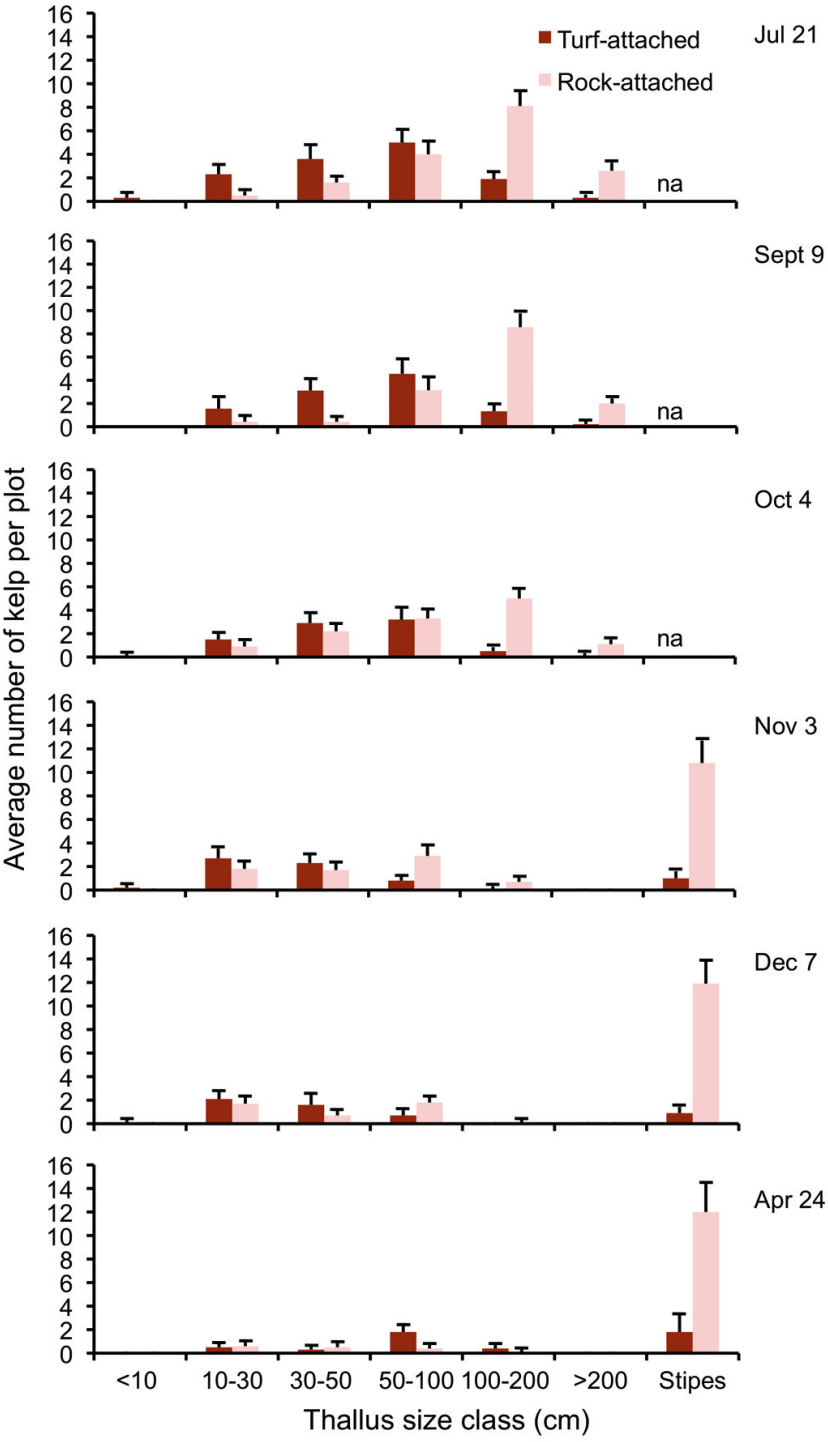

Fig. 6. Number (mean + SE) of turf- and rock-attached kelp *Saccharina latissima* in binned size classes (total length: <10, 10–30, 30–50, 50–100, 100–200, >200 cm) and kelp stipes (without blade tissue) within 10 plots (2 m diameter) at TL on 6 sampling dates from July 2016 to April 2017

minate in thallus death, progressively increased from November 3 (11.8) to April 24 (13.8); 90.4% of these stipes were rock-attached (Fig. 6).

DISCUSSION

Recruitment and persistence of kelp on turf algae and rocky substrates

Previous studies have shown an inhibitory effect of algal turfs and associated sediments on recruitment of kelp sporophytes (e.g. Chapman 1984, Connell & Russell 2010) by blocking spore settlement (Airoldi 2003, Gorman & Connell 2009, Deiman et al. 2012) or creating an inimical microenvironment (reduced light, oxygen, or nutrients) for post-settlement survival of the early life-history stages of kelp (Daly & Mathieson 1977, Devinny & Volse 1978). As far as we are aware, our study is the first to document extensive macroscopic recruitment of kelp sporophytes to filamentous and coarsely branched turf algae in the northwest Atlantic. In Nova Scotia, spore release and settlement of *Saccharina latissima* occurs in autumn (Chapman 1984), when the substrate is predominantly covered by turf algae (J. M. O'Brien pers. obs.), which likely accounts for the high rate of recruitment that we observed on turfs compared to coralline-encrusted rock. Although we found that kelp sporophytes grow to a macroscopic size on turf, as they increase in size their survival is reduced compared to sporophytes attached to rock. Therefore, just as high post-settlement mortality can reverse the distribution of recruits among turf and rock microhabitats expected from settler densities (Benedetti-Cecchi & Cinelli 1992), so too can post-recruitment processes reverse spatial patterns of adult abundance from patterns of recruit densities.

As we predicted, turf-attached kelp was predominately small (<30 cm at PH, <50 cm at FP and TL) while rock-attached kelp represented the majority of the larger kelp size classes. This likely reflects a differential loss by detachment, as hydrodynamic forces acting on a thallus increase with kelp size (Friedland & Denny 1995). Attachment strength is also expected to increase with size for rock-attached kelps (Thomsen et al. 2004). However, we found a very weak relationship between attachment strength

and size for turf-attached kelp, indicating these individuals may be even more vulnerable to dislodgement as they grow. Turf-attached kelps appear to reach a size threshold beyond which the holdfast cannot counteract drag and acceleration forces acting on the thallus. This threshold varies between sites of differing wave exposure, from approximately 30 cm at the most wave-exposed site (PH) to approximately 50 cm at TL and FP.

Variation in holdfast morphology and attachment strength

Phenotypic variation in blade and stipe morphology (plasticity) can increase survival and photosynthesis of kelp and other macroalgae (Gerard 1987, Friedland & Denny 1995, Buck & Buchholz 2005). However, the degree of holdfast plasticity and the adaptive benefit that it may provide remain poorly understood. As we predicted, holdfast morphology differed between turf- and rock-attached holdfasts. Turf-attached holdfasts had a significantly more elongated gross morphology, greater structural complexity (TL only), and greater allocation of biomass to the holdfast than rock-attached holdfasts. Holdfast growth begins in meristematic tissue at the tips of haptera (Novaczek 1981) and proceeds downward due to the negatively phototactic extension of the haptera (Buggeln 1974) and the high specific gravity of the holdfast as a whole (Schiel & Foster 2015). For rock-attached holdfasts contacting hard substrate and spreading outward, the growth pattern is likely governed by the underlying rocky surface, resulting in a short holdfast and small length-to-width ratio. Turf algae raise an attached holdfast above the substrate, and continued downward growth of haptera likely results in a longer holdfast and a greater length-to-width ratio. Similarly, in the absence of contact with the rock substrate, turf-attached holdfasts may continue to branch, leading to a greater average number of bifurcations per primary hapteron, as shown at TL. Continued growth and increased complexity of turf-attached holdfasts likely diverts more energy and resources away from the growth of other structures (Sjøtun et al. 1998, Rodriguez et al. 2016) compared to their rock-attached counterparts.

Increased allocation of biomass to the holdfast has also been documented in wave-exposed locations, where it reduces the risk of dislodgement (Sjøtun & Fredriksen 1995, Roberson & Coyer 2004). Differences in wave exposure may explain the site-specific variation in the allocation of biomass that we observed. Kelp in the more wave-exposed locations (PH, SC, DC) had a greater holdfast-to-total biomass ratio compared to less wave-exposed areas (TL, FP), although this did not necessarily coincide with greater attachment strength of turf-attached individuals (e.g. PH). Site-specific differences in the physical structure or composition of the turf may also have contributed to observed differences in holdfast morphology. For example, greater turf height may result in protracted growth of the haptera, with attendant changes in holdfast height and branching, and biomass accumulation. This may explain the significant interaction of site and substrate observed for the average number of bifurcations per primary hapteron.

In comparison to other kelp species for which attachment properties on rock have been measured, turf-attached *S. latissima* has much weaker attachment strength relative to its size, between 4% and 51% of that measured for rock-attached kelp (Table 3). Rock-attached holdfasts appear to have both physical and chemical attachment properties that enable the holdfast to solidly anchor and extend into interstitial crevices (Tovey & Moss 1978). Attachment strength of kelps on turf may be lower because turfs are typically comprised of thin filaments that can break or have small holdfasts or rhizoids that are readily detached. Paine (1979) showed that *Postelsia palmaeformis* can settle and grow on the calcareous algae *Corallina vancouveriensis*, but becomes dislodged when the articulated joints of the turf break when subjected to heavy wave action. Further, kelp haptera are often loosely entwined in the filaments and branches of turf algae and therefore likely to dislodge even when the turf remains largely intact. These mechanisms of detachment will vary with turf composition. Milligan & DeWreede (2000) showed that attachment strength of the kelp *Hedophyllum sessile* was greater on articulated coralline algae than non-calcareous encrusting red algae. Similarly, differences in the composition of turf algae may have contributed to the site-specific variation in attachment strength in our study. At sites where attachment strength was greater (SC, DC), the turf composition measured from turf in detached holdfasts included a high proportion of articulated coralline algae (*C. officinalis*) relative to delicately and coarsely branched fleshy forms. Despite site-specific variation in attachment, without a solid and stable substrate, there is an increased risk for the dislodgement of turf-attached kelp. At DC, dislodged kelp in depositional areas was predominately classified as formerly turf-attached.

Table 3. Comparison of mean (±SD) attachment strength (N), mean (±SD) thallus fresh weight (FW, g), and mean (±SD) blade surface area (SA, cm^2) where available, and measurement method between turf-attached *Saccharina latissima* in this study and literature records for rock-attached kelp species with similar holdfast morphology. Turf-attached *S. latissima* were collected from 4 sites (Paddy's Head, The Lodge, Duncan's Cove, Sandy Cove) from July to August 2016. n = sample size; ND = no data

Species	Substrate	Method	Attachment strength (N)	n	FW (g)	SA (cm^2)	Source
Saccharina latissima	Turf algae	Spring scale woven through holdfast and pulled perpendicular to substrate until dislodgement	10.1 (6.4)	91	50.7 (39.3)	707.6 (436.2)	This study
Laminaria setchellii	Rock	Spring scale clamped around stipe and pulled parallel to substrate until dislodgement	262.9 (113.5)	76	ND	486.9 (191.8)	Boizard (2007)
Agarum fimbriatum	Rock	Spring scale clamped around stipe and pulled perpendicular to substrate until dislodgement	23.4 (12.2)	120	97.5 (74.0)	ND	Duggins et al. (2003)
Costaria costata	Rock	Spring scale clamped around stipe and pulled perpendicular to substrate until dislodgement	26.2 (14.7)	104	72.2 (55.8)	ND	Duggins et al. (2003)
Laminaria japonica	Rock	String attached to spring scale, secured around stipe, and pulled parallel to substrate until dislodgement	19.9 (7.5)	10	192.7 (ND)	896.0 (320.2)	Kawamata (2001)
Ecklonia radiata	Rock	Nylon webbing attached to spring scale, secured around stipe, and pulled 30° to substrate until dislodgement	161.5 (50.1)	19	862.9 (663.9)	ND	Thomsen et al. (2004)
Ecklonia radiata	Limestone	Nylon webbing attached to spring scale, secured around stipe, and pulled 30° to substrate until dislodgement	162.5 (56.2)	19	831.5 (5996)	ND	Wernberg (2005)
Hedophyllum sessile	Rock	Spring scale clamped at base of blade and pulled parallel to substrate until dislodgement	84.4 (53.5)	34	ND	992.0 (629.5)	Milligan & DeWreede (2000)

Dislodgement and survival of kelp

Our manipulative transplant experiment supported the prediction that attachment substrate is a significant predictor of kelp mortality, with rock-attached kelp having a 68.9% reduced risk of mortality compared to turf-attached kelp. Early loss of kelp in the turf-attached and wave-exposed treatment is attributed to a minor wave event that removed weakly attached individuals (perhaps due to handling), selecting for the individuals with a higher wave dislodgement threshold at the onset of the experiment (see also Lee et al. 2004). As the hydrodynamic forces acting on the transplanted kelps increased with SWH in autumn, individuals with a higher threshold were lost and survival in all treatments decreased, eventually leading to the complete loss of turf-attached kelp in the exposed treatment.

Although attachment substrate was a significant predictor of kelp mortality, our results did not support the prediction that transplant survival would be reduced at the more wave-exposed location or affected by initial blade surface area. This can be explained in part by wave direction during the periods of greatest wave activity. The wave-protected site is only exposed to waves from the east. The periods of highest SWH during the study had a large easterly component, increasing wave forces and associated hydrodynamic drag at the more often wave-protected site. As the initial blade surface area of kelp transplants was similar in both locations, it is likely that the drag force acting on thalli would have been comparable. Furthermore, the individuals used in the experiment were collected from a wave-protected site at a greater depth (~7 m) than the depth to which they were transplanted (5 m). Therefore, their blade morphology and attachment strength may have been adapted to lower water movement (Gerard 1987, Buck & Buchholz 2005). Morphological features that were advantageous at the collection site may be maladaptive at the shallower depths of both the wave-protected and exposed treatments, which experience greater hydrodynamic forces. For example, large blades provide a greater surface area for photosynthesis in areas of low wave exposure (Gerard & Mann 1979), but a greater thallus size also can lead to greater drag forces in areas of high water movement that increase dislodgement.

The mensurative field experiment failed to support the prediction that the losses would be predominantly of turf-attached kelp in the largest size classes. Loss of turf-attached kelp occurred among all size classes and was accompanied by the loss of large rock-attached kelp. At the onset, there was more rock-attached kelp in the larger size classes and more turf-attached kelp in the smaller size classes. During periods of low SWH, there was a minimal loss of kelp. As the SWH increased there were increased losses of the largest size classes for both turf- and rock-attached kelp. However, the interaction between substrate and size class was consistent from June to December 2016, with smaller kelp being turf-attached and larger kelp rock-attached. By December, there was a greater loss of turf-attached than rock-attached kelp in the intermediate size class (50–100 cm), which is consistent with the apparent size threshold of turf-attached kelp determined in surveys carried out earlier in the summer. At the end of the experiment in April 2017, there were few remaining kelps in all size classes, with a complete loss of the smallest and largest individuals.

Our results suggest that drag and acceleration forces acting on the kelp thalli are the major cause of kelp loss. These hydrodynamic forces must be counteracted by a strong and stable attachment site to prevent dislodgement (Milligan & DeWreede 2000). For turf-attached kelp, the lack of such an attachment site increased the likelihood of dislodgement with increases during peak SWH in autumn and winter. Large turf-attached kelp would have experienced greater drag and acceleration forces as a result of a larger blade surface area (Friedland & Denny 1995). Consequently, there was an increased loss of large turf-attached kelp (>50 cm) compared to the smaller turf-attached kelp (<50 cm) that may have had a size refuge from wave dislodgement. Increasing wave forces may have led to holdfast loosening of rock-attached kelps as individual haptera became detached from their substrate, eventually causing holdfast failure (Dayton et al. 1984). However, hydrodynamic forces leading to holdfast dislodgement were likely not a major source of loss in rock-attached kelp, as suggested by the abundance of rock-attached stipes. Other studies have shown that kelps growing on more stable substrates are more likely to fracture at other parts of the thallus (Thomsen et al. 2004).

Loss of kelp in response to hydrodynamic forces can occur by mechanisms beyond holdfast dislodgement. Mortality can also occur by stipe breakage (Duggins et al. 2001) and erosion of the intercalary meristem (Johnson & Mann 1988), both of which can be exacerbated by the combined impacts of multiple stressors acting on kelp thalli. Daily mean SST during peak months (August–October) were higher in 2016 (Fig. S1; 16.5°C at surface; 13.8°C at 12 m depth) than the long-term average from 1980 – 2012 (13.8°C at surface; Scheibling et al. 2013). Peak SST during the experiment approached and exceeded the optimal growth range of *S. latissima* (10–15°C; Bolton & Lüning 1982, Simonson et al. 2015) and thresholds for tissue degradation (14°C) and loss (18–21°C; Simonson et al. 2015). Warm temperatures also increase settlement and growth of the invasive bryozoan *Membranipora membranacea*, which encrusts, weakens, and causes fragmentation of kelp blades (Saunders & Metaxas 2009, Scheibling & Gagnon 2009). Furthermore, *M. membranacea* has a settlement affinity to new tissue adjacent to the basal meristem (Brumbaugh et al. 1994, Denley et al. 2014), which may increase the likelihood of erosion of the meristem as the colony grows towards the stipe (Ryland & Stebbing 1971). The combined effects of increasing temperatures late in the summer and encrustation by *M. membranacea*, coupled with increased wave activity in the autumn, likely caused the considerable loss of blade tissue of the large rock-attached kelps, such that only bare stipes remained. The loss of meristematic tissue at the base of a kelp blade results in the degeneration of the stipe and holdfast, and removal from the population (Kennelly 1987).

CONCLUSIONS

Loss of canopy-forming algae and the replacement by turf algae is increasingly reported globally, and stabilized by various feedbacks (Filbee-Dexter & Wernberg 2018). Once established, turf algae can physically inhibit settlement of kelp spores by entrapping sediment (Airoldi 2003, Gorman & Connell 2009, Deiman et al. 2012) and reducing the availability of coralline-covered rock upon which kelp spores normally settle (Norton & Fetter 1981, Kennelly 1987). Some species of turf algae may also chemically alter the substrate, preventing settlement of kelp spores even after the turf is removed (Kennelly 1987). The turf-algal state can be further reinforced through intensified grazing of remaining kelp blades following defoliation events (Bennett et al. 2015, O'Brien et al. 2015) and kelp propagule supply-side limitations (O'Brien & Scheibling 2016).

We have demonstrated that kelp *Saccharina latissima* can recruit to turf algae, and that the holdfast

morphology of these individuals differs from rock-attached kelps. However, poor attachment properties lead to increased dislodgement, particularly during autumn and winter storms, which may create yet another feedback that perpetuates the turf-algal state. The only individuals in our mensurative experiment that were observed to develop a sorus (spore-bearing tissue on the blade) were rock-attached. Because turf-attached kelp are small, short-lived, and unlikely to reproduce, there is little chance of population recovery and formation of adult canopy that could outcompete turf through overgrowth and shading (Kennelly 1989, Clark et al. 2004). Our findings indicate that turf-attached kelp do not substantially contribute to the biomass or re-establishment of kelp beds in Nova Scotia, providing further evidence of the resilience of the novel, and potentially less desirable, turf-dominated state of the rocky subtidal ecosystem along the Atlantic coast.

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