



Mesograzer interactions with a unique strain of Irish moss *Chondrus crispus*: colonization, feeding, and algal condition-related effects

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ABSTRACT: Marine macroalgae are exposed to multiple sources of stress. As a result, perennial macroalga habitats have become depleted in many coastlines. Here, we investigated the role of mesograzers in the sharp decline of a unique strain of *Chondrus crispus* (the giant Irish moss) found solely in a lagoon in Atlantic Canada. This study was prompted by damage resembling grazing scars that appeared on the fronds as the population declined, for which no grazer had been identified. We identified potential grazers of the seaweed by deploying 4 types of experimental clumps of giant Irish moss and sampling the epifauna that colonized them. Laboratory assays were then run with an abundant species, the amphipod *Gammarus oceanicus*, to measure feeding rates and test whether this mesograzer is capable of consuming the alga and creating measurable damage. *G. oceanicus* readily consumed the Irish moss at a grazing rate of 5.24 mg amphipod⁻¹ d⁻¹ and created deep lateral grazing wounds similar to those observed in the field. An additional experiment was conducted to assess whether a co-acting stressor in the lagoon, the accumulation of fine sediments, could explain the appearance and spatially patchy distribution of the damage in the population. Giant Irish moss fronds that had been buried under sediment lost twice as much biomass as those that had not. These results suggest that grazer activity and declining conditions in the lagoon have a negative and additive effect on this unique strain of Irish moss, with clear implications for its restoration.

KEY WORDS: Mesograzers · Giant Irish moss · Colonization · Algal condition · Restoration

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1. INTRODUCTION

Marine macroalgae play foundation roles in trophic webs (Ellison et al. 2005), and provide habitat, food, and shelter for other organisms (Dayton 1985, Bégin et al. 2004). They are also harvested for commercial purposes (Zemke-White & Ohno 1999) or can be of interest due to their uniqueness in a given region or concerns regarding their conservation status (Bracken & Low 2012, Smale et al. 2013). With exposure to multiple stressors (e.g. warming, nutrient inputs, physical disruption, and invasions; Ellison

et al. 2005, Harley et al. 2012), the conservation of these algae is challenging, and protective measures are often not fully effective (see review by Gleason et al. 2006). As a result, perennial macroalgal habitats have declined in many coastal areas (Kautsky et al. 1986, Wahl et al. 2015). This has been the case for a unique strain of Irish moss *Chondrus crispus* which grows at a single location (Basin Head lagoon, Prince Edward Island, Atlantic Canada) and has been protected under the Oceans Act (DFO 2009) since 2005. Referred to as 'giant Irish moss' because of its unusually broad fronds, this strain differs from typical

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open-coast Irish moss in its vegetative life cycle, reproducing solely through fragmentation of the thalli (Tummon Flynn et al. 2018). This strain also differs in its attachment method as it lacks a holdfast and is reliant on its co-occurrence with blue mussels *Mytilus edulis*, which anchor its fronds to the seafloor with byssal threads. Despite conservation measures, the giant Irish moss population went into sharp decline in 2000 (Sharp et al. 2010) and was almost lost by 2013 (<2 m² remaining; Tummon Flynn et al. 2019).

Several stressors may have contributed to the collapse of giant Irish moss. These include poor water quality due to nutrient inputs (Sharp et al. 2010), the European green crab *Carcinus maenas* invasion (Tummon Flynn et al. 2019), Irish moss harvesting between 1977 and 2000 (Sharp et al. 2003), and the accumulation of fine sediments on the lagoon floor (DFO 2020). No single stressor has yet fully explained the decline, and it is suspected that multiple interacting factors are at play. An additional potential causative agent is a change in herbivore pressure, as the decline of giant Irish moss biomass was accompanied by a change in appearance suggestive of grazing damage, with the fronds becoming ragged and the apices damaged (Sharp et al. 2010). Similar changes in algal condition have been observed more recently (2016–2018) when tank-cultivated giant Irish moss was introduced to bolster the population (I. Novaczek pers. comm.).

It is well established that herbivores are capable of controlling algal biomass (Lubchenco 1978) and altering plant fitness and performance (Toth et al. 2007). Extensive collapses of macroalgal beds are usually attributed to outbreaks of large mobile grazers (e.g. sea urchins). As large grazers are not abundant in the Basin Head lagoon, the activity of smaller mobile herbivores, termed mesograzers (*sensu* Hay et al. 1987, Brawley 1992), comes to the forefront. Despite their small per capita effects, mesograzers occur in large numbers and can also affect benthic algal populations under certain circumstances (Arntes 1990, Gutow et al. 2020). The susceptibility of macroalgae to grazing is known to be altered by other stressors (e.g. desiccation and ultraviolet radiation; Renaud et al. 1990, Cronin & Hay 1996) that cause changes in seaweed attractiveness (e.g. nutrient content) or deterrent features (e.g. chemical defenses and toughness) (Van Alstyne 1989, Renaud et al. 1990, Pavia et al. 1999). The interaction of these stressors with herbivory can have additive or synergistic negative impacts on seaweed fitness and survival (Renaud et al. 1990, Cronin & Hay 1996).

Until now, efforts to explore the possible role of herbivory in the decline of giant Irish moss have been stalled, as no local species has been identified to have an appetite for this tough, unpalatable alga (Lubchenco 1978). Experiments with one of the most abundant grazers in the area, the periwinkle *Littorina littorea*, showed no effect on giant Irish moss biomass (Vandermeulen 2009). Similarly, the non-indigenous omnivorous green crab, whose invasion in the area coincided with the beginning of the giant Irish moss decline (Poirier et al. 2017), has been found to have a negligible consumptive impact on this strain (Tummon Flynn et al. 2019). The identification of alternative grazer species is therefore a logical next step in unravelling the causes of the giant Irish moss decline. Composition and abundance of mesograzers that associate with the giant Irish moss were documented, and their potential impact was evaluated through laboratory experiments using the most abundant species to test 3 hypotheses: (1) mesograzer feeding activity reduces algal biomass, (2) their feeding activity causes wounds and alters the condition of the fronds, and (3) mesograzer effects can be mediated by localized stress from heavy sedimentation in the lagoon. These hypotheses are rooted in previous evidence of grazing wounds in wild and cultivated giant Irish moss fronds and the decline in habitat quality experienced in the lagoon since the 1980s (Sharp et al. 2010).

2. MATERIALS AND METHODS

2.1. Epifauna colonization and mesograzer identification

Field manipulations were conducted near the location of the natural giant Irish moss bed in the Basin Head Marine Protected Area (MPA), a shallow lagoon system located in eastern Prince Edward Island, Atlantic Canada (Fig. 1; details in Tummon Flynn et al. 2019). The lagoon is characterized by soft bottoms and scattered beds of clams surrounded by salt marshes. To identify potential grazers of giant Irish moss, epifauna that colonize giant Irish moss were sampled using experimental clumps that were set out in Basin Head's Northeast Arm (Fig. 1; 46° 23' 25" N, 62° 6' 5.55" W). To avoid disturbing the remaining natural giant Irish moss population and to standardize clump size, experimental clumps were made using giant Irish moss grown in tank culture at the National Research Council (NRC) facilities in Sandy Cove, Nova Scotia, from fronds originally col-

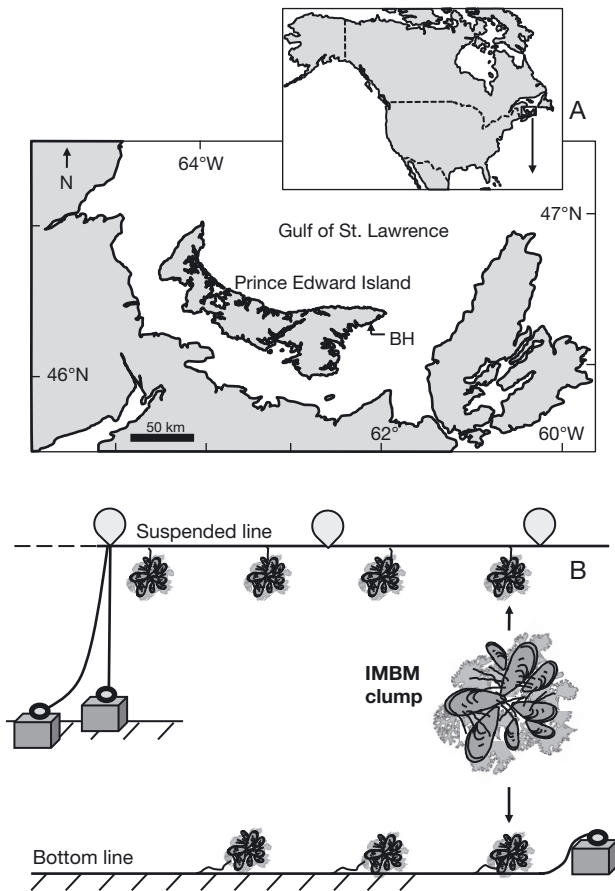


Fig. 1. (A) Location of Prince Edward Island in Atlantic Canada and the approximate location of Basin Head lagoon (BH). (B) Placement of giant Irish moss–blue mussel (IMBM) clumps in the water column and the bottom of BH. Other treatments included IM alone in the water column and bottom but are not portrayed in this figure

lected in Basin Head in 2008 (I. Novaczek pers. comm.). Four types of experimental clumps were created to sample associated epifauna: (1) seaweed with mussels on bottom lines, (2) seaweed with mussels on floating lines, (3) seaweed on its own on bottom lines, and (4) seaweed on its own on floating lines. Two of these treatments are illustrated in Fig. 1.

Giant Irish moss was shipped to Basin Head in May 2017 and hung on floating cultivation lines to grow and acclimate to Basin Head waters before experiments began. In late July 2017, the seaweed was retrieved, rinsed with seawater, cleared of any epibionts by gently scrubbing with fingertips, and spun in a salad spinner for 30 s before it was weighed and divided into clumps of ~50 g. Fronds showing signs of grazing were not used to make up clumps. Individual clumps were placed into plastic mussel socking (2 × 2 cm mesh size) to create ~15 cm diameter clumps,

similar in size to the remaining natural clumps recorded in the study area in 2015 (Tummon Flynn et al. 2019). Two 8 m longlines, one suspended in the water column and the other sunk to the lagoon seafloor, were maintained with buoys and concrete weights in waters ~1.0–1.5 m deep (Fig. 1). Clumps were hung at 0.5 m intervals along these lines. Suspended socks hung in the water column ~10 cm below the surface whereas those on the bottom line rested on the lagoon floor. For clumps including blue mussels, 10 large mussels (4–7 cm shell length, SL) were placed in the mussel socking with the seaweed to mimic natural clumps. Mussels were obtained from a private aquaculture lease in Tracadie Bay, Prince Edward Island (~50 km away), and were pre-treated with a 24 h freshwater bath, following Department of Fisheries and Oceans protocols to prevent the spread of invasive species. The mussels were also acclimatized to Basin Head waters for several weeks prior to placing them into mussel socking with the giant Irish moss. Within a few days, these mussels grew byssal threads attaching to the giant Irish moss, creating distinct seaweed–mussel clumps within the socking.

Experimental clumps made with NRC giant Irish moss were deployed for 2 wk, which was deemed enough time to allow colonization by mobile organisms based on studies of seaweed colonization (Virnstein & Curran 1986, Pavia et al. 1999) and observations in the study area. The first of two 14 d deployments (27 July to 10 August 2017) included Irish moss clumps suspended and resting on the seafloor (hereafter IM suspended and IM bottom, respectively). These treatments simulated conditions in which the seaweed is held in Basin Head during ongoing restoration efforts. The second 14 d deployment (10–24 August 2017) involved clumps made of a combination of Irish moss and blue mussels that were either suspended or deployed on the seafloor (IMBM suspended and bottom, respectively). Before deployment on the seafloor, the IMBM clumps were kept in mussel socking, allowing the mussels to grow byssal threads to knit to the seaweed. The staggered deployment of these 2 sets of treatments enabled us to preserve line placement in the narrow lagoon, keeping variables associated with site constant between treatments, including water depth, sediment firmness, and proximity to other habitats, including other cultivation lines where Irish moss used for restoration was being grown (see Virnstein & Curran 1986). The staggering of line deployments was not expected to bias colonization as they were both set out in late summer when no new settlement events

have been observed in the area. Replication level for each clump treatment was 15 (Table 1).

Upon retrieval (10 and 24 August), clumps were bagged underwater to prevent loss of organisms and then cut from the line. In the laboratory, samples were rinsed through a 500 μm sieve, and all retained organisms were preserved in 70% ethanol for subsequent sorting, identification, and counting. Identification used standard keys for the region (e.g. Brunel et al. 1998, Pollock 1998). Mussel survival was recorded at the end of the 14 d, with no substantial mussel mortality recorded in any of the 2 clump treatments made with mussels (on average <0.4 mussels treatment⁻¹ died).

2.2. Collection of experimental organisms for laboratory assays

The amphipod *Gammarus oceanicus* was chosen as a model (abundant) species to study the meso-grazer effects based on the results of the giant Irish moss colonization study (found abundantly in all clump treatments; see Section 3.1), historic fauna data from Basin Head (McCurdy 1979, Sharp et al. 2003), field observations, and literature indicating they feed on desiccant resistant macroalgae (Shacklock & Croft 1981). Adult *G. oceanicus* (9.28–13.32 mm length, measured alive in the natural curled position from the rostrum to the rear edge of telson) were collected by vigorously shaking socks of NRC-cultured giant Irish moss hanging on cultivation lines into 1 mm mesh sieve buckets. Giant Irish moss was obtained from the same lines. Amphipods

and seaweeds were collected 1 d before the beginning of the experiments and were transported to the laboratory within 2 h of collection. Seaweeds were kept in closed bags in a cooler with ice to prevent desiccation while amphipods were maintained in aquarium tanks filled with prepared seawater (Instant Ocean® Sea Salt, ~25 ppt, 18–20°C), an airstone, and exposed to a 12 h light:12 h dark cycle. Amphipods were starved 24 h prior to the beginning of experiments to standardize hunger levels (Beer-mann et al. 2018). Any visible epibionts (e.g. bryozoans) were gently scrubbed off the seaweed before it was used in experiments (previous use of this protocol caused no visible damage to Irish moss blades; Tummon Flynn et al. 2019)

2.3. Amphipod feeding rates

Laboratory assays were run between August and October 2017 to measure amphipod herbivory on the giant Irish moss (replication levels are summarized in Table 1). Amphipod grazing rates were quantified in 48 h trials run in 1 l plastic containers holding ~700 ml of prepared seawater. Each container held a ~50 mg piece of apical giant Irish moss tissue and 2 amphipods (grazing rates were standardized to mg of seaweed amphipod⁻¹ d⁻¹). Each replicate was paired with a control containing a piece of seaweed from the same frond but without grazers (Roa 1992). Seaweed pieces and their controls were gently blotted dry with paper towel and weighed pre- and post-assay on a 0.001 g accuracy balance. To compare amphipod treatments to controls, the change in biomass was determined for each trial by subtracting the final weight of each experimental

Table 1. Types of experiments, treatments, and their corresponding replication levels. Field experiments were conducted in 2 consecutive sets: from 27 July to 10 August 2017 (Irish moss [IM] treatments) and from 10–24 August 2017 (Irish moss–blue mussel [IMBM] treatments)

Type of experiment	Treatments	Replications
Field: clump colonization experiment	IM suspended	15
	IM bottom	15
	IMBM suspended	15
	IMBM bottom	15
Lab: grazing rates by amphipods	Amphipods	12
	Controls	12
Lab: effects on Irish moss condition index	Amphipods	15
	Controls	16
Lab: grazing rates and Irish moss health	Amphipods–healthy IM	15
	Control–healthy IM	16
	Amphipods–stressed IM	10
	Control–stressed IM	9

alga from the initial. To eliminate weight changes not related to grazing, a precise consumption rate of each assayed seaweed was calculated as rate of consumption = $G_f \times (C_f / C_i) - G_i$, where G and C represent the wet mass of Irish moss tissues and their paired controls, respectively, and the subscripts i and f represent measurements taken at the beginning and end of the experiment (see Yun & Molis 2012; equation adapted from Cronin & Hay 1996). To further verify that reductions in seaweed tissue weight were due to grazing, the presence of fecal matter in each replicate was recorded at the end of the experiments.

2.4. Seaweed condition

A second laboratory experiment investigated whether gammarids create noticeable grazing wounds on giant Irish moss fronds. One week feeding assays were run with fronds of giant Irish moss (~2 g wet weight, patted dry with paper towel) exposed or not (controls) to a standard number of amphipods (20 tank⁻¹). Replication numbers are summarized in Table 1. Water tank conditions were as described above, and the fronds were weighed down to the bottom of the tank with a small rock. A condition index (CI) adapted from the one developed by Sharp et al. (2010) (see also Tummon Flynn et al. 2019) was used to evaluate the condition of the fronds at the beginning and end of this experiment. Ten haphazardly chosen blades of each frond (typically 15–20 blades frond⁻¹) were inspected for visual evidence of grazing damage. Each blade was given a value of 1 (= intact) or 0 (= with evidence of grazing damage) and summed to estimate a CI in a 0–10 scale. Change in CI was used as a proxy of grazing damage and was calculated by subtracting the pre- and post-assay CI for each experimental alga. Only fronds with a pre-assay CI of ≥ 7 were used. Amphipods that died during the experiment were not replaced but the number of live amphipods in each replicate was checked at the termination of the experiment. For this, as well as all other assays, amphipod survival by the end of the experiment was consistently high (median survival = 18 out of 20). Presence of fecal matter in the tanks was also recorded to verify that decline in seaweed condition was due to grazing.

2.5. Impact of sedimentation on loss of biomass

An additional experiment was conducted to assess the influence of sedimentation stress on the loss of seaweed biomass during amphipod feeding. Methodology similar to the one described above was used to test for grazer effects, but for both healthy and sedimentation-stressed giant Irish moss. Healthy giant Irish moss was taken from the cultivation lines in Basin Head where the seaweeds grew without evidence of stress: they were deep red in colour, showed new tissue growth in the tips (Sharp et al. 2010) and normal measurements of photosynthetic efficiency (Tummon Flynn et al. 2018). In addition, the CI described above was also used to check for signs of stress, including necrosis or herbivory (median of 0 blades had evidence of either). A subset of healthy

fronds was placed in plastic mesh bags that were pegged into the subtidal sediment of Basin Head's Northeast Arm. Bags were covered in ~2–3 cm of fine surface sediments and left for 1 wk. This treatment simulated the conditions that natural and planted clumps endure during part of the spring/summer season, as a result of high sedimentation in some sites of the study area (DFO 2020). Tanks containing 2 g pieces of giant Irish moss were maintained without grazers (controls) or exposed to 20 amphipods tank⁻¹. Loss of biomass was estimated as the difference between final and initial wet mass for each tank. Replication levels are summarized in Table 1.

2.6. Statistical analyses

2.6.1. Epifauna colonization and mesograzer identification

Species composition and abundance of all the organisms colonizing the giant Irish moss clumps were documented to identify potential grazers of the alga. Non-metric multi-dimensional scaling (nMDS) plots based on Bray-Curtis similarities were then generated to visually inspect potential differences among the assemblages associated with each treatment. Data were fourth-root transformed to reduce the dominance of the most abundant species. The goodness of fit of the nMDS plots was assessed using the nMDS stress value; values < 0.2 were considered satisfactory representations of the actual differences among samples (Clarke et al. 2014). ANOSIM was then applied to assess the significance of the difference among assemblages associated with each type of clump. Additionally, SIMPER analysis was used to identify which species contributed the most to the dissimilarity between clump types. The nMDS, ANOSIM and SIMPER analyses were conducted using PRIMER 6 routines (Clarke et al. 2014). Replication levels for these and subsequent analyses are summarized in Table 1. The densities of the 4 most abundant mesograzer taxa (*G. oceanicus*, *G. mucronatus*, *G. lawrencianus*, and a species of the genus *Corophium*; see Section 3.1) were then compared among treatments using 4 separate 1-way ANOVAs, followed by Tukey's post hoc tests (these and subsequent analyses were done with Minitab® 18; Minitab). The data in these and subsequent analyses were tested for normality using Anderson-Darling normality test and for equal variance using Levene's test. In cases where assumptions were not met, the data were square-root, fifth-root, or ln transformed.

2.6.2. Amphipod feeding rates, seaweed condition, and impact of sedimentation

To assess differences in consumption rates, a 2-sample *t*-test was used to compare amphipod to control treatments. Due to normality assumption violations, a non-parametric Mann-Whitney *U*-test was used to compare the change in CI of fronds exposed to amphipod and control treatments. For the analysis of sedimentation effects on loss of biomass during grazing activity, data were ln transformed, and a 2-way ANOVA was performed to assess differences between weight changes due to grazing (amphipods versus control) and due to the condition of the seaweed (healthy versus stressed). Non-parametric Mann-Whitney *U*-tests were also used to assess between-treatment differences in amphipod survival.

3. RESULTS

3.1. Epifauna colonization and mesograzer identification

A total of 11 741 individuals representing 31 taxa colonized the giant Irish moss clumps (Table 2). Five species of mesograzers accounted for 96.5% of all collected invertebrates. Gammarid and corophiid amphipods were consistently the most abundant taxa, with 4 taxa of mesograzers making up 91.5% of all organisms found: *Gammarus oceanicus* (30.6%), *G. mucronatus* (14.1%), *G. lawrencianus* (19.9%), and *Corophium* spp. (26.9%). The 3 gammarid species are well-known macroalgal grazers whereas corophiid amphipods are generally considered deposit feeders that consume microalgae. Gas-

Table 2. Mean (\pm SE) abundance of associated fauna per ~50 g algal wet mass in 4 treatments deployed in Basin Head. IM: giant Irish moss; IMBM: giant Irish moss combined with mussels. A: amphipod; I: isopod; G: gastropod; D: decapod; P: polychaete; B: bivalve; (*) macroalgal grazers, based on Geiselman (1980), Hawkins (1983), Watson & Norton (1987), Norton et al. (1990), Pavia et al. (1999), Kelly et al. (2002), and Chenelot & Konar (2007)

Taxon	IM suspended	IM bottom	IMBM suspended	IMBM bottom
<i>Gammarus oceanicus</i> (A)*	60.50 \pm 6.89	39.70 \pm 6.41	44.10 \pm 3.94	95.60 \pm 7.75
<i>Gammarus mucronatus</i> (A)*	47.10 \pm 6.52	4.70 \pm 1.20	41.90 \pm 6.53	16.70 \pm 4.57
<i>Gammarus lawrencianus</i> (A)*	84.80 \pm 14.45	36.60 \pm 9.26	18.90 \pm 4.60	15.10 \pm 6.30
<i>Corophium</i> spp. (A)	35.30 \pm 10.07	5.40 \pm 1.10	117.70 \pm 17.73	52.50 \pm 5.72
<i>Unciola serrata</i> (A)	0	0	1.40 \pm 0.56	0.07 \pm 0.07
<i>Caprella linearis</i> (A)	0.60 \pm 0.25	0.07 \pm 0.07	1.13 \pm 0.45	0.07 \pm 0.07
<i>Paracaprella tenuis</i> (A)	2.60 \pm 0.80	0.13 \pm 0.09	2.80 \pm 0.95	0.07 \pm 0.07
<i>Jaera marina</i> (I)	0.07 \pm 0.07	0.67 \pm 0.27	0.07 \pm 0.07	1.13 \pm 0.41
<i>Idotea balthica</i> (I)*	0	0.07 \pm 0.07	0.07 \pm 0.07	0
<i>Idotea phosphorea</i> (I)*	0	0	0.33 \pm 0.19	0
<i>Littorina obtusata</i> (G)*	0	2.40 \pm 1.20	0	0
<i>Littorina littorea</i> (G)*	0.40 \pm 0.24	36.00 \pm 7.70	0.20 \pm 0.20	1.87 \pm 0.49
<i>Lacuna vincta</i> (G)*	0	0.13 \pm 0.09	0	0
<i>B. totteni</i> (<i>Boonea bisuturalis</i>) (G)	0	0	1.27 \pm 0.30	0.67 \pm 0.23
<i>Neptunea decemcostata</i> (G)	0	0	0.80 \pm 0.24	1.53 \pm 0.43
<i>Nassarius trivittatus</i> (G)	0	0	0.07 \pm 0.07	0
Hydrobiidae (G)	0	0.07 \pm 0.07	0	0
<i>Carcinus maenas</i> (D)	0.14 \pm 0.09	0.07 \pm 0.07	0	0
<i>Cancer irroratus</i> (D)	1.00 \pm 0.41	0.40 \pm 0.19	0.07 \pm 0.07	0.93 \pm 0.33
<i>Panopeus herbstii</i> (D)	0 \pm 0	0.73 \pm 0.15	0	0.47 \pm 0.13
Nereidae (P)	0.60 \pm 0.24	0.27 \pm 0.15	0.93 \pm 0.32	0.13 \pm 0.13
<i>Harmathoe extenuata</i> (P)	0	0.27 \pm 0.18	0.07 \pm 0.07	1.27 \pm 0.25
<i>Harmathoe imbricata</i> (P)	0	0.07 \pm 0.07	0.13 \pm 0.13	0.07 \pm 0.07
<i>Eusyllis blomstrandii</i> (P)	0	0	0	0.13 \pm 0.13
Phyllodocidae (P)	0	0.47 \pm 0.19	0	0
<i>Scolelepis squamata</i> (P)	0.20 \pm 0.11	0.07 \pm 0.07	0.07 \pm 0.07	0
<i>Periploma leanum</i> (B)	0	0	0.27 \pm 0.15	0.47 \pm 0.27
<i>Lyonsia hyalina</i> (B)	0	0	0.07 \pm 0.07	0
<i>Crassostrea virginica</i> (B)	0	0.07 \pm 0.07	0	0
Platyhelminthes	0	0	0.07 \pm 0.07	0
Oligochaeta	0	0	0.07 \pm 0.07	0
Total abundance	233.27 \pm 23.61	128.27 \pm 15.57	232.40 \pm 23.07	188.87 \pm 14.89
Number of taxa	12	21	21	20

tropoda followed as the next most abundant taxa (5.8%), including primarily *Littorina littorea* (4.9%) and then, in very small numbers, other amphipod species (1.2%) and isopods, polychaetes, decapods, bivalves, oligochaetes, and platyhelminthes (all <1%).

The visual inspection of species composition and abundance across samples (nMDS) is presented in Fig. 2 (stress value = 0.17). Samples were segregated by clump treatment type, and clump treatments differed significantly (ANOSIM $p < 0.001$ in all comparisons), suggesting that giant Irish moss cultivated for restoration purposes may be colonized by different faunal assemblages than giant Irish moss growing *in situ* in clumps with blue mussels. SIMPER analysis identified 5 taxa of importance in shaping differences in epifaunal assemblages associated with the different clumps. The species contributing the most to the dissimilarity between treatments included the 4 most abundant amphipods, *G. oceanicus*, *G. lawrencianus*, *G. mucronatus*, and *Corophium* spp., in

addition to the periwinkle *L. littorea* (Table 3). Levels of dissimilarity between individual treatments ranged from 44.63–69.81%.

The most abundant mesograzer species differed depending on a combination of vertical position (suspended or bottom) and mussel presence (IM or IMBM) (1-way ANOVAs, $p < 0.001$; Table 4, Fig. 3). However, the species most consistently found in high numbers was *G. oceanicus*, which was also significantly more abundant than other taxa in the clumps most closely resembling their natural state (IMBM clumps on the seafloor). That species was followed by *G. lawrencianus*, which was very abundant in the grow-out IM conditions. *Corophium* spp. were more prominent in IMBM treatments, while *G. mucronatus* was less abundant than the other amphipod species but were more common in the treatments suspended in the water column.

3.2. Amphipod feeding rates and seaweed condition

G. oceanicus fed heavily on giant Irish moss in all 3 laboratory assays. In the assay measuring amphipod feeding rates (Fig. 4A), seaweed exposed to amphipods for 48 h lost significantly more biomass than controls (2-sample *t*-test, $t_{22} = 7.16$, $p < 0.001$), and amphipod grazing rate was calculated as 5.24 mg amphipod⁻¹ d⁻¹. Amphipods consumed visible amounts of seaweed and left marks that were often deep, lateral wounds, extending far into the frond. Observations of fecal matter in the bottom of the tanks verified that amphipods were feeding and reductions in seaweed tissue weight were most likely due to grazing. In the 7 d seaweed conditions trials (Fig. 4B), condition decline compared to controls was significant (Mann-Whitney test, $W = 359.5$, $p < 0.001$). Median CI decrease was 4 out of 10, with sampled blades showing more visible grazing damage in amphipod

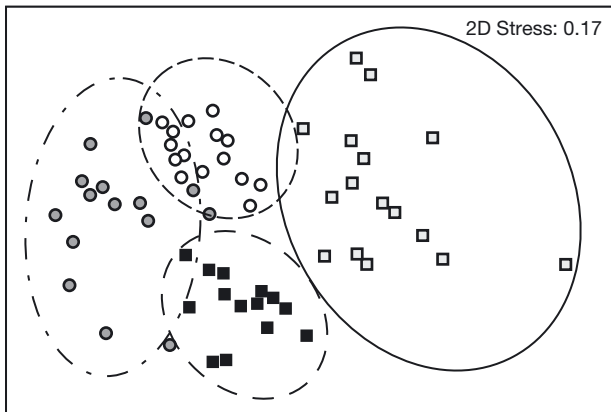


Fig. 2. Non-metric multidimensional scaling (nMDS) plot illustrating epifaunal species composition and abundance differences among the 4 types of clumps placed in Basin Head. Open circles: IM suspended; gray squares: IM bottom; gray circles: IMBM suspended; black squares: IMBM bottom. IM: Irish moss; BM: blue mussel

Table 3. Results of SIMPER analysis showing which taxa were contributing the most to the dissimilarity between giant Irish moss (IM) cultivation techniques. IMBM: Irish moss–blue mussel combination

Pairwise clump comparisons	Dissimilarity (%)	First 3 taxa driving dissimilarity		
IM _{Bottom} –IM _{Suspended}	59.02	<i>Gammarus lawrencianus</i>	<i>G. mucronatus</i>	<i>Littorina littorea</i>
IM _{Bottom} –IMBM _{Suspended}	69.81	<i>Corophium</i> spp.	<i>G. mucronatus</i>	<i>L. littorea</i>
IM _{Bottom} –IMBM _{Bottom}	63.22	<i>G. oceanicus</i>	<i>Corophium</i> spp.	<i>L. littorea</i>
IM _{Suspended} –IMBM _{Suspended}	48.07	<i>Corophium</i> spp.	<i>G. lawrencianus</i>	<i>G. mucronatus</i>
IM _{Suspended} –IMBM _{Bottom}	48.12	<i>G. lawrencianus</i>	<i>G. oceanicus</i>	<i>G. mucronatus</i>
IMBM _{Suspended} –IMBM _{Bottom}	44.63	<i>Corophium</i> spp.	<i>G. oceanicus</i>	<i>G. mucronatus</i>

Table 4. Results of 1-way ANOVAs comparing the abundances of the main amphipod species in 4 giant Irish moss cultivation treatments. Data underwent appropriate transformation (ln or square root) to meet ANOVA assumptions. **Bold:** significant

Taxa	Source of variation	df	SS	MS	F	p
<i>Gammarus oceanicus</i>	Treatment	3	116.3	38.77	15.31	<0.001
	Error	56	141.8	2.533		
<i>G. mucronatus</i>	Treatment	3	6.801	2.2669	29.35	<0.001
	Error	56	4.325	0.0772		
<i>G. lawrencianus</i>	Treatment	3	7.925	2.6417	12.10	<0.001
	Error	56	12.225	0.2183		
<i>Corophium volutator</i>	Treatment	3	73.08	24.3591	51.85	<0.001
	Error	56	26.31	0.4698		

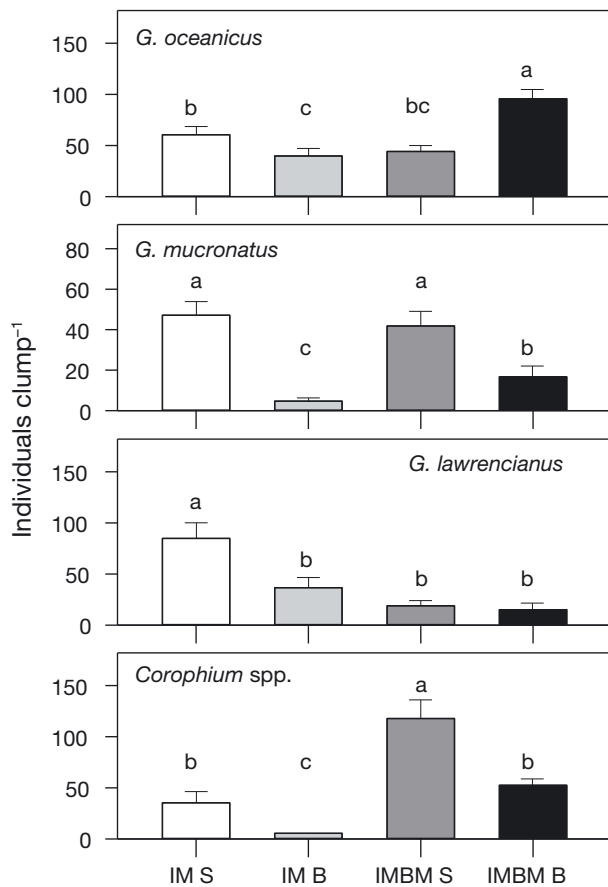


Fig. 3. Mean (+SE) densities of the most abundant amphipods colonizing the 4 types of clumps placed in Basin Head. IM: Irish moss; BM: blue mussel; S: suspended; B: bottom. Lowercase letters above the bars identify significant differences ($p < 0.05$) among clump types. Bar shading as in Fig. 2

treatments compared to controls (median change in CI of 0). Similar to the laboratory feeding trials, grazing did not bore through central areas but was rather concentrated first on the tips and edge of the thallus where large portions were bitten off (see Fig. A1 in the Appendix).

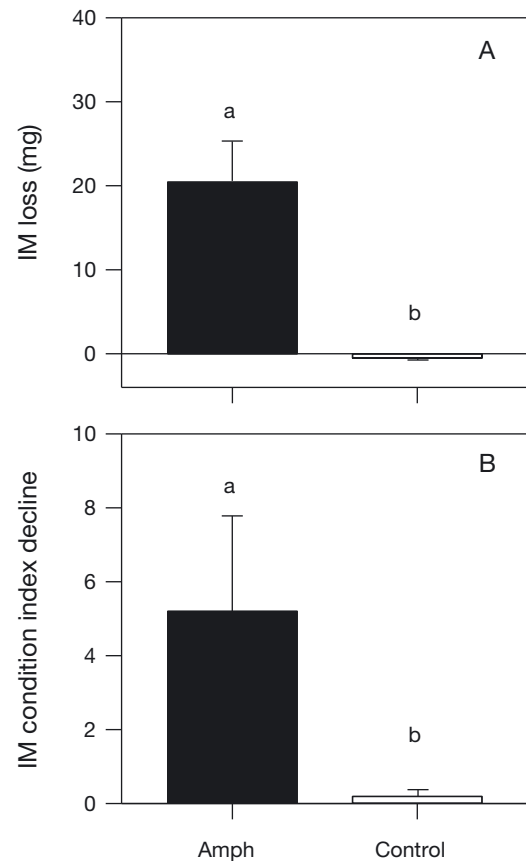


Fig. 4. (A) Mean (+SE) loss in biomass of giant Irish moss in 48 h trials exposed to 2 amphipods (Amph) and in control conditions (Control). (B) Mean (+SE) decline in giant Irish moss condition index in 7 d trials exposed to 20 amphipods and in control conditions. Lowercase letters above the bars identify significant differences ($p < 0.05$)

3.3. Impact of sedimentation on loss of biomass

Results of feeding trials assessing the influence of amphipods and the health of the giant Irish moss (i.e. healthy versus algae stressed by burial in sedi-

ment) are summarized in Fig. 5. Burial-stressed giant Irish moss fronds developed areas of evident necrosis, brittleness, and loss of pigmentation. Blades of giant Irish moss exposed to amphipods lost significantly more mass than those in the controls (2-way ANOVA, $F_{1,46} = 118.39$, $p < 0.001$; Fig. 5); and burial-stressed giant Irish moss lost significantly more mass than healthy giant Irish moss (2-way ANOVA, $F_{1,46} = 62.99$, $p < 0.001$). Over 1 wk of exposure to amphipods, Irish moss blades in the stressed treatment lost twice as much mass as those in the healthy Irish moss treatment. There was no significant interaction effect between amphipod presence and seaweed health (2-way ANOVA, $F_{1,46} = 2.20$, $p = 0.145$). As well as lateral grazing damage along the edges and tips of fronds, central holes appeared in some sediment-stressed plants where necrotic tissue was eaten away (see Fig. A1). Survival of amphipods in both treatments was similar (18 out of 20 amphipods survived; Mann-Whitney, $W = 187.0$, $p = 0.661$).

4. DISCUSSION

The virtual disappearance of the giant Irish moss beds in the 2000s precludes direct testing of hypotheses exploring their sudden decline. However, tank-cultivation of the seaweed and recent planting of it in its natural habitat have presented an opportunity to

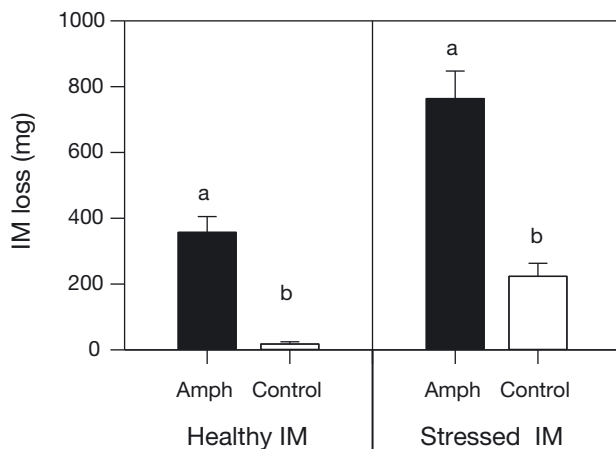


Fig. 5. Mean (+SE) loss in biomass of giant Irish moss (IM) in trials using healthy and stressed algal fronds exposed to amphipods (Amph) and control conditions (Control). Lowercase letters above the bars identify significant differences ($p < 0.05$) between seaweeds exposed to amphipods and the controls. Differences between healthy and stressed IM were also significant (without significant interaction between factors) but are not shown

gain insight into the causes of its collapse. Efforts to restore this unique strain have produced observations of a phenomenon originally described over a decade ago: the appearance of conspicuous damage to the fronds, likely due to grazing activity. These observations have reignited interest in the interactions between herbivores and this seaweed. By identifying mesograzers associated with giant Irish moss clumps and demonstrating their ability to damage the seaweed, this study takes a further step towards understanding their role in the decline and restoration of the giant Irish moss. Although this study focused on a singular variety of a seaweed species living at one geographic location, our findings with respect to interactions with herbivores and with habitat conditions have implications for seaweeds under grazing pressure elsewhere, particularly those at risk of disappearing or in the process of restoration (Smale et al. 2013).

4.1. Epifauna associated with giant Irish moss

All giant Irish moss clumps were colonized by abundant assemblages of mobile epifauna. Despite differences across treatments, a common feature was the numeric dominance of herbivores. This observation is similar to what has been described in another close association between a holdfast-lacking macroalga, a strain of *Fucus* sp., and blue mussel beds in the mudflats of the Wadden Sea, which likewise coexisted with high abundances of grazing herbivores, including periwinkles and gammarids (Albrecht & Reise 1994). In both cases, this association with mussels benefited the seaweed by holding it firm where other available hard substrate was scarce and, indirectly, supported high herbivore densities (see also Tummon Flynn et al. 2020). In the clumps studied here, 3 of the 4 most common species were gammarid amphipods. These species use macroalgae as a primary food source, although they also feed on microalgae, detritus, and animal tissue (Zimmerman et al. 1979, Hawkins 1983, Orav-Kotta 2004). Additionally, giant Irish moss clumps protect epifauna from physical stress and predators, as macroalgal canopies provide environments physically and biologically different from areas nearby lacking cover (Buschmann 1990, Bégin et al. 2004, Gutiérrez et al. 2019). The mobility of these epifaunal amphipods (able to travel 10s of m to km in the water column; Virnstein & Curran 1986) allows them to rapidly colonize macroalgae on both floating and bottom lines from adjacent habitats.

Differences in epifaunal communities colonizing the 4 cultivation treatments indicate that giant Irish moss clumps grown, held, and planted *in situ* for restoration purposes are exposed to different assemblages of organisms, and particularly different herbivore assemblages, throughout the process. The 5 taxa whose abundances were identified to be the driving force in compositional differences among treatments were all mesograzers (4 amphipod taxa and the gastropod *Littorina littorea*). While this study was not designed to identify the causes of such differences, it is presumed that the colonization patterns are reflective of differences in physical habitat (e.g. Dean & Connell 1987, Gutiérrez et al. 2019), with the blue mussels adding further 3-dimensional structure and secondary space, altering abiotic conditions (Commito & Rusignuolo 2000), and depositing pseudofaeces to fronds and benthic sediments. Habitat selection is likely also influenced by other factors, including food preferences, predation, and competition (e.g. Norling & Kautsky 2007, Beermann et al. 2018, Malyshev et al. 2020).

4.2. Amphipod feeding rates, seaweed condition and impact of sedimentation

Gammarus oceanicus readily consumed giant Irish moss in laboratory experiments, creating deep grazing wounds similar to those recorded in the field. The specialized forelimbs and mandibles of gammarid amphipods (Parker et al. 1993) allow them to manipulate and bite large pieces from tough macroalgae such as Irish moss (Shacklock & Croft 1981, D'Antonio 1985) that other herbivores (e.g. littorinids) tend to eschew (Lubchenco 1978). The palatability of this unique strain (giant Irish moss) appears to be similar to that of typical Irish moss, with grazing rates ($5.24 \text{ mg amphipod}^{-1} \text{ d}^{-1}$) close to those previously reported for *G. oceanicus* in culture ($\sim 6 \text{ mg amphipod}^{-1} \text{ d}^{-1}$; Shacklock & Croft 1981). Grazing rates per amphipod were much higher than those measured for small green crabs ($0.73 \text{ mg crab}^{-1} \text{ d}^{-1}$; Tummon Flynn et al. 2019), which had previously been suspected to feed on giant Irish moss. These results support our hypotheses that mesograzers, specifically gammarid amphipods, the most abundant taxa associated with the giant Irish moss bed (Sharp et al. 2003, this study), have the potential to reduce giant Irish moss biomass and create the grazing wounds that have been repeatedly observed in the field (see Fig. A1). This is the first evidence that identifies the organisms causing this damage.

Grazing damage in the giant Irish moss population has been temporally and spatially variable. Prior to 2005, the plants showed no evidence of grazing, aside from irregular tips late in the summer (McCurdy 1979). A pronounced ragged state of the fronds was first reported in the spring of 2005 (Sharp et al. 2010) with subsequent observations of grazing wounds in laboratory-grown giant Irish moss planted in the lagoon (spring, summer, and fall of 2015–2017; authors' pers. obs.). During restoration, grazing was spatially patchy; damage observed in the field was extensive but not ubiquitous, and healthy giant Irish moss could still grow in the lagoon (Tummon Flynn et al. 2018). In fact, despite the abundance of herbivores in the study area and in the experimental clumps, recent Irish moss restoration efforts are promising, with giant Irish moss coverage increasing from $< 2 \text{ m}^2$ in 2013 to an estimated 90 m^2 by 2018.

Our sedimentation experiment explored the possibility that increasing localized environmental stress in the Basin Head lagoon could at least partially explain the onset of and the pattern of damage if the seaweed were rendered disproportionately susceptible to herbivory. In the literature, multiple environmental stressors, e.g. light limitation, UV light, desiccation, burial, and even degradation into detritus, have been shown to change algal palatability and increase its consumption by grazers (Renaud et al. 1990, Cronin & Hay 1996, Kubicek et al. 2011, Braeckman et al. 2019). The Basin Head lagoon has experienced a general decline in habitat quality since the 1980s, including eutrophication, sedimentation, marsh erosion, loss of eelgrass beds, and climate change leading to thermal stress (Sharp et al. 2010). Environmental stressors such as light limitation due to shading by *Ulva* spp. mats and increased turbidity have also been noted to affect the condition of cultivated giant Irish moss and generally decrease growth. Sedimentation, in particular, has been identified as a primary threat to the survival of the population, and the negative influence of smothering by silt, marsh debris, and *Ulva* spp. on the health of planted clumps of giant Irish moss has included evidence of grazing damage as well as loss of biomass, development of necrotic tissue, and increased mortality. Additionally, the success of restoration efforts has been spatially variable and seems to be related to local current speeds that affect sedimentation rates and bottom firmness.

In this study, amphipod feeding on fronds stressed by silt burial for 7 d prior to trials resulted in a doubling of the loss of algal biomass compared to healthy giant Irish moss. Sediment-exposed algae showed visual signs of necrosis, brittleness, and loss of pig-

mentation, and the physical integrity of the Irish moss was sufficiently degraded that control algae exposed to sedimentation lost partial biomass without the action of grazers. As well as lateral bites, central holes appeared on the stressed fronds where necrotic tissue was eaten away. Surprisingly, there was no significant interactive effect between grazing by amphipods and the stress caused by burial, indicating the increase in biomass loss is likely an additive, rather than synergistic, effect of these 2 factors. Changes in seaweed palatability due to stress associated with sediment burial have been already addressed in the literature (e.g. Williams et al. 2013, Braeckman et al. 2019). Red seaweeds generally contain halogenated compounds that may be grazer-deterrent, and Irish moss crude extracts have acted as feeding deterrents against *L. littorea* (Geiselman 1980). It is likely that the amphipods chose the less protected tissues when given an option, hence the holes, possibly causing the patchy spacing of the damage in the field. All these factors point to the need to limit sedimentation and nutrient inputs to the lagoon, and to concentrate restoration efforts in areas less exposed to low currents and excessive deposition of fine sediments.

Estimating the overall impact of grazing damage on the giant Irish moss population is a complex endeavor. While the direct consumptive impact of mesograzers on macrophyte biomass is usually small, their effects can also be disproportionately large when grazer abundance is unevenly distributed, critical tissues (e.g. reproductive structures) are selectively consumed (Buschmann 1990, Poore et al. 2014), or grazer effects are concentrated on fewer individuals, e.g. when the abundance of macrophytes wanes (O'Brien 2018). Indirect effects can have even greater ramifications than direct removal of biomass (e.g. secondary tissue loss from frond breakage at weakened grazing sites; Krumhansl et al. 2011). The availability of alternative macroalgae species, as well as the nutritional quality and defenses of the latter species, will also affect the grazing pressures on giant Irish moss, and should be further explored. *G. oceanicus* tend to prefer more palatable, fast-growing green algae over tough, heavily defended perennials (Goecker & Kall 2003).

4.3. Implications for restoration

An important consideration is whether top-down control of seaweeds by grazing could cause a collapse like the one that decimated the giant Irish moss popu-

lation in the 2000s. The literature suggests that, despite their small per capita effects, mesograzers have the potential to strongly impact the fitness and structure of macroalgal communities (Shacklock & Croft 1981, Hauxwell et al. 1998), particularly on slow-growing perennial species (Poore et al. 2014). Mesograzer outbreaks have been linked with other large-scale macroalgae declines (Leidenberger et al. 2012, Wahl et al. 2015). However, the extent to which they control macroalgal standing stocks does not follow consistent patterns (Hay et al. 1987, Bell 1991, Duffy & Hay 1991), and grazer activity can also enhance macroalgal productivity through indirect positive effects (e.g. by removing epiphytes or controlling the abundance of competing ephemeral seaweeds; D'Antonio 1985, Duffy 1990). Restoration efforts, including the culture or hanging of Irish moss clumps, should expect colonization patterns like the one described here, attracting large numbers of amphipods and other grazers. Those hardly qualify as outbreaks, and as indicated above, indirect interactions with the Irish moss, competing seaweeds, and their own consumers may well balance their numbers at the scale of the lagoon.

The mesograzers identified and assessed here are not exotic species and, in fact, gammarid amphipods were recorded in high densities in the 1970s when the giant Irish moss thrived (McCurdy 1979, Sharp et al. 2003). Unfortunately, a lack of systematic monitoring precludes the quantification of changes in grazer abundances and their distribution on the plants. Additionally, although historical data on rates of sedimentation are not available (McCurdy 1979), a general shallowing of the lagoon has been noted along with a decline in sediment-stabilizing organisms (e.g. eelgrass and blue mussel populations; I. Novaczek pers. comm.). That information suggests that the most plausible explanation for the giant Irish moss collapse was the cumulative factors contributing to habitat decline, in which grazing damage was a symptom of an already stressed population. This aligns with the results of our experiments and the additive impact of grazing on stressed seaweed fronds referred to above. Hence, a further understanding of key stressors, including sedimentation and stress-mediated grazing, is important for the success of restoration efforts and the future of the giant Irish moss population.

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Appendix.



Fig. A1. (A) Fragmentation of a giant Irish moss frond due to tip and lateral wounds/damage in a sample from the field site (Basin Head). (B) Frond from laboratory trials showing tip and lateral wounds/damage after 1 wk of exposure to amphipods. In both (A) and (B), grazing is visible in the tip of a frond. In the holes at the center of the frond, the tissue became necrotic.

Photographs: © P. Tummon Flynn 2021 (A) and © K. D. Lynn 2021 (B)