Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats

Karen Filbee-Dexter*, Robert E. Scheibling

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

ABSTRACT: Severe storm events are important agents of disturbance that can transport large quantities of algal detritus from highly productive kelp beds (or forests) in shallow water to deeper, more food-limited areas. We measured canopy cover in shallow kelp beds (5 to 15 m depth) and the cover of detrital kelp in sedimentary habitats directly offshore of these beds (20 to 45 m) before and after Hurricane Earl, which struck the Atlantic coast of Nova Scotia in September 2010. The storm resulted in large losses of kelp canopy cover (from 71.0 to 38.7 %, averaged across sites) and significantly increased the cover of detrital kelp deposits below the kelp beds (from 1.5 to 3.4 %). Detrital deposits were more commonly found in a semi-protected bay than off an exposed headland and persisted in the bay for at least 6 wk. Sea urchins *Strongylocentrotus droebachiensis* were associated with detrital kelp deposits in offshore habitats. At sites with the greatest amount of detrital kelp, we estimated that sea urchins could consume this material within 2 mo, indicating that storm-generated detrital pulses may be an important form of trophic connectivity between adjacent ecosystems off this coast.

KEY WORDS: Defoliation · Hurricane impacts · Kelp beds · Macroalgal detritus · Sea urchin grazing

INTRODUCTION

Large-scale episodic disturbance events can profoundly alter the structure and function of marine benthic communities (Dayton 1971, Connell 1978, Sousa 1979). In kelp forests off California (USA), severe storms can cause major losses of large canopy-forming kelps (Seymour et al. 1989, Tegner et al. 1997) and reduce the resilience of the kelp forest to biotic forces, such as sea urchin grazing (Ebeling et al. 1985, Tegner & Dayton 1991) and competitive interactions with other macroalgae (Dayton & Tegner 1984). As these canopy kelps break-up or are dislodged, they entangle other kelps (Dayton 1985) and create floating rafts of drift algae (Hobday 2000). Prostrate kelps may be less vulnerable to breakage than canopy-forming species because of a lower risk of entanglement (Dayton & Tegner 1984, Dayton et al. 1984). Storm-mediated defoliation events also generate large pulses of blade fragments (Krumhansl & Scheibling 2011a) and dislodged thalli that provide trophic subsidies for benthic communities remote from the source of production (Bustamante et al. 1995, Vetter 1998, Britton-Simmons et al. 2009).

Kelp beds in the Northwest Atlantic are composed of prostrate kelps, such as *Laminaria digitata* and *Saccharina latissima* (Adey & Hayek 2011). Although the impact of extreme storm events on these kelp beds has not been documented, substantial losses of kelp biomass are expected to reduce primary production and biogenic habitat, which in turn would affect food web structure and energy flow to higher trophic levels (Wharton & Mann 1981). The sea urchin *Strongylocentrotus droebachiensis* is the

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dominant herbivore in kelp beds in the Northwest Atlantic and plays a pivotal role in determining community structure (Scheibling & Hatcher 2007). At high population densities, sea urchins destructively graze kelp beds, causing a shift to a barren state in the rocky subtidal zone (Mann 1977, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a). These kelp beds are re-established following periodic outbreaks of disease that eliminate sea urchins at shallow depths (<25 m) (Scheibling 1986, Johnson & Mann 1988). Deeper-living sea urchins persist in a thermal refuge from disease and provide larval recruits to the emergent kelp beds or form grazing aggregations along the lower margin of the beds, which drives the transition back to sea urchin barrens in this alternative stable-state system (Scheibling 1986, Lauzon-Guay et al. 2009). Particulate kelp detritus is continuously generated through the natural erosion of blades (Krumhansl & Scheibling 2011b) and the production of sea urchin feces (Sauchyn & Scheibling 2009a). Severe storm events could generate pulses of large detrital fragments and whole thalli that are likely an important food source for deeper-living sea urchins and other detritivores (Britton-Simmons et al. 2012, Kelly et al. 2012). Laminarian kelps are a preferred food of *S. droebachiensis* that maximizes growth and reproduction (Scheibling & Hatcher 2007), and the nutritional value of detrital kelp is enhanced through nitrogen enrichment during microbial decomposition (Norderhaug et al. 2003, Sauchyn & Scheibling 2009b) and the accumulation of a diverse epifaunal assemblage (Krumhansl & Scheibling 2012).

Detrital subsidies have been documented in other kelp ecosystems, although these studies are few and geographically limited and the role of storm events in the creation and transport of detrital material remains largely unexplored. In Western Australia, detrital exports from kelp beds subsidize adjacent sea grass beds (Wernberg et al. 2006, Vanderklift & Wernberg 2008). In the Chilean intertidal zone, sea urchins preferentially feed on drift kelp, which enables them to develop even larger gonads than sea urchins that feed only on attached kelp (Rodriguez 2003). Off Washington State (USA), sea urchins inhabiting barrens in the shallow subtidal zone below a kelp bed rely heavily on a drift kelp subsidy and have a similar reproductive output as sea urchins within the kelp bed (Britton-

Simmons et al. 2009). Off southern California, detritus exported from both a kelp forest and sea grass beds increases secondary production in adjacent habitats and is flushed by fall storms into a deep canyon, where it provides an energy subsidy for benthic communities at even greater depths and distances from the source of primary production (Vetter 1998, Vetter & Dayton 1999).

This study was conducted within a broader investigation of factors influencing the distribution of kelp and sea urchins on rocky and sedimentary substrata from the intertidal zone to ~100 m depth along the Atlantic coast of Nova Scotia. Hurricane Earl made landfall within our study region in early September 2010, presenting a rare opportunity to examine the effects of a severe storm on kelp canopy cover, drift algal deposits, and sea urchin distribution. The present study is the first to directly quantify both the loss of kelp canopy and deposition of drift kelp attributed to a single large storm event.

MATERIALS AND METHODS

Study sites and sampling design

To measure the effect of a severe storm on canopy loss in kelp beds and the deposition of detached blades and thalli, we sampled a series of sites along a gradient of wave exposure within St. Margarets Bay and on an adjacent headland at Splitnose Point, near Halifax, Nova Scotia, before and after Hurricane Earl struck the coast on 4 September 2010 (Fig. 1). St. Margarets Bay is a large semi-protected embayment that is exposed to ocean swell from the south.
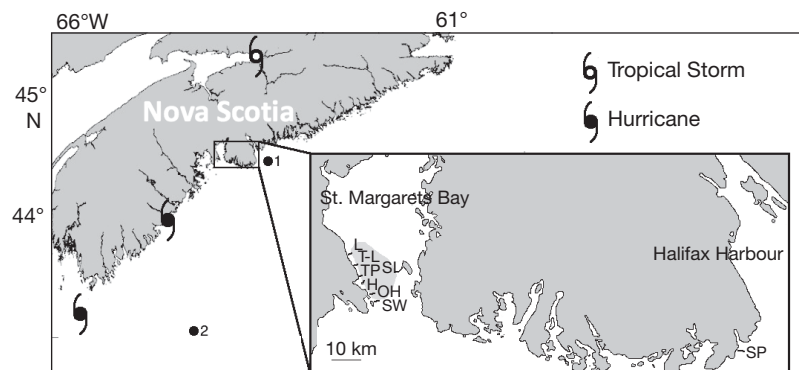

Fig. 1. Map of Nova Scotia showing track of Hurricane Earl on 4 Sept 2010 and study sites in St. Margarets Bay (L = The Lodge. T-L = Tilly-Lodge. TP = Tilly Point. H = Horse Island. OH = Owl's Head. SW = Southwest Island. SI = Shut-in Island) and off the headland at Splitnose Point (SP). Shaded area is a deep sedimentary basin (>60 m depth) in St Margarets Bay. (•1) Lahave Bank buoy; (•2) Halifax Harbour buoy

The western shore of the bay is rocky and steeply shelves into a deep (70 to 100 m) sedimentary basin; the eastern shore is more gently sloped with scattered islands. The deepest regions of the bay have a sandy bottom and are surrounded by areas of gravel interspersed with boulders (Hughes et al. 1972). The rocky subtidal zone (0 to 20 m depth) of the bay is dominated by prostrate kelps (*Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*) and grades to sand at its lower limit (Mann 1977). Along the headland at Splitnose Point, the substratum grades from exposed bedrock ledges in the shallow subtidal zone (<20 m depth) (Lauzon-Guay & Scheibling 2007a) to boulder fields and sandy substrata in deeper regions. Kelps (*Alaria esculenta*, *S. latissima*, and *L. digitata*) extend to depths of 20 m, depending on the extent of destructive grazing by sea urchins (Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007a,b).

Six sites along the western shore of St Margarets Bay (Southwest Island, Owl's Head, Horse Island, Tilly Point, Tilly-Lodge, and The Lodge) and one site off a large island along the eastern shore of the bay (Shut-in Island) were surveyed with video transects on 1 (Southwest Island only), 13 and 18 (Owl's Head only), and 31 August (Shut-in Island), prior to Hurricane Earl, and resurveyed on 13 and 26 September and 14 October 2010, after the storm (Appendix 1). Splitnose Point, on the headland near the western mouth of Halifax Harbour, was surveyed immediately before and after the hurricane, on 1 and 8 September, with 4 transects spaced at 100 m intervals alongshore (Appendix 1). To examine the persistence of deposits of drift kelp and the response of deep-living sea urchins to this food fall, video transects were also repeated at Southwest Island on 14 and 25 October 2010 and 5 February 2011 and at Owl's Head on 14 and 25 October 2010 and 5 February 2011.

Video transects

Our video transects ran perpendicular to the coastline from the mid-range to lower regions of the kelp bed to the operational depth of our equipment. At the start of the present study, our

camera system reached 50 m depth; we upgraded our equipment on 1 October 2010, which extended the transects at Southwest Island and Owl's Head to 90 m (Fig. 2a, Appendix 1). A digital video camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search Equipment) was towed at an average speed of 1.8 km h^{-1} from a 7 m research vessel (RV Nexus). The position of the wing above the bottom was monitored using real-time video and manually maintained at a relatively constant height above the bottom (1 to 2 m) by adjusting cable length using an electronic winch. To aid in positioning the wing and to measure scale in video frames, 2 fixed lasers spaced 20 cm apart were trained on the bottom. The depth and position of the vessel was recorded using side-imaging sonar (1198c Side Imaging Sonar, Humminbird) and lagged by 9 s to account for positional offset between the wing and the sounder. The transects were resurveyed after the storm by following prior GPS tracks.

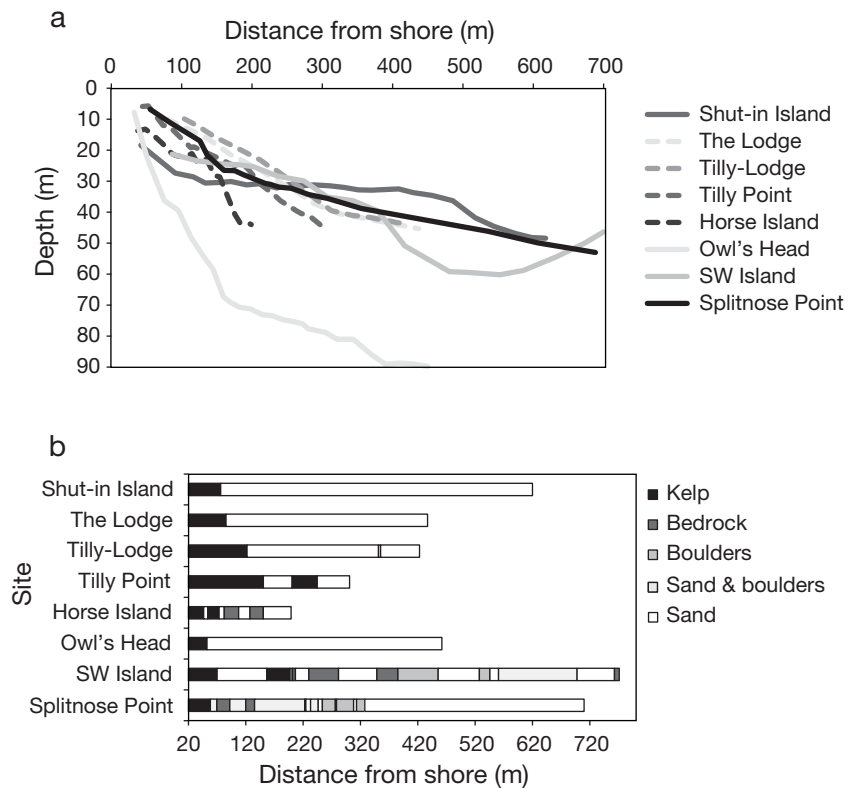Video data were exported from iMovie (version 3.0.3, Apple) into ImageJ (National Institute of

Fig. 2. (a) Depth profile and (b) substratum type for video transects at study sites. Transects off Owl's Head and Southwest Island extended beyond 45 m due to equipment upgrades on 1 October 2010 that facilitated deeper data collection

Health, USA) as frames (1 frame per 3 s of video record). For each video transect, we randomly sampled 12 frames in the kelp bed at 5 to 15 m depth and 30 frames below the kelp bed at 20 to 45 m depth at all sites except Horse Island and Shut-in Island. At the latter 2 sites, transects began below 15 m because of the steeply sloping bottom, and we sampled 12 frames in the kelp bed at 15 to 25 m and 30 frames below the kelp bed at 25 to 45 m. About 2% of frames were excluded from analysis because they were out of focus, taken high off the bottom, or poorly lit. These frames were replaced with other randomly selected frames. To determine the percentage of cover of attached kelp or detrital kelp deposits, we overlaid a grid of 104 points on each frame and recorded the presence of attached or detached kelp under each point. Approximately 0.6 to 2.0 m^2 of bottom area was captured in each frame. Sea urchins were counted in the same frames used for the detached kelp measurements at Southwest Island, Owl's Head, and Shut-in Island.

Substratum type was recorded continuously in all frames along each transect and categorized as (1) bedrock with attached kelp, (2) bedrock without attached kelp, (3) boulders, (4) sand and boulders, or (5) sand (Fig. 2b).

We used a 2-way analysis of variance (ANOVA), with period (2 levels: before or after the storm) and site (8 levels) as fixed factors to compare changes in kelp canopy cover or in the cover of detrital kelp below the kelp bed. Site was considered a fixed factor because we selected sites along a wave exposure gradient in St. Margarets Bay (approximately evenly spaced along the western side of the bay from the mouth to the inner bay) and included a headland site (Splitnose Point) where exposure was greatest. Raw data for the cover (%) of attached kelp satisfied the assumption of normality (Shapiro-Wilks test, $\alpha = 0.05$) and homogeneity of variance (Levene's test, $\alpha = 0.05$). However, the data for the coverage (%) of detrital kelp did not meet these assumptions, even after conventional transformation (square-root, log, logit, or arcsine), and raw data were analysed. For each site, post-hoc comparisons of coverage (%) before vs. after the hurricane, for attached or detrital kelp, were conducted using t-tests with a Simes-Hochberg sequential Bonferroni adjustment (Simes 1986, Hochberg 1988). For comparisons of the detrital kelp cover, we first tested for variance homogeneity using the F-ratio test. In cases where this assumption was not met, we used Welch's t-test with adjusted degrees of freedom.

Wave and current measurements

Significant wave height data were obtained from meteorological buoys at Lahave Bank (42.500° N, 64.02° W) and Halifax Harbour (44.500° N, 63.4° W) from 1 August to 14 October (www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm). As an indicator of the change in bottom currents before and after the hurricane, we measured the wavelength (distance between successive wave crests) and direction (normal to the crests) of sand waves in video frames at Southwest Island using scaling lasers.

Wave exposure indices

We predicted that sites on the headland and close to the mouth of St. Margarets Bay would experience higher wave action and therefore higher kelp defoliation and detritus deposition than more protected sites within the bay. We rated the sites in terms of exposure to storm-generated waves by direct observation during Hurricane Earl, using an 11 point scale. We based our rating on the direction of waves breaking on the shore and the intensity of the wave break. Splitnose Point was assigned the highest value (11) because it was on a headland (although this site was not directly observed during the storm, adjacent headlands near Halifax were observed). Within St. Margarets Bay, the sites were rated as follows: Shut-in Island (10), Southwest Island (9), Owl's Head (7), Horse Island (4), Tilly Point (3), Tilly-Lodge (2) and The Lodge (1). We also estimated site exposure based on the average fetch (m) measured every 10° within the directional range (140 to 210°) over which large swells can enter the mouth of St. Margarets Bay and bounded at 2000 km, the distance over which storms in the North Atlantic generate waves that propagate to the coast of Nova Scotia (Hart & Evans 2001). Wind data were not taken into account in our exposure calculation because wind direction was highly variable as the hurricane made landfall and was not representative of the direction of ocean swells. Site exposure based on fetch was strongly correlated with our observation-based rank (Pearson's product moment correlation, $r = 0.997$), and the rank order of fetch measurements was in complete concordance with the observation-based ranks.

We used linear regression to examine the effect of site exposure (observation-based rank) on the loss of kelp cover during the hurricane and the deposition of detrital kelp after the storm. Percentage cover data

for attached and detrital kelp were averaged for all frames of the relevant video segments in each transect. Model II linear regression was used to examine the relationship between the amount of detritus deposited and the loss of kelp cover at sites within St. Margarets Bay.

Consumption of drift algae by sea urchins

We estimated the consumption of detrital kelp deposits by sea urchins *Strongylocentrotus droebachiensis* in a cage experiment on a sandy bottom in St. Margarets Bay. Initial camera surveys were used to identify a region off The Lodge where sea urchins were rare: only 2 individuals were observed along a 50 m transect extending parallel to shore at ~42 m depth. We deployed 4 cages (length × width × height: $1.5 \times 0.5 \times 0.5$ m; mesh aperture: 4×4 cm) in a linear series at ~40 m intervals along this transect. Each cage contained 10 *Saccharina latissima* thalli freshly collected from a kelp bed at 14 m depth at The Lodge and secured to the cage bottom with plastic cable ties around the base of the stipes. The total wet weight of kelp (3.31 to 4.13 kg per cage) was measured using a spring scale (1 g accuracy) immediately before deployment. The kelp density in cages was similar to natural densities observed at Splitnose Point, Southwest Island, Owl's Head, and Horse Island in St. Margarets Bay (K. Filbee-Dexter unpubl. data). Two cages were supplied with 20 sea urchins (grazing treatment); the other 2 cages contained no sea urchins (autogenic control). Adult sea urchins (40 to 50 mm test diameter) were collected from barrens at 15 m depth off Pennant Point (a headland site near Splitnose Point) on 18 July 2011 and maintained in flow-through seawater tanks in the laboratory prior to use in this experiment. Replicates of each treatment were randomly allocated to the 4 positions along the array. The cages were retrieved after 4 d,

and the remaining kelp in each cage was re-weighed immediately with the spring scale to compare the mass loss in the grazing treatment (due to sea urchin grazing and kelp fragmentation) with that in the autogenic control (fragmentation only). In the laboratory, pre-weighed kelp fronds (3.19 kg) and 20 sea urchins (from the same collection used for the field experiment) were placed in a 1×0.6 m flowing seawater tank over the same 4 d period to measure grazing rate.

RESULTS

Kelp loss and drift algae deposition

Hurricane Earl made landfall near Lunenburg, Nova Scotia, as a Category 1 hurricane on 4 September 2010. The hurricane was associated with significant wave heights of 10 to 14 m (Fig. 3) and sustained wind speeds of 75 to 100 km h^{-1}. Weather buoys recorded maximum wave heights of 23.3 m off Halifax Harbour and 25.1 m on Lahave Bank. Large waves and pounding surf struck south- and southeast-facing coastlines, and the hurricane passed almost directly over our study area (Fig. 1). The waves reached the coast at low tide, exposing shallow kelp beds to extreme wave forces. Weather buoy recordings show that Hurricane Earl was a major wave event compared to normal wave activity during the autumn of 2010 (Fig. 3).

The hurricane was associated with a dramatic defoliation of the kelp bed at all of our sites, with the greatest losses of kelp cover at Splitnose Point, Tilly-Lodge, and Owl's Head (Fig. 4). The 2-way ANOVA showed a significant interaction of sampling period (before and after the storm) and site (Table 1). This result reflects an interaction in the magnitude of the effect and not the direction: post-hoc comparisons showed a significant decrease in kelp cover at each
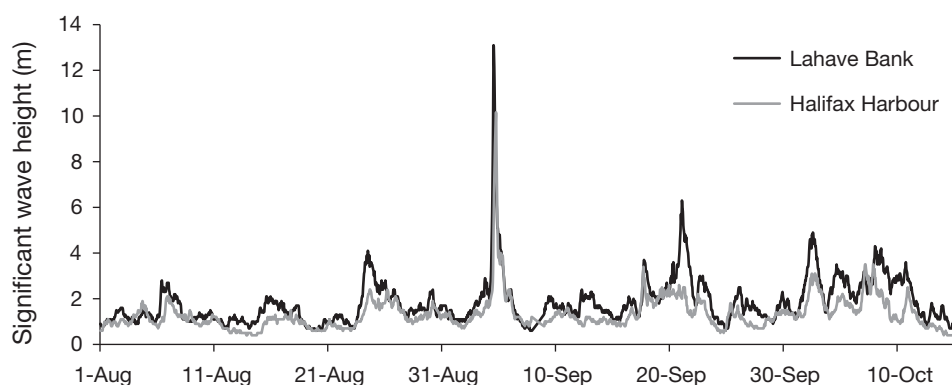
Fig. 3. Significant wave height recorded at Lahave Bank and Halifax Harbour buoys from 1 August to 15 October 2010. The peak in wave height on 4 September was caused by Hurricane Earl
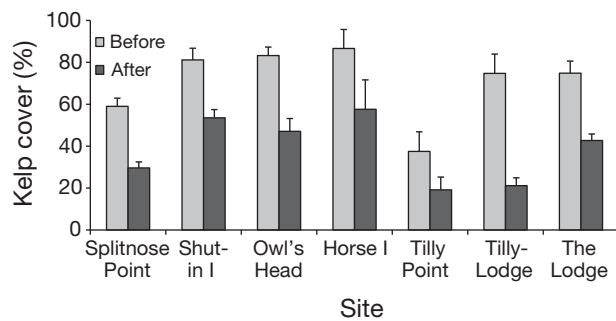
Fig. 4. Kelp cover (%) before and after Hurricane Earl at sites in St. Margarets Bay (Owl's Head, Horse Island, Tilly Point, Tilly-Lodge, Shut-in Island, and The Lodge) and near the mouth of Halifax Harbour (Splitnose Point). Owl's Head data are averaged across 3 transects, and Splitnose Point data are averaged across 4 transects. Sites are in order of decreasing exposure. Means + SE, n = 12. Each site has a significant loss in kelp cover following Hurricane Earl

Table 1. Two-factor ANOVA of the effect of site and sampling period (before and after Hurricane Earl) on coverage (%) of attached kelp and kelp detritus

Source	df	MS	F	p
Kelp cover				
Site	6	0.454	11.566	<0.001
Period	1	6.102	155.352	<0.001
Site × Period	6	0.161	4.091	0.001
Error	194	0.039		
Detritus cover				
Site	7	3.603	4.939	<0.001
Period	1	2.692	3.691	0.055
Site × Period	7	3.576	4.902	<0.001
Error	656	0.730		

site before and after the hurricane (Bonferroni-adjusted t-test, p < 0.017). The kelp cover decreased from 71.0% before to 38.7% after the storm, when averaged across all sites; defoliation was greatest at Tilly-Lodge, where the cover declined from 74.7 to 21.2%. Following the hurricane, coralline and filamentous red algae, which were understory species within the intact kelp bed, dominated the algal cover on the rocky seabed. Observations by divers at Splitnose Point on 8 September confirmed the extent of damage to kelp beds along the headlands: the kelp canopy was stripped, with only stipes and torn blades remaining in shallower wave-swept areas (Fig. 5a,b), and there were large accumulations of kelp detritus both within the remnant kelp bed and in the rocky barrens below it.

The cover of drift algae increased in deeper habitats below the kelp beds after Hurricane Earl

from 1.5% before to 3.4% after the storm, when averaged across all sites (Fig. 6). The 2-way ANOVA showed a significant interaction of sampling period and site (Table 1). This result also reflects variation in the magnitude of the effect across sites: post-hoc comparisons showed that detrital kelp cover significantly increased (p < 0.007) at Splitnose Point, Owl's Head and Shut-in Island; no significant change in detrital cover (p > 0.048) was detected at Southwest Island, Horse Island, Tilly-Lodge, and The Lodge. The increase in detrital cover at Tilly Point was marginally non-significant (p = 0.011); however, our test procedure was highly conservative (adjusted α = 0.010). At Splitnose Point, large amounts of detritus accumulated amid boulders at the lower margin of the kelp bed and in crevices among bedrock outcrops (Fig. 5c), but drift kelp was infrequently observed in deeper sandy regions. In contrast, extensive deposits of kelp detritus occurred on the sandy bottoms off Southwest Island and Shut-in Island. Near the lower margin of the kelp bed at these sites, the seabed was carpeted with detached kelp fronds that formed dense patches covering areas of up to 200 m². Further from the kelp bed, at 20 to 40 m depth, the bottom consisted of uniform sand waves, which accumulated large quantities of drift kelp in the troughs (Fig. 5d). Sand waves at 30 m depth off Southwest Island had average wavelengths of 0.70 m oriented at 107° and 1.10 m oriented at 111° before (13 August) and after (13 September) Hurricane Earl respectively, indicating a 57% increase in wavelength with little change in direction following the storm. These sand waves graded to rocky substrata and sand with scattered boulders at ~45 m depth (Fig. 2b). At other sites in St. Margarets Bay, drift kelp was more uniformly deposited on sediment bottoms offshore of the kelp beds and did not form wave-rows or large patches. At Owl's Head, sea urchins aggregated on drift kelp, typically with 3 to 4 individuals on a blade fragment every 1 to 3 m along a transect. Similar aggregations of sea urchins were observed in deep sedimentary habitats off Shut-in Island, Southwest Island, Horse Island, and Tilly Point.

Linear regression indicated that wave exposure was not a good predictor of the loss of kelp cover during the hurricane at sites within St. Margarets Bay ($r^2 = 0.051$, p = 0.443) (Fig. 7a). However, there was a significant positive relationship between detritus accumulation below the kelp beds and site exposure ($r^2 = 0.934$, p < 0.001) (Fig. 7b). When Splitnose Point is included in these analyses, the results are qualita-
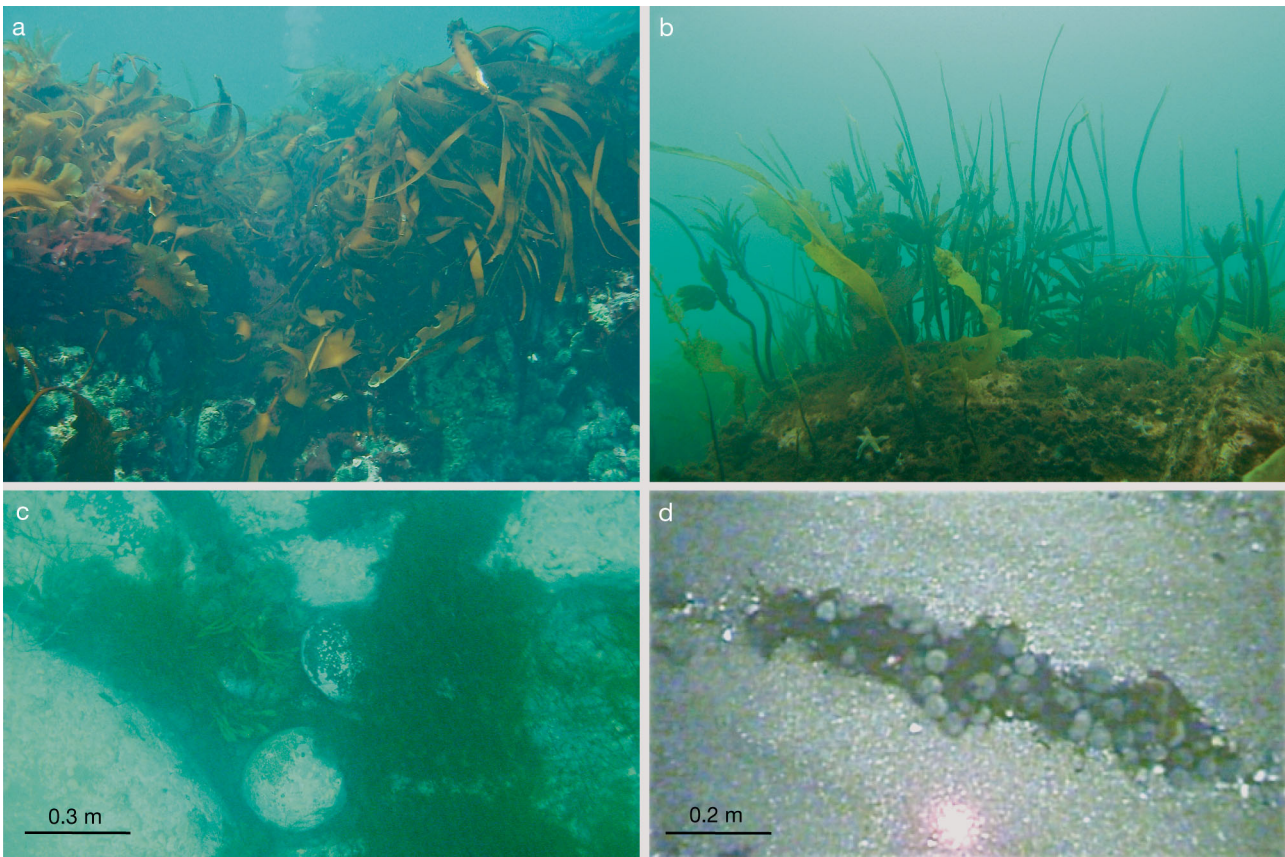
Fig. 5. (a) Splitnose Point kelp bed on 5 May 2008. (b) Defoliated kelp bed at the same location as (a) after Hurricane Earl on 8 September 2010. (c) Drift kelp off Splitnose Point at 18 m depth after Hurricane Earl on 13 September 2010. (d) Sea urchins aggregated on drift kelp off Southwest Island at 25 m depth before Hurricane Earl on 18 August 2010
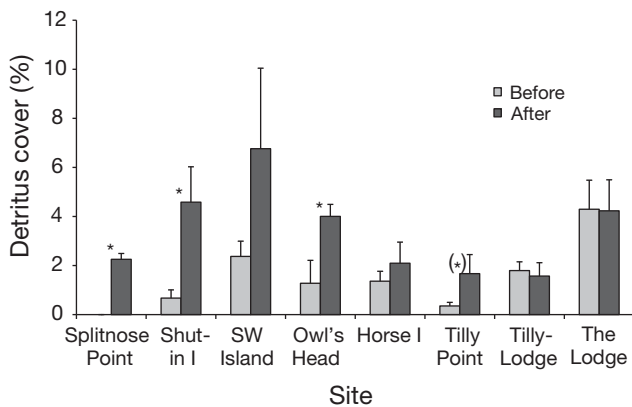

Fig. 6. Detritus cover (%) before and after Hurricane Earl at sites in St. Margarets Bay (Owl's Head, Horse Island, Tilly Point, Tilly-Lodge, Shut-in Island, and The Lodge) and near the mouth of Halifax Harbour (Splitnose Point). Owl's Head data are averaged across 3 transects, and Splitnose Point data are averaged across 4 transects. Sites are in order of decreasing exposure. Means + SE, n = 30. *: significant increase in detrital cover following Hurricane Earl. The change in detrital cover at Tilly Point (*) was marginally non-significant

tively similar (kelp loss: $r^2 = 0.061$, p = 0.594; detritus gain: $r^2 = 0.714$, p = 0.017). The increase in detritus at a site was not significantly related to the loss of kelp cover at that site ($r^2 = 0.164$, p = 0.184) (Fig. 7c).

Changes in sea urchin density and detrital deposits

Prior to Hurricane Earl, sea urchins were aggregated on drift algae on sand waves off Shut-in Island and Southwest Island. After the hurricane, sea urchins were no longer present on shallow sand waves (25 to 35 m depth) off Shut-in Island, where they previously occurred at an average density of 0.56 ind. m^{-2}, and the detritus cover on the sand waves increased to 4.6% from a pre-storm level of 0.7% (Fig. 6). Sea urchins also disappeared from sand waves off Southwest Island after the storm, and detritus cover (averaged across all frames in the sand-wave segment of video transects) increased to 6.8% from a pre-storm cover of 2.4%, with the greatest
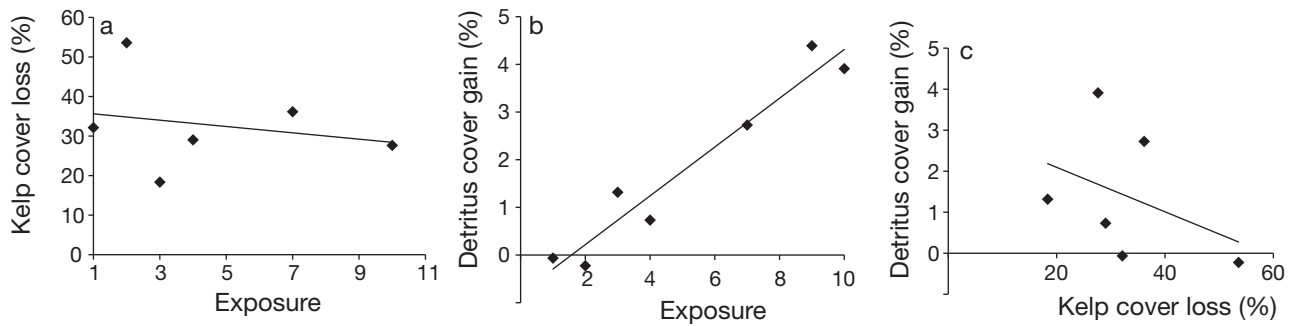
Fig. 7. Relationship (%) between (a) loss of kelp cover after Hurricane Earl and site exposure, (b) gain in kelp detritus cover after Hurricane Earl and site exposure, and (c) kelp cover loss and detritus cover gain for sites in St. Margarets Bay

increase at 15 to 20 m depth (from 16.3 to 38.6%; Fig. 8). These detrital deposits were still evident on 25 October 2010 but had dissipated by 4 February 2011. Deeper regions off Owl's Head (45 to 80 m) showed an increase in detritus cover following Hurricane Earl that persisted to February 2011 (Fig. 8). Sea urchins on drift kelp at Owl's Head did not decline in density following the hurricane (Fig. 8). These sea urchins were not associated with sand waves and occurred at greater depths than those off Southwest Island (where the basin is shallower). Sea urchins were also present in the deep sedimentary regions off Horse Island and Tilly Point (53 to 85 m), although the urchins were more sparsely distributed than those at similar depths off Owl's Head, Southwest Island, and Shut-in Island. Off the headland at Split-nose Point, sea urchins were abundant (reaching densities of 200 ind. m^{-2}) on bedrock ledges at 15 to 25 m depth, both before and after the storm (1 and 8 September 2010).

There was a marked loss of kelp biomass in cages with sea urchins (99.2 ± 14.2 g d^{-1}; mean ± SE, n = 2) and without sea urchins (70.9 ± 50.7 g d^{-1}) at 41 m depth in St. Margarets Bay. The kelp fronds in cages with sea urchins had signs of extensive grazing. The mass loss in cages without sea urchins is attributed to kelp fragmentation, which occurred at a rate of 2.6% d^{-1}. The increased loss in cages with sea urchins is attributed to the added effect of sea urchin grazing, including any increase in fragmentation caused by this grazing, which was estimated as 1.4 g ind.$^{-1}$ d^{-1} based on the difference in average mass loss between the treatments. Sea urchins in the laboratory grazed kelp at a rate of 1.9 g ind.$^{-1}$ d^{-1}. Consumption of caged kelp by mesograzers, such as amphipods, isopods, or small gastropods, is considered negligible because it occurs at a relatively slow rate compared to sea urchin grazing (Krumhansl & Scheibling 2012).

DISCUSSION

Kelp bed defoliation

Our study is the first to document the effects of a severe storm of known intensity on subtidal kelp beds and adjacent communities in the Northwest Atlantic. Hurricane Earl caused large-scale defoliation of kelp beds in the shallow subtidal zone (5 to 15 m depth) along the Atlantic coast of Nova Scotia and deposited drift algae in surrounding habitats in deeper waters (15 to 45 m). Averaged across all sites, the kelp cover was reduced by 46% after the hurricane, relative to pre-storm values. This loss of canopy cover during a single storm event is comparable to that recorded during major defoliation events associated with usual sea conditions or outbreaks of the invasive bryozoan *Membranipora membranacea*, which encrusts kelp and increases rates of blade breakage (Krumhansl et al. 2011). For example, Witman (1987) recorded a 64% reduction in kelp cover between July and November (from 28 to 10%) in Maine (USA), which he attributed to unusually high wave activity during the autumn of 1983. In Nova Scotia, Scheibling & Gagnon (2009) recorded major losses in kelp cover between June and November, with reductions of 63, 49, and 79% (relative to peak values) in 1993, 1997, and 1999, respectively, during periods of heavy encrustation by *M. membranacea*. *M. membranacea* was present at our sites at moderate levels of encrustation (Authors' pers. obs.) and may have contributed to the canopy loss we observed following Hurricane Earl.

The production and consumption of drift kelp is an important component of energy flow in the kelp bed ecosystem. Mann (1982) estimated that kelp beds in St. Margarets Bay produce 1750 g C m^{-2} yr^{-1} of kelp. When scaled to the total area of the bay, the primary productivity of kelps in the rocky subtidal zone
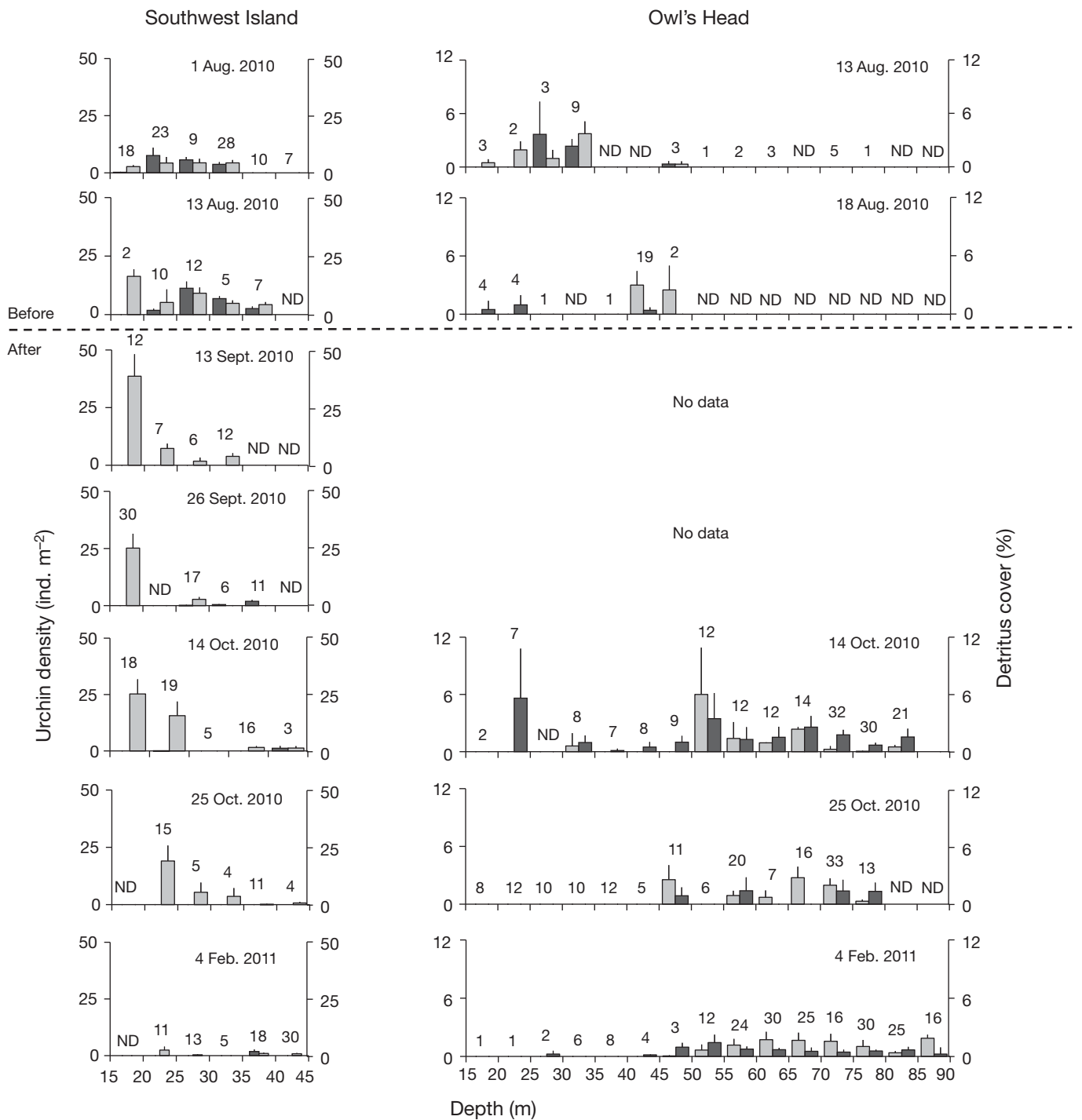
Fig. 8. Detrital kelp cover (%, light bars, right *y*-axis) and sea urchin density (ind. m^{-2}, dark bars, left *y*-axis) along depth gradient on a sand bottom adjacent to Southwest Island and Owl's Head before and after (dotted line) Hurricane Earl. Means + SE. The number of frames measured for each depth range are shown above bars. ND: no data

(600 g C m^{-2} yr^{-1}) is 3-fold greater than that of phytoplankton in the water column (200 g C m^{-2} yr^{-1}) (Ramus 1992). This massive amount of annual kelp production enters the marine food web mainly as de-

tritus (Mann 1988, Krumhansl & Scheibling 2011b). We observed large accumulations of detrital kelp on beaches, within the kelp bed, and in deep regions beyond the kelp bed directly after the passage of

Hurricane Earl. The pulsed delivery of algal detritus to these deep areas indicates that severe storm events may be a major pathway through which kelp production enters offshore benthic communities on sedimentary bottoms.

The impact of the hurricane in reducing kelp cover varied among sites, although more exposed sites did not experience higher kelp defoliation. This result is likely because kelps such as *Saccharina latissima* and *Laminaria digitata* are morphologically adapted to high wave forces and are more firmly attached by their holdfast at exposed sites (e.g. Splitnose Point) than at more protected areas (Gerard & Mann 1979, Thomsen et al. 2004), which may lower the risk of dislodgement in exposed areas, despite greater wave forces. Local variation in fetch, substratum type, and rugosity also may have contributed to variation in the degree of storm-mediated defoliation among sites.

Detrital kelp deposition

The amount of kelp cover lost after Hurricane Earl was not correlated with the increase of detrital cover directly offshore of a given site, suggesting that drift kelp is moved alongshore by currents and that deposits in a particular area may reflect the accumulation of material from kelp beds across a much larger span of coast. There was a strong positive relationship between the increase in detrital kelp cover and site exposure. This finding may be associated with deeper wave-mixing at more exposed sites, which deposits detritus across a greater depth range. Previous surveys of St. Margarets Bay show that hurricanes disrupt the summer thermocline (at ~30 m depth from June to September) and cause mixing to 50 m (Heath 1973). Bottom features are another important determinant of the amount of detrital deposition and its persistence in an area. Drift algae tend to accumulate in basins and deep canyons but not along the sloping continental shelf (Harrold et al. 1998). Off the headland at Splitnose Point, kelp detritus generated by Hurricane Earl collected around boulders and in crevices on bedrock ledges in the barrens immediately below the kelp bed, while deposits in deeper, more gradually sloping sandy regions (~55 m) were scant and short-lived. This pattern is likely because there are few topographic features to trap drift kelp, aside from scattered boulders on the sandy seabed, at this exposed site. Conversely, large detrital deposits in St Margarets Bay persisted for up to 6 wk, where they collected in deep sedimentary basins, such as at Owls Head, or in

areas of pronounced sand waves, such as Southwest Island and Shut-in Island. At 20 m depth in St Margarets Bay, clusters of drift kelp (72 g m^{-2}) can take longer than 4 mo to degrade (in the absence of sea urchins), increasing in nutritional value through microbial decomposition and accumulation of meio- and macrofauna (Krumhansl & Scheibling 2012). Thus, severe storm events can result in long-lasting pulses of high quality organic material in some offshore habitats.

Storm effects on sea urchin distribution and abundance

The impact of Hurricane Earl on deep-living sea urchins varied among sites. After the hurricane, sea urchins were absent on the expansive deposits of drift off Southwest Island and Shut-in Island at 15 to 35 m depth, where they had formerly been abundant. These sea urchins may have been displaced or buried by strong bottom currents or wave surge during the storm. Storm-induced bottom currents are typically stronger than regularly occurring tidal currents (Berné et al. 1988) and can alter sand waves in the subtidal zone (Viana et al. 1998). At depths of 15 to 25 m, storms often disrupt normal sand-wave patterns, creating more widely spaced, thicker waves in some regions and more closely spaced, thinner waves in others (Yang & Nio 1985). The present results suggest that this area experienced an increase in bottom current velocity. Siddon & Witman (2003) found that water velocities of 7.5 m s^{-1} are required to dislodge large sea urchins attached to bedrock, but much lower velocities are expected to displace sea urchins on sandy substrata to which they cannot firmly attach (Laur et al. 1986). No evidence of buried sea urchins or their tests appeared in our video transects, but sea urchins were found in deeper rocky areas off Southwest Island throughout the autumn. Sea urchins in shallow areas off Southwest Island could have been swept away by strong bottom currents during the storm, or they may have migrated offshore to deeper rocky habitats as wave action increased during the preceding 3 wk. Off Owl's Head, sea urchins persisted after Hurricane Earl on a sandy bottom without sand waves in a deep basin (40 to 90 m depth), where they were unaffected by the hydrodynamic forces generated by the storm at shallower depths. Thus, drift kelp deposited to sedimentary habitats adjacent to kelp beds after a hurricane may only benefit sea urchins in areas below the depth at which the storm displaces them.

Large influxes of drift kelp during storms may be important in maintaining dense sea urchin populations beyond the kelp beds in shallower water. In California, detrital exports from kelp forests enable sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) to graze passively, precluding the formation of destructive grazing fronts (Tegner & Dayton 1991). In Nova Scotia, the supply of drift kelp to deeper water also may reduce the likelihood of deep-living sea urchins migrating onshore, where they encounter and destructively graze kelp beds and form barrens (Scheibling et al. 1999, Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007a,b). Grazing fronts have periodically formed along the western shore of St. Margarets Bay (Scheibling et al. 1994, Lyons & Scheibling 2008), perhaps during times of low drift-kelp supply to the deep.

The turnover of drift kelp in deep areas in St. Margarets Bay is an indication of the long-term importance and persistence of detrital deposits and the rate at which this energy subsidy is incorporated into the benthic community. Sea urchins in cages at 42 m depth in the bay consumed drift kelp at a rate of 1.4 g ind.$^{-1}$ d^{-1}, which is within the recorded range for sea urchins grazing in shallow water (0.7 to 3.5 g ind.$^{-1}$ d^{-1}) (Lauzon-Guay & Scheibling 2007a) and comparable to the rate for caged individuals in the kelp bed at Splitnose Point (1.7 g ind.$^{-1}$ d^{-1}) (Sauchyn & Scheibling 2009a). Fragmentation of blades accounted for most of the mass loss of kelp within our cages. However, the extent of fragmentation may be overestimated in our experiment because lowering and hauling the cages may have artificially increased the hydrodynamic forces on the kelp. Also, a small gastropod mesograzer (*Lacuna vincta*) was abundant on the kelp and had extensively perforated the blades, making them more susceptible to breakage (Krumhansl & Scheibling 2011a, Krumhansl et al. 2011).

Kelp degradation rates observed in our experimental cages can be used to estimate the turnover time of detrital deposits. Deep-living sea urchins off Southwest Island and Owl's Head occurred at densities of 2 ind. m^{-2}. We used the average biomass of standing kelp (4.1 kg m^{-2}) measured in kelp beds with complete (100%) canopy cover in St. Margarets Bay and adjacent Mahone Bay from 1992 to 1995 (Scheibling et al. 1999) to approximate the biomass of drift kelp in deeper water from its cover on the seabed. Given an average cover for drift kelp within 1 m^2 of bottom off Southwest Island and Owl's Head of 4%, this translates to a biomass of 164 g m^{-2}. At an average sea urchin density of 2 ind. m^{-2} at these sites and a grazing rate of 1.4 g per urchin d^{-1} (from our cage

experiment), an average cover of drift kelp would be consumed in 58.6 d. This turnover rate indicates that the detrital deposits that we observed in late October at Owl's Head, 50 d after Hurricane Earl, could contain some drift kelp generated by the storm. The small amount of drift algae observed February 2011 in regions with sea urchins was likely not derived from the hurricane but detached by subsequent storms or by fragmentation due to other causes, such as grazing by *Lacuna vincta* or encrustation by *Membranipora membranacea*.

CONCLUSIONS

Hurricane Earl defoliated the kelp beds and deposited fragmented and dislodged kelp in deeper regions (15 to 45 m) beyond the kelp beds. This detrital export to food-limited communities exemplifies how a productive ecosystem can supply allochthonous subsidies to nearby habitats that increase overall secondary productivity. Given the predicted increase in the frequency of severe storm events along the Atlantic coast of Nova Scotia (Scheibling & Lauzon-Guay 2010), these pulses of drift algae are likely to become an increasingly important energy subsidy to the recipient benthic communities. The connectivity between kelp beds and neighbouring marine communities remains poorly understood. Elucidating biotic and abiotic processes that determine the spatio-temporal patterns of drift algal production and deposition and the response of the benthic community to detrital inputs is a promising and important area for future research.

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Appendix

Table A1. Locations of video transects at each site and date: start position coordinates, heading, length (m), and depth range. ND: no data

Site	Date	Position Coordinates	Heading (°)	Length (m)	Depth range (m)
Horse I	13/8/2010	44°32.02′ N, 64°00.76′ W	61	163	13–44
Horse I	13/9/2010	44°32.03′ N, 64°00.76′ W	73	87	22–42
The Lodge	18/8/2010	44°33.56′ N, 64°01.88′ W	67	359	14–35
The Lodge	13/9/2010	44°33.53′ N, 64°01.89′ W	89	344	10–45
Owl's Head 1	18/8/2010	44°31.53′ N, 64°00.36′ W	55	424	11–34
Owl's Head 1	14/10/2010	44°31.57′ N, 64°00.40′ W	50	279	24–74
Owl's Head 2	18/8/2010	44°31.34′ N, 64°00.17′ W	60	260	8–31
Owl's Head 2	14/10/2010	44°31.32′ N, 64°00.20′ W	65	298	10–71
Owl's Head 3	13/08/2010	44°31.19′ N, 64°00.11′ W	82	242	11–75
Owl's Head 3	26/9/2010	44°31.21′ N, 64°00.11′ W	90	118	11–42
Owl's Head 3	14/10/2010	44°31.20′ N, 64°00.12′ W	61	331	8–85
Owl's Head 3	25/10/2010	44°31.19′ N, 64°00.12′ W	90	240	10–76
Owl's Head 3	05/2/2011	44°31.20′ N, 64°00.12′ W	71	600	29–88
Shut-in I	31/8/2010	44°32.84′ N, 63°57.74′ W	200	540	18–48
Shut-in I	26/9/2010	44°32.84′ N, 63°57.74′ W	203	610	19–42
Southwest I	1/8/2010	ND	ND	ND	22–47
Southwest I	13/8/2010	44°30.67′ N, 63°59.74′ W	99	395	25–48
Southwest I	13/9/2010	44°30.63′ N, 63°59.82′ W	51	305	10–35
Southwest I	14/10/2010	44°30.68′ N, 63°59.83′ W	78	481	21–60
Southwest I	25/10/2010	44°30.67′ N, 63°59.83′ W	80	377	4–62
Southwest I	26/9/2010	44°30.66′ N, 63°59.82′ W	77	314	6–42
Southwest I	5/2/2011	44°30.68′ N, 63°59.83′ W	79	900	27–56
Splitnose Pt 1	1/9/2010	44°28.65′ N, 63°32.79′ W	101	1048	7–53
Splitnose Pt 1	8/9/2010	44°28.65′ N, 63°32.77′ W	88	250	4–20
Splitnose Pt 2	1/9/2010	44°28.57′ N, 63°32.83′ W	91	611	8–30
Splitnose Pt 2	8/9/2010	44°28.57′ N, 63°32.84′ W	89	575	5–20
Splitnose Pt 3	1/9/2010	44°28.39′ N, 63°32.90′ W	92	767	5–45
Splitnose Pt 3	8/9/2010	44°28.40′ N, 63°32.92′ W	91	375	5–24
Splitnose Pt 4	1/9/2010	44°28.15′ N, 63°32.99′ W	91	344	11–42
Splitnose Pt 4	8/9/2010	44°28.16′ N, 63°33.00′ W	100	390	9–25
Tilly Point	18/8/2010	44°32.31′ N, 64°00.93′ W	75	322	14–49
Tilly Point	26/9/2010	44°32.33′ N, 64°00.93′ W	94	263	6–45
Tilly-Lodge	18/8/2010	44°32.87′ N, 64°01.27′ W	108	335	10–45
Tilly-Lodge	26/9/2010	44°32.81′ N, 64°01.26′ W	84	333	8–32