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Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. *fragile*

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ABSTRACT: Invasive species have the potential to alter the dynamics of detrital subsidy from high to low productivity areas through changes in quantity and nutritional quality of detrital material. We examined the effect of the invasive alga *Codium fragile* ssp. *fragile* on the nature of detrital export from subtidal algal beds off Nova Scotia, Canada, by comparing changes in mass, nutritional quality (%C, %N, C/N ratio), concentration of dimethylsulfoniopropionate (DMSP, a secondary metabolite that deters grazers), and isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) between *C. fragile* and the native kelp *Saccharina latissima* at 4 wk intervals over 16 wk of degradation in cages on a sand bottom at 19 m depth. *C. fragile* degraded more slowly, and had a consistently lower C/N and higher DMSP concentration, than *S. latissima*. Isotope signatures did not differ between algal species: $\delta^{15}N$ became slightly enriched (~1‰) after 16 wk of degradation, with no change in $\delta^{13}C$. We also compared macrofaunal communities associated with degrading thalli of each algal species and found significantly higher abundances of invertebrates (mainly capitellid polychaetes) on *S. latissima* after 8 wk of degradation, resulting in lower evenness (J') and diversity (H') on *S. latissima* compared to *C. fragile*. Macrofaunal community composition became similar between algal species at 12 and 16 wk in concordance with decreases in C/N ratio in *S. latissima* and DMSP concentration in *C. fragile*. Our results indicate that differences in biochemical composition and the rate of degradation between *C. fragile* and native kelps result in community-level effects in areas linked to shallow algal beds via the transfer of detritus.

KEY WORDS: *Codium fragile* · Kelp · Degradation · Invasive species · Detritus · Stable isotopes

INTRODUCTION

The transfer of organic detritus from highly productive macroalgal beds to adjacent habitats can be an important trophic linkage (Duggins & Simenstad 1989, Bustamante et al. 1995, Bustamante & Branch 1996, Britton-Simmons et al. 2009), particularly if local productivity in the recipient community is low or of poor nutritional quality (Tenore & Hanson 1980, Bouillon et al. 2002, Wernberg et al. 2006). The supply of allochthonous material can represent a substantial energy subsidy in these situations, influencing patterns of community organization and secondary production (Bustamante et al. 1995). Invasive species have the potential to alter trophic connectedness by changing the species composition, productivity, and biomass of macroalgal assemblages and, in turn, the quantity and quality of exported detrital material (Krumhansl & Scheibling 2011).

Large quantities of detritus are produced from subtidal kelp beds annually through continuous erosion and fragmentation of blades and dislodgement of thalli (Chapman 1984, Tala & Edding 2007, Krumhansl & Scheibling 2011). This material can be transported inshore or alongshore to low-energy habitats at shallower or similar depths, or offshore to deeper sedimentary or rocky habitats with low local productivity (Chapman 1981, Mann 1982, Scheibling et al. 1999). Sea urchins can locate, trap, and rapidly consume algal detritus as it is transported or

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deposited in deeper waters (Vetter & Dayton 1999, Britton-Simmons et al. 2009). Where sea urchins are absent, however, deposits of detrital kelp may accumulate and remain on the order of months to years (Tzetlin et al. 1997, Vetter & Dayton 1998, Filbee-Dexter & Scheibling 2012), degrading slowly and being consumed by other macrofauna.

The green algal genus *Codium* has a broad geographic distribution and *C. fragile* ssp. *fragile* (formerly *tomentosoides*, Provan et al. 2008, hereafter *C. fragile*) is among the most invasive algal species worldwide (Carlton & Scanlon 1985, Trowbridge 1998). *C. fragile* was first introduced to Nova Scotia, Canada, in the late 1980s (Bird et al. 1993) and had spread along the entire Atlantic coast by 2007, forming monospecific meadows or mixed stands with native kelps (Chapman et al. 2002, Watanabe et al. 2010). In the NW Atlantic, *C. fragile* fragments in the fall and is dislodged from the substratum during winter storms (Begin & Scheibling 2003, D'Amours & Scheibling 2007). Large mats of drifting thalli and branched fragments of *C. fragile* have been observed in shallow sedimentary areas adjacent to dense stands of the alga; these mats can persist for months before they are transported offshore during storms (Watanabe et al. 2009). The effects of *C. fragile* on community dynamics have been well documented both within kelp beds (Scheibling & Gagnon 2006, Schmidt & Scheibling 2006, 2007) and in intertidal habitats (Jones & Thornber 2010, Lutz et al. 2010), but the fate of detrital fragments of *C. fragile* is unknown.

Macrophyte tissues usually have a high content of indigestible fibrous carbon and low contents of nitrogen and protein, which limits their nutritional value to most herbivores (Mann 1988). Consequently, much of the primary production from macrophyte assemblages, such as kelp beds and seagrass meadows, enters detrital pathways rather than being directly grazed (Mann 1988, Cebrian 1999). Macrophyte detritus is colonized by microbes that break down refractory carbon and draw in nitrogen from seawater, thereby increasing the nutritional value and facilitating consumption by a wider variety of consumers (Mann 1988). The rate of degradation is therefore largely dependent on the extent of microbial colonization and transformation and varies among macrophyte phyla (Tenore & Hanson 1980). Consumption of live macrophyte tissues may be restricted by secondary metabolites, such as phlorotannins found in high concentrations in kelps and other brown algae (Johnson & Mann 1986, Paul 1992, Iken et al. 2009). Phlorotannins break down as kelp degrades (Norderhaug et al. 2003), increasing the palatability of kelp for detritivores. Dimethylsulfoniopropionate (DMSP) is another secondary metabolite found in all macroalgal phyla, with highest concentrations in green algae (Van Alstyne & Puglisi 2007). DMSP is produced, and cleaved into dimethylsulfide (DMS) and acrylic acid, as an activated defense against herbivory (Van Alstyne et al. 2001, Van Alstyne & Houser 2003, Lyons et al. 2010). DMSP occurs in high concentration in *Codium fragile* and varies seasonally in response to changing water temperature and light intensity (Lyons et al. 2007, 2010). Like phlorotannins in kelps, concentration of DMSP may decrease during degradation of *C. fragile*, but this has not been examined.

Stable isotope ratios of C and N are widely used to track the flow of organic matter from primary producers to consumers in marine food webs (Peterson & Fry 1987). Microbial degradation can affect these isotopic ratios in algal tissues, although this has only been examined for a few species of marine macroalgae (Stephenson et al. 1986, Fenton & Ritz 1988, Hill & McQuaid 2009). In food webs where most of the primary production enters detrital pathways, degradation may obscure linkages based on isotopic signatures in live tissue, underscoring the importance of measuring changes in isotopic ratios during degradation of detritus.

In the present study, we examine the effect of *Codium fragile* on the nature of detrital export from shallow kelp beds by comparing changes in mass, nutritional quality and palatability, and isotopic composition between the invasive alga and native kelp *Saccharina latissima* (formerly *S. longicruris*, McDevit & Saunders 2010) at 4 wk intervals over 16 wk of degradation. To examine how changes in the quantity and nutritional quality of detrital material influence colonization by macrofauna, we concurrently measured changes in the macrofaunal assemblage associated with each algal species. These results improve our understanding of the dynamics of detrital subsidies from kelp beds and broaden our knowledge of the effects of invasive species beyond the habitats to which they have been introduced.

MATERIALS AND METHODS

Experimental design

The experimental site (The Lodge, 44° 33′ 32.98″ N, 64° 01′ 56.75″ W) is located near the mouth of a large semi-protected embayment, St. Margarets Bay, near

Halifax, Nova Scotia, Canada. The rocky substratum consists of ledges and boulders that grade to sand at ~17 m depth. Kelps (primarily *Saccharina latissima*, *Laminaria digitata*, and *Agarum cribosum*) form a dense canopy, which peaks in cover from May to July and declines from October to December (Krumhansl & Scheibling 2011). *Codium fragile* is interspersed with kelps, following a similar seasonal pattern in abundance (Schmidt & Scheibling 2005). Sandy substrata below the limit of boulders and ledges are devoid of attached fleshy macroalgae but periodically accumulate deposits of drift algae (K. Filbee-Dexter & R. E. Scheibling unpubl. data). Our experiment was conducted from 9 August to 29 November 2010 to coincide with seasonal decreases in the biomass of kelps and *C. fragile* in the shallow subtidal zone.

To measure changes in biochemical properties of algal tissues and colonization by macrofauna during degradation, we placed thalli of *Codium fragile* or *Saccharina latissima* into nylon-mesh (0.5 cm aperture) bags that were placed within plastic cages (33 × 33 × 27 cm, 2.5 cm aperture) anchored to the sandy seabed at 19 m depth. Large thalli of *S. latissima* (100 to 200 cm total length) and *C. fragile* (50 to 75 cm) without visible signs of degradation or heavy colonization by epibionts were haphazardly collected using SCUBA from the algal bed at 5 to 7 m depth. Thalli were cleaned of any epibionts, air dried for 1 min, and weighed into ~500 g (0.001 g precision) batches that mimicked small deposits of drift algae. These were loosely packed in labeled mesh bags (40 × 50 cm, 0.5 cm aperture), with 12 replicate bags per algal species, and kept in seawater until delivery to the seabed by divers. Bags were randomly allocated to 24 numbered cages that were anchored to the sand bottom and spaced at 1.5 m intervals along a single linear array running parallel to and approximately 4 to 6 m away from the lower margin of the algal bed. There were 3 replicates of each combination of 4 levels of time (4, 8, 12, or 16 wk of degradation) and 2 levels of species (*S. latissima*, *C. fragile*) in this factorial, completely randomized design. At each time interval, replicate bags of each algal species (n = 3) were collected and transported in coolers to the laboratory, where they were placed in flow-through seawater tanks and processed within 3 h. The mesh bags remained on the sediment surface throughout the experiment (i.e. were not buried), although some sedimentation occurred within bags as a result of reduced flow.

Temperature was measured at 30 min intervals at the experimental array using a HOBO pendant data logger (Onset Computer Corp.). Temperature was highly variable during the first 12 wk of the experimental period, ranging from 5.5 to 20.0°C, then stabilized over the last 4 wk (Fig. 1). Mean temperature during each sampling interval was relatively constant, ranging from 9.6 to 11.2°C.

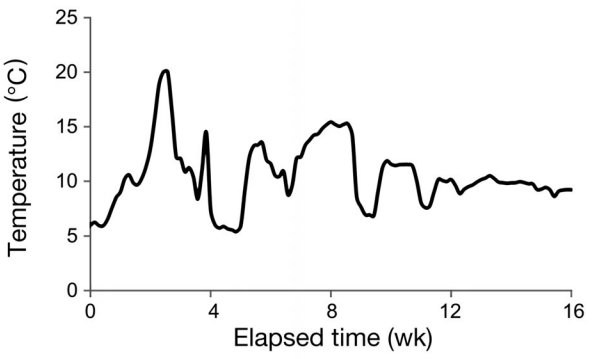

Fig. 1. Average daily temperature (°C) at the experimental array (19 m depth) over the 16 wk experimental period (9 August to 29 November 2010)

Sample processing and analyses

In the laboratory, the algal sample in each bag was cleaned of epibionts and weighed. Macrofauna (body size > 1 mm) on each algal sample or in the respective mesh bag were placed directly into 70% ethanol and identified (to the lowest taxonomic level possible) using a dissecting microscope. A section of each sample was rinsed in distilled water and dried at 60°C for 48 h until constant weight. Dried algal samples were ground to a fine homogeneous powder using a mortar and pestle and weighed into tin capsules and shipped to the Stable Isotopes in Nature Laboratory at the University of New Brunswick (Saint John, New Brunswick, Canada) for C and N content and isotopic ($\delta^{13}C$, $\delta^{15}N$) analysis. The isotopic value of each sample is reported in δ notation as:

$$\delta X(‰) = (R_{sample}/R_{standard} - 1) \times 1000$$

where $\delta X = \delta^{13}C$ or $\delta^{15}N$ and $R = {}^{13}C:{}^{12}C$ or ${}^{15}N:{}^{14}N$. PeeDee belemnite and air were used as standards for C and N, respectively.

A 1 cm^2 section of each algal sample was placed in a 14 ml glass vial containing 2 ml 10 M NaOH at the sea surface immediately upon delivery from the seabed and crimped with a Pharma-fix septa (Graze Alltech). Sections of tissue were selected from the middle of a branch for *Codium fragile* and central

region of a blade for *Saccharina latissima*. The vials were stored at room temperature in the dark to allow the DMS in each sample to equilibrate with the vial headspace. Samples were analyzed for both intracellular DMS and DMSP, collectively termed DMS(P). Then, 100 µl (*S. latissima*) or 10 µl (*C. fragile*) of vial headspace was analyzed by gas chromatography using a Shimadzu 2014 gas chromatograph fitted with a 25 m capillary column (Restek RTx-5MS, 0.25 mm ID) and sulfur-specific flame photometric detector (FPD) at the University of Glasgow, UK (injector port and column oven temperature, 45°C; detector temperature, 200°C). DMS peak retention time was ~1.5 min. Sample concentrations were quantified from DMSP standard calibration curves (DMSP standard from Research Plus Inc.), and normalized by sample dry weight (g). The limit of detection was 960 ng S per 100 µl injection (headspace); standard and sample precision was within 3%.

Statistical analyses

The effect of algal species (*Saccharina latissima* or *Codium fragile*) and elapsed time (fixed factors) on the mass (4 to 16 wk) and biochemical properties of algal tissues (0 to 16 wk) was analyzed using a 2-way analysis of variance (ANOVA), except for DMS(P) concentration which was analyzed using 1-way ANOVA for *C. fragile* only. Transplantation stress may have caused an increase in DMSP in the first 4 wk of the experiment (Lyons et al. 2010); therefore, only 4 to 16 wk were included in this analysis. The abundance of associated macrofauna, and species richness, Pielou's evenness index (J'), and Shannon's diversity index (H'), were also compared between algal species and over time (4 to 16 wk) using a 2-way ANOVA. Post hoc tests (Tukey's honestly significant difference [HSD] test, $\alpha = 0.05$) were used to identify patterns over time within each algal species. Wet mass and abundance data were log(x) transformed, and % C and % N data were arcsine transformed to meet the assumptions of normality (Shapiro-Wilk's test, $\alpha = 0.05$) and homogeneity of variance (Bartlett's test, $\alpha = 0.05$). Evenness data were normally distributed, but variances were heterogeneous. Transformation of these data did not improve variance homogeneity, and untransformed data were used.

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), based on Bray-Curtis similarity matrices calculated from square-root-transformed data, was used to examine the effect of algal species and elapsed time on macrofaunal composition. Homogeneity of multivariate dispersions was satisfied for community data grouped by algal species and elapsed time (permutational analysis of multivariate dispersions, $p > 0.05$; Anderson 2004). Cluster analysis was then used to determine similarities among samples. Taxa that most contributed to differences between algal species and among time intervals were identified using the similarities of percentages routine (SIMPER). The effects of algal species and elapsed time on the abundances of these taxa were analyzed using 2-way ANOVA. Macrofaunal abundance was log(x+1) transformed as required to meet the assumption of normality and homogeneity of variance. Multivariate analyses were conducted using PRIMER 6 software with the PERMANOVA+ package (Clarke & Gorley 2006).

Table 1. Two-way ANOVA of the effect of algal species and elapsed time (0, 4, 8, 12, and 16 wk) on the weight (g), % C, % N, $\delta^{13}C$, and $\delta^{15}N$ of degrading algal samples. Tukey's pairwise comparisons were made where time was significant. Lines connect non-significant subsets of treatment means

Response Factor	df	MS	*F*	p	Pairwise
Wet mass					
Algae	1	5.17	26.0	<0.001	
Time	3	4.57	23.0	<0.001	4 8 12 16
Time × Algae	3	0.53	2.67	0.083	
Residual	16	0.20			
% C					
Algae	1	0.29	723	<0.001	
Time	4	<0.01	1.40	0.270	
Time × Algae	4	<0.01	1.25	0.323	
Residual	20	<0.01			
% N					
Algae	1	<0.01	10.5	0.0041	
Time	4	<0.01	15.4	<0.001	0 4 8 12 16
Time × Algae	4	<0.01	2.20	0.1056	
Residual	20	<0.01			
δ^{13} C					
Algae	1	0.73	0.368	0.551	
Time	4	2.00	1.01	0.425	
Time × Algae	4	2.73	1.38	0.276	
Residual	20	1.98			
δ^{15} N					
Algae	1	<0.01	0.0060	0.936	
Time	4	0.99	5.42	0.004	0 4 8 12 16
Time × Algae	4	0.05	0.280	0.887	
Residual	20	0.09			

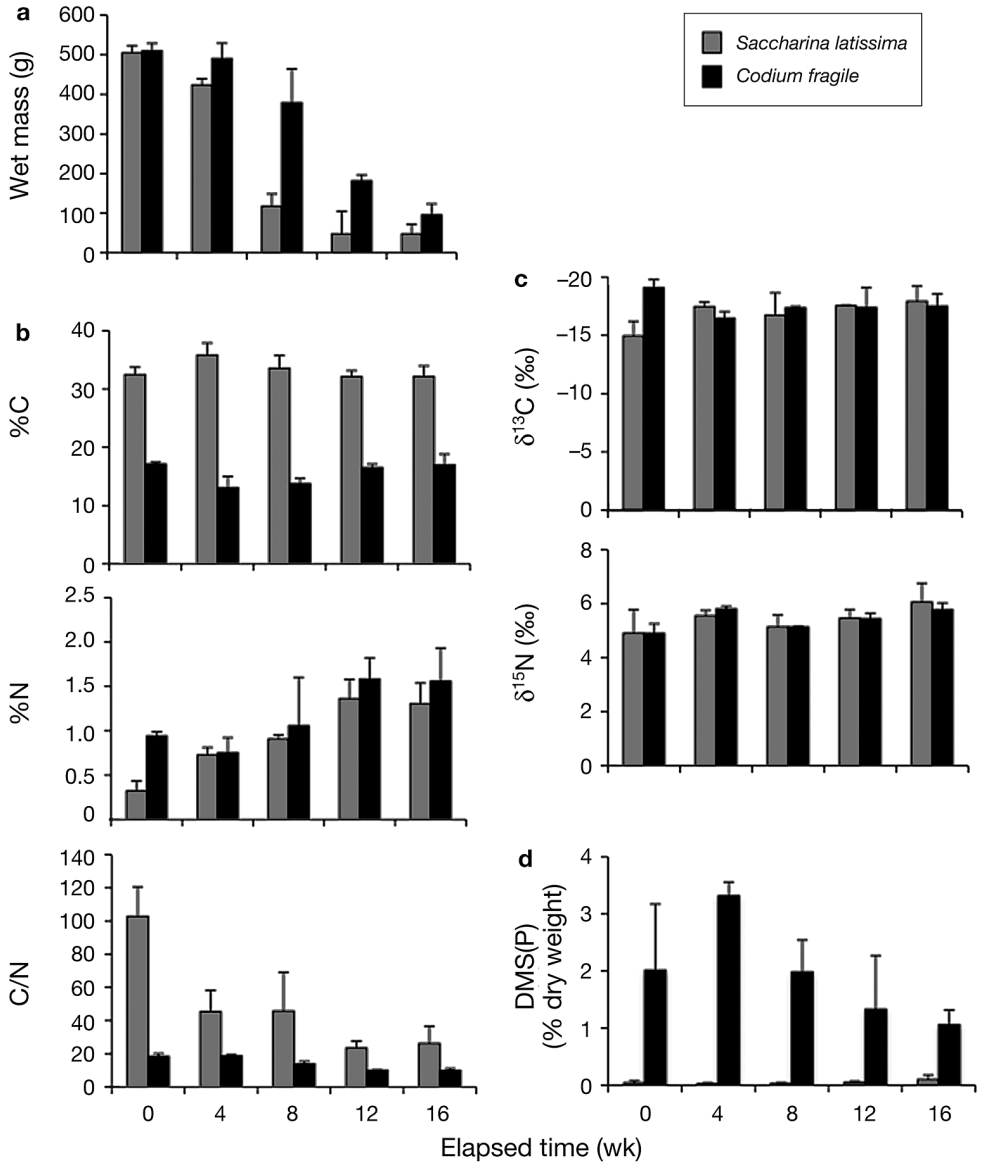

Fig. 2. *Saccharina latissima* and *Codium fragile*. (a) Wet mass (g), (b) % C, % N, C/N ratio, (c) $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), and (d) dimethylsulfide and dimethylsulfoniopropionate, DMS(P), concentration (% dry weight) of the 2 algal species at the start of the experiment and after 4, 8, 12, and 16 wk of degradation. Data are means (+1 SD, n = 3)

RESULTS

Changes in mass and biochemical composition

The wet mass of both *Saccharina latissima* and *Codium fragile* decreased (Table 1, Fig. 2a) to 9.5 and 18.4% of initial mass after 16 wk, respectively. Mass loss of *S. latissima* was greatest between 4 and 8 wk (63% decrease), while *C. fragile* showed a near linear decrease in mass between 4 and 16 wk. Carbon content of *S. latissima* (32.0%, averaged over all intervals) was approximately twice that of *C. fragile* (15.5%), and did not change significantly during degradation for either species (Fig. 2b, Table 1). Nitrogen content was significantly higher in *C. fragile* (1.18% averaged over all intervals) than in *S. latissima* (0.92%) and increased significantly in both species between 8 and 12 wk (Fig. 2b, Table 1). Consequently, the C/N ratio of both algal species decreased during the 16 wk of degradation, but this decrease was much greater for *S. latissima* (from 102.8 to 26.2) than for *C. fragile* (from 18.3 to 9.9) (Fig. 2b). $\delta^{13}C$ did not differ significantly between algal species or between sampling intervals (Fig. 2c,

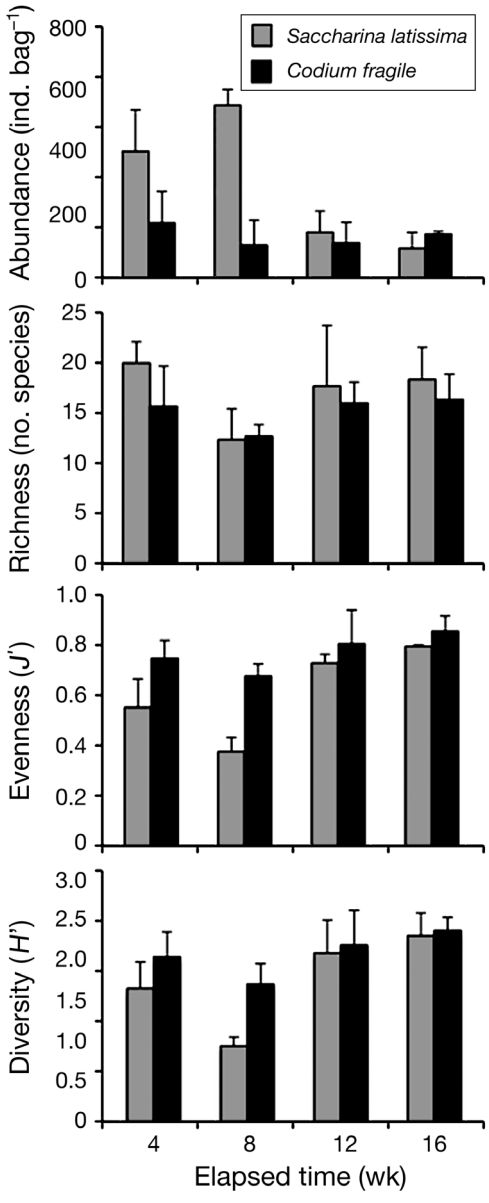

Fig. 3. *Saccharina latissima* and *Codium fragile*. The abundance (ind. bag^{-1}), richness (no. of species), evenness (*J'*), and diversity (*H'*) of macrofaunal communities associated with the 2 algal species after 4, 8, 12, and 16 wk of degradation. Data are means (+1 SD, n = 3)

Table 1), which ranged from −15.0 to −19.1‰. $\delta^{15}N$ did not differ between algal species but increased between 0 and 16 wk for *S. latissima* (6.1‰) and *C. fragile* (5.8‰) (Fig. 2c, Table 1).

The concentration of DMS(P) in degrading *Codium fragile* (1.0 to 3.3%) was 1 to 2 orders of magnitude higher than in degrading *Saccharina latissima* (0.03 to 0.1%) and decreased significantly between 4 and 16 wk ($F_{3,8}$ = 9.22, p = 0.006, Tukey's HSD: 4 > 12 = 16 wk) (Fig. 2d).

Macrofaunal communities

Macrofauna colonized both *Saccharina latissima* and *Codium fragile* within 4 wk, but differences in faunal abundance between species varied among sampling intervals, resulting in a significant interaction between algal species and elapsed time (Fig. 3, Table 2). Macrofaunal abundance was approximately 2 and 6 times greater on *S. latissima* than on *C. fragile* after 4 and 8 wk, respectively, but then decreased markedly on *S. latissima* between 12 and 16 wk, when abundance no longer differed between algal species (Fig. 3, Table 2). A total of 41 and 37 taxa (14 identified to family, 4 to genus, 23 to species) were associated with degrading *S. latissima* and *C. fragile,* respectively, throughout the experiment (Appendix 1). Taxonomic richness did not differ between algal species, with means ranging from 12 to 20 taxa on *S. latissima* and from 12 to 15 taxa on

Table 2. Two-way ANOVA of the effect of algal species (C: *Codium fragile*; S: *Saccharina latissima*) and elapsed time (4, 8, 12, and 16 wk) on the richness (no. of species), abundance (ind. bag^{-1}), evenness (*J'*), and diversity (*H'*) of macrofaunal communities associated with degrading algal samples. Tukey's pairwise comparisons were made where time or the interaction between algal species and time were significant. Lines connect non-significant subsets of treatment means: horizontal lines compare time intervals; vertical lines compare algal species when there is a significant interaction

Response Factor	df	MS	*F*	p	Pairwise
Richness					
Algae	1	22.0	1.98	0.178	
Time	3	36.0	3.24	0.050	
Time × Algae	3	5.49	0.493	0.692	
Residual	16	11.1			
Abundance					
Algae	1	2.98	11.3	0.004	
Time	3	0.99	3.77	0.032	
Time × Algae	3	1.23	4.68	0.016	C: 4 8 12 16 S: 4 8 12 16
Residual	16	0.26			
Evenness					
Algae	1	0.15	25.6	<0.001	
Time	3	0.11	18.1	<0.001	4 8 12 16
Time × Algae	3	0.02	3.24	0.050	
Residual	16	0.01			
Diversity					
Algae	1	0.66	7.10	0.017	
Time	3	1.19	12.7	<0.001	4 8 12 16
Time × Algae	3	0.16	1.71	0.205	
Residual	16	0.09			

C. fragile across sampling intervals (Fig. 3, Table 2). Richness was lowest on both species at 8 wk, although the effect of time was marginally non-significant (p = 0.050) (Table 2). Indices of evenness (*J'*) and diversity (*H'*) were significantly higher for *C. fragile* than *S. latissima* and varied significantly over time, with lowest values for both species at 8 wk (Fig. 3, Table 2).

Cluster analysis indicated >60% similarity among macrofaunal assemblages on *Saccharina latissima* that degraded for 4 and 8 wk, with 1 outlier at 8 wk. In contrast, macrofaunal assemblages on *Codium fragile* that degraded for 4 wk were highly variable in composition (<40% similarity) and distinct from samples of *S. latissima*. The similarity of samples of *C. fragile* increased slightly at 8 wk (55% similar) but remained distinct from those of *S. latissima*. Macrofaunal assemblages from algae that had degraded for 12 wk were more similar in composition between and within algal species; samples of both algal species showed >60% similarity at 16 wk. PERMANOVA detected a significant interaction between algal species and elapsed time in the composition of macrofaunal assemblages (Table 3), as differences between *S. latissima* and *C. fragile* diminished with algal degradation.

SIMPER analysis identified polychaetes of the family Capitellidae as contributing most to differences in macrofaunal assemblage between *Saccharina latissima* and *Codium fragile* and to changes over time on *S. latissima* (Appendix 2). Capitellidae were more abundant on *S. latissima* than *C. fragile* at 4, 8, and 12 wk but were rare on both algal species at 16 wk (Fig. 4, Table 4). The razor clam *Ensis directus* contributed most to differences between *S. latissima* and *C. fragile* at 16 wk and to differences between time intervals in *C. fragile*, with the highest abundances observed on *C. fragile* at 16 wk (Fig. 4, Table 4, Appendix 2). Relatively high abundances of amphipods of the family Gammaridae on both algal species at 4 wk contributed to differences between these samples and those that had degraded for 8, 12, and 16 wk (Fig. 4, Table 4, Appendix 2). SIMPER also identified shrimp (*Mysis* spp.) and a small gastropod (*Lacuna vincta*) as contributing to differences in community composition over the course of degradation on *C. fragile* (Appendix 2), but the effects of algal species and elapsed time on the abundance of each of these taxa were non-significant (Table 4).

Table 3. Two-way permutational multivariate analysis of variance (PERMANOVA) of the effect of algal species (*Codium fragile* and *Saccharina latissima*) and elapsed time (0, 4, 8, 12, and 16 wk) on overall macrofaunal community composition of degrading algal samples

Factor	df	MS	*F*	p
Time	3	0.00392	4.64	0.001
Algae	1	0.00261	3.08	0.001
Time × Algae	3	0.00187	2.21	0.002
Residual	16	0.0846		

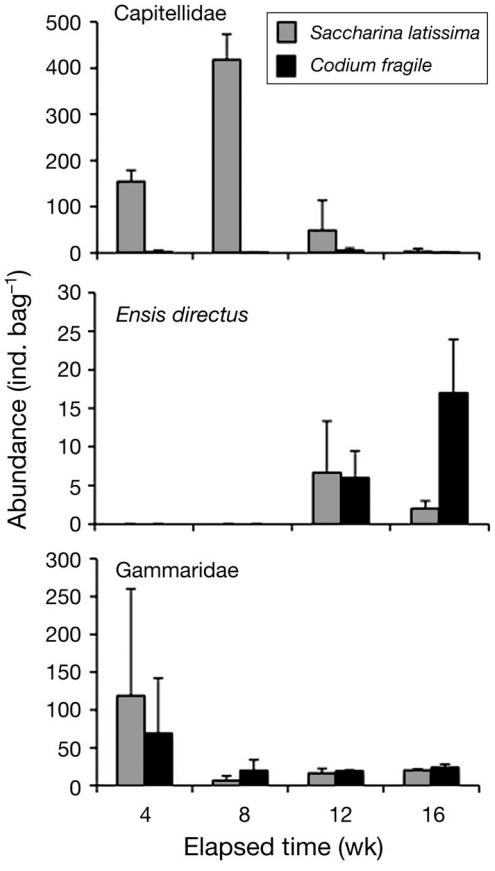

Fig. 4. Abundances of the taxa (Capitellidae, *Ensis directus*, and Gammaridae, as identified by SIMPER (similarity of percentages), that contributed most to differences in macrofaunal community composition on *Saccharina latissima* and *Codium fragile* after 4, 8, 12, and 16 wk of degradation, and that varied significantly over time or between algal species. Data are means (+1 SD, n = 3)

DISCUSSION

We have shown that detached thalli of *Saccharina latissima* and *Codium fragile* differ significantly in their rate of degradation, and the manner in which biochemical composition and nutritional quality change during degradation, indicating that displace-

Table 4. Two-way ANOVA of the effect of algal species (C: *Codium fragile*; S: *Saccharina latissima*) and elapsed time (4, 8, 12, and 16 wk) on the abundance (ind. bag^{-1}) of taxa identified by SIMPER as contributing most to differences in overall macrofaunal community composition between degrading algal samples. Tukey's pairwise comparisons were made where time or the interaction between algal species and time were significant. Lines connect non-significant subsets of treatment means: horizontal lines compare time intervals; vertical lines compare algal species when there is a significant interaction

Response Factor	df	MS	*F*	p	Pairwise
Capitellidae					
Algae	1	47.9	34.8	<0.001	
Time	3	8.95	6.50	0.004	
Time × Algae	3	8.41	6.11	0.006	C: 4 8 12 16 | S: 4 8 12 16
Residual	16	1.38			
Gammaridae					
Algae	1	0.43	0.531	0.477	
Time	3	2.94	3.60	0.037	4 8 12 16
Time × Algae	3	0.94	1.15	0.361	
Residual	16	0.76			
***Mysis* spp.**					
Algae	1	0.12	0.167	0.688	
Time	3	0.70	0.994	0.421	
Time × Algae	3	1.94	2.74	0.077	
Residual	16	0.71			
Lacuna vincta					
Algae	1	0.05	0.0373	0.849	
Time	3	0.70	0.568	0.644	
Algae × Time	3	1.68	1.37	0.288	
Residual	16	1.23			
Ensis directus					
Algae	1	1.33	6.39	0.022	
Time	3	7.00	33.5	<0.001	
Algae × Time	3	1.16	5.54	0.008	C: 4 8 12 16 | | | S: 4 8 12 16
Residual	16	0.21			

ment of native kelps by *C. fragile* alters the nature of detrital export from shallow subtidal areas. Degradation of *C. fragile* was delayed compared to *S. latissima*, resulting in a lower mass loss in *C. fragile* after 16 wk. The concentration of the grazing-deterrent compound DMS(P) (Van Alstyne & Houser 2003, Lyons et al. 2010) increased slightly in *C. fragile* 4 wk after transplantation, when mass loss was minimal, likely in response to a decrease in water temperature with depth (Lyons et al. 2010). Similarly, the concentration of DMS(P) in attached *C. fragile* at 5 to 7 m depth (the source of experimental thalli) increased over the course of the experiment from 2.0 to 7.0% (not shown) as temperatures decreased in the shallows from 23 to 7°C. High DMS(P) concentration in *C. fragile* may have deterred consumption by macrofauna initially, but as degradation progressed, DMS(P) concentration gradually declined along with algal mass, coinciding with a change in the taxonomic composition and abundance of associated macrofauna. Live tissue from *S. latissima* had a higher C/N ratio than *C. fragile*, and therefore a relatively low nutritional value for most consumers (Hessen 1992, Norderhaug et al. 2003). We observed a marked decrease in C/N ratio of degrading *S. latissima*, which generally is attributed to microbial colonization and transformation (Mann 1988, Duggins & Eckman 1997, Norderhaug et al. 2003). C/N ratio was much lower in *C. fragile* than in *S. latissima* and decreased minimally during degradation. This is consistent with previous work showing a higher protein content and lower C/N of *C. fragile* relative to other brown algal species, indicating higher nutritional quality (Cruz-Rivera & Hay 2001, Zhang et al. 2010).

Degradation did not affect $\delta^{13}C$ signatures of *Saccharina latissima* and *Codium fragile*. Stephenson et al. (1986) also found no change in $\delta^{13}C$ of *S. latissima* during degradation, and minimal depletion in $\delta^{13}C$ (~1‰) has been reported in other macroalgal species, including the kelp *Ecklonia radiata* (Fenton & Ritz 1988, Hill & McQuaid 2009). $\delta^{15}N$ signatures of *S. latissima* and *C. fragile* became slightly enriched during degradation, likely because of microbial assimilation of $\delta^{15}N$-enriched dissolved inorganic nitrogen (DIN) (Macko & Estep 1984). The magnitude and direction of changes in $\delta^{15}N$ during degradation vary across primary producer groups (Caraco et al. 1998, Hill & McQuaid 2009) in response to differences in microbial community composition, the C/N ratio of the organic substrate, and spatial variation in the $\delta^{15}N$ composition of DIN (Macko & Estep 1984, Lehmann et al. 2002). Changes in $\delta^{15}N$ during degradation may obscure interpretation of the trophic position of consumers in stable isotope analysis of benthic food webs. For example, $\delta^{13}C$ values in sea urchins collected in barrens up to 240 m from kelp beds indicate that drift kelp is an important food source (Kelly et al. 2012). However, these sea urchins have enriched $\delta^{15}N$ values relative to sea urchins in kelp beds, suggesting either a higher trophic position (i.e. consumption of some animal material) or greater consumption of degraded kelp.

Temperature also influences microbial activity (Tang et al. 2006, Piontek et al. 2009) and degradation rate of algal detritus (Rothausler et al. 2009). The

degradation rates of *Saccharina latissima* and *Codium fragile* may have fluctuated with daily temperatures, which varied by 8 to 15°C within each of the first 4 sampling intervals. However, mean temperature was relatively constant (10 to 11°C) across the 4 wk intervals, and this may have obscured shorter term variation in degradation rate related to temperature during the first 12 wk of the experiment.

Our experiment shows that detrital deposits of *Codium fragile* and *Saccharina latissima* in sedimentary habitats are rapidly colonized by a variety of macrofauna. This is consistent with previous studies suggesting that detrital material is a significant food subsidy to areas offshore of kelp beds (or forests) worldwide and an important trophic linkage between high and low productivity habitats (McLachlan 1985, Vetter & Dayton 1999, Rodriguez 2003, Britton-Simmons et al. 2009, Krumhansl & Scheibling 2011). Thalli of *C. fragile* degraded more slowly than those of *S. latissima* and accumulated a macrofaunal assemblage that was less abundant but more diverse than the assemblage on kelp. The diversity of associated macrofauna differed most between algal species during the first half of the experiment, when capitellid polychaetes were highly abundant on *S. latissima*, but rare or absent on *C. fragile*, resulting in a marked difference in evenness. Capitellids are highly opportunistic and non-selective feeders, and are commonly associated with food items with a high C/N ratio (Fauchald & Jumars 1979, Mamouridis et al. 2011). The abundance of capitellids on *S. latissima* decreased at 12 and 16 wk, coinciding with increases in diversity and evenness to similar levels as *C. fragile*, and increasing similarity of macrofaunal assemblages between algal species. These results concur with previous studies, indicating that changes in the detrital macrofaunal assemblage are tightly linked to changes in the C/N ratio associated with degradation (Norderhaug et al. 2003, Cebrian & Lartigue 2004, Van Alstyne et al. 2009). Gammarid amphipods also appear to be capable of consuming food with a lower nutritional quality. Abundance of these amphipods on both *S. latissima* and *C. fragile* was highest after 4 wk of degradation, suggesting they may be important early colonizers and facilitators of subsequent detrital breakdown. In contrast, the razor clam *Ensis directus* emerged on both algal species as degradation progressed, possibly in response to increased quantities of degraded algal particles, and was abundant on *C. fragile* at 16 wk.

Live and attached *Codium fragile* supports a more diverse community of epifauna and epiphytes than native kelps (Schmidt & Scheibling 2006, 2007) and other species of brown, red, and green algae (Jones & Thornber 2010, Lutz et al. 2010). This has been attributed to the highly branched morphology of *C. fragile*, which may provide more shelter from predators, greater surface area for attachment (Schmidt & Scheibling 2006, Drouin et al. 2011), and higher sedimentation rates (Schmidt & Scheibling 2007) compared to native species. Structural complexity also may influence detrital macrofaunal assemblages immediately following deposition of intact thalli but likely decreases in importance relative to nutritional quality and palatability as thallus structure breaks down. Differences in macrofaunal composition between attached thalli of *C. fragile* and *Saccharina latissima* in Nova Scotia are explained by lower abundances of gastropods and asteroids, and higher abundances of amphipods, harpacticoid copepods, and the nudibranch *Placida dendritica* on *C. fragile* (Schmidt & Scheibling 2006). These differences are not consistent with those that characterize degrading thalli of these species, indicating that different factors regulate the species-specific colonization patterns of live and detrital macroalgae.

In Nova Scotia, rates of fragmentation and dislodgement of *Codium fragile* are greatest in fall and early winter, resulting in an increased deposition of this detrital material at these times (Begin & Scheibling 2003, D'Amours & Scheibling 2007). However, the timing of fragmentation and attendant production of detritus by stands of *C. fragile* varies among regions and occurs throughout the year in some areas (Trowbridge 1996, 1998). Thalli of *C. fragile* used for this experiment were collected during the seasonal minimum in DMSP production coincident with high water temperatures (Lyons et al. 2010). In regions were fragmentation occurs during periods of low temperature in winter and spring (Fralick & Matheison 1973, Trowbridge 1993), the DMSP content of detrital fragments is likely higher, which may result in a greater deterrent effect on potential consumers and slower degradation rate than observed in our study.

Adult (>20 mm test diameter) sea urchins *Strongylocentrotus droebachiensis* were absent on the sandy bottom during our experiment. Juvenile sea urchins were common in the adjacent kelp bed (authors' pers. obs.), and small juveniles (<10 mm) occasionally were found on *Saccharina latissima* and *Codium fragile* throughout the 16 wk experiment. Where large sea urchins are abundant, they can consume drift algal deposits before substantial degradation occurs (Lyons & Scheibling 2008, Britton-Simmons et al. 2009). Consumption by sea urchins will greatly

accelerate the degradation process, as large fragments of algae are reduced to small (~2.4 mm diameter) fecal particles (Sauchyn & Scheibling 2009a). These feces are of higher nutritional quality (lower C/N ratio) than fresh algal material (Sauchyn & Scheibling 2009b), and degrade more rapidly than fresh kelp (Sauchyn & Scheibling 2009b). Our cages excluded other large detritivores and predators of macrofauna, such as lobsters and crabs, which also may contribute to the degradation of algal thalli and influence the structure of associated macrofaunal assemblages.

Our findings are consistent with previous studies that have documented shifts in macrofaunal assemblages on mudflats in response to changing detrital resources following algal species invasions (Bishop et al. 2010, Taylor et al. 2010), indicating that the effects of algal invaders can extend beyond the introduced habitat to those linked via the transfer of detrital material. Given the trophic importance of detrital pathways (Cebrian 1999, Cebrian & Lartigue 2004), these studies demonstrate that introductions of algal species can have more far-reaching impacts than previously considered.

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Appendix 1. Macrofaunal taxa on samples of degrading *Saccharina latissima* and *Codium fragile*. +: taxon present

Taxon	*S. latissima*	*C. fragile*
Arthropoda		
Mysis spp.	+	+
Gammaridae	+	+
Caprellidae	+	+
Hyperiidae	+	+
Pagurus acadianus	+	+
Cancer irroratus	+	+
Libinia emarginata	+	
Bodotriidae	+	+
Asellidae	+	+
Echinodermata		
Ophiopholis aculeata	+	+
Amphiolis squamata	+	+
Stronglyocentrotus droebachiensis	+	+
Asterias spp.	+	
Henricia sanguinolenta	+	+
Mollusca		
Littorina spp.	+	+
Lacuna vincta	+	+
Musculus spp.	+	+
Modiolus modiolus	+	+
Anomia simplex	+	+
Nucella lapillus	+	+
Buccinum undatum	+	+
Crenella glandula	+	+

Taxon	*S. latissima*	*C. fragile*
Mollusca (continued)		
Margarites groenlandicus	+	+
Ischnochiton ruber	+	+
Onchidoris bilamellata	+	+
Ensis directus	+	+
Placida dendritica	+	
Turbinilla interrupta	+	+
Haminoea solitaria	+	+
Euspira heros	+	+
Placopecten magellanicus	+	+
Annelida		
Capitellidae		
Nereididae	+	+
Sabellidae	+	+
Polynoidae	+	+
Dorvilleidae	+	+
Phyllodocida	+	+
Platyhelminthes		
Bdellouridae	+	+
Leptoplanidae	+	+
Nemertea		
Cephalothrichidae	+	
Chordata		
Pholis gunnellus	+	+

Appendix 2. Pairwise Bray-Curtis dissimilarities between macrofaunal communities associated with samples of *Saccharina latissima* (S) and *Codium fragile* (C), after 4, 8, 12, and 16 wk of degradation, from SIMPER analysis of square-root-transformed abundance data. Only taxa with dissimilarities >2.5 are shown

Comparison Taxon	Dissimilarity Avg.	Cum. %
C4 vs. S4		**53.8**
Capitellidae	11.3	20.7
Gammaridae	5.9	31.7
Polynoidae	3.2	37.6
Phyllodocida	3.0	43.2
C8 vs. S8		**63.8**
Capitellidae	25.1	39.3
Polynoidae	4.1	45.8
Mysis spp.	4.1	52.2
C12 vs. S12		**39.8**
Capitellidae	6.4	16.1
Neididae	3.1	23.9
Strongylocentrotus droebachiensis	2.6	30.3
C16 vs. S16		**42.4**
Ensis directus	3.4	8.0
Lacuna vincta	2.9	14.9
Crenella glandula	2.7	21.2
C4 vs. C8		**52.9**
Gammaridae	5.9	11.1
Neididae	3.6	18.0
Mysis spp.	3.5	24.5
Amphiolis squamata	3.4	30.9
Polynoidae	3.3	37.1
Lacuna vincta	3.0	42.7
C4 vs. C12		**52.3**
Gammaridae	5.4	10.4
Neididae	4.4	18.7
Amphiolis squamata	4.0	26.3
Ensis directus	3.1	32.3
Strongylocentrotus droebachiensis	2.7	37.4
S4 vs. S8		**44.5**
Capitellidae	7.2	16.1
Gammaridae	6.7	31.2
Mysis spp.	3.3	38.7
Polynoidae	2.6	44.4
S4 vs. S12		**43.4**
Capitellidae	7.2	16.6
Gammaridae	5.7	29.6
Mysis spp.	2.5	35.3
S4 vs. S16		**50.6**
Gammaridae	5.3	10.4
Amphiolis squamata	3.1	16.5
Lacuna vincta	3.1	22.7
Neididae	2.5	27.6
Buccinum undatum	2.5	32.5

Comparison Taxon	Dissimilarity Avg.	Cum. %
C4 vs. C16		**53.8**
Ensis directus	5.0	9.4
Gammaridae	4.8	18.3
Neididae	3.5	24.8
Crenella glandula	3.4	31.1
Lacuna vincta	3.0	36.6
Amphiolis squamata	2.7	41.6
C8 vs. C12		**49.3**
Mysis spp.	5.0	10.2
Ensis directus	3.6	17.6
Neididae	3.6	25.0
Amphiolis squamata	3.5	32.1
Polynoidae	3.3	38.9
Strongylocentrotus droebachiensis	3.1	45.1
Asellidae	2.8	50.7
C8 vs. C16		**54.9**
Ensis directus	5.8	10.6
Mysis spp.	4.3	18.4
Crenella glandula	4.2	26.0
Modiolus modiolus	4.2	33.6
Lacuna vincta	3.5	40.0
Anomia simplex	2.7	44.9
Polynoidae	2.6	49.6
Neididae	2.5	54.1
C12 vs. C16		**39.0**
Lacuna vincta	3.0	7.6
Modiolus modiolus	2.6	14.3
Strongylocentrotus droebachiensis	2.5	20.8
Anomia simplex	2.5	27.1
S8 vs. S12		**56.2**
Capitellidae	16.7	29.8
Polynoidae	3.6	36.2
Buccinum undatum	3.2	42.0
Lacuna vincta	2.6	46.7
Ensis directus	2.6	51.3
S8 vs. S16		**63.8**
Capitellidae	22.3	35.0
Polynoidae	3.9	41.0
Buccinum undatum	3.5	46.5
Mysis spp.	2.9	51.0
S12 vs S16		**37.6**
Capitellidae	6.4	17.1
Neididae	2.7	24.3

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