DETRITAL PRODUCTION IN KELP BEDS

by

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "DETRITAL PRODUCTION IN KELP BEDS" by Kira Aubin Krumhansl in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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I dedicated this dissertation to all things that lack charisma, but play an important role in the functioning of natural systems.

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ABSTRACT

Detrital subsidy from highly productive kelp beds and forests to adjacent habitats represents a major form of connectivity between coastal ecosystems that regulates regional patterns of community organization and production. In this thesis, I investigated environmental and biological factors that influence the rate of detrital production in Nova Scotian kelp beds, with emphasis on the role of invasive species in altering these dynamics. The rate of blade erosion of the dominant kelp species (*Saccharina latissima* and *Laminaria digitata*) increased significantly with the level of encrustation by the invasive bryozoan *Membranipora membranacea* and the extent of grazing damage by the native snail *Lacuna vincta*, and by increased water temperature and site exposure. The rate of detrital production (as dry mass) ranged from 0.5 to 1.71 kg m^{-2} y^{-1} across 5 sites, and increased linearly with kelp bed biomass. Spatial variation in the total level of grazing damage on kelp blades by *L. vincta* was explained in part by a negative relationship with site exposure, and the distribution of grazing along blades was regulated by kelp growth rate and the associated production of grazing-deterrent polyphenolics. Grazing damage by *L. vincta* that exceeded 0.5 to 1.0% of blade area caused increased rates of erosion during heavy wave action associated with a passing hurricane. The maximum stress before breakage, toughness, and extensibility of blade tissues decreased with the degree of encrustation by *M. membranacea* or grazing damage by *L. vincta*, which cause degradation and removal of the outer cell layers of kelp tissues, resulting in stress concentration and breakage at lower force applications than required to break undamaged tissues. The invasive green alga *Codium fragile* and *S. latissima* differed with respect to nutritional quality and changes in biochemical composition that occurred over the course of degradation on a sandy bottom adjacent to a kelp bed. Macrofaunal communities colonizing detrital deposits responded to these differences. These findings demonstrate that invasive species can alter the quantity and quality of detritus produced from subtidal kelp beds, and that their community-level effects can extend well beyond the invaded habitats via the export of detritus.

LIST OF ABBREVIATIONS USED

g	gram
kg	kilogram
μm	micrometer
mm	milimeter
cm	centimeter
m	meter
km	kilometer
t	time
min	minute
h	hour
d	day
wk	week
mo	month
y	year
ml	millilitre
μl	microlitre
ww	wet weight
dw	dry weight
no	number
ind	individual
N	Newton
Hz	Hertz
psi	pound per square inch
MJ	Megajoule
CC	Cranberry Cove
DP	Duncan's Cove Protected
DE	Duncan's Cove Exposed
SP	Splitnose Point
TL	The Lodge
G	Growth rate
H_f	Final hole position
B	Biomass
P	Productivity
L	Loss of tissue from the thallus
BL	Blade length
E	Erosion
EP	The ratio of erosion to productivity
D_M	Density of kelps within measured size range
D_M	Total kelp density
E_M	Erosion for the measured proportion of the population
REI	Relative exposure index
V_i	Average monthly windspeed
P_i	Frequency of winds

F_i	Fetch
%M	% Cover by *Membranipora membranacea*
% Gzd	% of distal area grazed by *Lacuna vincta*
Temp	Temperature
Exp	Exposure
N	North
S	South
E	East
W	West
MPa	Modulus of material stiffness
σ	Stress
ε	Strain
[illegible]	Extension
ANOVA	Analysis of Variance
ANCOVA	Analysis of Covariance
MANOVA	Multivariate Analysis of Variance
MANCOVA	Multivariate Analysis of Covariance
PERMANOVA	Permutational Multivariate Analysis of Variance
SIMPER	Similarities of percentages routine
df	Degrees of freedom
p	p-value
F	F test statistic
n	Sample size
SE	Standard error
SD	Standard deviation
R^2	Coefficient of determination
α	Significance level
b	Slope
MS	Mean squares
AIC	Akaike Information Criteria
w_i	Model probability
LL	Log liklihood
Λ	Λ test statistic
DIN	Dissolved inorganic nitrogen
DOM	Dissolved organic matter
POM	Particulate organic matter
UV	Ultraviolet
ROV	Remotely operated vehicle
DMSP	Dimethylsulfoniopropionate
USA	United States of America
UK	United Kingdom
NIH	National Institute of Health
J’	Pileau’s evenness
H’	Shannon diversity index

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First and foremost, I owe many thanks to my supervisor, Bob Scheibling. I've learned so much from Bob over the past 4 years, and feel supremely grateful for the opportunity to have him as a mentor. His endless energy and enthusiasm have been my main driving force through it all, even those tough periods of tear-soaked track changes and frozen winter field days. He's taught me the value of doing what I love, thinking critically about my work, constantly seeking the opportunity to learn, and a well-written manuscript. Most importantly, he's taught me the importance of balance in life, of taking the time to be active and do what I love in the midst of it all.

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CHAPTER 1
INTRODUCTION

Kelps (*Laminaria digitata* and *Saccharina latissima*) are the dominant macroalgae along the Atlantic coast of Nova Scotia, forming dense beds with high rates of primary productivity (Mann 1973). These kelp beds serve as a primary source of food and biogenic habitat for a diverse community of invertebrates and fishes. Previous studies suggest that most primary productivity in marine and terrestrial communities enters detrital pathways (Mann 1988, Cebrian 1999), but most of the work in Nova Scotia has focused on the dominant grazer pathway (e.g. Miller & Mann 1973, Wharton & Mann 1981, Lauzon-Guay & Scheibling 2007). The green sea urchin *Strongylocentrotus droebachiensis* forms dense aggregations that destructively graze kelp beds, driving the ecosystem-state transition between a highly productive kelp bed and low-productivity barrens dominated by coralline algae (Breen & Mann 1976, Lauzon-Guay et al. 2009). In 1999, widespread mass mortality of sea urchins due to an amoebic disease, with only minimal recovery of populations in localized areas (Brady & Scheibling 2005, Miller & Nolan 2008), enabled the re-establishment of kelp beds along most of the Atlantic coast of Nova Scotia (Watanabe et al. 2009a).

Kelps produce detritus through the gradual erosion and fragmentation of blades, and through breakage of stipes or dislodgement of whole thalli during storm events. Detritus can settle within kelp beds and serve as food for benthic invertebrates, or be advected to adjacent habitats, where it can serve as a significant energy source for the recipient community (Duggins et al. 1989, Bustamante & Branch 1995, Vetter 1995, Dugan et al. 2003). The magnitude of detrital production from Nova Scotian kelp beds has not been quantified, and little is known about the biotic and abiotic factors that regulate the rate of production. The potential for large-scale consequences of transitions in ecosystem state on the productivity of adjacent communities that receive detritus has not been considered.

During the past two decades, two invasive species have altered dynamics of the rocky subtidal ecosystem off Nova Scotia. The bryozoan *Membranipora membranacea* was first observed in the Gulf of Maine in 1987 (Lambert et al. 1992) and along the Atlantic coast of Nova Scotia in 1992 (Scheibling et al. 1999). *M. membranacea* encrusts kelp blades, with peak coverage of the bryozoan occurring in fall. Large-scale reductions in canopy cover (50-70% loss) occur at high levels of encrustation (>60% blade coverage) (Scheibling & Gagnon 2006, 2009, Saunders & Metaxas 2008). This has been attributed to increased brittleness of blades following encrustation, making them more susceptible to fragmentation by wave forces, although this hypothesis has not been tested explicitly.

Canopy losses caused by *Membranipora membranacea* facilitated the establishment and spread of the green alga *Codium fragile* by opening up space on the substratum (Scheibling et al. 1999, Watanabe et al. 2009a). Once established, *C. fragile* formed monospecific meadows that inhibited recruitment of kelps and other native macroalgae (Scheibling & Gagnon 2006). The abundance of *C. fragile* declined at the epicenter of introduction between 2000 and 2007 (Watanabe et al. 2009a) likely because its dislodgement by storms (D'Amours & Scheibling 2007) enabled the re-establishment of kelps (Watanabe et al. 2009a). Currently, *C. fragile* forms mixed stands with kelps in protected and semi-protected areas of the coast. Accumulations of detrital thalli and thallus fragments of *C. fragile* occur in low-energy areas, persisting for months until being flushed during large wave events (Watanabe et al. 2009b).

Membranipora membranacea and *Codium fragile* have the potential to alter the nature of detrital production from Nova Scotian kelp beds. Bryozoan encrustation of kelp blades may increase detrital production from kelp beds in the short term, but eventually cause declines as kelp bed biomass is reduced. The replacement of native kelps by *C. fragile* also reduces kelp biomass, and ultimately alters the species composition of algal detritus produced from subtidal habitats. Rates of consumption and degradation of this detritus are related to its nutritional quality (Mann 1988, Cebrian & Lartigue 2004, Hladyz et al. 2009), which likely differs between *C. fragile* and native kelps. Alterations in the quantity and quality of algal detritus produced in the rocky subtidal may have consequences for communities in adjacent habitats linked by the transfer of detritus. This represents a novel contribution to invasive species research, which focuses primarily on local effects of species introductions to biodiversity and ecosystem function (Scheibling et al. 1999, Scheibling & Gagnon 2006, Eastwood et al. 2007, Galil 2007, Schaffelke & Hewitt 2007).

The overarching goal of my thesis is to examine the dynamics of detrital production from Nova Scotian kelp beds, with emphasis on the role of invasive species in altering the quantity and quality of the detritus produced. In Chapter 2, I document rates of detrital production from kelp beds at 5 sites across a range of wave exposure and over 15 months, and examine the importance of various biological and environmental factors in regulating these rates. In Chapter 3, I investigate factors that regulate grazing by the dominant mesograzer on kelp blades, the gastropod *Lacuna vincta*, and the effect of this grazing damage on rates of kelp blade erosion under varying wave conditions. In Chapter 4, I combine biomechanical testing procedures and histology to identify the mechanistic linkage between increased rates of kelp blade erosion and encrustation by *M. membranacea* and grazing damage by *L. vincta*. In Chapter 5, I compare the degradation rate and nutritional quality during degradation of the native kelp *Saccharina latissima* to the invasive *Codium fragile* on a sandy bottom adjacent to a kelp bed in a field experiment, and examine differences in species composition of macrofauna associated with the degrading algal material. In Chapter 6, I review current knowledge of detrital production rates from kelp populations worldwide, and identify factors that commonly regulate this rate. I also summarize the literature documenting the fate of detrital production in sandy beaches, rocky bays, soft-sediment and rocky and subtidal habitats, and the deep sea, and the consequences of this subsidy for secondary production and community organization. I then discuss this body of empirical work in the context of spatial ecological theory to make predictions about the linkage between local productivity within kelp systems and regional-scale productivity. In Chapter 7, I integrate conclusions based on the foregoing chapters to summarize the contribution of my thesis to our overall knowledge of the production and fate of kelp detritus from kelp communities.

CHAPTER 2
DETRITAL PRODUCTION FROM NOVA SCOTIAN KELP BEDS: PATTERNS AND PROCESSES

The work presented in Chapter 2 also appears in:
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2.1 INTRODUCTION

The importance of connectivity between adjacent habitats in determining the structure of populations and communities is a central theme in contemporary marine ecological research (Polis & Hurd 1996, Huxel & McCann 1998, Nakano & Murakami 2001). Studies of connectivity in marine systems have focused largely on mobile species (Lindberg & Moberg 2003) or on widely dispersing larval stages (Lipcius et al. 2008). Less attention has focused on the role of energy exchange in the form of detritus in influencing patterns of abundance and productivity in recipient communities (Duggins et al. 1989, Polis & Hurd 1996, Polis et al. 1997). Studies that have explored this linkage provide evidence to suggest that exchange of detritus plays a significant role in determining population and community structure in areas adjacent to productive macroalgal beds. For example, invertebrate populations in intertidal habitats adjacent to subtidal kelp beds have greater secondary productivity than those in areas without a kelp subsidy (Duggins & Simenstad 1989, Bustamante et al. 1995, Bustamante & Branch 1996). This linkage is particularly strong when extremely productive ecosystems are adjacent to less productive ones (Polis & Hurd 1996), and where imported detritus serves as a primary source of food or habitat (Lenanton et al. 1982, Vetter 1998, Vetter 1999, Hyndes & Lavery 2005).

The interaction between native and introduced species is another area of expanding interest and concern among marine ecologists and resource managers, as evidence of the negative impacts of biological invasions accumulates (Thomsen et al. 2009, Sorte et al. 2010). This research has primarily addressed the direct effects of introductions on native populations and resulting changes in biodiversity and ecosystem function (Eastwood et al. 2007, Galil 2007, Schaffelke & Hewitt 2007). Indirect effects on the dynamics of material and energy exchange between invaded and adjacent native communities are largely unknown.

Kelp ecosystems are amongst the most productive in the world (Mann 1972, Smith 1988). In Nova Scotia, Canada, kelp beds often are located next to sea urchin barrens, characterized by low productivity and coralline-algal dominated assemblages (Chapman 1981, Mann 1982, Scheibling et al. 1999). The faunal assemblages that inhabit these barrens (Balch & Scheibling 2000, Knip & Scheibling 2007) and adjacent sedimentary habitats in deeper waters (Kenchington et al. 2006) may depend largely on allochthonous inputs from shallow algal beds, as has been observed for deep-water systems elsewhere (Lawson et al. 1993, Vetter 1995), although this connection remains unexplored in the Northwest Atlantic.

Kelp beds on the Atlantic coast of Nova Scotia are highly dynamic. Phase shifts between productive kelp beds and urchin barrens occur on a decadal time scale, driven by fluctuations in the abundance of the sea urchin *Strongylocentrotus droebachiensis* (Miller 1985, Scheibling et al. 1999, Lauzon-Guay et al. 2007). The introduction of the epiphytic bryozoan *Membranipora membranacea*, which encrusts kelp blades, has resulted in several large-scale defoliation events since 1993 (Scheibling & Gagnon 2006, Saunders & Metaxas 2008). A reduction in kelp biomass, due to the combined effects of urchin grazing and bryozoan-mediated defoliation, likely affects the dynamics of detrital subsidies to adjacent communities.

While kelp productivity has been measured extensively off Nova Scotia (Mann 1972, Chapman & Craigie 1977, Gerard & Mann 1979, Smith 1988), the rate of detrital production from these kelp assemblages has not been directly quantified. Wave exposure (Gerard & Mann 1979), nutrients (Chapman & Craige 1977) and temperature (Mann 1972) are known to affect rates of kelp production in Nova Scotia, but factors regulating rates of detrital production remain poorly understood. Wave exposure is expected to play an important role, as major losses in kelp biomass have been observed elsewhere following storms (Seymore et al. 1989, Reed et al. 2008). Temperature is linked to tissue degradation in kelps (Rothausier et al. 2009), and therefore is likely to increase erosion of blades. Biological factors that weaken kelp blades, such as encrustation by *Membranipora membranacea* (Dixon et al. 1981) and grazing by snails (mainly *Lacuna vincta*; Johnson & Mann 1986) also are expected to influence detrital production.

In this study, we provide direct estimates of the rate of detrital production from subtidal kelp beds by measuring the erosion and production of individual kelp blades over a seasonal cycle at various sites along the Atlantic coast of Nova Scotia near Halifax. The ratio of erosion to productivity (EP) was calculated as an indication of whether kelp beds are increasing (EP < 1) or decreasing (> 1) in biomass. Kelp population density and biomass were measured during each sampling period at each site, and used to estimate erosion per unit area for the portion of the population measured from individual rates. We concurrently measured a suite of physical and biological factors, including temperature, wave exposure, grazing damage by snails, and encrustation by *Membranipora membranacea.* We predicted that erosion of kelp blades would increase with each of these factors. Identifying the main factors driving rates of detrital production aids in understanding how natural and human-mediated environmental variation affects energy export from subtidal kelp beds.

2.2 METHODS

2.2.1 Study Sites

This study was conducted at 5 sites along the central region of the Atlantic coast of Nova Scotia from the western shore of St. Margaret's Bay to the western head of Halifax Harbour (Figure 2.1). Sites were selected to represent a range of wave exposures, and the presence or absence of *Membranipora membranacea* (Table 2.1). Splitnose Point was selected as the most exposed site and because it experiences moderate to high

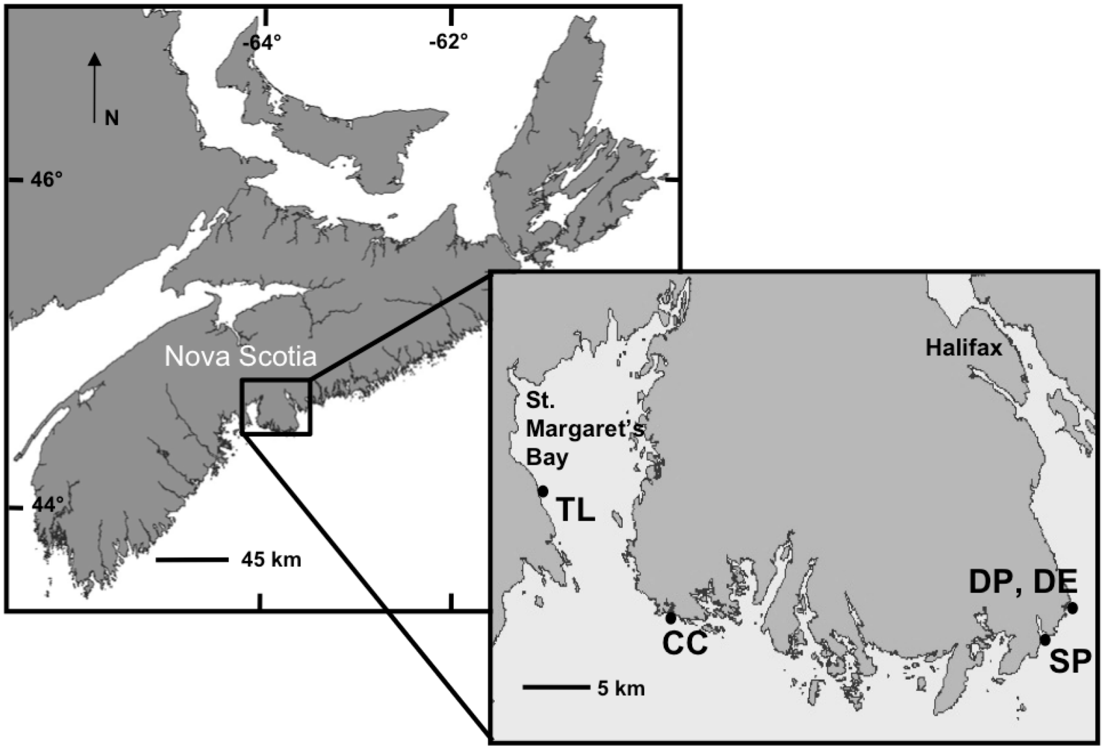

Figure 2.1 Location and physical and biological characteristics of the 5 study sites: Splitnose Point, Duncan's Cove Exposed, Duncan's Cove Protected, The Lodge, and Cranberry Cove. Kelps include *Laminaria digitata* and *Saccharina latissima*.

Table 2.1 Location and physical and biological characteristics of the 5 study sites: Splitnose Point, Duncan's Cove Exposed, Duncan's Cove Protected, The Lodge, and Cranberry Cove. Kelps include *Laminaria digitata* and *Saccharina latissima*. The last column indicates whether *Membranipora membranacea* grows epiphytically on kelps at each study site location.

Site	**Location (°N,°W)**	**Substratum**	**Exposure**	**Dominant Algae**	***Membranipora membranacea***
Splitnose Point	4428'38.45" 63°32'48.21"	Ledges	High, SSE	Kelps, *Desmarestia spp.*	Yes
Duncan's Cove Exposed	44°29'50.22" 63°31'24.26"	Channel between island and mainland, with boulders	Moderate, SE	Kelps	No
Duncan's Cove Protected	44°29'52.53" 63°31'34.99"	Small boulders	Low, E	Kelps	No
The Lodge	44°33'32.98" 64°01'56.75"	Small boulders and sand	Low-moderate, NNE	Kelps, *Chondrus crispus, Fucus spp., Desmarestia spp.*	Yes
Cranberry Cove	44°30'0.31" 63°55'22.71"	Boulders and sand, rocky outcrops	Low-moderate, SW	Kelps, *Fucus spp., Desmarestia spp.*	No

encrustation by *M. membranacea* in late summer to fall. Duncan's Cove Exposed is located ~3 km northeast of Splitnose Point within a channel between an island and the mainland. This site was selected because it experiences moderate to high levels of wave action. Duncan's Cove Exposed is more protected than Splitnose Point and contains a mix of ledges and small to large boulders. Duncan's Cove Protected is located ~0.25 km inshore of the exposed site and is protected from wave action, with kelps growing on small to medium sized boulders. The Duncan's Cove sites were selected because *M. membranacea* rarely occurs on kelp in this area. Cranberry Cove is located ~ 30 km southwest of Splitnose Point, and was selected as a low-moderately exposed site. Cranberry Cove contains sparse stands of kelp mixed with the invasive green alga *Codium fragile* growing on small boulders and large rock outcroppings. *M. membranacea* also rarely occurs at this site. The Lodge is a low-moderately exposed site located ~ 11 km northwest of Cranberry Cove on the western shore of St. Margaret's Bay. This site was selected because kelp density was low at the start of the study following declines in kelp canopy cover (~ 40%) following a high infestation of *M. membranacea* in fall 2006 (Saunders & Metaxas 2008). Measurements of individuals and populations of kelp were taken at 4-6 m depth at all sites, where *Saccharina latissima* and *Laminaria digitata* were the dominant canopy-forming kelps.

2.2.2 Productivity and Erosion

Productivity and erosion of kelps were measured using SCUBA during 6 sampling periods: July 2008, September 2008 and 2009, November 2008, February 2009, and May 2009. Measures were taken at all 5 sites during the July, September and May sampling periods, but logistical constraints of winter sampling limited February measurements to 3 sites (Splitnose Point, Duncan's Cove Protected, and Cranberry Cove). Measures were taken at only 2 sites (Splitnose Point and The Lodge) in the November sampling period because these sites experience the highest abundance of *Membranipora membranacea* during this season. Growth and erosion of *Saccharina latissima* was measured at all sites and sampling periods, while *Laminaria digitata* was measured at all sites and periods except Cranberry Cove (all periods) and Duncan's Cove Protected (July 2008), where this species was not particularly abundant. During each sampling period, 10-20 thalli of each species were haphazardly selected within a representative stand of kelp at each site, and individually labeled with a numbered tag. Only thalli of total length >30 cm for *L. digitata* and >50 cm for *S. latissima* were selected. Due to logistical constraints, sites could not be measured concurrently. Therefore, sampling periods differed by 1-2 wk across sites during each sampling month.

Growth and productivity were measured *in situ* using a modified "hole-punch method" after Tala & Edding (2005). A slightly different procedure was used for *Laminaria digitata* than *Saccharina latissima* because of morphological differences between species. *S. latissima* has a single blade, while *L. digitata* has a large broad blade that splits into smaller "digits" near the proximal end. Therefore, a single hole was punched at 10 cm above the base of the blade in *S. latissima*, while 3 holes were punched in *L. digitata*: one at 10 and another at 20 cm directly above the base of the blade (defined as the location where the blade is twice the width of the stipe), and a third hole at 20 cm above the base of the blade on an outer digit (Figure 2.2). Multiple holes in *L. digitata* ensured that blade length was re-measured on the same digit at the beginning and end of a sampling interval. Stipe length and blade length above each hole were measured with a flexible tape (1-cm precision) for each individual.

After 2-4 wk, marked kelps were collected and returned to the laboratory. Stipe length, growth hole position (as distance from the base of the blade), and final blade length were measured for each individual of *Saccharina latissima*. Growth rate of *S. latissima* as blade elongation (G_{SL}, cm d^{-1}) was calculated as:

$$G_{SL} = (H_f - 10)/t \qquad \text{Eqn 1}$$

where H_f is the final growth hole position (cm) and t is the time (d) between initial and final measurements. For *Laminaria digitata*, stipe length and the positions of each of the 3 holes above the base of the blade were measured. The blade length above each set of holes (central and outer blades) was then measured. Growth rate of *L. digitata* (G_{LD}) was calculated as:

$$G_{LD} = (((H_{f1} - 10) + (H_{f2} - 20) + (H_{f3} - 20))/3)/t \qquad \text{Eqn 2}$$

where H_{f1}, H_{f2}, and H_{f3} are the positions of the 2 inner and 1 outer holes, respectively.

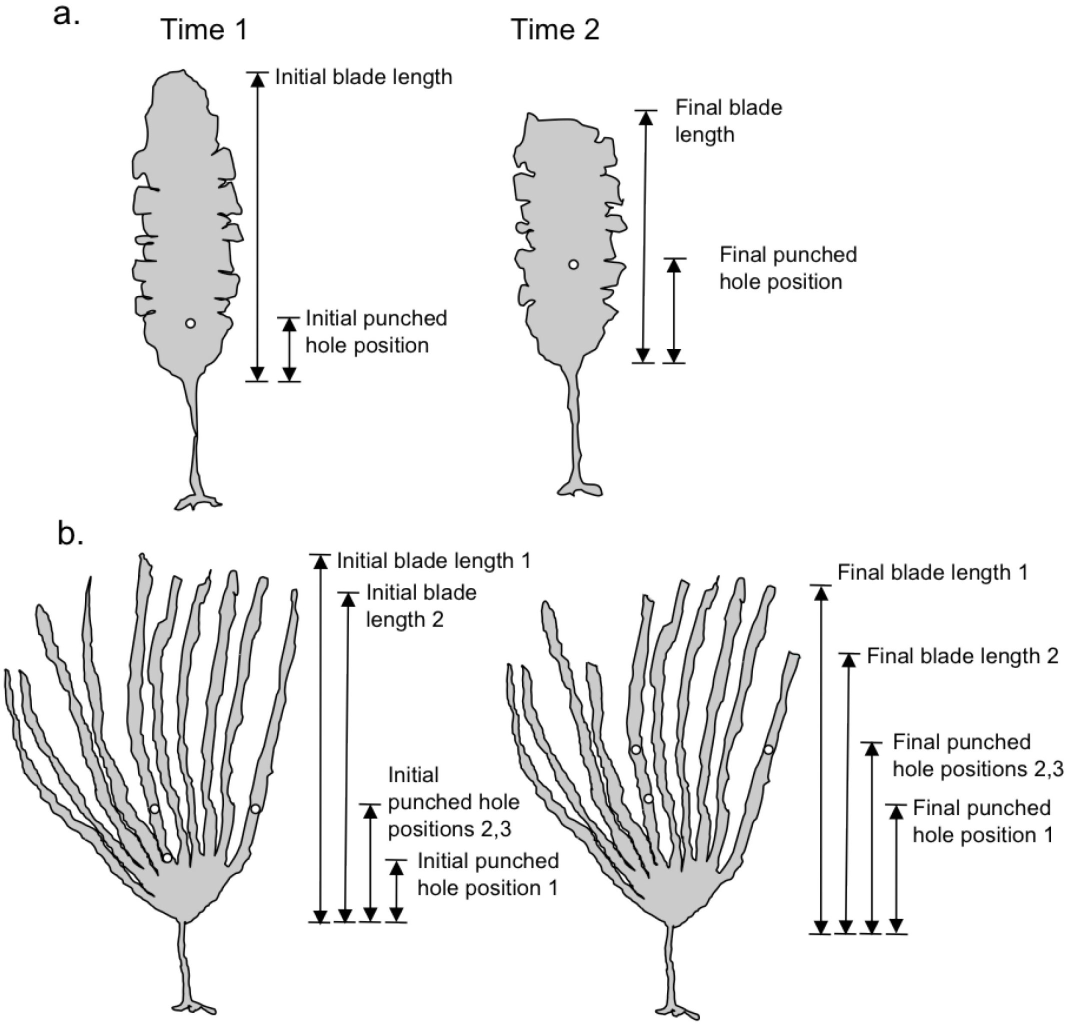

Figure 2.2 Diagram showing the hole-punching methods used to measure productivity and erosion in *Saccharina latissima* (a) and *Laminaria digitata* (b). Diagrams on the left show locations of punched holes and morphometric measurements taken at the start of the sampling period (Time 1). Diagrams on the right are the locations of punched holes and measurements taken at the time of collection (Time 2). Multiple holes are punched in thalli of *L. digitata* to ensure that the same "digits" were measured at the beginning and end of the study period.

To calculate productivity, blades were cut along their length into 10-20 cm-long sections, depending on the overall length of the blade, and wet weight was measured for each section. The basal section of the blade (between the base and growth hole) was then dried at 60 ºC for at least 48 h and weighed. The relationship between dry and wet weight was determined by linear regression, for each site and sampling period (Appendix 1). All regression models were significant at $\alpha = 0.05$, with $R^2 > 0.80$. Based on this relationship, dry biomass per unit length of blade (g cm^{-1}) was estimated for the remaining sections of the basal 1/3 of the blade from wet weight measures. The measured and estimated dry biomass per unit length in the basal 1/3 of the blade was then averaged to give B_{base} (g cm^{-1}). Productivity (P, g d^{-1}) was calculated as:

$$P = G \times B_{base} \qquad \text{Eqn 3}$$

where G represents G_{SL} or G_{LD} for calculating productivity in *Saccharina latissima* and *Laminaria digitata*, respectively.

For *Saccharina latissima*, the loss of tissue from the thallus (L, cm) was calculated as:

$$L = (BL_i + g) - BL_f \qquad \text{Eqn 4}$$

where BL_i and BL_f are initial and final blade length (cm), respectively, and g is the length of new tissue produced (cm). For *Laminaria digitata, L* was calculated for the center and outer digits using Equation 4, and then averaged to generate an estimate of tissue loss from the whole thalli. The relationship between wet and dry weight in the distal section of the thallus for both species was used to estimate the dry biomass per unit length in the distal 1/3 of the blade B_{distal} (g cm^{-1}). Erosion rate (E, g d^{-1}) was then calculated as:

$$E = (L / t) \times B_{distal} \qquad \text{Eqn 5}$$

The ratio of erosion to productivity (EP) was then calculated for each individual.

2.2.3 Population Measurements

Standing stock biomass and density of both kelp species at each site were measured during all sampling periods. 8 to 9 quadrats of 0.5 m^2 were haphazardly placed on the substrate in an area adjacent to the tagged kelp thalli. All individuals of *Saccharina latissima* and *Laminaria digitata* were collected from each quadrat, and individual stipe and total length was measured for each kelp individual >20 cm total length. The biomass (as wet weight) of all individuals of each species was weighed for each quadrat using a spring balance (10-g precision).

2.2.4 Detrital Production Estimates

Daily erosion per unit area (m^2) was estimated for each site and sampling period based on individual erosion rates. The density of kelps within the size range of thalli measured for erosion and productivity (D_M, individuals m^2) was determined for each site and sampling period from quadrat counts. Erosion rate per unit area (E_M, g m^{-2} d^{-1}) for the measured portion of the population was then calculated as:

$$E_M = E \times D_M \qquad \text{Eqn 6}$$

for each species. These values were averaged across sampling periods and multiplied by 365 to estimate annual detrital production for each site (Annual E_M, kg m^{-2}). The proportion (P_M) of the total population represented by E_M and Annual E_M was calculated as:

$$P_M = D_M / D_T \qquad \text{Eqn 7}$$

where D_T is the total density of kelps > 20 cm in length.

To relate annual detrital production to total kelp biomass, we converted wet biomass measures averaged across sampling periods for each site and species to dry weight using the ratio of dry to wet weight of marked kelp thalli (including stipe and holdfast). These conversion factors ranged from 0.124 (Splitnose Point) to 0.183 (Cranberry Cove) for *Saccharina latissima*, and 0.158 (Splitnose Point) to 0.162 (Duncan's Cover Protected) for *Laminaria digitata*.

2.2.5 Physical Factors

Seasonal variation in productivity and erosion were examined in relation to temperature and wave action. Temperature was recorded at 10- to 30-min intervals at each site using HOBO® Tidbit or Pendant Data Loggers (Onset Computer Corporation) deployed between 4 and 6 m depth (Chart Datum). A logger was continuously deployed at The Lodge during the 15-mo study; at the other sites, loggers were deployed intermittently. Linear regression was used to determine the relationship between average weekly temperature at The Lodge and each of the other sites individually. These models ($R^2 > 0.95$, $p < 0.0001$) were used to extrapolate temperature when direct measurements were not made. Temperature data were unavailable in July 2008 due to equipment malfunction.

A relative wave exposure index (REI) for each site was calculated using a modification of the index by Keddy (1982):

$$REI = \sum_{i=1}^{16} (V_\mathrm{i} \times P_\mathrm{i} \times F_\mathrm{i}) \qquad \text{Eqn 7}$$

where V_i is average monthly wind speed, P_i is frequency of winds, and F_i is fetch, from the i^{th} direction (north, north northeast, northeast, east northeast, etc in 16 increments of 22.5°). Fetch calculations were site-specific, while the same wind data, obtained from Environment Canada's National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca), were used for all sites. Typically effective fetch is used in this exposure index calculation, but our sites are located in semi- or non-enclosed areas, with fetch values of 1000s of km in some directions, making effective fetch calculations impractical. In these cases, fetch was bounded at 2,000 km, the distance within which storms in the Atlantic generate waves that propagate to the coast of Nova Scotia (Hart & Evans 2001).

2.2.6 Biological Factors

Percent cover of *Membranipora membranacea* on kelp blades was measured at the time of collection for each site and sampling period. Blades were placed under a plexiglass sheet and photographed using Canon G7 or G10 Powershot digital cameras. Colonies of *M. membranacea* on the full area of 1 randomly selected side of the blade were outlined using a marker and photographed. To calculate percent cover, the total blade area and the blade area covered by *M. membranacea* were measured using ImageJ (NIH). If blade dimensions exceeded that of the plexiglass sheet, as was the case for some individuals of *Laminaria digitata* at Splitnose Point, a randomly selected subsection of the thallus was measured.

The degree of blade damage by snail grazing (primarily *Lacuna vincta*) was measured for both kelp species to determine its effect on erosion rate. Grazing damage consists of perforations or superficial excavations that do not perforate the blade. Only perforations were measured. Photographs were taken of the complete blade of each individual at the time of final measurement, and the area of grazing holes was measured using image analysis. Erosion primarily occurs in the distal 1/3 of blades, and grazing intensity in this region is expected to affect erosion. Therefore, distal area grazed was used in later analysis.

2.2.7 Statistical Analysis

The effect of site and season (fixed factors) on 1) productivity; 2) erosion rate, and 3) the ratio of erosion to productivity (EP) were examined using 2-way Analysis of Variance (ANOVA) for seasons when measurements were taken at all sites (July and September 2008 and May and September 2009 for *Saccharina latissima*, and in September 2008 and May and September 2009 for *Laminaria digitata*). 1-way ANOVA was used to compare the effect of season at sites where winter measurements (February 2009) were taken for both species. Significance values were constrained to $\alpha = 0.01$ for 1-way ANOVA to compensate for inflation of Type I error rates during repeated 1-way ANOVA. Rate data were log (x+1) transformed and EP data were log (x) transformed to meet the assumptions of normality (Shapiro-Wilk test, $\alpha = 0.05$) and homogeneity of variance (Levene's test, $\alpha = 0.05$).

To examine factors that influence erosion rate and the EP ratio, data were averaged across individuals for each species at each site and sampling period for each measure. We used 2nd-order bias- corrected Akaike's Information Criteria (AICc), the values of maximized log-likelihood function, and model probabilities to assess the evidence supporting models that predict erosion rate and EP ratio, and to assess the relative importance of physical (temperature and site exposure) and biological (% cover by *Membranipora membranacea* and % distal area grazed) factors that may influence these measures. Using this approach, models can be ranked according to their AICc values, with the lowest AICc value indicating the best model to explain the data. Model probability (w_i) is the probability that a given model is actually the best model (Anderson 2008). We also used log-likelihood values and adjusted R^2 values for each model as a means of assessing fit. To examine the relative importance of each factor, we summed the model probabilities of all the models in which each factor appears. Factors with greater summed model probability values are ranked higher, in terms of importance, than factors with lower values (Anderson 2008). All models containing every possible combination of 3 or fewer factors were considered (14 possible models). AIC results decrease in validity if the number of parameters is high in relation to the number of observations (Anderson 2008). Therefore, models with greater than 3 factors were not considered because of the small number of observations. We present the top 5 models for each measure only. Linear regression analysis was used to determine the coefficient and standard error of each factor in the best model based on AICc. July 2008 data were not included in these analyses because temperature and wave data were not available. Variables were not found to be collinear following examination of tolerance values (tolerance < 0.60) (Van den Poel & Lariviere 2004).

2.3 RESULTS

2.3.1 Physical Factors

The highest temperatures recorded during our sampling periods were in July 2009 (monthly mean: 14.0-16.2 °C), and the lowest in February 2009 (0.6-0.9 °C) (Figure 2.3). There was little difference in September temperature between 2008 (12.6-15.2 °C) and 2009 (12.0-14.4 °C).

Exposure index varied within and across sites with seasonal trends in wind velocity and direction (Figure 2.3). Splitnose Point consistently had a higher level of exposure than other sites, while Duncan’s Cove Protected had the lowest exposure (Figure 2.3). Duncan’s Cove Exposed, Cranberry Cove, and The Lodge had similar levels of exposure across sampling months; the only large difference in exposure between these sites occurred in September 2008, when Duncan’s Cove Exposed had a lower exposure than Cranberry Cove and The Lodge (Figure 2.3).

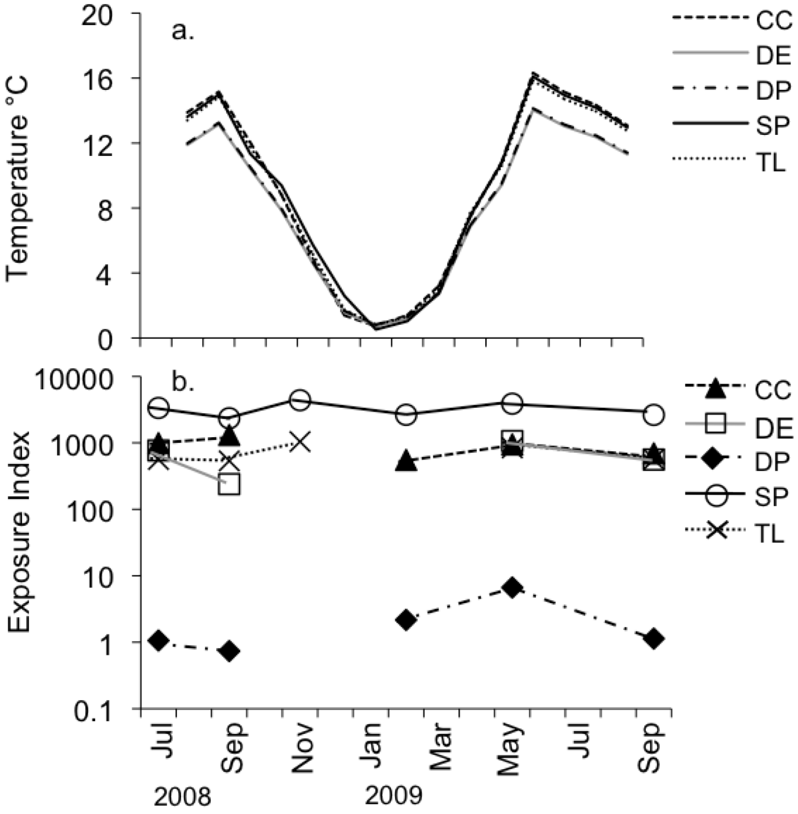

Figure 2.3 (a) Average monthly temperature (°C) for the 5 sampling sites (CC, Cranberry Cove; DE, Duncan's Exposed; DP, Duncan's Protected; SP, Splitnose Point; TL, The Lodge) from July 2008 to October 2009, and (b) exposure index calculated for each site during each sampling period.

2.3.2 Biological Factors

Membranipora membranacea was absent on both kelp species at Cranberry Cove and Duncan's Cove Protected during all sampling periods, and occurred in low abundance only in fall (September 2009) at Duncan's Cove Exposed (Figure 2.4). At Splitnose Point and The Lodge, *Saccharina latissima* and *Laminaria digitata* were encrusted by *M. membranacea* in fall (September and November 2008, September 2009), and cover was generally highest in November (*S. latissima* = 41%, *L. digitata* = 91%). Some bryozoan colonies persisted on *L. digitata* through the winter (February 2009) at Splitnose Point. Percent cover of *M. membranacea* tended to be lower on *S. latissima* than on *L. digitata* in fall.

Grazing intensity on the distal section of blades of *Laminaria digitata* was generally highest (0.2-3.26 % of the distal area grazed) in fall (September and November 2008, September 2009) and lowest in winter (February 2009), particularly at Splitnose Point and The Lodge (Figure 2.4). Grazing intensity on *Saccharina latissima* was generally low (< 2%) and less variable across sampling periods. Grazing intensity was the highest at The Lodge and Duncan's Cove Protected for *L. digitata*, and at The Lodge and Cranberry Cove for *S. latissima* (Figure 2.4).

2.3.3 Productivity and Erosion Rate

Productivity of *Saccharina latissima* followed a seasonal cycle with the highest rates of production in spring (May 2009: 0.14-0.39 g d^{-1}) and lowest in fall and winter (November 2008: 0.08-0.10 g d^{-1}, September 2008: 0.07-0.11 g d^{-1}, February 2009: 0.02-0.09 g d^{-1}, and September 2009: 0.07-0.12 g d^{-1}) (Table 2.2, Figure 2.5). Productivity differed significantly among sites around the spring peak, resulting in pronounced differences in amplitude of the seasonal cycle and a significant interaction between site and season ($F_{12, 303} = 3.96$, $p < 0.001$). The highest rate was recorded at The Lodge and the lowest at Cranberry Cove, where there was little seasonal variation and productivity in summer was similar to that in spring (Table 2.2, Figure 2.5). Productivity of *Laminaria digitata* followed a similar seasonal cycle as *S. latissima*: rates were highest in

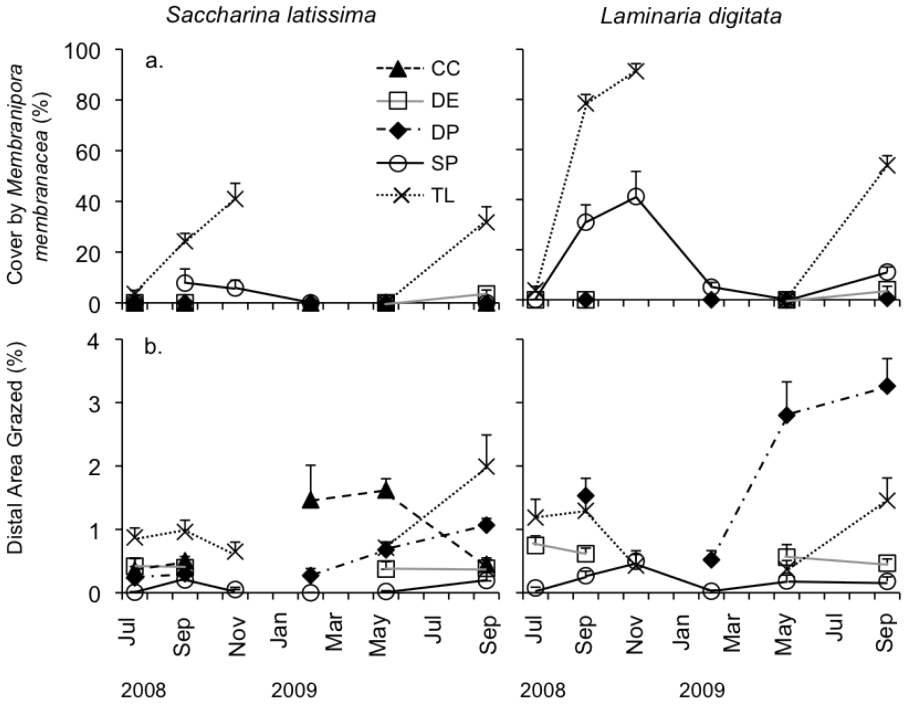

Figure 2.4 Seasonal mean (+ 1 SE) of (a) % cover of *Membranipora membranacea* and (b) % distal area grazed for blades of *Saccharina latissima* and *Laminaria digitata* at the 5 sampling sites (CC, Cranberry Cove; DE, Duncan's Exposed; DP, Duncan's Protected; SP, Splitnose Point; TL, The Lodge). Sample size is 10 to 20 thalli during each sampling period

Table 2.2 One-way ANOVA of seasonal changes in erosion and productivity rates and the ratio of erosion to productivity (EP) for *Saccharina latissima* and *Laminaria digitata* at the study sites where winter measurements were taken (CC = Cranberry Cove, DP = Duncan's Cove Protected, SP = Splitnose Point). Letters next to months indicate statistically significant groupings according to Tukey's HSD tests ($\alpha < 0.01$).

Site	**Variable**	**DF**	**SS**	**F**	**p**	**Tukey's HSD**
Sccharina latissima						
CC	Erosion (g d^{-1})	4	0.22	10.9	<0.001	May(A), Sep09(AB), July(AB), Sep08(B), Feb(C)
	Productivity (g d^{-1})		20.5	20.6	<0.001	July(A), May(AB), Sep09(BC), Sep08(CD), Feb(D)
	EP		18.0	10.0	<0.001	Sep09(A), Sep08(A), May(AB), July(BC), Feb(C)
DP	Erosion (g d^{-1})	4	0.13	16.0	<0.001	Sep09(A), May(A), Sep08(BC), July(B), Feb(C)
	Productivity (g d^{-1})		7.38	8.35	<0.001	May(A), July(AB), Sep09(BC), Feb(BC), Sep08(C)
	E:P		10.4	8.39	<0.001	Sep09(A), Sep08(AB), May(B), July(B), Feb(B)
SP	Erosion (g d^{-1})	5	0.44	4.91	0.001	Sep09(A), July(AB), Sep08(ABC), Nov(BC), Feb(ABC), May(C)
	Productivity (g d^{-1})		33.8	19.6	<0.001	May(A), July(A), Sep08(B), Nov(B), Sep09(B), Feb(C)
	E:P		41.1	5.90	<0.001	Feb(A), Sep09(A), Nov(AB), Sep08(AB), July(AB), May(B)
Laminaria digitata						
DP	Erosion (g d^{-1})	3	0.21	7.57	<0.001	Sep09(A), May(AB), Feb(BC), Sep08(C)
	Productivity (g d^{-1})		6.59	5.78	0.002	May(A), Feb(A), Sep09(AB), Sep(B)
	E:P		24.40	24.4	<0.00	Sep09(A), May(AB), Sep08(B), Feb(B)
SP	Erosion (g d^{-1})	5	1.36	3.27	0.009	Sep09(A), Nov(AB), Feb(AB), Sep08(AB), July(B), May(B)
	Productivity (g d^{-1})		22.93	11.6	<0.001	May(A), July(AB), Feb(ABC), Sep09(BCD), Nov(CD), Sep08(D)
	E:P		60.97	8.12	<0.001	Sep09(A), Nov(A), Sep08(A), Feb(AB), July(B), May(B)

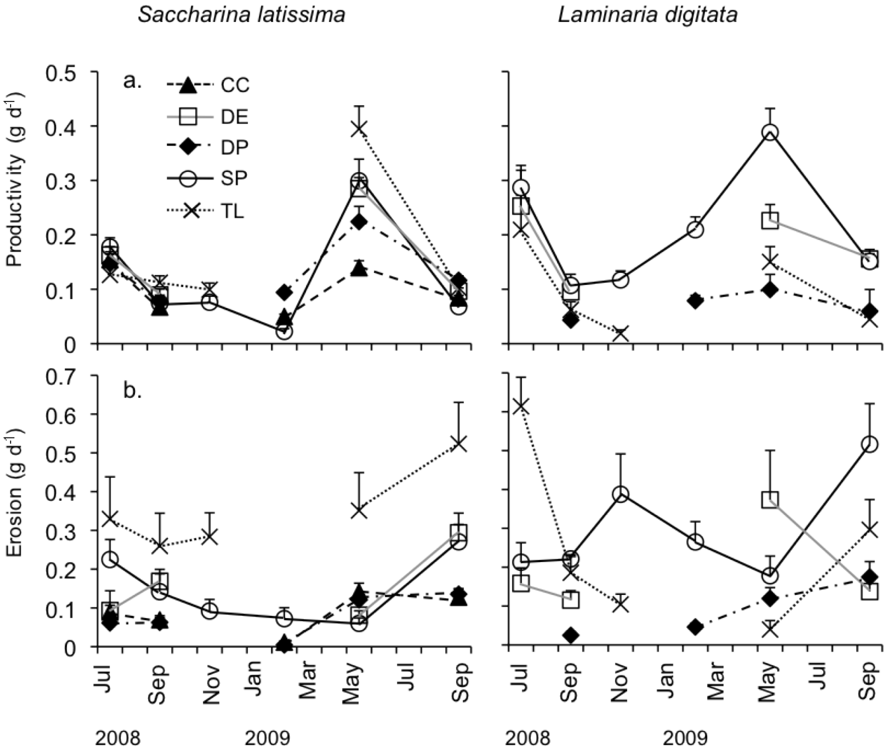

Figure 2.5 Seasonal mean (+ 1 SE) of (a) productivity and (b) erosion (g d^{-1}) for *Laminaria digitata* and *Saccharina latissima* at the 5 sampling sites (CC = Cranberry Cove, DE = Duncan's Exposed, DP = Duncan's Protected, SP = Splitnose Point, TL = The Lodge). Sample size is 10 to 20 thalli during each sampling period.

spring (May 2009: 0.15-0.39 g d^{-1}) and summer (July 2008: 0.21-0.29 g d^{-1}) and lowest in fall (September 2008: 0.04-0.11 g d^{-1}, November 2008: 0.02-0.12, and September 2009: 0.04-0.16 g d^{-1}) (Table 2.2, Figure 2.5). Productivity of *L. digitata* began to increase earlier in the year (February 2009) compared to *S. latissima* (Table 2.2, Figure 2.5). There were consistent differences in productivity among sites over time, resulting in significant effects of site ($F_{3,167} = 29.0$, $p < 0.001$) and season ($F_{2,167} = 36.5$, $p < 0.001$) with no interaction between these factors ($F_{6,167} = 4.67$, $p = 0.100$). Productivity of *L. digitata* was highest at Splitnose Point and lowest at Duncan's Cove Protected.

Unlike productivity, erosion rates of *Saccharina latissima* and *Laminaria digitata* varied over time with no clear seasonality or consistent differences among sites (Figure 2.5), as indicated by a significant interaction between site and season for both species (*S. latissima*: $F_{12,303} = 2.29$ $p = 0.009$; *L. digitata*: $F_{6,167} = 9.25$, $p < 0.001$). Erosion rates of *S. latissima* were highest at The Lodge (0.26-0.52 g d^{-1}) throughout the study and lowest at Cranberry Cove (0.01-0.14 g d^{-1}) and Duncan's Cove Protected (0.004-0.13 g d^{-1}) during most sampling periods (Table 2.2, Figure 2.5). At Duncan's Cove Exposed and Splitnose Point, erosion rates in 2009 were lowest in winter (February 2009: Splitnose Point = 0.02 g d^{-1}) and spring (May 2009: Duncan's Cove Exposed = 0.08, Splitnose Point = 0.06 g d^{-1}) and increased markedly by fall (September 2009: Duncan's Cove Exposed = 0.29, Splitnose Point = 0.27 g d^{-1}). Rates in fall were higher in 2009 (September) than in 2008 (September, November) at all sites, although the difference was not statistically significant at Cranberry Cove and Splitnose Point (Table 2.2). Erosion rate of *L. digitata* at Splitnose Point appeared to follow a reciprocal seasonal pattern to that of productivity, with low rates of erosion in spring (May 2009: 0.18 g d^{-1}) and summer (July 2008: 0.21 g d^{-1}), and high rates in fall (November 2008, September 2009: 0.39 and 0.52 g d^{-1} respectively) (Table 2.3, Figure 2.5). Increases in erosion between winter/spring (February/May) and fall (September) in 2009 also were observed at The Lodge and Duncan's Cove Protected; however, erosion rate at The Lodge declined between summer (July 2008) and fall (September/November) in 2008. In contrast to other sites, erosion at Duncan's Cove Exposed was highest in spring (May 2009: 0.37 g d^{-1}) and decreased markedly in fall (September 2009: 0.14 g d^{-1}). Erosion rate increased significantly with total length for each kelp species when measures were pooled across sites and seasons

(*L. digitata*: $F_{1,260} = 64.9$, $p < 0.001$, $R^2 = 0.19$, *S. latissima*: $F_{1,344} = 63.4$ $p < 0.001$, $R^2 = 0.15$); however, this relationship explained little of the overall variance in erosion.

2.3.4 The Ratio of Erosion to Productivity

The EP ratio for *Saccharina latissima* and *Laminaria digitata* showed no consistent temporal pattern across sites (Table, 2.2, Figure 2.6), and the interaction between site and season was significant for both species (*S. latissima*: $F_{12,303} = 3.96$, $p < 0.001$; *L. digitata*: $F_{6,167} = 10.7$, $p < 0.001$). Consistently high EP ratios were observed at The Lodge for *S. latissima*, where biomass remained low throughout the study period. The EP ratio was consistently at or slightly below 1 (except in February 2009) at Cranberry Cove for this species, where kelp biomass remained relatively constant across seasons (Figure 2.6). The EP ratio at Duncan’s Cove Exposed and Splitnose Point fluctuated widely between successive sampling periods but tended to be highest in fall (September 2008, 2009) and lowest in spring (May 2009). In 2009, a switch in the EP ratio from less than 1 in spring (May) to maximum values greater than 1 in fall (September) was associated with a marked decline in biomass of *S. latissima* at Splitnose Point, but only slight decreases at the other sites. EP values much less than 1 in winter at Duncan’s Cove Protected and Cranberry Cove corresponded to small increases in biomass from winter to spring in 2009. In 2008, EP ratios greater than 1 at The Lodge in summer and fall (July, September, November) were not associated with a decrease in biomass of *S. latissima* during this period (Figure 2.6).

For *Laminaria digitata*, the EP ratio was consistently high at The Lodge (except May 2009), where biomass remained low throughout all sampling periods (Figure 2.6). Conversely, the EP ratio remained close to 1 at Duncan’s Cove Exposed, corresponding to a general increase in biomass over the study period. At Splitnose Point, the EP ratio was high in fall (September/November 2008) and low in winter/spring (February/May 2009), corresponding to a switch from increasing to decreasing biomass around February. Increases in EP ratios between September 2008 and 2009 were observed at Duncan’s Cove Protected and The Lodge, while the ratio remained relatively constant at Duncan’s Cove Exposed and Splitnose Point over this interval (Table 2.2, Figure 2.6).

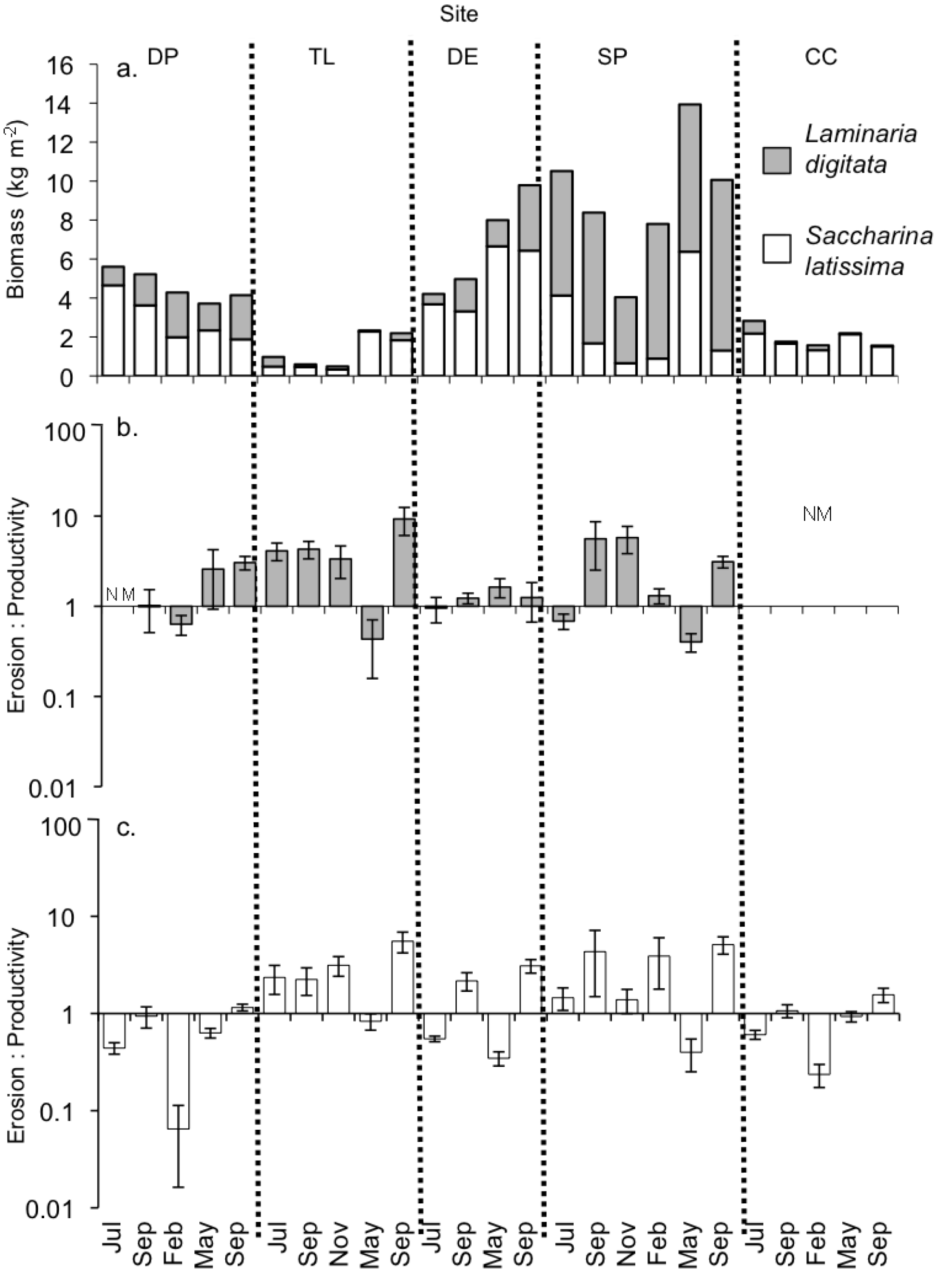

Figure 2.6 (a) Mean standing biomass (kg ww m^{-2}) of *Saccharina latissima* and *Laminaria digitata* and (b) the ratio of erosion to productivity (EP) at the five sampling sites (CC = Cranberry Cove, DE = Duncan's Exposed, DP = Duncan's Protected, SP = Splitnose Point, TL = The Lodge) during all sampling periods for (b) *Laminaria digitata* and (c) *Saccharina latissima*. EP data are plotted on a log scale. Sample size is 10 to 20 thalli during each sampling period.

2.3.5 Effects of Biological and Physical Factors on Erosion and EP Ratio

Cover by *Membranipora membranacea*, distal area grazed by snails, and temperature are factors (each positively related) in the best model of erosion rate of *Saccharina latissima* (Tables 2.3, 2.4). There is strong evidence that cover by *M. membranacea* is the main factor controlling this rate. Models including cover by *M. membranacea* were ranked as the best (ranks 1-5, and 7-8) (Appendix 2), and the sum of model probabilities containing this factor is high (0.91). The best model not including cover by *M. membranacea* had a model probability less than 0.05. There is also evidence that temperature and % distal area grazed are important factors driving this rate (both positively related), as the likelihood increases and the model probability is 3 times greater with the inclusion of these factors as compared to the model with *M. membranacea* cover alone. Furthermore, the sum of model probabilities containing area grazed and temperature are 0.60, and 0.67, respectively. In contrast, there is strong evidence to support exposure as the most important factor (positively related) explaining variation in erosion rate of *Laminaria digitata* (Tables 2.3, 2.4), as models containing this factor were ranked above all those that did not, and the sum of model probabilities containing this factor is 0.95 (Appendix 2). Area grazed (positively related) is also present in the top model, which performed slightly better than a model without it, providing weak evidence that it may be important to in determining the erosion rate of *L. digitata*. Models including cover by *M. membranacea* or temperature were also ranked as good models, however there is little evidence to suggest that they are important factors. Comparing the log-likelihood values of these models (ranked 3-5) to simpler nested models indicates that the fit improved little, and that the good fit of these models is due to other variables.

Cover by *Membranipora membranacea* was the only factor (positively related) in the top model for the EP ratio of *Saccharina latissima* (Tables 2.3, 2.4), and the sum of model probabilities containing this factor is very high (0.95) (Appendix 3). This indicates that there is strong evidence to support *M. membranacea* as the main factor driving the EP ratio for this species. Other high-ranked models explaining variation in the EP ratio of *S. latissima* include factors such as exposure, temperature, and grazing. However, the

Table 2.3 The 5 best models of physical (temperature, exposure) and biological (% cover by *Membranipora membranacea* [% M], % distal area grazed by snails [% Gzd]) factors explaining variation in erosion rate (g d^{-1}) and the ratio of erosion to productivity (EP) for *Saccharina latissima* and *Laminaria digitata.* Calculated are: 2nd-order bias-corrected Akaike's Information Criteria (AICc), the difference between the minimum AICc and the AICc of each model (ΔAICc), the log likelihood function, the model probability (w_i), and the R^2 value of each model.

Parameter	Model	AICc	ΔAICc	Log Likelihood	w_i	R^2
Saccharina latissima						
Erosion (g d^{-1})	%M + %Gzd + Temp	-89.81	0.000	48.65	0.361	0.48
	%M + Temp	-88.41	1.396	46.56	0.179	0.40
	%M + %Gzd	-87.79	2.019	46.25	0.131	0.38
	%M	-87.45	2.353	44.84	0.111	0.33
	%M + Exposure + Temp	-85.99	3.818	46.74	0.053	0.37
EP	%M	15.34	0.000	-6.561	0.311	0.31
	%M + Exposure	16.48	1.140	-5.889	0.176	0.32
	%M + Exposure + Temp	16.55	1.209	-4.527	0.170	0.30
	%M + Temp	17.25	1.902	-6.270	0.120	0.29
	%M + %Gzd	17.57	2.230	-6.434	0.102	0.28
Laminaria digitata						
Erosion (g d^{-1})	%Gzd + Exposure	-68.17	0.000	36.54	0.284	0.41
	Exposure	-68.03	0.132	35.16	0.266	0.35
	%M + Exposure	-66.25	1.914	35.59	0.109	0.34
	Exposure + Temp	-66.20	1.964	35.56	0.106	0.33
	%M + %Gzd + Exposure	-65.74	2.426	36.87	0.085	0.39
EP	%M + %Gzd	11.52	0.000	-3.300	0.553	0.72
	%M + %Gzd + Exposure	13.89	2.366	-2.945	0.169	0.71
	%M + %Gzd + Temp	14.29	2.768	-3.146	0.139	0.71
	%M	15.95	4.430	-6.834	0.060	0.60
	%M + Temp	16.90	5.3742	-5.988	0.038	0.61

Table 2.4 Coefficient estimate and standard error for each physical (temperature, exposure) and biological (% cover by *Membranipora membranacea* [%M], % distal area grazed by snails [% Gzd] factor present in the top model according to 2nd-order bias-corrected Akaike's Information Criteria (AICc) for erosion rate (g d^{-1}), and the ratio of erosion to productivity (EP) for *Saccharina latissima* and *Laminaria digitata*, determined by multiple linear regression analysis.

Species	**Parameter**	**Model**	**Estimate**	**Standard Error**
Saccharina latissima	Erosion (g d^{-1})	% M	0.04	0.02
		% Gzd	0.07	0.04
		Temp	0.01	0.00
	EP	% M	0.68	0.22
Laminaria digitata	Erosion (g d^{-1})	% Gzd	0.06	0.04
		Exposure	0.01	0.00
	EP	% M	1.21	0.19
		% Gzd	0.93	0.35

modest increases in log-likelihood values for these models relative to the simpler, best-ranked model indicates that there is little to no evidence to suggest these other factors are important, and the fit of these other models is determined primarily by cover of *M. membranacea*. There is also strong support for cover of *M. membranacea* as the key determinant of variation in the EP ratio for *Laminaria digitata*, as this factor (positively related) also appeared in the top 5 models for this measure (Table 2.3, 2.4), and the sum of model probabilities containing this factor is 0.99 (Appendix 3). There is also strong support for the role of area grazed (positively related) in EP ratio, as the model including this factor is 10 times more likely than the model with *M. membranacea* cover alone, and the sum of model probabilities containing this factor is 0.86.

2.3.6 Detrital Production Estimates

The proportion of the total population represented by our erosion rate measurements was > 0.50 for *Saccharina latissima* at 4 of the 5 sites, and > 0.60 for *Laminaria digitata* at 3 of the 4 sites where it was measured (Table 2.5). Individual erosion rates, averaged over all sampling periods for each species, ranged from 0.1 to 0.4 g d^{-1}. When multiplied by the average density of the measured population, detrital production rates due to erosion range from 0.8 to 2.8 g m^2 d^{-1} for *S. latissima* and from 0.3 to 3.9 g m^2 d^{-1} for *L. digitata* (Table 2.5). Combining species within kelp beds (except at Cranberry Cove, where *L. digitata* was rare and not measured during our study) gives estimates of annual detrital production ranging from 0.5 to 1.71 kg dw m^{-2}. Annual detrital production was strongly related ($R^2 = 0.83$) to average kelp biomass across sites (Figure 5.7), and was highest at Splitnose Point and lowest at Cranberry Cove.

2.4 DISCUSSION

The kelps *Saccharina latissima* and *Laminaria digitata* exhibit a distinct annual cycle of primary productivity in the Northwest Atlantic, with a spring peak and seasonal low in late fall/winter (Mann 1972, Chapman & Craigie 1977, Gagné et al. 1982, Brady-Campbell et al. 1984, this study). This cycle is driven by nutrient dynamics in the water column, which in turn are linked to ocean temperature, wave action, and site exposure

Table 2.5 Summary of measures of *Saccharina latissima* (SL) and *Laminaria digitata* (LD) averaged across sampling periods at each site: minimum and maximum total length (TL, cm) of measured individuals, density within the size range measured for erosion (D_M, individuals m^{-2}), proportion of D_M relative to total density of individuals >20 cm total length (D_T), individual erosion rates (E , g d^{-1}), and erosion rates per unit area for the measured portion of the population (E_M, g m^{-2} d^{-1}). Annual production of kelp detritus via erosion (Annual E_M, kg dw m^{-2}) combines E_M for both species standardized to 1 year.

Site	Min TL		Max TL		D_M		D_M /D_T		E		E_M		Annual E_M
	SL	LD	SL	LD	SL	LD	SL	LD	SL	LD	SL	LD	
CC	54	nm	172	nm	14	nm	0.36	nm	0.1	0.0	1.4	0.0	0.50
DP	78	49	183	105	19	8.8	0.62	0.29	0.1	0.1	1.3	1.0	0.82
DE	110	68	247	170	16	6.8	0.65	0.64	0.2	0.2	2.8	1.1	1.43
TL	81	42	185	105	5.3	1.3	0.52	0.75	0.4	0.3	1.9	0.3	0.82
SP	124	101	242	193	6.1	13	0.55	0.67	0.1	0.3	0.8	3.9	1.71

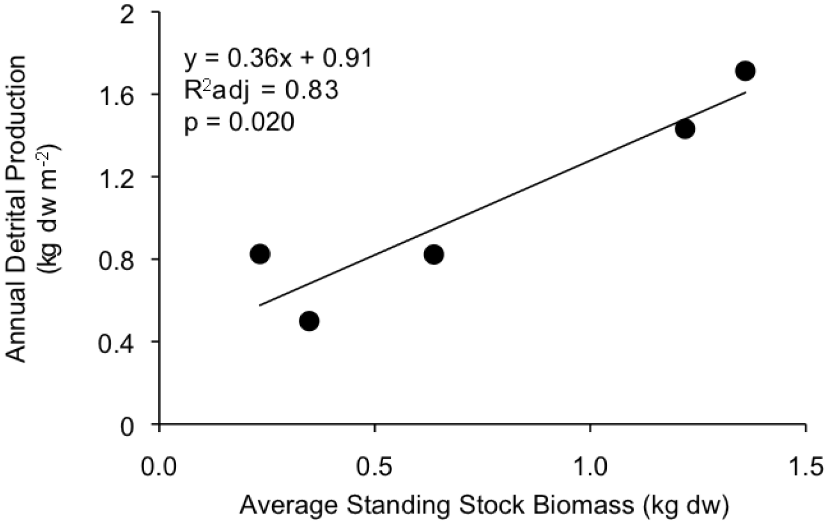

Figure 2.7 The relationship between total kelp standing biomass (kg dw m^{-2}), averaged across all sampling periods at each site, and annual detrital production (kg dw). Linear regression equation and line, R^2, and p-value are shown.

(Chapman & Craigie 1977, Gerard & Mann 1979, Dobrynin et al. 2010). We detected a significant interaction between site and sampling date, indicating seasonality in productivity is variable across sites. This variability is in part linked to encrustation by the invasive bryozoan *Membranipora membranacea*, which limits nutrient uptake by kelps (Hurd et al. 1994, 2000). This is evident in observed decreases in productivity relative to erosion (increases in EP ratio) with increasing bryozoan cover from spring/summer to fall at Splitnose Point and The Lodge in 2008 and 2009.

Erosion rate and the ratio of erosion to productivity for *Saccharina latissima* and *Laminaria digitata* varied markedly among sites and seasons. The significant interaction of these factors indicates that seasonal patterns in erosion rate and EP ratio differed among sites. For both measures, positive relationships were found with percent cover by *Membranipora membranacea* and area grazed by snails, indicating that these factors are important determinants of spatial and temporal variation. Erosion rate and EP ratio were highest at The Lodge and Splitnose Point, where the highest levels of encrustation by *M. membranacea* and grazing intensity were observed. Conversely, kelps were not encrusted by *M. membranacea* at Cranberry Cove and Duncan's Cove Protected, leading to low erosion rates and EP ratios at these sites. While consistent seasonal patterns in erosion and the EP ratio were not observed, peaks in these measures at the different sites typically corresponded to peaks in bryozoan cover or grazing intensity. For example, high bryozoan cover and grazing intensity led to high erosion rates and EP ratios at Splitnose Point and The Lodge in summer and fall for both kelp species. At the other 3 sites, where the bryozoan was rare or absent, high erosion rates and EP ratios were typically observed in spring during periods of high grazing intensity. Furthermore, increases in erosion rate between September 2008 and September 2009 at Duncan's Cove Protected corresponded to increases in grazing between years. Erosion was generally minimal during winter, when grazing intensity and bryozoan cover were at seasonal lows.

Extensive loss of kelp canopy following outbreaks of *Membranipora membranacea* has been documented in late fall/early winter in Nova Scotia and the Gulf of Maine (Berman et al. 1992, Lambert et al. 1992, Scheibling et al. 1999, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). Encrustation by the bryozoan purportedly renders kelp blades more friable (Dixon et al. 1981), increasing susceptibility to breakage and erosion by hydrodynamic forces, although this process has not been quantified or tested explicitly. Mesograzers such as snails, which create superficial abrasions, nicks or complete perforations of blades, also can reduce the ability of kelps and other seaweeds to withstand waves, as fractures form more readily at sites of tissue damage (Black 1976, Johnson & Mann 1986, Denny et al. 1989, Duggins et al. 2001). While previous work has suggested that these biological factors may affect detrital production rates, our study is the first to make direct linkages between cover by *M. membranacea*, grazing by snails, and kelp blade erosion.

Temporal and spatial variation in erosion rate also is influenced by the seasonal dynamics of temperature for *Saccharina latissima* and site exposure for *Laminaria digitata*. Warm temperatures are linked to low nutrient levels in the water column, leading to tissue degradation in kelps (Rothausier et al. 2009). The relationship between temperature and erosion was not observed for *L. digitata*, which may be attributed to differences in blade morphology between the two kelp species. Blade area of *S. latissima* is typically less than that of *L. digitata*, which may result in a lower capacity for nutrient uptake and a stronger influence of temperature-mediated nutrient levels on erosion rate for *S. latissima.* Erosion rate of *L. digitata* increased with site exposure, although this was not observed for *S. latissima*. Again, this may be due to morphological variation between species related to wave exposure. The “digits” of *L. digitata* were narrower and more numerous at exposed compared to protected sites, resulting in an increase in blade area with exposure (K. Krumhansl, unpublished data). The single blade of *S. latissima* also narrows with increasing wave exposure, but it remains broader and possibly more resistant to erosion than the highly digitate blade of *L. digitata* at wave-exposed sites. This likely leads to a greater dependence of erosion rate on wave exposure for *L. digitata* compared to *S. latissima*.

The ratio of erosion to production is an indication of whether a kelp bed is decreasing (EP ratio > 1) or increasing (< 1) in biomass. We observed some linkages between long-term patterns in total biomass and EP ratio, however these relationships were not consistent. For example, EP ratio was consistently high at The Lodge for both *Saccharina latissima* and *Laminaria digitata*, resulting in the lowest recorded biomass of all sites. At sites where EP ratio remained close to 1 (Cranberry Cove for *S. latissima*, and Duncan’s

Cove Protected for *L. digitata*), biomass increased or remained relatively constant during the study period. We expected that biomass would increase at sites were EP ratios were consistently lower than 1, but this was not observed. Some linkages between biomass changes and EP ratio were observed seasonally, including a decline in biomass from spring to fall at some sites for *S. latissima*, associated with increases in EP ratio. However, these measures were generally not well correlated in the short-term. A clearer relationship between seasonal patterns in EP ratio and biomass may be observed if biomass changes are measured over the same sampling intervals as erosion rate.

We demonstrate that a large quantity of detritus is produced annually by erosion of particulates and larger fragments from kelp thalli. These estimates were generated for a portion of the sporophyte population (albeit the majority in most cases) and are therefore conservative. However, the degree of underestimation is likely small because our measures are based on the larger size fraction of the population, and erosion rate is directly related to total length for both *Saccharina latissima* and *Laminaria digitata*. Thus, larger kelps contribute a much greater proportion of the total eroded material than individuals below our minimum size limit for measurement (30-40 cm total length). Another component of detrital production from subtidal kelp beds is the dislodgement of whole thalli that occurs during major storm events, such as passing hurricanes. Massive pulses of detrital material can be exported from kelp beds to adjacent intertidal and subtidal habitats during these sporadic events (Filbee Dexter & Scheibling in press), substantially augmenting the more gradual and continuous erosion and fragmentation of blade tissue measured in our study.

The amount of detrital material produced annually from erosion of both *Saccharina latissima* and *Laminaria digitata* ranged from 0.5 to 1.7 kg dry weight m^{-2} across sites. This is equivalent to 150 to 513 g C m^{-2}, as carbon composes 30% of blade tissue for both kelp species (Mann 1972). These values equal or exceed those recorded for phytoplankton production off the Atlantic coast of Nova Scotia, estimated at 190 g C m^{-2} (Platt 1971), indicating that particulate kelp detritus may be the main source of food for suspension- and deposit-feeders in deep-water communities in this region.

We found a positive relationship between the amount of material eroded annually and standing biomass. Long-term reductions in kelp biomass have been linked to encrustation of kelps by *Membranipora membranacea* (Scheibling & Gagnon 2006, 2009). At The Lodge, a 40% decline in canopy cover was documented 2 y prior to our study (Saunders & Metaxas 2008), and biomass remained low throughout the study. Therefore, while *M. membranacea* may increase the amount of material eroded from kelps in the short term, long-term decreases in kelp biomass due to bryozoan encrustation may ultimately lead to a decline in detrital production in kelp beds.

We have shown that a combination of environmental and biological factors affects rates of erosion and the ratio of erosion to productivity of kelps along the Atlantic coast of Nova Scotia, which in turn influence the dynamics of detrital export to surrounding habitats. These rates will be affected by ongoing changes in ocean climate and anthropogenic disturbances, such as species introductions. A positive effect of temperature on erosion rate indicates that warming can lead to changes in detrital production. We also have shown that encrustation by the invasive bryozoan *Membranipora membranacea* alters detrital production rates by increasing erosion rate relative to productivity in both *Saccharina latissima* and *Laminaria digitata.* This non-consumptive interaction between a native alga and an invasive bryozoan provides a striking example of an indirect effect of an introduced species on energy export from kelp beds.

The exchange of detrital material may be a significant form of connectivity between subtidal kelp beds and adjacent, less productive areas. Therefore, changes in rates of detrital production and export from kelp beds are likely to have important consequences for deep-water assemblages that rely on algal detritus as an energy source. Previous studies have demonstrated these effects in other systems, including effects of species introductions. For example, changes in amphipod assemblages have been attributed to increased detrital accumulation in areas invaded by the green alga *Caulerpa racemosa* in the Mediterranean (Vazquez-Luis et al. 2008). Similar effects have been observed in terrestrial ecosystems where detritus from non-native species may alter soil conditions and/or food availability (Wolkovich et al. 2009). Ultimately, understanding the roles of environmental and biological factors in the dynamics of detrital export from kelp beds will aid in predicting impacts of human-mediated changes to climate and habitat on the structure and function of coastal ecosystems.

CHAPTER 3
SPATIAL AND TEMPORAL VARIATION IN GRAZING DAMAGE BY THE GASTROPOD *Lacuna vincta* IN NOVA SCOTIAN KELP BEDS

The work presented in Chapter 3 also appears in:
Krumhansl KA, Scheibling RE (2011b) Spatal and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. Aquat Biol 13:163-173

3.1 INTRODUCTION

Mesograzers, such as small snails and crustaceans (Brawley 1992), can have large direct effects on benthic community organization by influencing the dynamics of early succession (Scheibling et al. 2009), reducing macrophyte biomass (Johnson & Mann 1986, Chenelot & Konar 2007), and cycling nutrients through consumption of detrital material (Robertson & Lucas 1983). Tissue damage by mesograzers also can increase the susceptibility of macrophytes to other forms of disturbance, such as breakage or dislodgement by hydrodynamic forces (Duggins et al. 2001, Krumhansl & Scheibling 2011a). These indirect effects may have important consequences for the structure and dynamics of both the local community and adjacent communities that depend on allochthanous inputs in the form of macrophyte detritus (Bustamante et al. 1995, Vetter 1995).

In kelp beds, the rate of consumption of macroalgal biomass by snails and other mesograzers is small relative to that of large and abundant grazers such as sea urchins (Lawrence 1975, Harrold & Pearse 1987). However, in areas where sea urchins are rare or absent, mesograzers may be the dominant herbivores (Kangas et al. 1982, Johnson & Mann 1986, Duggins et al. 2001, Chenelor & Konar 2007, Scheibling et al. 2009). In the northwest Atlantic, the gastropod *Lacuna vincta* is the only mesograzer known to consume macroscopic kelp sporophytes (Brady-Campbell et al. 1984, Johnson & Mann 1986). On the Atlantic coast of Nova Scotia, *L. vincta* is seasonally abundant in kelp beds, with peak densities (up to 2000 snails m^{-2}) during recruitment in February, and seasonal lows between August and October (Johnson & Mann 1986). *L. vincta* preferentially grazes kelps (Chavanich & Harris 2002), creating perforations or superficial excavations on the surface of blades. Johnson and Mann (1986) estimated that the cumulative effect of grazing by *L. vincta* was a removal of only 0.05 % of standing blade biomass of *Saccharina latissima* (formerly *Saccharina longicrurus*, MecDevit & Saunders 2010) in a kelp bed in St. Margarets Bay, Nova Scotia. However, population explosions of *L. vincta* in the Gulf of Maine have been associated with high levels of damage to kelp blades and canopy loss (Fralick et al. 1974). Krumhansl & Scheibling (2011a) linked variation in the rate of kelp blade fragmentation and erosion to damage along the distal ends of blades, suggesting that grazing by *L. vincta* can indirectly decrease kelp biomass and increase detrital production.

Spatial and temporal variation in grazing damage to kelps and other macroalgae in shallow marine habitats is caused by the interaction between various abiotic and biotic factors. Wave exposure generally has a negative effect on grazing rate (Duggins et al. 2001, Vanderklift et al. 2009, Taylor & Schiel 2010; but see also Robles & Robb 1993), although the underlying mechanisms and magnitude of this effect can vary among habitats. Structural properties and nutritional quality of blades also can vary seasonally with changes in water temperature (Sjotun et al. 1996, Abdullah & Fredriksen 2004). For example, warming temperatures can increase grazing damage by accelerating degradation of older tissues at the distal ends of blades (Rothausier et al. 2009), which reduces toughness and increases palatability (Molis et al. 2010).

The process of blade elongation, and variation in chemical or structural characteristics of tissues along kelp blades may influence the distribution of grazing damage on individual thalli. As new blade tissue is produced at the basal meristem, existing tissue continually progresses towards the distal end of the blade, where it fragments or gradually erodes. If grazing occurred randomly across the blade surface, we would expect an increase in the amount of grazer-damaged tissue with distance from the meristem and period of exposure to grazers. Polyphenolic content is highest near the meristem, which has been linked to low grazing rates in the basal region (Johnson & Mann 1986).

Encrustation of kelp blades by the invasive epiphytic bryozoan, *Membranipora membranacea* also may influence the distribution and intensity of grazing by *Lacuna vincta*. Blade encrustation peaks in September and October (~100 % cover on some kelp blades), and declines to extremely low levels from February to May (Scheibling & Gagnon 2009, Krumhansl & Scheibling 2011a). *L. vincta* is assumed to be strictly herbivorous (Iyengar & Harvell 2002) and *M. membranacea* may limit grazing by preempting space on blade surfaces. However, a positive association between cover of *M. membranacea* and density of *L. vincta* has been observed in the Gulf of Maine (Chavanich & Harris 2000).

In this study, we examine spatial and seasonal patterns in grazing damage by *Lacuna vincta* along blades of *Saccharina latissima* and *Laminaria digitata* at five sites varying in wave exposure and cover of *Membranipora membranacea*, and over 15 months. Grazing damage provides a time-integrated measure of the intensity and distribution of grazing that enables us to test the following predictions: 1) damage along kelp blades will be lowest near the base and highest at the distal end, 2) damage will decrease with the cover of *M. membranacea* on kelp blades, and 3) damage will be negatively related to wave action and positively related to temperature. We also experimentally examine the indirect effect of grazing damage on kelp blade breakage by simulating different levels of grazing damage on *S. latissima* in field experiments during moderate to heavy wave conditions.

3.2 METHODS

3.2.1 Grazing Damage Measurements

As part of a broader study of kelp production and erosion rates (Krumhansl & Scheibling 2011a), we measured grazing damage on kelps at 5 sites of varying wave exposure along the Atlantic coast of Nova Scotia: Duncan's Cove Exposed, Duncan's Cove Protected, Splitnose Point, The Lodge, and Cranberry Cove. The kelps *Saccharina latissima* and *Laminaria digitata* occur in monospecific or mixed stands as the dominant canopy-forming macroalgae at all sites. The morphology of *S. latissima* is characterized by a single, strap-like blade with ruffled margins. *L. digitata* has a broad blade that splits into “digits” near the distal end. Measurements were taken on kelps growing on substrates ranging from small boulders to rock ledges at 5 to 7 m depth. For detailed site descriptions, see Krumhansl & Scheibling (2011a).

Grazing damage was measured on 10–15 kelp thalli, > 25 cm blade length, that were haphazardly collected using SCUBA at 6 times over a 15-month period (July, September, November 2008; February, May, September 2009). Measurements were obtained at all sites in July, September (2008 and 2009), and May. In November, measurements were taken at The Lodge and Splitnose Point because the invasive bryozoan *Membranipora membranacea* occurs in high abundance during this period at these sites only. In February, logistical constraints limited our measurements to Duncan’s Cove Protected, Splitnose Point, and Cranberry Cove. Grazing damage on thalli of *Laminaria digitata* was not measured at Cranberry Cove (all sampling periods) or Duncan’s Cove Protected (July 2008) because this species was not abundant at these sites or seasons.

To measure grazing damage, thalli were pressed between two pieces of plexiglass and photographed. We characterized grazing damage as perforations (holes) or superficial excavations of the blade (Figure 3.1A,B). Excavations were difficult to delineate in photographs and have little effect on blade strength (Krumhansl et al. 2011); therefore, we measured perforations only. The area grazed in each of 3 equal sections of blade by length was measured by manually outlining grazed holes in ImageJ (NIH). This was divided by the area of the respective blade section to estimate of the percentage of blade area grazed in the base, middle and distal regions of blades. The area grazed in each section was then divided by the total area grazed on a blade to generate the percentage of total blade area grazed in each section. The total area of grazed holes in all sections was divided by the total blade area to estimate the percentage of blade area grazed.

Grazing damage was measured in relation to site exposure, temperature, and cover of *Membranipora membranacea*. The relative exposure of each site was determined by calculating a relative exposure index (REI, modified from Keddy 1982) using fetch and wind data (directional average wind speed and probability) for a 3-week period before each measurement (REI values presented in Krumhansl & Scheibling 2011a). This index uses wind data for a specific time period, and therefore index values vary both seasonally as well as spatially.

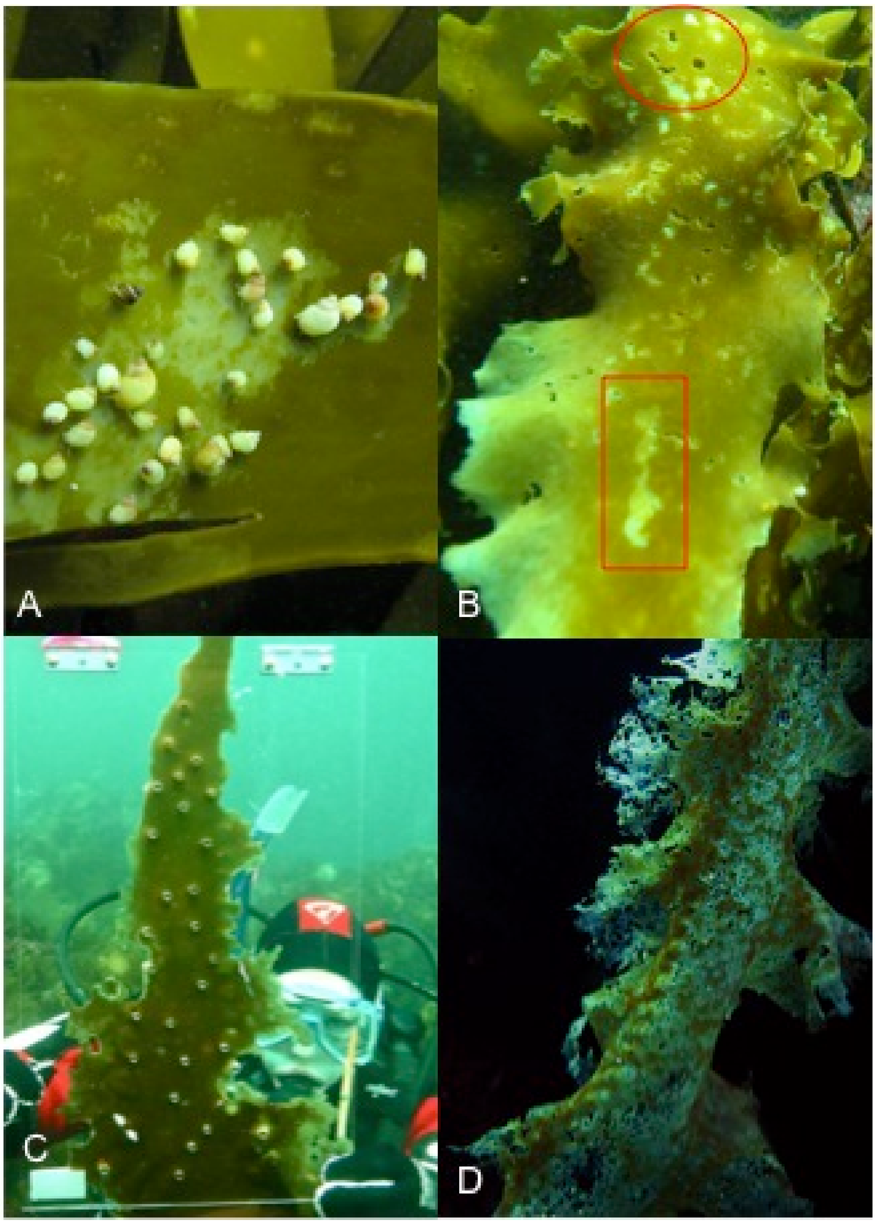

Figure 3.1 (A) *Lacuna vincta* actively grazing *Laminaria digitata* (B) Grazed perforations (circled), and excavations (inside rectangle) on a blade of *Saccharina latissima* (C) Applying the 30-hole simulated grazing treatment to the distal 45 cm of a blade of *S. latissima* (D) A heavily grazed blade of *S. latissima* at The Lodge in September 2010. Photographs by R. Scheibling.

Previous studies comparing wave-based exposure indices to those based on fetch have found good correlation between the two, suggesting that the latter can appropriately be used to approximate wave exposure at a particular site (Hill et al. 2010). Temperature was recorded using temperature loggers (Onset StowAway Tidbits or HOBO Pendant Data Loggers), and averaged for 3 weeks before each sampling period for analysis (Krumhansl & Scheibling 2011a). Temperature data were not available for the July 2008 sampling period. Percentage cover of *M. membranacea* was measured by photographing each collected thallus and outlining colonies of *M. membranacea*. Tracings were then photographed and the area measured using image analysis. The area covered by *M. membranacea* was divided by total blade area to measure the percentage of blade covered by the bryozoan for each thallus.

3.2.2 Simulated Grazing Experiment

The effect of grazing damage on rates of blade fragmentation was examined experimentally on *Saccharina latissima*. The experiment was conducted in August and September 2009 to correspond with the seasonal occurrence of storms and hurricanes, as well as a seasonal peak in kelp erosion rates (Krumhansl & Scheibling 2011a). Artificial holes were punched in the distal ends of blades of *S. latissima* at the Lodge to mimic grazing damage by *Lacuna vincta*. This was done by sandwiching the thallus in a hinged plexiglass folder with imbedded sections of copper tubing that punctured the thallus as the folder was closed (Figure 3.1C). Three levels of simulated grazing damage were applied to reflect the observed range of area grazed (0–25 cm^2, 0.0–1.4 % of blade area) on the distal end of kelp blades, and average size of perforations caused by grazing (0.32 cm^2 ± 0.08 SE, n = 57) on kelps at The Lodge in September 2008. Treatments consisted of 10 ("low grazing damage"), 30 ("moderate grazing damage"), and 60 ("high grazing damage") holes (i.e. losses of blade area of 3.2, 9.6, 19.2 cm^2 respectively) randomly distributed in a triangular area encompassing the distal 45 cm of blade, and a control with no artificial holes. Four experimental blocks were set parallel to the shore at a depth of 5 to 6 m. Eight kelps 120–250 cm in blade length with little grazing damage were selected in each block, and 2 individuals were randomly assigned to each of the treatments or control. A numbered tag was affixed to the holdfast of each experimental thallus to enable relocation.

Rate of blade breakage was measured during 2 experimental runs, beginning on 7 and 27 August and spanning two successive storm events varying in intensity. Breakage of each blade was measured using a modified "hole punch" method (see Krumhansl & Scheibling 2011a for details). A hole was punched 10 cm directly above the base of the blade (where the blade is twice the width of the stipe) using a sharpened piece of copper tubing, and total blade length was measured. After 3 weeks, each individual was collected and returned to the lab. Growth hole position (as distance from the base of the blade), and final blade length were measured. The loss in length due to breakage, accounting for growth, was then calculated and divided by the total number of days over which the measurements were taken. This generated an estimate of rate of breakage in cm d^{-1}. The distal 30–50 cm of each thallus (depending on the total blade length) was dried at 60 °C for 48 hours, and dry weight was measured. Dry weight was divided by the length of the segment to determine the dry weight biomass (g cm^{-1}) of the distal end of the blade. This measurement was then used to convert rate of blade breakage in cm d^{-1} to g d^{-1}.

We calculated the mean and maximum significant wave height, defined as the mean of the largest on third of waves measured, for each experimental trial from data recorded at a meterological buoy located at the mouth of Halifax Harbour (National Climate Data and Information Archive, http://www.meds-sdmm.dfo- mpo.gc.ca, buoy ID# C44258, 44°30 N, 63°24 W).

3.2.3 Statistical Analysis

To examine seasonal and spatial variation in the distribution of grazing damage, we analyzed the effects of site, season, and location on blade on the percentage of thallus area grazed by a factorial ANOVA, using a split-plot design. To achieve an orthogonal design, only time periods where sampling occurred at all sites were included in the analysis (*Saccharina latissima*: July and September 2008, May and September 2009; *Laminaria digitata*: September 2008, May and September 2009). Main-plot factors were site and time (both fixed factors), while the sub-plot factor was location on the blade (fixed factor) of each individual (random factor, nested within site and time). Data were not normally distributed (Shapiro-Wilk test, $p < 0.001$) and variances were heterogeneous (Levene's test, $p < 0.001$). Arcsine transformation of the percentage of thallus area grazed yielded similar results for tests of these assumptions of ANOVA; therefore we performed the analysis on untransformed data. Variance heterogeneity can inflate the Type I error rate; to adjust for this possibility, we use $\alpha = 0.01$ in this analysis.

We used an information-theoretic approach to examine factors that influence the extent of total grazing damage on thalli at a site scale. The percentage of total blade area grazed was averaged across individuals for each site and season, by species. 2^{nd}-order bias-corrected Akaike's Information Criteria (AICc), the values of the maximized log-likelihood function, and model probabilities were used to assess the relative strength of possible models containing temperature and/or site exposure (REI) in explaining variation in the percentage of total area grazed on thalli. To further assess the relative importance of each individual factor, the model probabilities of all models containing each individual factor were summed. Factors with higher summed model probabilities are considered to be more important than factors with lower values (Anderson 2008). Examination of tolerance values indicated that variables were not collinear (tolerance < 0.60) (Van den Poel & Lariviere 2004).

The effect of *Membranipora membranacea* on total grazing damage on thalli was examined for individuals of *Saccharina latissima* and *Laminaria digitata* at Splitnose Point and The Lodge during periods of peak encrustation (September and November 2008, and September 2009). Analysis of Covariance (ANCOVA) indicated that the slopes of the relationship between the percentage of blade covered by *M. membranacea* and total percent blade area grazed (where these were significant) did not significantly differ between sampling periods within each site ($p > 0.05$). Therefore, data were pooled across sampling periods at each site, and linear regression was used to detect significant relationships between bryozoan cover and snail grazing damage. Individual kelps with no grazing damage were excluded from these analyses. Data were arcsine transformed where necessary to meet the assumptions of bivariate normality (Shapiro-Wilk test, $p > 0.05$) and homogeneity of variance (Breusch-Pagan test, $p > 0.05$).

We used factorial ANOVA to examine the effect of experimental trial (fixed factor), treatment (fixed factor), and block (random factor) on erosion rates in the artificial grazing experiment. Experimental trial was considered fixed because of the deliberate timing of the trials in advance of specific storm events. The block effect was not significant ($p = 0.49$), so data were pooled across blocks for further analysis (Underwood 1997). Post-hoc comparisons between treatment levels were performed using Tukey's HSD tests. All data were log (x+1) transformed to meet the assumptions of normality (Shapiro-Wilk test, $p > 0.05$) and homogeneity of variance (Bartlett's test, $p > 0.05$). All statistical analyses were performed using JMP (v. 5.1, SAS institute).

3.3 RESULTS

3.3.1 Distribution of Grazing Damage Along Kelp Thalli

Grazing damage did not occur evenly along the length of blades on *Saccharina latissima* or *Laminaria digitata* (Figure 3.2). A highly significant 3-way interaction between site, time, and location on blade for both species indicates that temporal variation in the percentage of area grazed in each section of blade varied across sites (Table 3.1). For *S. latissima* and *L. digitata*, grazing was generally highest in the middle and distal section of blades, and lowest in the basal section, except at Splitnose Point where damage was low or absent in the middle of blades during all sampling periods except November (Figure 3.2). Damage in the basal section was lowest from November to May and highest in July and September at all sites except Duncan's Cove Protected and Splitnose Point (Figure 3.2). At Duncan's Cove Protected, grazing in the basal sections of *L. digitata* remained high from September 2008 to February 2009, but decreased from May to September 2009. In contrast, grazing in the basal sections of *S. latissima* at this site was low during all sampling periods except May. At Splitnose Point, damage in the basal sections of *L. digitata* was absent in September 2009 (*S. latissima* only). Damage was more heavily concentrated in the distal region of blades at Splitnose Point than at other sites for both species during all sampling periods (Figure 3.2).

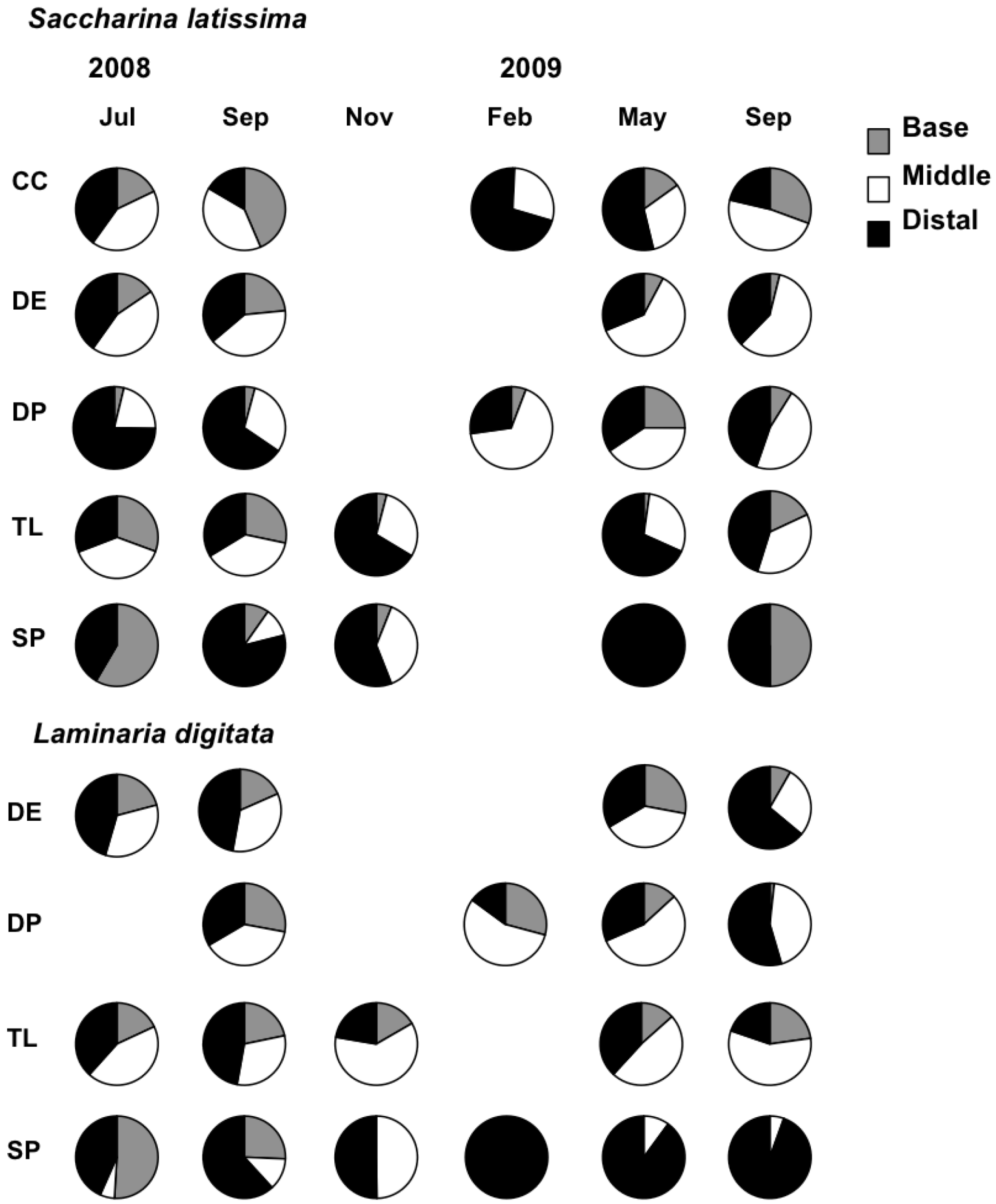

Figure 3.2 The relative percentage of total blade area grazed in the basal, middle, and distal sections of blades of *Saccharina latissima* and *Laminaria digitata* at 5 sites: Cranberry Cove (CC), Duncan's Cove Exposed (DE), Duncan's Cove Protected (DP), The Lodge (TL), Splitnose Point (SP) in all sampling months.

Table 3.1 Results of split-plot analysis of variance of the effect of site, season, and location on blade on total percentage of blade area grazed by snails on *Saccharina latissima* and *Laminaria digitata*. Main plot factors include site and season, and sub-plot factors include location on blade.

Factor	**df**	***F***	**p**
Saccharina latissima			
Site	4	35.2	< 0.001
Season	3	1.06	0.367
Season*Site	12	36.7	< 0.001
Main-plot error	240		
Location	2	19.5	< 0.001
Location*Site	8	3.53	< 0.001
Location*Season	6	3.90	0.001
Location*Site*Season	24	3.08	< 0.001
Sub-plot error	480		
Laminaria digitata			
Site	3	66.4	< 0.001
Season	2	13.1	< 0.001
Season*Site	6	14.5	< 0.001
Main-plot error	162		
Location	2	83.9	< 0.001
Location*Site	6	30.8	< 0.001
Location*Season	4	2.59	0.037
Location*Site*Season	12	3.55	< 0.001
Sub-plot error	324		

3.3.2 Seasonal and Spatial Trends in Grazing Intensity

The percentage of total blade area lost through grazing by *Lacuna vincta* ranged from 0.00–1.25 % for *Saccharina latissima*, and 0.00–1.50 % for *Laminaria digitata* (Figure 3.3). Seasonal trends in grazing damage on both *S. latissima* and *L. digitata* varied between sites, as indicated by a significant interaction between site and time for both species (Table 3.1, Figure 3.3). Some seasonality in grazing damage on *S. latissima* was evident at The Lodge, where the highest rates were observed in September 2008 and 2009 (0.79–0.93 %), and the lowest rates were observed in November 2008 and May 2009 (0.25–0.36 % in both months) (Figure 3.3). Grazing damage on *L. digitata* also increased from July to September 2008 at this site (0.37–0.60 %), but remained high in November 2008. A large increase in grazing damage on this species was then observed in September 2009 (1.50 %). This was similar to patterns observed at Duncan's Cove Protected, where grazing damage increased over the study on both *S. latissima* (0.16–0.70 %) and *L. digitata* (0.70–1.50 %), peaking in September 2009. Grazing was consistently lowest of all sites and showed little temporal variation at Splitnose Point and Duncan's Cove Exposed for *S. latissima* (Splitnose Point: 0–0.14 %, Duncan's Cove Exposed: 0.22–0.43 %) and *L. digitata* (Splitnose Point: 0.00–0.19 %, Duncan's Cove Exposed: 0.24–0.37 %). Grazing was consistently highest at Cranberry Cove for *S. latissima* (0.46–1.21 %), peaking in September 2008 and May 2009.

The total percentage of blade encrusted by *Membranipora membranacea* had a marginally significant positive effect on blade area grazed for *Saccharina latissima* at Splitnose Point (slope = 0.02), but this effect was not observed at The Lodge (Figure 3.4). There was no significant relationship between bryozoan cover and total percentage of blade area grazed for *Laminaria digitata* at either Splitnose Point or The Lodge.

3.3.3 Relationship with Physical Variables

REI was consistently highest at Splitnose Point (2346–4375), intermediate at Duncan's Cove Exposed (239–1062), The Lodge (535–1044), and Cranberry Cove (553–1313), and lowest at Duncan's Cove Protected (1–6). Temperature and site exposure were factors present in the best model explaining variation in grazing damage on blades of

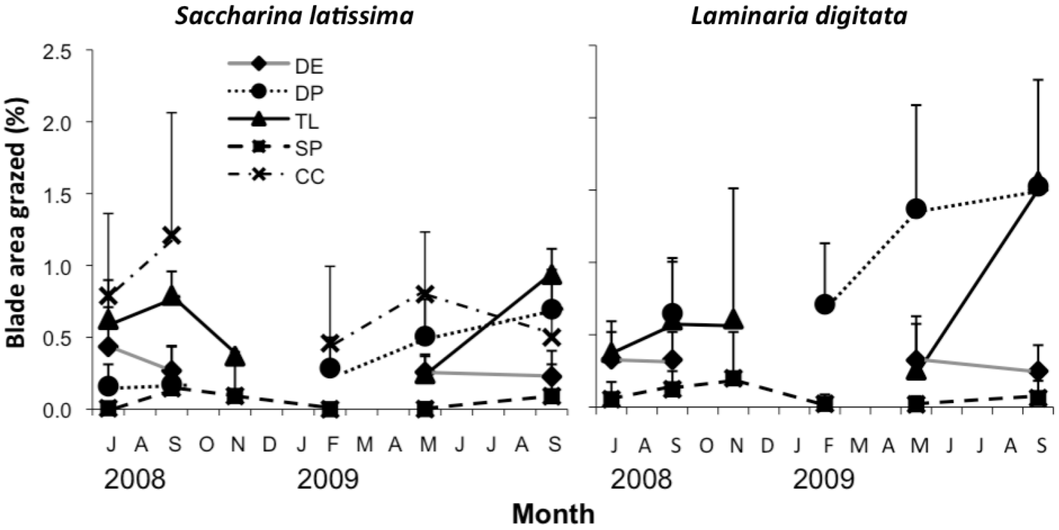

Figure 3.3 Percentage of total blade area grazed on *Saccharina latissima* and *Laminaria digitata* over 15 months at 5 sites: Duncan’s Cove Exposed (DE), Duncan’s Cove Protected (DP), The Lodge (TL), Splitnose Point (SP), and Cranberry Cove (CC). Data are mean + 1 standard deviation for 10-15 thalli at each sampling period.

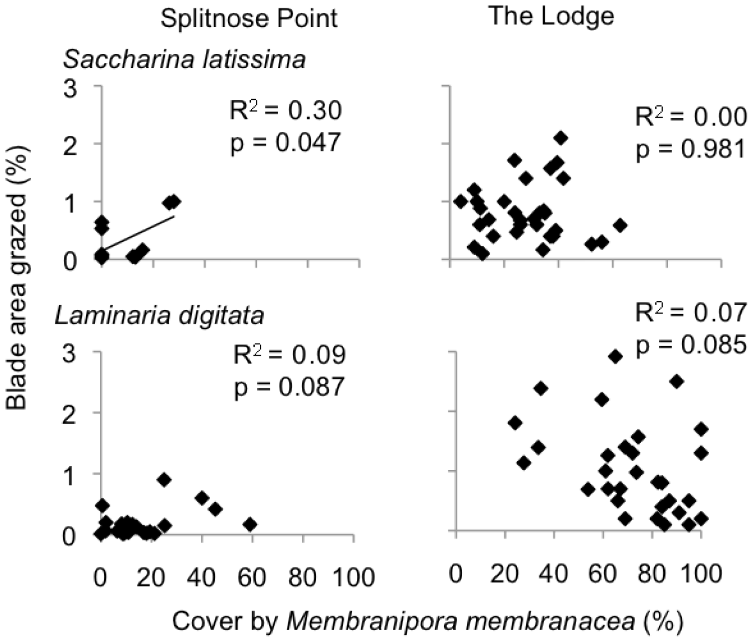

Figure 3.4 The relationship between total percentage of blade area grazed by *Lacuna vincta* on *Saccharina latissima* and *Laminaria digitata* and percentage of blade area covered by *Membranipora membranacea* for September and November 2008 and September 2009 at Splitnose Point and The Lodge. R^2 and p-values from linear regressions are indicated on each figure. A line is fitted where significant results were obtained.

Saccharina latissima, although the overall fit of this model was low ($R^2 = 0.24$; Table 3.2). Site exposure (negatively related) had a higher sum of model probabilities (0.88) than temperature (positively related, 0.58; Table 3.3), and explained more of the variation in grazing damage (Table 3.2). Site exposure (negatively related) was the only factor present in the top model explaining variation in grazing damage on *Laminaria digitata*, with a greater overall fit ($R^2 = 0.34$) than the model for *S. latissima* (Tables 3.2, 3.3) and a high sum of model probabilities (0.98). Temperature was likely unrelated to grazing damage for this species, indicated by low model likelihood, R^2 value (Table 3.2), and sum of model probabilities (0.30).

3.3.3 Simulated Grazing Experiment

Rate of blade breakage of kelps increased significantly with the level of simulated grazing damage in the first experimental trial, but not in the second (Table 3.4, Figure 3.5A). In Trial 1, erosion increased significantly between low and moderate damage (10- vs. 30-hole) treatments. During trial 2, erosion in all treatments was minimal and similar to that measured in the control and low damage treatments in Trial 1. Breakage usually occurred as fragmentation of large pieces of blade tissue. It was evident that tears in the blade tissue typically began at a simulated grazing hole.

Wave conditions differed markedly between trials (Figure 3.5B). During Trial 1, Hurricane Bill passed along the Atlantic coast of Nova Scotia as a Category 1 storm on 23 August, generating a maximum significant wave height of 9.0 m. During Trial 2, a weak tropical cyclone (Danny) generated a maximum significant wave height of 3.5 m on 30 August.

3.4 DISCUSSION

Grazing damage was not evenly distributed along the length of blades for either *Saccharina latissima* or *Laminaria digitata*, and varied spatially and seasonally. As we predicted, grazing damage was generally lowest in the basal section of blades, especially during the seasonal peak in kelp growth between February and May (Mann 1972,

Table 3.2 Coefficient estimates and standard errors for factors in the top model according to 2nd-order bias-corrected Akaike's Information Criteria explaining variation in the percentage of thallus area grazed for *Saccharina latissima* and *Laminaria digitata.* Factors included are site exposure (Exp) and temperature (Temp, °C).

Species	**Model**	**Estimate**	**SE**
Saccharina latissima	Exp	-1.0×10^{-4}	< 0.01
	Temp	2.0×10^{-2}	< 0.01
Laminaria digitata	Exp	-1.0×10^{-4}	< 0.01

Table 3.3 Akaike's Information Criteria (AIC) for all models containing site exposure (Exp) and temperature (Temp, °C) explaining variation in percentage of thallus are grazed for *Saccharina latissima* and *Laminaria digitata*, also including the 2nd-order bias-corrected Akaike's Information Criteria (AICc), the difference between the minimum AICc and the AICc of each model (ΔAICc), the log likelihood function (LL), the model probability (w_i), and the R^2 value of each model

Model	**AIC**	**AICc**	**n**	**ΔAICc**	**LL**	**w_i**	**R^2 adj**
Saccharina latissima							
Temp+Exp	-230.9	-230.2	20	0.00	117.47	0.465	0.24
Exp	-230.3	-230.0	20	0.21	116.13	0.418	0.18
Temp	-227.7	-227.5	20	2.75	114.85	0.117	0.11
Laminaria digitata							
Exp	-173.5	-173.2	16	0.00	87.74	0.698	0.34
Temp+Exp	-171.7	-171.4	16	1.8	86.85	0.288	0.32
Temp	-165.5	-165.5	16	7.7	83.9	0.015	0.00

Table 3.4 Results of analysis of variance of the effect of simulated grazing treatment on rate of blade breakage ($g\ d^{-1}$) of *Saccharina latissima* in 2 experimental trials, including a Tukey's HSD test for pairwise comparisons between treatment levels.

Factor	**df**	**F**	**P**	**Pairwise**
Combined				
Treatment	3	7.94	< 0.001	
Trial	1	11.8	0.001	
Treatment*Trial	3	4.73	0.006	Trial 1: 0 = 10 < 30 < 60
Error	47			
				Trial 2: 0 = 10 = 30 = 60

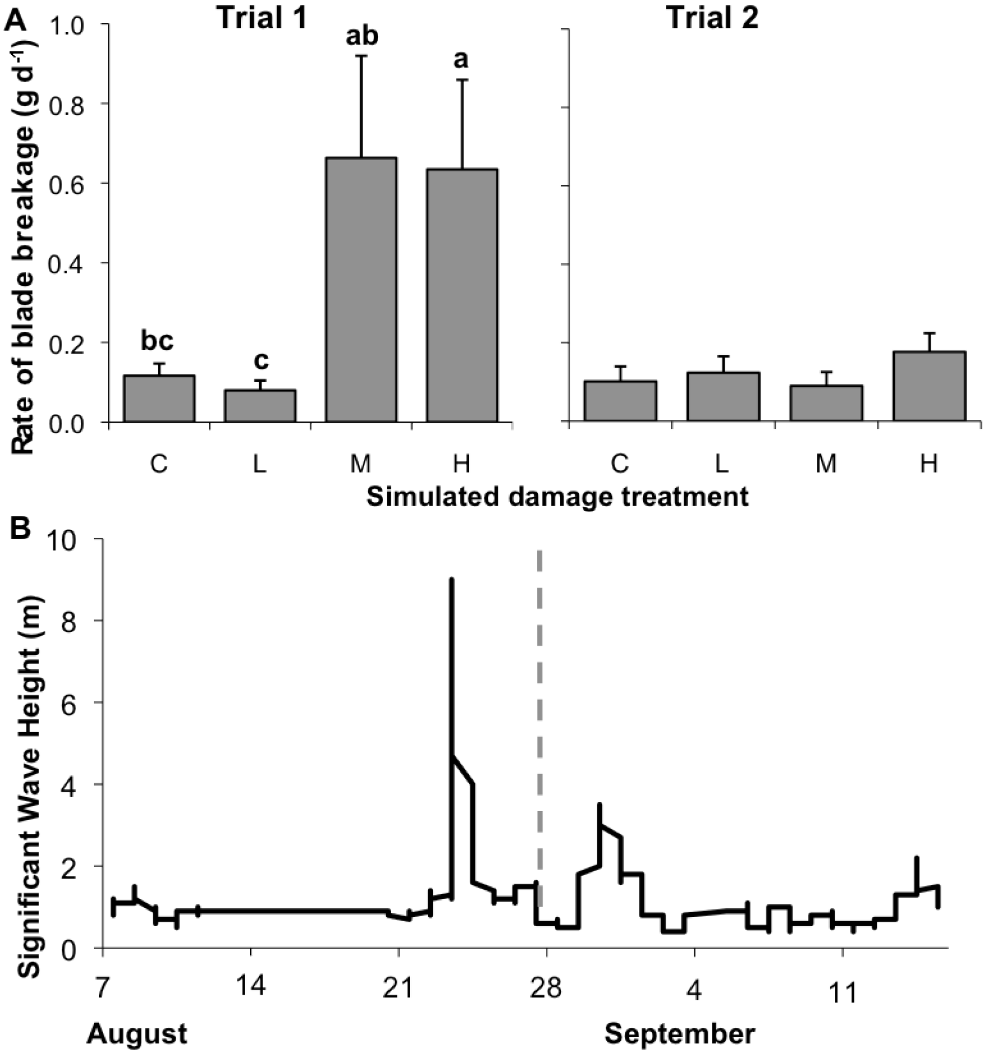

Figure 3.5 (A) Erosion rate (g d^{-1}) of *Saccharina latissima* at four levels of simulated grazing damage: control (C), low (L), moderate (M), and high (H) (0, 10, 30, 60 artificial holes per distal 45 cm of blade, respectively) in two experimental trials beginning on 7 and 27 August 2009 respectively. Data are mean + 1 standard error for 6-8 thalli in each treatment during each trial. Letters indicate statistically significant groupings. (B) Significant wave height (m) recorded hourly during both trials. Dashed line delineates the sequential trials.

Chapman & Craige 1977, Krumhansl & Scheibling 2011a). This may be explained by the lower exposure time of rapidly growing tissue to grazing, or by the presence of polyphenolics, which are known to peak during periods of rapid growth (Johnson & Mann 1986, Abdullah & Fredriksen 2004). Increases in grazing damage in the basal part of blades in July and September corresponded to seasonal reductions in growth rate and associated production of polyphenolics (Mann 1972, Abdullah & Fredriksen 2004, Krumhansl & Scheibling 2011a). Also as predicted, grazing was often greatest in the distal sections of blades, which was likely related to increased exposure time to grazing as well as greater palatability and decreased toughness of blade material associated with the degradation of aged tissues (Norderhaug et al. 2003, Molis et al. 2010).

We found no evidence to support our prediction that encrustation by the invasive bryozoan *Membranipora membranacea* limits grazing damage by *Lacuna vincta* on kelp blades. In contrast, a weak positive relationship between grazing damage and bryozoan cover was observed on *Saccharina latissima* at an exposed site (Splitnose Point) at low levels of cover (0–35 %). Local degradation of blade tissues under colonies of *M. membranacea* may facilitate grazing by decreasing tissue toughness or polyphenolics (Norderhaug et al. 2003, Molis et al. 2010). No effect of bryozoan cover on grazing damage was observed for *Laminaria digitata* at this site, or for both *L. digitata* and *S. latissima* at a second, more protected site (The Lodge), across a greater range of bryozoan cover. This suggests that even high bryozoan cover does not deter grazing, which is contrary to previous observations (Durante & Chia 1991, Chavanich & Harris 2000). *L. vincta* is capable of grazing through colonies of *M. membranacea* (O'Brien et al. submitted), incidentally consuming the bryozoan as has been shown for other invertebrates such as sea urchins (van Montfrans et al. 1984, Nestler & Harris 1994, Meidel & Scheibling, 1999). We occasionally observed *L. vincta* on colonies of *M. membranacea*, particularly in highly degraded parts of the blades.

Peaks in grazing damage of kelps did not correspond to a February peak in abundance of *Lacuna vincta* recorded in the Gulf of Maine and in Nova Scotia (Johnson & Mann 1986, Chavanich & Harris 2002). In contrast, we generally observed peak levels of damage in July and September, when snail density is expected to be at a seasonal low.

This discrepancy is likely explained by the prevalence of small snails (0–2 mm) with low grazing rates following recruitment in February (Johnson & Mann 1986). Larger snails (4–10 mm) that consume kelp at a faster rate are more prevalent from August to October (Johnson & Mann 1986), explaining higher damage during these months (Figure 3.1D). There were large interannual differences in grazing intensity between September 2008 and 2009 at some sites, possibly due to higher recruitment of *L. vincta* in 2009 than in 2008.

Between-site variation in grazing damage by *Lacuna vincta* on each kelp species was explained in part by a negative relationship with site exposure. As we predicted, grazing damage was consistently greater at sites with low and intermediate exposure to waves (Duncan's Cove Protected, Cranberry Cove, The Lodge, and Duncan's Cove Exposed) than the most exposed site (Splitnose Point). Previous studies have found a similar relationship between herbivory and exposure to waves and currents (Duggins et al. 2001, Vanderklift et al. 2009, Taylor & Schiel 2010), which has been attributed to increased dislodgement from algal substrates or bodily damage to grazers (Menge 1978), or altered foraging behaviour (Kawamata 1998, Lauzon-Guay & Scheibling 2007) with increased flow. Kelp blade thickness, toughness, and photosynthetic capacity also increase with wave exposure (Kraemer and Chapman 1991, Wing et al. 2007, Wernberg and Vanderklift 2010), which may result in greater resilience to herbivory and lower levels of grazing damage. Site exposure also may influence the spatial distribution and rates of settlement and recruitment if pre-metamorphic larvae are retained or induced to settle in low-energy environments (Wing et al. 1998, Palma et al. 2006). We also observed a relationship between site exposure and the distribution of grazing damage along blades. Contrary to expectation, grazing damage appeared to be more concentrated in the distal regions of blades at the most exposed site, Splitnose Point. This may be because toughness in the distal ends of blades is even more reduced, relative to basal tissues, at high wave exposures, where the ends are damaged by whiplash and abrasion with the substratum.

There was some evidence of a positive relationship between grazing damage and temperature for *Saccharina latissima* that is consistent with our prediction, but temperature explained only a small portion of the overall spatial or seasonal variation in grazing damage. The relatively low fit of our models is likely because they were based solely on environmental factors. Direct measures of abundance of *Lacuna vincta* may explain most of the observed variance in grazing damage.

September peaks in grazing damage to blades by *Lacuna vincta* are coincident with the seasonal occurrence of hurricanes off Nova Scotia. Results of our field experiment indicate a positive relationship between the extent of grazing damage and blade breakage in *Saccharina latissima* under heavy wave conditions generated by a passing hurricane. There was a strong effect of moderate and high levels of simulated damage on the rate of blade breakage when a passing hurricane generated a 9-m spike in significant wave height in Trial 1. In contrast, no effect at any level of simulated damage was detected in Trial 2, despite a passing tropical storm that generated a peak significant wave height of 3.5 m. This suggests a damage threshold (0.5–1.0 % loss of blade area) for increased breakage of kelp blades when wave forces also exceed a threshold value (3.5–9.0 m). Because the level of naturally occurring blade damage exceeds this damage threshold during the summer and fall hurricane season, *L. vincta* likely contributes to the massive loss of kelp biomass associated with passing hurricanes (personal observations), which occur at a rate of 5.3 y^{-1} in the Atlantic (Bender et al. 2010).

We have shown that the distribution of damage by *Lacuna vincta* on kelp blades varies spatially and temporally, likely due to seasonal patterns in growth and the nutritional quality of blade tissue. We did not find a strong relationship between grazing by *L. vincta* and the invasive bryozoan *Membranipora membranacea*, indicating that the bryozoan does not deter grazing by *L. vincta* on kelp blades. Spatial variation in the total level of grazing damage was negatively related to site exposure, explaining low levels of grazing damage at highly exposed sites. The direct effects of grazing by *L. vincta* are relatively small, as area grazed typically represents only a small percentage of the overall blade area (present study) and biomass (Johnson & Mann 1986). However, we experimentally show that grazing by *L. vincta* can have a large indirect effect on detrital production from kelp beds by increasing rates kelp blade breakage and erosion (Krumhansl & Scheibling 2011a), especially during large storm events such as hurricanes. This indirect effect may become increasingly important in light of a changing ocean climate, as storms and hurricanes that generate heavy wave conditions increase in frequency and intensity (Bender et al. 2010, Scheibling & Lauzon-Guay 2010).

CHAPTER 4
GRAZING DAMAGE AND ENCRUSTATION BY AN INVASIVE BRYOZOAN REDUCE THE ABILITY OF KELPS TO WITHSTAND BREAKAGE BY WAVES

The work presented in Chapter 4 also appears in:
Krumhansl KA, Lee MJ, Scheibling RE (2011) Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. J Exp Mar Biol Ecol 407: 12-18

4.1 INTRODUCTION

The biomass of macroalgal beds is largely dependent on the balance of productivity and the rate at which thalli erode, fragment or dislodge from the substrate during periods of heavy wave action (Seymore et al. 1989, Krumhansl & Scheibling 2011a). Macroalgae in rocky intertidal and subtidal zones have developed morphological and material adaptations to withstand extreme wave conditions. Thalli are composed of highly flexible material that reconfigures and orients to flow to reduce drag (Vogel 1984, Gaylord & Denny 1997, Boller & Carrington 2006), which is the primary force generating tension on blades. For many macroalgal species, the measured tensile strength of thalli exceeds the predicted force of drag in their natural habitats, suggesting that breakage or dislodgement is unlikely (Friedland & Denny 1995, Utter & Denny 1996, Denny et al. 1997). However, observational studies have shown that algal blades frequently fragment and dislodge (Seymore et al. 1989, Krumhansl & Scheibling 2011a), suggesting that external factors limit the ability of macroalgae to withstand breakage by waves (Utter & Denny 1996).

Fragmentation and dislodgement of large macroalgae, such as kelps, can occur through breakage at several points along the thallus. Failure at the holdfast and stipe are common, particularly at the junctions between stipe and holdfast, and stipe and blade (Seymore et al. 1989, Utter & Denny 1996, Duggins et al. 2001). This type of breakage has been the focus of most studies because it causes mortality of individual thalli. Failure may also occur in the middle of blades, resulting in fragmentation. This process does not cause mortality unless breakage occurs below the meristem at the base of the blade. Fragmentation of blades, however, can result in significant losses of biomass from subtidal kelp beds (Krumhansl & Scheibling 2011a).

Breakage by wave action is often the result of previous damage to part of the thallus through grazing, abrasion with the substrate, or physiological stress (Black 1976, Biedka et al. 1987). Grazing by herbivores may generate nicks, holes, and cuts that concentrate stress, leading to crack formation, propagation, and blade breakage at forces lower than the maximum recorded force-to-break undamaged macroalgal tissue. Cracks at the site of damage to a macroalgal blade can form during repetitive, low-force loading in wave-swept locations, propagating gradually until failure occurs (Mach 2009). Alternatively, damage may cause stress concentration at high wave forces that leads to rapid crack formation and propagation. In particular, breakage at the junction of stipe and holdfast has been linked to damage by herbivorous snails (Black 1976, Duggins et al. 2001) and urchins (Koel & Wainwright 1977, Biedka et al. 1987).

Seasonal variation in the rate of blade breakage of laminarian kelps along the Atlantic coast of Nova Scotia has been attributed to a combination of environmental and biological factors. Such factors include damage to blades caused by mesograzers (mainly the snail *Lacuna vincta*) and encrustation by the invasive bryozoan *Membranipora membranacea* (Krumhansl & Scheibling 2011a), although the direct effect of this damage on the material properties of blades has not been examined. *L. vincta* creates full perforations or partial-thickness grazing scars (excavations) on kelp blades, which may reduce the force to break blade tissue, increasing the incidence of blade breakage (Krumhansl & Scheibling 2011a,b). *M. membranacea* encrusts the surface of kelp blades, increasing rates of blade breakage (Krumhansl & Scheibling 2011a) leading to major canopy losses during periods of heavy wave action (Scheibling et al. 1999, Scheibling & Gagnon 2006). It has been proposed that the mechanism by which the bryozoan renders the kelp more prone to breakage is increased brittleness (Dixon et al. 1981), but this effect has not been tested explicitly.

Using a combination of materials testing and histological techniques, we have examined the effect of grazing damage by *Lacuna vincta* or encrustation by *Membranipora membranacea* on the material properties of laminarian kelps, including maximum stress (tensile strength) and strain (extensibility) before breakage, toughness, and stiffness. We predict that perforations and excavations generated by snail grazing and bryozoan encrustation will reduce the overall strength, extensibility, and amount of energy required to break kelp tissues. We also predict that *M. membranacea* will increase the stiffness of blades.

4.2 METHODS

4.2.1 Sample Collection

Samples of the kelps *Saccharina latissima* and *Laminaria digitata* were collected offshore of a site (The Lodge, 44° 33' 32.98''N, 64° 01' 56.75''W) on the western shore of St. Margarets Bay, Nova Scotia, Canada. Undamaged thalli and those encrusted by *M. membranacea* (>25 cm blade length) were collected from 4 to 7 m depth on November 28, 2009 using SCUBA. Kelp thalli with grazing damage were selected from the same depths on December 15, 2009. For regional comparisons of the effect of grazing damage by *L. vincta* on material properties of kelps, samples of *Laminaria complanata* (>25 cm) were collected in the same depth range at a site (Shady Cove, 48° 33' 9"N, 123° 3' 43"E) on San Juan Island, Washington, USA on March 22, 2010. After collection, kelps were transported in enclosed bins for no more than 2 hours to flow-through seawater tanks.

For kelps from Nova Scotia, the effect of encrustation by *Membranipora membranacea* on material properties of blade tissues was examined at two levels of encrustation: fully encrusted or lesioned. Fully encrusted samples were completely covered on both sides by *M. membranacea* with no visible signs of tissue degradation. After prolonged encrustation, kelp tissue beneath a colony of *M. membranacea* may become highly degraded, resulting in perforation of the blade, termed a lesion. Lesioned samples were selected from highly degraded areas adjacent to such a perforation (Figure 4.1). We expected lesions would reduce the tensile strength, extensibility, and toughness

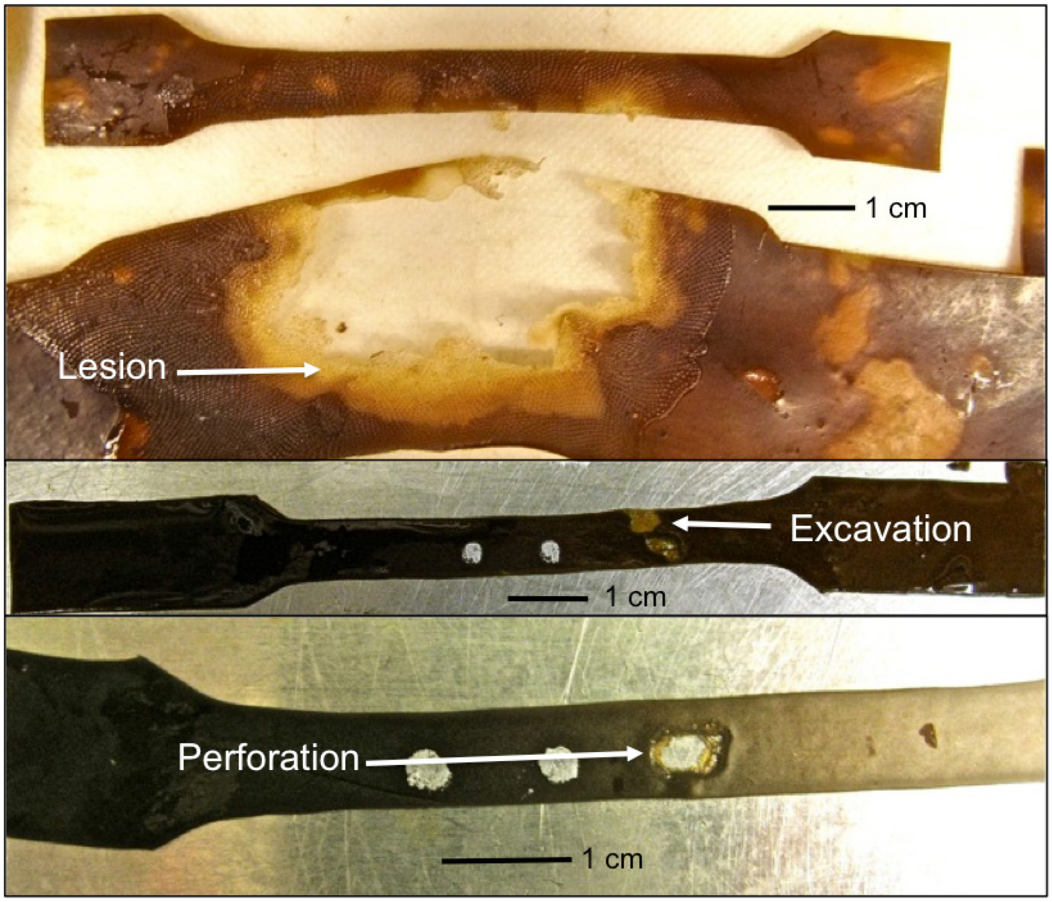

Figure 4.1 Photographs of lesioned, excavated, and perforated samples used to examine the effect of encrustation by *M. membranacea* and grazing damage on the material properties of kelps. Samples were excised from blade tissue in standard dimensions using a “dog-bone” template.

of kelp blades to a greater degree than encrustations. Similarly, the effect of the mesograzer *Lacuna vincta* was examined at two levels of grazing damage: excavations and full perforations of the blade (Figure 4.1). Excavations spanned all or part (40 to 100%) of the sample width in the testing region, while perforations were always smaller in diameter (6 to 55%) than the width of the sample. We expected perforations would reduce the tensile strength, extensibility, and toughness of kelp blades to a greater degree than excavations. Results from these four sample condition groups were compared to undamaged and non-encrusted sections of each blade. For samples from Washington, only the effect of grazing was examined.

4.2.2 Mechanical Testing

Standard pull-to-break uniaxial tensile tests were performed as per Carrington et al. (2001). In Nova Scotia, samples were tested using a computer-interfaced, 458-series MTS planar biaxial testing system. Extension was measured using video from a camera (Cohu CCD 4190) mounted above the sample, and interfaced with a Scion video capture board operating at 14.98 Hz. In Washington, samples were tested using a computer-interfaced tensometer (model 5565; Instron Corp., Canton, MA, USA) equipped with a non-contacting video extensometer (Model 2663, Instron Corp.). Both testing systems were equipped with load cells (100 N in Nova Scotia, 50 N in Washington). Samples of standard dimensions were excised from kelp using a “dog bone”-shaped template (ASTM/ISO D638-03, Figure 4.1) in a longitudinal direction on blades. The distance of the sample from the base of the blade was recorded. Thickness (0.01-mm precision) was measured in three locations on each sample using a non-rotating thickness gauge prior to testing. In Nova Scotia, samples were held in manually tightened grips lined with neoprene and fine sandpaper. Two white candy confection balls were placed 3-4 cm apart on the surface of the sample, defining the testing region. In Washington, samples were held in pneumatic grips lined with fine sandpaper at a pressure of 20 psi. Two silver dots were painted with solvent-based paint approximately 10 mm apart on the surface of the sample to define the testing region. Samples from this experiment were never observed to break at the silver dots, which was consistent with previous studies that used the same marking material on macroalgal samples (Carrington et al. 2001, Boller & Carrington 2007). Therefore it was assumed that samples were unaffected by the paint. Samples were photographed before testing, and sample width was measured in the testing region using image analysis (ImageJ). The sample was extended at a rate of 50 mm min^{-1} until breakage occurred. Samples were tested in open air at room temperature, and periodically wetted with seawater to prevent desiccation.

Applied force (N) was captured during extension for each sample. Stress (σ) was then calculated as:

$$\sigma = F/A$$

where F is force (N) and A is the initial cross-sectional area of the sample (mm^2). In Nova Scotia, extension at grips was measured during testing, and grip-to-grip strain (ε) was calculated as:

$$\varepsilon = \Delta l / l_o$$

where Δl is extension between the markers (mm) and l_o is the initial length of the testing region defined by the markers (mm). Strain in the testing region was calculated from grip-to-grip strain using a correction technique that related grip-to-grip extension to extension in the testing region. To generate this correction, the distance between dots was measured in still images (ImageJ, 0.01-mm precision) taken from the captured video at 10 evenly spaced increments by time throughout the course of the test, and divided by grip extension at the same time points. This ratio was then plotted against video frame number and a logarithmic function was fitted to the points ($R^2 > 0.90$). This function was then used to convert the grip-to-grip extension to extension in the testing region and this data was then synched to the captured load data. In Washington, a video extensometer measured extension of the testing region by tracking the movement of the silver dots throughout the course of the video (0.005 mm-precision) and strain was calculated as described. A tangent modulus of material stiffness (MPa) was calculated as the steepest slope of the stress-strain curve and toughness was calculated as the area under the stress-strain curve (MJ m^{-3}).

4.2.3 Statistical Analysis

Analysis of covariance (ANCOVA) was used to identify covariates common to all sample conditions that affect material properties for each species. Potential covariates were independently included in ANCOVA with condition as the main factor, and each material property (maximum stress before breakage, strain at fracture, modulus, and toughness) as the dependent variable. Linear regression was then used to determine the direction of the relationship between significant covariates and material properties. Linear regression was also used to examine the relationship between material properties and relevant independent variables within two levels of grazer damage (excavation and perforation width) for each kelp species. The effect of condition on material properties was examined using Multivariate Analysis of Covariance (MANCOVA) using statistically significant covariates for each kelp species where present, or MANOVA where no significant covariates were detected. 1-way ANCOVA or ANOVA followed by Tukey's HSD test were then used to compare sample condition groups for each material property. Data were square-root transformed where necessary to meet the assumptions of homogeneity of variance (Bartlett's test, $p < 0.05$) and normality (Shapiro-Wilk test, $p < 0.05$). Plots of the residuals versus predicted values were examined to test the assumption of linearity where linear regressions were used.

4.2.4 Histology

Histological techniques were used to examine the effect of *Membranipora membranacea* on blade tissues of *Saccharina latissima* and *Laminaria digitata* collected from The Lodge (4 to 7 m depth) on 18 November 2009. Kelps were transported and held as above, and processed within 24 hours of collection. Samples <1 cm^2 were excised from undamaged, encrusted, and lesioned sections (defined as above) and fixed in 7% formalin in seawater for 24 hours. Samples were then washed twice in 70% ethanol in preparation for dehydration, clearing, and paraffin wax infiltration using the ASP300 Leica Tissue Processor. Specimens were embedded in paraffin and cut into 5 µm-transverse sections using a Reichert-Jung rotary microtome and mounted onto superfrost plus slides (Fisherbrand). Slides were then oven dried at 37°C overnight before staining. Slides were de-paraffinized through xylene and graded alcohols and stained in 0.1% Saffranin for 6 minutes. Slides were then dehydrated in graded alcohols and mounted to cover slips with Cytoseal (Richard-Allan Scientific). The blade tissue sections were then examined using light microscopy (Nikon Eclipse E600 microscope) and photographed using a Nikon DXM1200F digital camera.

4.3 RESULTS

Stress-strain curves of *Saccharina latissima*, *Laminaria digitata*, and *Laminaria complanata* were typically characterized by an initial linear or j-shaped portion where the sample deformed until the limit of extension was reached, defined as the location where the curve changed shape (~0.1 strain for *S. latissima* and *L. complanata*, ~0.5-2.0 for *L. digitata*) (Figure 4.2). The sample then entered a second phase in which plastic deformation likely occurred, resulting in a curve that was concave downward until failure. Some curves from grazed condition groups never reached this second phase, failing within the linear or j-shaped region (Figure 4.2). The shapes of the curves for *S. latissima* and *L. complanata* were more uniform across sample conditions than were the curves of *L. digitata* (Figure 4.2).

ANCOVA showed that distance of the sample (for all conditions pooled) from the base of the blade had a significant effect on maximum stress before breakage in *Saccharina latissima* ($p = 0.044$) and on strain at fracture in *Laminaria complanata* ($p = 0.047$). In both cases the material property decreased with distance (linear regression, *S. latissima*: $b = -7.05 \times 10^3$, *L. complanata*: $b = -0.01$). There was no detectable effect of blade thickness on material properties in any of the three species of kelp, and no effect of distance from the base of the blade on material properties in *Laminaria digitata* ($p>0.05$). Therefore, distance from the base of the blade was included as a covariate in MANCOVA for *L. complanata* and *S. latissima*, and no covariates were used in MANOVA for *L. digitata*.

The material properties of kelp blades were significantly altered by encrustation and lesioning by *Membranipora membranacea* (*Saccharina latissima*: MANCOVA, df = 4, 24, $\Lambda = 0.155$, $F = 2.768$, $p = 0.003$, *L. digitata*: MANOVA, df = 4, 28, $\Lambda = 0.124$, $F = 5.10$, $p <0.001$). Encrusted and lesioned samples were significantly less tough, had a

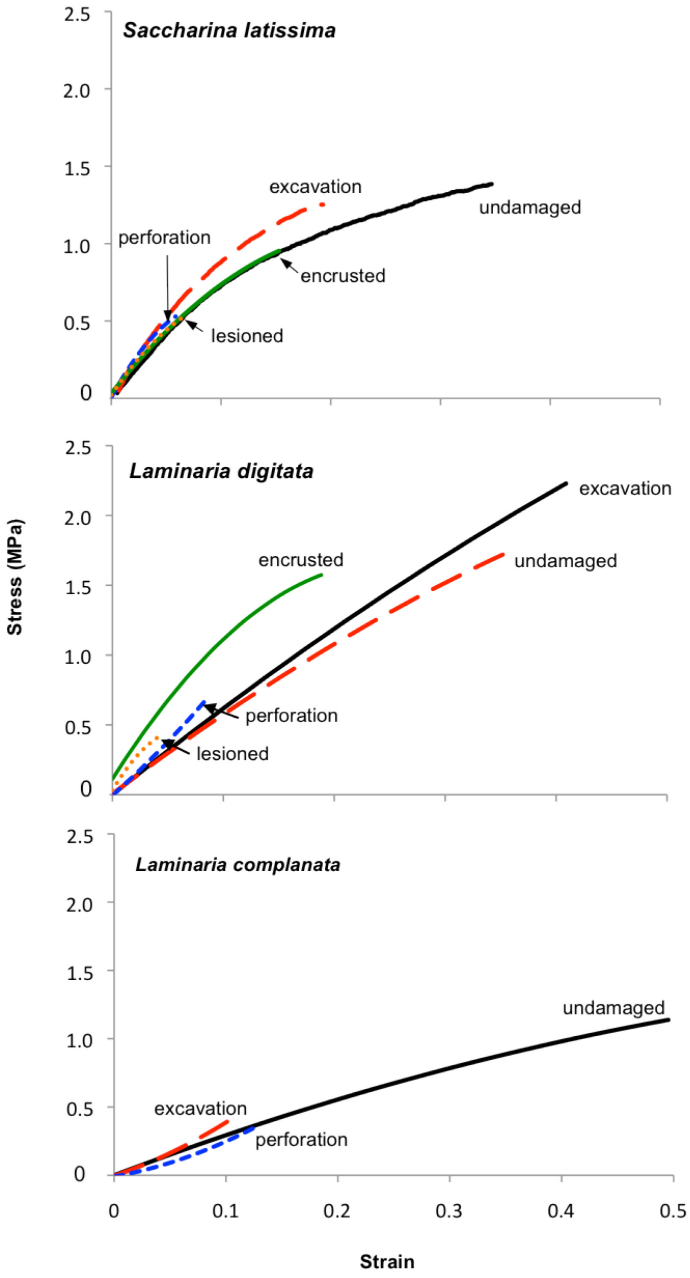

Figure 4.2 Examples of stress-strain curves for undamaged, perforated, excavated, lesioned, and encrusted samples from *Saccharina latissima*, *Laminaria digitata*, and *Laminaria complanata*. Example curves in figures best represent the means of each sample condition group.

Table 4.1 Results of ANOVA or ANCOVA (*distance from base of blade as a covariate) to examine differences between condition groups (undamaged, encrusted, lesioned, excavation, perforation) for each material property and kelp species.

Species	**Material Property**	**df**	**F**	**p**
Saccharina latissima	Maximum stress*	4,20	7.43	<0.001
	Toughness	4,25	14.3	<0.001
	Modulus	4,25	1.35	0.278
	Strain	4,25	11.45	<0.001
Laminaria digitata	Maximum stress	4,30	19.3	<0.001
	Toughness	4,30	18.4	<0.001
	Modulus	4,30	3.15	0.028
	Strain	4,30	9.61	<0.001
Laminaria complanata	Maximum stress	2,19	19.2	<0.001
	Toughness	2,19	27.2	<0.001
	Modulus	2,19	0.21	0.814
	Strain*	2,16	3.86	0.043

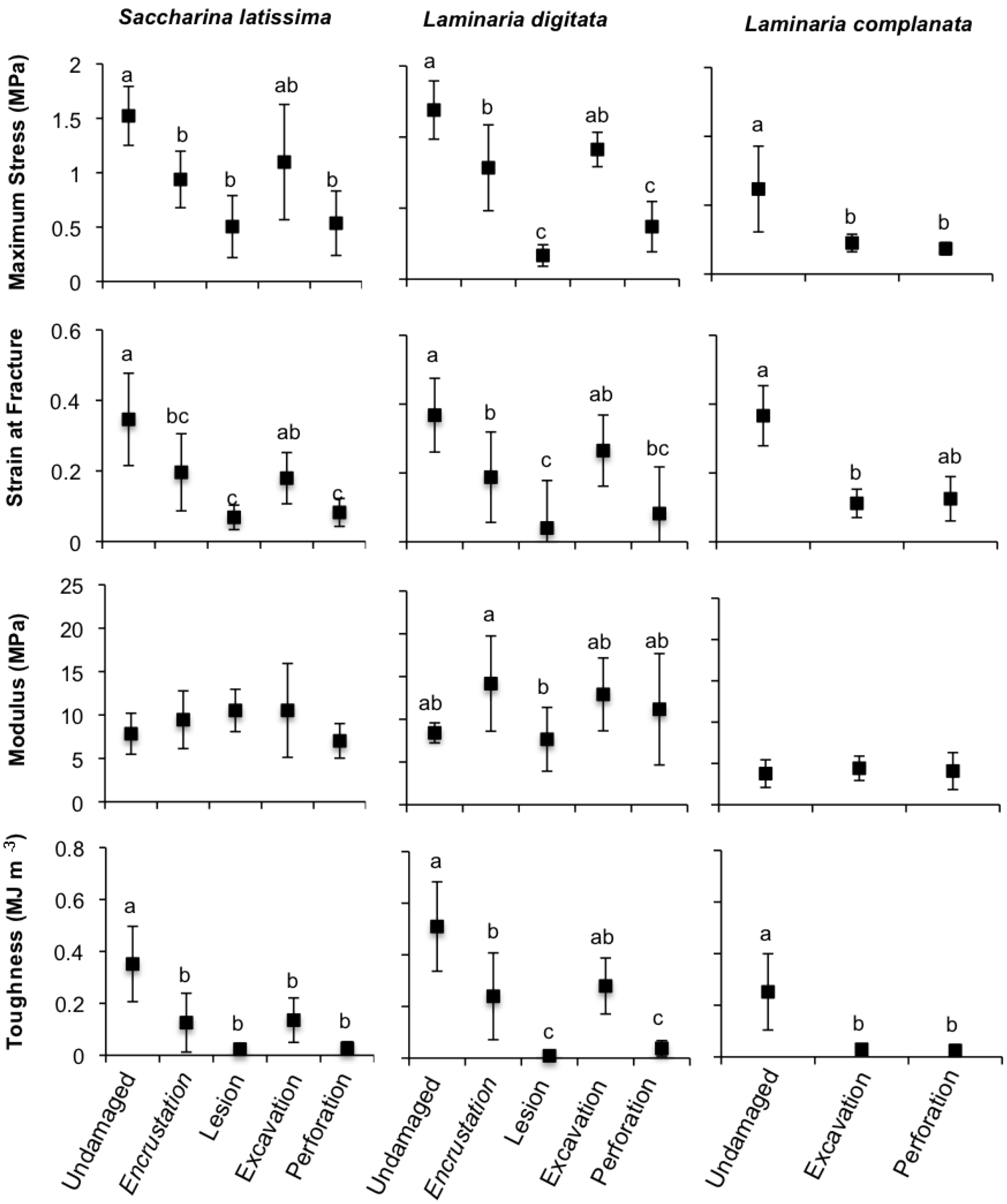

Figure 4.3 Mean (± 1 SD) maximum stress, strain at fracture, modulus, and toughness for undamaged, encrusted, lesioned, excavated, and perforated samples of *Saccharina latissima*, *Laminaria digitata*, and *Laminaria complanata* (n = 5-10). Letters denote statistically significant groupings.

lower maximum stress before breakage, and a lower strain at fracture than undamaged controls from both kelp species (Table 4.1, Figure 4.3). Lesions had a greater effect on toughness, strain at fracture, and maximum stress before breakage than did encrustation for samples from both kelp species, but this relationship was only significant for samples from *Laminaria digitata.* Encrustations and lesions did not alter the modulus of material stiffness relative to undamaged samples from either kelp species (Table 4.1, Figure 4.3).

Grazing damage by *Lacuna vincta* on kelp blades also had a significant effect on the material properties of *Saccharina latissima*, *Laminaria digitata*, and *Laminaria complanata* (MANCOVA, df = 2, 18, $\Lambda = 0.090$, $F = 2.35$, $p = 0.009$). Grazed perforations decreased the maximum stress before breakage, strain at fracture, and toughness relative to undamaged controls for samples from all three species (Table 4.1, Figure 4.3), having the same effect as lesions created by *Membranipora membranacea* on samples from *S. latissima* and *L. digitata*. Grazed excavations did not affect material properties of samples from *L. digitata* relative to undamaged controls, but lowered the toughness of samples from *S. latissima*. In contrast, the maximum stress, strain at fracture, and toughness of samples from *L. complanata* all were reduced by grazed excavations as compared to undamaged tissue. Neither grazed holes nor excavations affected the modulus of material stiffness for samples from *S. latissima*, *L. digitata*, or *L. complanata* (Table 4.1, Figure 4.3). There were no significant relationships between excavation and perforation widths and material properties for samples from any of the three kelp species.

Undamaged samples of *Saccharina latissima* and *Laminaria digitata* consisted of three distinct cell layers (Figure 4.4). The meristoderm is visible as several intact layers of small epidermal cells, with cells gradually increasing in size towards the cortex. The cortex consists of larger circular cells that are more elongate close to the central medulla. The medulla is a dense layer of elongate cells in the center of the tissue. The tissue structure of samples encrusted by *Membranipora membranacea* (not adjacent to a lesion) was similar to the structure of undamaged tissue, and we found no evidence that the bryozoan penetrates the meristoderm. In contrast, samples that were lesioned were missing the meristodermal layer completely, and were often also missing the majority of cortical cells. This effect was similar for both kelp species.

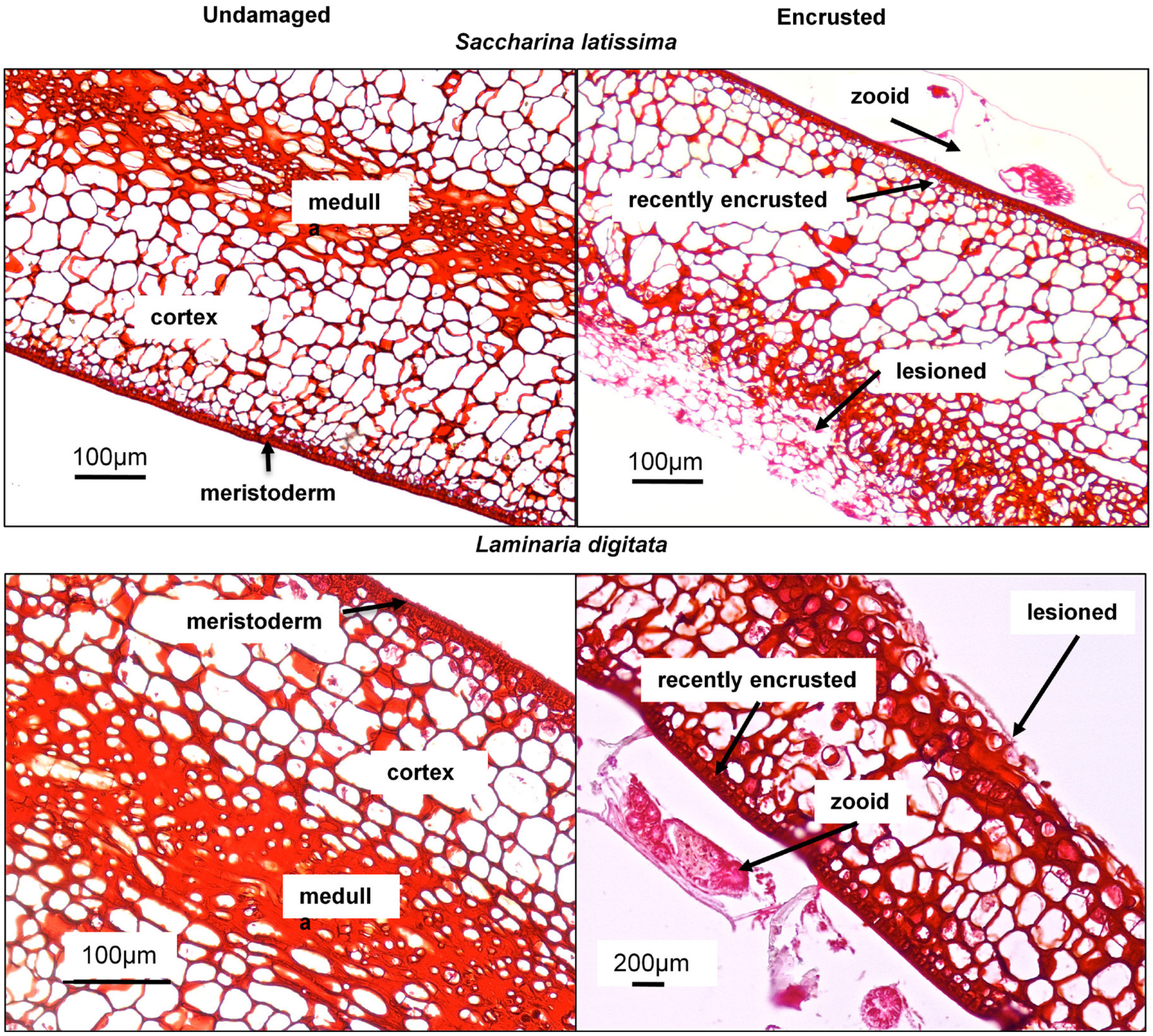

Figure 4.4 Transverse sections of undamaged (left) and tissue encrusted by *Membranipora membranacea* (right) on *Saccharina latissima* and *Laminaria digitata* prepared using histology techniques. Three distinct cell layers are visible in undamaged sections, while the meristoderm and cortex are highly reduced or absent on lesioned tissue.

4.4 DISCUSSION

Our study is the first to quantify a decrease in the tensile strength, extensibility, and toughness of kelp blades associated with encrustation by the invasive bryozoan *Membranipora membranacea.* Lesions that formed after prolonged encrustation caused a greater weakening of blades than did encrustation alone, suggesting that tissue strength decreases with increasing duration of bryozoan coverage. Histological preparations showed that encrustation by *M. membranacea* causes degradation of the meristoderm and eventually of the cortex, likely through shading (Oswald et al. 1984) and reductions in nutrient uptake (Hurd et al. 1994) and tissue pigment content (Hepburn et al. 2006). Such damage to the meristoderm may concentrate stress when the blade is experiencing drag-induced tension, leading to crack formation and propagation at lower force applications than required to break undamaged tissue (Mach 2009). While macroalgal tissue is highly flexible and extensible, less energy is required to propagate cracks once initiated by fatigue or damage (Denny et al. 1989, Mach 2009), suggesting that macroalgal blades are particularly susceptible to failure following damage, such as through bryozoan encrustation.

Contrary to our predictions, encrustation by *Membranipora membranacea* did not have an effect on the stiffness of kelp blade tissue when force was applied in tension. Stress and hydrodynamic drag increase with stiffness in tension (Gaylord & Denny 1997, Boller & Carrington 2007), such that stiffer blades are less able to withstand breakage by wave forces. The fact that we did not observe an effect of bryozoan encrustation on blade stiffness suggests that this factor may be less important than stress concentration at the point of cellular degradation of encrusted blades in causing observed increased rates of breakage (Krumhansl & Scheibling 2011a) and canopy loss (Lambert et al. 1992, Scheibling et al. 1999, Scheibling & Gagnon 2006). However, encrustation by *M. membranacea* also may increase stiffness in bending, which would reduce the flexibility of blades and contribute to blade breakage.

Full-thickness perforations created by the mesograzer *Lacuna vincta* also reduced the strength, extensibility, and toughness of blade tissue from *Saccharina latissima, Laminaria digitata,* and *Laminaria complanata*. While partial-thickness excavations did not have a significant effect on the material properties of *L. digitata*, they had a similar effect as perforations for *L. complanata* and reduced the toughness of *S. latissima*. Flaws introduced by grazer damage therefore likely also act as force concentrators, initiating cracks and breakage when in tension. We observed that sample failure always occurred at the site of a grazed perforation or excavation, and propagated in an across-blade direction perpendicular to the applied force. We note that cracks in kelp blades propagate more easily along the blade than across the blade because of the orientation of central medulla fibers (Vincent & Gravell 1986). This suggests that cracks initiated by grazer damage or encrustation would likely propagate along the blade at even lower force applications than we observed for across-blade propagation.

Force concentration is dependent on the shape of the flaw, with sharp-edged flaws concentrating force to a greater degree than more rounded flaws (Denny et al. 1989). We expected perforations to concentrate more force than excavations because they are sharp-edged and affect the entire blade thickness rather than a portion of it. This prediction was true for *Laminaria digitata* but not for *Laminaria complanata*. This suggests that the removal of meristoderm cells by partial-thickness grazing concentrates enough force to cause blade breakage in *L. complanata* at forces comparable to those causing breakage at perforations. We found some evidence that excavations reduce the ability of blades from *Saccharina latissima* to withstand breakage, although this species appears to be more resistant to partial-thickness damage than *L. complanata*. Our results indicate that *L. digitata* is the most resistant of the three kelp species to strength reductions caused by partial-thickness excavations. Interestingly, the magnitude of tissue strength reduction was not related to the size of the flaw for any of the three kelp species.

We observed significant decreases in the maximum stress before breakage and strain at fracture of blade tissue with increasing distance of the sample from the base of the blade for *Saccharina latissima* and *Laminaria complanata*. Kelp blades are often tattered and degraded at the distal end, in part due to abrasion with other blades and the substratum. Our results suggest that this damage and degradation causes the material to become more susceptible to breakage, which is consistent with previous observations that kelps erode gradually from the distal end, even in relatively calm conditions (Krumhansl & Schiebling 2011a). This effect was not observed for samples from *Laminaria digitata*, indicating that this species may be more resistant to damage at the distal end. *L. digitata* is often found shallower and in more exposed locations than *S. latissima* in Nova Scotia (Mann 1972), likely in part because it is less susceptible to breakage by wave action. The material properties of blade tissue of *L. digitata* differed in many respects from those of the two other kelp species. This can also be seen in the shapes of the stress-strain curves for the three kelp species considered, which differed more widely between sample conditions for *L. digitata* than for *S. latissima* and *L. complanata*. This indicates that, while the overall effect of damage to kelp blades is similar across species, natural variation in material properties exists between species, even in similar environments (Hale 2001).

Our results provide a mechanistic explanation for increased fragmentation of kelp blades (Krumhansl & Scheibling 2011a) leading to extensive canopy loss during periods of peak encrustation by *Membranipora membranacea* in Nova Scotia (Scheibling et al. 1999, Scheibling & Gagnon 2006, Saunders & Metaxas 2008) and the Gulf of Maine (Lambert et al. 1992). We have shown that grazing damage by *Lacuna vincta* also reduces breaking strength, likely leading to increased fragmentation during periods of high wave action (Krumhansl & Scheibling 2011b). Our findings support previous studies indicating that *L. vincta* and *M. membranacea* play major roles in the seasonal dynamics of detrital export from highly productive kelp beds to adjacent low-productivity habitats (Krumhansl & Scheibling 2011a).

CHAPTER 5
DETRITAL SUBSIDY FROM SUBTIDAL KELP BEDS IS ALTERED BY THE INVASIVE GREEN ALGA *Codium fragile* ssp. *fragile*

The work presented in Chapter 5 was accepted for publication:
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5.1 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 2011a).

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 2011a). 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 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 1998, Filbee-Dexter & Scheibling in press), 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 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, Lyons et al. 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 this 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. latissima,* McDevit & Saunders 2010) during degradation in a 16-week field experiment. To examine how changes in the quantity and nutritional quality of detrital material influence colonization by macrofauna, we also measured changes in the macrofaunal assemblage associated with each algal species over the course of degradation. 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.

5.2 METHODS

5.2.1 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. 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 2011a). *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 (Filbee-Dexter & Scheibling in press). 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 x 33 x 27 cm, 2.5-cm aperture) anchored to the sandy seabed at 19 m depth. Large thalli of *S. latissima* (100–200 cm total length) and *C. fragile* (50–75 cm) without visible signs of degradation or heavy colonization by epibionts were haphazardly collected using SCUBA from the algal bed at 5–7 m depth. Thalli were cleaned of any epibionts, air dried for 1 minute 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 x 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 4–6 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 weeks 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 hours. 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 weeks of the experimental period, ranging from 5.5 to 20.0°C, then stabilized over the last 4 weeks (Figure 5.1). Mean temperature during each sampling interval was relatively constant, ranging from 9.6 to 11.2°C.

5.2.2 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 hours 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 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:

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

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 10M 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 *C. fragile* and central region of a blade for *S. 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). 100µl (*S. latissima*) or 10µl (*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 FPD

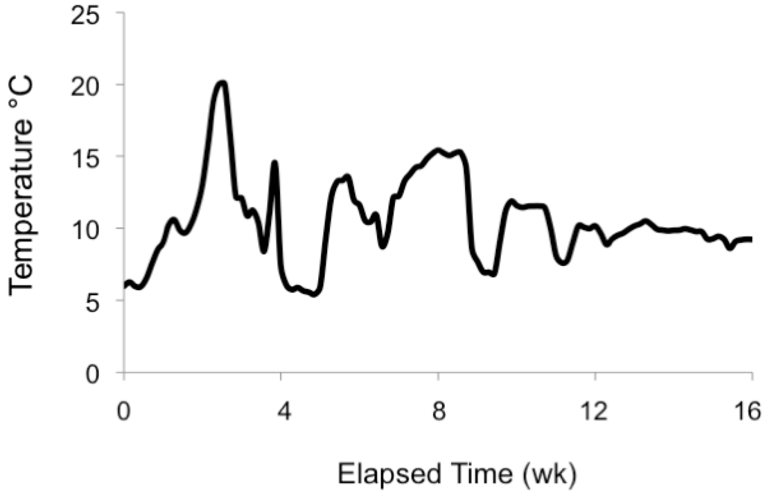


Figure 5.1 Average daily temperature (°C) at the experimental array (19 m depth) over the 16-wk experimental period (9 Aug – 29 Nov 2010).

detector at the University if 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 %.

5.2.3 Statistical Analyses

The effect of algal species (*Saccharina latissima* or *Codium fragile*) and elapsed time on the mass (4–16 weeks) and biochemical properties of algal tissues (0–16 weeks) 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 weeks of the experiment (Lyons et al. 2010); therefore only 4–16 weeks were included in this analysis. The abundance of associated macrofauna, species richness, Pielou's evenness index (J'), and Shannon diversity index (H') also were compared between algal species and over time (4–16 weeks) using a 2-way ANOVA. Post-hoc tests (Tukey's 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 were arcsine transformed to meet the assumptions of normality (Shapiro-Wilk 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).

5.3 RESULTS

5.3.1 Changes in Mass and Biochemical Composition

The wet mass of both *Saccharina latissima* and *Codium fragile* decreased during the 16-wk experiment (Table 5.1, Figure 5.2a) to 9.5 and 18.4 % of initial mass, respectively. Mass loss of *S. latissima* was greatest from 4 to 8 wk (63 % decrease), while *C. fragile* showed a near linear decrease in mass from 4 to 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 (Table 5.1, Figure 5.2b). Nitrogen content was consistently higher in *C. fragile* than in *S. latissima*, and increased significantly from 8 to 12 weeks in both species between 8 and 1 (Table 5.1, Figure 5.2b). Nitrogen content was consistently higher in *C. fragile* (0.75-1.58%) than in *S. latissima* (0.32-1.36%), and increased significantly in both species between 8 and 12 wk. Consequently, the C/N ratio of both algal species decreased during 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) (Figure 5.2b). $\delta^{13}C$ did not differ significantly between algal species, or during degradation (Table 5.1, Figure 5.2c), ranging from -15.0 to -19.1 ‰. $\delta^{15}N$ did not differ between algal species, but increased during degradation, with highest values at 16 wk for *S. latissima* (6.1 ‰) and *C. fragile* (5.8 ‰) (Table 5.1, Figure 5.2c).

The concentration of DMS(P) in degrading *Codium fragile* (1.0–3.3 %) was 1-2 orders of magnitude higher than in degrading *Saccharina latissima* (0.03–0.1 %), and decreased significantly from 4 to 16 wk ($F_{3,8} = 9.22$, p = 0.006, Tukey's HSD: 4 > 12 = 16 wk) (Figure 5.2d).

Table 5.1 2-way ANOVA of the effect of algal species (*Codium fragile*: C, and *Saccharina latissima*: S) and elapsed time (0, 4, 8, 12, and 16 wk) on the weight (g), % C, % N, δ^{13}C, and δ^{15}N of 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
Wet mass						
	Algae	1	5.17	26.0	<0.001	
	Time	3	4.57	23.0	<0.001	$\underline{4}\ \underline{8}\ \underline{12\ 16}$
	Time*Algae	3	0.53	2.67	0.083	
	Residual	16	0.20			
% C						
	Algae	1	4.08	612	<0.001	
	Time	3	0.01	1.63	0.205	
	Time*Algae	3	0.01	1.45	0.255	
	Residual	16	0.01			
% N						
	Algae	1	0.91	15.2	0.013	
	Time	3	1.05	17.6	<0.001	$\underline{0\ 4\ 8}\ \underline{12\ 16}$
	Time*Algae	3	0.26	4.29	0.365	
	Residual	16	0.06			
δ^{13}C						
	Algae	1	0.73	0.368	0.551	
	Time	3	2.00	1.01	0.425	
	Time*Algae	3	2.73	1.38	0.276	
	Residual	16	1.98			
δ^{15}N						
	Algae	1	<0.01	0.0060	0.936	
	Time	3	0.99	5.42	0.004	$\underline{0}\ \underline{\underline{4}}\ \underline{\underline{8\ \underline{12}}}\ \underline{16}$
	Time*Algae	3	0.05	0.280	0.887	
	Residual	16	0.09			

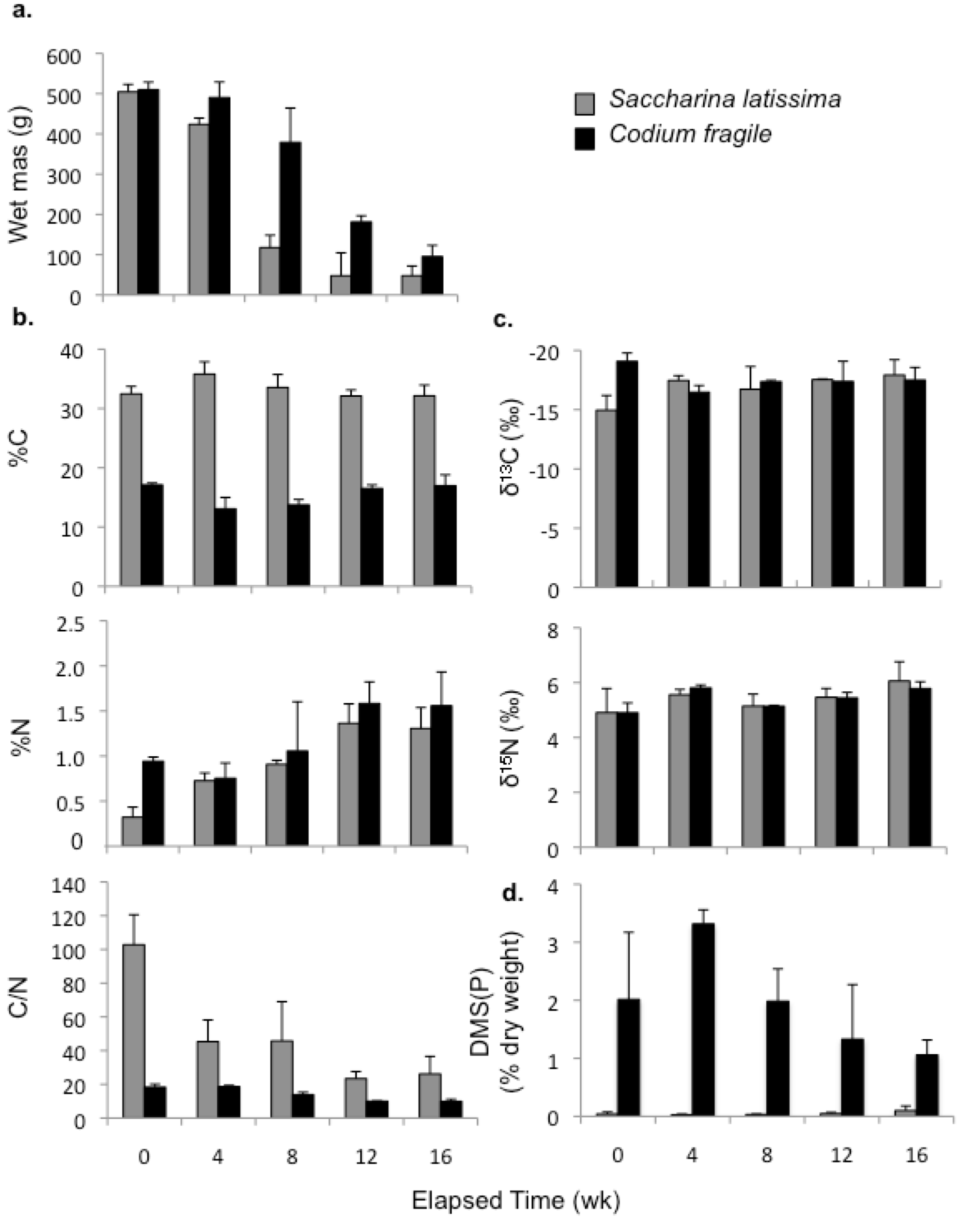


Figure 5.2 a) Wet mass (g), (b) % C, % N, C/N ratio, (c) δ^{13}C (‰), δ^{15}N (‰), and (d) DMS(P) concentration (% dry weight) of *Saccharina latissima* and *Codium fragile* at the start of the experiment, and after 4, 8, 12, and 16 wk of degradation. Data are mean + 1 standard deviation (n = 3).

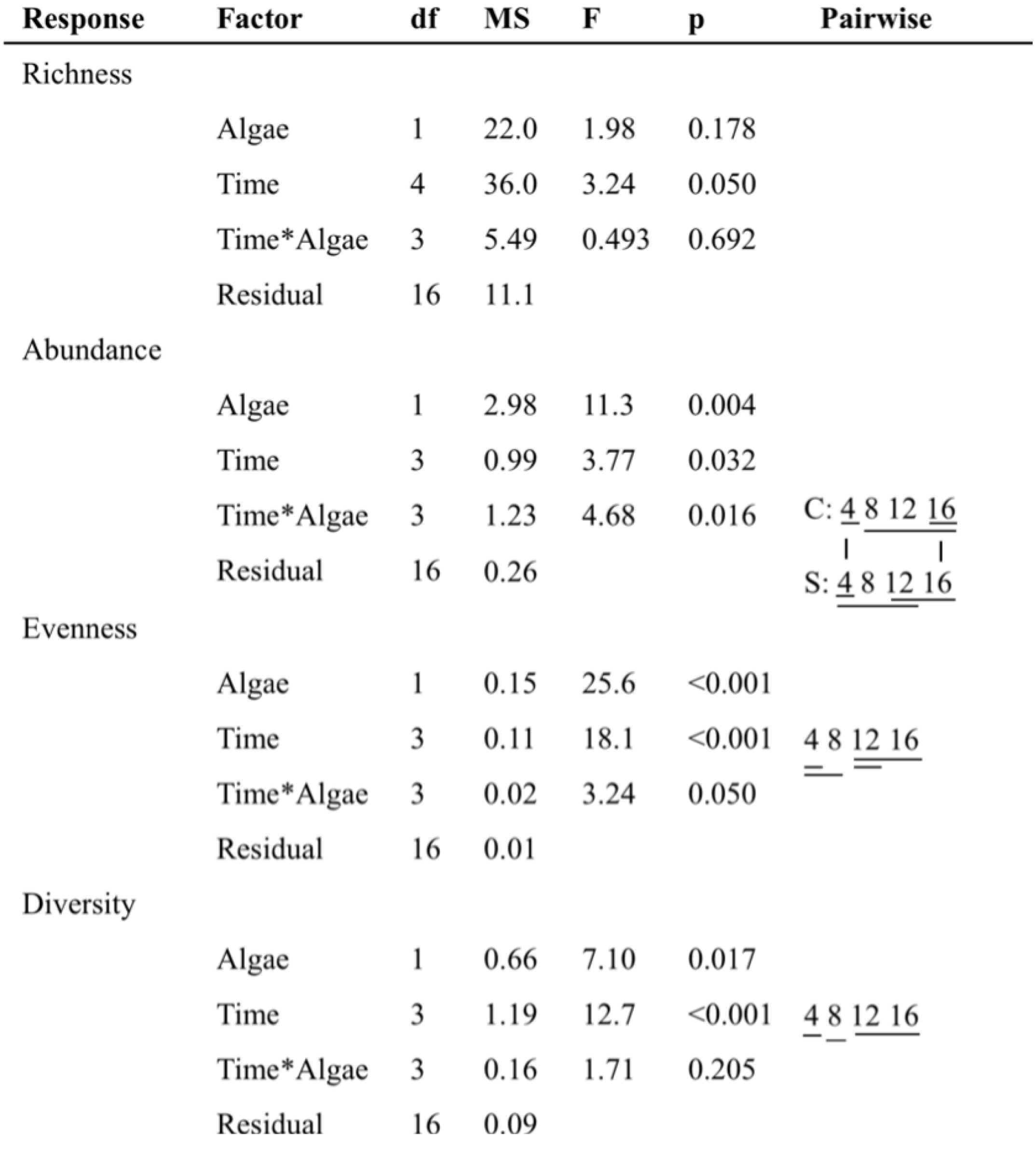
5.3.2 Macrofaunal Communities

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 (Table 5.2, Figure 5.3). 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* from 12 to 16 wk, when abundance no longer differed between algal species (Table 5.2, Figure 5.3). 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 4). 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 *C. fragile* across sampling intervals (Table 5.2, Figure 5.3). Richness was lowest on both species at 8 wk, although the effect of time was marginally non-significant ($p = 0.069$) (Table 5.2). 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 (Table 5.2, Figure 5.3).

Cluster analysis indicated > 60% similarity among macrofaunal assemblages on *Saccharina latissima* that degraded for 4 and 8 wk, with one 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 5.3), 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

Table 5.2 2-way ANOVA of the effect of algal species (*Codium fragile*: C, and *Saccharina latissima*: S) and elapsed time (0, 4, 8, 12, and 16 wk) on the richness (no. species), abundance (individuals 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	4	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
	Residual	16	0.26			S: 4 8 12 16
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			

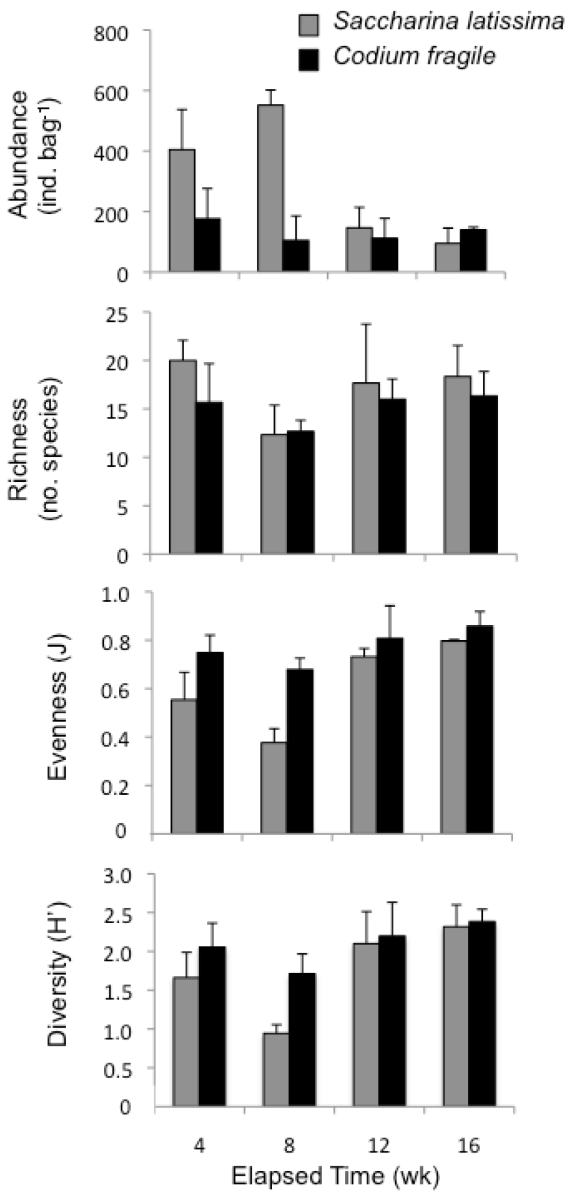


Figure 5.3 The abundance (ind. bag^{-1}), richness (no. species), evenness (J), and diversity (H') of macrofaunal communities associated with *Saccharina latissima* and *Codium fragile* after 4, 8, 12, and 16 wk of degradation. Data are mean + 1 standard deviation (n = 3).

Table 5.3 2-way 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		

Codium fragile, and to changes over time on *S. latissima* (Appendix 5). 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 (Table 5.4, Figure 5.4). The razor clam *Ensis directus* contributed most to differences between *S. latissima* and *C. fragile* at 16 wk, and to differences over time in *C. fragile*, with the highest abundances observed on *C. fragile* at 16 wk (Table 5.4, Figure 5.4, Appendix 5). 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 (Table 5.4, Figure 5.4, Appendix 5). 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 5), but the effects of algal species and elapsed time on the abundance of each of these taxa were non-significant (Table 5.4).

5.4 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 displacement 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* over 16 weeks. The concentration of the grazing-deterrent compound DMS(P) (Van Alstyne & Houser 2003, Lyons et al. 2010) increased slightly in *C. fragile* in the first 4 weeks of the experiment, when mass loss was minimal, likely in response to transplantation to deeper cooler water (Lyons et al. 2010). Similarly, the concentration of DMS(P) in attached *C. fragile* at 5–7 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

Table 5.4 2-way ANOVA of the effect of algal species (*Codium fragile*: C, and *Saccharina latissima*: S) and elapsed time (0, 4, 8, 12, and 16 wk) on the abundance (individuals 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: $\underline{4\ 8\ 12\ 16}$
	Residual	16	1.38			| S: $\underline{\underline{4}\ 8}\ \underline{\underline{12}\ 16}$
Gammaridae						
	Algae	1	0.43	0.531	0.477	
	Time	3	2.94	3.60	0.037	$\underline{4}\quad \underline{8\ \underline{12\ 16}}$
	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: $\underline{4\ 8}\ \underline{12\ 16}$
	Residual	16	0.21			| | | S: $\underline{4\ 8}\ \underline{\underline{12}\ \underline{16}}$

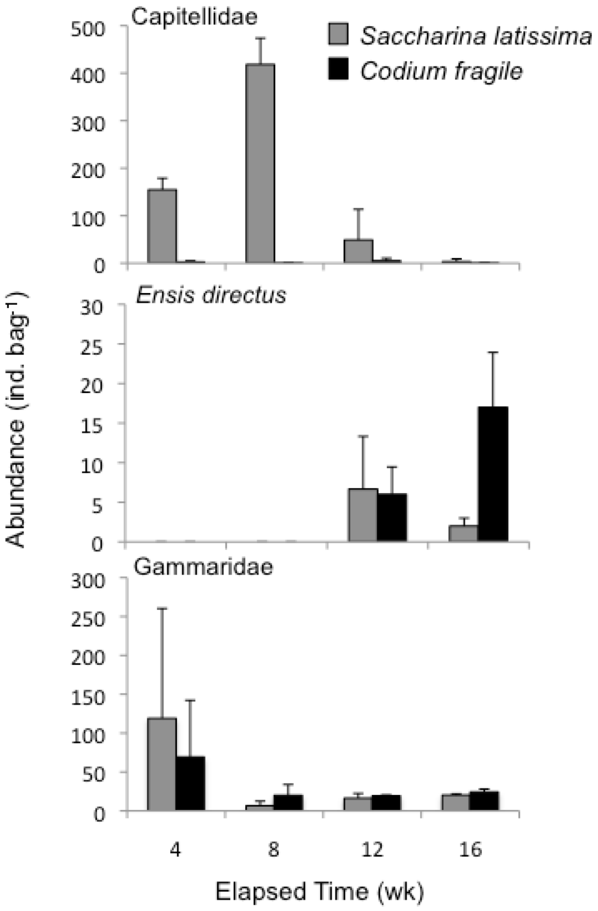


Figure 5.4 Abundances of the taxa (Capitellidae, *Ensis directus*, and Gammaridae (individuals bag^{-1}), as identified by SIMPER, that contributed most to differences in macrofaunal community composition on *Saccharina latissima* and *Codium fragile* after 4, 8, 12, and 16 wk of degradation, and that varied significantly over time or between algal species. Data are mean + 1 standard deviation (n = 3).

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, Lehman 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. in press). 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 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 four sampling intervals. However, mean temperature was relatively constant (10–11°C) across the 4-wk intervals, and this may have obscured shorter-term variation in degradation rate related to temperature during the first 12 weeks 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 2011a). 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 weeks, 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. Amphipods colonized both algal species in higher abundance during the early stages 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 weeks.

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 (Lutz et al. 2010, Jones & Thornber 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 *S. 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 *C. fragile* are greatest in fall and early winter resulting in 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 (Trowbridge 1993, Fralick & Matheison 1973), 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 (personal observations), and small juveniles (<10 mm) occasionally were found on *Saccharina latissima* and *Codium fragile* throughout the 16-week 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 & Scheibiling 2009a). These feces are of higher nutritional quality (lower C/N ratio) than fresh algal material (Sauchyn & Scheibiling 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. 2011), 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 algal species introductions can have more far-reaching impacts than previously considered.

CHAPTER 6

PRODUCTION AND FATE OF KELP DETRITUS

6.1 INTRODUCTION

Kelp species have a broad geographic distribution and are a major source of primary production and biogenic habitat in coastal zones of temperate and polar oceans worldwide (Dayton 1985a, Steneck et al. 2002). Kelp productivity is tightly linked to seawater nutrient concentrations (Chapman & Lindley 1980, Gagné et al. 1982), which are regulated by oceanographic processes and anthropogenic activities. Kelps support high secondary productivity in rich and diverse communities of invertebrates and fish, including many commercially important species such as abalone, lobster, and sea urchins. The sensitivity of kelps to environmental change and increasing fishing pressure are altering kelp productivity and biomass, which can have important follow-on effects on secondary production and ecosystem function both within kelp beds or forests (Dayton et al. 1992, Steneck et al. 2002) and in adjacent communities that receive kelp detritus.

There is growing recognition that the exchange of detritus is an important form of connectivity between distinct habitats that can influence spatial patterns of primary and secondary productivity (Polis et al. 1997, Loreau et al. 2003, Marczak et al. 2007), and that a significant proportion of energy produced in macrophyte communities enters detrital pathways (Mann 1988, Cebrian 1999). Kelps continuously produce detritus, which is consumed or decomposed within kelp beds or forests, or exported. Various studies have shown that kelp detritus is an important resource in adjacent communities (Duggins et al. 1989, Bustamante et al. 1995, Dugan et al. 2003, Vanderklift & Wernberg 2008), however a comprehensive understanding of the nature and extent of this subsidy is lacking. Although the production and fate of detritus have been reviewed for other marine macrophyte communities (e.g. seagrass beds, Heck et al. 2008; mangrove forests, Kristensen et al. 2008) reviews of kelp ecosystems provide only a cursory description of detrital pathways (Dayton 1985a, Steneck et al. 2002). Other reviews have considered detrital production and processing in terrestrial and aquatic ecosystems more broadly, without specific emphasis on kelp communities (Mann 1988, Cebrian & Lartigue 2004). The impact of anthropogenic pressures on kelp detrital production and export has not been considered.

In this review, I summarize estimates of detrital production from kelp populations worldwide for comparison with other macrophyte communities that contribute detritus to coastal habitats. I identify environmental and biological factors that regulate the rate of kelp detrital production and degradation, and examine the consequences of detrital kelp subsidies for community organization and productivity in a variety of marine habitats, including sandy beaches and rocky intertidal shores, rocky and sedimentary subtidal areas, and the deep-sea. I then frame this body of empirical work in the theoretical context of spatial ecology to explore the relationship between local kelp productivity and regional productivity. Finally, I discuss anthropogenic impacts to kelp ecosystems that are causing declines in kelp biomass, and highlight the broader implications of these declines to communities subsidized by kelp detritus.

6.2 PRODUCTION OF KELP DETRITUS

There are three morphological groupings of kelp species: canopy, stipate, and prostrate (Dayton 1985a, Steneck et al. 2002). All kelps are attached to the substrate by a root-like structure known as a holdfast. Canopy kelps have flexible stems or stipes that are supported by gas-filled bladders called pneumatocysts. The largest of the canopy kelps, the genus *Macrocystis,* has a primary stipe that gives rise to multiple secondary stipes, each with lateral blades along their extent, referred to as fronds. Other canopy kelps, such as the genus *Nereocystis*, have a single stipe supported by one large pneumatocyst, from which emanate multiple blades. Stipate kelps typically are smaller and have rigid stipes supporting a single blade, while prostrate kelps are the smallest and have blades that lay directly on the substrate. Stipate and prostrate kelps include species of the genera *Laminaria, Saccharina, Ecklonia, Lessonia,* and *Eisenia*. Populations of canopy kelps form so-called forests, while prostrate and stipate kelps form beds (Steneck et al. 2002).

Kelp detritus ranges in size from small particles to whole thalli. Whole thalli are lost through breakage at the base of the primary stipe or when holdfasts become detached from the substratum. Frond loss is the result of breakage of the secondary stipe for *Macrocystis* spp.; individual blades also can detach from secondary stipes with multiple blades. Breakage at the junction of stipe and blade for stipate and prostrate kelps is another form of blade loss. Loss of whole thalli and blade breakage below the basal meristem prevent re-growth of an individual, and are considered mortality. The distal ends of blades can erode rapidly or gradually, producing detrital fragments that range from small particulates to large sections of blade. Dissolved organic matter is released as kelp blades fragment and erode, and is estimated to account for 16–35% of annual energy production in kelps (Johnston et al. 1977, Hatcher et al. 1977, Mann et al. 1979, Newell et al. 1980).

Rates of dislodgement (including loss of whole thalli and fronds) and erosion (including blade loss and breakage) have been measured (as dry mass or C) for kelp populations spanning the temperate range of kelps worldwide (Table 6.1, Figure 6.1). Measures of variability associated with these estimates are absent or inconsistent across measures, and therefore not included. Although the range of kelps extends into the high arctic, erosion rate has only been recorded for a single population of *Laminaria solidungula* in the Beaufort Sea, Alaska, USA (Dunton 1984), which was the lowest of all kelp populations studied (26 g m^{-2} y^{-1}, 8 g C m^{-2} y^{-1}). Erosion rate spans three orders of magnitude globally, with the highest rate measured for *Lessonia* spp. in Chile (11,071 g m^{-2} y^{-1}, 2,657 g C m^{-2} y^{-1}), reflecting a high blade density of these species (2369–3019 blades m^{-2}) (Tala & Edding 2007). Erosion rates of *Ecklonia* spp. were moderately high across all locations, and erosion of *Laminaria* spp., *Saccharina* spp., and *Macrocystis pyrifera* were in the mid to low end of the range. Erosion of *Saccharina latissima* (formerly *Saccharina longicruris, Laminaria longicruris* or *L. saccharina*; McDevitt & Saunders 2010) was an order of magnitude greater in Nova Scotia, Canada than in Scotland, indicating high variability among populations of the same species in different geographic locations. Erosion rate of a cultured population of *Undaria pinnatifida* in northern Japan was the lowest value recorded of all populations worldwide.

Table 6.1 Estimated rates of productivity, blade erosion, dislodgement of whole fronds and thalli (g dry mass m^{-2} y^{-1} and g C m^{-2} y^{-1}), and percent of productivity lost to erosion and dislodgement for kelp populations worldwide. One measurement is presented for the combined contribution of all kelp species present in a particular location. The number in the first column indicates the location of measurements in Fiure 6.1.

	Location	Species	Productivity		Erosion		% Eroded	Dislodgement		% Dislodged	Source
			(g $m^{-2}y^{-1}$)	(g C $m^{-2}y^{-1}$)	(g $m^{-2}y^{-1}$)	(g C $m^{-2}y^{-1}$)		(g $m^{-2}y^{-1}$)	(g C $m^{-2}y^{-1}$)		
1	Beaufort Sea, Alaska, USA	*Laminaria solidungula*	28	9	26	8	90.7	-	-		Dunton 1984
2	British Colombia, Canada	*Macrocystis integrifolia*						774	232		Druehl and Wheeler 1986
3	Monterey Bay, California, USA	*Macrocystis pyrifera*	2389	664	414	115	17.3	1170	325	49.0	Gerard 1976
4	Tongoy, Chile	*Lessonia nigrescens,* *Lessonia trabeculata*	23424	5622	11071	2657	47.3	-	-		Tala and Edding 2007
5	Falkland Islands	*Macrocystis pyrifera*	2721	766	-	-		565	157	20.8	Van Trussenbroek 1993
6	Nova Scotia, Canada	*Laminaria digitata,* *Saccharina latissima*	951	289	1058	322	111.3	-	-		Krumhansl & Scheibling 2011
7	Nova Scotia, Canada	*Laminaria digitata,* *Saccharina latissima*	-	-	-	-		74	22		Chapman 1984
8	Rhode Island, USA	*Laminaria digitata,* *Saccharina latissima*	6152	1938	-	-		2798	839	45.5	Brady-Campbell et al. 1984
9	Loch Creran, Scotland	*Laminaria latissima*	395	120	160	48	40.5	-	-		Johnston et al. 1977
10	Cape Town, South Africa	*Laminaria pallida,* *Ecklonia maxima*	1614	450	1129	343	70.0	97	29	6.2	Newell et al. 1982
11	Perth, Australia	*Ecklonia radiata*	-	-	-	-		662	201		Hatcher et al. 1987
12	Goat Island Bay, Leigh, New Zealand	*Ecklonia radiata*	3000	912	1500	456	50.0	-	-		Novackez 1984
13	Otsuchi Bay, Japan	*Undaria pinnatifida* (cultured)	33	10	9	3	28.3	-	-		Yoshikawa et al. 2001
14	Shimizu, Japan	*Ecklonia cava*	2800	851	2547	774	91.0	-	-		Hyashida 1977

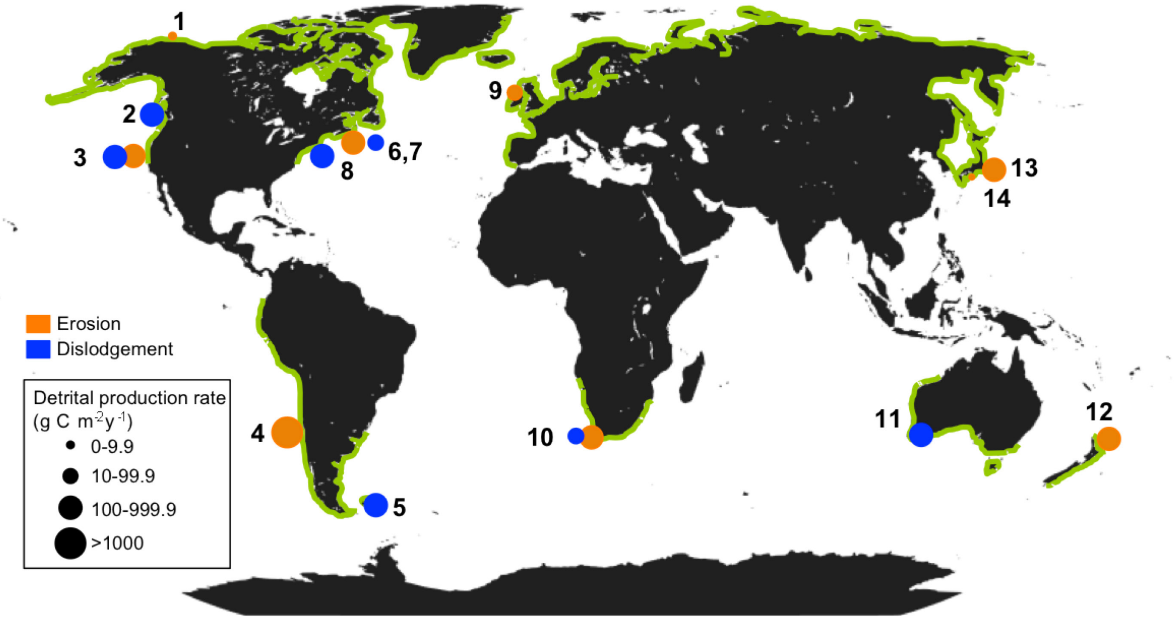


Figure 6.1 Global distribution of kelps (green shading) and locations (numbered) where rates of kelp production, erosion (orange circles) and dislodgement (blue circles) have been measured (Table 6.1). Circle area represents the magnitude of measured rates; overlapping circles indicate locations where erosion and dislodgement rates were measured simultaneously.

Across all populations, erosion accounted for 17.3 to 111.3% of annual primary productivity (Table 6.1). Although erosion rate was highest for *Lessonia* spp. in Chile, the amount of material eroded accounted for less than half (47.3%) of the annual primary production. In contrast, *Ecklonia cava* in southern Japan had the second highest erosion rate (2547 g m^{-2} y^{-1}, 774 g C m^{-2} y^{-1}) but 91% of biomass produced annually was eroded. Annual erosion exceeded production for populations of *Laminaria digitata* and *Saccharina latissima* in Nova Scotia, indicating that the standing biomass of these species decreased over the measurement period.

Few studies have documented dislodgement rates for kelp populations (Table 6.1). Interestingly, measurements from populations of *Laminaria digitata* and *Saccharina latissima* in two separate locations represented the minimum (Nova Scotia, Canada) and maximum (Rhode Island, USA) rates of the range recorded (74–2798 g m^{-2} y^{-1}, 22–839 g C m^{-2} y^{-1}). Dislodgement accounted for 6.2 to 49.0% of annual productivity, which is lower than the range presented for erosion. Only two studies have simultaneously measured erosion and dislodgement rates in a single kelp population (Gerard 1976, Newell et al. 1982). For *Macrocystis pyrifera*, dislodgement rate (50% of annual production) was an order of magnitude greater than erosion rate (17%) (Gerard 1976). The opposite was observed for populations of *Laminaria pallida* and *Ecklonia maxima* in South Africa, where dislodgement accounted for a small portion of biomass produced annually (6%) as compared to erosion (70%). Erosion rate also exceeded dislodgement rate in populations of *Laminaria digitata* and *Saccharina latissima* in Nova Scotia (Chapman 1984, Krumhansl & Scheibling 2011a), and *Ecklonia radiata* in northern New Zealand and Western Australia (Novaczek 1984, Hatcher et al. 1987). The relative importance of erosion and dislodgement to detrital production may be related to kelp morphology, with larger canopy-forming kelps producing more detritus through dislodgement than smaller canopy-forming and prostrate kelps. Spatial and temporal variation in physical processes that cause dislodgement also may account for differences in the relative importance of this mode of detrital production among kelp populations. Erosion is likely to be greater than dislodgement rate in areas less prone to physical disturbance, or during periods when disturbance events are less frequent.

6.3 FACTORS REGULATING PRODUCTION OF KELP DETRITUS

Kelp detritus is produced through wave and current-driven water motion. Losses in kelp biomass through dislodgement and erosion are greatest during storms that generate high flow rates (Gerard 1976, Luning 1979, Gunnill 1985, Seymore et al. 1989, Reed et al. 2008, Cavanaugh et al. 2011). During periods when maximum wave heights frequently exceed 2.5 m, as much as 30% of thalli and fronds of *Macrocystis pyrifera* are lost (Gerard 1976), and losses of density and biomass can range from 65 to 100% during the largest wave events (maximum wave height >5 m) (Ebeling et al. 1985, Seymore et al. 1989, Reed et al. 2008). Detached fronds and thalli may become entangled with attached kelps, causing substantial increases in drag that lead to further dislodgement (Gerard 1976, Seymore et al. 1989, Brown et al. 1997). Poorly attached kelps, and those that have settled on small cobbles and biogenic structures such as mussels are more likely to become dislodged from the substratum at higher flow rates (Gunnill 1985, Witman 1987, Scheibling & Gagnon 2009). Erosion occurs continuously, even during relatively calm conditions (Reed et al. 2008, Krumhansl & Scheibling 2011a). Loss of fronds and blade area may actually increase the survivorship of kelps in strong flow by reducing drag on thalli (Gunnill 1985).

The importance of hydrodynamic forces in determining kelp survivorship and biomass is corroborated by morphological variation in kelps along spatial gradients of wave and current exposure. Kelps in areas of high flow are typically more streamlined or strap-like, less crenulated or undulate, have thicker stipes and blades, and are more firmly attached at the holdfast than kelps in low-flow environments (Gerard & Mann 1979, Wernberg & Vanderklift 2010, Koehl et al. 2008, Miller et al. 2011). Nevertheless, dislodgement and erosion are typically greater at sites with high wave exposure than at more protected sites (Duggins et al. 2003, Krumhansl & Scheibling 2011a).

Damage to kelp stipes and blades through abrasion, epiphytism, and grazing greatly reduce the ability of kelps to withstand dislodgement and breakage by waves and currents. Knicks, holes and flaws in kelp tissues concentrate stress when the thallus is in tension, leading to crack formation and propagation at lower force applications than required to break undamaged tissues (Black 1976, Koehl & Wainwright 1977, Biedka et al. 1987, Duggins et al. 2001, Krumhansl et al. 2011). For example, grazing damage by snails and sea urchins on kelp stipes and holdfasts has been linked to stipe breakage and holdfast dislodgement (Koehl & Wainwright 1977, Biedka et al. 1987, Duggins et al. 2001). Perforations generated by snails reduce the strength of kelp blade tissues (Black 1976, Krumhansl et al. 2011), which accounts, in part, for seasonal variation in erosion rate (Krumhansl & Scheibling 2011a) and loss of kelp biomass during storms (Krumhansl & Scheibling 2011b). Encrustation of kelp blades and stipes by bivalves and bryozoans also increase drag and induce flaws in blade tissues that lead to dislodgement and breakage (Brady-Campbell et al. 1984, Brown et al. 1997, Krumhansl & Scheibling 2011a, Krumhansl et al. 2011). In particular, encrustation of kelp blades by the bryozoan *Membranipora membranacea* in its invaded range (east and west coasts of North America) causes quantifiable reductions in blade strength (Krumhansl et al. 2011), resulting in widespread defoliation of kelp beds during periods of high wave action (Scheibling et al. 1999, Scheibling & Gagnon 2009).

Water temperature and nutrient availability can affect the quality of kelp blade tissue and, in turn, erosion rate. Low nitrate in summer corresponds to a seasonal minimum in kelp growth rate (Mann 1973, Gagné et al. 1982, Brown et al. 1997). During this period, temperature, irradiance and sedimentation on blades are high (Gunnill 1985, Brown et al. 1997), causing tissue degradation and increasing the susceptibility of blades to breakage (Gunnill 1985, Brown et al. 1997). Older thalli may erode more rapidly than juvenile kelps (Brown et al. 1997, Krumhansl & Scheibling 2011a).

6.4 COMPARISON OF DETRITAL PRODUCTION RATES AMONG MACROPHYTE COMMUNITIES

Annual rates of erosion and dislodgement averaged among kelp populations measured globally (Table 6.1) are 448 ± 770 (mean ± 1 SD) and 257 ± 278 g C m^{-2} y^{-1} respectively. Summing these quantities yields an estimated average detrital production rate of 705 g C m^{-2} y^{-1}. The average productivity of these kelp populations is 864 g C m^{-2} y^{-1}, indicating that detrital production accounts for the large majority of kelp primary production (81.7%). Similar global estimates of detrital production exist for other macrophyte communities. Seagrass ecosystems produce on average 817 g C m^{-2} y^{-1} (including above and below ground production), of which 650 g C m^{-2} y^{-1} (79.5%) enters detrital pathways (Mateo et al. 2006).

Mangrove forests contribute a significant amount of detritus in the form of leaf litter to coastal marine communities. Productivity of mangroves (1788 g C m^{-2} y^{-1}) typically exceeds that that of seagrass or kelps, but annual leaf litter estimates (456 g C m^{-2} y^{-1}) represent only 25.5% of primary production (Kristensen et al. 2008). Salt marshes are also highly productive and produce a significant quantity of detritus annually. Bouchard & Lefeuvre (2000) estimated productivity of marsh grasses (*Pucinellia maritima, Suaeda maritime, Aster tripolium, Salicornia* spp., *Atriplex portulacoides, Elytrigia aetherica, Festuca rubra*) in France at 4370 g C m^{-2} y^{-1}, of which 3330 g C m^{-2} y^{-1} (76.2%) entered detrital pathways. Haines (1977) presents a more moderate estimate of detrital production (648 g C m^{-2} y^{-1}) from a salt marsh in Georgia, USA comprised of *Spartina alterniflora*, which is similar to detrital production rates from salt marshes in Argentina comprised of *S. alterniflora* (788 g C m^{-2} y^{-1}) and *S. densiflora* and (862 g C m^{-2} y^{-1}) (Montemayor et al. 2011).

Few studies have directly quantified detrital production from macroalgal communities other than kelp beds or forests, and these measurements are primarily for other large brown algae. Fucales form extensive beds in intertidal and shallow subtidal habitats, and are often a dominant component of beach wrack (Josselyn & Mathieson 1980, Yatsuya et al. 2007). Josselyn & Mathieson (1980) estimated that *Ascophyllum nodosum* and *Fucus vesiculosus* in an estuarine system produce detritus at rates of 540 and 414 g C m^{-2} y^{-1} respectively, although these estimates were based on wrack deposited on shore. The rate of detrital production from a population of *Sargassum muticum* in a Danish estuary was estimated at 136 g C m^{-2} y^{-1}, while *Halidrys siliquosa* produced substantially less detritus (6.3 g C m^{-2} y^{-1}) in the same area (Pedersen et al. 2005).

A comparison of these studies indicates that detrital production accounts for a similar percentage of primary production in kelp, seagrass, and salt marsh communities (76–82%), representing the majority of primary production. In contrast, most of the primary production in mangrove communities accumulates as standing stock biomass

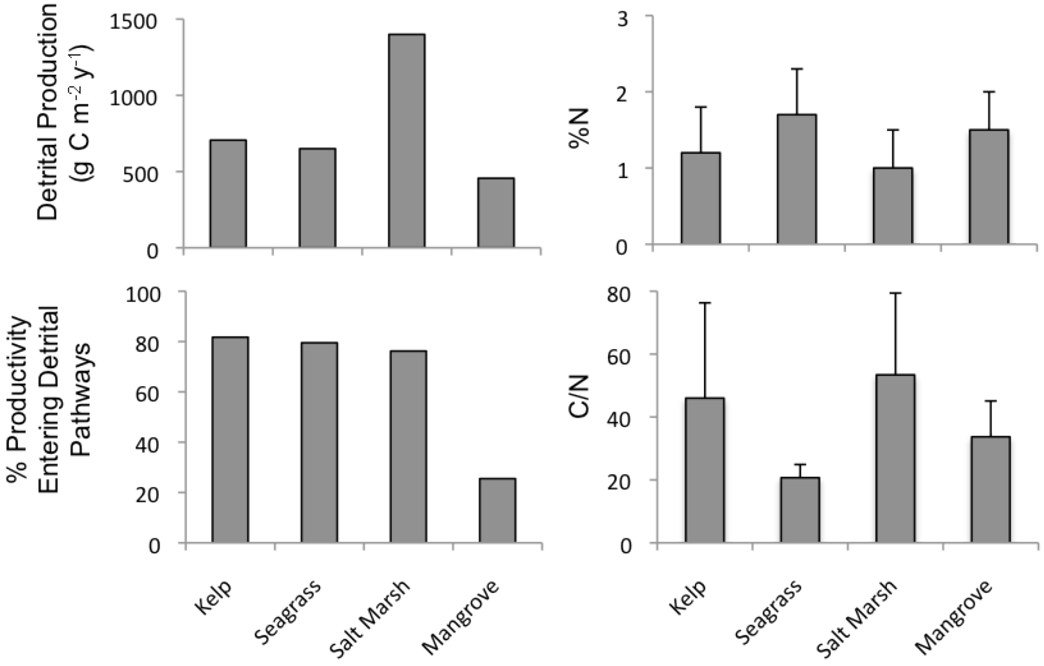


Figure 6.2 Average detrital production rates (g C m^{-2} y^{-1}), the percentage of primary productivity entering detrital pathways, the average percentage of nitrogen and C/N ratio (+1 SD) for kelp (n = 7), seagrass (n = 6), salt marsh (n = 7), and mangrove communities (n = 6). %N and C/N were calculated from a range of species within each macrophyte type. Kelp sources: Norderhaug et al. 2003, Hepburn et al. 2007, Krumhansl & Scheibling, in press, Cerda et al. 2009, Schaal et al. 2010; salt marsh sources: Montemayor et al. 2011, Simoes et al. 2011, Tobias et al. 2010, Dai et al. 2009; seagrass sources: Smit et al. 2006, Mateo et al. 2006, Mascaro et al. 2009, MacArthur et al. 2011, Prado and Heck 2011; mangrove sources: Thongtham and Kristensen 2005, Nordhaus et al. 2011.

(Lugo & Snedaker 1975, Lee et al. 1990, Kristensen et al. 2008). The decomposition rate and ability of organisms to consume plant and algal material is related to its nutritional quality and palatability, specifically to the C/N ratio, % N, content of fibrous material (cellulose, lignin), and concentration of secondary metabolites (Mann 1988, Cebrian & Lartigue 2004, Hladyz et al. 2009, Krumhansl & Scheibling in press). Based on the C/N ratio and % N, kelp generally is more nutritious than salt marsh grass and less nutritious than seagrass and mangrove leaves, although these values are highly variable across macrophyte species (Figure 6.2). The presence, identity, and concentration of secondary metabolites also differ widely among macrophytes, and have varying effects on consumers. Lower consumption, assimilation, and degradation rates of vascular plants relative to kelps and other macroalgae are likely related to a higher content of fibrous material (or lower labile fraction) (Smith & Foreman 1984, Tenore et al. 1984, Mann 1988, Cebrian 1999, Hladyz et al. 2009). Consumers often prefer kelp and other macroalgal detritus to vascular plant detritus (Smit et al. 2006, Doropoulos et al. 2009), and more refractory material accumulates in vascular plant than macroalgal communities (Cebrian & Lartigue 2004).

A combination of hydrodynamics, geomorphology, and sediment characteristics influences the export and deposition of macrophyte detritus (Kotta et al. 2008, Britton-Simmons et al. 2012). For example, the direction and distance of detrital transport from marshes is highly dependent on freshwater input, wind and tidal flows (Dame & Allen 1996), and sediment characteristics, such as softness and penetrability, that affect the likelihood that detritus is trapped and buried (Kristensen et al. 2008, Montemayor et al. 2011). Less detritus may be retained in kelp beds and forests relative to seagrass meadows, salt marshes, and mangrove forests because kelps grow only on rocky substrata in areas with moderate to high wave exposure, where trapping and burial are unlikely. Low-energy bays and soft-sediment habitats accumulate kelp detritus at rates that exceed local kelp productivity (Bustamante et al. 1995, Bustamante & Branch 1996, Vetter 1995), indicating that kelp detritus is concentrated in low-energy environments.

6.5 DEGRADATION OF KELP DETRITUS

The rate of kelp degradation depends on the chemical and physical characteristics of detritus, and the environmental conditions under which degradation is occurring. Degradation occurs more rapidly at higher water temperatures (Bedford & Moore 1984, Rothausler et al. 2009), and under high flow conditions where mechanical breakdown occurs (Tenore et al. 1984, Alkemade & van Rikswijk 1993). Physical processes also play a role in regulating the environmental conditions within detrital accumulations. Re-suspension exposes a greater surface area of detritus to microbial colonization (Stahlberg et al. 2006) and increases the concentration of dissolved oxygen (Tenore et al. 1984, Kristensen 1994, Okey 1997, Okey 2003). Smaller detrital particles degrade at a faster rate than larger fragments because they have a higher surface area relative to their volume for microbial colonization (Smith & Foreman 1984). Microbial respiration is reduced when algal material is dried onshore, resulting in slower degradation rates compared to wet material (Newell et al. 1985).

Nutritional quality increases throughout the course of kelp degradation (Smith & Foreman 1984, Mann 1988, Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling in press). Microbial colonization and transformation increase the % N in kelp tissues, leading to a gradual decrease in the C/N ratio (Mann 1988, Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling in press). Phlorotannins occur in varying concentrations among kelp species and are known to deter grazing (Johnson & Mann 1986, Iken et al. 2009), reduce growth in filter feeders by decreasing assimilation efficiency (Duggins & Eckman 1997), and deter colonization by microbes (Ragan & Golombitza 1986). Phlorotannin concentration decreases rapidly during degradation, and the largest increases in nitrogen occur in species that undergo the greatest reduction in phlorotannins (Duggins & Eckman 1997). Assimilation efficiency, survival and growth of several species of polychaetes, mussels, and amphipods are reduced when fed a single diet of fresh kelp, but are enhanced when fed aged kelp particles (Cranford & Grant 1990, Duggins & Eckman 1997, Norderhaug et al. 2003). Species with different nutritional preferences and physiological tolerances colonize algal material at varying times over the course of degradation in response to changing environmental conditions and nutritional quality of the detritus (Bedford & Moore 1984, Fauchald & Jumars 1979; Okey 2003, Mamouridis et al. 2011, Krumhansl & Scheibling in press).

6.6 EXPORT OF KELP DETRITUS: TRANSPORT MECHANISMS AND SINKS

Kelp detritus can settle within kelp beds and forests, where it serves as food for the local assemblage of benthic invertebrates (Dunton & Schell 1987, Tutschulte & Connell 1988, Norderhaug et al. 2003, Schaal et al. 2009), or be advected by waves and currents to adjacent or distant habitats. The transfer of resources across habitat boundaries plays a central role in shaping ecological patterns and processes (Huxel et al. 2004, Heck et al. 2008, Lamberti et al. 2010). Resource subsidies influence almost all levels of ecology, from behavior (Harrold & Reed 1985, Rodriguez 2003) and species interactions (Spiller et al. 2010), to productivity (Bustamante & Branch 1996, Polis & Hurd 1996), food web stability (Huxel & McCann 1998, Huxel et al. 2002, Marleau et al. 2010), and population dynamics (Bustamante et al. 1995, Barrett et al. 2005). Nutrients and detritus subsidize lower trophic levels, while carrion and prey subsidize higher trophic levels. Subsidies have a greater effect when they occur at lower trophic levels where species are more specialized than consumers at higher trophic levels (Polis & Hurd 1996, Huxel & McCann 1998, Marczak et al. 2007). Resource subsidies have the greatest effect when productivity or the amount of an equivalent resource is lower in the recipient community than in the source community (Polis & Hurd 1996, Marczak et al. 2007). Subsidies can be reciprocal (Nakano & Murikami 2001); for example, when imported kelp detritus is processed and nutrients are returned to the source (Gravel et al. 2010a).

The proportion of detritus that is exported from kelp beds and forests is unknown, but the consequences of detrital subsidies for recipient populations and communities have been documented in a variety of habitats. Kelp detritus is transported alongshore and tends to accumulate in low-energy depositional areas such as sandy beaches, embayments

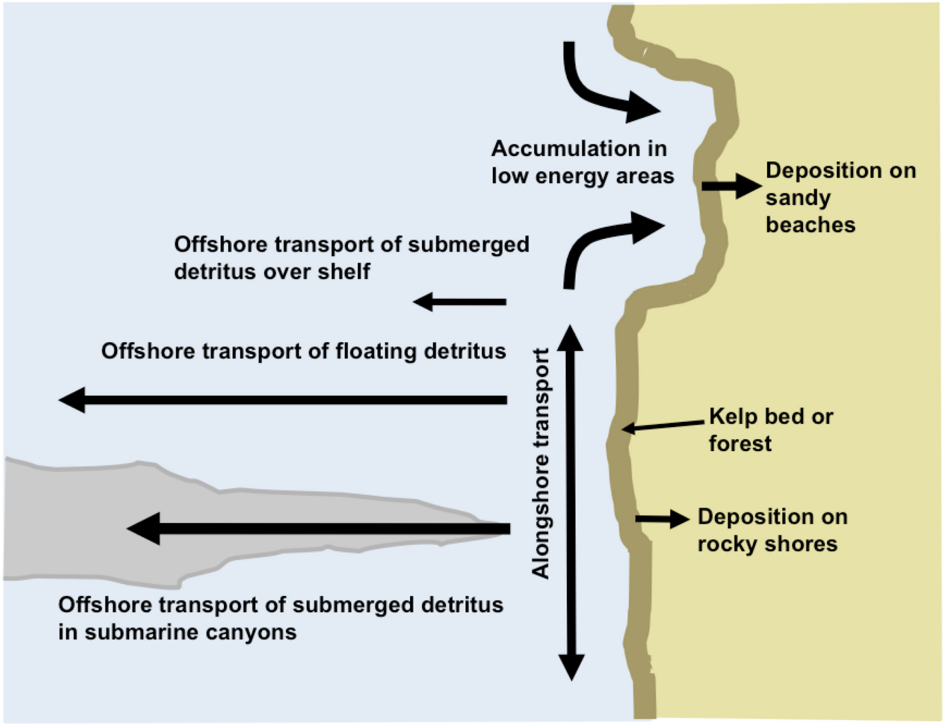


Figure 6.3 Detrital transport mechanisms in coastal systems. Arrows indicate the direction and relative magnitude (as line thickness) of transport.

and deep basins, resulting in patchy deposits of high biomass in intertidal or subtidal habitats (Figure 6.3) (Gerard 1976, Bustamante et al. 1995, Britton-Simmons et al. 2012). It also can be dispersed far offshore by bottom currents, or as rafts of floating thalli carried by surface currents and winds, to provide a subsidy for communities in the deep sea.

6.6.1 Onshore Transport and Deposition

6.6.1.1 Sandy Beaches

Kelp detritus plays a significant role in shaping community dynamics on sandy beaches, and is perhaps the most well known example of kelp detrital subsidy to an adjacent community. Sandy beaches have very low local primary productivity (0–50 g C m^{-2} y^{-1}; Brown 1964, Munro et al. 1978, Griffiths et al. 1983, Colombini & Chelazzi 2003), largely because sandy sediments are highly mobile and thus unsuitable for attachment by macrophytes or formation of benthic diatom assemblages (Griffiths et al. 1983). Imported detritus is the primary food source for resident fauna and microbes. Rates of kelp deposition (as wet mass) range from 1200 to 2200 kg m^{-1} y^{-1} for *Laminaria pallida* and *Ecklonia maxima* in South Africa (Koop & Field 1980, Stenton-Dozey & Griffiths 1983), from 450 to 548 kg m^{-1} y^{-1} for *Macrocystis pyrifera* in California, USA (Hayes 1974, Dugan et al. 2011), and from 180 to 1450 kg m^{-1} y^{-1} for *Ecklonia radiata* in Western Australia (Hansen 1984). Deposition of kelp detritus varies by season in response to changing water temperatures and wave conditions (Stenton-Dozey & Griffiths 1983, Koop & Field 1980).

Detrital processing by microbes and meio- and macrofauna on sandy beaches plays a key role in coastal nutrient cycling (Pearse et al. 1942, Dugan et al. 2011). Bacteria and protozoans rapidly colonize detrital kelp deposits on beaches, causing surficial lesions and cell lysis that release dissolved and particulate organic matter into the sediments (Figure 6.4) (Koop et al. 1982). Carbon in this leachate is converted to microbial biomass and remineralized (Koop et al. 1982), directly absorbed by meiofauna (Koop & Griffiths 1982, McLachlan 1985), or returned to the sea via tidal forcing or rainwater run-off. Nitrogen in the leachate is rapidly remineralized and nitrified, and accumulated as

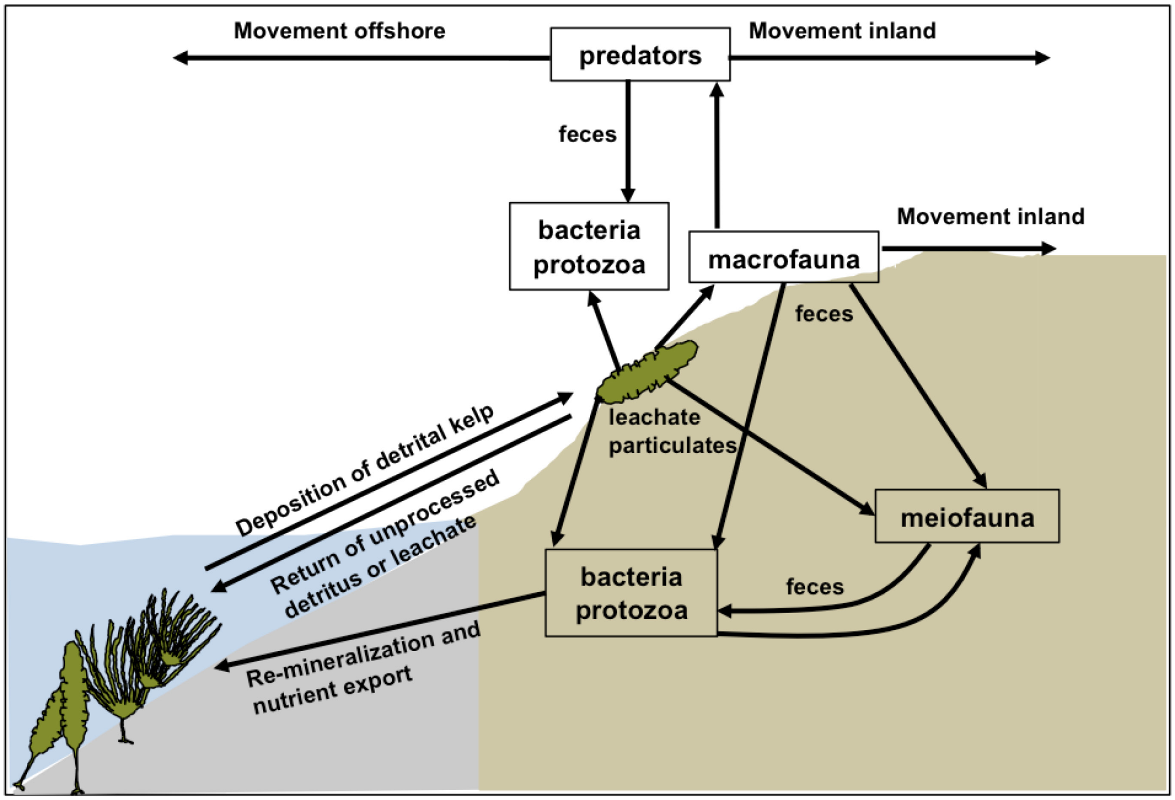


Figure 6.4 Energy flow associated with faunal and microbial processing of kelp detritus in sandy beach ecosystems.

dissolved inorganic nitrogen (DIN) in sediments beneath kelp deposits (Dugan et al. 2011). Koop et al. (1982) found that very little DIN is returned to the sea following remineralization in beach sands in South Africa. In contrast, Dugan et al. (2011) showed that DIN in surf-zone water in California was positively correlated with DIN in intertidal sediments, suggesting export from beach sediments. Beaches can act as sources or sinks of nitrogen depending on the rate of erosion of beach sediments (Colombini & Chelazzi 2003, Dugan et al. 2011). Dissolved organic matter (DOM) may also return to the sea before bacterial processing (Dugan et al. 2011).

Deposits of kelp detritus on beaches also are readily colonized by meio- and macrofauna (Hayes 1974, Koop et al. 1982, Griffiths et al. 1983, McLachlan 1985, Inglis 1989, Dugan et al. 2003). Species distributions are tightly linked to kelp deposition, with highest microbial and faunal abundance, biomass, and diversity occurring in the vicinity of detritus (Griffiths et al. 1983, McLachlan 1985, Dugan et al. 2003). Amphipods, isopods, dipterans, and coleopterans are the predominant macrofaunal consumers of kelp detritus (Griffiths & Stenton-Dozey 1981, Lavoie 1985, McLachlan 1985, Griffiths et al. 1983, Dugan et al. 2003). Their grazing activity releases particulates, leachates, and fecal pellets (Figure 6.4), which stimulates the growth of bacteria and infaunal invertebrates, such as bivalves, nematodes, and oligochaetes (Newell et al. 1982, Griffiths et al. 1983, McLachlan 1985). Meiofauna in sediments directly absorb DOM and consume bacteria associated with kelp leachate and fecal pellets (Griffiths et al. 1983). Invertebrates can consume up to 75% of the biomass of detrital kelp in some beach systems (Griffiths & Stenton-Dozey 1981, Griffiths et al. 1983, Lastra et al. 2008), or as little as 5–9% in others (Koop et al. 1982, Inglis 1989), indicating large variability in the importance of these consumers in detrital processing. Macrofauna also can slow the process of degradation in some systems by preferentially consuming highly degraded material, which retards microbial colonization and breakdown (Bedford & Moore 1984). The extent of microbial and meio- and macrofaunal colonization and processing of detritus are determined by the residence time of detrital deposits, which in turn is regulated by physical factors, such as beach morphology, weather, and tides, and characteristics of the detrital material (e.g. buoyancy) (Orr et al. 2005). Long-term deposition of kelp detritus may have detrimental effects on species distribution and abundance on beaches by creating areas of anoxia, low pH, or high hydrogen sulfide concentration (McLachlan 1985, Colombini & Chelazzi 2003), or by providing a physical barrier to burrowing (Soares et al. 1996).

Kelp deposition on beaches and the associated accumulation of meio- and macrofauna attract predators such as birds, carnivorous ispopods and coleopterans, crustaceans, and arachnids (Griffiths et al. 1983, Bradley & Bradley 1993, Anderson & Polis 1998, Dugan et al. 2003, Mellbrand et al. 2011). Consumption of kelp-associated fauna can account for a significant portion of the diets of these predators (Griffiths et al. 1983, Mellbrand et al. 2011), which then act as vectors for the landward transport of marine-derived material (Anderson & Polis 1998, Mellbrand et al. 2011). In particular, islands with low terrestrial relative to marine productivity are heavily influenced by the input of marine detritus (Polis & Hurd 1996, Anderson & Polis 1998).

6.6.1.2 Rocky Intertidal Habitats

A strong linkage also can occur between subtidal kelp beds or forests and adjacent rocky intertidal communities through the transfer of detritus. While detrital deposition tends to be low in rocky intertidal areas with high wave exposure, deposition on semi-exposed and sheltered rocky shores can be substantial (Rodriguez 2003, Bustamante & Branch 1996, Bustamante et al. 1995). For example, Bustamante et al. (1995) showed that, on average, 960 g m^{-2} d^{-1} (wet mass) was deposited in a sheltered rocky bay in South Africa, exceeding local estimates of kelp productivity.

Invertebrate grazers on rocky shores may depend more on imported kelp detritus than intertidal micro- and macroalgae (Bustamante et al. 1995, Rodriguez 2003). On the central Chilean coast, sea urchins emerge from cryptic habitats in response to kelp deposition (Rodriguez & Farina 2001), forming aggregations that rapidly consume detritus (Rodriguez 2003). Sea urchins receiving this subsidy develop larger gonads than those consuming only autochthonous production (Rodriguez 2003). On rocky shores in South Africa, the limpet *Patella grenatina* traps and consumes detrital kelp when submerged at high tide (Bustamante et al. 1995). Kelp is a major component of the diet of limpets, whose spatial distribution is correlated with the biomass of deposited kelp (Bustamante et al. 1995). Experimentally restricting access to detrital kelp reduced survival and biomass of limpets, indicating that this subsidy is a major determinant of distribution and abundance of this intertidal grazer (Bustamante et al. 1995).

Particulate detritus produced during erosion of kelp blades is utilized by intertidal and subtidal benthic filter feeders (Bustamante & Branch 1996, Kaehler et al. 2006). Kelp particulates are the dominant form of particulate organic matter (POM) within kelp beds and forests (Bustamante & Branch 1996) and can occur in concentrations exceeding that of phytoplankton across an offshore range of more than 14 km (Kaehler et al. 2006). In South Africa, kelp constitutes the largest proportion of the diets of intertidal filter-feeding mussels and barnacles, and spatial variation in filter-feeder biomass is related to near-shore concentrations of particulate kelp (Bustamante & Branch 1996). Duggins et al. (1989) linked high rates of secondary production in intertidal mussels and barnacles in Alaska to subsidy by nearby subtidal kelps. More recently, Tallis (2009) demonstrated that kelp constitutes 10-88% of the diets of filter feeders inhabiting intertidal areas near river mouths in Washington, USA, generally exceeding the dietary contribution of intertidal macroalgae and seagrasses.

6.6.2 Offshore and Alongshore Transport and Deposition

6.6.2.1 Rocky Subtidal Habitats

Barren habitats occur in the rocky subtidal zone and are generated through the grazing action of sea urchins, which denude the substratum of erect fleshy macroalgae. Barrens are characterized by low local productivity (Breen & Mann 1976, Chapman 1981, Miller 1985), but receive macroalgal subsidies from adjacent kelp beds and forests (Dayton 1985b, Basch & Tegner 2007, Britton-Simmons et al. 2009, Filbee-Dexter & Scheibling in press). Basch & Tegner (2007) found that up to 250–400 g m^{-2} of *Macrocystis pyrifera* (wet mass) accumulates at 8–18 m depth off California. Similarly, Britton-Simmons et al. (2009) recorded an average of 514 g m^{-2} of detrital kelp (*Laminaria*) (wet mass) at 23 m depth in Washington. When detritus is abundant within kelp forests and adjacent areas, sea urchins do not graze attached kelps but instead form sedentary aggregations or hide within cryptic habitats where they trap detritus as it is transported along-bottom or accumulates (Mattison et al. 1977, Dean et al. 1984, Harrold & Reed 1985, Rogers-Bennett et al. 1995, Basch & Tegner 2007, Vanderklift & Wernberg 2008, Britton-Simmons et al. 2009). When detrital supply becomes limited, sea urchins increase their rate of movement and form grazing fronts that rapidly consume stands of attached kelps (Dayton 1985b, Ebeling et al. 1985, Harrold & Reed 1985). Low detrital supply, therefore, triggers the transition from a highly productive kelp forest to a low-productivity sea urchin barren.

The onshore advance of grazing fronts of sea urchins is generally limited by wave action, either directly or via the whiplash effect of kelps (Velimirov & Griffiths 1979, Dayton 1985b, Scheibling et al. 1999, Konar & Estes 2003, Lauzon-Guay & Scheibling 2007). In Nova Scotia, this wave-mediated upper limit of destructive grazing enables kelp beds to persist in shallow bands along the coast (Brady & Scheibling 2005), while dense populations of sea urchins in adjacent barrens subsist in part on the supply of kelp detritus from the shallows (Kelly et al. in press). Sea urchins supplied with detrital kelp develop larger gonads than those without access to this food resource (Rogers-Bennett et al. 1995, Basch & Tegner 2007, Britton-Simmons et al. 2009). Detrital kelp is less abundant along exposed coastlines relative to more sheltered coastlines or bays (Dayton 1985b, Filbee-Dexter & Scheibling in press). As a result, sea urchins in barrens on exposed coasts are of lower nutritional condition than those feeding directly on kelps in the shallow subtidal zone, whereas sea urchins in deep depositional areas in protected bays are well nourished (Dayton 1985b, Brady & Scheibling 2006, Filbee-Dexter K & Scheibling RE, unpubl data). Detrital subsidy to sea urchins decreases with distance from the kelp bed or forest (Mattison et al. 1977, Rogers-Bennett et al. 1995, Kelly et al. in press), but has been documented for sea urchins on reefs up to 8 km from the kelp source (Vanderklift & Wernberg 2008).

Fecal pellets from urchins and other grazers as well as kelp particulates are transported offshore where they are consumed by filter- and deposit-feeding macroinvertebrates, meiofauna and microbes, enhancing secondary production across a range that can extend > 14 km from the kelp source (Duggins et al. 1989, Kaehler et al. 2006). Along the Atlantic coast of Nova Scotia, Canada, sea urchins form dense grazing fronts that advance onshore consuming kelp at a rate of 454–530 g d^{-1} (dry mass) across a meter-span of front. This translates to an estimated fecal production rate of 74–81 g y^{-1} per linear meter of front, or 20,720 kg d^{-1} across an estimated 280 km of coastline spanned by these grazing fronts in the mid to late 1990s (Sauchyn & Scheibling 2009a). The small (~2 mm diameter) fecal pellets are a highly nutritious food source relative to live kelp, and nitrogen, lipid, and available energy content increase rapidly during degradation (Sauchyn & Scheibling 2009b).

6.6.2.2 Soft-sediment Habitats

Kelp detritus is transported alongshore or offshore via tidal, bottom, or surface currents to unvegetated soft-sediment habitats ranging from the surf zone to the bathyal and abyssal depths (Figure 6.3). Submarine canyons trap submerged detritus as it is transported by alongshore currents, accumulating massive quantities of material and acting as conduits for detrital transport to the deep sea (Josselyn et al. 1983, Vetter 1995, 1996, Vetter & Dayton 1998, Harrold et al. 1998, Okey 2003). Kelp detritus transported over the continental shelf is more likely to be consumed or buried before arrival at the deep sea, compared to that transported via submarine canyons (Vetter & Dayton 1999). However, the abundance of detrital kelp can decrease by 95% between 30 and 900 m depth in submarine canyons in canyons off California (Vetter & Dayton 1999); detrital kelp is sparse (2.5×10^{-2} g C m^{-2}) at depths of >1 km (Smith 1983). Long-distance transport of kelp detritus offshore is more likely to occur via surface dispersal of floating rafts, which ultimately lose buoyancy and sink to the deep sea (Smith 1983, Bernardino et al. 2010). Detrital accumulations (mats) in shallow habitats and submarine canyons are expansive during periods of calm wave action in spring and summer, while wave surge associated with fall and winter storms causes detrital flushing or mat compaction in deeper regions (Vetter 1995, Vetter 1998, Okey 2003).

Kelp detritus is a primary source of food in subtidal soft-sediment habitats, as it is for sandy beaches, attracting diverse assemblages of detritivores, predators, and microbes, whose distribution and secondary production are largely determined by the availability of detritus (Lenanton et al. 1982, Bedford & Moore 1984, Kim 1992, Vetter 1995, 1996, Okey 1997, Harrold et al. 1998, Vetter & Dayton 1998, 1999, Hyndes & Lavery 2005, Bernardino et al. 2010, Krumhansl & Scheibling in press). Secondary production rates in detrital mat communities in submarine canyons exceed that of most other natural systems (Vetter 1995). Juvenile fish use mats of kelp detritus as nursery habitat, feeding on associated amphipods, leptostraceans, and copepods (Lenanton et al. 1982, Vetter 1998, Hyndes & Lavery 2005). Vetter (1998) experimentally demonstrated that predation rate on these crustaceans decreases with mat thickness, indicating that detrital mats also provide structural protection. During calm conditions, thick bacterial mats colonize the surface of detrital deposits, causing crustaceans to move into open patches where they are more susceptible to predators (Vetter 1998). The bacterial mats are unable to form during periods of frequent wave disturbance (Vetter 1998).

Community dynamics within mats of detrital kelp and underlying sediments are largely dependent on the size and residence time of deposits, which in turn are determined by physical processes and the rate of consumption by large herbivores, such as sea urchins (Scheibling & Raymond 1990, Kim 1992, Okey 1997, Norkko et al. 2000, Okey 2003). In small deposits with short residence times, or in ephemeral deposits in wave- or current-swept locations, faunal abundance and diversity are locally enhanced relative to the surrounding sediments (Lenanton et al. 1982, Vetter 1995, 1996, Harrold et al. 1998, Vetter & Dayton 1998, 1999, Hyndes & Lavery 2005). In larger and more persistent deposits, hypoxic conditions can develop in the bottom layers of detrital mats. In some cases this leads to widespread anoxia and decreased microbial and faunal abundances within the deposit and underlying sediments (Tzetlin et al. 1997, Mokievsky et al. 2005, Scheibling & Raymond 1990). Local hypoxia also can occur in sediments beneath small deposits with relatively short residence times (Thrush 1986, Vetter 1996, Vetter & Dayton 1998, Okey 2003, Bernardino et al. 2010). Opportunistic species that tolerate low oxygen and high sulfide conditions, such as capitellid and dorvellid worms, can occur in high abundance beneath deposits (Levin & Smith 1984, Thrush 1986, Vetter 1996, Okey 2003, Bernardino et al. 2010). More diverse faunal assemblages may accumulate in the vicinity of detritus, where the adverse effects of organic enrichment are less severe (Thrush 1986). In large, persistent deposits, a greater diversity of fauna can occur on the surface and edges of mats, where detrital material is freshly deposited and turns over more rapidly than material in lower layers (Tzetlin et al. 1997).

Kelp detritus also is deposited in intertidal surfgrass and subtidal seagrass beds (Hori 2006, Wernberg et al. 2006). Wernberg et al. (2006) documented large deposits of detrital kelp within seagrass beds hundreds of meters from a kelp source in southwestern

Australia. These deposits attracted assemblages of herbivorous fish, which in some locations consumed most of the detritus within days (Wernberg et al. 2006). When given a choice, herbivores and detritivores that inhabit seagrass beds preferentially consume kelp and other macroalgae over seagrasses (Smit et al. 2006, Doropoulos et al. 2009). Stable isotope analysis has revealed that seagrass is a less important dietary source than imported and autochthonous macroalgae, periphyton, and epiphytic algae in seagrass food webs (Stephenson et al. 1986, Smit et al. 2006). Doropoulos et al. (2009) suggest that the importance of macroalgal subsidies to seagrass beds varies seasonally in response to changing levels of production by autochthonous macroalgae and periphyton.

6.6.3 Long Distance and Sea-Surface Transport

Kelps and other macroalgal species with pneuomatocysts are buoyant after dislodgement from the substrate, and can accumulate in rafts that drift with surface currents and winds (Helmuth et al. 1994, Hobday 2000a, Hinojosa et al. 2010). The estimated wet biomass of floating rafts of giant kelp (*Macrocystis pyrifera*) in California and Chile can range from 100 to 1500 kg km^{-2} (Hobday 2000a, Hinojosa et al. 2010). In South Africa, rafts of *M. pyrifera* can be up to 6 m in diameter and 1 m deep, and contain as many as 200 individual thalli (Helmuth et al. 1994). Dispersal of rafts is low when prevailing winds are onshore (Harrold & Lisen 1989) or in areas with large freshwater input such as fjords (Hinojosa et al. 2010). Kelp rafts may disperse hundreds of kilometers in areas with strong unidirectional currents (Helmuth et al. 1994, Fraser et al. 2010). The dispersal and spatial distribution of kelp rafts vary seasonally in response to changing wind and current patterns (Harrold & Lisen 1989, Hobday 2000a, Hinojosa et al. 2010).

The dispersal of a kelp raft is also dependent on environmental and biological factors that affect buoyancy (Rothausler et al. 2009). Rothausler et al. (2009, 2011a, 2011b) have tested the interactive effects of temperature, UV, and grazing by amphipods on the photosynthesis, growth, and reproduction of floating *Macrocystis pyrifera. M. pyrifera* is able to withstand a wide range of UV conditions by adjusting photosynthetic pigments and photochemical reactions (Rothausler et al. 2011a, 2011b), but photosynthesis, growth, and reproduction are greatly reduced in water temperatures above 20°C, which cause degradation and loss of buoyancy (Rothausler et al. 2009, 2011a). The effect of grazing amphipods on biomass and buoyancy is highest at moderate water temperatures (15–20°C) where grazing rate exceeds kelp growth (Rothausler et al. 2009). At low temperatures (<15°C), kelp growth can compensate for biomass lost to grazers (Rothausler et al. 2009). These results indicate that raft dispersal is greatest in waters below 15°C. Low seawater nitrate levels may also reduce buoyancy (Hobday 2000a).

Kelp rafts accumulate diverse communities of invertebrates while drifting (Edgar 1987, Hobday 2000b, Thiel & Gutow 2005). Some organisms remain attached to kelps following dislodgement from the substrate, while others settle or become attached to rafts as they are encountered during drifting. It has been hypothesized that rafting is an important mechanism of long-distance dispersal for invertebrates (Highsmith 1985, Edgar 1987, Helmuth et al. 1994, Fraser et al. 2010), particularly those species with a short-duration larval phase or those that brood their young to a benthic stage (Highsmith 1985, Helmuth et al. 1994). Evidence for this includes genetic linkages between broadly distributed populations of brooding species (Fraser et al. 2009), and the discovery of individuals brooding young on kelp rafts (Helmuth et al. 1994). Holmquist (1994) proposed that dispersal via rafting is more effective than larval dispersal because of a lower risk of mortality. Kelps remain reproductive while drifting (Rothausler et al. 2009), and propagules of other algal and plant species have been collected from kelp rafts (Edgar 1987), indicating that dispersal via kelp rafts is not limited to invertebrates.

6.7 KELP DETRITAL SUBSIDIES AND METAECOSYSTEM DYNAMICS

It is evident from the large body of literature encompassed by this review that detrital subsidies from kelp communities play a major role in linking adjacent marine and terrestrial ecosystems, with significant consequences for community dynamics and productivity in subsidized areas. There is growing recognition that material flows, including those of nutrients and energy, play a key role in shaping ecological patterns and processes across a range of scales (Gravel et al. 2010a, b, Marleau et al. 2010). This has led to the development of metaecosystem theory, which combines the perspectives of metapopulation and metacommunity theory and landscape ecology (Loreau et al. 2003, Massol et al. 2011).

The theoretical constructs of metapopulation and metacommunity dynamics were developed to explain mechanisms of species persistence on local scales in terms of the interaction of processes occurring across multiple scales (Logue et al. 2011). For both theories, the main mechanism of spatial coupling between populations or communities is the dispersal of organisms. Landscape ecology, by contrast, focuses on documenting patterns on a landscape scale that result from material flows between ecosystems (Loreau et al. 2003). Metaecosystem theory is essentially a conjunction of landscape ecology and metapopulation and metacommunity theory: it considers a set of local ecosystems that are connected by the spatial flows of energy and materials as well as the dispersal of organisms (Loreau et al. 2003, Massol et al. 2011). Metaecosystem theory extends the simpler concept of spatial subsidy by examining properties on multiple scales that emerge from flows between ecosystems, and by focusing more on reciprocal than unidirectional flows (Loreau et al. 2003, Gravel et al. 2010a). What emerges is a robust theoretical framework to examine the relationship between the local persistence and functioning of ecosystems and regional dynamics (Gravel et al. 2010a, b). Kelp beds or forests can be useful models for exploring this relationship because of their strong linkage to adjacent systems through the transfer of detritus.

In a metaecosystem, locally high primary productivity results in high regional productivity as detritus and nutrients flow between habitat patches (Massol et al. 2011). High regional productivity promotes high propagule production, which enhances the regional persistence of species (Massol et al. 2011). Compelling evidence for this exists in landscapes that include kelp beds or forests, which are highly productive on a local scale. For example, large quantities of kelp detritus flow into adjacent sandy beach communities, enhancing local production (Figure 6.4). Detritivorous macrofauna and their predators may move farther onshore, transporting kelp-derived nutrients in the form of feces and carrion, to promote higher rates of terrestrial productivity than would occur in the absence of this flow. Beach fauna and microbes degrade and remineralize nutrients from kelp detritus, and physical processes return inorganic nutrients, detrital particles, and fecal pellets to subtidal habitats for direct use by kelps or for further processing. The transfer of detritus to beaches and subsequent recycling and return of nutrients to the water column represents a reciprocal subsidy between subtidal kelp beds or forests and sandy beaches. In this example, high local productivity in kelp communities is both the cause and consequence of high regional productivity.

To extend this concept, we can consider another situation in which a transition from high to low regional productivity occurs in response to a change in kelp productivity that is mediated by a species interaction operating on a local scale. High detrital kelp abundance enhances sea urchin productivity and reproductive output in rocky barrens offshore of kelp beds or forests, causing recruitment pulses and an increase in the sea urchin population (Figure 6.5). With greater demand for detrital resources, the supply becomes limited, triggering the transition from passive feeding on detrital kelp to active grazing by sea urchin fronts on attached kelps. Fronts proceed gradually until reaching the upper, wave-mediated depth limit of grazing. At this stage, kelp populations have been substantially reduced, resulting in low detrital production. Accordingly, subsidies to adjacent inshore and offshore habitats also are reduced, resulting in low secondary production in recipient communities. This conceptual model describes a sequence of changes in regional productivity during a shift from 1) a high productivity state, in which kelp productivity and detrital subsidy to adjacent areas is high, through 2) a transitional state during which sea urchins destructively graze kelp to expand barrens, and culminating in 3) a low productivity state in which kelp productivity and detrital subsidy are low (Figure 6.5). Sea urchin fecal production is high during active grazing of detrital and attached kelps in the first and second stages (Sauchyn et al. 2011), but greatly reduced as attached kelp biomass and the supply of detrital material decrease. Other factors that reduce kelp biomass and detrital supply, such as encrustation by the invasive bryozoan *Membranipora membranacea*, also can trigger the transition from a high to a low regional productivity state (Scheibling et al. 1999, Krumhansl & Scheibling 2011a). This alternative stable-state system has traditionally been viewed from the perspective of local productivity. From a metaecosystem perspective, however, these state-shifts also can drive transitions in regional productivity.

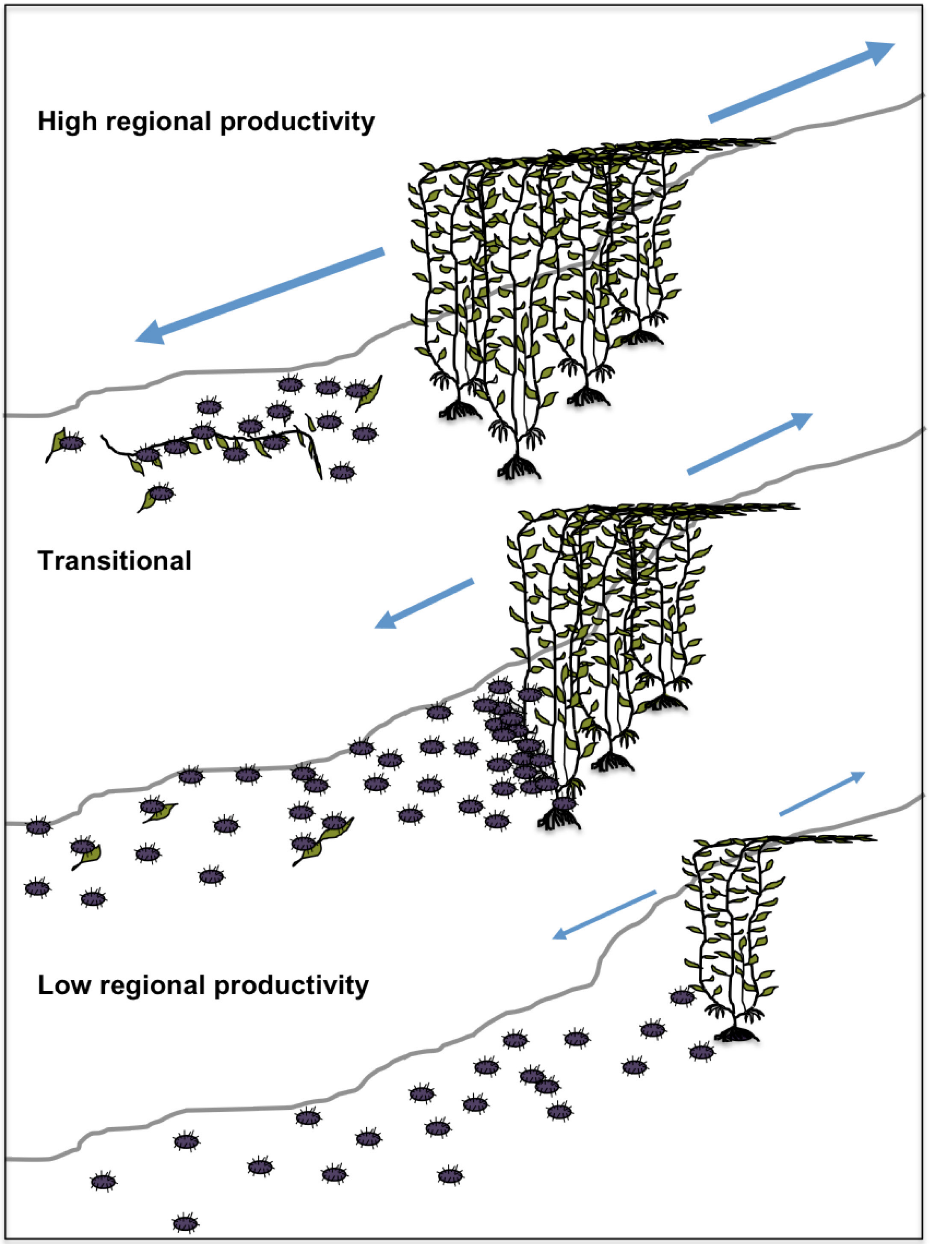


Figure 6.5 High regional productivity, transitional, and low regional productivity states of adjacent barrens and kelp forest communities associated with the transition from passive trapping of kelp detritus by sea urchins to active grazing on attached kelps. Arrow thickness indicates the magnitude of detrital flows in the inshore and offshore directions.

Gravel et al. (2010a) suggest that spatial flows of a limiting nutrient can alter landscape level source-sink dynamics. Specifically, sources may be converted to sinks if spatial flows decrease nutrient concentrations in the source patch. Under most conditions, kelp beds or forests are considered sources and sandy beaches sinks. Large-scale kelp mortality can occur during severe wave events and periods of high seawater temperature, effectively decreasing nutrient concentrations (kelp biomass) in the source patch. Following the large initial pulse of detritus generated during the mortality event, detrital flows from the source patch are reduced while kelp biomass and production are low, and the kelp bed or forest no longer acts as a source. Inorganic nutrients accumulated in beach sands from the immediate and long-term processing of kelp detritus are returned to the subtidal zone and promote the re-growth of kelps. At this stage, the beach is the source because the magnitude of nutrient transfer from beaches to subtidal kelps exceeds transfer in the opposite direction. Source-sink dynamics in this context also could be mediated by seasonal asymmetries in detrital deposition and nutrient export from beach sands.

6.8 HUMAN IMPACTS ON KELP BIOMASS AND DETRITAL SUBSIDY

Anthropogenic pressures on natural systems have mounted over the past centuries, resulting in profound changes in the marine environment (Worm et al. 2005, Lotze et al. 2006, Jackson 2008). Kelp ecosystems are no exception to this trend, and may be particularly sensitive given their proximity to human populations. A suite of anthropogenic factors cause declines in kelp biomass and population size, which can have regional as well as local effects on ecosystem structure and function through a reduction in detrital production (Krumhansl & Scheibling 2011a). Primary emphasis on anthropogenic impacts to kelp beds or forests has been on the indirect effects of fishing high-level predators, which releases sea urchin populations from top-down controls (Steneck et al. 2002). The role of climate change in the decline of kelp populations also has been noted due to the sensitivity of kelps to fluctuations in environmental variables, such as water temperature and salinity (Steneck et al. 2002, Martinez et al. 2003, Springer et al. 2010). The disruption of upwelling cycles during El Nino years may cause local warming, which leads to large-scale canopy loss (Gunnill 1985, Steneck et al. 2002, Martinez et al. 2003, Vasquez et al. 2006, Foster & Schiel 2010, Springer et al. 2010).

Storms that cause large wave events also reduce kelp biomass (Gerard 1976, Luning 1979, Gunnill 1985, Seymore et al. 1989, Reed et al. 2008), and are likely to have greater long-term effects as the incidence of severe storm events increases (Easterling et al. 2000, Byrnes et al. 2011). Declines in kelp biomass also have occurred in response to coastal pollution (Steneck et al. 2002, Foster & Schiel 2010) and development and extraction activities that disrupt subtidal habitat (Pulfrich et al. 2003) and cause run-off of toxic materials, warm water, and sediments (Medina et al. 2005, Springer et al. 2010). The introduction and spread of non-native algal species can replace kelps and alter the nutritional characteristics of detritus entering adjacent communities (Bishop et al. 2010, Krumhansl & Scheibling in press).

Direct removal of kelp-canopy through harvesting also can have severe repercussions for kelp biomass and detrital production. Kelp is primarily used for human consumption (Peteiro & Freire 2011, Rothman et al. 2006), alginic acid extraction (Vasquez 2008, Vea & Ask 2011), and as feed for cultured abalone (Troell et al. 2006, Macchiavello et al. 2010). Canopy harvesting has increased dramatically in recent decades (Rothman et al. 2006, Vasquez 2008, Thompson et al. 2010, Vea & Ask 2011). Kelp is currently harvested in many countries worldwide (including the USA, Canada, Mexico, South Africa, Chile, Australia, New Zealand, Japan, China, Taiwan, Ireland, Norway, the UK, and Iceland) and markets continue to expand (Adams et al. 2009, 2011). Historically, kelp harvesting involved collection of beach-cast material; however, since the 1960s this has been replaced by direct harvesting, particularly of canopy kelps, in response to increasing demand (Vasquez 2008, Vea & Ask 2011). With growing concern that wild populations of kelp cannot sustain harvesting at the current rate, the harvest potential of currently unexploited areas, such as the Arctic, is being investigated (Sharp et al. 2008) and suspended culture of kelps has been developed in some bays and offshore areas (Troell et al. 2006, Macchiavello et al. 2010, Peteiro & Freire 2011, Radiarta et al. 2011). Kelp mariculture may relieve some of the pressure on natural populations, but little is known about its ecological impact. Cultured kelp is a source of detritus (Yoshikawa et al. 2001), but at high density suspended kelps can reduce current speeds (Shi et al. 2011) and may cause organic enrichment of local sediments and anoxia.

Research on the effects of kelp canopy removal has largely developed from a fisheries perspective, with the goal of designing harvesting strategies that maximize landings and minimize impacts to kelp growth and reproduction (Christie et al. 1998, Vasquez 2008, Lorentzen et al. 2010, Thompson et al. 2010). Current harvesting strategies involve 1) trimming fronds in a manner that allows for regrowth and/or reproduction, 2) targeted harvesting of larger individuals in a population, and 3) removal of only a certain portion of total kelp biomass (Springer et al. 2010, Vea & Ask 2011). A few studies have examined the impacts of canopy removal on organisms inhabiting kelp beds or forests, with emphasis on commercially targeted species (Lorentzen et al. 2010, Thompson et al. 2010), In general, these studies have not detected direct negative effects, but the empirical evidence is limited. The impact of canopy removal on detrital pathways remains unexplored. A decline in shorebird abundance in California from 1969 to 1973 was associated with a reduction in subtidal kelp cover over this period due to a decrease in wrack-associated prey items (Bradley & Bradley 1993). Beach grooming and the collection of beach-cast kelp have large negative effects on species richness, abundance, and biomass of macrofauna and shorebirds (Kirkman & Kendrick 1997, Dugan et al. 2003), but these activities remain completely unregulated in most areas.

6.9 CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Although most of the primary production of kelp beds and forests flows through detrital pathways, detrital production has been quantified for relatively few kelp populations. These measurements are sparsely distributed throughout the temperate range of kelps and are highly variable within and among kelp species, underscoring the need for more location and species-specific measurements. There is only one estimate for an Arctic kelp population, and detrital production rates are missing entirely for many kelp genera (e.g. *Nereocystis*, *Agarum*, *Alaria*, *Costaria*, *Pterogophora*). Variation in detrital production rates and the relative importance of erosion vs. dislodgement as production processes may be related to characteristics of particular kelp species (e.g. morphotype) or populations (e.g. density), or to the physical environment (e.g. wave exposure, temperature regime, latitude). Understanding the mechanisms that regulate detrital production on large spatial scales would provide insight into the potential response of communities to environmental change, which may be greatest at the lower and higher latitudinal limits of kelps. A more complete quantification of detrital production throughout the geographic range of kelps is required to address these hypotheses and to improve our ability to model energy flow through coastal systems.

Future studies also should attempt to standardize measures of detrital production and variance, and to concurrently measure both erosion and dislodgment. A number of studies have presented erosion measurements in units that are relevant only on a per individual basis (e.g. as cm d^{-1}, Dean & Hurd 2007, Miller et al. 2011; or relative erosion, Brown et al. 1997). Although these measurements can be used to examine spatial and temporal dynamics of erosion, measurements at the population level (e.g. as g m^{-2} d^{-1} or g C m^{-2} d^{-1}, Krumhansl & Scheibling 2011a) are more useful in developing energy flow models or for comparisons among geographically distinct populations. Only two studies (Gerard 1976, Newell & Field 1983) have simultaneously measured detrital production by erosion and dislodgement. Measurement of only one or the other of these important mechanisms can significantly underestimate detrital production from kelp beds and forests.

The extent of detrital subsidy by kelps is determined by the magnitude and direction of detrital export. The proportion of detrital production exported or retained has been well quantified for seagrass (Heck et al. 2008), salt marsh (Gallagher et al. 1980, Dame & Stilwell 1984, Bouchard & Lefeuvre 2000) and mangrove communities (Kristensen et al. 2008), likely because these macrophyte assemblages typically occur in semi-enclosed bays or estuaries where exported material can be readily trapped and measured. Kelp communities, on the other hand, generally occur on semi-protected or exposed coasts where trapping and quantifying material flows is considerably more difficult. Export rates in kelp ecosystems can be estimated as the difference between simultaneous measures of detrital production and accumulation within kelp beds or forests. Residence time of kelp fragments or thalli manually deposited within kelp beds or forests can provide insight into environmental factors that govern detrital export rates and seasonal variation. The relative importance of inshore vs. offshore transport can be estimated by relating detrital production rates to arrival rates in habitats along an onshore/offshore gradient. Transport direction and distance also can be measured by tracking labeled detrital fragments and thalli (e.g. with flagging tape) using diver surveys, towed video, or ROVs.

A comprehensive understanding of energy flow in coastal systems requires consideration of all local sources of macrophyte detritus. The relative contribution of kelps and other types of macrophytes to detrital food webs is related to the magnitude of detrital production, export, and deposition in various habitat types, which in turn are related to local hydrodynamics, geomorphology, and substrate characteristics. Transport also is determined by the physical properties of detritus, including size, shape, and buoyancy (Watanabe et al. 2009), which differ among macrophyte types. The composition of detrital deposits affects their turnover rate and patterns of colonization by microbes and meio- and macrofauna (on the surface of detritus and in underlying sediments). Future research should emphasize comparisons of detrital production rates, transport, and depositional dynamics between kelps and other dominant macrophytes. Examining the species composition of macrophytes in detrital deposits across broad scales within regions could indicate the relative importance of different detrital sources to macrofaunal communities in various habitat types. The link between spatial patterns of production and deposition of different macrophyte species may be clearer when these species occupy different physical environments.

Kelp detritus subsidizes consumers in a wide range of marine and terrestrial habitats, acting as a major form of connectivity in coastal systems that enhances species abundance, diversity, productivity, and reproductive output. Most studies examining the consequences of detrital subsidies in receiving communities have been conducted over relatively short time scales. Seasonal dynamics in some detritus-based communities (e.g. in submarine canyons or on sandy beaches) are related to variation in physical factors that determine the size and residence time of detrital deposits. In many habitats the deposition of kelp detritus is a sporadic occurrence. Receiving communities may be adapted to protracted periods of low food abundance punctuated by detrital food pulses that occur over short time scales (Sears et al. 2004). These pulsed depositional events may play an important role in maintaining gamma diversity, especially in the deep sea (Bernardino et al. 2010). Long-term environmental changes and reductions in kelp populations may have different and more pronounced consequences for detritus-based communities than changes resulting from short-term environmental variability.

Many of the species that consume detritus within kelp beds and forests and in adjacent systems (e.g. sea urchins, abalone, sea cucumbers, mussels) are the basis of valuable coastal fisheries. These species also are prey for higher trophic-level consumers (e.g. lobsters, ground fish, sea otters) that have commercial or ecological importance (Dayton et al. 1998, Steneck et al. 2002). Consequently, the provisioning of detrital food webs is a major ecosystem service provided by kelp beds and forests. Loss of kelp biomass threatens this important function through reduction or elimination of detrital production. Kelp populations require more than 6 years to recover from canopy harvesting (Lorentzen et al. 2010), and declines on the order of decades have been documented following overfishing, repeated El Nino events, or freshwater and sewage run-off (Mann 1977, Dayton et al. 1998, Steneck et al. 2002, Foster and Schiel 2010). Dire ecological and economic consequences can be expected as a result of these long-term declines in kelp canopy. Effective management of coastal ecosystems and resources demands a broader consideration of the role of detrital flows from kelp and other marine macrophytes in determining overall productivity on regional scales.

CHAPTER 7
GENERAL CONCLUSIONS

Most of the primary production in kelp communities worldwide enters detrital pathways. Kelp detritus is exported to a wide range of marine and terrestrial habitats, where it serves as an important resource at the base of food webs (Chapter 6). Spatial patterns in the abundance, growth, reproduction and diversity of organisms in communities that receive kelp detritus are largely determined by the magnitude of subsidy. As a result, local rates of kelp productivity and detrital production are linked to community dynamics on broad spatial scales. Although there have been considerable advances in our understanding the fate of kelp detritus, few studies have quantified the flux of this material from kelp beds or forests, or examined factors that influence the rate of detrital production. My thesis contributes to this body of knowledge and elucidates the impact of invasive species on the dynamics of detrital production in a rocky subtidal ecosystem off the Atlantic coast of Nova Scotia.

I have shown that Nova Scotian kelp beds produce detritus continuously through the erosion of blade tissue from the distal end, with annual losses that range from 0.5–1.71 kg dry mass m^{-2} (Chapter 2). The interactive effects of blade encrustation by the invasive bryozoan *Membranipora membranacea,* grazing by the snail *Lacuna vincta,* site exposure to wave action, and water temperature regulate spatial and temporal patterns in erosion. Peaks in erosion rate and the ratio of erosion to productivity occur when blade encrustation by *M. membranacea* or grazing damage in the distal ends of blades are highest. In Chapter 4, I found that prolonged encrustation by *M. membranacea* leads to degradation of the outer cell layers of blade tissues, which concentrates stress when the blade is in tension, leading to breakage at lower force applications than required to break undamaged tissues. Grazing by *L. vincta* that penetrates the full thickness of blade tissues causes similar reductions in blade strength, explaining increased rates of detrital production associated with high levels of bryozoan encrustation and grazing damage.

Spatial variation in erosion rate also was attributed to a positive relationship with wave exposure for *Laminaria digitata* (Chapter 2). Kelps at the site where wave exposure was the highest (Splitnose Point) consistently had the lowest level of grazing damage by *Lacuna vincta*, but variation in erosion rate over time followed the same temporal pattern as the level of grazing damage on blades. Grazing damage may have a greater effect on erosion rate at sites with higher wave exposure, where even small levels of damage can induce breakage (Duggins et al. 2001). This is consistent with the observation that erosion was low at the most wave-protected site (Duncan's Cove Protected) where the level of grazing damage on *L. digitata* was highest. Biomechanical tests indicate that although more energy is required to break undamaged blade tissues of *L. digitata* compared to *Saccharina latissima*, the magnitude of the reduction in tissue toughness due to grazer-induced perforations is greater for *L. digitata* (Chapter 4). This may indicate that *L. digitata* is more prone to grazer-induced increases in erosion than *S. latissima.* In contrast, erosion rate and the level of grazing damage on blades of *S. latissima* increased with water temperature, but this effect was not observed for *L. digitata*. This indicates that *S. latissima* may be more susceptible to tissue degradation at higher water temperatures.

By examining spatial and temporal patterns in grazing damage by *Lacuna vincta* along kelp blades (Chapter 3), I found that only a small percentage of the total blade area is grazed on *Saccharina longiruris* (0.00-1.25%) and *Laminaria digitata* (0.00-1.50%). Grazing is typically concentrated in the middle and distal end of blades where the concentration of polyphenolic compounds is lowest (Johnson & Mann 1986), and tissue toughness is reduced relative to recently produced tissue. Grazing in basal regions of blades is lowest during peak periods of kelp growth in spring, which is coincident with the greatest production of polyphenols at the basal meristem (Abdullah & Fredriksen 2004). Grazing at the distal ends of blades above a threshold value of 0.5 to 1.0% of blade area leads to significant increases in the rate of blade erosion during storms that generate significant wave heights exceeding 3.5 m. Grazing damage above this threshold is commonly observed on kelp blades in summer and fall, and is coincident with the peak occurrence of hurricanes off Nova Scotia. This indicates that *L. vincta* plays a significant role in seasonal losses of kelp canopy. Grazing damage is likely to have a greater negative effect on kelp populations as the incidence of severe storms increases (Bender et al. 2010, Scheibling & Lauzon-Guay 2010).

These results indicate that epifauna on kelp blades can have direct as well as indirect effects on kelp physiology and biomass. Encrustation by *Membranipora membranacea* shades blade tissues (Oswald et al. 1984), directly reducing photosynthesis, nutrient uptake, and tissue pigment (Hurd et al. 1984, Hepburn et al. 2006), which cause cellular degradation and a weakening of blade tissues. This indirectly results in losses of kelp canopy. The direct loss of kelp biomass to grazing by *L. vincta* is minute, but grazing damage also causes blade weakening that leads to major losses during storms. These indirect effects play a significant role in regulating canopy biomass and the rate of detrital production from subtidal kelp beds.

In a field experiment, I found that the nutritional quality and biochemical changes occurring during degradation differ between the invasive green alga *Codium fragile* and the native kelp *Saccharina latissima* (Chapter 5). *C. fragile* has a higher nutritional value (lower C/N ratio) than *S. latissima*, but the concentration of the anti-herbivory compound DMSP is two orders of magnitude higher in *C. fragile* than *S. latissima*. The C/N ratio and concentration of DMSP decreased in both algal species during degradation, becoming similar after 12 to 16 weeks. These results indicate that changes in the macroalgal species composition of detritus through the replacement of kelps by *C. fragile* has altered the quality of detritus produced from subtidal macroalgal beds. Macrofaunal communities consuming degrading algal material responded to these differences in nutritional quality and palatability. Macrofaunal species composition, diversity, and abundance differed between algal species to a greater degree during the initial stages of degradation than in the advanced stages when detrital quality became similar.

Diverse communities of organisms rapidly colonized and consumed detritus placed on the sandy seabed below a kelp bed (Chapter 5), demonstrating that macroalgal detritus subsidizes food webs in adjacent habitats. Little is known about the fate of kelp detritus produced in kelp beds off Nova Scotia, but emerging evidence suggests that detritus is also an important food resource for deep populations of sea urchins (Filbee-Dexter & Scheibling in press, Kelly et al. in press). Deep-living sea urchins migrate shoreward to repopulate shallow habitats following disease-induced mass mortalities (Brady & Scheibling 2006). By provisioning these deep populations of sea urchins, kelp detritus may be important in the long-term dynamics of the alternative-state system in the rocky subtidal zone. Future work in Nova Scotia should focus on examining the spatial extent and temporal variation of kelp subsidy to deep-living sea urchins, as well as documenting the utilization of kelp detritus by a wider range of consumers in other habitats, including sandy beaches and the rocky intertidal zone.

The magnitude of detrital production is positively related to the standing biomass of kelp beds (Chapter 2). This indicates that factors that reduce kelp biomass in the long term may ultimately lead to a decline in detrital production rates. The lowest biomass of all sites was recorded at The Lodge, where encrustation by *Membranipora membranacea*, grazing by *Lacuna vincta*, and erosion rates were consistently high. The low biomass at this site may be the long-term consequence of persistent blade encrustation and high levels of grazing damage. *Codium fragile* was only present at 2 of the 5 sites, which included The Lodge and Cranberry Cove, both of which had very low standing stock biomass. *M. membranacea* does not encrust kelps at Cranberry Cove, but grazing damage is high at this site. This indicates that *M. membranacea*, *L. vincta*, and *C. fragile* may all contribute to long-term declines in kelp biomass, and consequently to declines in the rate of detrital production from subtidal kelp beds.

My findings indicate that the introductions of *Membranipora membranacea* and *Codium fragile* to Nova Scotia have altered the quantity and quality of detritus produced from subtidal kelp beds. Macrofaunal communities in adjacent habitats respond to these changes in detrital resources. This indicates that the effects of these invasive species extend well beyond their ranges via changes in the quantity and quality of detrital exports (Bishop et al. 2010, Taylor et al. 2011). Previous work in Nova Scotia has largely emphasized the local effects of declines in kelp biomass that are a result of destructive grazing by sea urchins, storms, and species invasions. This thesis provides the first evidence that these declines also may affect communities in adjacent habitats that are subsidized by kelp detritus, with broad-scale consequences for secondary productivity.

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APPENDIX 1: LINEAR REGRESSION MODELS

Appendix 1. Linear regression models generated from the relationship between wet weight and dry weight for blade tissue in *Saccharina latissima* and *Laminaria digitata* at each site and during each sampling period.

Sampling Period	**Site**	***S. latissima***	**R^2**	***L. digitata***	**R^2**
July 2008	CC	y = 0.2095x + 0.2561	0.9679	NA	NA
	DE	y = 0.1636x - 0.6254	0.8021	y = 0.2767x - 3.1465	0.9091
	DP	y = 0.1437x + 0.2936	0.9707	NA	NA
	TL	y = 0.2217x + 0.4634	0.9689	y = 0.2650x - 1.8475	0.9046
	SP	y = 0.1434x + 0.205	0.9702	y = 0.1624x + 0.2841	0.8840
September 2008	CC	y = 0.2045x - 0.1033	0.8785	NA	NA
	DE	y = 0.1636x - 0.6254	0.8021	y = 0.1500 + 0.7404	0.8873
	DP	y = 0.1859x + 0.2133	0.8182	y = 0.1714x +0.1406	0.9054
	TL	y = 0.1661x - 0.4027	0.8860	y = 0.2198x - 0.6231	0.9803
	SP	y = 0.1434x + 0.205	0.9702	y = 0.1624x + 0.2841	0.8840
November 2008	TL	y = 0.1802x – 0.9854	0.9193	y = 0.1872x + 0.2187	0.9818
	SP	y = 0.1556x – 0.5932	0.9602	0.1798x + 0.2595	0.9226
February 2009	CC	y= 0.1142x - 0.2741	0.9061	NA	NA
	DP	y = 0.1199x + 0.0317	0.9577	y = 0.1368x - 0.0389	0.9592
	SP	y = 0.1224x - 0.3955	0.9894	y = 0.1236x + 0.6040	0.9194
May 2009	CC	y = 0.1444x - 0.2199	0.9726	NA	NA
	DE	y = 0.1136x + 0.1949	0.9438	y = 0.1264x + 0.0873	0.9653
	DP	y = 0.1274x - 0.323	0.9434	y = 0.1344x - 0.2702	0.9559
	TL	y = 0.1023x + 2.2951	0.8732	y = 0.1312x + 0.3412	0.9937
	SP	y = 0.1391x - 2.1842	0.9351	y = 0.1373x - 0.9716	0.9862
September 2009	CC	y = 0.2045x - 0.1033	0.8785	NA	NA
	DE	y = 0.1456x - 0.4258	0.724	y = 0.1682x + 0.4325	0.9271
	DP	y = 0.1636x - 0.6254	0.8021	y = 0.1714x + 0.1406	0.9054
	TL	y = 0.1646x + 0.1011	0.8320	y = 0.1600x + 0.9668	0.8857
	SP	y = 0.1709x + 0.955	0.8743	y = 0.1435x - 0.3239	0.8500

APPENDIX 2: AIC MODEL RESULTS FOR EROSION RATE

Appendix 2. AIC results for all possible combinations of ≤ 3 factors explaining variation in erosion rate (g d^{-1}) for *Saccharina latissima* and *Laminaria digitata*, including: uncorrected Akaike's Information Criteria (AIC), the number of observations (n), second-order bias corrected AIC (AICc), the difference between the minimum AICc and the AICc for each model (ΔAICc), the log likelihood function, the model probability (w_i), and the R^2 value of each model.

Species	**Model**	**AIC**	**n**	**AICc**	**ΔAICc**	**Log Likelihood**	**w_i**	**R^2**
Saccharina latissima	% M + % Gzd + Temp	-91.31	20	-89.81	0.000	48.65	0.361	0.48
	% M + Temp	-89.12	20	-88.41	1.396	46.56	0.179	0.40
	% M + % Gzd	-88.49	20	-87.79	2.019	46.25	0.131	0.38
	% M	-87.67	20	-87.45	2.353	44.84	0.111	0.33
	% M + Exp + Temp	-87.49	20	-85.99	3.818	46.74	0.053	0.37
	% Gzd + Temp	-86.37	20	-85.67	4.138	45.19	0.046	0.31
	% M + Exp	-86.10	20	-85.39	4.414	45.05	0.040	0.30
	% M + % Gzd + Exp	-86.49	20	-84.99	4.812	46.25	0.033	0.34
	% Gzd + Exp + Temp	-85.25	20	-83.75	6.052	45.63	0.017	0.30
	Temp	-83.52	20	-83.30	6.509	42.76	0.014	0.17
	% Gzd	-82.11	20	-81.89	7.917	42.06	0.007	0.11
	Exp + Temp	-81.52	20	-80.81	8.993	42.76	0.004	0.12
	% Gzd + Exp	-80.70	20	-80.00	9.810	42.35	0.003	0.08
	Exp	-78.72	20	-78.50	11.31	40.36	0.001	-0.06
Laminaria digitata	% Gzd + Exp	-69.09	16	-68.17	0.000	36.54	0.284	0.412
	Exp	-68.32	16	-68.03	0.132	35.16	0.266	0.351
	% M + Exp	-67.17	16	-66.25	1.914	35.59	0.109	0.337
	Exp + Temp	-67.12	16	-66.20	1.964	35.56	0.106	0.335
	% M + % Gzd + Exp	-67.74	16	-65.74	2.426	36.87	0.084	0.388
	% Gzd + Exp + Temp	-67.25	16	-65.25	2.912	36.63	0.066	0.369
	% M + Exp + Temp	-65.61	16	-63.61	4.559	35.80	0.029	0.301
	% M	-63.54	16	-63.25	4.912	32.77	0.024	0.124
	% M + % Gzd	-61.76	16	-60.84	7.330	32.88	0.007	0.069
	% M + Temp	-61.56	16	-60.63	7.531	32.78	0.007	0.058
	% Gzd	-60.90	16	-60.61	7.552	31.45	0.007	-0.033
	Temp	-60.62	16	-60.34	7.826	31.31	0.006	-0.051
	% Gzd + Temp	-59.59	16	-58.67	9.499	31.79	0.002	-0.065
	%M + % Gzd + Temp	-59.86	16	-57.86	10.31	32.93	0.002	-0.085

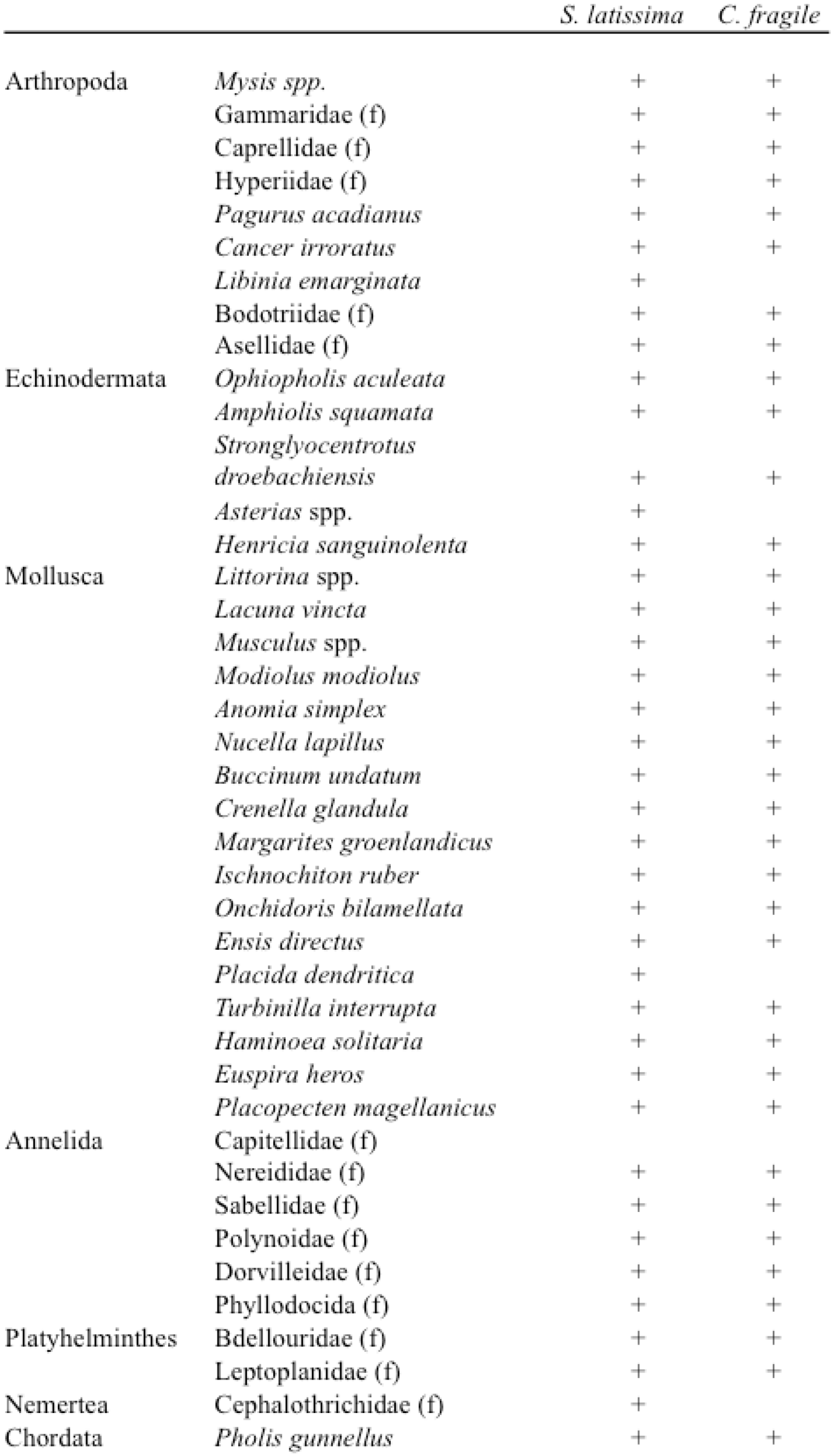
APPENDIX 3: AIC MODEL RESULTS FOR EP RATIO

Appendix 3. AIC results for all possible combinations of ≤ 3 factors explaining variation in the ratio of erosion to productivity for *Saccharina longicruris* and *Laminaria digitata*, including: uncorrected Akaike's Information Criteria (AIC), the number of observations (n), second-order bias corrected AIC (AICc), the difference between the minimum AICc and the AICc for each model (ΔAICc), the log likelihood function, the model probability (w_i), and the R^2 value of each model.

Species	Model	AIC	n	AICc	ΔAICc	Log Likelihood	w_i	R^2
Saccharina latissima	% M	15.12	16	15.34	0.000	-6.561	0.311	0.31
	% M + Exposure	15.78	16	16.48	1.140	-5.889	0.176	0.32
	% M + Exp + Temp	15.05	16	16.55	1.209	-4.527	0.170	0.30
	% M + Temp	16.54	16	17.25	1.902	-6.270	0.120	0.29
	% M + % Gzd	16.87	16	17.57	2.230	-6.434	0.102	0.28
	% M + % Gzd + Exp	17.78	16	19.28	3.933	-5.889	0.043	0.28
	% M + % Gzd + Temp	18.34	16	19.84	4.498	-6.171	0.033	0.26
	Exp	21.62	16	21.84	6.495	-9.809	0.012	0.05
	Temp	22.01	16	22.23	6.890	-10.01	0.010	0.03
	Exp + Temp	21.75	16	22.45	7.107	-8.873	0.009	0.08
	% Gzd + Exp	23.15	16	23.85	8.511	-9.574	0.004	0.02
	% Gzd	23.69	16	23.91	8.566	-10.84	0.004	-0.06
	% Gzd + Exp + Temp	23.15	16	24.65	9.303	-8.574	0.003	0.05
	% Gzd + Temp	23.99	16	24.70	9.355	-10.00	0.003	-0.03
Laminaria digitata	% M+ % Gzd	10.60	16	11.52	0.000	-3.300	0.553	0.72
	% M + % Gzd + Exp	11.89	16	13.89	2.366	-2.945	0.169	0.71
	% M + % Gzd + Temp	12.29	16	14.29	2.768	-3.146	0.138	0.71
	% M	15.67	16	15.95	4.430	-6.834	0.060	0.60
	% M + Temp	15.98	16	16.90	5.374	-5.988	0.038	0.61
	% M + Exp	16.49	16	17.41	5.886	-6.243	0.029	0.60
	% M + Exp + Temp	17.16	16	19.16	7.632	-5.578	0.012	0.60
	Temp	28.79	16	29.08	17.553	-13.40	<0.001	0.09
	% Gzd + Exp	29.44	16	30.36	18.836	-12.72	0.000	0.10
	Exp + Temp	29.94	16	30.86	19.337	-12.97	0.000	0.07
	% Gzd	30.83	16	31.12	19.594	-14.42	0.000	-0.03
	Exp	30.86	16	31.15	19.622	-14.43	0.000	-0.03
	% Gzd + Temp	30.65	16	31.58	20.051	-13.33	0.000	0.03
	% Gzd + Exp + Temp	29.84	16	31.84	20.314	-11.92	0.000	0.12

APPENDIX 4: MACROFAUNA

Appendix 4. Macrofaunal taxa on samples of degrading *Saccharina latissima* and *Codium fragile*: + indicates taxon present; (f) indicates family.



		S. latissima	*C. fragile*
Arthropoda	*Mysis spp.*	+	+
	Gammaridae (f)	+	+
	Caprellidae (f)	+	+
	Hyperiidae (f)	+	+
	Pagurus acadianus	+	+
	Cancer irroratus	+	+
	Libinia emarginata	+	
	Bodotriidae (f)	+	+
	Asellidae (f)	+	+
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	+	+
	Margarites groenlandicus	+	+
	Ischnochiton ruber	+	+
	Onchidoris bilamellata	+	+
	Ensis directus	+	+
	Placida dendritica	+	
	Turbinilla interrupta	+	+
	Haminoea solitaria	+	+
	Euspira heros	+	+
	Placopecten magellanicus	+	+
Annelida	Capitellidae (f)		
	Nereididae (f)	+	+
	Sabellidae (f)	+	+
	Polynoidae (f)	+	+
	Dorvilleidae (f)	+	+
	Phyllodocida (f)	+	+
Platyhelminthes	Bdellouridae (f)	+	+
	Leptoplanidae (f)	+	+
Nemertea	Cephalothrichidae (f)	+	
Chordata	*Pholis gunnellus*	+	+

APPENDIX 5: SIMPER RESULTS

Appendix 5. Macrofaunal taxa on samples of degrading *Saccharina latissima* (S) and *Codium fragile* (C): + indicates taxon present; (f) indicates family.

Comparison **Taxa**	**Dissimilarity**			**Dissimilarity**	
	Avg	Cum. %		Avg	Cum. %
C4 vs. S4		**53.8**	**C4 vs C16**		**53.8**
Capitellidae	11.3	20.7	*Ensis directus*	5.0	9.4
Gammaridae	5.9	31.7	Gammaridae	4.8	18.3
Polynoidae	3.2	37.6	Nerididae	3.5	24.8
Phyllodocida	3.0	43.2	*Crenella glandula*	3.4	31.1
C8 vs. S8		**63.8**	*Lacuna vincta*	3.0	36.6
Capitellidae	25.1	39.3	*Amphiolis squamata*	2.7	41.6
Polynoidae	4.1	45.8	**C8 vs. C12**		**49.3**
Mysis spp.	4.1	52.2	*Mysis spp.*	5.0	10.2
C12 vs. S12		**39.8**	*Ensis directus*	3.6	17.6
Capitellidae	6.4	16.1	Nerididae	3.6	25.0
Nerididae	3.1	23.9	*Amphiolis squamata*	3.5	32.1
Strongylocentrotus droebachiensis	2.6	30.3	Polynoidae	3.3	38.9
C16 vs. S16		**42.4**	*Strongylocentrotus droebachiensis*	3.1	45.1
Ensis directus	3.4	8.0	Asellidae	2.8	50.7
Lacuna vincta	2.9	14.9	**C8 vs. C16**		**54.9**
Crenella glandula	2.7	21.2	*Ensis directus*	5.8	10.6
C4 vs. C8		**52.9**	*Mysis spp.*	4.3	18.4
Gammaridae	5.9	11.1	*Crenella glandula*	4.2	26.0
Nerididae	3.6	18.0	*Modiolus modiolus*	4.2	33.6
Mysis spp.	3.5	24.5	*Lacuna vincta*	3.5	40.0
Amphiolis squamata	3.4	30.9	*Anomia simplex*	2.7	44.9
Polynoidae	3.3	37.1	Polynoidae	2.6	49.6
Lacuna vincta	3.0	42.7	Nerididae	2.5	54.1
C4 vs. C12		**52.3**	**C12 vs C16**		**39.0**
Gammaridae	5.4	10.4	*Lacuna vincta*	3.0	7.6
Nerididae	4.4	18.7	*Modiolus modiolus*	2.6	14.3
Amphiolis squamata	4.0	26.3	*Strongylocentrotus droebachiensis*	2.5	20.8
Ensis directus	3.1	32.3	*Anomia simplex*	2.5	27.1
Strongylocentrotus droebachiensis	2.7	37.4			

Comparison	**Taxa**	**Dissimilarity**	
		Avg.	Cum %
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
Nerididae		2.5	27.6
Buccinum undatum		2.5	32.5
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
Nerididae		2.7	24.3

APPENDIX 6: PUBLICATIONS

Krumhansl KA, Lee MJ, Scheibling RE (2011) Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. J Exp Mar Biol Ecol 407: 12-18

Krumhansl KA, Scheibling RE (2011a) Detrital production in Nova Scotian kelp beds: patterns and processes. Mar Ecol Prog Ser 421:67-82

Krumhansl KA, Scheibling RE (2011b) Spatal and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. Aquat Biol 13:163-173

Krumhansl KA, Scheibling RE (in press) Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* spp. *fragile*

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