PROCESSES REINFORCING REGIME SHIFT TO TURF-FORMING ALGAE IN A KELP BED ECOSYSTEM

by

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Dedicated to my always-changing family who made me the person I am today, and who will continue to grow with me as I move forward.

You push the damper in, you pull the damper out
	On the road again
The smoke goes up the chimney just the same
	Just can't wait to get on the road again
Glory, glory Hallelujah
	The life I love is making music with my friends
The smoke goes up the chimney just the same
	And I can't wait to get on the road again

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ABSTRACT

Canopy-forming brown algae (kelps and fucoids) that provide habitat structure on temperate rocky reefs increasingly are replaced by assemblages of low-lying and pervasive turf algae, driving concerns that these shifts represent a stable degraded reef state. In this thesis, I elucidate the reinforcing processes and feedbacks that inhibit recovery of subtidal kelp beds following large-scale losses, and stabilize regime shifts to turf algae in Nova Scotia. Field observations and a kelp-thinning experiment showed that density and grazing intensity of the snail *Lacuna vincta* on the dominant kelp species *Saccharina latissima* increased non-linearly with decreasing kelp biomass. This enhances direct and indirect kelp tissue loss creating a positive feedback between disturbances that defoliate kelp (hurricanes, outbreaks of the invasive epiphytic bryozoan *Membranipora membranacea*) and grazing. An active feeding preference of *L. vincta* for sporogenous over vegetative tissue, correlated with the distribution of anti-grazing phlorotannins, resulted in intense grazing on sori of *S. latissima* during seasonal spore production that reduced kelp fecundity. Estimates of potential reproductive output (spores m^{-2}) at 5 sites suggested low density of reproductive adults in degraded kelp populations imposes propagule supply constraints that are exacerbated by grazing losses. Limited kelp recruitment occurred over 5 years of observations at 2 sites that were characterized by pervasive turf algae following canopy defoliation. High tissue loss and mortality of juvenile sporophytes were related to effects of grazing by *L. vincta*, encrustation by *M. membranacea*, and high temperatures. Kelp cover and density remained low after 5 years at both sites and turf-forming, opportunistic and invasive algae dominated reefs. A global meta-analysis of interactions between turf algae and other foundation species indicated that canopies of macroalgae or established corals generally suppress the abundance of turf algae on reefs, but that turf algae inhibit establishment of canopy algae recruits and expansion of coral colonies. Competition from turf algae likely maintains regime shifts on temperate and tropical reefs by inhibiting recovery of foundation species following disturbances that enable turf algae to establish. Stabilizing feedbacks that maintain shifts to turf algal assemblages bear consequences for communities dependent on the foundation species they replace.

LIST OF ABBREVIATIONS AND SYMBOLS USED

mL	Millilitre
L	Litre
°C	Degrees Celsius
rpm	Revolutions per minute
g	Gravity of Earth
mg	Milligram
g	Gram
nm	Nanometre
μm	Micrometre
mm	Millimetre
cm	Centimetre
m	Metre
km	Kilometre
min	Minute
h	Hour
d	Day
wk	Week
mo	Month
yr	Year
Jan	January
Feb	February
Mar	March
Apr	April
Jun	June
Jul	July
Aug	August
Sep	September
Oct	October
Nov	November
Dec	December
SWH	Significant Wave Height
%	Percent
log	Logarithm
ANOVA	Analysis of Variance
n	Sample size
R^2	Coefficient of determination
α	Significance level
SD	Standard deviation
SE	Standard error
p	p-value
HSD	Honest significant difference
t	t test statistic
F	F test statistic

df	Degrees of freedom
MS	Mean square
CI	Confidence interval
β	Regression coefficient
SS	Sum of squares
RSS	Residual sum of squares
LR	Likelihood ratio
HR	Hazard ratio
g	Hedges' standardized mean difference
$\overline{Y}_{competitor}$	Mean response in treatment with competitor present
$\overline{Y}_{no\,competitor}$	Mean response in treatment with competitor absent
S_{Pooled}	Pooled standard deviation
J	Small sample size correction for Hedges' g
Q_M	SS of subgroup means about grand mean in meta-analysis
r	Pearson product moment correlation coefficient
k	Number of studies
τ	Kendall's tau rank correlation coefficient
DW	Dry weight
na	Not available
nd	No data
NM	Not measured
no	Number
ind	Individual
sp	Species (singular)
spp	Species (plural)
ssp	Subspecies
LD	*Laminaria digitata*
SL	*Saccharina latissima*
Sp	Sporangia
P	Paraphyses
Me	Meristoderm
C	Cortex
Md	Medulla
p	Grazing perforation
s	sorus tissue
v	vegetative tissue
e	Superficial grazing excavation
B_k	Dry kelp biomass
D_s	Snail density
G	Grazing intensity on kelp (% blade area grazed)
G_i	Grazing index on kelp blade region i
P_i	Proportion of kelp blade region i grazed by snails
T_i	Total area of kelp blade region i
$\overline{P}$	Average of P_i for all regions within a kelp blade
F_{-g}	Kelp fecundity discounting grazing
F_g	Loss of kelp fecundity due to grazing

A_{t}	Total sorus area
A_{g}	Sorus area grazed
D_{s}	Sporangial density
D_{r}	Density of reproductive kelp
D_{tot}	Total kelp density
$R_{\mathrm{-g}}$	Kelp potential reproductive output discounting grazing
R_{g}	Kelp potential reproductive output lost to grazing
$R_{\mathrm{+g}}$	Kelp potential reproductive output accounting for grazing
H_f	Final position of hole-punch
G	Kelp growth rate
t	Time
T	Rate of gross tissue loss from kelp
L_i	Kelp initial blade length
L_f	Kelp final blade length
M	Percent blade area encrusted by *Membranipora membranacea*
B	Kelp blade surface area
D	Depth stratum
K	Kelp
Cf	*Codium fragile* ssp. *tomentosoides*
Dv	*Desmarestia viridis*
T	Turf algae
Br	Annual and perennial brown algae
EAC	Epilithic Algal Community
EAM	Epilithic Algal Matrix
CanAlg	Canopy algae
EstabCor	Established corals
ArtCor	Articulated coralline turf algae
Cort/Br	Corticated/coarsely branching turf algae
Filam	Filamentous turf algae
Micro	Microscopic canopy algae recruits
Macro	Macroscopic canopy algae recruits
RecrCor	Coral recruits
Lat	Latitude
Long	Longitude
N	North
S	South
E	East
W	West
BH	Birchy Head
CC	Cranberry Cove
DE	Duncan’s Cove Exposed
DP	Duncan’s Cove Protected
GBR	Great Barrier Reef
NS	Nova Scotia
PH	Paddy’s Head
SC	Sandy Cove

SMB	St. Margarets Bay
SP	Splitnose Point
TL	The Lodge
USA	United States of America
JMO	John Michael O'Brien
RES	Robert Eric Scheibling
SCUBA	Self-Contained Underwater Breathing Apparatus
PVC	Polyvinyl chloride
C/N	Carbon to Nitrogen ratio
CO_2	Carbon dioxide
N	Normality of a solution
Na_2CO_3	Sodium carbonate
Chl *a*	Chlorophyll *a*
DOC	Dissolved organic carbon
NSERC	Natural Sciences and Engineering Research Council of Canada
NIH	National Institutes of Health
et al.	Et alia
e.g.	Exempli gratia
i.e.	Id est

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CHAPTER 1

INTRODUCTION

Marine ecosystems globally are increasingly threatened by a combination of human impacts (Halpern et al. 2008a) that are changing the context in which key ecological interactions and processes operate. Predicting the cumulative effect of multiple stressors on individual organisms, populations, communities, and ecosystems remains difficult owing to the range of spatial scales over which stressors are integrated (Russell & Connell 2012), complex non-additive (antagonistic or synergistic) interactions among stressors (Crain et al. 2008, Darling & Côté 2008), interactions with internal ecosystem dynamics (Conversi et al. 2015, Lyons et al. 2015), and threshold or non-linear responses (Griffen et al. 2016). Of particular concern is when one or more drivers push an ecosystem beyond a critical threshold to cause a regime (or phase) shift: a sudden and large change in ecosystem structure and function that is persistent over ecological time scales (Möllman et al. 2015). Regime shifts pose a major management challenge as they are associated with loss of ecosystem services (Rocha et al. 2015) and because they are difficult to anticipate and reverse. Once the transition occurs, a new set of mutually reinforcing feedbacks often stabilizes the new ecosystem state (Biggs et al. 2012).

Shallow rocky reefs support productive kelp beds or forests along one quarter of the world's coastlines (Filbee-Dexter & Scheibling 2014), but are among the marine ecosystems experiencing the highest cumulative human impacts (Halpern et al. 2008a). Much of the prolific primary productivity of kelps in temperate and polar regions is exported to detrital foodwebs fuelling secondary production in less productive adjacent communities (Krumhansl & Scheibling 2012). However, kelp abundance has declined over the last 50 years in 38% of ecoregions with available data (Krumhansl et al. 2016), and increasingly loss of kelp and other canopy-forming brown macroalgae (e.g. fucoids) is associated with the proliferation of pervasive turf-forming algal assemblages (Connell et al. 2014, Filbee-Dexter & Wernberg 2018). Turf algae form monospecific or mixed assemblages of low-lying, densely packed algal branches and filaments in shallow reef systems worldwide (Connell et al. 2014), but are generally suppressed beneath macroalgal canopies on temperate reefs (Johnson & Mann 1988, Irving & Connell 2006b), and by intense grazing on healthy coral reefs (Marshell & Mumby 2015). The proliferation of turf algae on degraded reefs suggests that climate change and other human impacts are tipping the balance between key seaweed competitors to induce large changes in ecosystem structure (Connell et al. 2011, Harley et al. 2012), although whether these changes are mediated predominantly by reversals of competitive hierarchies remains equivocal.

There is concern that shifts to turf-dominated assemblages may represent a stable ecosystem state on temperate reefs (Gorman & Connell 2009, Moy & Christie 2012, Filbee-Dexter & Wernberg 2018), although research to date has largely focused on documenting the extent of shifts and identifying the main drivers. Shifts can occur over large spatial scales (10s – 100s km) and generally are associated with gradual or anomalous ocean warming that directly impacts kelp (Moy & Christie 2012, Wernberg et al. 2016) or large inputs of nutrients and sediment in urbanized areas that promote turf expansion (Eriksson et al. 2002, Gorgula & Connell 2004). There has been considerable effort to identify complex interactions between global (warming, acidification) and local (nutrient enrichment) stressors and other factors (herbivory) that promote or mediate turf expansion using factorial mesocosm experiments (Russell et al. 2009, Falkenberg et al. 2015, Ghedini et al. 2015). Expansive cover of turf-forming algae can limit recruitment of kelps and fucoids (Gorman & Connell 2009, Bellgrove et al. 2010), but less attention has been given to identifying other reinforcing processes that will determine the stability of this ecosystem state. Emerging evidence suggests that density-dependent processes and changes in the nature and types of ecological interactions with changing environmental conditions and canopy loss may create important feedbacks in this context (Bennett & Wernberg 2014, Bennett et al. 2015b).

Changing environmental conditions and human impacts are altering the context of ecological interactions in subtidal kelp beds on the Atlantic coast of Nova Scotia with implications for ecosystem structure and function. Historically, regime shifts on shallow reefs occurred when aggregations of green sea urchins *Strongylocentrotus droebachiensis* destructively grazed productive beds of the dominant kelp species *Saccharina latissima* and *Laminaria digitata* to form barrens with low productivity and structure (Breen & Mann 1976, Scheibling et al. 1999). Mass mortalities of sea urchins from recurrent introductions by large storms of an amoebic disease with temperature-dependent dynamics allowed periods of kelp recovery (Scheibling 1984, Feehan et al. 2012). Increasing frequency of disease-mediated mass mortality in response to 3 decades of ocean warming and increasing storm intensity along this coast now effectively precludes destructive grazing by sea urchins and favours kelp persistence (Scheibling et al. 2013).

However, ocean warming in this region also has been associated with a decline in kelp abundance on a coastal scale (Filbee-Dexter et al. 2016). The invasive epiphytic bryozoan *Membranipora membranacea* has caused recurrent canopy defoliation since its introduction to this region in the early 1990's (Scheibling et al. 1999, Scheibling & Gagnon 2009). Temperature-dependent settlement and growth of the bryozoan on kelp blades (Saunders & Metaxas 2008, 2009) cause extensive loss of canopy cover during warmer years (Scheibling & Gagnon 2009) due to weakening of the blade tissue after prolonged encrustation (Krumhansl et al. 2011). Loss of kelp has resulted in a shift in ecosystem structure to rocky reefs now dominated by turf-forming and invasive algal assemblages in many protected and semi-protected embayments along the central Atlantic coast (Filbee-Dexter et al. 2016). While the spatial extent and drivers of this shift are well described, whether the turf-dominated state will persist and potential feedbacks maintaining this configuration are key unknowns.

Environmental change and altered ecological interactions may impact the production and loss of kelp biomass and the demographic processes that limit kelp recovery and reinforce a turf algae dominated state. In the absence of dense populations of sea urchins, the small gastropod *Lacuna vincta* is the numerically dominant grazer in Nova Scotian kelp beds. While this mesograzer directly consumes only a small fraction of kelp biomass in dense beds (Johnson & Mann 1986), indirect tissue losses are much greater during large wave events due to tears that initiate from grazing perforations (Krumhansl & Scheibling 2011b, Krumhansl et al. 2011). Given the preference of *L. vincta* for the dominant kelp *S. latissima* over other macroalgae (Johnson & Mann 1986, Chavanich & Harris 2002), if grazing dynamics are contingent on kelp density (i.e. a functional or numerical response) the direct and indirect effects of *L. vincta* on kelp in turf-dominated habitats could be intensified. Effects of grazing will be greater if damage occurs on valuable reproductive tissues, especially since the low density of reproductive adults in degraded habitats is likely to limit propagule supply. However, the distribution of grazing damage on kelps during seasonal spore production is unknown. Low kelp recruitment to degraded habitats may reinforce shifts to turf, in combination with reduced growth and survival post-recruitment. Juvenile kelp sporophytes might be more vulnerable to grazing. Increased tissue loss and risk of mortality due to encrustation by *M. membranacea* (Levin et al. 2002, Krumhansl & Scheibling 2011a) and high seawater temperatures (Simonson et al. 2015) could further exacerbate this bottleneck.

The main objective of my doctoral research is to elucidate the reinforcing processes and feedbacks that inhibit recovery of kelp beds following large-scale losses and stabilize regime shifts to turf algae along the Atlantic coast of Nova Scotia. I focus on density-dependent (grazing, propagule supply) and post-recruitment processes (grazing, epiphytism, physical stress) that lead to increased tissue loss, recruitment limitation, and mortality of recovering kelp populations to the advantage of their spatial competitors. In Chapter 2, I examine how large-scale disturbances that defoliate kelp beds (outbreaks of *M. membranacea*, hurricanes) alter local-scale grazing dynamics of *L. vincta* on kelp through field observations and a kelp-thinning experiment that simulated disturbance, and evaluate the consequences for indirect tissue loss. In Chapter 3, I assess the impact of *L. vincta* on fecundity of *S. latissima* from grazing on localized reproductive tissues (sori) during the annual reproductive peak, and explore how the interplay between grazing losses and density of reproductive adults can impose propagule supply limitations. In Chapter 4, I investigate the contribution of recruitment, growth, and survival of young sporophytes to recovery of degraded kelp populations, and evaluate the opposing sources of post-recruitment tissue loss and mortality (grazing, encrustation by *M. membranacea*, high temperatures) by following cohorts of juvenile kelps at 2 sites and monitoring kelp populations and macroalgal composition of the surrounding community over 5 years.

In Chapter 5, I expand the context of my primary research using meta-analysis techniques to evaluate the broader role of competitive interactions in mediating regime shifts between turf algae and foundation species (canopy algae, corals) on temperate and tropical reefs globally, and explore variation in these interactions between life-history stages of foundation species, functional groups of turf algae, and intertidal and subtidal reefs. I also discuss the contribution of disturbance and stress to regime shift dynamics and how their effects might be integrated with competitive interactions to better evaluate the stability of regime shifts to turf algae. In Chapter 6, I synthesize the conclusions of Chapters 2 to 5, and discuss the contributions of my thesis to our understanding of the stability and consequences of regime shifts to turf-forming algae and loss of key structural species on shallow reefs.

CHAPTER 2

POSITIVE FEEDBACK BETWEEN LARGE-SCALE DISTURBANCE AND DENSITY-DEPENDENT GRAZNG DECREASES RESILIENCE OF A KELP BED ECOSYSTEM[*]

2.1 ABSTRACT

I examined how large-scale disturbances that defoliate kelp beds (outbreaks of an invasive bryozoan, hurricanes) alter local-scale grazing dynamics of an abundant herbivore, the gastropod *Lacuna vincta*, on the Atlantic coast of Nova Scotia. From field observations and a 5-wk kelp-thinning experiment that simulated disturbance, I found that snail density and grazing intensity on kelp (*Saccharina latissima*) increased non-linearly with decreasing kelp biomass, as it varied within a site. Grazing intensity on *S. latissima* also increased non-linearly with decreasing standing kelp biomass across 5 sites spanning 40 km (linear distance) of coast and 2 years, but I did not find strong support for this relationship for the kelp *Laminaria digitata*. Intensification of grazing augments the indirect effect of *L. vincta* on *S. latissima* (increased blade erosion and fragmentation), and drives it beyond a threshold for further losses of kelp biomass with subsequent storms. This positive feedback between large-scale disturbances and local-scale grazing could reinforce the depletion of kelp and facilitate turf-forming algae on Nova Scotian rocky reefs. I conclude that interactions of large-scale external perturbations with local-scale natural and anthropogenic perturbations must be considered to understand how drivers of ecosystem change collectively disrupt the balance of top-down and bottom-up forces to cause shifts to unexpected community states.

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[*] The research presented in Chapter 2 also appears in:

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2.2 INTRODUCTION

Large biological or physical disturbances may render populations increasingly vulnerable to further disturbances and processes that elicit, reinforce, or hasten further decline (Gilpin & Soulé 1986, Fagan & Holmes 2006, Brook et al. 2008). Of particular concern for management and conservation is when natural disturbances or anthropogenic impacts interact unpredictably to produce non-additive effects (antagonism and synergism) or establish positive feedback loops (Sala et al. 2000, Burkepile & Hay 2006, Brook et al. 2008, Crain et al. 2008, Halpern et al. 2008b). Synergies between perturbations (i.e. the total effect is greater than the sum of individual effects) are particularly common in marine systems, leading to larger or more rapid changes than anticipated (Crain et al. 2008). Consequences of such interactions include: delayed population recovery (Hughes & Connell 1999, Wernberg et al. 2010), population decline and increased extinction risk (van Katwijk et al. 1999, Brook et al. 2008), loss of biodiversity (Sala et al. 2000), and rapid changes to ecosystem structure and function (Paine et al. 1998, Hobbs et al. 2009).

Predicting and managing undesirable interactions among perturbations is complicated by the range of scales over which perturbations are compounded (global, regional, local). Impacts caused by disturbances originating at large spatial and temporal scales (e.g. climate-driven impacts) may act synergistically with the local anthropogenic stressors on which they are superimposed (e.g. nutrient loading, fishing pressure; Harley et al. 2006, Halpern et al. 2008b, Wernberg et al. 2011), driving unexpected shifts to novel community states (Hobbs et al. 2009, Russell et al. 2009). An improved understanding of the mechanisms by which perturbations interact may facilitate prediction of undesirable synergisms (Lyons et al. 2015). Ecologically mediated interactions, where the effect of one perturbation on a community modifies the strength of species interactions and thus the effect of a second perturbation, may be an important interaction mechanism behind ecological regime shifts (Wernberg et al. 2010, Lyons et al. 2015). The intensity of herbivory on macroalgae, for instance, may increase or decrease under future ocean warming and acidification scenarios, leaving uncertainty in the future structure of seaweed-dominated assemblages (Harley et al. 2012). How large-scale anthropogenic impacts modify local-scale perturbations intrinsic to a system, like herbivory, is therefore a critical knowledge gap. These types of interactions are arguably more difficult to mitigate through local management action compared to those involving purely anthropogenic stressors. Large disturbances that intensify grazing on competitively dominant macroalgae could facilitate competitors leading to shifts in community structure.

Major shifts in the structure of seaweed assemblages of rocky coastlines are already underway. The replacement of productive canopy-forming macroalgae (kelps and fucoids) by turf-forming algal assemblages is increasingly reported from temperate rocky reefs globally (Eriksson et al. 2002, Worm & Lotze 2006, Connell et al. 2008, Perkol-Finkel & Airoldi 2010, Andersen et al. 2011, Moy & Christie 2012). Stressors that favour the persistence of turf-forming algae and inhibit the recovery of canopy-forming species include eutrophication (Gorman et al. 2009), sediment loading (Airoldi 1998, Eriksson et al. 2002), fouling epiphytes (Andersen et al. 2011), ocean warming (Wernberg et al. 2010, 2013) and acidification (Russell et al. 2009, Connell & Russell 2010), and general anthropogenic disturbance (Benedetti-Cecchi et al. 2001). These perturbations affect rocky coastlines at various spatial scales and it is held that synergistic effects of multiple drivers can cause or exacerbate these large-scale shifts in community structure (Russell et al. 2009, Perkol-Finkel & Airoldi 2010, Moy & Christie 2012), although the nature of their interaction may depend on the specific identity of the drivers involved (Strain et al. 2014).

Comparable shifts in community structure have been observed along the Atlantic coast of Nova Scotia. The rocky subtidal zone, normally characterized by productive kelp beds (*Saccharina latissima*, *Laminaria digitata*), has become dominated by mixed assemblages of turf-forming algae, primarily filamentous red (*Polysiphonia* spp., *Callithamnion* spp., *Antithamnion* spp.) and brown (ectocarpoids) algae, that are particularly pervasive at sheltered sites from late spring to fall. This system is regularly impacted by large-scale disturbances. The encrusting bryozoan *Membranipora membranacea* was first reported in Nova Scotia in 1992 (Scheibling et al. 1999). Since introduction, *M. membranacea* has become continuously distributed along the Atlantic coast of Nova Scotia (Watanabe et al. 2010). Reduced kelp tissue strength following encrustation (Krumhansl et al. 2011) results in large-scale defoliation of kelp beds in fall (Scheibling et al. 1999, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). Defoliation of kelp along broad stretches of coast also may occur at this time owing to hurricanes tracking through the region (Filbee-Dexter & Scheibling 2012). Understanding how these large regional impacts modify local-scale processes may offer some insight into structural shifts from kelp- to turf-dominated subtidal communities.

Reductions in kelp abundance resulting from these biological and physical disturbances could alter the grazing dynamics of the small gastropod *Lacuna vincta*. This is a numerically abundant mesograzer (1000s m^{-2} at seasonal peaks) that occurs on diverse algal substrates, but preferentially consumes kelp (Johnson & Mann 1986). *Lacuna vincta* is the principal grazer of kelp on the Atlantic coast of Nova Scotia when sea urchins (*Strongylocentrotus droebachiensis*) are rare (Johnson & Mann 1986). This is increasingly the case due to recurrent disease-mediated mortality of sea urchins in shallow water (Scheibling et al. 2010, Feehan et al. 2012). Although direct consumption of kelp biomass by snails generally is small (but see Fralick et al. 1974), the indirect effects of grazing are much greater, including increased blade erosion and fragmentation caused by grazing holes and superficial excavations (Johnson & Mann 1986, Krumhansl & Scheibling 2011a,b, Krumhansl et al. 2011). Therefore, changes in the grazing intensity of *L. vincta* can have important implications for the persistence of kelp beds. Reductions in kelp abundance may alter grazing intensity by changing the abundance of kelp relative to snails, the rate of kelp consumption per snail (functional response) or a combination of both (total response).

In this study, I examined how large-scale disturbances (recurrent outbreaks of *M. membranacea* and hurricane damage) that reduce kelp abundance alter local-scale grazing dynamics of *L. vincta*. I measured within-site spatial variation in kelp biomass and snail density on kelp in combination with a kelp-thinning experiment to test my predictions that 1) snails will be more heavily concentrated on kelp (*S. latissima*, *L. digitata*) where it is sparse and biomass is lower, and 2) grazing intensity on *S. latissima* will increase with thinning of kelp. I extended my second prediction to both kelp species and a broader scale by examining standing kelp biomass and grazing damage on *S. latissima* and *L. digitata* at 5 sites in 2 consecutive years. I hypothesized that both species of canopy-forming kelp would be more heavily grazed at sites with lower kelp abundance.

2.3 MATERIALS AND METHODS

2.3.1 Site Descriptions

Data for the various components of this study were collected between 2008 and 2013 from 6 sites along the Chebucto Peninsula and in St. Margarets Bay southwest of Halifax, NS: Paddy's Head, Duncan's Cove Protected, Duncan's Cove Exposed, Splitnose Point, Cranberry Cove, and The Lodge (Table 2.1, Fig. 2.1). Paddy's Head is moderately exposed with a substratum of ledges and medium to large boulders on gently-sloping bedrock. At the time of this study, kelp (predominantly *Saccharina latissima*) occurred in sparse and thin patches among pervasive filamentous turf-forming algae (Fig. 2.2A). Duncan's Cove Protected is a sheltered site supporting a dense, mixed kelp canopy of *S. latissima* and *Laminaria digitata* on small and medium-size boulders. Data from the remaining sites were collected as a part of a previous study on detrital production that included Duncan's Cove Protected (Krumhansl & Scheibling 2011a). These sites vary in substratum type (ledges, boulders, bedrock, rocky outcrops), wave exposure (low to high), and relative abundance of kelp species (*S. latissima* and *L. digitata*; Table 2.1). For detailed site descriptions, see Krumhansl & Scheibling (2011a). All collections and manipulations were made at 4 – 6 m depth.

2.3.2 Grazing Dynamics within Sites

To examine the potential response of *Lacuna vincta* to spatial variation in kelp abundance within a site (metres to 10s of metres), kelp biomass and snail density on kelp were measured using SCUBA at Paddy's Head, once in both July and September 2012. All macroscopic kelp (*S. latissima* and *L. digitata*) and snails on the kelp were collected in 5 – 8 haphazardly sampled 1 m^2 quadrats and placed in separate fine-mesh bags. Kelp and snails were returned to the laboratory in closed bins and placed immediately in flow

Table 2.1. Location and characteristics of 6 study sites on the Chebucto Peninsula and shores of St. Margarets Bay along with a description of the data collected from each. Types of data collected include:
B_k = dry kelp biomass, D_s = density of *Lacuna vincta*, G = grazing intensity on kelp. The range in average kelp biomass observed at each site over the period of data collection is split by species (SL = *Saccharina latissima*, LD = *Laminaria digitata*).

Site	Lat/Long	Exposure	Kelp biomass (g m^{-2})	Data Collection Period	Data Type
Paddy's Head (PH)	44° 31.624' N 63° 57.080' W	Moderate, NW	SL: 20 – 75 LD: 0 – 4	2012: Jul, Sep	B_k, D_s
Duncan's Cove Protected (DP)	44° 29.875' N 63° 31.583' W	Low, E	SL: 350 – 686 LD: 14 – 380	2008: Sep 2009: Sep 2013: Jun – Jul	B_k, G^* B_k, G^* B_k, D_s, G
Duncan's Cove Exposed (DE)	44° 29.837' N 63° 31.404' W	Moderate, SE	SL: 497 – 1094 LD: 290 – 591	2008: Sep 2009: Sep	B_k, G^* B_k, G^*
Splitnose Point (SP)	44° 28.641' N 63° 32.804' W	High, SSE	SL: 179 – 245 LD: 1040 – 1536	2008: Sep 2009: Sep	B_k, G^* B_k, G^*
Cranberry Cove (CC)	44° 30.005' N 63° 55.379' W	Low – Moderate, SW	SL: 348 – 382 LD: 7 – 19	2008: Sep 2009: Sep	B_k, G^* B_k, G^*
The Lodge (TL)	44° 33.491' N 64° 01.493' W	Low – Moderate, NNE	SL: 71 – 317 LD: 28 – 70	2008: Sep 2009: Sep	B_k, G^* B_k, G^*

* data collected as part of broader study on kelp detrital production (Krumhansl & Scheibling 2011a)

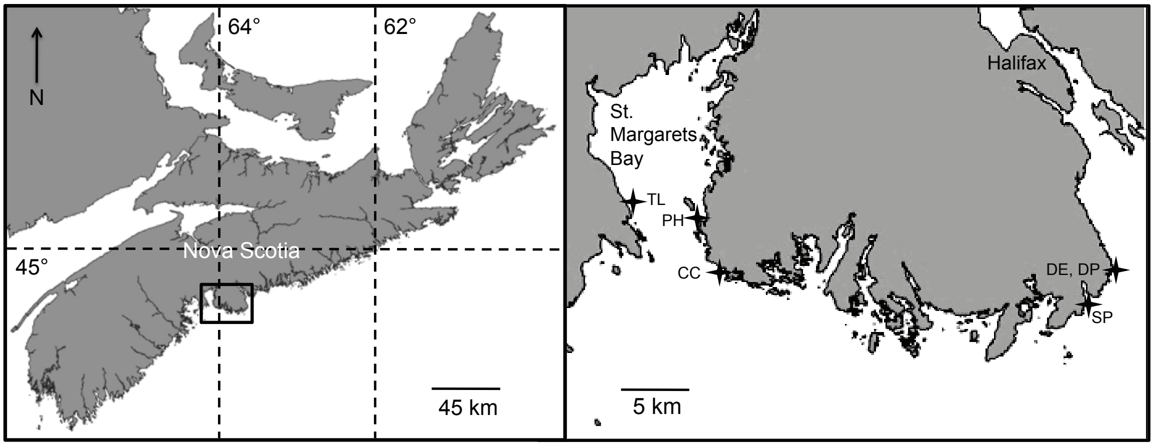

Fig. 2.1. Map of study area in central region of Atlantic coast of Nova Scotia, Canada showing locations of 6 study sites along the Chebucto Peninsula and shores of St. Margarets Bay: Paddy's Head (PH), Duncan's Cove Protected (DP), Duncan's Cove Exposed (DE), Splitnose Point (SP), Cranberry Cove (CC), and The Lodge (TL).

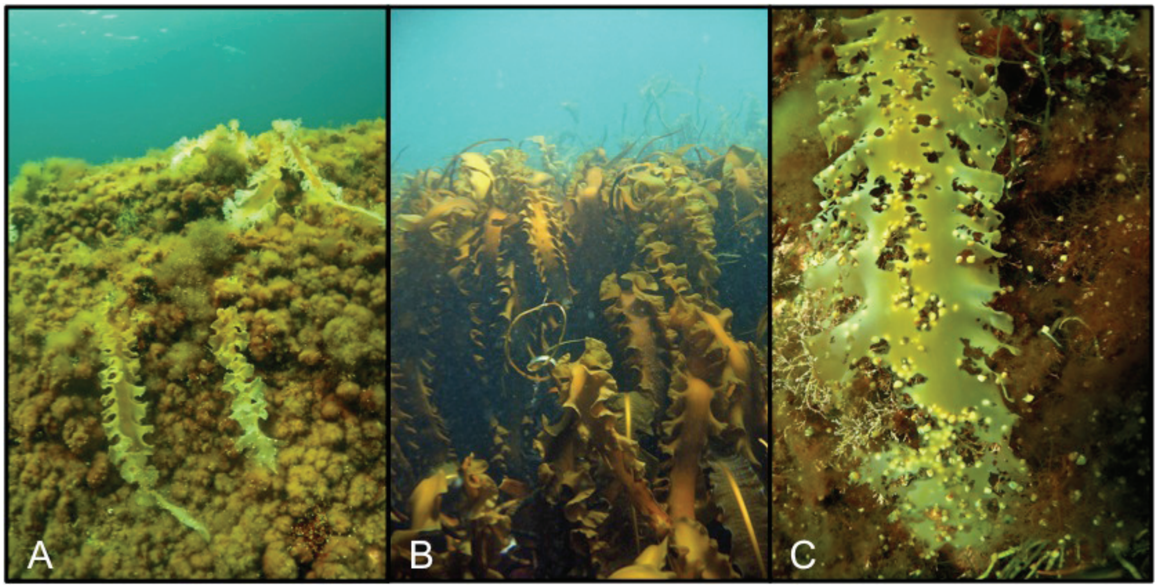

Fig. 2.2. (A) Sparse kelp (*Saccharina latissima*) amid a pervasive mat of turf-forming algae at Paddy's Head in June 2012; (B) Dense stand of kelp (*S. latissima*, *Laminaria digitata*, and *Alaria esculenta*) at Splitnose Point in May 2007; (C) Dense aggregation of *Lacuna vincta* on an isolated blade of *S. latissima* extensively perforated by grazing at Paddy's Head in June 2012. *Photo credit*: R.E. Scheibling.

through seawater holding tanks. To measure snail density on kelp (snails g kelp^{-1} m^{-2}), all snails from each quadrat were removed from the kelp and counted. Stipes (including holdfast) and blade tissue of each species were weighed (0.001 g precision) separately after drying for 5 min on paper towel. In July, tissue subsamples from the stipe and mid blade of all measured individuals of each species were weighed as above and then oven-dried at 60 °C for 48 h to calculate wet to dry weight conversions using linear regression (*S. latissima*: n = 47, *L. digitata*: n = 7). Regressions for each tissue type and species were significant at $\alpha = 0.05$ with $R^2 > 0.96$ (Appendix A: Table A1) and used to estimate the dry kelp biomass (g) of both species combined in each quadrat.

The effect of kelp abundance on the density and grazing intensity of *L. vincta* was tested in a manipulative field experiment from 19 June to 25 July 2013 at Duncan's Cove Protected. This site was chosen for its high background density of kelp and because *M. membranacea* is typically rare, allowing greater control over kelp abundance. SCUBA divers manipulated kelp density (and thus biomass) in experimental plots in a kelp bed to simulate the severe thinning and gap creation caused by biological and physical disturbances that dislodge and defoliate kelp (e.g. outbreaks of *Membranipora membranacea*, hurricane damage). Although such disturbances can defoliate kelp across broader spatial scales (Saunders & Metaxas 2008, Scheibling & Gagnon 2009, Filbee-Dexter & Scheibling 2012), the scale of my manipulations was limited by logistical constraints.

At the start of the experiment, 12 circular plots (1.2 m radius, ~ 4.5 m^2) marked with a central eyebolt and numbered tag were established along the 4 – 5 m depth contour. Plots were positioned to achieve ~ 7 m spacing between plot centres and as much homogeneity in background kelp density as possible. Half the plots were randomly assigned to a kelp thinning treatment and the other half served as controls. In thinned plots, divers removed all macroscopic kelp at the holdfast within the plot, except for 4 individuals (*S. latissima* only) 50 – 70 cm in blade length that were marked with flagging tape. One of these individuals was located in the plot centre and the remaining 3 were equally spaced along the perimeter of a smaller circular subplot (1 m^2) in the centre of the larger plot (Appendix A: Fig. A1). Centralizing kelp thalli in this way minimized edge effects while achieving a kelp density of ~ 1 thallus m^{-2} in the larger plot, consistent with observed kelp density for the time of year at other, low density kelp sites (Fig. 4.6, 4.7). Snails were shaken loose from removed kelp thalli and allowed to re-distribute among algal substrates. The kelp was bagged and discarded on shore. *Lacuna vincta* is an annual species (Johnson & Mann 1986), and it was assumed that the re-distribution of snails in thinned plots would be similar in effect to settlement of a new cohort to a kelp bed from the plankton. No kelp was removed from control plots, but 7 individuals in the same size range as thinned plots were flagged in like fashion (1 central thallus and 6 equally spaced thalli along the perimeter of the central subplot; Appendix A: Fig. A1), which permitted increased replication in anticipation of loss through dislodgement. Average kelp density in control plots was 21 ± 10 thalli m^{-2} (mean ± SD, n = 6). Of the kelp removed from thinned plots, 5 individuals from each plot (n = 30) were retained and transported back to the laboratory to estimate the baseline grazing intensity of *L. vincta* on *S. latissima*. A baseline density of snails was obtained 6 d later when all kelp and snails were collected from five 1 m^2 quadrats in the area between plots, placed in separate fine-mesh bags, and returned to the laboratory in closed bins. After 1 month, all kelp and snails on kelp were collected from the central 1 m^2 subplots and placed separately in fine mesh bags to estimate final snail density in the laboratory. Collected thalli included those individuals flagged at the beginning of the experiment, which were subsequently used to estimate final grazing intensity.

Methods for measuring snail density on kelp (snails g $kelp^{-1}$ m^{-2}) and kelp biomass (g) at the beginning and end of the experiment were as described above. At both times, tissue subsamples of 4 – 6 individuals of each kelp species were retained from each 1 m^2 quadrat or subplot for wet to dry weight conversions. All regressions were significant at $\alpha = 0.05$ with $R^2 > 0.85$ (Appendix A: Table A1). To measure grazing intensity, defined as the percent of blade area grazed by *L. vincta*, at the beginning and end of the experiment, the central part of the blade of collected individuals was separated from the convoluted margins and photographed. Before photographing, the margins were further sectioned and pressed between Plexiglas® sheets. Due to their convoluted morphology, the surface area of the blade margins of *S. latissima* is much larger once sectioned. Grazing intensity was determined from photographs by outlining and measuring the blade area and total area of grazing damage on the blade using ImageJ

(National Institutes of Health). *L. vincta* creates superficial excavations and full perforations of the blade, but only full perforations were delineated in photographs and used to estimate grazing intensity.

2.3.3 Grazing Dynamics across Sites

To investigate how grazing intensity of *L. vincta* on canopy-forming kelps varies with kelp abundance at broader spatial scales (10s of km), measurements of grazing intensity on *S. latissima* and *L. digitata* and standing kelp biomass across 5 sites from a separate study on detrital production and spanning ~ 40 km (linear distance) of coast were used (Krumhansl & Scheibling 2011a). Over this range, standing kelp biomass may differ between sites by orders of magnitude (Table 2.1, Fig. 2.2A,B). Measurements were taken at Duncan's Cove Protected, Duncan's Cove Exposed, Splitnose Point, Cranberry Cove, and The Lodge in September in both 2008 and 2009 at the peak of grazing intensity (Krumhansl & Scheibling 2011b). Grazing damage was measured on 10 – 23 haphazardly collected thalli of each species (> 25 cm blade length), except for *L. digitata* at Cranberry Cove, which was not measured in either sampling period because it was rare at this site. The percent of the blade area grazed of collected thalli was measured as above, although whole thalli were photographed without sectioning the blade margins. Standing kelp biomass at the sites was estimated at each sampling period by weighing all individuals of both species in each of 8 – 9 quadrats of 0.5 m^2 with a spring scale (10 g precision). Tissue subsamples (stipe and blade) of each species were taken from collected thalli during each sampling period for wet to dry weight conversions as above. All regressions were significant at $\alpha = 0.05$ with $R^2 > 0.8$ (Appendix A: Table A1). Conversions for *L. digitata* at Cranberry Cove were taken from literature values from a comparable site and season (Mann 1972a).

2.3.4 Statistical Analysis

Regression techniques were used to determine the effect of kelp abundance on snail density using data from collections at Paddy's Head and the field experiment at

Duncan's Cove Protected. Power functions were fit to the relationships between snail density (D_s, snails g kelp^{-1} m^{-2}) and dry kelp biomass (B_k, g), in quadrats or subplots, of the form: $D_s = \alpha\ (B_k)^{\beta}$. If the number of snails on kelp in an area is constant regardless of kelp biomass (no aggregative response) or decreases more slowly than kelp biomass (type II aggregative response; see Gascoigne & Lipcius 2004), then I expect a strong, declining power-fitting relationship between snail density on kelp and kelp biomass because biomass is essentially plotted by its inverse. Separate regressions were fit for the July and September sampling periods at Paddy's Head, and the combined data from the beginning and end of the field experiment. For comparison, a regression line also was fit to the combined Duncan's Cove Protected and Paddy's Head data (July sampling period). Regression parameters were estimated using non-linear regression with the 'nls' function in R (R Core Team 2012).

To demonstrate that observed differences in snail density in the field experiment between treatments were not confounded by differences in kelp consumption by snails, the mean thallus biomass of flagged plants in thinned and control plots were compared with a 2-tailed independent samples *t*-test. Snail density per thallus (rather than per g kelp) of all kelps > 30 cm blade length in subplots also was compared between treatments with a 2-tailed independent samples *t*-test. For both tests, untransformed data met assumptions of normality (Shapiro-Wilk test, $p > 0.05$) and homogeneity of variances (Bartlett's test, $p > 0.05$)

Nested ANOVA was used to test for differences in the mean grazing intensity (% blade area grazed) between thinned and control plots at the end of the field experiment and the baseline site average at the start of the experiment with kelp thinning treatment as a fixed factor and plot as a random factor nested within treatment. Grazing data were $\log_{10}$-transformed to achieve normality (Shapiro-Wilk test, $p > 0.05$) and homogeneity of variance (Bartlett's test, $p > 0.05$). Where differences were detected, pairwise comparisons were made using Tukey's HSD test at a 95% family-wise confidence level.

The relationships between grazing intensity and kelp abundance for 1) *S. latissima* within a site (Duncan's Cove Protected 2013) and 2) *S. latissima* and *L. digitata* across sites (5 sites 2008/2009) represent the total response (see Murdoch & Oaten 1975) of *L. vincta* to kelp abundance. That is the product of shifts in the per capita consumption rate of snails (functional response; not explored explicitly here) and the number of snails per kelp (addressed above). I apply the advice of Trexler et al. (1988) for determining the general shape of functional response curves (i.e. type I, II, or III) to these total response curves, which may have analogous shapes, prior to more detailed curve-fitting (details provided in Appendix B). In all cases it was determined that grazing was negatively density-dependent throughout all ranges of kelp biomass (i.e. type II total response) (Appendix B: Table B1, B2). Subsequently, I used power functions (as above) to model this response. Due to the error structure of these data (variance increasing with the mean), parameters were estimated by simple linear regression following a linearizing transformation of the power function: $\log Y = \log \alpha + \beta (\log B_k)$ to meet model assumptions. Back-transformed regression lines are presented for these data. All analyses were performed using R statistical software (Version 2.15.1, R Core Team 2012).

2.4 RESULTS

2.4.1 Grazing Dynamics within Sites

The density of *Lacuna vincta* on kelp (*Saccharina latissima* and *Laminaria digitata*) at Paddy's Head varied with kelp abundance. In July and September 2012, snail density increased non-linearly with decreasing kelp biomass in 1 m^2 quadrats (Fig. 2.3). A non-linear relationship was supported by a significant fit of the power function for September and a marginally non-significant fit for July (Table 2.2). Snail density in quadrats with the least kelp was ~ 2 times greater than in quadrats with the most kelp in July (13 – 31 vs. 10 – 12 snails g $kelp^{-1}$ m^{-2}), and an order of magnitude greater in September (61 vs. 2 – 3 snails g $kelp^{-1}$ m^{-2}). The substantial difference in September was partly owing to the lowest observed kelp biomass at this time being much lower than in July (Fig. 2.3).

The outcome of the manipulative field experiment at Duncan's Cove Protected in 2013 was consistent with observations at Paddy's Head in the previous year. Kelp biomass ranged widely in control plots at the end of the experiment (191 – 1070 g), and

Table 2.2. Coefficient estimates and standard errors of power models of the form: $Y = \alpha (B_k)^{\beta}$. Y is snail density or grazing intensity (% kelp blade area grazed) on *Saccharina latissima* or *Laminaria digitata* and B_k is kelp biomass at the respective sites (see Table 2.1 for site abbreviations) in 2008/2009, 2012, or 2013.

Site and sampling period	Parameter	Estimate	SE	*t*	p
Snail Density					
PH Jul 2012	α	44.674	18.584	2.404	0.053
	β	-0.264	0.117	-2.253	0.065
PH Sep 2012	α	103.872	13.195	7.872	<0.01
	β	-0.934	0.144	-6.466	<0.01
DP Jun-Jul 2013	α	63.211	15.229	4.151	<0.001
	β	-0.382	0.049	-7.773	<0.001
DP Jun-Jul 2013/PH Jul 2012	α	57.975	10.486	5.529	<0.001
	β	-0.353	0.044	-8.015	<0.001
Grazing intensity					
Saccharina latissima					
DP Jul 2013*	log(α)	2.337	0.577	4.053	<0.01
	β	-0.270	0.106	-2.538	<0.05
DP, DE, SP, CC, TL Sep 2008/2009*	log(α)	4.067	1.472	2.763	<0.05
	β	-0.785	0.226	-3.473	<0.01
Laminaria digitata					
DP, DE, SP, CC, TL Sep 2008/2009*	log(α)	3.514	2.739	1.283	0.247
	β	-0.674	0.412	-1.638	0.153

* indicates where regression parameters were determined by linear regression following log-log transformation.

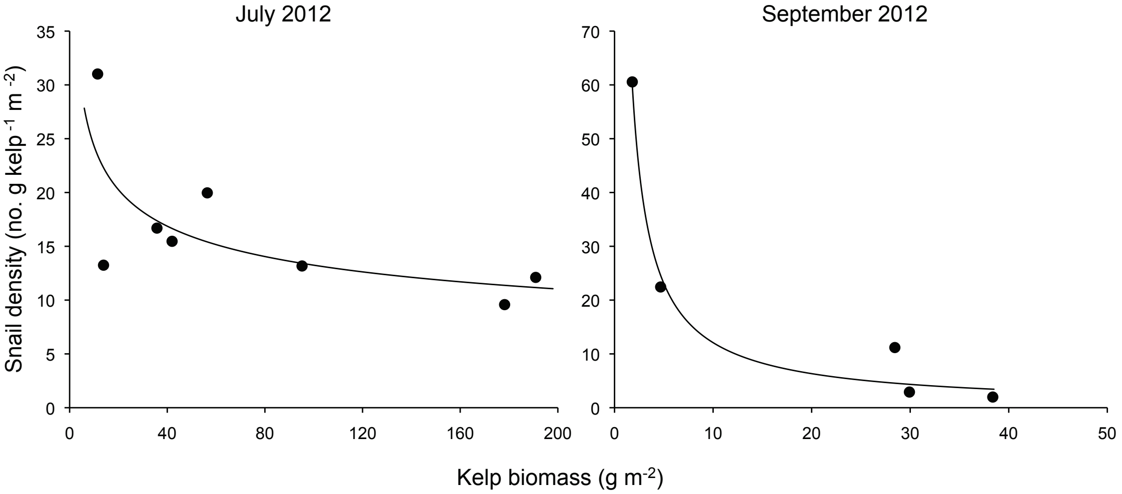

Fig. 2.3. The relationship between density of *Lacuna vincta* on kelp (*Saccharina latissima* and *Laminaria digitata*) and kelp biomass in 1 m^2 quadrats at Paddy's Head in July and September 2012 (July: $R^2 = 0.469$, $p = 0.065$; September: $R^2 = 0.842$, $p < 0.01$). Note difference of scale on both axes for each sampling period.

was comparable to the range observed for the site at the start in June (163 – 761 g; Fig. 2.4). Snail density varied little over this range with little difference between control plots (mean ± SD: 5 ± 2 snails g kelp^{-1} m^{-2}) and baseline values in June (7 ± 2 snails g kelp^{-1} m^{-2}). Kelp biomass in thinned plots was lower (39 – 149 g) and snail density rapidly increased to 3.5 times that observed in the highest biomass control plot (14 vs. 4 snails g kelp^{-1} m^{-2}; Fig. 2.4). Kelp biomass and snail density in thinned plots were within the range observed at Paddy's Head (July), and the observational data closely approximate the power relationship that describes the experimental data (Table 2.2, Fig. 2.4). The mean thallus biomass of flagged individuals in control and thinned plots did not differ significantly (t_{39} = -1.03, p = 0.307; Fig. 2.5). However, the number of snails per thallus was significantly higher (by 2-fold) in thinned plots (t_{10} = -3.05, $p < 0.05$; Fig. 2.5). Therefore, it is unlikely that the observed increase in snail density (per g kelp) in thinned plots is a result of confounding differences in snail consumption (and reduction of biomass) of kelp between treatments.

Grazing intensity on *S. latissima* did not differ between control plots at the end of the field experiment (mean ± SE: 1.9 ± 0.04%) and the baseline site average at the start (1.5 ± 0.02%; Table 2.3, Fig. 2.6). However, grazing intensity in thinned plots (3.6 ± 0.07%) was significantly higher than control and baseline plots (Table 2.3, Fig. 2.6). There was no effect of the nested factor plot (Table 2.3). Grazing intensity varied with local kelp abundance similarly to snail density though there was much more variability around this relationship (Fig. 2.6). Grazing intensity increased non-linearly with decreasing kelp biomass in experimental 1 m^2 subplots and the power function was a significant fit (Table 2.2, Fig. 2.6).

2.4.2 Grazing Dynamics across Sites

In accordance with observations within sites, grazing intensity of *L. vincta* on *S. latissima* also increased as standing kelp biomass decreased across sites (Fig. 2.7), and the power function was a significant fit to this non-linear relationship (Table 2.2). Grazing intensity on *L. digitata* across sites followed the same general trend (Fig. 2.7). However, there was greater variability and a relative scarcity of points around the

Table 2.3. Nested ANOVA comparing the mean grazing intensity (% blade area grazed) between thinned and control experimental plots in July, and the baseline site average in June 2013 at Duncan's Cove Protected. Pairwise comparisons based on Tukey's HSD test at 95% family-wise confidence level.

Source	df	MS	*F*	p	Pairwise
Treatment	2	0.984	25.0	<0.001	Baseline = Control < Thinned
Plot(Treatment)	15	0.062	1.57	0.111	
Error	59	0.039			
Total	76				

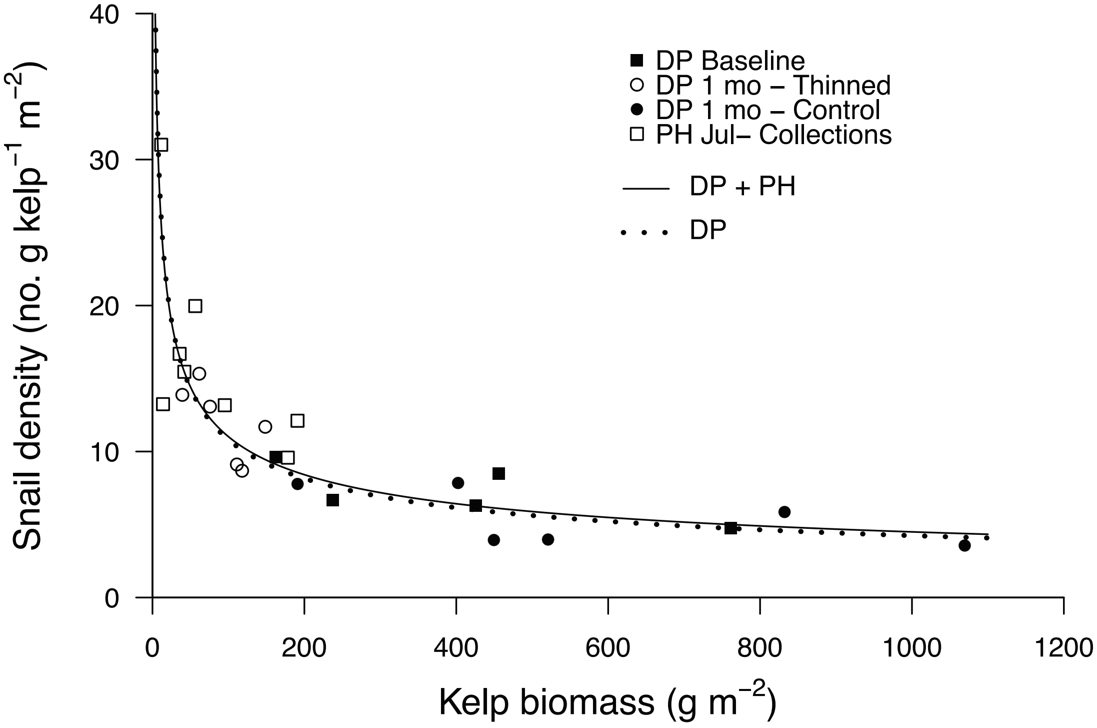

Fig. 2.4. The relationship between density of *Lacuna vincta* on kelp (*Saccharina latissima* and *Laminaria digitata*) and kelp biomass in 1 m^2 quadrats and circular subplots from a manipulative field experiment at Duncan's Cove Protected (DP) in June/July 2013. Plotted points are data from quadrats at the start of the experiment (black squares), plots thinned of kelp by clearing (white circles), and control plots (black circles) at the end of the experiment. Data from Paddy's Head (PH) in July 2012 are also plotted (white squares). Separate regressions are fit to DP 2013 data only (dotted line: $R^2 = 0.741$, $p < 0.001$) and DP 2013/PH 2012 data (solid line: $R^2 = 0.977$, $p < 0.001$).

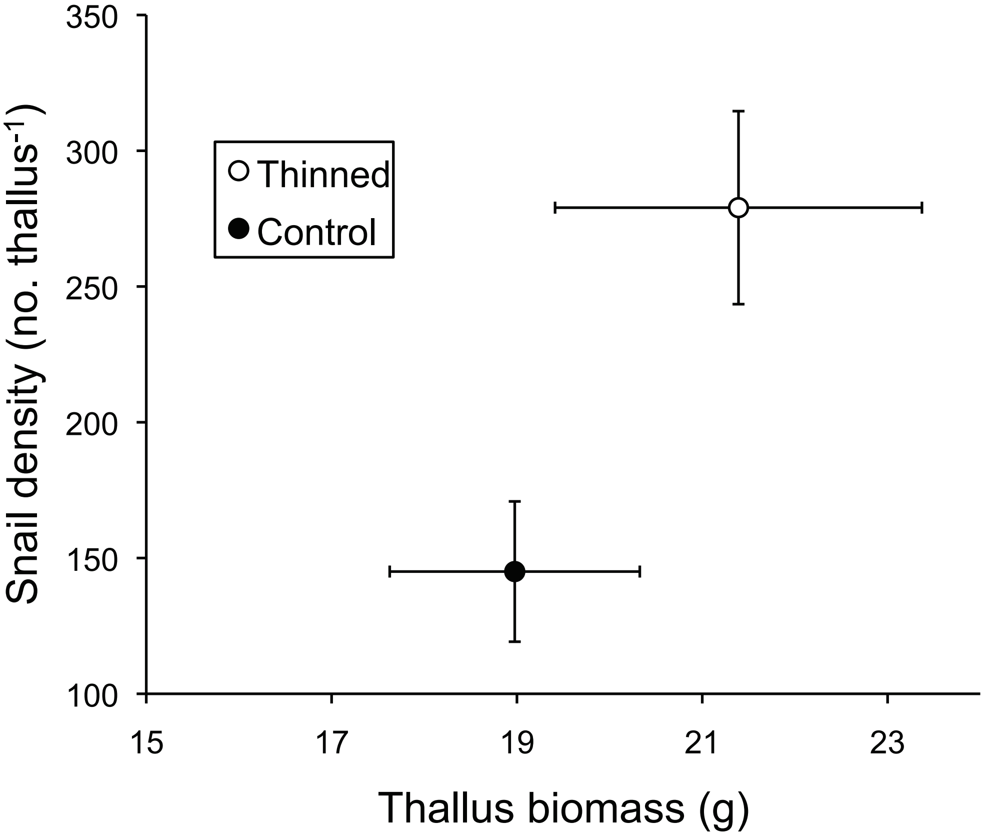

Fig. 2.5. Dry weight of flagged kelp thalli (*Saccharina latissima*) and density of *Lacuna vincta* (snails thallus^{-1}) on kelps > 30 cm in blade length (*S. latissima* and *Laminaria digitata*) in experimental plots thinned of kelp by clearing (white circle) and controls (black circle) at Duncan's Cove Protected in July 2013. Data are mean (± SE) dry weight of kelp (Thinned: n = 17; Control: n = 24) and snail density (n = 6).

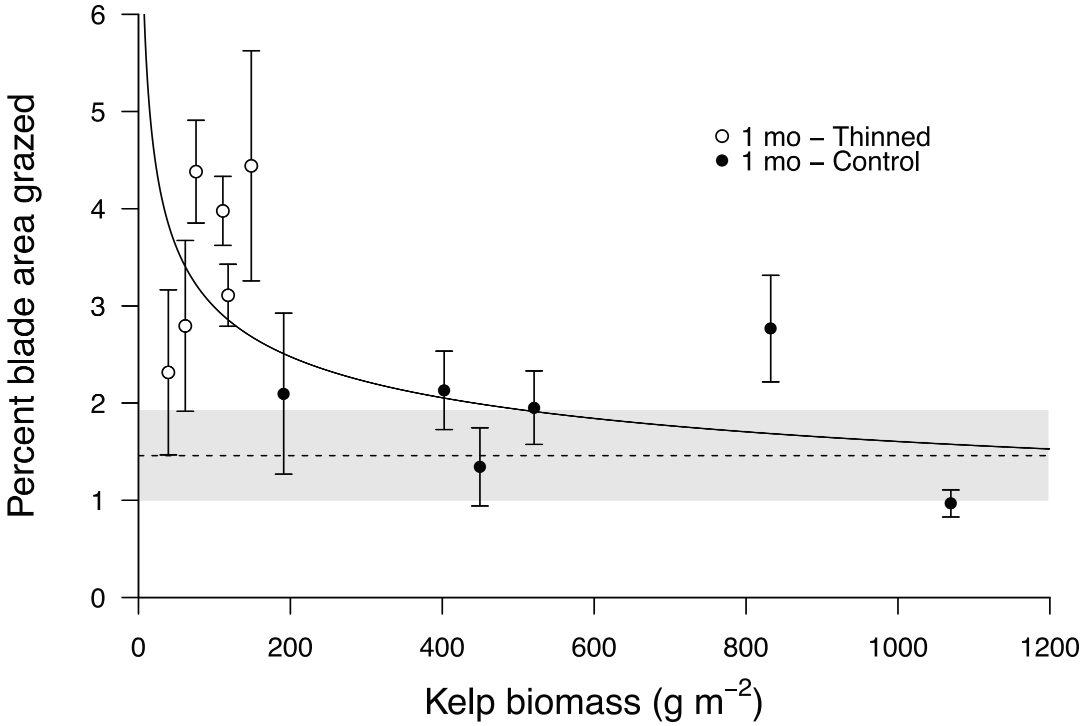

Fig. 2.6. The relationship between grazing intensity on kelp (*Saccharina latissima*) by *Lacuna vincta* and kelp biomass in 1 m^2 circular subplots from a manipulative field experiment at Duncan's Cove Protected in June/July 2013. Points are data from plots thinned of kelp by clearing (white circles) and control plots (black circles) at the end of the experiment. Data are mean (± SE) percent of blade area grazed (n = 3 – 6). Also shown is the baseline grazing intensity at the start of the experiment in June (dashed line = site average, grey box = 95% CI). Regression line is back-transformed prediction from fitting linearized power model to data ($R^2 = 0.392$, $p < 0.05$).

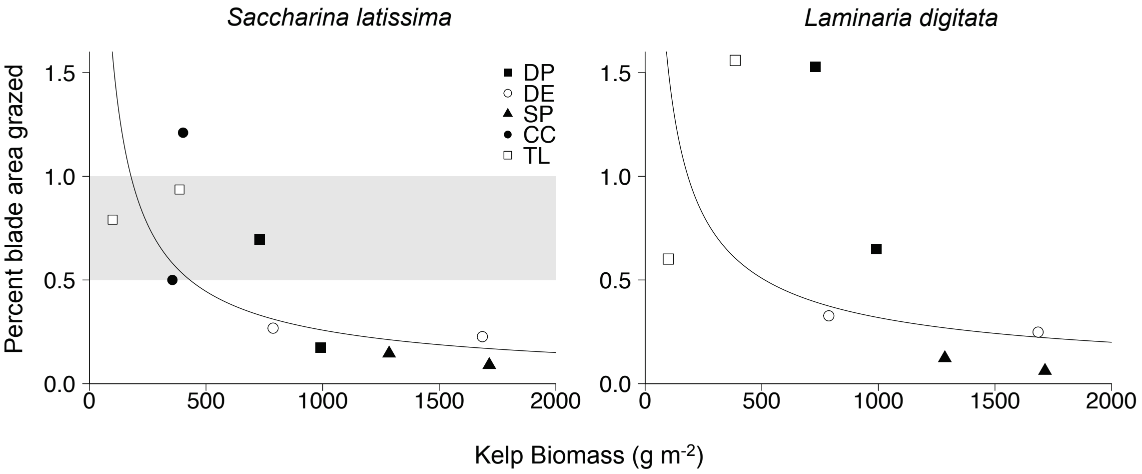

Fig. 2.7. The relationship between grazing intensity on kelp (*Saccharina latissima* and *Laminaria digitata*) by *Lacuna vincta* and standing kelp biomass at 5 sites (DP, DE, SP, CC, TL; see Table 2.1 for site abbreviations) in September 2008/2009. Data are mean percent of blade area grazed (n = 10 – 23 thalli in each sampling period) against mean kelp biomass at each site (n = 8 – 9 quadrats of 0.5 m^2). Regression lines are back-transformed predictions from fitting linearized power models to data (*S. latissima*: R^2 = 0.601, p < 0.01; *L. digitata*: R^2 = 0.309, p = 0.153). The grey box indicates a threshold range of grazing damage (0.5 – 1% blade area grazed) beyond which a stepwise increase in blade fragmentation is expected with large wave events for *S. latissima* (Krumhansl & Scheibling 2011b).

regression line at lower kelp biomass (Fig. 2.7), and this relationship was non-significant (Table 2.2). If grazing intensity on *S. latissima* by *L. vincta* exceeds a threshold at 0.5 – 1%, there is a stepwise increase in blade fragmentation with large wave events (Krumhansl & Scheibling 2011b). The increase in grazing intensity with decreasing standing kelp biomass in my study exceeded even the more conservative 1% threshold (Fig. 2.7). Grazing intensity was generally higher in the field experiment at Duncan's Cove Protected compared to 2008/2009 levels and exceeded the 1% threshold in all but the highest biomass control plot (Fig. 2.6, 2.7).

2.5 DISCUSSION

Both field observations and experimental manipulation supported my predictions of the response of *Lacuna vincta* to changes in kelp abundance within a site. As I expected, snail density on kelp increased where kelp density and biomass were lower, suggesting a tendency for *L. vincta* to become concentrated on the remaining individuals as kelp becomes more sparse (Fig. 2.2C). I also observed higher grazing intensity on individual blades of *Saccharina latissima* following experimental thinning of kelp as predicted. In large part this is likely a direct result of the increasing density of snails on those individuals rather than changes in the consumption rate of individual snails (although a functional response was not explicitly investigated). Furthermore, increases in snail density and grazing intensity with decreasing kelp abundance were consistently non-linear. Thus, changes in kelp abundance are expected to result in disproportionate changes in grazing pressure. Although the non-linear relationship was relatively weaker for grazing intensity as compared to snail density, this may have been an experimental artifact. Variability in the time for snails to recolonize following kelp thinning could explain why grazing intensity in some thinned plots was lower than expected (Fig. 2.6). Nonetheless, I found that individual thalli were increasingly grazed by *L. vincta* as kelp abundance decreased (Fig 2.2C).

Variation in grazing intensity across sites was partly explained by kelp abundance. As I predicted, *S. latissima* was most heavily grazed at sites where standing kelp biomass was low. Evidence to support this prediction for *Laminaria digitata* was equivocal, suggesting this species may be more resistant to herbivory by *L. vincta*. Material properties (strength, toughness) of the blade tissue would indicate that, of the two species, *L. digitata* is more resistant to breakage under stress and reductions in strength following grazing (Krumhansl et al. 2011) and perhaps more difficult to excavate. As with grazing within a site, grazing intensity on *S. latissima* increased non-linearly with decreasing kelp biomass across sites, although overall grazing was markedly lower. Methodological differences between the 2 periods (2008/2009 & 2013) may have contributed to the discrepancy in grazing intensity, as sectioning the blade before photographing (as in 2013) would capture more damage along the convoluted blade margins where grazing is concentrated (Johnson & Mann 1986). Inter-annual variability in snail recruitment may also have been a contributing factor. Despite this difference, the total response of *L. vincta* to kelp abundance both within and across sites is (at least for *S. latissima*) most consistent with a type II shape (i.e. asymptotically declining).

A concern with consumers showing a type II total response is their potential to cause Allee effects in their prey populations, i.e. inversely density-dependent population growth at low population size or density (Sinclair et al. 1998, Gascoigne & Lipcius 2004, Courchamp et al. 2008). Under these circumstances predation events are spread among more individuals at high population density (the dilution effect), but concentrated on fewer individuals when density or numbers are low (Courchamp et al. 2008). Likewise, I observed a "dilution" of snails and grazing damage as kelp became increasingly dense. Consumer-driven Allee effects typically arise when the prey is secondary in the diet of the consumer, such that the consumer population is not depleted with its prey (Courchamp et al. 2008). Because *L. vincta* is a generalist herbivore, I do not expect a numerical response to changes in kelp abundance even though kelp is the preferred dietary item (Johnson & Mann 1986). The fact that *L. vincta* is a mesograzer and typically does not consume kelp thalli entirely adds a further complication. Whether increasing grazing intensity with decreasing kelp abundance translates to a decline in the per capita rate of increase will depend to a large extent on the indirect effects of grazing on kelp.

Although direct consumption of macroalgae by mesograzers may be relatively minor, the indirect effects of grazing on growth, tissue loss, and mortality can be substantial (Johnson & Mann 1986, Duggins et al. 2001, Krumhansl & Scheibling 2011a,b, Poore et al. 2014). The levels of grazing damage observed in this study represent a relatively small portion of the blade area, and the difference in grazing intensity between treatments in my field experiment did not cause an appreciable difference in thallus biomass. However, I expect increased grazing intensity at low kelp abundance to indirectly enhance the loss of biomass from individual thalli. Grazing damage by *L. vincta* increases the erosion rate of tissue from the distal end of kelp blades (Krumhansl & Scheibling 2011a) and causes considerable blade fragmentation from *S. latissima* during large wave events if grazing intensity exceeds a threshold at 0.5 – 1% (Krumhansl & Scheibling 2011b). My findings suggest that the removal of kelp by hurricane damage and recurrent outbreaks of *Membranipora membranacea* may intensify the direct impact (i.e. grazing damage) and in turn the indirect impact (i.e. increased erosion and fragmentation) of *L. vincta* on *S. latissima*. Furthermore, increases in grazing intensity beyond a relatively low threshold level, as I observed for *S. latissima*, presages even further losses of kelp biomass with subsequent storm events. Thus, disturbance-generated gaps in the canopy and low kelp biomass at sites following major thinning events are likely to persist due to high levels of blade erosion and fragmentation or possibly mortality if tissue loss occurs below the meristem. Defoliation of kelp canopy has been an important pre-requisite for replacement of kelp by other macroalgae (e.g. *Codium fragile* ssp. *fragile*) in this system in the past (Scheibling & Gagnon 2006, 2009). This positive feedback between large-scale disturbances that impact the broader region and local-scale grazing could suppress kelp dominance and favour the persistence of competing turf-forming algae on subtidal reefs in Nova Scotia following canopy loss.

It is proposed that shifts on temperate rocky reefs from canopy- to turf-dominated algal assemblages are facilitated by synergies between multiple drivers (Russell et al. 2009, Connell & Russell 2010, Moy & Christie 2012). That view is consistent with what I report here. Self-reinforcing feedbacks between multiple drivers are expected to produce synergies over time (Brook et al. 2008). Owing to a positive feedback between large-scale disturbances (*M. membranacea* outbreaks, hurricanes) and the mesograzer *L. vincta*, their combined effect on loss of kelp biomass from subtidal beds is likely greater than predicted from the sum of their independent effects. This synergy, which can drive the proliferation of turf-forming algae following initial removal of a foundation species such as kelp, underscores the importance of maintaining intact kelp populations (Eriksson et al. 2009, Falkenberg et al. 2012). However, the type II interaction that characterizes this particular grazer-kelp system renders it potentially unstable in the face of perturbation (Murdoch & Oaten 1975, Sinclair et al. 1998). While intact kelp populations with high standing biomass should be more resilient to the indirect impacts of grazing, anticipated climate-mediated increases in the frequency and intensity of bryozoan infestations in Nova Scotia (Scheibling & Gagnon 2009, Saunders et al. 2010) and hurricanes in the North Atlantic (Webster et al. 2005, Bender et al. 2010) should increasingly maintain kelp biomass within a range where *L. vincta* exerts a stronger top-down influence.

Ecosystem shifts in marine systems, such as shifts from kelp- to turf-dominated assemblages, appear to result from drivers that change the balance between production and consumption of key primary producers, which in turn alters their abundance (Burkepile & Hay 2006, Connell et al. 2011, Harley et al. 2012). The replacement of *S. latissima* and other perennial macroalgae by filamentous turf-forming algae along the west and Skagerrak coasts of Norway and Sweden appears to be a consequence of ocean warming and eutrophication that favour both turf-forming algae and epiphytic algae that decrease survival of kelp (Eriksson et al. 2002, Andersen et al. 2011, Moy & Christie 2012). In South Australia, pervasive turfs that replace kelp forests (*Ecklonia radiata*) are facilitated by nutrient enrichment (Gorman et al. 2009), which may be exacerbated by synergism with future ocean warming and acidification (Russell et al. 2009, Connell & Russell 2010). Though this system generally lacks strong herbivory (Connell et al. 2011), molluscan grazers have some capacity to mediate turf expansion (Russell & Connell 2005, Falkenberg et al. 2014). Eutrophication also has caused the proliferation of ephemeral and filamentous algae in shallow subtidal habitats of the Baltic Sea, which is exacerbated by cascading effects of overfishing that decrease the abundance of invertebrate grazers (Eriksson et al. 2009). In contrast, subtidal fucoid algae in other areas of the Baltic and intertidal fucoids in Nova Scotia may be replaced by ephemeral algae following eutrophication even when grazers of the microscopic stages of ephemeral algae are present (Worm & Lotze 2006). My study highlights a special case where conditions that increase top-down control facilitate turf-forming algae because the dominant herbivore is a grazer of the canopy-forming species. These examples indicate that an understanding of the context-dependence of top-down and bottom-up forces, and the conditions that disrupt their relative strengths, is required to predict shifts from canopy- to turf-dominated assemblages on rocky reefs (Burkepile & Hay 2006, Connell et al. 2011).

I have shown that large-scale disturbances that defoliate kelp beds can lead to increased densities of *L. vincta* on kelp and thus intensified grazing on surviving individuals, which could reinforce or accelerate the depletion of kelp and facilitate growth of turf-forming algae. Shifts to turf-dominance likely impair important ecosystem functions attributed to kelp beds including high primary production (Krumhansl & Scheibling 2011a), habitat provision to important commercial species (Wharton & Mann 1981), and the flow of energy and resource subsidies to less productive adjacent communities via kelp detritus (Filbee-Dexter & Scheibling 2012, Kelly et al. 2012, Krumhansl & Scheibling 2012). Owing to the non-independent interaction between large-scale disturbances and local-scale grazing dynamics described here, projected climate-mediated declines in kelp biomass and detrital production (Krumhansl et al. 2014) may occur more rapidly than predicted. My results underscore the importance of considering the potential for anthropogenic impacts to modify natural biological perturbations through ecologically mediated interactions when making an integrative assessment of how various drivers of ecosystem change combine across global, regional, and local scales.

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CHAPTER 3

NIPPED IN THE BUD: MESOGRAZER FEEDING PREFERENCE CONTRIBUTES TO KELP DECLINE[*]

3.1 ABSTRACT

Small invertebrate grazers can disproportionately affect plant fitness by discriminately consuming valuable tissues, but the context and attendant consequences of this activity at higher levels of ecological organization rarely are considered. To assess the impact of a gastropod mesograzer *Lacuna vincta* on fecundity and potential reproductive output of the habitat-forming kelp *Saccharina latissima*, I measured the intensity and distribution of grazing damage on kelp blades at 5 sites of varying kelp density, during the annual reproductive peak (October–November) in Nova Scotia. I found most grazing damage on reproductive individuals consisted of superficial excavations, and was concentrated on the central sorus (region where sporangia develop) compared to the vegetative blade margins. Grazing intensity on sori (% grazed) averaged 29.6% across sites and sampling periods. The distribution of grazing on non-reproductive individuals was opposite to that of reproductive ones, indicating that snails shift feeding from blade margins to the centre as sori develop. Choice and no-choice feeding assays in the laboratory revealed that focused grazing on sori is likely due to an active feeding preference for sporogenous over vegetative tissue. This preference was correlated with the distribution of chemical defense between tissues (phlorotannin content was ~2.5 times higher in vegetative tissue than sori), but not nutritional quality (no difference in C/N ratio). I deduce, with support from histological observations, that consumption of sorus

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O’Brien JM, Scheibling RE (2016) Nipped in the bud: mesograzer feeding preference contributes to kelp decline. Ecology 97:1873–1886 tissue by *L. vincta* reduces fecundity of *S. latissima*. Extrapolating my results to estimate potential reproductive output within kelp beds suggests that spore supply and recruitment limitation may be predominantly imposed by the scarcity of reproductive individuals in the most degraded kelp beds. However, loss of reproductive output to grazing could extend recruitment limitations that impede recovery of waning kelp populations in Nova Scotia.

3.2 INTRODUCTION

The capacity of herbivores to alter abundance and distribution of primary producers, with attendant consequences for ecosystem structure and function, is well established (Lubchenco & Gaines 1981, Crawley 1983). However, a complex suite of plant (e.g. structural or chemical defenses, nutritional value), herbivore (e.g. size, density, mobility, preferences) and environmental characteristics mediates the strength of this important interaction (Lubchenco & Gaines 1981). Consequently, evaluating the impact of an herbivore on individual plant fitness may be difficult without detailed knowledge of these particulars. For example, small invertebrate herbivores like insects can affect plant fitness disproportionately to their size and total tissue consumption when grazing is concentrated on flowers directly (Krupnick & Weis 1999) or on foliage of adjacent branches that contribute to seed production due to plant sectoriality (Marquis 1992). The latter can be ameliorated by induction of secondary chemicals that disperse grazing (Marquis 1992). Mapping the effects of small herbivores on individual plant fitness, deduced from controlled laboratory experiments or variable field conditions, to impacts at the population or community level likely introduces further complexities and context-dependencies.

Mesograzers are a diverse group of small (~ 0.1 – 2.5 cm) marine invertebrate herbivores (isopods, amphipods, gastropods, etc.) that have eluded generalizations (Brawley 1992). Many mesograzers naturally occur at high densities (1000s per m^2), but their small size and short life span may effectively limit their ability to overgraze habitat-forming macrophytes (Brawley 1992; but see Tegner & Dayton 1987). Compared to large mobile grazers, such as fish, sea urchins and crabs, direct consumption of macrophyte tissue by mesograzers often is relatively minor (Johnson & Mann 1986, Poore et al. 2014). However, the associated cost of herbivory to individual plants is a function of both the amount and distribution of consumption (Lubchenco & Gaines 1981, Poore 1994). The uneven spatial distribution and indirect effects of partial grazing damage, characteristic of mesograzers, have complicated evaluation of their impacts (Poore et al. 2014), but certain principles are useful starting-off points for future efforts.

Indirect effects of mesograzers on habitat-forming macrophytes often exceed tissue losses from direct consumption (Black 1976, Johnson & Mann 1986, Krumhansl & Scheibling 2011b) and relate to the division of grazing between macrophytes and smaller primary producers, and among tissues within macrophytes. Mesograzers can both reduce or enhance plant growth rates and biomass by removing photosynthetically active tissue (Van Alstyne 1990, Poore et al. 2014) or epiphytes (Howard & Short 1986, Reynolds et al. 2014) respectively. Likewise, some mesograzers excavate macrophyte tissue, facilitating grazing by other species (Molis et al. 2010), while others facilitate macrophytes by grazing competitors (Falkenberg et al. 2014). By concentrating hydrodynamic forces that initiate breaks (Krumhansl et al. 2011), grazing scars also augment gradual erosion of macrophyte tissue (Krumhansl & Scheibling 2011a) or cause abrupt and substantial tissue loss through fragmentation (Krumhansl & Scheibling 2011b). Depending upon whether damage and subsequent tissue loss is confined distally or occurs at key basal structures (e.g. stipes), mesograzers can promote (Black 1976, de Bettignies et al. 2012) or reduce (Black 1976, Duggins et al. 2001) macrophyte survival respectively, in strong hydrodynamic regimes. Damage to tissues that contribute largely to growth and reproduction (e.g. meristems, sporangia, gametangia) also is predicted to bear further fitness consequences. Therefore, information on the intensity and distribution of grazing, as well as feeding preferences, is requisite to delineating the diverse roles of mesograzers.

Tissues contributing more to individual fitness, such as reproductive structures, are expected to be more heavily defended against herbivory (Rhoades 1979). Compared to vegetative tissue, the sporogenous tissue of kelps (order Laminariales) commonly contains higher concentrations of phlorotannins (Steinberg 1984, Van Alstyne et al. 1999b, Pansch et al. 2008), a group of brown-algal polyphenolic compounds that can deter feeding by gastropods and other invertebrate grazers (Geiselman & McConnell 1981, Steinberg et al. 1995). However, reproductive structures may have higher nitrogen content (Pansch et al. 2008), making them potentially more attractive to nitrogen-limited herbivores (Mattson 1980). Certain mesograzers discriminate between food items of differing nutritional quality (Cruz-Rivera & Hay 2000), but the interplay with chemical defenses is complex (Cruz-Rivera & Hay 2003). Because mesograzers can be contextually deterred by or attracted to valuable macrophyte tissues (Steinberg 1984, Pansch et al. 2008), coincident measures of within-plant distribution of grazing damage and plant characteristics, such as chemical defense and nutritional quality, are beneficial.

The distribution of grazing, chemical deterrents, and nutritional qualities among tissues of habitat-forming brown algae (orders Laminariales, Fucales) have been largely considered in the context of herbivore resistance and defense theory (e.g. Steinberg 1984, Pavia et al. 2002, Pansch et al. 2008), and thus from the perspective of individual plant fitness. However, indirect effects of mesograzers on fitness of macrophytes also must be placed in the ecological context of their populations. As a first step, Toth et al. (2007) evaluated the fitness consequences of chemical defense and snail grazing on individuals in a natural seaweed population. However, the consequences of reductions to individual growth, survival, or fecundity, once integrated to population metrics (productivity, abundance, reproductive output), may vary with context. For example, population-level impacts may be more severe in macrophyte stands recovering from intense perturbation, compared to dense stands, due to feedbacks and density-dependent effects on growth, survival, or recruitment. Particularly for habitat-forming brown algae, a more complete perspective on stand structure will require elucidating the density-dependent reproductive processes and feedbacks throughout their complicated life histories (Schiel & Foster 2006). Grazer-induced changes to individual fitness, and in turn to population dynamics of foundation species, such as habitat-forming macrophytes, could bear broad implications for benthic communities.

Evaluating the impact of mesograzers on habitat-forming macrophytes is increasingly pertinent in systems where the predominant, larger grazers have been extirpated or are rare. In the rocky subtidal zone on the Atlantic coast of Nova Scotia, recurrent disease-mediated mortality events remove green sea urchins *Strongylocentrotus* *droebachiensis* from shallow water (Feehan et al. 2012). The gastropod *Lacuna vincta* currently is the primary grazer of the dominant canopy-forming kelp *Saccharina latissima*. The small fraction of available tissue removed by this mesograzer is not evenly distributed within kelp thalli. The intercalary meristem is defended heavily with phlorotannins, lower in nutritional quality, and largely avoided, as is the tough, less nutritious stipe (Johnson & Mann 1986). Most damage is concentrated in the blade margins and distally where tissue toughness is lowest and nutritional quality highest, increasing indirect tissue losses from these regions (Johnson & Mann 1986, Krumhansl & Scheibling 2011a,b). The seasonal peak in snail size structure and grazing intensity in the fall (Johnson & Mann 1986, Krumhansl & Scheibling 2011b) also coincides with the seasonal development of sporogenous tissue on kelp blades localized within central sori. Most spore production by *S. latissima* occurs from October to November (Chapman 1984), but the distribution of grazing damage among sporogenous and vegetative tissues at this time, when it could have an acute impact on kelp fitness and population dynamics, is unknown.

Here, I evaluate the impact of grazing damage by *L. vincta* on individuals and populations of *S. latissima* during its annual reproductive peak by surveying kelp beds at 5 sites over this 2-month period. To evaluate impacts on individual kelp fecundity, I measure the grazing intensity on sori and compare the within-blade distribution of grazing between individuals with and without sori. I complement field measures with feeding assays and tissue-specific measurements of C/N ratio and phlorotannin content in the laboratory. I predict that the distribution of grazing damage within reproductive kelp blades in the field can be explained by the feeding preference of *L. vincta* between sporogenous and vegetative tissues, and that both grazing damage and feeding preference are correlated with between-tissue variation in nutritional quality or chemical defense. With the ultimate aim to extend predictions to the population level, I infer consequences of superficial grazing damage for individual kelp fecundity by examining cell layers of kelp sori using histology. Finally, I combine measures of sorus area grazed and density of reproductive individuals with available information on sporangial density per sorus area to estimate potential reproductive output of kelp beds and assess the relative impacts of losses to grazing and decreasing kelp abundance on this output and consequences for recruitment. I hypothesize that loss of reproductive output due to grazing will be more critical as kelp abundance wanes as it further depletes density-dependent spore supply.

3.3. MATERIALS AND METHODS

3.3.1 Surveys and Kelp Collections during Reproductive Peak

To assess the impact of grazing by *L. vincta* on the fecundity and potential reproductive output of the kelp *S. latissima* during its annual reproductive peak in Nova Scotia (Chapman 1984), I conducted SCUBA-based surveys on 5 subtidal reefs in October and November 2013. The sites, spanning 31.5 km of coast (linear distance) from the mouth of Halifax Harbour to the mouth of St. Margarets Bay, covered a range of expected grazing intensities (Krumhansl & Scheibling 2011b) and included: Cranberry Cove (44° 30.005' N, 63° 55.379' W), Duncan's Cove Exposed (44° 29.837' N, 63° 31.404' W), Duncan's Cove Protected (44° 29.875' N, 63° 31.583' W), Sandy Cove (44° 27.758' N, 63° 42.420' W), and Splitnose Point (44° 28.641' N, 63° 32.804' W). At each sampling period, the number of reproductive (i.e. mature sorus developed) and non-reproductive individuals ≥ 20 cm total length were counted along a 30-m transect at 4 – 8 m depth, either within a 2-m swath if kelp density was ≤ 5 thalli m^{-2} or in ten 0.5-m^2 quadrats at random transect positions at greater kelp density. Subsequently, 8 – 12 reproductive individuals and 4 – 9 non-reproductive individuals within a similar size range were collected adjacent to the transect, transported in closed bins on ice to the laboratory, and held in flow-through seawater tanks no more than 72 h until additional measurements could be made (see next section). Due to logistical constraints, Cranberry Cove was not sampled in November.

3.3.2 Intensity and Distribution of Grazing Damage within Kelp Blades

To evaluate the intensity of grazing damage on sori and the distribution of grazing damage within collected reproductive individuals, kelp blades were mounted between 2 Plexiglas® sheets, illuminating from behind the section where a mature sorus had developed on one randomly selected side of the blade (Appendix C: Fig. C1A). I traced all grazing damage within this blade section on clear acetate sheets, distinguishing between superficial excavations (Appendix C: Fig. C1B) and full perforations of the blade (Appendix C: Fig. C1A). I also delineated the boundaries of the central sorus and the margins of the vegetative portion of the blade adjacent to it. After photographing and digitizing tracings, I obtained the following measurements using ImageJ (National Institutes of Health): area of sorus (cm^2), area of vegetative blade adjacent to sorus, and total area of grazing excavations and perforations within these blade regions. I then calculated the grazing intensity on sori as percentage of sorus area grazed.

To compare the within-blade distribution of grazing damage between kelp blades with and without a sorus, I traced and measured as above the grazing damage on non-reproductive kelp blades within a section of the blade corresponding to the position of the sorus on reproductive individuals. I further subdivided this blade section into a central region proportional in size to the average area represented by the sorus on reproductive individuals from that site and sampling period and a region combining both blade margins. Using individual measurements obtained from reproductive and non-reproductive kelp blades, I calculated the following grazing index adapted from Johnson & Mann (1986) for both blade regions (centre and margins):

$$G_i = \left(P_i / \overline{P}\right) \cdot \left(T_i / \sum T_i\right)$$

where G_i is the grazing index for region i, P_i is the proportion of region i grazed by *L. vincta* (the total area of grazing excavations and perforations in region i divided by the total area, T_i, of region i), and $\overline{P}$ is the average proportion grazed by snails for both regions. This index weights damage in each region by the relative size of the region, is independent of the total amount of grazing damage, and reflects the distribution of damage among regions.

3.3.3 Laboratory Feeding Experiments

To ascertain whether the distribution of grazing damage within reproductive kelp blades observed in the field can be explained by grazer preferences for specific tissues I conducted no-choice and choice feeding assays in the laboratory. Reproductive kelp (*S. latissima*) and snails (*L. vincta*) were collected at Splitnose Point from 6 – 8 m depth 1 or 2 days before each experiment, transported in closed bins to the laboratory and placed in flow-through seawater holding tanks. Snails were allowed to feed *ad libitum* on the kelp from which they were collected.

In the no-choice assay, I excised replicate circular kelp tissue samples (3.4 cm diameter; 1 per blade) from either the sorus (sporogenous tissue) or the adjacent blade margin (vegetative tissue; Appendix C: Fig. C1A). Tissue samples were photographed on each side while illuminated from beneath and placed separately in cylindrical, perforated feeding arenas (10 cm diameter, 8 cm height; 2-mm perforations and 1-mm mesh top). Half the feeding arenas for each tissue type were randomly assigned to a treatment with 4 snails 3 – 6 mm in shell height (n = 4 per tissue type). The other half served as autogenic controls with no snails (n = 4). Arenas with samples were uniformly positioned (~ 10 cm spacing) in a seawater table (135 × 70 × 14 cm) with a continuous flow (~ 14 L min^{-1}) of ambient seawater, where they were maintained for 6 d (13 – 19 November 2014). At the end of the experiment, tissue samples were re-photographed to determine the change in the total area grazed (cm^2) between days 1 and 6 measured using ImageJ. This included changes due to grazing, autogenic changes, and measurement error.

In choice assays, replicate tissue samples were excised along the sorus margin of individual kelp blades and divided to yield 2 equally sized half-discs (1 sporogenous, 1 vegetative). Paired tissue samples were placed in the same feeding arena, providing a choice while keeping the total amount of material consistent with the no-choice assay. Otherwise, the experiment was conducted as described above using the same seawater table. I conducted 2 trials of the choice assay from 6 – 12 November 2013 (n = 10) and 10 – 16 December 2013 (n = 12) respectively.

3.3.4 Biochemical Analyses and Histology

To test the prediction that patterns of grazing and preference would be correlated with tissue-specific variation in nutritional quality and/or chemical defense, I used kelp collected on 9 December 2013, in advance of the second trial of the choice experiment, for separate quantification of C/N ratio and phlorotannin content. Phlorotannin levels in kelp will remain constant for up to 4 d post-collection if tissues are kept cool and moist (Van Alstyne et al. 1999a). Materials were transported less than 2 h in closed bins on ice before storage in flow-through seawater tanks at ambient temperature. Within 48 h of collection, I excised paired sporogenous and vegetative tissue samples free of epibionts from the sorus margin of individual blades of *S. latissima*, 20 – 60 cm from the intercalary meristem to minimize along-blade variations in biochemical qualities, and immediately stored them at -10 °C (C/N, n = 15) or -80 °C (Phlorotannins, n = 20) for subsequent analyses.

C/N tissue samples were oven-dried to a constant weight at 60 °C for 48 h. I then ground dried tissues using a mortar and pestle to a fine homogeneous powder. Approximately 1.5 mg of sample were weighed into tin capsules and carbon and nitrogen content measured with a Costec ECS 4010 CHNSO analyzer using acetanilide as a standard (detection limit = 0.001 mg).

Phlorotannin tissue samples were freeze-dried and ground to a fine powder as above. To extract soluble phlorotannins, I used a variation on methods described in Koivikko et al. (2005). Aliquots of dried tissue (100 mg) from each sample were placed in 5 mL of 70% acetone overnight at 4 °C in darkness with continuous shaking (150 rpm). After centrifugation (10 min at 2700 *g*), I removed 0.05 mL aliquots from the supernatant to quantify phlorotannin content (% dry mass) using a variation on the Folin-Ciocalteu assay (Van Alstyne 1995). I added 1.0 mL each of distilled water and 40% Folin-Ciocalteu reagent (Sigma-Aldrich) to the 0.05 mL aliquots from each sample, gently mixed, and allowed to rest for 5 min. Upon adding 1.0 mL of 2 N Na_2CO_3, samples were incubated for 30 min at 50 °C, after which absorbance was read at 765 nm using a Cary WinUV 4000 spectrophotometer (Agilent Technologies, detection limit =

0.23 mg). Known concentrations of phloroglucinol (1,3,5-Trihodroxybenzene, Sigma-Aldrich) were used to construct a standard curve.

To evaluate the consequences of superficial grazing damage on sori by *L. vincta* for the fecundity of individual kelp thalli, I used histological techniques to examine the cell layers of the sorus of *S. latissima*. On 15 November 2013, reproductive kelp was collected at Sandy Cove from 4 – 8 m depth and transported in closed bins on ice within 2 h to the laboratory. I immediately excised tissue samples (≤ 1 cm^2) from mature sorus tissue that was either undamaged or superficially excavated by *L. vincta* and fixed them in 7% formalin neutralized in seawater for 24 h. Following 2 rinses in 70% ethanol, samples were dehydrated and infiltrated with paraffin wax using a Leica ASP300 tissue processor and embedded in paraffin blocks with a Leica EG1150 embedding centre. I cut embedded samples into 5-µm transverse sections using a Leica RM2255 semi-automatic microtome and mounted them on positively charged slides (Globe Scientific, Inc.). After oven-drying overnight at 37 °C, slides were de-paraffinized with xylene and graded alcohols, stained for 6 min in 0.1% Saffranin, and finally dehydrated with graded alcohols and xylene. I mounted stained slides to cover slips with Cytoseal (Richard-Allan Scientific), examined sorus tissue sections via light microscopy (Zeiss Axioplan2) and took photographs of representative sections using a mounted digital camera (Zeiss AxioCam HRc).

3.3.5 Loss of Kelp Bed Potential Reproductive Output

To estimate the loss of potential reproductive output (spores m^{-2} bottom) within kelp beds due to grazing, I combined individual measures of sorus area, sorus area grazed, and density of reproductive individuals with the average sporangial density on reproductive *S. latissima* reported by Chapman (1984) from a kelp bed in southwestern Nova Scotia in October and November (3.79×10^5 and 3.76×10^5 cm^{-2} of sorus respectively). Assuming (1) equal sorus area (Kain 1975) and equal grazing intensity on both sides of kelp blades, (2) 32 spores per sporangium (Schreiber 1930), (3) the same effect of superficial grazing and full perforations, and (4) non-viability of ingested spores, I estimated the fecundity discounting grazing (F_{-g}, spores individual^{-1}) and loss of fecundity due to grazing (F_g) for each collected individual as:

$$F_{-g} = 2\left(A_t \cdot D_s \cdot 32\right)$$

$$F_g = 2\left(A_g \cdot D_s \cdot 32\right)$$

where A_t and A_g are the total sorus area and sorus area grazed (cm^2) respectively, and D_s is the sporangial density in the month of collection (sporangia cm^{-2} sorus). Averaging these individual estimates for each site and sampling period, I calculated potential reproductive output (spores m^{-2} bottom) discounting grazing (R_{-g}), lost to grazing (R_g), and the difference, which accounts for grazing (R_{+g}), as:

$$R_{-g} = \overline{F}_{-g} \cdot D_r$$

$$R_g = \overline{F}_g \cdot D_r$$

$$R_{+g} = R_{-g} - R_g$$

where D_r is the density of reproductive kelp (individuals m^{-2}) for a given site and sampling period. To assess the relative impacts of grazing damage and decreasing kelp abundance on the potential reproductive output of kelp beds, I plotted estimates of potential reproductive output against the density of reproductive individuals from their respective sites and sampling periods.

3.3.6 Statistical Analysis

All analyses were performed using R statistical software (Version 3.1.3) and IBM SPSS Statistics software (Version 21.0.0.1). Data for Cranberry Cove were excluded from all analyses to achieve designs with no missing cells. I tested the effects of month (October, November) and site (DE, DP, SC, SP) on grazing intensity on sori, as proportion grazed, using beta regression with a logit link. Beta regression is useful for modeling continuous variables restricted to the standard unit interval, like proportions, as it incorporates the natural asymmetry and heteroscedasticity of these data by assuming a more flexible beta distribution (Ferrari & Cribari-Neto 2004). The model is not a special case of generalized linear models, but employs similar principles of relating the expectation of the response to regressors through a linear predictor and link function (Ferrari & Cribari-Neto 2004). Model fitting via Maximum Likelihood estimation of regression parameters was done using the 'betareg' function in the R package 'betareg' (Cribari-Neto & Zeileis 2010). I tested the effects of month, site, and their interaction by comparing hierarchical models using likelihood-ratio tests with the 'lrtest' function in the 'lmtest' R package (Zeileis & Hothorn 2002). Residual diagnostic plots indicated good model fit.

To analyze spatial and temporal trends in the distribution of grazing damage within reproductive compared to non-reproductive kelp blades, I used a split-plot ANOVA testing the effects of 3 between-plot factors and 1 within-plot factor on the index of snail grazing on kelp blades. Between-plot factors were month (fixed: October, November), site (random: DE, DP, SC, SP) and reproductive state (fixed: reproductive, non-reproductive). The within-plot factor was blade region (fixed: centre, margin) of individual kelp blades (random; nested within factorial combination of month, site, and reproductive state). Because the design was unbalanced due to unequal replication, I calculated Type III sums of squares (Quinn & Keough 2002). Untransformed data met the assumption of homogeneity of between-plot treatment variances (Levene's test, $p > 0.05$). However, 2 of 16 between-plot treatment groups did not meet the assumption of normality (Shapiro-Wilk test, $p < 0.05$). As transformation did not improve normality and ANOVA is robust to this assumption (Quinn & Keough 2002), I proceeded with analysis of untransformed data. Because there were only 2 levels of blade region, the assumption of sphericity of the within-plot factor was trivial.

I applied the framework of Peterson & Renaud (1989) for analyzing preference experiments to the no-choice and choice feeding assays. However, due to heteroscedasticity of the data, linear models were fit using generalized least squares, allowing unequal variances. Joint estimation of relative variances and regression parameters via Restricted Maximum Likelihood, and subsequent Wald tests for significance of model terms based on the finite sample F-statistic, were done using the ‘gls’ and ‘anova’ functions in the ‘nlme’ R package, respectively (Pinheiro et al. 2015). For the no-choice assay, I tested the effects of tissue type (sporogenous, vegetative) and herbivore (i.e. snails) presence/absence (fixed factors) on the changes in area of kelp tissue samples grazed (cm^2), allowing herbivore treatments to have unequal variance. Rejection of the null hypothesis of no interaction between tissue type and herbivore presence/absence implies unequal feeding rates between tissue types in arenas with snails. For the choice assays, I tested the effects of herbivore presence/absence and trial (fixed factors) on the differences between paired sporogenous and vegetative kelp tissue samples in the change in area grazed (cm^2), allowing variances to differ between each combination of herbivore and trial. To adjust for the difference in replication between trials 1 and 2, I used Type III sums of squares in tests of model terms. Diagnostic plots indicated appropriate dispersion of residuals and fit of models.

The differences between paired sporogenous and vegetative kelp tissue samples in C/N ratio and phlorotannin content (% dry mass) each were analyzed using paired *t*-tests. In both cases, the assumption of normality was met (Shapiro-Wilk test, $p > 0.05$).

3.4 RESULTS

3.4.1 Intensity and Distribution of Grazing Damage within Kelp Blades

During October and November, the peak months of reproduction for *S. latissima*, mature sori were grazed by *L. vincta* at all 5 sites (Fig. 3.1). Grazing intensity on sporogenous tissue differed among sites but not between months, and there was no significant interaction between month and site, for the 4 sites sampled in each month (Appendix C: Table C1). Average grazing intensity on sori was consistently highest at Duncan’s Cove Exposed, reaching a peak of 46.4% (± 18.0% SD) in October, and lowest at Splitnose Point (12.2% ± 11.4% in November), with an average across sites and months of 29.6% ± 10.7% (Fig. 3.1). Grazing damage on sori comprised largely superficial excavations; only 2.7% of observations involved full perforations of the blade (Fig. 3.1).

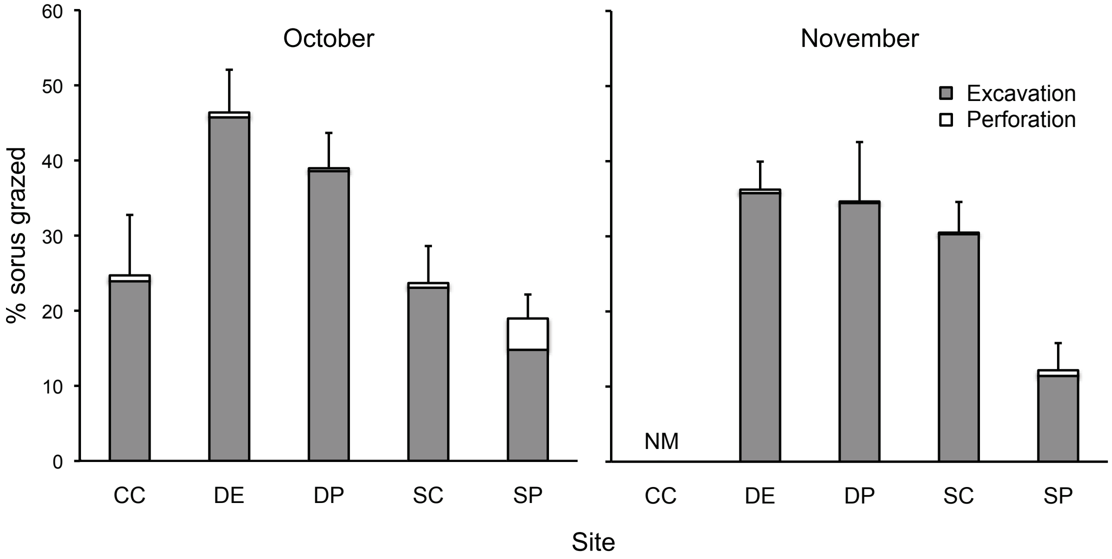

Fig. 3.1. Grazing intensity of *Lacuna vincta* on mature sori of kelp *Saccharina latissima* at 5 sites (Cranberry Cove - CC, Duncan's Cove Exposed - DE, Duncan's Cove Protected - DP, Sandy Cove - SC, Splitnose Point - SP) in Oct and Nov 2013. Data are mean (+ 1 SE) percent of sorus area grazed (n = 8 – 12 individuals in each sampling period). Grey bars are superficial excavations, white bars are full perforations of the blade. NM = not measured.

The distribution of grazing damage within individual kelp blades at this time was strongly dependent on the reproductive state of the individual. A highly significant interaction between blade region and reproductive state indicates that the grazing index for the blade centre relative to the margins was contingent on whether a mature sorus had developed on the blade or not (Table 3.1). On reproductive individuals the index generally was higher for the central sorus, relative to vegetative tissue in the blade margins adjacent, with the exception of Cranberry Cove (October) and Splitnose Point (November) where the index was comparable in both blade regions (Fig. 3.2). In contrast, on non-reproductive individuals the grazing index was consistently higher for blade margins, relative to the central equivalent to the location of the sorus, at all sites and sampling periods (Fig. 3.2). Examination of the simple effects of blade region confirms a directional change in effect with reproductive state (Region | Reproductive = 0.415, $F_{1,6}$ = 79.9, $p < 0.001$; Region | Non-reproductive = -0.685, $F_{1,6}$ = 143, $p < 0.001$).

3.4.2 Laboratory Feeding Experiments

In the no-choice feeding assay, there was no significant interaction between tissue type and herbivore presence/absence (Wald test: $F_{1,12}$ = 0.028, p = 0.870), while the main effect of herbivore was significant ($F_{1,12}$ = 16.8, p = 0.002) indicating that *L. vincta* grazed sporogenous and vegetative tissue samples from *S. latissima* to an equal extent (Fig. 3.3). In contrast, snails grazed a significantly greater area of sporogenous than vegetative kelp tissue (~ 4 to 6 times) in treatment arenas after 6 d ($F_{1,40}$ = 17.6, $p < 0.001$) in the choice assays (Fig. 3.3). Trial had no effect on the difference in area grazed between tissue types ($F_{1,40}$ = 0.004, p = 0.950) and there was no interaction between trial and herbivore presence/absence ($F_{1,40}$ = 0.039, p = 0.845). This consistently higher grazing on sporogenous tissue when snails were provided a choice, given equal grazing on either tissue type in the no-choice assay, is indicative of an active feeding preference for sporogenous tissue. Any changes in area grazed in control arenas (mean ± SD) were negligible (No-choice: -0.002 ± 0.014 cm^2; Choice, Trial 1: 0.115 ± 0.293 cm^2; Trial 2, -0.004 ± 0.008 cm^2) and likely represent measurement error (i.e. misclassification at the start or end of experiment of minimal pre-existing grazing damage).

Table 3.1. Results of a split-plot ANOVA comparing effects of month and site of collection, reproductive state, and blade region on an index of grazing by snails (*Lacuna vincta*) calculated for kelp blades (*Saccharina latissima*) collected from 4 sites (DE, DP, SC, SP; see Fig. 3.1 for site abbreviations) in Oct and Nov 2013.

Source	df	MS	*F*	p
Between plots (i.e. blades)				
Month	1	0.001	0.375	0.584
Site	3	0.004	0.306	0.821
Reproductive state	1	2.11	351	**< 0.001**
Month × Site	3	0.003	0.223	0.880
Month × Reproductive state	1	0.003	0.346	0.598
Site × Reproductive state	3	0.006	0.501	0.682
Month × Site × Reproductive state	3	0.009	0.723	0.540
Individual (Month × Site × Reproductive state)	115	0.012		
Within plots (i.e. blades)				
Region	1	1.15	14.9	**0.031**
Month × Region	1	0.043	0.806	0.436
Site × Region	3	0.077	1.61	0.192
Reproductive state × Region	1	18.4	197	**< 0.001**
Month × Site × Region	3	0.053	1.11	0.347
Month × Reproductive state × Region	1	< 0.001	0.009	0.930
Site × Reproductive state × Region	3	0.094	1.95	0.125
Month × Site × Reproductive state × Region	3	0.049	1.03	0.383
Individual (Month × Site × Reproductive state) × Region	115	0.048		

Note: Significant results ($p < 0.05$) are highlighted in boldface type.

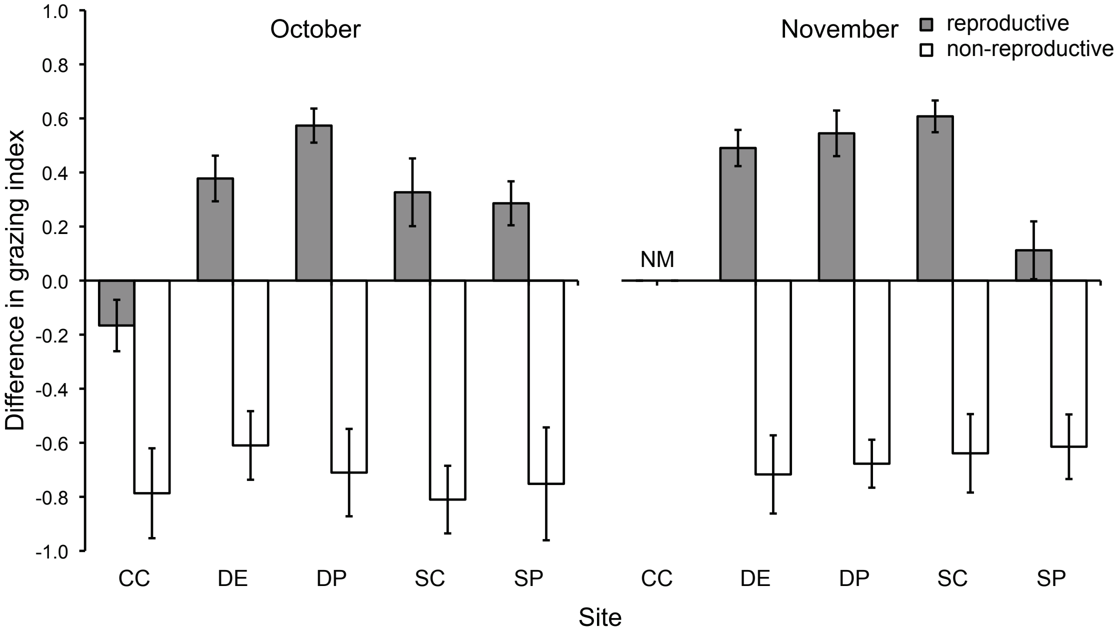

Fig. 3.2. Difference in grazing index (mean ± SE) between central region and margins of individual blades of *Saccharina latissima* (positive values indicate higher index in central region) collected from 5 sites (CC, DE, DP, SC, SP; see Fig. 3.1 for site abbreviations) in Oct and Nov 2013. Grey bars are reproductive individuals with a mature sorus (n = 8 – 12), white bars are non-reproductive individuals (n = 4 – 9). NM = not measured.

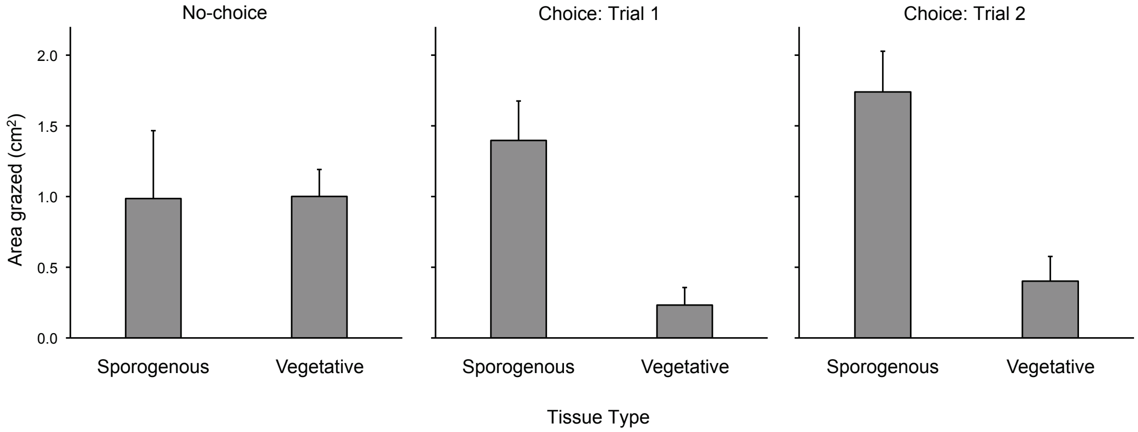

Fig. 3.3. Change in extent of grazing damage from *Lacuna vincta* on kelp tissue samples (*Saccharina latissima*) in feeding arenas after 6 d. Sporogenous tissue from sorus and adjacent vegetative tissue were provided separately (No-choice, n = 4) or paired (Choice: Trial 1, n = 10; Trial 2, n = 12). Data are mean (+ 1 SE) area grazed in arenas with snails (data for control arenas without snails not shown).

3.4.3 Biochemical Analyses and Histology

The mean (± SE) C/N ratio was comparable between sporogenous (24.7 ± 0.9) and vegetative tissue (24.2 ± 0.5) of *S. latissima* with no significant difference between paired tissue samples ($t_{14} = 0.741$, $p = 0.471$). The mean (± SE) phlorotannin content of vegetative kelp tissue (2.6 ± 0.2% dry mass) was ~ 2.5 times that of adjacent sporogenous tissue (1.1 ± 0.1% dry mass; $t_{19} = -8.86$, $p < 0.001$).

Transverse sections through undamaged tissue from the sorus of *S. latissima* revealed 5 cell layers (Fig. 3.4). The central medulla consists of loosely aggregated cells and is flanked on either side by the cortex of large circular cells. Cells decrease in size towards the outer meristoderm of small densely packed cells in several layers containing numerous plastids. An intact layer of oblong sporangia bearing packets of spores emerges tangentially from the basal epidermal cells. These are surrounded by sterile paraphyses. The darkly staining club-shaped tips of the paraphyses form a layer that extends above the sporangia. The structure of sorus tissue that had been superficially grazed by *L. vincta* showed that sporangia and paraphyses had been completely removed leaving the meristoderm mostly intact (Fig. 3.4). Grazing occasionally penetrated further into the meristoderm and cortex.

3.4.4 Loss of Kelp Bed Potential Reproductive Output

My estimates of potential reproductive output indicated that in both months of the reproductive peak of *S. latissima*, at each of the sampled sites, a prodigious number of spores would have been borne by the fecund portion of the kelp population, with potential for release if grazing damage was discounted (Appendix C: Table C2). These ranged from 21.2 to 1140.6×10^{7} spores m^{-2} bottom, at Cranberry Cove (October) and Duncan's Cove Protected (November) respectively. The potential reproductive output at a given site and time decreased with the density of reproductive individuals in the population (Fig. 3.5), which in turn decreased generally with the total density of kelp (Appendix C: Table C2). The density of reproductive individuals varied among the 5 sites (CC < DE < SP < DP, SC) and within one site (Duncan's Cove Protected) between

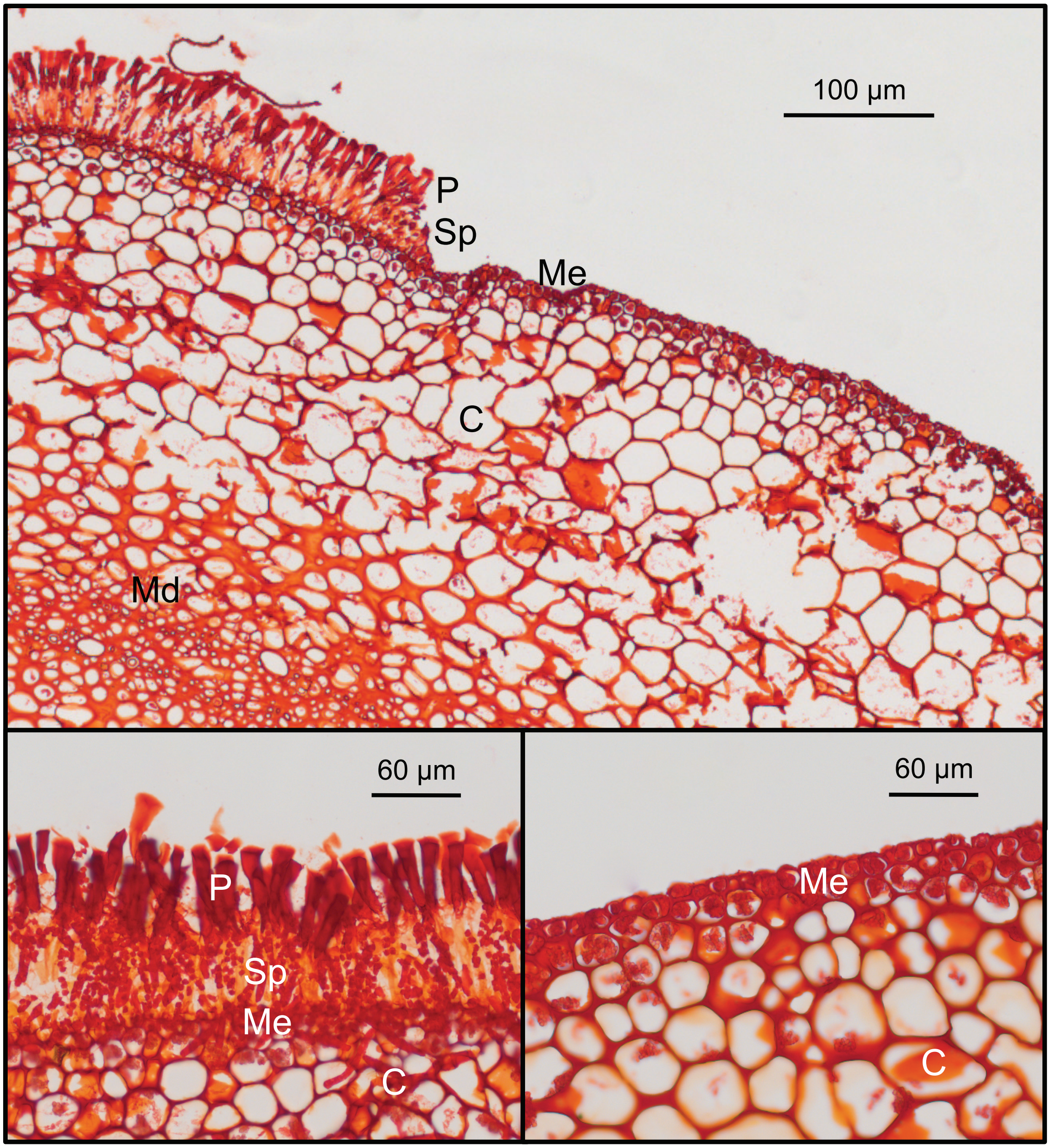

Fig. 3.4. Transverse sections of Saffranin-stained sorus tissue from *Saccharina latissima* undamaged (left) and superficially excavated by *Lacuna vincta* (right). Undamaged sporangia (Sp) and sterile paraphyses (P) disappear sharply at the boundary of a grazing scar (top panel) leaving the underlying meristoderm (Me), cortex (C), and medulla (Md) intact. At higher magnification (bottom panels) it is clear that paraphyses and sporangia are completely removed by grazing.

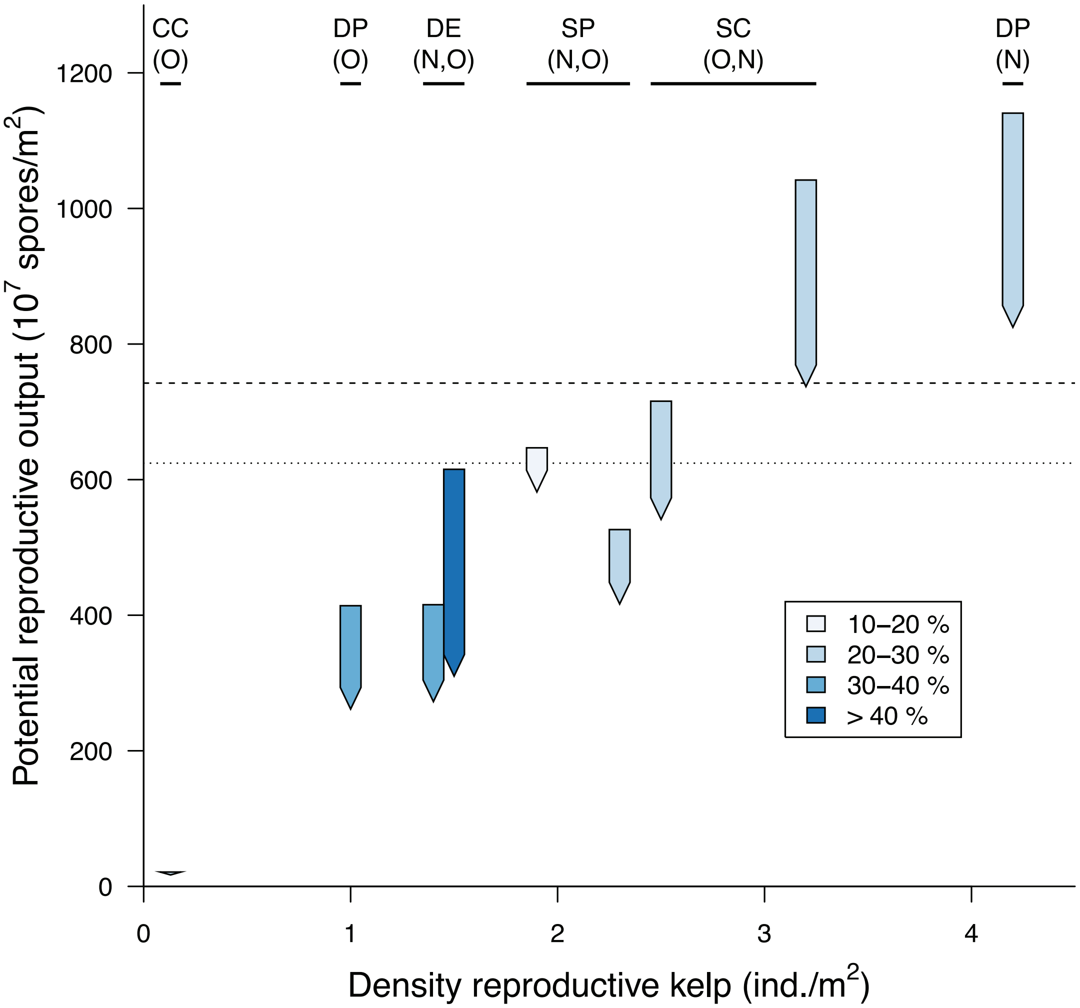

Fig. 3.5. Estimated loss of potential reproductive output (spores m^{-2} bottom) of kelp *Saccharina latissima* due to grazing of sori on reproductive individuals by *Lacuna vincta* at 5 sites (CC, DE, DP, SC, SP; see Fig. 3.1 for site abbreviations) in Oct (O) and Nov (N) 2013. Top of arrow is estimated potential reproductive output discounting grazing damage, tip is output accounting for grazing. Estimates are shown in relation to the density of reproductive individuals (i.e. mature sorus developed) at time of sampling. Blue tone indicates an increasing percentage of potential reproductive output lost to grazing (light to dark). Lines indicate potential reproductive output reported by Chapman (1984) for another Nova Scotia kelp bed in Oct (dashed) and Nov (dotted) 1981, at the reproductive peak.

October and November (Fig 3.5; Appendix C: Table C2). It appeared that some non-reproductive individuals in October at Duncan's Cove Protected had developed sori by November. Grazing of sori by *L. vincta* also contributed to decreases in potential reproductive output, attenuating initial estimates that discounted grazing (Fig 3.5; Appendix C: Table C2). Estimates of potential reproductive output lost to grazing fell within a narrower range (Appendix C: Table C2), but with similar absolute losses of spores representing proportionally greater decreases at lower kelp densities (Fig. 3.5).

3.5 DISCUSSION

3.5.1 Distribution of Grazing on Kelp: Effects of Grazer Feeding Preference and Blade Tissue Quality

Grazing damage by *L. vincta* was unevenly distributed within kelp blades during the seasonal reproductive period of *S. latissima*. This unequal allocation of grazing among macrophyte tissues is characteristic of mesograzers (Poore et al. 2014). Consistent with previous work (Johnson & Mann 1986), most grazing on non-reproductive individuals was concentrated within the vegetative blade margins. A shift towards the blade centre of reproductive individuals represents a previously undocumented reversal in the distribution of grazing with development of the sorus. Changes in the distribution of grazing by *L. vincta*, coincide with other phenological events in the life cycle of *S. latissima*, such as peaks and troughs in growth and phlorotannin production (Krumhansl & Scheibling 2011b). As I predicted, the distribution of grazing damage on reproductive kelp blades was consistent with the feeding preference of *L. vincta*. The propensity of mesograzers to discriminate between macrophyte tissues gives rise to the potential for indirect and disproportionate effects of partial grazing on individual fitness (Poore 1994, Poore et al. 2014). The active feeding preference for sporogenous tissue observed here suggests that partial grazing damage disproportionately affects kelp fitness by reducing fecundity.

I did not find evidence to support my prediction that the feeding preference of *L. vincta* and the distribution of grazing damage within reproductive kelp blades in the field would be correlated with tissue-specific variation in nutritional quality. Although the distribution of grazing by *L. vincta* among thallus regions of non-reproductive *S. latissima* is correlated with variation in nutritional quality (Johnson & Mann 1986), the C/N ratios of sporogenous and vegetative tissue of reproductive kelp measured here were indistinguishable. This is consistent with *S. latissima* in other biogeographic regions (Gevaert et al. 2001) and other kelp species for which nitrogen content or C/N ratio of sporogenous and vegetative tissues have been compared (Steinberg 1984, Molis et al. 2010). Even in kelp species where nitrogen content is higher in sporogenous tissue, this is not always consistent with the feeding preferences of mesograzers (Pansch et al. 2008). However, as with other kelps, the spores of *S. latissima* contain large reserves of storage lipids (Steinhoff et al. 2011). Like some other marine herbivores, the feeding preference of *L. vincta* for sporogenous tissue may correlate more with lipid or caloric content than nitrogen (Prado & Heck 2011).

As I predicted, the preference of *L. vincta* for sporogenous tissue was consistent with the distribution of phlorotannins among tissues. Phlorotannin content was higher in vegetative tissue compared to the preferred sorus. *L. vincta* avoids consumption of other chemically defended tissues of *S. latissima* (Johnson & Mann 1986), and the concentration of phlorotannins in the vegetative blade margins measured here is sufficient to deter grazing by gastropods (Geiselman & McConnell 1981). This distribution of chemical defenses is perhaps counterintuitive. Optimal defense theory postulates that defenses are produced by plants at a cost and allocated to tissues, such as reproductive structures, that contribute most to individual fitness (Rhoades 1979). Indeed, many kelps allocate more phlorotannins to sori and sporophylls than to non-meristemic vegetative tissue (Steinberg 1984, Van Alstyne et al. 1999b, Pansch et al. 2008). My results are more consistent with fucoid brown algae in which reproductive tissue often is less defended than vegetative tissue (Tuomi et al. 1989, Van Alstyne et al. 1999b). Predictions of the optimal defense theory often are contingent on subjective assessments of the fitness value of various tissues (Van Alstyne et al. 1999b, Pavia et al. 2002). It has been suggested that for kelps with an ontogeny akin to *S. latissima*, reproduction is dependent on production and maintenance of the vegetative blade that bears the developing sorus (Johnson & Mann 1986, Pansch et al. 2008). Thus, additional fitness value and necessity for herbivore resistance are conferred to vegetative blade tissue. The pattern I observed also is predicted by the growth-differentiation balance hypothesis due to a trade-off between growth and defense production in actively growing tissues (Herms & Mattson 1992).

3.5.2 Effects of Grazing on Fecundity, Reproductive Output and Resilience of Kelp Beds

Selective consumption of reproductive structures by mesograzers is not necessarily detrimental to macrophyte fitness. Amphipods in the genus *Hyale* preferentially consume cystocarpic tissue of red algae in the genus *Iridaea*, but in the process tear open cystocarps and release carpospores that might otherwise remain on fronds (Buschmann & Santelices 1987, Buschmann 1991). These amphipods also may disperse carpospores that stick to appendages or survive digestion (Buschmann & Santelices 1987, Buschmann & Bravo 1990). While I found most grazing damage on kelp sori consisted of superficial excavations, it is unlikely that *L. vincta* facilitates the release of spores from sporangia. Histology indicated sporangia were completely removed rather than torn open. The possibility remains that *L. vincta* could disperse ingested spores in fecal pellets. However, the capacity of propagules of late succession, perennial macroalgae to survive digestion by molluscan herbivores is very low to non-existent (Santelices & Correa 1985, Santelices & Ugarte 1987). Therefore, even superficial excavations of kelp sori by *L. vincta* could effectively reduce individual fecundity by rendering ingested spores non-viable.

The impact of *L. vincta* on individual kelp fecundity appears to be more severe at some sites than others. I found that grazing intensity by *L. vincta* on sori of *S. latissima* remained constant throughout the reproductive peak, but with consistent between-site differences. Spatial variability in grazing intensity by mesograzers can arise on scales of metres to kilometres due to patchiness in grazer abundance (Graham 2002, Krumhansl & Scheibling 2011b, Poore et al. 2014). Because the indirect effects of partial grazing may increase as linear (Poore et al. 2014) or stepwise functions of grazing intensity (Krumhansl & Scheibling 2011b), these too are not expected to be uniform among individuals and sites. Kilometre-scale variability in overall grazing intensity on kelp by *L. vincta* arises from negative relationships with both site exposure (Krumhansl & Scheibling 2011b) and kelp abundance (Chapter 2). Therefore, I might expect indirect effects to be amplified as kelp abundance wanes, particularly within sheltered sites and embayments. Grazing intensity on sori and concomitant loss of fecundity was consistently lower at my most exposed site (Splitnose Point) compared to the most protected (Duncan's Cove Protected), and consistently highest at Duncan's Cove Exposed where reproductive and overall kelp density were lower (Fig. 3.1; Appendix C: Table C2). Furthermore, spores lost to grazing represented a greater proportion of the potential reproductive output from within kelp beds where density was low.

Loss of individual fecundity and potential reproductive output within kelp beds portend changes in population resilience and community structure. Subtidal reefs on the Atlantic coast of Nova Scotia, particularly in protected embayments, have seen a decades-long decline in abundance of kelp giving way to communities dominated by turf-forming and invasive macroalgae (Filbee-Dexter et al. 2016). Canopy recovery is contingent on recruitment from within kelp beds and long distance colonization; both of which directly relate to spore supply. Because the density of settling spores determines whether subsequently germinating microscopic gametophytes are in sufficient proximity for fertilization (Reed 1990), successful sporophyte recruitment hinges on adult sporophyte density and their individual fecundity (i.e. potential reproductive output). By elevating spore densities further into the tails of the dispersal curve, higher reproductive outputs also extend effective colonization distance (Gaylord et al. 2006).

Threshold spore settlement densities necessary for recruitment (Reed 1990), and other potential non-linearities in the relationship between spore density and macroscopic recruitment, make predictions of population impacts from spore losses less certain, although first-order approximations are possible. Chapman (1984) reported potential reproductive output in a Nova Scotian kelp bed during October and November of 742.4×10^7 and 624.3×10^7 spores m^{-2} bottom respectively. After 1 year, 1 macroscopic sporophyte m^{-2} recruited to the benthos on average, providing benchmarks for potential reproductive output sufficient for sporophyte recruitment. At the highest densities of reproductive thalli reported here (3 – 4 individuals m^{-2}), large losses to grazing did not decrease potential reproductive output below these benchmarks (Fig. 3.5). At intermediate densities (1.5 – 2.5 individuals m^{-2}), potential reproductive output discounting grazing was comparable to the benchmarks, but large and proportionally more severe losses to grazing could reduce reproductive output to well below them (Fig. 3.5). At lower densities of reproductive thalli, the estimate of output was already well below the benchmarks when grazing was discounted. Grazing further reduced output, but minimally at the lowest density (0.13 individuals m^{-2}; Cranberry Cove, October) where reproductive output was < 3.5% of the benchmarks (Fig. 3.5). My results suggest spore supply and recruitment limitation may arise at low to intermediate kelp densities. While I predicted that the loss of reproductive output to grazing would be most critical at the lowest kelp densities, reduced spore supply associated with scarcity of reproductive individuals may already be limiting and supersede the loss to grazing at the lower range of kelp density. However, selective consumption of kelp sori by *L. vincta* causes greater relative declines in reproductive output as kelp abundance wanes, and could hamper kelp bed recovery by extending the upper range of kelp density over which spore supply is limiting.

Protracted or stalled recovery is a common phenomenon on other temperate, rocky coastlines where canopy-forming macroalgae have been lost in favour of low-lying filamentous forms (Gorman & Connell 2009, Schiel & Lilley 2011, Moy & Christie 2012). It has been widely documented that a matrix of algal filaments and bound sediments impedes recruitment of canopy-forming algae by limiting propagule establishment (Råberg et al. 2005, Gorman & Connell 2009, Alestra et al. 2014). Mesograzers and larger molluscan herbivores may mediate canopy recovery by countering expansion of turf-forming species (Russell & Connell 2005, Falkenberg et al. 2014). However, recruitment limitation also arises from constraints on propagule supply (Clark et al. 1998). I propose that, where such shifts in community structure have occurred, attrition of the canopy itself imposes supply limitations. My results suggest that mesograzers may hinder recovery by exacerbating these supply limitations. Even relatively minor grazing events have the potential to impose additional consequences for the reproductive output of kelps with diverse reproductive strategies. This can occur through direct consumption of sporogenous tissue of seasonally reproducing species (this study) or through energetic trade-offs with growth and biomass recovery following grazing of vegetative tissue in continuously reproducing kelps (Graham 2002). These divergent possibilities indicate that indirect effects of mesograzers on habitat-forming macrophytes likely depend on the distribution of grazing among and within primary producers.

3.5.3 Conclusions

I have shown that mesograzers (*L. vincta*) can have a disproportionate effect on habitat-forming macrophytes (*S. latissima*), despite incomplete consumption, by discriminately grazing valuable tissues. An active feeding preference for reproductive tissue, inversely correlated with the within-blade distribution of a chemical deterrent, led to a reversal in the distribution of grazing within kelp blades at reproductive maturity. Concentrated grazing on sori at the peak of the reproductive period reduced the fecundity of *S. latissima*. This period coincides with when the largest, fastest-grazing snails dominate the demographic structure of populations of *L. vincta* (Johnson & Mann 1986). Given the small size and short life span of mesograzers relative to their food, my results underscore the necessity of considering the within-plant distribution and timing of grazing. My estimates of reproductive output within kelp beds suggest grazing by *L. vincta*, in combination with loss of reproductive individuals, could impose recruitment limitation as kelp beds become increasingly degraded. The paucity of reproductive individuals may render spore supply critically low in the most degraded beds, while loss of spores to grazing may limit prospects for recovery by imposing limitations even as kelp density increases. Explicating the link between propagule supply and recruitment of habitat-forming macrophytes with complex life cycles, such as kelps, will be imperative to refine the role of *L. vincta* in hampering kelp recovery in Nova Scotia, and the wider role of supply limitation in the continued loss of macroalgal habitats globally.

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CHAPTER 4

RECRUITMENT, TISSUE LOSS, AND SURVIVORSHIP LIMIT RECOVERY OF KELP FOLLOWING LARGE-SCALE DEFOLIATION

4.1 ABSTRACT

Recovery of canopy-forming macroalgae following large-scale degradation is contingent on recruitment processes and subsequent growth and survival. Constraints on propagule supply and establishment reinforce canopy loss in turf-algal assemblages that replace kelps and fucoids, but post-recruitment processes that hinder growth and survival of juvenile individuals (epiphytic overgrowth, grazing, physical stress) also could impede recovery. To investigate the contribution of recruitment, growth, and survival of young sporophytes to recovery of degraded kelp populations, and evaluate the opposing sources of post-recruitment tissue loss and mortality, I followed cohorts of juvenile sporophytes of the dominant kelp *Saccharina latissima* and monitored kelp recruitment, population abundance and structure, and macroalgal composition of the surrounding community, for 5 years following defoliation in 2 formerly abundant populations in St. Margarets Bay, Nova Scotia (The Lodge, Paddy's Head). Large decreases in blade area of juveniles were related to cover by the invasive bryozoan *Membranipora membranacea*, grazing damage by small snails *Lacuna vincta*, and warm temperatures, which collectively skewed the balance between growth and tissue loss. Risk of death for kelp juveniles was relatively constant at The Lodge but increased over time at Paddy's Head, where the median time-at-death was a third of that recorded at The Lodge (108 d vs. 307 d). Reduced survival at both sites was directly related to encrustation by *M. membranacea*, but also associated with warm temperatures. Seasonal increases in abundance of *S. latissima* at Paddy's Head largely were driven by low, episodic recruitment that did not exceed annual losses, sustaining low kelp cover over 5 years. More consistent recruitment and greater survivorship at The Lodge facilitated modest gains in kelp density and cover each year,

especially following an anomalously cold winter to form a sparse canopy in 2015, but these gains were reversed following high peak temperatures in summer/fall 2016. Lack of kelp recovery and persistence of mats of turf-forming, opportunistic and invasive algae at both sites highlight the need to protect intact kelp populations growing in favourable conditions to maintain positive interactions that increase resilience to undesirable regime shifts.

4.2 INTRODUCTION

Stands of canopy-forming brown seaweeds (e.g. kelp, fucoids) on temperate reefs have the capacity to close small ($cm^2 – m^2$) disturbance-generated gaps in the canopy (Kennelly 1987, Gorman & Connell 2009), and regenerate seasonal losses of biomass (Johnson & Mann 1988, Sales & Ballesteros 2012), through growth and recruitment. High growth rates (Mann 1972b), high fecundity (Chapman 1984), and localized dispersal (Dayton et al. 1984, Johnson & Brawley 1998) facilitate these processes and favour persistence of established stands. However, the pervasive impacts of human activity can lead to loss of canopy-forming algae on much larger scales (Benedetti-Cecchi et al. 2001), which is becoming a more common occurrence on temperate rocky reefs. Over the last 50 years kelp abundance worldwide has declined in 38% of ecoregions with available data (Krumhansl et al. 2016). Loss of kelps and other canopy-forming algae increasingly has been associated with the proliferation of low-lying turf-forming algae in the last decade, which fundamentally change the structure and stabilizing feedbacks operating in these communities (Filbee-Dexter & Wernberg 2018). With this greater extent and severity of canopy loss, recovery increasingly is contingent on the ability of new individuals to recruit, grow, and survive in the altered habitat even while the conditions that led to the original degradation persist.

Recovery of kelps and fucoids following extensive canopy defoliation may be limited by constraints on recruitment to macroscopic stages. A low density of reproductive adults in such habitats is predicted to impose limitations on propagule supply and recruitment (Bennett & Wernberg 2014; Chapter 3). For kelps, replenishment from distance source populations is dependent on their abundance and fecundity (Gaylord et al. 2006), or episodic events of high spore release overlapping with strong storms (Reed et al. 1988). Recruitment limitation also results from competition with turf-forming algae that proliferate in canopy-free conditions and pre-empt space, preventing propagules from establishing, or smother early post-settlement stages of canopy algae (Isæus et al. 2004, Gorman & Connell 2009). While mechanistic studies support the prediction of low recruitment following extensive canopy loss, long-term observations of interannual patterns of recruitment to evaluate this prediction and the scope for recovery are limited.

Even where macroscopic recruitment of kelp is successful, physical stress acting on individual sporophytes in canopy-free conditions also could limit capacity for recovery. Kelps are cold temperate and polar species and both gradual ocean warming (Andersen et al. 2013, Filbee-Dexter et al. 2016) and anomalous heat wave conditions (Wernberg et al. 2013) have been implicated in large-scale declines in kelp abundance and lack of recovery in the North Atlantic and off Western Australia respectively. Although various kelp species have shown some capacity to acclimate to warmer seawater temperatures (Davison et al. 1991, Staehr & Wernberg 2009, Andersen et al. 2013), warming beyond the thermal optimum for growth of a species, or its capacity to acclimate, can significantly reduce photosynthetic performance (Andersen et al. 2013), tissue strength (Simonson et al. 2015), and growth and survival (Simonson et al. 2015, Wilson et al. 2015). Furthermore, high light conditions in the absence of kelp canopy can be stressful for recruits and juvenile sporophytes (Toohey & Kendrick 2007). Even if kelps are able to acclimate to warmer temperatures, the necessary metabolic adjustments can reduce the physiological performance and growth of recruits in response to high light conditions, thereby limiting their ability to contribute to canopy recovery (Wernberg et al. 2010).

Post-recruitment constraints that limit recovery of kelp populations also can arise from biological interactions that mediate survival or the balance between growth and tissue loss. Extensive epiphytic growth on kelps may limit rates of nutrient uptake (Hurd et al. 1994) and photosynthesis (Cancino et al. 1987), and increase drag (Anderson & Martone 2014) and tissue loss from breakage and erosion (Dixon et al. 1981, Krumhansl & Scheibling 2011a). High epiphyte loads are expected under warmer (Scheibling &

Gagnon 2009, Bennett & Wernberg 2014) and more eutrophied coastal conditions (Worm & Sommer 2000, Worm & Lotze 2006), and have been associated with extensive loss of kelp canopy and sporophyte mortality in degraded habitats along the Skagerrak coast of Norway (Andersen et al. 2011), where *Saccharina latissima* has been replaced by turf algae (Moy & Christie 2012). Herbivory can cause a population bottleneck for kelps when grazers, such as gastropods, kelp crabs, and sea urchins, selectively consume juvenile sporophytes (Dean et al. 1984, Chenelot & Konar 2007, Dobkowski 2017). While larger adult sporophytes may reach a size refuge from grazing (Lubchenco 1983), smaller juveniles may be particularly vulnerable to grazing-induced tissue loss (Dobkowski 2017) and mortality (Franco et al. 2017). Furthermore, intensified grazing on the few remaining individuals following canopy defoliation can reinforce or accelerate the transition to a turf algae-dominated state (Bennett et al. 2015b; Chapter 2).

Along the Atlantic coast of Nova Scotia, large-scale declines in kelp abundance associated with 3 decades of ocean warming (Scheibling et al. 2013) and the introduction of the invasive encrusting bryozoan *Membranipora membranacea* in the early 1990’s (Scheibling et al. 1999) have driven large-scale changes in community structure to reefs dominated by turf-forming and invasive algae (Filbee-Dexter et al. 2016). Growth rate and tissue strength of the dominant kelp *Saccharina latissima* decline at seawater temperatures > 14 ºC, and tissue loss and mortality increase at > 18 ºC (Simonson et al. 2015). Prolonged encrustation by *M. membranacea* reduces kelp tissue strength (Krumhansl et al. 2011), increasing the likelihood of blade erosion and breakage with wave action (Krumhansl & Scheibling 2011a), which has led to recurrent defoliation of kelp canopy during severe outbreaks of the bryozoan (Scheibling & Gagnon 2009). Grazing by the small gastropod *Lacuna vincta* also weakens blade tissue (Krumhansl et al. 2011) and indirectly contributes to canopy loss through increased erosion and fragmentation with wave action (Krumhansl & Scheibling 2011a,b). However, grazing has not been explicitly linked to reduced survivorship. While this body of research provides a mechanistic understanding of how various physical and biological factors might limit kelp bed recovery, an understanding of how the combined effects of these factors are integrated over the lifespan of an individual thallus is impeded by the lack of a longitudinal perspective in a field context.

In this study, I investigate the potential contribution of recruitment, growth, and survival of young sporophytes to recovery of degraded kelp populations, and evaluate the countervailing sources of post-recruitment tissue loss and mortality. I track the fate of cohorts of juvenile (30 – 50 cm) sporophytes of *Saccharina latissima* in 2 formerly abundant kelp populations within a large embayment (St. Margarets Bay) on the central Atlantic coast of Nova Scotia, following extensive canopy loss. I relate tissue loss and mortality of these cohorts to ongoing community-level shifts by measuring seasonal and interannual patterns of kelp recruitment, population abundance and size structure, and macroalgal composition over the next 5 years. Based on predictions of 1) low recruitment rates and 2) high rates of tissue loss and mortality of young sporophytes, associated with physical (warm temperatures, wave forces) and biological (encrustation by *M. membranacea*, grazing by *L. vincta*) factors that weaken tissue strength, I hypothesized that a degraded community state, characterized by low kelp abundance and pervasive mats of turf-forming, opportunistic and invasive algae, would persist.

4.3 MATERIALS AND METHODS

4.3.1 Site Descriptions

I made recurring observations on rocky, subtidal reefs from June 2012 to August 2017 at 2 moderately exposed sites near the mouth of St. Margarets Bay (SMB) on the Atlantic coast of Nova Scotia: The Lodge (44° 33.491' N, 64° 01.493' W) and Paddy's Head (44° 31.624' N, 63° 57.080' W; see Fig 1.1). These sites were selected because of a long history of previous research on kelp canopies, which were extensively defoliated at the onset of my study (Fig. 4.1A). The Lodge is located on the western shore of SMB and 7 km from Paddy's Head on the opposite shore. The substratum at The Lodge consists of gently grading granitic bedrock with small to medium sized boulders and small sand patches to 18-m depth (Chart Datum). At Paddy's Head, sloping bedrock, raised ledges, and medium- to large-sized boulders grade to sand at 6-m depth.

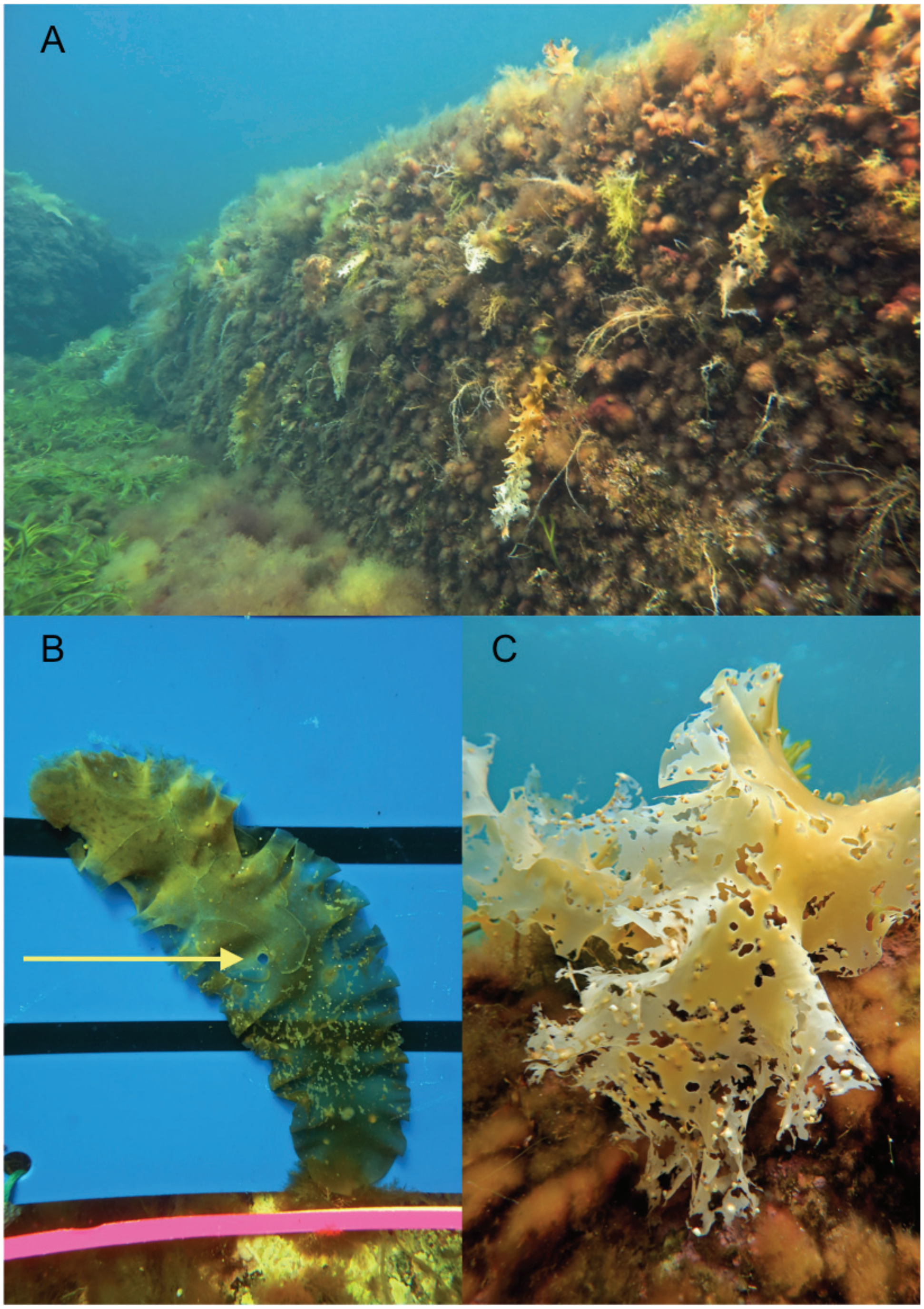

Fig. 4.1. A) Extensive cover of turf algae with scattered kelp (*Saccharina latissima*) and small patches of invasive green alga *Codium fragile* ssp. *tomentosoides* (left background) at Paddy's Head. B) Tagged juvenile sporophyte, encrusted on distal end by *Membranipora membranacea*, pressed between a transparent acrylic sheet and a blue backboard with graduation markings at 10-cm intervals. Yellow arrow identifies hole-punch to measure growth. C) Kelp frond densely populated by *Lacuna vincta* and heavily perforated by grazing damage. *Photo credit*: R.E. Scheibling.

To facilitate continuing observations, I established fixed plots at each site marked by a numbered float or tag attached to a central eyebolt anchored with marine epoxy (Z-Spar A-788 Splash Zone Compound) to the rock substratum. At The Lodge, 33 plots in rows of 8 (1 row of 9) ran parallel to the shore along 4 depth strata between 7 and 10 m (Chart Datum). Adjacent rows were offset to maintain 7 m between plot centres. At Paddy's Head, 12 plots were haphazardly placed between 4 and 6 m depth to reflect the varied bathymetric features of the site (boulders, bedrock, ridges).

4.3.2 Growth and Survival of Kelp Juveniles

To investigate the potential for new individuals to contribute to kelp bed recovery through growth and survival, I tracked cohorts of juvenile (30 – 50 cm thallus length) sporophytes of the dominant kelp, *Saccharina latissima*, at each site. On 8 and 12 June 2012, SCUBA divers tagged 64 juveniles at The Lodge and 51 at Paddy's Head, respectively. Only individuals not encrusted by *Membranipora membranacea* and with minimal grazing damage were selected. Plants were uniquely identified with a numbered tag attached to an eyebolt anchored immediately adjacent to the plant. I selected one individual to the north and south of each plot at The Lodge and at least 1 m from the plot centre to minimize contacts with divers working in the plots (see section 4.3.3). Tagged plants at Paddy's Head were scattered haphazardly in the area between and within plots.

To evaluate survivorship of juveniles, I conducted censuses of tagged individuals at approximately monthly intervals from June to October 2012 at Paddy's Head and from June to November 2012 and April to November 2013 at The Lodge. The presence of a broken stipe or absence of a holdfast immediately adjacent to the numbered tag provided unambiguous evidence of mortality. Dislodgement of tags resulted in those individuals becoming right-censored from the cohort, although tag loss was rare at both sites (2 at The Lodge and 1 at Paddy's Head). To document the fate of each tagged plant and relate survivorship to levels of encrustation by *M. membranacea* (Fig. 4.1B) and grazing damage by *L. vincta* (Fig. 4.1C), I took repeated, high-resolution photographs *in situ* with an underwater camera (Canon S100). On each sampling date, divers lightly pressed each photographed plant between a transparent acrylic sheet and a blue backboard for contrast with graduation markings at 10-cm intervals (Fig. 4.1B). I used image analysis software (ImageJ, National Institutes of Health, USA) to measure changes in blade surface area (cm^2) and the percent of the blade area perforated from grazing by *L. vincta* or encrusted by *M. membranacea* on one haphazardly selected side of the blade.

To measure rates of blade growth (linear extension from intercalary meristem) and gross tissue loss (from distal end), I used a hole-punch technique (Krumhansl & Scheibling 2011a). On each sampling date, a small hole (0.5 cm diameter) was punched 10 cm above the junction of the stipe and blade of each tagged plant (Fig. 4.1B). The final position of the hole on the subsequent sampling date (H_f, cm) was determined from photographs and used to calculate growth rate (G, cm d^{-1}) over the interval between sampling dates as:

$$G = \left(H_f - 10\right)/\mathrm{t}$$

where t is the number of days between sampling dates. The rate of gross tissue loss (T, cm d^{-1}) also was calculated from measures derived from photographs as:

$$T = \left(\left(L_i + \left(H_f - 10\right)\right) - L_f\right)/\mathrm{t}$$

where L_i and L_f are the initial blade length (cm) and final blade length (cm) on the next sampling date, respectively. These rates were measured over roughly monthly sampling intervals except overwinter and late summer 2013 at The Lodge (~ 6 mo and 2 mo respectively). If excessive tissue loss eroded a blade below the punched hole, growth and gross tissue loss could not be measured. If no growth had occurred, a new hole was punched immediately below the first.

4.3.3 Kelp Population Dynamics and Macroalgal Composition

To compare the fate of tagged juveniles with that of the entire kelp population at each site, I made repeated measures of kelp abundance (percent cover, density) and population size structure (thallus length) within the fixed plots concurrent with the tagging study. After its conclusion, I continued to monitor kelp populations until August 2017. This non-destructive sampling was originally done at the same monthly frequency as the tagging study, but reduced in 2013 to a seasonal frequently. Disappearance of some floats throughout 2015 at The Lodge meant that certain plots could not be re-located, so that by the following year only 24 of the original 33 plots could be sampled.

To measure kelp cover (mainly *S. latissima*, but also *Laminaria digitata* and *Agarum clathratum*), divers placed crosshairs, constructed of 4 rotating, 0.9 m-long PVC arms (1.3 cm diameter), at the plot centre for scale and photographed the seabed within this area with an underwater camera (Canon S100, Canon PowerShot G10 or G7X). Planar cover of kelp in a circular area (2.54 m^2) around the plot centre was measured from photographs with ImageJ (NIH) using a point-intercept method. The superimposed grid contained 100 systematically spaced points per square metre. To simultaneously estimate kelp density and assess size structure, divers also measured the stipe and total thallus length (0.5 cm precision) of all individuals > 10 cm total length (*S. latissima* only) within a 1-m radius of the plot centre (3.14 m^2). This method also facilitated monitoring levels of recruitment over the study period. I considered recruits to be individuals 10 – 30 cm in total length. Higher kelp densities at The Lodge in August and October 2015 and in June 2016 necessitated sub-sampling due to logistical constraints, and only 16 or 17 plots, distributed evenly among depth strata, were sampled.

To evaluate changes in macroalgal composition over the study period at each site, I measured the percent cover of other abundant macroalgal groups from the photographs of fixed plots using the point-intercept method. These groups included turf-forming algae, the invasive green alga *Codium fragile* ssp. *tomentosoides*, the annual brown alga *Desmarestia viridis* whose blooms can form a plumose canopy, and a category of other less abundant perennial and annual brown macroalgae (*Ascophyllum nodosum*, *Fucus* spp., *Sacchariza dermatodea*, and *Chorda filum*). Turf-forming algae comprised a tangled matrix of low-lying filamentous (e.g. *Ceramium* spp., *Rhodomela confervoides*, *Bonnemaisonia hamifera*, *Polysiphonia* spp., *Chaetomorpha linum*, *Callithamnion* sp., *Sphacelaria* sp., *Hincksia* sp.), coarsely branching (e.g. *Phyllophora pseudoceranoides*, *Coccotylus truncatus*, *Chondrus crispus*), and articulated coralline (*Corallina officinalis*) algae.

To place the changes in kelp abundance and macroalgal composition measured in the present study in a more extended historical context, I searched for comparable measures of the macroalgal community (kelp density, macroalgal cover) at these sites from previous published and unpublished research (Appendix D: Table D1).

4.3.4 Temperature and Wave Data

Patterns of juvenile survival and kelp population dynamics also were interpreted in light of seawater temperatures and wave conditions over the study period. Bottom temperature was recorded at 10-min intervals using HOBO® Pendant Data Loggers deployed at 4-m depth at Paddy's Head and 8-m depth at The Lodge (the approximate midpoint of the 4 depth strata in the plot array). I calculated daily averages to construct a temperature series at each site for the duration of the tagging study and to calculate an average temperature in each year over the period of peak temperatures in summer/fall (August, September, October) and the winter trough (February and March) for the entire study. Wave data (hourly observations of significant wave height, m) for the Halifax Harbour Buoy (Station 44258, 44.500º N 63.400º W) located 44 km from Paddy's Head and 50 km from The Lodge were obtained over the study period from an online wave database (http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm) maintained by the Marine Environmental Data Section of the Canadian Department of Fisheries and Oceans. I calculated daily averages of significant wave height (SWH) from hourly observations to construct a time series of wave activity during the tagging study. To relate trends in kelp population dynamics with interannual variation in large wave events, I also examined the distribution of daily averages of SWH for each year of the study within a 6-month period with the highest predicted storm and wave activity (October to March) using box plots. Wave data for this period were not available for 2015.

4.3.5 Statistical Analysis

All analyses were conducted in R version 3.1.3 (R Core Team 2015). To examine whether variation in net tissue loss among tagged kelp juveniles was related to encrustation by *M. membranacea* or grazing damage by *L. vincta*, I used multiple regression techniques. For each sampling interval during the period of peak encrustation and grazing damage in 2012 (August to November at The Lodge, July at Paddy's Head), I fit separate multiple linear regression models evaluating the combined main effects of encrustation (percent blade area covered by *M. membranacea*) and grazing (percent blade area grazed), measured at the start of a sampling interval, on the net change in blade surface area by the subsequent sampling date. Net change in blade area was standardized by expressing it as a proportion of initial blade area. While encrustation by *M. membranacea* at Paddy's Head peaked in October, the sample size (2 surviving juveniles) was insufficient to evaluate the effects on tissue loss at this time.

To evaluate the effects of encrustation by *M. membranacea*, grazing damage from *L. vincta*, and thallus size on the survival of individual kelp juveniles over the course of the tagging study, I used extended Cox proportional hazards models fit with the 'coxph' function in the 'Survival' package (Therneau 2015). In these models the percent blade area covered by *M. membranacea*, percent blade area grazed, and initial blade surface area (cm^2) were treated as time-dependent variables such that the hazard (risk of death at sampling date) was predicted by the value of these variables measured on the previous sampling date. Tag identification number was used as a 'cluster' term to account for non-independence from multiple observations on the same subjects by computing robust standard errors for coefficient estimates using the Wei-Lin-Weissfeld estimator (Wei et al. 1989). I fit separate models to the data for each site, and the model for The Lodge also included a time-independent variable, depth stratum, with 4 levels (7 m, 8 m, 9 m, 10 m), which was a proxy for temperature and wave energy (both decrease with depth). Ties were handled with the Efron approximation, which is more accurate and computationally efficient than the EXACT or Breslow methods (Hertz-Picciotto & Rockhill 1997). For Paddy's Head, I initially fit a full model including the above variables and all possible interactions. For The Lodge, the full model included main effects and 2-way interactions only because the number of events (i.e. deaths) would be low relative to the number of variables if higher order interactions were included, and the associated coefficient estimates would be unreliable (Peduzzi et al. 1995). I then used a step-down model selection procedure in which the current model was compared to the nested model with the highest log-likelihood value and one variable less using likelihood ratio tests. I used Wald tests to evaluate the significance of the model coefficients in the final model because they do not assume independence of repeated observations (i.e. tag identification) within a cluster (Therneau 2015).

4.4 RESULTS

4.4.1 Interannual Variation in Seasonal Temperatures and Large Wave Events

Average daily temperature during the peak warm period between August and October ranged from 11.9 ºC (The Lodge 2013) to 15.7 ºC (Paddy's Head 2017) and showed an increasing trend from 2012 to 2017 at both sites (Appendix D: Fig. D1), that was statistically significant at The Lodge (TL: $R^2 = 0.687$, $p = 0.041$; PH: $R^2 = 0.512$, $p = 0.110$). Average daily temperature during the winter trough in February and March ranged from 0.2 ºC (Paddy's Head 2015) to 2.8 ºC (The Lodge 2016) with no significant trend (Appendix D: Fig. D1) at either site (TL: $R^2 = 0.016$, $p = 0.841$; PH: $R^2 = 0.039$, $p = 0.752$).

There were no consistent trends in the median daily significant wave height during the fall and winter between years of the study, but there were differences in the frequency and magnitude of the largest wave events (Appendix D: Fig. D2). In fall 2014 and winter 2015, there were fewer outlier wave events in the upper range of the distribution and these were smaller in magnitude compared to other years of the study (Appendix D: Fig. D2).

4.4.2 Juvenile Kelp Growth and Survival

For tagged juvenile kelp sporophytes at The Lodge, the percent of blade area encrusted by the invasive bryozoan *Membranipora membranacea* and grazed by *Lacuna vincta* increased throughout summer and fall in 2012 (Fig. 4.2A,C). Cover by *M. membranacea* reached a peak in September (mean, 63%) and remained high into November (Fig. 4.2A). The level of grazing damage increased in August and persisted at a similar low level (~ 1%) into November (Fig. 4.2C). Tissue loss exceeded growth over the first 4 months (Fig. 4.3), when there were extended periods with temperatures > 14 ºC (Fig. 4.4A), and particularly at the peak of encrustation by *M. membranacea* in September when wave action was increasing (Fig. 4.4C) and the rate of tissue loss was highest. Consequently, the mean blade surface area of surviving plants decreased in each month (Fig. 4.2E) until temperatures dropped below 14 ºC in October (Fig. 4.4A) and growth began to exceed tissue loss (Fig. 4.3). Net tissue loss (blade area) over sampling intervals was significantly and positively related to the degree of encrustation by *M. membranacea* for intervals within the period of peak cover (September to October, October to November; Table 4.1, Fig. 4.5), but not for the sampling interval prior to this peak (August to September; Table 4.1). Net tissue loss was not significantly related to grazing damage by *L. vincta* for any sampling interval during the period of peak grazing (Table 4.1).

Growth of tagged juveniles never exceeded the rate of tissue loss at Paddy's Head, where growth was lower and tissue loss greater than at The Lodge (Fig. 4.3). Accordingly, the mean blade surface area of surviving plants declined precipitously from June to October 2012 (Fig 4.2F). Low growth rates also corresponded with extended periods of temperatures above 14 ºC, exceeding those at The Lodge where plants were at a greater depth (Fig. 4.4B). As at The Lodge, the percent of blade area encrusted by *M. membranacea* increased throughout summer and fall at Paddy's Head, but peaked later (17% in October) and was only one fourth of the peak cover at The Lodge (Fig. 4.2B). In contrast, the percent of blade area grazed by *L. vincta* peaked earlier (6.7%, in July) at Paddy's Head and was 6-fold greater than peak grazing damage at The Lodge in 2012 (Fig. 4.2D). The greatest decrease in blade surface area at Paddy's Head at this time when

Table 4.1. Multiple linear regression models of net tissue loss (proportion of blade area lost) of tagged juvenile kelp sporophytes (*Saccharina latissima*) at 2 sites (The Lodge, Paddy's Head) over 4 sampling intervals in 2012 coinciding with the peak in encrustation by the invasive bryozoan *Membranipora membranacea* and grazing damage by *Lacuna vincta* at those sites. Variables tested in the models are the percent of blade area covered by *M. membranacea* (M) and percent of blade area grazed by snails (G) at the start of the sampling period.

Site	Sampling Interval	df	Variable	Coefficient estimate	SE	*t*	p
The Lodge	Aug – Sep	56	Intercept	0.24	0.08	3.16	**< 0.01**
			M	0.001	0.002	0.723	0.473
			G	0.03	0.03	1.28	0.205
The Lodge	Sep – Oct	47	Intercept	0.16	0.15	1.06	0.295
			M	0.01	0.002	2.54	**0.014**
			G	-0.06	0.05	-1.28	0.208
The Lodge	Oct – Nov	31	Intercept	-0.34	0.15	-2.23	**0.033**
			M	0.01	0.002	3.41	**< 0.01**
			G	0.05	0.06	0.980	0.334
Paddy's Head	Jul – Aug	39	Intercept	0.31	0.07	4.60	**< 0.001**
			M	-0.01	0.01	-1.30	0.202
			G	0.02	0.01	2.74	**< 0.01**

Note: Significant regression coefficients are highlighted by p-values in boldface type.

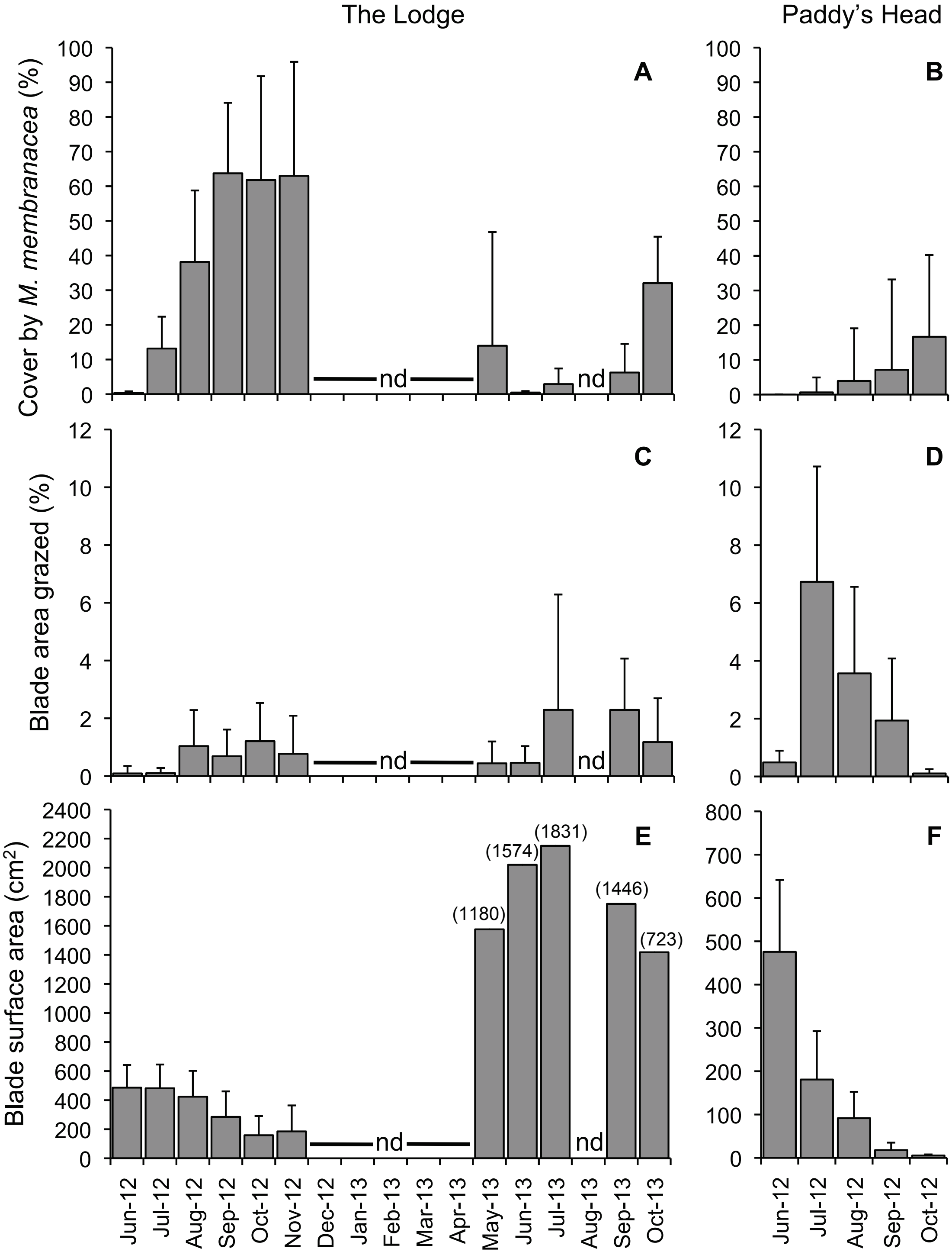

Fig. 4.2. Fate of surviving tagged juvenile kelp sporophytes (*Saccharina latissima*) at The Lodge (Left Column, n = 3 – 64) and Paddy's Head (Right Column, n = 2 – 51) from June 2012 to October 2013. A – B) Percent of blade area encrusted by *Membranipora membranacea*. C – D) Percent of blade area fully perforated by grazing from *Lacuna vincta*. E – F) Surface area (cm^2) of blade tissue (Note: difference in scale of y-axis between columns). Data are means + 1 SD; nd = no data. Errors extending beyond scale of y-axis are indicated in parentheses above bar.

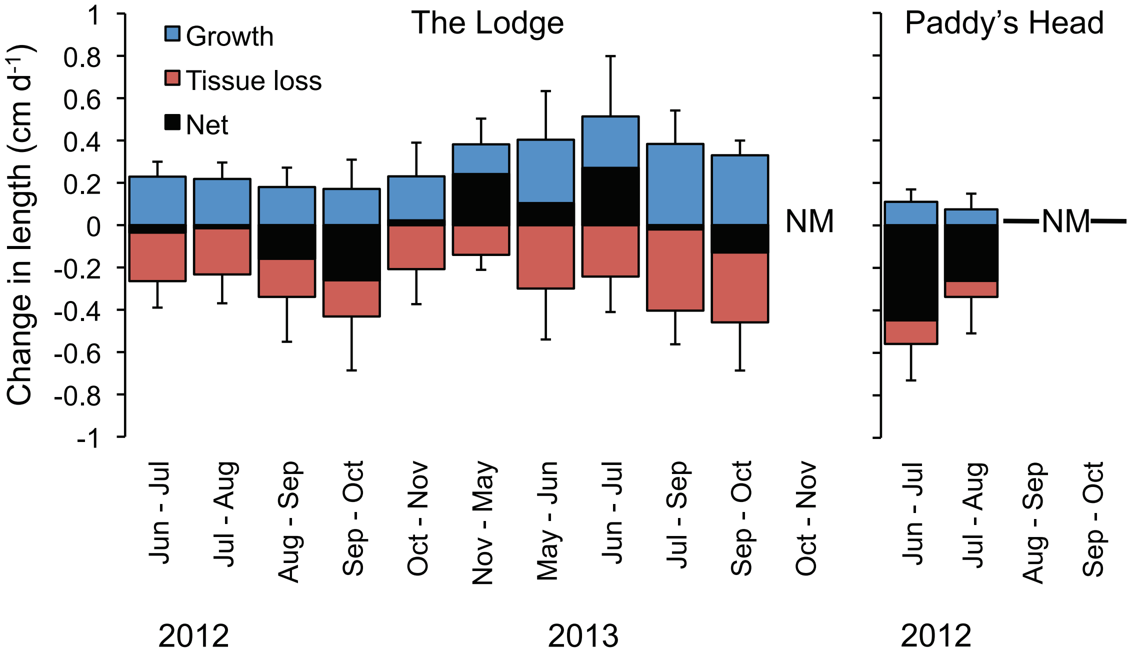

Fig. 4.3. Rates of blade growth, gross tissue loss, and net change (cm d^{-1}) of surviving tagged juvenile kelp sporophytes (*Saccharina latissima*) at The Lodge (Left Panel, n = 3 – 61) and Paddy's Head (Right Panel, n = 20 – 34) from June 2012 to October 2013. Rates correspond to change over the sampling interval indicated (roughly monthly, but up to 2 to 6 mo on two occasions at The Lodge). Data are means + 1 SD; NM = not measured.

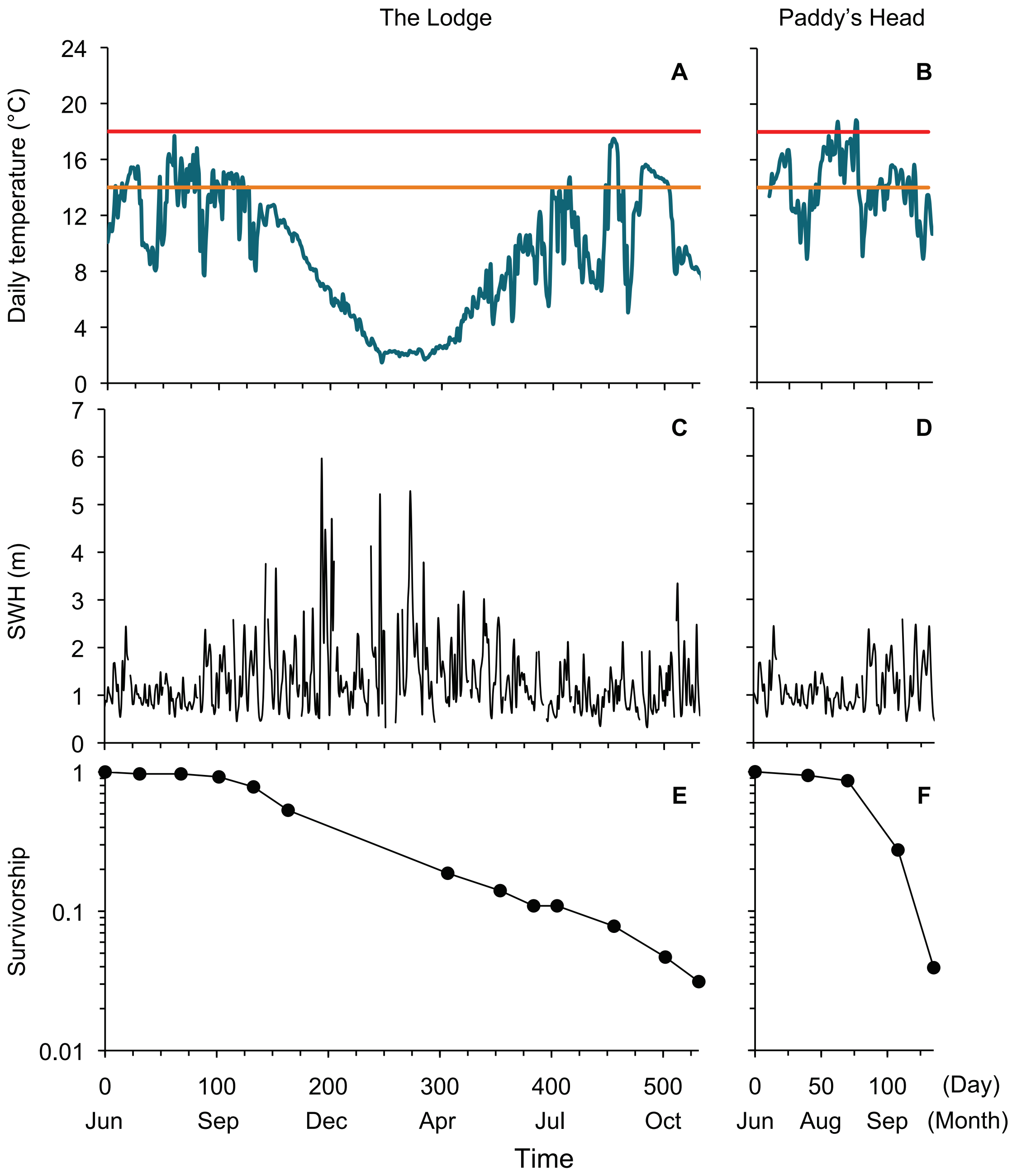

Fig. 4.4. A – B) Daily temperature (ºC) at 8 m and 4 m, respectively, C – D) daily significant wave height (m), and E – F) survivorship of tagged juvenile kelp sporophytes (*Saccharina latissima*) at The Lodge (Left Column, n = 64) and Paddy's Head (Right Column, n = 51) over the course of the tagging study beginning June 2012. Time is the elapsed number of days from the onset of the study and the associated month. Note: survivorship is plotted on a log-scale. Orange line indicates temperature above which growth and tissue strength of *S. latissima* are reduced (Simonson et al. 2015). Red line indicates temperature above which tissue loss and mortality of *S. latissima* increase (Simonson et al. 2015).

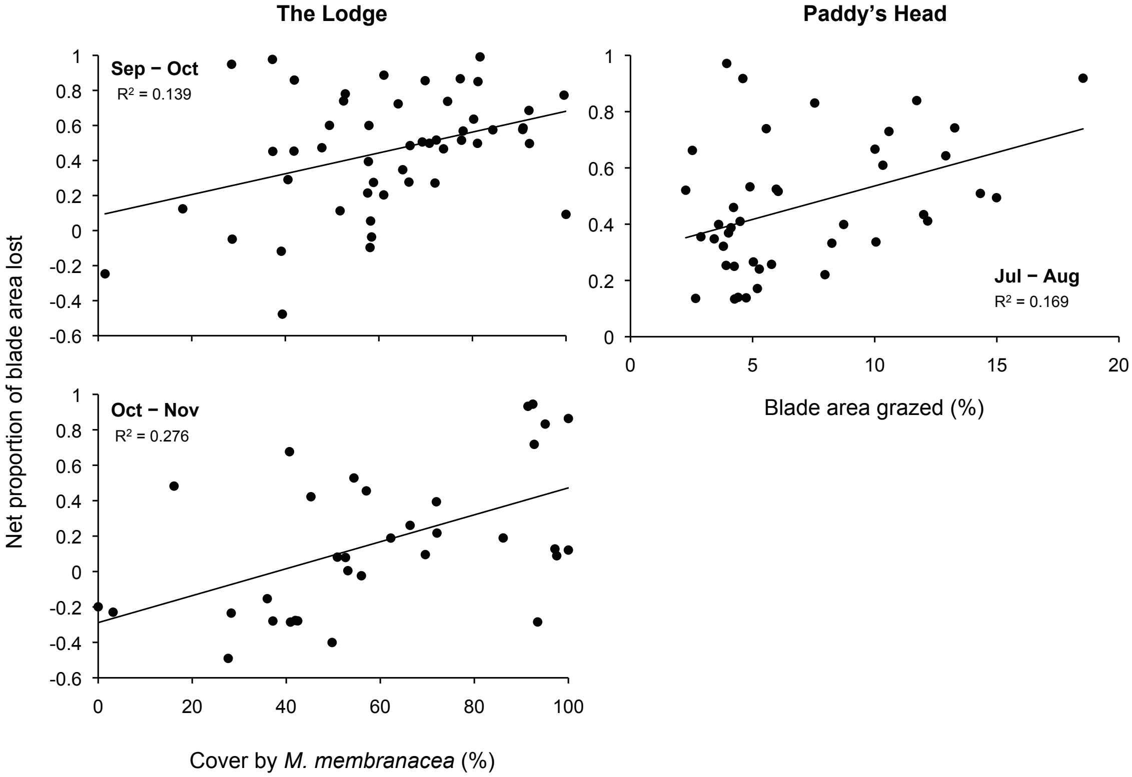

Fig. 4.5. Relationship between net tissue loss (proportion of blade area lost) of tagged juvenile kelp sporophytes (*Saccharina latissima*) and percent of blade area covered by *Membranipora membranacea* or grazed by snails (*Lacuna vincta*) at 2 sites (The Lodge, Paddy's Head) over 3 sampling intervals (Jul – Aug, Sep – Oct, Oct – Nov) in 2012 coinciding with the peak in encrustation and grazing damage at those sites. Cover by *M. membranacea* at The Lodge and grazing damage at Paddy's Head were significant predictors of net tissue loss for the sampling intervals shown (Table 4.1). R^2 values are for simple linear regressions. Negative proportions indicate net gain in blade area.

grazing intensity was increasing (Fig. 4.2D,F) coincided with a large wave event with significant wave heights > 2 m (Fig. 4.4D). Net tissue loss (blade area) following the peak in grazing damage was significantly and positively related to the percent of blade area grazed by *L. vincta* (Table 4.1, Fig. 4.5), but not the degree of encrustation by *M. membranacea* (Table 4.1).

Increasing cover of *M. membranacea*, grazing damage by *L. vincta*, and tissue loss at The Lodge and Paddy's Head were followed by decreased survivorship of each cohort later in the summer and fall, but the patterns of survival differed between the two sites (Fig. 4.4E,F). The risk of death at The Lodge increased slightly in fall 2012 when significant wave height was increasing (Fig. 4.4C) and cover by *M. membranacea* was high (Fig. 4.2A), but was otherwise relatively constant through time (Fig. 4.4E). At Paddy's Head, the risk of death increased over time (Fig. 4.4F) and the median time-at-death (since tagging) was only one third of that at The Lodge (108 d vs. 307 d). A large drop in survivorship of juveniles at Paddy's Head between August and September followed an extended period of temperatures > 14 ºC with peaks > 18 ºC (Fig. 4.4B,F), and corresponded with increased significant wave height > 2 m (Fig. 4.4D). This also was the time when cover by *M. membranacea* was increasing (Fig. 4.2B).

Despite differences in patterns of survival between sites, extended Cox proportional hazards models indicated that survival of juveniles at both sites was significantly related to the degree of encrustation by *M. membranacea* (The Lodge: Wald statistic = 4.56, df = 1, p = 0.033; PH: Wald statistic = 10.58, df = 1, p = 0.001), and not to any of the other predictors (initial blade surface area, percent of blade area grazed by *L. vincta*, and depth stratum) or any interactions between them (Table 4.2, 4.3). The effect of depth at The Lodge was only marginally non-significant (Table 4.2). The hazard ratios (TL: HR = 1.012, PH: HR = 1.008) indicated that an increase in blade area covered by *M. membranacea* of 50% is associated with an approximately 1.8- and 1.5-fold increase in the risk of death at The Lodge and Paddy's Head, respectively. Only 2 individuals remained at Paddy's Head by October 2012, whereas over half the cohort survived until November 2012 at The Lodge (Fig. 4.4E).

Table 4.2. Step-down model selection procedure comparing nested extended Cox proportional hazards models of survival of tagged juvenile kelp sporophytes (*Saccharina latissima*) at The Lodge from 8 June 2012 to 22 November 2013. Variables are initial blade surface area (B), percent blade area covered by *Membranipora membranacea* (M), percent blade area grazed by *Lacuna vincta* (G), depth stratum (D), and 2-way interactions. The specific model comparisons, likelihood ratio (LR) statistics, degrees of freedom, significance, and outcome of the likelihood ratio tests are shown.

Comparison	LR	df	p	Result
BM + BG + BD + MG + MD + GD + B + M + G + D vs. BG + BD + MG + MD + GD + B + M + G + D	0.016	1	0.900	Drop BM
BG + BD + MG + MD + GD + B + M + G + D vs. BD + MG + MD + GD + B + M + G + D	0.397	1	0.529	Drop BG
BD + MG + MD + GD + B + M + G + D vs. BD + MD + GD + B + M + G + D	1.72	1	0.190	Drop MG
BD + MD + GD + B + M + G + D vs. MD + GD + B + M + G + D	2.13	3	0.546	Drop BD
MD + GD + B + M + G + D vs. GD + B + M + G + D	2.30	3	0.512	Drop MD
GD + B + M + G + D vs. B + M + G + D	3.04	3	0.386	Drop GD
B + M + G + D vs. B + M + D	0.013	1	0.908	Drop G
B + M + D vs. M + D	0.025	1	0.874	Drop B
M + D vs. M	6.85	3	0.078	Drop D

Table 4.3. Step-down model selection procedure comparing nested extended Cox proportional hazards models of survival of tagged juvenile kelp sporophytes (*Saccharina latissima*) at Paddy's Head from 12 June 2012 to 19 October 2012. Variables are initial blade surface area (B), percent blade area covered by *Membranipora membranacea* (M), percent blade area grazed by *Lacuna vincta* (G), and their interactions. The specific model comparisons, likelihood ratio (LR) statistics, degrees of freedom, significance, and outcome of the likelihood ratio tests are shown.

Comparison	LR	df	p	Result
BMG + BG + BM + MG + B + M + G vs. BG + BM + MG + B + M + G	0.768	1	0.381	Drop BMG
BG + BM + MG + B + M + G vs. BG + BM + B + M + G	0.007	1	0.936	Drop MG
BG + BM + B + M + G vs. BG + B + M + G	0.174	1	0.676	Drop BM
BG + B + M + G vs. B + M + G	0.613	1	0.437	Drop BG
B + M + G vs. M + G	0.049	1	0.825	Drop B
M + G vs. M	0.122	1	0.726	Drop G

Of the individuals that survived through the fall at The Lodge, approximately 19% survived until the following spring (Fig. 4.4E). The loss of individuals over this period was associated with the highest wave activity observed during the tagging study (Fig. 4.4C). However, over this period of cooler winter/spring temperatures (Fig. 4.4A), growth exceeded tissue loss (Fig. 4.3), and there was an order of magnitude increase in the mean blade surface area of surviving individuals by May 2013 (Fig. 4.2E). Cooler temperatures prevailed at The Lodge in 2013 compared to 2012 (Fig. 4.4A; Appendix D: Fig. D1), and high rates of growth that exceeded tissue loss throughout the spring and early summer (Fig. 4.3) resulted in increases in blade surface area from May to July (Fig. 4.2E). The individuals that survived into the late summer and fall were more heavily grazed by *L. vincta* (Fig. 4.2C) and became increasingly encrusted by *M. membranacea* in October, although not to the same degree as in 2012 (Fig. 4.2A). Increased rates of tissue loss over this period (Fig. 4.3) resulted in reductions in blade area (Fig. 4.2E). By November 2013 only 2 individuals of the original cohort remained.

4.4.3 Kelp Population Dynamics and Macroalgal Composition

The fates of the cohorts of juvenile kelps at each site also were reflected by changes in abundance and size structure of kelp populations over the duration of the tagging study. Decreases in kelp cover, density (Fig. 4.6, 4.7) and median size (Fig. 4.8) mirrored decreases in blade surface area and survivorship of tagged individuals throughout summer and fall 2012. Over this period, size distributions of kelp at both sites became increasingly right skewed with the fragmentation or loss of larger individuals (Fig. 4.8, 4.9). Such changes were particularly pronounced and rapid at Paddy’s Head compared to The Lodge. Growth of surviving tagged individuals at The Lodge from winter to early summer 2013 (Fig. 4.3) was matched by an increase in the median size (Fig. 4.8) and a broadening of the size distribution (Fig. 4.8, 4.9) in the wider population over this time. This growth, in combination with an influx of new recruits in April 2013 (Fig. 4.6, 4.9), resulted in an increase in kelp density and cover over this period (Fig. 4.6). As in 2012, kelp cover, density (Fig. 4.6), and median size (Fig. 4.8) at The Lodge declined in the fall of 2013. However, peak summer/fall temperatures were cooler

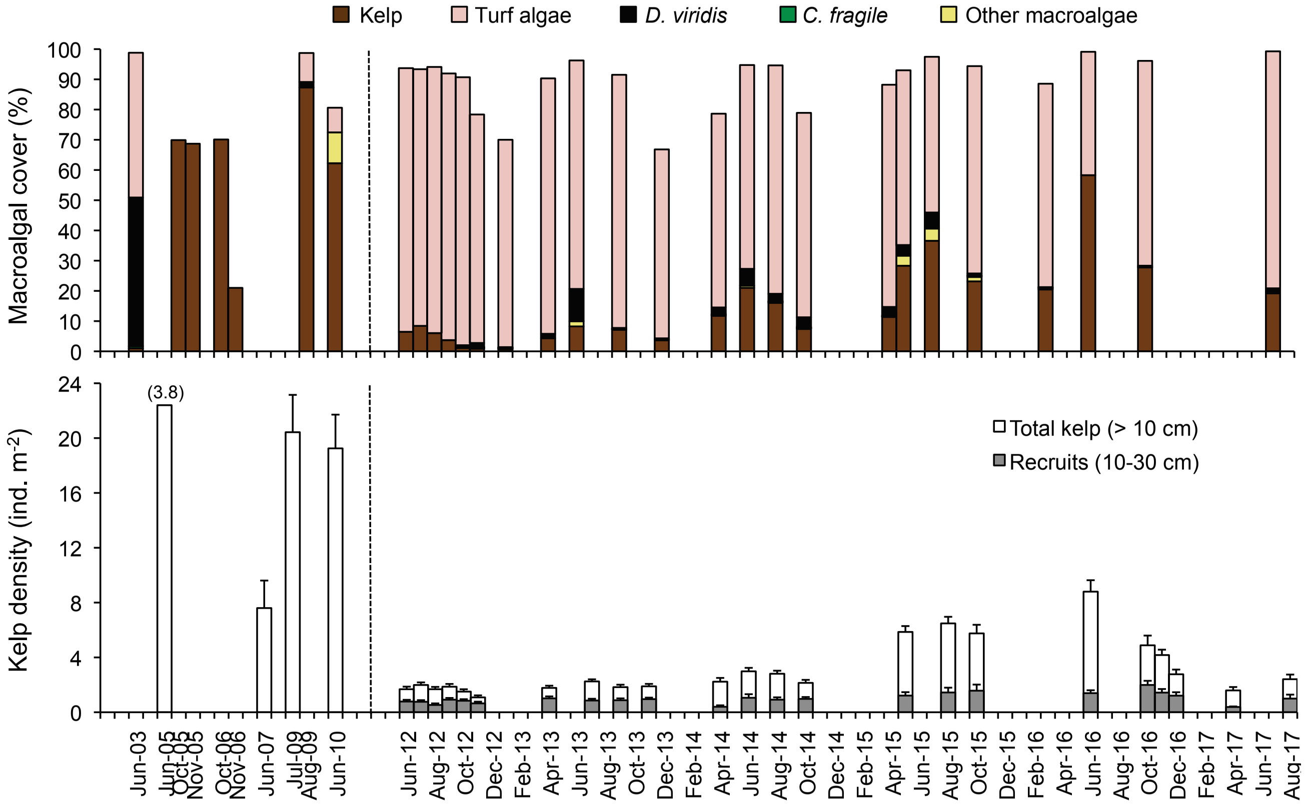

Fig. 4.6. Macroalgal composition (Top Panel) and kelp abundance and recruitment (Bottom Panel) at The Lodge from June 2003 to August 2017. Data are mean percent cover (n = 4 – 33) of key macroalgal groups (kelp, turf-forming algae, *Desmarestia viridis*, *Codium fragile* ssp. *tomentosoides*, and other perennial and annual brown macroalgae) and mean (+ 1 SE) density (ind. m^{-2}) of *Saccharina latissima* (n = 4 – 33), respectively. Total kelp density (> 10 cm thallus length) and density of recruits (10 – 30 cm thallus length) are shown. Data after June 2012 were collected from fixed plots during the present study. Earlier data is from other published and unpublished research. Gaps in the record indicate periods with missing data. Note: recruitment data not available before 2012. Errors extending beyond scale of y-axis are indicated in parentheses above bar. Cover of other macroalgal groups not available for sampling times where only kelp cover is shown.

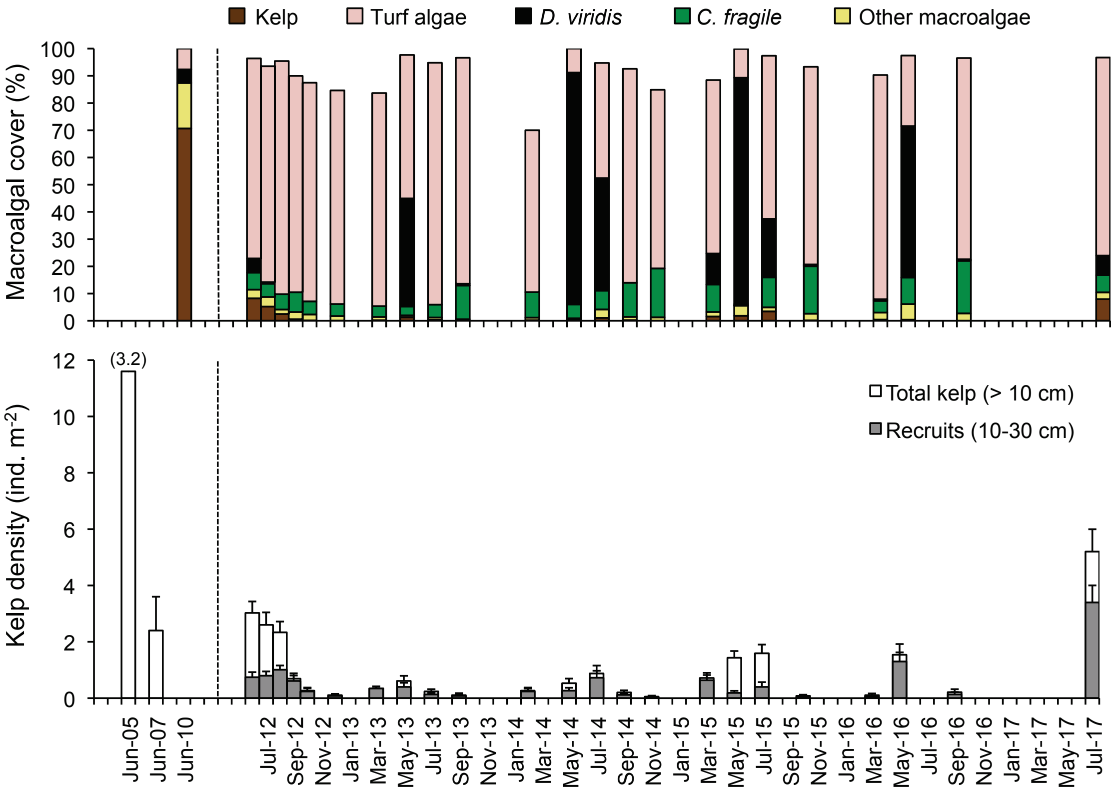

Fig. 4.7. Macroalgal composition (Top Panel) and kelp abundance and recruitment (Bottom Panel) at Paddy's Head from June 2005 to July 2017. Data are mean percent cover (n = 8 – 12) of key macroalgal groups (kelp, turf-forming algae, *Desmarestia viridis*, *Codium fragile* ssp. *tomentosoides*, and other perennial and annual brown macroalgae) and mean (+ 1 SE) density (ind. m^{-2}) of *Saccharina latissima* (n = 12 – 20), respectively. Total kelp density (> 10 cm thallus length) and density of recruits (10 – 30 cm thallus length) are shown. Data after June 2012 were collected from fixed plots during the present study. Earlier data is from other published and unpublished research. Gaps in the record indicate periods with missing data. Note: recruitment data not available before 2012. Errors extending beyond scale of y-axis are indicated in parentheses above bar.

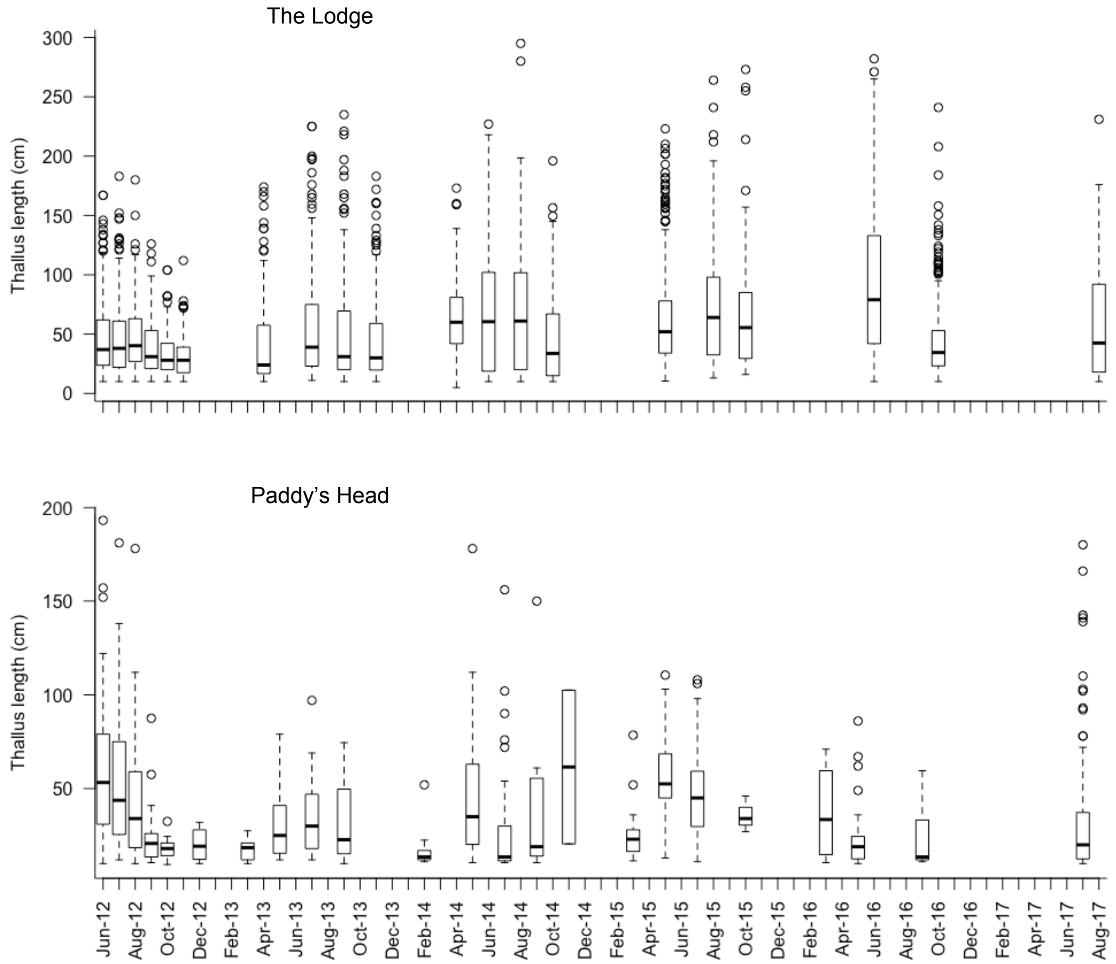

Fig. 4.8. Box plots illustrating seasonal and annual changes in the size distribution of kelp populations (*Saccharina latissima*) in fixed plots at The Lodge (Top Panel) and Paddy's Head (Bottom Panel) from June 2012 to August 2017. Data are thallus lengths of individuals larger than 10 cm. Black band is the median, the box indicates the 1st and 3rd quartiles, whiskers are the lowest and highest values within 1.5 interquartile range of the 1st and 3rd quartiles, respectively, and individual points are outliers.

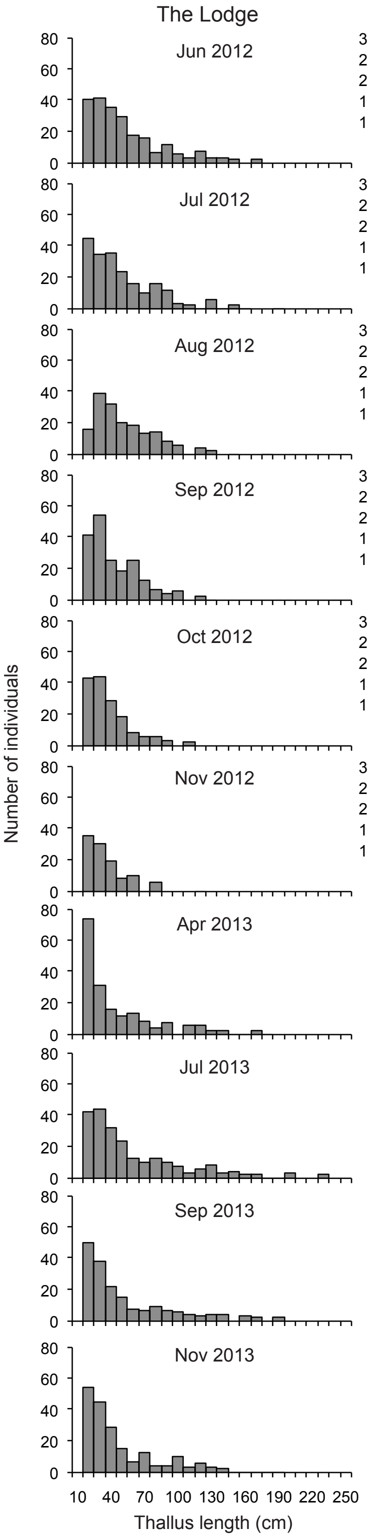

Fig. 4.9. Size distributions of kelp populations (*Saccharina latissima*) in fixed plots at The Lodge (Left Column) and Paddy's Head (Right Column) during the tagging study. Data are the number of individuals in 10-cm bins of thallus length (cm). Note: individuals < 10 cm not counted.

compared to the previous year (Appendix D: Fig. D1) and seasonal losses were not as great. The size distribution at The Lodge continued to be highly skewed, but larger individuals up to 200 cm in length remained by November 2013 (Fig. 4.8, 4.9).

Seasonal changes in the kelp populations at both sites also were evident beyond the tagging study, but interannual variability and overall trajectories differed between sites. At Paddy's Head, seasonal increases in abundance were largely driven by low levels of episodic recruitment in the spring (Fig. 4.7). However, these increases did not exceed annual losses, and low kelp cover and density were sustained over 5 years (Fig. 4.7). By the last sampling date in July 2017, kelp cover remained low despite a particularly strong pulse of recruitment (Fig. 4.7). Seasonal fluctuations in the size distribution also were evident, but due to the predominance of small recruits and repeated annual losses, the median thallus length remained under 50 cm, and the size distribution highly right-skewed (Fig. 4.8). Seasonal cycles in the kelp population also occurred at The Lodge. However, losses in the late summer/fall were largely expressed in cover (Fig. 4.6) and the size distribution (Fig. 4.8), but not density (Fig. 4.6). In contrast to Paddy's Head, recruitment was more consistent throughout the year, and increases in kelp cover, density (Fig. 4.6), and median size (Fig. 4.8) occurred in each year from 2012 to 2016, especially following a particularly cold winter in 2015 (Appendix D: Fig. D1) when large wave events were smaller and less frequent compared to previous years (Appendix D: Fig. D2). The size distribution of kelp also became wider and less skewed over this time (Fig. 4.8), and a sparse, partial canopy formed by June 2016 (Fig. 4.6). However, large losses in kelp cover and density in fall and winter 2016 reversed much of the gains over the previous 4 years (Fig. 4.6). These losses coincided with the warmest peak summer/fall temperatures observed since the onset of the study (Appendix D: Fig. D1).

With low kelp cover at both sites throughout the study period, other macroalgal groups dominated the benthic cover (Fig. 4.1A). Turf-forming algae were consistently the major component of the macroalgal assemblage at both sites (Fig. 4.1A, 4.6, 4.7), reaching upwards of 89% cover and rarely falling below 50% cover. Other macroalgal groups formed a smaller component of cover at The Lodge, but were more prevalent at Paddy's Head where they often were more abundant than kelp when present (Fig. 4.6, 4.7). At Paddy's Head, the annual brown alga *Desmarestia viridis* and invasive green alga *Codium fragile* ssp. *tomentosoides* displayed seasonal cycles (Fig. 4.7). Thick spring blooms of *D. viridis* carpeted much of the seabed in May each year, but were highly ephemeral (Fig. 4.7). *C. fragile* ssp. *tomentosoides* was more persistent, but tended to be most abundant in the fall (September to November; Fig. 4.7). Other perennial and annual brown macroalgae were less prevalent, but at times were more abundant than kelp (Fig 4.7).

Data prior to 2012 indicate a reversal in the patterns of kelp abundance and macroalgal composition documented after the onset of the present study. Planar cover at both sites was generally dominated by kelp and other perennial brown algae (up to 87% at The Lodge and 71% at Paddy's Head) with minimal cover of turf-forming algae (Fig. 4.6, 4.7). High average densities of *S. latissima* (up to 22.4 ind. m^{-2} at The Lodge and 11.6 ind. m^{-2} at Paddy's Head) were 2 to 3 times higher than maximum densities attained after 2012 (Fig. 4.6, 4.7). These data also reveal periods of canopy defoliation and dominance by turf and other macroalgae in 2003 and 2006 at The Lodge, and 2007 at Paddy's Head (Fig. 4.6, 4.7). Whereas a full canopy did not reform past 2012 after 5 years at either site, high kelp density and cover were attained in as little as 2 – 3 years after past defoliation events (Fig. 4.6, 4.7).

4.5 DISCUSSION

4.5.1 Low Recruitment Limits Capacity for Kelp Recovery

As predicted, I observed consistently low recruitment (often < 1 ind. m^{-2}) at both study sites over the course of 5 years, particularly at Paddy's Head (compare with 45 – 80 ind. m^{-2} in canopy gaps; Johnson & Mann 1988, Scheibling et al. 1999). This suggests that constraints on recruitment to the macroscopic sporophyte stage limit the rate of population recovery in these degraded habitats. Several non-exclusive mechanisms may contribute to this bottleneck. With large-scale canopy loss of kelps or fucoids, the scarcity of reproductive adults likely limits propagule supply and the capacity for local replenishment from within a population (Bennett & Wernberg 2014; Chapter 3). Supply constraints may be particularly critical for kelps as low spore settlement density can result in fertilization failure at the gametophyte stage (Reed 1990). In Nova Scotia these constraints are exacerbated by the mesograzer *Lacuna vincta*, which preferentially consumes sorus tissue (Chapter 3). Loss of the moderating effect of a kelp canopy also might limit the supply and establishment of propagules and subsequent recruitment. For example, modification of flow within canopies likely promotes the retention and settlement of spores (Graham 2003). Furthermore, water motion and sediment accumulation are reduced within kelp canopies (Irving & Connell 2006b) as fronds slow impinging currents and sweep the substratum, which may enhance spore settlement and attachment (Gaylord et al. 2002, Deiman et al. 2012). Low and sporadic recruitment rates at Paddy's Head suggest pulsed inputs from a distant source (Reed et al. 1988). The appearance of small recruits at The Lodge was more consistent within and between years than at Paddy's Head, which may have contributed to greater gains in kelp cover at the former site. However, a sufficient supply of propagules in itself does not guarantee population recovery of canopy-forming algae if novel features of the degraded habitat lead to repeated recruitment failure (Perkol-Finkel & Airoldi 2010).

As expected, in the absence of a kelp canopy, the rocky substratum at both sites continued to be dominated by turf-forming algae, seasonal blooms of the annual brown alga *Desmarestia viridis*, and stands of the invasive green alga *Codium fragile* ssp. *tomentosoides* (at Paddy's Head). Turf algae, *Desmarestia* spp. and *C. fragile* typically are excluded by dense kelp and fucoid canopies, but quickly occupy disturbance-generated gaps (Dayton et al. 1984, Reed & Foster 1984, Scheibling et al. 1999, Scheibling & Gagnon 2006, Tamburello et al. 2013) and may exclude kelp once established. Following its introduction to the Atlantic coast of Nova Scotia in the early 1990's, *C. fragile* established dense meadows that inhibited kelp recruitment (Scheibling & Gagnon 2006); the smaller patches that persisted at Paddy's Head over the course of this study may have had a similar effect. Similarly, turf-forming algae bind and accumulate large quantities of inorganic sediment (Gorman & Connell 2009, Filbee-Dexter et al. 2016), and this dense matrix of algal branches, filaments, and sediment can have an inhibitory effect on settlement and establishment of kelp microscopic propagules and macroscopic recruits (Isæus et al. 2004, Gorman & Connell 2009). High densities of small grazers in turf also can hinder recruitment of small sporophytes (Dayton et al.

1984). Given its ephemeral nature and low abundance at the time of spore settlement, it is unclear whether *D. viridis* likewise limits kelp recruitment, but the seasonality of these blooms may complement the inhibitory effects of turf algae and *C. fragile*. Extensive, dense blooms of *D. viridis* shaded young sporophytes in spring during my study, which has been shown to reduce growth of juveniles of the kelp *Agarum cribrosum* (Gagnon et al. 2003). *D. viridis* also releases sulphuric acid during the bloom dieback in fall (Blain & Gagnon 2013), which may negatively impact sporophyte survival.

4.5.2 High Tissue Loss and Mortality of Sporophytes Limit Capacity for Recovery

Results of the tagging study supported the prediction that the ability of juvenile sporophytes to make net gains in blade area and contribute to canopy recovery would be impaired by physical and biological agents that skewed the balance between blade growth and tissue loss. Large losses over the summer and fall at The Lodge and Paddy's Head were related to the degree of encrustation by *M. membranacea* and grazing by *L. vincta*, respectively. Grazing perforations and weakening of underlying tissue from prolonged encrustation both reduce the breaking strength of kelp blades (Krumhansl et al. 2011). This appears to have increased the susceptibility of young juveniles to blade breakage during large wave events after peaks in encrustation and grazing. A large wave event in summer 2012, before the peak cover of *M. membranacea* at The Lodge, did not result in sizeable tissue losses, which is consistent with earlier work in Nova Scotia that found no simple relationship between canopy loss and 3 measures of wave energy (Scheibling & Gagnon 2009). Prolonged periods of seawater temperatures above 14 ºC in summer 2012 may have further skewed the balance between blade growth and erosion as both the growth rate and tissue strength of *S. latissima* decline at this temperature (Simonson et al. 2015). The resulting decrease in blade area of tagged plants was associated with declines in total kelp cover and a truncation of the size structure at both sites, particularly at Paddy's Head where the 2 surviving tagged individuals had only small fragments of blade remaining in October 2012. In contrast, individuals at The Lodge that survived this bottleneck after temperatures dropped in late fall were able to compensate with prolific growth over winter when nutrient concentrations are high (Chapman & Craigie 1977). This was reflected by a greater increase in kelp canopy cover at this site over the following year compared to Paddy's Head.

Differences in the patterns of survival between tagged juveniles at The Lodge and Paddy's Head also were reflected by changes in kelp density at these sites. The risk of mortality at The Lodge appeared relatively constant through time, which was consistent with the shape of survival curves of tagged cohorts of *S. latissima* measured before the introduction of *M. membranacea* (Chapman 1984, 1986), as well as those of other perennial kelp species (Dayton et al. 1984). Mortality of young sporophytes is expected to be highest before they reach the sizes at which they were tagged in this study, and to decline thereafter (Schiel & Foster 2006). However, the risk of mortality at Paddy's Head increased over time, which is more comparable to survival curves for annual kelps (Coyer & Zaugg-Haglund 1982, McConnico & Foster 2005). Nonetheless, survival at both sites was related to the degree of encrustation by *M. membranacea*, which is not surprising given that this bryozoan can encrust entire blades leading to fragmentation below the meristem. This result was consistent with high mortality of *S. latissima* observed in the NE Atlantic associated with high epiphyte loads (Andersen et al. 2013) and extensive canopy loss in Nova Scotia during past bryozoan outbreaks (Saunders & Metaxas 2008, Scheibling & Gagnon 2009), but contrary to the effects of *M. membranacea* on larger, surface-canopy kelps in its native NE Pacific range, where complete defoliation does not occur (Dixon et al. 1981).

Contrary to my prediction, survival was not related to grazing intensity by *L. vincta* at either site. This result is surprising given the extensive grazing damage observed on blades of juvenile sporophytes at Paddy's Head. If grazing had been concentrated on the stipe rather than the blade, *L. vincta* may have had a larger effect on the loss of whole plants, as has been observed for other kelp-mesograzer interactions (Black 1976, Duggins et al. 2001). Grazing by *L. vincta* was largely concentrated on the margins and distal end of the blade in tagged juveniles, consistent with previous studies of grazing by this snail on adults of *S. latissima*, which similarly observed tissue losses without mortality (Johnson & Mann 1986, Krumhansl & Scheibling 2011a,b). In other kelp systems, this type of grazer-induced tissue loss actually may enhance survival by reducing drag if grazing occurs before periods of high wave activity (de Bettignies et al. 2012). However, rapid mortality of the cohort at Paddy's Head meant that nearly all individuals were lost before the stormiest part of the year. Time to 50% mortality of the cohort (2.5 – 3.5 months) was less than half that measured by Chapman (1986) for *S. latissima* in the early 1980's (~ 8 months). Even at The Lodge, where survivorship was greater, time to 50% mortality of the cohort (5.5 months) was low relative to Chapman's estimate, indicating that for these currently degraded kelp populations, low survivorship of recruits coupled with low rates of recruitment limit the capacity for kelp-bed recovery.

Observations from the tagging study and monitoring of kelp population dynamics suggested that warm seawater temperatures also constrain the rate of kelp recovery through direct effects on kelp. The effect of depth on survival at The Lodge, was marginally non-significant, but indicated a trend toward a higher risk of mortality for plants in the shallowest stratum (7 m) where warmer temperatures and stronger wave forces acting on thalli are expected. This was consistent with the higher overall rate of mortality of tagged juveniles at even shallower depths at Paddy's Head (4 – 6 m), and the occurrence of the greatest loss of tagged plants as wave heights increased following an extended period of temperatures > 14 ºC with peaks in excess of 18 ºC. These temperatures are high enough to induce significant weakening of blade strength and mortality (Simonson et al. 2015). However, the short duration of temperatures > 18 ºC suggests indirect loss resulting from tissue weakening as a more likely cause than direct mortality. I also observed higher growth and lower tissue loss of tagged juveniles at The Lodge compared to Paddy's Head in 2012, which may reflect warmer summer/fall temperatures at the latter site (Simonson et al. 2015, Wilson et al. 2015). The smaller decrease in canopy cover at The Lodge in 2013 compared to 2012 also may be related to cooler temperatures in 2013, while the higher growth rate may have been related to the larger size of plants by that time (Mann 1972b). The large decrease in kelp abundance at the Lodge in 2016 coincided with the warmest peak temperatures observed at the site during my study, further suggesting a link between warm temperatures and canopy loss.

The effects of physical factors (temperature, wave forces) on kelp bed recovery may be largely indirect, through the interaction with *M. membranacea* rather than direct effects on kelp. For example, the positive relationship between the extent of kelp canopy loss and seawater temperature likely reflects interannual variability in bryozoan growth and consequently blade cover, both of which are positively correlated with temperature (Scheibling & Gagnon 2009, Saunders & Metaxas 2009), rather than an effect of temperature *per se*. Likewise, the onset and intensity of settlement by *M. membranacea* and severity of subsequent outbreaks are positively correlated with winter sea temperature (Saunders & Metaxas 2008). The relatively large increase in kelp abundance at The Lodge in 2015, following the lowest winter minimum temperatures observed over the study, coincided with the late onset and low settlement of *M. membranacea* that year (Danielle Denley, Dalhousie University, pers. comm.). The frequency and intensity of large wave events over fall and winter also were lower in 2014/2015 compared to other years of the study, which may have mitigated the extent of kelp mortality related to encrustation by *M. membranacea* and facilitated greater gains in kelp abundance in 2015.

4.5.3 Regime Shifts and Scope for Recovery Following Degradation of Kelp Ecosystems

A closed canopy of dense kelp failed to form at either site during 5 years of observation, and the macroalgal communities remained largely dominated by mixed-species assemblages of low-lying turf-forming algae. The skewed size distributions of kelp throughout the study indicated that the sparse populations largely comprised smaller individuals. Abundant kelp was recorded at both sites in June 2010, before the onset of this study, indicating that up to 7 years could have elapsed since the loss of the canopy without recovery. Recovery of kelp populations from past disturbances in Nova Scotia has generally been more rapid. Barrens devoid of fleshy macroalgae, created by outbreaks of destructive sea urchin grazing throughout the 1970’s to 1990’s, were fully re-colonized by kelp canopies within 1.5 to 4 years following mass mortalities of urchins (Scheibling 1986, Johnson & Mann 1988, Scheibling et al.1999). This recovery was facilitated by spore inputs from refuge kelp populations in the wave swept shallows beyond the limits of urchin grazing (Johnson & Mann 1988). Even after the introduction of *M. membranacea* in the 1990’s, recovery of the kelp canopy from extensive defoliation events generally occurred within 1 to 3 years (Scheibling & Gagnon 2009;

Fig. 4.6), most likely through the growth of juvenile sporophytes, previously in arrested developmental stages in the understorey (Kinlan et al. 2003, Toohey & Kendrick 2007). My findings suggest that limits on kelp recruitment and sporophyte growth and survival are increasingly eroding the resilience of this ecosystem to kelp canopy loss, and that this large and persistent shift in community structure to turf-dominated reefs may represent a regime shift. Limited or protracted recovery is typical of intertidal and subtidal rocky reef communities globally where large canopy-forming macroalgae have been replaced by turf-forming assemblages, and various feedbacks and stressors stabilize the degraded canopy-free state (Schiel & Lilley 2011, Moy & Christie 2012, Wernberg et al. 2016, Filbee-Dexter & Wernberg 2018). As with these systems, the prospect of canopy recovery in Nova Scotia before the next major disturbance appears to be low. Interestingly, the increased probability of disease-mediated mass mortality of sea urchins in response to ocean warming and increasing storm intensity along this coast was predicted to favour the persistence of kelp beds in this region by precluding destructive overgrazing of kelp (Scheibling & Lauzon-Guay 2010, Scheibling et al. 2013), but may now further stabilize the turf-algal dominated state.

Feedbacks and other stabilizing processes that limit recovery, reinforce kelp loss, and maintain degraded turf-dominated community states highlight the challenge for ecologists to identify relevant actions for decision-makers before regime shifts occur that may be difficult to reverse. I have shown that limits on recruitment and high rates of tissue loss and mortality of young sporophytes, related to the combined effects of epiphytism, grazing, warm temperatures, and wave forces, impede recovery of kelp populations following large-scale canopy defoliation. These results underscore the need to protect intact kelp populations so that positive interactions that increase resilience are maintained. High adult densities should ensure a greater supply of kelp propagules (Graham 2003; Chapter 3), and the reduction by a dense canopy of water flow, sediment accumulation, and understorey competitors (Irving & Connell 2006b) can facilitate propagule establishment and recruitment. The dilution of grazing damage among more individuals (Chapter 2) and amelioration of physical stress (Bennett & Wernberg 2014, Bennett et al. 2015a) within a full canopy also may promote higher growth and lower tissue loss of individual sporophytes. Spatial variation in coastal water temperature also should be considered in protection measures. Kelp abundance in Nova Scotia remains higher on exposed headlands and outer bays where cooler temperatures prevail compared to inner bays (Filbee-Dexter et al. 2016). Given the temperature dependence of outbreak dynamics of *M. membranacea* (Scheibling & Gagnon 2009) and feeding rates of herbivores (Krumhansl & Scheibling 2011b, Harley et al. 2012), protecting kelp populations in regional "cool spots" should mitigate the direct and indirect effects of temperature on kelp. By conserving positive interactions in intact kelp populations growing in more favourable environmental conditions, we can expect a more encouraging outlook for these ecologically important habitats.

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CHAPTER 5

TURF WARS: COMPETITION BETWEEN FOUNDATION AND TURF-FORMING SPECIES ON TEMPERATE AND TROPICAL REEFS AND ITS ROLE IN REGIME SHIFTS*

5.1 ABSTRACT

Shifts in competitive balance between key functional groups are often inferred to drive regime shifts in tropical and temperate marine ecosystems that increasingly involve changes in spatial dominance by foundation species (e.g. reef-building corals, canopy-forming algae) to turf-forming algae differing in structural complexity. To disentangle competitive interactions from other processes that may contribute to these shifts, I conducted a global meta-analysis of manipulative competition experiments between these groups. Shading and abrasion by canopy-forming algae had consistently negative effects on abundance of turf-forming algae, but tending toward larger effects on delicate filamentous compared to articulated coralline and corticated/coarsely branching turf. Competitive effects of turf-forming algae on canopy species were limited to early life-history stages, and similarly varied between turf functional groups. Conversely, shorter filamentous turf assemblages typical of tropical reefs had no significant effect on settlement and survival of coral larvae. Interactions between turf-forming algae and established coral colonies through a variety of mechanisms were negative overall, but variable in magnitude. These indicate that corals suppress turf abundance, but not vice versa. However, turf-forming algae significantly impacted coral growth and tissue mortality. I suggest reefs with extensive cover of foundation species are resistant to

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O'Brien JM, Scheibling RE (2018) Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. Mar Ecol Prog Ser 590:1–17 [Feature Article] competitive effects of turf algae, but competition will inhibit recovery of reefs following disturbances that enable turf algae to establish. Integrating accurate estimates of the competitive effects of foundation and turf-forming species into spatial and dynamic models will improve predictions of the stability of these undesirable regime shifts and recovery potential under alternative climate and management scenarios.

5.2 INTRODUCTION

There is growing recognition that diverse types of marine regime shifts—striking and abrupt changes in the structure of ecological communities (Möllmann et al. 2015)—are the outcome of one or more external drivers altering the internal dynamics of ecosystems (Connell et al. 2011, Conversi et al. 2015). These internal dynamics include interactions between trophic levels (e.g. predator-prey interactions) or within trophic levels (e.g. competition; Conversi et al. 2015). Indeed, even before a contemporary theoretical framework surrounding these critical transitions developed (e.g. Scheffer et al. 2001), there was early recognition that classic Lotka-Volterra models of two-species competition with unstable coexistence could describe dynamics consistent with regime shifts (Knowlton 1992). The drivers impacting on these internal ecosystem dynamics are diverse, frequently co-occur, and are common across many types of marine regime shifts (Rocha et al. 2015). The resulting changes involve key species or groups that structure the community, often are persistent over ecological time scales (Möllmann et al. 2015), and can lead to loss of ecosystem services (Rocha et al. 2015).

Such regime shifts on tropical and temperate reefs are increasingly reported to involve changes in spatial dominance from various foundation species to turf-forming algae. Foundation species, such as reef-building corals in order Scleractinia and canopy-forming algae in orders Laminariales and Fucales, have a large effect on community structure, sometimes disproportionate to their abundance (Dayton 1975). In contrast, ‘turf-forming’ algae broadly describe algal assemblages that vary considerably in composition (single- or multi-species assemblages) and morphology (filamentous, corticated and coarsely branching, or articulated coralline algae), but are united by some consistent physical and functional characteristics. Generally, these assemblages form a pervasive, low-lying, and dense matrix of algal filaments, branches and associated sediment (Connell et al. 2014). This is in contrast to the isolated individuals or patches of the component species that may occur on relatively pristine reefs.

On many degraded temperate rocky intertidal and subtidal reefs globally, turf-forming assemblages have replaced canopy-forming brown algae such as kelps and fucoids (Benedetti-Cecchi et al. 2001, Connell et al. 2008, Moy & Christie 2012, Filbee-Dexter et al. 2016). Turf algae also form a conspicuous component of the epilithic algal community or matrix (EAC or EAM) in healthy tropical coral reef assemblages and contribute considerably to the total primary productivity and trophic transfer, especially in lagoon, reef flat, and back-reef habitats (Hatcher & Larkum 1983, Carpenter 1985, Klumpp & McKinnon 1992, Wismer et al. 2009). Nonetheless, turf algae are disproportionately represented within assemblages interacting with coral colonies at their boundary (Barott et al. 2012b, Wild et al. 2014, Jorissen et al. 2016) and can rapidly colonize space following large-scale coral mortality (McClanahan et al. 2001, Adjeroud et al. 2009, Mellin et al. 2016). Algal turf forms the dominant component of benthic cover on many degraded coral reefs, rather than erect macroalgae (Haas et al. 2010, Vermeij et al. 2010, Barott et al. 2012b). However, the geographic extent and frequency of regime shifts from coral to turf algae are difficult to evaluate as global analyses have focused on erect macroalgae (Bruno et al. 2009). Turf algae are structurally complex (Dijkstra et al. 2017), but on a fundamentally smaller scale compared to the habitat architecture, canopy structure, and standing biomass provided by the dominant foundation species on temperate and tropical reefs. Their proliferation therefore is considered a degraded reef state with respect to 3-dimensional structure and associated ecosystem services. Consequently, efforts to disentangle the processes behind the shifting nature of the interactions between these broad groups of organisms have intensified in both temperate and tropical systems.

Competition is thought to be a key ecological interaction between foundation species and turf-forming algae that contributes to or maintains regime shifts in reef ecosystems (McCook et al. 2001, Connell et al. 2013). Here I define competition as the negative effect one species or group has on the performance of another by consuming or interfering with access to resources (Keddy 2001). Despite structural and taxonomic disparities, foundation and turf-forming species may compete for nutrients and light. However, competition for space may be particularly intense, as it is a resource often in short supply on shallow benthic reefs and highly correlated with access to these other resources (Worm & Karez 2002). This interaction can be largely hierarchical with established corals and closed stands of canopy algae dominating over turf algae across a range of habitats (Johnson & Mann 1988, McCook 2001). Nonetheless, when turf algae proliferate to pervade benthic habitat and form a thick and dense matrix, they can inhibit the establishment of macroalgal propagules (Bellgrove et al. 2010, Connell & Russell 2010) and coral larvae (Birrell et al. 2005). Consequently, turf algae are thought to become competitively superior under anthropogenically-altered conditions that stimulate their growth (e.g. reduced herbivory, enriched nutrients; Gorgula & Connell 2004, Barott et al. 2012b), thus reducing the resilience of foundation species to natural disturbances (Birrell et al. 2005, Connell et al. 2011) or facilitating direct overgrowth of established corals (Vermeij et al. 2010). Therefore, regime shifts toward spatial dominance by turf algae in response to reef degradation may follow from a shift in the competitive balance between these key groups.

This assessment is sometimes based on observations that, along gradients of anthropogenic influence (urbanization, nutrient input, fishing pressure), the relative abundances of foundation species and turf algae (Benedetti-Cecchi et al. 2001, Gorgula & Connell 2004, Gorman et al. 2009, Wild et al. 2014), or the apparent outcome of interactions between them, are reversed (Barott et al. 2012b). However, numerous other anthropogenic stressors lead to reef degradation (Rocha et al. 2015) and may directly influence nutrient enrichment and fishing (Ban et al. 2014) or combine in unexpected, non-additive ways (Strain et al. 2014). Many of these anthropogenic impacts are forms of stress or disturbance to corals and canopy algae. Here I define stress as external factors that limit growth and reproduction by diverting resources to prevent or repair damage (i.e. disruptive stress *sensu* Davison & Pearson 1996). In contrast, disturbances are external factors (physical or biological) that cause partial or total removal of biomass (Grime 2001). Species-specific environmental responses that underlie theories of coexistence (e.g. Chesson 1994) emphasize environmental fluctuations rather than interspecific competition in driving patterns of relative abundance. Given that turf algae are often highly stress-tolerant and resistant or resilient to disturbance (Hay 1981, Airoldi 1998), forms of stress and disturbance that disproportionately affect foundation species may indirectly benefit turf algae. Trade-offs between competitive ability, stress-tolerance, and resistance to disturbance form the basis of models of alternative evolutionary strategies and highlight that changes in patterns of dominance (i.e. numerical supremacy) are not necessarily an outcome of competitive interactions (Grime 2001, Keddy 2001). In their formative review, McCook et al. (2001) concluded that despite limited experimental evidence, coral-algal competition is likely a widespread process. However, a systematic evaluation of controlled experiments that separate competitive interactions between turf algae and corals or canopy algae from other processes is needed to weigh their contribution to such regime shifts on tropical and temperate reefs.

Here I provide the first quantitative synthesis, to my knowledge, of competitive interactions between foundation species and turf-forming algae across temperate and tropical marine ecosystems to disentangle the role of competition in mediating regime shifts involving these groups. I conduct a meta-analysis of experiments measuring the effects of canopy algae or corals and turf algae on one another to quantify the magnitude and direction of these effects and explore sources of variation (e.g. between foundation species life-history stages, turf algae functional groups). Because the definition of competition that I draw upon emphasizes both the effects and mechanisms of competition, I also review and summarize the mechanisms of competition indicated in the literature to underlie these interactions. I then discuss how the results of this synthesis inform our understanding of the process by which regime shifts between foundation species and turf algae may be driven by shifts in the balance of competition and address alternative mechanisms involving the disproportionate effects of stress and disturbance on these competing groups. I conclude with an outline for future research to explore the integrative effects of competition, stress, and disturbance in mediating regime shifts to turf algae and the stability of this generally undesirable ecosystem state.

5.3 MATERIALS AND METHODS

5.3.1 Literature Search and Data Extraction

To assemble an exhaustive collection of studies measuring the competitive effects of canopy algae or corals and turf-forming algae on one another I conducted a systematic literature search of Title, Abstract, and Keyword fields of the following databases: ‘Web of Science’ Core Collection (1900-2017), ‘Biological Abstracts’ (1926-2017), ‘Aquatic Sciences and Fisheries Abstracts’ (1960-2017), and ‘Dissertations and Theses Global’ (1980-2017). I retrieved experimental studies in temperate rocky marine systems (intertidal or subtidal) using the following combinations of search terms or less restrictive subsets: (Canopy* OR Kelp* OR Laminariales OR Rockweed* OR Macroalga* OR Fucoid* OR Fucus OR Fucales OR Brown-alga* OR Habitat-form*) AND (Turf* OR Filament* OR Mat-form* OR "Epilithic Alga*" OR "EAC" OR "EAM") AND (Compet* OR (Recruitment NEAR/5 Inhibit*) OR Canopy-Understor$y OR "Plant-Plant interaction*") AND (Experiment* OR Quantitative OR Empiric*). These search terms preclude studies on the effects of epiphytes. While some facultative algal epiphytes may decrease the performance of canopy algae (Worm & Sommer 2000) and might also be present in turf assemblages (Kiirikki 1996), I did not consider the effect of the epiphytic form to be a competitive effect of turf-forming algae *per se*. To retrieve equivalent studies from tropical reef systems, I conducted separate searches with the search term combinations: (Coral* OR Scleractinia*) AND (Turf* OR Filament* OR Mat-form* OR "Epilithic Alga*" OR "EAC" OR "EAM" OR "Cyanobacter*") AND (Compet* OR Coral-Alga* OR (Recruitment NEAR/5 Inhibit*)) AND (Experiment* OR Quantitative OR Empiric*). I also examined the reference lists of the relevant publications to identify additional relevant studies.

After screening titles and abstracts for obviously unrelated false positives, I further assessed the relevance of remaining publications identified from the literature search. I considered studies in the field, laboratory, or experimental mesocosms for inclusion in analyses provided they met the following 4 criteria (final yield = 69 publications):

1) Studies were manipulative experiments comparing the performance of the focal group or species (canopy algae or coral, turf-forming algae) between two treatments in which the hypothesized competing group or species (turf-forming algae, canopy algae or coral) was either absent or present. This included competitor removal (pulse or press), competitor addition, and transplantation type manipulations as well as manipulations of the competitor's effect (e.g. pre-treatment of seawater with the competitor, interference with the mechanism of interaction). Studies lacking proper controls, that manipulated the competitor indirectly (e.g. through herbivore exclusion), or that quantitatively compared units where interactions were naturally occurring or absent were excluded.

2) The two treatments were independently replicated.

3) For temperate systems, the response of turf algae was measured between late spring to late summer to separate competitive effects from seasonal changes in algal growth and productivity.

4) Information required to calculate effect sizes (means, sample sizes, and standard errors, standard deviations, or confidence intervals for both treatments) was reported or could be extracted from the article, or the raw data were made available by the authors or in a digital online repository.

To extract data for effect size calculations from this collection of studies, I used graph-digitizing software, PlotDigitizer v. 2.6.2 (http://plotdigitizer.sourceforge.net/), whenever the information was not reported in the text or tables. I considered multiple measures of the performance of individual species and functional or morphological groups for analyses including abundance variables (% cover, density, biomass), growth (size or change in size of whole/parts of organisms), survival (% survival, % mortality, coral tissue damage/mortality), and response variables indicating the organism's physiological status or level of stress (e.g. effective quantum yield, density of coral symbiotic zooxanthellae, Chl *a* content). If a study reported multiple response variables measuring the same phenomenon, I chose the variable most comparable with other studies in the analyses (turf algae abundance: % cover > biomass; canopy algae recruitment: density > % cover > biomass; coral physiological status: zooxanthellae density > effective quantum yield and Chl *a* content). For studies reporting results as a time series, I extracted data at the last time point within the seasonal constraints described above or, if recruitment was measured, during the recruitment period. For factorial experiments crossing competition orthogonally with other factors (e.g. temperature, sedimentation, herbivory, nutrient enrichment), I measured the effect of the competitor at the ambient level or in the absence of the additional factors. The aim of the analysis was to isolate, as much as possible, competitive interactions from the influence of external variables. This approach is a necessary first step towards determining how these interactions may be altered under changing external conditions.

Studies were further categorized by the life-history stage of canopy algae (microscopic recruit, i.e. embryo, zygote, microscopic germling; macroscopic recruit; adult) or coral (recruit, i.e. larva to primary polyp; established, i.e. juvenile to adult) and functional group of turf-forming algae (filamentous; corticated/coarsely branching; articulated coralline). This functional group designation of turf algae captures a gradient of increasing thallus longevity and decreasing mass-specific productivity (Steneck & Dethier 1994). I included benthic cyanobacteria (e.g. *Lyngbya* spp.) in the filamentous category because they may be mixed with filamentous algae in tropical turf assemblages (McCook 2001) and appear similar on a macroscopic and functional level. Temperate reef studies were also grouped into intertidal or subtidal assemblages.

5.3.2 Effect Sizes and Data Analysis

I measured the effect of the competitor for each study as the bias-corrected standardized mean difference, Hedges' *g* (Hedges & Olkin 1985), between the competitor present and competitor absent treatments as follows:

$$\text{Hedges' } g = \frac{\overline{Y}_{competitor} - \overline{Y}_{no\,competitor}}{S_{Pooled}}(J)$$

where $\overline{Y}_{competitor}$ and $\overline{Y}_{no\,competitor}$ are the mean responses in the competitor present and absent treatments, respectively, S_{Pooled} is the pooled standard deviation of the two groups, and J is a correction factor based on sample sizes. A negative value of g indicates a reduction in performance of the focal group in response to the competitor. For publications that reported results for multiple independent experiments or replicated experiments at multiple sites separated by greater than 1 km, at different times of the year, in different years, or with different species/functional groups, I calculated effect sizes for each of these experiments separately. These were treated as independent studies. When multiple response variables measuring different phenomena were reported for replicates within the same experiment (e.g. growth and survival), effect sizes were measured for each response variable, but treated in separate analyses.

To calculate overall effect sizes across studies for each combination of response variable, competitors (canopy algae, coral, turf-forming algae), life-history stage of canopy algae or coral, and functional group of turf for which there was sufficient data, I used random effects or mixed effects models. The random effects model attributes variation between individual effect estimates to within-study variance (sampling error) and between-study variance (variation in true effect sizes; Borenstein et al. 2009). The mean effect size is calculated by weighting study-specific estimates by the inverse of their variance, which includes a common between-study variance. I used the DerSimonian and Laird approximation to estimate the between-study variance (DerSimonian & Laird 1986). Mixed effects models allow for systematic comparisons of subgroups of the data (moderator analysis) to be made by testing the significance of the heterogeneity between groups (Q_M), and assume fixed differences in the true effect between subgroups, but treat effects within subgroups as random (Borenstein et al. 2009). I used mixed effects models to test the null hypotheses of no difference in effect of canopy algae on the abundance of turf algae between 1) functional groups of turf and 2) intertidal and subtidal reefs. Similarly, I tested the null hypotheses of no difference in effect of turf algae on the abundance of canopy algae recruits between 1) functional groups of turf, 2) microscopic and macroscopic recruits, and 3) intertidal and subtidal reefs. A subset of canopy manipulation experiments measured the response of multiple functional groups of turf algae within the same plots. Treating these measures as independent will over- or underestimate the precision of the effect size estimates if they are positively or negatively correlated, respectively (Borenstein et al. 2009). Because the non-independence issue was relevant to a minority of canopy manipulation experiments (27%), and those for which I had raw data indicated that correlations among functional groups were weak ($r < 0.3$) and typically negative, I opted to treat measures of different functional groups within the same plot as independent in the analyses. My calculations ignoring correlations likely overestimate variances around these mean effect sizes and my inferences based on them therefore more conservative.

To evaluate evidence of publication bias I used funnel plots to aid visual interpretation. A scarcity of studies with small sample sizes (large SE) and non-significant outcomes results in a linear relationship between sample size and effect size and an asymmetric funnel plot. I tested for asymmetry of funnel plots using Kendall's rank correlation between standardized effect sizes and standard errors ($\alpha = 0.10$). I also calculated Rosenthal's fail-safe number for each overall effect size or subgroup mean as a sensitivity analysis, which estimates the number of unpublished studies with null effects that, if included (unweighted) among the studies located by the meta-analyst, would be required to reduce the significance below $\alpha = 0.05$ (Rosenthal 1979). For comparison, I also calculated Rosenberg's fail-safe number, which is based on weighted meta-analysis and estimates the weight of a single additional study, relative to the average of those included in the model, with a null effect necessary to reduce the significance below $\alpha = 0.05$ (Rosenberg 2005). These computations were made with the fail-safe number calculator available online (Rosenberg 2005). All other analyses were conducted in R version 3.1.3 (R Core Team 2015) using the 'metafor' package (Viechtbauer 2010).

There was evidence of funnel plot asymmetry indicative of publication bias for the abundance of turf algae competing with canopy algae (Appendix E: Table E1, Fig. E1A) or coral (Appendix E: Table E1, Fig. E1B), and coral growth (Appendix E: Table E1, Fig. E1F), but not the other variables (Appendix E: Table E1, Fig. E1D–E,G,H). It should be noted that some funnel plots were based on a relatively small number of studies, and asymmetry may emerge by chance (Jennions et al. 2013). Of those variables showing funnel plot asymmetry, Rosenthal's fail-safe numbers indicated the results were relatively robust to overestimates of the true effect size (Appendix E: Table E1). Rosenberg's fail-safe numbers indicated that results of all models would be more sensitive to publication bias in comparison to Rosenthal's fail-safe.

5.3.3 Mechanisms of Competition

In addition to the systematic search for manipulative experiments measuring the competitive effects of canopy algae or corals and turf-forming algae on one another, I also surveyed the extracted literature and their references for studies reporting or evaluating the mechanisms by which these groups suppress the performance of their competitors.

5.4 RESULTS AND DISCUSSION

5.4.1 Description of Datasets

From the 69 publications reporting results of manipulative experiments that met my inclusion criteria (Appendix F), I extracted 193 effect sizes (Hedges' *g*) measuring the impact of foundation species on the performance of turf-forming algae or vice versa. These involved a variety of different species and genera (Appendix G: Table G1). The majority (73%) of these effect sizes came from experiments in temperate rocky reef systems and the number of publications and study-specific effect sizes contributing to each overall effect size calculation varied considerably (Appendix G: Table G2). Both tropical and temperate studies were distributed broadly across the globe, but with some regional biases (Fig. 5.1; Appendix G: Table G1). Tropical studies were concentrated within the Great Barrier Reef (18) and Caribbean (17) with the remainder scattered across the Philippine Sea (4), North (5) and South Pacific (4), South Atlantic (1), and Florida Keys (3). Temperate studies were conducted on the west (49) and east (14) coasts of North America, in the NE Atlantic (8), Baltic Sea (10) and Mediterranean Sea (20), around Australia and New Zealand (37), and in the Korea Strait (3), but with noticeable gaps on the west coasts of South America and Africa. The year of publication of studies included in the analyses ranged from 1981 to 2017 with an increasing frequency through time (Fig. 5.2). A large increase in the number of publications began in the late 1990s and early 2000s concurrent with the first publications of experiments on tropical reefs (Fig. 5.2). The duration (mean ± SD) of experiments ranged from 5 d ± 2 d (median = 5 d) for

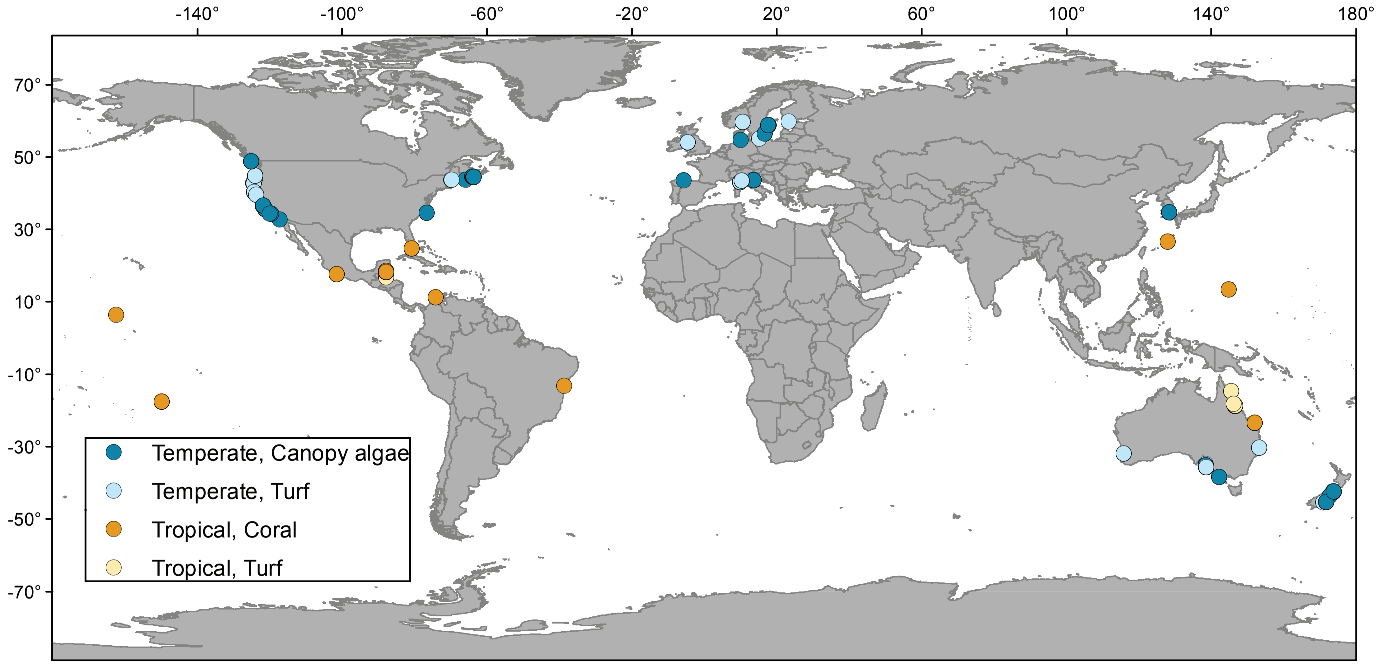

Fig. 5.1. Locations of studies included in meta-analyses of competition experiments on temperate (cool colours) and tropical reefs (warm colours) between foundation (canopy algae, corals) and turf-forming species. Legend indicates whether canopy algae, coral, or turf algae is the focal group of the experiment for which the response is measured.

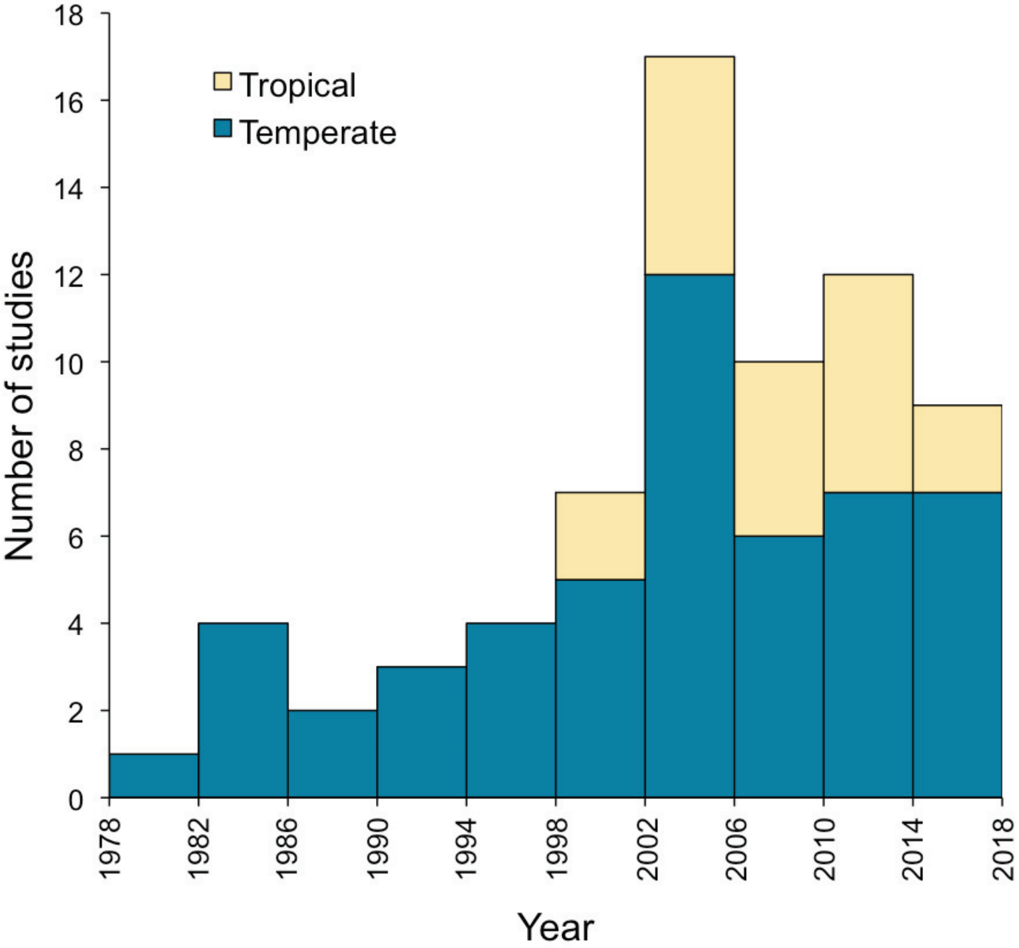

Fig. 5.2. Publication frequency at 4-yr intervals of studies included in meta-analyses of competition experiments on temperate and tropical reefs between foundation (canopy algae, corals) and turf-forming algal species.

studies on the effects of filamentous turfs on the survival of coral recruits to 706 d ± 763 d (median = 485 d) for studies on the effects of canopy algae on the abundance of articulated coralline turfs (Appendix G: Table G2). The average study duration rarely spanned multiple years (Appendix G: Table G2).

5.4.2 Competitive Effects on Temperate Reefs

Canopy algae had significant negative effects on all 3 functional groups of turf-forming algae, but with a trend toward a greater negative effect on more delicate filamentous turf algae compared to the articulated coralline and corticated/coarsely branching groups (Fig. 5.3A). However, the mixed effect model indicated turf functional group did not explain significant variation in effect of canopy algae ($Q_M = 2.80$, $p = 0.246$). Currents and water flow are reduced within canopies of brown algae (Jackson & Winant 1983, Irving & Connell 2006b), which could inhibit turf algae by affecting recruitment or the rate of nutrient uptake. However, there is little experimental evidence to support a strong effect of reduced water flow *per se* on algal assemblages in the understorey (Wernberg et al. 2005, Russell 2007). More commonly, canopies of brown algae suppress the growth of turf-forming algae in the understorey by reducing the availability of light (Kim 2002, Connell 2005, Wernberg et al. 2005, Russell 2007) or through the abrading, sweeping motion (‘whiplash’) of algal fronds (Irving & Connell 2006a,b, Russell 2007) with water movement (Fig. 5.4A,B). The more robust morphology and increased shade tolerance (Häder et al. 2003, Toohey et al. 2004, Irving & Connell 2006a) of articulated coralline and corticated/coarsely branching turf algae may impart greater resistance to the effects of shading and abrasion/whiplash by canopy algae. Alternatively, the trend towards smaller effects on these groups may reflect a facilitating effect of brown algal canopies in some circumstances (Appendix E: Fig. E2, E3). In contrast to fugitive species, so called obligate understorey species are much reduced in abundance when the ameliorating effect of the canopy to temperature, high light, and desiccation stress is removed (Dayton 1975, Cervin et al. 2005). Consequently, compared to subtidal reefs, the mean effect of canopy algae on turf algae was significantly less negative on intertidal reefs where more intense physical stress would

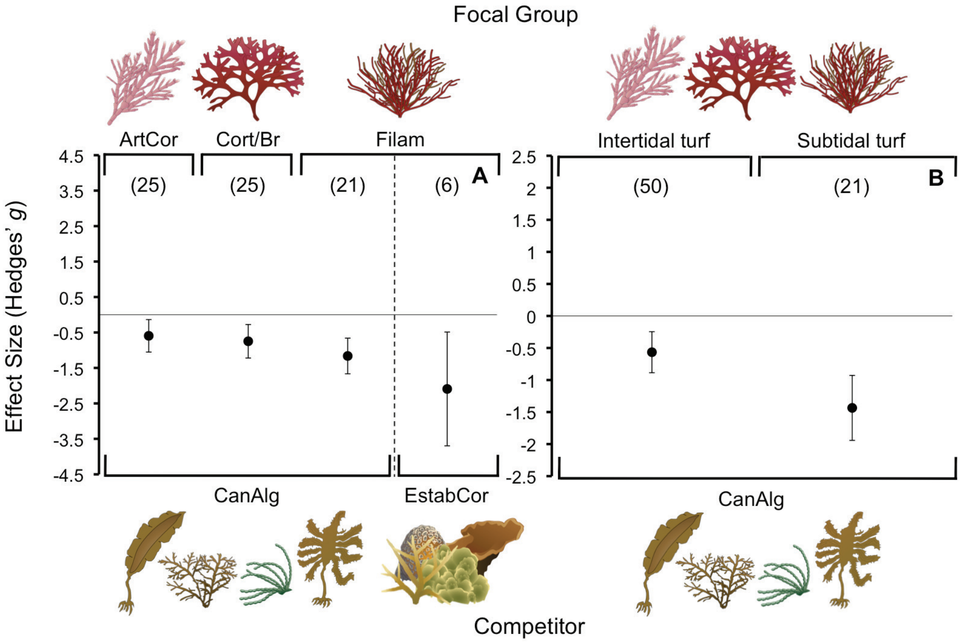

Fig 5.3. Competitive effects (standardized mean difference) of canopy algae and established corals (Competitors: CanAlg, EstabCor) on abundance of turf-forming algae (Focal Groups). Effects are grouped by turf algae in (A) 3 functional groups: articulated coralline algae (ArtCor), corticated/coarsely branching (Cort/Br), and filamentous algae (Filam) and (B) intertidal and subtidal assemblages. Data are mean effect sizes calculated from mixed or random effects models and 95% confidence intervals. Number of study-specific effect sizes contributing to each overall effect size shown at top of figure directly above data points. Image credits: Tracey Saxby (*Chondrus*, *Hormosira*, *Cystoseira*, *Acropora*, plate and encrusting coral), Joanna Woerner (*Porites lobata*) & Dieter Tracey (filamentous algae), IAN Image Library (ian.umces.edu/imagelibrary/).

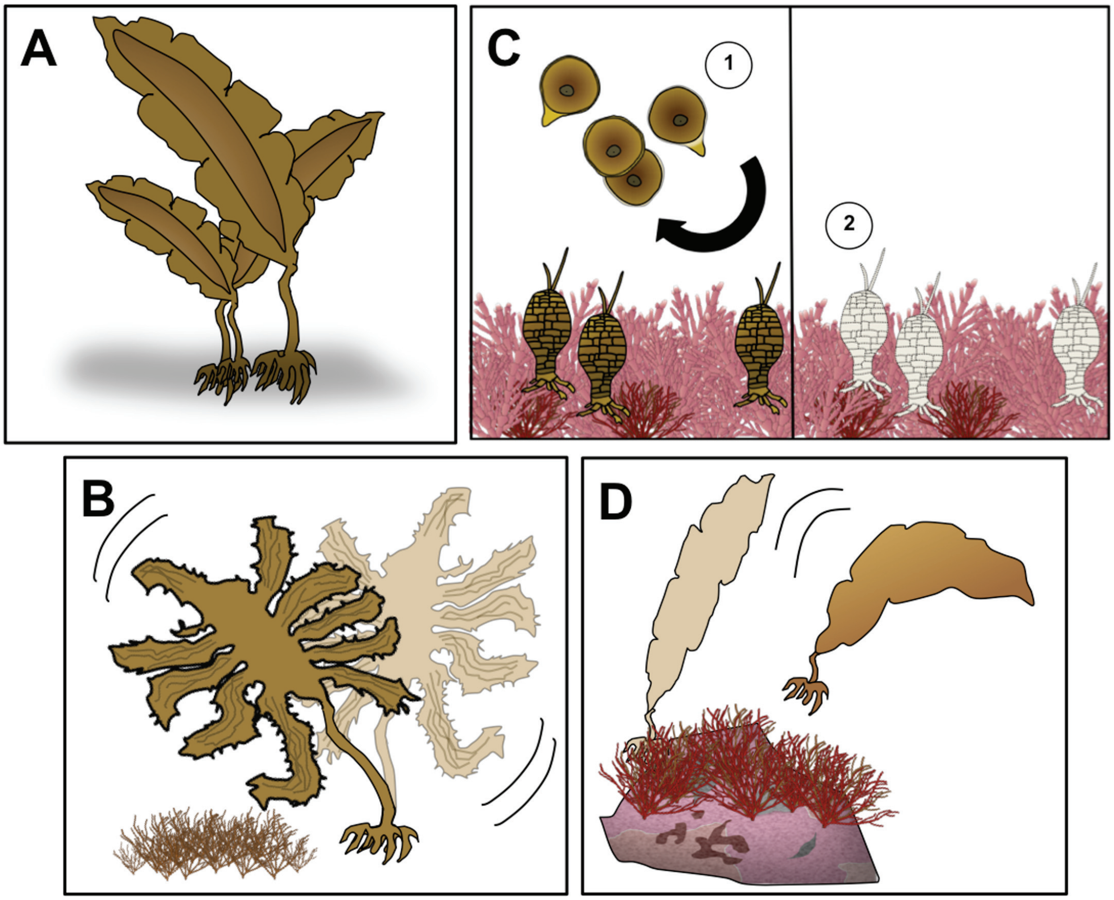

Fig 5.4. Mechanisms of competition between canopy algae and turf-forming algae. Canopy algae suppress turf algae through (A) shading and (B) abrasion/whiplash. Turf algae (C) inhibit early life-history stages of canopy algae by forming a settlement barrier [1] or increasing post-settlement mortality via sediment smothering, shading, overgrowth, or allelopathic exudates [2] and (D) cause post-recruitment mortality of macroscopic recruits via dislodgement/sloughing. Image credit: Dieter Tracey (filamentous algae), IAN Image Library (ian.umces.edu/imagelibrary/).

make the ameliorating effect of the canopy more beneficial (Fig. 5.3B; $Q_M = 8.07$, $p < 0.01$).

While adult canopy algae directly suppress turf-forming algae, reciprocal effects of turf-forming algae are largely limited to the early life-history stages of canopy algae. I found only 2 publications investigating effects of turf-forming algae on adults. These studies reported either neutral (Benedetti-Cecchi et al. 1996) or facilitating effects (Barner et al. 2016). Turf-forming algae limited recruitment of kelps and fucoids, but the mean effects also varied between functional groups of turf (Fig. 5.5A). Turf functional group explained significant heterogeneity in effect sizes ($Q_M = 8.45$, $p = 0.015$). Corticated/coarsely branching and filamentous turf algae had significant negative effects on the abundance of recruits (Fig. 5.5A). In contrast, the negative effect of articulated coralline algae on recruit abundance was small and non-significant (mean = -0.34, CI = -0.99/0.31; Fig. 5.5A). While most individual studies reported negative effects, others reported positive effects of articulated coralline turfs, all of which were intertidal studies (Appendix E: Fig. E4). Pooled across all functional groups of turf algae, the overall effect size for studies on intertidal reefs did not differ from zero and was significantly different from studies on subtidal reefs (Fig. 5.5B; $Q_M = 16.9$, $p < 0.001$). The greater frequency of positive interactions in intertidal compared to subtidal assemblages may provide support for the stress-gradient hypothesis (Bertness & Callaway 1994), suggesting that the ameliorating effects of turf algae on physical extremes in temperature (Brawley & Johnson 1991) and water motion (Vadas et al. 1990) experienced by intertidal algal propagules outweigh potential negative effects. Positive effects on propagules and recruits also may arise if turf algae limit the movement or activity of grazers (Harris et al. 1984, Benedetti-Cecchi & Cinelli 1992). The mean effect of turf algae on microscopic recruits was also twice as large compared to macroscopic recruits (Fig. 5.5C), suggesting that the most intense competition from turf occurs at the earliest life-history stages. However, life-history stage was marginally non-significant when included as a moderator in a mixed effect model ($Q_M = 3.62$, $p = 0.057$).

Variation between functional groups of turf algae in their effects on recruitment of canopy algae, and a larger effect on microscopic recruits, might also reflect variation in the mechanisms of competition. The dense matrix of algal branches in turf assemblages

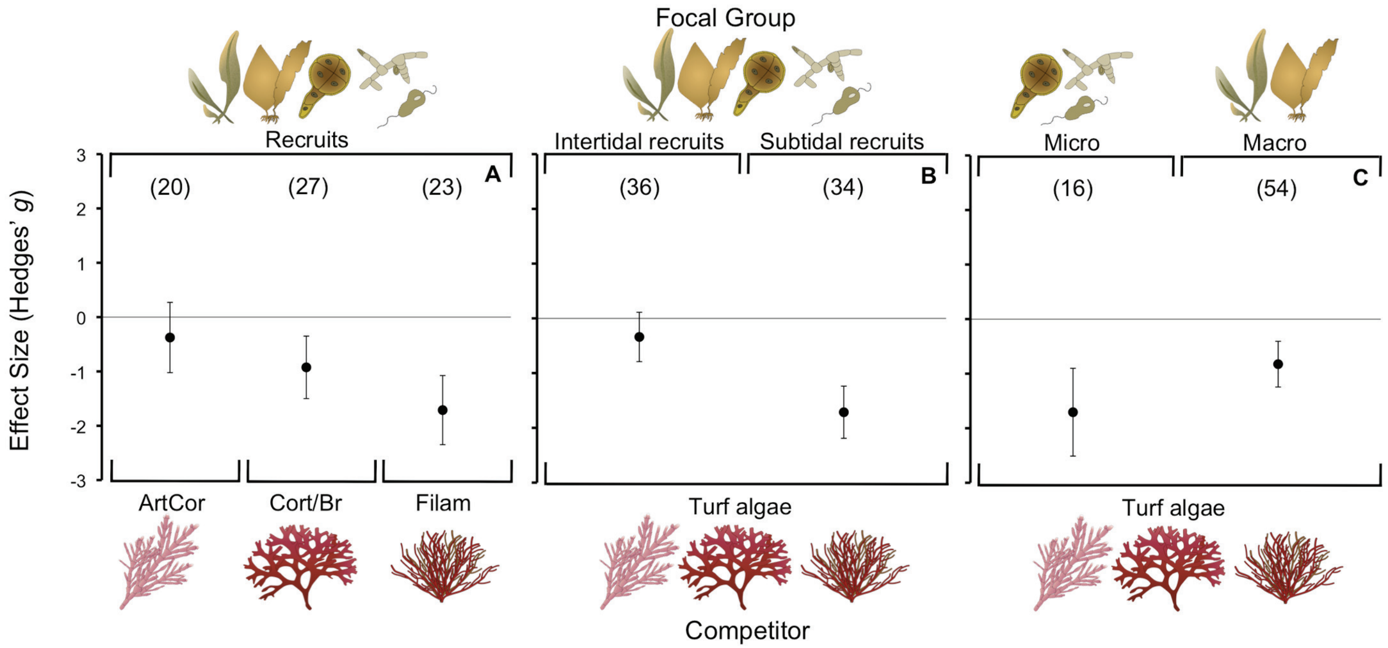

Fig 5.5. Competitive effects (standardized mean difference) of turf-forming algae (Competitors) on abundance of early life-history stages of canopy algae (Focal Groups). Effects are grouped by (A) turf functional group (see Fig 1), (B) intertidal and subtidal assemblages, and (C) microscopic (Micro: zygotes, embryos, germlings) and macroscopic (Macro) recruits. Data are mean effect sizes calculated from mixed effects models and 95% confidence intervals. Number of study-specific effect sizes contributing to each overall effect size shown at top of figure directly above data points. Image credits: Tracey Saxby (*Chondrus*) & Dieter Tracey (filamentous algae), IAN Image Library (ian.umces.edu/imagelibrary/).

forms a settlement barrier to propagules of canopy algae (Fig. 5.4C; Isæus et al. 2004, Råberg et al. 2005, Bellgrove et al. 2010) that is exacerbated by associated sediments (Alestra et al. 2014). Inorganic sediments prevent attachment of fucoid zygotes and kelp spores (Devinny & Volse 1978, Schiel et al. 2006, Deiman et al. 2012) or smother attached microscopic stages (Devinny & Volse 1978, Isæus et al. 2004). Fine-branching filamentous forms may create a more tightly woven matrix of algal branches or more effectively trap and stabilize sediments than coarsely branching forms. In addition to smothering by sediments, turf algae can directly cause post-settlement mortality of recruits (Fig. 5.4C). The effects of corticated turf algae and fast-growing filamentous forms via overgrowth (Steen 2004) and shading (Worm & Chapman 1998, Steen 2004) may be particularly large on microscopic recruits, but decrease once canopy algae reach a size refuge. Limited evidence suggests some filamentous forms also release exudates that decrease settlement success and increase post-settlement mortality (Råberg et al. 2005, Svensson et al. 2013), but similar allelopathic effects for articulated coralline algae are equivocal (Bellgrove et al. 2010, Alestra et al. 2014). Post-recruitment mortality can also result from dislodgement of macroscopic recruits attached to certain forms of turf algae (K. Burek *unpublished Honours thesis, Dalhousie University*; Fig. 5.4D). While filamentous and corticated/coarsely branching turf forms greatly reduce the attachment strength of kelp (K. Burek *unpublished Honours thesis, Dalhousie University*), articulated coralline algae may strengthen attachment (Milligan & DeWreede 2000).

5.4.3 Competitive Effects on Tropical Reefs

In contrast to temperate reefs, filamentous turf algae on tropical reefs had no significant effect on the survival of settling coral larvae and primary polyps (Fig. 5.6). This may reflect latitudinal differences in the nature of turf assemblages, which tend to be composed largely of short (mm – cm), cropped filamentous forms on tropical reefs (e.g. Wismer et al. 2009, Harris et al. 2015), but reach greater heights (cm – 10s cm) on temperate reefs (e.g. Berger et al. 2003, Bellgrove et al. 2010). The greater size of coral larvae compared to kelp spores and motility compared to fucoid zygotes could also explain this latitudinal difference. However, variation between tropical turf assemblages in their effect on coral settlement and recruitment (Appendix E: Fig. E5) may be related to turf height, density, and composition (Birrell et al. 2005). Particular assemblages of tropical turf algae inhibit coral recruitment by forming a barrier to settlement (Fig. 5.7A; Birrell et al. 2005) or overgrowing small settlers (Fig. 5.7B; Birkeland 1977, Bak & Engel 1979). It also is possible that coral larvae avoid turf algae by responding to chemical cues as has been shown for other tropical macroalgae (Dixson et al. 2014).

My results not only suggest that filamentous turfs generally do not limit the establishment of corals, but also that previously established corals have a strong negative, albeit highly variable, effect on the abundance of turf algae (Fig. 5.3). This variability might be in part a consequence of the smaller number of studies contributing to the overall effect size in the latter case. However, there also is considerable variation in relative competitive ability among different species (White & O'Donnell 2010) and morphological groups of corals (Swierts & Vermeij 2016), which may reflect disparities in the mechanisms of competition. Shading of turf algae is more typical of tabulate corals (Fig. 5.7C; Baird & Hughes 2000). Other documented mechanisms such as space pre-emption and overgrowth of turf algae (Fig. 5.7D; McCook 2001, Diaz-Pulido & McCook 2002, Barott et al. 2012b) are more effective in encrusting and massive colonies than in branching corals (Swierts & Vermeij 2016). Digestion of adjacent turf algae by mesenterial filaments (Fig. 5.7D) has been reported for some coral species experiencing bleaching, but the generality of this phenomenon is unknown (Marhaver 2011). Because of limitation in sample size, I lumped coral forms (e.g. branching, mounded, plate-like, etc.) under one category of established corals, but variation in coral composition among studies (Appendix G: Table G1) likely contributes to increased variability of the mean effect.

In comparison to temperate rocky reefs, the mechanisms by which tropical turf algae directly interact with and suppress competitors once established are more varied (Fig. 5.7E). However, the effect of filamentous turf algae on established corals across studies was not consistent between response variables. While the mean effects were always negative in direction, these were only significant for growth and survival (Fig. 5.6). In contrast, effects on abundance and physiological status were highly variable and non-significant (Fig. 5.6). Again, this may reflect the comparatively fewer studies

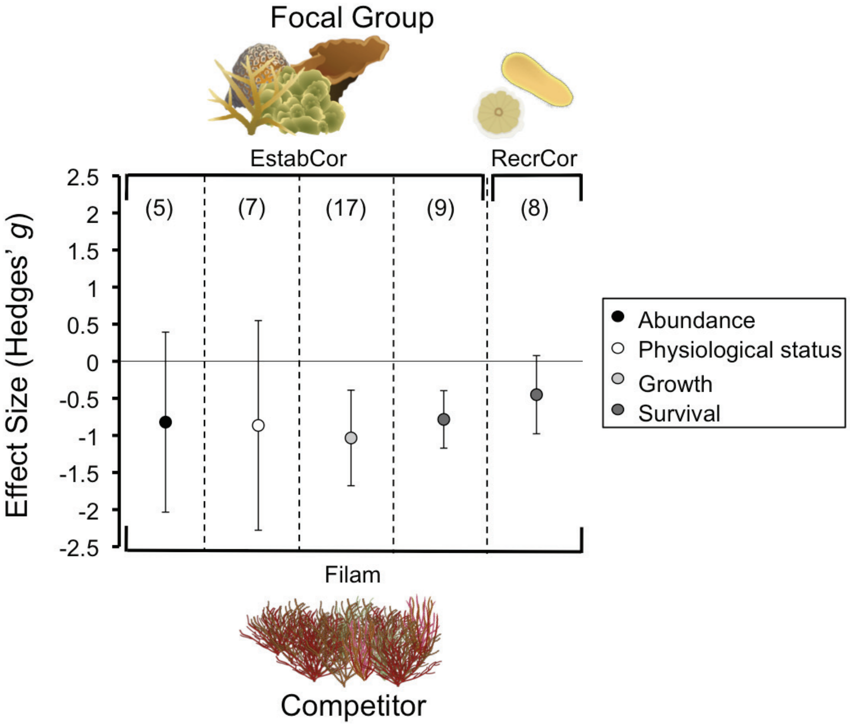

Fig 5.6. Competitive effects (standardized mean difference) of filamentous (Filam) turf-forming algae (Competitor) on abundance, physiological status, growth, and survival of established corals or recruits (Focal Groups: EstabCor, RecrCor). Data are mean effect sizes calculated from random effects models and 95% confidence intervals. Number of study-specific effect sizes contributing to each overall effect size shown at top of figure directly above data points. Image credits: Tracey Saxby (*Acropora*, plate and encrusting coral, *Chaetomorpha*), Joanna Woerner (*Porites lobata*), Dieter Tracey (filamentous algae), & Diana Kleine (non-branching filamentous algae), IAN Image Library (ian.umces.edu/imagelibrary/).

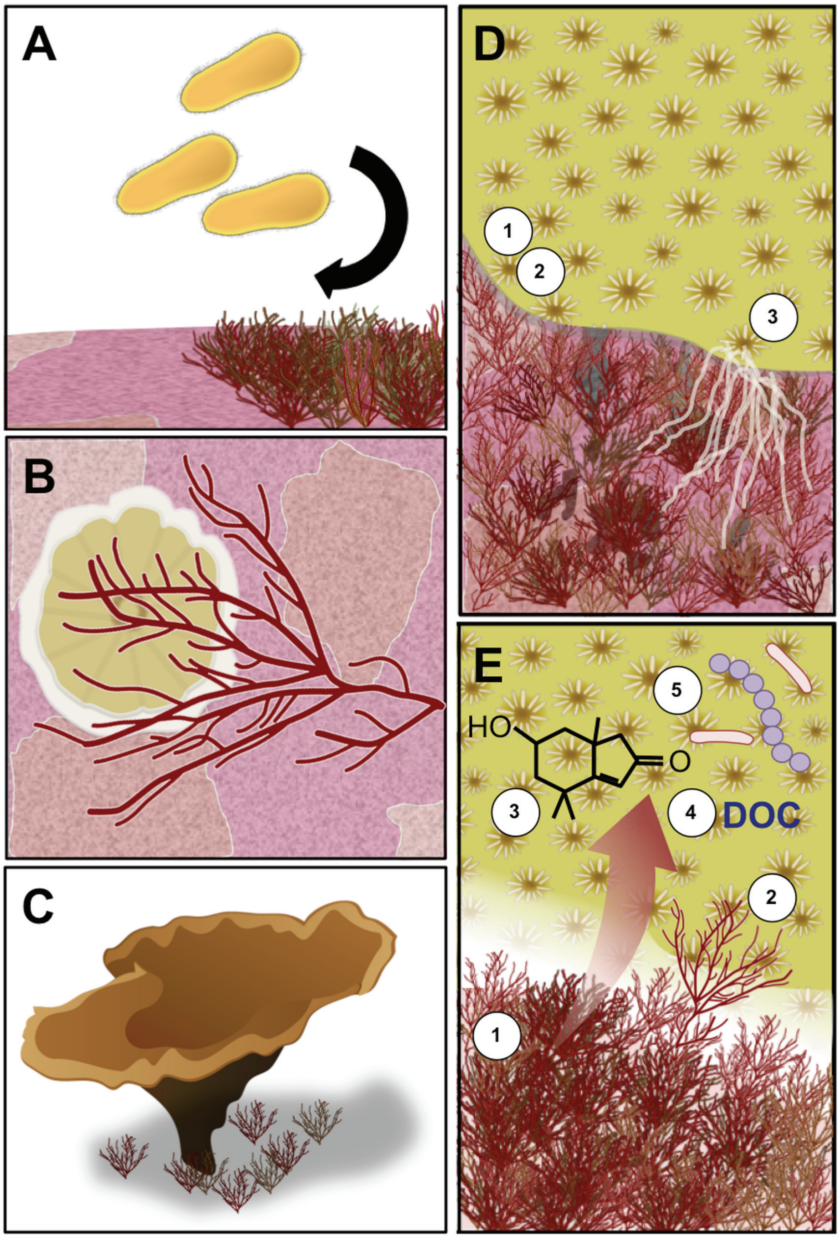

Fig 5.7. Mechanisms of competition between reef-building corals and turf-forming algae. Turf algae inhibit early-life history stages of coral by (A) forming a settlement barrier to coral larvae and (B) overgrowth of small recruits. Established corals suppress turf algae through (C) shading or (D) at the interaction zone through space pre-emption [1], overgrowth [2], and digestion by mesenterial filaments [3]. Turf algae (E) suppress established corals by space pre-emption [1], overgrowth [2], allelopathy [3], and various turf-mediated physical and biological processes at the interaction zone described in detail in the text (e.g. releasing dissolved organic carbon [4], stimulating microbial and pathogenic activity [5]). Image credits: Tracey Saxby (plate coral, *Chaetomorpha*), Dieter Tracey (filamentous algae), & Diana Kleine (non-branching filamentous algae), IAN Image Library (ian.umces.edu/imagelibrary/).

contributing to these effect sizes, or variability in competitive ability among coral species and growth forms. Turf algae can pre-empt space or overgrow corals (Fig. 5.7E; Barott et al. 2012b, Gowan et al. 2014, Jorissen et al. 2016), but branching corals may be more susceptible to overgrowth than encrusting or massive colonies (Swierts & Vermeij 2016).

Alternatively, variable effects of different turf assemblages on corals between and within performance measures may result from differences in turf composition and physical structure. Some filamentous turf algae may produce allelopathic chemicals that cause bleaching and necrosis of coral tissue and facilitate overgrowth (Fig. 5.7E), but this appears to be highly species-specific (Jompa & McCook 2003a,b) and coral species vary in their susceptibility to these chemicals (Bonaldo & Hay 2014). There are also a number of turf-mediated processes occurring at the coral-algae interaction zone that lead to bleaching, necrosis, and algal overgrowth of coral tissue, effects that are exacerbated with increasing height of the turf (Jorissen et al. 2016). Turf algae exude photosynthate (Fig. 5.7E; Haas et al. 2010), which stimulates microbial activity (Fig. 5.7E; Smith et al. 2006), increases abundance of pathogens (Barott et al. 2012a), decreases dissolved oxygen (Smith et al. 2006) and leads to hypoxia at night (Wangpraseurt et al. 2012, Jorissen et al. 2016). There is also an increase in the thickness of the diffusive boundary layer at the interaction zone, which could limit coral respiration and photosynthesis and promote the accumulation of allelochemicals and harmful metabolites (Wangpraseurt et al. 2012, Jorissen et al. 2016). Therefore, while there was an overall strong negative effect of established corals on tropical turfs, reciprocal effects of turf appear to be more context-dependent, and the prevailing direction of the hierarchy may depend on factors that alter the standing biomass and species composition of turf.

5.4.4 Relative Importance of Competition in Mediating Regime Shifts

My results suggest regime shifts from foundation species to turf-forming algae could be mediated in part by changes to the competitive balance between these two groups. Predictions of patch occupancy models indicate that a species or group that is an inferior competitor locally can exclude a superior competitor regionally if an absolute competitive hierarchy is relaxed (i.e. if the probability of a superior competitor becoming established is lower in patches occupied by an inferior competitor than in unoccupied patches) and the colonization rate of the inferior competitor is sufficiently high (Klausmeier & Tilman 2002). Evidence here illustrates that under ambient conditions, established brown algal canopies and coral colonies generally suppress turf algae, but that turf assemblages, particularly filamentous forms, can inhibit establishment of algal recruits or limit expansion of established corals. Filamentous algae generally have high maximum specific growth rates (Pedersen & Borum 1996, Bokn et al. 2003) and rapid nutrient uptake rates (Pedersen & Borum 1997). Therefore, factors that stimulate their growth, and thereby increase standing biomass or colonization rate of open space, theoretically could lead to reef-scale declines in the abundance of foundation species. Specific data on the patch dynamics, rates of dispersal, colonization and vegetative propagation of turf assemblages are scarce (but see Airoldi 2000, Diaz-Pulido & McCook 2002). However filamentous algae are often among the first colonists of open space on temperate (Hawkins & Harkin 1985, Irving & Connell 2006b) and tropical reefs (Woodley et al. 1981, Adjeroud et al. 2009).

Growth of turf algae can be stimulated by a number of factors modified by anthropogenic activity. Elevated nutrients in urbanized and eutrophic areas support increased growth rates (Pedersen & Borum 1997, Lotze & Schramm 2000) and abundance of temperate turf algae (Gorgula & Connell 2004, Russell et al. 2009). However, heightened nutrient concentrations alone do not always stimulate turf growth and increase standing biomass on tropical reefs (Hatcher & Larkum 1983, Larkum & Koop 1997, Russ & McCook 1999, Burkepile & Hay 2006). Nutrient delivery and uptake are also mediated by water flow (Carpenter et al. 1991, Williams & Carpenter 1998). Given their reliance on passive diffusion of CO_2 in the absence or decreased efficiency of carbon concentrating mechanisms (Hepburn et al. 2011, Falkenberg et al. 2013a), increased concentrations of CO_2 associated with future ocean acidification also are expected to stimulate growth of tropical (Ober et al. 2016) and temperate (Connell & Russell 2010) turf algae, particularly when combined with nutrient enrichment (Russell et al. 2009, Falkenberg et al. 2012). Tropical fish grazers also maintain turf assemblages at a low standing biomass (Hatcher & Larkum 1983, Marshell & Mumby 2015) and cropped-height (Vermeij et al. 2010), but generally do not limit areal extent (Burkepile & Hay

2006). Likewise, the abundance of temperate turf algae is reduced by crustacean and molluscan grazers (Worm et al. 2001, Scheibling et al. 2009, Falkenberg et al. 2014). While the ability of grazers to counter the enriching effects of heightened nutrients and CO_2 is variable (Worm et al. 2001, Vermeij et al. 2010, Ghedini et al. 2015), the highest rates of turf algae growth, and greatest potential for competition-mediated regime shifts, can be expected when enrichment is combined with weak top-down control where grazing intensity is naturally low or reduced by overfishing.

Increased spatial dominance of turf algae also could occur without invoking changes to competitive hierarchies if increasing stress and disturbance disproportionately afflict canopy algae and corals. This may be the case if there is a trade-off between competitive ability and stress tolerance (Keddy 2001), vulnerability to disturbance (Dayton et al. 1984), or colonization rate (Sousa 1979). Anthropogenic influences that act as a resource to turf algae can also be a form of disruptive stress to foundation species. For example, increased oceanic uptake of CO_2 benefits tropical turf algae (Ober et al. 2016), but consequent acidification impedes calcification rates and growth of reef-building corals (Gattuso et al. 1998, Jokiel et al. 2008). Further, while warming seawater temperatures can synergistically enhance turf algae growth in response to CO_2 enrichment (Connell & Russell 2010), they also impose chronic stress on canopy algae (Wernberg et al. 2010, Simonson et al. 2015) and corals (Carricart-Ganivet et al. 2012), or generate disturbance in the form of pulse events such as heat waves (Smale & Wernberg 2013, Wernberg et al. 2013), El Niño (McClanahan et al. 2001), and other sea surface temperature anomalies (Eakin et al. 2010). Likewise, sedimentation is often a form of stress or disturbance for established corals (Rogers 1990, Nugues & Roberts 2003) or early life-history stages of coral (Birkeland 1977, Birrell et al. 2005) and canopy algae (Devinny & Volse 1978). However, turf algae commonly tolerate high sediment loads (Airoldi 1998, Connell 2005, Eriksson & Johansson 2005) and even exacerbate the effects of sedimentation on foundation species by binding and accumulating sediments through a reduction in along-bottom flow (Purcell 2000, Gorman & Connell 2009, Filbee-Dexter et al. 2016). Physical disturbances such as hurricanes and tropical cyclones (Gardner et al. 2005, Osborne et al. 2011, Filbee-Dexter & Scheibling 2012), and biological disturbances such as outbreaks of crown-of-thorns starfish (Osborne et al.

2011) or coral disease (Aronson & Precht 2001) and tissue loss induced by heavy fouling of canopy algae (Scheibling et al. 1999), also cause large-scale removal or mortality of foundation species. Moreover, anthropogenic impacts that cause disruptive stress may increase the effective intensity of such disturbances by prolonging recovery times (Gaylord et al. 2015).

Large disturbance events may likewise intensify the effects of stress on foundation species if decreasing adult density results in a loss of positive interactions. Algal canopies ameliorate physical stress from high light intensity, promoting increased adult growth (Bennett et al. 2015a). Furthermore, movement of fronds across the bottom limits sediment accumulation (Connell 2005, Wernberg et al. 2005, Irving & Connell 2006b) and temperature-mediated epiphyte growth, which facilitates recruitment of canopy algae (Bennett & Wernberg 2014). Loss of other density-dependent processes inhibits recovery of foundation species and benefits turf algae directly or indirectly. The large increase in open space associated with coral mortality greatly expands the foraging area for herbivores and effectively decreases grazing rate per area of substratum (Williams et al. 2001). Conversely, on temperate reefs a low density of canopy algae can intensify grazing on remaining individuals (Chapter 2) or new recruits (Bennett et al. 2015b). Recruitment limitation following loss of adults also may arise from a dwindling supply of propagules and concomitant supply-side constraints on tropical (Hughes et al. 2000, Vermeij & Sandin 2008) and temperate reefs (Bennett & Wernberg 2014; Chapter 3).

5.4.5 Conclusions and Future Directions

Through this synthesis of the literature from tropical and temperate reefs I have shown that corals and canopy algae generally exert a negative effect on the abundance of turf-forming algae, but that the competitive effect of turf algae depends on the functional form of turf and life-history stage of the interacting foundation species. Moreover, variability in the effect of competitors often can be interpreted in light of the competitive mechanisms at play. Since the predominant effect of turf algae is to limit the establishment of canopy algae or expansion of established corals, it is possible that factors stimulating turf growth and expansion alone (decreased herbivory, nutrient enrichment, increased CO_2) may shift the competitive balance in favour of turf, resulting in reefs that are depauperate of corals or canopy algae. However, factors that stimulate turf growth are often concomitant with anthropogenic stressors or disturbances to foundation species (Gorman et al. 2009, Rocha et al. 2015) that may benefit turf algae indirectly. My results suggest competition plays a role in mediating regime shifts from foundation to turf-forming species, but it remains to be seen if the main effect of anthropogenic stressors is promoting the growth of turf (shifting the balance between competitors) or reducing the abundance of foundation species (disproportionately limiting one competitor). The reality likely falls somewhere in between where recovery of foundation species following adult losses is made increasingly difficult by proliferating turf algae that limit recruitment of canopy algae or expansion of residual coral colonies.

To accurately parse out the relative importance of competition, stress, and disturbance requires more factorial competition experiments in the field and laboratory. These ecological processes do not operate independently. Few studies included in this analysis were factorial experiments that tested interactions of competition with herbivory, nutrient or CO_2 enrichment, or other forms of stress and disturbance that potentially mediate competitive interactions (Appendix G: Table G2). Experiments conducted along natural gradients in the field also will be useful in this respect, and have revealed the existence of gradients in competition intensity in terrestrial ecosystems (Keddy 2001). Only four studies included here aimed to replicate experiments in space or time to make use of natural gradients (McCook 2001, Venera-Ponton et al. 2011, Corado-Nava et al. 2014, Barner et al. 2016). Furthermore, many competition experiments are often conducted on relatively short time scales (Appendix G: Table G2) following pulse removals. Since there may be a divergence between the short-term dynamics of small-scale interactions and the long-term outcome of competition on a reef scale, it would be beneficial to extend experiments across multiple years. Synthesizing observational/correlative studies also would extend generality of this study’s conclusions.

While it is not always feasible to conduct field experiments on the relevant spatial and temporal scales, especially when there are multiple crossed factors, spatial (e.g.

interacting particle systems) and dynamic models will be useful in this regard. Models that take into account competitive effects are powerful tools that allow ecologists to predict the equilibrium abundance of foundation species like corals and canopy algae at increasing levels of external forcing variables (e.g. grazing pressure, nutrient input, sedimentation, temperature). As such, they provide a platform to explore the integrative effects of competition, disturbance, and stress. Importantly, they can reveal at what levels of the forcing variables abrupt changes in abundance are expected and whether such changes may be easily reversed by returning the forcing variable to below the level that caused the shift (i.e. whether the regime shift is continuous or discontinuous). Such models have been applied to regime shifts in response to coral reef degradation (Mumby 2009, Fung et al. 2011), but typically assume minimal or no effects of turf algae. Furthermore, I have shown that grouping the competitive effects of turf into one functional group will not accurately capture the dynamics of competition. Improved estimates of the magnitude and direction of the effects of foundation and turf-forming species, the associated uncertainty, and systematic sources of variability will improve the utility of such models to evaluate the stability of these undesirable regime shifts and potential for recovery under alternative climate and management scenarios.

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CHAPTER 6

DISCUSSION

Concerns that assemblages of turf-forming algae constitute a stable ecosystem state on shallow reefs are linked to the difficulty of reversing conditions to recover important foundation species. In my thesis, I have shown that identifying how key ecological interactions and processes change with environmental conditions and context is necessary to understand their contribution to the stability of this new state. Grazing intensity by the snail *Lacuna vincta* changes with available kelp biomass (Chapter 2), indicating that the direct and indirect effects of this mesograzer are likely to be greater on kelp depauperate reefs. However, the strength of the relationship between grazing intensity and kelp biomass was weaker for *Laminaria digitata* compared to *Saccharina latissima*, suggesting that the effects of grazing on kelp recovery may depend on species composition. In Chapter 4, I found current recruitment and survivorship of young sporophytes in degraded kelp beds are low compared to measures in the 1980's (Chapman 1986, Johnson & Mann 1988), indicating that demographic processes on rocky reefs in Nova Scotia have changed over 3 decades of ocean warming, and with increasing grazing intensity by *L. vincta*, introduction of the invasive bryozoan *Membranipora membranacea*, and proliferation of turf algae. Competitive interactions with turf algae also can inhibit recruitment of foundation species, but effects are context dependent with no overall effect on intertidal reefs, coral reefs, and by articulated coralline turf algae compared to other functional groups (Chapter 5). Context dependency of ecological interactions and impacts of multiple stressors on ecosystems (Crowe et al. 2013) support the notion that each particular reef system may be more or less vulnerable to a persistent shift to turf algae based on its unique characteristics in space and time.

Examining the effects of stressors and the nature of interactions throughout the life cycle of key species can help to identify important bottlenecks that inhibit recovery of foundation species and reinforce shifts to turf algae. Turf algae have little direct effect on adult canopy algae, but inhibition of early life history stages is a widespread feedback mechanism on temperate reefs (Chapter 5). In contrast, effects of turf algae on growth and tissue mortality of established coral colonies appear to be a more important constraint on coral recovery following turf proliferation on tropical reefs. In addition to low recruitment, I found that large tissue losses and mortality of juvenile sporophytes in Nova Scotia represent another bottleneck to kelp recovery (Chapter 4). Encrustation by *M. membranacea* increased juvenile mortality, and net loss of blade area was driven by the effects of *M. membranacea*, high temperatures, and *L. vincta* skewing the balance between growth and tissue loss. Direct and indirect tissue losses induced by grazing by *L. vincta* extend to adult sporophytes and likely this is an important agent of canopy loss during large wave events (Chapter 2; Krumhansl & Scheibling 2011b). Furthermore, I found that the indirect effects of grazing are enhanced by the active feeding preference of *L. vincta* for sporogenous tissue. This leads to a shift in the distribution of grazing on *S. latissima*, with extensive grazing of soral patches (11.4% – 46.4%) and loss of fecundity during seasonal spore production (Chapter 3). The link between spore production and macroscopic recruitment, however, remains a key knowledge gap that needs to be addressed to assess the recovery potential of kelp populations.

Threshold and non-linear responses are defining characteristics of regime shift dynamics and can lead to "ecological surprise" (Conversi et al. 2015). Elucidating threshold and non-linear dynamics that underlie the stability of shifts to turf algae in Nova Scotia is a major contribution of my thesis. The common 2 x 2 factorial design of most multiple stressor experiments precludes identification of such dynamics (Griffen et al. 2016). By examining grazing dynamics over a range of kelp biomass in a field experiment that simulated disturbance by *M. membranacea* and hurricane damage, I showed that snail density and grazing intensity by *L. vincta* increase non-linearly as available kelp biomass decreases (Chapter 2). This increases the likelihood that grazing intensity on sparse individuals on degraded reefs will exceed a threshold (0.5 – 1%) for increased tissue loss during large wave events (Krumhansl & Scheibling 2011b). By estimating potential reproductive output from kelp populations, I found that spore production in highly degraded kelp beds is unlikely to be sufficient for macroscopic recruitment due to the low density of reproductive adults (Chapter 3). Furthermore, large losses of spores to grazing by *L. vincta* may increase the risk that reproductive output falls below limiting levels. Estimates of competitive effects of foundation and turf-forming species on one another (Chapter 5) can be integrated into spatial and dynamic models to further improve our ability to identify threshold and non-linear responses to environmental drivers and other regime shift characteristics.

My findings also contribute to the changing view on the role of density-dependence in kelp ecosystems. Earlier research emphasized intraspecific competition and negative density-dependence as controls on kelp population dynamics (Reed & Foster 1984, Reed 1990). However, recent studies suggest that recovery of kelp and other canopy-forming algae following large-scale losses is hindered by loss of positive or facilitating interactions (Wernberg et al. 2010, Bennett & Wernberg 2014, Bennett et al. 2015a). The dilution of grazing by *L. vincta* among more individual plants demonstrates the positive effects of a dense kelp canopy (Chapter 2), in sharp contrast to the intense grazing I observed on kelp juveniles on defoliated reefs (Chapter 4). Limited propagule supply (Chapter 3) and recruitment (Chapter 4) on turf-dominated reefs also highlight the positive effects of a dense kelp canopy on reproductive output. Closed macroalgal canopies also suppress turf algae through shading and abrasion (Chapter 5), which may facilitate recruitment. Most of the competition experiments in my meta-analysis in Chapter 5 manipulated competitor presence/absence. Given that the outcome of interactions between canopy algae and turf algae may depend on their relative abundance, future research should aim to identify thresholds of canopy loss for turf invasion, and vice versa, by using gradients of removal (e.g. Benedetti-Cecchi et al. 2015).

Scaling up small-scale experiments and observations to larger spatial scales and higher levels of ecological organization presents both a challenge and an opportunity in ecology. In Chapter 2, I found that the response of *L. vincta* to spatial variation in kelp abundance on a scale of m to 10s of m was similar to the response to variation on a scale of 10s of km, providing stronger support for the hypothesis that grazing damage is intensified on fewer individuals as kelp density decreases. In Chapter 4, I nested detailed observations on cohorts of juvenile sporophytes within ongoing multiyear monitoring of kelp populations at 2 sites. I found that changes in growth, tissue loss, blade area and survival patterns of cohort members closely matched changes in kelp density, cover, and size structure in the wider populations, indicating that the processes affecting individuals (grazing, epiphytism) were influencing population dynamics. I suggest that such longitudinal studies using repeated photographic sampling *in situ* also provide a means to examine the time-integrated effects of multiple stressors on kelp. In contrast, in Chapter 3 I found that scaling up observations on individuals to populations modified my conclusions. Results of feeding experiments and tissue-specific measures of phlorotannin content in the laboratory matched the distribution of grazing on reproductive individuals in the field (concentrated on sorus tissue). While histological preparation of sorus tissue indicated grazing by *L. vincta* reduces individual fecundity of *S. latissima*, my estimates of potential reproductive output (spores m^{-2} bottom) at 5 sites indicate that, while low densities of reproductive individuals ($< 1\ m^{-2}$) may be more limiting than grazing losses and high densities ($3 – 4\ m^{-2}$) may mitigate the effects of grazing, grazing may have the greatest impact on reproductive output at intermediate densities of reproductive individuals.

I have shown that various feedbacks and processes reinforce kelp loss and shifts to turf assemblages on temperate reefs, indicating that the degraded state will persist. Low kelp abundance and high cover of turf-forming, invasive, and opportunistic algae remained after 5 years of observation at 2 sites, following canopy defoliation (Chapter 4). The next direction in scaling up observations will be examining impacts of these shifts on ecosystem structure and function. The value of kelp beds and forests as a food source and habitat for diverse fish and invertebrates has long been recognized. While turf algae do not provide the same canopy structure, their structural complexity (fractal dimension) can be higher than canopy algae with simple morphologies, which leads to increased abundance and diversity of smaller invertebrates (e.g. amphipods, isopods, small gastropods) in turf assemblages (Milne & Griffiths 2014, Dijkstra et al. 2017). Likewise, algal diversity also may increase in the absence of a canopy (Pinho et al. 2015). Despite low standing biomass, rates of biomass-specific primary productivity are high among turf algae, especially filamentous forms, on temperate and tropical reefs (Carpenter 1985, Copertino et al. 2005). However, the net annual production per unit area may be lower for turf algae compared to canopy algae (Copertino et al. 2005). The impact of regime shifts to turf algae on higher trophic levels and patterns of regional productivity and diversity are less clear. Most primary production from shallow kelp beds globally is exported as detritus to adjacent marine and terrestrial communities, where it is an important resource subsidy that increases productivity and diversity of recipient communities (Krumhansl & Scheibling 2012). Evaluating the degree of connectivity of turf algal assemblages with other communities via detrital pathways, and the quantity and quality of the resource subsidy will be another important direction of future research.

Interestingly, climate has been a driving force behind changes in the predominant regime shift dynamics on subtidal reefs in Nova Scotia. With increasing intensity of strong storms in the region and more than 3 decades of ocean warming, the probability of disease-induced mass mortality of sea urchins *Strongylocentrotus droebachiensis* has increased (Scheibling & Lauzon-Guay 2010, Scheibling et al. 2013), which decreases the likelihood of transitions to urchin barrens and pushes the system towards an algal state. At the same time, changing climatic conditions likely have favoured the transition towards a turf-dominated state over a kelp state. Passing hurricanes cause large-scale kelp defoliation (Filbee-Dexter & Scheibling 2012) and high seawater temperatures have direct negative effects on growth, tissue strength, and survival of the dominant kelp species in Nova Scotia (Simonson et al. 2015, Wilson et al. 2015; Chapter 4). I found interannual patterns of kelp cover at one site were linked to trends in peak and minimum temperatures (Chapter 4). Warming conditions also favour more severe outbreaks of *M. membranacea* and associated kelp loss (Scheibling & Gagnon 2009). Likewise, grazing by *L. vincta* is temperature-dependent (Krumhansl & Scheibling 2011b) and model hindcasting suggests that grazing intensity has increased steadily since 1976 (Krumhansl et al. 2014). Projected loss of kelp biomass under alternative climate scenarios (Krumhansl et al. 2014) may further stabilize the turf algae state by weakening the important drift kelp subsidy from kelp beds to refuge populations of sea urchins in deeper waters that contribute to destructive grazing on shallow reefs through larval supply and migration (Filbee-Dexter 2016).

Results of my global synthesis of competitive interactions between foundation species and turf-forming algae (Chapter 5) indicate that recovery of foundation species from large-scale losses due to disturbance and acute or chronic stress will be hindered by turf algae that limit recruitment of canopy algae and expansion of established coral colonies. This thesis identifies further density-dependent and post-recruitment processes that inhibit recovery of kelp beds following large-scale losses and reinforce regime shifts to turf algae in Nova Scotia. Intensified grazing on sparse kelp, decreased kelp propagule supply due to low density of reproductive adults and preferential grazing of sorus tissue, low recruitment, and high tissue loss and mortality of juvenile sporophytes due to the combined effects of grazing by *L. vincta*, high temperatures, and encrustation by *M. membranacea* likely erode the resilience of kelp populations.

Previous research has emphasized the importance of mitigating regime shifts to turf algae through the local management of water quality to counter synergies with global stressors on turf expansion (e.g. Falkenberg et al. 2013b). However, regime shifts to turf in Nova Scotia have occurred in the absence of intense urbanization and nutrient inputs (Filbee-Dexter et al. 2016), and many of the drivers and feedback mechanisms are less amenable to local management. Barring multilateral action on climate change that may alleviate the direct and indirect effects of temperature on kelp, my research indicates that protecting intact kelp populations on headlands with cooler water temperatures is critical to maintaining positive canopy interactions and avoiding the reinforcing processes that currently maintain low kelp cover and turf-dominated reef states in protected and semi-protected bays.

APPENDIX A: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 2

Table A1. Estimated parameters from linear regressions of dry weight against wet weight of blade and stipe (including holdfast) tissue of *Saccharina latissima* and *Laminaria digitata* from 6 sites (Cranberry Cove- CC, Duncan's Cove Exposed- DE, Duncan's Cove Protected- DP, The Lodge- TL, Splitnose Point- SP, Paddy's Head- PH) and 5 sampling periods. na: not available; parameters taken from Mann 1972a.

Site	Period	Tissue	*S. latissima*	R^2	df	*L. digitata*	R^2	df
CC	Sep 2008	Blade	y = 0.200x	0.99	20	y = 0.214x	na	na
		Stipe	y = 0.297x	0.92	22	y = 0.124x	na	na
DE	Sep 2008	Blade	y = 0.149x	0.97	10	y = 0.159x	0.97	15
		Stipe	y = 0.155x	0.99	10	y = 0.211x - 0.288	0.99	12
DP	Sep 2008	Blade	y = 0.189x	0.99	9	y = 0.200x	0.99	14
		Stipe	y = 0.190x	0.97	9	y = 0.165x	0.99	15
TL	Sep 2008	Blade	y = 0.153x	0.99	15	y = 0.208x	0.99	13
		Stipe	y = 0.168x	0.97	15	y = 0.205x	0.99	12
SP	Sep 2008	Blade	y = 0.146x	0.97	12	y = 0.166x	0.98	15
		Stipe	y = 0.146x	0.99	11	y = 0.133x	0.85	14
CC	Sep 2009	Blade	y = 0.183x	0.99	18	y = 0.214x	na	na
		Stipe	y = 0.339x - 2.18	0.93	12	y = 0.124x	na	na
DE	Sep 2009	Blade	y = 0.160x	0.99	15	y = 0.175x	0.99	13
		Stipe	y = 0.214x	0.87	16	y = 0.181x	0.99	13
DP	Sep 2009	Blade	y = 0.192x	0.99	12	y = 0.176x	0.99	14
		Stipe	y = 0.172x	0.99	12	y = 0.152x	0.99	14
TL	Sep 2009	Blade	y = 0.174x	0.99	13	y = 0.189x	0.99	11
		Stipe	y = 0.168x	0.93	12	y = 0.218x	0.99	11
SP	Sep 2009	Blade	y = 0.131x	0.99	12	y = 0.180x	0.99	16
		Stipe	y = 0.157x	0.99	10	y = 0.161x	0.98	12
PH	Jul 2012	Blade	y = 0.230x	0.98	46	y = 0.230x	0.98	6
		Stipe	y = 0.160x	0.96	46	y = 0.217x	0.99	6
DP	Jun 2013	Blade	y = 0.156x	0.98	21	y = 0.125x	0.99	22
		Stipe	y = 0.129x	0.98	24	y = 0.165x	0.96	20
DP	Jul 2013	Blade	y = 0.25x - 0.283	0.95	29	y = 0.156x + 0.172	0.88	27
		Stipe	y = 0.165x	0.99	29	y = 0.177x	0.99	25

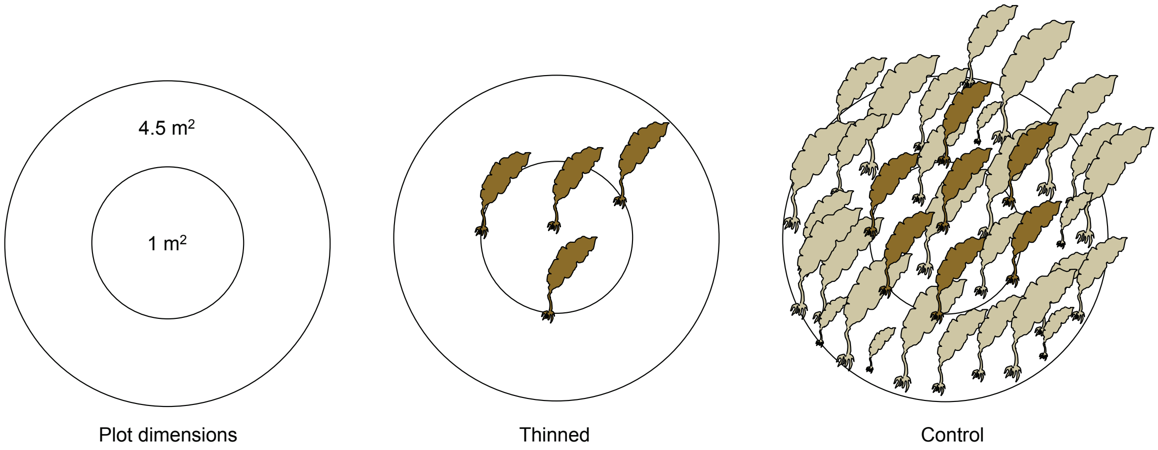

Fig. A1. Illustration of the dimensions of circular experimental plots from kelp-thinning experiment at Duncan's Cove Protected in June/July 2013 consisting of a sub-plot within a larger one. The spatial arrangement of kelp thalli within thinned and control plots is shown. Dark brown thalli indicate individuals that were identified at the start of the experiment and on which grazing damage was measured at the end. Light brown thalli indicate unmarked individuals in control plots

Literature Source

Mann KH (1972a) Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. I. Zonation and biomass of seaweeds. Mar Biol 12:1-10

APPENDIX B: DESCRIPTION OF METHODS FOR DETERMINING GENERAL SHAPE OF TOTAL RESPONSE CURVES

Trexler et al. (1988) describe methods for determining the general shape of functional response data (i.e. type I, II, or III) based on analysis of predation rate using least squares regression following arcsine transformation or logistic regression if data are binary. This approach fits a phenomenological expression that characterizes the density dependence of the response expressed as a proportion rather than an amount consumed. In this form, the slope of the relationship near the origin is distinct between response types, and polynomial expressions (often quadratic or cubic) flexibly fit type II and III shapes (Juliano 2001). A model is selected by backward elimination starting with higher order expressions. A best-fitting model with a significant negative second-order term and positive first-order term indicates a region of positively density-dependent predation or grazing (i.e. type III response), while a negative first-order term indicates negative density dependence (i.e. type II response; Trexler et al. 1988, Juliano 2001). A non-significant slope indicates a density-independent response (i.e. type I; Trexler et al. 1988). Because this approach is phenomenological, serving only as a diagnostic tool for determining the general form of the response, it should be equally useful for determining the shape of total response curves, which also can be described as type I, II, or III.

To determine the shape of the total response of *Lacuna vincta* to kelp abundance, a cubic polynomial and all reduced models were fit to the proportion of blade area grazed (plot or site averages) against kelp biomass (within plot or site) for each data set using the ‘lm’ function in R (R Core Team 2012) following arcsine transformation of proportion data. The biomass of both kelp species were combined for all analyses as there was no relationship between the abundance of each species across sites, and grazing intensity was positively correlated between species. The fit of higher-order polynomial models were compared to reduced models using partial *F* statistics. In all cases the best-fitting expression was a first-order model with negative slope indicating grazing was negatively density-dependent throughout all ranges of kelp biomass (type II total response; Table B1, B2).

Literature Cited

Juliano SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, 2nd ed. Oxford University Press, New York, p 178-196

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/

Trexler JC, McCulloch CE, Travis J (1988) How can the functional response best be determined? Oecologia 76:206-214

Table B1. Partial *F* test results comparing the fit of polynomial expressions (third- to second-order; second- to first-order) describing the relationship of grazing intensity versus kelp biomass within a kelp bed for *Saccharina Latissima* (Duncan's Cove Protected- DP 2013) and across sites for *S. latissima* and *Laminaria digitata* (Cranberry Cove- CC, Duncan's Cove Exposed- DE, DP, The Lodge- TL, Splitnose Point- SP 2009/2009). G = arcsine transformation of proportion of blade area grazed, B_k = combined kelp biomass of both species (g DW). SS_{extra} is the additional unexplained variation resulting from dropping a higher-order term from the model.

Data Source	Model	df	RSS	SS_{extra}	*F*	p
DP 2013	*Saccharina latissima*					
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2 + \beta_3(B_k)^3$	8	7.35×10^{-3}			
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2$	9	7.97×10^{-3}	0.62×10^{-3}	0.674	0.436
	$G = \beta_0 + \beta_1(B_k)$	10	8.12×10^{-3}	0.15×10^{-3}	0.166	0.693
Site Averages 2008/2009	*Saccharina latissima*					
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2 + \beta_3(B_k)^3$	6	1.86×10^{-3}			
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2$	7	2.40×10^{-3}	0.54×10^{-3}	1.74	0.235
	$G = \beta_0 + \beta_1(B_k)$	8	2.46×10^{-3}	0.06×10^{-3}	0.186	0.679
Site Averages 2008/2009	*Laminaria digitata*					
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2 + \beta_3(B_k)^3$	4	2.48×10^{-3}			
	$G = \beta_0 + \beta_1(B_k) + \beta_2(B_k)^2$	5	4.29×10^{-3}	1.81×10^{-3}	2.92	0.163
	$G = \beta_0 + \beta_1(B_k)$	6	4.88×10^{-3}	0.59×10^{-3}	0.685	0.446

Table B2. Coefficient estimates and standard errors for best fitting polynomial expression describing the relationship of grazing intensity versus kelp biomass within a kelp bed for *Saccharina latissima* (DP 2013) and across sites for *S. latissima* and *Laminaria digitata* (CC, DE, DP, TL, SP 2008/2009; see Table B1 for site abbreviations). G = arcsine transformation of proportion of blade area grazed, B_k = combined kelp biomass of both species (g DW).

Data source	Species	Best fitting model	Estimate	SE	*t*	p
DP 2013	*S. latissima*	$G = \beta_0 + \beta_1(B_k)$	β_0 1.81×10^{-1} β_1 -6.83×10^{-5}	1.19×10^{-2} 2.58×10^{-5}	15.183 -2.649	< 0.001 < 0.05
Site Averages 2008/2009	*S. latissima*	$G = \beta_0 + \beta_1(B_k)$	β_0 9.86×10^{-2} β_1 -4.53×10^{-5}	1.03×10^{-2} 1.03×10^{-5}	9.564 -4.396	< 0.001 < 0.01
Site Averages 2008/2009	*L. digitata*	$G = \beta_0 + \beta_1(B_k)$	β_0 1.13×10^{-1} β_1 -4.73×10^{-5}	2.05×10^{-2} 1.86×10^{-5}	5.493 -2.542	< 0.01 < 0.05

APPENDIX C: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 3

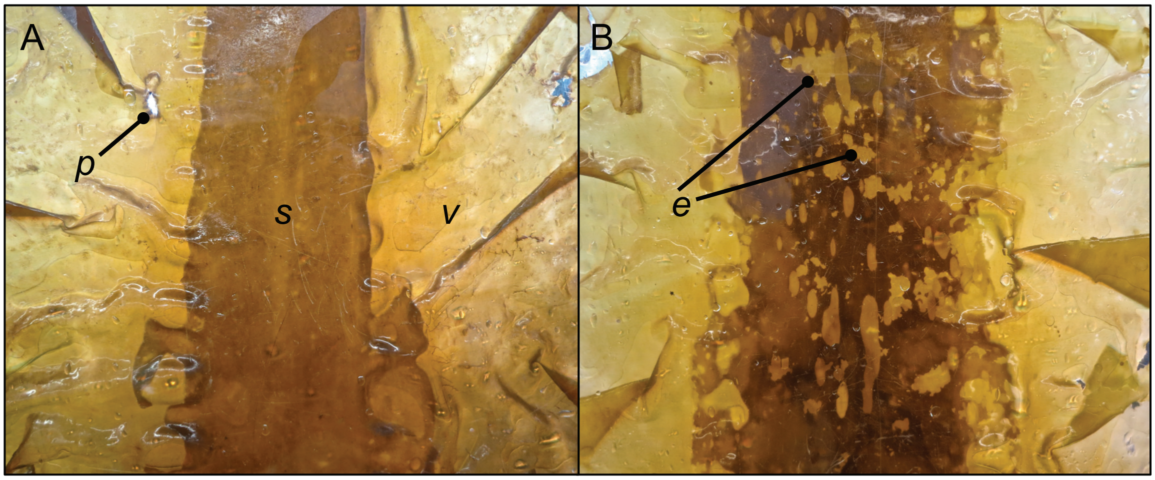

Fig. C1. Reproductive kelp *Saccharina latissima* showing region where mature sorus (*s*) is developed and vegetative tissue (*v*) in the adjacent blade margins. (A) Blade with minimal grazing except for isolated perforations (*p*) of the blade margins. Sorus is solid, dark brown in appearance. (B) Extensively grazed blade. Sorus mottled by superficial grazing excavations (*e*). *Photo credit*: J.M. O'Brien.

Table C1. Likelihood ratio (LR) tests comparing hierarchical beta regression models for effects of month (Oct, Nov) and site of collection (Duncan's Cove Exposed, Duncan's Cove Protected, Sandy Cove, Splitnose Point) on grazing intensity (proportion grazed) on kelp sori (*Saccharina latissima*) by *Lacuna vincta*.

Model Term	df	LR	p
Month	1	0.884	0.347
Site	3	30.3	**< 0.001**
Month × Site	3	4.35	0.226

Note: Significant results ($p < 0.05$) are highlighted in boldface type.

Table C2. Density of kelp *Saccharina latissima* (D_{tot}, individuals/m^2), density of reproductive kelp (D_r, i.e. mature sorus developed), estimated potential reproductive output discounting grazing damage by *Lacuna vincta* (R_{-g}, spores/m^2 bottom), lost to grazing (R_g), and accounting for grazing (R_{+g}) at 5 sites (Cranberry Cove - CC, Duncan's Cove Exposed - DE, Duncan's Cove Protected - DP, Sandy Cove - SC, Splitnose Point - SP) in Oct and Nov 2013.

Month	Site	D_{tot}	D_r	R_{-g} (× 10^7)	R_{+g} (× 10^7)	R_g (× 10^7)
Oct	CC	1.1*	0.13*	21.2	16.9	4.3
Oct	DE	4.1*	1.5*	615.2	310.1	305.1
Oct	DP	8.4 ± 1.3	1.0 ± 0.6	414.0	261.5	152.5
Oct	SC	12.2 ± 1.5	2.5 ± 1.1	715.7	541.2	174.5
Oct	SP	5.1 ± 0.9	2.3 ± 0.6	526.3	416.5	109.8
Nov	DE	8.2*	1.4*	415.5	272.5	143.0
Nov	DP	23.2 ± 4.2	4.2 ± 1.3	1140.6	824.7	315.9
Nov	SC	17.4 ± 3.0	3.2 ± 1.1	1041.9	737.2	304.7
Nov	SP	2.5*	1.9*	646.9	581.8	65.1

* From survey of 30-m transect within 2-m swath (no estimate of error)

APPENDIX D: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 4

Table D1. Summary of supplementary data on kelp abundance and macroalgal composition at The Lodge (TL) and Paddy's Head (PH) from 2003 to 2010 prior to the onset of the present study. The year, month, site, and depth of sampling are provided along with the macroalgal groups and variables measured, the quadrat size sampled, sample size, and source of data. K = kelp (*Saccharina latissima* only if indicated by subscript 'SL'), Cf = *Codium fragile* ssp. *tomentosoides*, Dv = *Desmarestia viridis*, T = turf-forming algae, Br = other perennial and annual brown macroalgae.

Year	Site	Month	Depth (m)	Macroalgae	Measure	Quadrat (m^2)	n	Source
2003	BH*	Jun	7	K_{SL}, Cf, Dv, T	Cover	0.73	20	Lyons & Scheibling 2008
2005	TL	Jun	8	K_{SL}	Density	0.25	20	Saunders & Metaxas 2008
2005	TL	Oct, Nov	8	K_{SL}	Cover	–	17 – 20	Saunders & Metaxas 2008
2006	TL	Oct, Nov	8	K_{SL}	Cover	–	8 – 14	Saunders & Metaxas 2008
2007	TL	Jun	8	K_{SL}	Density	0.25	21	Saunders & Metaxas 2008
2009	TL	Jul	7 – 10	K_{SL}	Density	1	7	C. Feehan, *unpublished*
2009	TL	Aug	7 – 10	K, Cf, Dv, T, Br	Cover	2	4	C. Feehan, *unpublished*
2010	TL	Jun	8 – 10	K, Cf, Dv, T, Br	Cover	1	4	C. Feehan, *unpublished*
2010	TL	Jun	7 – 8	K_{SL}	Density	1	4	C. Feehan, *unpublished*
2005	PH	Jun	4	K_{SL}	Density	0.25	20	Saunders & Metaxas 2008
2007	PH	Jun	4	K_{SL}	Density	0.25	16	Saunders & Metaxas 2008
2010	PH	Jun	6 – 9	K, Cf, Dv, T, Br	Cover	1	8	C. Feehan, *unpublished*

* BH = Birchy Head located 3.5 km from The Lodge

Literature Sources

Lyons DA, Scheibling RE (2008) Context-dependent survival of the invasive seaweed *Codium fragile* ssp. *tomentosoides* in kelp bed and urchin barren habitats off Nova Scotia. Aquat Biol 2:17–27

Saunders M, Metaxas A (2008) High recruitment of the introduced bryozoan *Membranipora membranacea* is associated with kelp bed defoliation in Nova Scotia Canada. Mar Ecol Prog Ser 369:139–151

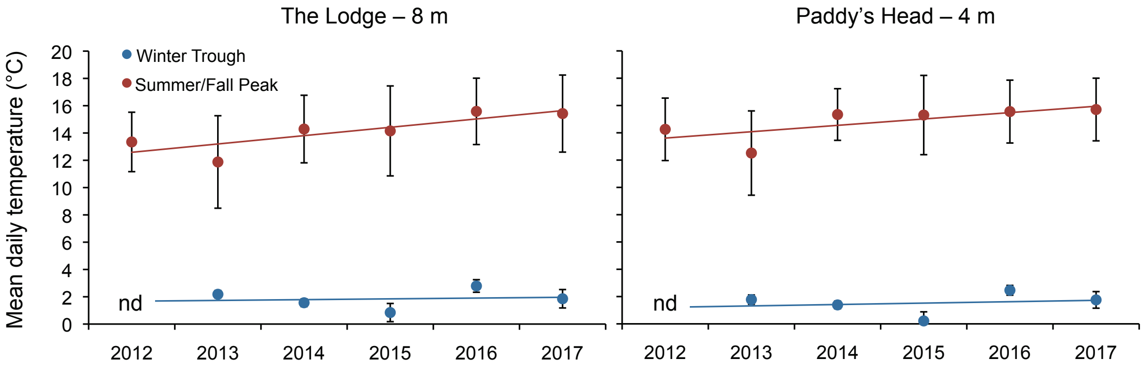

Fig. D1. Mean (± SD) daily temperature (ºC) at 8 m at The Lodge (Left Panel) and 4 m at Paddy's Head (Right Panel) during the period of peak summer/fall temperatures (August, September, October: red symbols) and the winter trough (February, March: blue symbols) in each year from 2012 to 2017; nd = no data.

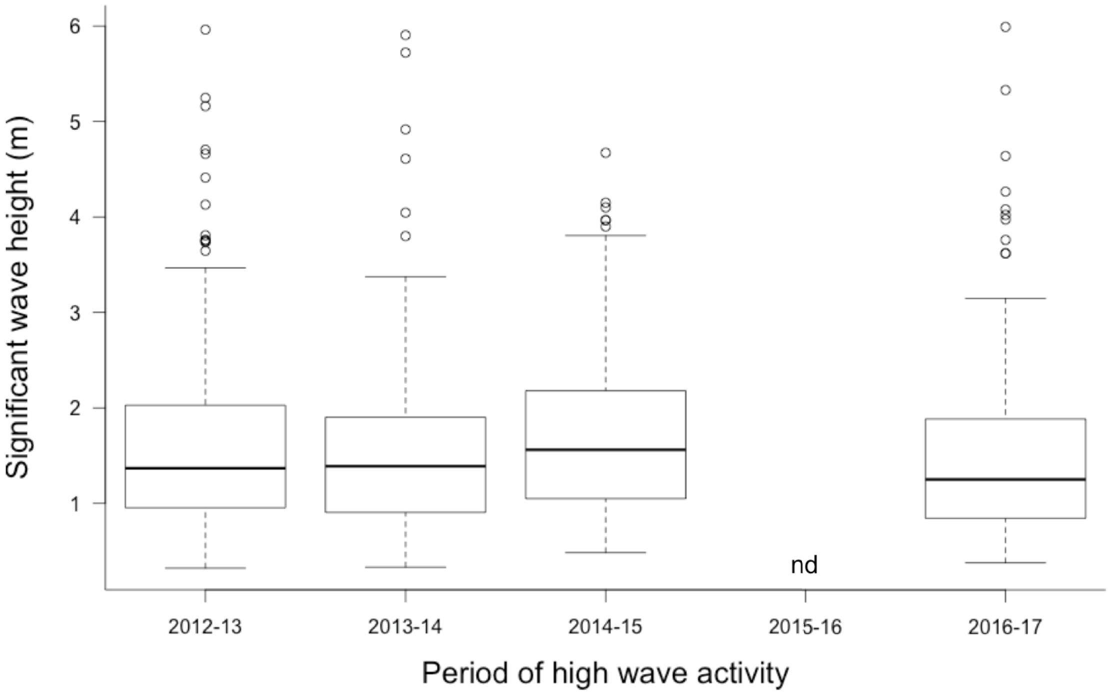

Fig. D2. Box plots illustrating interannual variation in large wave events over fall and winter from 2012 to 2017. Data are daily average significant height (m) within the 6-mo period of the year with the highest anticipated wave activity (October to March). Black band is the median, the box indicates the 1st and 3rd quartiles, whiskers are the lowest and highest values within 1.5 interquartile range of the 1st and 3rd quartiles, respectively, and individual points are outliers. nd = no data.

APPENDIX E: FUNNEL PLOTS, FOREST PLOTS, AND RESULTS OF DIAGNOSTIC TESTS FOR CHAPTER 5 META-ANALYSES

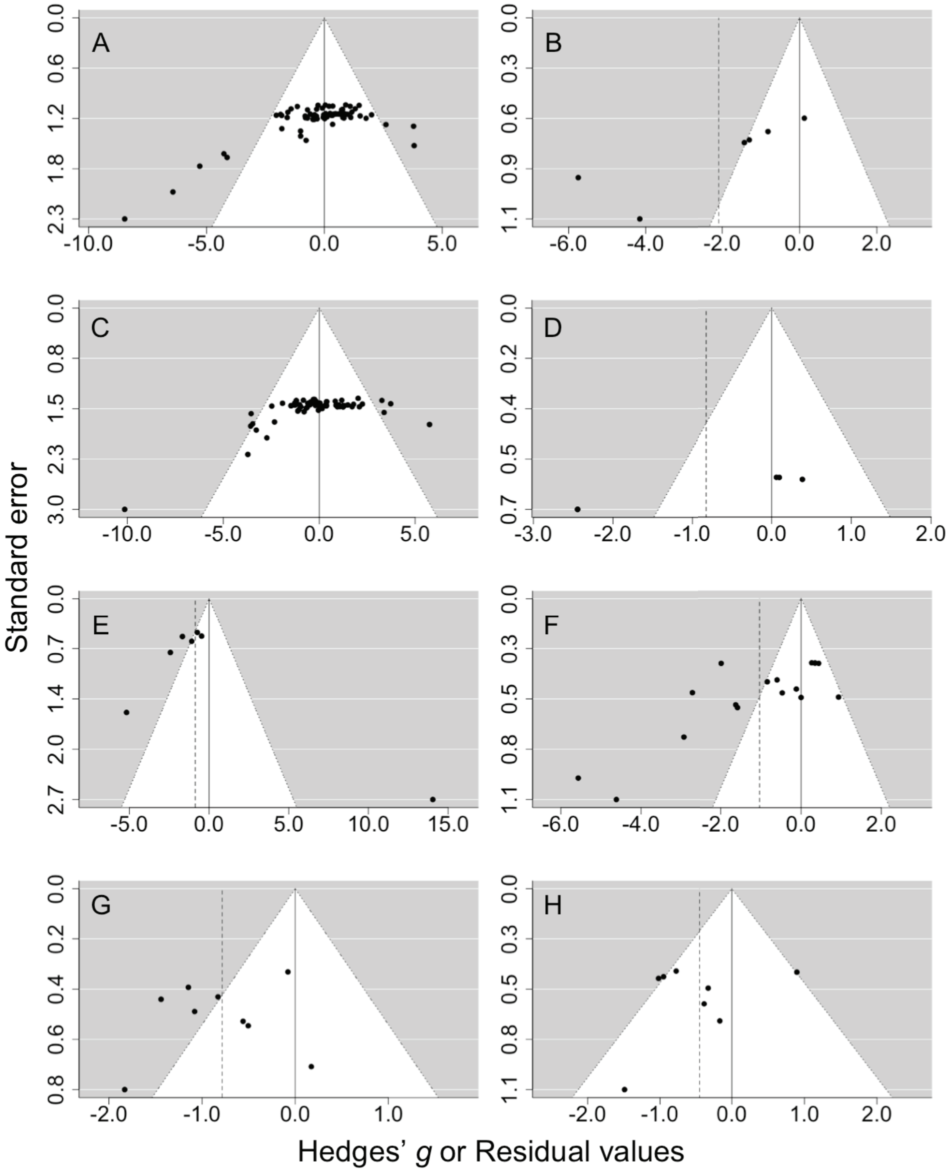

Fig. E1. Funnel plots for random and mixed effects models synthesizing effects of foundation species and turf algae on one another. Effects of (A) canopy algae and (B) established corals on turf algae abundance and effects of turf algae on (C) abundance of canopy algae recruits, established coral (D) abundance, (E) physiological status, (F) growth, (G) survival and (H) coral recruit survival. Data are standard errors plotted against study-specific effect sizes (Hedges' *g*) or residual values (for mixed effects models). Solid vertical line indicates the null value and borders of white triangle denote pseudo 95% CI and critical effect size for significance at given SE. Dashed vertical line indicates mean overall effect size for random effects model.

Table E1. Results of diagnostic tests for publication bias and related sensitivity analyses. The focal group, competing group, subgroup membership, and response variable measured in each random or mixed effects model are indicated in the first 4 columns. Kendall's τ and p-values are for rank correlation tests for funnel plot asymmetry. Rosenberg's fail-safe number is based on weighted meta-analysis. Rosenthal's fail-safe number is unweighted. Fail-safe numbers greater than $5k + 10$ are considered robust (k = number of studies). CanAlg = canopy algae, EstabCor = established corals, RecrCor = recruiting corals, ArtCor = articulated coralline turf, Cort/Br = corticated/coarsely branching turf, Filam = filamentous turf, Intertidal and Subtidal = intertidal and subtidal assemblages, respectively, and Micro and Macro = microscopic and macroscopic canopy algae recruits, respectively.

Focal Group	Competitor	Subgroup	Response Variable	Kendall's τ	p	Rosenberg's Fail-safe	Rosenthal's Fail-safe	Robust Fail-safe
Turf	CanAlg	-	Abundance	-0.22	0.006	169	2804	365
Turf	CanAlg	ArtCor	Abundance	na	na	12	218	135
Turf	CanAlg	Cort/Br	Abundance	na	na	5	321	135
Turf	CanAlg	Filam	Abundance	na	na	16	395	115
Turf	CanAlg	Intertidal	Abundance	na	na	52	911	260
Turf	CanAlg	Subtidal	Abundance	na	na	17	498	115
CanAlg	Turf	-	Abundance	-0.13	0.116	82	4560	360
CanAlg	Turf	ArtCor	Abundance	na	na	na	na	na
CanAlg	Turf	Cort/Br	Abundance	na	na	5	674	145
CanAlg	Turf	Filam	Abundance	na	na	14	911	125
CanAlg	Turf	Intertidal	Abundance	na	na	na	na	na
CanAlg	Turf	Subtidal	Abundance	na	na	50	3208	180
CanAlg	Turf	Micro	Abundance	na	na	2	414	90
CanAlg	Turf	Macro	Abundance	na	na	38	1874	280
Turf	EstabCor	Filam	Abundance	-0.87	0.017	1	76	40
EstabCor	Turf	Filam	Abundance	-0.33	0.435	na	na	na
EstabCor	Turf	Filam	Physiology	-0.24	0.562	na	na	na
EstabCor	Turf	Filam	Growth	-0.41	0.022	3	297	95
EstabCor	Turf	Filam	Survival	0.06	0.920	5	78	55
RecrCor	Turf	Filam	Survival	0.00	1.00	na	na	na

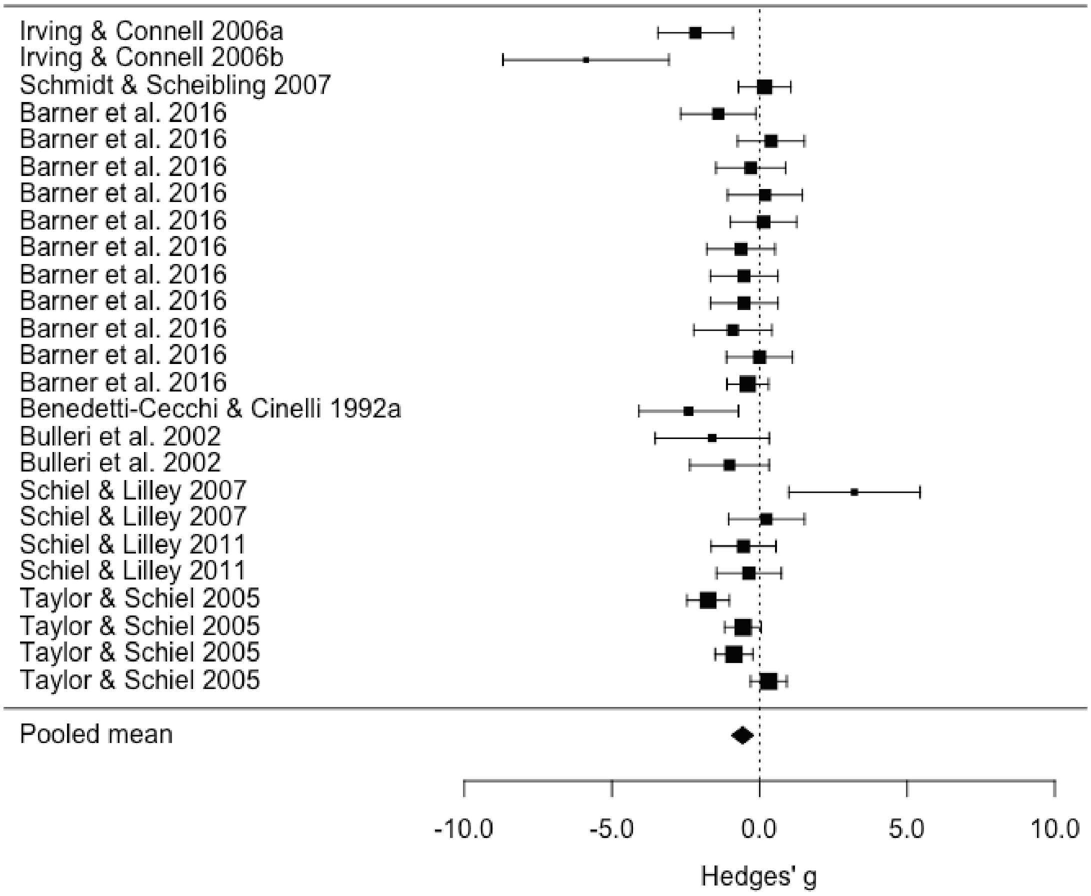

Fig. E2. Forest plot showing effects (Hedges' *g*) of canopy algae on the abundance of articulated coralline turf algae. Squares are study-specific effect sizes. Symbol size indicates the relative weight in the mixed effects model. Error bars are 95% CI, which denote a null effect when overlapping the vertical line. The overall effect size is shown by the polygon centred at the mean with 95% CI limits indicated at the corners.

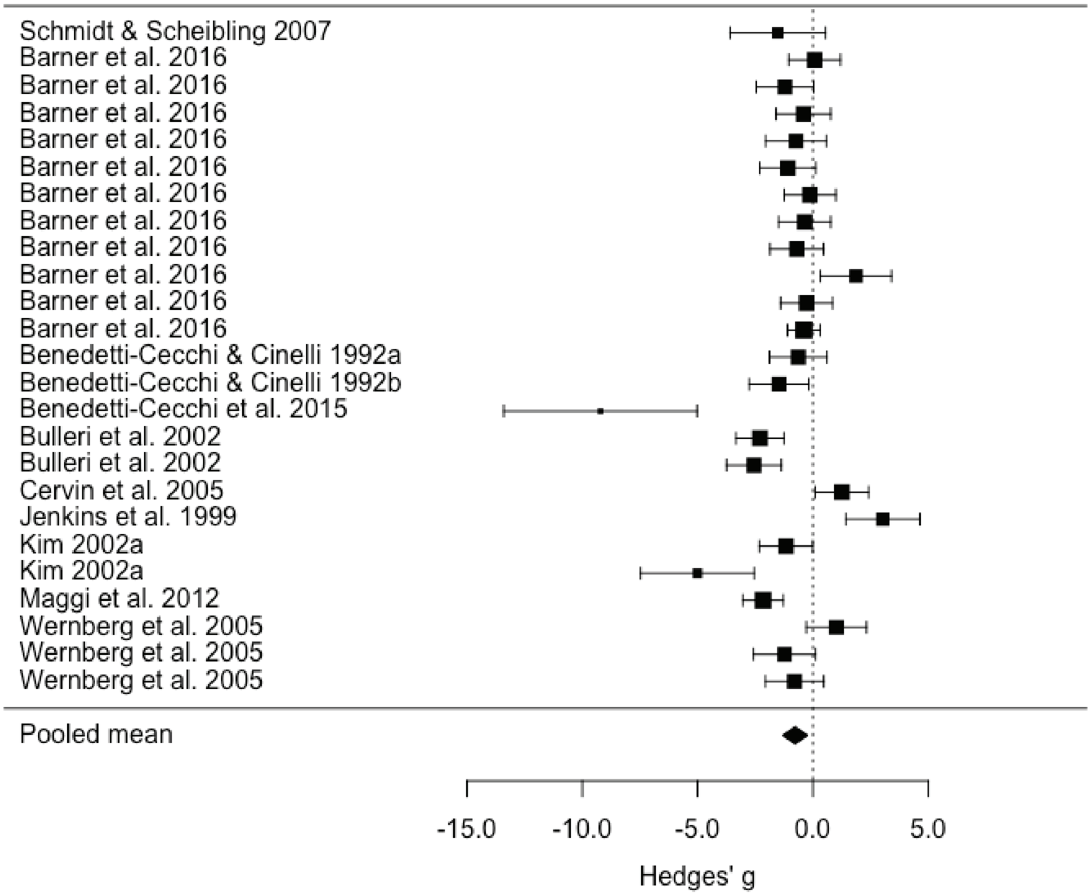

Fig. E3. Forest plot showing effects (Hedges' *g*) of canopy algae on the abundance of corticated/coarsely branching turf algae. Squares are study-specific effect sizes. Symbol size indicates the relative weight in the mixed effects model. Error bars are 95% CI, which denote a null effect when overlapping the vertical line. The overall effect size is shown by the polygon cantered at the mean with 95% CI limits indicated at the corners.

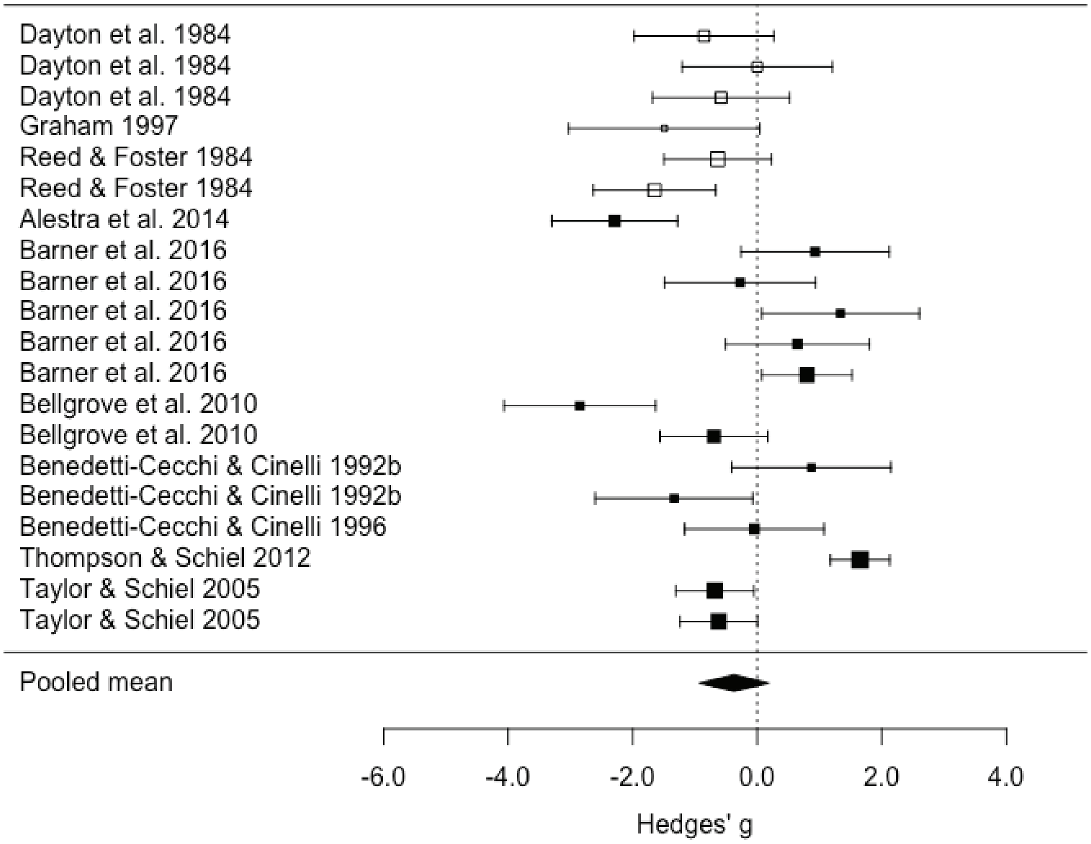

Fig. E4. Forest plot showing effects (Hedges' *g*) of articulated coralline turf algae on the abundance of canopy algae recruits. Squares are study-specific effect sizes. Symbol size indicates the relative weight in the mixed effects model. Open and filled symbols indicate subtidal and intertidal studies, respectively. Error bars are 95% CI, which denote a null effect when overlapping the vertical line. The overall effect size is shown by the polygon cantered at the mean with 95% CI limits indicated at the corners.

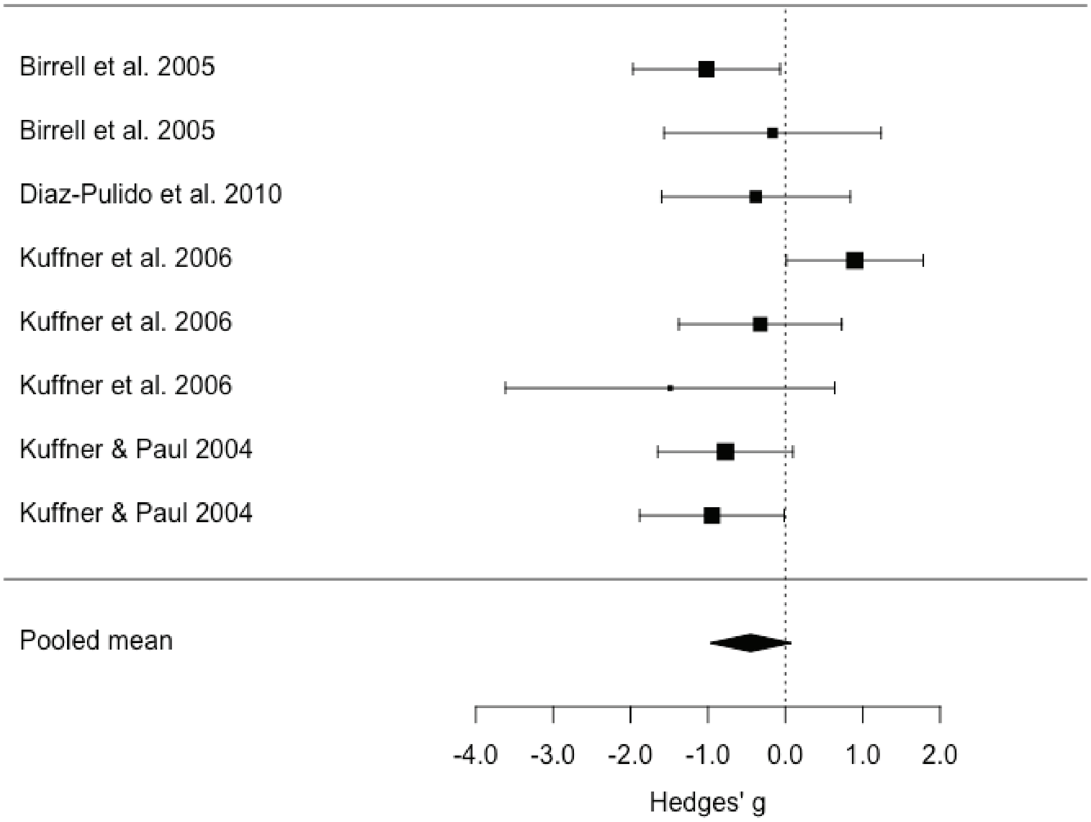

Fig. E5. Forest plot showing effects (Hedges' *g*) of filamentous turf algae on the survival of coral larvae and primary polyps. Squares are study-specific effect sizes. Symbol size indicates the relative weight in the random effects model. Error bars are 95% CI, which denote a null effect when overlapping the vertical line. The overall effect size is shown by the polygon cantered at the mean with 95% CI limits indicated at the corners.

APPENDIX F: LIST OF PUBLICATIONS INCLUDED IN CHAPTER 5 META-ANALYSES

Alestra T, Schiel DR (2014) Effects of opportunistic algae on the early life history of a habitat-forming fucoid: influence of temperature, nutrient enrichment and grazing pressure. Mar Ecol Prog Ser 508:105–115

Alestra T, Tait LW, Schiel DR (2014) Effects of algal turfs and sediment accumulation on replenishment and primary productivity of fucoid assemblages. Mar Ecol Prog Ser 511:59–76

Andrew NL, Viejo RM (1998) Ecological limits to the invasion of *Sargassum muticum* in northern Spain. Aquat Bot 60:251–263

Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. J Exp Mar Biol Ecol 251:117–132

Barner AK, Hacker SD, Menge BA, Neilsen KJ (2016) The complex net effect of reciprocal interactions and recruitment facilitation maintains an intertidal kelp community. J Ecol 104: 33–43

Barner AK, Hacker SD, Menge BA, Nielsen KJ (2015) Data from "The complex net effect of reciprocal interactions and recruitment facilitation maintains an intertidal kelp community." Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.7950f

Bellgrove A, McKenzie PF, McKenzie JL, Sfiliagoj B (2010) Restoration of the habitat-forming fucoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. Mar Ecol Prog Ser 419:47–56

Bender D, Diaz-Pulido G, Dove S (2012) Effects of macroalgae on corals recovering from disturbance. J Exp Mar Biol Ecol 429:15–19

Benedetti-Cecchi L, Cinelli F (1992a) Canopy removal experiments in *Cystoseira*-dominated rockpools from the Western coast of the Mediterranean (Ligurian Sea). J Exp Mar Biol Ecol 155:69–83

Benedetti-Cecchi L, Cinelli F (1992b) Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. Mar Ecol Prog Ser 90:183–191

Benedetti-Cecchi L, Cinelli F (1996) Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. Mar Ecol Prog Ser 135:145–161

Benedetti-Cecchi L, Tamburello L, Maggi E, Bulleri F (2015) Experimental perturbations modify the performance of early warning indicators of regime shift. Curr Biol 25:1867–1872

Berger R, Henriksson E, Kautsky L, Malm T (2003) Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. Aquat Ecol 37:1–11

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. Mar Pollut Bull 51:408–414

Brawley SH, Johnson LE (1991) Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. J Phycol 27:179–186

Bulleri F, Benedetti-Cecchi L, Acunto S, Cinelli F, Hawkin SJ (2002) The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. J Exp Mar Biol Ecol 267:89–106

Cervin G, Åberg P, Jenkins SR (2005) Small-scale disturbance in a stable canopy dominated community: implications for macroalgal recruitment and growth. Mar Ecol Prog Ser 305:31–40

Cetz-Navarro NP, Espinoza-Avalos J, Hernández-Arana H, Carricart-Ganivet JP (2013) Biological responses of the coral *Montastraea annularis* to the removal of filamentous turf algae. PLoS ONE 8(1): e54810. doi:10.1371/journal.pone.0054810

Chapman ARO (1984) Reproduction, recruitment, and mortality in two species of *Laminaria* in southwest Nova Scotia. J Exp Mar Biol Ecol 78:99–109

Connell SD, Russell BD (2010) The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proc R Soc B 277:1409–1415

Corado-Nava NA, Rodríguez D, Rivas G (2014) Algal turfs colonization effect on *Pocillopora capitata* (Anthozoa: Scleractinia) growth at Mexican tropical Pacific. Revista Mexicana de Biodiversidad 85:1086–1092

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Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organization of a benthic community. Ecol Monogr 70:237–263

Falkenberg LJ, Russell BD, Connell SD (2012) Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forest. PLoS ONE 7: e33841. doi:10.1371/journal.pone.0033841

Falkenberg LJ, Connell SD, Coffee OI, Ghedini G, Russell BD (2015) Species interactions can maintain resistance of subtidal algal habitats to an increasingly modified world. Glob Ecol Conserv 4:549–558

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APPENDIX G: CHARACTERISTICS OF STUDIES INCLUDED IN CHAPTER 5 META-ANALYSES

Table G1. Species identity and location of experiments included in meta-analyses. The foundation species (coral, canopy algae) and turf-forming species or genera manipulated in each publication, region in which the studies were conducted, and latitude and longitude are provided. The table is organized by the particular combination of focal group and competitor interacting. Foundation species are categorized by life-history stage and turf algae by functional group (articulated coralline, corticated/coarsely branching, filamentous). GBR = Great Barrier Reef.

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Focal Group = Coral (established), Competitor = Turf (filamentous)					
Bender et al. 2012	*Acropora aspera*, *A. pulcra*	*Feldmannia mitchelliae*	GBR	-23.43667	151.87917
Cetz-Navarro et al. 2013	*Orbicella annularis*	*Polysiphonia*, *Lophosiphonia*, *Herposiphonia*, *Parviphycus*, *Centroceras*, *Ceramium*, *Anotrichium*, *Bryobesia*, *Lyngbya*, *Dichothrix*, *Padina* (diminutive stage)	Caribbean	18.50417	-87.75650
Corado-Nava et al. 2014	*Pocillopora capitata*	Mixed filamentous turf	North Pacific	17.62200	-101.55217
Jompa & McCook 2003a	*Porites lobata*, *P. lutea*, *P. australiensis*	*Anotrichium tenue*	GBR	-18.68500	146.58667
Jompa & McCook 2003b	*Porites cylindrica*	*Corallophila huysmansii*	GBR	-18.68333	146.58667

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
McCook 2001	*Porites lobata*	*Sphacelaria*, *Hincksia*, *Jania*, *Centroceras*, *Ceramium*, *Enteromorpha*, *Cladophora*, *Polysiphonia*, Cyanophyta, Dictyotales diminutive stages	GBR	-18.68100 -18.72083 -18.18650	146.58733 146.57967 146.17200
Quan-Young & Espinoza Avalos 2006	*Orbicella faveolata*	*Polysiphonia*, *Lophosiphonia*, *Parviphycus*, *Herposiphonia*, *Centroceras*, *Amphiroa*, *Jania*, *Ceramium*, *Sphacelaria*, *Padina* (diminutive stage)	Caribbean	18.25000	-87.83333
Ramos et al. 2014	*Sideastrea stellata*	Mixed filamentous turf	South Atlantic	-13.13350	-38.73650
Smith et al. 2006	*Acropora*, *Favia*, *Fungia*, *Hydnophora*, *Montastraea*, *Montipora*, *Pavona*, *Pocillopora*, *Porites*, *Stylophora*	Mixed filamentous turf	North Pacific	6.44533	-162.39667
Titlyanov et al. 2007	*Porites lutea*	*Lyngbya bouillonii*	Philippine Sea	26.63333	127.86667
Venera-Ponton et al. 2011	*Porites astreoides*	*Anotrichium*, *Bryopsis*, *Ceramium*, *Gelidiella*, *Gelidiopsis*, *Herposiphonia*, *Polysiphonia*, *Sphacelaria*, *Ulva*, Cyanophyta, *Jania*, *Amphiroa*, macroalgae diminutive stages	Caribbean	11.29033	-74.23267
White & O'Donnell 2010	*Acropora striata*, *Montipora floweri*, *Porites australiensis*, *Pocillopora verrucosa*	*Polysiphonia* spp.	South Pacific	-17.47600	-149.79033

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Focal Group = Coral (recruit), Competitor = Turf (filamentous)					
Birrell et al. 2005	*Acropora millepora*	Mixed filamentous turf	GBR	-18.61667	146.49000
Diaz-Pulido et al. 2010	*Platygyra daedalea*	*Hincksia*, *Polysiphonia*, *Sphacelaria*	GBR	-23.44350	151.91200
Kuffner et al. 2006	*Porites astreoides*	*Lyngbya polychroa*, *L. confervoides*	Florida Keys	24.79967	-80.80150
Kuffner & Paul 2004	*Acropora surculosa*, *Pocillopora damicornis*	*Lyngbya majuscula*	Philippine Sea	13.41000	144.80867
Focal Group = Turf (filamentous), Competitor = Coral (established)					
Baird & Hughes 2000	*Acropora hyacinthus*	Mixed filamentous turf	GBR	-14.68333	145.46667
McClanahan et al. 2002	*Acropora cervicornis*	*Hincksia mitchelliae*, *Enteromorpha prolifera*	Caribbean	16.76700	-87.78833
McCook 2001	*Porites lobata*	*Sphacelaria*, *Hincksia*, *Jania* *Centroceras*, *Ceramium*, *Enteromorpha*, *Cladophora*, *Polysiphonia*, Cyanophyta, Dictyotales diminutive stages	GBR	-18.68500 -18.69333 -18.18167	146.58500 146.57333 146.17000
Focal group = Canopy algae (recruit), Competitor = Turf (articulated coralline)					
Alestra et al. 2014	*Hormosira banksii*	*Corallina officinalis*	New Zealand	-42.41667	173.70000

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Barner et al. 2016	*Saccharina sessile*	*Bossellia plumosa*, *Corallina* spp., *Calliarthron tuberculosum*	N. America (west coast)	44.83167 44.31983 44.24500 40.34167 44.84050	-124.05933 -124.10950 -124.12033 -124.36317 -124.05617
Bellgrove et al. 2010	*Hormosira banksii*	*Corallina officinalis*	Australia	-38.39867	142.07500
Benedetti-Cecchi & Cinelli 1992b	*Cystoseira brachycarpa*, *C. compressa*	*Corallina elongata*	Mediterranean	43.50000	10.33333
Benedetti-Cecchi & Cinelli 1996	*Cystoseira brachycarpa*, *C. compressa*	*Corallina elongata*	Mediterranean	43.50000	10.33333
Dayton et al. 1984	*Macrocystis pyrifera*, *Laminaria setchellii*	*Calliarthron* spp.	N. America (west coast)	35.66283 35.66133	-121.28383 -121.28517
Graham 1997	*Macrocystis pyrifera*,	*Calliarthron* spp.	N. America (west coast)	36.64017	-121.92800
Reed & Foster 1984	*Macrocystis pyrifera*, *Pterygophora californica*, *Nereocystis luetkeana*	*Calliarthron tuberculosum*	N. America (west coast)	36.54833	-121.93883
Taylor & Schiel 2005	*Durvillaea antarctica*	*Haloptilon roseum*, *Jania micrarthrodia*, *Corallina officinalis*	New Zealand	-45.18333 -42.41667	171.63333 173.73333
Thompson & Schiel 2012	*Undaria pinnatifida*	*Corallina officinalis*	New Zealand	-43.60983	172.68050

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Focal group = Canopy algae (recruit), Competitor = Turf (corticated/coarsely branching)					
Andrew & Viejo 1998	*Sargassum muticum*	*Gelidium latifolium*, *Calliblepharis jubata*, *Chondrus crispus*	Bay of Biscay	43.61133	-5.77467
Barner et al. 2016	*Saccharina sessile*	*Cryptopleura/Hymenena* complex, *Constantinea simplex*, *Microcladia borealis*, *Odonthalia floccosa*, *Dilsea californica*, *Osmundea spectabilis*	N. America (west coast)	44.84050 44.82850 42.84717 42.71450 40.35100 39.59550	-124.05617 -124.06633 -124.56417 -124.47717 -124.36517 -123.79033
Brawley & Johnson 1991	*Pelvetia fastgiata*	*Mastocarpus papillatus*, *Endocladia muricata*	N. America (west coast)	36.62383	-121.91283
Cervin et al. 2005	*Ascophyllum nodosum*, *Fucus serratus*, *F. vesiculosus*	*Chondrus crispus*, *Gelidium pusillum*, *G. latifolium*, *Osmundea* spp., *Lomentaria articulata*	Irish Sea	54.08333	-4.61667
Chapman 1984	*Saccharina latissima*, *Laminaria digitata*	*Chondrus crispus*, *Phyllophora truncata*	N. America (east coast)	43.65683	-65.82383
Dayton et al. 1984	*Macrocystis pyrifera*	*Gelidium robustum*	N. America (west coast)	32.70300	-117.26583
Graham 1997	*Macrocystis pyrifera*	*Chondracanthus*, *Cryptopleura*, *Prionitis*, *Rhodymenia*, *Sarcodiotheca*, *Gelidium*	N. America (west coast)	36.61533	-121.89183
Kang et al. 2005	*Ecklonia stolonifera*	*Gelidium amansii*, *Gracilaria textorii*, *Gigartina tenella*, *Lomentaria catenata*, *Pachymeniopsis lanceolata*	Korea Strait	34.76933 34.76067 34.75500	128.38250 128.39033 128.39550

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Kim 2002b	*Fucus gardneri*, *Pelvetopsis limitata*	*Mazzaella cornucopiae*	N. America (west coast)	48.81983	-125.17500
Perkol-Finkel & Airoldi 2010	*Cystoseira barbata*	*Gelidium latifolium*, *Gigartina* spp., *Chondracanthus acicularis*	Mediterranean	43.55950 43.54717	13.61050 13.63000
Sousa et al. 1981	*Egregia laevigata*, *Macrocystis pyrifera*, *Cystoseira osmundacea*	*Gigartina canaliculata*, *Laurencia pacifica*, *Gastroclonium coulteri*	N. America (west coast)	34.41667	-119.68333
Worm & Chapman 1996	*Fucus distichus*	*Chondrus crispus*	N. America (east coast)	44.45000	-63.71667
Worm & Chapman 1998	*Fucus distichus*	*Chondrus crispus*	N. America (east coast)	44.45000	-63.71667
Focal group = Canopy algae (recruit), Competitor = Turf (filamentous)					
Alestra & Schiel 2014	*Hormosira banksii*	*Ulva* spp.	New Zealand	-42.41333	173.70500
Berger et al. 2003	*Fucus vesiculosus*	*Cladophora glomerata*, *Enteromorpha intestinalis*, *Pilayella littoralis*	Baltic Sea	58.80067	17.65983
Connell & Russell 2010	*Ecklonia radiata*	*Feldmannia* spp.	Australia	-35.10700 -35.14633 -35.17883	138.46833 138.46350 138.46033
Duffy & Hay 2000	*Sargassum filipendula*	*Enteromorpha* spp., *Cladophora ruchingeri*	N. America (east coast)	34.65117	-76.72350
Gorman & Connell 2009	*Cystophora* spp., *Ecklonia radiata*, *Sargassum* spp.	*Feldmannia* spp.	Australia	-35.10700 -35.14633 -35.17883	138.46833 138.46350 138.46033

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Harris et al. 1984	*Macrocystis pyrifera*, *Pterygophora californica*	*Giffordia*, *Ectocarpus*	N. America (west coast)	34.41667	-119.95000
Isæus et al. 2004	*Fucus serratus*	*Polysiphonia fucoides*, *Sphacelaria arctica*	Baltic Sea	56.42100	16.59350
Johnson & Mann 1988	*Saccharina latissima*	*Antithamnion* spp., *Ceramium rubrum*, *Polysiphonia* spp., *Acrothrix novae-angliae*	N. America (east coast)	44.57250	-63.93367
				44.59167	-64.06167
Råberg et al. 2005	*Fucus vesiculosus*	*Pilayella littoralis*	Baltic Sea	58.81417	17.63633
Steen 2004	*Fucus serratus*, *F. distichus*	*Enteromorpha compressa*	Norway	59.66667	10.63333
Thompson & Schiel 2012	*Undaria pinnatifida*	*Halopteris congesta*	New Zealand	-43.60983	172.68050
Worm et al. 2001	*Fucus vesiculosus*	*Enteromorpha* spp., *Pilayella littoralis*, *Cladophora rupestris*, *Ceramium strictum*, *Polysiphonia violaceae*	Baltic Sea	54.68567	10.00367
Focal group = Turf (articulated coralline), Competitor = Canopy algae					
Barner et al. 2016	*Saccharina sessile*	*Bossellia plumose*, *Corallina* spp., *Calliarthron tuberculosum*	N. America (west coast)	44.84050	-124.05617
				44.83167	-124.05933
				44.82850	-124.06633
				44.31983	-124.10950
				44.24500	-124.12033
				42.84717	-124.56417
				42.71450	-124.47717
				40.35100	-124.36517

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
				40.34167 39.59550	-124.36317 -123.79033
Benedetti-Cecchi & Cinelli 1992a	*Cystoseira compressa*, *C. crinita*	*Corallina elongata*, *C. granifera*	Mediterranean	43.45800	10.35450
Bulleri et al. 2002	*Cystoseira amentacea*	*Corallina elongata*, *Haliptilon virgatum*	Mediterranean	43.04917	9.80033
Irving & Connell 2006a	*Ecklonia radiata*	*Haliptilon roseum*	Australia	-35.63933	138.54317
Irving & Connell 2006b	*Ecklonia radiata*	*Haliptilon roseum*	Australia	-35.60833	138.58767
Schiel & Lilley 2007	*Hormosira banksii*	*Corallina officinalis, Jania* spp., *Haliptilon roseum*	New Zealand	-42.42767 -42.43200	173.71283 173.70383
Schiel & Lilley 2011	*Hormosira banksii*	*Corallina officinalis, Jania* spp.	New Zealand	-42.41667 -45.35000	173.68333 170.85000
Schmidt & Scheibling 2007	*Saccharina latissima*, *Laminaria digitata*	*Corallina officinalis*	N. America (east coast)	44.49917	-63.92150
Taylor & Schiel 2005	*Durvillaea antarctica*	*Haloptilon roseum*, *Jania micrarthrodia*, *Corallina officinalis*	New Zealand	-45.18333 -42.41667	171.63333 173.73333
Focal group = Turf (corticated/coarsely branching), Competitor = Canopy algae					
Barner et al. 2016	*Saccharina sessile*	*Cryptopleura/Hymenena* complex, *Constantinea simplex*, *Microcladia borealis*, *Odonthalia floccosa*, *Dilsea californica*, *Osmundea spectabilis*	N. America (west coast)	44.84050 44.83167 44.82850 44.31983 44.24500 42.84717	-124.05617 -124.05933 -124.06633 -124.10950 -124.12033 -124.56417

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
				42.71450 40.35100 40.34167 39.59550	-124.47717 -124.36517 -124.36317 -123.79033
Benedetti-Cecchi & Cinelli 1992a	*Cystoseira compressa*, *C. crinita*	*Feldmannophycus*, *Gelidium*, *Hypnea*, *Laurencia*, *Rytiphloea*, *Alsidium*	Mediterranean	43.45800	10.35450
Benedetti-Cecchi & Cinelli 1992b	*Cystoseira brachycarpa*, *C. compressa*	*Laurencia obtusa*, *Rytiphloea tinctoria*	Mediterranean	43.50000	10.33333
Benedetti-Cecchi et al. 2015	*Cystoseira amentacea*	Unspecified	Mediterranean	43.03533	9.79850
Bulleri et al. 2002	*Cystoseira amentacea*	*Laurencia obtusa*, *Chondria* spp., *Gastroclonium clavatum*	Mediterranean	43.04917	9.80033
Cervin et al. 2005	*Ascophyllum nodosum*, *Fucus serratus*, *F. vesiculosus*	*Chondrus crispus*, *Gelidium pusillum*, *G. latifolium*, *Osmundea* spp., *Lomentaria articulata*	Irish Sea	54.08333	-4.61667
Jenkins et al. 1999	*Ascophyllum nodosum*, *Fucus serratus*	*Chondrus crispus*	Irish Sea	54.06583	-4.62683
Kim 2002a	*Fucus gardneri*, *Pelvetopsis limitata*	*Mazzaella cornucopiae*	N. America (west coast)	48.81983	-125.17500
Maggi et al. 2012	*Cystoseira brachycarpa*, *C. compressa*, *C. crinita*	*Gelidium*, *Hypnea*, *Laurencia*, *Rytiphloea*	Mediterranean	43.48683	10.31867
Schmidt & Scheibling 2007	*Saccharina latissima*, *Laminaria digitata*	*Chondrus crispus*, *Mastocarpus stellatus*	N. America (east coast)	44.49917	-63.92150

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Wernberg et al. 2005	*Ecklonia radiata*	*Pterocladia lucida*, *Rhodymenia sonderi*, *Hypnea* spp.	Australia	-31.83717	115.71417
Focal group = Turf (filamentous), Competitor = Canopy algae					
Benedetti-Cecchi & Cinelli 1992a	*Cystoseira compressa*, *C. crinita*	*Ceramium tenuissimum*, *Cladophora* spp., *Sphacelaria cirrosa*	Mediterranean	43.45800	10.35450
Benedetti-Cecchi & Cinelli 1992b	*Cystoseira brachycarpa*, *C. compressa*	*Cladophora rupestris*, *Ceramium* spp., *Polysiphonia* spp.	Mediterranean	43.50000	10.33333
Bulleri et al. 2002	*Cystoseira amentacea*	*Ceramium*, *Chaetomorpha*, *Enteromorpha*	Mediterranean	43.04917	9.80033
Falkenberg et al. 2012	*Ecklonia radiata*	*Feldmannia* spp.	Australia	-34.79300	138.48517
Falkenberg et al. 2015	*Ecklonia radiata*	*Feldmannia* spp.	Australia	-35.56433	138.62333
Ghedini et al. 2015	*Ecklonia radiata*	Unspecified	Australia	-35.56433	138.62333
Irving & Connell 2006a	*Ecklonia radiata*	*Feldmannia*, *Ectocarpus*, *Sphacelaria*, *Giffordia*	Australia	-35.63933	138.54317
Irving & Connell 2006b	*Ecklonia radiata*	*Feldmannia*, *Ectocarpus*, *Sphacelaria*, *Giffordia*	Australia	-35.60833	138.58767
Johnson & Mann 1988	*Saccharina latissima*	*Bonnemaisonia hamifera*	N. America (east coast)	44.57250 44.59167	-63.93367 -64.06167
Kiirikki 1996	*Fucus vesiculosus*	*Cladophora glomerata*, *Enteromorpha* spp., *Pilayella littoralis*	Baltic Sea	59.82633	23.24217
Palmer & Sideman 1988	*Ascophyllum nodosum*, *Fucus distichus*	*Ulothrix flacca*	N. America (east coast)	43.72167 43.71833	-69.99000 -69.85500

Reference	Foundation Species	Turf-Forming Species	Location	Lat	Long
Provost et al. 2017	*Ecklonia radiata*	Unspecified	Australia	-30.30283	153.15833
Russell & Connell 2005	*Ecklonia radiata*	*Feldmannia* spp.	Australia	-35.60700	138.58983
Schmidt & Scheibling 2007	*Saccharina latissima*, *Laminaria digitata*	*Bonnemaisonia hamifera*, *Chaetomorpha melagonium*	N. America (east coast)	44.49917	-63.92150
Steen 2004	*Fucus serratus*, *F. distichus*	*Enteromorpha compressa*	Norway	59.66667	10.63333
Wernberg 2006	*Fucus serratus*	*Cladophora rupestris*, *C. glomerata*, *Pilayella littoralis*	Baltic Sea	55.03850	15.14350

Table G2. Summary of characteristics of studies contributing to overall effect sizes in random effects models (or subgroup means in mixed effects models). The focal group of the experiments, competing group manipulated, and response variable measured are indicated in the first 3 columns, followed by the number of publications with experiments meeting inclusion criteria (n) and the number of study-specific effect sizes extracted from those publications (n). The average (mean ± SD; median) duration (d) of experiments contributing effect sizes and the number of experiments that also crossed competitor manipulation with other factors suspected of mediating the interaction (herbivory, nutrient or CO_2 enrichment, physical stress or disturbance) are also provided. ArtCor = articulated coralline turf, Cort/Br = corticated/coarsely branching turf, Filam = filamentous turf, Micro/Macro = Microscopic/Macroscopic canopy algae recruits, CanAlg = Canopy algae, and RecrCor and EstabCor = recruiting and established corals, respectively.

Focal Group	Competitor	Response Variable	Publications (n)	Study-specific effects (n)	Duration (d)	Studies crossed with other factors (n)		
						Herbivory	Enrichment	Stress or Disturbance
ArtCor	CanAlg	Abundance	9	25	706 ± 763; 485	0	0	0
Cort/Br	CanAlg	Abundance	11	25	506 ± 388; 440	2	0	1
Filam	CanAlg	Abundance	16	21	173 ± 191; 76	2	8	4
Micro/Macro	ArtCor	Abundance	10	20	251 ± 211; 183	2	0	1
Micro/Macro	Cort/Br	Abundance	13	27	209 ± 173; 120	2	0	0
Micro/Macro	Filam	Abundance	12	23	123 ± 131; 66	3	2	0
Filam	EstabCor	Abundance	3	6	96 ± 78; 60	0	0	0
EstabCor	Filam	Abundance	2	5	223 ± 46; 213	0	0	0
EstabCor	Filam	Physiology	3	7	164 ± 89; 183	0	0	0
EstabCor	Filam	Growth	7	17	119 ± 75; 105	1	0	0
EstabCor	Filam	Survival	6	9	161 ± 87; 167	1	0	0
RecrCor	Filam	Survival	4	8	5 ± 2; 5	0	0	1
Total			69	193	226 ± 353; 120	11	9	7

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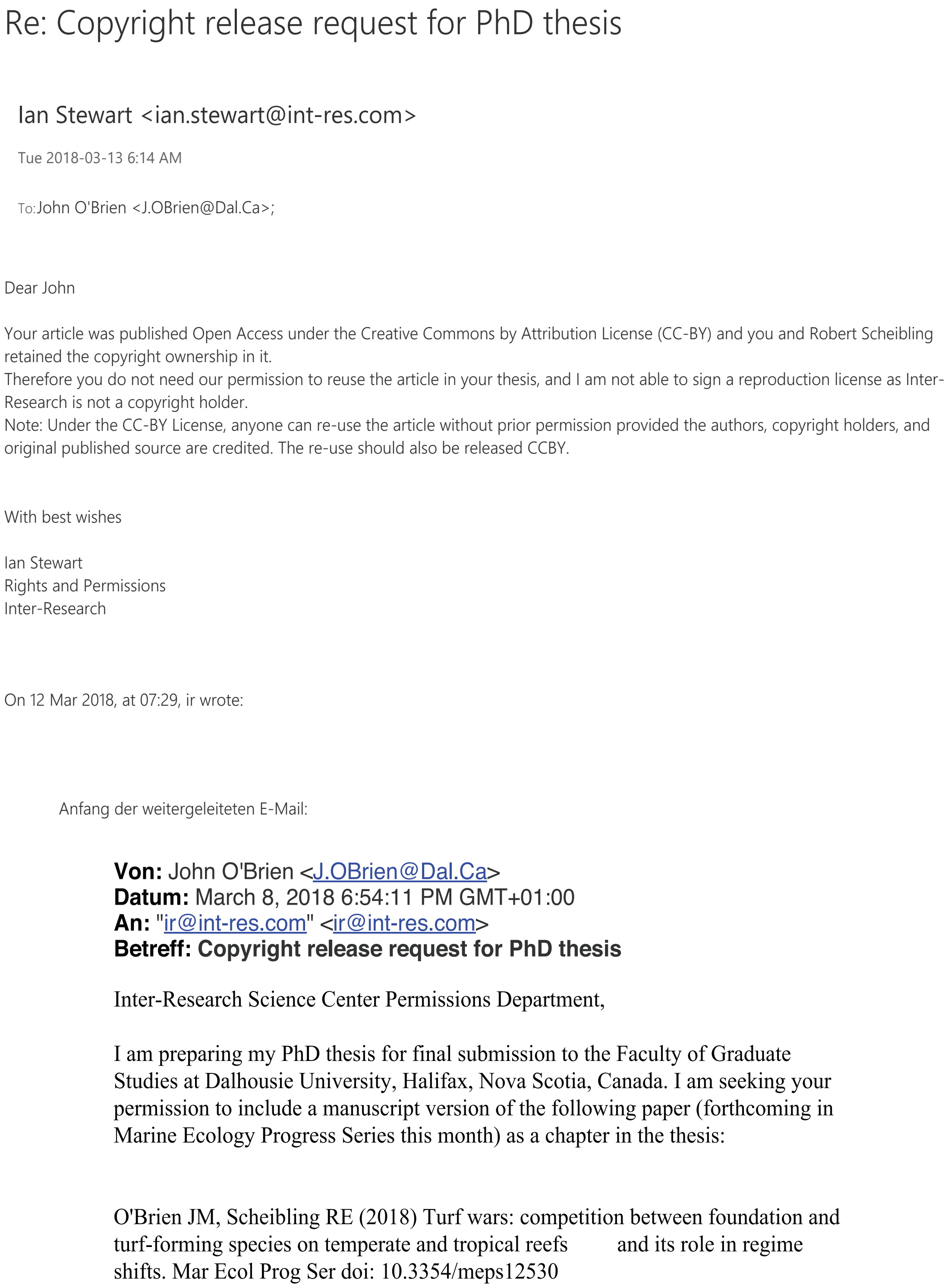

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