REGIME SHIFTS IN A KELP BED ECOSYSTEM AND LINKAGES WITH DEEP-LIVING SEA URCHINS

by

Karen Filbee-Dexter

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
July 2016

To my Grandmother, Bernice Dexter. She attended Dalhousie University from 1936 to 1939, and graduated at the age of 19 with a Bachelor of Arts in History and Psychology. At age 97, she knows the entire contents of this thesis.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

In kelp ecosystems, abrupt shifts occur when high densities of sea urchins destructively graze attached kelp, creating unproductive barrens devoid of erect macroalgae. In this thesis, I assessed the stability of urchin barrens along temperate and polar coasts globally and investigated the role of deep-living sea urchins (*Strongylocentrotus droebachiensis*) in driving shallow regime shifts in Nova Scotia. Shifts between barrens and kelp beds in many parts of the world represent regime shifts, in accordance with alternative stable-state dynamics. Sea urchins in deep subtidal environments along the Atlantic coast of Nova Scotia serve as a source of adults that eventually form grazing aggregations at the deep margins of kelp beds or contribute to the pool of planktonic larvae that settle in shallow habitats. Pulses of drift kelp were generated during a strong storm event that caused large losses of kelp canopy and exported kelp to deeper regions (15 to 45 m), where sea urchins were highly associated with kelp detritus. Sea urchins rapidly located pre-weighted kelp fronds deployed at 45 and 60 m depth, and consumed them for months. Urchins collected from 60 m depth had large gonads and spawned outside of the main spring spawning season in shallow water, suggesting periodic detrital subsidy enhances their reproductive condition. Longterm dive records and coastal surveys show that kelp biomass has declined by over 84% over the past 4–6 decades, and a shift has occurred from kelp beds to rocky reefs dominated by opportunistic turf-forming and invasive algae. This shift is associated with warming sea temperatures and predicted to reduce the amount of kelp entering detrital food webs. Drift algae and sea urchins occurred across a range of benthic habitats, but most frequently

within 1.5 km of the coast in depressions. We found that shallow regions where destructive grazing fronts have been documented over the past 4 decades were closer to predicted habitats of deep-living sea urchin compared to regions that remained in a kelp bed state during the same period, indicating these urchins play an important role in driving shifts from kelp beds to barrens on a coastal scale.

LIST OF ABBREVIATIONS USED

mg	Milligram
g	Gram
kg	Kilogram
µm	Micrometre
mm	Millimetre
cm	Centimetre
m	Meter
km	Kilometre
ml	Millilitre
s	Second
min	Minute
h	Hour
d	Day
wk	Week
mo	Month
yr	Year
BC	Before Christ
Jun	June
Jul	July
Aug	August
Oct	October
Sum	Summer
°C	Degrees Celsius
mmol	Millimole
K	Kelp
B	Barrens
M	Non-kelp macroalgal bed
Obs	Observations
Exp	Experimental transplantation or removal
GI	Gonad index
LI	Latency of response spawning induction
MO	Proportion of mature ova
TD	Test diameter
F	Fertilized
U	Unfertilized
UN	Unfertilized with nucleolus
F1	Forward shift threshold
F2	Reverse shift threshold
SST	Sea surface temperature

DNA	Deoxyribonucleic acid
no	Number
ND	No data
Log	Logistic
RFM	Random forest model
Sensit	Sensitivity
Specif	Specificity
TSS	True Skill Statistic
χ^2	Chi-square
n	Sample size
ind	Individual(s)
SE	Standard error
SD	Standard deviation
LR	Likelihood ratio
GLM	Generalized linear model
ANOVA	Analysis of Variance
PERMANOVA	Permutational Multivariate Analysis of Variance
t (perm)	PERMANOVA test statistic
r	Pearson's product moment correlation
p	P-value
α	Significance level
R^2	Coefficient of determination
ACF	Autocorrelation function
z	Z score
I	Moran's Index
ROC	Receiver operating curve
AUC	Area under the receiver operating curve
df	Degrees of freedom
F	Fischer statistic
AIC	Akaike information criterion
MS	Mean Square
BPI	Bathymetric position index
DEM	Digital elevation model
ROV	Remotely operated underwater vehicle
Lat	Latitude
Long	Longitude
N	North
S	South
E	East
W	West
GPS	Global Positioning System

USA	United States of America
OH	Owl’s Head
DC	Duncan’s Cove
WI	Whitehead Island
LDI	Little Duck Island
MC	Mill Cove
L	The Lodge
T-L	Tilly-Lodge
TP	Tilly Point
H	Horse Island
SW	Southwest Island
SP	Splitnose Point
I	Island
Pt	Point
L	Ledge
Hd	Head
Rd	Road
R	Rock
RS	Right side
H	Headland
O	Outer bay
I	Inner bay
Quad	Quadrat
Trans	Transect
N	No
Y	Yes
DG	David Gray
DL	Devin Lyons
JL	John Lindley
RES	Robert E. Scheibling
KFD	Karen Filbee-Dexter
DDW	Deep dive wing
RV	Research vessel
Sp	Specie
Spp	Species
C	Carbon
KCL	Potassium Chloride
Chl *a*	Chlorophyll *a*
CTS	Coastal Time Series
TRITON	Temperate reefs in Tasmania with lobsters and urchins
MODIS	Moderate Imaging Resolution Spectroradiometer
UTM	Universal Transverse Mercator
IPCC	Intergovernmental Panel on Climate Change
NSERC	Natural Sciences and Engineering Research Council
et al.	Et alia

ACKNOWLEDGEMENTS

I am very grateful to have had the opportunity to work with Bob. He has inspired me to pursue a career in marine research, fueled my curiosity about natural systems, and been an amazing mentor, friend and supporter. It has been a wonderful five years, and I am glad to have been a "fun-seeker" in the Scheibling lab. I was also fortunate to have an excellent committee. Sandra Walde is the reason I majored in biology. Her first year lectures were inspiring, insightful and just plain fascinating! Hal Whitehead has been a great source of statistical advice throughout my degree. Anna Metaxas has been a wonderful role model. I admire her passion and big picture approach to marine research. John Lindley was instrumental in creating the tow camera system, and installing all manner of contraptions on our research vessel. It was a pleasure to work with a number of fishers, especially Ben Miller, Chris Mackenzie, and David Gray.

Thanks to my friends Aly, Hannah, Tara, Kelly and Ila for wanting me to be great and loving me even though I talk about sea urchins for hours. Thanks to my partner Mike Gniewek for the constant support and laughter throughout this degree. He taught me how to write my first scientific paper 9 years ago and has refused to edit my writing ever since! I also cannot forget my other life partner Dana Archibald. We chased an Olympic dream together during my first 2 years of this PhD. The drafts of Chapters 2 and 3 were written on various trains between regattas in Europe. To my labmates Kira, Colette, and John – what can I say? It has been a blast. I will always remember all the good days on the water and all the crazy days where everything went wrong and we laughed anyway.

Lastly, thanks to Mum and Dad, for teaching me to love the ocean long before I slipped below the surface to explore its depths.

It is of great use to the sailor to know the length of his line, though he cannot with it fathom all the depths of the ocean. – John Locke.

CHAPTER 1

INTRODUCTION

1.1. ABRUPT AND PERSISTENT CHANGE IN MARINE ECOSYSTEMS

Marine ecosystems currently face multiple stressors, including changing climate, habitat loss, invasive species, overfishing and pollutants (IPCC 2014, Halpern et al. 2015). As the number and intensity of impacts on biological systems increase (Hoekstra et al. 2005), and the capacity of ecosystems to absorb these impacts dwindles, there is an urgent need to understand dynamics of ecosystem change and curb the loss of important ecosystem services (Drijfhout et al. 2015). Of particular concern to managers are major changes in ecosystems that are difficult to predict and reverse (Folke et al. 2004, Rocha et al. 2015). A classic example is a regime shift, which is defined as an abrupt and persistent reconfiguration of an ecosystem's structure and function (Biggs et al. 2015).

Regime shifts have been observed in a variety of ecosystems globally and are expected to become more frequent and severe with increasing anthropogenic impacts and environmental change (Steffen et al. 2007). Well-studied examples include collapse from coral-dominated to macroalgae-dominated reefs (Hughes et al. 2013), and shifts from clear lakes to eutrophic lakes (Carpenter 2003). These shifts generally occur when an ecosystem is pushed beyond a critical threshold where reinforcing processes or feedbacks maintaining the current community configuration (or stable state) are overcome, resulting in an abrupt transition to a new configuration (or alternative stable state). This can be triggered by a gradual change in the system or an external perturbation, in ecosystems with more than one possible stable state. Regime shifts in ecology also have been referred to as phase shifts or critical transitions (Rocha et al, 2015); there are some differences in how the term is used in other disciplines. For example, oceanographers use regime shift to describe decadal changes in ocean systems driven by climate, and community ecologists (especially coral reef ecologists) often inconsistently use phase shifts to describe both non-linear change and abrupt, persistent changes in community structure. In this thesis I use the terms phase shift and regime shift interchangeably, but currently refer to these dynamics as regime shifts to be consistent with recent synthetic reviews (e.g. Biggs et al, Hughes et al. 2013, Rocha et al. 2015).

1.2. REGIME SHIFTS IN KELP BED ECOSYSTEMS OF NOVA SCOTIA

In kelp ecosystems, regime shifts occur when high densities of sea urchins destructively graze attached kelp, creating barrens devoid of erect macroalgae (Ling et al. 2015). Urchin barrens have lower structural complexity and productivity compared to kelp beds (or forests), which provide food and biogenic habitat for a diverse community of invertebrates and fishes, and are often difficult to recover. Shifts between urchin barrens and kelp beds have been studied for decades on temperate rocky reefs world-wide, and researchers have identified reinforcing feedbacks maintaining each state, as well as critical thresholds for shifts between states, in many areas (Dean et al. 1984, Leinass & Christie 1996, Konar & Estes 2003, Vásquez et al. 2006, Lauzon-Guay & Scheibling 2007a, Ling et al 2009). Despite these efforts, alternative stable-state dynamics remain notoriously difficult to predict because only a small change in the kelp state can trigger a dramatic collapse to barrens.

On rocky reefs along the Atlantic coast of Nova Scotia, changes in the abundance and behaviour of the green sea urchin *Strongylocentrotus droebachiensis* have historically triggered overgrazing of the dominant kelp species, *Saccharina latissima* and *Laminaria digitata* (Scheibling et al. 1999). In the early 1970s dense aggregations of sea urchins overgrazed kelp beds in a large embayment along the Nova Scotian coast near Halifax (Breen & Mann 1976). By the late 1970s, widespread destructive grazing had created barrens that spanned 1000 km of coastline (Miller 1985). Kelp beds re-established after outbreaks of an amoebic disease (paramoebiasis) in 1981–83 that caused mass mortalities of sea urchins (Scheibling 1984). In the early 1990s localized shifts to barrens occurred once again in this region, as sea urchins migrated from deeper regions and formed grazing fronts along the lower margin of kelp beds (Scheibling et al. 1999, Miller & Nolan 2008). Kelp beds re-established again in the late 1990s to early 2000s following another series of disease outbreaks (Scheibling et al. 2013), and sea urchins currently are restricted to depths > 15 m (where there is a thermal refuge from disease) along most the coast (Feehan & Scheibling 2014).

Spatial linkages between sea urchins in deep subtidal habitats and destructive grazing events in shallow kelp beds are key unknowns in the alternative-state dynamics of the rocky subtidal ecosystem of Nova Scotia. Deep-living sea urchins can serve as a source of adult migrants or larval recruits that repopulate shallow reefs after disease-induced mass mortalities (Scheibling et al. 1999, Brady & Scheibling 2005). *Strongylocentrotus droebachiensis* inhabits a vertical range from the intertidal zone to 300 m depth (Jensen 1974), but little is known about its distribution, abundance or reproductive condition beyond the depth limit of nontechnical scientific diving (Scheibling & Hatcher 2013). These deeper habitats have little to no *in situ* primary production, and sea urchins living there likely rely on external inputs of plant-derived food. Emerging evidence suggests that drift kelp is an important food resource for deep-living sea urchins that could influence their reproductive output and contribution to the larval pool (Kelly et al. 2011). Although large quantities of drift kelp are exported from shallow kelp beds by erosion and fragmentation of blades (Krumhansl & Scheibling 2011a), little is known about the spatial extent and timing of deposition in deep areas.

The Atlantic coast of Nova Scotia is one of 24 globally identified ocean warming hotspots (Hobday & Pecl 2014), and has experienced increases in sea surface temperatures (Scheibling et al. 2013) and the frequency of severe storms (Lauzon-Guay et al. 2010), over the past 30−35 years. These changes have altered the dynamics of the rocky subtidal ecosystem by increasing the frequency of sea urchin disease events and causing shifts to new and more degraded macroalgal beds dominated by mats or meadows of turf-forming and invasive algae (Watanabe et al. 2010, O'Brien et al. 2015). Understanding the extent of these changes in kelp beds, and the implications for nearby communities dependent on drift kelp subsidy, can provide insight into the future stability and functioning of this system.

1.3. OUTLINE OF THE THESIS

In this thesis, I investigate linkages between deep subtidal habitats and nearby kelp bed ecosystems, with emphasis on the role of deep-living sea urchins in driving shallow regime shifts to barrens. In Chapter 2, I synthesize available information on temporal and spatial patterns of occurrence of barrens and kelp beds on temperate and polar coasts world-wide. I document the various drivers of shifts between ecosystem states, threshold levels that trigger abrupt change, and feedback mechanisms that stabilize each state. In Chapter 3, I examine the magnitude and potential impact of hurricane-mediated defoliation of kelp beds and pulsed delivery of drift kelp to offshore sedimentary habitats with deep-living sea urchins. In Chapter 4, I document long-term changes in the kelp community and show that mean kelp biomass has declined by 85 – 99% over the past 4 – 6 decades, and a shift has occurred from luxuriant kelp beds to rocky reefs dominated by opportunistic turf-forming and invasive algae, with negative consequences for coastal productivity and drift subsidy. In Chapter 5, I experimentally measure the response of *Strongylocentrotus droebachiensis* in deep subtidal habitats to drift subsidy and the turnover time of this material. I also examine the reproductive capacity of deep-living sea urchins and compare this to sea urchins in shallow kelp beds. In Chapter 6, I quantify the extent of drift kelp deposition in deep subtidal areas off Nova Scotia and create the first predictive map of drift subsidy in a marine ecosystem. In Chapter 7, I create a predictive distribution map of deep-living sea urchins and draw inferences about the spatial linkage between deep sea urchins and foci of destructive grazing of shallow kelp beds that can spread over coastal scales. In Chapter 8, I integrate conclusions based on the foregoing chapters to summarize the contribution of my thesis to our overall knowledge of shifts between kelp beds and barrens, our understanding of linkages between deep and shallow subtidal environments, and the drivers and dynamics of long-term changes in kelp ecosystems.

CHAPTER 2

SEA URCHIN BARRENS AS ALTERNATIVE STABLE STATES OF COLLAPSED KELP ECOSYSTEMS

The work presented in Chapter 2 also appears in:

Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25. [Feature Article]

2.1. ABSTRACT

Sea urchin barrens are benthic communities on rocky subtidal reefs that are dominated by urchins and coralline algae; in the absence of intense herbivory by urchins, these barrens support luxuriant seaweed communities such as kelp beds (or forests). Barrens can extend over 1000s of km of coastline or occur in small patches (10s to 100s of m) within a kelp bed. They are characterized by low primary productivity and low food-web complexity relative to kelp communities and are generally considered a collapsed state of the kelp ecosystem. To assess the stability of sea urchin barrens and potential for return to a kelp-dominated state, we document temporal and spatial patterns of occurrence of barrens along temperate and polar coasts. We examine the various drivers of phase (or regime) shifts in these areas, the threshold levels of urchin abundance that trigger abrupt changes in ecosystem state, and the feedback mechanisms that stabilize each state. Although longitudinal (decadal) studies are limited, we find evidence in several regions that transitions between barrens and kelp beds are characterized by discontinuous phase shifts, with different thresholds for forward (to barrens) and reverse (to kelp beds) shifts, in accordance with alternative stable-state dynamics. In other areas, barrens may reflect regime shifts associated with large-scale oceanographic changes. Accelerating climate change and increasing anthropogenic impacts play important roles in altering alternative stable-state dynamics and triggering phase shifts. Recovery of the kelp state may be possible through management or remediation measures, but this necessitates a clear understanding of the thresholds and stabilizing factors for a given system.

2.2. INTRODUCTION

Sea urchin barrens are benthic communities that are dominated by herbivorous sea urchins and coralline red algae on rocky reefs devoid of seaweed (Fig. 2.1) (Pearse et al. 1970). Barrens generally occur in regions that can support kelp beds (or forests), which are highly productive and provide habitat and food for many ecologically and commercially important fish and invertebrate species (Konar & Estes 2003, Ling 2008, Bonaviri et al. 2012). Over the last 4 decades, transitions between kelp beds and sea urchin barrens have been widely reported along temperate coastlines globally (Sala et al. 1998, Pinnegar et al. 2000, Steneck et al. 2002). These transitions, termed phase shifts, generally occur when a change in sea urchin grazing intensity moves the system from one stable (i.e. robust to relatively small perturbations) community state to another (Lawrence

1975, Steneck et al. 2002). Sea urchin barrens have much lower primary productivity and habitat structural complexity than kelp beds and consequently can be considered a collapse of the kelp state (Simenstad et al. 1978, Chapman & Johnson 1990, Sivertsen 1996, Graham 2004, Christie et al. 2009). Since kelp beds are key components of coastal ecosystems that provide important services to resident communities (Mann 1973, Levin 1994, Krumhansl & Scheibling 2012b), understanding the factors that cause phase shifts to urchin barrens, and that enable kelp beds to recover, is crucial for the proper management of these ecosystems.

Of particular concern to managers is the possibility that sea urchin barrens are a stable state of the subtidal ecosystem, maintained by various feedback mechanisms that prevent recovery of the kelp-dominated state after the initial driver of the phase shift has been relaxed or reversed (Lauzon-Guay et al. 2009, Ling et al. 2009). This type of transition is termed a discontinuous phase shift (Fig. 2.2a) and characterizes an alternative stable-state system (Lewontin 1969, Scheffer et al. 2001, Collie et al. 2004, Mumby et al. 2007, Fung et al. 2011). It is discontinuous because the threshold for the forward shift to the barrens state is at a different level than the threshold for the reverse shift back to the kelp state. In contrast, the forward and reverse transitions of a continuous phase shift (Fig. 2.2b) occur around the same threshold level (Petraitis & Dudgeon 2004). There is mounting evidence from marine systems (such as kelp beds, seagrass beds and coral reefs) that collapse to less productive or structurally complex states occurs at a critical threshold of a forcing variable (Sutherland 1974, Scheffer et al. 2001, Petraitis & Dudgeon 2004, Casini et al. 2009). However, few studies have conclusively documented alternative stable-state dynamics (Knowlton 2004), and these have focused mainly on tropical coral reefs (Jackson 1997, Mumby et al. 2007, Dudgeon et al. 2010, Fung et al. 2011).

Despite compelling evidence of discontinuous phase shifts to sea urchin barrens for several regions, including Alaska, USA (Estes et al. 1998), Nova Scotia, Canada (Lauzon-Guay et al. 2009), and Tasmania, Australia (Ling et al. 2009), the existence of barrens as a true alternative stable state of kelp ecosystems remains controversial. Petraitis & Dudgeon (2004) argue that inadequate information on the mechanisms that create and stabilize kelp beds and urchin barrens precludes their classification as alternative stable-state systems but that they remain strong candidates for this designation. Other explanations for large-scale shifts between kelp beds and barrens are that they represent continuous phase shifts between states, most likely caused by ongoing anthropogenic impact (Connell & Sousa 1983, Petraitis & Dudgeon 2004), or that they are part of a larger oceanic regime shift to coralline-dominated barrens (Dayton et al. 1998, Lees et al. 2006, Wernberg et al. 2011). If shifts to sea urchin barrens are part of an oceanic regime shift, these transitions will likely involve an abrupt, long-term (decadal) change in oceanographic conditions occurring at large spatial scales and impacting multiple trophic levels (DeYoung et al. 2004, Lees et al. 2006).

In a comprehensive review of sea urchin grazing behaviour on kelps and other macroalgae, Lawrence (1975) summarized existing records of the distribution of sea urchin-dominated barren grounds. Steneck et al. (2002) reviewed the literature on kelp ecosystem collapses in temperate and boreal regions worldwide, including transitions to sea urchin barrens and possible forcing variables of phase shifts. Ecosystem-specific reviews of alternations between kelp and barrens states also exist for Chile (Vásquez &

Buschmann 1997), Maine, USA (Steneck et al. 2013), Nova Scotia (Scheibling et al. 2013) and the Northeast Atlantic (Norderhaug & Christie 2009). Here, we document the extent and history of occurrence of sea urchin barrens amid kelp-bed ecosystems worldwide to compile evidence on the nature of phase shifts and potential for alternative stable states. We include several canopy-forming brown algal communities (of the genera Sargassum and Cystoseira) in the Mediterranean in our survey, as these macroalgae are functionally and taxonomically similar to kelps (Round 1967) and offer further insights into the formation of sea urchin barrens. We begin by briefly reviewing the theoretical framework of alternative stable-state dynamics and the associated terminology, which has been used inconsistently and often inaccurately in the large and growing body of literature on the subject. We then examine the drivers of phase shifts between kelp beds and barrens and the feedback mechanisms that stabilize each community state. Lastly, we examine shifts to sea urchin barrens in the context of changing marine environments, and investigate the implications of a collapse in kelp ecosystems for marine management and conservation.

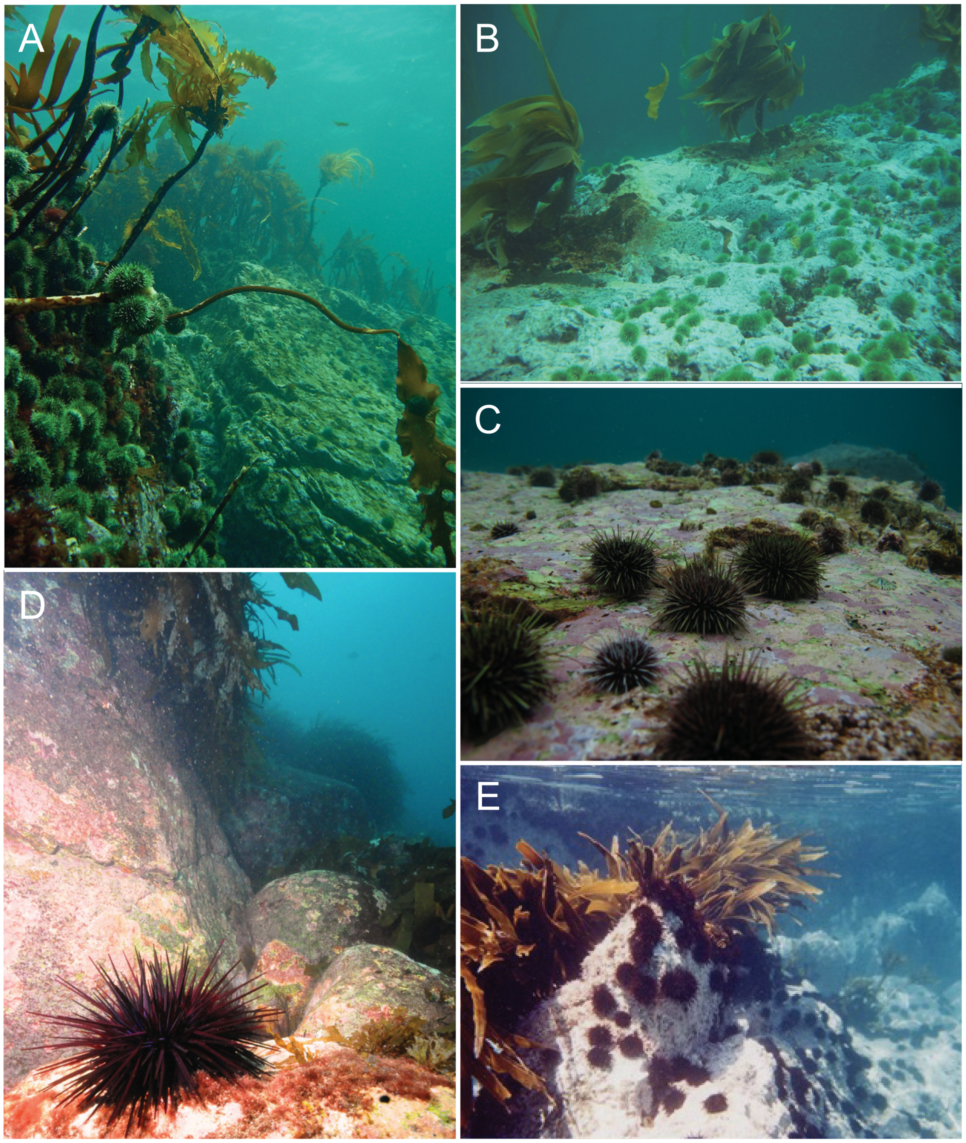
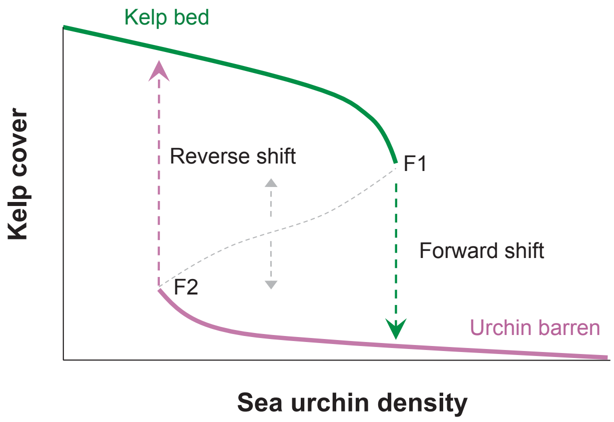


Fig. 2.1. (A) Destructive grazing front of sea urchins *Strongylocentrotus droebachiensis* advancing into a kelp bed near Halifax, Nova Scotia, Canada. Photo credit: R. E. Scheibling. (B) Extensive urchin barrens *S. polyacanthus* in the Aleutian Islands, USA. Photo credit: B. Konar. (C) Urchins *S. droebachiensis* on scoured coralline algae in barrens in Norway. Photo credit: C. W. Fagerli. (D) Range-expanding urchin *Centrostephanus rodgersii* forming patchy barrens in a kelp bed in southeast Tasmania. Photo credit: S. D. Ling. (E) *S. nudus* grazing a kelp bed in Japan. Photo credit: D. Fujita.

A. Discontinuous phase shift



B. Continuous phase shift

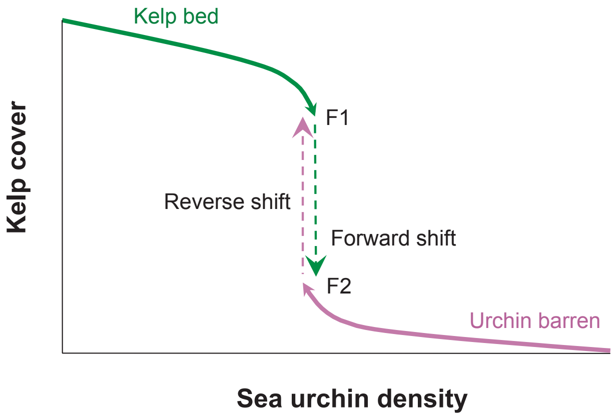


Fig. 2.2. (A) Discontinuous phase shift. As a kelp ecosystem (upper green path) approaches the threshold sea urchin density F1, a small increase in density will forward-shift the kelp-bed state to a barrens state. Once barrens have formed, a reverse shift (lower pink path) back to the kelp-bed state occurs when sea urchin density is reduced below the F2 threshold. The difference between F1 and F2 thresholds indicates the strength of hysteresis in the system. The dashed gray line represents the region of instability between the 2 alternative stable states. (B) Continuous phase shift. The forward shift threshold F1 and reverse shift threshold F2 occur at the same sea urchin density. The barren state only persists with high urchin densities and the kelp state immediately recovers when densities are reduced. Redrawn from Scheffer et al. (2001).

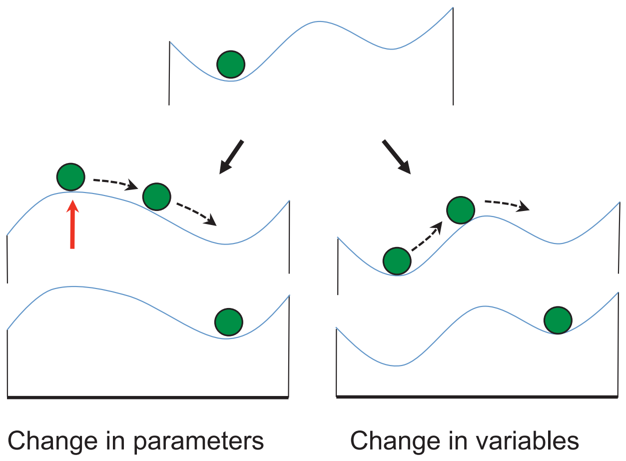


Fig. 2.3. Ball-in-cup diagram of alternative stable states. A ball represents a particular community state that exists on a landscape representing all possible states (2 states are considered for simplicity). Cups represent domains of attraction within that landscape. Each ball is continually ‘vibrating’ within these domains in response to seasonal cycles and natural variability in the ecosystem. The depth of a basin approximates resilience to these natural variations and small perturbations in the environment. Domains of attraction are also modified as system parameters change over time. The ecosystem can shift from one state to another (as represented by displacement of the ball) by either a change in state variables that moves the ball to a new domain of attraction or a change in state parameters that alters the landscape. Top diagram: initial condition with a community in 1 of 2 possible states; red vertical arrow: change in domains of attraction; dashed black arrows: shifts from one domain of attraction to another. Redrawn from Beisner et al. (2003).

2.3. ALTERNATIVE STABLE STATES

The concept of alternative stable states had its theoretical underpinnings in the models of Lewontin (1969), Sutherland (1974) and May (1977). Peterson (1984) provided evidence of state shifts among naturally occurring communities and identified the concept of stability as a critical aspect of alternative stable-state theory. He proposed a simple criterion as evidence of alternative stable states: different self-replacing communities can potentially dominate a given site. Connell & Sousa (1983) presented stricter criteria that required each state to exist at a long-term stable equilibrium (longer than 1 complete turnover of the dominant species) and the system to return to this point following a relatively small perturbation or disturbance, such as a fluctuation in a species' density or a storm event. They suggested that long-term (decadal) studies are required to distinguish alternative stable states. Additional conditions for stability are that each state must persist in the absence of the perturbation(s) that triggered the transition and be maintained by feedbacks that strengthen a current state (Petraitis & Latham 1999).

When this theoretical framework is applied to natural systems, this definition of stability becomes critical (Grimm & Wissel 1997). The requirement that the state must exist for the lifespan of the dominant species under similar environmental conditions can be difficult to assess because: (1) it requires long-term research (e.g. over 100 yr for the red sea urchin *Strongylocentrotus franciscanus*; Ebert & Southon 2003), (2) it does not allow for natural variation in environmental conditions, and (3) selection of dominants can be subjective in systems with many abundant species. For this reason, our review focuses on the stabilizing mechanisms and feedback loops that create domains of stability, instead of defining stability as the elapsed time in a state. Here, we define a stable state as a distinct community assemblage with feedback mechanisms that, under normal environmental conditions, confer resistance or resilience of the community to relatively small perturbations (see Table 2.1 for a glossary of ecological terms).

An important property of alternative stable states is hysteresis (Scheffer et al. 2001). Hysteresis occurs when an alternative state persists after the driver of the transition is relaxed or reversed. Hysteresis is created by various stabilizing mechanisms that inhibit return to the previous state. Therefore, for a kelp bed to re-establish in the barrens state, sea urchin density (a proxy for herbivory) would have to decrease well below the threshold density that caused the initial shift to barrens (Fig. 2.2a) (Breen & Mann 1976, Ling et al. 2009). The difference between thresholds for shifts in either direction determines the degree of hysteresis and the range of sea urchin densities that can occur in either a kelp or a barrens state. Transitions between 2 states without hysteresis are continuous phase shifts and are readily reversed by relaxing the forcing variable to the threshold level that caused the shift (Fig. 2.2b) (Petraitis & Dudgeon 2004). For example, phase shifts triggered by anthropogenic drivers may result in an ecosystem state that is only stabilized by the presence of continuing anthropogenic perturbation, such that the original state is recovered when human impact ceases (Knowlton 2004).

From a modelling perspective, a system can undergo a phase shift to a new state when a change in either state variables or system parameters passes a threshold where stabilizing mechanisms maintaining the original state are overcome (Fig. 2.3) (Beisner et al. 2003). State variables are system quantities (e.g. kelp biomass, abundances of urchins or their predators, larval supply) that change quickly in response to feedback mechanisms within the ecosystem. System parameters are measures that describe the behaviour of state variables and their interactions (e.g. grazing rate, per capita predation, settlement rate). Parameters can either change independently of state variables or be subject to slow feedback mechanisms originating within the system state (Table 2.1). A phase shift due to a strong perturbation or gradual change in state variables can shift the community from one state to another without affecting the stability landscape or parameters of the system.

In this type of transition, the system can exist in 2 or more community states under the same set of environmental conditions. Conversely, a large change in system parameters will alter the behaviour of the state variables, which could destabilize a community and shift it to another domain of stability. Some examples of changes in parameters that have caused shifts between kelp beds and coralline barrens are the increased mortality rate of sea urchins due to disease outbreaks associated with warming ocean temperatures and storm severity in Nova Scotia (Scheibling & Lauzon-Guay 2010), the increased survival rate of sea urchins due to changes in ocean currents in Tasmania (Ling 2008), and the change in crab predation rates due to large-scale overfishing of groundfish in Maine (Steneck et al. 2004). It is difficult to conceive of a marine system existing under a relatively constant set of parameters for decades, particularly when seasonal cycles, natural variability and anthropogenic impacts are continually changing the community landscape. Therefore, domains of stability represent dynamic community assemblages that are constantly being modified as system parameters change over time.

Table 2.1. Glossary of ecological terms, with examples from kelp bed and urchin barrens community states.

Term	Definition	Examples
Alternative stable-state ecosystem	An ecosystem that experiences discontinuous phase shifts, meaning it can exist in 2 stable states under the same environmental conditions.	Sea urchin barrens and kelp beds.
Continuous phase shift	Transition from one ecosystem state to another where the threshold for the forward shift is at the same level as the threshold for the reverse shift back to the previous state	A shift to barrens, where the kelp bed can re-establish when urchin grazing intensity decreases to the threshold density triggering the initial shift.
Discontinuous phase shift	Transition from one ecosystem state to another where the threshold for the forward shift is at a different level than the threshold for the reverse shift back to the previous state.	A shift to barrens, where the kelp bed does not re-establish until urchin grazing intensity decreases well below the threshold density triggering the initial shift.
Driver	A forcing agent that causes a change in state variable(s) or parameter(s) that results in a phase shift.	Overfishing or recovery of urchin predators, urchin recruitment pulse, disease outbreak, storm event or loss of kelp that results in an increase or decrease in sea urchin grazing intensity.
Ecosystem state	The arrangement of species or populations within an ecosystem and their interactions with the physical environment.	Abundances of macroalgal species, coralline algae and sea urchins, as well as the 3-dimensional structure of the kelp bed and its associated properties.
Oceanic regime shift	Changes in oceanographic processes and marine system functioning that are persistent, occur at a large spatial scale and over multiple trophic levels, and are related to climate oscillations or change.	Shifts to barrens caused by El Niño-Southern Oscillation events in California and Chile, and southern intrusion of the Eastern Australian Current off Tasmania.
Resilience	The properties that return an ecosystem to its original community state after a disturbance or perturbation.	The time it takes to return a kelp bed or a barrens community to its normal community structure and organization after a perturbation.

Term	Definition	Examples
Stability	The result of various feedback mechanisms that, under normal environmental conditions, enable a community to persist in a given state, and resist or be resilient to small perturbations.	A kelp bed that stays essentially unchanged under constant environmental conditions, is resistant to increases in urchin density, and is resilient to small perturbations such as canopy loss, temperature change or predator decline.
State parameter	Measure that governs the behaviour of state variables and how they interact in an ecosystem.	Urchin grazing rate, kelp growth rate, recruitment rates, per capita predation rates. These measures can vary with changes in ocean currents, ocean temperature and large-scale overfishing.
State variable	Property of an ecosystem that responds to changes in parameters.	Kelp biomass, sea urchin density, predator abundance, larval abundance.

2.4. KELP DISTRIBUTION AND ECOLOGY

Kelps are large brown seaweeds (class Phaeophyceae, order Laminariales) that inhabit temperate or polar coastal regions throughout the world (Fig. 2.4, Appendix A: Table A1) (Steneck & Dethier 1994, Dayton et al. 1999, Steneck et al. 2002). They exhibit 3 basic morphologies that characterize kelp stands as forests (stipitate and canopy-forming kelps, with fronds suspended by floats) or beds (prostrate forms, without floats) (Steneck et al. 2002). Canopy kelps (e.g. *Macrocystis pyrifera*, *Nereocystis leutkeana*, *Ecklonia maxim*, and *Alaria fistulosa*) can extend to the ocean surface, forming extensive forests along the western coasts of North and South America. They also are scattered throughout South Africa, Southern Australia and New Zealand. Stipitate kelps (e.g. *Laminaria japonica*, *Lessonia trabeculata* and *Ecklonia radiata*) form midwater stands extending from the Japan Sea across the North Pacific to California, USA. Prostrate kelps (e.g. *Saccharina latissima* and *Laminaria digitata*) form low-lying kelp beds throughout much of the North Atlantic and are the dominant forms in Greenland, Norway and along the east coast of Canada to Maine. (For simplicity, here we generally designate kelp communities as beds, unless the distinction as forest is important.)

Kelps typically live a maximum of 25 yr (Steneck & Dethier 1994) and grow best in high-nutrient, cold-water areas (Tegner et al. 1996). They have high rates of primary production (Dayton 1985) and support a variety of herbivorous and detritivorous species that graze attached or drift kelp (Duggins et al. 1989, Krumhansl & Scheibling 2012b). Kelps also are host to various suspension feeders and micropredators (Ling 2008) and serve as important nursery habitats for many fish (Bodkin 1988, Levin 1994). Periods of high recruitment and primary productivity enable kelp beds to rapidly increase in biomass, while periods of severe storm activity (Filbee-Dexter & Scheibling 2012), intensive grazing (Vadas & Steneck 1988), low light or nutrient conditions (Dayton 1985, Tegner & Dayton 1991, Tegner et al. 1996), and warm water (Dayton et al. 1999) erode or defoliate kelp beds.

2.5. GLOBAL DISTRIBUTION OF SEA URCHIN BARRENS

Open clearings that are denuded of seaweeds and have high densities of sea urchins have been observed in shallow rocky habitats worldwide (Table 2.2, Fig. 2.4). The spatial extent of these barrens can range from 1000s of km of coastline to small patches (100s of m in extent) within a kelp bed (Table 2.2). Urchin barrens are dominated by invertebrate species, mainly sea urchins, but also sea stars, mussels and brittle stars. They are devoid of fleshy and filamentous algae and are primarily covered by encrusting coralline algae of low nutritional value. Coastal areas dominated by sea urchin barrens typically retain some localized or spatially limited stands of kelp and other seaweeds. For example, kelps have a refuge from urchin grazing in wave-swept shallow waters without sea ice (Lauzon-Guay & Scheibling 2007c), and form small patches throughout urchin barrens in some areas (Vásquez & Buschmann 1997, Konar 2000).

Depending largely on the time span and intensity of research in different regions, sea urchin barrens have been documented under 3 types of conditions: (1) through multiple phase shifts between kelp beds and urchin barrens, (2) following a single phase shift from a kelp to a barrens state, or vice versa, and (3) in areas that might otherwise support kelp, although a phase shift has not been observed. In what follows, we survey the occurrence of sea urchin barrens throughout the global range of kelps (and some other canopy-forming brown algae) and consider the drivers of phase shifts that have led to barrens.

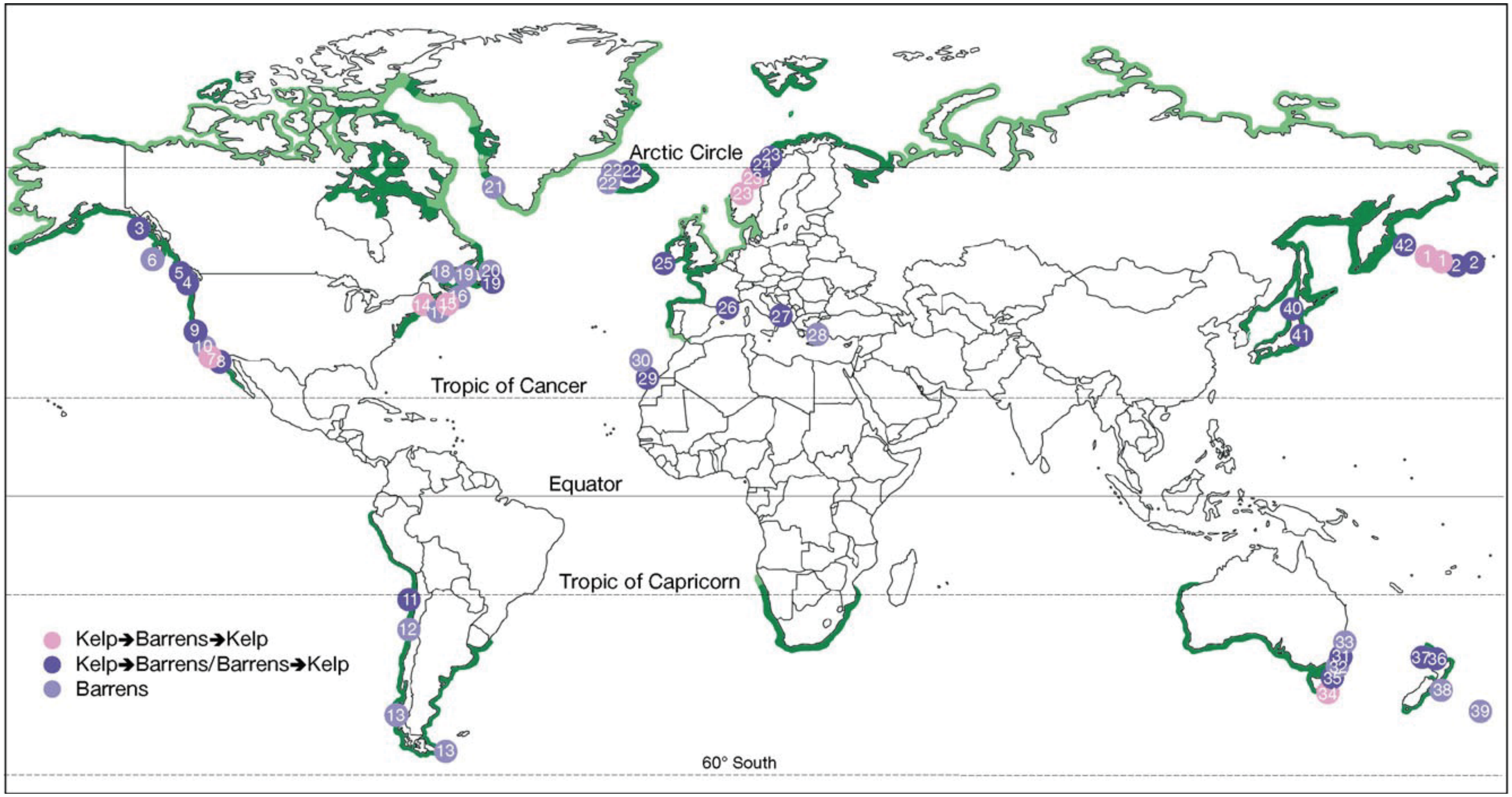


Fig. 2.4. Global occurrence of sea urchin barrens documented throughout the range of kelp. Numbered locations (colored circles) indicate areas where urchin barrens have been documented: (1) through the course of multiple phase shifts between kelp beds and barrens (pink), (2) following a single phase shift from a kelp to a barrens state, or vice versa (dark purple), and (3) in areas that might otherwise support kelp, although a phase shift has not been observed (light purple). Details for each numbered location are listed in Table 2.2. Locations outside the kelp range indicate barrens within communities of canopy-forming brown algae that are functionally and taxonomically similar to kelps. Dark green shading represents observed range of kelp (Raffaelli & Hawkins 1996, redrawn from Steneck et al. 2002). Light green shading represents the range of potential occurrence of kelp, based on the light and temperature requirements for kelp (approximated by latitude) (Krumhansl & Scheibling 2012b, K. A. Krumhansl pers. comm.). Dark green areas in the Beaufort Sea, Canadian Arctic, Greenland and northern Europe represent recorded kelp beds within the potential range of kelp (Appendix A).

Table 2.2. Survey of sea urchin barrens documented throughout the range of kelp beds. Phase shift indicates whether barrens have been documented through transitions between kelp and barrens (e.g. K→B→K), following a single phase shift from a kelp to a barrens state or vice versa (K→B or B→K), and in areas that might otherwise support kelp (B). Scale indicates the length of coastline where barrens were found. Barrens stability is given as time documented in a barrens state. Listed macroalgae genera and urchin species represent the dominant organism(s) in kelp and barrens state. Map no. corresponds to numbered location in Fig. 2.4. K: kelp forest or bed; B: sea urchin barrens; M: non-kelp macroalgal bed. –: no data

Location	Phase shift	Scale (km)	Driver(s)	Stability (yr)	Study period	Macroalgae genus	Urchin species	Map no.	Source
Northeast Pacific									
Aleutian Islands, USA	K→B→K →B	~400	Fluctuations in otter abundance (hunt, mortality)	100	560 BC–1998	*Laminaria*	*Strongylocentrotus polyacanthus*	1	Simenstad et al. (1978), Estes et al. (1998), Doroff et al. (2003)
	B→K	100	Otter predation	–	1985–87	*Laminaria*	*S. polyacanthus*,	2	Duggins et al. (1989)
	B→K	400	Otter predation	–	1970–72	*Alaria, Laminaria*	*S. franciscanus*	1	Estes & Palmisano (1974)
	B→K	500	Otter predation	–	1970–72	*Laminaria*, *Agarum*	*S. polyacanthus*	1	Estes et al. (1978)
Alaska, USA	B→K	40	Otter predation	–	1975–79	*Laminaria*	*S. droebachiensis*, *S. franciscanus*, *S. purpuratus*	3	Duggins (1980)
British Columbia, Canada	B→K	200	Otter predation	23	1987–2009	*Nereocystis*, *Pterygophora*	*S. franciscanus*	4	Watson & Estes (2011)
	B→K	10	Otter predation	10–20	1979	*Nereocystis*, *Laminaria*	*S. franciscanus*	5	Breen et al. (1982)
	B	100		1	1994	*Laminaria*	*S. franciscanus*	6	Jamieson & Campbell (1995)
California, USA	K→B→K	2	Storms	2	1979–84	*Macrocystis, Pterygophora*	*S. franciscanus*	7	Ebeling et al. (1985)
	K→B	0.1	Destructive grazing	4	1973–78	*Macrocystis*	*S. purpuratus*, *S. franciscanus*	8	Dayton et al. (1984)
	B→K	600	Urchin disease	5	1971–77	*Macrocystis*, *Laminaria*	*S. franciscanus*	9	Pearse & Hines (1979)
	B	0.5	Otter predation	–	1959–61	*Macrocystis*	*S. franciscanus*	10	McLean (1962)

Location	Phase shift	Scale (km)	Driver(s)	Stability (yr)	Study period	Macroalgae genus	Urchin species	Map no.	Source
Southeast Pacific									
Chile	K→B	0.64	La Niña event	6	1996–2004	*Macrocystis*, *Lessonia*	*Tetrapygus niger*, *Loxechinus albus*	11	Vega et al. (2005), Vásquez et al. (2006)
	B	2000[a]		7	1989–96	*Lessonia*	*T. niger*	12	Vásquez & Buschmann (1997)
	B	0.65		–	1973	*Macrocystis*	*L. albus*	13	Dayton (1985)
	B	0.15		–	1973	*Macrocystis*	*L. albus*	13	Dayton (1985)
Northwest Atlantic									
Maine, USA	K→B→K	300	Overfishing, urchin harvest	20	1930s–2000s	*Laminaria*	*S. droebachiensis*	14	Steneck et al. (2004)
Nova Scotia, Canada	K→B→K	0.08	Urchin increase, urchin disease	4	1992–98	*Laminaria*	*S. droebachiensis*	15	Scheibling et al. (1999)
	K→B	–	Recruitment pulse	19	1968–87	*Laminaria*	*S. droebachiensis*	15	Hart & Scheibling (1988)
	B→K	130	Urchin disease	–	1995	*Laminaria*	*S. droebachiensis*	15	Scheibling et al. (1999)
	B	2900		–	1980	*Laminaria*	*S. droebachiensis*	16	Moore & Miller (1983)
	B	150		–	1978–79	*Laminaria*	*S. droebachiensis*	17	Wharton (1980)
Quebec, Canada	B	0.09		35	2001	*Alaria*	*S. droebachiensis*	18	Dumont et al. (2004)
Newfoundland, Canada	B→K	–	Manual urchin removal	2	–	*Alaria*, *Desmarestia*	*S. droebachiensis*	19	Keats et al. (1991)
	B	80		23	1966–69	*Alaria*	*S. droebachiensis*	20	Himmelman (1986)
Greenland	B	0.08		3	2007–10	*Laminaria*	*S. droebachiensis*	21	Blicher (2010)
Iceland	K→B	0.2	Deep migration	1	1994	*Laminaria*	*S. droebachiesis*	22	Hjörleifsson et al. (1995)
Northeast Atlantic									
Norway	K→B→K	700	Urchin increase, urchin disease	18	1992–93	*Laminaria*	*S. droebachiensis*	23	Skadsheim et al. (1995)
	K→B	2000	Urchin increase	40	1970s–2009	*Laminaria*	*S. droebachiensis*	23	Norderhaug & Christie (2009)
	B→K	10	Manual urchin removal	14–18	1988–91	*Laminaria*	*S. droebachiensis*	24	Leinaas & Christie (1996)
Ireland	B→M	1	Predation, urchin disease	10	1994–2010	*Cystoseira*, *Sargassum*	*Paracentrotus lividus*	25	Trowbridge et al. (2011)
France	M→B	20	Overfishing	15	1906–93	*Cystoseira*	*P. lividus*	26	Thibaut et al. (2005)

Location	Phase shift	Scale (km)	Driver(s)	Stability (yr)	Study period	Macroalgae genus	Urchin species	Map no.	Source
Italy	M→B	30	Mussel fishery	12	2002	*Cystoseira*	*P. lividus*, *Arbacia lixula*	27	Guidetti et al. (2003)
	M→B	210	Mussel fishery	–	1990	*Cystoseira*	*P. lividus*, *A. lixula*	27	Fanelli et al. (1994)
Greece	B	90		1	2007–08	*Cystoseira*	*P. lividus*, *A. lixula*	28	Giakoumi et al. (2012)
East Atlantic									
Canary Islands	K→B	2.6	Overfishing	3	2001–04	*Sargassum*	*Diadema* aff. *antillarum*	29	Hernández et al. (2008)
	K→B	30	Overfishing	–	2003	*Cystoseira*, *Sargassum*	*Diadema* aff. *antillarum*	29	Tuya et al. (2005)
	B	50	High recruitment	21	2002–05	*Sargassum*	*Diadema* aff. *antillarum*	29	Hernández et al. (2010)
Savage Island	B	158		4	1998	*Cystoseira*, *Sargassum*	*Diadema* aff. *antillarum*	30	Alves et al. (2001)
Southwest Pacific									
Australia	B→K	0.16	Manual removal	2	1985–87	*Ecklonia*, *Sargassum*	*Centrostephanus rodgersii*	31	Andrew & Underwood (1993)
	B	2.75		2	2008–09	*Ecklonia*	*C. rodgersii*	32	Gladstone & Masens (2009)
	B	250^a		–	–	*Ecklonia*	*C. rodgersii*	33	Andrew & Underwood (1989)
Tasmania, Australia	K→B→K	15	Current change, lobster increase	20	1978–2004	*Ecklonia*	*C. rodgersii*	34	Ling (2008)
	K→B	400	Current change	5–20	1978–2005	*Ecklonia*	*C. rodgersii*	35	Johnson et al. (2005)
	K→B	0.1	Destructive grazing	0.5	2000–01	*Undaria*	*Heliocidaris erythrogramma*	34	Valentine & Johnson (2005)
New Zealand	K→B	200	Predation	2	1990	*Ecklonia*	*Evechinus chloroticus*	36	Schiel (1990)
	K→B	10	Predation	18	1978–2001	*Ecklonia*	*E. chloroticus*	37	Shears & Babcock (2003)
	B	1000^a		4	1975–79	*Laminaria*	*E. chloroticus*	38	Choat & Schiel (1982)
	B	0.025		–	1987	*Macrocystis*	*E. chloroticus*	39	Schiel et al. (1995)

Location	Phase shift	Scale (km)	Driver(s)	Stability (yr)	Study period	Macroalgae genus	Urchin species	Map no.	Source
Northwest Pacific									
Japan	K→B	100s	Destructive grazing, urchin removal	80	1930s–2000s	*Undaria*	*S. nudus*	40	Fujita (1998)
	K→B	10s	Destructive grazing	30–60	1930s–90s	*Undaria*	*S. nudus*	41	Tamaki et al. (2005)
	B→K	–	Urchin removal	0.2	2006–07	*Saccharina*, *Undaria*	*S. nudus*	40	Watanuki et al. (2010)
	B→K	2	Urchin exclusion	1	2003–05	*Undaria*	*S. nudus*	41	Tamaki et al. (2009)
Russia	B→K	0.1	Otter predation	5–15	1972–86	*Laminaria*	*S. polyacanthus*	42	Oshurkov et al. (1988)

[a] Likely an overestimate of range.

Table 2.3. Threshold sea urchin density and biomass required to trigger forward shifts from kelp to barrens states (K→B) and reverse shifts from barrens to kelp states (B→K) in Alaska, California, Chile, Nova Scotia, Norway and Tasmania. Thresholds were measured using field observations (Obs) during phase shifts or experimental transplantation or removal of sea urchins (Exp). Biomass decrease indicates the percentage decrease in threshold biomass between forward and reverse shifts. Measures were obtained from specific study sites and may not reflect thresholds for entire regions

Region	Method	Threshold density (ind. m^{-2})		Threshold biomass (kg m^{-2})		Biomass decrease (%)	Mean urchin mass (g)	Kelp biomass (kg m^{-2})	Source
		K→B	B→K	K→B	B→K				
Alaska, USA	Exp	72	16	1.81[a]	0.41[a]	77	25	–	Konar & Estes (2003)
California, USA	Obs	14	2–3	2.81[a]	0.4–0.61[a]	82[b]	200	0.2–0.6	Dean et al. (1984), Dayton et al. (1992)
Chile	Obs	36	20–28	–	–	–	–	–	Vásquez et al. (2006)
Nova Scotia, Canada	Obs, Exp	31–65	–	1.5–3.2[c]	0.15–0.25	91[b]	49	2.0–5.0	Breen & Mann (1976), Chapman (1981), Lauzon-Guay & Scheibling (2007a), Scheibling et al. (1999)
Norway	Obs, Exp	45–75	10	1.0–1.7[a]	0.22[a]	84[b]	22	1.0	Hagen (1995), Leinaas & Christie (1996), Sjøtun et al. (1998)
Tasmania, Australia	Obs, Exp	4–10	0.2–1.2	0.9–2.3[d]	0.05–0.28[d]	90[b]	230	0.8	Ling 2008, Ling et al. (2009), Pecorino et al. (2012), Marzloff et al. (2013)

[a] Urchin biomass calculated as mean individual mass multiplied by mean density; [b] Mid-point in biomass range used in calculation; [c] Biomass measured during destructive grazing; [d] Biomass range estimated from TRITON model of alternative stable states (Marzloff et al. 2013)

2.5.1. Barrens in regions with documented multiple phase shifts

Ecosystems where multiple shifts between kelp and barrens states have been documented provide important information on the drivers of these transitions and the stability of each state. Drivers of changes in urchin grazing intensity vary between these systems, but grazing typically increases after periods of high urchin recruitment and drift kelp shortage, and decreases with predation, overfishing and disease (Fig. 2.5). The first evidence of kelp beds alternating with sea urchin barrens comes from the Aleutian Islands in the Northwest Pacific, where sea otters are major predators of the sea urchin *Strongylocentrotus polycanthus* (Fig. 2.5a). Early European explorers described subtidal areas in the Aleutians as a lush kelp forest with abundant sea otter populations (Simenstad et al. 1978). By the 1800s, extensive hunting for the fur trade had decimated sea otter populations and caused the sea urchin population to increase and destructively graze kelp forests (Simenstad et al. 1978). This shifted the system to stable coralline barrens. Legal protection of sea otters in 1911 enabled sea otter populations to recover and reduce sea urchin densities to a level where kelp forests could re-establish (Estes & Palmisano 1974). The recovered kelp forests (*Alaria fistulos* and *Laminaria* spp.) were maintained for decades, until otter populations began to sharply decline due to predation by killer whales in the 1990s (Estes et al. 1998). This enabled sea urchin populations to increase once again and destructively graze kelp, leading to the formation of barrens across most of the Aleutian archipelago (Doroff et al. 2003). The Aleutians also provide a unique historical record of the state of the coastal ecosystem based on the contents of aboriginal middens (Simenstad et al. 1978). High abundances of fish and sea otter remains in middens from 580 BC suggest a kelp forest state, whereas high abundances of sea urchins and limpets in middens from 80 BC suggest a barrens state, providing evidence of localized transitions from kelp forests to coralline algal barrens over 2000 yr ago, possibly associated with aboriginal overharvest of sea urchin predators (Simenstad et al. 1978).

In California, there is similar archeological evidence of short-lived, localized shifts from giant kelp *Macrocystis pyrifera* forests to barrens thousands of years ago (Erlandson et al. 1996). Phase shifts from kelp forests to sea urchin barrens were recorded in California in the 1950s (Dayton et al. 1984) and were attributed mainly to the fishery-induced collapse of spiny lobster and sheepshead fish populations (Dayton et al. 1998), predators of sea urchins that filled the functional role of sea otters after the fur trade had eliminated them in the 1800s (Fig. 2.5b). These sea urchin barrens persisted in California until the 1960s, when the reintroduction of sea otters led to reinstatement of kelp forests in some areas (McLean 1962, Ebert 1968). However, widespread kelp forest recovery did not occur until the mid-1970s, when a fishery opened for red sea urchins *Strongylocentrotus franciscanus* (Dayton et al. 1998). In 1988, localized phase shifts to urchin barrens were documented following a winter storm event, and they persisted until sea urchin disease outbreaks in 1991 enabled kelp forest recovery (Dayton et al. 1992, Tegner et al. 1997). Presently, kelp forests dominate much of the Californian coast, although patchy urchin barrens occur amid these forests, and kelp only occupies a third of the range measured in 1911 (Tegner et al. 1996).

Shifts between kelp forests and barrens also have been associated with changing oceanographic conditions due to the El Niño-Southern Oscillation. In California, El Niño events in 1957–1959, 1982–1984 and 1992–1993 disrupted upwelling and brought warm, nutrient-depleted waters to coastal regions (Tegner & Dayton 1991, Dayton et al. 1998, Dayton et al. 1999). This reduced kelp biomass, and in some regions created temporary barrens that were recolonized by kelps during La Niña conditions (Tegner & Dayton 1987, Tegner et al. 1997). Conversely, in an 8-yr study of a kelp forest (*Macrocystis integrifolia* and *Lessonia trabeculata*) in northern Chile, Vásquez et al. (2006) documented a 3-fold increase in recruitment of sea urchins *Tetrapygus niger* and a sharp decline of kelp cover during a La Niña event in 1999. This created a barrens state that was stable for 4 yr until the kelp forest re-established in 2003.

In the Northwest Atlantic, kelp beds (*Saccharina latissima*) in Maine have exhibited 3 distinct phases in the last century (Steneck et al. 2004) (Fig. 2.5c). The historical state was dominated by large predatory fish, such as cod, haddock and wolfish, which controlled sea urchin *Strongylocentrotus droebachiensis* populations and maintained the kelp-bed state (Steneck 1997). In the mid-1960s, the functional loss of predatory fish due to fishing enabled sea urchin populations to increase, driving the transition to urchin barrens (Lamb & Zimmerman 1964, Steneck et al. 2004). The barrens state persisted until 1987, when an urchin fishery opened and decreased densities to the point at which kelp beds could re-establish (McNaught 1999). Currently the kelp-bed state is maintained by crab predation, which limits sea urchin recruitment and keeps urchin populations at low densities (Steneck et al. 2004, 2013).

In Eastern Canada, a shift from kelp beds (*Laminaria digitata* and *Saccharina latissima*) to barrens was first recorded in the late 1960s to the early 1970s, when dense aggregations of sea urchins overgrazed kelp in a large embayment near Halifax, Nova

Scotia (Breen & Mann 1976, Wharton & Mann 1981) (Fig. 2.5d). By the late 1970s, barrens dominated the entire Atlantic coast of Nova Scotia, until recurrent outbreaks of amoebic disease in 1980–1983 caused mass mortalities of sea urchins that enabled kelp beds to re-establish (Scheibling 1984, 1986, Jones 1985, Miller 1985). Initial increases in sea urchin density within kelp beds were attributed to declines of predatory fishes, crabs and lobsters (Wharton & Mann 1981, Bernstein & Mann 1982) or possible recruitment events (Hart & Scheibling 1988). The kelp beds transitioned to barrens again in the early 1990s after sea urchin density increased along the deep margins of kelp beds and recovered in the late 1990s following a widespread recurrence of disease in 1995 and 1999 (Scheibling et al. 1999, Brady & Scheibling 2005, Kelly et al. 2011). Disease outbreaks in Nova Scotia have been linked to storm activity and warm water temperatures and are becoming increasingly more frequent (Scheibling & Lauzon-Guay 2010, Scheibling et al. 2013). Consequently, kelp beds currently dominate much of the Nova Scotian coast, although barrens exist locally along headlands off central Nova Scotia and the southwestern shore (Feehan et al. 2013).

In the Northeast Atlantic, luxuriant beds of *Laminaria hyperborea* historically dominated the western coast of Norway (Skadsheim et al. 1995). In 1975, record high densities of the sea urchin *Strongylocentrotus droebachiensis* destructively grazed kelp beds (Skadsheim et al. 1995) (Fig. 2.5e) and extensive urchin barrens were created, although sea urchins were unable to remove mature kelp beds under low temperature and high light conditions (Leinaas & Christie 1996). Sea urchin die-offs in the early 1990s, due to either a macroparasitic infection (Sivertsen 1996) or an unidentified waterborne pathogen (Skadsheim et al. 1995), returned parts of the coast to the kelp-bed state.

Currently, northern Norway is dominated by decades-old sea urchin barrens, although kelp beds are re-establishing in southern and central Norway, most likely as a result of low sea urchin recruitment associated with warmer ocean temperatures and increased larval mortality (Sivertsen 2006, Fagerli et al. 2013).

In the Southwest Pacific, a long-term change in the East Australian Current introduced the sea urchin *Centrostephanus rodgersii* to coastal Tasmania in the late 1970s (Edgar et al. 2004). This influx of sea urchins caused areas with particularly high sea urchin densities along the northeastern coast of Tasmania to shift from a kelp-dominated (*Ecklonia radiata* and *Phyllospora comosa*) state to barrens (Fig. 2.5f) (Johnson et al. 2005, Ling 2008, Johnson et al. 2011). The resilience of kelp beds to these shifts has likely been reduced by the spiny lobster fishery, which removes an urchin predator from the system (Ling et al. 2009, Ling & Johnson 2012).

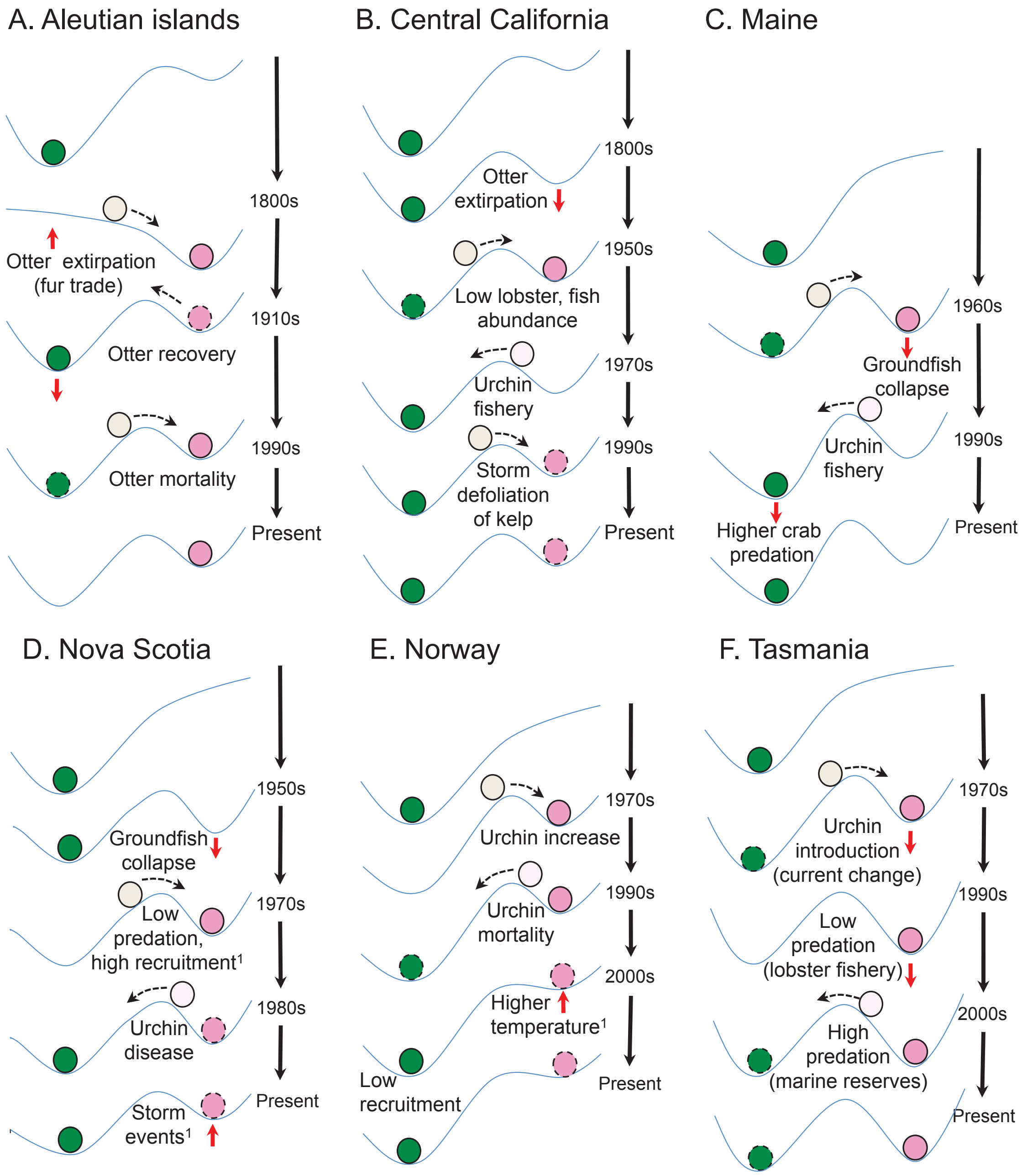


Fig. 2.5. Ball-in-cup diagrams representing phase shifts between kelp beds and sea urchin barrens in 6 regions: (A) Aleutian Islands, USA, (B) Central California, USA, (C) Maine, USA, (D) Nova Scotia, Canada, (E) Norway and (F) Tasmania, Australia. For each region, the top diagram (in chronological order) represents the earliest known community assemblage (determined by archeological evidence for the Aleutian Islands, California and Maine); this is followed by documented phase shifts and associated drivers leading to the present community state. See 'Barrens in regions with documented multiple phase shifts' for detailed explanation of drivers and dynamics for each region. Green balls

represent kelp states, pink balls represent barren states and light green or light pink balls indicate a transitional stage (e.g. kelp bed with active urchin grazing patches or barrens with kelp regrowth). Balls with dashed lines represent patchy kelp or barrens; balls with solid lines represent extensive kelp or barrens. Red vertical arrows represent changes in domains of attraction (resilience); dashed black arrows represent shifts from one domain of attraction to another. [a]A statistical association, not a mechanistic driver.

2.5.2. Barrens in regions with one or no documented phase shift

Isolated phase shifts between kelp forest and barrens states do not offer direct evidence for alternative stable states but can provide information about drivers of transitions and the potential stability of sea urchin barrens. Likewise, long-term reports of sea urchin barrens that occur within the range of kelp distribution, but without documented phase shifts, can provide information about the global prevalence and stability of the barrens state.

In the Northeast Pacific, along the coast of British Columbia, Canada, phase shifts from sea urchin (*Strongylocentrotus franciscanus*) barrens to kelp forests (*Nereocystic luetkeana*) were documented following the reintroduction of sea otters in the late 1960s (Breen et al. 1982) and their subsequent range expansion in the 1980s and 1990s (Watson & Estes 2011). Coastal surveys from 1987 to 2009 showed that kelp forests occurred in areas with continuously high abundances of sea otters, whereas urchin barrens were found in areas where otters were absent (Watson & Estes 2011). According to local fishermen, parts of the coast were urchin barrens for decades prior to sea otter re-introduction (Breen et al. 1982). A localized phase shift from kelp forests to urchin barrens also was documented off British Columbia when destructive grazing by sea urchins *S. droebachiensis* removed a kelp forest (Foreman 1977).

In the Northwest Pacific, a similar transition from barrens to a kelp state occurred when sea otters re-colonized the Commander Islands in Russia, reducing sea urchin *Strongylocentrotus polyacanthus* densities and enabling the reestablishment of kelp beds (*Saccharina dentigera*) (Oshurkov et al. 1988). On the east coast of Japan, sea urchins *Strongylocentrotus nudus* caused a phase shift from kelp forest (*Undaria pinnatifida* and *Laminaria japonica*) to barrens in Ogatsu Bay in the 1990s and prevented kelp regrowth for over 11 yr (Tamaki et al. 2005, 2009). Along the west coast of Hokkaido, Japan, sea urchins were documented overgrazing the kelp forest in the 1930s, and formed extensive coralline barrens by the 1960s (Matsunaga et al. 1999, Fujita 2010, Graham 2010). These barrens are most common in areas with low water movement and have been reduced in some areas by harvesting and remediation (sea urchin removal) efforts (Fujita 2010).

In the Southeast Pacific, stable sea urchin (*Tetrapygus niger*) barrens, interspersed with patches of kelp (*Macrocystis integrifolia* and *Lessonia trabeculata*), extend along much of the 2000 km of coastline of northern Chile (Vásquez & Buschmann 1997). The resilience of these barrens has likely been increased by unregulated macroalgal harvesting that targets kelp (Vásquez 2008). In southern Chile, only a few localized barrens, maintained by sea urchin *Loxechinus albus* grazing, have been reported within large tracts of kelp forest (Dayton 1985). Throughout most of this region, sea urchins passively consume drift kelp and do not actively graze kelp stands (Vásquez et al. 1984).

In the Northwest Atlantic, extensive *Strongylocentrotus droebachiensis* barrens exist along the western, eastern and southern coasts of Newfoundland and southern coast of Labrador, Canada (Keats 1991). Observations of barrens in these regions span periods of 40 yr, among the longest on record. Although phase shifts to kelp have not been documented in these areas (Keats 1991), kelp beds (*Saccharina latissima*) occur in some protected bays adjacent to barrens (Hooper 1975, Keats et al. 1990). Sea urchin removal experiments in Newfoundland showed that macroalgae colonized barrens, but low-lying beds of the brown alga *Desmarestia aculeata* often dominated the assemblage instead of kelp (Keats et al. 1990). In contrast, the majority of the Greenland coast appears to be largely kelp-dominated (*Saccharina* spp.), with dense patches of *S. droebachiensis* observed in some regions (Krause-Jensen et al. 2012). Blicher (2010) described a sea urchin barrens spanning 200 m along the east coast of Greenland, within a protected fjord in the Godthåbsfjord system.

In the Northeast Atlantic, Hjörleifsson et al. (1995) documented sea urchin fronts that emerged from deeper water to graze a kelp bed (*Laminaria hyperborea*) and form barrens in Iceland. Along the northern coasts of Norway and western Russia, approximately 2000 km of kelp beds (*L. hyperborea*) were destructively grazed in the early 1970s, and sea urchin (*Strongylocentrotus droebachiensis*) barrens have persisted for almost 40 yr (Propp 1977, Sivertsen 1997, Norderhaug & Christie 2009). Long-term monitoring of a localized sea urchin (*Paracentrotus lividus*) barrens in Lough Hyne, Ireland, captured a transition to large brown algae (*Cystoseira foeniculacea* and *Sargassum muticum*) in the 1990s that persisted for at least 10 yr (Kitching 1987, Trowbridge et al. 2011). Declines in sea urchin populations within the lough may have been due to disease or predation (Trowbridge et al. 2011).

In the Mediterranean, along the Albères coast in Southern France, 20 km of macroalgal beds (*Cystoseira* spp.) collapsed to barrens in the 1970s and have not recovered (Thibaut et al. 2005). The possible causes included overfishing of sea urchin

Paracentrotus lividus predators and the recent prohibition on sea urchin collection (Thibaut et al. 2005). In the Adriatic Sea, transitions from macroalgal beds (*Cystoseira amentacea*) to stable (9 yr) sea urchin (*P. lividus*) barrens have occurred along 200 km of coastline (Fanelli et al. 1994, Guidetti et al. 2002, Guidetti et al. 2003). These shifts are attributed to the destructive date mussel fishery, which breaks apart reefs, increasing the availability free space and small spatial refugia. This enhances settlement and recruitment rates of sea urchins, resulting in higher urchin densities on impacted reefs (Guidetti et al. 2003). Management of the fishery enabled macroalgae to recolonize some areas, but urchin barrens persist along most of the coast. *Paracentrotus lividus* barrens also have been described amid macroalgal-dominated (*Cystoseira* spp.) reefs in the Aegean Sea off the coast of Greece (Giakoumi et al. 2012).

In the Southwest Pacific, urchin barrens have been documented in Eastern Australia and New Zealand. In New South Wales, Australia, about 50% of 2000 km of rocky coastline exists in a stable sea urchin (*Centrostephanus rodgersii*) barrens state (Andrew and Underwood 1989, Andrew & Underwood 1993, Andrew & Byrne 2007, Connell & Irving 2008, Gladstone & Masens 2009). Small-scale experimental removals of sea urchins from these barrens caused a shift to macroalgal-dominated habitats (*Ecklonia radiata*) (Fletcher 1987). Along the coasts of New Zealand, urchin barrens have been documented throughout kelp forests (*E. radiata*) (Shears & Babcock 2007). In northern New Zealand, the benthos at 6–8 m depth is dominated by sea urchins *Evechinus chloroticuon* on coralline algal crusts and has persisted for at least 10 yr (Schiel 1990). Establishment of a marine reserve in this region resulted in phase shifts from urchin barrens to kelp forests that were attributed to an increase in fish and invertebrate predators of sea urchins (Leleu et al. 2012).

Notwithstanding the numerous examples of urchin barrens worldwide, the extent of phase shifts to barrens has in some cases been overstated or exaggerated in the literature. Past reviews have described entire coastlines that alternate between kelp beds and sea urchin barrens, or coastal regions that have remained in a kelp-bed state for thousands of years prior to overfishing (e.g. Steneck et al. 2002). What the evidence actually shows is that 10s to 100s of km of temperate coastline in regions around the world, at depth ranges between wave-swept shallows and light-limited deeper waters, can transition between a stable barrens state and a kelp- or macroalgal-dominated state (Table 2.2). The only data on kelp systems older than 200 yr come from a handful of midden sites in Alaska, California and Maine (Erlandson et al. 1996, Bourque et al. 2008, Erlandson et al. 2008). Although these findings contribute greatly to our understanding of the dynamics of kelp ecosystems (Steneck et al. 2002), they cannot be used to make broad conclusions about the historical state of kelp or barrens ecosystems throughout the world. Furthermore, much of the research on kelp beds and sea urchin barrens comes from well-studied areas, where attention was initially directed to high urchin densities or dramatic ecosystem shifts. As researchers continue to return to regions where barrens have previously been documented, we may be left with a lopsided view of the scale and importance of transitions. Fig. 2.4 shows large spans of coastal kelp regions where sea urchin barrens have not been documented, mainly due to the lack of research. This indicates the need for a broader perspective to accurately assess the worldwide extent of sea urchin barrens.

2.6. THRESHOLDS FOR PHASE SHIFTS AND STATE STABILITY

Field observations or sea urchin removal and transplantation experiments in Alaska, California, Chile, Nova Scotia, Norway and Tasmania provide estimates of thresholds of urchin density or biomass for phase shifts. These studies consistently show that the threshold required to initiate destructive grazing is much greater than that which enables kelp recovery (Table 2.3). This difference between thresholds for forward and reverse shifts indicates hysteresis in these dynamics and provides strong evidence of discontinuous phase shifts between alternative stable states. The percentage decrease in the threshold biomass of sea urchins between forward and reverse shifts ranged from 77 to 91% in these regions. Threshold densities varied markedly among regions, reflecting differences in body size of the dominant sea urchin species, while biomass thresholds were relatively consistent, with order of magnitude differences between forward shifts to barrens (1–3 kg m^{-2}) and reverse shifts to kelp beds (0.1–0.6 kg m^{-2}). Thresholds for phase shifts can vary locally with changes in hydrodynamic conditions. Strong wave action can inhibit aggregative feeding behaviour of sea urchins by limiting their ability to climb kelp stipes and anchor blades (Lauzon-Guay & Scheibling 2007c). Experimental transplantation of sea urchins in kelp beds in Alaska and Nova Scotia showed that the density threshold for destructive grazing was lower within kelp beds than along the kelp–barrens interface at the edge of beds, where wave action is greater (Konar & Estes 2003, Feehan et al. 2012). The biomass of kelp also can directly influence the threshold urchin biomass for destructive grazing and a shift to barrens (Lauzon-Guay & Scheibling 2007a, Lauzon-Guay et al. 2009).

Once threshold urchin densities are attained, phase shifts between kelp beds and barrens are relatively abrupt. Destructive grazing creates positive feedback mechanisms that accelerate the shift to barrens. Actively grazing sea urchins have unlimited, high quality food, which enables them to grow rapidly and allocate a large amount of energy to reproduction (Meidel & Scheibling 1998). Because highly fecund sea urchins are aggregating in high densities, fertilization rates are maximal (Meidel & Scheibling 2001, Lauzon-Guay & Scheibling 2007b), which likely increases larval supply and recruitment to barrens on regional scales. Similarly, when sea urchin densities in barrens drop significantly, the release from grazing triggers an immediate response: filamentous algae and diatoms appear within days of urchin removal, and kelps recruit and grow into canopies within 1 to 3 yr (Duggins 1980, Harrold & Reed 1985, Johnson & Mann 1988, Tegner et al. 1997, McNaught 1999, Konar & Estes 2003, Ling 2008, Ford & Meux 2010, Watanuki et al. 2010, Watson & Estes 2011).

There are 2 types of feedback mechanisms that stabilize the community assemblage in the barrens state: processes that reduce kelp recruitment on barrens and processes that allow sea urchins to maintain high densities on barrens (Fig. 2.6). Sea urchins in barrens prevent kelp recruitment by continually scraping coralline algal crusts, consuming the surficial layers along with any microalgal films and macroalgal recruits (Chapman 1981). This reduces the survival of kelp sporophytes in barrens (Jones & Kain 1967). Sea urchin exclusion experiments in the Gulf of St. Lawrence, Canada, found that kelp recruitment was 100 times higher on barrens without urchins than on barrens with urchins (Gagnon et al. 2004). In widespread barrens, the urchin-dominated state may be further stabilized by a lack of reproductive source populations of kelp that provide spores for recruitment (Keats 1991). Kelp spores are short-lived and typically settle within 5 to 10 m of the parent plant (Norton 1992, Gaylord et al. 2012), although maximum dispersal distances of up to 5 km have been measured for some species (e.g. *Laminaria hyperborea*, Norton 1992; *Macrocystis pyrifera*, Gaylord et al. 2006). In Nova Scotia, barrens adjacent to shallow stands of reproductive kelp sporophytes re-established kelp beds within 18 mo following urchin mass mortality, whereas it took 4 yr for kelp beds to recover on barrens that were 3 km away from the nearest reproductive kelps (Johnson & Mann 1988). Likewise, sea urchin removal experiments conducted within extensive barrens off Newfoundland, Canada, did not result in colonization by kelp after 3 yr, because the nearest reproductive kelps were several kilometers away from the removal plots (Keats 1991, Keats et al. 1990). This effect may be mitigated in barrens where a few remaining sporophytes are exposed to elevated light, nutrients and currents, which can result in greater fecundity. In the Aleutian Islands, individual sporophytes of *Eualaria fistulosa* in barrens produced 3 times more spores than individual sporophytes in adjacent kelp forests (Edwards & Konar 2012). In California, some kelp species form free-floating rafts that can disperse spores over great distances and may mitigate the loss of reproductive sporophytes in widespread barrens (Hobday 2000).

Despite the lack of kelp and other fleshy macroalgae as food sources, sea urchins can maintain high densities on barrens by allocating fewer resources to reproduction and growth, undergoing morphological changes in their body wall (Edwards & Ebert 1991), and reabsorbing parts of their body wall or gut (Pearse et al. 1970). High densities of sea urchins in barrens can offset decreased individual reproductive output, enabling populations to sustain moderately high fertilization rates and contribute to the larval pool

(Lauzon-Guay & Scheibling 2007b). However, since sea urchins have a planktonic larval stage of 2–3 mo and can disperse distances of up to 100 to 1000 km (Huggett et al. 2005), any positive impact of a larger larval pool on sea urchin settlement would likely be limited to large-scale barrens (100s of km).

Settlement of sea urchins in barrens is enhanced by a chemical cue associated with coralline algae that induces settlement and metamorphosis of sea urchin larvae (Pearse & Scheibling 1990). Therefore, by preventing kelps and other fleshy or filamentous macroalgae from overgrowing and outcompeting corallines, sea urchin grazing in barrens facilitates the supply of new individuals to the population (Miner et al. 2006, Hernández et al. 2010). Baskett & Salomon (2010) generated discontinuous phase shifts between barrens and kelp beds in a model that incorporated sea urchin grazing on kelp, competition between kelp and coralline algae, and facilitation of sea urchin recruitment by coralline algae. Sea urchins in barrens likely experience lower post-settlement mortality due to predation compared with kelp beds, which also acts to increase recruitment and stabilize a barrens state. The low structural complexity of barrens, compared with the 3-dimensional structure of kelp beds, limits available habitat for predators of sea urchins, such as decapod crustaceans and fish (Levin 1994, Konar & Estes 2003, Gianguzza et al. 2010), including those that prey on the early juvenile stages (Hacker & Steneck 1990, Bonaviri et al. 2012).

The decrease in kelp cover during a shift to the barrens state reduces the supply of kelp detritus both to shallow kelp bed (Ebeling et al. 1985) and to adjacent habitats in deeper regions (Vanderklift & Kendrick 2005, Krumhansl & Scheibling 2011a). Resident sea urchins in kelp beds, like those in deeper regions, generally feed passively on drift kelp (Harrold & Reed 1985, Filbee-Dexter & Scheibling 2012). When this subsidy declines, urchins emerge from shelters to actively graze attached kelp and augment populations in barrens, providing another form of feedback that can stabilize the barrens state.

A healthy kelp bed is maintained by various feedback mechanisms that prevent the increases in sea urchin density that lead to destructive grazing and the formation of barrens (Fig. 2.6). Algal films and understory algae inhibit settlement of sea urchin larvae by reducing the availability of open space on rocky substrata (Trowbridge et al. 2011). High levels of predation on juvenile urchins in kelp habitats compared with barrens limits recruitment (Tegner & Dayton 1981, Leinaas & Christie 1996, Scheibling 1996). Sea urchins within kelp beds often are cryptic, sheltering in spatial refuges from predators (e.g. crevices, undersides of boulders, and kelp hodlfasts); few reach a size refuge from all but the largest predators (Scheibling & Hamm 1991, Clemente et al. 2007).

The physical structure of kelp beds also can prevent sea urchin grazing. The wave-driven whiplash and sweeping motion of large kelps impedes urchins from moving into kelp beds (Vásquez 1992, Konar 2000, Tamaki et al. 2009). In experimental kelp removals in Alaska, Konar & Estes (2003) showed that sea urchins advanced beyond the deep margins of kelp forests (at 8–13 m depth) when kelp was removed but not when kelp was replaced with physical mimics, indicating that the sweeping motion of kelp arrested the onshore advance of grazing aggregations. Dislodgment of sea urchins may also be higher in kelp beds compared with barrens. In a laboratory study using a flume, Kawamata (2010) showed that sea urchins attached to turf algae stopped actively moving and were dislodged at lower water velocities than when attached to bare rock.

The high production of detrital material within kelp beds (Krumhansl & Scheibling 2012b) provides an important subsidy for resident sea urchins (Harrold & Reed 1985) and offshore populations (Britton-Simmons et al. 2009, Filbee-Dexter & Scheibling 2012). This reliance on passive detrivory lowers grazing intensity on attached kelp (Day & Branch 2000) and likely reduces adult migration into kelp beds. In contrast, detrital subsidy from a highly productive kelp state can also enhance reproductive output of offshore sea urchin populations (Britton-Simmons et al. 2009, Filbee-Dexter & Scheibling 2014a), which could increase the larval pool and, consequently, settlement of sea urchins in the kelp bed.

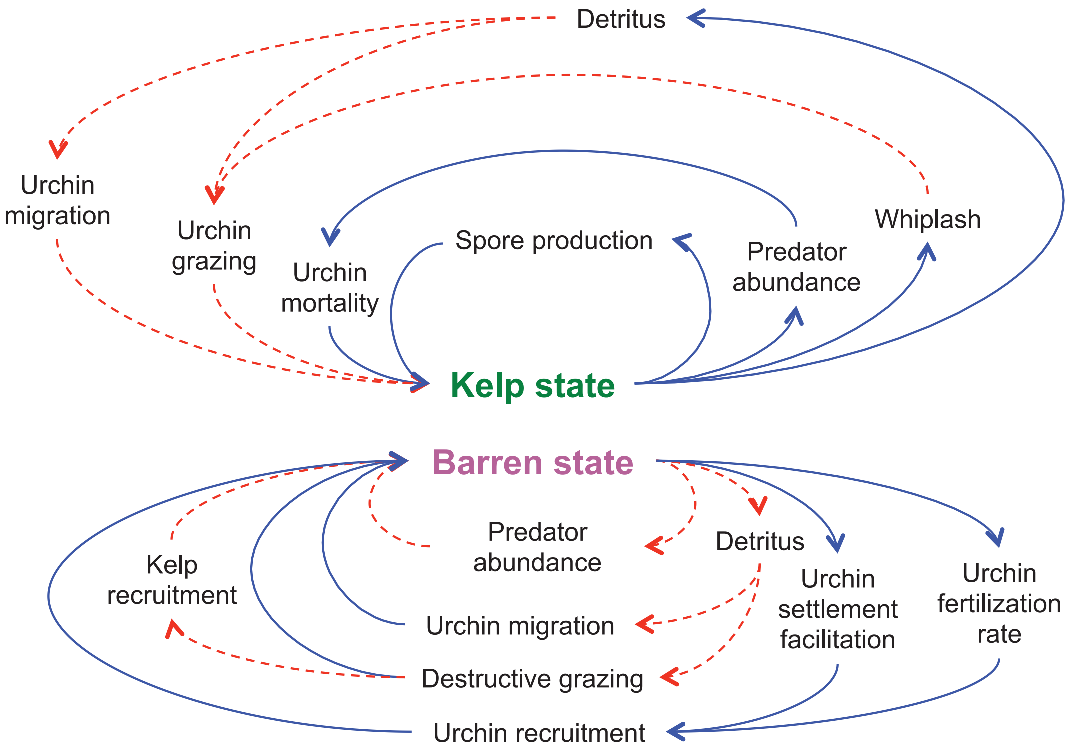


Fig. 2.6. Stabilizing feedback mechanisms for the kelp-bed and sea urchin barrens states. Blue (solid line) is positive and red (dashed line) is negative feedback; 2 sequential negative feedbacks indicate an indirect positive feedback.

2.7. ARE SEA URCHIN BARRENS AN ALTERNATIVE STABLE STATE?

With some exceptions, sea urchin barrens generally result from discontinuous phase shifts and therefore are considered an alternative stable state of kelp ecosystems (Table 2.2). Phase shifts between kelp beds and sea urchin barrens show evidence of hysteresis after a transition (Table 2.3), and both the kelp and barrens states are stabilized by numerous feedback mechanisms and are resistant to small perturbations or fluctuations in sea urchin densities. Sea urchin barrens can persist for decades and exist under environmental conditions similar to those of kelp beds. Most shifts to barrens are driven by localized changes in state variables and parameters and as such are not a part of a larger oceanic regime shift linked to climate change or climate oscillations. Exceptions are the phase shifts observed in Tasmania and California that are caused by changing ocean currents. The rapidly changing ocean temperature in Tasmania due to the increased southern penetration of the Eastern Australian Current may constitute an oceanic regime shift (Johnson et al. 2011). Likewise, periodic changes in coastal upwelling in California due to the El Niño-Southern Oscillation also may represent an oceanic regime shift (Tegner & Dayton 1987, Dayton & Tegner 1990).

We find little evidence supporting prior arguments that human-induced shifts between kelp beds and barrens constitute continuous phase shifts that are maintained by ongoing anthropogenic impacts (Connell & Sousa 1983, Petraitis & Dudgeon 2004). In ecosystems where human perturbations cause phase shifts, hysteresis still occurs and the alternative state persists after the human control is relaxed (Tables 2.2, 2.3). However, human activities such as moratoria on otter hunting, expanding sea urchin fisheries, or continued depletion of groundfish are likely increasing the occurrence of phase shifts in kelp ecosystems (Scheffer et al. 2001, Knowlton 2004). The dramatic changes in sea urchin densities that are required to trigger phase shifts may be difficult to achieve through natural causes but could readily occur through strong anthropogenic perturbations (Knowlton 2004). Given that humans are increasingly impacting ocean ecosystems globally, the implications of human perturbations in triggering phase shifts in kelp ecosystems are of growing concern.

In kelp ecosystems that exhibit alternative state dynamics, the recovered community state often differs from the state that existed prior to a collapse. For example, in Maine, the groundfish associated with kelp beds in the 1930s and subsequently depleted by coastal fisheries were not re-established with the return to the kelp state in the 1990s (Steneck et al. 2004). In California, the sheepshead fish and lobster populations that controlled sea urchins in kelp forests in the 1930s did not recover in kelp forests in the 1970s (Dayton et al. 1998). In the Aleutian Islands, sea otter populations in re-established kelp forests are encountering a new agent of mortality in the form of killer whale predation (Estes et al. 1998, Tegner & Dayton 2000). In the last 3 decades, climate change has been implicated in lowering recruitment of sea urchins in Norway (Fagerli et al. 2013, increasing the frequency of disease outbreaks that cause mass mortality of sea urchins in Nova Scotia (Scheibling et al. 2013), and modifying currents that have expanded the range of sea urchins into Tasmania (Johnson et al. 2011). The escalating influences of humans in each of these regions may be causing phase shifts to new, more deteriorated ecosystem states with fewer species, less biomass and increased levels of human impact, rather than alternations between 2 persistent community configurations. Although human perturbations may be altering the resilience of these communities, they still exhibit broad domains of attraction in both the kelp-dominated and urchin barrens state, which allows their classification as alternative stable-state systems.

2.8. IMPLICATIONS FOR MANAGEMENT OF KELP-BASED ECOSYSTEMS

Given that phase shifts to barrens often are considered as manifestations of the collapse of a kelp-based ecosystem, various strategies have been attempted to recover the productive kelp state. By definition, system recovery can be challenging after a discontinuous phase shift because of hysteresis, making it difficult to reverse a collapse (Scheffer et al. 2001). Even so, some forms of management, particularly those focused on controlling populations of urchin predators, have been effective in restoring kelp forests. Actions to re-establish populations of the sea otter *Enhydra lutris*, considered a keystone species in the North Pacific for its cascading effects on kelp abundance (Paine 1969), provide an early example of this strategy. Historical moratoria on sea otter hunting effectively restored populations in eastern Russia, western Alaska and California, and together with sea otter translocations across the eastern Pacific, led to the recovery of kelp forests in many regions (Estes & Palmisano 1974, Breen et al. 1982). Currently, sea otter populations are declining because of oil spills (Bodkin et al. 2002), disease (Kannan et al. 2006) and killer whale predation (Doroff et al. 2003). Wilmers et al. (2012) proposed that proper otter conservation strategies would maximize kelp forest abundance in the northeast Pacific and create an important carbon sink.

The establishment of marine reserves also can restore predator populations and recover the kelp state. In New Zealand, increased lobster and predatory fish populations, and substantial re-growth of kelp, was documented in marine protected areas compared with unregulated areas (Babcock et al. 1999, Shears & Babcock 2003, Shears et al. 2006, Leleu et al. 2012). In the Adriatic Sea, the percentage cover of barrens was lower in marine reserves where fishing prohibitions are strictly enforced than in unmonitored areas where poaching occurs (Guidetti et al. 2003). In Tasmania, marine reserves increased spiny lobster populations and maintained the kelp state by limiting the potential for destructive grazing by sea urchins through higher predation rates (Ling & Johnson 2012). However, the effectiveness of such protection strategies can be limited. In Tasmania, a large-scale experimental introduction of thousands of spiny lobsters into both widespread barrens and patchy barrens amid kelp beds resulted in no increase in kelp cover in widespread barrens and only a small increase in kelp cover in patchy barrens (S. D. Ling pers. comm.). This indicates that the barrens state is extremely resilient to kelp recovery (Marzloff et al. 2013), and only preventative management to increase the resilience of the kelp-bed state may be effective in halting phase shifts to barrens.

Judicious management of fisheries may recover kelp assemblages. Sea urchin fisheries in Maine and California have reduced sea urchin densities below thresholds that maintain barrens, enabling a reverse shift to a kelp-dominated state (Tegner & Dayton

1991, Steneck et al. 2004). In Nova Scotia, the sea urchin fishery manages the stock by targeting the grazing front at the deep edge of a kelp bed (Miller & Nolan 2000). This halts or slows the advance of fronts until trailing sea urchins in the barrens encounter the kelp and re-establish aggregations, allowing for a sustainable harvest (Miller & Nolan 2000). In California, commercial kelp harvesters prevented sea urchin grazing fronts from advancing into kelp forests using quick lime, before the establishment of an urchin fishery (North 1971). In Japan, artificial reefs have been suspended above the substratum on buoyed arrays to exclude sea urchins, resulting in the recovery of kelps for commercial harvest (Tamaki et al. 2009).

An unexplored strategy for conserving the kelp state could involve managing human impacts that affect feedback mechanisms in kelp systems. For example, minimizing kelp harvesting or coastal sedimentation due to runoff would increase kelp biomass. This would increase the supply of drift kelp, which could prevent behavioural switches to active grazing in resident sea urchins. Similarly, seeding barren areas with reproductive kelp fronds could enhance kelp settlement in regions with limited spores. A better understanding of the feedback mechanisms that stabilize the barrens state may help inform management strategies.

Two major challenges face effective management of kelp-bed and barrens ecosystems. First, management strategies require a clear understanding of individual ecosystems, as the relative importance of stabilizing mechanisms and drivers of state shifts can vary with species composition, trophic interactions, functional redundancy and environmental conditions that are unique to each system. Successful management of barrens has mainly been limited to well-studied systems where the drivers of transitions are well understood. Further research is needed in other regions of the kelp range, such as South America, Africa, Asia and the Arctic. Second, it is not possible to manage phase shifts resulting from environmental changes, such as warming oceans, increased storm severity, and altered currents (Ebeling et al. 1985, Ling 2008, Harley et al. 2012, Scheibling et al. 2013). These changes may be mitigated to some extent by maintaining high biodiversity and species richness within kelp beds (Folke et al. 2004), as phase shifts to barrens tend to be more common in systems with low trophic complexity and low functional redundancy (Steneck et al. 2002). However, future impacts of climate change on these ecosystems greatly exceed the management capacities of coastal areas and would require a larger global initiative that prevents further environmental change in ocean ecosystems.

2.9. PERSPECTIVES FOR FUTURE RESEACH

Kelp forests or beds are complex ecosystems that have the potential to drastically change in terms of both structure and function through phase shifts to sea urchin barrens. To fully understand whether barrens represent an alternative stable state of kelp ecosystems, further longitudinal studies of kelp and barrens communities are required. Manipulative field experiments typically provide the strongest evidence of alternative stable states and can be used to elucidate thresholds for state shifts as well as system-specific feedback mechanisms that can stabilize both kelp and barrens states. For example, sea urchin removal experiments not only indicate the potential macroalgal community that can develop within barren grounds but also can be used to quantify thresholds for recovery of the kelp state. Long-term monitoring programs and statistical models are also useful in evaluating the stability and organization of different ecosystem states (Johnson et al. 2013, Marzloff et al. 2013). A major source of uncertainty in kelp and barrens ecosystems is the period between sea urchin larval release and settlement. In the majority of these ecosystems, the fate of larvae produced by resident populations in barrens, kelp beds or nearby deep areas is largely unexplored and likely plays an important role in both driving density-induced phase shifts and stabilizing the barrens or kelp state.

There are several trends in the global occurrence of sea urchin barrens that may warrant further research. It is unclear why barrens dominate throughout eastern Canada, western Russia and northern Norway but are rarely documented along the coasts of Greenland and Iceland, regions with similar species composition and environmental conditions. Sea urchin barrens also tend to be more widespread and phase shifts occur more frequently along temperate coasts in the northern hemisphere than along tropical and south temperate coasts. The trend of increasing marine species richness and ecosystem complexity from the Arctic to the tropics (Gray 2001) may explain this discrepancy because the more simplified food webs in temperate ecosystems may collapse more readily. Southern kelp beds also occur in upwelling zones, which may have altered feedbacks and dynamics compared with temperate ecosystems.

Considerable attention has been directed towards establishing criteria for defining an alternative stable state (Connell & Sousa 1983, Beisner et al. 2003, Petraitis & Dudgeon 2004). However, in a practical sense, regardless of whether phase shifts between kelp beds and barrens reflect an actual alternative stable-state system, the barrens state typically exhibits multiple feedback mechanisms that can inhibit kelp recovery for decades. As Knowlton (2004) aptly observed, in the context of marine conservation, it probably makes little difference in human time scales if sea urchin barrens persist indefinitely; what matters is that the system can undergo a long-term departure from prevailing conditions that is difficult to reverse.

2.10. ACKNOWLEDGEMENTS

We thank A. Metaxas, S. Ling, C. Feehan, K. Krumhansl, S. Walde and H. Whitehead for helpful comments on earlier drafts of the manuscript. This research was funded by a Discovery Grant to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F.-D. was supported by a Dalhousie Killam Scholarship and an NSERC Canada Graduate Scholarship.

CHAPTER 3

HURRICANE-MEDIATED DEFOLIATION OF KELP BEDS AND PULSED DELIVERY OF KELP DETRITUS TO OFFSHORE SEDIMENTARY HABITATS

The work presented in Chapter 3 also appears in:

Filbee-Dexter K, Scheibling RE (2012) Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. Mar Ecol Prog Ser 455:51–64.

3.1. ABSTRACT

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

3.2. INTRODUCTION

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

Kelp beds in the Northwest Atlantic are composed of prostrate kelps, such as *Laminaria digitata* and *Saccharina longicruris* (Adey & Hayek 2011). Although the impact of extreme storm events on these kelp beds has not been documented, substantial losses of kelp biomass are expected to reduce primary production and biogenic habitat, which in turn would affect food web structure and energy flow to higher trophic levels (Wharton & Mann 1981). The sea urchin *Strongylocentrotus droebachiensis* is the dominant herbivore in kelp beds in the Northwest Atlantic and plays a pivotal role in determining community structure (Scheibling & Hatcher 2007). At high population densities, sea urchins destructively graze kelp beds, causing a shift to a barren state in the rocky subtidal zone (Mann 1977, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a). These kelp beds are re-established following periodic outbreaks of disease that eliminate sea urchins at shallow depths (<25 m) (Scheibling 1986, Johnson & Mann 1988). Deeper-living sea urchins persist in a thermal refuge from disease and provide larval recruits to the emergent kelp beds or form grazing aggregations along the lower margin of the beds, which drives the transition back to sea urchin barrens in this alternative stable-state system (Scheibling 1986, Lauzon-Guay et al. 2009). Particulate kelp detritus is continuously generated through the natural erosion of blades (Krumhansl & Scheibling 2011a) and the production of sea urchin feces (Sauchyn & Scheibling 2009a). Severe storm events could generate pulses of large detrital fragments and whole thalli that are likely an important food source for deeper-living sea urchins and other detritivores (Britton-Simmons et al. 2012, Kelly et al. 2012). Laminarian kelps are a preferred food of *S. droebachiensis* that maximizes growth and reproduction (Scheibling & Hatcher 2007), and the nutritional value of detrital kelp is enhanced through nitrogen enrichment during microbial decomposition (Norderhaug et al. 2003, Sauchyn & Scheibling 2009b) and the accumulation of a diverse epifaunal assemblage (Krumhansl & Scheibling 2012a).

Detrital subsidies have been documented in other kelp ecosystems, although these studies are few and geographically limited and the role of storm events in the creation and transport of detrital material remains largely unexplored (Krumhansl & Scheibling 2012b). In Western Australia, detrital exports from kelp beds subsidize adjacent sea grass beds (Wernberg et al. 2006, Vanderklift & Wernberg 2008). In the Chilean intertidal zone, sea urchins preferentially feed on drift kelp, which enables them to develop even larger gonads than sea urchins that feed only on attached kelp (Rodriguez 2003). Off Washington State (USA), sea urchins inhabiting barrens in the shallow subtidal zone below a kelp bed rely heavily on a drift kelp subsidy and have a similar reproductive output as sea urchins within the kelp bed (Britton-Simmons et al. 2009). Off southern California, detritus exported from both a kelp forest and sea grass beds increases secondary production in adjacent habitats and is flushed by fall storms into a deep canyon, where it provides an energy subsidy for benthic communities at even greater depths and distances from the source of primary production (Vetter 1998, Vetter & Dayton 1999).

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

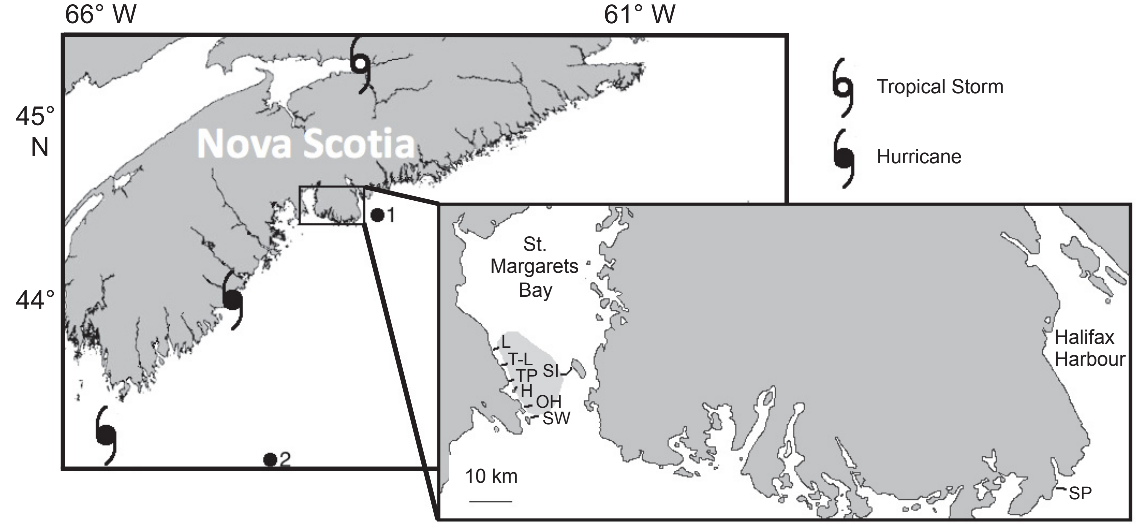


Fig. 3.1. Map of Nova Scotia showing track of Hurricane Earl on 4 Sept 2010 and study sites in St. Margarets Bay (L = The Lodge. T-L = Tilly-Lodge. TP = Tilly Point. H = Horse Island. OH = Owl's Head. SW = Southwest Island. SI = Shut- in Island) and off the headland at Splitnose Point (SP). Shaded area is a deep sedimentary basin (> 60 m depth) in St Margarets Bay. (•1) Halifax Harbour buoy; (•2) Lahave Bank buoy.

3.3. MATERIALS AND METHODS

3.3.1. Study sites and sampling design

To measure the effect of a severe storm on canopy loss in kelp beds and the deposition of detached blades and thalli, we sampled a series of sites along a gradient of wave exposure within St. Margarets Bay and on an adjacent headland at Splitnose Point, near Halifax, Nova Scotia, before and after Hurricane Earl struck the coast on 4 September 2010 (Fig. 3.1). St. Margarets Bay is a large semi-protected embayment that is exposed to ocean swell from the south. The western shore of the bay is rocky and steeply shelves into a deep (70 to 100 m) sedimentary basin; the eastern shore is more gently sloped with scattered islands. The deepest regions of the bay have a sandy bottom and are surrounded by areas of gravel interspersed with boulders (Hughes et al. 1972). The rocky subtidal zone (0 to 20 m depth) of the bay is dominated by prostrate kelps (*Saccharina longicruris*, *Laminaria digitata*, and *Agarum clathratum*) and grades to sand at its lower limit (Mann 1977). Along the headland at Splitnose Point, the substratum grades from exposed bedrock ledges in the shallow subtidal zone (<20 m depth) (Lauzon-Guay & Scheibling 2007a) to boulder fields and sandy substrata in deeper regions. Kelps (*Alaria esculenta*, *S. longicruris*, and *L. digitata*) extend to depths of 20 m, depending on the extent of destructive grazing by sea urchins (Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007a,c).

Six sites along the western shore of St Margarets Bay (Southwest Island, Owl’s Head, Horse Island, Tilly Point, Tilly-Lodge, and The Lodge) and one site off a large island along the eastern shore of the bay (Shut-in Island) were surveyed with video transects on 1 (Southwest Island only), 13 and 18 (Owl’s Head only), and 31 August (Shut-in Island), prior to Hurricane Earl, and resurveyed on 13 and 26 September and 14 October 2010, after the storm (Appendix B: Table B1). Splitnose Point, on the headland near the western mouth of Halifax Harbour, was surveyed immediately before and after the hurricane, on 1 and 8 September, with 4 transects spaced at 100 m intervals alongshore (Appendix B: Table B1). To examine the persistence of deposits of drift kelp and the response of deep-living sea urchins to this food fall, video transects were also repeated at Southwest Island on 14 and 25 October 2010 and 5 February 2011 and at Owl's Head on 14 and 25 October 2010 and 5 February 2011.

3.3.2. Video transects

Our video transects ran perpendicular to the coastline from the mid-range to lower regions of the kelp bed to the operational depth of our equipment. At the start of the present study, our camera system reached 50 m depth; we upgraded our equipment on 1 October 2010, which extended the transects at Southwest Island and Owl's Head to 90 m (Fig. 3.2a, Appendix B: Table B1). A digital video camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search Equipment) was towed at an average speed of 1.8 km h^{-1} from a 7 m research vessel (RV Nexus). The position of the wing above the bottom was monitored using real-time video and manually maintained at a relatively constant height above the bottom (1 to 2 m) by adjusting cable length using an electronic winch. To aid in positioning the wing and to measure scale in video frames, 2 fixed lasers spaced 20 cm apart were trained on the bottom. The depth and position of the vessel was recorded using side-imaging sonar (1198c Side Imaging Sonar, Humminbird) and lagged by 9 s to account for positional offset between the wing and the sounder. The transects were resurveyed after the storm by following prior GPS tracks.

Video data were exported from iMovie (version 3.0.3, Apple) into ImageJ (National Institute of Health, USA) as frames (1 frame per 3 s of video record). For each video transect, we randomly sampled 12 frames in the kelp bed at 5 to 15 m depth and 30 frames below the kelp bed at 20 to 45 m depth at all sites except Horse Island and Shut-in Island. At the latter 2 sites, transects began below 15 m because of the steeply sloping bottom, and we sampled 12 frames in the kelp bed at 15 to 25 m and 30 frames below the kelp bed at 25 to 45 m. About 2% of frames were excluded from analysis because they were out of focus, taken high off the bottom, or poorly lit. These frames were replaced with other randomly selected frames. To determine the percentage of cover of attached kelp or detrital kelp deposits, we overlaid a grid of 104 points on each frame and recorded the presence of attached or detached kelp under each point. Approximately 0.6 to 2.0 m^2 of bottom area was captured in each frame. Sea urchins were counted in the same frames used for the detached kelp measurements at Southwest Island, Owl's Head, and Shut-in Island.

Substratum type was recorded continuously in all frames along each transect and categorized as (1) bedrock with attached kelp, (2) bedrock without attached kelp, (3) boulders, (4) sand and boulders, or (5) sand (Fig. 3.2b).

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

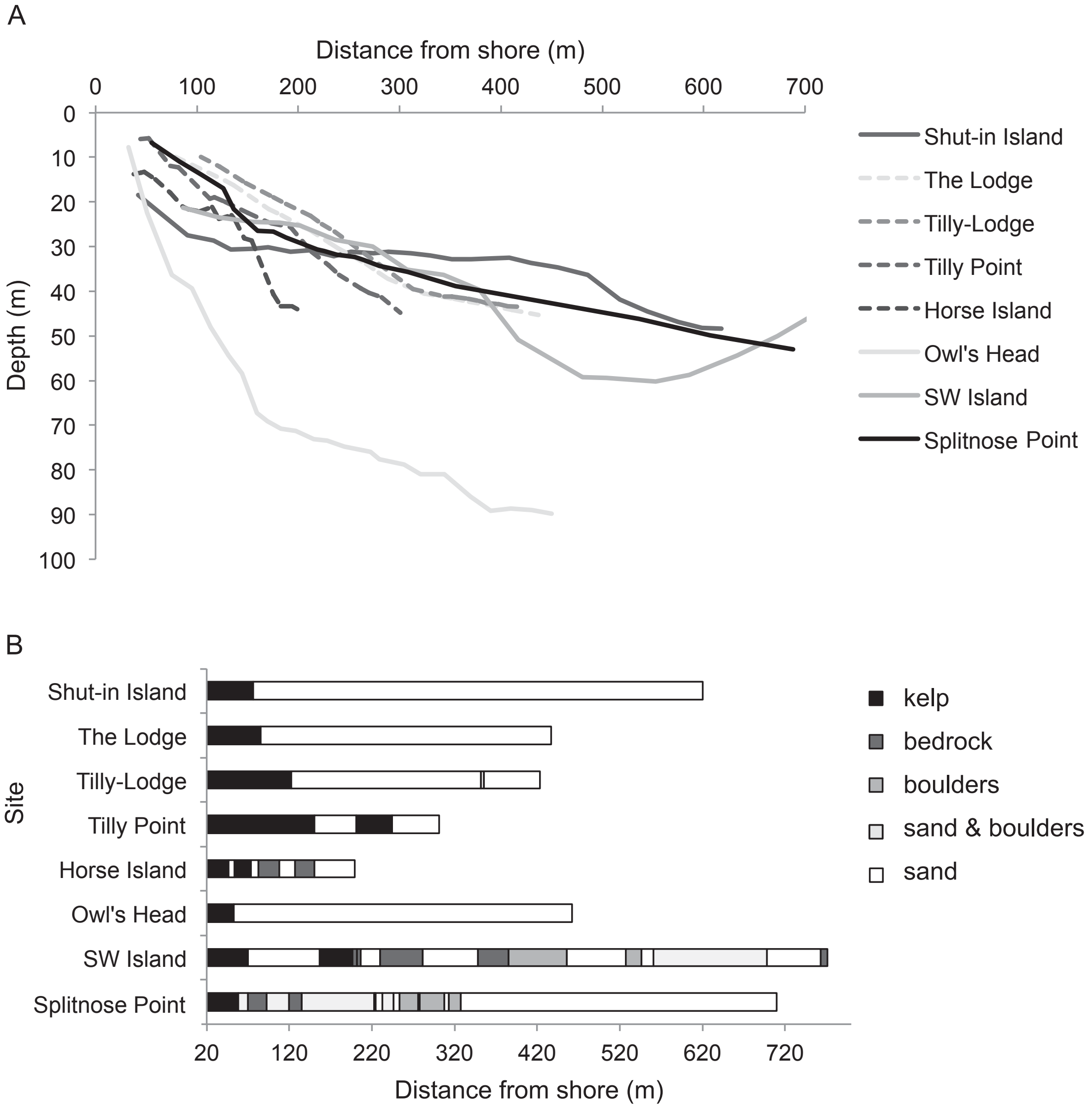


Fig. 3.2. a) Depth profile and (b) substratum type for video transects at study sites. Transects off Owl's Head and Southwest Island extended beyond 45 m due to equipment upgrades on 1 October 2010 that facilitated deeper data collection.

3.3.3. Wave and current measurements

Significant wave height data were obtained from meteorological buoys at Lahave Bank (42.500° N, 64.02° W) and Halifax Harbour (44.500° N, 63.40° W) from 1 August to 14 October (www.meds-sdmm.dfo- mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm). As an indicator of the change in bottom currents before and after the hurricane, we measured the wavelength (distance between successive wave crests) and direction (normal to the crests) of sand waves in video frames at Southwest Island using scaling lasers.

3.3.4. Wave exposure indices

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

We used linear regression to examine the effect of site exposure (observation-based rank) on the loss of kelp cover during the hurricane and the deposition of detrital kelp after the storm. Percentage cover data for attached and detrital kelp were averaged for all frames of the relevant video segments in each transect. Model II linear regression was used to examine the relationship between the amount of detritus deposited and the loss of kelp cover at sites within St. Margarets Bay.

3.3.5. Consumption of drift algae by sea urchins

We estimated the consumption of detrital kelp deposits by sea urchins *Strongylocentrotus droebachiensis* in a cage experiment on a sandy bottom in St. Margarets Bay. Initial camera surveys were used to identify a region off The Lodge where sea urchins were rare: only 2 ind. were observed along a 50 m transect extending parallel to shore at ~42 m depth. We deployed 4 cages (length × width × height: 1.5 × 0.5 × 0.5 m; mesh aperture: 4 × 4 cm) in a linear series at ~40 m intervals along this transect. Each cage contained 10 *Saccharina longicruris* thalli freshly collected from a kelp bed at 14 m depth at The Lodge and secured to the cage bottom with plastic cable ties around the base of the stipes. The total wet weight of kelp (3.31 to 4.13 kg per cage) was measured using a spring scale (1 g accuracy) immediately before deployment. The kelp density in cages was similar to natural densities observed at Splitnose Point, Southwest Island, Owl's Head, and Horse Island in St. Margarets Bay (Filbee-Dexter & Scheibling 2016). Two cages were supplied with 20 sea urchins (grazing treatment); the other 2 cages contained no sea urchins (autogenic control). Adult sea urchins (40 to 50 cm test diameter) were collected from barrens at 15 m depth off Pennant Point (a headland site near Splitnose Point) on 18 July 2011 and maintained in flowing seawater tanks in the laboratory prior to use in this experiment. Replicates of each treatment were randomly allocated to the 4 positions along the array. The cages were retrieved after 4 d, and the remaining kelp in each cage was re-weighed immediately with the spring scale to compare the mass loss in the grazing treatment (due to sea urchin grazing and kelp fragmentation) with that in the autogenic control (fragmentation only). In the laboratory, pre-weighed kelp fronds (3.19 kg) and 20 sea urchins (from the same collection used for the field experiment) were placed in a 1 × 0.6 m flowing seawater tank over the same 4 d period to measure grazing rate.

3.4. RESULTS

3.4.1 Kelp loss and drift algae deposition

Hurricane Earl made landfall near Lunenburg, Nova Scotia, as a Category 1 hurricane on 4 September 2010. The hurricane was associated with significant wave heights of 10 to 14 m (Fig. 3.3) and sustained wind speeds of 75 to 100 km h^{-1}. Weather buoys recorded maximum wave heights of 23.3 m off Halifax Harbour and 25.1 m on Lahave Bank. Large waves and pounding surf struck south- and southeast-facing coastlines, and the hurricane passed almost directly over our study area (Fig. 3.1). The waves reached the coast at low tide, exposing shallow kelp beds to extreme wave forces. Weather buoy recordings show that Hurricane Earl was a major wave event compared to normal wave activity during the autumn of 2010 (Fig. 3.3).

The hurricane was associated with a dramatic defoliation of the kelp bed at all of our sites, with the greatest losses of kelp cover at Splitnose Point, Tilly-Lodge, and Owl's Head (Fig. 3.4). The 2-way ANOVA showed a significant interaction of sampling period (before and after the storm) and site (Table 3.1). This result reflects an interaction in the magnitude of the effect and not the direction: post-hoc comparisons showed a significant decrease in kelp cover at each site before and after the hurricane (Bonferroni-adjusted *t*-test, $p < 0.017$). The kelp cover decreased from 71.0% before to 38.7% after the storm, when averaged across all sites; defoliation was greatest at Tilly-Lodge, where the cover declined from 74.7 to 21.2%. Following the hurricane, coralline and filamentous red algae, which were understory species within the intact kelp bed, dominated the algal cover on the rocky seabed. Observations by divers at Splitnose Point on 8 September confirmed the extent of damage to kelp beds along the headlands: the kelp canopy was stripped, with only stipes and torn blades remaining in shallower wave-swept areas (Fig. 3.5a,b), and there were large accumulations of kelp detritus both within the remnant kelp bed and in the rocky barrens below it.

The cover of drift algae increased in deeper habitats below the kelp beds after Hurricane Earl from 1.5% before to 3.4% after the storm, when averaged across all sites (Fig. 3.6). The 2-way ANOVA showed a significant interaction of sampling period and site (Table 3.1). This result also reflects variation in the magnitude of the effect across sites: post-hoc comparisons showed that detrital kelp cover significantly increased ($p < 0.007$) at Splitnose Point, Owl's Head and Shut-in Island; no significant change in detrital cover ($p > 0.048$) was detected at Southwest Island, Horse Island, Tilly-Lodge, and The Lodge. The increase in detrital cover at Tilly Point was marginally non-significant ($p = 0.011$); however, our test procedure was highly conservative (adjusted $\alpha = 0.010$). At Splitnose Point, large amounts of detritus accumulated amid boulders at the lower margin of the kelp bed and in crevices among bedrock outcrops (Fig. 3.5c), but drift kelp was infrequently observed in deeper sandy regions. In contrast, extensive deposits of kelp detritus occurred on the sandy bottoms off Southwest Island and Shut-in Island. Near the lower margin of the kelp bed at these sites, the seabed was carpeted with detached kelp fronds that formed dense patches covering areas of up to 200 m^2. Further from the kelp bed, at 20 to 40 m depth, the bottom consisted of uniform sand waves, which accumulated large quantities of drift kelp in the troughs (Fig. 3.5d). Sand waves at 30 m depth off Southwest Island had average wavelengths of 0.70 m oriented at 107° and 1.10 m oriented at 111° before (13 August) and after (13 September) Hurricane Earl respectively, indicating a 57% increase in wavelength with little change in direction following the storm. These sand waves graded to rocky substrata and sand with scattered boulders at ~45 m depth (Fig. 3.2b). At other sites in St. Margarets Bay, drift kelp was more uniformly deposited on sediment bottoms offshore of the kelp beds and did not form wave-rows or large patches. At Owl's Head, sea urchins aggregated on drift kelp, typically with 3 to 4 individuals on a blade fragment every 1 to 3 m along a transect. Similar aggregations of sea urchins were observed in deep sedimentary habitats off Shut-in Island, Southwest Island, Horse Island, and Tilly Point.

Linear regression indicated that wave exposure was not a good predictor of the loss of kelp cover during the hurricane at sites within St. Margarets Bay ($r^2 = 0.051$, $p = 0.443$) (Fig. 3.7a). However, there was a significant positive relationship between detritus accumulation below the kelp beds and site exposure ($r^2 = 0.934$, $p < 0.001$) (Fig. 3.7b). When Splitnose Point is included in these analyses, the results are qualitatively similar (kelp loss: $r^2 = 0.061$, $p = 0.594$; detritus gain: $r^2 = 0.714$, $p = 0.017$). The increase in detritus at a site was not significantly related to the loss of kelp cover at that site ($r^2 = 0.164$, $p = 0.184$) (Fig. 3.7c).

Table 3.1. Two-factor ANOVA of the effect of site and sampling period (before and after Hurricane Earl) on coverage (%) of attached kelp and kelp detritus.

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

3.4.2. Changes in sea urchin density and detrital deposits

Prior to Hurricane Earl, sea urchins were aggregated on drift algae on sand waves off Shut-in Island and Southwest Island. After the hurricane, sea urchins were no longer present on shallow sand waves (25 to 35 m depth) off Shut-in Island, where they previously occurred at an average density of 0.56 individuals m^{-2}, and the detritus cover on the sand waves increased to 4.6% from a pre-storm level of 0.7% (Fig. 3.6). Sea urchins also disappeared from sand waves off Southwest Island after the storm, and detritus cover (averaged across all frames in the sand-wave segment of video transects) increased to 6.8% from a pre-storm cover of 2.4%, with the greatest increase at 15 to 20 m depth (from 16.3 to 38.6%; Fig. 8). These detrital deposits were still evident on 25 October 2010 but had dissipated by 4 February 2011. Deeper regions off Owl's Head (45 to 80 m) showed an increase in detritus cover following Hurricane Earl that persisted to February 2011 (Fig. 3.8). Sea urchins on drift kelp at Owl's Head did not decline in density following the hurricane (Fig. 3.8). These sea urchins were not associated with sand waves and occurred at greater depths than those off Southwest Island (where the basin is shallower). Sea urchins also were present in the deep sedimentary regions off Horse Island and Tilly Point (53 to 85 m), although the urchins were more sparsely distributed than those at similar depths off Owl's Head, Southwest Island, and Shut-in Island. Off the headland at Splitnose Point, sea urchins were abundant (reaching densities of 200 ind. m^{-2}) on bedrock ledges at 15 to 25 m depth, both before and after the storm (1 and 8 September 2010).

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

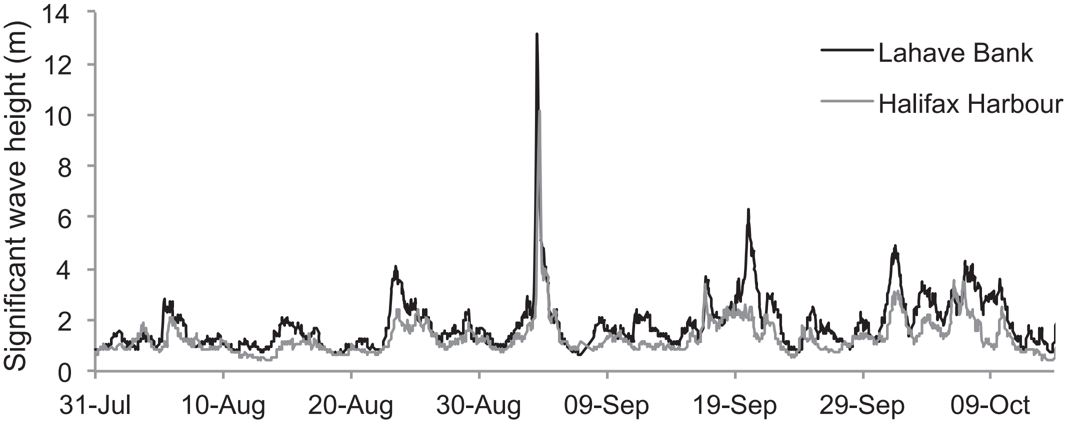


Fig. 3.3. Significant wave height recorded at Lahave Bank and Halifax Harbour buoys from 1 August to 15 October 2010. The peak in wave height on 4 September was caused by Hurricane Earl.

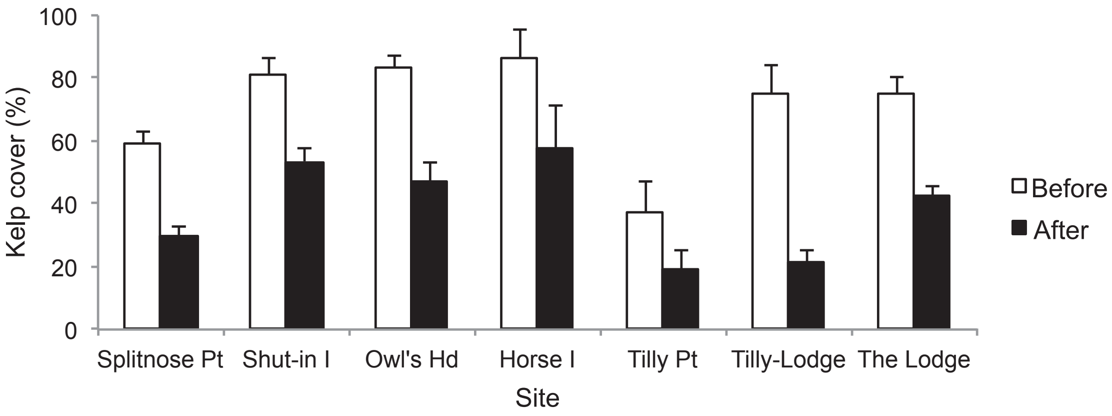


Fig. 3.4. Kelp cover (%) before and after Hurricane Earl at sites in St. Margarets Bay (Owl's Head, Horse Island, Tilly Point, Tilly-Lodge, Shut-in Island, and The Lodge) and near the mouth of Halifax Harbour (Splitnose Point). Owl's Head data are averaged across 3 transects, and Splitnose Point data are averaged across 4 transects. Sites are in order of decreasing exposure. Means + SE, n = 12. Each site has a significant loss in kelp cover following Hurricane Earl.

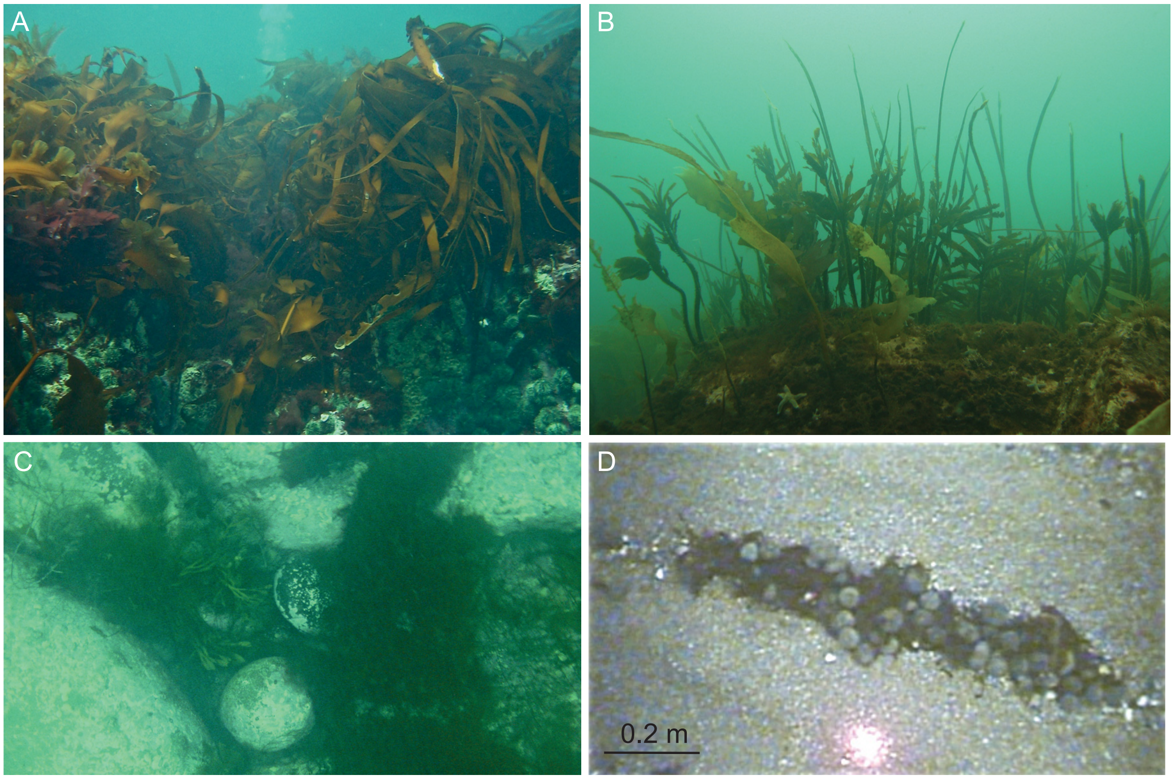


Fig. 3.5. (a) Splitnose Point kelp bed on 5 May 2008. (b) Defoliated kelp bed at the same location as (a) after Hurricane Earl on 8 September 2010. (c) Drift kelp off Splitnose Point at 18 m depth after Hurricane Earl on 13 September 2010. (d) Sea urchins aggregated on drift kelp off Southwest Island at 25 m depth before Hurricane Earl on 18 August 2010.

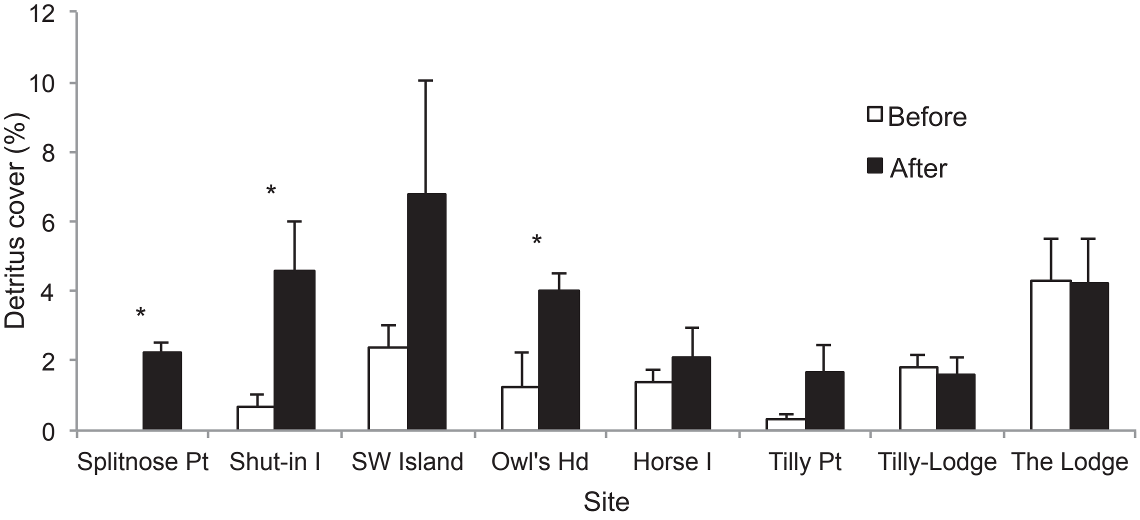


Fig. 3.6. Detritus cover (%) before and after Hurricane Earl at sites in St. Margarets Bay (Owl's Head, Horse Island, Tilly Point, Tilly-Lodge, Shut-in Island, and The Lodge) and near the mouth of Halifax Harbour (Splitnose Point). Owl's Head data are averaged across 3 transects, and Splitnose Point data are averaged across 4 transects. Sites are in order of decreasing exposure. Means + SE, n = 30. *: significant increase in detrital cover following Hurricane Earl. The change in detrital cover at Tilly Point was marginally non-significant.

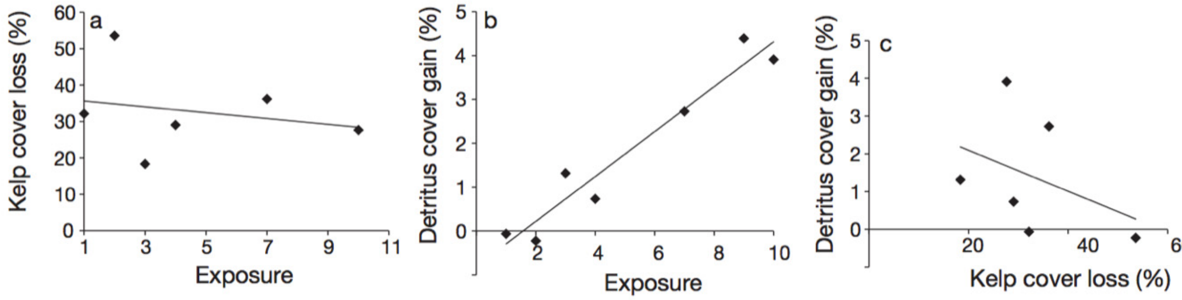


Fig. 3.7. Relationship (%) between (a) loss of kelp cover after Hurricane Earl and site exposure, (b) gain in kelp detritus cover after Hurricane Earl and site exposure, and (c) kelp cover loss and detritus cover gain for sites in St. Margarets Bay.

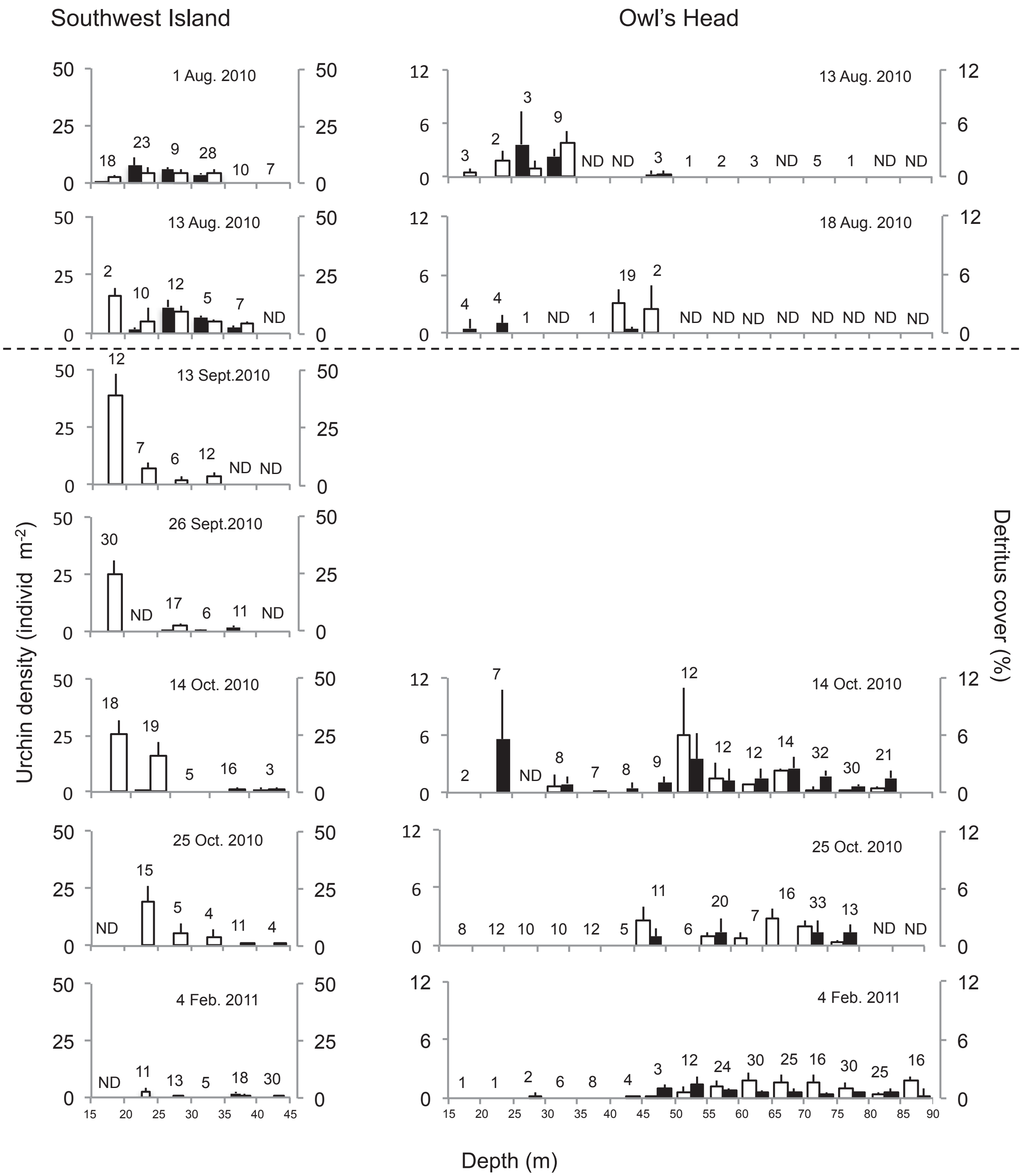


Fig. 3.8. Detrital kelp cover (%, light bars, right y-axis) and sea urchin density (ind. m–2, dark bars, left y-axis) along depth gradient on a sand bottom adjacent to Southwest Island and Owl's Head before and after (dotted line) Hurricane Earl. Means + SE. The number of frames measured for each depth range are shown above bars. ND: no data.

3.5. DISCUSSION

3.5.1 Kelp bed defoliation

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

The production and consumption of drift kelp is an important component of energy flow in the kelp bed ecosystem. Mann (1982) estimated that kelp beds in St.

Margarets Bay produce 1750 g C m^{-2} yr^{-1} of kelp. When scaled to the total area of the bay, the primary productivity of kelps in the rocky subtidal zone (600 g C m^{-2} yr^{-1}) is 3-fold greater than that of phytoplankton in the water column (200 g C m^{-2} yr^{-1}) (Ramus 1992). This massive amount of annual kelp production enters the marine food web mainly as detritus (Mann 1988, Krumhansl & Scheibling 2011a). We observed large accumulations of detrital kelp on beaches, within the kelp bed, and in deep regions beyond the kelp bed directly after the passage of Hurricane Earl. The pulsed delivery of algal detritus to these deep areas indicates that severe storm events may be a major pathway through which kelp production enters offshore benthic communities on sedimentary bottoms.

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

3.5.2. Detrital kelp deposition

The amount of kelp cover lost after Hurricane Earl was not correlated with the increase of detrital cover directly offshore of a given site, suggesting that drift kelp is moved alongshore by currents and that deposits in a particular area may reflect the accumulation of material from kelp beds across a much larger span of coast. There was a strong positive relationship between the increase in detrital kelp cover and site exposure. This finding may be associated with deeper wave-mixing at more exposed sites, which deposits detritus across a greater depth range. Previous surveys of St. Margarets Bay show that hurricanes disrupt the summer thermocline (at ~30 m depth from June to September) and cause mixing to 50 m (Heath 1973). Bottom features are another important determinant of the amount of detrital deposition and its persistence in an area. Drift algae tend to accumulate in basins and deep canyons but not along the sloping continental shelf (Harrold et al. 1998). Off the headland at Splitnose Point, kelp detritus generated by Hurricane Earl collected around boulders and in crevices on bedrock ledges in the barrens immediately below the kelp bed, while deposits in deeper, more gradually sloping sandy regions (~55 m) were scant and short-lived. This pattern is likely because there are few topographic features to trap drift kelp, aside from scattered boulders on the sandy seabed, at this exposed site. Conversely, large detrital deposits in St Margarets Bay persisted for up to 6 wk, where they collected in deep sedimentary basins, such as at Owls Head, or in areas of pronounced sand waves, such as Southwest Island and Shut-in Island. At 20 m depth in St Margarets Bay, clusters of drift kelp (72 g m^{-2}) can take longer than 4 mo to degrade (in the absence of sea urchins), increasing in nutritional value through microbial decomposition and accumulation of meio- and macrofauna (Krumhansl & Scheibling 2012a). Thus, severe storm events can result in long-lasting pulses of high quality organic material in some offshore habitats.

3.5.3. Storm effects on sea urchin distribution and abundance

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

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

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

Kelp degradation rates observed in our experimental cages can be used to estimate the turnover time of detrital deposits. Deep-living sea urchins off Southwest Island and Owl's Head occurred at densities of 2 ind. m^{-2}. We used the average biomass of standing kelp (4.1 kg m^{-2}) measured in kelp beds with complete (100%) canopy cover in St. Margarets Bay and adjacent Mahone Bay from 1992 to 1995 (Scheibling et al. 1999) to approximate the biomass of drift kelp in deeper water from its cover on the seabed. Given an average cover for drift kelp within 1 m^2 of bottom off Southwest Island and Owl's Head of 4%, this translates to a biomass of 164 g m^{-2}. At an average sea urchin density of 2 individuals m^{-2} at these sites and a grazing rate of 1.4 g per urchin d^{-1} (from our cage experiment), an average cover of drift kelp would be consumed in 58.6 d. This turnover rate indicates that the detrital deposits that we observed in late October at Owl's Head, 50 d after Hurricane Earl, could contain some drift kelp generated by the storm. The small amount of drift algae observed February 2011 in regions with sea urchins was likely not derived from the hurricane but detached by subsequent storms or by fragmentation due to other causes, such as grazing by *Lacuna vincta* or encrustation by *Membranipora membranacea*.

3.5.4. Conclusions

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

3.6. ACKNOWLEDGEMENTS

We thank J. Lindley, C. Feehan, K. Krumhansl, F. Francis, and J. Byrk for field and laboratory assistance and J.-S. Lauzon-Guay and K. Krumhansl for comments on earlier drafts of the manuscript. This research was funded by a Discovery Grant and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F-D. was supported by a NSERC Canada Graduate Scholarship.

CHAPTER 4

DETRITAL KELP SUBSIDY SUPPORTS HIGH REPRODUCTIVE CONDITION OF DEEP-LIVING SEA URCHINS IN A SEDIMENTARY BASIN

The work presented in Chapter 4 also appears in:

Filbee-Dexter K, Scheibling RE (2014) Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. Aquat Biol 23: 71–86

4.1. ABSTRACT

Highly productive kelp beds off Nova Scotia, Canada export detrital material to adjacent sedimentary habitats in deeper waters. We evaluated the importance of this subsidy to sea urchins *Strongylocentrotus droebachiensis* in less productive habitats. Gonad index and gut content of urchins on sediments at 60 m depth were measured monthly from September 2010 to May 2013 in a large semi-protected bay, and compared to concurrent measurements of sea urchins at 8 m depth off a nearby headland. Detrital algal cover in the bay was measured using a towed camera system. Seasonal patterns in algal deposition and gut contents of deep-living urchins indicated that detritus was the predominant food source from March to October. We observed lower gonad indices in deep-living sea urchins compared to those at 8 m, but deep-living urchins spawned outside of the main spring season, suggesting periodic detrital subsidy enhances their reproductive condition. Food availability and temperature appear to control the timing of gametogenesis, and phytodetritus may cue gamete release in these deep habitats. To evaluate the response of deep-living urchins to detrital subsidy, and turnover time of this material, we deployed lines baited with kelp thalli at 45 and 60 m depth and measured rates of encounter and consumption of kelp detritus by sea urchins, using the towed camera. Sea urchins aggregated on kelp within hours of deployment, and consumed it after 3 to 5 mo. Our findings suggest kelp detritus represents an important energy source that can support a high reproductive capacity in deep-living urchins.

4.2. INTRODUCTION

The flow of material and energy between habitats plays an important role in structuring marine communities (Polis et al. 1997, Nakano & Murakami 2001, Marczak et al. 2007). In kelp bed ecosystems, macroalgal primary production is largely restricted to the shallow subtidal zone (generally <25 m depth) because light is limiting in deeper waters. This shallow band of production can form a substantial proportion of the overall production in temperate coastal waters (Witman 1988). About 90% of organic material produced in kelp beds is not directly consumed, but enters detrital food webs where it rafts onto beaches, is exported to pelagic ecosystems, or enters deeper benthic communities (reviewed by Krumhansl & Scheibling 2012b). This detrital material ranges from small particles that erode off the distal ends of kelp fronds to large fragments or whole thalli that are torn off during periods of high wave action or when tissue is weakened by grazing damage, encrustation or sporogenesis (Krumhansl & Scheibling 2011b, de Bettignies et al. 2013).

On the Atlantic coast of Nova Scotia, the sea urchin *Strongylocentrotus droebachiensis* is a dominant herbivore in the rocky subtidal zone. At high population density, sea urchins overgraze kelp and create expansive coralline algal barrens (Scheibling 1986, Scheibling et al. 1999, Filbee-Dexter & Scheibling 2014b). In the 1990s and 2000s, phase shifts to barrens occurred when sea urchins migrated from deeper regions and formed aggregations at the lower margin of kelp beds that advanced shoreward as destructive grazing fronts (Scheibling et al. 1999, Brady & Scheibling 2005). More recently, widespread kelp beds have been re-established following recurrent disease outbreaks caused by a pathogenic amoeba, *Paramoeba invadens*, which appears to be periodically introduced into coastal waters where it causes mass mortality of *S. droebachiensis* in shallow habitats (Scheibling & Hennigar 1997, Feehan et al. 2012, Scheibling et al. 2013). Sea urchins have a thermal refuge in deeper waters (>20 m depth), where temperatures remain below the 12°C threshold for propagation of paramoebiasis (Scheibling & Stephenson 1984). These urchins are a source of adult migrants and larval recruits that could repopulate the shallows (Brady & Scheibling 2005).

Off wave-exposed headlands in Nova Scotia, where rocky substrata usually extend to greater depths before burial by sediments, deep-living sea urchins inhabit persistent barrens (Brady & Scheibling 2005, Kelly et al. 2012). Sea urchins in deep barrens subsist mainly on microbial films and coralline algae (Johnson & Mann 1982). Deep-living urchins are also found in sedimentary habitats below the rocky subtidal zone at 25 to 90 m depth, particularly in depositional areas where kelp detritus accumulates. These can occur in protected embayments or within small depressions amid shoals or along exposed headlands (Brady & Scheibling 2005, Filbee-Dexter & Scheibling 2012, unpubl. data, Kelly et al. 2012). Brady & Scheibling (2006) found low rates of growth and reproduction in poorly nourished sea urchins in persistent barrens at 24 m depth along a wave-exposed headland, compared to urchins within or adjacent to kelp beds in shallower water. However, our general knowledge of the ecology of deep populations of *S. droebachiensis* off Nova Scotia and elsewhere is limited compared to populations in the shallow subtidal zone.

In less productive habitats below the depth limit of kelp beds, the spatial extent and duration of detrital subsidy can play an important role in supporting sea urchin populations (Rogers-Bennett et al. 1995, Basch & Tegner 2007, Britton-Simmons et al. 2009). Sea urchins associated with accumulations of kelp detritus have been documented in deep submarine canyons off central California (Harrold et al. 1998) and in other rocky subtidal habitats in Alaska (Duggins et al. 1989), Washington (Britton-Simmons et al. 2009) and Western Australia (Vanderklift & Wernberg 2008). Since gonadal production in sea urchins is tightly linked to food availability (Keats et al. 1987, Meidel & Scheibling 1999, Wahle & Peckham 1999, Christiansen & Siikavuopio 2007), detrital subsidy is expected to enhance the reproductive capacity of deep-living sea urchins, and hence their contribution to the supply of larvae to shallow populations. Patterns of detrital kelp production (Krumhansl & Scheibling 2011a, Filbee-Dexter & Scheibling 2012) and degradation (Krumhansl & Scheibling 2012a) have been measured in Nova Scotia, however the seasonal variation and extent of detrital deposition to deep subtidal habitats have not been quantified. Kelly et al. (2012) found that sea urchins in habitats beyond the kelp bed edge (25 to 30 m depth and 240 m offshore) with access to kelp detritus had higher gonad indices than those living in barrens, but sea urchins at greater depths have not been studied.

In the North Atlantic, *S. droebachiensis* has an annual reproductive cycle with a major spawning period in March/April (reviewed by Scheibling & Hatcher 2013). Reproductive periodicity is primarily cued by changes in temperature (Walker & Lesser 1998, Garrido & Barber 2001, Kirchhoff et al. 2010), photoperiod (Böttger et al. 2006, Siikavuopio et al. 2007, Kirchhoff et al. 2010) and phytoplankton abundance (Starr et al. 1994, Gaudette et al. 2006, Himmelman et al. 2008). Some populations also spawn in late summer and autumn (August to November), but this second spawning event is thought to occur only in food-rich habitats (Keats et al. 1987, Meidel & Scheibling 1998, Lyons & Scheibling 2007). Gonads are the main energy storage organ in sea urchins, and in habitats with insufficient food the gonad can be re-absorbed and gametogenesis suspended without spawning (Guillou et al. 2000).

During video surveys off headlands and within large embayments between Halifax and Mahone Bay on the southwestern shore of Nova Scotia in 2010, we documented sea urchin populations in sedimentary basins at 40 to 100 m depth that were associated with deposits of kelp detritus (Filbee-Dexter & Scheibling 2012). We expected these sea urchins to have a higher reproductive capacity than populations remote from a source of attached or detrital kelp (Britton-Simmons et al. 2009, Kelly et al. 2012). Here, we describe the reproductive cycle of the deep-living population in St. Margarets Bay and compare it to a population in a shallow kelp bed. We measure the contribution of kelp detritus to the diet of deep-living urchins and document temporal patterns in detrital deposition over a 3 yr period. We also measure the response time of sea urchins to detrital kelp deposition and the turnover time of this material in a field experiment.

4.3. MATERIALS AND METHODS

4.3.1. Study sites

Our main study site was located off Owl’s Head (44° 31.18' N, 64° 00.40' W) in St. Margarets Bay, a large semi-protected embayment 50 km southwest of Halifax, Nova Scotia. The shallow rocky subtidal zone (5 to 20 m depth) of the bay is typically dominated by kelp (*Saccharina latissima, Laminaria digitata* and *Agarum cribrosum*), and deeper regions (to ~100 m depth) consist of sedimentary bottom. Owl’s Head is an exposed point along the western shore of St. Margarets Bay, where the granitic bottom shelves steeply into a deep basin (40 to 100 m depth) that is protected from the open ocean by a sill (50 m depth) extending across the bay’s entrance. Our shallow-water (8 m depth) reference site was at Duncan’s Cove (44° 29.54' N, 63° 31.20' W), a partially exposed headland at the western mouth of Halifax Harbour. The substratum at Duncan’s Cove consists of granite ledges and boulders, covered by dense kelp (*S. latissima* and *L. digitata*). The deep and shallow sites were spatially separated (by 38 km) as shallow adult populations of *Strongylocentrotus droebachiensis* do not occur in St. Margarets Bay or along adjacent headlands where they have been eliminated by recurrent outbreaks of paramoebiasis.

4.3.2. Sea urchin collection and analysis

We monitored the reproductive cycle of *S. droebachiensis* at 60 m depth at Owl's Head and at 8 m depth at Duncan's Cove (hereon, deep and shallow urchins, respectively). Large adults (test diameter >35 mm) were collected at both sites at approximately monthly intervals between August 2010 and May 2013. Deep urchins were collected from June to October using small purpose-built traps (0.4 m diameter plastic trays, baited with sardines) or a trawl (2 cm nylon mesh bag within a 0.5 × 0.5 m metal frame, towed from a 5.5 m research vessel), and from November to May using commercial lobster traps baited with chum (fermented herring) and set by a local fisher. Bait was placed inside a perforated metal container to prevent sea urchins from consuming it; purpose-built traps were retrieved after 1 d and lobster traps after 1 or 2 d. Collection methods varied seasonally as we were prohibited from deploying lobster traps outside the lobster fishing season, and we were unable to trawl or deploy our own traps during the season because of the large number of commercial traps and associated floating lines at Owl's Head. Measurements of sea urchin test diameter (8.5 to 111 mm) from each collection method revealed that lobster traps were able to catch smaller individuals than trawls or purpose-built traps. Consequently, sea urchins <35 mm were omitted from our analyses. Shallow urchins >35 mm were collected on encounter by divers at Duncan's Cove.

The gonad index (GI) was calculated for each sample of sea urchins (n = 9 to 23 individuals per sample, depending on trawl and trap success) as gonad wet weight expressed as a percentage of the total body wet weight (including coelomic fluid). The sex of individuals was determined by examining a gonadal smear under a compound microscope. Sea urchins with little to no gonad, or without clear ovaries or testes, were designated unsexed (8.0% of dissected urchins). An index of the latency of response to spawning induction (LI) (either by collection, dissection, or addition of 1 to 2 ml (depending on sea urchin size) of 0.55 M KCl to excised gonads in a petri dish) was determined by recording the time (min) to gamete release on a 6-point scale: (1) not observed after 20 to 60 min following addition of KCl, (2) observed after 10 to 20 min following addition of KCl, (3) observed after 5 to 10 min following addition of KCl, (4) observed after 0 to 5 min following addition of KCl, (5) observed upon dissection, and (6) observed upon collection. For sea urchins collected between August 2011 and May 2013, fertilization rates of 5 ripe females (the first 5 to release eggs during dissection or after induction with KCl) were measured as the proportion of eggs (n = 30 eggs ind.$^{-1}$) showing an elevated perivitelline membrane 1 h after addition of 0.05 ml sperm. Sperm was collected from 1 to 3 ripe males (that were dissected around the same time as the females), checked for motility, mixed in a pipette and added to 100 ml vials of seawater containing eggs of individual females.

Gut contents of all collected specimens were macroscopically analyzed to determine the relative contribution of different food sources: macroalgae, coralline algae/sediment and invertebrate/animal matter. Approximately 2.5 ml of gut content collected from each sea urchin during dissection was spread across a 1 × 5 cm grid to estimate the percentage cover of each food source. Content that could not be macroscopically identified was examined with a dissecting microscope.

4.3.3. Detrital abundance

To monitor kelp and other macroalgal detritus available to deep urchins at Owl's Head, we surveyed the seabed throughout the reproductive-sampling period in 16 video transects between August 2010 and November 2013 (Appendix C: Table C1). Surveys were conducted using a digital video camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor dive wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search Equipment) that was towed at an average speed of 0.51 m s^{-1} from a 7 m research vessel (RV 'Nexus'). Two dive lights and 2 fixed lasers (spaced 20 cm apart) were attached to either side of the camera to light the bottom and provide scale in the video record. The camera was maintained at 1 m above bottom using a hydraulic slip-ring winch with a shipboard controller (Shark Marine Technologies). Video transects began at 45 m depth and extended perpendicular to shore to 75 m depth. For the surveys conducted between August 2010 and February 2011, we measured depth along the video transect using side-imaging sonar (1198c Side Imaging Sonar, Humminbird), lagged by 60 s to account for the positional offset between the camera and the vessel. For surveys after February 2011, we used an acoustic transponder to directly record the depth of the camera (Tracklink 1500 USBL tracking system, LinkQuest). The 60 s positional offset was determined by comparing records from the acoustic transponder and side-imaging sonar for the same video transects.

Each video transect was viewed in iMovie (version 9.0.4, Apple) in real time, and percentage cover of algal detritus along the transect was qualitatively assessed and entered into an Excel macro, synchronized with the video time. The Excel macro tabulated measurements in sample units of 1 s intervals, which was long enough to avoid frame overlap. The accuracy of the detritus measurement was evaluated by selecting 25 frames from the transect conducted on 21 June 2013, overlaying each image with a 100-point grid, measuring percentage cover of detritus, and comparing it to the qualitative measurement of the same frame (paired *t*-test, $p = 0.938$).

4.3.4. Environmental cues

Photoperiod over a 3 yr period (August 2010 to December 2013) was estimated for our study area after Meeus (1999) using a web-interfaced calculator (www.gcstudio.com/suncalc.html). Temperature records from 8 and 60 m depth at the mouth of Halifax Harbour (~10 km SSE of Duncan's Cove) were acquired from the Coastal Time Series (CTS) database (http://bluefin2.dfo-mpo.gc.ca/ctsqry/index-e.html). To obtain a continuous record of phytoplankton concentration at Owl's Head and Duncan's Cove, we acquired 8 d composite chlorophyll *a* (chl *a*; mg m^{-3}) measurements in a 4 km^2 area at both sites from NASA's Ocean Color project SeaWiFS and MODIS satellite-based sensors (http://oceancolor.gsfc.nasa.gov/ cgi/l3). Satellite-based measures at Duncan's Cove corresponded with chl *a* measures at the mouth of Halifax Harbour (~10 km SSE of Duncan's Cove), acquired from the CTS database at 1 m depth (Pearson's $r = 0.986$, $p < 0.001$, $n = 43$).

4.3.5. Field experiment: response to detrital kelp subsidy

To examine rates of encounter and consumption of kelp detritus by sea urchins in the sedimentary basin off Owl's Head, we deployed 2 weighted nylon lines, baited with single thalli of *S. latissima* attached at the holdfast (with plastic cable-ties) at 1 m intervals along a 40 m target section of each line, on 21 June 2013. Each line was marked at each interval with flagging tape for scale. *S. latissima* was collected from Splitnose Point (2.4 km southwest of Duncan's Cove) on 19 July 2013 and held in flowing sea water tanks for 36 h. Thalli of similar biomass and length were selected for the experiment (mean ± SD, 227 ± 89 g, n = 90). The lines were anchored at one end and stretched along the 45 and 60 m depth contours using our research vessel. A line without kelp also was placed ~3 m inshore of the experimental line at each depth as a procedural control to account for potential line effects on sea urchin behavior or trapping of kelp detritus. Surveys using a towed video camera were taken immediately following and 2 d after deployment of the experimental lines to examine the initial response of sea urchins. Subsequent surveys were conducted at 1 to 4 wk intervals (21 June to 4 October 2013) to examine the rate of kelp consumption and decomposition, and changes in sea urchin density over time (Appendix C: Table C1). From 4 to 6 video transects were completed on every sampling day, each beginning in the kelp bed, intersecting the experimental lines (at different points along the 40 m target area) and ending at 80 to 100 m depth. Video data were exported from iMovie (version 3.0.3, Apple) into ImageJ (National Institute of Health) as frames. For each video transect, we selected 1 or 2 frames with a clear image of a kelp thallus attached to the 45 or 60 m depth lines. We outlined the thallus in each frame in ImageJ and calculated the surface area of kelp (using the flagging tape for scale), and recorded the number of sea urchins in contact with kelp. Urchin density on the seafloor surrounding the experimental lines was measured in the 10 consecutive frames before and after the line appeared in the video for each transect.

Natural variation in abundance of macroalgal detritus and sea urchins also was documented during the experiment by measuring percentage cover of detritus and urchin frequency (ind. frame^{-1}) along an extended video transect, ranging from 135 to 227 m from the kelp edge. These video surveys followed the same GPS track as transects used to monitor the detrital algae cover at this site between August 2010 and May 2013.

4.4. RESULTS

4.4.1. Reproductive cycle of deep and shallow populations

Seasonal cycles in GI of *Strongylocentrotus droebachiensis* were more similar among years at 8 than 60 m depth, both in the timing and magnitude of GI peaks, and the occurrence of spawning periods (indicated by sharp declines in GI 1 to 2 mo after peaks). In general, peaks in GI occurred in late winter (February to March) and late summer or autumn (August to October) each year (Fig. 4.1). The maximum GI recorded was 33.1 and 38.9% in deep and shallow urchins respectively. The primary spawning period (greatest decline in GI) at 60 m generally occurred in autumn between September and November, and male and female spawning was less synchronized than in shallow populations (Fig 4.1c). Spring spawning events differed substantially between sites, occurring in all 3 yr at 8 m, but only in 2011 at 60 m. Spawning events with smaller declines in GI occurred also during autumn at 8 m between August and October (Fig. 4.1b).

LI was positively correlated with GI over the sampling period for both deep and shallow sea urchins (Table 4.1), with rapid gamete release in spring and autumn and weak or no spawning in winter and summer (Fig. 4.1). This biannual pattern was clearer in LI than GI and showed less variation in the timing and strength of peaks. LI measures were less consistent in the final sampling year, with increases lasting longer than usual at 60 m depth in October 2012 and occurring earlier at 8 m depth in January 2013 (Fig. 4.1c,d). The seasonal pattern of *in vitro* fertilization rate also was concordant with patterns of GI and LI, with the highest proportion of fertilized ova in spring and autumn (Fig. 4.2). The proportion of mature ova (without a nucleolus) was positively correlated with GI over the sampling period (Table 4.1). It was lowest in early winter and highest in spring and autumn, and remained relatively high in summer months between spawning periods (Fig. 4.2). The proportion of mature ova and GI both were positively correlated with urchin size (test diameter) for deep and shallow urchins; LI was correlated with size for only the deep location (Table 4.1). Mean adult size was similar in the deep (55.9 ± 5.14 mm) and shallow (58.3 ± 2.80 mm) populations, however maximum size was much greater for deep (112 mm) than shallow urchins (79.1 mm). Deep urchins also had long, brittle spines and tended to have lighter, thinner tests than shallow urchins. The ratio of males to females was similar in shallow (1.14, n = 210) and deep urchins (1.08, n = 505) and did not differ significantly from 1:1 at either depth ($\chi^2_{8m} = 0.933$, $p = 0.334$; $\chi^2_{60m} = 0.715$, $p = 0.398$).

Daily photoperiod during autumn and spring spawning periods was similar (10 to 13 h) but differed in the direction of change (Fig. 4.3a). Seawater temperature at 8 m depth at Duncan's Cove was warmest (12 to 20°C) between August and October, coinciding with the autumn spawning, and coldest (1 to 3°C) between February and March, coinciding with the spring spawning (Fig. 4.3a). Temperature at 60 m depth at Owl's Head ranged from 1 to 7°C, and was lowest between February and April, and highest between November 2011 and January 2012, and August 2012 and January 2013 (Fig. 4.3a). Chlorophyll concentration (a proxy for phytoplankton abundance) at Owl's Head showed substantial inter-annual variability. As expected, seasonal peaks in chlorophyll occurred in autumn 2010 to 2012, and spring 2011, with highest concentrations (>10 mg m^{-3}) in April, May, and November 2011 and October 2012, and lowest concentrations (<4 mg m^{-3}) during summer and in some winter months (Fig. 4.3b). Out-of-season peaks also occurred in January 2012 and 2013, and no phytoplankton increase was documented in spring 2012 and 2013 (Fig. 4.3b). Chlorophyll measures near Duncan's Cove were also variable, but tended to peak in autumn 2011 and 2012 and spring 2011 and 2012, with slight increases in September and October 2010, and March 2013 (Fig. 4.3b).

4.4.2. Gut contents and availability of detrital algae for deep sea urchins

Algal material (mainly kelp and other brown algae) was present in the guts of 95% of sea urchins (n = 533) from 60 m depth at Owl's Head. Gut contents consisted almost entirely of algal detritus during spring/summer, while sediment, filamentous algae, and animal matter accounted for 15 to 27% of the content in autumn/winter

(Appendix C: Table C2). Brown algae (mainly kelp) were present in the guts of all sea urchins (n = 214) along the kelp bed at 8 m depth at Duncan's Cove; 95% of these urchins had no other observable material in the gut (Fig. 4.4a).

Seasonal changes in gut contents of deep urchins at Owl's Head reflected the annual pattern of abundance of algal detritus in the study area between August 2010 and November 2013 (Fig. 4.4b). For paired samples (n = 9, <30 d apart), the proportion of algal material in urchin gut contents was positively related to detrital cover on the bottom, although the correlation coefficient was on the margin of statistical significance (Pearson's r = 0.579, p = 0.051). Mean cover of detritus increased in late summer/early autumn in 2012 and 2013, and decreased in late autumn/winter throughout the 3 yr sampling period. Detrital cover was greatest in August or October/November in each year, and lowest in January/February 2011 and 2013 (there was no winter sampling in 2012, but detrital cover was minimal in July) (Fig. 4.4b). A dredged sample of algal detritus from 60 m depth on 20 July 2012 was primarily composed of the kelp *Agarum cribrosum* with moderate amounts of other kelps (*Saccharina latissima, Laminaria digitata*), foliose red algae, and the annual brown alga *Desmarestia viridis*.

4.4.3. Experimental response of sea urchins to detrital kelp subsidy

The fate of kelp thalli attached to lines placed at 45 and 60 m depth at Owl's Head, and the density of *S. droebachiensis* that aggregated on these thalli over time, differed markedly between depths (Table 4.2, Fig. 4.5). Sea urchins located kelp at the 45 m line within 2 h of deployment, forming aggregations of 12 ind. thallus^{-1}, on average, within 2 d, which doubled in size by Day 21 (Figs. 4.5a, 4.6). The area of transplanted kelp thalli began to decline at that point, and fronds were fragmented and mostly consumed by Day 82. Sea urchins were not observed on kelp at the 60 m line by Day 34 and density was only 5 ind. thallus^{-1} by Day 59, at which time there had been no significant decrease in thallus area and fronds were intact with no sign of degradation. Mean urchin density on kelp at the 60 m line increased to 12 ind. thallus^{-1} by the end of the experiment on Day 105, by which time kelp cover had been reduced by half (Fig. 4.6). A 2-way ANOVA of kelp area showed a significant effect of both elapsed time and depth. Post hoc comparisons indicated that kelp area (pooled over depths) decreased significantly between 34 and 82 d after deposition. A 2-way ANOVA of urchin density on kelp (ind. thallus^{-1}) showed a significant interaction of time and depth. Post hoc comparisons showed that urchin density was significantly lower on the 45 m line on Day 105 compared to all other sampling times, and urchin density significantly increased on the 60 m line 59 and 105 d after deposition (Table 4.2). Sea urchin density on kelp fronds was positively correlated with the number of urchins on the seafloor (ind. frame^{-1}) immediately before and after each line for data pooled throughout the experiment (Pearson's r = 0.38, $p < 0.001$, n = 175). A 1-way ANOVA showed no effect of elapsed time on the number of urchins in contact with the procedural control line ($F_{6,7} = 0.738$, p = 0.636) and on the kelp area in contact with the procedural control line ($F_{6,7} = 0.458$, p = 0.820), indicating that the weighted lines did not influence sea urchin density or detrital kelp deposition.

The extended video transects that intersected the experimental lines revealed patches of macroalgal detritus on sedimentary bottom, and accumulations of sea urchins on and around these deposits (Fig. 4.7). The effect of detrital cover on urchin frequency (ind. frame^{-1}) along these transects was examined with a generalized linear model (GLM) performed using R software (MASS package). GLM residuals were modelled with a negative binomial distribution and a log-link function. Likelihood ratio (LR) tests showed no significant effect of sampling date ($LR_4 = 3.84$, $p = 0.427$) and no interaction between detrital cover and date ($LR_4 = 1.37$, $p = 0.848$) on urchin frequency; therefore data were pooled over the duration of the experiment. To reduce spatial autocorrelation due to continuous sampling along video transects, an effective sample size of N/12 estimated using the autocorrelation function (ACF) and yielding 240 frames or 5 frames min^{-1} of video, was used. This analysis showed a significant positive effect of detrital cover on urchin frequency along these transects ($z = 5.74$, $p < 0.001$, deviance explained = 15.8%). The seafloor surrounding the 45 m line had a greater number of sea urchins and cover of detritus than the 60 m line (Fig. 4.7). Total detrital cover increased along these transects during the experiment, although the general pattern of distribution was maintained (Fig. 4.7).

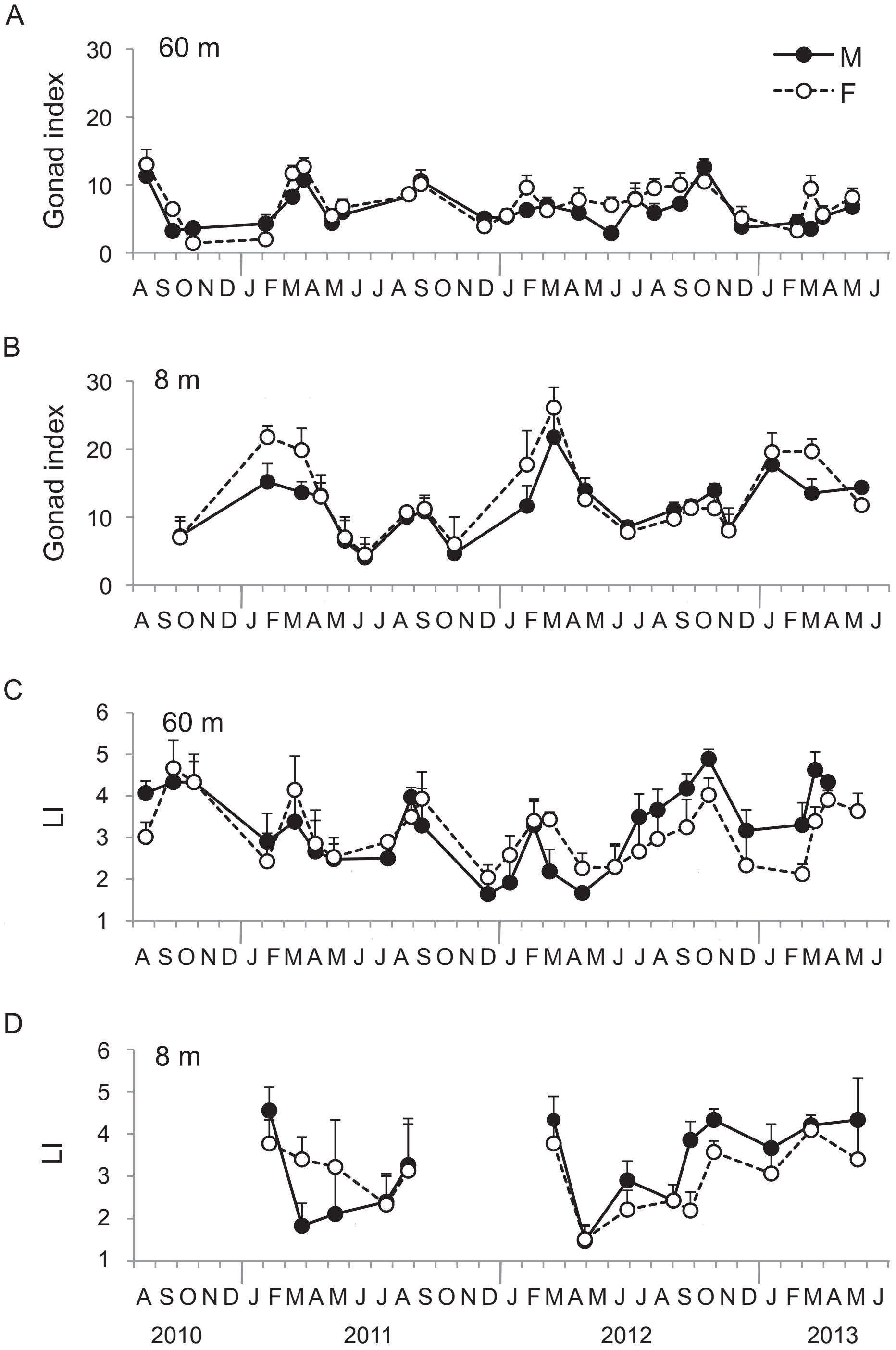


Fig. 4.1. *Strongylocentrotus droebachiensis*. Gonad index (% body weight that is gonad) of males and females at (A) Owl's head (60 m depth) from August 2010 to May 2013, and (B) Duncan's Cove (8 m depth) from February 2011 to May 2013; male n = 1 to 19, female n = 2 to 18. Latency of response index to spawning induction (LI) of males and females at (C) Owl's head and (D) Duncan's Cove. LI ranges from 1 (did not spawn by 1 h after induction) to 6 (spawned during collection); male n = 4 to 20, female n = 1 to 19. Data are means ± SE.

Table 4.1. *Strongylocentrotus droebachiensis*. Correlation matrix (Pearson's r, *p = 0.01, **p = 0.001; sample size in parentheses) for gonad index (GI), latency of response index to spawning induction (LI), proportion of mature ova (MO) and sea urchin test diameter (TD) at Owl's Head (OH, 60 m depth) and Duncan's Cove (DC, 8 m depth).

	OH				DC			
	GI	LI	MO	TD	GI	LI	MO	TD
Gonad index	1.00				1.00			
Latency of response index	0.35** (566)	1.00			0.45** (226)	1.00		
Proportion of mature ova	0.43** (136)	0.44** (136)	1.00		0.39* (41)	0.11 (41)	1.00	
Test diameter	0.35** (518)	0.29** (518)	0.31** (136)	1.00	0.21* (211)	0.08 (211)	0.40* (41)	1.00

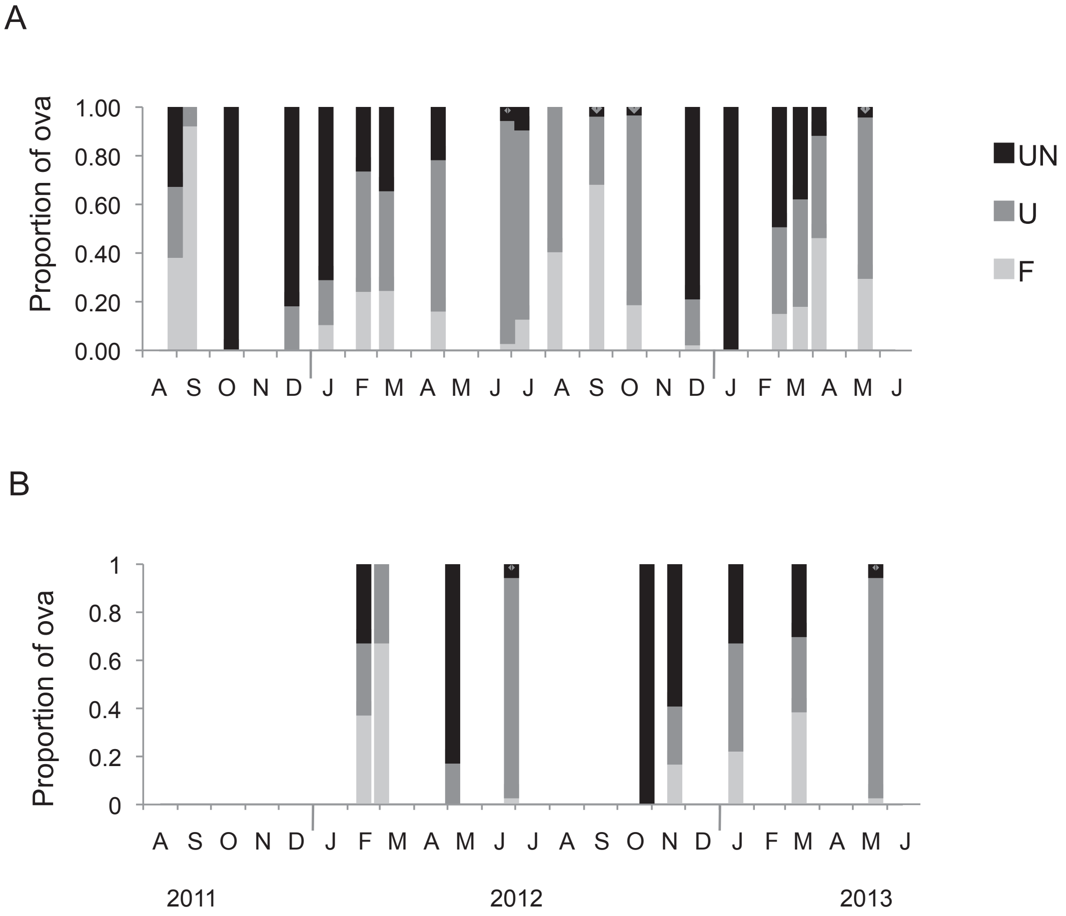


Fig. 4.2. *Strongylocentrotus droebachiensis*. Proportion of ova (n = 60) fertilized (F), unfertilized without nucleolus (U) or unfertilized with nucleolus (UN) 1 h after addition of sperm in sea urchins at (A) Owl's head (60 m depth) from August 2011 to May 2013, and (B) Duncan's Cove (8 m depth) from February 2012 to May 2013.

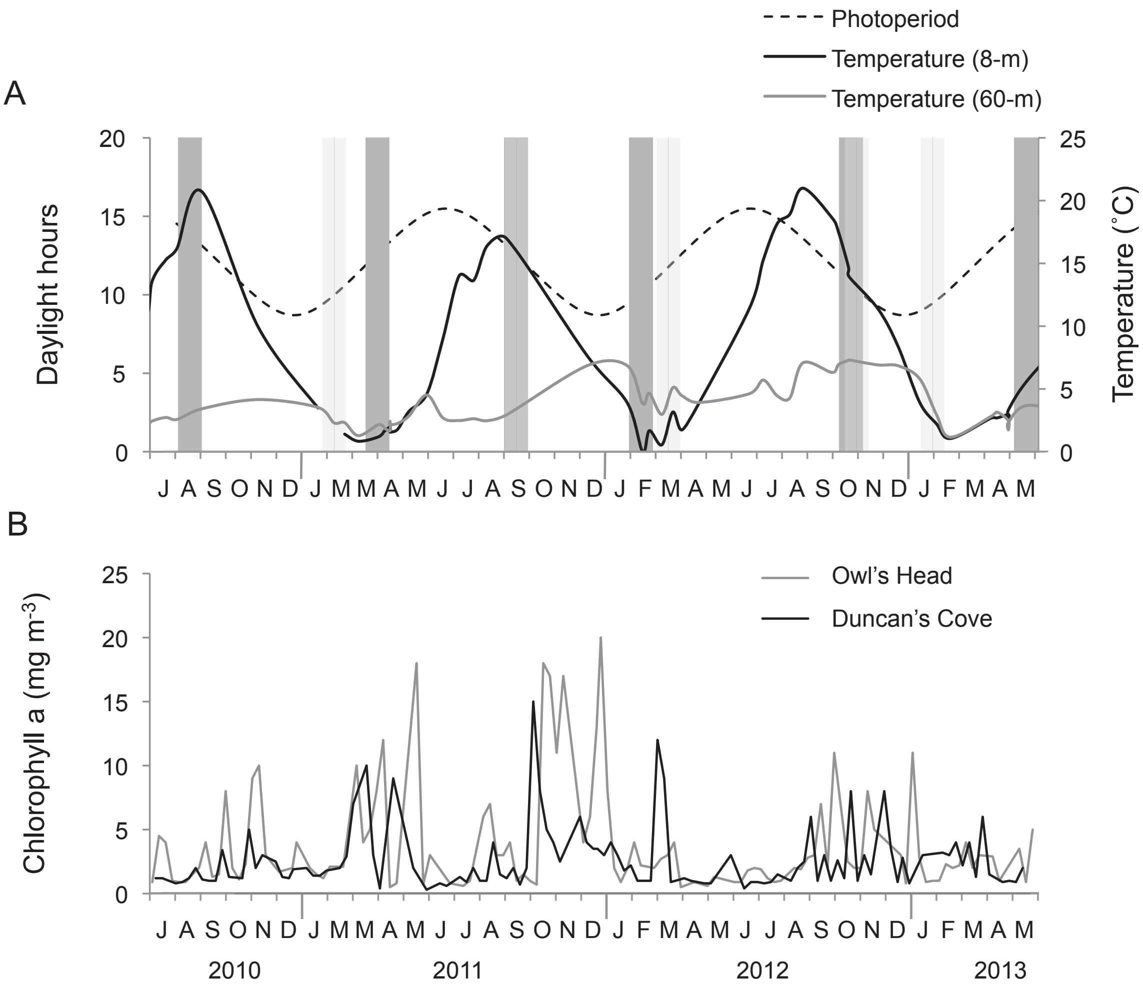


Fig. 4.3. *Strongylocentrotus droebachiensis*. (A) Mean daily temperature at 8 m and 60 m depth, and daylight hours, in the study area from July 2010 to June 2013. Shaded bars indicate spring and autumn spawning periods of sea urchins based on decreases in GI and increases in LI at Owl's Head (60 m depth, dark grey) and Duncan's Cove (8 m depth, light grey). (B) Chl a concentration at Duncan's Cove and Owl's Head from July 2010 to June 2013.

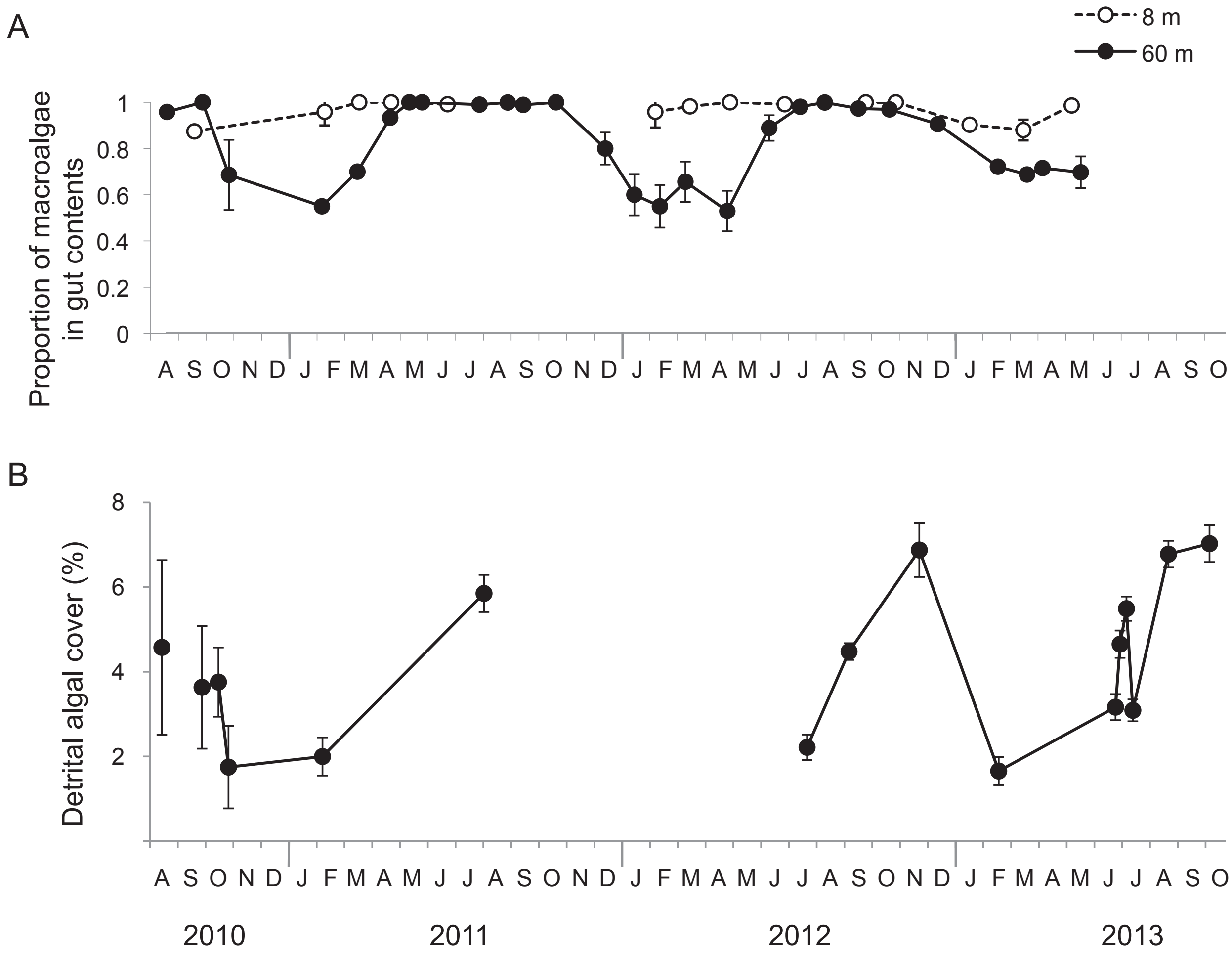


Fig. 4.4. *Strongylocentrotus droebachiensis*. (A) Proportion of algae (excluding coralline algae) in gut contents of sea urchins at Owl's Head (60 m depth) and Duncan's Cove (8 m depth) from August 2010 to November 2013. (B) Mean detrital algal % cover across a 45 to 75 m depth gradient at Owl's Head, near the collection site. Data are means ± SE.

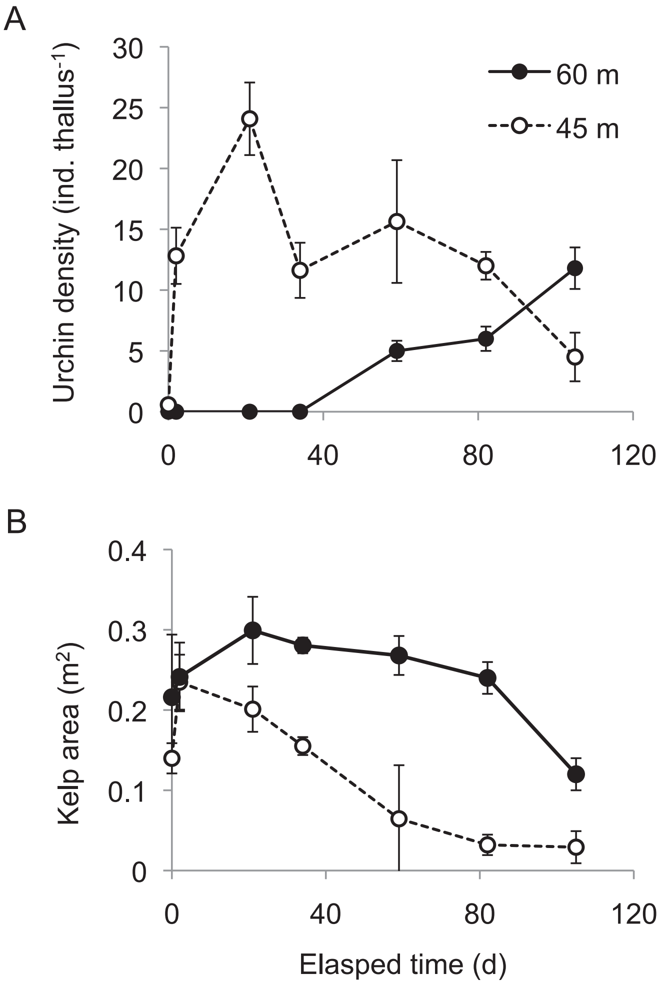


Fig. 4.5. *Strongylocentrotus droebachiensis*. Mean kelp area and density (urchin thallus^{-1}) on 45 and 60 m experimental lines at Owl's Head from 21 June to 4 October 2013. Data are mean ± SE; n = 6 to 12. Note: kelp had not fully settled on the bottom when lines were surveyed directly after deployment, resulting in an increase in kelp area on Day 2.

Table 4.2. *Strongylocentrotus droebachiensis.* Two-way ANOVA of effects on area of kelp thalli or density of sea urchins on kelp (urchins thallus^{-1}) of fixed factors depth (45 and 60 m) and elapsed time (2, 14, 34, 59, 82, 105 d) at Owl's Head. Urchin density is square-root transformed to satisfy assumption of homoscedasticity (Levene's test, α = 0.01). Significant post hoc comparisons (Tukey's test, α = 0.05) are given.

Source	df	MS	*F*	p	Tukey's post hoc tests
Kelp area					
Time	5	0.043	13.0	<0.001	Time
Depth	1	0.226	68.0	<0.001	2 = 14 = 34 > 59 = 82 > 105
Time × Depth	5	0.006	1.81	0.129	
Error	48	0.003			
Urchin density					
Time	5	2.67	7.80	<0.001	Time × Depth
Depth	1	79.5	232	<0.001	45 m: 105 < 82 = 59 = 34 = 14 = 2
Time × Depth	5	7.58	22.1	<0.001	60 m: 105 > 82 = 59 > 14 = 34 = 2
Error	48	0.342			2, 14, 34, 59, 82 d: 45 > 60
					105 d: 60 > 45

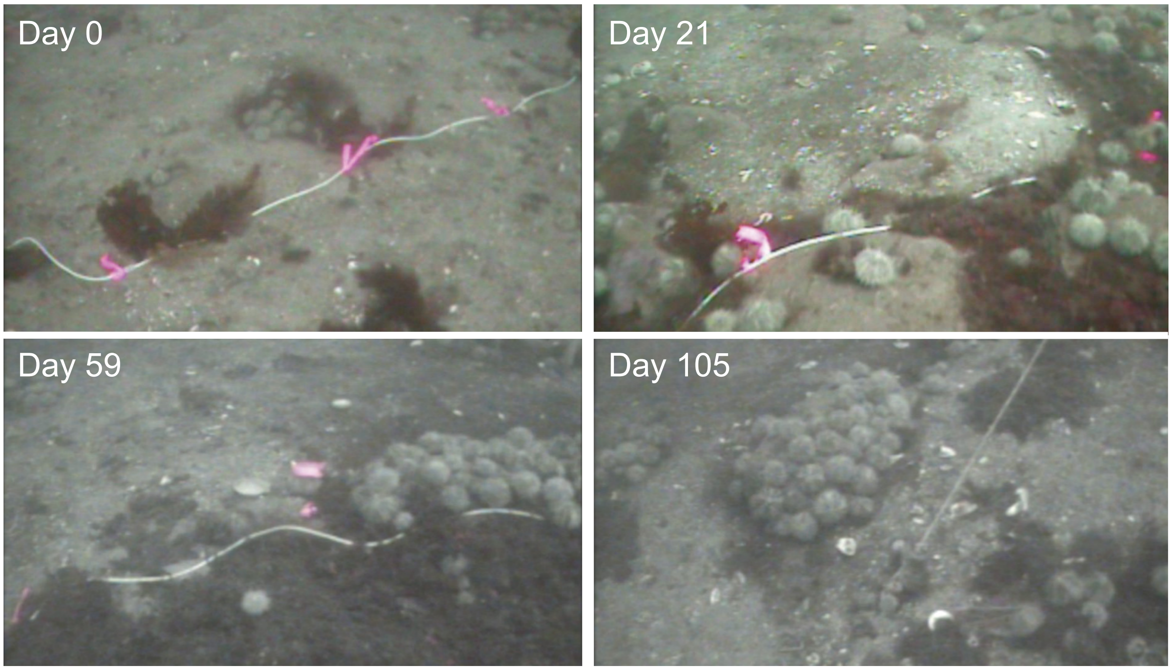


Fig. 4.6. Video frame grabs of weighted lines baited with kelp fronds at 45 m depth on Days 0, 21, 59 and 105 of the field experiment at Owl's Head in 2013, showing rapid detection of kelp by *Strongylocentrotus droebachiensis* within 2 h, dense urchin aggregations and kelp degradation after 21 and 59 d, and bare line by 105 d after deployment. Flagging tape indicates 1 m intervals along a line.

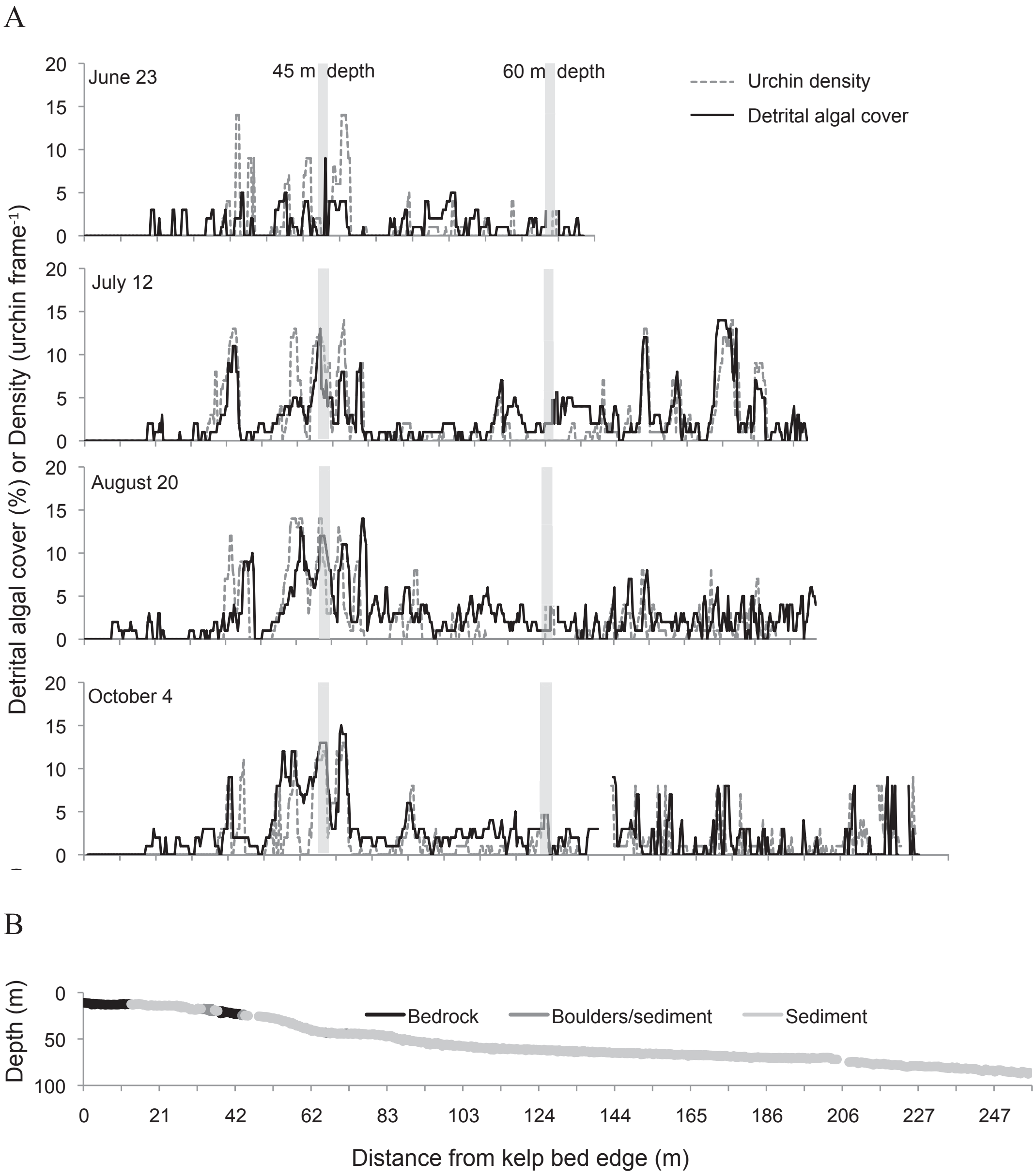


Fig. 4.7. A) Detrital algal cover and sea urchin abundance along video transects on 23 Jun, 12 Jul, 20 Aug and 4 Oct at Owl's Head. Experimental lines baited with kelp fronds (deployed on 21 Jun) are indicated by shaded grey bars at 45 and 60 m depth. B) Substratum type along the depth profile on video transects. Transects began in the kelp bed at 8 m depth and extended offshore to 95 m depth.

4.5. DISCUSSION

4.5.1. Detrital kelp subsidy and reproductive condition of deep-living urchins

Previous studies have recorded a decrease in gonad size and fecundity with increasing depth and distance from macroalgal beds for *Strongylocentrotus droebachiensis* (Keats et al. 1984, Bertram & Strathmann 1998, Wahle & Peckham 1999, Brady & Scheibling 2006, Kelly et al. 2012) and congeneric species (Rogers-Bennett et al. 1995, Wahle & Peckham 1999, Konar & Estes 2003). In contrast, we found that sea urchins at 60 m depth in a sedimentary basin can have comparable or in some cases greater reproductive effort (mean GI at spring or autumn peak: 10 to 12%) than those living in rocky barrens at 6 to 24 m depth adjacent to kelp beds at other sites in St. Margarets Bay (8 to 10%; Meidel & Scheibling 1998) or at the mouth of Halifax Harbour (6 to 9%; Brady & Scheibling 2006) in past decades. Kelly et al. (2012) observed a similar increase in mean GI of sea urchins (from 11 to 22%), and supply of detrital kelp, within a depositional basin at 25 m depth along transects running offshore from a kelp bed near Duncan’s Cove in 2009. Britton-Simmons et al. (2009) found that *S. franciscanus* feeding on macroalgal detritus at 24 m depth also a had similar GI compared to sea urchins in barrens at 6 m depth in the San Juan Islands, Washington, USA. The maximum GI of shallow and deep urchins in our study (39 and 33% respectively) was comparable to the highest measures recorded for *S. droebachiensis* under optimized feeding conditions (35 to 38%; Meidel & Scheibling 1999, Siikavuopio et al. 2007). The supply of detrital macroalgae, mainly kelp, likely explains the relatively high GI in deep urchins. Not only is kelp a high quality and preferred food of *S. droebachiensis* (Scheibling & Hatcher 2013), but the nutritional quality of kelp detritus is also enriched by microbial degradation (Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling 2012a).

S. droebachiensis generally does not form dense populations below 30 m depth as it does in the shallow barrens along the coast of Nova Scotia (Scheibling et al. 1999, Brady & Scheibling 2005). This likely is because the rocky substratum off the wave-exposed headlands does not accumulate substantial quantities of detrital macroalgae as it slopes continuously into deeper sedimentary areas. Ideally, we would have included in our sampling design a site at 60 m depth with minimal deposition of kelp detritus to directly test the effect of this subsidy on sea urchin reproductive capacity and periodicity. However, in extensive video surveys along the coast, we have found that in areas with little or no detritus sea urchins are so sparsely distributed (Filbee-Dexter & Scheibling *in review*) that regular collections for reproductive analyses would have been impossible within the logistical constraints of this study. This observation in itself supports our conclusions about the importance of detrital subsidy for deep urchin populations.

Sea urchin abundance was positively related to detrital cover in video surveys, and our field experiment indicates that *S. droebachiensis* can locate and consume this food resource for months. The presence of magroalgal detritus on the seafloor and in the guts of deep-living urchins varied seasonally throughout our 3 yr study at Owl's Head, with peaks in late summer and autumn. High wave action, storm events, and heavy encrustation by the bryozoan *Membranipora membranacea* combine to increase dislodgment, fragmentation and erosion of kelp resulting in increased detrital deposition during this period (Scheibling & Gagnon 2009, Krumhansl & Scheibling 2011a, Filbee-Dexter & Scheibling 2012). The non-uniform pattern of macroalgal detritus along our video transects indicates subtle bottom features that may retain detritus in certain areas. For example, a large amount of detritus accumulated amid sparse boulders and decreased in slope at 40 to 45 m depth, which in turn was associated with high sea urchin densities.

The rapid response to kelp detritus on our experimental line at 45 m depth demonstrates that *S. droebachiensis* can locate a nearby subsidy within hours, and may be constantly searching for food in deeper waters. The slower response to the 60 m line (59 d had elapsed before the first urchins were observed there) suggests that sea urchins are unable to detect or respond to detritus 10s to 100s of meters distant, and may only encounter it through random movement. Once deposited, kelp detritus degrades slowly at depth and persists as a food source for macrofaunal communities for up to 4 mo in the absence of sea urchins (Krumhansl & Scheibling 2012a). We also observed minimal loss of transplanted kelp at the 60 m experimental line over nearly 2 mo before sea urchins located it. Even for kelp on the 45 m line that was immediately located by sea urchins, the turnover rate was slow (on the scale of months). In a caging experiment at 41 m depth off Owl’s Head in 2011, we found that sea urchins consumed detached kelp at a rate of 1.4 g ind.$^{-1}$ d^{-1} (Filbee-Dexter & Scheibling 2012), which is within the range recorded for *S. droebachiensis* grazing in shallow water (Lauzon-Guay & Scheibling 2007a). From these results, we estimated that it would take ~2 mo for sea urchins off Owl’s Head to consume an average deposit of detrital kelp (Filbee-Dexter & Scheibling 2012), which approximates the time in which the majority of kelp was consumed on both experimental lines in our present study.

Laboratory feeding studies have shown that while a critical nutritional level is required for the initiation and progression of gametogenesis in *S. droebachiensis*, changes in food availability at later stages of the reproductive cycle affect gonad growth but do not influence the timing of gamete release (Minor & Scheibling 1997, Meidel & Scheibling 1998, 1999). Under optimal environmental conditions, gametogenesis can take about 6 mo (Walker & Lesser 1998). Maximum food availability occurred at Owl's Head during peaks in macroalgal detritus between September and November, ~6 mo prior to spring peaks in GI. This subsidy may have been supplemented with phytodetritus from the autumn phytoplankton bloom, which is expected to reach 60 m depth within 1 to 2 d of cell death, assuming a sinking rate of 100 m d^{-1} for coastal aggregates (Alldredge & Gotschalk 1990). Likewise, phytodetritus from the spring bloom deposits between March and April, in time for initiation of gametogenesis. At Owl's Head in 2012, the spring phytodetritus subsidy was 2 mo later than in previous years, and was followed by an autumn peak in GI that occurred 1 to 2 mo later than in previous years. The late phytoplankton bloom, combined with limited detrital kelp deposition between March and April 2012, may have delayed gametogenesis.

Gonad growth in sea urchins is the result of either a build-up of nutrient reserves in nutritive phagocytes prior to gametogenesis, or an increase in the size or number of germinal cells in the gonad during gametogenesis (Walker et al. 2013). The higher spring peak in GI at 8 m (particularly in females) compared to 60 m depth may reflect a better overall nutritional environment at the shallow site, where sea urchins generally had continuous access to attached and detrital kelp within and around the kelp bed. Likewise, increases in GI in deep regions may reflect energy storage (rather than gametogenesis) following periods of abundant food. This may have occurred in early autumn 2012 following the late summer supply of detritus.

Trophic linkages between algal beds that export detritus and the recipient species typically occur on the scale of kilometers and can have an important influence on community structure (Kirkman & Kendrick 1997, Vanderklift & Wernberg 2008, Britton-Simmons et al. 2012). For example, kelp detritus that rafts onto beaches can allow fauna to reach high abundance in a habitat where local production is low (reviewed by Colombini et al. 2003). Detached kelps such as *Macrocystis pyrifera* and *Ecklonia radiata* can be transported 10s to 100s of kilometers by along-shore currents and thereby provide spores or food to neighboring areas (Harrold & Lisin 1989, Vanderklift & Wernberg 2008). Detrital kelp is an important food source for sea urchins that passively trap and consume drifting fronds along the Pacific coast of the USA, the central Chilean coast, and the coast of Western Australia (Krumhansl & Scheibling 2012b). In the Northwest Atlantic, *Strongylocentrotus pallidus* has been observed consuming fronds of *Saccharina latissima* at 2500 m depth off the Scotian Shelf (A. Metaxas pers. comm.), indicating that this subsidy occurs over much larger spatial scales than documented in our study.

Another important linkage between shallow and deep sea urchin populations could be their contribution to larval production in the rocky subtidal ecosystem. Kelp detritus not only provides energy that deep sea urchins use to produce gonads, but also aggregates them at high densities on detrital deposits. This can increase fertilization rate

(Lauzon-Guay & Scheibling 2007b) by increasing both the number of spawning individuals and synchrony of gamete release (Starr et al. 1990, Wahle & Peckham 1999, Lauzon-Guay & Scheibling 2007b). A positive relationship between test size and GI for both deep and shallow urchins, combined with a larger maximum size for deep urchins, suggests that per capita gonadal production is greater in the deep.

4.5.2. Environmental cues and reproductive periodicity

Previous studies in Alaska, Eastern Canada, the Gulf of Maine, Norway and the Barents Sea have documented a distinct annual reproductive cycle for shallow populations (<25 m depth) of *S. droebachiensis*, with a peak in GI between March/April followed by a sharp decline, indicating relatively synchronous spawning in late winter or early spring (Himmelman 1978, Falk-Petersen & Lønning 1983, Keats et al. 1984, Munk 1992, Meidel & Scheibling 1998). Populations in the St. Lawrence Estuary, Canada have been observed to spawn in June/July (Starr et al. 1993, Oganesyan 1998). Histological analysis of the gonads of sea urchins from Nova Scotia indicates that gametogenesis commences in summer and is fueled in part by nutritive phagocytes produced in spring (Meidel & Scheibling 1998). For shallow populations of *S. droebachiensis*, changes in photoperiod (Böttger et al. 2006, Siikavuopio et al. 2007, Kirchhoff et al. 2010) or temperature (Walker & Lesser 1998, Garrido & Barber 2001, Kirchhoff et al. 2010) appear to control the timing of gametogenesis.

The presence of seasonal increases in GI of *S. droebachiensis* in spring and autumn, and the high proportion of mature ova and short response time to spawning induction at these peaks, indicates that deep-living urchins, like those in the shallow kelp bed, may be capable of spawning outside of the main spring season documented for shallow populations. This generally has been observed only under optimal feeding (Shpigel et al. 2004) or manipulated environmental conditions (Walker & Lesser 1998) in laboratory experiments, or under conditions of high food availability in the field (Keats et al. 1987, Meidel & Scheibling 1998, Brady & Scheibling 2006). The high proportion of sea urchins that readily spawned upon dissection (LI > 5) in both autumn and spring suggest that individuals can spawn twice a year. At 8 m depth, a higher spring peak in GI is consistent with previous studies of *S. droebachiensis* in shallow, food-rich habitats (Meidel & Scheibling 1998, Brady & Scheibling 2006), and indicates that the autumn peak likely reflects a secondary spawning period.

GI increases in our study coincided roughly with rapid changes in photoperiod, albeit in opposing directions in spring and fall (see also Brady & Scheibling 2006). Gattuso et al. (2006) measured irradiance reaching the seafloor in coastal oceans using satellite (SeaWIFS) data collected between 1998 and 2003. They calculated that approximately 0.004 to 0.023 mmol photons m^{-2} s^{-1} reached 60 m depth within 25 km of Owl's Head (Appendix C: Fig. C1). Tube feet of *S. droebachiensis* in shallow water react to low light irradiances of 5 mmol photons m^{-2} s^{-1} (Lesser et al. 2011), which approximates light levels at 35 to 40 m depth at Owl's Head. Therefore, photoperiod likely does not play a role in reproductive timing at 60 m depth, although it may indirectly influence spawning by affecting phytoplankton production (Platt & Jassby 1976).

Differences in temperature between 8 and 60 m depth also may account for differences in GI peaks between shallow and deep urchins. Gonadal production increases with temperature up to ~10°C, beyond which temperatures are too warm for oocyte maturation (Walker & Lesser 1998, Garrido & Barber 2001, Siikavuopio et al. 2006). Seawater temperature at 8 m dropped from 10 to 7°C from October to December, enabling oocyte maturation before the spring spawn, but exceeded 10°C from July to October, which could inhibit maturation and limit the autumn spawn (Brady & Scheibling 2006). Sea urchins at 60 m at Owl's Head experience consistently cold bottom temperatures (3 to 7°C). The lower summer temperatures at this depth are more conducive to oocyte maturation and autumn spawning compared to shallow waters. Moderately warm temperatures between September and January should enable gonad growth at 60 m, however, low detrital abundance and meager gut contents indicate that sea urchins are food-limited during this period.

Phenolic compounds associated with phytoplankton have been shown to induce spawning in *S. droebachiensis* from shallow populations under laboratory conditions (Starr et al. 1994), although this relationship is less clear in compiled field observations (Starr et al. 1993, Scheibling & Hatcher 2013). Phytodetritus following a bloom may provide an important cue at 60 m depth where changes in temperature, photoperiod and lunar cycles are damped. Reproductive periodicity in the deep-sea urchin *Echinus affinus* is strongly linked to seasonal pulses of phytodetritus (Tyler & Gage 1984, Campos-Creasey et al. 1994). Possible mechanisms to explain this association are: (1) sea urchins utilize phytodetritus for rapid gametogenesis and spawn shortly thereafter, (2) sea urchins time gamete release with favorable conditions for planktonic larval development, or (3) sea urchins initiate and synchronize gametogenesis with phytodetritus and spawn after a constant period of vitellogenesis (Eckelbarger & Watling 1995). Decreases in GI at 60 m in our study occurred 1 to 2 wk following phytoplankton blooms in autumn of all sampling years, and in spring 2011. This suggests that phytodetritus triggers gamete release in deep urchins, and could explain why spawning events were not documented at Owl's Head during spring 2012 and 2013, when blooms were not recorded on satellite imagery. The proportion of mature ova and LI remained high during summer 2012, indicating that gametogenesis occurred prior to the spring, but deep urchins did not spawn and retained their mature gonads until autumn. Similarly, a strong spawning event did not occur at 8 m depth in autumn 2012 even though GI and LI were high, and winter increases in GI and LI occurred earlier in 2013 than in other years, possibly because ripe gametes were retained from the autumn. It appears that although sea urchins have the capacity to release gametes in spring and autumn, spawning may only take place if it is cued by favorable environmental conditions.

4.5.3. Ecological implications of detrital subsidies for deep-living sea urchin populations

Our study underscores the importance of energy subsidies, originating in highly productive kelp beds within a relatively narrow rocky coastal zone, on the secondary productivity of adjacent communities in sedimentary habitats in deeper waters. Krumhansl et al. (2014) modelled the historical and future production of detritus in Nova Scotian kelp beds, and predicted that changes in ocean climate (increasing temperature and storm severity) will decrease detrital production. This would have negative effects on growth and reproduction of populations in adjacent habitats, such as deep-living urchins that receive a detrital subsidy.

Our findings demonstrate that reproductive capacity of deep-living *S. droebachiensis* is substantial in areas with an abundant supply of detritus, and can rival that of sea urchins in the shallow kelp beds that are a major source of this subsidy. The degree to which larvae produced by these deep populations are either locally retained or contribute to recruitment in kelp beds warrants further exploration. Interestingly, the vast body of research on sea urchin–kelp interactions in Nova Scotia and elsewhere (Filbee-Dexter & Scheibling 2014b) has focused almost entirely on a narrow band of rocky bottom between the intertidal zone and ~25 m depth. To a large extent, this reflects logistical constraints to direct observation within a 'blind zone' that exists between the deep (offshore) limit of non-technical scuba diving and the shallow (onshore) limit of camera platforms or submersibles deployed from large oceanographic vessels. Using a towed camera system deployed from a small coastal vessel has enabled us to visualize this blind zone for the first time off Nova Scotia. Our observations indicate that deep-living sea urchins, and the detrital subsidy upon which they rely, likely play a key role in the connectivity between adjacent habitats that influence ecosystem dynamics on much a broader scale than previously recognized.

4.6. ACKNOWLEDGEMENTS

We thank J. Lindley, C. Feehan, K. Krumhansl, F. Francis, and C. Robertson for field and laboratory assistance, and B. Miller for winter sea urchin collections. A.

Metaxas and 3 anonymous reviewers provided helpful comments on earlier drafts of the manuscript. This research was funded by a Discovery Grant and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F-D. was supported by a NSERC Canada Graduate Scholarship and a Dalhousie Killam Scholarship.

CHAPTER 5

LARGE-SCALE DEGRADATION OF A KELP ECOSYSTEM IN AN OCEAN WARMING HOTSPOT

The work presented in Chapter 5 also appears in:

Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Mar Ecol Prog Ser 543:141–152

5.1. ABSTRACT

Understanding the impacts of climate change on biological systems requires observational data over multi-decadal time spans and broad spatial scales. Extensive research at an ocean warming hotspot off Nova Scotia, Canada, enabled us to evaluate the impact of 3 decades of observed temperature rise on a coastal marine ecosystem. Here, we document changes in the kelp community from sites monitored since 1949, 1968 and 1984, and from coastal surveys in 1982, 2000, 2007 and 2014. We show that mean kelp biomass has declined by 85–99% over the past 4–6 decades, and a catastrophic phase shift has occurred from luxuriant kelp beds to rocky reefs dominated by opportunistic turf-forming and invasive algae. This shift likely represents a persistent change, driven by

multiple biotic and abiotic interactions, with positive feedback mechanisms (e.g. sediment accumulation) that stabilize the invasive/turf-algal state. This study is the first to show multi-decadal declines in kelp related to warming temperatures in the Northwest Atlantic. The large-scale degradation of an important coastal ecosystem within a warming hotspot presents a troubling example of the instability of marine systems in a rapidly changing ocean environment.

5.2. INTRODUCTION

Strong inference on the impacts of climate change on biological systems demands observational data over multi-decadal time spans and regional to global spatial scales (Parmesan et al. 2011). This is particularly challenging in marine systems, given a paucity of long-term data and the often-restrictive cost of large-scale surveys (Ducklow et al. 2009). Also, effects of rising ocean temperature frequently are masked by natural variability in ocean–atmospheric trends (Mochizuki et al. 2010 and anthropogenic impacts, such as overfishing and pollution (Brown et al. 2011). Regions in which ocean temperatures have changed most rapidly over the last 50 yr, termed warming hotspots, can act as natural laboratories for understanding climate change impacts (Pandolfi & Jackson 2006, Hobday & Pecl 2014).

Kelp beds (or forests) extend across a quarter of the world's coastlines (~26.7%, calculated from the observed range in Fig. 4 of Filbee-Dexter & Scheibling 2014b) and form some of the planet's most productive ecosystems, providing goods and services that coastal societies rely on for sustenance and economic stability (Vásquez et al. 2014).

Their functionality is derived largely from the structure of the beds themselves, which create complex 3-dimensional habitat for various life stages of fish and benthic invertebrates (Christie et al. 2003, Graham 2004). Kelps also provide food for numerous marine species (Norderhaug et al. 2003, Edgar et al. 2004) and detrital subsidies to adjacent shorelines and deep-water communities via dislodged fronds or fragments (Krumhansl & Scheibling 2012b). Like many other coastal ecosystems worldwide, kelp beds have been heavily altered and degraded by human activity during the last century (Steneck et al. 2002, Lotze et al. 2006).

Kelps generally require cold, nutrient-rich water and have a limited capacity for dispersal (Dayton 1985). They are particularly vulnerable to increases in ocean temperature that cause declines in reproduction or growth, or exceed physiological tolerance limits (Harley et al. 2012, Wernberg et al. 2013). Changing environmental conditions can also increase kelp loss indirectly by influencing biotic interactions, such as herbivory or epiphytism, that weaken kelp blades and increase fragmentation (Schiel et al. 2004, Andersen et al. 2011, Krumhansl et al. 2011b). Kelps typically inhibit growth of other seaweeds through shading (Kennelly 1989, Russell 2007), and loss of kelp canopy can facilitate establishment of understory species, including opportunistic or invasive macroalgae (Connell et al. 2008).

In the past 2 decades, shifts from dominance of kelp to turf-forming or invasive algae have been documented in South and Western Australia (Connell et al. 2008, Wernberg et al. 2013), Spain (Fernández 2011), France (Davoult et al. 2011), Sweden (Eriksson et al. 2002), Norway (Moy & Christie 2012), the western United States (Schiel et al. 2004) and Atlantic Canada (Scheibling & Gagnon 2009). Sediment accumulation by turfs and invasive algae inhibits kelp recruitment, limiting population recovery (Airoldi 2003, Schmidt & Scheibling 2007, Connell & Russell 2010). Researchers have identified the effects of acidification, eutrophication and extreme warming events in driving these shifts on metropolitan coasts (Airoldi et al. 2008, Connell & Russell 2010, Wernberg et al. 2013). Studies in Spain (Fernández 2011), Portugal (Tuya et al. 2012), Norway (Moy & Christie 2012) and Japan (Vergés et al. 2014) suggest that kelp loss along these coasts is the result of ocean warming in recent decades.

The Atlantic coast of Nova Scotia, Canada, historically has supported a luxuriant kelp bed ecosystem, dominated by *Saccharina latissima* and *Laminaria digitata*. Although episodes of intensive grazing by sea urchins (*Strongylocentrotus droebachiensis*) periodically destroyed kelp beds along large tracts of coastline (Wharton & Mann 1981), they were subsequently reinstated following sea urchin mass mortality from disease (Scheibling et al. 2013). Early research on kelp beds in a large embayment near Halifax (St. Margarets Bay) documented large standing biomass and primary productivity comparable to tropical rainforests (Mann 1972). Two species of invasive canopy-forming macroalgae co-occur with kelps in Nova Scotia: *Fucus serratus* and *Codium fragile fragile.* Introduced to disparate parts of the coast in the late 1800s and early 1990s, respectively, these seaweeds have expanded their range throughout eastern Canada in recent decades (Johnson et al. 2012, Matheson et al. 2014). Establishment of *C. fragile fragile* in Nova Scotia was facilitated by competitive release following defoliation of kelp beds by an invasive encrusting bryozoan *Membranipora membranacea* (Scheibling & Gagnon 2006, 2009). A similar process may have contributed to a recent range expansion of *F. serratus* along the central Atlantic coast of Nova Scotia (Johnson et al. 2012).

The Atlantic coast of Nova Scotia is one of 24 globally identified ocean warming hotspots (Hobday & Pecl 2014; Fig. 5.1), and has experienced increases in both summer (0.064°C yr^{-1}) and winter (0.039°C yr^{-1}) sea temperatures over the past 30–35 yr (Scheibling et al. 2013). During surveys in the last 5 yr we observed that kelp beds in St. Margarets Bay and elsewhere along the Nova Scotian coast have been replaced with mats or meadows of turf-forming and invasive algae. The extent and stability of this phase shift is unknown. An extensive body of empirical and theoretical research on the dynamics of this kelp-bed ecosystem, conducted over the past 5 decades (reviewed by Scheibling et al. 2013, Filbee-Dexter & Scheibling 2014b), makes it a useful model for examining the impact of warming sea temperatures. Here, we quantify the extent of kelp loss on the Atlantic coast of Nova Scotia and its replacement with opportunistic turf-forming and invasive algae, and assess the hypothesis that this shift is related to 3 decades of gradual ocean warming.

5.3. MATERIALS AND METHODS

5.3.1. Coastline surveys and long-term monitoring

Long-term data on kelp biomass and cover were compiled from published and unpublished studies spanning 30 to 65 yr (from 1949, 1968 or 1984 to 2014) at 3 sites along the Atlantic coast of Nova Scotia: one on the southwestern coast in Lobster Bay

(Whitehead Island, WI) and 2 on the central coast, in St. Margarets Bay (Mill Cove, MC) and at the mouth of Mahone Bay (Little Duck Island, LDI; Fig. 5.1, Appendix D: Table D1). In each study, divers collected kelps (*Saccharina latissima*, *Laminaria digitata* and *Agarum clathratum*) in summer/fall at 4–12 m depth in replicate 0.25–1 m^2 quadrats (n = 5–36), except in 1949, when a 0.42 m^2 metal grab was deployed from a wooden dory. For years with multiple sampling dates (1977, 2012 and 2014) we averaged across all samples. Kelp beds experienced destructive grazing events by sea urchins that created extensive coralline algal barrens along the Atlantic coast in the 1970s and again in the late 1980s through the 1990s (Filbee-Dexter & Scheibling 2014b). For our analysis, we considered only areas where kelp beds had re-established (>1 yr) following sea urchin mass mortality due to disease. Changes in kelp biomass or percent cover at each site were analyzed using a linear model or generalized linear model (GLM) with a Gaussian distribution and a log link function. The link function was determined using residual deviance; the link function and error distribution were assessed by inspection of residuals versus fitted values and normality plots. The autocorrelation structure of residuals was assessed using semi-variograms (R package nlme); no corrections were required.

We also measured change in percent cover at a greater spatial resolution and over the depth range of kelp at 7 sites from surveys in 1982 (Moore & Miller 1983) and 2014. Kelp cover was estimated visually by divers in 1982, and by analysis of images from a towed camera (tow speed: ~1 $m\ s^{-1}$ at 1 m above bottom) in 2014, in transects extending perpendicular to shore from the intertidal zone to the deep margin of the kelp bed (Appendix D: Table D2).

To examine the algal community composition over the last 14 yr, we measured percent cover of 4 types of non-encrusting macroalgae (kelp, turf-forming algae, and 2 species of canopy-forming invasive algae, *Codium fragile fragile* and *Fucus serratus*) from video surveys conducted at 22 sites along 145 km of coastline by Watanabe et al. (2010) in fall (September–November) 2000 and 2007, and repeated by us in fall 2014 (Appendix D: Table D2). At each site, video was recorded at 3 and 5 m depth, either by a diver swimming along a 25 m transect or using the towed camera along a 100 m transect. For each transect, 20 video frames (1 frame every 5 s) were analyzed, using only frames with a clear image on rocky substrata at depths suitable for kelp/macroalgal growth. We measured percent cover by overlaying a 10 × 10 grid of points onto each frame and counting the number of points over each algal type (Watanabe et al. 2010). Algal community composition was compared among 3 years (random factor: 2000, 2007 and 2014) and 3 coastal environments (fixed factor: headland, outer bay and inner bay; Appendix D: Fig. D1) using permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons using PERMANOVA *t*-statistic (Anderson et al. 2008). All PERMANOVA and post hoc comparisons used Bray-Curtis distances with 4999 permutations per test.

5.3.2. Turf and sediment collection

To examine relationships between kelp cover and turf-forming algae and sediments associated with turfs, we sampled twenty 1 m^2 quadrats in St. Margarets Bay in July/August 2014 using a stratified random sampling design (2 quadrats at ~3.5 km intervals alongshore). Each quadrat was photographed to measure canopy cover of kelp.

We then cleared kelp and other canopy algae from a 0.1 m^2 inset to photograph the understory, and collected turf-forming algae and associated sediments with a suction sampler (1 mm^2 mesh collection bag). Turf samples (cleaned of sediments) were oven-dried at 60°C for 72 h and weighed to obtain dry mass. Sediments extracted from turf samples were heated in a muffle furnace at 400°C for 6 h and weighed to obtain dry mass of inorganic sediment.

5.3.3. Temperature effects on kelp

To determine whether spatial variability in kelp cover can be explained by spatial variability in peak sea temperature, we acquired daily sea surface temperature (SST) off Nova Scotia for the annual thermal peak (August to mid-September) for 2002–2014 from MODIS Aqua SST images (11 mm daytime, 4 × 4 km spatial resolution) using Ocean Color Web (http://oceancolor.gsfc.nasa.gov/cgi/l3). We constructed grids of 3 × 3 SST pixels (12 × 12 km) that encapsulated our 22 survey sites along the central Atlantic coast (1–3 sites per grid), and the WI site on the southwestern coast, at relevant scales to capture variation in coastal environments (headland, outer and inner bay; see Appendix D: Table D2, Fig. D1). SST averaged over pixels (n = 9) within grids and over days during the annual peak (n = 45) for each year was then averaged across the 12 yr for each grid. Kelp percent cover, averaged over sites within grids, was then averaged for surveys in 2000, 2007 and 2014 (2007 and 2014 for WI). The effect of peak SST on kelp cover, measured at the grid scale and over a similar period, was analyzed using a GLM with a Gaussian distribution and a log link function (determined using residual deviance and graphical methods). To ensure model results were not influenced by spatial structure in our data, we assessed spatial autocorrelation of kelp cover from the central Atlantic sites (R package spdep). Moran's *I* tests using distance matrices based on Euclidean distances (Moran's *I* = 0.51, p = 0.306) and the 3-nearest neighbor method (Moran's *I* = 0.87, p = 0.194) indicated no significant spatial autocorrelation across sites.

To examine long-term trends in peak sea temperatures along the coast of Nova Scotia, which could explain declines in kelp biomass and cover, mean daily temperatures were acquired for 2004–2014 from a data logger (StowAway TidbiT Temp Logger, onset Computer) at 4 m depth at a site on the western shore of St. Margarets Bay (The Lodge, 4 km SSE of MC). To extend this record, mean daily temperatures from 1979 to 2004 were acquired from the Department of Fisheries and Oceans Canada (DFO) Coastal Time Series (CTS) database (http://bluefin2.dfo-mpo.gc.ca/ctsqry/index-e.html) from thermographs at 2 to 6 m depth within a 20 km radius of The Lodge. Given that dominant kelps in Nova Scotia lose tissue strength at sea temperatures >14°C and die if temperatures exceed 18°C for ≥2 wk or 20°C for ≥1 wk (Simonson et al. 2015b), we calculated the total number of days with sea temperatures above 5 levels at 2°C increments from 12 to 20°C for each year from 1979 to 2014. We also used these data to examine whether periods of peak temperatures that may influence the impacts on kelp of grazers, epiphytes and algal competitors were increasing along the coast.

PERMANOVAs were performed using the PERMANOVA+ add-on for Primer v.6 (Anderson et al. 2008). All other analyses were conducted using R v.3.1.0.

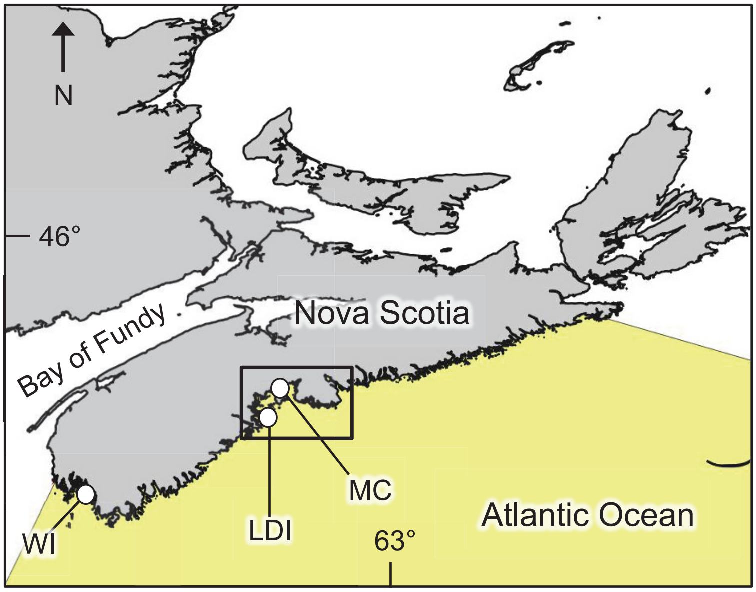


Fig. 5.1. Eastern Canada, showing locations of coastal surveys (box) and long-term study sites (WI: Whitehead Island; LDI: Little Duck Island; MC: Mill Cove) on the central and south-western coasts of Nova Scotia, within an ocean warming hotspot (yellow shading, after Hobday & Pecl 2014).

5.4. RESULTS

Diving surveys at 3 sites along the Atlantic coast of Nova Scotia, spanning 30 to 65 yr, showed that average biomass (kg m^{-2}) of mature kelp beds has declined by 85.0, 99.4 and 97.4% (WI, MC, and LDI, respectively) (Fig. 5.2a, Table 5.1). Declines in kelp biomass at these sites have led to a significant reduction in canopy cover (Fig. 5.2b, Table 5.1). This was more pronounced at LDI and MC (central coast) compared with WI (southwestern coast). At a greater spatial resolution, surveys in 1982 and 2014 showed that average kelp cover over this period declined by 89% across 7 sites spanning 110 km of coastline (Fig. 5.3). Surveys at 22 sites spanning 145 km of coastline in 2000, 2007 and 2014 indicated that the rocky bottom was dominated by turf-forming algal species (cover averaged across years: 52%; primarily filamentous red and brown algae) and 2 invasive canopy-forming species, *Codium fragile fragile* (12%) and *Fucus serratus* (18%), with kelp cover accounting for only 17% (Fig. 5.4). The number of sites at which *F. serratus* accounted for >10% of bottom cover increased from 5 to 8 between 2000 and 2014, due to replacement of kelp or *C. fragile fragile* at sites southwest of Mahone Bay (Fig. 5.4). PERMANOVA showed a significant effect of coastal environment on algal community composition ($p < 0.001$), but no effect of year or the interaction of year and environment (Table 5.2). Pair-wise comparisons indicated that algal communities differed between headlands, outer bays and inner bays (Table 5.2). Samples from St. Margarets Bay in 2014 show that biomass of turf-forming algae is negatively related to kelp cover (Fig. 5.5a,c). We also found a strong positive relationship between the mass of inorganic sediment and biomass of turf-forming algae (Fig. 5.5b,d).

A strong negative relationship exists between the seasonal peak in SST, averaged from 2002 to 2014, and percent cover of kelp, averaged for surveys in 2000, 2007 and 2014, indicating that kelp beds in warmer parts of the coast, such as large bays, have lower kelp cover (50% explained deviance GLM; Table 5.3, Fig. 5.6). Average sea temperature at 2–6 m depth on the central Atlantic coast of Nova Scotia increased by 1.58°C between 1979 and 2014, the period over which we observed substantial kelp loss (Fig. 5.3). Importantly, there has been a significant increase in the number of days with temperatures above thresholds for kelp tissue degradation (14°C) and mortality (18°C for ≥2 wk or 20°C for ≥1 wk) (Simonson et al. 2015b) (Fig. 5.7).

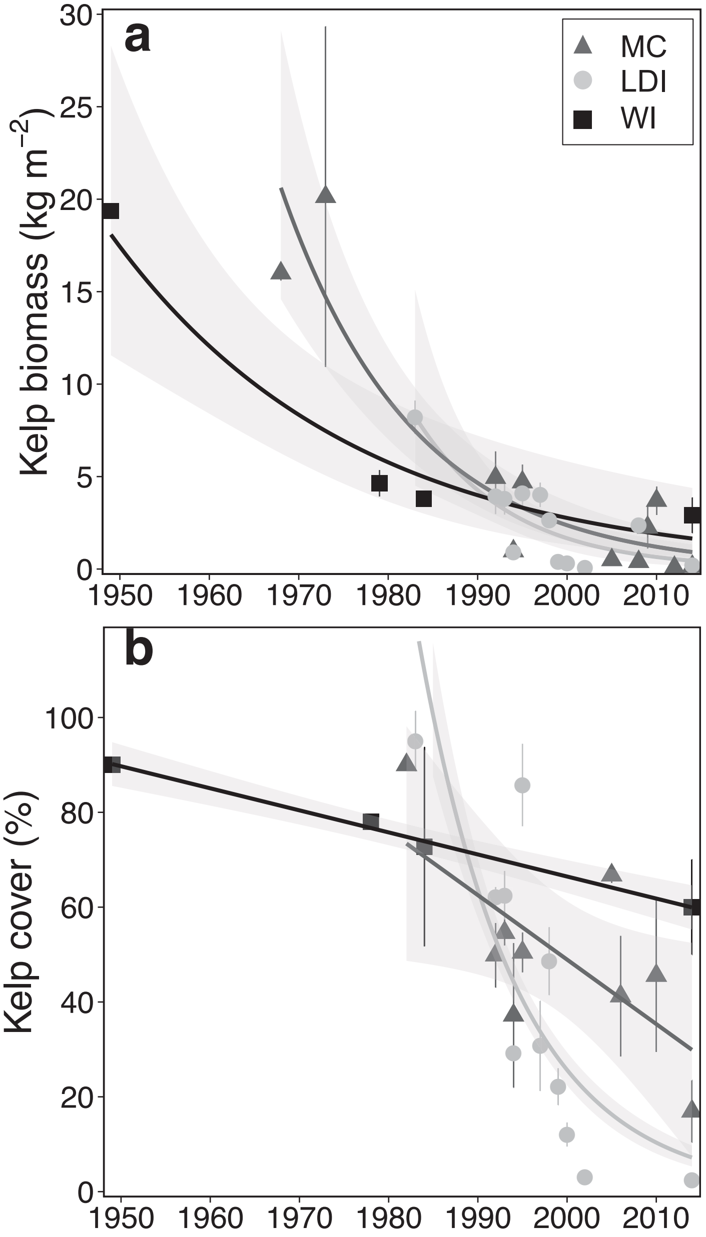


Fig. 5.2. (a) Kelp biomass (kg m−2) and (b) kelp cover (%) at 3 long-term study sites in Nova Scotia: Whitehead Island (WI), Little Duck Island (LDI) and Mill Cove (MC). Data are means ± SE for n = 5−36 quadrats (in some cases error bars are obscured by symbol). Trend lines ± 95% CI are fit using linear models or GLM (Gaussian, log link) (see Table 5.1).

Table 5.1. Model results for changes in kelp biomass or cover at 3 long-term sites in Nova Scotia (WI: Whitehead Island; LDI: Little Duck Island; MC: Mill Cove). Models are linear or generalized linear models (GLM: Gaussian, link = log). R^2 or explained deviance (%) describes fit to data (n = number of records) for respective model types.

Site/Model	Estimate	SE	*t*	p
Biomass				
WI: GLM				
Explained deviance = 87%; n = 4				
(Intercept)	59.7	17.1	3.5	0.073
Year	–0.03	0.01	–3.9	0.077
LDI: GLM				
Explained deviance = 71%; n = 12				
(Intercept)	190.1	37.6	5.1	<0.001
Year	–0.09	0.02	–5	0.001
MC: GLM				
Explained deviance = 47%; n = 11				
(Intercept)	120.8	23.4	5.1	0.001
Year	–0.06	0.01	–5	0.001
Cover				
WI: Linear				
$R^2 = 0.99$; n = 4				
(Intercept)	996.6	53.6	18.6	0.003
Year	–0.46	0.03	–17.2	0.003
LDI: Linear				
$R^2 = 0.65$; n = 11				
(Intercept)	6827	1654	4.1	0.003
Year	–3.39	0.83	–4.1	0.003
MC: GLM				
Explained deviance = 51%; n = 9				
(Intercept)	61.7	20.9	2.95	0.022
Year	–0.03	0.01	–2.75	0.028

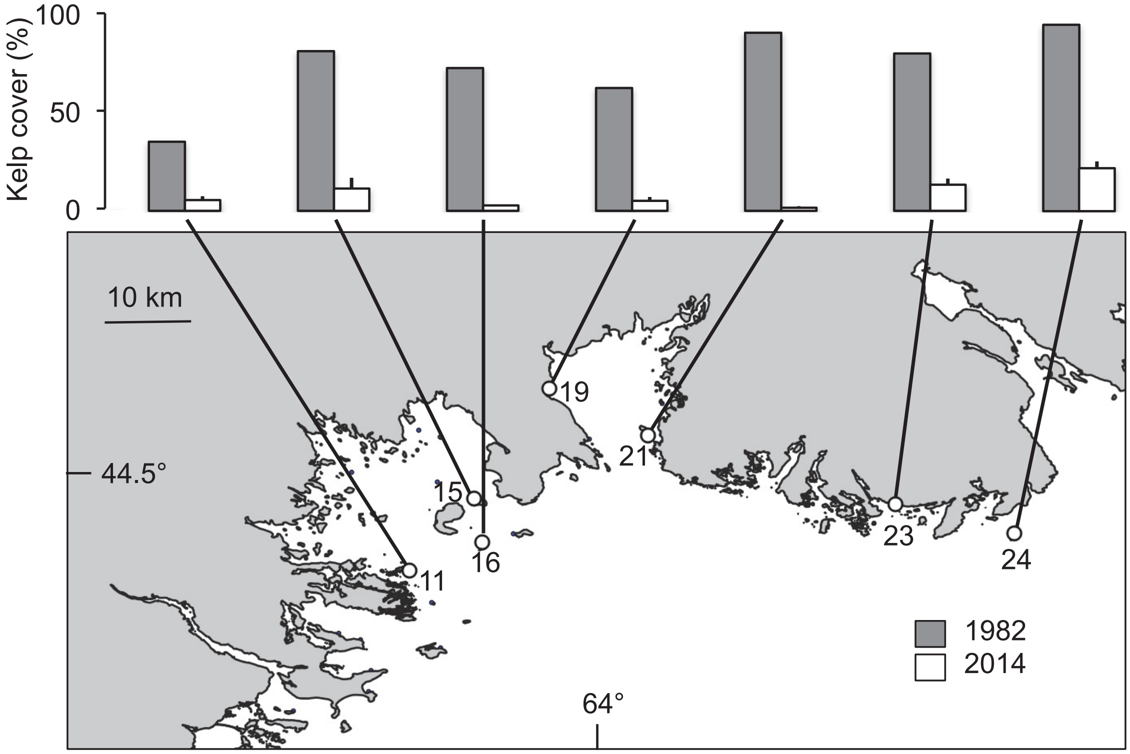


Fig. 5.3. Mean kelp cover (%) at 7 sites on the central Atlantic coast of Nova Scotia in 1982 and 2014. SE are shown for 2014, but were not available for 1982. For site locations, names/numbers and coordinates, see Appendix D.

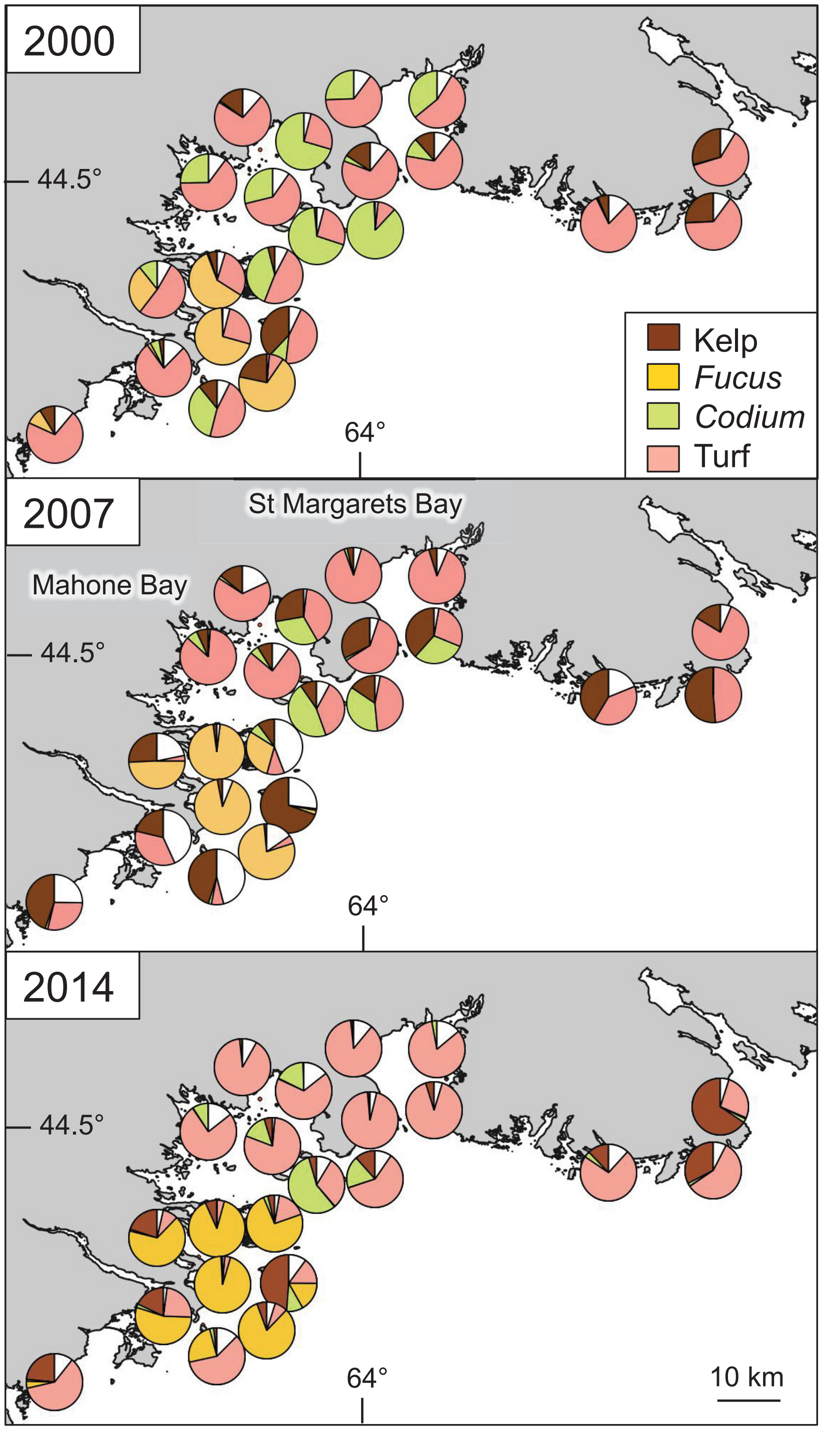


Fig. 5.4. Mean cover (%) of 4 macroalgal groups (kelp, *Fucus serratus*, *Codium fragile* spp. *fragile* and turf-forming algae) at 22 sites on the central coast of Nova Scotia in 2000, 2007 and 2014. White sections of pie charts refer to substratum that was unresolved, covered in crustose coralline algae or unsuitable for attached algae (e.g. sand patches). To minimize overlap, some charts are offset from site locations. For site locations, names/numbers and coordinates see Appendix D.

Table 5.2. Permutational multivariate analysis of variance (PERMANOVA) of effects of year (random factor: 2000, 2007 and 2014) and coastal environment (fixed factor: headland, H; outer bay, O; and inner bay, I), on algal community composition using Bray-Curtis dissimilarities. Also shown are pairwise comparisons using the PERMANOVA *t*-statistic. Tests are based on 4999 permutations

Source	df	MS	Pseudo-*F*	p (perm)
Environment	2	1.71	22.1	<0.001
Year	2	0.28	2.11	0.067
Environment × Year	4	0.08	0.59	0.839
Error	57	0.13		
Pairwise comparison		***t***		**p (perm)**
O vs. I		6.19		0.022
I vs. H		3.38		0.020
H vs. O		4.10		0.015

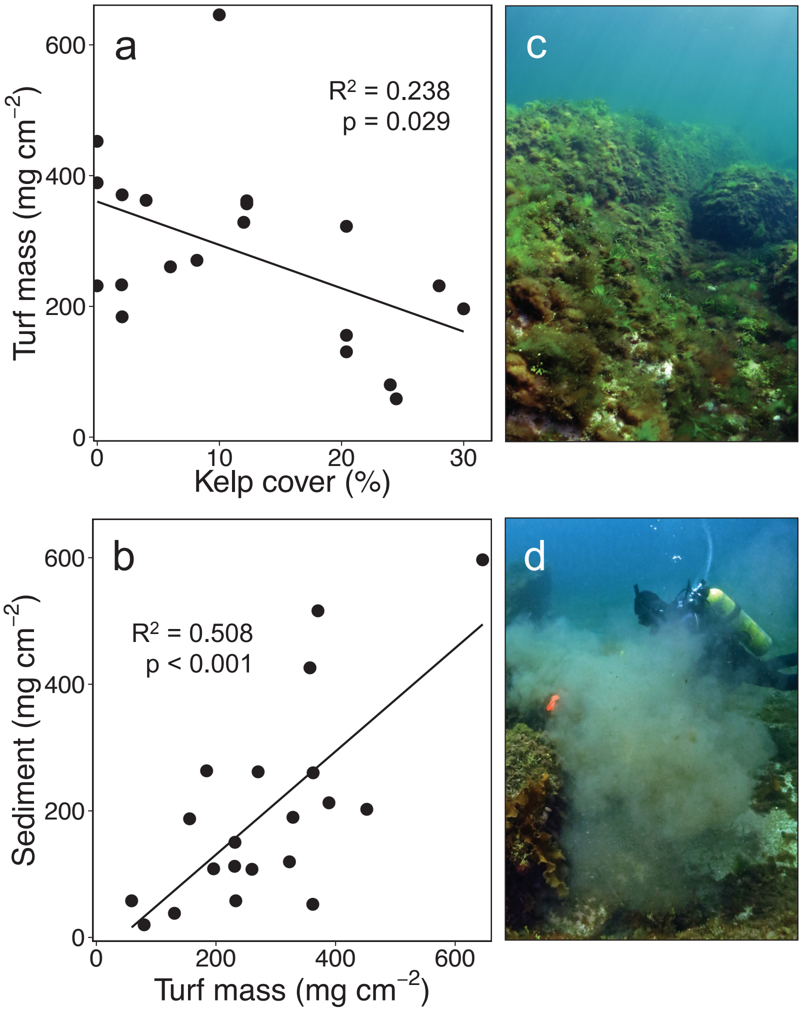


Fig. 5.5. Relationship between (a) dry mass (mg cm^{-2}) of turf-forming algae and kelp cover (%), and (b) dry mass of inorganic sediment (mg cm^{-2}) and turf-forming algae in St Margaret's Bay in 2014. Trend lines are based on linear regression of turf mass against kelp cover ($y = -6.7x + 381$) and sediment mass against turf mass ($y = 0.83x - 32$). Photographs show (c) turf algae at 4–5 m depth in St. Margarets Bay (2013) and (d) a sediment plume generated by a diver scraping turf from coralline-encrusted boulders (2014). Photographs: R. E. Scheibling.

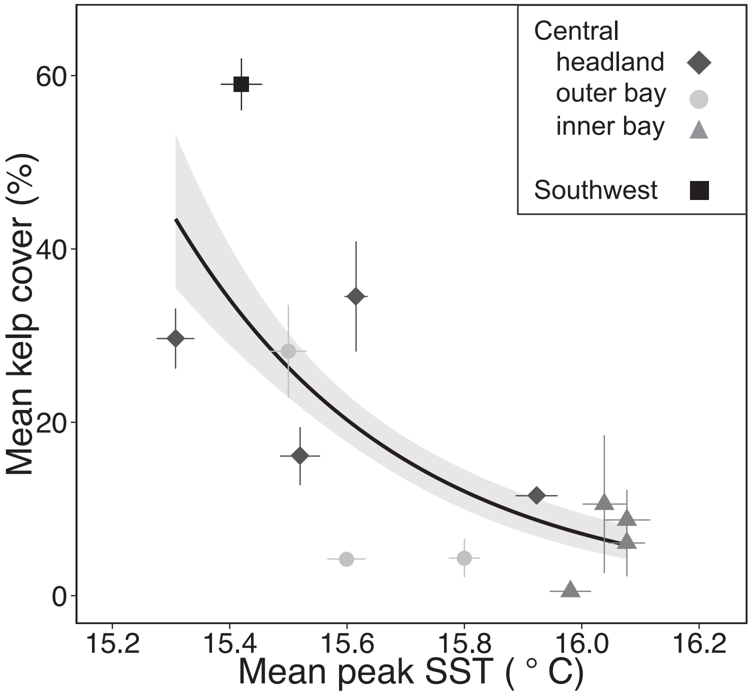


Fig. 5.6. Relationship between mean kelp cover (%) in 2000, 2007 and 2014 and mean peak (August–mid September) sea surface temperature (SST; °C) in 2002–2014 within grids representing 3 coastal environments along the central Atlantic coast of Nova Scotia (headland, outer bay, inner bay) and a site on the southwestern coast at the mouth of the Bay of Fundy (Whitehead Island). Vertical and horizontal error bars are ±1 SE of mean kelp cover and SST (n = 3 and 13 yr, respectively). Trend line ± 95% CI was fit using a GLM (Gaussian, log link). For site and grid locations see Appendix D.

Table 5.3. Generalized linear model (Gaussian, link = log) results for the relationship between average peak sea surface temperature (SST; 2002–2014) and average kelp cover (2000, 2007 and 2014) measured in grids that encapsulate 22 survey sites along the central Atlantic coast and one site on the southwestern coast of Nova Scotia. Results using data from the central Atlantic grids only are also shown. Model family and link function were selected using residual deviance and graphical methods

Coefficient	Estimate	SE	*t*	p
All grids				
(Intercept)	41.6	15.3	2.7	0.022
SST	–2.5	1.0	–2.5	0.032
Null deviance	3205 on 11 df			
Residual deviance	1602 on 10 df			
Deviance explained	0.50			
Central Atlantic grids				
(Intercept)	35.0	12.2	2.9	0.018
SST	–2.1	0.8	–2.6	0.027
Null deviance	1352 on 10 df			
Residual deviance	687 on 9 df			
Deviance explained	0.49			

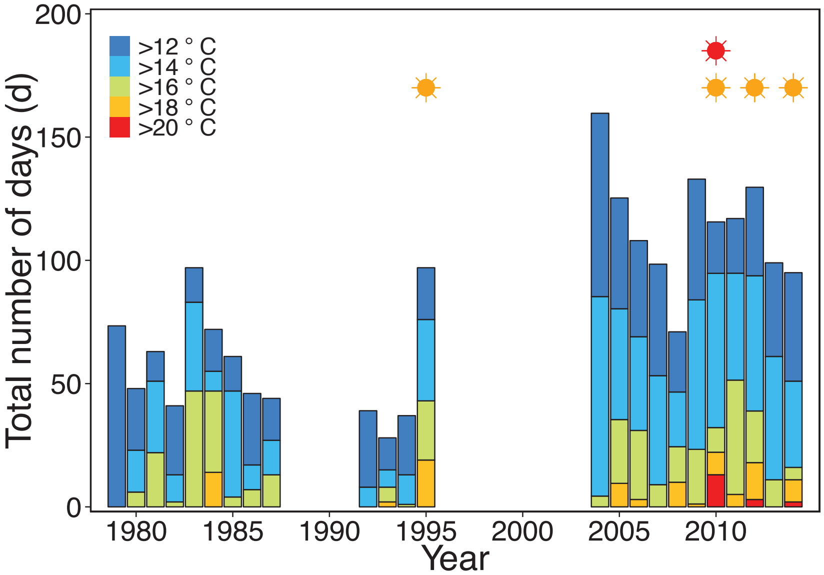


Fig. 5.7. Total number of days (d) with mean sea temperature above each of 5 levels (12, 14, 16, 18 and 20°C) in years from 1979−2014. Orange and red stars indicate years when sea temperature exceeded 18°C for ≥2 wk or 20°C for ≥1 wk, respectively, thresholds expected to cause significant kelp mortality. Records are from 2 to 6 m depth at sites within a 20 km radius of St. Margarets Bay (data sources: Department of Fisheries and Oceans Canada (DFO) Coastal Time Series (CTS) database — http://bluefin2.dfo-mpo.gc.ca/ctsqry/, and the present study). Gaps in record indicate years with missing data.

5.5. DISCUSSION

5.5.1. Temperature as a driver of kelp loss and ecosystem change

We show that kelp biomass off Nova Scotia has declined by 85–99% over the past 4–6 decades, resulting in a catastrophic phase shift from kelp beds to rocky reefs dominated by opportunistic turf-forming and invasive algae along the central Atlantic coast. This shift has been associated with warming sea temperatures that are modifying biological processes and interactions that contribute to kelp loss. Mean annual maximum (August–October) temperatures over the last 3 decades along the central coast (Scheibling et al. 2013) have approached or exceeded the upper limit of the optimal growth range of *Saccharina latissima* (10–15°C; Bolton & Lüning 1982) and *Laminaria digitata* (11–13°C; Pérez 1971). Although slow growth may not directly impact kelp condition, it could leave thalli more vulnerable to overgrowth by epiphytes (Andersen et al. 2011), including the encrusting bryozoan *Membranipora membranacea*. Perhaps more damaging are prolonged periods of thermal stress during peak temperatures. In the last decade, sea temperature repeatedly exceeded thresholds shown in laboratory experiments to cause serious cellular damage to kelp tissue, resulting in decreased strength and extensibility, or increased mortality (Simonson et al. 2015b).

Rising sea temperatures also indirectly affect rates of kelp tissue loss and mortality by favouring growth of *M. membranacea* (Saunders et al. 2010). Extensive overgrowth of kelp blades by bryozoan colonies decreases tissue strength, increasing fragmentation of blades during fall and winter storms (Krumhansl et al. 2011). This has resulted in a progressive loss of kelp canopy along the central Atlantic coast of Nova Scotia since the early 1990s (Scheibling & Gagnon 2009). Increased recruitment of *M. membranacea* has been attributed to warm winter temperatures (Saunders & Metaxas 2008) and the growth rate of the bryozoan is highly dependent on annual maximum temperatures in summer/autumn (Scheibling & Gagnon 2009, Saunders et al. 2010). In modelling the effects of rising temperature on detrital kelp production, Krumhansl et al. (2014) predicted that temperatures along this coast prior to 1983 would have been unsuitable for *M. membranacea* to establish colonies on kelp, even if it had been introduced over that period.

Although we found compelling evidence linking kelp loss in Nova Scotia to warming sea temperature in recent decades, identifying ecosystem-level responses to changes in ocean climate is complicated by local anthropogenic stressors (e.g. overfishing, eutrophication, pollution, species introduction) that can influence these dynamics (Strain et al. 2014). Interactions among multiple stressors can be nonlinear and temperature dependent (Crain et al. 2008). For example, the combined impacts of encrustation by *M. membranacea*, grazing by *Lacuna vincta* (O'Brien et al. 2015) and tropical storms (Filbee-Dexter & Scheibling 2012) that are increasing in severity with warming ocean temperatures (Scheibling et al. 2013) likely are operating synergistically to increase kelp defoliation during autumn and winter months (Krumhansl et al. 2014). In contrast, Simonson et al. (2015a) found that the temperature effects on kelp tissue did not influence settlement of *M. membranacea* or grazing by *L. vincta* on kelp blades in laboratory experiments, indicating that direct and indirect effects of temperature-mediated changes in kelp tissue, at least for these processes, were likely additive in terms of kelp loss.

In a review of the health of macroalgal beds in the Northeast Atlantic, Mineur et al. (2015) identified warming temperatures and invasive species as the 2 key threats facing these ecosystems. Understanding the extent to which range shifts induced by changing climate are mediated by biological interactions has become a critical question in climate change research (HilleRisLambers et al. 2013). These interactions can include changes in abundance of competitors that prevent invasive species from colonizing new habitats, environmental conditions that favour growth or reproduction of invasive over native species, or changes in consumption or disease severity (HilleRisLambers et al. 2013). In the Northwest Atlantic, kelp defoliation by *M. membranacea* facilitates colonization by the invasive macroalga *Codium fragile fragile* (Levin et al. 2002, Scheibling & Gagnon 2006). *Codium fragile fragile*, like *M. membranacea*, also benefits from warming temperatures, with maximal growth at ~24°C and a lower thermal threshold for reproduction at 12°C (Hanisak 1979). The effect of temperature on range expansion of another invasive macroalga, *Fucus serratus*, is less clear (Johnson et al. 2012). Temperature is known to affect embryonic growth, with maximum development at 18°C (Arrontes 1993), which may explain the dominance of *F. serratus* in the warmest regions of Nova Scotia (Johnson et al. 2012). Our surveys show that *C. fragile fragile* currently is a relatively minor component of the algal assemblage compared with *F. serratus* or turf-forming algae.

Currently, kelp beds off Nova Scotia occur mainly along the cooler headlands, and we found the greatest biomass and cover at WI, where strong tidal flushing from the

Bay of Fundy results in cool sea temperatures and high nutrient availability (Garrett & Loucks 1976). Neighbouring coastlines in the northern Gulf of Maine, northern Gulf of St. Lawrence and Newfoundland are also colder than the Atlantic coast of Nova Scotia (Drinkwater 1996, Mathieson et al. 2003). In these regions, spread of *F. serratus* and *C. fragile fragile* has been somewhat limited (Mathieson et al. 2003, Johnson et al. 2012) and encrustation by *M. membranacea* is less extensive than in Nova Scotia (Sisson 2005, Caines & Gagnon 2012). Perhaps for these reasons, healthy kelp beds continue to dominate rocky reefs in these neighbouring areas (Merzouk & Johnson 2011).

5.5.2. Phase shift to invasive-/turf-algal dominated reefs

Kelp beds in Nova Scotia experience natural cycles of canopy loss during late summer and autumn, when temperatures peak and storm intensity increases (Krumhansl & Scheibling 2011a), followed by periods of rapid recruitment and growth during cold winter and spring months (Scheibling et al. 1999). Positive feedback mechanisms that limit the seasonal regeneration of kelp beds can stabilize the alternative invasive-/turf-algal state. Fast-growing turfs and invasive algae such as *C. fragile fragile* overgrow crustose coralline algae and have branching morphologies that trap and accumulate sediment (Airoldi 2003, Schmidt & Scheibling 2007, Connell & Russell 2010). This limits suitable hard substratum required for spore settlement and reduces rates of germination and survival of kelp gametophytes (Devinny & Volse 1978, Kennelly 1989). Allee effects on kelp populations also may stabilize the alternative algal state. A sudden or prolonged loss of kelp results in declining fertilization rates as reproductive sporophytes become rare (Dayton 1985). This is compounded by the short dispersal range of spores (typically 1–10 m, Gaylord et al. 2012), which limits the rate and extent of population recovery (Johnson & Mann 1988). Furthermore, decreased sporophyte density will concentrate grazing by *L. vincta* on fewer remaining plants, where they target reproductive tissue directly and indirectly accelerating kelp loss (O'Brien et al. 2015, O'Brien & Scheibling 2016). It is also possible that reefs dominated by opportunistic and invasive species are less stable than kelp beds because of faster turnover rates, complicating our ability to predict subsequent changes in ecosystem state (HilleRisLambers et al. 2013).

An important change in community dynamics of Nova Scotian kelp beds is the recent elimination of sea urchins *Strongylocentrotus droebachiensis* on a coastal scale due to recurrent outbreaks of disease (Scheibling et al. 2013). Sea urchins destructively grazed kelp beds along this coast in the 1970s, 1980s and 1990s, creating widespread coralline-algal barrens (Wharton & Mann 1981, Scheibling et al. 1999). Episodic outbreaks of disease and mass mortality of sea urchins enabled kelp beds to re-establish within 2–3 yr (Scheibling et al. 1999). Current projections based on ocean warming and tropical storm activity indicate a high probability of disease every year (Scheibling et al. 2013, Buchwald et al. 2015). This has prevented recolonization of the shallow zone by sea urchins, and should lead to dominance of kelps or other macroalgal species. Historically, low-density populations of sea urchins within kelp beds (Feehan & Scheibling 2014) may have limited turfs and other understory algae (Sumi & Scheibling 2005). Elimination of these sea urchin populations by recurrent disease outbreaks (Feehan & Scheibling 2014) may have rendered the kelp-bed community more vulnerable to a shift to turf-forming algae.

Replacement of kelp beds with mats or meadows of invasive and turf-forming algal species is occurring within the context of global declines in kelp biomass due to human impacts (Steneck et al. 2002, Filbee-Dexter & Scheibling 2014b, Mineur et al. 2015) and a trend towards increased dominance of turf-forming algae in various marine ecosystems, including coral reefs (McCook et al. 2001), coastal macroalgal beds (Benedetti-Cecchi et al. 2001, Wernberg et al. 2013), seagrass meadows (Waycott et al. 2009) and rocky intertidal assemblages (Airoldi et al. 2008). These shifts have been attributed to various anthropogenic stressors, including changing oceanographic conditions (warming, acidification), eutrophication, sediment loading and disease (Pedersen & Borum 1996, Gorgula & Connell 2004, Schiel et al. 2004, Andersen et al. 2011, Mineur et al. 2015). However, unlike other more populated coastlines, Nova Scotia is largely undeveloped. The average population density within the 4 counties that span our study region (Shelburne, Queens, Lunenburg and Halifax) has remained relatively constant between 1996 (22.7 km^{-2}) and 2011 (24.4 km^{-2}) (Statistics Canada 2001, 2012). This suggests that local anthropogenic impacts, such as changes in water quality or sediment loading, are not a necessary pre-condition for phase shifts from kelps to turf-forming or invasive algae.

Understanding ecosystem dynamics on multi-decadal time scales remains a challenging but increasingly urgent aim of community ecology, particularly from a socioeconomic perspective. Empirical studies of temporal variability in marine ecosystem structure often are limited to a few decades, requiring the use of mathematical models to investigate stability over longer time scales (Savage et al. 2000). This is especially true for subtidal reefs, which usually require scuba or submersible camera technology for sampling. For example, there are few quantitative data on coral species abundance on tropical reefs before the 1960s (Pandolfi & Jackson 2006). Our record of large-scale decline in Nova Scotian kelp beds over 4–6 decades is exceptional both in extent and location within an ocean warming hotspot. This long-term change in an ecologically and economically important coastal system presents a cautionary message for other marine ecosystems in the face of rapid environmental change.

5.6. ACKNOWLEDGEMENTS

We thank J. Lindley, J. O'Brien, E. Bonang and E. Higgins for field or laboratory assistance. K. Krumhansl, A. Metaxas and J. O'Brien provided helpful comments on an early draft. This research was funded by a Discovery Grant and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F.-D. was supported by a NSERC Canada Graduate Scholarship and a Dalhousie Killam Scholarship.

CHAPTER 6

SPATIAL PATTERNS AND PREDICTORS OF DRIFT ALGAL SUBSIDY IN DEEP SUBTIDAL ENVIRONMENTS

The work presented in Chapter 6 also appears in:

Filbee-Dexter K, Scheibling RE (2016) Spatial patterns and predictors of drift algal subsidy in deep subtidal environments. Est Coasts. DOI 10.1007/s12237-016-0101-5ww

6.1. ABSTRACT

The movement of resource subsidies across natural systems can have important effects on recipient communities, and has emerged as a key research area in ecology. Detrital subsidies are critical in marine ecosystems where communities are reliant on external sources of primary production, yet few studies have quantified the spatial extent of drift algae at coastal scales. Using observations of the seafloor (up to 140 m depth) from tow-camera surveys along 145 km of Nova Scotia coast, and bathymetric data of this region, we created the first predictive map of drift subsidy in a marine ecosystem. We used a random forest model to generate our predictions, which correctly classified

95% of observations into a presence or absence of drift. Distance from source, slope and bathymetric position index (elevation relative to surrounding landscape) were the main predictor variables of the occurrence of drift. Drift algae occurred across a range of benthic habitats within our study area, but most frequently within 1.4 km of the coast on flat bottoms or in regions with zero or negative bathymetric position index. Such areas were coincident with seafloor depressions and flat low-energy habitats. Repeated observations at some locations indicated that areas with steep slopes or large curvature tended to have variable patterns of drift compared to areas with little or no slope or curvature. We predict that deep subtidal environments receiving drift subsidy will be impacted by the declines in kelp biomass projected for this region (and others) due to changes in ocean climate.

6.2. INTRODUCTION

The movement of resource subsidies across natural systems, and its effects on recipient communities, has emerged as an important area of research in terrestrial and aquatic ecology (Polis et al. 1997). Empirical studies over the past two decades have shown that energy flow across neighbouring systems, in the form of nutrients (Anderson & Polis 1999, Ellis et al. 2006, Kolb et al. 2010), prey (Rose & Polis 1998, Nakano et al. 1999, Murakami & Nakano 2002, Willson et al. 2010) or detritus (Duggins et al. 1989, Polis & Hurd 1995, Norkko et al. 2000), can alter patterns of species abundance and composition at lower trophic levels (Barrett et al. 2005), with attendant changes in food web structure (Hajal & Wise 2002, Piovia-Scott et al. 2011). These spatial subsidies can have important consequences for meta-ecosystem dynamics and functioning (Loreau et al. 2003, Gravel et al. 2010), especially when links occur between habitats of high and low productivity, or when recipient communities are limited by the subsidized resource (Polis et al. 1997).

Once such linkage in coastal marine ecosystems is the export of detached kelp and other large seaweeds (termed "drift algae") to deeper offshore areas with little *in situ* primary production, where they support a diverse array of primary and secondary consumers (Duggins & Eckman 1997, Vetter 1998, Krumhansl & Scheibling 2012b). Drift algae are produced through erosion, fragmentation and breakage (Krumhansl & Scheibling 2011a, de Bettignies et al. 2013) and are an important food source for detritivores and benthic invertebrates, resulting in enhanced faunal abundance and diversity compared to surrounding habitats (Harrold et al. 1998, Hyndes et al. 2012, Hyndes et al. 2014, Ramirez-Llodra et al. 2016). Vetter (1998) showed that mats of trapped drift algae in submarine canyons at 153 – 454 m depth off California, USA, supported communities with some of the highest productivity measured in natural systems. Britton-Simmons et al. (2009) found that drift kelp in subtidal habitats at 30 – 170 m depth off Washington, USA, provided food and habitat for sea urchins and small invertebrates. Similarly, Filbee-Dexter and Scheibling (2014a) attributed high rates of reproduction of sea urchins at 60 m depth off Nova Scotia, Canada, to periodic inputs of drift kelp, and Krumhansl and Scheibling (2012a) quantified the development a rich macrofaunal community on this kelp as it degraded. While deposits of drift material clearly play a key role in structuring marine benthic communities, this dynamic is technically challenging to investigate beyond the depth limit of scientific diving, and few studies have quantified the spatial extent of drift subsidy at coastal scales (but see Britton-Simmons et al. 2012).

In highly connected ecosystems, impacts to a source community will have consequences for recipient communities that extend beyond the spatial bounds of the impacted system. Kelp beds (or forests) range across a quarter of the world's coastlines (Filbee-Dexter & Scheibling 2014b) and, like many other coastal ecosystems worldwide, have been heavily altered and degraded by human activity during the last century (Steneck et al. 2002, Lotze et al. 2006, Filbee-Dexter et al. 2016). In recent decades, kelp loss due to sea urchin grazing, ocean warming, and eutrophication has been documented in Australia (Connell et al. 2008, Ling et al. 2009, Wernberg et al. 2012), Spain (Fernández 2011), Portugal (Tuya et al. 2012), France (Davoult et al. 2011), Sweden (Eriksson et al. 2002), Norway (Moy & Christie 2012) the western United States (Schiel et al. 2004), Japan (Vergés et al. 2014), and Atlantic Canada (Filbee-Dexter et al. 2016).

In Nova Scotia, 90% of kelp biomass enters detrital food webs (Mann 1988), where it rafts onshore or is exported to greater depths (Krumhansl & Scheibling 2012b). To document the export of this detrital production within a coastal ecosystem, we examined spatial patterns of deposition and retention of drift algae along the Atlantic coast of Nova Scotia. We quantified the distribution of drift algae in deep subtidal habitats with video surveys and used statistical modeling to relate the occurrence of drift to environmental variables. We show that drift algae are common in deep subtidal habitats, and that their pattern of occurrence depends largely on the bathymetry of the seafloor and distance to source of algal production. Our model accurately predicts landscape patterns of drift algal subsidy that likely supports enhanced benthic community production along this coast.

6.3. MATERIALS AND METHODS

6.3.1. Video surveys of drift algae

The seafloor along the Atlantic coast of Nova Scotia from Halifax Harbour to Liverpool was surveyed for drift algae from August 2010 to September 2015 (Fig. 6.1). Surveys were conducted using a digital video-camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor dive wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search Equipment) that was towed at an average speed of 0.7 m s^{-1} from a 7-m research vessel or a 9-m sailboat. Two fixed lasers and two dive lights were attached to either side of the camera to provide scale (20 cm) and light the bottom, respectively, in the video record. The camera was maintained ~ 2 m above bottom using a hydraulic slip-ring winch with a ship-board controller (Shark Marine Technologies). Most video transects began in kelp beds at 2 − 5 m depth or off submerged shoals or ledges and extended perpendicularly across depth contours to a maximum depth of 140 m. For surveys conducted between August 2010 and February 2011, we measured depth along a video transect using side-imaging sonar (1198c Side Imaging Sonar, Humminbird), lagged by 20 s every 10 min to account for the positional offset between camera and vessel. For surveys after February 2011, we used an acoustic transponder to directly record depth of the camera (Tracklink 1500 USBL tracking system, LinkQuest). The positional offset for surveys conducted before

February 2011 was determined by comparing records from the acoustic transponder and side-imaging sonar for the same video transects. In total, 117 transects were conducted across the entire study area (Appendix E: Table E1), amounting to 48,531 analyzed video frames, each encompassing ~ 1 m^2 of seafloor.

To measure drift algae in video surveys, each transect was viewed in iMovie (version 9.0.4, Apple) in real time and the presence or absence of drift algae was entered into an Excel macro, synchronized with the video time. The Excel macro tabulated measurements every second, which was sufficient to avoid frame overlap. We aggregated these point observations of drift algae in 900 m^2 grid squares (30-m cell resolution; n = 7459), which matched the resolution and spatial boundaries of our environmental predictor data (see section 6.3.2. Modeling abundance of drift algae). Grids with at least 1 observation of drift algae were assigned a presence and grids with no observations of drift algae were assigned an absence measure. The number of observations within each grid ranged from 1 to 42, with 90% of grids containing 3 – 18 observations.

6.3.2. Modeling abundance of drift algae

To acquire explanatory variables for our predictive distribution model, we used environmental layers that we deemed important for the deposition of drift algae (Appendix E: Table E2). Coastal maps of bottom type, bottom current and a digital elevation model (DEM) of 30-m cell resolution (created by combining point and contour data from the Canadian Hydrographic Service and the Nova Scotia Geomatics Centre) were obtained from the Department of Fisheries and Oceans, Canada (DFO) (Greenlaw et al. 2013). The processed bathymetry data was used to produce 6 additional layers of seafloor terrain properties using Spatial Analyst and Benthic Terrain Model tools (ARCGIS 9.3): slope; planar, profile and standard curvature; and fine-scale and broad-scale bathymetric position index (BPI). Standard curvature describes concavity (e.g., trough or depression) or convexity (e.g., ridge) of the seafloor, planar curvature describes concavity/convexity measured perpendicular to the aspect of the slope, and profile curvature describes concavity/convexity measured parallel to the aspect of the slope. Fine-scale and broad-scale BPI are measures of a location relative to its surrounding area, and also describe concavity (negative values) or convexity (positive values) of the seafloor. We used a 90-m and 300-m radius for fine-scale and broad-scale respectively, which corresponded to the spatial scale of shoals and near-shore basins in our study area. BPI values near zero represent flat areas or areas with constant slope. To approximate the nearest distance to a source of attached macroalgae, we calculated the distance to coast as the shortest length from the centre of a 30-m grid cell to shore (km) using ARCGIS. Our video surveys showed that kelp beds occurred within 0.5 km from shore, with an average distance of 0.23 km, supporting our approximation. We only included one hydrographic variable (bottom current) in our initial model, which was available in a low-resolution layer for our study area (~1 measure per 4 – 5 km^2). Other important hydrographic data for predicting the movement of drift algae, such as the direction of bottom currents and water mass properties, were not available. The variables included in our final model were selected using variable correlation analysis and misclassification rates of random forest models using different subsets of predictor variables (Appendix E).

To evaluate the relative importance of predictor variables in determining the occurrence of drift algae we used a random forest model. Random forest is an advanced version of a classification and regression tree that successively splits data into categories based on single variables (Breiman 2001). Each tree is grown from a randomized subset of predictor variables. It uses an algorithm to grow a large number of trees (in our case 1000), and then averages the output to produce a vector of the most common variables contributing to splits in the data (Breiman 2001). The model output for this study was the probability of classifying a grid as a presence (1) or absence (0) observation of drift. We selected this model type because it is one of the most accurate learning algorithms available and has demonstrated high performance in predicting species distributions (Iverson et al. 2008, Li & Wang 2013). A random forest model is ideal for cases with noisy, non-linear data and strong interaction effects, and does not overfit complex models (Iverson et al. 2008, Li & Wang 2013). It also is only moderately influenced by geographical attributes, such as spatial autocorrelation, compared to generalized additive models or generalized linear models (Marmion et al. 2009).

The analysis was conducted with the randomForest package in R. Relationships between predictor variables and the response variable were visualized using partial dependence plots, which show the effect of one variable on the probability of drift algae while controlling for effects of other variables in the model (Hastie et al. 2001). We evaluated the explanatory power of our model using rates of misclassification, which is a goodness of fit measure for random forest models (Appendix E).

6.3.3. Temporal pattern of drift algae

During our 5-year study we revisited several regions of the coast, which resulted in a subset of coordinate points being sampled multiple times. To examine temporal change in patterns of drift algae, we identified 112 grid cells (30-m cell resolution) that contained coordinate points surveyed more than once and determined whether the presence or absence of drift algae changed between sampling dates. For 6 coordinate points with more than 2 observations, we only compared the earliest and latest. To identify if bathymetric features influenced the temporal pattern of occurrence of drift algae, we compared environmental features between grids with unchanged patterns of algal occurrence and grids with variable patterns of occurrence using a random forest model.

6.3.4. Predictive mapping

We produced a map of occurrence of drift algae between Port Joli and Jeddore (Fig. 6.1) using our random forest model based on direct observations of drift and the environmental layers for this section of coast. We used two forms of cross-validation to evaluate the accuracy of our random forest model (Hijmans 2012). First, to evaluate our model performance within the main study area, we randomly partitioned our observations into a training sample (70% of points) and a testing sample (30%). We repeated this 20 times, and for each iteration fitted the model with training data and evaluated its predictions for sites of known presence or absence of drift algae using testing data. Second, to evaluate our model with statistically independent data, i.e. not spatially autocorrelated with training data (Araújo et al. 2005), we conducted 8 additional transects near the southern-most region of our map near Port Joli (~50 km southwest of our study area; Fig. 6.1). For these transects, we altered our sampling method by drifting alongshore with the wind and current instead of steaming perpendicular to the coast. We used these observations of the seafloor (n = 156 grid cells) to test the accuracy of our model predictions in an area not used to build the model. We assessed model performance for both these areas using the area under the receiver-operator-curve (Hanley & McNeil 1982), and the true skill statistic (Allouche et al. 2006) (Appendix E).

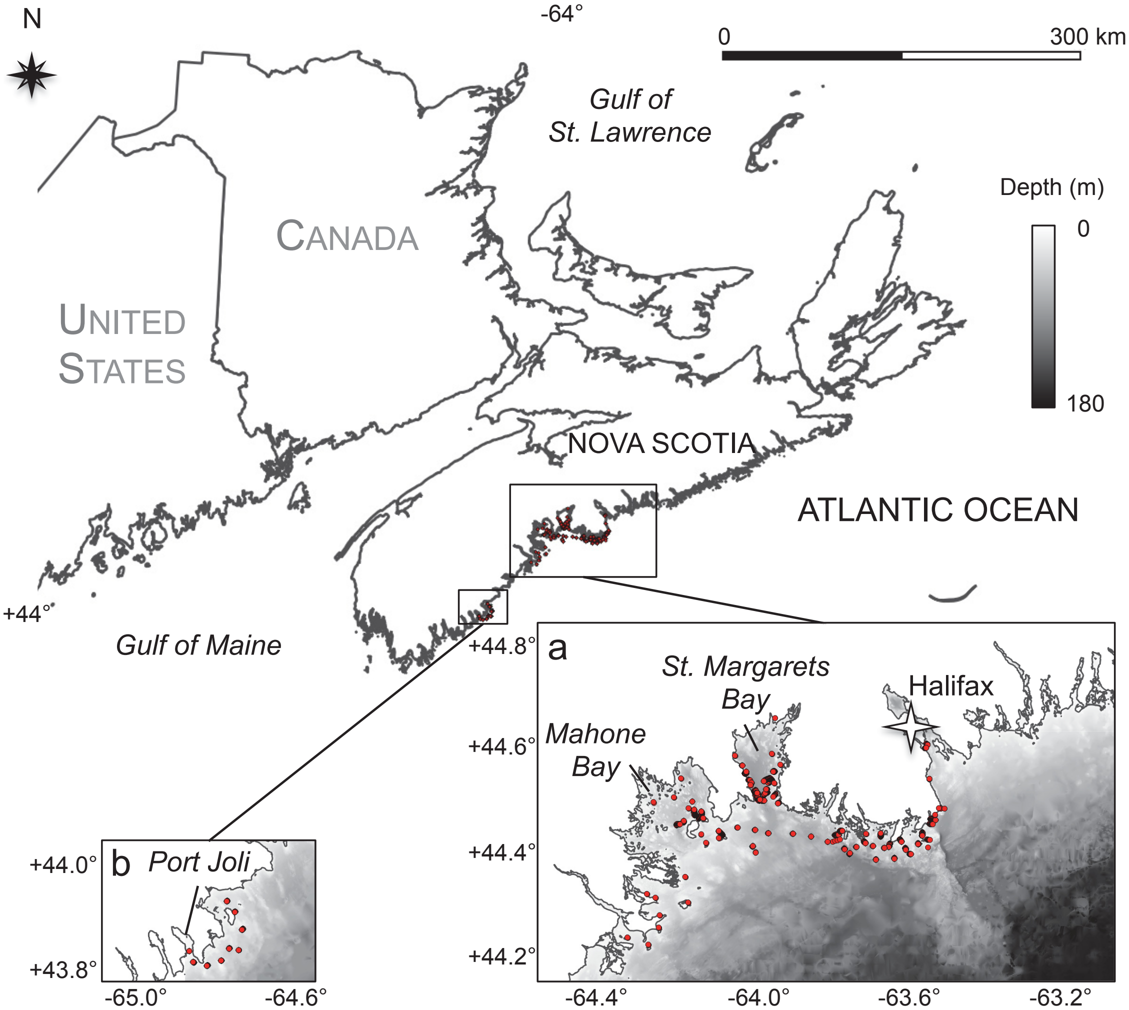


Fig. 6.1. Map of central Atlantic coast of Nova Scotia surveyed between 2010 and 2015. Insets are main study area with locations of transects used to create our predictive model (Box a) and independent test area with locations of transects used for validation of the model (Box b). Depth raster for a 30-m grid cell resolution is shown for each area. For transect locations see Appendix E, Table E1. Map projection is UTM Zone 20 N, WGS84.

6.4. RESULTS

6.4.1. Spatial distribution of drift algae in video surveys

Drift algae were observed in 68 out of 117 transects (Appendix E: Table E1), and 23.2% of survey grids, in our primary study area along 145 km of the central Atlantic coast of Nova Scotia (Fig. 6.1). Deposits primarily consisted of the orders Laminariales (kelps) and Desmarestiales, and to a lesser extent Fucales, along with various red and green (e.g. *Codium fragile fragile*) algae. This composition was consistent with that of a dredged sample of algal detritus from 60 m depth in St. Margarets Bay (Filbee-Dexter & Scheibling 2014a). Visual examination of video records showed drift accumulating throughout the subtidal zone from 25 to 95 m depth, and up to 4.7 km offshore. Drift often occurred along the deep margin of kelp beds, in troughs of sand waves, deep sedimentary basins, and around shallow bedrock ledges and shoals (Fig. 6.2a,b). Algae in deep depositional areas (> 50 m depth) often were associated with groundfish and benthic invertebrates, such as shrimp, brittle stars and sea urchins (Fig. 6.2b).

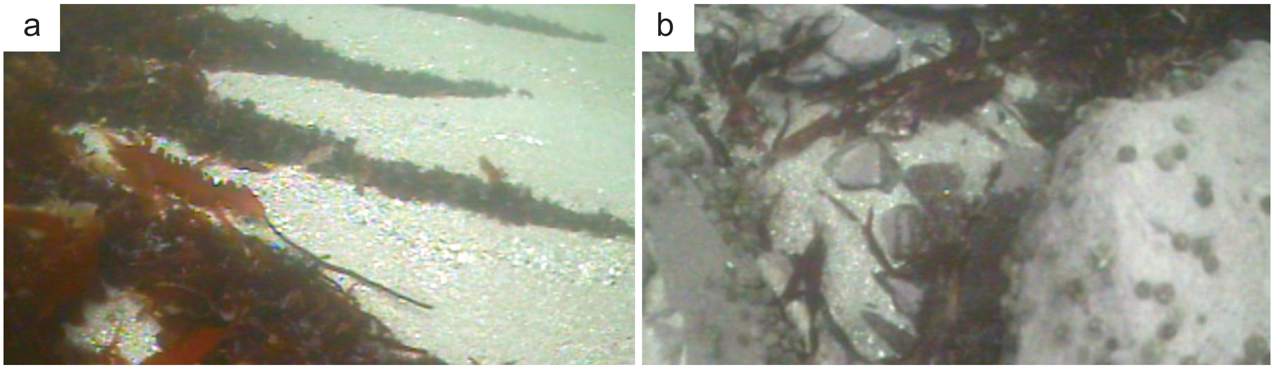


Fig. 6.2. Video frame-grabs showing drift algae a) in troughs of sand waves at 20 m depth and b) accumulating in a 45-m deep depression adjacent to bedrock ledges.

6.4.2. Predictive mapping of drift algae

Bathymetric data and associated terrain properties provided highly reliable predictions of occurrence of drift algae using a random forest model. Of 10 predictor variables used in the initial model, 6 were retained in the final model, which reduced the correct classification rate of the observations of drift algae from our original study area from 95.1 to 94.6% (Table 6.1). Standard curvature and profile curvature were eliminated because they were highly correlated with planar curvature (Nicodemus et al. 2010), which we selected as a better predictor of detrital deposition using conditional variable importance in our random forest model. Bottom current and bottom type were eliminated because they had the lowest conditional importance measures and their exclusion did not impact the model performance (Table 6.1). This was likely due to the low spatial resolution of these data for our study area. Cross-validation using testing and training data subsets yielded an AUC of 0.95, indicating excellent predictive power within our study area (Table 6.1, Appendix E: Fig. E1). Cross-validation using independent observations from Port Joli yielded an AUC of 0.74, indicating moderately good predictive power for regions of the coast outside of our study area (Table 6.1, Appendix E: Fig. E1).

A predictive map of drift algae based on our final model, shows a high probability of drift occurring close to shore, around shoals, in basins and in deep bays, and a low probability of occurrence close to exposed headlands and in offshore areas (Fig. 6.3). Three predictor variables, broad-scale BPI, distance to coast, and slope, explained most of the variation in occurrence of drift algae (Table 6.2). Broad-scale BPI was the most important predictor, with drift algae observed more frequently in depressions (large negative BPI) or relatively flat environments (BPI near 0) compared to ridges (large positive BPI) (Fig. 6.4a). Distance to coast was the second most important predictor, and was used to classify positive occurrence of drift algae in regions within 1.4 km of shore (Fig. 6.4b). Slope was the third most important predictor, with drift algae observed more frequently in flat habitats compared to steeply sloped habitats (Fig. 6.4c). This variable was partly indicative of flow regime, because highly sloping habitats generally are associated with increased currents compared to flat habitats (Mohn & Beckmann 2002, White 2006). However, drift algae also accumulated on the steep seabed close to shore and on the sloped sides of depressions, suggesting that the relationship between drift and slope was weaker in regions close to shore or with large negative BPI (Fig. 6.5). The remaining 3 predictor variables depth, fine-scale BPI, and planar curvature, captured the shape of the bottom in the immediate vicinity of the observed drift algae. The occurrence of drift algae was greater at 35 – 64 m depth, in depressions and in regions with high negative or positive planar curvature values compared to regions with little or no curvature, indicating that habitats with localized bathymetric features, such as troughs or ridges, accumulated more drift compared to flat habitats.

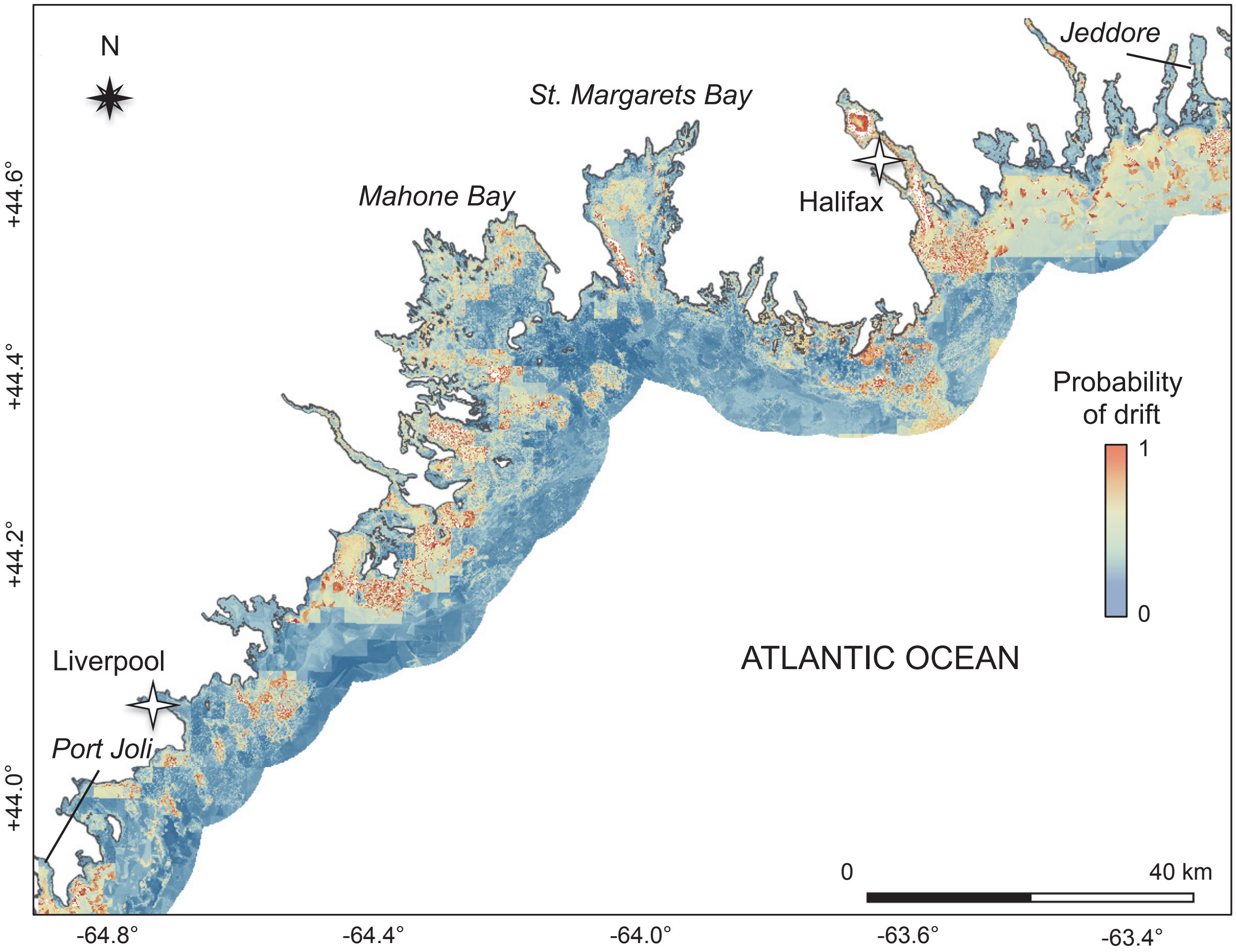


Fig. 6.3. Predictive map of occurrence of drift algae along the central Atlantic coast of Nova Scotia based on predictor variables in Appendix E, Table E2. Grid cell resolution is 30 m. Map projection is UTM Zone 20 N (WGS84).

Table 6.1. Validation and accuracy assessments for random forest model used to predict occurrence of drift algae in the study area. Error is percentage of correctly classified grids. Sensitivity (Sensit) is probability that the model will correctly classify a presence. Specificity (Specif) is probability that the model will correctly classify an absence. True Skill Statistic (TSS) is a measure of accuracy that normalizes error by that which would have occurred by chance alone (Appendix E).

Validation method	AUC[1]	Error	Sensit	Specif	TSS[2]
Independent data	0.735	0.24	0.742	0.766	0.508
Cross-calibration for final model	0.946[3]	0.05	0.800	0.982	0.782
Cross-calibration for original model using all predictor variables	0.951[3]	4.97	0.725	0.967	0.692

[1] AUC ≥ 0.9 indicates excellent, 0.8–0.9 good, and 0.7–0.8 moderate predictive power; 0.5 indicates model not different from random. [2] TSS = 1.0 indicates perfect accuracy; 0 indicates model not different from random. [3] AUC based on the average of 20 cross-calibrations.

Table 6.2. Conditional importance of 6 predictor variables used in random forest model to predict occurrence of drift algae in the study area.

Variable	Conditional Importance
Broad-scale BPI	0.041
Distance to coast	0.035
Slope	0.029
Depth	0.016
Fine-scale BPI	0.015
Planar curvature	0.008

Table 6.3. Conditional importance of 5 predictor variables used in random forest model to predict change in occurrence of drift algae in the study area.

Variable	Conditional importance
Curvature	7.16
Slope	6.36
Depth	6.20
Broad-scale BPI	5.34
Distance to coast	4.97

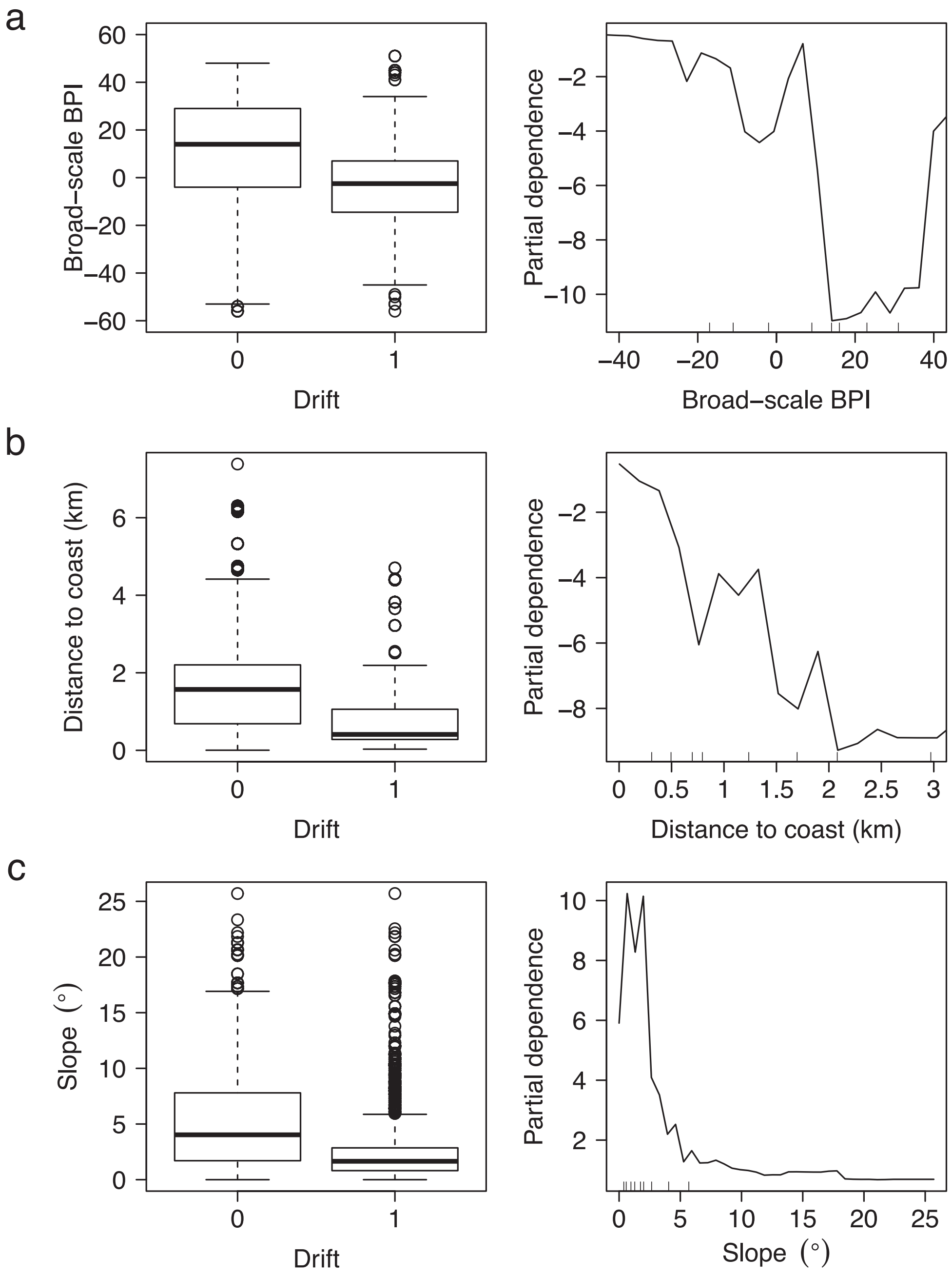


Fig. 6.4. Box-plots (left column) of the 3 main predictor variables from the random forest model for grids in the study area where drift was absent (0) or present (1): a) broad-scale bathymetric position index (BPI), b) distance to coast, and c) slope (left column). Bottom and top of box incases first and third quartiles, strong horizontal line is median, whiskers bound the 95th percentile range, circles are outliers. Associated partial dependence plots (right column) show model predictions of drift occurrence according to the respective predictor variable, when all other variables are held constant at their mean.

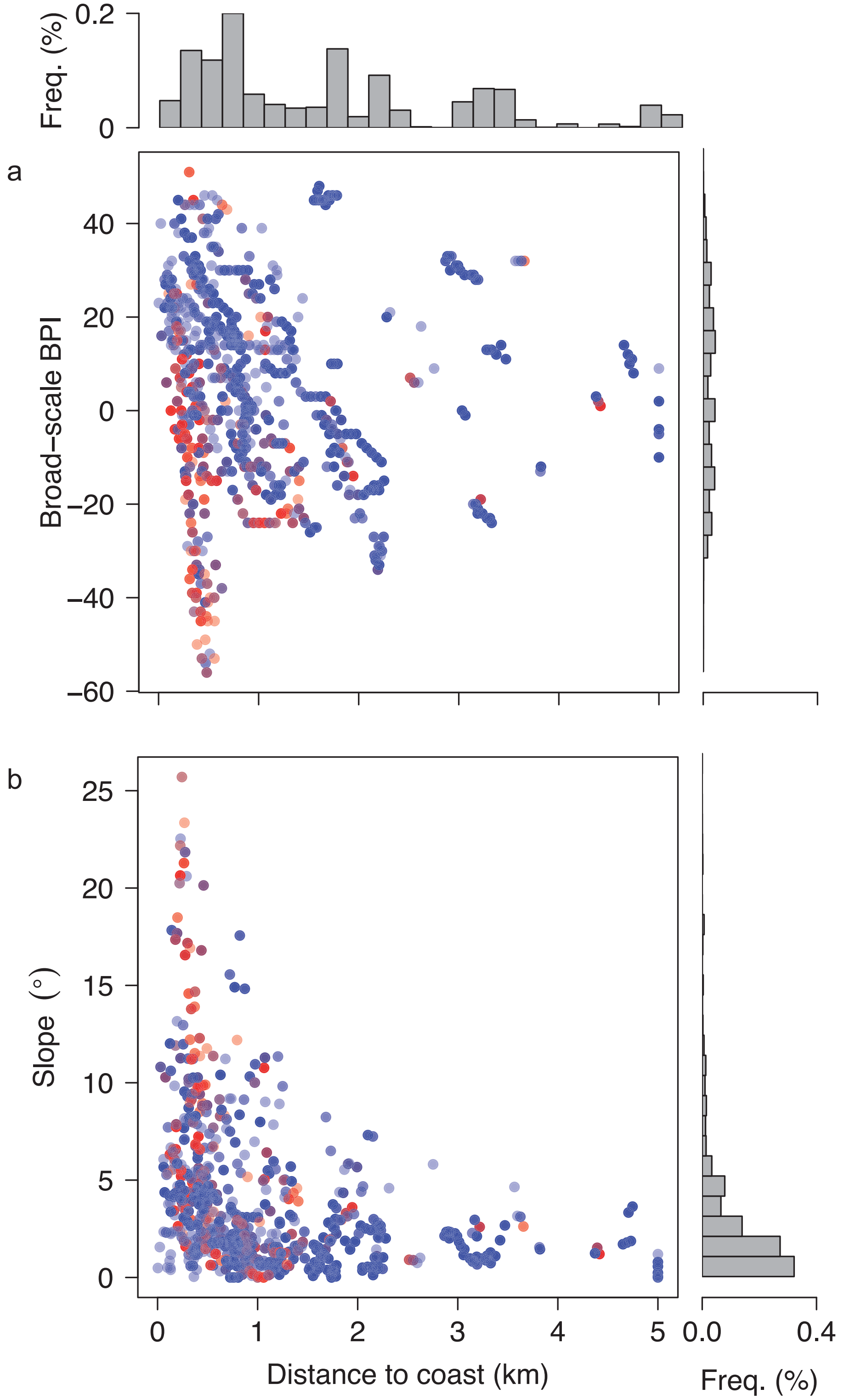


Fig. 6.5. Relationship of predictor variables a) broad-scale bathymetric position index (BPI) or b) slope to distance to coast (bounded by 5 km). Each point is a presence (red) or absence (blue) observation of drift in a grid in the study area. Red or blue tones are

semi-transparent (shown as the lightest tones), such that darker points indicate combinations with more than one like observation and purple tones indicate varying combinations of presence and absence observations. Histograms show the relative frequency of counts (N = 7459) of each predictor variable.

6.4.3. Temporal variation in occurrence of drift algae

Drift occurrence (presence or absence) varied between sampling dates in 25 out of 112 (22.3%) repeated observations in the same sampling grids. Five predictor variables (curvature, slope, depth, broad-scale BPI, and distance to shore) were used in the random forest model to classify constant or variable occurrence of drift algae between sampling times (Table 6.3). The final model correctly classified 63.3% of the repeated observations (AUC = 0.70) and identified curvature, slope and depth as the three most important variables used to classify whether the occurrence of drift algae changed over time (Table 6.3). Areas of seafloor with large curvature or steep slopes tended to have variable patterns of drift algae compared to areas with little or no curvature or slope (Fig. 6.6a,b). There was no clear relationship between depth and constant or variable occurrence of drift algae (Fig. 6.6c).

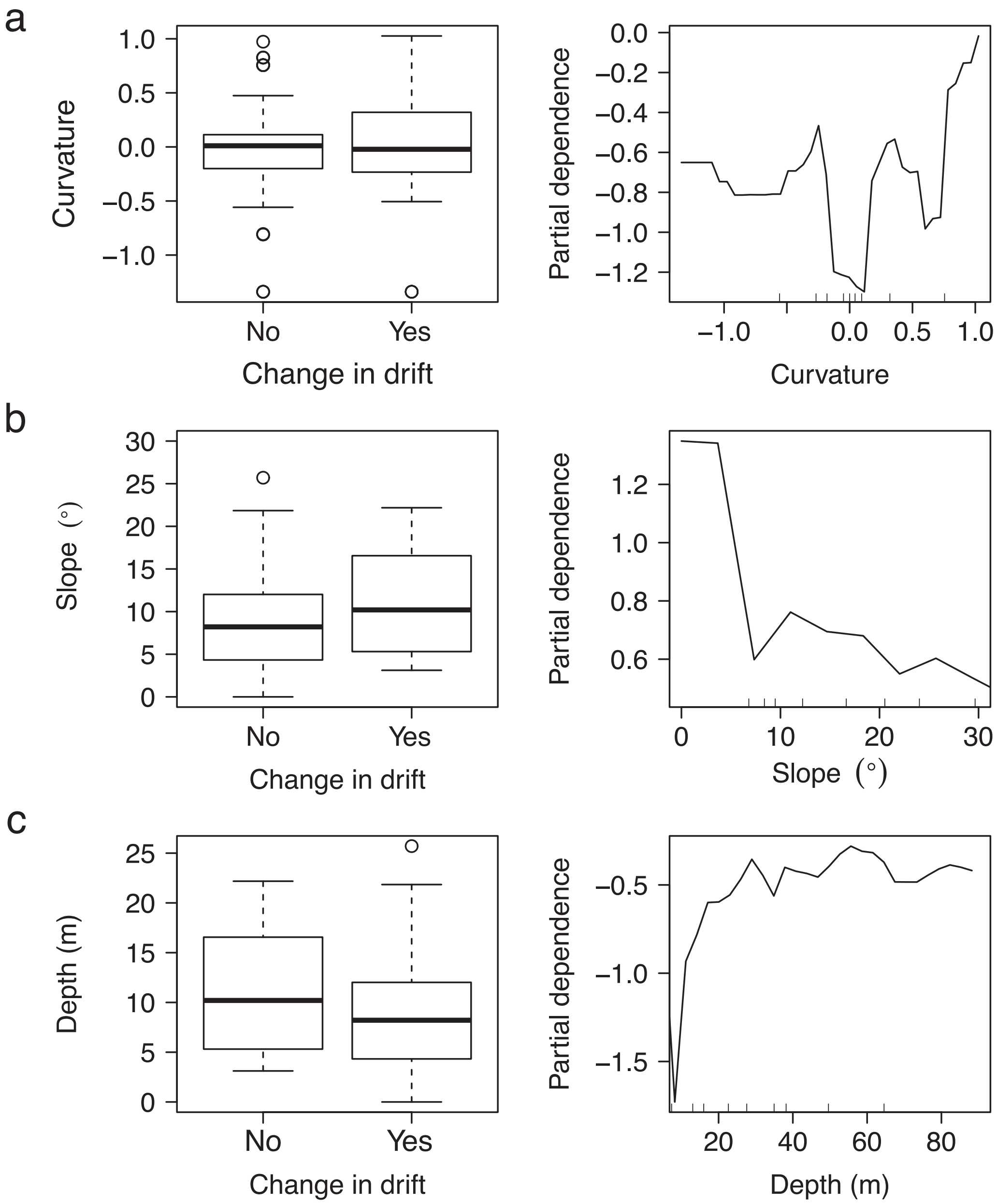


Fig. 6.6. Box-plots (left column) of the 3 main predictor variables from the random forest model for grids in the study area where drift was constant (no change) or variable (change): a) curvature, b) slope, and c) depth (left column). Bottom and top of box incases first and third quartiles, strong horizontal line is median, whiskers bound the 95th percentile range, circles are outliers. Associated partial dependence plots (right column) show model predictions of change in drift occurrence according to the respective predictor variable, when all other variables are held constant at their mean.

6.5. DISCUSSION

6.5.1. Physical determinants of spatial and temporal patterns of drift algal distribution

Spatial patterns of drift algae that we recorded in the nearshore subtidal zone of Nova Scotia, along 145 km of coastline and down to 140 m depth, were used to create the first predictive map of drift subsidy in a marine ecosystem. Drift algae occurred across a range of benthic habitats within this broad area (3,045 km^2), but tended to occur most frequently within 1.4 km of the coast, on flat bottoms or in regions with zero or negative BPI. Such areas were coincident with seafloor depressions, valleys, and flat low-energy habitats at 30 – 95 m depth. Our findings are consistent with decreases in drift abundance with increasing distance from kelp beds that previously have been observed in this area (Kelly et al. 2012) and in California (Mattison et al. 1976, Hobday 2000). Britton-Simmons et al. (2012) found similar patterns of drift distribution in relation to seafloor shape and depth in the San Juan Archipelago off Washington.

Deep accumulations of drift algae are not necessarily linked to proximate shallow macroalgal beds (Biber 2007a, Biber 2007b). Filbee-Dexter and Scheibling (2012) found that loss of canopy cover in shallow kelp-beds following a strong storm event was not correlated with increased drift deposition directly offshore of a given site, suggesting that the drift moves alongshore and deep accumulations originate from kelp beds across a broad span of coast. Researchers tracking the movement of detached kelp in shallow kelp beds in California found that drift algae were a highly dynamic resource, especially in areas with energetic oceanographic conditions (Gerard 1976). While the majority of video transects in our study captured a unique observation of the seafloor over the 5-year sampling period, repeated transects in some areas indicate that 22% of these observations of drift presence or absence changed between sampling intervals.

Regions of the seafloor with steep slopes or negative curvature had high temporal variability in occurrence of drift, suggesting movement of drift through these areas. These bathymetric features often are associated with high topographic relief (Huang et al. 2011) and increased current velocity (e.g. exposed bedrock where sediment is swept away by high flow) (Wilson et al. 2007). Conversely, habitats with little curvature or low angle slopes had less temporal variability in occurrence of drift algae, indicating that drift remains in these areas until it is consumed or degraded. This is supported by repeated observations of the seafloor at 25 – 75 m depth in a sedimentary basin in St. Margarets Bay, which showed a relatively constant spatial pattern of occurrence of drift over time, although the abundance of drift varied seasonally (Filbee-Dexter & Scheibling 2014a). Our predictive map, therefore, identifies deep environments that have a persistent standing stock of drift, and others that have transient depositions. Pulsed and constant resource dynamics influence benthic communities differently (Yang et al. 2008), so temporal patterns of drift occurrence will have consequences for benthic fauna using this food source.

6.5.2. Drift as a subsidy

Our results show that drift algae are a common potential food source in deep subtidal habitats along the Atlantic coast of Nova Scotia, and concur with findings from the San Juan Archipelago in Washington, USA, where drift kelp was observed in 97% of ROV transects at 30 – 170 m depth (Britton-Simmons et al. 2012). In contrast, drift algae were not commonly observed on the continental shelf off California at 87 – 357 m depth, but apparently transported into submarine canyons at 153 – 454 m (Harrold et al. 1998). For most coastal systems, the availability of drift algae in deep habitats is unknown; documenting its abundance and distribution is a critical step in understanding its role in coastal productivity (Krumhansl & Scheibling 2012b).

The influx of large quantities of drift algae is expected to substantially enhance secondary production of benthos in areas with little or no autotrophic primary production. These deep zones act as sinks for species dependent on algae as a source of primary production (Pulliam 1988). Sink populations can be sustained if they are open to spatial flows of food energy from independent source populations. Drift kelp is a primary source of food in deep subtidal regions, and attracts a diverse community of detritivores, microbes and consumers (reviewed by Krumhansl & Scheibling 2012b). Drift in our video transects was associated with shrimps and sea urchins, and commercially important groundfish and lobsters. These species either consume drift directly, prey on small invertebrates that consume drift, or use the structure of detrital mats for protection (Vetter 1998, Hyndes & Lavery 2005, Filbee-Dexter et al. 2014a, Duggins et al. 2016). There is evidence from seagrass systems that drift algae can alter food webs by benefiting opportunistic or mobile taxa over infaunal species (Norkko et al. 2000). The coupling of shallow kelp beds and deep subtidal environments through spatial resource subsidies can enrich sink environments and facilitate the establishment of ecological communities that do not depend on immigration from source populations (Gravel et al. 2010).

A known consumer of drift algae in Nova Scotia is the sea urchin *Strongylocentrotus droebachiensis* (Johnson & Mann 1982, Filbee-Dexter & Scheibling 2014a), which plays a key role in driving shifts between kelp beds and sea urchin barrens in shallow subtidal habitats (Filbee-Dexter & Scheibling 2014b). Sea urchins living in deep subtidal habitats feed passively on drift algae and a reduction in this resource may alter their reproductive output and trigger migration into the shallows (Filbee-Dexter & Scheibling 2014a). In California, reduced drift kelp caused *S. franciscanus* and *S. purpuratus* to emerge from shelters and actively graze attached kelp, resulting in a shift to sea urchin barrens (Ebeling et al. 1985, Harrold 1985). These dynamics involve reciprocal transfers of energy and matter, where spatial flow of food to deep subtidal zones could result in the flow of larvae or migrants back into source environments (Filbee-Dexter & Scheibling 2014b).

6.5.3. Implications for future research

Our findings add to a growing body of evidence that drift algae are an important source of primary production entering deep subtidal environments, and underscore the need for further research to quantify the impact of this energy subsidy for recipient communities. Our predictive map identifies offshore depositional areas for drift along the coast of Nova Scotia where benthic productivity likely will decrease with attendant changes in food web structure or energy flow if this resource becomes limiting. The shallow subtidal ecosystem of this region is undergoing a shift in algal dominance from kelp beds to invasive and turf-forming algae species: kelp biomass has declined by 84 – 99% in the past 4 decades and the degraded state is maintained by feedback mechanisms that inhibit kelp recovery (Filbee-Dexter et al. 2016). This shift alters the composition of drift (Krumhansl & Scheibling 2012a) and is predicted to reduce the amount of biomass entering detrital food webs (Krumhansl et al. 2014), that likely will have important bottom-up effects on benthic food webs with broader consequences for the coastal ecosystem. For example, decreased diversity and abundance of beach macrofauna and shorebirds has been attributed to declines in canopy cover of nearby kelp forests or removal of beach-cast drift in Southern California (Dugan et al. 2003). Shifts from kelp beds to turf-algal dominated reefs are occurring globally (Moy & Christie 2012, Wernberg et al. 2012, Filbee-Dexter et al. 2016), and a broader consideration of the importance of drift subsidy on overall coastal productivity is needed.

Our study showed that bathymetric measures alone can be sufficient to accurately predict patterns of drift subsidy on a coastal scale. This approach could have broad application in future benthic mapping studies given the paucity of oceanographic data in many regions, and the prohibitive cost of sampling the seafloor over large areas (Becker et al. 2009). Despite our high model performance, the Type I error rate in cross-validation results (i.e. not all suitable habitat types had drift in our surveys) indicates that other factors may influence drift distribution at small spatial scales (Kopecky and Dunton 2006). Information on bottom currents, water mass properties, and seafloor type, may be required to resolve fine-scale patterns of occurrence of drift algae.

Our predictive model is correlative, and requires little knowledge of mechanistic links between ocean environment and the transport and deposition of drift. Future studies should investigate processes responsible for drift movement, deposition and retention across deep subtidal habitats. Information on the ocean conditions that enable passive transport of algal fragments along the sea floor could be used to create mechanistic distribution models of drift algal subsidy. These models have been effectively used to predict distributional shifts of marine species under climate change (Buckley et al. 2010, Leroux et al. 2013), and similar approaches could be applied to resource subsidies. Future integration of landscape ecology with spatial subsidies promises novel insights into meta-ecosystem dynamics and the consequences of altering spatial flows.

6.6. ACKNOWLEDGEMENTS

We are indebted to J. Lindley for his invaluable help with the design and operation of the tow-camera system. We thank K. Krumhansl, C. Feehan, J. O'Brien, R. Buchwald, F. Francis, A. Harding, and C. Robertson for assisting with field work and image analysis. A. Metaxas and H. Whitehead provided helpful comments on an earlier draft of the manuscript. This research was funded by a Discovery Grant, a Research Tools and Instruments Grant, and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F-D. was supported by a NSERC Canada Graduate Scholarship and a Dalhousie Killam Scholarship.

CHAPTER 7

THE PRESENT IS THE KEY TO THE PAST: LINKING REGIME SHIFTS IN KELP BEDS TO THE DISTRIBUTION OF DEEP-LIVING SEA URCHINS

7.1. ABSTRACT

Understanding processes that drive sudden shifts in ecosystem structure and function has become an important research area for coastal management. In kelp bed ecosystems, regime shifts occur when high densities of sea urchins destructively graze kelp and create coralline algal barrens. While the importance of predation and disease in mediating shifts between kelp beds and barrens on shallow rocky reefs has been well documented, little is known about the role of deep-living urchins in these alternative stable-state dynamics. In this study we examine the distribution of deep-living urchins along the central Atlantic coast of Nova Scotia to gain insight into their role in triggering shifts from kelp beds to barrens on shallow rocky reefs. We documented urchin distribution and abundance in tow-camera surveys down to 140 m depth and across 140 km of coast and created a predictive species-distribution model using these observations and spatial data on environmental factors that likely delineate suitable habitat for urchins. We used a random forest model to generate our predictions, which correctly classified

91% of observations into a positive or negative occurrence of urchins. Sea urchins predominantly occurred within 1.5 km of shore, in depressions and flat habitats between 40 and 85 m depth. We found that shallow regions where destructive grazing fronts have been documented over the past 4 decades were closer to deep-living sea urchin habitats compared to regions that remained in a kelp bed state during the same period. Our study indicates that deep-living urchins play an important role in driving shallow regime shift dynamics, and that their distribution can help identify areas of coast that are most vulnerable to a collapse to barrens.

7.2. INTRODUCTION

Sudden, long-lasting shifts in ecosystem structure and function have been documented in various coastal marine habitats (Scheffer et al. 2001), including seagrass beds (Viaroli et al. 2008), coral reefs (Norström et al. 2009) and macroalgal beds (Filbee-Dexter & Scheibling 2014b). These regime (or phase) shifts often have substantial impacts on ecosystem services and human economies, and can be difficult to reverse (Rocha et al. 2015). Understanding processes that drive sudden shifts between alternative system states, and the critical thresholds at which such changes are triggered, has become an increasingly important area of research for management, in the face of multiple anthropogenic stressors operating at local to global scales (Folke et al. 2004).

In kelp beds (or forests), regime shifts occur when high densities of sea urchins destructively graze attached kelp, creating barrens devoid of erect macroalgae (Filbee-

Dexter & Scheibling 2014b, Ling et al. 2015). Urchin barrens have lower structural complexity and productivity than kelp beds and are stabilized by positive feedback mechanisms that inhibit recovery of the kelp bed state (Filbee-Dexter & Scheibling 2014b). Drivers of a shift to barrens vary across kelp ecosystems and include: declines in urchin predators (Dayton et al. 1998, Watson & Estes 2011), recruitment pulses during favourable environmental conditions (Hart & Scheibling 1988, Sivertsen 2006), altered grazing behaviour (Harrold 1985), and range extensions due to warming ocean temperatures (Vásquez et al. 2006, Ling et al. 2009). While factors controlling sea urchin populations within kelp beds have been extensively studied (Filbee-Dexter & Scheibling 2014b, Ling et al. 2015), the extent to which urchins in deeper regions (> 15 m depth) contribute to shallow destructive grazing, either through larval supply or onshore movement to nearby kelp beds, remains largely unknown.

Strongylocentrotid sea urchins have been observed moving onshore from deep water to form grazing aggregations along the deep margins of kelp beds (or forests) in Nova Scotia, Canada (Scheibling et al. 1999, Brady & Scheibling 2005); California (Ebeling et al. 1985), Alaska (Konar & Estes 2003) and Maine (Johnson et al. 2013) in the USA; and Iceland (Hjörleifsson et al. 1995). These grazing fronts can advance across entire rocky reefs to create extensive barrens. In Nova Scotia and Maine, sea urchin fishers target these fronts as they are comprised of large individuals with high quality gonads (Meidel & Scheibling 1998, Miller & Nolan 2008) that are rapidly replenished by urchins from greater depths (Scheibling et al. 1999, Johnson et al. 2013). Our knowledge of the distribution and abundance of these deep-living urchins is limited however, compared to populations in shallow subtidal habitats, and their role in driving transitions to barrens is unknown. Sea urchins from deep barrens (> 15 m depth) often are sparsely distributed and malnourished, subsisting on coralline algal crusts and microalgal films that limit growth and reproduction (Brady & Scheibling 2006, Kelly et al. 2012). In some areas however, deep populations are subsidized by periodic inputs of drift kelp, resulting in reproductive rates comparable to those recorded in shallow grazing fronts (Britton-Simmons et al. 2012, Kelly et al. 2012, Filbee-Dexter & Scheibling 2014a).

The green sea urchin *Strongylocentrotus droebachiensis* historically has been the dominant herbivore on rocky reefs along the Atlantic coast of Nova Scotia (Mann 1977). This species ranges from the intertdal zone to 300 m depth, but relatively little is known about its distribution and abundance beyond the depth limit (~ 40 m) of nontechnical scientific diving (Scheibling & Hatcher 2013). In the early 1970s dense aggregations of urchins overgrazed kelp beds in a large embayment (St. Margarets Bay) near Halifax, Nova Scotia (Breen & Mann 1976). By the late 1970s, waves of destructive grazing created barrens that spanned ~500 km (linear distance) of coast (Wharton & Mann 1981). Kelp beds re-established following recurrent outbreaks of an amoebic disease between 1981 and 1983 that caused mass mortalities of sea urchins (Scheibling 1986). Transmission of this disease in *S. droebachiensis* is strongly temperature dependant, and only leads to mortality when sea temperature exceeds a threshold around 12°C (Scheibling & Stephenson 1984). In the early 1990s sea urchins moved from deeper regions, within a thermal refuge from disease, and formed grazing fronts along the lower margin of kelp beds, resulting in localized shifts to barrens (Scheibling et al. 1999) and heralding the onset of an urchin roe fishery (Miller & Nolan 2008). Kelp beds recovered again in the late 1990s to early 2000s, after another series of disease outbreaks

(Scheibling et al. 2013). Currently, the range of shallow water sea urchins is restricted to a few localized areas of coast and the roe fishery has collapsed (Scheibling & Lauzon-Guay 2010).

Here we examine the current distribution of deep-living sea urchins along the central Atlantic coast of Nova Scotia to gain insight into their putative role in triggering shifts from kelp beds to barrens on shallow rocky reefs over the past 4 decades. We recorded the occurrence of sea urchins down to 140 m depth in video surveys along this coast, and used these observations and available bathymetric and environmental data to create a predictive map of sea urchin distribution below the shallow reefs. In addition we compiled records of destructive grazing events over the last 44 years to examine whether shallow kelp beds close to areas predicted to support deep-living urchin populations were more likely to have shifted to barrens compared to kelp beds located further from these areas.

7.3. METHODS

7.3.1. Video surveys of sea urchin populations

Deep-living urchins (putatively *Strongylocentrotus droebachiensis*) were surveyed along the central Atlantic coast of Nova Scotia between August 2010 and August 2015. Surveys were conducted using a digital video camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor dive wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search

Equipment) towed at an average speed of 0.5 m s^{-1} from a 7-m motorized research vessel or 9-m sailing vessel. For details of the tow camera system, acoustic depth measurements, and video transects see Francis et al. (2014). In total, 113 transects were conducted across the entire study area (Fig. 7.1; Appendix F: Table F1), amounting to 41,795 analyzed video frames, each encompassing ~ 1 m^2 of seafloor.

Each video transect was viewed in iMovie (version 9.0.4, Apple) in real time, and urchin abundance (measured as counts from 0 to ≥ 15 urchins $frame^{-1}$), bottom type and percentage cover of drift algae along the transect were recorded in an Excel macro, synchronized with the video time. The program tabulated records in 1-s intervals to avoid frame overlap. The accuracy of urchin counts were assessed by exporting 90 min of video into Image J as frames (1 frame per 30 s), counting urchins in each frame and comparing that to counts for the same frames assessed in real time using the program (Pearson's r = 0.90; paired *t*-test, n = 180, p = 0.79). We estimated size structure of urchin populations in video transects in August and September 2010 using scale lasers in frames that enabled accurate measurements of test diameter (n = 260 frames). We also used lasers to estimate the frame area, which ranged from 0.25 to 4 m^2 (mean ~ 1 m^2) depending on the height of the camera off the bottom. Video frames outside this range or of poor quality were recorded as a missing observation in the program. Bottom type was classified into 6 categories: bedrock or boulders with attached kelp or other macroalgae (mainly *Desmarestia* spp., *Codium fragile* ssp. *fragile*, *Fucus* spp., and unidentified red algae), bedrock with no attached macroalgae, boulders, boulders and sediment, and sediment. Sediment grain size and type (e.g. mud, silt, sand) was undiscernable in many of the frames, so we grouped sedimentary habitats into a single category ("sediment").

7.3.2. Modeling sea urchin distribution

We used 18 environmental predictor variables for our sea urchin distribution model (Appendix F: Table F2). A coastal map of bottom type and a digital elevation model (DEM) of 30-m cell resolution (created using a combination of contour, sounding and multibeam data from the Canadian Hydrographic Service and the Nova Scotia Geomatics Centre) were obtained from the Department of Fisheries and Oceans, Canada (DFO) (Greenlaw et al. 2013). The processed bathymetry data were used to produce 14 additional layers of the seafloor using Spatial Analyst and Benthic Terrain Model tools (Wright et al. 2005): slope; planar, profile and standard curvature; aspect; and 9 bathymetric position index (BPI) measures. Standard curvature describes concavity (e.g., trough or depression) or convexity (e.g., ridge) of the seafloor, planar curvature describes concavity/convexity measured perpendicular to the aspect of the slope, and profile curvature describes concavity/convexity measured parallel to the aspect of the slope. BPI is a measure of the depth of a location relative to the depth of the surrounding area, and also describes concavity or convexity of the seafloor. BPI values near zero represent flat areas or areas with constant slope. We calculated 9 BPI layers using a 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, and 1.6 km radius around each grid cell. To approximate the nearest distance to shallow kelp/barrens habitats, we calculated the distance to coast as the shortest length from the centre of a grid cell to shore (km) using ARCGIS. Our video surveys showed that kelp beds occurred, on average, 0.23 km from shore, supporting our approximation. We also included a layer of drift algae that we created using observations from the same video transects used in this study (Filbee-Dexter & Scheibling 2016). The predictor variables included in our final model were selected using variable correlation analysis and misclassification rates using different subsets of predictor variables (Appendix F).

To examine the relationship between the distribution of deep-living urchins and predictor variables, we transformed our video-frame records of urchin abundance into presence/absence data that matched the resolution and spatial boundaries of our predictor data, and aggregated point observations of sea urchin occurrence in grid squares of 30-m cell resolution (n = 7459). Grids with at least 1 occurrence record were assigned a presence measure, and grids with no occurrence were assigned an absence. The number of frames within each grid ranged from 1 to 42, with 90% of grids containing 3 – 18 frames.

We used a random forest model (RFM) to evaluate the relative importance of predictor variables in determining the suitable sea urchin habitat. RFM is an advanced version of a classification and regression tree algorithm that successively splits data into categories based on single variables (Breiman 2001). The algorithm “grows” a large number of classification trees (in our case 1000), each from a randomized subset of predictor variables, and then averages the output to produce a vector of the most common variables contributing to splits in the data. The model output for this study was the probability of classifying a grid as presence (1) or absence (0) of sea urchins. We selected this model type because it is one of the most accurate learning algorithms available, with demonstrated high performance in predicting species distributions (Iverson et al. 2008). RFM is ideal for cases with noisy, non-linear data and strong interaction effects, and does not overfit complex models (Li & Wang 2013). It is only moderately influenced by spatial autocorrelation, compared to generalized additive models or generalized linear models (Marmion et al. 2009). The analysis was conducted with the randomForest package in R using 3 predictor variables for each split, and stopping (pruning) trees after 3 splits. Relationships between predictor variables and the response variable were visualized using partial dependence plots, which show the effect of one variable on sea urchin occurrence while controlling for effects of other variables in the model (Hastie et al. 2001). We evaluated the explanatory power of our model using rates of misclassification (Breiman 2001), and used a conditional variable importance index to rank these predictor variables for overall importance in classifying sea urchin habitat (Appendix F).

Our predictive model of suitable urchin habitat in deep subtidal environments encompassed an offshore area of 3045 km^2 and down to 140 m. We used cross-validation to evaluate the accuracy of our model by randomly partitioning observations into a “training” sample (70% of points) and a “testing” sample (30%). We repeated this 20 times, and for each iteration fitted the RFM with training data and evaluated its predictions for sites of known presence or absence of urchins using testing data (Fielding & Bell 1997). We evaluated how well the RFM predicted the testing data using the area under the receiver-operator-curve (AUC; Hanley & McNeil 1982). We verified that spatial autocorrelation between presence and absence locations did not overinflate the AUC by creating a null model that predicted the “testing sample” based solely on geographic distance to the nearest “training sample” point (Hjimans 2012). The predictive performance of this null model was not different from chance (Table 7.1), so no other corrections for spatial autocorrelation were required. Model reliability was assessed using threshold-dependent model evaluation indices (Liu et al. 2005): sensitivity, specificity, and the true skill statistic (Allouche et al. 2006).

7.3.3. Links to shallow destructive grazing events

To explore the spatial relationship between sea urchins in deep subtidal habitats and historic records of destructive grazing of kelp on shallow reefs, we compiled records of urchin grazing aggregations or shallow (< 15 m depth) urchin barrens ("barrens" hereon) in our study area, based on published and unpublished data from 1972 to 2015 (Appendix G: Table G1). We only included records from areas that also supported kelp and, whenever possible, distinguished barrens created by urchins grazing in fronts at the deep margin of kelp beds vs. those in grazing aggregations within the beds. We divided these records into two periods, representing major regime shifts from kelp to barrens over the last 44 years. The first began in 1972 when grazing fronts were first observed in St. Margarets Bay (Breen & Mann 1976) and ended in 1981 when the entire Atlantic coast had shifted to barrens (Wharton & Mann 1981). The second period began in 1984, following kelp bed recovery due to outbreaks of disease in 1981–1983 that eliminated shallow urchin populations along the entire Atlantic coast (Scheibling 1986). The second period encompassed several localized shifts to barrens between 1991 and 2015, however the coast did not fully transition to barrens due to recurrent outbreaks of urchin disease (Scheibling et al. 2013). We also identified locations in a kelp bed state by randomly selecting coordinates along regions of the coast with no record of destructive grazing. We verified that these locations supported kelp beds at times when others were in a barrens state using published and unpublished observations of the areas and maps of suitable bedrock habitat (Appendix G: Table G1). In total we randomly selected 17 kelp locations within St. Margarets Bay that matched the spatial extent of 17 barrens locations documented between 1972 and 1981, and 36 kelp locations between the western mouth of Mahone Bay (Little Duck Island) and Halifax Harbour that matched the spatial extent of 36 barrens locations documented between 1992 and 2015 (Fig. 7.1).

To test the hypothesis that deep areas adjacent to shallow barrens have a higher likelihood of containing urchin populations compared to deep areas adjacent to kelp-bed locations, we calculated probability of occurrence of urchins within circular buffers (areas around a coordinate point) at each barrens or kelp location. For the first period we used buffer radii of 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, and 6.4 km to encompass the bounds of St. Margarets Bay (maximum width ~ 10 km), and expanded this series to 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 12.8, 25.6 and 51.2 km to capture variation in coastal environments (headlands, shoal grounds, inner and outer bays) for the second period. For each period, we plotted the relationship between radius length and average probability of sea urchin occurrence for both barrens and kelp locations, and used 95% confidence intervals to compare the difference in this relationship between location types over a range of spatial scales. The autocorrelation structure of the response was assessed for barrens and kelp locations during each period using semi-variograms (R package nlme); no corrections were required.

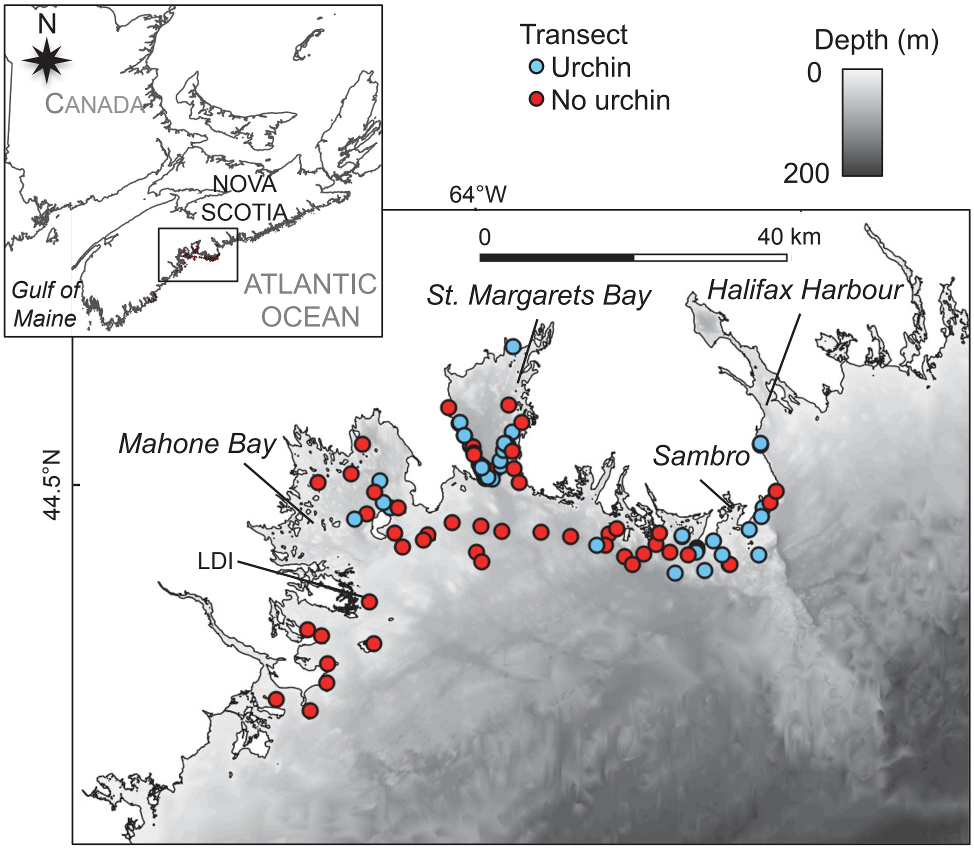


Fig. 7.1. Map of central Atlantic coast of Nova Scotia surveyed between 2010 and 2015 showing location of video transects with presence (blue) or absence (red) of sea urchins. Depth raster is shown for study area. For transect locations see Table A1. Map projection is UTM Zone 20 N, WGS84.

7.4. RESULTS

7.4.1. Sea urchin distribution and abundance from video samples

Sea urchins were observed on shallow barrens and in deep sedimentary basins throughout our study area. Mean sea urchin abundance generally ranged from 1 to 4 urchins frame^{-1} at depths < 25 m, where the seabed was mostly composed of rocky substrata (~ 69% of shallow frames; Fig. 7.2) with attached kelp and other macroalgae (51% of frames with rocky substrata). At depths of 25 to 100 m, mean abundance was generally lower (often < 1 urchin frame^{-1}) and the seabed was composed mainly of sediments (~ 77% of frames), sometimes interspersed with rocks (10% of frames), boulder fields or bedrock (~ 13% of frames) (Fig. 7.2). Video records showed sea urchins in small depressions amid shoals, in depositional areas with drift algae, and in habitats with other benthic invertebrates, such as sand dollars, brittle stars, scallops and shrimp. Mean horizontal test diameter of sea urchins in deep habitats was 5.4 (± 0.4 SD) cm and ranged from 2 to 11 cm (n = 814 urchins).

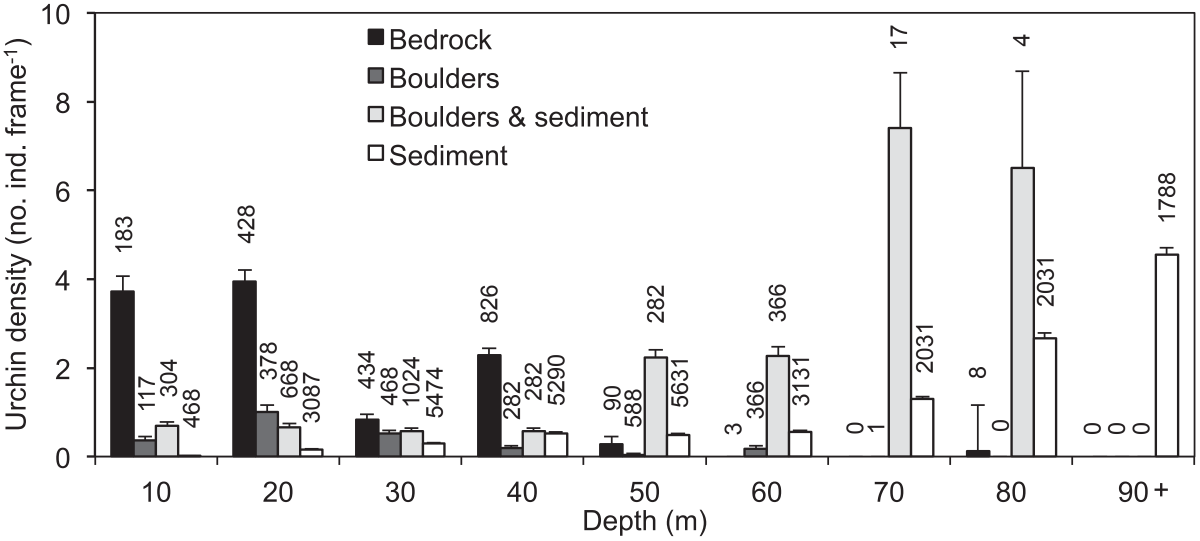


Fig. 7.2. Urchin density (no. individuals frame^{-1}) across depth (5 to 95 m) and habitat type. Data are mean ± SD. Numbers above each bar are analyzed frames for each habitat type in each depth bin.

7.4.2. Predictive map

A predictive distribution map of sea urchins based on our final model, showed deep-living sea urchins in four main areas: 1) the deepest part of St. Margarets Bay along the western shore near the mouth of the bay, 2) surrounding the Sambro ledges at the western entrance to Halifax Harbour, 3) within Halifax Harbour, and 4) around several islands near the head of Mahone Bay (Fig. 7.3). Our environmental variables provided reliable predictions of urchin distribution using a RFM (Table 7.1). Of 18 predictor variables used in the initial model, 7 were retained in the final model, with effectively no reduction in the correct classification (Table 7.2). Distance to the coast was the most important predictor, and was used to classify urchin habitat as primarily within 1.5 km of shore (Fig. 7.4a). Of the 9 BPI variables examined in the model, we used only the 2 most important predictors, which we designated as fine-scale and broad-scale BPI (radius of

0.6 and 1 km, respectively). Broad-scale BPI was the second most important predictor, with urchins occurring in depressions (negative BPI) compared to ridges (positive BPI) and flat habitats (BPI near zero) (Fig. 7.4b). Fine-scale BPI was the third most important predictor and was used to classify urchin habitat in areas with negative BPI, which describes depressions, and zero or small positive BPI, which describes bottom features such as flat areas, small shoals and ledges (Fig. 7.4c). Depth was the fourth most important predictor, with sea urchins tending to occur at depths of < 25 m and between 40 – 85 m, which correspond to near-shore barrens and deep sedimentary basins in Halifax Harbour, Mahone Bay and St. Margarets Bay (Fig. 7.5a; Fig. 7.6). The remaining three predictor variables used in our final RFM were drift, slope and standard curvature (Table 7.2). Habitats with any probability of drift appeared more suitable for urchins than habitats with little to no probability of drift (Fig. 7.5b). Regions with little to no slope or negative curvature (depressions) appeared more suitable than steep regions or areas of positive curvature (Fig. 7.5c).

The variables bottom type, planar curvature, profile curvature and aspect were not used in our final model because they had low importance measures and their removal had a negligible effect on model performance. Pairwise correlations between environmental variables were generally low ($r < 0.23$), with the exception of fine-scale BPI, broad-scale BPI and depth, which were significantly correlated ($r > 0.63$). These variables were retained in our final model because they each explained more of the response data than the predictor variables drift, slope and curvature, and their individual removal reduced the model performance.

Cross-validation indicated that our final RFM performed well in predicting urchin habitats along the central coast of Nova Scotia. Bootstrapped cross-validation using testing and training data subsets yielded an AUC of 0.85, indicating good predictive power within our study area (Appendix F). The misclassification rate was 9.29%, and was low as a result of high specificity (the model was more accurate at correctly identifying areas without sea urchins, compared to areas with sea urchins; Table 7.1).

Table 7.1. Validation and accuracy assessments for RFM used to predict occurrence of sea urchins in the study area. Error is percentage of incorrectly classified grids. Sensitivity (Sensit) is probability that the model will correctly classify a presence. Specificity (Specif) is probability that the model will correctly classify an absence. True Skill Statistic (TSS) is a measure of accuracy that normalizes error by that which would have occurred by chance alone.

Validation method	AUC[1]	Error	Sensit	Specif	TSS[2]
Cross-calibration for final model	0.851	0.09	0.41	0.98	0.38
Cross-calibration for original model using all predictor variables	0.846	0.09	0.41	0.97	0.38
Null model using geographic distance	0.498	-	-	-	-

[1] AUC ≥ 0.9 indicates excellent, 0.8–0.9 good, and 0.7–0.8 moderate predictive power; 0.5 indicates model not different from random. Calculation is based on the average of 20 cross-calibrations.

[2] TSS = 1.0 indicates perfect accuracy; 0 indicates model not different from random.

Table 7.2. Conditional importance of 7 predictor variables used in random forest model to predict sea urchin occurrence in the study area.

Variable	Conditional Importance
Distance to coast	159
Broad-scale BPI	152
Fine-scale BPI	143
Depth	138
Drift algae	85
Slope	83
Standard curvature	63

7.4.3. Spatial links to historic urchin barrens

Shallow sea urchin barrens were documented at 13 locations along the western shore of St. Margarets Bay and 4 locations on the eastern shore between 1972 and 1981 (Fig. 7.1). Of 17 observations of barrens, 4 were created by patchy grazing within the kelp bed, 1 was created by urchin grazing fronts at the deep margin of a kelp bed, and 12 were unknown. Kelp beds during this period occurred at 17 locations along the northern and eastern shores and at the entrance St. Margarets Bay (Fig. 7.1). Beyond a threshold radius of 0.3 km from a site, there was a significantly higher probability of deep-living sea urchins adjacent to a barrens site compared to a kelp bed site (Fig. 7.7a). This difference was most pronounced between 0.3 and 1 km radius. Shallow sea urchin barrens were documented at 2 locations near the western mouth of Mahone Bay, 5 locations in St. Margarets Bay, 15 locations around Sambro Ledges, 7 locations at the western mouth of Halifax Harbour, and 6 locations within Halifax Harbour between 1984 and 2015 (Fig. 7.1). Of 36 records of barrens, 27 were formed by grazing fronts at the deep margin of a kelp bed and 9 were of unknown formation. Kelp beds during this period occurred at 3 locations near Little Duck Island, 5 locations in Mahone Bay, 3 locations in St. Margarets Bay, 14 locations along headlands between Mahone Bay and Sambro, 4 locations offshore of Sambro, and 7 locations in Halifax Harbour (Fig. 7.1). There was a significantly higher probability of deep-living sea urchins adjacent to a barrens site compared to a kelp bed site (Fig. 7.7b). Similar to the previous period, this difference was most pronounced between a 0.1 and 3 km radius from a site.

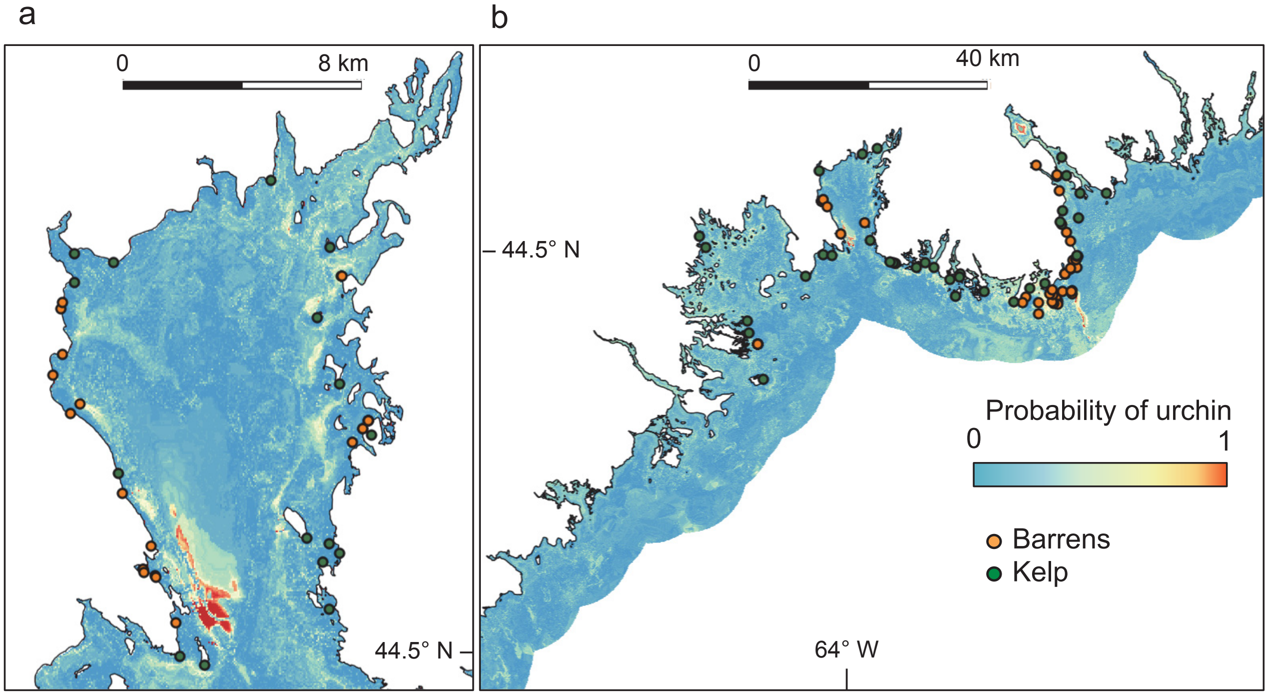


Fig. 7.3. Maps showing probability of sea urchins along the Atlantic coast of Nova Scotia and location of barrens (orange circles) and kelp beds (green circles) a) in St. Margarets Bay between 1972 and 1981, the period from initial observation of destructive grazing in the bay (Breen & Mann 1976) to complete transition to barrens on a coastal scale (Wharton & Mann 1981), and b) along the central region of the coast after 1984, following a second regime shift once disease had eliminated barrens along the whole coast. Map projection is UTM Zone 20 N (WGS84). Predictive map of sea urchins is based on predictor variables in Table 7.2. Grid cell resolution is 30 m.

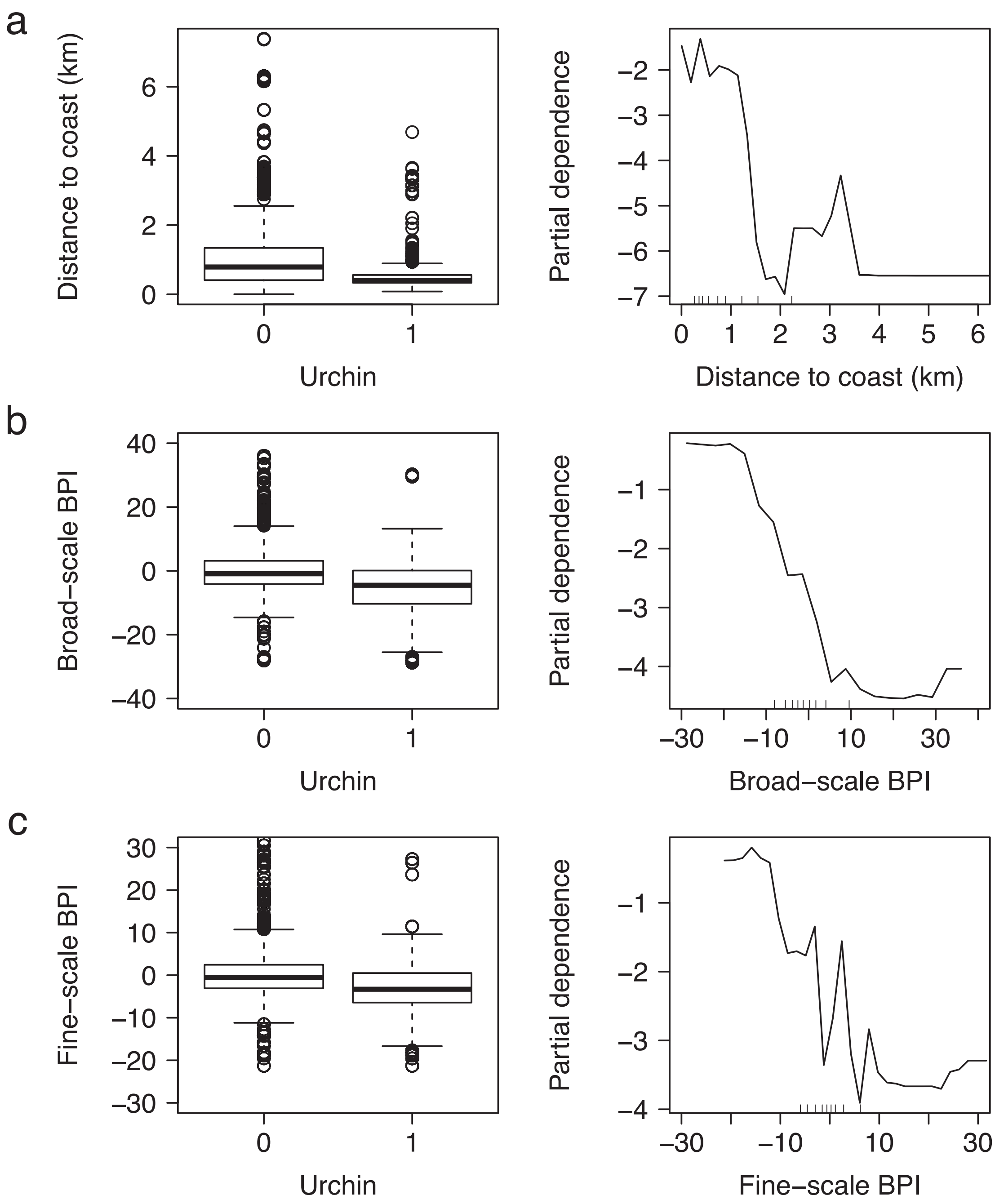


Fig. 7.4. Box-plots (left column) of the 3 most important predictor variables from the random forest model for grids in the study area where sea urchins were absent (0) or present (1): a) distance to coast, b) broad-scale bathymetric position index (BPI), and c) fine-scale BPI. Bottom and top of box incases first and third quartiles, strong horizontal line is median, whiskers bound the 95th percentile range, and circles are outliers. Associated partial dependence plots (right column) show model predictions of sea urchins according to the respective predictor variable, when all other variables are held constant at their mean.

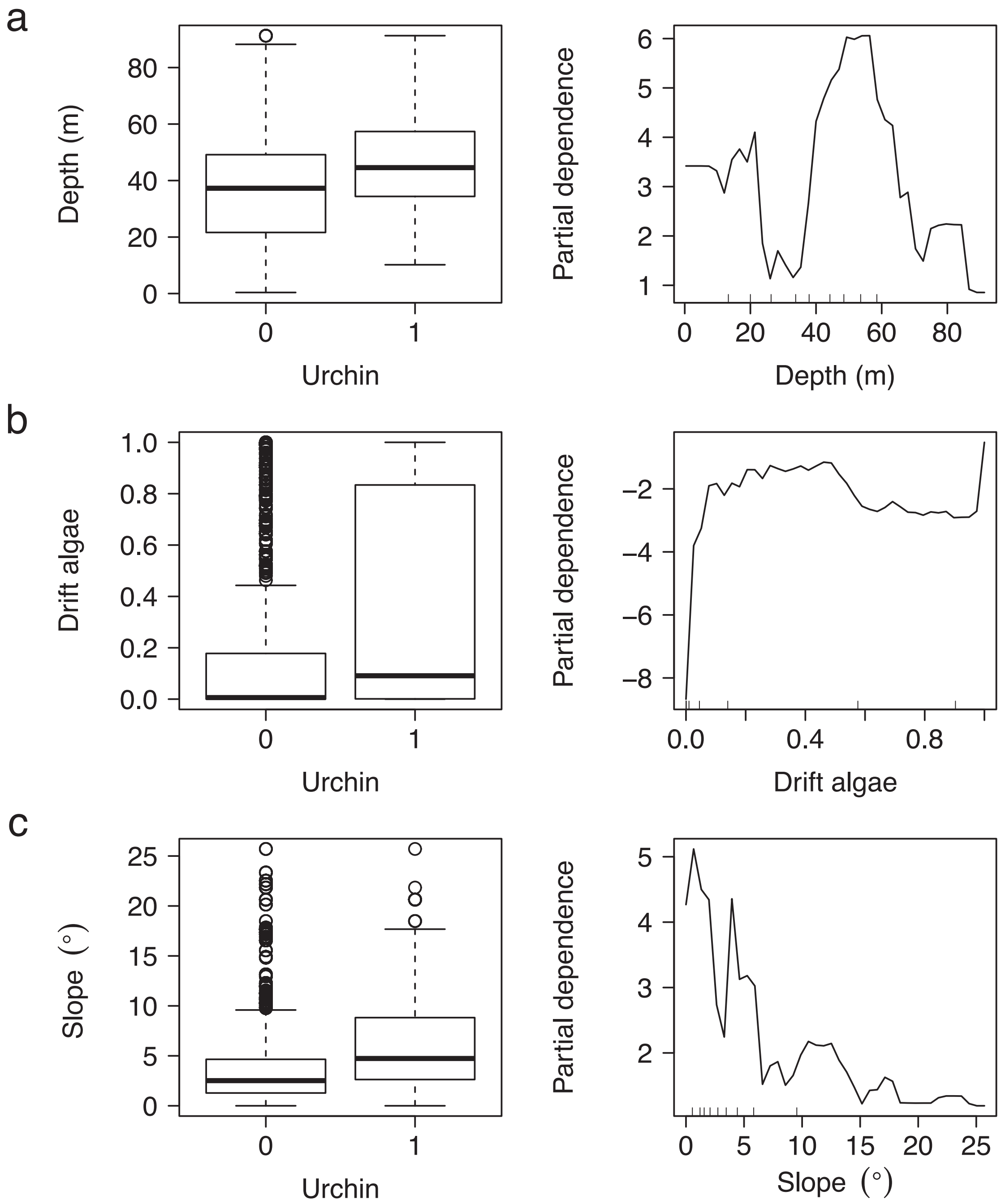


Fig. 7.5. Box-plots (left column) of 3 predictor variables of secondary importance from the random forest model for grids in the study area where sea urchins were absent (0) or present (1): a) depth, b) drift algae, and c) slope (left column). Bottom and top of box incases first and third quartiles, strong horizontal line is median, whiskers bound the 95th percentile range, and circles are outliers. Associated partial dependence plots (right column) show model predictions of sea urchins according to the respective predictor variable, when all other variables are held constant at their mean.

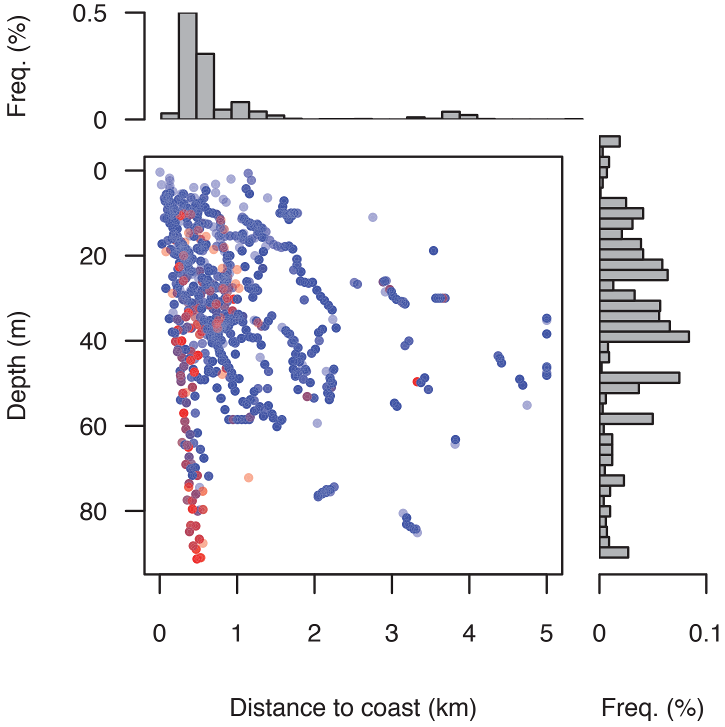


Fig. 7.6. Relationship of predictor variables depth and distance to coast. Each point is a presence (red) or absence (blue) observation of sea urchins in a grid in the study area. Red or blue tones are semi-transparent (shown as the lightest tones), such that darker points indicate combinations with more than one like observation and purple tones indicate varying combinations of presence and absence observations. Histograms show the relative frequency of counts (n = 7459) of each predictor variable.

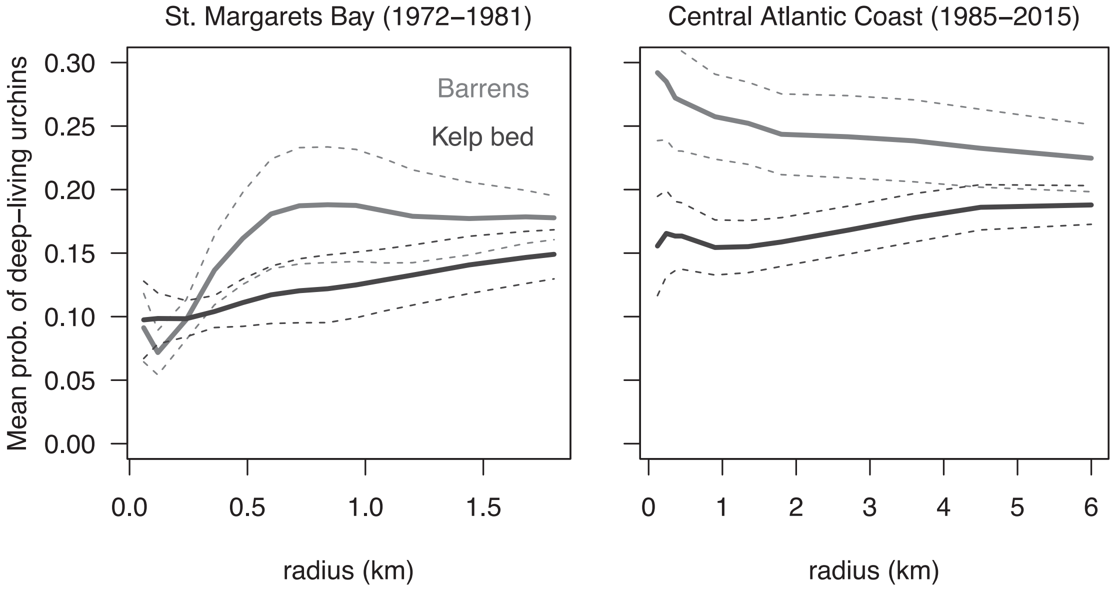


Fig. 7.7. Average probability of occurrence of sea urchins within circular buffers (areas around a coordinate point) around barrens (grey) or kelp (black) locations (Fig. 7.3) during two periods of regime shift: between 1972 and 1981 in St. Margarets Bay, and between 1991 and 2015 along the central Atlantic coast of Nova Scotia.

7.5. DISCUSSION

7.5.1. Physical and biological determinants of sea urchin distribution

Our video records showed that *Strongylocentrotus droebachiensis* did not form dense populations below 30 m depth, unlike urchins in shallow kelp beds and barrens in Nova Scotia and elsewhere in the Northwest Atlantic (Meidel & Scheibling 2001). Deep-living urchins were sparsely distributed in most areas, but abundant on granite shoals at western entrance to Halifax Harbour and below 40 m depth in the deepest regions of Mahone Bay, St. Margarets Bay and Halifax Harbour. Our predictive model showed that suitable sea urchin habitats were predominantly located within 1.5 km of the coast and in regions with negative broad-scale BPI and negative or zero fine-scale BPI, which characterize depressions, basins and localized areas (< 1.1 km^2) of flat seabed. These regions have reduced flow compared to areas with positive BPI, and should retain drift algae and small detrital particles (e.g. phytodetritus) that are important food sources for deep-living urchins (Campos-Creasey et al. 1994, Filbee-Dexter & Scheibling 2014a). Less suitable habitats included regions > 3.4 km from the coast or at depths > 85 m, flat areas > 3.1 km^2, and convexities of the seafloor.

Observations from our video transects suggest that *Strongylocentrotus droebachiensis* prefer rocky substrata in high-energy shallows, but showed no clear preference for bottom type in deeper regions. The variables bottom type and slope, which can strongly affect urchin attachment (Laur et al. 1986), were not important predictors in our model, suggesting that attachment strength becomes less important with increasing depth. These results are consistent with studies by Britton-Simmons et al. (2012) and Vetter et al. (1998) that found deep-living urchins (*S. franciscanus*) in low-energy sedimentary basins or submarine canyons in Washington and California, respectively. In contrast González-Irusta et al. (2015) found that depth, bottom type, and slope were the most important predictors of suitable habitat for other sea urchins (*Centrostephanus longispinus*, *Coelopleurus floridanus*, *Stylocidaris affinis*, *Cidaris cidaris*) at 158 – 1663 m depth on a seamount near the Canary Islands, where BPI, curvature and aspect were not important predictors.

Linkages between shallow kelp beds and deep subtidal habitats appear to play an important role in influencing the distribution of deep-living urchins. Abundance of *Strongylocentrotus droebachiensis* was positively related to drift algae in our video surveys, and our predictive model indicates that urchins were more likely to occur in habitats in close proximity to a source of attached algae and with a high probability of occurrence of drift algae. The export of drift from productive kelp beds to habitats with little to no *in situ* production, recorded in our video transects, is greatest within 1.5 km of the coast (Filbee-Dexter & Scheibling 2016). *Strongylocentrotus pallidus* has been observed consuming fronds of *Saccharina latissima* at 2500 m depth off the Scotian Shelf (A. Metaxas, Dalhouise University, pers. comm.), indicating that this subsidy occurs over a much larger range than our study documents. In a field experiment in St. Margarets Bay, Filbee-Dexter and Scheibling (2014a) showed that *Strongylocentrotus droebachiensis* at 60 m depth can locate and consume drift kelp (*Saccharina latissima*) for months, and that access to this food resource supports high reproductive capacity in these populations. Similarly, Britton-Simmons et al. (2009) found that drift kelp at 30 –

90 m depth in subtidal habitats off Washington, USA, provided food for the sea urchin *Strongylocentrotus franciscanus*, which had comparably sized gonads as shallow populations. Although urchin densities in deep subtidal habitats in our study area were lower than densities in shallow kelp beds, deep populations occupy a much greater area than shallow ones, which may offset a lower fertilization rate in determining overall larval production (Lauzon-Guay & Scheibling 2007b). Drift subsidy from highly productive kelp beds, therefore, is expected to enhance reproductive output of deep-living urchins and the supply of larvae to shallow kelp beds.

7.5.2. Spatial links to historic urchin barrens

Our results suggest that kelp beds adjacent to deeper habitats that sustain abundant populations of *Strongylocentrotus droebachiensis* are more likely to shift to barrens compared to more distant kelp beds. Localized episodes of destructive grazing causing shifts to barrens between 1972 and 1981 in St. Margarets Bay, and between 1991 and 2014 over most of the Atlantic coast of Nova Scotia, were documented at sites adjacent to areas where deep populations of urchins are predicted by our model: in sedimentary habitats at 40 to 90 m depth and on bedrock shoals < 25 m depth. Although the spread of barrens formed after 1991 was arrested due to recurrent outbreaks of urchin disease (Scheibling & Lauzon-Guay 2010), the initial shift to barrens along the outer western coast of St. Margarets Bay in the early 1970s eventually propagated throughout the entire bay and beyond, as part of a coast-wide phenomenon in the late 1970s (Wharton & Mann 1981). This suggests that sites adjacent to deep-living urchins were early tipping points of a regime shift that propagated on a coastal scale.

The shift from kelp beds to urchin barrens is likely accelerated by positive feedback mechanisms, associated with destructive grazing, that serve to increase larval supply and recruitment to barrens on regional scales. Actively grazing urchins have unlimited high-quality food (kelp), which enables high rates of growth and reproduction (Meidel & Scheibling 1998). They aggregate in high densities at grazing fronts, maximizing local fertilization rate and larval production (Lauzon-Guay & Scheibling 2007b). Urchin larvae settle preferentially on crustose coralline algae (Pearce & Scheibling 1991), the dominant algal form following destructive grazing. However, a significant spatial relationship between deep-living urchins and locations of historic barrens is probably a result of onshore movement of adults, and not larval dispersal. *Strongylocentrotus droebachiensis* has a planktonic larval duration of 28 − 147 d (Hart & Scheibling 1988). Therefore any positive effect of local populations of deep-living urchins on the overall larval pool would likely be distributed over broad coastal scales (100s – 1000s of km). In St. Margarets Bay for example, seawater retention time is estimated to be 5 – 10 d in the surface layer (10 m), and 10 – 30 d in the deeper layer (Heath 1973). Therefore most urchin larvae produced within the bay would be flushed away before they reached competency, making it unlikely that the spatial relationship that we observed between deep-living urchins and shallow barrens along the western shore results from larval retention. In contrast, there is direct evidence of onshore movement in certain areas. Scheibling et al. (1999) tracked the advance of urchin grazing fronts into kelp beds from deeper sedimentary or rocky habitats along the western shore of St. Margarets Bay and at Little Duck Island at the mouth of Mahone Bay. Brady and Scheibling (2005) documented the onshore movement of sea urchins from 25 m depth, after they were eliminated by disease on shallow bedrock ledges off Sambro near the western mouth of Halifax Harbour.

Despite evidence of onshore advance of grazing fronts from depths below 25 m, Filbee-Dexter and Scheibling (2014a) found that spatial distribution of *Strongylocentrotus droebachiensis* did not change in video surveys at 45 – 75 m depth on the outer western shore of St. Margarets Bay (at Owl's Head) between June and October 2013, indicating that onshore movement may not occur when deep-living urchins have access to a drift algal subsidy. However, we expect that a reduction in the supply of drift algae, or an increase in density of deep-living urchins, could trigger onshore movement from deep regions. In California, reduced drift kelp caused *S. franciscanus* to emerge from shelters and actively graze attached kelp (Mattison et al. 1976), resulting in a shift to barrens (Ebeling et al. 1985).

A deep-living congener, *Strongylocentrotus pallidus*, overlaps in distribution and hybridizes with *S. droebachiensis* in the Northwest Atlantic (Gagnon & Gilkinson 1994). To examine species-specificity of the linkage between shallow and deep-living sea urchins, we collected specimens for genetic analysis from 8 – 20 m depth in kelp beds near the entrance to Halifax Harbour and from 60 m in St. Margarets Bay. Of 54 individuals sequenced from shallow depths, 52 were *S. droebachiensis* and 2 were *S. droebachiensis* with *S. pallidus* mitochondrial DNA (J. Addison, University of New Brunswick at St John, unpublished data), indicating introgressive hybridization (Addison & Pogson 2009). Of 66 individuals sequenced from 60 m, 17 were *S. pallidus* and 49 were *S. droebachiensis*; 9 of these 49 were from a population lineage similar to samples of sea urchins collected from 72 – 120 m depth on the Scotian Shelf in DFO dredge surveys, and 40 were from a lineage similar to the 54 individuals that we collected at 8 – 20 m depth (J. Addison, unpublished data). This supports our assumption that the deep-living sea urchins in our study area are predominantly *S. droebachiensis*, and provides evidence of a high level of gene flow between shallow and deep subtidal habitats.

7.5.3. Conclusions and implications for future research

Our study sheds light on mechanisms driving regime shifts in the shallow rocky subtidal habitats along the Atlantic coast of Nova Scotia and the role of deep-living urchins in these dynamics. Deep populations of *Strongylocentrotus droebachiensis* persist in a cold thermal refuge from disease that causes mass mortality of shallow populations and triggers the shift from barrens to kelp beds (Scheibling & Stephenson 1984). They serve as a source of adults that eventually form grazing aggregations at the deep margins of recovering kelp beds or contribute to the pool of planktonic larvae that settle in shallow habitats, including kelp beds (Scheibling et al. 1999, Brady & Scheibling 2005). Both onshore movement and larval supply can increase urchin density to a critical threshold that triggers destructive grazing of kelp and the shift to barrens (Lauzon-Guay & Scheibling 2010). However, increased frequency of disease makes it unlikely that shallow urchin populations will recover their historic densities along the coast of Nova Scotia (Feehan & Scheibling 2014).

Our study enables us to draw inferences about the spatial linkage between deep-living urchins and foci of destructive grazing of shallow kelp beds that can spread at coastal scales. This linkage helps to explain spatial patterns of past shifts to urchin barrens in the coastal ecosystem, and to identify parts of the coast of Nova Scotia where kelp beds are most vulnerable to collapse. Our findings highlight the importance of incorporating knowledge of deeper, less-studied subtidal habitats in our understanding of the dynamics of shallow coastal areas subject to abrupt change in ecosystem structure and functioning.

The connectivity between kelp beds and neighboring deep communities remains poorly understood in many coastal systems. Investigating the importance of energy subsidies, originating in kelp beds along a shallow band of coast, in structuring benthic communities in deeper waters is an important area for future research, particularly in light of major declines in kelp biomass in coastal ecosystems associated with anthropogenic stressors on a global scale (Moy & Christie 2012, Wernberg et al. 2012, Filbee-Dexter et al. 2016). Projected declines in drift (Krumhansl et al. 2014) can be incorporated into predictive species distribution models to further examine consequent changes in distribution of benthic assemblages in deeper coastal areas. A key source of uncertainty in the alternative-state dynamics of kelp and barrens ecosystems concerns the source and magnitude of supply of sea urchin larvae to shallow coastal habitats, which likely plays an important role in both driving density-induced phase shifts and stabilizing the barrens or kelp state. Biophysical modeling (Daigle et al. 2014) or genetic markers (Hellberg et al. 2002, Banks et al. 2007) could be used to explore the fate of larvae produced in deep areas and their likelihood of settling in shallow kelp bed habitats.

7.6. ACKNOWLEDGEMENTS

We thank J. Lindley for his invaluable help with the design and operation of the tow-camera system. We thank K. Krumhansl, C. Feehan, J. O’Brien, R. Buchwald, F. Francis, A. Harding, and C. Robertson for assisting with field work and image analysis, and J. Addison for genetic analyses. We thank H. Whitehead and D. Lyons for helpful advice and discussion during preparation of the manuscript. This research was funded by a Discovery Grant, a Research Tools and Instruments Grant, and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F-D. was supported by a NSERC Canada Graduate Scholarship and a Dalhousie Killam Scholarship.

CHAPTER 8

CONCLUSION

The growing complexity and severity of anthropogenic impacts on natural systems presents a major challenge for human societies that rely on predictable ecosystem behavior (Drijfhout et al. 2015). Identifying critical thresholds for ecological collapse, and feedback mechanisms that maintain alternate community configurations, is an important step in understanding abrupt and persistent changes in ecosystems, which usually are associated with high costs for human societies (Folke et al. 2004). Alternations between kelp beds and barrens are one of the best-studied examples of these dynamics in marine ecosystems. This thesis shows that transitions between kelp beds and barrens represent regime shifts, and that linkages between shallow and deep subtidal habitats play an important role in these dynamics.

My review of the literature (Chapter 2) indicates that shifts between barrens and kelp beds (or forests) occur on temperate and polar coasts throughout the world, with different thresholds for shifts to barrens and reverse shifts to kelp beds. Numerous stabilizing feedback mechanisms create these two alternative stable states, and multiple co-occurring drivers operating at both global (e.g. climate change) and local (e.g. coastal fisheries) scales drive changes in sea urchin densities that trigger shifts in ecosystem state. Although it is not possible to manage global drivers such as climate change, adaptive management and a focus on reducing local impacts may be effective strategies for maintaining kelp beds in many of these systems. In Chapter 2, I also identified large regions of coastal kelp where sea urchin barrens have not been documented, and spans of coastlines that should support kelp yet remain unstudied, particularly in South America and the Canadian Arctic. This indicates the need for further research to accurately assess the global extent of regime shifts to barrens.

The large body of research on shifts between barrens and kelp-dominated states is limited to a narrow band of rocky bottom between wave-swept shallow regions and light-limited deeper waters (Chapter 2). My thesis underscores the importance of incorporating information from deep subtidal habitats, adjacent to kelp beds, in this research. Connections between these deep and shallow habitats are complex and involve reciprocal flows of energy and individuals. In Nova Scotia, there is a strong spatial relationship between predicted locations of deep-living sea urchins and foci of sea urchin outbreaks leading to destructive grazing along the Atlantic coast (Chapter 7). This relationship suggests that sea urchins living in deep subtidal habitats migrate onshore to encounter and overgraze shallow kelp beds. Deep-living sea urchins, depending on available food resources, can have a high reproductive capacity, making them a source of larvae for recruitment to sea urchin populations on a coastal scale (Chapter 4). Increased larval supply, for example, can enable sea urchins to repopulate kelp beds re-established after disease has eliminated urchins in shallow barrens, and trigger further outbreaks of destructive grazing to cause a shift back to barrens. Increased survival of sea urchin larvae due to favourable environmental conditions (Hart & Scheibling 1988) likely results in higher recruitment to both deep and shallow subtidal habitats, increasing sea urchin densities along a much broader scale than previously recognized.

Deep-living sea urchins to a large extent are reliant on drift kelp and other forms of algal detritus produced in productive shallow habitats (Chapter 3,7). This subsidy can be an important food source for sea urchins over the course of a year (Chapter 4). Drift kelp is common in deep subtidal habitats where it occurs in depressions and flat regions close to the coast (Chapter 6). The flow of drift from shallow kelp beds to deep subtidal habitats appears to inhibit sea urchins from actively searching for food (Chapter 4). However, a decline in kelp biomass could increase foraging movements of deep-living sea urchins resulting in encounter with the deep margins of kelp beds, where they form grazing fronts. Increased density of adult sea urchins along these fronts create positive feedbacks that accelerate the shift to barrens, resulting in abrupt transitions that can spread on a coastal scale and are difficult to prevent (Chapter 2). Locating sea urchin populations in deep habitats may help identify regions of the coast that are vulnerable to collapse to barrens, and monitoring changes in the distribution and abundance of deep-living sea urchins may provide early warning of shifts to barrens. These findings are widely applicable to kelp ecosystems in other regions that experience similar onshore migration from deep areas, such as Iceland (Hjorleifsson et al. 1995), California (Ebeling et al. 1985), Alaska (Konar & Estes 2003) and Maine (Johnson et al. 2012).

The extent to which regime shifts have cascading effects on marine communities that rely on these systems for habitat and food is an important area of research. This thesis shows that multiple impacts along the coast of Nova Scotia appear to be creating new and further degraded ecosystems with lower macroalgal biomass and structural complexity. Rising temperatures and invasive species, such as *Membranipora membranacea*, have modified biotic interactions that are contributing to large-scale declines in kelp in this region (Chapter 5). Acute perturbations such as hurricanes also are increasing in frequency and can cause defoliation of shallow kelp beds (Chapter 3). The resulting turf and invasive algae-dominated reefs are stabilized by feedback mechanisms, such as sediment accumulation (Chapter 5) and reduced supply of kelp propagules (O'Brien et al. 2015). I predict that large-scale changes in kelp biomass will impact the structure and functioning of adjacent ecosystems receiving drift kelp subsidy, with broader consequences for the coastal ecosystem. Future studies are needed to more fully understand processes of drift transport, degradation and deposition in deep subtidal habitats, and the potential impact of this subsidy not only for sea urchins, but also for benthic communities at large.

The two sudden changes in the kelp bed ecosystem that I explored in this thesis, namely the shift to barrens by destructive grazing of sea urchins and the collapse of reestablished kelp beds and their replacement by stands of invasive or turf algae, have taken place along different parts of the Atlantic coast of Nova Scotia in the recent past. Over the last 1 to 2 decades, the range of shallow sea urchin populations, and therefore the extent of destructive grazing of kelp, has become restricted to headlands along a few localized sections of coast due to increasingly more frequent outbreaks of sea urchin disease (Chapter 7). While kelp beds currently persist on headlands along much of the coast, kelps within the warmer and more protected embayments (such as St Margarets Bay) have largely given way to low lying invasive or turf forming algae, a likely consequence of the direct and indirect effects of ocean warming (Chapter 5). These patterns of change in space and time underscore the importance of information on spatial variability in species distributions, habitat type, environmental stressors, and biotic interactions in understanding the stability of kelp bed ecosystems along this coast.

Assessing ecosystem stability on an empirical basis is challenging particularly for marine systems because it requires observational data over long time-spans and broad spatial scales. Long-term data is generally sparse on subtidal reefs (e.g. Pandolfi & Jackson 2006), which usually require scuba or submersible camera technology for sampling. Our observational data for the rocky subtidal ecosystem off Nova Scotia is remarkable both in duration and spatial extent. Records from 5 decades of diving-based research enabled us to evaluate the impact of observed temperature rise on kelp beds along the central Atlantic coast (Chapter 5). These records combined with extensive towed-camera surveys were essential to linking the spatial pattern of historic shifts to barrens with predicted maps of sea urchin distribution created using modern camera and computing technology. This underscores the importance of long-term monitoring initiatives, coastal surveys and field experiments in understanding the stability of kelp bed ecosystems.

Early work on ecosystem stability and alternative stable states was entirely theoretical (Lewontin 1969, May 1973, 1977), born out of curiosity of natural system behaviour, rather than concern of human-driven collapse. In recent decades, verifying the existence of alternative ecosystem states and understanding the nature critical transitions and stabilizing feedbacks has profound implications for ecosystem management (Scheffer et al. 2001, Folke et al. 2004). Currently, ecologists are documenting loss of complex and diverse ecosystems worldwide (IPCC 2014), discovering no-analog communities

(Williams & Jackson 2007), and struggling to untangle the complex interactions between multiple stressors (Crain et al. 2008). We are in a time of unprecedented change, and predicting the manner in which these changes will impact the equilibrium of nature is a daunting task for scientists and society at large. During my 5-year graduate degree I witnessed 2 shifts in ecosystem structure due to rising temperatures and disease, a severe hurricane, and environmental conditions and marine communities never before seen in this region. Although these events were personally disturbing to observe, they also provided an ideal study system in which to explore the dynamics of change. We have a narrowing window of opportunity to recover degraded ecosystems and prevent further collapse, and successful measures will require innovative strategies and a clearer understanding of processes that impart stability or lead to abrupt change. My hope is that this thesis and the publications that emanate from it is a step in that direction.

Appendix A. Kelp beds documented in Arctic for Chapter 2

Table A1. Documented kelp beds in the Beaufort Sea, Canadian Arctic, Greenland and northern Europe.

Region	Kelp species	Source
Alaska, USA		
Stefensson Sound	*Laminaria solidungula*, *Saccharina latissima*	Dunton et al. (1982)
Demarcation Point	*L. solidungula*, *S. latissima*	Wiencke et al. (2007)
Camdem Bay	*L. solidungula*, *S. latissima*	Wiencke et al. (2007)
Chukchi Sea	*L. solidungula*, *S. latissima*	Mohr et al. (1957)
Prince Patrick Island	*S. latissima*	Wiencke et al. (2007)
Canadian Arctic		
Bylot Island	*S. latissima*	Wilce et al. (2009)
Cape Hatt	*S. latissima*, *Alaria esculenta*	Cross et al. (1987)
Pangnirtung Fiord	*Laminaria sp.*	Cross et al. (1987)
Brock Island	*L. solidungula*	Lee (1973)
Ungava Bay	*A. esculenta*, *L. solidungula*, *L. digitata*, *S. latissima*	Sharp et al. (2009)
Lancaster South	*A. esculenta*, *L. solidungula*, *S. groenlandica*, *S. latissima*	Cross et al. (1987)
Foxe Basin	*A. esculenta*, *L. solidungula*, *S. groenlandica*, *S. latissima*	Chapman & Lindley (1981)
Hudson Bay	*A. esculenta*, *L. solidungula*, *L. digitata*, *S. latissima*	Mathieson et al. (2010)
Greenland		
Siorapoluk to Nuuk	*S. latissima*, *Agarum clathratum*, *L. solidungula*	Krause-Jensen et al. (2012)
Disko Island	*S. latissima*	Bischoff & Wiencke (1993)
Young Sound	*S. latissima*	Glud et al. (2009)
Northern Europe		
Svalbard	*L. digitata*, *L. solidungula*, *S. latissima*, *A. esculenta*, *Saccorhiza dermatodea*	Hop et al. (2002)

Region	Kelp species	Source
Kingsfjorden	*L. digitata*, *L. solidungula*, *S. latissima*, *A. esculenta*, *S. dermatodea*	Wiencke et al. (2007)
White Sea	*L. digitata*, *L. hyperborea*, *S. latissima*, *A. esculenta*, *S. dermatodea*	Mikhaylova (1999)

Literature Source

Bischoff B, Wiencke C (1993) Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland). Helgol Meeresunters 47:167−191

Cross WE, Wilce RT, Fabijan MF (1987) Effects of experimental releases of oil and dispersed oil on Arctic near-shore macrobenthos. III. Macroalgae. Arctic 40:211−219

Dunton KH, Reimnitz E, Schonberg S (1982) An arctic kelp community in the Alaskan Beaufort Sea. Arctic 35:465−484

Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. Bot Mar 52:559−572

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167−208

Krause Jensen D, Marbà N, Olesen B, Sejr MK and others (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. Glob Change Biol 18:2981−2994

Mikhaylova TA (1999) The initial stages of experimental forming of *Laminaria* communities in the White Sea. Bot Zh 84:56–66

Mohr JL, Wilimovsky NJ, Dawson EY (1957) An arctic Alaskan kelp bed. Arctic 10:45−52

Sharp G, Allard M, Lewis A, Semple R, Rochefort G (2008) The potential for seaweed resource development in sub-arctic Canada; Nunavik, Ungava Bay. J Appl Phycol 20:491–498

Wiencke CM, Clayton N, Gómez I, Iken K and others (2007) Life strategy, ecophysiology and ecology of seaweeds in polar waters. In: Amils R, Ellis-Evans C, Hinghofer- Szalkay HG (eds) Life in extreme environments. Springer, Dordrecht, p 213–244

Wilce RT, Pedersen PM, Sekida S (2009) *Chukchia pedicellata* gen. et sp. nov. and *C. endophyticanov.* comb., Arctic endemic brown algae (Phaeophyceae). J Phycol 45:272 – 286

Appendix B. Locations of video transects for Chapter 3

Table B1. Locations of video transects at each site and date: start position coordinates, heading, length (m), and depth range. ND: no data.

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

Site	Date	Position Coordinates	Heading (°)	Length (m)	Depth range (m)
Splitnose Pt 3	1/9/2010	44°28.39’ N, 63°32.90’ W	92	767	5–45
Splitnose Pt 3	8/9/2010	44°28.40’ N, 63°32.92’ W	91	375	5–24
Splitnose Pt 4	1/9/2010	44°28.15’ N, 63°32.99’ W	91	344	11–42
Splitnose Pt 4	8/9/2010	44°28.16’ N, 63°33.00’ W	100	390	9–25
Tilly Point	18/8/2010	44°32.31’ N, 64°00.93’ W	75	322	14–49
Tilly Point	26/9/2010	44°32.33’ N, 64°00.93’ W	94	263	6–45
Tilly-Lodge	18/8/2010	44°32.87’ N, 64°01.27’ W	108	335	10–45
Tilly-Lodge	26/9/2010	44°32.81’ N, 64°01.26’ W	84	333	8–32

Appendix C. Locations of video transects and gut contents of sea urchins for Chapter 4

Table C1. Video transects at Owl's Head: date, start position coordinates, heading, length (m), and depth range. (-) indicates missing data.

Date	Transect type	Position Coordinates	Heading (°)	Length (m)	Depth range (m)
13/08/2010	Detritus survey	44° 31.19 N 64° 00.11 W	82	242	11-75
26/09/2010	Detritus survey	44° 31.21 N 64° 00.11 W	90	118	11-42
14/10/2010	Detritus survey	44° 31.57 N 64° 00.40 W	50	279	24-74
25/10/2010	Detritus survey	44° 31.19 N 64° 00.12 W	90	240	10-76
5/02/2011	Detritus survey	44° 31.20 N 64° 00.12 W	80	780	29-88
20/07/2012	Detritus survey	44° 31.20 N 64° 00.11 W	90	750	10-80
04/09/2012	Detritus survey	44° 31.23 N 64° 00.14 W	100	710	5-90
15/02/2013	Detritus survey	-	-	-	-
20/06/2013	Field experiment	44° 31.29 N 64° 00.15 W	98	260	20-70
23/06/2013	Field experiment	44° 31.29 N 64° 00.15 W	100	266	20-69
28/06/2013	Field experiment	44° 31.31 N 64° 00.14 W	110	549	34-74
12/07/2013	Field experiment	44° 31.29 N 64° 00.13 W	102	330	28-71
25/07/2013	Field experiment	44° 31.33 N 64° 00.18 W	115	355	15-68
5/08/2013	Field experiment	44° 27.20 N 63° 46.94 W	78	611	10-25
20/08/2013	Field experiment	44° 31.31 N 64° 00.17 W	100	654	20-90
11/09/2013	Field experiment	44° 31.30 N 64° 00.10 W	100	646	40-92
04/10/2013	Field experiment	44° 31.29 N 64° 00.10 W	112	740	1-90
15/11/2013	Detritus survey	44° 32.29 N 64° 00.91 W	100	830	10-70

Table C2. Mean proportion of macroalgae (excluding coralline algae), sediment and animal sources in gut contents of sea urchins *Strongylocentrotus droebachiensis* at Owl's Head (OH, 60 m depth) and Duncan's Cove (DC, 8 m depth) from August 2010 to May 2013.

Date	Location	Kelp	Sediment	Animal
8/18/2010	OH	0.96	0.04	0.00
9/26/2010	OH	1.00	0.00	0.00
10/25/2010	OH	0.69	0.31	0.00
2/4/2011	OH	0.55	0.45	0.00
3/15/2011	OH	0.70	0.05	0.25
4/20/2011	OH	0.93	0.07	0.00
5/11/2011	OH	1.00	0.00	0.00
5/25/2011	OH	1.00	0.00	0.00
7/27/2011	OH	0.99	0.01	0.00
8/27/2011	OH	1.00	0.00	0.00
9/13/2011	OH	0.99	0.00	0.01
10/19/2011	OH	1.00	0.00	0.00
12/12/2011	OH	0.80	0.20	0.00
1/13/2012	OH	0.60	0.40	0.00
2/10/2012	OH	0.55	0.45	0.00
3/9/2012	OH	0.66	0.34	0.00
4/24/2012	OH	0.53	0.36	0.11
6/9/2012	OH	0.89	0.11	0.00
7/13/2012	OH	0.98	0.03	0.00
8/9/2012	OH	1.00	0.00	0.00
9/15/2012	OH	0.97	0.03	0.00
10/19/2012	OH	0.97	0.03	0.00
12/11/2012	OH	0.91	0.08	0.01
2/15/2013	OH	0.72	0.17	0.11
3/19/2013	OH	0.69	0.31	0.00
4/5/2013	OH	0.72	0.28	0.00
5/17/2013	OH	0.70	0.22	0.08

Date	Location	Kelp	Sediment	Animal
9/17/2010	DC	0.87	0.12	0.00
2/7/2011	DC	0.96	0.04	0.04
3/17/2011	DC	1.00	0.00	0.00
4/21/2011	DC	1.00	0.00	0.00
6/22/2011	DC	0.99	0.01	0.00
2/5/2012	DC	0.96	0.04	0.00
3/14/2012	DC	0.98	0.02	0.00
4/27/2012	DC	1.00	0.00	0.00
6/26/2012	DC	0.99	0.01	0.00
9/27/2012	DC	1.00	0.00	0.00
10/26/2012	DC	1.00	0.00	0.00
1/15/2013	DC	0.90	0.00	0.10
3/15/2013	DC	0.88	0.00	0.12
5/7/2013	DC	0.99	0.01	0.00

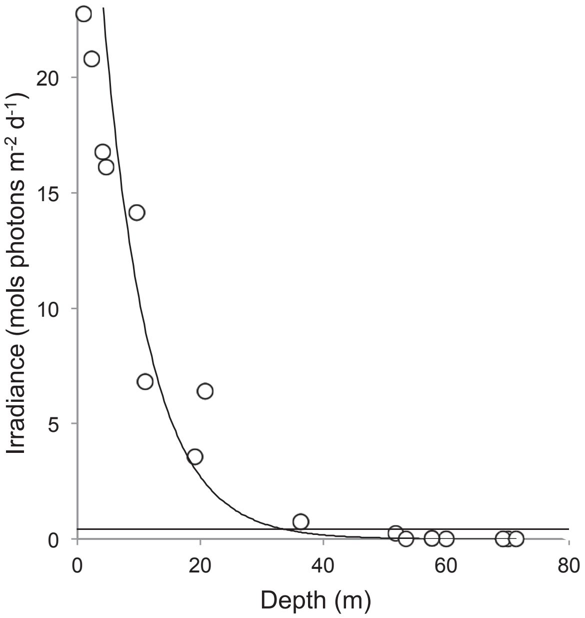


Fig. C1. Irradiance reaching seafloor at various depths within 25 km of Owl's Head, based on satellite measurements by Gattuso et al. (2006). Horizontal line indicates minimum irradiance detected by tube feet of *Strongylocentrotus droebachiensis* (Lesser et al. 2011).

Appendix D. Long-term records of kelp abundance, and locations of coastal surveys and SST grids for Chapter 5

Table D1. Records of kelp biomass and cover at 3 sites in Nova Scotia between 1949 and 2014. Samples were collected from quadrats (n = sample size). Sites are on the southwestern coast (Whitehead Island, WI) and along the central Atlantic Coast (Little Duck Island, LDI; Mill Cove, MC) of Nova Scotia. Data are mean (+ SE); –: no data.

Year	Month	Site	Depth (m)	Quad. (m^2)	n	Biomass (kg m^{-2})	Cover (%)	Source
1949	Sum.[a]	WI	5–10	0.42[b]	–	19.4 (0.33)	90[c]	MacFarlane 1952
1978	–	WI	10	1	10–15	–	78 (5)	Wharton & Mann 1981
1979	7,8	WI	4.5–8	0.25	–	4.64 (0.71)	–	Tremblay & Chapman 1980
1983	8	WI	8–10	1	12	3.81 (0.14)	72.7 (21)	Scheibling 1986
2014	11	WI	5–8	1	25	2.9 (0.95)	60 (10)	This study
1984	7	LDI	8–10	1	12	8.21 (0.9)	95 (6.4)	Scheibling et al. 1999
1992	9–10	LDI	6, 8	1	10	3.94 (0.97)	75.7 (3.1)	Scheibling et al. 1999
1993	6–10	LDI	6, 8	1	10	3.79 (0.85)	65.4 (5.9)	Scheibling et al. 1999
1994	6,8–10	LDI	6, 8	1	10	0.9 (0.04)	27.5 (4.1)	Scheibling et al. 1999
1995	6–7,10	LDI	6, 8	1	14	4.1 (0.67)	76.3 (11.4)	Scheibling et al. 1999
1997	7,9,10	LDI	6	1	10	4.01 (0.66)	39.1 (7.7)	Kelly et al. 2011
1998	6–10	LDI	8	1	10	2.64 (0.42)	43.5 (6.5)	Kelly et al. 2011
1999	6–8,10	LDI	8	1	5	0.4 (0.01)	36.6 (5.4)	Kelly et al. 2011
2000	8	LDI	6, 8	1	9	0.3 (0.13)	13.4 (2.7)	Kelly et al. 2011
2002	8	LDI	6, 8	1	16	0.07 (0.02)	3.1 (0.2)	Kelly et al. 2011
2008	8	LDI	8	1	8	2.36 (0.38)	–	Kelly et al. 2011
2014	8	LDI	8	1	8	0.21 (0.04)	2.4 (0.5)	This study
1968	Sum.[a]	MC	4–8	0.25	31	16 (0.4)	–	Mann 1972
1973	6–8	MC	4–12	0.5	5	20.1 (9.2)	–	Breen & Mann 1976
1977	Sum.[a]	MC	8	0.25	10	3.6[c]	–	Chapman 1981
1982	Sum.[a]	MC	4–14	80[d]	1	–	60 (0)	Moore & Miller 1983
1992	10	MC	8	1	10	4.94 (0.71)	91.5 (5.5)	Scheibling et al. 1999
1993	6,8–9	MC	8	1	10	2.1 (0.48)	65.6 (8.9)	Scheibling et al. 1999
1994	6,8–9	MC	6–10	1	10	0.97 (0.22)	33.5 (5.3)	Scheibling et al. 1999
1995	6,8,10	MC	6–10	1	10	4.7 (0.95)	45.8 (9.4)	Scheibling et al. 1999
2005	10–11	MC	4, 8	–	73	–	66.8 (1.6)	Saunders & Metaxas 2008
2006	10–11	MC	4, 8	–	44	–	41.2 (1.6)	Saunders & Metaxas 2008

Year	Month	Site	Depth (m)	Quad. (m^2)	N	Biomass (kg m^{-2})	Cover (%)	Source
2008	7,9	MC	4, 6	0.5	16–18	0.39 (0.06)	–	Krumhansl et al. 2011
2009	8–9	MC	4, 6	0.5	16–18	1.97 (0.43)	–	Krumhansl et al. 2011
2010	6	MC	8	1	8	3.7 (0.77)	46.6 (9.5)	C. Feehan[e]
2012	6	MC	8	1	10	0.07 (0.004)	–	J. O'Brien[e]
2014	6,7,11	MC	8	1	8	0.1 (0.02)	16.9 (6.5)	This study

[a] Sampled during summer (Sum), exact months not available. [b] Kelp collected with 0.42 m^2 metal grab from a wooden dory. [c] SE not available. [d] Cover measured along transect. [e] Unpublished data.

LITERATURE SOURCE

Breen PA, Mann KH (1976) Destructive grazing of kelp by sea urchins in eastern Canada. J Fish Res Board Can 33:1278–1283

Chapman ARO (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. Mar Biol 62:307–311

Kelly JR, Scheibling RE, Balch T (2011) Invasion-mediated shifts in the macrobenthic assemblage of a rocky subtidal ecosystem. Mar Ecol Prog Ser 437:69–78

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

MacFarlane C (1952) A survey of certain seaweeds of commercial importance in southwest Nova Scotia. Can J Botany 30:78–97

Mann KH (1972) 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

Moore DS, Miller RJ (1983) Recovery of macroalgae following widespread sea urchin mortality with a description of the shallow, hard-bottom habitat on the Atlantic coast of Nova Scotia. Can Tech Rep Fish Aquat Sci 1230

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

Scheibling RE (1986) Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. Oecologia 68:186–198

Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. Can J Fish Aquat Sci 56:2300–2314

Tremblay C, Chapman ARO (1980) The local occurrence of *Agarum cribrosum* in relation to the presence or absence of its competitors and predators. Proc Nova Scotian Ins Sci 30:165–170

Wharton WG, Mann KH (1981) Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. Can J Fish Aquat Sci 38:1339–134

Table D2. Locations of study sites along the southwestern and central Atlantic coast of Nova Scotia. Long-term study sites are Whitehead Island (WI), Little Duck Island (LDI), and Mill Cove (MC). Coastal surveys were at 7 sites in 1982 (Moore & Miller 1983) and 2014 (this study), and at 23 sites in 2000 and 2007 (Watanabe et al. 2010), and in 2014 (this study). Grids used for SST analysis that encapsulate sites in headlands (H), outer bays (O) and inner bays (I) are numbered east to west. Site numbers and grid locations correspond to Fig. D1.

Site	#	SST Grid	Latitude (°N)	Longitude (°W)	Long-term	Coastal Surveys			
						1982	2000	2007	2014
Whitehead I	1	WI	43.665	65.867	✓			✓	✓
Puddingpan I	2	H1	44.061	64.564			✓	✓	✓
E Spectacle I	3	H2	44.250	64.330			✓	✓	✓
W Ironbound I	4	H2	44.238	64.276			✓	✓	✓
Pt Enrage	5	H2	44.270	64.250			✓	✓	✓
Rose Bay	6	O1	44.293	64.248			✓	✓	✓
The Ovens	7	O1	44.325	64.259			✓	✓	✓
Feltzen South	8	O1	44.332	64.282			✓	✓	✓
Cross I	9	O2	44.317	64.174			✓	✓	✓
Little Duck I	10	O2	44.365	64.183	✓		✓	✓	✓
Hell Racketts	11	-	44.399	64.207		✓			✓
Sheep L	12	I1	44.503	64.268			✓	✓	✓
Graves Shoal	13	I1	44.548	64.197			✓	✓	✓
Coachman’s L	14	I2	44.493	64.177			✓	✓	✓
Little Tancook I	15	I2	44.475	64.138		✓	✓	✓	✓
Flat I	16	O3	44.429	64.130		✓	✓	✓	✓
E Ironbound I	17	O3	44.438	64.097			✓	✓	✓
Tilley Pt	18	I3	44.538	64.016			✓	✓	✓
Mill Cove	19	I4	44.592	64.058	✓	✓	✓	✓	✓
Luke I	20	I3	44.576	63.939			✓	✓	✓
Shut-in I	21	I3	44.542	63.954		✓	✓	✓	✓
Woody I	22	H3	44.449	63.714			✓	✓	✓
Terrence Bay	23	-	44.469	63.691		✓			✓
Sambro I	24	-	44.438	63.565		✓			✓
Gill Cove	25	H4	44.485	63.535			✓	✓	✓
Duncan's Cove	26	H4	44.498	63.525			✓	✓	✓

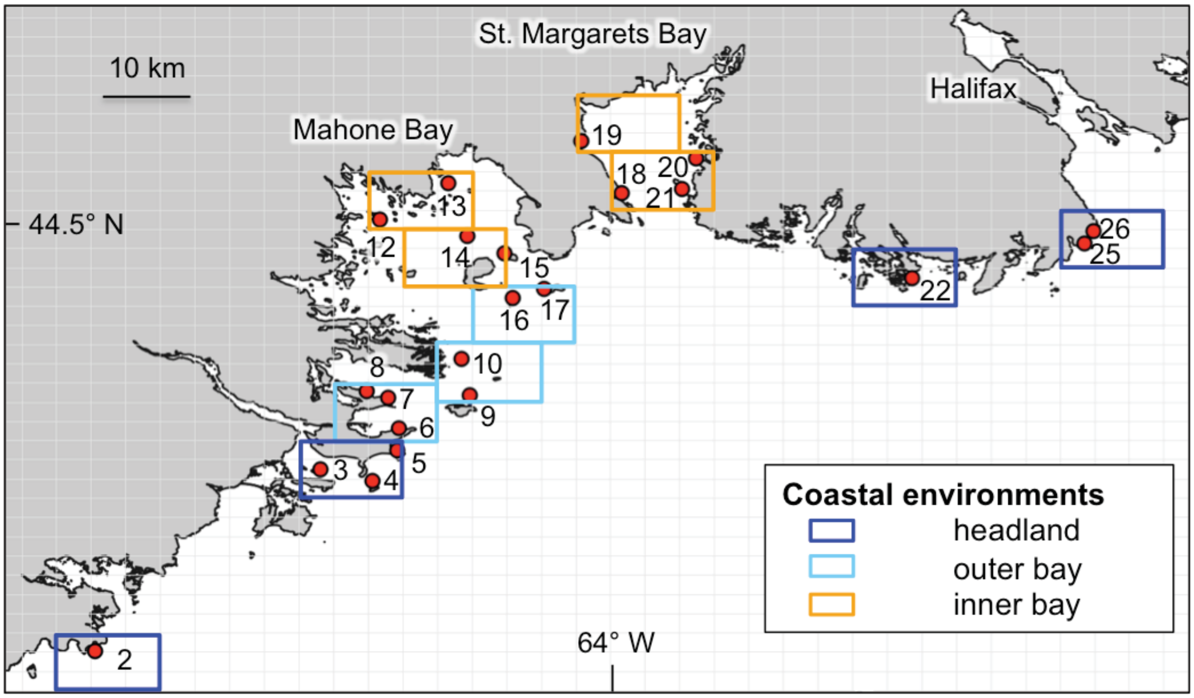


Fig. D1. Numbered locations of sites on the central Atlantic coast surveyed in 2000 and 2007 (Watanabe et al. 2010), and resurveyed in 2014 (this study). Grids used for SST analysis that encapsulate headland, outer bay and inner bay coastal environments are indicated.

Appendix E. Methods and results for predictive model of occurence of drift algae for Chapter 6

Table E1. Video transects in study area and validation site: transect number, depth range, start and end position coordinates, and observation of drift. No data = ND.

Trans No.	Depth (m) Min	Max	Coordinates (Lat. Lon.) Start Position	End Position	Drift
1	14.6	31.7	44.573 -64.04	44.574 -64.038	N
2	24.0	58.8	44.574 -64.038	44.511 -63.991	Y
3	10.0	53.2	44.520 -64.002	ND	Y
4	58.5	74.0	44.520 -64.000	DN	Y
5	20.3	73.1	44.516 -64.005	44.516 -63.996	Y
6	45.8	49.1	44.520 -63.980	44.521 -63.980	N
7	22.1	28.7	44.512 -63.995	44.520 -64.001	Y
8	23.7	55.9	44.520 -64.001	44.523 -64.001	Y
9	7.4	55.7	44.523 -64.001	44.523 -64.003	Y
10	15.1	65.1	44.524 -63.972	44.523 -63.977	Y
11	40.2	52.9	44.530 -63.973	44.530 -63.976	Y
12	41.5	55.4	44.542 -63.967	44.543 -63.971	Y
13	13.0	49.7	44.548 -63.961	44.545 -63.968	Y
14	14.5	32.7	44.563 -63.954	44.563 -63.958	N
15	6.8	53.6	44.478 -63.546	44.476 -63.534	Y
16	4.5	44.9	44.559 -64.031	44.559 -64.028	Y
17	23.3	47.5	44.548 -63.962	44.549 -63.966	Y
18	4.7	37.4	44.511 -63.997	44.512 -63.994	Y
19	11.5	24.6	44.510 -63.996	44.509 -63.991	Y
20	7.3	38.2	44.547 -64.021	44.546 -64.017	Y
21	16.4	42	44.546 -64.017	44.520 -64.001	Y
22	11.3	42	44.520 -64.001	44.520 -64.001	Y
23	7.2	49.7	44.511 -63.997	44.512 -63.993	Y
24	6.0	43.6	44.511 -63.997	44.511 -63.993	Y
25	14.4	46.3	44.510 -63.996	44.510 -63.992	Y
26	24.5	61	44.510 -63.991	44.510 -63.987	Y
27	5.3	44	44.511 -63.997	44.512 -63.993	Y
28	9.2	59.6	44.522 -64.004	44.523 -64.002	Y
29	61.6	72.4	44.523 -64.001	44.523 -64.000	Y

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Drift
30	9.4	75.3	44.526 -64.007	44.528 -64.002	Y
31	7.0	46.1	44.539 -64.016	44.542 -64.013	Y
32	6.5	55.6	44.559 -64.031	44.562 -64.028	Y
33	19	69.7	44.520 -64.002	nd	Y
34	26.7	61.7	44.511 -63.994	44.510 -63.991	Y
35	34.7	83.2	44.522 -64.003	44.523 -63.999	Y
36	11.0	81.1	44.525 -64.006	44.526 -64.001	Y
37	11.9	38.5	44.431 -63.652	44.429 -63.653	Y
38	26.0	40.1	44.428 -63.653	44.428 -63.653	Y
39	16.5	41.4	44.426 -63.654	44.425 -63.654	N
40	5.3	17.8	44.443 -64.088	44.451 -64.097	N
41	10.8	37.4	44.474 -64.15	44.487 -64.143	Y
42	11.8	31.4	44.480 -64.161	44.490 -64.162	Y
43	23.9	29.2	44.466 -64.188	44.469 -64.189	Y
44	18.0	56.6	44.460 -64.207	44.463 -64.198	Y
45	9.5	24.5	44.453 -63.568	44.430 -63.578	Y
46	26.9	91.7	44.520 -64.001	44.519 -63.996	Y
47	9.5	70	44.522 -64.003	44.521 -64.000	Y
48	5.8	86.3	44.522 -64.003	44.522 -63.997	Y
49	21.3	72.9	44.522 -64.002	44.521 -64.009	Y
50	8.3	90.1	44.522 -64.003	44.521 -63.996	Y
51	29.4	92.6	44.522 -64.002	44.520 -63.996	Y
52	11.4	23.5	44.511 -63.996	44.511 -63.995	N
53	29.6	89.1	44.521 -64.002	44.517 -63.997	Y
54	22.1	61.3	44.51 -63.995	44.509 -63.985	Y
55	24.4	63.6	44.509 -63.985	44.508 -63.98	Y
56	31.7	42.5	44.550 -63.964	44.550 -63.965	Y
57	42.8	62	44.550 -63.966	44.545 -63.981	Y
58	3.9	58	44.423 -64.009	44.424 -64.008	N
59	53.1	81.8	44.412 -64.000	nd	N
60	74.9	139.6	44.412 -63.600	44.412 -63.599	Y
61	13.4	39.7	44.412 -63.599	44.412 -63.597	N
62	14.5	32.7	44.663 -63.954	44.563 -63.958	N
63	21.4	33.1	44.511 -63.995	44.511 -63.994	Y
64	0.5	61.7	44.511 -63.993	44.510 -63.991	Y
65	34.7	83.2	44.522 -64.003	44.523 -63.999	Y
66	9.8	50.1	44.446 -63.795	44.447 -63.785	Y
67	11.0	29.1	44.453 -63.782	44.454 -63.776	Y
68	30.0	76.0	44.433 -63.800	44.438 -63.548	N

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Drift
69	34.0	48.1	44.424 -63.552	44.611 -63.559	Y
70	31.0	60.0	44.551 -63.550	44.552 -63.550	Y
71	30.0	34.4	44.553 -63.550	44.497 -63.510	Y
72	21.0	34.0	44.468 -63.549	44.467 -63.540	Y
73	14.0	44.0	44.521 -63.950	44.516 -63.956	Y
74	34.0	40.0	44.505 -63.941	44.504 -63.944	Y
75	42.1	43.3	44.505 -64.167	44.505 -64.167	Y
76	33.8	35.7	44.458 -64.049	44.458 -64.048	Y
77	46.3	49.4	44.454 -64.003	44.454 -64.002	N
78	39.9	42.7	44.448 -63.968	44.448 -63.967	N
79	65.5	68.3	44.448 -63.905	44.448 -63.904	Y
80	65.5	68.3	44.443 -63.857	44.443 -63.856	Y
81	49.4	52.1	44.423 -63.666	44.423 -63.666	N
82	44.2	46	44.426 -63.696	44.426 -63.695	N
83	53.7	56.1	44.424 -63.739	44.424 -63.739	N
84	63.1	64.9	44.433 -63.814	44.433 -63.813	N
85	30.6	37.2	44.423 -63.611	44.420 -63.611	N
86	9.1	18.4	44.439 -63.626	44.435 -63.622	N
87	29.4	42.1	44.444 -63.676	44.445 -63.676	N
88	34.9	40.8	44.445 -63.676	44.450 -63.676	N
89	5.9	47.2	44.435 -63.719	44.431 -63.714	N
90	79	81.8	44.420 -63.769	44.419 -63.769	N
91	88.5	90.7	44.411 -63.756	44.413 -63.755	N
92	51.4	62.7	44.402 -63.688	44.401 -63.688	Y
93	48.9	54.2	44.405 -63.640	44.403 -63.640	N
94	3.0	50.0	44.249 -64.329	44.250 -64.330	N
95	3.0	50.0	44.237 -64.275	44.238 -64.276	N
96	3.0	50.0	44.269 -64.249	44.270 -64.250	N
97	3.0	50.0	44.292 -64.247	44.293 -64.248	N
98	3.0	50.0	44.324 -64.258	44.325 -64.259	N
99	3.0	50.0	44.331 -64.281	44.332 -64.282	N
100	3.0	50.0	44.316 -64.173	44.317 -64.174	N
101	3.0	50.0	44.364 -64.182	44.365 -64.183	N
102	3.0	50.0	44.428 -64.129	44.429 -64.130	N
103	3.0	50.0	44.437 -64.096	44.438 -64.097	N
104	3.0	50.0	44.444 -64.142	44.445 -64.143	N
105	3.0	50.0	44.474 -64.137	44.475 -64.138	N
106	3.0	50.0	44.492 -64.176	44.493 -64.177	N
107	3.0	50.0	44.502 -64.267	44.503 -64.268	N

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Drift
108	3.0	50.0	44.512 -64.214	44.513 -64.215	N
109	3.0	50.0	44.547 -64.196	44.548 -64.197	N
110	3.0	50.0	44.537 -64.015	44.538 -64.016	N
111	3.0	50.0	44.591 -64.057	44.592 -64.058	N
112	3.0	50.0	44.595 -63.960	44.596 -63.961	N
113	3.0	50.0	44.575 -63.938	44.576 -63.939	N
114	3.0	50.0	44.541 -63.953	44.542 -63.954	N
115	3.0	50.0	44.448 -63.713	44.449 -63.714	N
116	3.0	50.0	44.484 -63.534	44.485 -63.535	N
117	3.0	50.0	44.497 -63.524	44.498 -63.525	N

Table E2. Data sets used to develop predictive models. All raster data sets were resampled to 30 m resolution to match DEM and derived rasters.

Occurrence data	
Drift	Presence and absence observations of drift algae from video surveys (aggregated into 30-m resolution grids)
Predictor variables	
Depth (DEM)	Digital elevation model (DEM) created using a combination of multibeam, contour and sounding data from the Canadian Hydrographic Service (CHS) and the Nova Scotia Geomatics Centre (30-m resolution)
Slope	Derived from DEM in ArcGIS (v10.2, ESRI, Inc.)
Curvature	Derived from DEM in ArcGIS
Planar curvature	Derived from DEM in ArcGIS. Created using aspect raster derived from DEM
Profile curvature	Derived from DEM in ArcGIS. Created using aspect raster derived from DEM
Bathymetric position index – fine	Derived from DEM in ArcGIS – 3 cell neighborhood. Created using Jenness Tools extension to ArcGIS (Jenness et al. 2013)
Bathymetric position index – broad	Derived from DEM in ArcGIS – 10 cell neighborhood. Created using Jenness Tools extension to ArcGIS (Jenness et al. 2013)
Distance from coast	Derived using Euclidean distance function in ArcGIS Spatial Analyst from Nova Scotia Coast high resolution line data (Greenlaw et al. 2013)
Current	Near-bottom current speed for Gulf of Maine from Department of Fisheries and Oceans (DFO; M. Greenlaw)
Bottom type	Seabed type determined using surficial geology, geomorphology, CHS and substrate samples from DFO in the coastal western Maritimes Region (Greenlaw et al. 2013)

Model calibration and evaluation

The random forest model was created with the randomForest package in R using 3 predictor variables for each split, and pruning trees after 3 splits. We used the conditional variable importance index in the R party package to rate the 10 predictor variables for overall importance in influencing the occurrence of drift algae in the model. This index is calculated as the number of misclassified observations that occur when the variable of interest in the dataset is replaced with conditionally permuted values that are within defined combinations of the other variables in the model (Strobl et al. 2008). The conditional variable importance index accounted for correlations between curvature, BPI and slope, which resulted in substitution among these 3 variables in the models, so that the overall importance of each variable was lower than if we included only 1 or 2 of them in the models. We eliminated variables with low conditional importance measures and checked that their exclusion did not impact the model performance using classification error.

We evaluated the effectiveness of the random forest model in predicting both the testing data and independent data from Port Joli using two procedures: the area under the receiver-operator-curve (Hanley & McNeil 1982), and the true skill statistic (Allouche et al. 2006). AUC is the most commonly used measure of model quality for species distribution models (Merckx et al. 2011). The receiver-operator-curve (ROC) describes the trade-off between model specificity (probability the model will correctly classify a presence) and sensitivity (probability the model will correctly classify an absence) for each probability threshold used to estimate occurrence of drift algae from the random forest model. The probability threshold is a value used to transform the model's probability scores into binary presence and absence predictions. The ROC curve shows specificity and sensitivity for all possible thresholds between 0 and 1, generating multiple points for a given model that range from 100% chance of correctly classifying a presence to 100% chance of correctly classifying an absence. Values of AUC range from 0.5 (model is not different from random expectation) to 1.0 (perfect accuracy). Because practical applications of these types of models often require presence/absence maps of a species or resource, we also transformed our model's probability scores into presence and absence predictions using a single threshold value (Table E3). We selected the threshold that minimizes the distance to the top left corner (0,1) of the ROC plot (Liu et al. 2005). We evaluated model performance using TSS, which compares the number of correct predictions, minus those expected to occur by chance alone, to a hypothetical set of perfect predictions. In this way the TSS is independent of prevalence (i.e. it corrects for high accuracy associated with predicting the absence of very rare species), making it more accurate than the commonly used Cohen's Kappa statistic (Allouche et al. 2006). Values of TSS range from -1.0 to 1.0 (perfect accuracy), with a score of 0 indicating model is not different from random expectation.

References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232.

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36.

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

Merckx B, Steyaert M, Vanreusel A, Vincx M, Vanaverbeke J (2011) Null models reveal preferential sampling, spatial autocorrelation and overfitting in habitat suitability modelling. Ecolog Model 222:588–597.

Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for random forests. BMC Bioinformatics 9:307.

Table E3. Confusion matrix used to evaluate performance of final random forest model in predicting occurrence of drift algae in the study area using probability threshold of 0.30.

		Validation data set	
		Absence	Presence
Model	Absence	6600	255
	Presence	121	483

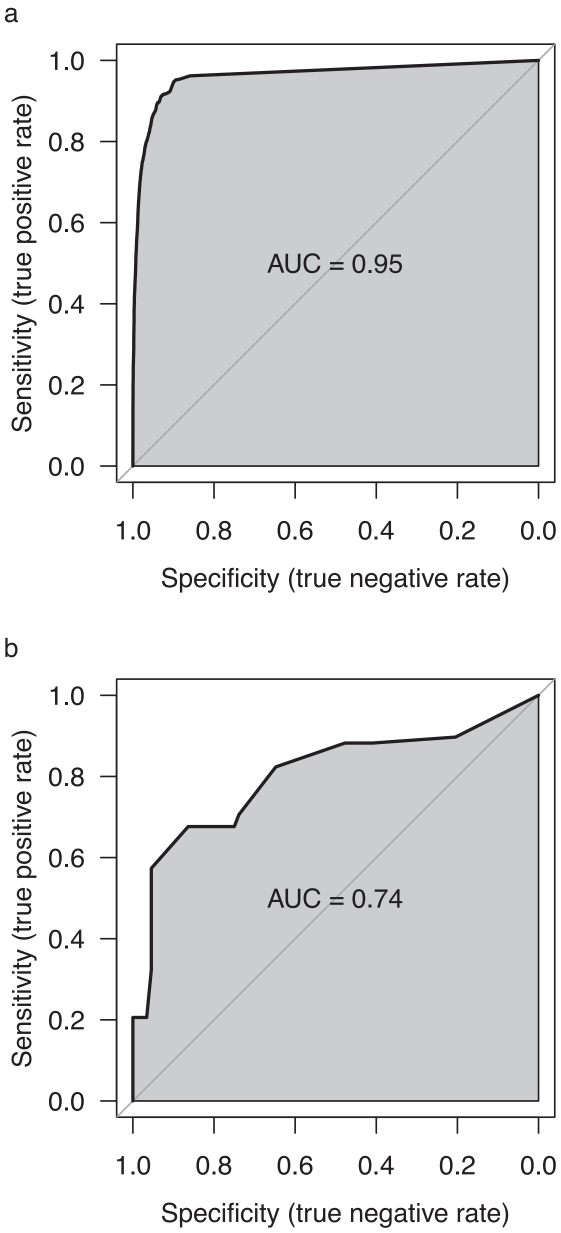


Fig. E1. Model evaluation plot for random forest model calibrated using a) testing data from our study area and b) independent data collected near Port Joli, 50 km southwest of our study area. Plots are receiver-operator-curve (ROC) indicating relationship between model specificity and model sensitivity for each probability threshold used to estimate occurrence of drift algae in the model. Area under the curve (AUC) is gray polygon. Diagonal line shows ROC curve if model expectation is not different from random

Appendix F. Methods and results for predictive model of distribution of deep-living sea urchins for Chapter 7

Table F1. Video transects in study area and validation site: transect number, depth range, start and end position coordinates, and observation of urchins. No data = ND.

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Urchin
1	14.6	31.7	44.573 -64.04	44.574 -64.038	N
2	24.0	58.8	44.574 -64.038	44.511 -63.991	Y
3	10.0	53.2	44.520 -64.002	ND	Y
4	58.5	74.0	44.520 -64.000	ND	Y
5	20.3	73.1	44.516 -64.005	44.516 -63.996	Y
6	45.8	49.1	44.520 -63.980	44.521 -63.980	N
7	22.1	28.7	44.512 -63.995	44.520 -64.001	Y
8	23.7	55.9	44.520 -64.001	44.523 -64.001	Y
9	7.4	55.7	44.523 -64.001	44.523 -64.003	Y
10	15.1	65.1	44.524 -63.972	44.523 -63.977	Y
11	40.2	52.9	44.530 -63.973	44.530 -63.976	Y
12	41.5	55.4	44.542 -63.967	44.543 -63.971	Y
13	13.0	49.7	44.548 -63.961	44.545 -63.968	Y
14	14.5	32.7	44.563 -63.954	44.563 -63.958	Y
15	6.8	53.6	44.478 -63.546	44.476 -63.534	Y
16	4.5	44.9	44.559 -64.031	44.559 -64.028	Y
17	23.3	47.5	44.548 -63.962	44.549 -63.966	Y
18	4.7	37.4	44.511 -63.997	44.512 -63.994	N
19	11.5	24.6	44.510 -63.996	44.509 -63.991	N
20	7.3	38.2	44.547 -64.021	44.546 -64.017	Y
21	16.4	42	44.546 -64.017	44.520 -64.001	N
22	11.3	42	44.520 -64.001	44.520 -64.001	N
23	7.2	49.7	44.511 -63.997	44.512 -63.993	N
24	6.0	43.6	44.511 -63.997	44.511 -63.993	Y
25	14.4	46.3	44.510 -63.996	44.510 -63.992	Y
26	24.5	61	44.510 -63.991	44.510 -63.987	Y
27	5.3	44	44.511 -63.997	44.512 -63.993	Y
28	9.2	59.6	44.522 -64.004	44.523 -64.002	Y
29	61.6	72.4	44.523 -64.001	44.523 -64.000	Y
30	9.4	75.3	44.526 -64.007	44.528 -64.002	Y
31	7.0	46.1	44.539 -64.016	44.542 -64.013	N
32	6.5	55.6	44.559 -64.031	44.562 -64.028	Y

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Urchin
33	19	69.7	44.520 -64.002	ND	N
34	26.7	61.7	44.511 -63.994	44.510 -63.991	Y
35	34.7	83.2	44.522 -64.003	44.523 -63.999	Y
36	11.0	81.1	44.525 -64.006	44.526 -64.001	Y
37	11.9	38.5	44.431 -63.652	44.429 -63.653	N
38	26.0	40.1	44.428 -63.653	44.428 -63.653	Y
39	16.5	41.4	44.426 -63.654	44.425 -63.654	Y
40	5.3	17.8	44.443 -64.088	44.451 -64.097	N
41	10.8	37.4	44.474 -64.15	44.487 -64.143	Y
42	11.8	31.4	44.480 -64.161	44.490 -64.162	Y
43	23.9	29.2	44.466 -64.188	44.469 -64.189	N
44	18.0	56.6	44.460 -64.207	44.463 -64.198	Y
45	9.5	24.5	44.453 -63.568	44.430 -63.578	Y
46	26.9	91.7	44.520 -64.001	44.519 -63.996	Y
47	9.5	70	44.522 -64.003	44.521 -64.000	Y
48	5.8	86.3	44.522 -64.003	44.522 -63.997	Y
49	21.3	72.9	44.522 -64.002	44.521 -64.009	Y
50	8.3	90.1	44.522 -64.003	44.521 -63.996	Y
51	29.4	92.6	44.522 -64.002	44.520 -63.996	Y
52	11.4	23.5	44.511 -63.996	44.511 -63.995	N
53	29.6	89.1	44.521 -64.002	44.517 -63.997	Y
54	22.1	61.3	44.51 -63.995	44.509 -63.985	Y
55	24.4	63.6	44.509 -63.985	44.508 -63.980	Y
56	31.7	42.5	44.550 -63.964	44.550 -63.965	Y
57	42.8	62	44.550 -63.966	44.545 -63.981	Y
58	3.9	58	44.423 -64.009	44.424 -64.008	N
59	53.1	81.8	44.412 -64.000	ND	N
60	74.9	139.6	44.412 -63.600	44.412 -63.599	Y
61	13.4	39.7	44.412 -63.599	44.412 -63.597	N
62	14.5	32.7	44.663 -63.954	44.563 -63.958	Y
63	21.4	33.1	44.511 -63.995	44.511 -63.994	Y
64	0.5	61.7	44.511 -63.993	44.510 -63.991	Y
65	34.7	83.2	44.522 -64.003	44.523 -63.999	Y
66	9.8	50.1	44.446 -63.795	44.447 -63.785	N
67	11.0	29.1	44.453 -63.782	44.454 -63.776	N
68	30.0	76.0	44.433 -63.800	44.438 -63.548	N
69	34.0	48.1	44.424 -63.552	44.611 -63.559	Y
70	31.0	60.0	44.551 -63.550	44.552 -63.550	N
71	30.0	34.4	44.553 -63.550	44.497 -63.510	Y

Trans	Depth (m)		Coordinates (Lat. Lon.)		
No.	Min	Max	Start Position	End Position	Urchin
72	21.0	34.0	44.468 -63.549	44.467 -63.540	Y
73	14.0	44.0	44.521 -63.950	44.516 -63.956	N
74	34.0	40.0	44.505 -63.941	44.504 -63.944	N
75	42.1	43.3	44.505 -64.167	44.505 -64.167	Y
76	33.8	35.7	44.458 -64.049	44.458 -64.048	N
77	46.3	49.4	44.454 -64.003	44.454 -64.002	N
78	39.9	42.7	44.448 -63.968	44.448 -63.967	N
79	65.5	68.3	44.448 -63.905	44.448 -63.904	N
80	65.5	68.3	44.443 -63.857	44.443 -63.856	N
81	49.4	52.1	44.423 -63.666	44.423 -63.666	N
82	44.2	46	44.426 -63.696	44.426 -63.695	N
83	53.7	56.1	44.424 -63.739	44.424 -63.739	N
84	63.1	64.9	44.433 -63.814	44.433 -63.813	Y
85	30.6	37.2	44.423 -63.611	44.420 -63.611	Y
86	9.1	18.4	44.439 -63.626	44.435 -63.622	Y
87	29.4	42.1	44.444 -63.676	44.445 -63.676	Y
88	34.9	40.8	44.445 -63.676	44.450 -63.676	Y
89	5.9	47.2	44.435 -63.719	44.431 -63.714	N
90	79	81.8	44.420 -63.769	44.419 -63.769	N
91	88.5	90.7	44.411 -63.756	44.413 -63.755	N
92	51.4	62.7	44.402 -63.688	44.401 -63.688	Y
93	48.9	54.2	44.405 -63.640	44.403 -63.640	Y
94	3.0	50.0	44.249 -64.329	44.250 -64.330	N
95	3.0	50.0	44.237 -64.275	44.238 -64.276	N
96	3.0	50.0	44.269 -64.249	44.270 -64.250	N
97	3.0	50.0	44.292 -64.247	44.293 -64.248	N
98	3.0	50.0	44.324 -64.258	44.325 -64.259	N
99	3.0	50.0	44.331 -64.281	44.332 -64.282	N
100	3.0	50.0	44.316 -64.173	44.317 -64.174	N
101	3.0	50.0	44.364 -64.182	44.365 -64.183	N
102	3.0	50.0	44.428 -64.129	44.429 -64.130	N
103	3.0	50.0	44.437 -64.096	44.438 -64.097	N
104	3.0	50.0	44.444 -64.142	44.445 -64.143	N
105	3.0	50.0	44.474 -64.137	44.475 -64.138	N
106	3.0	50.0	44.492 -64.176	44.493 -64.177	N
107	3.0	50.0	44.502 -64.267	44.503 -64.268	N
108	3.0	50.0	44.512 -64.214	44.513 -64.215	N
109	3.0	50.0	44.547 -64.196	44.548 -64.197	N
110	3.0	50.0	44.537 -64.015	44.538 -64.016	N

Trans No.	Depth (m) Min	Max	Coordinates (Lat. Lon.) Start Position	No.	Min
111	3.0	50.0	44.591 -64.057	44.592 -64.058	N
112	3.0	50.0	44.595 -63.960	44.596 -63.961	N
113	3.0	50.0	44.575 -63.938	44.576 -63.939	N

Table F2. Data sets used to develop predictive models. All raster data sets were resampled to 30 m resolution to match DEM and derived rasters.

Occurrence data	
Sea urchin	Presence and absence observations of sea urchins from video surveys (aggregated into 30-m resolution grids)
Predictor variables	
Depth	Digital elevation model (DEM) created using a combination of (DEM) multibeam, contour and sounding data from the Canadian Hydrographic Service (CHS) and the Nova Scotia Geomatics Centre (30-m resolution)
Slope	Derived from DEM in ArcGIS (v10.2, ESRI, Inc.)
Standard curvature	Derived from DEM in ArcGIS
Planar curvature	Derived from DEM in ArcGIS. Created using aspect raster also derived from DEM
Profile curvature	Derived from DEM in ArcGIS. Created using aspect raster also derived from DEM
Bathymetric Position Index	Derived from DEM in ArcGIS using 2, 4, 8, 12, 16, 20, 24, 28, 32 cell neighborhood. Inner radius = 1 cell
Distance from coast	Derived using euclidean distance function in ArcGIS Spatial Analyst from Nova Scotia Coast high resolution line data (Greenlaw et al. 2013)
Bottom type	Seabed type determined using surficial geology, geomorphology, CHS and substrate samples from DFO in the coastal western Maritimes Region (Greenlaw et al. 2013)
Drift	Probability of drift algae created using predictive distribution model with 5% misclassification error (Filbee-Dexter & Scheibling 2016)

Model calibration and evaluation

The random forest model (RFM) was created with the randomForest package in R using 3 predictor variables for each split, and pruning trees after 3 splits. We used the conditional variable importance index in the R party package to rate the 18 predictor variables for overall importance in influencing the positive classification of sea urchins in the model. This index is calculated as the number of misclassified observations that occur when the variable of interest in the dataset is replaced with conditionally permuted values that are within defined combinations of the other variables in the model (Strobl et al. 2008). The conditional variable importance index accounted for correlations between fine and broad-scale BPI, which resulted in substitution among these 2 variables in the models, so that the overall importance of each variable was lower than if we included only 1 of them in the models. We eliminated variables with low conditional importance measures and checked that their exclusion did not impact the model performance using classification error.

We evaluated the effectiveness of the RFM in predicting the testing data using two procedures: the area under the receiver-operator-curve (Hanley & McNeil 1982), and the true skill statistic (Allouche et al. 2006). AUC is the most commonly used measure of model quality for species distribution models (Merckx et al. 2011). The receiver-operator-curve (ROC) describes the trade-off between model specificity (probability the model will correctly classify a presence) and sensitivity (probability the model will correctly classify an absence) for each probability threshold used to estimate occurrence of sea urchins from the RFM. The probability threshold is a value used to transform the model's probability scores into binary presence and absence predictions. The ROC curve shows specificity and sensitivity for all possible thresholds between 0 and 1, generating multiple points for a given model that range from 100% chance of correctly classifying a presence to 100% chance of correctly classifying an absence. Values of AUC range from 0.5 (model is not different from random expectation) to 1.0 (perfect accuracy). Because practical applications of these types of models often require presence/absence maps of a species or resource, we also transformed our model's probability scores into presence and absence predictions using a single threshold value of 0.2. We selected the threshold that minimizes the distance to the top left corner (0,1) of the ROC plot (Liu et al. 2005). We evaluated model performance using true test statistic (TSS), which compares the number of correct predictions, minus those expected to occur by chance alone, to a hypothetical set of perfect predictions. In this way the TSS is independent of prevalence (i.e. it corrects for high accuracy associated with predicting the absence of very rare species), making it more accurate than the commonly used Cohen's Kappa statistic (Allouche et al. 2006). Values of TSS range from -1.0 to 1.0 (perfect accuracy), with a score of 0 indicating model is not different from random expectation.

Reference

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232.

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36.

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

Merckx B, Steyaert M, Vanreusel A, Vincx M, Vanaverbeke J (2011) Null models reveal preferential sampling, spatial autocorrelation and overfitting in habitat suitability modelling. Ecolog Model 222:588–597.

Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for random forests. BMC Bioinformatics 9:307.

Appendix G. Historic records of kelp beds and urchin overgrazing for Chapter 7

Table G1. Records of urchin grazing aggregations (fronts) or barrens (barrens) and kelp beds (kelp) in our study area over the last 44 years based on published and unpublished data between 1972 and 2015. Barrens were created by sea urchins grazing in fronts at the deep margin of kelp beds (deep) or in patchy aggregations within the beds (patch). Kelp locations were randomly selected along regions of the coast with no record of destructive grazing, and verified using published and unpublished data. Records were divided into 2 periods representing 2 regime shifts from kelp to barrens: 1) 1972 – 1981, and 2) 1984 – 2015. Sources of unpublished records or personal observations: DG = David Gray, urchin harvester, Sambro, Nova Scotia; DL = Devin Lyons, Dalhousie University; JL = John Lindley, Dalhousie University; KFD = K. Filbee-Dexter, RES = R.E. Scheibling.

Year	Site	Long.	Lat.	Grazing	Period	State	Source
1968, 73	Luke I	-63.9294	44.5765	unknown	1	barren	1
1970, 78-80	Boutilier’s Pt	-63.9270	44.5790	unknown	1	barren	1,2,3
1971, 75	NW Cove (W)	-64.0240	44.5330	unknown	1	barren	4
1972	Horse I (W)	-64.0170	44.5310	unknown	1	barren	5
1973	SW I	-64.0082	44.5167	patch	1	barren	5
1973	The Lodge	-64.0317	44.5560	patch	1	barren	5
1973	Birchy Hd	-64.0500	44.5830	patch	1	barren	5
1973	Horse I (E)	-64.0169	44.5304	unknown	1	barren	5
1973	Fox Pt (N)	-64.0589	44.6119	patch	1	barren	5
1979	NW Cove (E)	-64.0220	44.5320	unknown	1	barren	6
1979	Beacons	-64.0190	44.5400	unknown	1	barren	2
1979	Paul's Pt	-63.9336	44.5725	unknown	1	barren	7
1979	Mill Cove	-64.0540	44.5800	unknown	1	barren	2
1979	Fox Pt (BWR)	-64.0580	44.6140	unknown	1	barren	2
1979	Davy Pt	-63.9390	44.6230	unknown	1	barren	2
1979	Fox Pt (S)	-64.0580	44.5980	deep	1	barren	2
1980	Mill Cove	-64.0617	44.5917	unknown	1	barren	7
1979	SW I	-64.0063	44.5065		1	kelp	8
1979	Strawberry I	-63.9957	44.5039		1	kelp	8
1979	Hubbards	-64.0533	44.6288		1	kelp	2
1979	Red Bank	-64.0365	44.6262		1	kelp	2
1979	Meisners Pt	-63.9696	44.6520		1	kelp	2
1979	Micou's I	-63.9442	44.6317		1	kelp	2
1979	Wedge I	-63.9494	44.6102		1	kelp	2
1979	Frank George I	-63.9394	44.5901		1	kelp	2

Year	Site	Long.	Lat.	Grazing	Period	State	Source
1979	Glen Margaret	-63.9255	44.5746		1	kelp	2
1979	Shut-in I	-63.9527	44.5431		1	kelp	2
1979	Paddy's Hd	-63.9458	44.5358		1	kelp	2
1979	Lower Dung	-63.9387	44.5385		1	kelp	2
1979	The Lodge	-64.0335	44.5619		1	kelp	2
1979	Seabright	-63.9394	44.6229		1	kelp	2
1979	Hubbards	-64.0530	44.6200		1	kelp	2
1979	Sheep I	-63.9429	44.5414		1	kelp	2
1979	Indian H	-63.9429	44.5214		1	kelp	2
1997	Ferguson Cove	-63.5570	44.6000	unknown	2	barren	9
2010	Pennant Pt.	-63.6254	44.4419	unknown	2	barren	JL
2011	Bear Cove	-63.5424	44.5388	unknown	2	barren	JL
2013	Pt Pleasant	-63.5624	44.6211	unknown	2	barren	this study
2013	Pt Pleasant	-63.5632	44.6233	unknown	2	barren	this study
2015	Jubliee Rd	-63.6068	44.6379	unknown	2	barren	JL
2009-10	Gill Cove	-63.5283	44.4967	unknown	2	barren	10
1992-95	Mill Cove	-64.0530	44.5817	deep	2	barren	11,12
1992-95	Little Duck I	-64.1830	44.3667	deep	2	barren	12,13
1999,02	Chebucto Hd	-63.5182	44.5026	deep	2	barren	14
2009, 11	Black R	-63.5300	44.4517	unknown	2	barren	10
2009, 13	Duncan's Cove	-63.5200	44.4867	unknown	2	barren	10, JL
2002	Portuguese Cove	-63.5346	44.5250	deep	2	barren	14
2002	Gill Cove	-63.5332	44.4840	deep	2	barren	14
2003	Birchy Hd	-64.0500	44.5830	deep	2	barren	15
2008	Owl's Hd	-64.0020	44.5206	deep	2	barren	DL
2011	Sambro I	-63.5662	44.4388	deep	2	barren	DG
2011	Sambro I	-63.5604	44.4365	deep	2	barren	DG
2011	Sambro I	-63.5629	44.4402	deep	2	barren	DG
2011	Mad R	-63.5602	44.4314	deep	2	barren	DG
2011	Shag R	-63.5682	44.4321	deep	2	barren	DG
2011	Sambro I	-63.5715	44.4346	deep	2	barren	DG
2011	Gull R	-63.5697	44.4450	deep	2	barren	DG
2011	Whaleback R	-63.5767	44.4463	deep	2	barren	DG
2011	The Sisters	-63.5293	44.4471	deep	2	barren	DG
2011	Chubb R	-63.5492	44.4500	deep	2	barren	DG
2011	Polluck Shoal	-63.5716	44.4522	deep	2	barren	DG
2011	Bull R	-63.6320	44.4335	deep	2	barren	DG
2011	Horse Shoal	-63.5990	44.4169	deep	2	barren	DG
2011	Colt Shoal	-63.5987	44.4335	deep	2	barren	DG
2014	Duncan's I	-63.5227	44.4982	deep	2	barren	JL

Year	Site	Long.	Lat.	Grazing	Period	State	Source
2005-15	Splitnose Pt	-63.5457	44.4768	deep	2	barren	16,10,17
2009	Horse I	-64.0129	44.5330	deep	2	barren	RES
2004	Shut-in I	-63.9628	44.5499	deep	2	barren	RES
2003	Birchy Hd	-64.0415	44.5730	deep	2	barren	18
1995	Cross I	-64.1692	44.3146	deep	2	barren	RES
2001	Saddle I	-64.0482	44.5015		2	kelp	19
2010	Hubbards	-64.0599	44.6267		2	kelp	KFD
2010	Sandy Cove RS	-63.5580	44.4676		2	kelp	KFD
2011	Rogues Roost	-63.7632	44.4752		2	kelp	this study
2011	Hearn I	-63.7649	44.4699		2	kelp	this study
2011	Pennant Pt.	-63.6503	44.4340		2	kelp	this study
2011	Dartmouth	-63.5525	44.6506		2	kelp	KFD
2011	McNabs I	-63.5429	44.6227		2	kelp	KFD
2011	McNabs I	-63.5147	44.5969		2	kelp	KFD
2012	Chebucto Hd	-63.5196	44.5032		2	kelp	this study
2012	Chebucto Hd	-63.5203	44.5042		2	kelp	this study
2012	Halibut Bay	-63.5523	44.5504		2	kelp	20, KFD
2012	Herring Cove	-63.5504	44.5705		2	kelp	this study
2014	Shag R	-64.2004	44.3829		2	kelp	KFD
2014	Oak I	-64.2926	44.5102		2	kelp	KFD
2014	Wreck Cove	-63.9088	44.4920		2	kelp	this study
2014	Flemming I	-63.8544	44.4841		2	kelp	this study
2014	Shad Bay	-63.8355	44.4919		2	kelp	this study
2014	O Gull I	-63.8169	44.4843		2	kelp	this study
2014	Saul I	-63.7840	44.4662		2	kelp	this study
2014	Mackerel Cove	-63.6171	44.4551		2	kelp	this study
1982, 2010	Boutilier Pt	-63.9697	44.6517		2	kelp	20, this study
1982, 2014	Rake I	-64.2051	44.4008		2	kelp	20, this study
1982, 2014	Betty I	-63.7718	44.4420		2	kelp	20, this study
1984, 2014	Halibut Bay	-63.5562	44.5542		2	kelp	21, this study
1985, 2014	Polly Cove	-63.8982	44.4892		2	kelp	22, this study
1995, 2009	Feltzen S	-64.2870	44.3320		2	kelp	20, 23
2000, 2007, 2014	Big I	-64.3064	44.5257		2	kelp	24
2000, 2007, 2014	Woody I	-63.7129	44.4498		2	kelp	24, 25
2001, 2007, 2014	Coachman’s L	-64.0854	44.4690		2	kelp	19, 25
2001, 2007, 2014	Little Tancook	-64.1260	44.4674		2	kelp	19, 25
2001, 2011-2013	Gravel I	-64.0306	44.4999		2	kelp	19, 26

Year	Site	Long.	Lat.	Grazing	Period	State	Source
2001, 2012	Grassy I	-64.1280	44.4240		2	kelp	19, 25
2005-2006, 2010-15	Paddy's Hd	-63.9506	44.5236		2	kelp	27, KFD
2006, 2008-2009	Cranberry Cove	-63.9017	44.4904		2	kelp	28, 29
2008, 2009	Sandy Cove	-63.5868	44.4617		2	kelp	20

Published Sources

1. Bernstein B, Mann K (1982) Changes in the nearshore ecosystem of the Atlantic coast of Nova Scotia, 1968-1981. Sci Council Studies 4:101–105

2. Chapman A (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. Mar Biol 62:1–5

3. Miller R (1985) Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. Mar Biol 84:275–286

4. Lang C, Mann K (1976) Changes in sea urchin populations after the destruction of kelp beds. Mar Biol 36:321–326

5. Breen, PA, Mann KH (1976) Destructive grazing of kelp by sea urchins in Eastern Canada. J Fish Res Board Can 33:1278–1283

6. Wharton WG, Mann KH (1981) Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of american lobster, *Homarus americanus*, on the Atlantic Coast of Nova Scotia. Can J Fish Aquat Sci 38:1339-1349

7. Johnson CR, Mann KH (1982). Adaptations of *Strongylocentrotus droebachiensis* for survival on barren grounds in Nova Scotia. In: Lawrence JM (ed) Echinoderms Proceedings of the International Conference. Balkema, Rotterdam.

8. Mann K (1972) 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

9. Scheibling RE, Anthony S (2001) Feeding, growth and reproduction of sea urchins (*Strongylocentrotus droebachiensis*) on single and mixed diets of kelp (*Laminaria spp.*) and the invasive alga *Codium fragile ssp. tomentosoides*. Mar Biol 139:139-146

10. Kelly, JR, Krumhansl KA, Scheibling RE (2012) Drift algal subsidies to sea urchins

in low-productivity habitats. Mar Ecol Prog Ser 452:145–157

11. Balch, T, Scheibling RE (2000) Temporal and spatial variability in settlement and recruitment of echinoderms in kelp beds and barrens in Nova Scotia. Mar Ecol Prog Ser 205:139-154

12. Scheibling RE, Hennigar AW (1997) Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. Mar Ecol Prog Ser 152:155-165

13. Scheibling RE, Hennigar AW, Balch T (2011) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin - kelp interactions in Nova Scotia. Can J Fish Aquat Sci 56:2300–2314

14. Brady SM, Scheibling RE (2005) Repopulation of the shallow subtidal zone by green sea urchins (*Strongylocentrotus droebachiensis*) following mass mortality in Nova Scotia, Canada. J Mar Biol Assoc UK 85:1511–1517

15. Lyons DA, Scheibling RE (2009) Range expansion by invasive marine algae: rates and patterns of spread at a regional scale. Divers Distrib 15:762–775

16. Lauzon-Guay J-S, Scheibling RE (2007) Behaviour of sea urchin *Strongylocentrotus droebachiensis* grazing fronts: food-mediated aggregation and density-dependent facilitation. Mar Ecol Prog Ser 329:191-204

17. Harding PC, Scheibling RE (2015) Feed or flee: Effect of a predation-risk cue on sea urchin foraging activity. J Exp Mar Biol Ecol 466:59–69

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

19. Theriault C, Scheibling R, Hatcher B, Jones W (2006) Mapping the distribution of an invasive marine alga (*Codium fragile* spp. *tomentosoides*) in optically shallow coastal waters using the compact airborne spectrographic imager (CASI). Can J Remote Sens 32:315-329

20. Moore DS, Miller RJ (1983) Recovery of macroalgae following widespread sea urchin mortality with a description of the shallow, hard-bottom habitat on the Atlantic coast of Nova Scotia. Can Tech Rep Fish Aquat Sci 1230

21. Scheibling, R 1986 Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. Oecologia 68:186–198

22. Rice EL, Kenchington TJ, Chapman ARO (1985) Intraspecific geographic-morphological variation patterns in *Fucus distichus* and *F. evanescens*. Mar Biol

88:207–215

23. Yorke AF, Metaxas A (2011) Interactions between an invasive and a native bryozoan (*Membranipora membranacea* and *Electra pilosa*) species on kelp and *Fucus* substrates in Nova Scotia, Canada. Mar Biol 158:2299–2311

24. Watanabe S, Scheibling RE, Metaxas A (2010) Contrasting patterns of spread in interacting invasive species: *Membranipora membranacea* and *Codium fragile* off Nova Scotia. Biol Invas 12:2329-2342

25. Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Mar Ecol Prog Ser 543:141–152

26. Feehan CJ, Scheibling RE, Brown MS, Thompson KR (2016) Marine epizootics linked to storms: Mechanisms of pathogen introduction and persistence inferred from coupled physical and biological time-series. Limnol Oceanogr 61:316-329

27. Saunders MA, 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

28. Schmidt AL, Scheibling RE (2007) Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. J Exp Mar Biol Ecol 341:110-130

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

Appendix F. Copyright agreement letters

From: Marita Bruns <marita@int-res.com>
Subject: **Re: Permission to include journal article in PhD thesis**
Date: April 11, 2016
To: Karen Filbee-Dexter <kfilbeedexter@gmail.com>

Dear Karen Filbee-Dexter,

We herewith give publisher permission for you to use the articles mentioned below in your PhD thesis, provided proper acknowledgement is being made to the original source of publication.

Best wishes

Marita Bruns
Inter-Research Science Center
Nordbuente 23,
21385 Oldendorf/Luhe,
Germany
Tel: +49-4132-7127 Fax: +49-4132-8883
http://www.int-res.com

Am 11.04.2016 um 21:14
Karen Filbee-Dexter <kfilbeedexter@gmail.com>:

Inter-Research Permission Department,

I am preparing my PhD thesis for submission to the Faculty of Graduate Studies at Dalhousie University, Halifax, Nova Scotia, Canada. I am seeking your permission to include a manuscript version of the following papers as a chapter in the thesis:

Filbee-Dexter, K, and R E Scheibling. 2012. Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. *Marine Ecology Progress Series* 455: 51–64. doi:10.3354/meps09667.

Filbee-Dexter, K, and R E Scheibling. 2014a. Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. *Aquatic Biology* 23: 71–86.

Filbee-Dexter, K, and R E Scheibling. 2014b. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series* 495: 1–25. doi:10.3354/meps10573.

Filbee-Dexter, K, C J Feehan, and R E Scheibling. 2016. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Marine Ecology Progress Series* 543: 141–152. doi:10.3354/meps11554.

Canadian graduate theses are reproduced by the Library and Archives of Canada (formerly National Library of Canada) through a non-exclusive, worldwide license to reproduce, loan, distribute, or sell theses. I am also seeking permission for the material described above to be reproduced and distributed by the LAC (NLC). Further details about the LAC (NLC) thesis program are available on the LAC (NLC) website (www.nlc- bnc.ca).

Full publication details and a copy of this permission letter will be included in the thesis.

Yours sincerely,

Karen Filbee-Dexter

From: Springer <springerauthorquery@springeronline.com>
Subject: **Copyright Transfer Statement (CTS) for your article in Estuaries and Coasts (101)**
Date: April 23, 2016
To: Karen Filbee-Dexter <kfilbeedexter@gmail.com>

Confirmation of your Copyright Transfer

Dear Author,

Please note: This e-mail is a confirmation of your copyright transfer and was sent to you only for your own records.

The copyright to this article, including any graphic elements therein (e.g. illustrations, charts, moving images), is hereby assigned for good and valuable consideration to Coastal and Estuarine Research Federation effective if and when the article is accepted for publication and to the extent assignable if assignability is restricted for by applicable law or regulations (e.g. for U.S. government or crown employees). Author warrants (i) that he/she is the sole owner or has been authorized by any additional copyright owner to assign the right, (ii) that the article does not infringe any third party rights and no license from or payments to a third party is required to publish the article and (iii) that the article has not been previously published or licensed.

The copyright assignment includes without limitation the exclusive, assignable and sublicensable right, unlimited in time and territory, to reproduce, publish, distribute, transmit, make available and store the article, including abstracts thereof, in all forms of media of expression now known or developed in the future, including pre- and reprints, translations, photographic reproductions and microform. Springer may use the article in whole or in part in electronic form, such as use in databases or data networks for display, print or download to stationary or portable devices. This includes interactive and multimedia use and the right to alter the article to the extent necessary for such use. Authors may self-archive the Author's accepted manuscript of their articles on their own websites. Authors may also deposit this version of the article in any repository, provided it is only made publicly available 12 months after official publication or later. He/she may not use the publisher's version (the final article), which is posted on SpringerLink and other Springer websites, for the purpose of self-archiving or deposit. Furthermore, the Author may only post his/her version provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be provided by inserting the DOI number of the article in the following sentence: "The final publication is available at Springer via http://dx.doi.org/[insert DOI]".

Prior versions of the article published on non-commercial pre-print servers like arXiv.org can remain on these servers and/or can be updated with Author's accepted version. The final published version (in pdf or html/xml format) cannot be used for this purpose. Acknowledgement needs to be given to the final publication and a link must be inserted to the published article on Springer's website, by inserting the DOI number of the article in the following sentence: "The final publication is available at Springer via http://dx.doi.org/[insert DOI]". Author retains the right to use his/her article for his/her further scientific career by including the final published journal article in other publications such as dissertations and postdoctoral qualifications provided acknowledgement is given to the original source of publication.

Articles disseminated via http://link.springer.com are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks, and consortia.

Thank you very much.
Kind regards,
Springer Author Services
233 Spring Street New York, NY 10013 USA
phone: +1 212 460 1500; fax: +1 212-460-1700
customerservice@springer.com

Article details:
Article title: SPATIAL PATTERNS AND PREDICTORS OF DRIFT ALGAL SUBSIDY IN DEEP SUBTIDAL ENVIRONMENTS
Corresponding author: Karen Filbee-Dexter
DOI: 10.1007/s12237-016-0101-5

BIBLIOGRAPHY

Addison JA, Pogson GH (2009) Multiple gene genealogies reveal asymmetrical hybridization and introgression among Strongylocentrotid sea urchins. Mole Ecol 18:1239–1251

Adey WH, Hayek LC (2011) Elucidating marine biogeography with macrophytes: quantitative analysis of the North Atlantic supports the thermogeographic model and demonstrates a distinct subarctic region in the Northwestern Atlantic. Northeast Nat 18:1–128

Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. Oceanogr Mar Biol Annu Rev 41:161–236

Airoldi L, Balata D, Beck MW (2008) The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. J Exp Mar Biol Ecol 366:8–15 doi:10.1016/j.jembe.2008.07.034

Alldredge AL, Gotschalk CC (1990) The relative contribution of marine snow of different origins to biological processes in coastal waters. Cont Shelf Res 10:41–58 doi:10.1016/0278-4343(90)90034-J

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Alves F, Chícharo LM, Serrao E, Abreu AD (2001) Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). Sci Mar 65:383–392 doi:10.3989/scimar.2001.65n4383

Andersen SG, Steen H, Christie H, Fredriksen S, Moy FE (2011) Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: implications for forest recovery. J Mar Biol 2011:690375

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER. Guide to software and statistical methods. PRIMER-E Ltd, Plymouth

Anderson WB, Polis GA (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332

Andrew N, Byrne M (2007) Ecology of *Centrostephanus*. In: Lawrence JM (ed) Edible sea urchins: biology and ecology. Elsevier, Amsterdam, p 191–204

Andrew NL, Underwood AJ (1989) Patterns of abundance of the sea urchin *Centrostephanus rodgersii* (Agassiz) on the central coast of New South Wales, Australia. J Exp Mar Biol Ecol 131:61–80 doi:10.1016/0022-0981(89)90011-7

Andrew NL, Underwood AJ (1993) Density-dependant foraging in the sea urchin *Centrostephanus rodgersii* on shallow subtidal reefs in New South Wales, Australia. Mar Ecol Prog Ser 99:89–98 doi:10.3354/meps099089

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. Glob Change Biol 11:1504–1513

Arrontes J (1993) Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. Mar Ecol Prog Ser 93:183–193 doi:10.3354/meps093183

Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134 doi:10.3354/meps189125

Banks SC, Piggott MP, Williamson JE, Bové U, Holbrook NJ, Beheregaray LB (2007) Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. Ecology 88:3055–3064

Barrett K, Anderson WB, Wait DA, G LL, Polis GA, Rose MD (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 109:145–153

Basch LV, Tegner MJ (2007) Reproductive responses of purple sea urchin (*Strongylocentrotus purpuratus*) populations to environmental conditions across a coastal depth gradient. Bull Mar Sci 81:255–282

Baskett ML, Salomon AK (2010) Recruitment facilitation can drive alternative states on temperate reefs. Ecology 91:1763–1773 doi:10.1890/09-0515.1

Becker JJ, Sandwell DT, Smith WHF, Braud J, Binder B, Depner J, Fabre D, Factor J, Ingalls S, Kim S-H, Ladner R, Marks K, Nelson S, Pharaoh A, Trimmer R, Rosenberg Von J, Wallace G, Weatherall P (2009) Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. Mar Geod 32:355–371

Beisner BE, Haydon DT, Cuddington K (2003) Alternative stable states in ecology. Front Ecol Environ 1:376–382 doi:10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150 doi:10.3354/meps214137

Berné S, Auffret JP, Walker P (1988) Internal structure of subtidal sandwaves revealed by high-resolution seismic reflection. Sedimentology 35:5–20 doi:10.1111/j.1365-3091.1988.tb00902.x

Bernstein BB, Mann KH (1982) Changes in the nearshore ecosystem of the Atlantic coast of Nova Scotia, 1968–81. NAFO Sci Counc Stud 5:101–105

Bertram DF, Strathmann RR (1998) Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. Ecology 79:315–327

Biber PD (2007a) Transport and persistence of drifting macroalgae (Rhodophyta) are strongly influenced by flow velocity and substratum complexity in tropical seagrass habitats. Mar Ecol Prog Ser 343:115–122

Biber PD (2007b) Hydrodynamic transport of drifting macroalgae through a tidal cut. Estuar Coast Shelf S 74:565–569

Bischoff B, Wiencke C (1993) Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland). Helgol Meeresunters 47:167–191 doi:10.1007/BF02430357

Blicher ME (2010) Structure and dynamics of marine macrozoobenthos in Greenland and the link to environmental drivers. PhD dissertation, Greenland Climate Research Centre & Department of Biology, Greenland Institute of Natural Resources, University of Copenhagen

Bodkin JL (1988) Effects of kelp forest removal on associated fish assemblages in central California. J Exp Mar Biol Ecol 117:227–238 doi:10.1016/0022-0981(88)90059-7

Bodkin JL, Ballachey BE, Dean TA, Fukuyama AK and others (2002) Sea otter population status and the process of recovery from the 1989 ‘Exxon Valdez’ oil spill. Mar Ecol Prog Ser 241:237–253 doi:10.3354/meps241237

Bolton JJ, Lüning K (1982) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. Mar Biol 66:89–94 doi:10.1007/BF00397259

Bonaviri C, Gianguzza P, Pipitone C, Hereu B (2012) Micropredation on sea urchins as a potential stabilizing process for rocky reefs. J Sea Res 73:18–23 doi:10.1016/j.seares.2012.06.003

Böttger SA, Devin MG, Walker CW (2006) Suspension of annual gametogenesis in North American green sea urchins (*Strongylocentrotus droebachiensis*) experiencing invariant photoperiod—applications for land-based aquaculture. Aquaculture 261:1422–1431 doi:10.1016/j.aquaculture.2006.09.018

Bourque BJ, Johnson BJ, Steneck RS (2008) Possible prehistoric fishing effects on coastal marine food webs in the Gulf of Maine. In: Erlandson J, Rick T (eds) Human impacts on ancient marine ecosystems: a global perspective. University of California Press, Berkeley, CA, p 165–185

Brady SM, Scheibling RE (2005) Repopulation of the shallow subtidal zone by green sea urchins (*Strongylocentrotus droebachiensis*) following mass mortality in Nova Scotia, Canada. J Mar Biol Assoc UK 85:1511–1517 doi:10.1017/S0025315405012713

Brady SM, Scheibling RE (2006) Changes in growth and reproduction of green sea urchins, *Strongylocentrotus droebachiensis* (Müller), during repopulation of the shallow subtidal zone after mass mortality. J Exp Mar Biol Ecol 335:277–291 doi:10.1016/j.jembe.2006.03.016

Breen PA, Carson TA, Foster JB, Stewart EA (1982) Changes in subtidal community structure associated with British Columbia sea otter transplants. Mar Ecol Prog Ser 7:13–20 doi:10.3354/meps007013

Breen PA, Mann KH (1976) Destructive grazing of kelp by sea urchins in eastern Canada. J Fish Res Board Can 33:1278–1283 doi:10.1139/f76-164

Breiman L (2001) Random Forests. Mach Learn 45:5–32

Britton-Simmons KH, Foley G, Okamoto D (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. Aquat Biol 5:233–243 doi:10.3354/ab00154

Britton-Simmons KH, Rhoades AL, Pacunski RE, Galloway AWE, Lowe AT, Sosik EA, Dethier MN, Duggins DO (2012) Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. Limnol Oceanogr 57:176–184

Brown CJ, Schoeman DS, Sydeman WJ, Brander K and others (2011) Quantitative approaches in climate change ecology. Glob Change Biol 17:3697–3713 doi:10.1111/j.1365-2486.2011.02531.x

Buchwald R, Feehan CJ, Scheibling RE, Simpson ABG (2015) Low temperature tolerance of a sea urchin pathogen: implications for benthic community dynamics in a warming ocean. J Exp Mar Biol Ecol 469:1–9 doi:10.1016/j.jembe.2015.04.006

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecol Lett 13:1041–1054

Bustamante RH, Branch GM, Eekhout S (1995) Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. Ecology 76:2314–2329 doi:10.2307/1941704

Caines S, Gagnon P (2012) Population dynamics of the invasive bryozoan *Membranipora membranacea* along a 450-km latitudinal range in the subarctic northwestern Atlantic. Mar Biol 159:1817–1832 doi:10.1007/s00227-012-1972-z

Campos-Creasey LS, Tyler PA, Gage JD, John AWG (1994) Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis.* Deep-Sea Res I 41:369–388 doi:10.1016/0967-0637(94)90009-4

Casini M, Hjelm J, Molinero JC, Lövgren J and others (2009) Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proc Natl Acad Sci USA 106:197–202 doi:10.1073/pnas.0806649105

Chapman ARO (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margarets Bay, eastern Canada. Mar Biol 62:307–311 doi:10.1007/BF00397697

Chapman ARO, Johnson CR (1990) Disturbance and organization of macroalgal assemblages in the northwest Atlantic. Hydrobiologia 192:77–121 doi:10.1007/BF00006228

Chapman ARO, Lindley JE (1981) Productivity of *Laminaria solidungula* in the Canadian high Arctic: a year-round study. In: Levring T (ed) 10th International Seaweed Symposium Proceedings. Walter de Gruyter, Berlin, p 247–252

Choat JH, Schiel DR (1982) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. J Exp Mar Biol Ecol 60:129–162 doi:10.1016/0022-0981(82)90155-1

Christiansen JS, Siikavuopio SI (2007) The relationship between feed intake and gonad growth of single and stocked green sea urchin (*Strongylocentrotus droebachiensis*) in a raceway culture. Aquaculture 262:163–167 doi:10.1016/j.aquaculture.2006.09.043

Christie H, Jørgensen NM, Norderhaug KM, Waage-Nielsen E (2003) Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian coast. J Mar Biol Assoc UK 83:687–699 doi:10.1017/S0025315403007653h

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–233 doi:10.3354/meps08351

Clemente S, José CH, Toledo K, Brito A (2007) Predation upon *Diadema antillarum* in barren grounds in the Canary Islands. Sci Mar 71:745–754 doi:10.3989/scimar.2007.71n4745

Collie JS, Richardson K, Steele JH (2004) Regime shifts: Can ecological theory illuminate the mechanisms? Prog Oceanogr 60:281–302 doi:10.1016/j.pocean.2004.02.013

Colombini I, Chelazzi L, Gibson RN, Atkinson RJA (2003) Influence of marine allochthonous input on sandy beach communities. Oceanogr Mar Biol Annu Rev 41:115–159

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310 doi:10.1126/science.199.4335.1302

Connell JH, Sousa WP (1983) On evidence needed to judge ecological stability or persistence. Am Nat 121:789–824 doi:10.1086/284105

Connell S, Russell B, Turner D, Shepherd A, Kildea T, Miller D, Airoldi L, Cheshire A (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar Ecol Prog Ser 360:63–72

Connell SD, Irving AD (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. J Biogeogr 35:1608–1621 doi:10.1111/j.1365-2699.2008.01903.x

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 Biol Sci 277:1409–1415 doi:10.1098/rspb.2009.2069

Connell SD, Russell BD, Turner DJ, Shepherd SA, Kildea T, Miller D, Airoldi L, Cheshire A (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar Ecol Prog Ser 360:63–72 doi:10.3354/meps07526

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315 doi:10.1111/j.1461-0248.2008.01253.x

Cross WE, Wilce RT, Fabijan MF (1987) Effects of experimental releases of oil and dispersed oil on Arctic nearshore macrobenthos. III. Macroalgae. Arctic 40:211–219

Daigle RM, Metaxas A, deYoung B (2014) Fine-scale distribution and spatial variability of benthic invertebrate larvae in an open coastal embayment in Nova Scotia, Canada (M Hart, Ed.). PLOS ONE 9:e106178

Davoult D, Engel CR, Arzel P, Knoch D, Laurans M (2011) Environmental factors and commercial harvesting: exploring possible links behind the decline of the kelp *Laminaria digitata* in Brittany, France. Cah Biol Mar 52:429–435

Day EG, Branch GM (2000) Evidence for a positive relationship between juvenile abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* in the south-western Cape, South Africa. S Afr J Mar Sci 22:145–156 doi:10.2989/025776100784125834

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41:351–389 doi:10.2307/1948498

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16:215–245 doi:10.1146/annurev.es.16.110185.001243

Dayton PK (1985) The structure and regulation of some South American kelp communities. Ecol Monogr 55:447–468 doi:10.2307/2937131

Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Tresca DV (1984) Patch dynamics and stability of some California kelp communities. Ecol Monogr 54:253–289 doi:10.2307/1942498

Dayton PK, Tegner MJ (1984) Catastrophic storms, El Niño, and patch stability in a Southern California kelp community. Science 224:283–285 doi:10.1126/science.224.4646.283

Dayton PK, Tegner MJ (1990) Bottoms beneath troubled waters: benthic impacts of the 1982–1984 El Niño in the temperate zone. In: Glynn PW (ed) Global consequences of the 1982–1983 El Niño-Southern Oscillation. Elsevier Oceanography Series, Amsterdam, p 433–466

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol Appl 8:309–322 doi:10.1890/1051-0761(1998)008[0309:SBGARE]2.0.CO;2

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: the role of the oceanographic climate. Ecol Monogr 69:219–250 doi:10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2

Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421–445 doi:10.2307/2937118

de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Mohring MB (2013) Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. Limnol Oceanogr 58:1680–1688 doi:10.4319/lo.2013.58.5.1680

Dean TA, Schroeter SC, Dixon JD (1984) Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two species of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). Mar Biol 78:301–313 doi:10.1007/BF00393016

Devinny JS, Volse LA (1978) Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. Mar Biol 48:343–348 doi:10.1007/BF00391638

DeYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: data considerations. Prog Oceanogr 60:143–164 doi:10.1016/j.pocean.2004.02.017

Doroff AM, Estes JA, Tinker MT, Burn DM, Evans TJ (2003) Sea otter population declines in the Aleutian archipelago. J Mammal 84:55–64 doi:10.1644/1545-1542(2003)084<0055:SOPDIT>2.0.CO;2

Drijfhout S, Bathiany S, Beaulieu C, Brovkin V, Claussen M, Huntingford C, Scheffer M, Sgubin G, Swingedouw D (2015) Catalogue of abrupt shifts in Intergovernmental Panel on Climate Change climate models. Proc Natl Acad Sci 112:E5777-E5786.

Drinkwater KF (1996) Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s. J Northw Atl Fish Sci 18:77–97 doi:10.2960/J.v18.a6

Ducklow HW, Doney SC, Steinberg DK (2009) Contributions of long-term research and time series observations to marine ecology and biogeography. Annu Rev Mar Sci 1:279–302 doi:10.1146/annurev.marine.010908.163801

Dudgeon SR, Aronson RB, Bruno JF, Precht WF (2010) Phase shifts and stable states on coral reefs. Mar Ecol Prog Ser 413:201–216 doi:10.3354/meps08751

Dugan JE, Hubbard DM, McCrary MD, Pierson MO (2003) The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar Coast Shelf S 58S:25–40

Duggins DO (1980) Kelp beds and sea otters: an experimental approach. Ecology 61:447–453 doi:10.2307/1937405

Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. Mar Biol 128:489–495 doi:10.1007/s002270050115

Duggins DO, Gómez-Buckley MC, Buckley RM, Lowe AT, Galloway AW, Dethier MN (2016) Islands in the stream: kelp detritus as faunal magnets. Mar Biol 163:17

Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173doi:10.1126/science.245.4914.170

Dumont C, Himmelman JH, Russell MP (2004) Size-specific movement of green sea urchins *Strongylocentrotus droebachiensis* on urchin barrens in eastern Canada. Mar Ecol Prog Ser 276:93–101 doi:10.3354/meps276093

Dunton KH, Reimnitz E, Schonberg S (1982) An arctic kelp community in the Alaskan Beaufort Sea. Arctic 35:465–484

Ebeling AW, Laur DR, Rowley RJ (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar Biol 84:287–294 doi:10.1007/BF00392498

Ebert EE (1968) California sea otter – census and habitat survey. Underwat Nat 5:20–23

Ebert TA, Southon JR (2003) Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb ^{14}carbon. Fish Bull 101:915–922

Eckelbarger KJ, Watling L (1995) Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. Invertebr Biol 114:256–269 doi:10.2307/3226880

Edgar GJ, Barrett NS, Morton AJ, Samson CR (2004) Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. J Exp Mar Biol Ecol 312:67–87 doi:10.1016/j.jembe.2004.06.005

Edwards MS, Konar B (2012) A comparison of dragon kelp *Eualaria fistulosa*, (Phaeophyceae) fecundity in urchin barrens and nearby kelp beds throughout the Aleutian archipelago. J Phycol 48:897–901 doi:10.1111/j.1529-8817.2012.01139.x

Edwards PB, Ebert TA (1991) Plastic responses to limited food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus.* J Exp Mar Biol Ecol 145:205–220 doi:10.1016/0022-0981(91)90176-W

Ellis JC, Fariña JM, Witman JD (2006) Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. J Anim Ecol 75:565–574

Eriksson BK, Johansson G, Snoeijs P (2002) Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. J Phycol 38:284–296 doi:10.1046/j.1529-8817.2002.00170.x

Erlandson JM, Kennett DJ, Ingram BL, Guthrie DA and others (1996) An archaeological and palaeontological chronology for Daisy Cove (CA-SMI-261), San Miguel Island, California. Radiocarbon 38:355–373

Erlandson JM, Rick TC, Estes JA, Graham MH, Braje TJ, Vellanoweth RL (2008) Sea otters, shellfish, and humans: a 10,000 year record from San Miguel Island, California. J Archaeol Sci 35:2144–2152 doi:10.1016/j.jas.2008.01.014

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060 doi:10.1126/science.185.4156.1058

Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian islands, Alaska. Ecology 59:822–833 doi:10.2307/1938786

Estes JA, Tinker MT, Williams TM (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476 doi:10.1126/science.282.5388.473

Fagerli CW, Norderhaug KM, Christie HC (2013) Lack of sea urchin settlement may explain kelp forest recovery in overgrazed areas in Norway. Mar Ecol Prog Ser 488:119–132

Falk-Petersen IB, Lønning S (1983) Reproductive cycles of two closely related sea urchin species, *Strongylocentrotus droebachiensis* (OF Müller) and *Strongylocentrotus pallidus* (GO Sars). Sarsia 68:157–164

Fanelli G, Piraino S, Belmonte G, Geraci S, Boero F (1994) Human predation along Apulian rocky coasts (SE Italy): desertification caused by *Lithophaga lithophaga* (Mollusca) fisheries. Mar Ecol Prog Ser 110:1–8 doi:10.3354/meps110001

Feehan C, Scheibling RE, Lauzon-Guay JS (2012) Aggregative feeding behavior in sea urchins (*Strongylocentrotus droebachiensis*) leads to gap formation and destructive grazing in a Nova Scotian kelp bed. Mar Ecol Prog Ser 444:69–83 doi:10.3354/meps09441

Feehan C, Scheibling RE, Lauzon-Guay JS (2012) An outbreak of sea urchin disease associated with a recent hurricane: support for the 'killer storm hypothesis' on a local scale. J Exp Mar Biol Ecol 413:159–168 doi:10.1016/j.jembe.2011.12.003

Feehan CJ, Johnson-Mackinnon J, Scheibling RE, Lauzon-Guay JS, Simpson AGB (2013) Validating the identity of *Paramoeba invadens*, the causative agent of recurrent mass mortality of sea urchins in Nova Scotia, Canada. Dis Aquat Org 103:209–227 doi:10.3354/dao02577

Feehan CJ, Scheibling RE (2014) Disease as a control of sea urchin populations in Nova Scotian kelp beds. Mar Ecol Prog Ser 500:149–158 doi:10.3354/meps10700

Fernández C (2011) The retreat of large brown seaweeds on the north coast of Spain: the case of *Saccorhiza polyschides*. Eur J Phycol 46:352–360 doi:10.1080/09670262.2011.617840

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. Mar Ecol Prog Ser 543:141–152

Filbee-Dexter K, Scheibling RE (2012) Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. Mar Ecol Prog Ser 455:51–64 doi:10.3354/meps09667

Filbee-Dexter K, Scheibling RE (2014a) Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. Aquat Biol 23:71–86

Filbee-Dexter K, Scheibling RE (2014b) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25 doi:10.3354/meps10573

Filbee-Dexter K, Scheibling RE (2016) Spatial patterns and predictors of drift algal subsidy in deep subtidal environments. Est Coasts doi:10.1007/s12237-016-0101-5

Fletcher WJ (1987) Interactions among subtidal Australian sea urchins, gastropods and algae: effects of experimental removals. Ecol Monogr 57:89–109 doi:10.2307/1942640

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Syst 35:557–581 doi:10.1146/annurev.ecolsys.35.021103.105711

Ford T, Meux B (2010) Giant kelp community restoration in Santa Monica Bay. Urban Coast 2:43–46

Foreman RE (1977) Benthic community modification and recovery following intensive grazing by *Strongylocentrotus droebachiensis.* Helgol Meeresunters 30:468–484 doi:10.1007/BF02207855

Francis FTY, Filbee-Dexter K, Scheibling RE (2014) Stalked tunicates *Boltenia ovifera* form biogenic habitat in the rocky subtidal zone of Nova Scotia. Mar Biol 161:1375–1383

Fujita D (1998) Strongylocentrotid sea urchin-dominated barren grounds on the Sea of Japan coast of northern Japan. In: Mooi R, Telford M (eds) Echinoderms. Balkema, Rotterdam, p 659–664

Fujita D (2010) Current status and problems of isoyake in Japan. Bull Fish Res Agency 32:33–42

Fung T, Seymour RM, Johnson CR (2011) Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92:967–982 doi:10.1890/10-0378.1

Gagnon JM, Gilkinson KD (1994) Discrimination and distribution of the sea urchins *Strongylocentrotus droebachiensis* (OF Müller) and *S. pallidus* (GO Sars) in the Northwest Atlantic. Sarsia 79:1–11.

Gagnon P, Himmelman JH, Johnson LE (2004) Temporal variation in community interfaces: kelp-bed boundary dynamics adjacent to persistent urchin barrens. Mar Biol 144:1191–1203 doi:10.1007/s00227-003-1270-x

Garrett CJR, Loucks H (1976) Upwelling along the Yarmouth shore of Nova Scotia. J Fish Res Board Canada 33:116–117 doi:10.1139/f76-013

Garrido CL, Barber BJ (2001) Effects of temperature and food ration on gonad growth and oogenesis of the green sea urchin, *Strongylocentrotus droebachiensis.* Mar Biol 138:447–456 doi:10.1007/s002270000473

Gattuso JP, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D (2006) Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. Biogeosciences 3:489–513 doi:10.5194/bg-3-489-2006

Gaudette J, Wahle RA, Himmelman JH (2006) Spawning events in small and large populations of the green sea urchin *Strongylocentrotus droebachiensis* as recorded using fertilization assays. Limnol Oceanogr 51:1485–1496 doi:10.4319/lo.2006.51.3.1485

Gaylord B, Nickols KJ, Jurgens L (2012) Roles of transport and mixing processes in kelp forest ecology. J Exp Biol 215:997–1007 doi:10.1242/jeb.059824

Gaylord B, Reed DC, Raimondi PT, Washborn L (2006) Macroalgae spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecol Monogr 76:481–502 doi:10.1890/0012-9615(2006)076[0481:MSDICE]2.0.CO;2

Gerard VA (1976) Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. PhD dissertation. University of California Santa Cruz, Santa Cruz.

Gerard VA, Mann KH (1979) Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. J Phycol 15:33–41 doi:10.1111/j.0022-3646.1979.00033.x

Giakoumi S, Cebrian E, Kokkoris GD, Ballesteros E, Sala E (2012) Relationships between fish, sea urchins and macroalgae: the structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. Estuar Coast Shelf Sci

109:1–10 doi:10.1016/j.ecss.2011.06.004

Gianguzza P, Bonaviri C, Milisenda G, Barcellona A, Agnetta D, Vega Fernández T, Badalamenti F (2010) Macroalgal assemblage type affects predation pressure on sea urchins by altering adhesion strength. Mar Environ Res 70:82–86 doi:10.1016/j.marenvres.2010.03.006

Gladstone W, Masens O (2009) Monitoring and assessment of urchin barrens as a marine condition indicator. Hunter-Central Rivers Catchment Management Authority, University of Newcastle

Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. Bot Mar 52:559–572 doi:10.1515/BOT.2009.074

González-Irusta JM, González-Porto M, Sarralde R, Arrese B, Almón B, Martín-Sosa P (2015) Comparing species distribution models: a case study of four deep sea urchin species. Hydrobiologia 745:43–57

Gorgula SK, Connell SD (2004) Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. Mar Biol 145:613–619 doi:10.1007/s00227-004-1335-5

Graham MH (2004) Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. Ecosystems 7:341–357 doi:10.1007/s10021-003-0245-6

Graham MH (2010) Comparisions between East-Asian isoyake and deforestation in global kelp ecoystems. Bull Fish Res Agen 32:47–50

Gravel D, Mouquet N, Loreau M, Guichard F (2010) Patch dynamics, persistence, and species coexistence in metaecosystems. Am Nat 176:289–302

Gray JS (2001) Marine diversity: the paradigms in patterns of species richness examined. Sci Mar 65:41–56 doi:10.3989/scimar.2001.65s241

Greenlaw ME, Gromack AG, Basquill SP, Agatsuma Y, DS M, Lynds JA, Taylor RB, et al. (2013) A physiographic coastline classification of the scotian shelf bioregion and environs: the Nova Scotia coastline and the New Brunswick Fundy Shore. CSAS Research Document :051

Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334 doi:10.1007/s004420050090

Guidetti P, Fanelli G, Fraschetti S, Terlizzi A, Boero F (2002) Coastal fish indicate human-induced changes in the Mediterranean littoral. Mar Environ Res 53:77–94 doi:10.1016/S0141-1136(01)00111-8

Guidetti P, Fraschetti S, Terlizzi A, Boero F (2003) Distribution patterns of sea urchins and barrens in shallow Mediterranean rocky reefs impacted by the illegal fishery of the rock-boring mollusc *Lithophaga lithophaga*. Mar Biol 143:1135–1142 doi:10.1007/s00227-003-1163-z

Guillou M, Lumingas LJ, Michel C (2000) The effect of feeding or starvation on resource allocation to body components during the reproductive cycle of the sea urchin *Sphaerechinus granularis* (Lamarck). J Exp Mar Biol Ecol 245:183–196 doi:10.1016/S0022-0981(99)00162-8

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology 71:2269–2285 doi:10.2307/1938638

Hagen NT (1995) Recurrent destructive grazing of successionally immature kelp forests by green sea urchins in Vestfjorden, Northern Norway. Mar Ecol Prog Ser 123:95–106 doi:10.3354/meps123095

Hajal J, Wise DH (2002) Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. Ecology 83:3141–3151

Hanisak MD (1979) Growth patterns of *Codium fragile* ssp. *tomentosoides* in response to temperature, irradiance, salinity, and nitrogen source. Mar Biol 50:319–332 doi:10.1007/BF00387009

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36

Harley CD, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham MH (2012) Effects of climate change on global seaweed communities. J Phycol 48:1064–1078 doi:10.1111/j.1529-8817.2012.01224.x

Harrold C (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1–11

Harrold C, Light K, Lisin S (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. Limnol Oceanogr 43:669–678 doi:10.4319/lo.1998.43.4.0669

Harrold C, Lisin S (1989) Radio-tracking rafts of giant kelp: local production and regional transport. J Exp Mar Biol Ecol 130:237–251

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169 doi:10.2307/1939168

Hart MW, Scheibling RE (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. Mar Biol 99:167–176 doi:10.1007/BF00391978

Hart RE, Evans JL (2001) A climatology of the extratropical transition of Atlantic tropical cyclones. J Clim 14:546–564 doi:10.1175/1520-0442(2001)014<0546:ACOTET>2.0.CO;2

Hastie T, Friedman J, Tibshirani R (2001) Unsupervised Learning. New York: Springer.

Heath RA (1973) Flushing of coastal embayments by changes in atmospheric conditions. Limnol Oceanogr 18:849–862 doi:10.4319/lo.1973.18.6.0849

Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. Bull Mar Sci 70:273–290.

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688.

Hernández JC, Clemente S, Girard D, Pérez-Ruzafa Á, Brito A (2010) Effect of temperature on settlement and postsettlement survival in a barrens-forming sea urchin. Mar Ecol Prog Ser 413:69–80 doi:10.3354/meps08684

Hernández JC, Clemente S, Sangil C, Brito A (2008) Actual status of the sea urchin *Diadema antillarum* populations and macroalgal cover in marine protected areas compared to a highly fished area (Canary Islands eastern Atlantic Ocean). Aquat Conserv 18:1091–1108 doi:10.1002/aqc.903

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688

HilleRisLambers J, Harsch, MA, Ettinger AK, Ford KR, Theobald EJ (2013) How will biotic interactions influence climate change-induced range shifts? Ann N Y Acad Sci 1297:112–125

Himmelman JH (1978) Reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis.* Can J Zool 56:1828–1836 doi:10.1139/z78-249

Himmelman JH (1986) Population biology of sea urchins on rocky barrens. Mar Ecol Prog Ser 33:295–306

Himmelman JH, Dumont CP, Gaymer CF, Vallières C, Drolet D (2008) Spawning synchrony and aggregative behaviour of cold-water echinoderms during multi-species mass spawnings. Mar Ecol Prog Ser 361:161–168 doi:10.3354/meps07415

Hjörleifsson E, Kassa O, Gunnarsson K (1995) Grazing of kelp by green sea urchins in Eyyjafjordu, North Iceland. In: Skjoldal HR, Hopkins C, Erikstad KK, Leinass HP (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, p 593–597

Hobday AJ (2000) Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight. Mar Ecol Prog Ser 195:101–116 doi:10.3354/meps195101

Hobday AJ (2000) Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. J Exp Mar Biol Ecol 253:75–96 doi:10.1016/S0022-0981(00)00250-1

Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish 24:415–425 doi:10.1007/s11160-013-9326-6

Hochberg Y (1988) A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75:800–803 doi:10.1093/biomet/75.4.800

Hooper RG (1975) Bonne Bay marine resources. An ecological and biological assessment. Parks Canada, Halifax

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208 doi:10.1111/j.1751-8369.2002.tb00073.x

Huang Z, Brooke BP, Harris PT (2011) A new approach to mapping marine benthic habitats using physical environmental data. Cont Shelf Res 31:S4–S16

Huggett M, King C, Williamson JE, Steinberg P (2005) Larval development and metamorphosis of the Australian diadematid sea urchin *Centrostephanus rodgersii.* Invertebr Reprod Dev 47:197–204 doi:10.1080/07924259.2005.9652160

Hughes RN, Peer DL, Mann KH (1972) Use of multivariate analysis to identify functional components of the benthos in St. Margarets Bay, Nova Scotia. Limnol Oceanogr 17:111–121 doi:10.4319/lo.1972.17.1.0111

Hyndes GA, Lavery PS (2005) Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? Estuar Coast Shelf S 63:633–643

Hyndes GA, Lavery PS, Doropoulos C (2012) Dual processes for cross-boundary subsidies: incorporation of nutrients from reef-derived kelp into a seagrass ecosystem. Mar Ecol Prog Ser 445:97–107

Hyndes GA, Nagelkerken I, McLeod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol Rev 89:232–254

Iverson L, Prasad A, Matthews S (2008) Modeling potential climate change impacts on the trees of the northeastern United States. Mitig Adapt Strateg Glob Change 13:487–516

Jackson JB (1997) Reefs since Columbus. Coral Reefs 16:S23–S32 doi:10.1007/s003380050238

Jamieson GS, Campbell A (1995) Red sea urchins and kelp in northern British Columbia. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier Science, Amsterdam, p 537–547

Johnson CR, Banks SC, Barrett NS, Cazassus F and others (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J Exp Mar Biol Ecol 400:17–32 doi:10.1016/j.jembe.2011.02.032

Johnson CR, Ling SD, Ross DJ, Shepherd S, Miller KJ (2005) Establishment of the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania: first assessment of potential threats to fisheries. Project Report. School of Zoology and Tasmanian Aquaculture and Fisheries Institute, Hobart

Johnson CR, Mann KH (1982) Adaptations of *Strongylocentrotus droebachiensis* for survival on barren grounds in Nova Scotia. In: Lawrence JM (ed) Echinoderms: proceedings of the international conference. AA Balkema, Rotterdam, p 277–283

Johnson CR, Mann KH (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecol Monogr 58:129–154 doi:10.2307/1942464

Johnson LE, Brawley SH, Adey WH (2012) Secondary spread of invasive species: historic patterns and underlying mechanisms of the continuing invasion of the European rockweed *Fucus serratus* in eastern North America. Biol Invasions 14:79–97 doi:10.1007/s10530-011-9976-z

Johnson TR, Wilson JA, Cleaver C, Morehead G, Vadas R (2013) Modeling fine scale urchin and kelp dynamics: Implications for management of the Maine sea urchin fishery. Fish Res 141:107–117 doi:10.1016/j.fishres.2012.05.008

Johnson TR, Wilson JA, Cleaver C, Morehead G, Vadas R (2013) Modeling fine scale urchin and kelp dynamics: Implications for management of the Maine sea urchin fishery. Fisheries Research 141:107–117

Jones GM (1985) *Paramoeba invadens* n. sp. (Amoebida, Paramoebidae), a pathogenic amoeba from the sea urchin *Strongylocentrotus droebachiensis* in Eastern Canada. J Protozool 32:564–569 doi:10.1111/j.1550-7408.1985.tb03075.x

Jones NS, Kain JM (1967) Subtidal algal colonization following the removal of Echinus. Helgol Meeresunters 15:460–466 doi:10.1007/BF01618642

Kannan K, Agusa T, Perrotta E, Thomas NJ, Tanabe S (2006) Comparison of trace element concentrations in livers of diseased, emaciated and non-diseased southern sea otters from the California coast. Chemosphere 65:2160–2167 doi:10.1016/j.chemosphere.2006.06.003

Kawamata S (2010) Inhibitory effects of wave action on destructive grazing by sea urchins: a review. Bull Fish Res Agency 32:95–102

Keats DW (1991) Refugial *Laminaria* abundance and reduction in urchin grazing in communities in the Northwest Atlantic. J Mar Biol 71:867–876

Keats DW, Hooper RG, Steele DH, South GR (1987) Field observations of summer and autumn spawning by *Strongylocentrotus droebachiensis*, green sea urchins, in eastern Newfoundland. Can Field Nat 101:463–465

Keats DW, South GR, Steele DH (1990) The effects of an experimental reduction in grazing by green sea urchins on a benthic macroalgal community in eastern Newfoundland. Mar Ecol Prog Ser 68:181–193 doi:10.3354/meps068181

Keats DW, Steele DH, South GR (1984) Depth-dependent reproductive output of the green sea urchin, *Strongylocentrotus droebachiensis* (OF Müller), in relation to the nature and availability of food. J Exp Mar Biol Ecol 80:77–91 doi:10.1016/0022-0981(84)90095-9

Kelly JR, Krumhansl KA, Scheibling RE (2012) Drift algal subsidies to sea urchins in low-productivity habitats. Mar Ecol Prog Ser 452:145–157 doi:10.3354/meps09628

Kelly JR, Scheibling RE, Balch T (2011) Invasion-mediated shifts in the macrobenthic assemblage of a rocky subtidal ecosystem. Mar Ecol Prog Ser 437:69–78 doi:10.3354/meps09284

Kennelly SJ (1989) Effects of kelp canopies on understorey species due to shade and scour. Mar Ecol Prog Ser 50:215–224 doi:10.3354/meps050215

Kirchhoff NT, Eddy S, Brown NP (2010) Out-of-season gamete production in *Strongylocentrotus droebachiensis*: photoperiod and temperature manipulation. Aquaculture 303:77–85 doi:10.1016/j.aquaculture.2010.03.003

Kirkman H, Kendrick GA (1997) Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. J Appl Phycol 9:311–326 doi:10.1023/A:1007965506873

Kitching JA (1987) Ecological studies at Lough Hyne. Adv Ecol Res 17:115–189 doi:10.1016/S0065-2504(08)60245-7

Knowlton N (2004) Multiple ‘stable’ states and the conservation of marine ecosystems. Prog Oceanogr 60:387–396 doi:10.1016/j.pocean.2004.02.011

Kolb GS, Jerling L, Hambäck PA (2010) The impact of cormorants on plant–arthropod food webs on their nesting islands. Ecosystems 13:353–366

Konar B (2000) Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. Oecologia 125:208–217 doi:10.1007/s004420000440

Konar B, Estes JA (2003) The stability of boundary regions between kelp beds and deforested areas. Ecology 84:174–185 doi:10.1890/0012-9658(2003)084[0174:TSOBRB]2.0.CO;2

Kopecky AL, Dunton KH (2006) Variability in drift macroalgal abundance in relation to biotic and abiotic factors in two seagrass dominated estuaries in the Western Gulf of Mexico. Estuaries Coast 29:617–629

Krause-Jensen D, Marbà N, Olesen B, Sejr MK and others (2012) Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. Glob Change Biol 18:2981–2994 doi:10.1111/j.1365-2486.2012.02765.x

Krumhansl KA, Lauzon-Guay JS, Scheibling RE (2014) Modeling effects of climate change and phase shifts on detrital production of a kelp bed. Ecology 95:763–774 doi:10.1890/13-0228.1

Krumhansl KA, Lee JM, Scheibling RE (2011) Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. J Exp Mar Biol Ecol 407:12–18 doi:10.1016/j.jembe.2011.06.033

Krumhansl KA, Scheibling RE (2011a) Detrital production in Nova Scotian kelp beds: patterns and processes. Mar Ecol Prog Ser 421:67–82 doi:10.3354/meps08905

Krumhansl KA, Scheibling RE (2011b) Spatial and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. Aquat Biol 13:163–173 doi:10.3354/ab00366

Krumhansl KA, Scheibling RE (2012a) Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. *fragile.* Mar Ecol Prog Ser 456:73–85 doi:10.3354/meps09671

Krumhansl KA, Scheibling RE (2012b) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302 doi:10.3354/meps09940

Lamb I, Zimmerman M (1964) Marine vegetation on Cape Anne, Essex County, Massachusetts. Rhodora 66:217–254

Laur DR, Ebeling AW, Reed DC (1986) Experimental evaluations of substrate types as barriers to sea urchin (*Strongylocentrotus* spp.) movement. Mar Biol 93:209–215 doi:10.1007/BF00508258

Lauzon-Guay J, Scheibling R (2010) Spatial dynamics, ecological thresholds and phase shifts: modelling grazer aggregation and gap formation in kelp beds. Mar Ecol Prog Ser 403:29–41

Lauzon-Guay JS, Scheibling RE (2007a) Behaviour of sea urchin *Strongylocentrotus droebachiensis* grazing fronts: food-mediated aggregation and density-dependent facilitation. Mar Ecol Prog Ser 329:191–204 doi:10.3354/meps329191

Lauzon-Guay JS, Scheibling RE (2007b) Importance of spatial population characteristics on the fertilization rates of sea urchins. Biol Bull (Woods Hole) 212:195–205 doi:10.2307/25066602

Lauzon-Guay JS, Scheibling RE (2007c) Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. Mar Biol 151:2109–2118 doi:10.1007/s00227-007-0668-2

Lauzon-Guay JS, Scheibling RE, Barbeau MA (2009) Modeling phase shifts in a rocky subtidal ecosystem. Mar Ecol Prog Ser 375:25–39 doi:10.3354/meps07758

Lawrence JM (1975) On the relationships between marine plants and sea urchins. Oceanogr Mar Biol Annu Rev 13:213–286

Lee RKS (1973) General ecology of the arctic benthic marine algae. Arctic 26:32–43

Lees K, Pitois S, Scott C, Frid C, Mackinson S (2006) Characterizing regime shifts in the marine environment. Fish Fish 7:104–127 doi:10.1111/j.1467-2979.2006.00215.x

Leinaas HP, Christie H (1996) Effects of removing sea urchins (*Strongylocentrotus droebachiensis*): stability of the barren state and succession of kelp forest recovery in the east Atlantic. Oecologia 105:524–536 doi:10.1007/BF00330016

Leleu K, Remy-Zephir B, Grace R, Costello MJ (2012) Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. Biol Conserv 155:193–201 doi:10.1016/j.biocon.2012.05.009

Leroux SJ, Larrivée M, Boucher-Lalonde V, Hurford A, Zuloaga J, Kerr JT, Lutscher F (2013) Mechanistic models for the spatial spread of species under climate change. Ecol Appl 23:815–828

Lesser MP, Carleton KL, Böttger SA, Barry TM, Walker CW (2011) Sea urchin tube feet are photosensory organs that express a rhabdomeric-like opsin and PAX6. Proc R Soc B 278:3371–3379

Levin PS (1994) Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environ Biol Fishes 40:271–281 doi:10.1007/BF00002517

Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83:3182–3193 doi:10.1890/0012-9658(2002)083[3182:CWEONS]2.0.CO;2

Lewontin RC (1969) Meaning of stability. Brookhaven Symp Biol 22:13–24

Li X, Wang Y (2013) Applying various algorithms for species distribution modelling. Integrative Zool 8:124–135

Ling S, Johnson CR, Ridgway K (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Glob Change Biol 15:719–731

Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia 156:883–894 doi:10.1007/s00442-008-1043-9

Ling SD, Johnson CR (2012) Marine reserves reduce risk of climate-driven phase shift by reinstating size-and habitat-specific trophic interactions. Ecol Appl 22:1232–1245 doi:10.1890/11-1587.1

Ling SD, Johnson CR, Frusher SD, Ridgeway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Natl Acad Sci USA 106:22341–22345 doi:10.1073/pnas.0907529106

Ling SD, Scheibling RE, Rassweiler A, Johnson CR, Shears N, Connell SD, Salomon AK, Norderhaug KM, Perez-Matus A, Hernández JC, Clemente S, Blamey LK, Hereu B, Ballesteros E, Sala E, Garrabou J, Cebrian E, Zabala M, Fujita D, Johnson LE (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. Philos T R Soc B 370:20130269–20130269

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393

Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6:673–679

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809 doi:10.1126/science.1128035

Lyons DA, Scheibling RE (2007) Differences in somatic and gonadic growth of sea urchins (*Stronglyocentrotus droebachiensis*) fed kelp (*Laminaria longicruris*) or the invasive alga *Codium fragile* ssp. *tomentosoides* are related to energy acquisition. Mar Biol 152:285–295 doi:10.1007/s00227-007-0682-4

Lyons DA, Scheibling RE (2008) Context-dependant survival of the invasive seaweed *Codium fragile* ssp. *tomentosoides* in kelp bed and urchin barren habitats off Nova Scotia. Aquat Biol 2:17–27 doi:10.3354/ab00035

Mann KH (1972) Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar Biol 14:199–209

Mann KH (1973) Seaweeds: their productivity and strategy for growth. Science 182:975–981 doi:10.1126/science.182.4116.975

Mann KH (1977) Destruction of kelp-beds by sea urchins: a cyclical phenomenon or irreversible degradation? Helgol Mar Res 30:455–467

Mann KH (1982) Ecology of coastal waters. A systems approach. University of California Press, Berkeley, CA.

Mann KH (1988) Production and use of detritus in various freshwater estuarine, and coastal marine ecosystems. Limnol Oceanogr 33:910–930 doi:10.4319/lo.1988.33.4_part_2.0910

Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88:140–148 doi:10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2

Marmion M, Luoto M, Heikkinen RK, Thuiller W (2009) The performance of state-of-the-art modelling techniques depends on geographical distribution of species. Ecol Model 220:3512–3520

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15:59–69

Marzloff MP, Johnson CR, Little LR, Soulie JC, Ling SD, Frusher SD (2013) Sensitivity analysis and pattern-oriented validation of TRITON, a model with alternative community states: insights on temperate rocky reefs dynamics. Ecol Model 258:16-32

Matheson K, McKenzie CH, Sargent P, Hurley M, Wells T (2014) Northward expansion of the invasive green algae *Codium fragile* spp. *fragile* (Suringar) Hariot, 1889 into coastal waters of Newfoundland, Canada. BioInvasions Rec 3:151–158 doi:10.3391/bir.2014.3.3.03

Mathieson AC, Dawes CJ, Harris LG, Hehre EJ (2003) Expansion of the Asiatic green alga *Codium fragile* subsp. *tomentosoides* in the Gulf of Maine. Rhodora 105:1–53

Mathieson AC, Moore GE, Short FT (2010) A floristic comparison of seaweeds from James Bay and three contiguous Northeastern Canadian Arctic sites. Rhodora 112:396–434 doi:10.3119/09-12.1

Matsunaga K, Kawaguchi T, Suzuki Y, Nigi G (1999) The role of terrestrial humic substances on the shift of kelp community to crustose coralline algae community of the southern Hokkaido Island in the Japan Sea. J Exp Mar Biol Ecol 241:193–205 doi:10.1016/S0022-0981(99)00077-5

Mattison JE, Trent JD, Shanks AL, Akin TB, Pearse JS (1976) Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. Mar Biol 39:25–30

May RM (1973) Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton

May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–476 doi:10.1038/269471a0

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417 doi:10.1007/s003380000129

McLean JH (1962) Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol Bull 122:95–114 doi:10.2307/1539325

McNaught DC (1999) The indirect effects of macroalgae and micropredation on the post-settlement success of the green sea urchin in Maine. PhD dissertation, University of Maine, Orono, ME

Meeus JH (1999) Astronomical algorithms. Willman-Bell, VA

Meidel SK, Scheibling RE (1998) Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. Mar Biol 131:461–478 doi:10.1007/s002270050338

Meidel SK, Scheibling RE (1999) Effects of food type and ration on reproductive maturation and growth of the sea urchin *Strongylocentrotus droebachiensis.* Mar Biol 134:155–166 doi:10.1007/s002270050534

Meidel SK, Scheibling RE (2001) Variation in egg spawning among subpopulations of sea urchins *Strongylocentrotus droebachiensis*: a theoretical approach. Mar Ecol Prog Ser 213:97–110 doi:10.3354/meps213097

Merzouk A, Johnson LE (2011) Kelp distribution in the northwest Atlantic Ocean under a changing climate. J Exp Mar Biol Ecol 400:90–98 doi:10.1016/j.jembe.2011.02.020

Miller RJ (1985) Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. Mar Biol 84:275–286 doi:10.1007/BF00392497

Miller RJ, Nolan SC (2000) Management of the Nova Scotia sea urchin fishery: a nearly successful habitat based management regime. Fisheries and Oceans Science, Canadian Stock Assessment Secretariat, Ottawa

Miller RJ, Nolan SC (2008) Management Methods for a Sea Urchin Dive Fishery with Individual Fishing Zones. J Shellfish Res 27:929–938

Miner CM, Altstatt JM, Raimondi PT, Minchinton TE (2006) Recruitment failure and shifts in community structure following mass mortality limit recovery prospects of black abalone. Mar Ecol Prog Ser 327:107–117 doi:10.3354/meps327107

Mineur F, Arenas F, Assis J, Davies AJ and others (2015) European seaweeds under pressure: consequences for communities and ecosystem functioning. J Sea Res 98:91–108 doi:10.1016/j.seares.2014.11.004

Minor MA, Scheibling RE (1997) Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis.* Mar Biol 129:159–167 doi:10.1007/s002270050156

Mochizuki T, Ishii M, Kimoto M, Chikamoto Y and others (2010) Pacific decadal oscillation hindcasts relevant to near-term climate prediction. Proc Natl Acad Sci USA 107:1833–1837 doi:10.1073/pnas.0906531107

Mohr JL, Wilimovsky NJ, Dawson EY (1957) An arctic Alaskan kelp bed. Arctic 10:45–52

Moore DS, Miller RJ (1983) Recovery of macroalgae following widespread sea urchin mortality with a description of the nearshore hard-bottom habitat on the Atlantic coast of Nova Scotia. Can Tech Rep Fish Aquat Sci 1230

Moy FE, Christie H (2012) Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. Mar Biol Res 8:309–321 doi:10.1080/17451000.2011.637561

Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101

Munk JE (1992) Reproduction and growth of green urchins *Strongylocentrotus droebachiensis* (Müller) near Kodiak, Alaska. J Shellfish Res 11:245–254

Murakami M, Nakano S (2002) Indirect effect of aquatic insect emergence on a terrestrial insect population through birds predation. Ecol Lett 5:333–337

Nakano S, Miyasaka H, Kuhara N (1999) Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441

Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc Natl Acad Sci USA 98:166–170 doi:10.1073/pnas.98.1.166

Nicodemus KK, Malley JD, Strobl C, Ziegler A (2010) The behaviour of random forest permutation-based variable importance measures under predictor correlation. BMC Bioinformatics 11:110

Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar Biol Res 5:515–528 doi:10.1080/17451000902932985

Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborean* to kelp forest consumers and the importance of bacterial degradation to food quality. Mar Ecol Prog Ser 255:135–144 doi:10.3354/meps255135

Norkko J, Bondsorff E, Norkko A (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. J Exp Mar Biol Ecol 248:79–104

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306

North WJ (1971) The biology of giant kelp beds (*Macrocystis*) in California: introduction and background. Nova Hedwigia 32:1–68

Norton TA (1992) Dispersal by macroalgae. Br Phycol J 27:293–301 doi:10.1080/00071619200650271

O'Brien JM, Scheibling RE (2016) Nipped in the bud: mesograzer feeding preference contributes to kelp decline. Ecology. doi:10.1890/15-1728.1

O’Brien JM, Scheibling RE, Krumhansl KA (2015) Positive feedback between large-scale disturbance and density-dependent grazing decreases resilience of a kelp bed ecosystem. Mar Ecol Prog Ser 522:1–13 doi:10.3354/meps11193

Oganesyan SA (1998) Reproductive cycle of the echinoid S*trongylocentrotus droebachiensis* in the Barents Sea. In: Mooi R, Telford M (eds) Echinoderms. AA Balkema, Rotterdam, p 765–768

Oshurkov VV, Bazhin AG, Lukin VI, Sevostyanov VF (1988) Sea otter predation and the benthic community structure of Commander Islands. Biol Mora 6:50–60

Paine RT (1969) A note on trophic complexity and community stability. Am Nat 103:91–93 doi:10.1086/282586

Pandolfi JM, Jackson JB (2006) Ecological persistence interrupted in Caribbean coral reefs. Ecol Lett 9:818–826 doi:10.1111/j.1461-0248.2006.00933.x

Parmesan C, Duarte C, Poloczanska E, Richardson AJ, Singer MC (2011) Overstretching attribution. Nat Clim Change 1:2–4 doi:10.1038/nclimate1056

Pearce CM, Scheibling RE (1990) Induction of metamorphosis of larvae of the green sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. Biol Bull 179:304–331 doi:10.2307/1542322

Pearce CM, Scheibling RE (1991) Effect of macroalgae, microbial films, and conspecifics on the induction of metamorphosis of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). J Exp Mar Biol Ecol 147:147–162

Pearse JS, Clark ME, Leighton DL, Mitchell CT, North WJ (1970) Marine waste disposal and sea urchin ecology. In: North WJ (ed) Kelp Habitat Improvement Project, California Annual Report, 1969 to 1970. California Institute of Technology, Pasadena, CA, p 1–93

Pearse JS, Hines AH (1979) Expansion of a central California kelp forest following the mass mortality of sea urchins. Mar Biol 51:83–91 doi:10.1007/BF00389034

Pecorino D, Lamare MD, Barker MF (2012) Growth, morphometrics and size structure of the Diadematidae sea urchin *Centrostephanus rodgersii* in northern New Zealand. Mar Freshw Res 63:624–634 doi:10.1071/MF12040

Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. Mar Ecol Prog Ser 142:261–272 doi:10.3354/meps142261

Pérez R (1971) Ecologie, croissance et régénération, teneurs an acide alginique de *Laminaria digitata* sur les côtes française de la Manche. Rev Trav Inst Pêches Marit 35:287–346

Peterson CH (1984) Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? Am Nat 124:127–133 doi:10.1086/284256

Petraitis PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities. J Exp Mar Biol Ecol 300:343–371 doi:10.1016/j.jembe.2003.12.026

Petraitis PS, Latham RE (1999) The importance of scale in testing the origins of alternative community states. Ecology 80:429–442 doi:10.1890/0012-9658(1999)080[0429:TIOSIT]2.0.CO;2

Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and others (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200 doi:10.1017/S0376892900000205

Piovia-Scott J, Spiller DA, Schoener TW (2011) Effects of experimental seaweed deposition on lizard and ant predation in an island food web. Science 331:461–463

Platt T, Jassby AB (1976) The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J Phycol 12:421–430

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316 doi:10.1146/annurev.ecolsys.28.1.289

Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc Nat Acad Sci 92:4382–4386

Propp MV (1977) Ecology of the sea urchin *Strongylocentrotus droebachiensis* of the Barents Sea: metabolism and regulation of abundance. Sov J Mar Biol 3:27–37

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Raffaelli D, Hawkins S (1996) Intertidal ecology. Chapman & Hall, London

Ramirez-Llodra E, Rinde E, Gundersen H, Christie H, Fagerli CW, Fredriksen S, Gitmark JK, Norling K, Walday MG, Norderhaug KM (2016) A snap shot of the short-term response of crustaceans to macrophyte detritus in the deep Oslofjord. Sci Rep 6:23800

Ramus J (1992) Productivity of seaweeds. In: Falkowski PG, Woodhead D (eds) Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, NY p 239–255

Rocha J, Yletyinen J, Biggs R, Blenckner T, Peterson G (2015) Marine regime shifts: drivers and impacts on ecosystems services. Philos T R Soc B 370:20130273–20130273

Rodriguez SR (2003) Consumption of drift kelp by intertidal populations of the sea urchins *Tetrapygus niger* on the central Chilean coast: possible consequences at different ecological levels. Mar Ecol Prog Ser 251:141–151 doi:10.3354/meps251141

Rogers-Bennett L, Bennett WA, Fastenau HC, Dewees CM (1995) Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. Ecol Appl 5:1171–1180 doi:10.2307/2269364

Rose MD, Polis GA (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007

Round FE (1967) The ecology of benthic algae. In: Jackson DE (ed) Algae and man. Plenum Press, New York, NY, p 138–184

Russell BD (2007) Effects of canopy-mediated abrasion and water flow on the early colonization of turf-forming algae. Mar Freshw Res 58:657–665 doi:10.1071/MF06194

Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades and the structure of algal assemblages; evaluation of an old but untested paradigm. Oikos 82:425–439 doi:10.2307/3546364

Sauchyn LK, Scheibling RE (2009a) Fecal production by sea urchins in native and invaded algal beds. Mar Ecol Prog Ser 396:35–48 doi:10.3354/meps08296

Sauchyn LK, Scheibling RE (2009b) Degradation of sea urchin feces in a rocky subtidal ecosystem: implications for nutrient cycling and energy flow. Aquat Biol 6:99–108 doi:10.3354/ab00171

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 doi:10.3354/meps07669

Saunders M, Metaxas A, Filgueira R (2010) Implications of warming temperatures for population outbreaks of a nonindigenous species (*Membranipora membranacea*, Bryozoa) in rocky subtidal ecosystems. Limnol Oceanogr 55:1627–1642 doi:10.4319/lo.2010.55.4.1627

Savage M, Sawhill B, Askenazi M (2000) Community dynamics: what happens when we rerun the tape? J Theor Biol 205:515–526 doi:10.1006/jtbi.2000.2055

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596 doi:10.1038/35098000

Scheibling RE (1984) Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada. Helgol Meeresunters 37:233–242 doi:10.1007/BF01989308

Scheibling RE (1986) Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. Oecologia 68:186–198 doi:10.1007/BF00384786

Scheibling RE (1996) The role of predation in regulating sea urchin populations in eastern Canada. Oceanol Acta 19:421–430

Scheibling RE, Feehan CJ, Lauzon-Guay JS (2013) Climate change, disease and the dynamics of a kelp-bed ecosystem in Nova Scotia. In: Fernández-Palocios JM, Nascimiento LD, Hernández JC, Clement S, González A, Diaz-González JP (eds) Climate change: perspectives from the Atlantic: past, present and future. Servicio de Publicaciones de la Universidad de La Laguna, Tenerife, p 41–81

Scheibling RE, Gagnon P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Mar Ecol Prog Ser 325:1–14 doi:10.3354/meps325001

Scheibling RE, Gagnon P (2009) Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora membranacea* in Nova Scotian kelp beds. Mar Ecol Prog Ser 390:1–13 doi:10.3354/meps08207

Scheibling RE, Hamm J (1991) Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. Mar Biol 110:105–116 doi:10.1007/BF01313097

Scheibling RE, Hatcher BG (2007) Ecology of *Strongylocentrotus droebachiensis*. In: Lawrence JM (ed) Edible sea urchins: biology and ecology, 2nd edn. Elsevier Science, Amsterdam, p 353–392

Scheibling RE, Hatcher BG (2013) *Strongylocentrotus droebachiensis*. In: Lawrence JM (ed) Edible sea urchins: biology and ecology. Elsevier Science, Amsterdam, p 381–412

Scheibling RE, Hennigar A, Balch T (1994) The dynamics of destructive grazing of kelp beds by sea urchins in Nova Scotia. In: David B, Guille A, Feral JP, Roux M (eds) Echinoderms through time: Proc 8th Int Echinoderms Conf Dijon. AA Balkema, Rotterdam, p 871

Scheibling RE, Hennigar AW (1997) Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. Mar Ecol Prog Ser 152:155–165 doi:10.3354/meps152155

Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. Can J Fish Aquat Sci 56:2300–2314 doi:10.1139/f99-163

Scheibling RE, Lauzon-Guay JS (2010) Killer storms: North Atlantic hurricanes and disease outbreaks in sea urchins. Limnol Oceanogr 55:2331–2338 doi:10.4319/lo.2010.55.6.2331

Scheibling RE, Stephenson RL (1984) Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. Mar Biol 78:153–164 doi:10.1007/BF00394695

Schiel DR (1990) Macroalgal assemblages in New Zealand: structure, interactions and demography. Hydrobiologia 192:59–76 doi:10.1007/BF00006227

Schiel DR, Andrew NL, Foster MS (1995) The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand. Mar Biol 123:355–367 doi:10.1007/BF00353627

Schiel DR, Steinbeck JR, Foster MS (2004) Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. Ecology 85:1833–1839 doi:10.1890/03-3107

Schmidt AL, Scheibling RE (2007) Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. J Exp Mar Biol Ecol 341:110–130 doi:10.1016/j.jembe.2006.10.003

Seymour RJ, Tegner MJ, Dayton PK, Parnell PE (1989) Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. Estuar Coast Shelf Sci 28:277–292 doi:10.1016/0272-7714(89)90018-8

Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Mar Ecol Prog Ser 246:1–16 doi:10.3354/meps246001

Shears NT, Babcock RC (2007) Quantitative description of mainland New Zealand's shallow subtidal reef communities. Science for Conservation 280, Department of Conservation, Wellington

Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take marine park. Biol Conserv 132:222–231 doi:10.1016/j.biocon.2006.04.001

Shpigel M, McBride SC, Marciano S, Lupatsch I (2004) The effect of photoperiod and temperature on the reproduction of European sea urchin *Paracentrotus lividus.* Aquaculture 232:343–355 doi:10.1016/S0044-8486(03)00539-8

Siddon CE, Witman JD (2003) Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Mar Ecol Prog Ser 261:99–110 doi:10.3354/meps261099

Siikavuopio SI, Christiansen JS, Sæther BS, Dale T (2006) Effects of temperature and season on gonad growth and feed intake in the green sea urchin (*Strongylocentrotus droebachiensis*). Aquaculture 255:389–394 doi:10.1016/j.aquaculture.2005.12.021

Siikavuopio SI, Christiansen JS, Sæther BS, Dale T (2007) Seasonal variation in feed intake under constant temperature and natural photoperiod in the green sea urchin (*Strongylocentrotus droebachiensis*). Aquaculture 272:328–334 doi:10.1016/j.aquaculture.2007.09.003

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411 doi:10.1126/science.200.4340.403

Simes JR (1986) An improved Bonferroni procedure for multiple test of significance. Biometrika 73:751–754 doi:10.1093/biomet/73.3.751

Simonson EJ, Metaxas A, Scheibling RE (2015a) Kelp in hot water: II. Effects of warming seawater temperature on kelp quality as a food source and settlement substrate. Mar Ecol Prog Ser 537:105–119 doi:10.3354/meps11421

Simonson EJ, Scheibling RE, Metaxas A (2015b) Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. Mar Ecol Prog Ser 537:89–104 doi:10.3354/meps11438

Sisson CG (2005) Life history dynamics and biogeography of a nudibranch with contrasting developmental modes: a hypothesis for the evolution of larval types. J Nat Hist 39:1719–1733 doi:10.1080/00222930400024709

Sivertsen K (1996) Incidence, occurrence and distribution of the nematode *Echinomermella matsi* in its echinoid host, *Strongylocentrotus droebachiensis*, in northern Norway. Mar Biol 126:703–714 doi:10.1007/BF00351337

Sivertsen K (1997) Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. Can J Fish Aquat Sci 54:2872–2887 doi:10.1139/f97-186

Sivertsen K (2006) Overgrazing of kelp beds along the coast of Norway. J Appl Phycol 18:599–610 doi:10.1007/s10811-006-9064-4

Sjøtun K, Fredriksen S, Rueness J (1998) Effect of canopy biomass and wave exposure on growth in *Laminaria hyperborea* (Laminariaceae: Phaeophyta). Eur J Phycol 33:337–434

Skadsheim A, Christie H, Leinaas HP (1995) Population reductions of *Strongylocentrotus droebachiensis* (Echinodermata) in Norway and the distribution of its endoparasite *Echinomermella matsi* (Nematoda). Mar Ecol Prog Ser 119:199–209 doi:10.3354/meps119199

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium of species diversity. Ecology (USA) 60:1225–1239 doi:10.2307/1936969

Starr M, Himmelman JH, Therriault JC (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. Science 247:1071–1074 doi:10.1126/science.247.4946.1071

Starr M, Himmelman JH, Therriault JC (1993) Environmental control of green sea urchin, *Strongylocentrotus droebachiensis*, spawning in the St Lawrence Estuary. Can J Fish Aquat Sci 50:894–901 doi:10.1139/f93-103

Starr M, Therriault JC, Conan GY, Comeau M, Robichaud G (1994) Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. J Plankton Res 16:1137–1147 doi:10.1093/plankt/16.9.1137

Statistics Canada (2001) Shelburne (Code 1201), Queens (Code 1204), Lunenburg (Code 1206), and Halifax (Code 1209), Nova Scotia (table) Community Profile, 2001 Census. Statistics Canada Catalogue no. 93F0053XIE, Ottawa, Canada

Statistics Canada (2012) Shelburne (Code 1201), Queens (Code 1204), Lunenburg (Code 1206), and Halifax (Code 1209), Nova Scotia (table) Community Profile, 2011 Census. Statistics Canada Catalogue no. 98-316-XWE, Ottawa, Canada

Steneck RS (1997) Fisheries-induced biological changes to the structure and function of the Gulf of Maine ecosystem In: Wallace GT, Braasch EF (eds) Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop. Regional Association for Research on the Gulf of Maine, Hanover, ME, p 151-165

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498 doi:10.2307/3545860

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459 doi:10.1017/S0376892902000322

Steneck RS, Leland A, McNaught DC, Vavrinec J (2013) Ecosystem flips, locks, and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. Bull Mar Sci 89:31–55 doi:10.5343/bms.2011.1148

Steneck RS, Vavrinec J, Leland AV (2004) Accelerating trophic-level dysfunction in kelp forests ecosystems of the Western North Atlantic. Ecosystems 7:323–332 doi:10.1007/s10021-004-0240-6

Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoldi L (2014) Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. Glob Chang Biol 20:3300–3312 doi:10.1111/gcb.12619

Sumi CB, Scheibling RE (2005) Role of grazing by sea urchins *Strongylocentrotus droebachiensis* in regulating the invasive alga *Codium fragile* ssp. *tomentosoides* in Nova Scotia. Mar Ecol Prog Ser 292:203–212 doi:10.3354/meps292203

Sutherland JP (1974) Multiple stable points in natural communities. Am Nat 108:859–873 doi:10.1086/282961

Tamaki H, Kusaka K, Fukuda M, Arai S, Muraoka D (2009) *Undaria pinnatifida* habitat loss in relation to sea urchin grazing and water flow conditions, and their restoration effort in Ogatsu Bay, Japan. J Water Environ Technol 7:201–213 doi:10.2965/jwet.2009.201

Tamaki H, Takahashi H, Fukaya A, Fukuda M, Arai S, Muraoka D (2005) The distributional patterns of *Undaria pinnatifida* (Harvey) Suringar and sea urchins related to water velocity condition in Ogatsu Bay, Miyagi Prefecture. Jpn J Phycol 53:131–135

Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Mar Ecol Prog Ser 5:255–268 doi:10.3354/meps005255

Tegner MJ, Dayton PK (1987) El Niño effects on southern California kelp forest communities. Adv Ecol Res 17:243–279 doi:10.1016/S0065-2504(08)60247-0

Tegner MJ, Dayton PK (1991) Sea urchins, El Niños, and the long term stability of Southern California kelp forest communities. Mar Ecol Prog Ser 77:49–63 doi:10.3354/meps077049

Tegner MJ, Dayton PK (2000) Ecosystem effects of fishing in kelp forest communities. ICES J Mar Sci 57:579–589 doi:10.1006/jmsc.2000.0715

Tegner MJ, Dayton PK, Edwards PB, Riser KL (1996) Is there evidence for the long-term climatic change in southern California kelp forests? Calif Coop Ocean Fish Investig Rep 37:111–126

Tegner MJ, Dayton PK, Edwards PB, Riser KL (1997) Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. Mar Ecol Prog Ser 146:117–134 doi:10.3354/meps146117

Thibaut T, Pinedo S, Torras X, Ballesteros E (2005) Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). Mar Pollut Bull 50:1472–1489 doi:10.1016/j.marpolbul.2005.06.014

Thomsen MS, Wernberg T, Kendrick GA (2004) The effect of thallus size, life stage, aggregation, wave exposure and substratum condition on the forces required to break or dislodge the small kelp *Ecklonia radiata.* Bot Mar 47:454–460 doi:10.1515/BOT.2004.068

Trowbridge CD, Little C, Pilling GM, Stirling P, Miles A (2011) Decadal-scale changes in the shallow subtidal benthos of an Irish marine reserve. Bot Mar 54:497–506 doi:10.1515/BOT.2011.057

Tuya F, Cacabelos E, Duarte P, Jacinto D and others (2012) Patterns of landscape and assemblage structure along a latitudinal gradient in ocean climate. Mar Ecol Prog Ser 466:9–19 doi:10.3354/meps09941

Tuya F, Sanchez-Jerez P, Haroun RJ (2005) Influence of fishing and functional group of algae on sea urchin control of algal communities in the eastern Atlantic. Mar Ecol Prog Ser 287:255–260 doi:10.3354/meps287255

Tyler PA, Gage JD (1984) The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, North-East Atlantic Ocean). Mar Biol 80:63–74 doi:10.1007/BF00393129

Vadas RL, Steneck RS (1988) Zonation of deep water benthic algae in the Gulf of Maine. J Phycol 24:338–346

Valentine JP, Johnson CR (2005) Persistence of sea urchin (*Heliocidaris erythrogramma*) barrens on the east coast of Tasmania: inhibition of macroalgal recovery in the absence of high densities of sea urchins. Bot Mar 48:106–115 doi:10.1515/BOT.2005.025

Vanderklift MA, Kendrick GA (2005) Contrasting influence of sea urchins on attached and drift macroalgae. Mar Ecol Prog Ser 299:101–110 doi:10.3354/meps299101

Vanderklift MA, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia 157:327–335 doi:10.1007/s00442-008-1061-7

Vásquez JA (1992) *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: a case study for a structural and geographical comparisons. In: Seeliger U (ed) Coastal plants of Latin America. Academic Press, San Diego, CA, p 77–89

Vásquez JA (2008) Production, use and fate of Chilean brown seaweeds: resources for a sustainable fishery. J Appl Phycol 20:457–467 doi:10.1007/s10811-007-9308-y

Vásquez JA, Buschmann AH (1997) Herbivore–kelp interactions in Chilean subtidal communities: a review. Rev Chil Hist Nat 70:41–52

Vásquez JA, Castilla JC, Santelices B (1984) Distributional patterns and diets of four species of sea urchins in giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. Mar Ecol Prog Ser 19:55–63 doi:10.3354/meps019055

Vásquez JA, Vega JA, Buschmann AH (2006) Long term variability in the structure of kelp communities in northern Chile and the 1997–98 ENSO. J Appl Phycol 18:505–519 doi:10.1007/s10811-006-9056-4

Vásquez JA, Zuñiga S, Tala F, Piaget N, Rodríguez DC, Vega JA (2014) Economic value of kelp forests in northern Chile: values of goods and services of the ecosystem. J Appl Phycol 26:1081–1088 doi:10.1007/s10811-013-0173-6

Vega JMA, Vasquez JA, Buschmann AH (2005) Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales: Phaeophyta) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997–98. Rev Chil Hist Nat 78:33–50

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira F, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Gupta Sen A, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Roy Soc B 281:20140846–20140846

Vetter EW (1998) Population dynamics of a dense assemblage of marine detritivores. J Exp Mar Biol Ecol 226:131–161 doi:10.1016/S0022-0981(97)00246-3

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep-Sea Res Pt II 45:25–54

Vetter EW, Dayton PK (1999) Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar Ecol Prog Ser 186:137–148 doi:10.3354/meps186137

Viana AR, Faugres JC, Stow DAV (1998) Bottom-current-controlled sand deposits a review of modern shallow- to deep-water environments. Sediment Geol 115:53–80 doi:10.1016/S0037-0738(97)00087-0

Viaroli P, Bartoli M, Giordani G, Naldi M, Orfanidis S, Zaldivar JM (2008) Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquat Conserv: Mar Freshw Ecosys 18:S105–S117

Wahle RA, Peckham SH (1999) Density-related reproductive trade-offs in the green sea urchin, *Strongylocentrotus droebachiensis.* Mar Biol 134:127–137 doi:10.1007/s002270050531

Walker CW, Lesser MP (1998) Manipulation of food and photoperiod promotes out-of-season gametogenesis in the green sea urchin, *Strongylocentrotus droebachiensis*: implications for aquaculture. Mar Biol 132:663–676 doi:10.1007/s002270050431

Walker CW, Lesser MP, Unuma T (2013) Sea urchin gametogenesis – structural, functional and molecular/genomic biology. In: Lawrence JM (ed) Edible sea urchins: biology and ecology, 3rd edn. Elsevier Science, Amsterdam, p 25–43

Watanabe S, Scheibling RE, Metaxas A (2010) Contrasting patterns of spread in interacting invasive species: *Membranipora membranacea* and *Codium fragile* off Nova Scotia. Biol Invasions 12:2329–2342 doi:10.1007/s10530-009-9647-5

Watanuki A, Aota T, Otsuka E, Kawai T, Iwahashi Y, Kuwahara H, Fujita D (2010) Restoration of kelp beds on an urchin barren: Removal of sea urchins by citizen divers in southwestern Hokkaido. Bull Fish Res Agency 32:83–87

Watson J, Estes JA (2011) Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecol Monogr 81:215–239 doi:10.1890/10-0262.1

Waycott M, Duarte CM, Carruthers TJ, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381 doi:10.1073/pnas.0905620106

Wernberg T, Russell BD, Moore PJ, Ling SD and others (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp Mar Biol Ecol 400:7–16

Wernberg T, Smale DA, Tuya F, Thomsen MS and others (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78–82 doi:10.1038/nclimate1627

Wernberg T, Vanderklift MA, How J, Lavery PS (2006) Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia 147:692–701 doi:10.1007/s00442-005-0318-7

Wharton WG (1980) The distribution of sea urchin-dominated barren grounds along the south shore of Nova Scotia. Can Tech Rep Fish Aquat Sci 954:33–47

Wharton WG, Mann KH (1981) Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Seotia. Can J Fish Aquat Sci 38:1339–1349 doi:10.1139/f81-180

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Front Ecol Environ 5:475–82

Willson JD, Winne CT, Pilgrim MA, Romanek CS, Gibbons JW (2010) Seasonal variation in terrestrial resource subsidies influences trophic niche width and overlap in two aquatic snake species: a stable isotope approach. Oikos 119:1161–1171

Wilmers CC, Estes JA, Edwards M, Laidre KL, Konar B (2012) Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. Front Ecol Environ 10:409–415 doi:10.1890/110176

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar Geod 30:3–35

Witman JD (1987) Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecol Monogr 57:167–187 doi:10.2307/1942623

Witman JD (1988) Stability of Atlantic kelp forests. Trends Ecol Evol 3:285–286 doi:10.1016/0169-5347(88)90099-7

Wright DJ, Lundblad ER, Larkin EM, Rinehart RW (2005) ArcGIS Benthic Terrain Modeler [a collection of tools used with bathymetric data sets to examine the deepwater benthic environment]. Oregon State University, Corvallis

Yang CS, Nio SD (1985) The estimation of palaeohydrodynamic processes from subtidal deposits using time series analysis methods. Sedimentology 32:41–57 doi:10.1111/j.1365-3091.1985.tb00491.x

Yang L, Bastow J, Spence K (2008) What can we learn from resource pulses? Ecology 89:621–634