

Large-scale degradation of a kelp ecosystem in an ocean warming hotspot

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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.

KEY WORDS: Kelp beds · Turf algae · Invasive seaweeds · Climate change · Phase shift · Rocky reefs · Seawater temperature

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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 2014) 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 2012). Like many other coastal ecosystems worldwide, kelp beds have been heavily altered and degraded by human activity dur-

ing 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. 2011). 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*

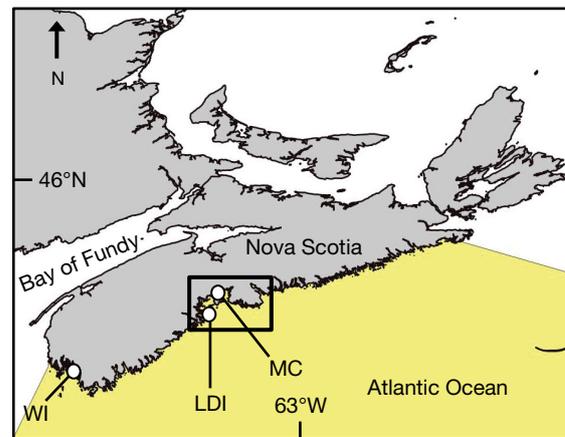


Fig. 1. Eastern Canada, showing locations of coastal surveys (box) and long-term study sites (WI: Whitehead Island; LDI: Little Duck Island; MC: Mill Cove) on the central and southwestern coasts of Nova Scotia, within an ocean warming hotspot (yellow shading, after Hobday & Pecl 2014)

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. 1), and has experienced increases in both summer ($0.064^{\circ}\text{C yr}^{-1}$) and winter ($0.039^{\circ}\text{C yr}^{-1}$) 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 2014), 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.

MATERIALS AND METHODS

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. 1, see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m543p141_supp.pdf). 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 m² quadrats (n = 5–36), except in 1949, when a 0.42 m² 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 2014). 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 (see Table S2 in Supplement 2 at www.int-res.com/articles/suppl/m543p141_supp.pdf).

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 coast-

line by Watanabe et al. (2010) in fall (September–November) 2000 and 2007, and repeated by us in fall 2014 (see Table S2 in Supplement 2). 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; see Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m543p141_supp.pdf) 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.

Turf and sediment collection

To examine relationships between kelp cover and turf-forming algae and sediments associated with turfs, we sampled twenty 1 m² 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 m² inset to photograph the understory, and collected turf-forming algae and associated sediments with a suction sampler (1 mm² 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.

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 µm daytime, 4 × 4 km spatial resolution) using Ocean Color Web (<http://>

oceancolor.gsfc.nasa.gov/cgi/13). 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 Table S2, Fig. S1 in Supplement 2). 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 $>14^\circ\text{C}$ 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.

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. 2a, Table 1). Declines in kelp biomass at these sites have led to a significant reduction in canopy cover (Fig. 2b, Table 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. 3). Surveys at 22 sites spanning 145 km of coastline in

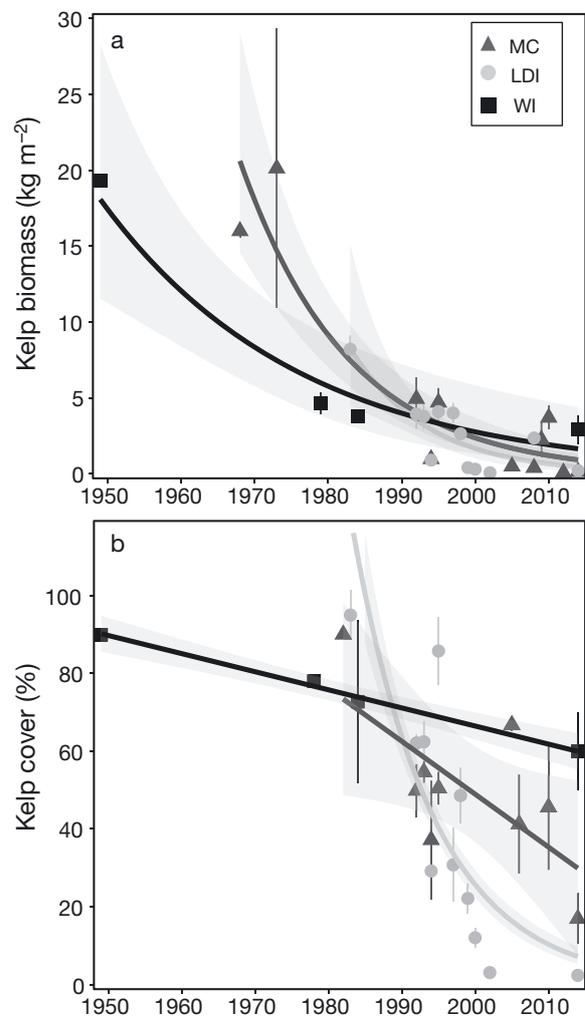


Fig. 2. (a) Kelp biomass (kg m^{-2}) and (b) kelp cover (%) at 3 long-term study sites in Nova Scotia: Whitehead Island (WI), Little Duck Island (LDI) and Mill Cove (MC). Data are means \pm SE for $n = 5$ –36 quadrats (in some cases error bars are obscured by symbol). Trend lines \pm 95% CI are fit using linear models or GLM (Gaussian, log link) (see Table 1)

Table 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). R² 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

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. 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. 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 2). Pairwise comparisons indicated that algal communities

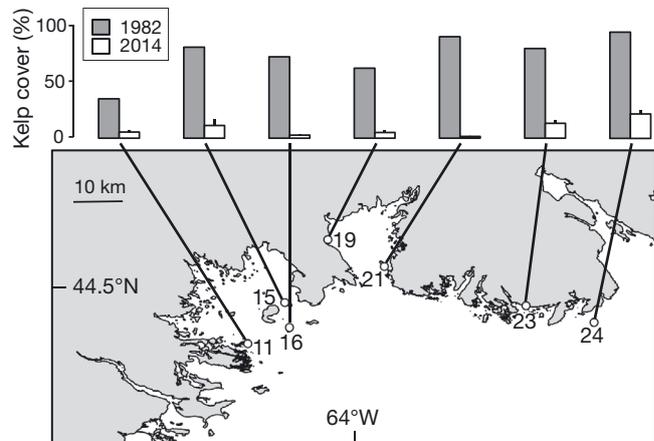


Fig. 3. Mean kelp cover (%) at 7 sites on the central Atlantic coast of Nova Scotia in 1982 and 2014. SE are shown for 2014, but were not available for 1982. For site locations, names/numbers and coordinates, see Table S2, Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m543p141_supp.pdf

differed between headlands, outer bays and inner bays (Table 2). Samples from St. Margarets Bay in 2014 show that biomass of turf-forming algae is negatively related to kelp cover (Fig. 5a,c). We also found a strong positive relationship between the mass of inorganic sediment and biomass of turf-forming algae (Fig. 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

Table 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

lower kelp cover (50% explained deviance GLM; Table 3, Fig. 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. 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. 7).

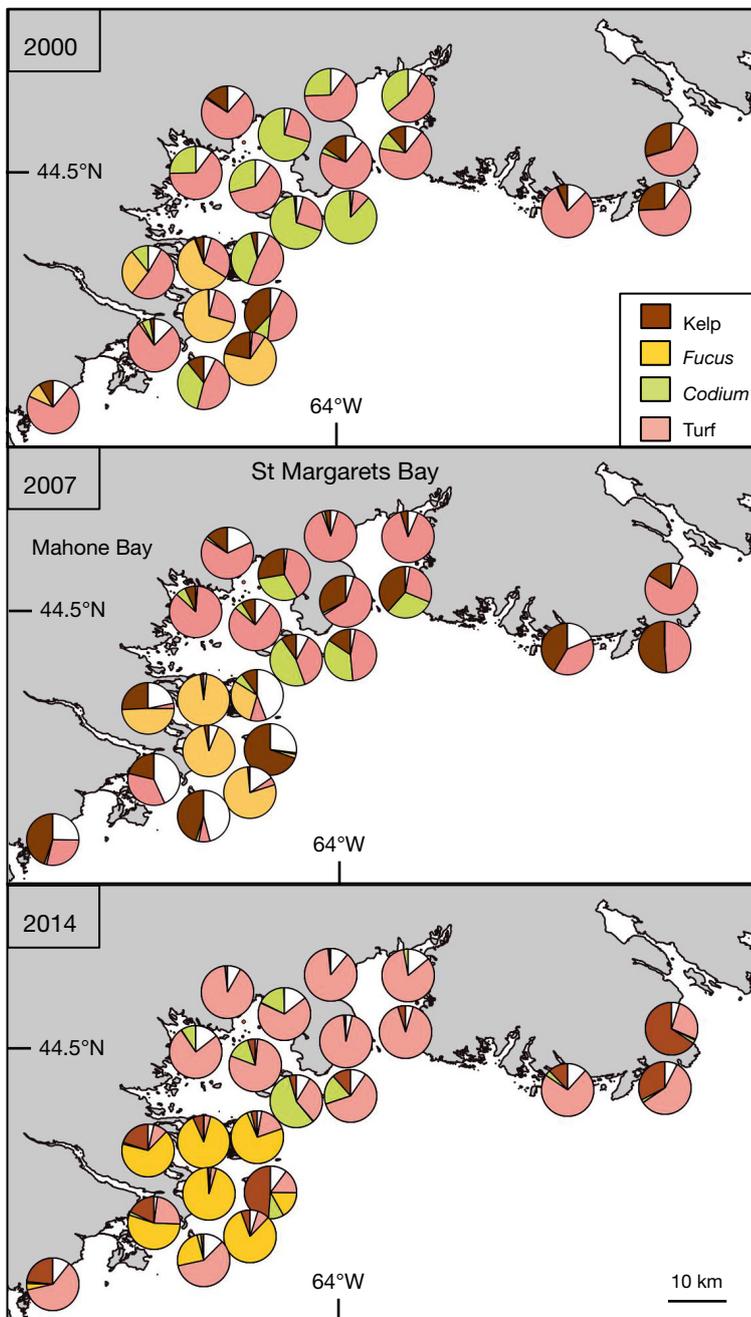


Fig. 4. Mean cover (%) of 4 macroalgal groups (kelp, *Fucus serratus*, *Codium fragile fragile* and turf-forming algae) at 22 sites on the central coast of Nova Scotia in 2000, 2007 and 2014. White sections of pie charts refer to substratum that was unresolved, covered in crustose coralline algae or 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 Table S2, Fig. S1 in Supplement 2

DISCUSSION

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 *Membranopora 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

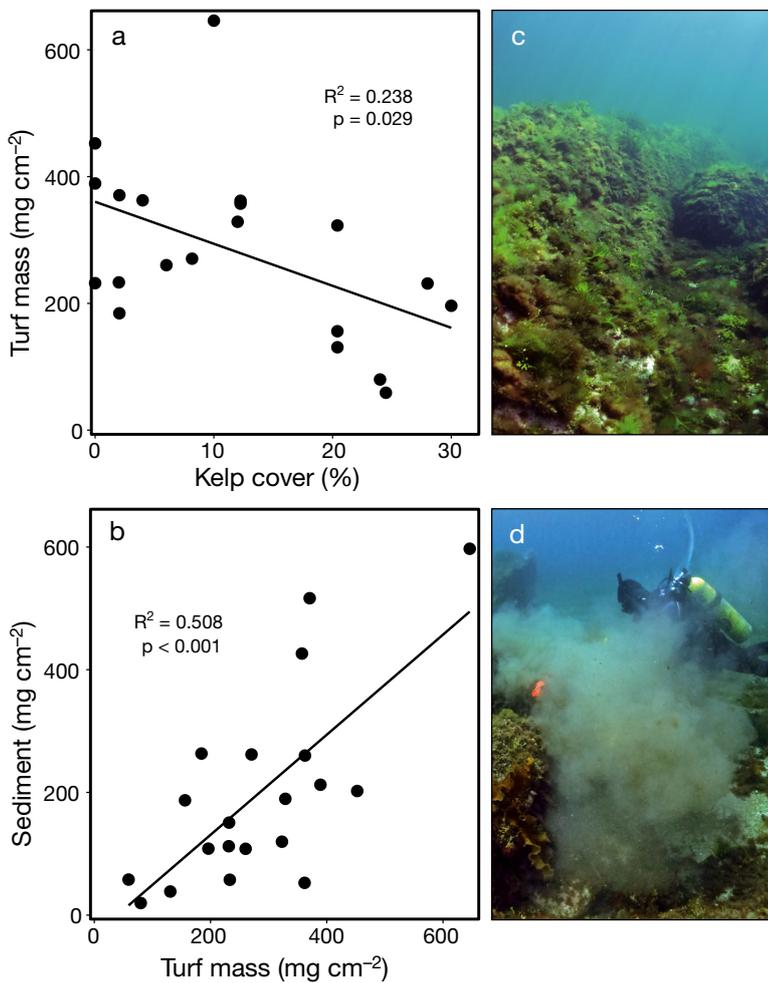


Fig. 5. Relationship between (a) dry mass (mg cm⁻²) of turf-forming algae and kelp cover (%), and (b) dry mass of inorganic sediment (mg cm⁻²) and turf-forming algae in St Margaret's Bay in 2014. Trend lines are based on linear regression of turf mass against kelp cover ($y = -6.7x + 381$) and sediment 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

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. membra-*

nacea 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

Table 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			

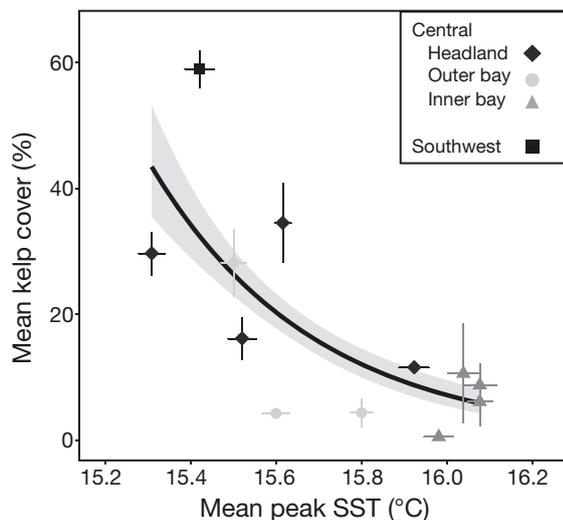


Fig. 6. Relationship between mean kelp cover (%) in 2000, 2007 and 2014 and mean peak (August–mid September) sea surface temperature (SST; °C) in 2002–2014 within grids representing 3 coastal environments along the central Atlantic coast of Nova Scotia (headland, outer bay, inner bay) and a site on the 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 Table S2, Fig. S1 in Supplement 2

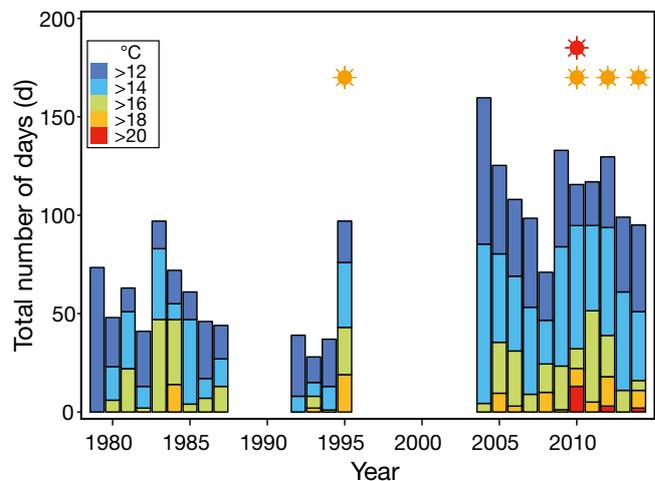


Fig. 7. Total number of days (d) with mean sea temperature above each of 5 levels (12, 14, 16, 18 and 20°C) in years from 1979–2014. Orange and red stars indicate years when sea temperature exceeded 18°C for ≥2 wk or 20°C for ≥1 wk, respectively, thresholds expected to cause significant kelp mortality. 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

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).

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 2011), 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 (Devlin & 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. vineta* on fewer remaining plants, where they target reproductive tissue, directly and indirectly accelerating kelp loss (O'Brien et al. 2015, J. O'Brien unpubl. data). 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 2014, 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.

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