Kelp distribution in the northwest Atlantic Ocean under a changing climate

Anissa Merzouk [a], Ladd Erik Johnson [a,b,*]

[a] Centre d'étude et de valorisation des algues marines (CEVAM), Québec-Océan, Canada
[b] Département de biologie, Université Laval, Québec, QC, Canada G1V 0A6

A B S T R A C T

Warming of the planet has accelerated in recent years and is predicted to continue over the next century. Environmental consequences include increasing water temperatures, and evidence of ecological responses to current warming in marine coastal ecosystems is found in poleward shifts in the geographic range of species as well as changes in the composition of nearshore benthic communities. Most evidence has, however, been obtained from intertidal studies, but similar shifts should be occurring for subtidal communities as well, especially for the ecologically important kelp species that provide both food and shelter to a multitude of organisms. Kelp may be particularly vulnerable to climate change due to their cold-water affinities and limited dispersal ability. A major biogeographic transition occurs along northwest Atlantic shores of Canada between subarctic and boreal zones where major shifts can be seen in the composition of kelp assemblages of *Alaria esculenta*, *Laminaria digitata*, *Saccharina longicruris* and *Saccharina latissima*. Here we review the historic and recent distribution and abundance of these species and find no evidence of changes in the past century. However, sparse coverage of data, inconsistent methodology and a lack of adequate time series prevent us from concluding that no changes have occurred, especially with respect to natural variation and anthropogenic alteration. These shortcomings illustrate the need for identifying sentinel species and sites for studies dedicated to the specific questions of climate-induced changes in kelp abundance and distribution. We suggest that a combination of traditional and modern tools (e.g., benthic surveys and climate model forecasting, respectively) offers the best path forward.

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1. Introduction

Climate change is very likely to have both direct and indirect consequences on the biota and the structure and function of marine ecosystems. The major consequence of climate change is an increase in atmospheric and sea surface temperatures (SST) in response to anthropogenic emissions of greenhouse gasses. Global average increase in SST was 0.6 ± 0.2 °C during the last century (IPCC, 2001, 2007), but polar and cold-temperate regions have been especially affected. In the North Atlantic, mean annual temperatures have risen by more than 1.5 °C since 1950, more than twice the global average. Global climate change models predict an acceleration of the current warming trend during the first half of this century, with the earth becoming warmer than any period during the past 40 million years (Houghton, 2001; IPCC, 2001).

When facing an environmental challenge outside the normal range of phenotypic variability, populations may respond in one of three ways: (i) Migration: dispersal shifts the distribution towards a more favorable area; (ii) Adaptation: selection shifts the phenotypic reaction norm of individuals to match the new environment; and (iii)

Extinction: neither migration nor adaption occurs, and the species becomes extinct (Clarke, 1996). As the climate continues to warm, it is hypothesized that the first response will be seen as a poleward shift in the ranges of species (Graham and Grimm, 1990; Fields et al., 1993; Southward et al., 1995; Parmesan, 1996; Sagarin et al., 1999; Parmesan and Yohe, 2003). Although still at an early stage in the projected trends, such ecological responses to recent climate change are already clearly visible (Walther et al., 2002), and well-documented latitudinal shifts in species distribution have already been observed on rocky shores in Europe (Herbert et al., 2003; Simkanin et al., 2005; Herbert et al., 2007; Lima et al., 2007; Mieszkowska et al., 2006, 2007; Hawkins et al., 2008, 2009), along the Atlantic and Pacific coasts of North America (Barry et al., 1995; Bertness et al., 1999; Sagarin et al., 1999; Zacherl et al., 2003; Harley et al., 2006) and in the southern hemisphere (Rivadeneira and Fernandez, 2005; Ling and Johnson, 2009). In general, coldwater-adapted species are decreasing in abundance and retreating poleward while warm-water species are increasing in abundance and advancing, in some cases by as much as 50 km per decade, much faster than most recorded shifts of terrestrial species (Helmuth et al., 2006). However, most of these studies have been conducted in intertidal habitats that are easily accessible but where conditions both in and out of water may contribute to emerging patterns thereby confounding interpretations. In contrast, very few studies

have dealt with subtidal habitats and in particular with the ecologically important canopy-forming macroalgae such as kelps (Müller et al., 2009).

Kelps (brown algae of the order Laminariales) are particularly important components of nearshore benthic communities as they can form dense beds with wet-weight biomass often exceeding 20 kg m^{-2} on rocky shores where they typically grow to depths of 10–25 m (see reviews by Kain, 1979; Steneck et al., 2002; Bartsch et al., 2008). Kelp beds are among the most productive ecosystems in the world (Mann, 1973; Fredriksen, 2003; Rysgaard and Nielsen, 2006) and provide food, shelter and nursery grounds for a variety of organisms. Temperature is one of the most important factors controlling the geographic distribution of seaweeds, and their tolerances to high (summer maxima) and low (winter minima) temperatures generally define their biogeographical boundaries (Luning, 1984; van den Hoek and Luning, 1988; van den Hoek et al., 1990; Adey and Steneck, 2001). Moreover, the low dispersal ability of many kelps (Norton, 1992) may limit their ability to "track" large-scale environmental changes.

The northwest Atlantic coast of Canada straddles an important biogeographic boundary between subarctic "northern" waters and warmer boreal "southern" waters (Adey and Steneck, 2001) where many kelp species reach their regional northern or southern limits of distribution. In the face of increasing water temperature we would expect a latitudinal retreat in the distribution of coldwater kelp species (e.g., *Alaria esculenta*) coupled with a poleward expansion by those with warmer water affinities (e.g., *Saccharina* spp. and *Laminaria digitata*) across this boundary. In this region, increased water temperature will not only have direct physiological effects, but will also induce indirect effects that can modify the biogeographic range of seaweeds; in particular, decreases in sea-ice cover (shading and scouring) in winter and increases in water column stratification in summer may occur. Warmer winters and sea surface temperatures should result in less sea-ice cover, less intense ice scouring, increased winter precipitation, and earlier melting in the spring. These changes should, in turn, increase light and nutrient availability, modify sedimentation and disturbance processes in subtidal environments, and result in a general range expansion, both latitudinally and bathymetrically. However, the complexity of the interactions between temperature, ice cover, and light makes predicting the underlying dynamics of the community exceptionally difficult (Clarke et al., 2007). For example, Lima et al. (2007) did not see the shifts predicted by earlier models (Breeman, 1990) in the distribution of *Laminaria hyperborea* and *Saccharina latissima* along Iberian shores.

While global warming and its associated direct and indirect effects are important determinants of the future evolution of coastal marine ecosystems, the modern context also involves human-induced stressors such as overfishing, habitat loss, invasive species, and pollutants. Direct responses of kelp beds to global climate-driven change are thus superimposed on these often smaller-scale processes (Hawkins et al., 2008, 2009). Complex interactions between these stressors will potentially exacerbate nonlinear responses of ecosystems (i.e., thresholds and tipping points) and progressively limit the adaptive capacity of natural systems to cope with rapid climate change (Ling et al., 2009).

Here we review the literature for information on the geographic distribution and local abundance of subtidal kelp species across the northwest Atlantic coast of Canada and the USA. Our objectives were specifically to: (1) assess the state of our knowledge of these key organisms; (2) look for evidence of shifts in distribution or abundance over historical and recent times; and (3) propose a conceptual model for understanding the complex interactions determining kelp distributions under a changing climate in this region.

2. Methods

Published literature was reviewed for data on the distribution and abundance of key kelp species of the northwest Atlantic Ocean:

Saccharina longicruris (Bachelot de la Pylaie) Kuntze (formerly *Laminaria longicruris*), *S. latissima* (L.) Lane, Mayes, Druehl & Saunders (formerly *L. saccharina*), *L. digitata* (Hudson) J.V. Lamouroux, and *A. esculenta* (L.) Greville. These kelp species were selected because literature was available dating back to the 1850s and because any shifts in their distributions should be detected as both a retraction in the southern range limit for *A. esculenta* and a northward gain in range for the other three species. The northwest Atlantic coast in Canada has been divided into boreal and subarctic biogeographic regions based on temperature and environmental conditions (Briggs, 1974), but as proposed by Adey and Steneck (2001), the subarctic region extends south down into the Gulf of St. Lawrence, encompassing Labrador, the northern half of Newfoundland, and the northern gulf shore of Quebec (Fig. 1). Thus we compiled data on the geographic distribution of these kelps, as well as on density and standing crop biomass, for each of four regions: the Gulf of Maine/Bay of Fundy, the Atlantic coast of Nova Scotia, the St. Lawrence Estuary/southern Gulf of St. Lawrence, and the northern Gulf of St. Lawrence/Newfoundland/Labrador (Fig. 1). The first three all fall into the boreal zone whereas the last is part of the subarctic. Early literature on algal inventories has already been reviewed (Cardinal, 1968; South and Cardinal, 1970) for eastern Canada (including Quebec, Newfoundland and the Maritime provinces of Nova Scotia, New Brunswick, and Prince Edward Island) and the Canadian Arctic (including Hudson Bay), and we depended primarily on these sources for pre-1970 information. Similar reviews by Mathieson et al. (1998, 2008, 2010) were used for the Gulf of Maine.
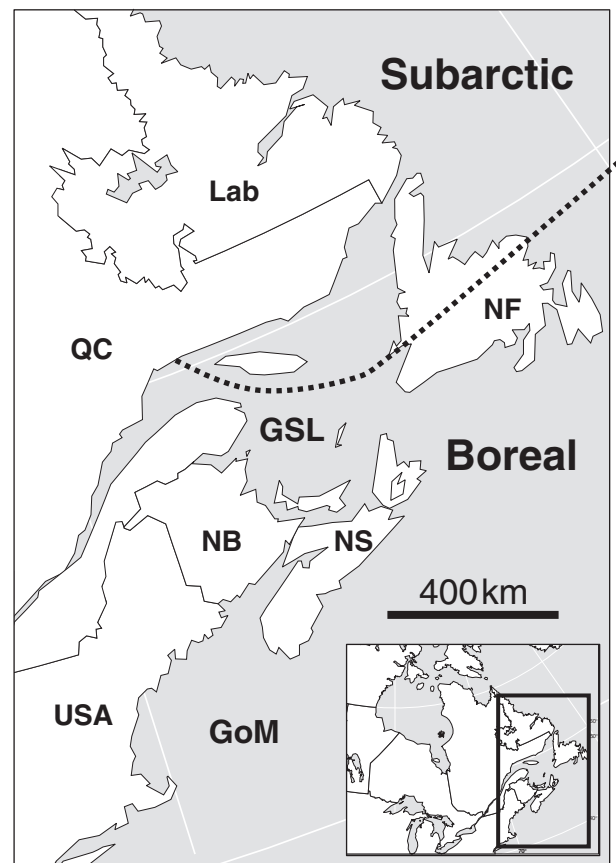

Fig. 1. Map of the northwest Atlantic coast showing the transition between subarctic and boreal biogeographic zones. GoM = Gulf of Maine; GSL = Gulf of St. Lawrence; Lab = Labrador; NB = New Brunswick; NF = Newfoundland; NS = Nova Scotia, QC = Quebec.

3. Results

The available literature before the 1970s largely contained only information about the presence of species in broadly-defined areas, but all four species were observed in all four regions (Table 1). Details on sampling techniques (e.g., search effort and habitats surveyed) were generally lacking for historical studies and even precise details on number and location of sites were not provided (although consultation with herbarium specimens could reveal some information on locations). More recent literature over the past 10 years was surprisingly even less complete and for some regions (e.g., the southern Gulf of St. Lawrence), no published literature was found with which comparisons could be made. Technical details were, however, more generally specified although some aspects were still often lacking (e.g., criteria for site selection).

A. esculenta was clearly the dominant kelp in the subarctic region, but still extended south into the boreal region of the Gulf of Maine, the Bay of Fundy and the southern tip of Nova Scotia. Its presence in the transition zone (i.e., the southern limit of its distribution) did not appear to change between the earliest observations (Table 1; Harvey, 1852; Eaton, 1873; Lawson, 1870; Farlow, 1881; Hay and MacKay, 1887) and the latest published data (Scheibling and Gagnon, 2009; Adey and Hayek, 2011). In the subarctic region, it can form dense beds, reaching densities of over 50 individuals m^{-2} and biomass up to 6 kg m^{-2} wet weight (Table 2). From the sparse quantitative data collected over a large geographic area, no significant long-term change in abundance or standing stock could be observed in *A. esculenta*-dominated kelp beds, and the wide range in abundance can be attributed to the strong influence of sea urchin grazing (Gagnon et al., 2004) or ice scour (Keats et al., 1985) in these communities.

L. digitata is a boreal species ranging from Long Island Sound in the south to the subarctic-boreal transition zone in the north where it generally dominates more wave-exposed shores and is often observed in mixed assemblages with either *S. longicruris* or *S. latissima*. Recent literature on *L. digitata* is somewhat sparse (often lumped with other kelps), but the species distribution has not appeared to have changed in the 150 years between the earliest and most recent observations (Table 1).

S. longicruris and *S. latissima* are also boreal kelp species, but are more abundant in protected bays and less wave-exposed shores. While *S. latissima* is the dominant kelp in the Gulf of Maine, Rhode Island and Long Island Sound (Brady-Campbell et al., 1984; Lee and Brinkhuis, 1986; Mathieson et al., 1998, 2010; Levin et al., 2002; Vadas et al., 2004), *S.*

longicruris dominates in kelp beds along the coasts of Nova Scotia, the Gaspé Peninsula and the St. Lawrence maritime estuary (MacFarlane, 1952; Cardinal, 1968; South and Cardinal, 1970; Mann, 1972, 1973; Scheibling, 1986; Scheibling et al., 1999; Scheibling and Gagnon, 2009). No poleward shift in their distributions is apparent from the compiled literature, but the more recent articles (Adey and Hayek, 2011) did not mention these species in the communities of the core subarctic region of the Labrador coast (Table 1) even though dense populations can be found farther north (e.g., Ungava Bay; Wilce, 1959; Sharp et al., 2008). In the boreal zone both species can reach extremely high abundance (up to 60 ind. m^{-2}) and biomass (typically 5 kg m^{-2}, but as high as 25 kg m^{-2} in some studies), but only when sea urchin abundances are low (Tables 3 and 4). Again, data are sparsely distributed, but enough quantitative data have been recorded along the Atlantic shore of Nova Scotia (Fig. 2) to document the drastic decrease in maximum densities and abundances of kelps from the 1950s (maximal biomass of 29 kg m^{-2}) to the early 1980s

Table 2

Kelp (*Alaria esculenta* and *Laminaria digitata*) density and biomass reported for the subarctic region, including the northern Gulf of St. Lawrence (Quebec), northern Newfoundland and Labrador. (Not including Ungava Bay, but see Sharp et al., 2008).

Year	Species	Density (individuals m^{-2})	Wet biomass (kg m^{-2})	Reference
1978	*A. esculenta*		<0.2	Himmelman et al. (1983) with urchins
1980	*A. esculenta*	66	3.3	Himmelman et al. (1983) 2 years after urchin removal
1979	*A. esculenta*		0.7	Keats et al. (1985)
1980	*A. esculenta*		1.6	Keats et al. (1985)
1981	*A. esculenta*		5.0	Keats et al. (1985) with no spring ice scour
1982	*A. esculenta*		5.8	Keats et al. (1985) with no spring ice scour
1983	*A. esculenta*		1.9	Keats et al. (1985)
2003	*A. esculenta*		0.3–1.8	Adey and Hayek (2011): exposed sites 0.5–10 m
2003	*L. digitata*		0.0–0.75	Adey and Hayek (2011): exposed sites 0.5–10 m
2003	*A. esculenta*		0–0.2	Adey and Hayek (2011): protected sites 0.5–10 m
2000	*A. esculenta*	12, 37		Gagnon et al. (2004): mean values from 2 sites
2001	*A. esculenta*	7, 21		Gagnon et al. (2004): mean values from 2 sites
2002	*A. esculenta*	5, 35		Gagnon et al. (2004): mean values from 2 sites

Table 1

Historic and recent observations of key kelp species (*Alaria esculenta*, *Laminaria digitata*, *Saccharina longicruris* and *S. latissima*) along the northwest Atlantic shores from the Gulf of Maine to northern Labrador. "Historic" refers to pre-2000 studies whereas "Recent" refers to studies published in the past 10 years. "–" represent situations where no published information exists although personal observations and personal communications indicate that the species are present in most cases (e.g., *Saccharina longicruris* in the St. Lawrence Estuary).

Species	Boreal — Gulf of Maine and Bay of Fundy		Boreal — Atlantic coast of Nova Scotia		Boreal — Estuary and southern Gulf of St. Lawrence		Subarctic — Quebec North Shore, northern Newfoundland and Labrador	
	Historic	Recent	Historic	Recent	Historic	Recent	Historic	Recent
A. esculenta	X[a]	X[b]	X[c]	X[d]	X[e]	–	X[f]	X[g]
L. digitata	X[h]	X[b]	X[c]	X[d]	X[e]	–	X[f]	X[i]
S. latissima	X[h]	X[b]	X[c]	–	X[e]	–	X[f]	X[i]
S. longicruris	X[h]	X[b]	X[c]	X[d]	X[e]	–	X[f]	–

Pre-1970 references from South and Cardinal (1970). Historic distributions for all species also mentioned in Taylor (1957).
[a] Eaton (1873).
[b] Mathieson et al. (2010), Adey and Hayek (2011).
[c] Lawson (1870), Hay and MacKay (1887), Bell and MacFarlane (1933, 1938).
[d] Scheibling and Gagnon (2009), Adey and Hayek (2011).
[e] Klugh (1931), Gauvreau (1939, 1956), Cardinal (1968).
[f] Wilce (1959, 1965).
[g] Gagnon et al. (2004), Adey and Hayek (2011).
[h] Farlow (1881).
[i] Adey and Hayek (2011).

(no significant biomass and densities less than 5 ind. m^{-2}) in response to expanding urchin populations (see below). Following massive urchin mortalities, abundances and densities increased sharply from 1983 to 1995 to reach high values (>50 ind. m^{-2} and >5 kg m^{-2}, respectively). Although subsequent data in the 2000s are limited, it appears that densities declined as biomass increased (27 kg m^{-2}; Adey and Hayek,

Table 3
Kelp (*Alaria esculenta*, *Laminaria digitata*, *Saccharina longicruris* and *S. latissima*) density and biomass reported for the Atlantic coast of Nova Scotia.

Year	Species	Density (individuals m^{-2})	Wet biomass (kg m^{-2})	Reference
1952	"*Laminaria*" spp. (also *Saccharina*)		0–29.0	MacFarlane (1952)
1968–70	*S. longicruris*, *L. digitata*		4.9–16.0	Mann (1972)
1977–78	*S. longicruris*		4.4	Gerard and Mann (1979)
1982–83	*S. longicruris*, *L. digitata*, *A. esculenta*		0.25–4.25	Miller (1985)
1982–83	*S. longicruris*, *L. digitata*		3.2	Smith (1988)
1984	*S. longicruris*, *L. digitata*	5.0–7.8	0–0.23	Scheibling (1986) 1 year after urchin die off
1984	*S. longicruris*, *L. digitata*	16.5–35.8	5.53–8.31	Scheibling (1986) 3 years after urchin die off
1984	*S. longicruris*, *L. digitata*	23.2–30.1	7.58–9.88	Scheibling (1986) 4 years after urchin die off
1984	*S. longicruris*, *L. digitata*	11.8	4.75	Scheibling (1986) unchanged kelp bed
1984	*S. longicruris*, *L. digitata*	0.4–3.1	0–0.065	Scheibling (1986) unchanged urchin barrens
1992	*S. longicruris*	20–55	1.0–5.0	Scheibling et al. (1999)
1992	*S. longicruris*	38.0		Scheibling and Gagnon (2009)
1993	*S. longicruris*	21.0		Scheibling and Gagnon (2009)
1994	*S. longicruris*	40.0		Scheibling and Gagnon (2009)
1995	*S. longicruris*	45.0		Scheibling and Gagnon (2009)
1997	*S. longicruris*	26.0		Scheibling and Gagnon (2009)
1998	*S. longicruris*	60.0		Scheibling and Gagnon (2009)
2000	*S. longicruris*	8.0		Scheibling and Gagnon (2009)
2002	*S. longicruris*	8.0		Scheibling and Gagnon (2009)
2005	*L. digitata*		0.5–24.2	Adey and Hayek (2011): exposed sites 0.5–10 m
2005	*S. latissima*		0.6–3.3	Adey and Hayek (2011): exposed sites 0.5–10 m
2005	*A. esculenta*		0.02–0.35	Adey and Hayek (2011): exposed sites 0.5–10 m
2005	*L. digitata*		0.0–0.9	Adey and Hayek (2011): protected sites 0.5–5 m
2005	*S. longicruris*		0.0–1.8	Adey and Hayek (2011): protected sites 0.5–5 m
2005	*S. latissima*		0.25–3.0	Adey and Hayek (2011): protected sites 0.5–5 m

Table 4
Kelp (*Alaria esculenta*, *Laminaria digitata*, *Saccharina longicruris* and *S. latissima*) density and biomass reported for the Gulf of Maine and Long Island Sound.

Year	Species	Density (individuals m^{-2})	Wet biomass (kg m^{-2})	Reference
1980–81	*S. latissima*	50–150	1–11.25[a]	Brady-Campbell et al. (1984)
1985–87	*S. longicruris*	25–1000	2.5–47.0	Egan and Yarish (1990)
1990–91	*S. latissima*	8–64		Lambert et al. (1992)
1995–96	*S. longicruris*		0–5.0[a]	Vadas et al. (2004)
2005–06	*L. digitata*		0.5–1.8	Adey and Hayek (2011): exposed sites 0.5–10 m
2005–06	*S. longicruris*		0.00–3.2	Adey and Hayek (2011): exposed sites 0.5–10 m
2005–06	*S. latissima*		0.06–1.9	Adey and Hayek (2011): exposed sites 0.5–10 m
2005–06	*A. esculenta*		0.01–4.1	Adey and Hayek (2011): exposed sites 0.5–10 m
2005–06	*L. digitata*		0.0–0.08	Adey and Hayek (2011): protected sites 0.5–5 m
2005–06	*S. longicruris*		0.0–3.5	Adey and Hayek (2011): protected sites 0.5–5 m
2005–06	*S. latissima*		1.2–1.8	Adey and Hayek (2011): protected sites 0.5–5 m
2005–06	*A. esculenta*		0.0–0.08	Adey and Hayek (2011): protected sites 0.5–5 m

[a] Converted from reported dry weights: WW = 5 DW for kelp; Chapman and Chapman, 1980).

2011), a pattern consistent with self-thinning during the maturation of kelp beds.

4. Discussion

One of the predicted effects of rising sea surface temperature (SST) has been to induce changes in the geographic distribution of marine organisms, especially in coastal environments where temperature increases have been greatest (Müller et al., 2009). Based on historical data (e.g., Fischer-Piette, 1937), long time series (e.g., Southward et
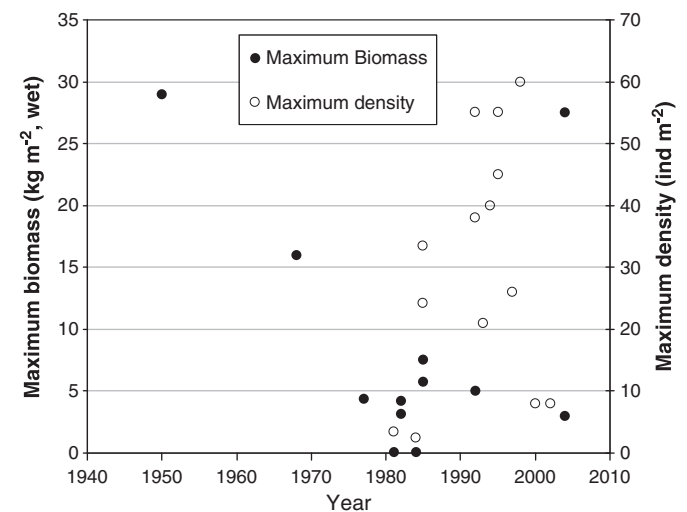
Fig. 2. Maximum densities and biomass of kelp reported from the Atlantic coast of Nova Scotia from 1950 to 2004. The high and low values for 2004 represent exposed and protected sites, respectively.

al., 1995) and modeling exercises (e.g., Müller et al., 2009), the expansion of the distribution ranges of species and communities toward the poles in response to ocean warming has been observed in many marine coastal communities around the globe. Meta-analyses of a variety of both marine and terrestrial taxa have shown that more species are advancing poleward than are retreating (Parmesan, 1996; Parmesan and Yohe, 2003). In marine environments where warm and cold species coexist, it is likely that the colder water taxa can persist because they are competitively superior in terms of growth rates and maximum body size (Poloczanska et al., 2008; Hawkins et al., 2009). However, *A. esculenta* is competitively inferior to *L. digitata* in the northeast Atlantic (Hawkins and Harkin, 1985), where it is confined to more exposed shores and can colonize sheltered environments only if *L. digitata* is removed.

For marine species, abundant evidence comes from studies of sessile or sedentary invertebrates. In California, shifts in species abundance from the 1930s to the 1990s provide evidence of climate-induced changes in community composition of intertidal invertebrates with an increase in SST of just 0.75 °C (Barry et al., 1995; Sagarin et al., 1999). The abundance of most southern species (10 out of 11) increased, whereas most (5 out of 7) northern species declined, with no trend for cosmopolitan species. Similarly, geographic distributions and population abundance of species on rocky shores of the northeastern Atlantic have changed over the last 60 years (reviewed by Southward et al., 1995, 2005; Hawkins et al., 2008, 2009), and in the British Isles, major range extensions of intertidal invertebrates have been observed in response to warming (as much as 1 °C increase) from the early 1990s onwards: relative abundances of warm-water species have increased, and those of northern species have declined (Hiscock et al., 2004; Mieszkowska et al., 2006, 2007; Hawkins et al., 2009). On the North American side of the Atlantic Ocean, the southern edge of the range of mussels (historically in North Carolina, USA) has shifted poleward, probably in response to global warming (Jones et al., 2009). Similarly, in the southern hemisphere, an increase in SST of 2 °C over 60 years appears to have driven range expansion of sea urchins toward the pole, where their overgrazing has significantly impacted kelp bed distribution (Ling and Johnson, 2009; Johnson et al., 2011-this issue).

Ample evidence also comes from studies of seaweeds. Historical comparisons of intertidal algae in the Gulf of Maine (Mathieson et al., 1998) revealed that 13 out of 32 species showed reduction in their distributions (although along an elevation gradient, not a latitudinal one) while none exhibited expansion, possibly due to the general warming trend or effects of air pollution during intertidal exposure. In Portugal, average temperature increased 0.7 °C over 50 years, and warm-water species generally expanded their range northwards (Lima et al., 2007). In contrast, cold-water seaweeds showed no particular trend with the number of species that shifted north or south about the same.

For kelp in particular, changes have been observed in a number of species worldwide. On Honshu Island (Japan), the biomass of cold water kelp species (*Laminaria japonica* and *Costaria costata*) has declined while species with warm affinities (*Undaria* spp. and *Ecklonia stolonifera*) have increased in tandem with an SST increase of 1 °C (Kirihara et al., 2006). In Europe, the boreal kelp *L. hyperborea* is already exhibiting a shift in its distribution toward the pole, recently expanding to Spitsbergen and suffering local extinctions at certain locations along the Iberian peninsula near its southern limit (Müller et al., 2009). Interestingly, *L. digitata* and *S. latissima*, also species with colder water affinities, have not yet shown any shift in their southernmost limits in Portugal (Lima et al., 2007). For *A. esculenta*, major range retractions poleward have been recorded in the northeast Atlantic in Ireland (Simkanin et al., 2005; Mieszkowska et al., 2006) and Norway (S. Fredriksen, pers. comm.).

In contrast, many seaweeds examined in these studies showed no shift in their biogeographical distribution. Likewise, an extensive study (Stuart-Smith et al., 2010) conducted over the last decade in Tasmania did not detect any major shifts in the distribution of species in subtidal reef communities, including macroalgae. They hypothesized that their study encompassed a relatively stable period following a more abrupt change, and that community responses to ocean warming may follow nonlinear, step-like trajectories. In large-scale field surveys of subtidal communities over the past 40 years, Adey and Hayek (2011) did not observe significant latitudinal shifts in the distributions of algal species in the subarctic or boreal regions of the western Atlantic. This finding is consistent with our more extensive review of the distribution of key kelp species, including *A. esculenta*, the most reactive kelp species on the other side of the Atlantic Ocean. The absence of latitudinal displacement can be explained in general by the fact that most species of macroalgae have distribution ranges that span temperature gradients of several degrees and display ecotypes that are capable of growing and reproducing over a wide range of temperatures (Bolton and Luning, 1982). The development of ecotypes and differing morphologies suggests that many macroalgae have an ability to adjust and optimize carbon fixation (photosynthesis) and biosynthesis (respiration) to the prevailing temperature and local environmental conditions (Staehr and Wernberg, 2009). For example, *S. latissima*, a boreal species, appears poorly adapted to survive prolonged periods of both low nitrogen and low temperature, yet ecotypes of this species extend into the Arctic (Korb and Gerard, 2000).

The lack of distributional shifts in the northwest Atlantic flora is, however, particularly surprising as the global pattern of increases in SST in the twentieth century (IPCC, 2007) was particularly pronounced in the North Atlantic Ocean and in coastal environments (Müller et al., 2009). Moreover, the northwest Atlantic coast is especially well suited to observe shifts in species distributions since it constitutes the transition zone between subarctic and boreal communities, and the dominant kelps in both regions are at the limit of their regional distribution range (i.e., southern limit for *A. esculenta* and northern limit for *Saccharina* spp.).

The nature of the literature reviewed here can in part explain the absence of any observed response to climate change. The literature pertaining to kelps on northwest Atlantic shores, while abundant and dating back to the 1850s, consists mostly of species inventories with little data on the abundance of individual species or the composition of the communities. Simple presence or absence of species in an area is an insensitive parameter (Tingley and Beissinger, 2009) and does not permit distinguishing fine-scale changes in populations (e.g., decreases in abundance) or communities (e.g., shifts in dominance). For example, *A. esculenta* was reported in southern Nova Scotia and in the Gulf of Maine in the 1880s and early 1900s and Adey and Hayek (2011) also recently reported the presence of this species in the same regions. Their quantitative data showed, however, that this species was only a minor constituent of the communities, representing <1% of the macroalgal biomass. Likewise, they recorded the presence of *S. longicruris* in the core subarctic region off the Labrador coast, but again at <1% of the macroalgal biomass. Without data on the historical abundance of this species in these regions, it is impossible to judge if shifts in abundance or dominance are occurring. Moreover, the warming trend is often not uniform (e.g., cycles of warm and colder period in the British Isles; Hawkins et al., 2009), and multiple baselines may be needed to associate long-term changes in marine communities and global warming.

4.1. Practical problems in broad scale and long-term studies

Part of the problem in detecting long-term changes at larger scales (100s of km) is due to the lack of quantitative sampling of rocky bottoms before SCUBA permitted *in situ* sampling beginning in the 1940s. Comparisons between quantitative studies are still difficult,

however, due to the different methods used to quantify kelp including density, biomass and percent cover. Of these, biomass is likely to be the most comparable as it integrates both the density and size-frequency of the population. In contrast, percentage cover is likely to be the least useful, and indeed, we were unable to incorporate some extensive and otherwise interesting studies (e.g., Wharton and Mann, 1981) due to this limitation. In addition, sampling protocols are often poorly described, and thus it is unknown whether any sampling bias for high kelp abundance occurred at the level of site, depth or quadrat selection. Added to this problem is the fact that sites have rarely been resampled (but see Miller, 1985; Scheibling, 1986; Scheibling et al., 1994, 1999; Scheibling and Gagnon, 2009) and thus any comparison of data from studies conducted in different places in different years is confounded − differences attributed to temporal changes (e.g., increased SST) may simply reflect spatial heterogeneity.

Identification issues have also compounded the problem, but more problematic is a lack of taxonomic discrimination as kelps are often counted and grouped together without regard to species composition, i.e., a functional group approach (Steneck and Watling, 1982). Many recent studies of kelp communities have not focussed specifically on kelp but rather on the effects of urchin population dynamics or invasive species (see below), and the macroalgal community is seldom described in great taxonomic detail. Thus changes in abundance of common species become impossible to determine as does the presence of rare species.

4.2. Short-term fluctuations versus long-term trends

Beyond these more practical problems, there are also challenges in the detection of changes over the temporal scale of climate change (10s to 100s of years) when many other ecological and environmental processes are operating on shorter time scales (decadal NAO or simple interannual variation) and induce greater responses in kelp assemblages, if only in the short-term (see examples below). Distinguishing various sources of temporal variation is a challenge for all studies of species responses to climate change, but is especially problematic for kelp as their subtidal habit hides them from direct view and their short life spans (usually 2–5 years) create the potential for a dynamic system with spatial patterns changing rapidly in response to environmental conditions. Moreover, in the northwest Atlantic, long-term studies are exceedingly rare, leaving us unable to assess the patterns and drivers of changes in kelp distribution. Exceptions are a series of studies in central Atlantic Nova Scotia (Scheibling, 1986; Scheibling et al., 1994, 1999; Scheibling and Gagnon, 2009) and a recent study of the northern Gulf of St. Lawrence that was able to use aerial photographs to document changes over 20 years in the aggregate kelp assemblage over a 15-km-long shore (P. Gagnon, unpubl. data).

The magnitude of human-induced and weather-induced changes in coastal communities occurring over short time scales and at local spatial scales can be much greater than those due to increased SST and thus may overshadow the response of kelp to climate change. Indeed, such effects have completely changed the seascape in some areas of the northwest Atlantic. The most dramatic was the destruction of Nova Scotian kelp beds during the 1970s by the green sea urchin, *Strongylocentrotus droebachiensis* (Miller, 1985; Scheibling, 1986). Urchin grazing can reduce kelp beds to so-called "barren zones" where biodiversity and productivity are greatly diminished (Himmelman et al., 1983). Steneck et al. (2002) have proposed that this shift was due to the overexploitation of apex predators (cod and other large groundfish) in the Gulf of Maine and Atlantic Canada that normally kept populations of urchins in check, thereby maintaining the kelp-dominated state. Historical data on kelp beds are lacking, but the barren-zone community state is now found throughout the subarctic and in most of the boreal region — kelp beds are only found where they are protected from grazing by environmental refuges (e.g., low salinity and high wave action) or physical shelter (e.g., boulders surrounded by soft sediments). The exceptions are in Atlantic Nova Scotia, where cyclic (decadal) disease outbreaks in sea urchin populations can occur (Scheibling, 1986; Scheibling and Raymond, 1990) during periods of increased water temperature associated with on-shore movement of hurricanes (Scheibling and Raymond, 1990; Scheibling and Hennigar, 1997). The mass mortality of urchin populations leads to rapid recovery (<3 years) of kelp beds. A similar regime shift occurred in the Gulf of Maine when sea urchins were overfished, again reducing grazing pressure and initiating the recovery of kelp beds (Steneck et al., 2002).

Biological invasions have also the potential to alter kelp assemblages and are occurring with increasing frequency in this system (Chapman and Fletcher, 2002). The most striking example is the recent invasion by *Codium fragile*, an introduced green alga that is replacing kelp along the Atlantic shores of Nova Scotia. Interestingly, the establishment of *Codium* can be facilitated by another invasive species, an encrusting bryozoan (*Membranipora membranacea*) that promotes kelp frond loss (Scheibling and Gagnon, 2006). Once established as dense meadows, *C. fragile* prevents re-colonization by kelp and can persist as the dominant canopy-forming seaweed for prolonged periods.

These more local effects may interact synergistically with climate change. For example, temperature-dependent outbreaks of urchin disease could be more likely under elevated SST, either directly (increased temperatures) or indirectly (increased hurricane frequency). Likewise, the severity of *Membranipora* outbreaks is dependent on
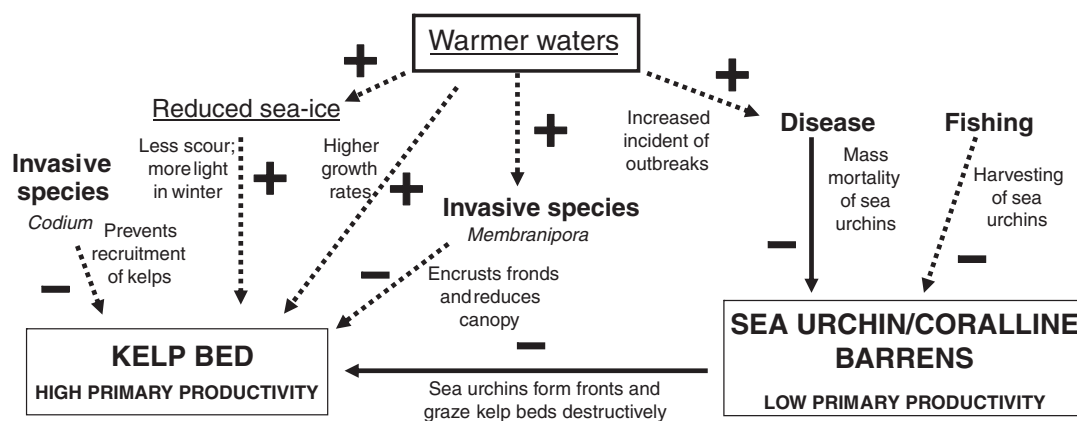

Fig. 3. Schematic representation of ecological interactions within kelp bed ecosystems of the northwest Atlantic Ocean and potential effects of changing environmental conditions induced by climate change. Climate change-induced factors are underlined. Anthropogenic effects (fishing, invasive species, and climate change) are represented by dashed arrows. (Note these interactions do not include any direct negative effects of climate change beyond the reaction norms of the kelp species themselves.)

warm temperatures in late summer and fall, which are more likely achieved if SST becomes higher in general. The combination of direct and indirect effects of climate change thus makes the already complex ecological interaction between kelp bed stability and urchin population dynamics even more complex and difficult to predict (Ling and Johnson, 2009), but increasing temperatures should favor kelp productivity in general in the northwest Atlantic (Fig. 3).

The ensemble of these circumstances (i.e., limited data and alternative drivers of temporal variation) prevents us from determining if climate-induced shifts in distribution or dominance are indeed occurring. Despite a long history of observations and a reasonable number of studies, the data are still too limited to draw any firm conclusions in the northwest Atlantic. Essentially, we have low power in the statistical sense to reject the null hypothesis of no change, and the lack of detailed studies and inconsistent methodology combined with natural and anthropogenic variation puts us in a poor position to judge the influence of climate change.

4.3. Future work: monitoring and modeling

Given that the knowledge of species response is critical for ecosystem management and that the temporal scale of the problem exceeds our normal experience, we must track changes in species abundance and distribution in a coordinated manner instead of relying on compilations of studies that are not specifically aimed at this question. Such monitoring programs are not glamorous, but are necessary to identify long-term trends at large spatial scales. Since we cannot track all species everywhere, the challenge is to identify which species are the best indicators and where are the key locations to monitor. For northwest Atlantic shores, *A. esculenta* is an obvious choice, with its global southern limit in the boreal region. The shores where the transitions between subarctic and boreal waters occur (the Quebec and Newfoundland sides of the Gulf of St. Lawrence and the Atlantic coast of Newfoundland; Fig. 1) would be promising candidate areas for standard, systematic surveys.

Selecting such sentinel species and the sensitive locations in which to follow them is a daunting task. Good natural history and basic biology are, of course, essential knowledge, but the use of forecasting techniques that can predict environmental changes associated with climate change may provide good guidance (e.g., shifts in isotherms; Hughes, 2000). For macroalgae, earlier, simpler studies (Breeman, 1990) have been followed by ones based on more sophisticated climate models, and more precise predictions can now be made for specific species in specific regions (Keser et al., 2005; Müller et al., 2009). These studies have already identified a number of North Atlantic cold temperate and polar seaweeds that are predicted to extend their distribution into the High Arctic through the end of the 21st century as well as retreat along the northeast Atlantic coast, including the local extinction of several kelp species (*L. digitata*, *L. hyperborea* and *S. latissima*) in Europe. *L. hyperborea* has already exhibited progressive poleward shift along European coastlines, and changes in the local abundance of *S. latissima* and *L. digitata* may be associated with changes in temperatures (Müller et al., 2009). More specific to the northwest Atlantic, various scenarios of predicted climate change have been developed for commercially important species of kelp (which do not, unfortunately, include *A. esculenta*), and while all scenarios show some retraction of species ranges along southern limits, more striking changes occur within the existing range, with large-scale local extinctions predicted in certain regions, e.g., the southern Gulf of St. Lawrence (Van Guelpen et al., 2007).

5. Conclusions

In spite of the important role of kelp in the nearshore temperate ecosystems of the northwest Atlantic Ocean and their vulnerability to perturbation by climate change, we can find no evidence based on the reviewed literature for latitudinal shifts in the geographic distribution of key kelp species. Moreover, observed changes in local abundance could not be distinguished from natural or other anthropogenic changes. These results appear due primarily to a lack of adequate baseline information, and we suggest that efforts be made through biological and modeling studies to identify sentinel species and sites in this region. Increasing sea surface temperatures and other indirect climate-related effects will likely decrease the resilience of kelp beds, potentially leading to loss in abundance and range of this key component of coastal ecosystems — we must be better prepared to predict the magnitude and extent of this threat.

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