The effect of global climate change on the future distribution of economically important macroalgae (seaweeds) in the northwest Atlantic

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Abstract

An increase in greenhouse gas emissions has led to a rise in average global air and ocean temperatures. Increased sea surface temperatures can cause changes in species' distributions, particularly those species close to their thermal tolerance limits. We use a bioclimate envelope approach to assess potential shifts in the range of marine macroalgae harvested in North American waters: rockweed (*Fucus vesiculosus* Linnaeus, 1753), serrated wrack (*Fucus serratus* Linnaeus, 1753), knotted wrack (*Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863), carrageen moss (*Chondrus crispus* Stackhouse, 1797), and three kelp species (*Laminaria digitata* (Hudson) J.V. Lamouroux, 1813; *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl et G.W. Saunders, 2006; and *Saccharina longicruris* (Bachelot de la Pylaie) Kuntze, 1891). We determined species' thermal limits from the current sea surface temperatures associated with their geographical distributions. Future distributions were based on sea surface temperatures projected for the year ~2100 by four atmosphere-ocean general circulation models and earth system models for regional concentration pathways (RCPs) 4.5 and 8.5. Future distributions based on RCP 8.5 indicate that the presence of all but rockweed (*F. vesiculosus*) is likely to be threatened by warming waters in the Gulf of St. Lawrence and along the Atlantic coast of Nova Scotia. Range retractions of macroalgae will have significant ecological and economic effects including impacts on commercial fisheries and harvest rates and losses of floral and faunal biodiversity and production, and should be considered in the designation of marine protected areas.

Key words: seaweeds, climate change, global climate models, earth system models, climate envelope, range forecasting

Introduction

With unprecedented increases in greenhouse gas emissions and a warming climate, marine ecosystems will incur major changes in ecological structure and function. Species are likely to react in one of three ways: adapting, migrating to more appropriate climate conditions, or becoming extirpated from their original distribution (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006). Climate change has already had observable impacts on the distribution of marine species including seaweeds (Perry et al. 2010). Seaweeds (hereafter referred to as macroalgae) are particularly sensitive

as the adult form of many species is sessile. Indeed, a poleward range retraction of kelp has been observed on the coasts of Spain (Fernández 2011; Díez et al. 2012), Portugal (Tuya et al. 2012), France (Cosson 1999), Norway (Moy and Christie 2012), Australia (Wernberg et al. 2011), and Japan (Tanaka et al. 2012). Expansion of macroalgal ranges is dependent on the dispersal of spores to appropriate habitats and there is evidence that this is occurring. Poleward range extensions of rock-weed (*Fucus vesiculosus* Linnaeus, 1753) (Jueterbock et al. 2013; Nicastro et al. 2013), a brown sea-weed species (*Bifurcaria bifurcata* R. Ross, 1958), a bushy seaweed species (*Cystoseira tamariscifolia* (Hudson) Papenfuss, 1950) (Mieszkowska et al. 2006), and a kelp species *Laminaria hyperborea* (Gunnerus) Foslie, 1884 (Müller et al. 2009) have been linked to increasing temperatures. Although some macroalgae can adapt to warming through northward shifts of their range, it can be at the expense of overall distribution and loss of genetic diversity within a species (Nicastro et al. 2013).

Local extirpation of macroalgae, or even reduced production due to warming stress, will have broad ecological impacts. Macroalgae include foundation species that provide habitat for other taxa. The canopy and understory of macroalgae provide shelter and nursery grounds for a large number of species, including those with direct economic importance (e.g., Rangeley and Kramer 1995; Steneck et al. 2002; Bartsch et al. 2008; Christie et al. 2009). Macroalgal communities are highly productive ecosystems fueling high rates of secondary production (Mann 1973; Fredriksen 2003; Krumhansl and Scheibling 2012).

Macroalgae have considerable direct economic importance. Globally, they provide goods and services for human consumption, fertilizers, animal feed additives, pet foods, and cosmetics (Rebours et al. 2014; Ugarte and Sharp 2012). On the eastern coast of Canada artisanal and commercial harvesting occurs in all five of the Atlantic provinces (Chopin and Ugarte 2006).

In this study we consider the fate of these economically important species with climate change in the northwest Atlantic as demonstrated in a companion study by Khan et al. (2013, fig. 1). Because temperature has been linked to changes in macroalgal distributions elsewhere, we apply a bioclimate envelope approach based on current sea surface temperatures (SSTs) and temperatures projected from global climate models to project future distributions. We consider the following species: serrated wrack (*Fucus serratus* Linnaeus, 1753), rockweed (*F. vesiculosus*), knotted wrack (*Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863), carrageen moss (*Chondrus crispus* Stackhouse, 1797), and three kelps, *Laminaria digitata* (Hudson) J.V. Lamouroux, 1813; *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl et G.W. Saunders, 2006; and *Saccharina longicruris* (Bachelot de la Pylaie) Kuntze, 1891. Because air temperatures are highly correlated with sea surface temperatures (Cayan 1980; Galbraith and Larouche 2013) our bioclimate envelope should also be a proxy for intertidal macroalgae sensitive to extremes in air temperature (e.g., Schonbeck and Norton 1978).

Methods

Although a bioclimate envelope does not include all factors responsible for a species' distribution, it provides a useful conservation tool at our sub-continental scale of investigation (Watling et al. 2013; Torossian et al. 2016). We developed bioclimate envelopes using the SSTs associated with the bathymetric and latitudinal limits of each species in the northwest Atlantic. We used daily SST data for the period 1982–1999 available in the Group for High Resolution Sea Surface Temperature (GHRSST) database (Reynolds et al. 2007). The GHRSST data are produced on a 0.25° grid and represents the surface 10 m. The data were downloaded from the Physical Oceanography Distributed Active Archive Center (podaac.jpl.nasa.gov/dataset/NCDC-L4LRblend-GLOB-AVHRR_OI), imported as network common data form (NetCDF) files, converted to raster, and clipped to include the boundaries of the study area. We selected the months of February and August, which generally represent extremes in winter and summer SSTs within the target region. Hudson Bay was excluded from the analysis as sea ice in this

region produced anomalous SSTs. Bathymetry data were obtained from the General Bathymetric Chart of the Oceans 1-min grid, created in 2003 and updated in 2008 (gebco.net/). The current limits for the northern and southern latitudinal and bathymetric range were assessed from both reports in the literature (e.g., Taylor 1957; Sears 2002; Van Guelpen et al. 2007) and specimen holdings of the Atlantic Reference Centre of Fisheries and Oceans Canada. Present day SSTs were derived from GHRSST data as described by Khan et al. (2013). The bioclimate envelope was defined by determining the minimum February and maximum August SSTs within each species' range (Table 1).

Future distributions for the year 2100 were determined using SSTs projected by four different atmosphere-ocean general circulation models (AOGCMs) and earth system models (ESMs) used for the Intergovernmental Panel on Climate Change's (IPCC) 5th Assessment Report (AR5) and the output of runs from two representative concentration pathways (RCPs), RCP 4.5 and RCP 8.5 (Khan et al. 2013, fig. 1). Model selections were based on models' spatial resolution, ability to simulate present climate, and period of the model run including historical availability of historical projections. We used an ensemble of four AOGCMs and ESMs: the Canadian Centre for Climate Modelling and Analysis (CCCMA) CanESM2, the Met Office Hadley Centre HadGEM2-ES, the National Aeronautics and Space Administration (NASA) Goddard Institute for Space Studies (GISS) GISS-E2-R, and the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) CSIRO-Mk3.6. From each model's output we selected two RCPs (4.5 and 8.5) used in the IPCC's AR5. RCP 8.5 represents the most severe climate change projected, reaches a radiative forcing >8.5 W·m^{-2} by 2100, and continues to increase. In RCP 4.5 radiative forcing is stabilized at 4.5 W·m^{-2} after 2100, thus projecting less dire climate change. As model projections vary, we averaged the SSTs for each RCP projected by each of the four models to create an ensemble average (i.e., average of the data used for each map) change in SST for the target region.

Climate model SST data were obtained from the Program for Climate Model Diagnosis and Intercomparison (PCMDI) Earth System Gateway (ESG) (cmip.llnl.gov/cmip5/). Climate projections from the PCMDI ESG were downloaded as NetCDF files and were viewed through the NASA GISS Panoply program to obtain time-step information. Data were imported into a geographic information system (GIS) application as a feature layer. The files were then exported in Microsoft Excel and tabulated to calculate the average for each period for every climate model projection and pathway. We used data for February and August from the periods

Table 1. Present geographic and thermal range of each of the target species in the northwest Atlantic.

| Species | Common name | Latitudinal range (°N) | | Bathymetric limits (m) | Thermal limits (°C) | |
		South	North		February	August
Saccharina longicruris	kelp	41.3	79.8	2–60	−1.8	21.5
Saccharina latissima	kelp	41.3	79.8	2.5–30	−1.8	21.5
Laminaria digitata	kelp	41.3	62	0–40	−1.7	21.5
Fucus vesiculosus	rockweed	35	80	0–10	−1.8	27.4
Chondrus crispus	Irish moss/carrageen moss	40	60	0–20	−1.8	21.8
Ascophyllum nodosum	knotted wrack	41.5	66	0–10	−1.8	20.1
Fucus serratus	serrated wrack	44.3	47	0–10	−1.2	18.1

1961–1999 and 2071–2100 to create change fields representing SST changes occurring at year 2100 (Fig. 1).

Spatial resolution varies among the AOGCMs and ESMs, but all change fields were scaled to 4 km × 4 km using an inverse distance-weighted function to enable comparisons to modern climatologies derived from GHRSST data. The power of the function was set to two. A minimum of eight neighbouring data points were used for each interpolation. Interpolation through land was eliminated by using a barrier mask. The barrier limited the search for neighboring data to only those input sample points on the same side of the barrier as the processed cell. Interpolation was performed by the Spatial Analyst extension in ArcMAP (ESRI V 10).

We used a GIS analysis to identify areas where both the future minimum February and maximum August SSTs are within the thermal boundaries and bathymetric limits of the species and to determine the future range of each species. The coarse resolution of the bathymetric layer made species' ranges appear discontinuous. To compensate, the ARCGIS buffer tool was used to link a one-pixel coastal zone (∼15 km) with species depths. The current and potential future distributions were then mapped to determine potential gain or loss in each species' range.

For each species the latitudinal expansion and contraction (in km) was assessed by determining the distance between the most northern (and southern) projected and present extents of the range. The area considered was limited to the northernmost extent of the Newfoundland–Labrador Shelf large marine ecosystem, as sea ice presents challenges for climate modelling and there is considerable uncertainty in projections of future SSTs where sea ice is prevalent.
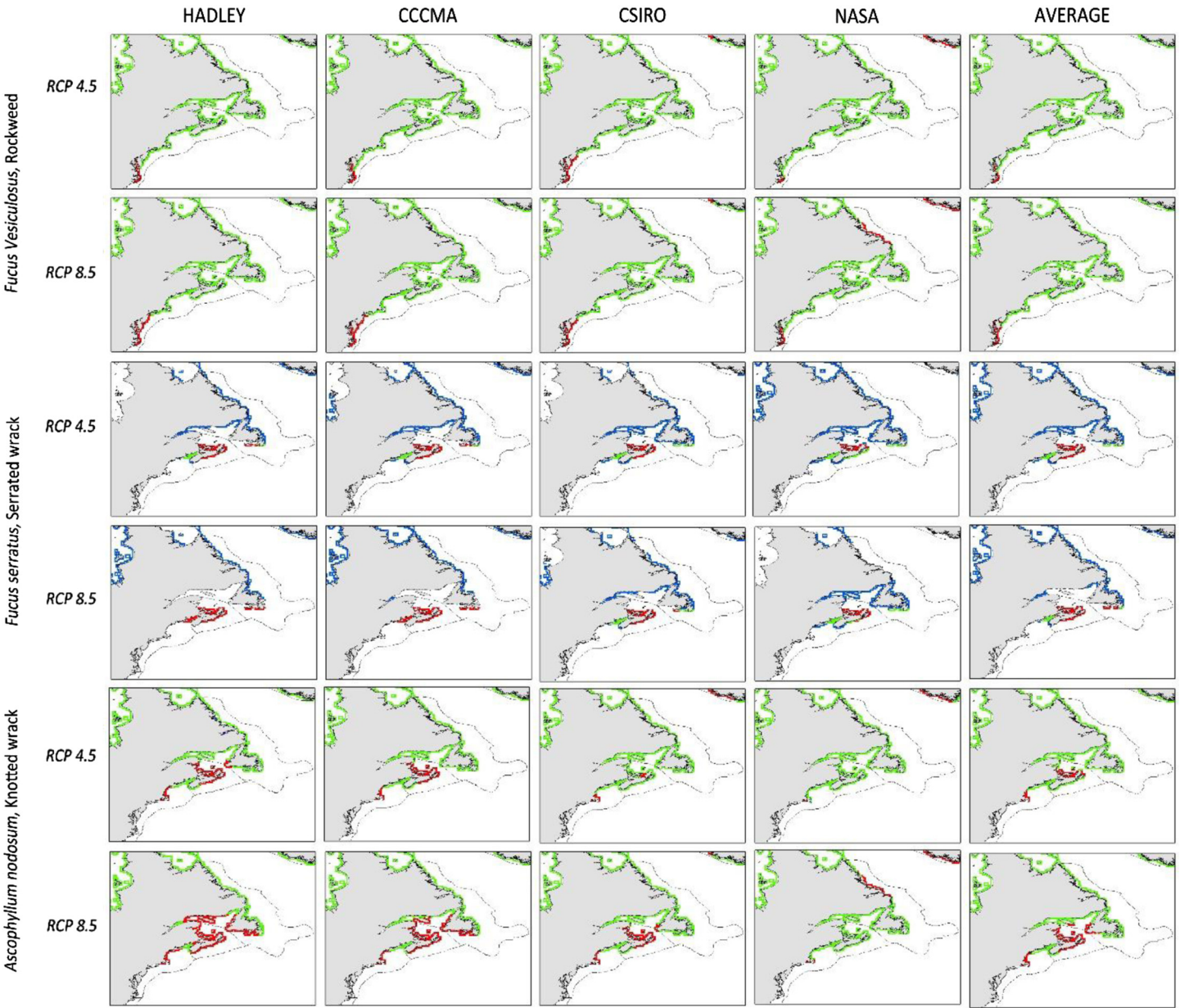
Results

Maps of all species' predicted distributions are shown in Figs. 2 and 3. Output from the NASA model projects less temperature increase in our target area than the Hadley, CCMA, and CSIRO models, thus, using NASA projections alone we would assume less change in species' ranges. However, under both the RCP 8.5 and the more limited change of RCP 4.5 model projections, some retraction of range is indicated for each species. As expected, the northward retraction is greater with the greater warming projected under scenario RCP 8.5 (Fig. 4).

The present range of *S. latissima, S. longicruris, L. digitata, A. nodosum*, and *F. vesiculosus* already extends poleward beyond our study area (Taylor 1957, table 1; Sears 2002). However, three species
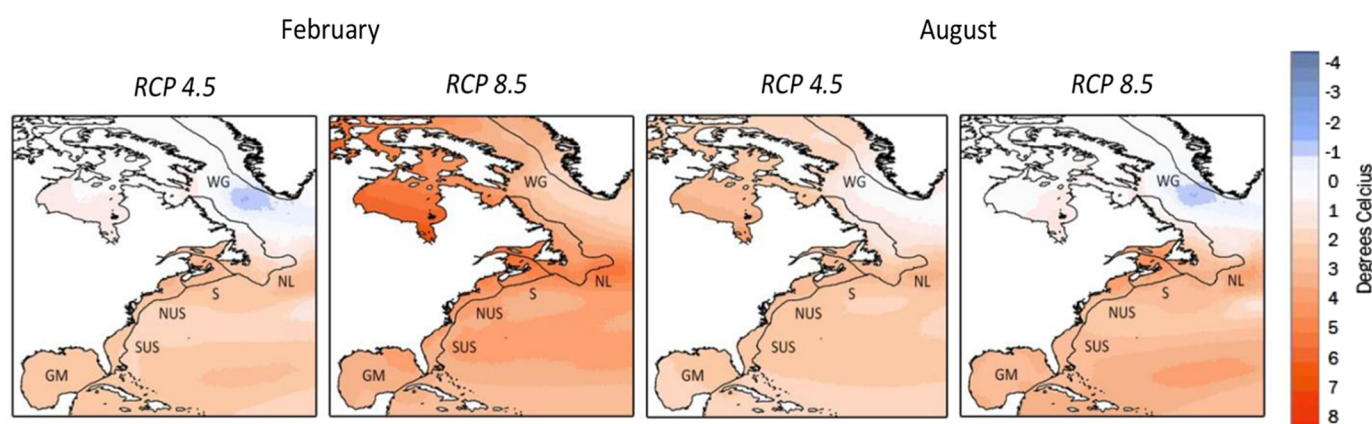

Fig. 1. Ensemble average changes in sea surface temperatures in six large marine ecosystems: West Greenland Shelf (WG), Newfoundland–Labrador Shelf (NL), Scotian Shelf (S), Northeast US Continental Shelf (NUS), Southeast US Continental Shelf (SUS), and the Gulf of Mexico (GM). RCP, regional concentration pathway.

Fig. 2. Changes predicted in the thermal range of *Fucus vesiculosus, Fucus serratus*, and *Ascophyllum nodosum* in the northwest Atlantic as a result of sea surface temperature changes expected in the year 2100 projected by four atmosphere-ocean general circulation models and earth system models through RCPs 4.5 and 8.5. Ensemble is the average of all four models. Red indicates loss of thermal range, green no loss or gain, and blue increase. RCP, regional concentration pathway; Hadley, Met Office Hadley Centre; CCCMA, Canadian Centre for Climate Modelling and Analysis; CSIRO, Australian Commonwealth Scientific and Industrial Research Organization; NASA, National Aeronautics and Space Administration.

(*S. longicruris, S. latissima*, and *F. vesiculosus*) are found at ∼80°N and there is little coastline left for poleward range expansion in the northwest Atlantic. The remaining three species are likely to have appropriate physical habitat available for poleward range expansion in the northwest Atlantic. Unfortunately, the geographical limitations of our analyses do not allow us to assess possibilities of
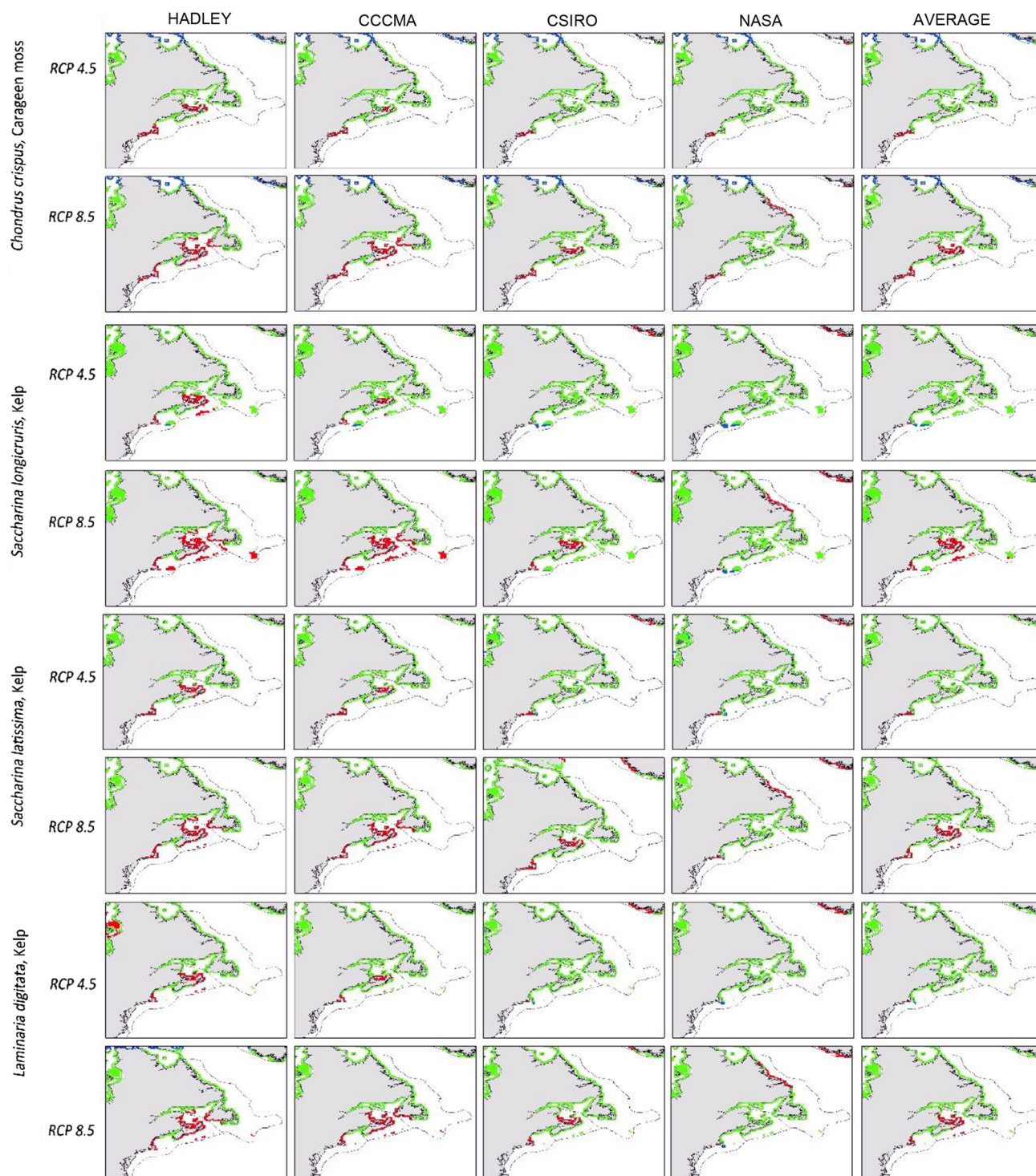
Fig. 3. Changes predicted in the thermal range of *Chondrus crispus*, *Saccharina longicruris*, *Saccharina latissima*, and *Laminaria digitata* the northwest Atlantic as a result of sea surface temperature changes expected in the year 2100 projected by four atmosphere-ocean general circulation models and earth system models through RCPs 4.5 and 8.5. Ensemble is the average of all four models. Red indicates loss of thermal range, green no loss or gain, and blue increase. RCP, regional concentration pathway; Hadley, Met Office Hadley Centre; CCCMA, Canadian Centre for Climate Modelling and Analysis; CSIRO, Australian Commonwealth Scientific and Industrial Research Organization; NASA, National Aeronautics and Space Administration.
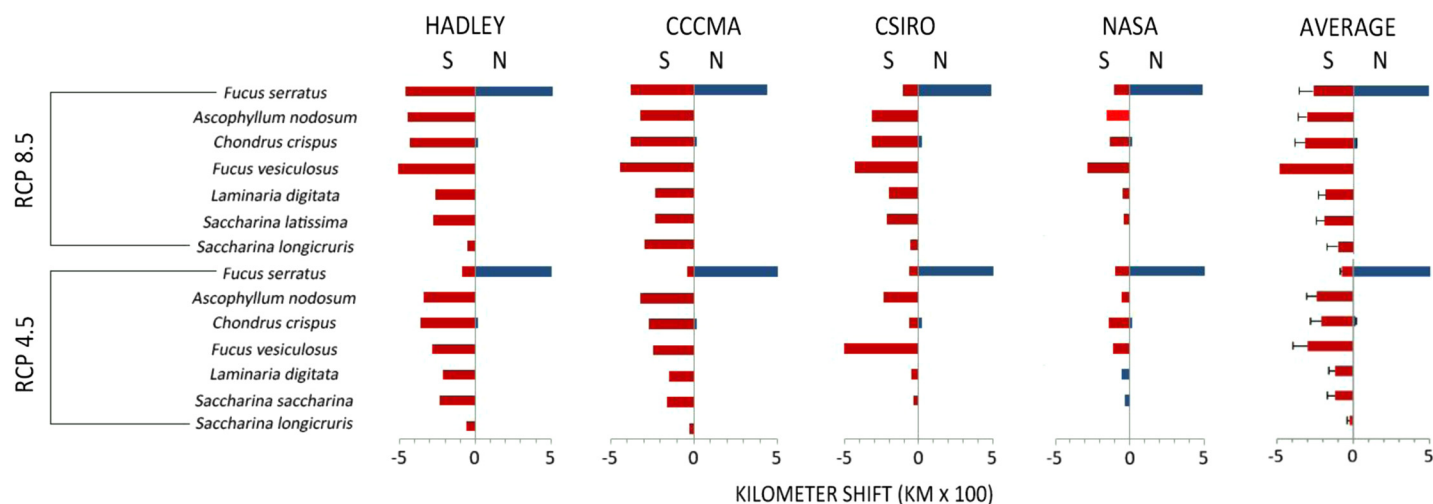
Fig. 4. Latitudinal shift (hundreds of km) of commercially important macroalgae species in the northwest Atlantic predicted using output from four atmosphere-ocean general circulation models and earth system models as well as the model ensemble average for RCP 4.5 and RCP 8.5. Blue indicates range expansion and red indicates range retraction. RCP, regional concentration pathway; Hadley, Met Office Hadley Centre; CCCMA, Canadian Centre for Climate Modelling and Analysis; CSIRO, Australian Commonwealth Scientific and Industrial Research Organization; NASA, National Aeronautics and Space Administration.

range expansion in the northernmost regions, limiting our assessments to loss of area of these species in the northwest Atlantic (**Figs. 2** and **3**). In contrast, *F. serratus* presently occupies little coastline of the northernmost waters and may actually attain a larger range as seas warm. Under all projections new thermal habitat may become available for *C. crispus*, but the poleward shift will not compensate for the retraction at the southern edge of its range (**Fig. 4**).

Discussion

Range retractions of these macroalgae will have significant direct effects on local economies and ecology, and ecological effects will have indirect economic effects. Cascade effects may occur as loss of the macroalgal canopies negatively impact recruitment, growth, and survival of understory organisms (e.g., Bertness et al. 1999), resulting in compounded impacts. These impacts are likely to be greatest for species that have limited potential for poleward range expansion that would counterbalance range retraction. The following discussion focusses on how higher SSTs will impact these species, the habitats they provide, and harvests.

Seeley and Schlesinger (2012) reviewed the ecological services of *A. nodosum*, which grows attached to rocks in the intertidal and subtidal zones. It forms extensive beds that float as a canopy at high tide. Seeley and Schlesinger (2012) noted the importance of *A. nodosum* to other organisms. For instance the algal fronds support epiphytes, and the beds provide habitat for more than 100 invertebrate taxa that, in turn, provide prey for vertebrates. In US and Canadian waters *A. nodosum* beds are used as habitat by 34 fish species including the American eel and Atlantic cod. Six of these fish species are designated with special conservation status in the US, Canada, or both. Of the more than 17 bird species that utilize *A. nodosum*, 10 are designated with special conservation status (Seeley and Schlesinger 2012). Thus, reduced population or local extirpation of *A. nodosum* will further threaten already endangered species.

On the northwest Atlantic coast, *F. vesiculosus* can be found growing with *A. nodosum*, although the former is more prevalent on exposed coasts (Schmidt et al. 2011; Larsen 2012). Research on the habitat that *F. vesiculosus* provides on the Baltic coast revealed that the invertebrate assemblage it held had nearly twice the biomass compared with sites with no algae (Wikström and Kautsky 2007). We have found no comparable synthesis for the northwest Atlantic, but conclude that similar losses of fauna will occur where *F. vesiculosus* faces range retraction in the northwest Atlantic.

Smale et al. (2013) reviewed faunal diversity supported by kelp species in the northeastern Atlantic. They noted that a single kelp plant can support approximately 40 macroinvertebrate species. In addition, kelp provides habitat for other sessile flora and fauna. Kelp forests are nursery grounds for juvenile invertebrates and fish such as Atlantic cod and pollock, as well as feeding grounds for many fish species and fish predators. By extension, we can assume that the extirpation of kelp from portions of its existing range in the northwest Atlantic will have wide-reaching impacts on marine species diversity and production (Wilson et al. 2015).

Populations in warmer water that have not been extirpated may still be affected. Where temperatures remain or approach the optimal range, production will be maintained or enhanced (as demonstrated by experiments conducted by Wilson et al. 2015). However, populations located at the new, warmer edge of the range (where higher temperatures resulted in a poleward shift) will be subject to heat stress, which results in decreased production.

Warmer waters will have indirect impacts on the macroalgae as a habitat or as a harvestable resource by enabling expansion of invasive species that act as competitors, herbivores, or disease agents, as well as other herbivores that simply are expanding their range poleward with warming. Merzouk and Johnson (2011) provided the following example of the complex ecological interactions possible as kelp beds of the northwest Atlantic are subject to warmer waters. Warmer waters may result in increased incidence of disease in sea urchins, a major herbivore of kelp. (In high enough populations, sea urchins can decimate kelp beds.) However, if warmer waters enhance growth of invasives, such as the alga *Codium* Stackhouse, 1797 that reduces kelp recruitment or the encrusting alga *Membranipora* de Blainville, 1830 that reduces photosynthetic capacity, then kelp beds would decline (Merzouk and Johnson 2011).

Warming SSTs may affect the ability to harvest macroalgae. Harvests will no longer be possible where ranges have retracted and may no longer be economically feasible where production is decreased. Commercial harvests could be relocated poleward, but the northern portions of these macroalgal ranges are along the coasts of Newfoundland and Labrador where infrastructure, transportation networks, and labour are more limited. Thus, such geographical shifts are likely unfeasible. Local communities that harvest macroalgae from beds or collect detrital material washed up on shorelines will have to find alternative resources.

Conclusions

The most important species for commercial harvests are *A. nodosum* and *F. vesiculosus*. Where heat stress lowers their production, rates of harvests will have to be reassessed to assure that ecological values will not be compromised. This will require monitoring of productivity and air and water temperatures. Our modelled projections suggest where productivity and temperature monitoring might best be focussed. The approach that would provide the greatest benefit would be to use the projections developed from the Hadley or CCMA models that indicate the greatest warming and range retraction. For instance, populations in the Gulf of St. Lawrence and along Atlantic Nova Scotia (with the exception of *F. vesiculosus*) are likely to be threatened. Minimally, the future distributions predicted with the model ensemble average should be used.

These future SSTs and ranges of key macroalgal foundation species should be considered in plans for designation of future marine protected areas. As Canada strives to meet its goal of 10% of marine ecosystems protected (by 2020), consideration should be given to locations near present poleward edges of ranges as these will have the greatest chance of ensuring protection of macroalgal habitat with the inevitable climate warming.

We have not examined the possibility of algae adapted to warmer waters expanding their ranges poleward or if any have direct economic value. However even if new valuable species do appear, adaptation by industrial and artisanal users will likely be required with respect to harvest and processing methods.

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Author contributions

LVG, GP, and GLC conceived and designed the study. AHK, LVG, and GP performed the experiments/collected the data. AHK, EL, and GLC analyzed and interpreted the data. EL and GLC contributed resources. AHK, EL, and GLC drafted or revised the manuscript.

Competing interests

The authors have declared that no competing interests exist.

Data accessibility statement

All relevant data are within the paper and available from the sources mentioned in the Methods section.

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