



# Interactive effects of increasing temperature and nutrient loading on the habitat-forming rockweed *Ascophyllum nodosum*



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## ABSTRACT

Perennial seaweeds are dominant primary producers and foundation species along rocky shores, providing essential ecosystem functions and services. Although increasingly affected by various anthropogenic activities, the cumulative effects of multiple stressors are little known. We tested the interactive effects of nutrient enrichment and increased water temperatures on growth, nitrogen retention and carbon storage in juvenile *Ascophyllum nodosum* from Nova Scotia, Canada (44° 29.9' N, 63° 31.7' W) using a multi-factorial laboratory experiment. Temperature strongly affected growth, significantly reducing weight and length gain from 16 °C to 20 °C and 24 °C. Medium nutrient enrichment enhanced while high enrichment slowed rockweed growth at lower temperatures, yet these effects disappeared with warming. Nitrogen retention in rockweed tissue significantly increased with nutrient enrichment and decreased with warming, whereas carbon storage remained unaffected. These individual and interactive effects of nutrient loading and climate warming may alter the structure and function of rockweed habitats with potentially far-reaching ecological and economic consequences.

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## 1. Introduction

Perennial seaweeds play critical roles in coastal ecosystems (Worm and Lotze, 2006). Laminarians (kelps) and fucoids are foundation species that form canopies, providing important ecological services: they are involved in nutrient cycling; store nitrogen and carbon; and add energy to food webs (Worm et al., 2000; Schmidt et al., 2011; Seeley and Schlesinger, 2012). Additionally, they provide essential habitat and shelter for invertebrate, vertebrate and algal communities (Thompson et al., 2002; Schmidt et al., 2011; Tuya et al., 2011; Wernberg et al., 2011).

The fucoid rockweed *Ascophyllum nodosum* (L.) Le Jolis (hereafter *Ascophyllum*) is found along rocky shores of the temperate North Atlantic Ocean as well as parts of the Arctic Ocean (Sharp, 1987). In the northwest Atlantic, it ranges from New Jersey to Baffin Island in the Canadian Arctic; in the northeast Atlantic, it extends from northern Portugal to the White Sea in the Russian Arctic (Sharp, 1987; Kerin, 1998). Given the diversity and importance of the ecological services rockweed provides, it is listed as a “high-priority” species for protection in the United States and Canada (Wippelhauser, 1996), a “priority species” in North-

ern Ireland (Morton, 2011) and a “high-sensitivity species” in the UK (Hill and White, 2008). However, rockweed is also economically important with commercial harvests increasing in recent decades (Seeley and Schlesinger, 2012).

Like other ecologically important coastal ecosystems, rockweed habitats are exposed to increasing anthropogenic impacts, including nutrient loading, climate change and direct harvesting (Lotze et al., 2006; Worm and Lotze, 2006; Schmidt et al., 2011). On a global scale, humans have doubled nitrogen loading to coastal waters in post-industrial times (Millennium Ecosystem Assessment, 2005), whereas on local scales, nitrogen and phosphorus loading has increased up to 10-fold (Lotze et al., 2006). Rockweeds and other vegetation, such as seagrass meadows and wetlands, contribute to nutrient cycling and storage thereby diminishing the effects of land-derived nutrient export to the open ocean (Lotze et al., 2006). *Ascophyllum* can also store nitrogen and phosphorus in its tissues to accommodate seasonal changes in nutrient supply (Fletcher, 1996; Chopin et al., 1996, 1997). However, increased nutrient loading can change the species composition and abundance of primary producers (Duarte, 1995) and alter a coastal ecosystem’s ability to store and cycle nutrients (Worm et al., 2000). Although slight increases in nutrient levels have been shown to enhance rockweed growth, high nutrient levels can result in overgrowth by ephemeral algae (Kraberg and Norton, 2007). In some areas, *Ascophyllum* has been

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declining because of overgrowth and replacement by ephemeral algae (Ruessens, 1973; Fletcher, 1996; Worm and Lotze, 2006).

Anthropogenic greenhouse gas emissions have also increased exponentially in the post-industrial era resulting in a net warming effect (Solomon, 2007). Surface seawater temperature (SST) has increased in the Canadian Maritimes since 2000 (Ugarte et al., 2009) and in Eastern North America is predicted to rise by 3 °C in the 21st century (Solomon, 2007). The growth rate of *Ascophyllum* is sensitive to changes in water temperature (Vadas et al., 1976, 1978; Wilce et al., 1978; Keser et al., 1998). Moderate increases in temperature can lead to faster apical growth and extend the season of optimal growth. With greater increases in temperature, however, growth slows or stops and high temperatures can be lethal for *Ascophyllum* (Keser et al., 1998; Wilson et al., 2015). Thus, increasing temperature is predicted to shift the distribution range of rockweed northward (Jueterbock et al., 2013) and shift the composition of *Ascophyllum*-dominated habitats to mixed fucoid beds by favouring more opportunistic fucoid species like *Fucus vesiculosus* (Ugarte et al., 2010).

While more attention has been devoted to the cumulative and interactive effects of environmental or anthropogenic factors on aquatic ecosystems in recent years (see review by Crain et al., 2008), significant gaps remain in our understanding of the effects of multiple stressors on species' growth and function (Wernberg et al., 2012). For annual green algae, rising temperatures and nutrient loading have shown strong synergistic effects on growth (Lotze and Worm, 2002). In the case of *Ascophyllum*, the interactive effects of nutrient loading and a warming climate are so far unknown. In Norway, however, the combined effects of eutrophication and warming have been shown to cause the collapse of kelp forest (Moy and Christie, 2012). Thus, we could expect potentially strong cumulative effects on rockweed growth and nutrient storage with potential consequences on the ecosystem structure, function and the services it provides. Therefore, the aim of this study was to investigate the individual and interactive effects of rising temperatures and nutrient loading on rockweed growth and carbon and nutrient storage. To do so, we performed a multi-factorial laboratory experiment with juvenile rockweed plants exposed to three levels of temperature and four levels of nutrient enrichment in a fully crossed design. Our results provide insight into this seaweed's response to nutrient enrichment, climate change and their interaction, which can help predict the future role that *Ascophyllum* may play in coastal community structure, ecosystem services as well as the viability of expanding rockweed harvests.

## 2. Materials and methods

### 2.1. Collection of *Ascophyllum* plants

On June 29th, 2011, *Ascophyllum* plants of approximately the same length and age were harvested from the intertidal zone at Duncan's Cove, Nova Scotia, Canada (44° 29.9' N, 63° 31.7' W). This site is a small embayment on the open Atlantic coast and protected from wave exposure. At low tide, plants with their holdfast were scraped from rocks; intact fronds were removed from the holdfast and stored in glass jars filled with seawater in a cooler overnight. Fronds were then sorted; all those selected for the experiment were between 5 and 9 cm in length and had not yet laid down the first air vesicle. This ensured that all fronds were sexually immature and, therefore, somatic growth could be examined in the absence of reproductive tissue growth.

### 2.2. Nutrient and temperature treatments

Four nutrient concentrations and three temperatures were chosen to represent different nutrient enrichment and climate

warming scenarios. Nutrient treatments were prepared using stock solutions of sodium nitrate and sodium phosphate and contained nitrate (NO<sub>3</sub>) and phosphate (PO<sub>4</sub>) in a 10:1 ratio, which is comparable to ratios observed in the field (Lotze and Worm, 2002). The four treatment levels represented ambient (control), low, medium and high levels of nutrient enrichment (NO<sub>3</sub>/PO<sub>4</sub> at 0/0, 4/0.4, 20/2 and 100/10 μmol L<sup>-1</sup> respectively). These four levels correspond to background summer (0/0) and winter (4/0.4) concentrations seen in open coastal waters off Nova Scotia, concentrations in nutrient-loaded Atlantic Canadian estuaries (20/2) and concentrations in highly eutrophic regions, such as areas in the Baltic and North Seas (100/10) (Lotze and Worm, 2002).

For the three temperature treatments, the lowest temperature (16 °C) was chosen to represent early summer (May–June) and 20 °C to represent late summer (August–September) seawater conditions in protected coastal areas of Nova Scotia, Canada (Lotze and Worm, 2002; Wilson et al., 2015). The upper temperature of 24 °C was selected because a warming of Eastern North America by ~3 °C during the 21st century is predicted by Multi-Model Data (MMD) models (Solomon, 2007). The large number of experimental units made it logistically necessary to incubate replicates in three adjacent temperature controlled chambers set at 16, 20 and 24 °C (Lotze and Worm, 2002; Clark et al., 2013). However, each plant was held in its own 1-L microcosm, which was supplied with seawater and air from a common source, and exposed to the same light treatment. A control experiment (see below) confirmed that *Ascophyllum* growth did not differ among chambers when set at the same temperature, therefore eliminating the potential effects of pseudo-replication. Temperature within microcosms was monitored throughout the experiment using HOBO® Pendant Temp/Light Data Loggers as well as verified daily with a VWR™ QUARTZ digi-thermo, revealing consistent variation of ±1 °C. All microcosms were exposed to a 14:10 h light:dark cycle with fluorescent light tubes (Coralife 50/50) providing ambient irradiance. Irradiance was monitored daily with a light meter (LI-COR Inc. LI-250A) as well as continuously using HOBO® Pendant Temp/Light Data Loggers and kept constant at 100–120 μmol m<sup>-2</sup> s<sup>-1</sup>.

### 2.3. Laboratory experiment

The experiment ran for nine weeks in July and August 2011 since the main growth period for *Ascophyllum* in the north Atlantic falls between summer and early fall (Peckol et al., 1988; Åberg, 1992; Vadas et al., 2004). Until the start of the experiment, fronds were acclimated to and kept at 16 °C and ambient nutrient concentrations for twelve days. Then, all fronds were towel dried and weighed (wet weight), photographed and the length was measured to the nearest mm. Each frond was then housed in a 1 l glass jar containing 900 ml of filtered (0.1 μm) seawater sourced from Halifax Harbour, enriched with different levels of nutrients according to their treatment group. Five replicates were used for each temperature x nutrient treatment for a total of 60 experimental units. Fronds were tied to stainless steel nuts to anchor them at the base of the jars so that they stood erect. Air stones continually supplied air to each jar to ensure water movement. The jars in the 24 °C chamber were placed in water baths in order to dissipate excess heat that built up more quickly in these experimental units.

Nutrients were replaced from stock solutions every three days. At the same time, each glass jar was cleaned and each frond gently scrubbed to remove bacterial growth and epiphytes. Since our main interest was to quantify the direct effects of temperature and nutrients on the growth of *Ascophyllum*, epiphytes were continually removed to eliminate any confounding effects of shading or nutrient competition.

The weight and length of each frond was measured at 16-day intervals. For each interval, the changes were calculated by sub-

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