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Nutrients influence the thermal ecophysiology of an intertidal macroalga: multiple stressors or multiple drivers?

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Abstract. Urbanization of coastlines is leading to increased introduction of nutrients from the terrestrial environment to nearshore habitats. While such nutrient influxes can be detrimental to coastal marine organisms due to increased eutrophication and subsequent reduced oxygen, they could also have positive effects (i.e., increased food availability) on species that are nitrogen-limited such as macroalgae. Nutrient enrichment in this environment thus has the potential to counteract some of the negative impacts of increasing temperatures, at least for some species. Characterizing the physiological response of organisms to simultaneous changes in multiple drivers such as these is an important first step in predicting how global climate change may lead to ecological responses at more local levels. We evaluated how nutrient enrichment (i.e., nitrogen availability) affected the growth of *Fucus vesiculosus*, a foundational macroalgal species in the North Atlantic rocky intertidal zone, and found that nutrient-enriched algal blades showed a significant increase in tissue growth compared to individuals grown under ambient conditions. We further quantified net photosynthesis by ambient and nutrient-enriched tissues at saturating irradiance over a range of temperature conditions (6–30°C). Respiration was unaffected by nutrient treatment; however, there was a significant increase in photosynthetic oxygen production for nutrient-enriched tissue compared to ambient, but only at elevated (≥18°C) temperatures. This study contributes to a growing body of literature showing the complexity of responses to changes in multiple drivers, and highlights the importance of studying the impacts of global climate change within the context of more local environmental conditions.

Key words: ecophysiology; environmental drivers; Fucus vesiculosus; *macroalgae; nutrient enrichment; photosynthesis.*

INTRODUCTION

A major scientific challenge is to forecast how the relative sensitivity of interacting species to multiple stressors will translate into ecosystem-level effects (Crain et al. 2008, Gunderson et al. 2016). Coastal marine environments, at the interface of the terrestrial and marine environments, are among the most rapidly changing habitats, and among the most vulnerable (Scavia et al. 2002). Numerous biological responses related to global environmental change have been reported in coastal zones (Sagarin et al. 1999, Harley et al. 2006, Doney et al. 2012, Howard et al. 2013) including altered patterns of organism phenology (Edwards and Richardson 2004, Harley et al. 2006, Mills et al. 2013), native species ranges (Barry et al. 1995, Hawkins et al. 2009, Mills et al. 2013), and the expansion of invasive species (Carlton 2000, Stachowicz et al. 2002). In many cases climatic factors such as temperature and ocean pH have been shown to interact with non-climatic stressors (Gunderson et al. 2016) and in particular there is an increasing emphasis on the role that an organism's nutritional state may play in alleviating, at least to some degree, physiological stress (Connell et al. 2013). Studies have also highlighted that increases in drivers typically considered as "stressors" may, under some levels, instead enhance performance and survival (Connell et al. 2013). There is also recognition of the often overwhelming role of local environmental conditions in driving idiosyncratic responses at local scales (Freestone and Inouye 2006, Helmuth et al. 2014, Stein et al. 2014, Kroeker et al. 2016), including the role of local adaptation (Untersee and Pechenik 2007, Somero 2010, Hoffman and Sgrò 2011). All of these factors point to the inherent risks in resorting to generic predictions of how environmental change will likely affect ecosystems in any particular location (Helmuth et al. 2014) and point to a critical need to understand underlying mechanisms (Seebacher and Franklin 2012).

While the many physiological and genetic differences that dictate the response of individuals, populations and species to local environmental conditions are complex, understanding the relative vulnerability of organisms such as producers, keystone consumers, and ecosystem engineers can lend insight into community-level processes (Monaco and Helmuth 2011, Woodin et al. 2013). In intertidal and shallow coastal zones, macroalgae serve as basal producers as well as provide critical habitat that support many other species. *Fucus vesiculosus* is one of the most prevalent and ubiquitous macroalgal species

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within the intertidal and shallow subtidal zones in the North Atlantic ocean and the Baltic Sea, thus contributing to ecosystem function over a large spatial range (Lubchenco 1978, Pearson et al. 2000, Nygård and Ekelund 2006). Multiple studies have evaluated the thermal performance (e.g., growth, photosynthesis) of *F. vesiculosus* in the context of environmental factors relevant to global climate change (Pearson et al. 2000, Nygård and Dring 2008, Graiff et al. 2015). While such studies often note a fairly wide thermal tolerance, range contractions at equatorial range boundaries apparently related to increasing temperature have been reported (Nicastro et al. 2013). However, considerably less is known about the potential interactions of nutrient availability and temperature in driving the ecophysiology of this species. Here we experimentally explore the interactive effects of these two drivers, testing the hypothesis that under some suites of conditions elevated temperature and nutrients may have a net positive effect.

The net positive and negative impacts of elevated nutrients, and in particular nitrogen, on coastal zones has enormous significance (e.g., Rabalais et al. 2009). The anthropogenic introduction of nitrogen through agriculture, fossil fuel combustion, and other human activities (i.e., land clearing and draining wetlands) has dramatically altered the global cycle of nitrogen (Vitousek et al. 1997). Human activities have nearly doubled the rate at which nitrogen enters terrestrial systems and has greatly increased the nitrogen subsequently transferred to estuarine and coastal ocean systems through rivers and watersheds (Nixon 1995, Howarth 2008). The increased development and urbanization of coastal communities has further exacerbated the problem by increasing surface water run-off (Nixon 1995, Valiela et al. 1997, Nixon and Buckley 2002, Howarth 2008). Coastal ecosystems are quite sensitive to external perturbations, and under extreme nutrient addition eutrophication and anoxia can occur with severe ecosystem-level consequences (Galloway et al. 2004, Rabalais et al. 2009).

Nitrogen levels in rocky intertidal, shallow subtidal, and pelagic environments are typically well below the more moderate to high levels found in estuarine, wetland, and river-outlet systems (de Jonge et al. 2002, Howarth and Marino 2006, Bricker et al. 2008). As a result, these systems are likely to be nutrient limited, and small increases in available nitrogen can have a large impact on organisms typically exposed to very low nitrogen levels. High nitrogen inputs from sewage and fertilizer run-off from coastal development (Nixon 1995, Valiela et al. 1997, Howarth 2008) can thus cause large-scale microalgal blooms (Nixon and Buckley 2002, Bricker et al. 2008), which influence water oxygen levels and potentially influence other macrophyte, invertebrate, and fish species in the affected habitats (Heugens et al. 2001, Orth et al. 2006, Thornber et al. 2008, Altieri and Gedan 2014). Additionally, nitrogen additions to the environment can lead to increased epiphytic growth on macrophytes (Worm and Sommers 2000, Bracken et al. 2007), as well as alter grazing pressure from herbivores resulting from changes in tissue palatability (Cronin and Hay 1996*a*, *b*, Worm and Sommers 2000, Hughes et al. 2004).

A growing body of literature has also pointed to the positive influence that nutritional state can have on the physiological sensitivity of plants and animals to changes in their environment, and especially to temperature (Galloway et al. 2004, 2008, Connell et al. 2013). For example, several studies have shown that increased food availability can increase tolerance to otherwise stressful temperatures in marine invertebrates (e.g., Schneider et al. 2010), although others have shown contradictory results (Fabricius et al. 2013). However, considerably less is known about effects of nutrient enrichment on marine macroalgae under elevated temperatures. Macrophytes are typically thought to be nitrogen limited (Galloway et al. 2004, Elser et al. 2007, Harpole et al. 2011), suggesting that some increase in available nitrogen could enhance productivity (Vitousek et al. 1997, Galloway et al. 2004, 2008). Increases in available nitrogen have been shown to increase plant productivity and biomass accumulation over short temporal scales (Blanchette et al. 2000, Stachowicz 2001, Bracken 2004, Elser et al. 2007, Harpole et al. 2011). In terrestrial environments, nitrogen supply can directly affect photosynthetic production and leaf litter decomposition rates (Hunt et al. 1988, Berg and Tamm 1991, Boxman et al. 1995). In marine and coastal ecosystems, nitrogen can be seasonally limiting at high latitudes and chronically limiting at lower latitudes (Sarmiento et al. 1993, Herbert 1999), thus influencing organism production and success in these respective environments. Increases in environmental nutrient levels increase algal tissue growth, tissue nutrient levels, and the production of protective chemicals that deters herbivory (Van Alstyne and Pelletreau 2000).

In coastal marine systems, the distribution of environmental nitrogen limitation differs both geographically and temporally (Lapointe 1987, Fujita et al. 1989, Wootton et al. 1996, Van Alstyne and Pelletreau 2000). Though phosphorus and iron serve important roles as nutrients available for algal productivity, nitrogen has been shown to be most influential in northern temperate coastal waters (Van Alstyne and Pelletreau 2000, Bracken 2004, Perini and Bracken 2014, Bracken et al. 2015). Fast-growing macrophytes are more dependent on environmental nutrient levels compared to large, slow-growing plants, suggesting that maximum growth rates are associated with high sensitivity to nutrients (Pedersen 1995). The carbon/nutrient balance hypothesis (CNBH) predicts that when nutrient levels are abundant macroalgae will allocate carbon to tissue growth, and when nutrient levels are deplete the plant will allocate carbon to anti-herbivore defenses (i.e., carbon-based phlorotannins in *Fucus*; Cronin and Hay 1996*b*, Van Alstyne and Pelletreau 2000). Plant growth is often more limited by low nutrient availability than from photosynthesis (Chapin 1980); therefore, it is important to consider environmental nutrient levels when quantifying growth and photosynthetic production over time.

It therefore remains unclear how increased nitrogen delivery may affect coastal ecosystems dominated by macroalgae undergoing temperature increases resulting from global climate change. Macroalgae are responsible for a considerable amount of the photosynthetic productivity in coastal marine habitats (Nixon et al. 1986, Binzer and Sand-Jensen 2002, Binzer et al. 2006, Dethier and Williams 2009). Although aerial exposure, desiccation, and high light stress have all been shown to negatively affect photosynthetic production during extreme exposure conditions (Underwood and Jernakoff 1984, Harley 2003, Williams and Dethier 2005, Lamote et al. 2012), temperature is positively correlated with photosynthesis and growth in macrophytes at lower levels until a temperature optimum is reached (Smith and Berry 1986, Matta and Chapman 1995, Colvard et al. 2014). However, any additional increase in temperature, though small, beyond this optimal thermal state can result in a dramatic decline in organism performance due to changes in both respiration and photosynthesis. Therefore, increasing temperatures have a net positive effect until some threshold (optimum temperature), above which the organism experiences thermal stress (Colvard et al. 2014). How temperature and nutrients interact remains relatively underexplored for many basal producers, including *F. vesiculosus*. Understanding the synergistic effects of changes in temperature and nutrients on basal producers such as these will inform our understanding of how foundational species within intertidal and shallow subtidal communities will respond to predicted environmental conditions in the coming decades.

We evaluated how long-term nutrient enrichment (i.e., nitrogen) affected photosynthesis and tissue growth in *Fucus vesiculosus* when exposed to short-term temperature increases. *F. vesiculosus* has served as a model organism in North Atlantic rocky intertidal and Baltic shallow subtidal systems because of its ubiquitous nature (Nicastro et al. 2013), its ease in laboratory use (Lubchenco 1983, Serrão et al. 1999, Pearson et al. 2000, Nygård and Ekelund 2006), and because of its importance as a basal producer and source of biological habitat (Dijkstra et al. 2012). This study quantified the photosynthetic response of ambient and nutrient-enriched *F. vesiculosus* over a range of irradiance and seawater temperature combinations representative of both current and elevated temperatures in the southern Gulf of Maine (Mills et al. 2013, Saba et al. 2016). We chose to evaluate the algal thermal response over short, more acute exposures to elevated temperature since intertidal and shallow subtidal species such as *F. vesiculosus* typically experience quite rapid changes in their thermal environment, especially in shallow water (Pfister et al. 2007, Colvard et al. 2014). In this study we did not examine the potential role of changes in the thermal and desiccation regimes of macroalgae during aerial exposure, but instead focus on temperatures during submergence.

METHODS

Study organism and location

We examined the thermal performance (photosynthesis and tissue growth) of *Fucus vesiculosus* individuals in response to ambient and nutrient-enriched states. All algal tissue used in these experiments was collected from non-reproductive individuals collected in July 2014 from the mid-intertidal region (~1.0 m above mean lower low water, MLLW) of rocky shores near the Northeastern University Marine Science Center in Nahant, Massachusetts, USA (42.42° N, 70.90° W). All individuals were placed in a flow-through seawater system with a simulated tide for 24 h prior to the start of each experimental trial. Only whole individuals with little to no tissue damage were used, and all epiphytic algae and grazing invertebrates were removed prior to the start of the experiment. The experiment was conducted in July and August 2014 for 36 d.

Experimental design

This study consisted of two treatment levels, ambient and nutrient-enriched, each with 10 replicate experimental mesocosms (7.5 L) consisting of four *F. vesiculosus* individuals per mesocosm. A mixed semi-diurnal tidal cycle was simulated in the experimental mesocosms, mimicking the tidal elevation at which the algae were collected. Each mesocosm had an independent water supply and contained a nutrient dispenser constructed from a perforated PVC cap with a 3% agar solution (Perini and Bracken 2014). The nutrient-enriched treatment contained a 2.0 M solution of sodium nitrate ($NaNO_3$) added to the nutrient dispensing agar solution; preliminary tests confirmed that concentrations were adequate to produce the desired level of elevated nitrogen in seawater. The ambient (control) treatment did not contain any added $NaNO_3$ (i.e., nutrients). To ensure proper nutrient levels in the mesocosms for the duration of the study the nutrient dispensers were replaced weekly, and weekly seawater samples (15 mL) were collected from each mesocosm in order to confirm seawater nitrogen levels. To determine nutrient uptake throughout the duration of the experimental trials (36 d) ~3 cm of tissue was clipped weekly from a fifth, sacrificial *F. vesiculosus* individual per mesocosm. At the end of the experiments, all *F. vesiculosus* individuals were dried at 70°C in a drying oven (Thermo Scientific HERAtherm Oven, Nahant, MA USA) for at least 48 h, and dry tissue mass recorded in order to normalize all photosynthesis measurements. The dried algal tissue was then ground to a fine powder using a Retch Mixer Mill MM400, in order to quantify the percent nitrogen levels in the tissue using a Thermo Scientific Flash EA 1112 NC soil analyzer. Nitrogen levels in the collected seawater were analyzed using a Unisense NO_x Biosensor, which provided a quantitative value of total nitrate and nitrite (μmol/L NO_x), hereafter referred to as nitrogen. Nitrogen levels in the algal tissue and in the seawater collected from the experimental mesocosms at the end of the study were statistically analyzed using two sample *t*-tests, comparing ambient and nutrient-enriched conditions.

Tissue growth

Growth was calculated as a rate of change in algal tissue wet weight and projected surface area. Tissue wet weight was recorded using a Mettler Toledo MS 105DU scale (0.0001 g sensitivity) at the start and end of the experiment, with algal tissue dabbed dry to remove surface seawater. Relative growth rate of *F. vesiculosus* tissue was calculated as the difference in mass change, standardized to initial tissue weight, over the time of the experiment (36 d). Photographs were taken of all individuals ($n = 40$ treatment^{-1}) at the start and end of the experiment, and the change in the projected surface area was calculated using ImageJ software (v. 1.37). To analyze differences in growth between treatments, relative growth rate (g/d) and normalized difference of the projected surface area (cm^2), we performed nonparametric Mann-Whitney *U*-tests, since the data did not meet the assumptions of normality and homoscedasticity.

Photosynthesis vs. irradiance

An Ocean Optics Neofox FOSPOR-R oxygen sensor was used to quantify oxygen production as a function of irradiance (PE curves) for *F. vesiculosus* algae at three temperatures. Each PE curve consisted of a 20-min exposure in the dark (0 μmol photons·m^{-2}·s^{-1}), and a 5-min exposure to each consecutive irradiance level (0, 15, 50, 75, 125, 230, 450, 820, and 1440 μmol photons·m^{-2}·s^{-1}). An external light source (300-W quartz-halogen lamp projector) and neutral density filters were used to create the nine irradiance conditions. All respiration and photosynthesis measurements were conducted in a 1-L closed system chamber that was continually mixed. A linear regression of oxygen levels inside the chamber vs. time was calculated once the level became stable while in the dark (0 μmol photons·m^{-2}·s^{-1}) and for each consecutive irradiance level. PE curves were conducted at three different temperature conditions (10°, 14°, and 18°C), with five individuals selected haphazardly from the respective experimental mesocosms for each temperature condition. All measurements were conducted between days 28 and 30 of the experiment to ensure elevated nitrogen levels in the algal tissue for the nutrient-enriched treatment. The three temperatures chosen for the PE curves are representative of average (10°C), warm (14°C), and hot (18°C) seawater temperatures during the summer season for this location, verified from a temperature logger located at ~1.0 m MLLW tidal elevation near the Marine Science Center in Nahant, Massachusetts (Appendix S1: Fig. S1). All temperature manipulations for the closed photosynthetic chambers were provided by a recirculating water bath (VWR 1147P, Thermo Scientific Pittsburgh, PA USA).

Best curve fits were applied to all points for each PE curve as described in Colvard et al. (2014) using the following photosynthesis equation (Jassby and Platt 1976):

$$P_{\text{net}} = P_{\text{gross,max}} \times \tanh[\alpha \times I / P_{\text{gross,max}}] - R_{\text{d}} \qquad (1)$$

where P_{net} is the net photosynthesis (μmol O$_2$·g dry mass^{-1}·h^{-1}), $P_{\text{gross,max}}$ is the maximum rate of gross photosynthesis at a saturating irradiance (μmol O$_2$·g dry mass^{-1}·h^{-1}), R_{d} is the respiration rate in the dark (μmol O$_2$·g dry mass^{-1}·h^{-1}), I is irradiance (μmol photons m^{-2}·h^{-1}), and α is the initial slope of the PE curves ([μmol O$_2$/g dry mass] × [μmol photons/m^2]$^{-1}$). $P_{\text{gross,max}}$ and R_{d} were measured through laboratory experiments, where $P_{\text{gross,max}}$ was calculated posthoc using the equation

$$P_{\text{gross,max}} = P_{\text{net,max}} + R_{\text{d}} \qquad (2)$$

where $P_{\text{net,max}}$ is the maximum rate of net photosynthesis at a saturating irradiance. Based on preliminary results and from the findings in Colvard et al. (2014) for *F. gardneri*, $P_{\text{gross,max}}$ and R_{d} for *Fucus* spp. are temperature dependent; therefore, different irradiance and temperature combinations resulted in different calculated P_{net} values. The P_{net} equation provided by Jassby and Platt (1976) does not account for photoinhibition (β). Previous photosynthetic measurements of *F. vesiculosus* suggested that photoinhibition was not observed at high, ecologically relevant irradiances (N. Colvard *unpublished data*). An ANCOVA was used to analyze the effect of treatment (i.e., nutrient), temperature (covariate), and the treatment × temperature interaction for the PE curves. For purposes of statistical analysis, light was $\log(x + 1)$ transformed to meet assumptions of normality and homoscedasticity, confirmed by plot of residuals.

Photosynthetic thermal performance

Photosynthetic thermal performance was measured using an Ocean Optics Neofox FOSPOR-R (Ocean Optics, Dunedin, FL USA) oxygen sensor inserted into a 1-L closed chamber system, where temperature was controlled by a recirculating water bath. All measurements were conducted between days 30 and 36 of the experiment. We haphazardly selected five *F. vesiculosus* individuals per experimental treatment for each temperature measured. All algal individuals were dark adapted inside a closed water bath at the desired temperature for at least 30 min prior to any recorded measurements. Dark respiration (R_{d}) measurements were conducted by shading the chamber and water bath, and recording the reduction in percent oxygen (%O$_2$) for 20 min. The rate of %O$_2$ change inside the chamber was calculated once the rate stabilized, after which an external light source (300-W quartz-halogen lamp projector) was turned on to induce photosynthesis. Maximum net photosynthesis ($P_{\text{net,max}}$) was recorded following 20 min exposure at a saturating irradiance (1000 μmol photons·m^{-2}·s^{-1}), determined from the PE curves. The rate of %O$_2$ change for $P_{\text{net,max}}$ was calculated once the rate stabilized from exposure to light. $P_{\mathrm{gross,max}}$ was calculated as $P_{\mathrm{net,max}} + R_{\mathrm{d}}$. R_{d} and $P_{\mathrm{net,max}}$ at temperatures between 6° and 30°C were measured using an adaptive mesh refinement approach (Berger and Oliger 1984) where measurements were recorded at smaller intervals near the optimum (i.e., P_{max}). This provided a more precise determination of the thermal optimum performance. Irradiance for $P_{\mathrm{net,max}}$ measurements was provided by an external halogen lamp light source.

Best curve fits were applied to the photosynthetic performance measurements for *F. vesiculosus* as a function of seawater temperature in the dark (R_{d}) and at a saturating irradiance ($P_{\mathrm{gross,max}}$). R_{d} was determined by fitting a linear regression curve to the respiration (i.e., consumption of O_2) measurements with increasing seawater temperature. $P_{\mathrm{gross,max}}$ was determined by fitting the photosynthetic performance with a curvilinear, third-degree polynomial. ANCOVAs were used to analyze the effect of treatment (i.e., nutrient), temperature (covariate), and the treatment × temperature interaction for R_{d} and $P_{\mathrm{gross,max}}$ data.

Chlorophyll fluorescence measurements

The photosynthetic thermal performance measurements (R_{d} and $P_{\mathrm{gross,max}}$) provided an understanding of how elevated nitrogen influenced the whole algal individual, but we also wanted to characterize how specific tissue regions of *F. vesiculosus* were affected by elevated tissue nitrogen levels. Therefore, we used a Pulse Amplitude Modulation chlorophyll fluorometer (Jr. PAM, Walz, Effeltrich, Germany) to measure light induction curves on the apical tip and thallus wing tissue of *Fucus vesiculosus*. The apical tip has been shown to be the primary growing region of *Fucus* algae (King and Schramm 1976, Bonsdorff and Nelson 1996), and the wing or thallus tissue comprises a large portion of the photosynthetically active tissue of *F. vesiculosus* (Hemmi et al. 2005). All fluorescence measurements were conducted at the conclusion of the nutrient enrichment experiment (day 36). Ten individuals were haphazardly selected for both ambient and nutrient-enriched treatments, one alga from each replicate mesocosm. These individuals were dark adapted for at least 30 min prior to fluorescence measurements and all trials were conducted at 18°C in 35-μm filtered seawater. Light induction curves were used to describe characteristic changes in chl *a* fluorescence yield upon illumination of dark-adapted photosynthetic tissue. From the light induction curves, maximum quantum yield of PSII (ϕ_{PSII}) and non-photochemical quenching (NPQ) values were analyzed. The parameter ϕ_{PSII} can be used as a proxy for the photosynthetic capacity of the alga, whereas NPQ is closely related to the dissipation of excess light energy into heat in order to avoid photodamage. Two-way ANOVAs were used to compare the measured algal tissue (apical tip and thallus wing), the nutrient treatment, and the tissue × nutrient interaction for ϕ_{PSII} and NPQ. In order to determine differences in treatment within a tissue region, we used posthoc two sample *t* tests.

Net photosynthesis model

Using ecologically relevant irradiance (I, 0–1500 μmol photons·m^{-2}·s^{-1}) and seawater temperature (0–30°C) combinations, we used the equation to calculate P_{net} (Eq. 1) to predict net photosynthesis (P_{net}) for ambient and nutrient-enriched conditions. These predictive models are based on the best curve fits for $P_{\mathrm{gross,max}}$ (a curvilinear, third-degree polynomial fit) and R_{d} (a linear fit) for both treatments. $P_{\mathrm{gross,max}}$, R_{d}, and α (initial slope of PE curves) were temperature dependent for ambient and nutrient-enriched conditions. Since the P_{net} model is only valid when *F. vesiculosus* is submerged, during periods of aerial exposure at low tide P_{net} was assumed to be 0 (Colvard et al. 2014).

Driving the P_{net} model with environmental conditions recorded near Nahant, Massachusetts from May 2013 to December 2014 provided an estimate of *F. vesiculosus* performance in the field during that interval. Seawater temperature data were obtained from an offshore NOAA buoy (NDBC Buoy: 44013) and compared to an in situ HOBO pendant logger located at +1 m MLLW in Nahant, Massachusetts. Aerial irradiance (I_{air}) was recorded from a weather station (Onset S-LIA-M003 PAR sensor, Onset Computer Corporation Bourne, MA USA). Underwater irradiance was calculated from aerial irradiance and water depth following Beer's Law

$$I_{\mathrm{d,uw}}(z) = I_{\mathrm{air}} \times e^{(-\mathrm{Kd} \times z)}$$

$I_{\mathrm{d,uw}}$ is the downwelling underwater irradiance (μmol photons·m^{-2}·s^{-1}) at depth z (m), I_{air} is the downwelling irradiance measured in air (μmol photons·m^{-2}·s^{-1}), and K_{d} is the vertical light attenuation coefficient for Nahant, Massachusetts (0.480 m^{-1}, based on MWRA Water Quality measurements; data *available online*).[3] Water depth (z) was estimated from tidal predications at an intertidal elevation of +1 m MLLW (Xtide; data *available online*).[4] Therefore, when the tidal height was <+1 m MLLW, the modeled alga was assumed to be aerially exposed and $P_{\mathrm{net}} = 0$.

We calculated the yearly average P_{net} for *F. vesiculosus* located at Nahant, Massachusetts from hourly recorded environmental data, and compared those results to a simulated increase in seawater temperature +3°C above recorded temperatures, which is the anticipated average rise in seawater temperature by the end of the century for this region (IPCC 2014, Saba et al. 2016). Note that this approach does not account for projected changes in variance and thus is only a rough estimator of future changes, particularly considering that increases of this magnitude have already been reported in the Gulf of Maine (Mills

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[3] www.mwra.com/harbor/html/wq_data.htm

[4] tbone.geol.sc.edu/tide

et al. 2013). These evaluations were done over a tidal range of –1.0 to +2.0 m MLLW, at 0.5-m intervals. Statistical tests were run using RStudio (Version 0.99.467; 2009-2015 RStudio, 250 Northern Ave, Boston, MA 02210).

RESULTS

Seawater collected from the experimental mesocosms demonstrated elevated nitrogen levels in the nutrient-enriched treatment (20.95 ± 6.88 µmol/L NO_x [mean ± SE]) mesocosms for the duration of the experiment (36 d). Analysis of seawater collected from the ambient (control) experimental mesocosms showed no change in nitrogen levels for the duration of the experiment (2.41 ± 0.33 µmol/L NO_x; Table 1). The results from a two-sample t test showed these water nitrogen levels were significantly different from one another ($t = 2.01$, $P < 0.001$). Following the 36-d incubation period, the measured nitrogen levels in *Fucus vesiculosus* tissue were elevated in the nutrient-enriched treatment (1.741% ± 0.025% N) compared to the tissue incubated under ambient conditions (1.178% ± 0.012% N; Table 1). Results from a two-sample t test showed these tissue nitrogen levels were significantly different from one another ($t = 20.44$, $P < 0.001$).

Tissue growth

A nonparametric Mann-Whitney U test showed significant differences in the relative growth rate of *F. vesiculosus* tissue between ambient and nutrient-enriched individuals following the 36-d duration of incubation ($W = 312$, $P < 0.001$; Table 1). Nutrient-enriched tissue demonstrated elevated tissue growth rate (0.021 ± 0.001 g/d) compared to ambient (0.016 ± 0.001 g/d). A nonparametric Mann-Whitney U test showed there was also a significant difference in the change in projected surface area between ambient (0.669 ± 0.43 cm^2) and nutrient-enriched tissues (0.873 ± 0.061 cm^2; $W = 548.5$, $P = 0.024$; Table 1).

Photosynthesis vs. irradiance

The ANCOVA showed significant effects of temperature ($F_{1,228} = 26.998$, $P < 0.001$), light ($F_{1,228} = 953.895$, $P < 0.001$), treatment × temperature ($F_{1,228} = 10.834$, $P < 0.001$), and temperature × light ($F_{1,228} = 18.776$, $P < 0.001$). The effect of treatment (nutrients) showed a trend toward significance ($F_{1,228} = 3.516$, $P = 0.062$), and all other interactions were nonsignificant. Nutrient-enriched *Fucus vesiculosus* tissue had higher photosynthesis levels than ambient tissue, but only at the highest temperature (18°C) recorded for the photosynthesis vs. irradiance curves (PE curves; Fig. 1). The initial slope (α) of the PE curves for all nutrient and temperature combinations were similar (Appendix S1: Table S1). The half-saturation constant (I_K) for the PE curves showed similar values for ambient (44.355 µmol·m^2·s^{-1}) and

TABLE 1. Summary of the experimental results and statistics for ambient (control) and nutrient-enriched (treatment) conditions for the mesocosm containers and *Fucus vesiculosus* tissue.

Treatment	Seawater N (µmol/L)	*F. vesiculosus* tissue N (%)	Relative Growth Rate (g/d)	Projected surface area of *F. vesiculosus* (cm^2)	ϕ_{PSII}		NPQ	
					Apical tip	Thallus wing	Apical tip	Thallus wing
Ambient	2.41 ± 0.33	1.178 ± 0.012	0.016 ± 0.001	0.669 ± 0.043	0.71 ± 0.007	0.68 ± 0.006	1.63 ± 0.331	0.81 ± 0.140
Nutrient-enriched	20.95 ± 6.88	1.741 ± 0.025	0.021 ± 0.001	0.873 ± 0.061	0.74 ± 0.012	0.70 ± 0.005	2.07 ± 0.253	1.14 ± 0.077
Statistics	$t = 2.01$, $P < 0.001$	$t = 20.44$, $P < 0.001$	$W = 312$, $P < 0.001$	$W = 548.5$, $P = 0.024$	$t = 3.003$, $P = 0.007$	$t = 2.420$, $P = 0.026$	$t = 2.295$, $P = 0.034$	$t = 3.737$, $P = 0.002$

Notes: The measured nitrogen in the experimental mesocosm containers is the average (±SE) µmol/L nitrogen in seawater samples collected throughout the duration of the experiment. The measured %N in *F. vesiculosus* is the average (±SE) from the experimental tissue following the enrichment period and corresponding photosynthesis and growth measurements. The relative growth rate (g/d) and projected surface area growth (cm^2) measurements of *F. vesiculosus* are the average (±SE) for the two treatment conditions. The Quantum Yield of PSII (ϕ_{PSII}) and Non-photochemical Quenching (NPQ) results are the average (±SE) of the apical tip and thallus wing region of *F. vesiculosus* ($n = 10$) from ambient and nutrient-enriched conditions. Statistical results for ϕ_{PSII} and NPQ are apical tip and thallus wing region, respectively.

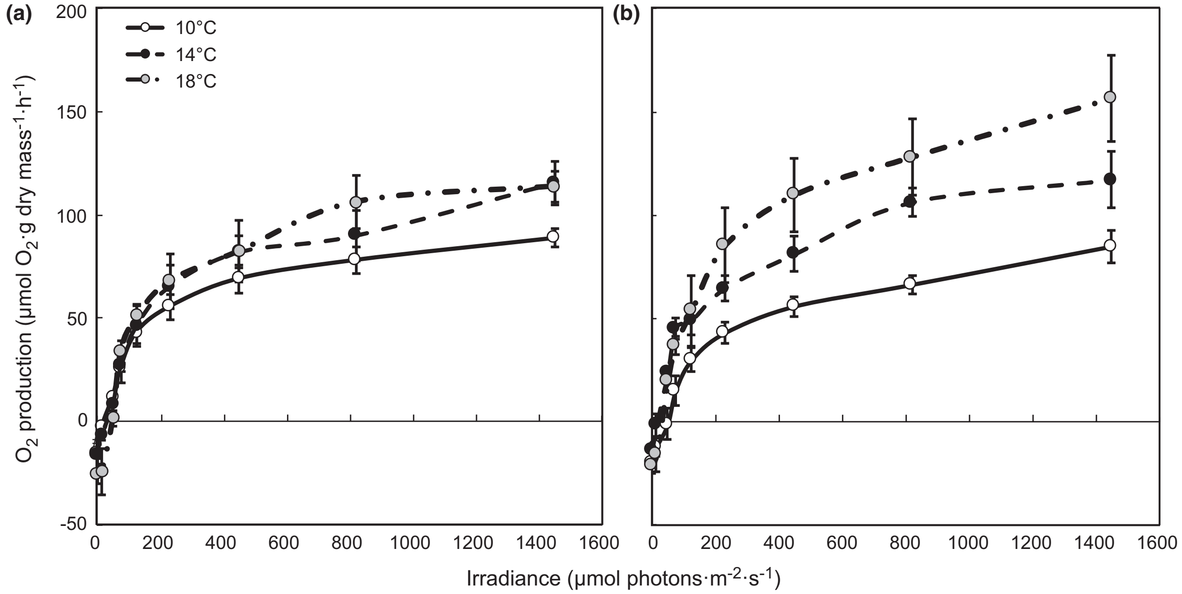

FIG. 1. Photosynthesis vs. irradiance curves for (A) ambient (control) and (B) nutrient-enriched (treatment) individuals at 10°C (white circle, solid line), 14°C (black circle, dashed line), and 18°C (gray circle, dashed line). These temperatures are representative of average (10°C), warm (14°C), and hot (18°C) seawater temperature conditions during summer months in Nahant, Massachusetts, USA. There was a significant effect of temperature and trend toward significance for the treatment (nutrients) Values are mean ± SE.

nutrient-enriched (42.438 μmol·m^2·s^{-1}) treatments at 10°C, and for ambient (57.728 μmol·m^2·s^{-1}) and nutrient-enriched (58.524 μmol·m^2·s^{-1}) treatments at 14°C. The I_K for the 18°C measurements had the greatest difference between ambient (56.922 μmol·m^2·s^{-1}) and nutrient-enriched (78.252 μmol·m^2·s^{-1}) treatments (Appendix S1: Table S1). None of the PE curves demonstrated photosynthetic inhibition (β) at high light levels, and therefore β was not included in the photosynthetic analyses.

Photosynthetic thermal performance

Measurements of *F. vesiculosus* respiration in the dark (R_d) showed a near-linear response in oxygen consumption (presented as CO_2 production) as temperature increased from 6° to 30°C (Fig. 2). The ANCOVA demonstrated a significant effect of temperature ($F_{1,85} = 212.848$, $P < 0.001$), however, there was no effect of the nutrient treatment ($F_{1,85} = 2.189$, $P = 0.143$) nor an effect of the treatment × temperature interaction ($F_{1,85} = 0.398$, $P = 0.530$).

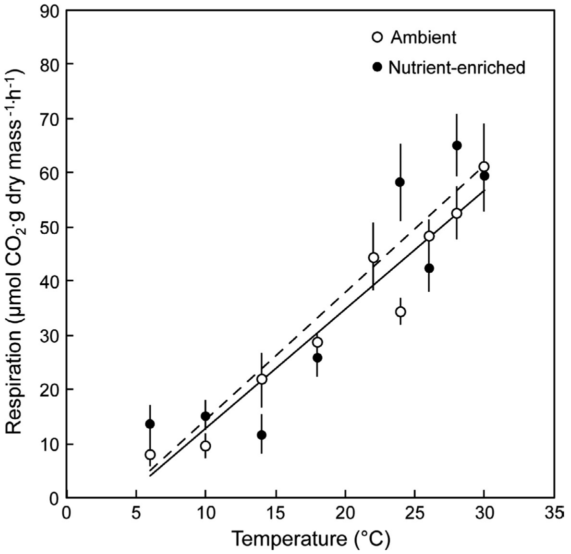

FIG. 2. Dark respiration (R_d) measurements of ambient (open circle, solid regression line) and nutrient-enriched (solid circle, dashed regression line) *F. vesiculosus* tissue were conducted using an adaptive mesh approach from 6° to 30°C. The recorded respiration values are the mean (± SE) of $n = 5$ individuals per temperature condition. There was a significant effect of temperature, with increasing respiration with increasing temperature conditions. There was no effect of treatment (nutrients) or the temperature × treatment interaction.

We fit curvilinear, third-degree polynomial curves to the maximum gross photosynthesis ($P_{\mathrm{gross,max}}$) data for nutrient-enriched and ambient individuals. The ANCOVA showed a significant effect of treatment (nutrients; $F_{1,75} = 30.195$, $P < 0.001$), and temperature^3 ($F_{1,75} = 33.032$, $P < 0.001$), and treatment × temperature interaction ($F_{1,75} = 5.157$, $P = 0.026$). Maximum photosynthetic production occurred at 26°C, followed by a decrease in $P_{\mathrm{gross,max}}$ at 28° and 30°C for both treatment conditions (Fig. 3). Posthoc statistical analysis comparing ambient and nutrient-enriched individuals at each respective temperature conditions showed there was no difference in $P_{\mathrm{gross,max}}$ between the two nutrient treatments at low temperatures (6–14°C); however, for temperatures ≥18°C $P_{\mathrm{gross,max}}$ was greater for nutrient-enriched tissue compared to ambient (Fig. 3). Although the treatment

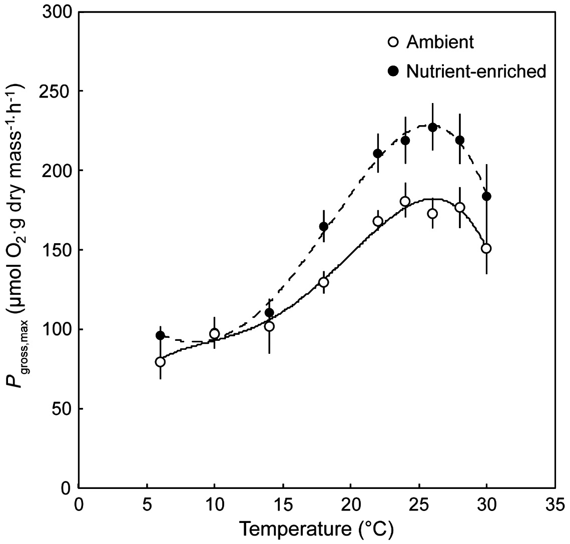

FIG. 3. Maximum gross photosynthesis ($P_{gross,max}$) of ambient (open circle, solid curve line) and nutrient-enriched (solid circle, dashed curve line) *F. vesiculosus* with curvilinear, third-degree polynomial curve fits were measured using an adaptive mesh approach from 6° to 30°C in order to determine the thermal optimum. The recorded $P_{gross,max}$ values are the mean (± SE) of $n = 5$ individuals per temperature condition. There was a significant effect of temperature, treatment (nutrients), and temperature × treatment, driven by the increase in $P_{gross,max} \geq 18°C$.

× temperature interaction was weak, the position of the treatment lines was consistent across the levels of the covariate (temperature).

Chlorophyll fluorescence measurements

The two-way ANOVA of the maximum quantum yield of PSII (ϕ_{PSII}) data revealed there were significant differences between tissue ($F_{1,36} = 15.852$, $P < 0.001$) and treatment ($F_{1,36} = 13.066$, $P < 0.001$), though no difference between the tissue × treatment interaction ($F_{1,36} = 0.208$, $P = 0.651$). In order to specifically evaluate the difference between treatments within a tissue region, posthoc *t* tests were used. This analysis showed there was a significant effect of nutrient concentration on ϕ_{PSII} for the apical tip tissue ($t = 3.003$, $P = 0.007$), with the nutrient-enriched condition having greater yield (0.739 ± 0.012) compared to the ambient condition (0.712 ± 0.007). Post hoc analysis evaluating the thallus wing tissue showed ϕ_{PSII} for nutrient-enriched tissue (0.703 ± 0.005) to be greater than ambient (0.675 ± 0.006; $t = 2.420$, $P = 0.026$; Table 1).

The two-way ANOVA of the non-photochemical quenching (NPQ) showed a significant difference between treatment ($F_{1,36} = 16.169$, $P < 0.001$) and a marginal difference between tissue ($F_{1,36} = 3.042$, $P = 0.090$), though no difference was detected between the tissue × treatment interaction ($F_{1,36} = 0.066$, $P = 0.799$). A post hoc *t* test showed there was a significant effect of nutrient level on NPQ for the apical tip tissue ($t = 2.295$, $P = 0.034$), with the ambient condition (1.635 ± 0.331) having greater quenching levels compared to nutrient-enriched tissue (0.810 ± 0.140). Posthoc analysis evaluating the thallus wing tissue showed NPQ for the ambient condition (2.071 ± 0.253) was significantly greater than nutrient-enriched tissue (1.136 ± 0.077; $t = 3.737$, $P = 0.002$; Table 1).

Net photosynthesis model

Based on temperature and irradiance values recorded near Nahant, Massachusetts, the P_{net} models suggested that *F. vesiculosus* rarely experience environmental conditions needed to reach optimal production at any tidal elevation (Fig. 4). Comparisons of average P_{net} for current (+0°C) recorded temperatures and an increase of 3°C with ambient nutrient conditions and elevated nutrient levels showed notable differences, with the highest yearly average P_{net} occurring in nutrient-enriched tissues at elevated temperatures (Fig. 4).

DISCUSSION

Fucus vesiculosus incubated in a nutrient-enriched treatment had higher oxygen production at warmer seawater temperatures, elevated maximum quantum yield of PSII (a proxy for photosynthetic capacity), a decrease in non-photochemical quenching (a mechanism to ameliorate light stress), an increase in the relative growth rate, and an increase in the difference in project surface area

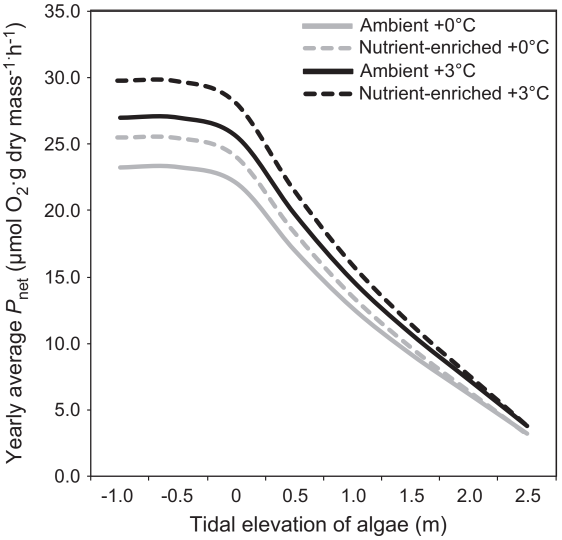

FIG. 4. The yearly average net photosynthesis (P_{net}) modeled over a tidal elevation range of −1.0 to 2.5 m at current seawater temperature (+0°C, gray lines) and the projected increase in seawater temperature by 2090 in the North Atlantic (+3°C, black lines). The solid lines indicate ambient nutrient levels and the dashed lines indicate the nutrient-enriched conditions. There are notable increases in yearly average P_{net} with elevated seawater temperature and nutrient enrichment.

growth rate compared to algae incubated under ambient conditions. These results support previous research findings that demonstrated elevated nitrogen levels led to increased photosynthetic performance and survival in macrophytes, as well as increased productivity and biomass accumulation on short temporal scales (Vitousek et al. 1997, Stachowicz 2001, Bracken 2004, Galloway et al. 2004, 2008). These results suggest that, as conditions continue to warm, this foundational macroalgal species would likely experience increased productivity and tissue growth under moderate increases in nitrogen in the Southern Gulf of Maine. Nitrogen levels in *F. vesiculosus* tissue have been shown to exhibit a seasonal periodicity, with higher %N in the winter months, due to storm mixing and increased terrestrial run-off, and lower %N in the summer months, when the stored nitrogen is more readily used during increased photosynthesis and growth (Townsend 1991, Perini and Bracken 2014). Tissue N levels from the nutrient-enriched treatment in the current study (1.741 ± 0.025) are representative of levels recorded in tissue sampled in the field at Nahant during May (1.996 ± 0.056) and October (1.951 ± 0.041), compared to lower levels measured in July and August (1.499 ± 0.087) when this experiment was conducted (N. Colvard *unpublished data*). The elevated levels used in this experiment are thus representative of those in the field, but at levels that typically occur only under cooler temperatures. Increased temperature and irradiance levels in July and August allow for greater growth and photosynthetic production of the nitrogen-enriched algal tissue than ambient conditions. The increased growth in the nitrogen-enriched treatment is likely the result of a shift in carbon allocation, described by the carbon nitrogen balance hypothesis (CNBH; Cronin and Hay 1996*b*, Van Alstyne and Pelletreau 2000).

Contextually, the seawater nitrogen levels recorded for the nutrient-enriched conditions (20.95 ± 6.88 μmol/L NO_x [mean ± SE]) are representative of elevated nitrogen levels for the rocky intertidal of New England (Perini 2013), which could be driven by environmental conditions such as winter storm mixing, terrestrial run-off, or the added influx from combined sewer overflows (Lapointe 1987, Nixon 1995, Wootton et al. 1996, Howarth 2008). This study only exposed the *Fucus* algae to these elevated conditions for one month and demonstrated significant increases in tissue nitrogen and subsequent tissue growth. However, it is not clear what impact these elevated seawater nitrogen levels would have on *Fucus* algae over a longer duration, how much nitrogen would accumulate in the tissue, and how these changes may influence the ecology of this primary producer. Additionally, these nitrogen values are well below moderate nitrogen levels for river, wetland, and estuarine environments (de Jonge et al. 2002, Howarth and Marino 2006, Bricker et al. 2008). From 1993 to 2015, the Boston Harbor nitrogen levels ranged from 0 to 69 μmol/L NO_x (NO_2 + NO_3), whereas the Mystic River nitrogen levels ranged from 0.01 to 290 μmol/L NO_x and the Charles River nitrogen levels have ranged from 0.02 to 202 μmol/L NO_x (based on MWRA Water Quality measurements, see footnote 2). Though the nitrogen levels used in this study are not representative of eutrophic conditions, in the traditional sense (Bricker et al. 2008), these levels do provide an initial indication of how *Fucus* algae may respond to elevated levels during the warmest time period of the year.

Changes in environmental nitrogen levels in the field would also likely impact the abundance of microalgae (i.e., phytoplankton), and other nutrient-limited macroalgae (i.e., *Ulva*; Nixon and Buckley 2002, Cabello-Pasini and Figueroa 2005, Bricker et al. 2008, Xu et al. 2016). This potential change in micro- and macroalgal abundance associated to increased nitrogen could lead to decreased irradiance levels available for *Fucus* growth and production, both via reduction of light in the water column as well as from the increased growth of epiphytes (Worm and Sommers 2000, Hughes et al. 2004). Increased nutrient availability also has been shown to affect palatability of some macroalgae to herbivores (e.g., Cronin and Hay 1996*a*). While evaluating the differential effects of changes in light, temperature, and nutrients on multiple interacting species of micro- and macroalgae and their herbivores would provide critical insights into ecosystem-wide effects, such a holistic approach was beyond the scope of this study.

There was no observed difference between nutrient treatments for *F. vesiculosus* respiration, suggesting there is no added cost or stress on dark respiration with added nitrogen. Therefore, future seawater temperature increases will likely have a greater impact on *F. vesiculosus* respiration than will nutrient enrichment. However, photosynthetic oxygen production was greater for the nutrient-enriched tissue compared to tissue grown under ambient conditions, specifically for seawater temperatures between 18° and 30°C. The results showed that 26°C is the thermal optimum for *F. vesiculosus* while submerged for both the ambient and nutrient-enriched treatments. The initial positive effect of temperature (<26°C) on oxygen production is based on the rate of carbon fixation during photosynthesis (Davison 1991), with an increased rate of fixation as seawater temperature increased. The decline in oxygen production at temperatures above 26°C is likely attributed to temperature sensitive enzymes of photophosphorylation and electron transport and plastoquinone diffusion (Davison 1991). Therefore, these results suggest that for *Fucus* at this location, seawater temperatures >26°C are thermally stressful, and thus these conditions negatively affect enzymatic activity and proper transport of energy within the photosynthetic cellular structures. At temperatures below this optimum, however, increases in temperature will likely lead to increases in net productivity.

Seawater temperatures for Nahant, Massachusetts recorded hourly from May 2013 to May 2015 logged a maximum of 26.0°C, the optimal temperature for photosynthetic production, only four times in two years

(Appendix S1: Fig. S1), suggesting that this species has not yet reached its thermal optimum for this location (Stuart-Smith et al. 2015). Average seawater temperatures in the Northwest Atlantic are projected to increase an average of 3°C by the end of the century (Saba et al. 2016), which may allow for increases in *Fucus vesiculosus* productivity. Since *F. vesiculosus* serves as a foundation species in this habitat (Dijkstra et al. 2012), this anticipated success would likely influence the success of other rocky intertidal organisms that directly or indirectly depend on *F. vesiculosus* for their own survival. These projected increases in average temperature, however, do not account for higher variance and thus higher extremes that accompany increases in mean temperature, and thus *Fucus* may also experience a higher risk of mortality (Woodin et al. 2013). For example, a summer heat wave in 2012 produced sea surface temperatures in the Gulf of Maine that were up to 3°C warmer than the average from the reference period of 1982–2011 (Mills et al. 2013), thus demonstrating that interannual variability in weather can exceed predicted changes in long-term average conditions. These rare, extreme events can potentially have deleterious effects on some intertidal organisms whose physiology is driven by local conditions and not broad scale climate shifts, per se.

Human activity has largely altered the delivery of nutrients into the natural environment, with nitrogen serving as one of the largest nutrients entering terrestrial and aquatic systems (Howarth et al. 2002). Reactive nitrogen, such as nitrates and ammonium, is delivered to the environment through point sources (i.e., outflow from wastewater treatment plants) and non-point sources (i.e., agricultural fertilizer run-off; Driscoll et al. 2003). Although efforts have been made to regulate point source emissions of reactive nitrogen into the environment, less attention has been given to control non-point sources, which can be difficult to do as there are direct and indirect effects from over-enrichment in exposed systems (Howarth et al. 2002, Driscoll et al. 2003, Compton et al. 2011). Predicting the effects that these nutrient additions will have on ecosystems is not always straightforward, especially when they co-occur with changes in temperature. While the negative effects of nutrient addition are well documented, their potential compensatory or positive effects are less recognized (Connell and Ghedini 2015). For organisms that are currently nutrient-limited, and especially those living at temperatures frequently below their thermal optimum, increased performance may occur under future conditions. The subsequent effect of increased productivity of basal consumers and habitat-forming organisms on ecosystem function is likewise complex. Initial changes in temperature and nutrient levels may drive increases in producer growth with follow-on effects on biodiversity and the uptake of carbonate. However, these initial increases are expected to be followed by rapid declines in function as physiological (Monaco and Helmuth 2011) and ecological tipping points (Connell and Ghedini 2015) occur when conditions exceed optimum. These highly nonlinear, unimodal responses to environmental change can confound efforts to detect early indicators of ecosystem collapse difficult (Hewitt and Thrush 2010, Scheffer et al. 2012). Mechanistic studies such as the one presented here can therefore serve as a valuable means of predicting the suites of conditions that will likely lead to critical ecological transitions (Seebacher and Franklin 2012).

This study showed that nutrient enrichment had a synergistic, positive effect on oxygen production for *Fucus vesiculosus* (Rhee and Gotham 1981, Staehr and Sand-Jensen 2006, Rosa et al. 2013) experiencing higher temperature conditions. These findings underscore the potential resilience of this basal producer in the Southern Gulf of Maine to future environmental changes, at least in the near term. These physiological responses will further affect interspecific interactions with other organisms within the assemblage and their success in an ever-changing environment (Bracken 2004), potentially dampening initial responses to increasing temperatures (Connell et al. 2011). It also points to the need to consider abiotic factors such as temperature and nutrients not just as stressors, but, at some levels, as drivers of increased performance (Connell et al. 2013). Scaling-up from the often idiosyncratic responses of species to changes in multiple stressors will require a detailed understanding of what drives physiological vulnerability, recognizing that changes that are stressful to one species may enhance performance of another, even in the same community (Harley et al. 2006, 2012, Helmuth 2009).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.1475/full

Data Availability

Data associated with this paper have been deposited in Dryad: https://doi.org/10.5061/dryad.d21t5