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Abstract

Variability in primary producers' responses to environmental change may buffer higher trophic levels against negative impacts to basal resource composition. Then again, in instances where consumers rely on a few species to meet their energetic requirements at specific times of the year, altered community production dynamics may significantly impact food web resilience. In high latitude kelp forests, a complementary annual phenology of seaweed production supports coastal marine consumers' metabolic needs across large seasonal variations in their environment. Yet, marine consumers in these systems may face significant metabolic stress in future winter environments, particularly if they lack the resources to support their increased energetic demands. In this study we investigate how the growth and nutritional value of three dominant, coexisting macroalgal species found in subpolar kelp forests will respond to ocean acidification and warming in future winter and summer seasons. We find that the three kelps *Macrocystis pyrifera*, *Hedophyllum nigripes*, and *Neoagarum fimbriatum* differ in their vulnerability to future environmental conditions, and that the seasonal environmental context of nutrient and light availability shapes these responses. Our results suggest that poleward fringe populations of *M. pyrifera* may be relatively resilient to anticipated ocean warming and acidification. In contrast, ocean warming conditions caused a decrease in the biomass and nutritional quality of both understory kelps. Considering the unique production phenology of *H. nigripes*, we emphasize that negative impacts to this species in future winters may be of consequence to consumer energetics in this system. This work highlights how interspecific variation in autotrophs' responses to global change can disrupt the diversity and phenological structure of energy supply available to higher trophic levels.

Introduction

Global environmental change is already affecting primary producers worldwide (Cavicchioli et al., 2019; Terrer et al., 2019; Walker et al., 2021). Anticipating how physiological effects on autotrophs affect higher trophic levels requires an understanding of how the quantity, quality, and identity of these basal resources will shift (Ainsworth & Long, 2004; Koch et al., 2013; Maschler et al., 2022). Species-specific variation in response to elevated CO_2 concentrations and temperatures may lead to a restructuring of primary producer community composition as well as a disruption of the phenology of production in many systems (Cornwall et al., 2012; Franklin et al., 2016; Poorter, 1988; Ullah et al., 2018). Further, effects of environmental change on the nutritional value or palatability of basal resources can significantly impact consumer energetics and food web structure (Campanyà-Llovet et al., 2017; Cebrian et al., 2009; Facey et al., 2014; Rosenblatt & Schmitz, 2016). There is a need to compare the responses of dominant, coexisting primary producers to global environmental change to assess whether interspecific variability can buffer the emergent, bottom-up effects in these ecosystems (e.g., Gilbert et al., 2020; Liu et al., 2018).

In marine ecosystems, macroalgae (seaweeds) support complex coastal food webs (Graham, 2004; Hurd et al., 2014). Similar to terrestrial plants, global environmental change is expected to affect macroalgal growth and biomass (Harley et al., 2012). In the absence of evolution, elevated temperatures with ocean warming (OW) may enhance algal primary productivity within optimal temperature ranges, and negatively impact productivity once thermal optima are exceeded (Eggert, 2012; Hurd et al., 2014; Kram et al., 2016). The effects of elevated seawater pCO_2 and reduced pH with ocean acidification (OA) on the photosynthesis of non-calcified seaweeds are expected to differ based on each species' carbon use strategy (Cornwall et al., 2012; Hepburn et

al., 2011; Hurd et al., 2020, but see Paine et al., 2023). Further, elevated temperature and pCO_2 can interact with each other and other environmental variables, such as light and nutrient availability, to shape species' responses (Celis-Plá et al., 2015; Hollarsmith et al., 2020; King et al., 2017, 2020; Ladah & Zertuche-González, 2022). Thus, effects on individual species will hinge on how environmental change layers onto the natural temporal and spatial variability of abiotic resources in a particular ecosystem (Kroeker et al., 2020).

In addition to the direct effects of global environmental change on macroalgal primary production and growth, OW and OA can alter their value to consumers. Increased temperatures will affect the rate of algal nutrient uptake (Raven & Geider, 1988), and increased pCO_2 can increase thallus nitrogen content (Falkenberg et al., 2013; but see Olischläger et al., 2014). Increased nitrogen content can enhance a seaweed's palatability to herbivores that preferentially consume nitrogen-rich food sources (Duffy & Paul, 1992; Hillebrand et al., 2000; Russell & Connell, 2007). However, the presence of secondary metabolites that may deter grazing, such as phenolic compounds, may be a stronger determinant of herbivores' consumption (Amsler et al., 2005; Demko et al., 2017; Granado & Caballero, 2001; Steinberg, 1985). Elevated pCO_2 and temperature can reduce, increase, or have no effect on seaweed phenolic concentrations depending on the species (Arnold et al., 2012; Kumar et al., 2018; Phelps et al., 2017) and their relative access to light and nutrients (Celis-Plá et al., 2015). Future alterations to seaweeds' secondary metabolic processes have strong potential to change consumptive interactions and energy flow through the base of coastal food webs (Doubleday et al., 2019; Duarte et al., 2016; Jin et al., 2020).

Interspecific variation in macroalgal responses to environmental change will alter the composition of seaweed communities and could disrupt the phenology of consumers' food

supply (Harley et al., 2012). These effects will be particularly evident in seasonally dynamic environments. High latitude marine ecosystems are characterized by large annual variations in temperature, pCO_2, light, and nutrients that influence the seasonal dynamics of primary production and algal physiology (Bell & Kroeker, 2022; Takahashi et al., 1993; Tian et al., 2001). Increases in temperature and pCO_2 will overlay current fluctuations in temperature, pCO_2, light, and nutrients in these systems, giving rise to novel environmental scenarios that will drive seasonally distinct effects on macroalgal physiology (Graiff et al., 2015; Gunderson et al., 2016; Harley et al., 2012; Kroeker et al., 2020). The energetic linkages among trophic levels in seasonally dynamic marine food webs are highly dependent on tight temporal alignment between food supply and consumer demand (Sydeman & Bograd, 2009). Thus, shifts in the seasonal phenology of macroalgal production and quality could lead to mismatches in the timing and strength of these consumptive interactions (Wahl et al., 2020). This may be particularly consequential at high latitudes if consumers experience heightened seasonal windows of metabolic stress under future environmental change (Kroeker et al., 2021).

The goal of this study was to quantify potential shifts in the quantity and quality of three dominant, coexisting seaweed species to ocean acidification and warming. Our study took place in Sitka Sound, Southeast Alaska, a high latitude region of the North Pacific where pronounced increases in sea surface temperatures and decreases in sea surface pH are anticipated in the next century (IPCC, 2018; Mathis et al., 2015) We focus on three large, canopy forming kelp species that dominate macroalgal biomass within the giant kelp forests of this region: *Macrocystis pyrifera*, *Hedophyllum nigripes*, and *Neoagarum fimbriatum*. The annual growth regimes of these three species are distinct in Sitka Sound (Bell & Kroeker, 2022), which may reflect underlying differences in their physiological optima and tolerances. *H. nigripes* is a cold-adapted

understory kelp found primarily in Arctic and sub-Arctic waters (Dankworth et al., 2020; Grant et al. 2020; McDevit & Saunders, 2010). This species' annual growth is controlled by a strong endogenous clock, with blade elongation initiating in January and curtailing abruptly in early summer (Bell & Kroeker, 2022; Lüning, 1993). In contrast, the more temperate kelps *M. pyrifera* and *N. fimbriatum* sustain relatively high growth rates through spring, summer, and early fall (Bell & Kroeker, 2022). Additionally, while *M. pyrifera* dominates the understory kelps in absolute biomass and production rates, *H. nigripes* and *N. fimbriatum* are consistently more nitrogen dense per gram of tissue (Bell & Kroeker, 2022). Thus, the co-occurrence of these kelps currently functions to provide a complementary energy supply to coastal consumers throughout the calendar year (Kroeker et al., 2021).

To isolate the seasonal effects of environmental change on these kelp species, we grew adult sporophyte blades of each macroalga within two, month-long experiments in winter (Feb-March) and summer (Aug-Sept). Experimental controls were designed to approximate current environmental conditions in Sitka Sound (Bell et al., 2022; Bell & Kroeker, 2022; Kroeker et al., 2021), and OA and OW treatments were based on projected end-of-century scenarios of ocean acidification and warming for this region (IPCC 2018; Mathis et al., 2015). At the end of the experiments, we assessed the seasonal impact of OW and OA on kelp growth rates, thallus nitrogen content, and carbon acquisition strategy based on thallus $\delta^{13}C$ values. Finally, to test whether kelp palatability was impacted by future warming and acidification, we used tissue of *H. nigripes* and *N. fimbriatum* grown during the experiments to perform feeding assays with a common kelp forest consumer. We hypothesized that the three kelp species would differ in their sensitivity to ocean warming and acidification. We also anticipated that impacts to the biomass and quality of *H. nigripes* in future winter conditions could be particularly consequential to kelp

forest consumers, given the early season growth and nitrogen-rich resource that this species represents during a metabolically demanding season (Bell & Kroeker, 2022; Kroeker et al., 2021).

This research responds to the call for a more nuanced understanding of how global change will alter marine primary producer resources by integrating natural variation in environmental drivers (Campanyà-Llovet et al., 2017; Rosenblatt & Schmitz, 2016; Wahl et al., 2020). We build from our close understanding of the natural environmental variability and kelp production dynamics in this system to isolate seasonally specific effects of OW and OA on three foundational seaweed species and interpret the potential impact of these changes on community structure and trophic interactions (Cebrian et al., 2009; Harley et al., 2017; Seibold et al., 2018). This work improves our understanding of how asynchronous responses among co-occurring primary producers to global environmental change may shape the bottom-up effects on the ecosystems they support.

Materials and methods

Seasonal experiments for kelp species

To tease apart the effects of seasonal variation in light availability and nutrients on the response of high-latitude kelp species to pH and temperature, we conducted two separate studies: a 'winter' experiment from February 12 – March 18, 2020 (35 d), and a 'summer' experiment from August 15 – September 16, 2020 (32 d). In our experimental design, analysis, and reporting, we endeavored to follow best practices for OA research with macroalgae (Cornwall et al., 2012; Cornwall & Hurd, 2016). Both experiments took place at the Sitka Sound Science Center in a flow-through seawater system drawing source water from 20 m depth (MLLW) in Sitka Sound, Alaska. Incoming seawater was filtered to 20 µm and routed through a UV filter

(Smart UV®, Pentair) before diverging into two temperature-controlled (TITAN® heat pump and Optima compact heaters, AquaLogic) recirculating tanks representing treatments for 'current' or control temperatures (7°C in winter; 14°C in summer) and 'future' OW projections (11°C in winter; 18°C in summer)(IPCC, 2018) by season. From here, temperature regulated seawater was pumped into eight header tanks where pH was maintained at setpoint levels for control conditions (pH_T 7.6 in winter; pH_T 7.9 in summer) and 'future' OA projections (pH_T 7.2 in winter; pH_T 7.5 in summer)(Mathis et al., 2015) through a relay system (*N* = 2 header tanks per pH/temperature treatment). In both seasonal experiments, achievable pH_T setpoints for our control treatments were constrained by the ambient pH of incoming seawater and were therefore lower than the typical seasonal in situ pH_T minima observed on local rocky reefs by ~0.1 – 0.2 pH units (Kroeker et al., 2021). However, the lower-than-average pH values of our control treatments did still fall within the observed pHs captured across all years of in situ environmental data. We chose to maintain the projected end-of-century pH offset for this region (~0.4 pH units) to define our OA treatment setpoints relative to our achievable control pH levels. A DuraFET sensor (Honeywell) in each header tank communicated real-time pH measurements to a controller (UDA 2152, Honeywell, integrated with LabVIEW, National Instruments) that regulated injection of pre-equilibrated low pH seawater through solenoid valves into the headers to maintain pH at treatment set points. The low pH (~6) seawater was produced by bubbling pure CO_2 gas into two tanks of seawater flowing from each temperature-controlled tank. Once in each header tank, the CO_2 and temperature-equilibrated seawater was continuously mixed before delivery to 24 experimental aquaria (*N* = 3 aquaria per header) at an average flow-through rate of 2-2.5 L min^{-1} $aquaria^{-1}$.

Seawater nutrient concentrations were not manipulated, and thus reflected what was delivered through source water inflow to the system during each experiment. Due to the complex controls of nutrient flux onto the Northeast Pacific shelves, there is little consensus on how seasonal nutrient supply in Sitka Sound may change in the future (Hermann et al., 2009; Hood & Scott, 2008; Jenckes et al., 2022; Romero et al., 2022). Therefore, we chose to assume that nutrient availability, like seasonal light availability, would not differ significantly in this region in the future. All aquaria were fitted with a full-spectrum light (Aqua Illumination) that provided seasonally relevant regimes of photosynthetically active radiation spectra and photoperiod within the aquaria based on observations during overcast days in Sitka Sound (Bell et al., 2022). The entire experimental system was shielded from external light sources, and aquaria positions were randomized by treatment and relative location within the system to minimize spatial variation among the random factors *aquaria* and *header*.

We monitored temperature, salinity, DO, and pH_{NBS} daily in each aquarium with a handheld meter (YSI). To capture diel variation in these parameters associated with organismal photosynthesis and respiration, we also performed these measurements every three hours in each aquarium for 24 hrs, once during the winter experiment (March 4-5) and twice during the summer experiment (August 30-31, Sept 14-15). We collected seawater for determination of nutrient concentrations within the experimental system at the beginning, middle, and end of each experiment (N = 6 samples^{-1} treatment^{-1} experiment^{-1}). To compare in situ nutrient data with aquaria conditions during the experiment, we also collected benthic seawater at Talon Is. (57.073 N, 135.414 W), Sitka Sound, for determination of nutrient concentrations in February and August 2020 (N=3 samples^{-1} season^{-1}). Seawater for nutrient samples was immediately filtered through a 0.2 µm filter and frozen until analysis for dissolved inorganic nitrogen content as NO_x

(NO_3 + NO_2) and ammonium (NH_4^+) on a Lachat QuikChem 8000 Flow Injection Analyzer (detection limits: < 0.28 μM NO_x, < 2.40 μM NH_4; average run measurement error < 0.1 μM NO_x < 0.8 μM NH_4).

Discrete water samples for carbonate chemistry analysis were collected from each aquarium and header tank at the beginning, middle, and end of each experiment. These samples were collected without aeration and poisoned with saturated $HgCl_2$ (0.025%) in glass bottles within 20 minutes. Airtight samples were transported to the University of California Santa Cruz (UCSC) for analysis within 3.5 years of collection. We measured water sample pH spectrophotometrically (Shimadzu, UV-1800) using *m*-cresol purple following best practices (Dickson et al., 2007), with a mean standard error of 0.0013 pH units among sample triplicates. We measured water sample total alkalinity (TA) using open cell titration (Metrohm, 905 Titrandro) and corrected against certified reference materials of CO_2 in seawater (Dickson laboratory, Scripps Institute of Oceanography). Mean standard error was 0.87 μmol kg^{-1} SW^{-1} among sample triplicates. To calculate water sample pH on the total hydrogen ion concentration scale (pH_T; mol kg^{-1} SW^{-1})(Dickson, 1993), we used our laboratory measurements of spectrophotometric pH and TA, YSI measurements of temperature and salinity recorded concurrently with discrete water sample collection, and stoichiometric dissociation constants (Dickson & Millero, 1987; Mehrbach et al., 1973) as inputs to the program CO2SYS (Lewis & Wallace, 1998; Pierrot et al., 2006). We then used calculated pH_T values to calibrate the continuous pH dataseries recorded by the DuraFET sensor in each header tank.

Kelp used in both winter and summer experiments came from 4.5-7.5 m depth at Talon Is. (57.073 N, 135.414 W), Sitka Sound. We collected these experimental 'individuals' as whole thalli (*Neoagarum fimbriatum* and *Hedophyllum nigripes),* or as single blades with their attached

230 pneumatocysts that were cut from young sporophytes at approximately 1 m above their holdfasts
231 (*Macrocystis pyrifera)*. During transport to the laboratory and prior to the start of the
232 experiments (< 2 d), we held all algae continuously in ambient flow-through seawater (winter
233 experiment: ~6°C, pH_T 7.8; summer experiment: ~13.5°C, pH_T 8.0). We removed individuals
234 briefly only to clean off epiphytes and record initial morphometrics (maximum blade length,
235 total wet mass) after trimming all blades to 10 cm total length. We also took pictures of each
236 trimmed blade to estimate total surface area using ImageJ (NIH v1.8.0).
237 In both the winter and summer experiments, we randomly assigned 3 individuals of each kelp
238 species to each experimental aquaria (N = 18 individuals $species^{-1}$ $treatment^{-1}$). We affixed
239 individuals upright in aquaria by placing their stipes or pneumatocysts through three-strand line
240 suspended over the open ends of 5 cm tall PVC stands. After all seaweeds were processed for
241 initial morphometrics, we gradually changed pH and temperature in treatment tanks stepwise
242 over the course of 3 d to reach final setpoints. During the experiment, kelps were visually
243 checked daily for necrosis and were lightly brushed biweekly during aquaria cleaning to remove
244 diatoms.
245 At the end of each experiment, individuals were measured and photographed for final
246 morphometrics. Due to the difficulty in capturing three-dimensional tissue growth and the error
247 inherent in wet mass measurements, we estimated kelp growth rates using three different metrics:
248 wet mass (g), maximum blade length (cm), and total blade surface area (cm^2). We used the initial
249 ($G_{initial}$) and final (G_{final}) measurements of each metric to calculate three relative growth rates
250 (RGR; % d^{-1}) for each individual using the equation:

$$RGR_{(mass,\ length\ or\ surface\ area)} = \frac{log(\frac{G_{final}}{G_{initial}}) \cdot 100}{\Delta t} \quad (1)$$

where Δt (d) is the total days elapsed between the beginning and end of the experiment. Relative growth rates were used for subsequent statistical analyses of experimental results. Absolute blade length extension rates were used to compare experimental growth to *in situ* kelp growth measurements (Bell & Kroeker, 2022).

From each individual, we excised new blade tissue grown during the experiment adjacent to the intercalary meristem and pooled this tissue for all species replicates in each aquarium. A portion of this tissue was frozen at -20°C for use in feeding assays (see *Algal palatability assays*, below). The other portion of this tissue was dried at 60°C for >24 hr and analyzed for nitrogen (N) content (% dry mass) and $\delta^{13}C$ values (‰) by the UCSC Stable Isotope Laboratory using a CE Instruments NC2500 elemental analyzer coupled to a Thermo Scientific DELTAplus XP isotope ratio mass spectrometer via a Thermo-Scientific Conflo III (routine measurement error ≤ 1.0 %C and ≤ 0.2 %N). We also analyzed blade tissue from non-experimental kelp individuals collected at Talon Is. in each season ('field controls'; N=6 species^{-1} season^{-1}) for elemental and isotopic analysis.

We quantified variability in relative growth rates, nitrogen content, and $\delta^{13}C$ values of each kelp species during each experiment using linear mixed-effects models (R; R Core Team 2022). We specified *pH*, *temperature* and the *interaction between pH and temperature* as fixed factors. In models of growth rate, we specified *aquaria* nested in *header* as random intercepts using restricted maximum likelihood. In models of kelp species' tissue nitrogen content and $\delta^{13}C$ values, in which samples were pooled by aquaria, we specified *header* as the random intercept

using restricted maximum likelihood. We used Q-Q plots and Tukey-Anscombe plots to confirm that all models satisfied the assumption of normality and that group variances were roughly similar (Winter, 2013). To conservatively account for the influence of heteroscedasticity, we used Satterthwaite's method for t-tests to determine p-values for the effects of fixed factors. When we detected an interaction between fixed factors, we computed estimated marginal means for pairwise contrasts among factor combinations with Satterthwaite's method for determining degrees of freedom. Finally, in the case of one species' response to experimental treatments ($\delta^{13}C$ values of *M. pyrifera* in winter), where there was no interaction among fixed factors but each factor had a significant and 'opposite' effect on algal response, we used a custom contrast to test whether the combined treatment effect of winter OW and OA was significantly distinct from the kelp's response in winter control conditions.

Algal palatability assays

We used tissue from *H. nigripes* and *N. fimbriatum* individuals grown in the laboratory (see *Seasonal experiments for kelp species*, above) to investigate whether future ocean conditions affect the palatability of these understory kelp species in either season. In April 2021, we modified methods used by Hay et al. (1994) to create 'gels' of homogenized kelp tissue suspended in agar and enmeshed in squares of window screen. Each 30 cm^2 gel was formed from 0.1547 ± 0.0004 g (mean ± SE) of freeze dried (FreeZone, Labconco) *H. nigripes* or *N. fimbriatum* tissue growth in either the control treatment or the combination OW and OA treatment from each seasonal experiment. The total number of gels used for the feeding assays was limited by the available kelp tissue grown during each experiment, and was consequently lower for gels made from tissue grown in the winter experiment (*H. nigripes*: N = 11 gels $treatment^{-1}$, *N. fimbriatum*: N = 12 gels $treatment^{-1}$) versus the summer experiment (*H. nigripes*:

296 N = 24 gels treatment^{-1}, *N. fimbriatum*: N = 23 gels treatment^{-1}). We ran 'no-choice' palatability
297 assays by feeding these seaweed gels to the common kelp forest grazer, *Strongylocentrotus*
298 *droebachiensis* (green urchin). Urchins with a test diameter of 24 ± 3 mm were collected from
299 the intertidal, starved for 48 hrs, and then placed in a flow-through chamber with a single gel in
300 ambient seawater conditions (~7 °C, ~8.0 pH) for 48 hrs. We photographed each gel before and
301 after the assay and determined relative consumption of seaweeds grown under different
302 treatments as a proxy for palatability using Image J (NIH v1.8.0). We assessed differences in
303 relative consumption of *N. fimbriatum* or *H. nigripes* tissue using two-way Analysis of Variances
304 (ANOVAs) with fixed factors of *treatment*, *season*, and the *interaction between treatment and*
305 *season*. All data were checked for normality using QQ-plots and homoscedasticity was tested by
306 visual inspection of the residuals. A Tukey's HSD post hoc comparison of means was used to
307 determine significant pairwise differences among treatments.
308
309 **Results**
310 *Seasonal experiments for kelp species*
311 Experimental conditions
312 Replicate experimental aquaria were successfully maintained at pH_T and temperature setpoints
313 offset by -0.4 pH units and +4°C between control and OA and OW treatments within each
314 seasonal experiment (Table 1). Discrete water samples confirmed that pCO_2 also differed by
315 treatment and experiment. Salinity and total alkalinity did not differ among treatment aquaria
316 within each seasonal experiment. Dissolved oxygen concentrations were up to 1 mg/L higher in
317 aquaria assigned a lower temperature treatment compared to aquaria with elevated temperatures
318 within each experiment. Light regimes were maintained uninterrupted throughout each seasonal

experiment at PPFD 10-25 μmol m^{-2} s^{-1}, 7.5 h d^{-1} (winter experiment) and PPFD 40-80 μmol m^{-2} s^{-1}, 11 h d^{-1} (summer experiment). Diel pH cycles within aquaria due to algal photosynthesis and respiration were up to 0.05 pH units during the winter and up to 0.1 pH units in the summer experiment, but did not differ among treatments.

Due to analytical error, there were insufficient samples to assess the relative nutrient concentrations among all treatments in either experiment. Experimental nutrient concentrations of NO_x and NH_4 are reported as mean values in each experiment (Table 1). While experimental NOx concentrations were similar to observations in the field, average ammonium concentrations within aquaria during the summer experiment were notably higher than were observed concurrently in situ. Seawater samples collected at Talon Is. had average nutrient concentrations of 16.7 mg L^{-1} NO_x and 7.6 mg L^{-1} NH_4 in February and 1.4 mg L^{-1} NO_x and 2.8 mg L^{-1} NH_4 in August.

Kelp growth

Treatment effects on kelp growth rates were consistent regardless of growth metric. Hereafter, we report growth results in terms of relative change in individuals' wet mass (RGR_{mass}), which can best capture three-dimensional changes in individuals' stipe, pneumatocyst or blade morphologies.

The effects of OW and OA on kelp growth differed among species (Fig. 1). For one species (*H. nigripes*), growth was lower in OW treatments compared to control treatments in both seasonal experiments (winter: $p < 0.001$, Appendix S1: Table S1; summer: $p < 0.001$, Appendix S1: Table S2). Another species' (*N. fimbriatum*) growth was lower under elevated temperatures in the summer experiment compared to growth in the control treatment ($p < 0.001$, Appendix S1: Table S4), but was not impacted under winter OW conditions (Appendix S1: Table S3). This is in

contrast to growth of the kelp *M. pyrifera*, which was not affected by OW in either winter (Appendix S1: Table S5) or summer (Appendix S1: Table S6) experiments. There was no effect of pH or the interaction between temperature and pH on the growth of any species in the summer experiment. In the winter experiment, there was a marginally significant interaction between temperature and pH on *H. nigripes*' growth ($p = 0.057$). Post-hoc contrasts among treatments indicate that this interaction was driven by the marginally significant effect of OA in combination with OW on the RGR_{mass} of *H. nigripes* compared to the control treatment ($p = 0.054$), while *H. nigripes'* growth under OW alone was significantly lower than in the control treatment ($p < 0.001$) and OA alone had no effect on the species' growth ($p = 0.972$). There was no effect of pH or the interaction between temperature and pH on the growth of *N. fimbriatum* or *M. pyrifera* in the winter experiment.

In the winter experiment, blade length extension rates of *H. nigripes* grown in control pH and temperature treatments were lower than observed growth rates for this understory kelp in Sitka Sound in February and March (Appendix S1: Figure S1) (Bell & Kroeker, 2022). Blade length extension rates of both *N. fimbriatum* and *H. nigripes* in control pH and temperature conditions of the summer experiment were comparable to observed length extension rates in August and September in Sitka Sound (Bell & Kroeker, 2022). We do not have in situ blade extension data for *M. pyrifera* to enable comparison of experiment versus field growth rates.

Nitrogen content

All three kelp species exhibited lower tissue nitrogen content (as % tissue dry mass) when grown under OW conditions compared to control treatments in at least one of the seasonal experiments (Fig. 2). Nitrogen content of *H. nigripes* was reduced under elevated temperatures in the winter experiment ($p = 0.004$, Appendix S1: Table S7), but not the summer experiment (Appendix S1:

Table S8). Meanwhile, elevated temperatures reduced the tissue nitrogen content of *N. fimbriatum* in both winter ($p = 0.005$, Appendix S1: Table S9) and summer ($p = 0.007$, Appendix S1: Table S10) experiments compared to control treatments. There was no effect of either pH or the interaction of temperature and pH on %N of *H. nigripes* or *N. fimbriatum* in either season. Similar to *H. nigripes*, nitrogen content of *M. pyrifera* tissue in the winter experiment was lower under elevated temperatures than in control conditions ($p < 0.001$, Appendix S1: Table S11), but was not affected by OW in the summer experiment. *M. pyrifera* was unique among the three kelps in that its nitrogen content was increased in the winter OA treatment relative to winter control conditions ($p = 0.003$), although there was no interaction between pH and temperature. Because the effects of pH and temperature on *M. pyrifera*'s %N in winter were similar in magnitude but opposite in 'direction', %N of *M. pyrifera* tissue grown under the combined OW and OA treatment was not statistically distinguishable from tissue grown in control conditions ($p = 0.577$). In the summer experiment, *M. pyrifera* %N was not affected by temperature, pH, or the interaction between factors (Appendix S1: Table S12).

$\delta^{13}C$ values

Ocean acidification treatments reduced thalli $\delta^{13}C$ values relative to control treatments in both seasons for *H. nigripes* (winter: $p < 0.001$, Appendix S1: Table S13; summer: $p = 0.004$, Appendix S1: Table S14) and *N. fimbriatum* (winter: $p = 0.001$, Appendix S1: Table S15; summer: $p < 0.001$, Appendix S1: Table S16)(Fig. 3). In contrast, tissue $\delta^{13}C$ values of *M. pyrifera* were not reduced under low pH conditions in the winter experiment (Appendix S1: Table S17), but were reduced under OA relative to control treatments in the summer experiment ($p = 0.004$, Appendix S1: Table S18). Elevated temperatures also impacted *H. nigripes*' tissue $\delta^{13}C$ values, but in a different manner in each season. In the winter experiment, $\delta^{13}C$ values of *H.*

388 *nigripes*' thalli grown in higher temperatures were elevated compared to $\delta^{13}C$ values of thalli in
389 control treatments ($p = 0.031$), whereas $\delta^{13}C$ values of *H. nigripes*' thalli in summer experiment
390 OW conditions were reduced relative to controls ($p = 0.006$). We did not detect an interactive
391 effect of pH and temperature on *H. nigripes*' tissue $\delta^{13}C$ in either season. There was no effect of
392 OW or the interaction between OW and OA on the $\delta^{13}C$ values of *N. fimbriatum* or *M. pyrifera*
393 in either experiment.

394 *Algal palatability assays*

395 Palatability of *H. nigripes'* tissue differed between treatment and season (Appendix S1: Table
396 S19; interaction between treatment and season: $p = 0.051$). Urchins consumed over 30% more *H.*
397 *nigripes'* tissue grown in future summer OW and OA than tissue grown under controls in the
398 summer experiment (Fig. 4; $p = 0.024$). Conversely, urchins consumed similar quantities of *H.*
399 *nigripes* tissue from the winter experiment, regardless of the treatment conditions during growth
400 ($p = 0.969$). There was no effect of pH and temperature treatment, season, or their interaction on
401 the palatability of *N. fimbriatum* tissue (Appendix S1: Figure S2; Appendix S1: Table S20).
402

403 **Discussion**

404 Our study indicates that in high latitude coastal systems, future ocean warming will decrease the
405 growth and nutritional content of certain kelps while ocean acidification will primarily drive
406 changes in species' carbon use strategy. We also found that kelps' responses to future shifts in
407 temperature and carbonate chemistry will depend on the seasonal environmental context,
408 including the relative availability of light and nutrients in each season. Furthermore, these
409 overlapping environmental drivers may indirectly affect higher order consumers via changes to
410 seaweed palatability in certain seasons. Given the inherent differences in distributions, life

histories, and annual production dynamics among the subtidal kelps in this study (Bell & Kroeker, 2022; Dankworth et al., 2020; Schiel & Foster, 2015), we were unsurprised to find that seasonal scenarios of ocean warming and acidification elicited distinct responses in each macroalgal species. This research demonstrates that changing environmental conditions will shift the seasonal quality and quantity of basal resources in kelp ecosystems at high latitudes, likely reducing the functional biodiversity of these communities (Schlenger et al., 2021). Prior research in this system identified that future winter seasons may represent a period of vulnerability for calcified consumers, due to the overlap of enhanced physiological stress from low pH/high pCO_2 seawater at a time when macroalgal food supply is naturally at an annual minimum (Bell & Kroeker, 2022; Kroeker et al., 2021). Our research expands this projection by revealing that consumers' stress in future winters may be compounded by pronounced reductions in macroalgal biomass and nutritional content primarily due to warming in this season.

Of the three kelps we considered, the high latitude endemic *H. nigripes* was the only species to exhibit reduced growth under ocean warming scenarios in both winter and summer experiments. Optimal temperatures for growth and gametogenesis in this species have been shown to occur at ≤ 10°C and decline above 15°C (Druehl, 1967; Franke et al., 2021; Longtin & Saunders, 2016). Indeed, current in situ productivity of *H. nigripes* declines dramatically starting in August in Sitka Sound (Bell & Kroeker, 2022), and our sensor data reveal this is just as seawater temperatures approach 15°C. Elevated temperatures in summer with ocean warming are likely to extend this seasonal period of reduced growth for *H. nigripes* in the future. Additionally, *H. nigripes*' low growth in the winter experiment under a future OW scenario of 11°C suggests that other environmental variables such as relative light availability and nutrient supply may interact with temperature to define this species' seasonal thermal optima.

Distinct from *H. nigripes*, growth of the other two, more temperate, kelp species was not vulnerable to the elevated temperatures expected in future winters. The understory kelp *N. fimbriatum* displayed reduced growth only under summer OW conditions. In Sitka Sound, growth of *N. fimbriatum* thalli is observed year-round, although blade extension rates are generally higher in summer than winter (Bell & Kroeker, 2022). While future summer OW conditions may challenge the thermal tolerance of this species during the warmest months of the year, its capacity for continuous production in this system could buffer a reduction in its growth in this particular season. Growth of the giant kelp *M. pyrifera* was unaffected by OW scenarios in either seasonal experiment, suggesting that production of this species may be resilient to future warming during future winter and summers at high latitudes. Sitka Sound is situated at the poleward edge of *M. pyrifera*'s continuous range extent (Druehl, 1970, 1981). Although intrapopulation variation in thermal tolerance has been observed in this species (Hollarsmith et al., 2020), these northern fringing *M. pyrifera* populations may possess enough phenotypic plasticity to afford a relative tolerance to anticipated OW conditions in this region (Becheler et al., 2022; King et al., 2020).

In contrast to the species-specific responses of growth rate to future environmental conditions, all three kelps in this study exhibited reduced tissue nitrogen content under winter scenarios of ocean warming. Currently in Sitka Sound, kelp nitrogen content increases in winter due to the ample seawater nutrient supply and low energetic requirements during this season of low light and low temperature (Bell & Kroeker, 2022). While the energetic expense of nutrient acquisition can be limited by low light levels (Hurd et al., 2014; Roleda & Hurd, 2019), some kelps, including *H. nigripes* and *M. pyrifera,* readily uptake nitrate at equal or higher rates in the dark compared to the light by mobilizing carbohydrate reserves (Harrison et al., 1986; Korb &

Gerard, 2000; Wheeler & Srivastava, 1984). However, the additional metabolic demand for nutrients that can occur under elevated temperatures may undermine these kelps' ability to maintain nitrogen reserves in their tissues even when nutrients are replete, as has been seen in temperate and Arctic populations of *Saccharina latissima* (Olischläger et al., 2014). Our results underscore the unexpected vulnerability of these high latitude kelps to nutritional depletion during a season associated with plentiful nutrient supply, even when projected future winter temperatures fall well within their current annual thermal range.

Seasonal differences in OW's impact on kelp nitrogen content likely arise from an interaction between environmental nutrient supply, temperature, and light on kelps' nitrogen uptake kinetics and usage (Endo et al., 2017; Mabin et al., 2019). As far as we are aware, there are few other studies that have considered the impact of OW on kelp nutritional content specifically under winter conditions of high nutrients combined with temperatures on the lower end of species' annual thermal range. More commonly, prior research has been set up similar to our summer experiment and reflect our results for *H. nigripes* and *M. pyrifera* in these conditions: OW treatments are chosen to exceed kelps' annual thermal maxima under low to moderate nitrogen concentrations (0.5-3 uM NOx), and these scenarios have no impact on kelp tissue nitrogen content (e.g., Brown et al., 2014; Mabin et al., 2019). Yet, we find it surprising that summer OW conditions had no effect on any of *M. pyrifera*'s measured physiological responses, given the documented vulnerability of this species to high temperature and low nutrient conditions in other studies (Schmid et al., 2020; Umanzor et al., 2021). We suspect that the results of our summer experiment may have been unintentionally influenced by a supplemental supply of nutrients to our system. The intake for our experimental system drew seawater just offshore from a natural river mouth, which was distinguished by an accumulation of decomposing salmon carcasses

during the second half of our summer experiment. We believe the concentrated outflow of nutrients from these fish in river water (authors' unpublished data) was picked up by our system's intake, leading to elevated ammonium concentrations in our aquaria compared to typical summer seawater nutrient concentrations in situ (Bell & Kroeker, 2022, and this study). We also interpret that the higher mean tissue nitrogen content of the kelps grown in these aquaria compared to observed nitrogen content of kelps at this time of year in situ (Bell & Kroeker, 2022) reflects how readily the macroalgae assimilated this supply of ammonium (Cedeno et al., 2021; Hurd et al., 2014). Therefore, the apparent resilience of kelps in our study to summer heat stress may have been due to the added heat tolerance conferred by having relatively high nitrogen reserves (Fernández et al., 2020; Gerard, 1997; Schmid et al., 2020). We anticipate that under a more realistic simulation of seasonal environmental nutrient depletion, the negative effects of OW on kelp physiology may have been more pronounced in future summer scenarios. Subtidal kelps can experience substantial fluctuations in light that were not captured in this experiment. Many high latitude seaweeds' photosynthesis saturation points occur at much higher irradiances than are required for growth, enabling these species to capitalize on enhanced carbon assimilation under large fluctuations in light (Gómez et al., 2009; Scheschonk et al., 2019; Wiencke et al., 2009). Thus, the lack of variability in our light levels might have contributed to the lower growth rates observed for *H. nigripes* in the winter experiment compared to a field setting (Bell & Kroeker, 2022). Moreover, a greater supply of light could improve *H. nigripes*' resilience to elevated temperatures in winter (Andersen et al., 2013; Nejrup et al., 2013). In view of the potential consequences that reduced *H. nigripes* biomass could represent for consumers in future winters, we advise further research into the interactive effects of light availability and OW on this species' production.

The clear response of all three kelp species' $\delta^{13}C$ values to OA conditions suggests that these kelps capitalize on enhanced CO_2 availability to optimize their carbon acquisition strategies. Presumably, the reduced $\delta^{13}C$ values indicate a downregulation of carbon concentrating activity with concomitant energetic savings (Cornwall et al., 2012, 2015; Hepburn et al., 2011). However, this spare energy did not appear to be consistently invested into new growth, except perhaps by ameliorating the negative impacts of OW on *H. nigripes* growth under winter conditions. In *M. pyrifera*, an increase in tissue nitrogen content under winter OA conditions indicates that this extra energy may have been mobilized to enhance nutrient uptake and assimilation. Intriguingly, this effect compensated for reduced nitrogen content under elevated winter temperatures when the two treatments were applied in tandem, suggesting a mitigating effect of OA on *M. pyrifera*'s nitrogen utilization in warmer future winters. Aside from these results, it is unclear whether the potential energetic benefits of OA conditions may lead to other ecologically consequential changes for these kelp species.

Our results also suggest that the combination of OW and OA may have biochemical effects on algal palatability beyond what we considered in our study. The increase in urchins' consumption of *H. nigripes* tissue grown in future summer ocean conditions could indicate a decrease in secondary metabolites, causing the algae to be more susceptible to grazing (Arnold et al., 2012; Hemmi & Jormalainen, 2002; Swanson & Fox, 2007). Increased grazing could also result from a decrease in nutritional quality in the seaweed blade, causing compensatory feeding (Cruz-Rivera & Hay, 2000; L. Falkenberg et al., 2014; Rodríguez et al., 2018). While we did not observe an effect of summer OA and OW on *H. nigripes*' nitrogen content, reduced nutritional value could also be driven by a decrease in fatty acid, lipid, or mineral content (Britton et al., 2020; Zhang et al., 2021). Our feeding assay results only begin to hint at the additional effects that OA and OW

may have on macroalgal physiochemical structure, and they reinforce the importance of testing the emergent effects of environmental change on food web interactions (Jin et al., 2020; Jin & Gao, 2021).

Altogether, our experimental results for these three common canopy-forming subtidal kelp species paint a picture of how the macroalgal energy supply in this system may shift in the future. Our finding that future warming had a greater impact than ocean acidification on the growth and nutritional quality of high latitude kelps is consistent with studies of macroalgae in other high latitude and subtropical habitats (Graba-Landry et al., 2018; Wahl et al., 2020). The vulnerability of the pan-Arctic understory species *H. nigripes* is particularly noteworthy. In the winter, the reduction of both the biomass and quality of this species could represent an energetically devastating loss for calcified rocky reef consumers facing additional metabolic stress associated with OA in the future (Kroeker et al., 2021). Meanwhile, high latitude populations of the more temperate kelp species *M. pyrifera* may be relatively resilient to the effects of OA and OW. Giant kelp may therefore continue to dominate total macroalgal production on reefs where it forms the surface canopy (Bell & Kroeker, 2022). However, consumers cannot rely on this species alone to fulfill their nutritional needs (Kroeker et al., 2021). Thus, the combination of OA and OW threatens not only the functional biodiversity of the macroalgal community on these high latitude reefs, but also the resilience of the consumer community that depends on their production.

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Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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989 **Tables**

990 Table 1: Seawater conditions in experimental aquaria by treatment and seasonal experiment.

	Winter Experiment				Summer Experiment			
	Control	OA	OW	OA & OW	Control	OA	OW	OA & OW
Dissolved Oxygen (mg/L)	9.5±0.9	9.3±1.2	8.5±1.4	8.4±1.5	8.5±0.2	8.4±0.2	7.9±0.3	7.8±0.2
Salinity (ppt)	31.3±0.3	31.4±0.3	31.3±0.3	31.4±0.3	31.0±0.2	31.0±0.2	31.1±0.2	31.1±0.2
Temperature (°C)	7.2±0.1	7.3±0.1	10.9±0.7	10.9±0.6	14.1±0.1	14.2±0.1	18.0±0.9	18.0±0.8
pH_T	7.65±0.01	7.21±0.01	7.66±0.01	7.28±0.01	7.88±0.01	7.46±0.02	7.84±0.01	7.51±0.02
*p*CO2 (µatm)	1011±22	2843±87	1001±23	2502±50	592±21	1667±103	648±14	1513±67
TA (µmol/kg)	2120±15	2122±14	2121±15	2125±14	2116±5	2116±5	2116±5	2115±5
$[NO_3^-]$	16.3±1.3				3.7±0.4			
$[NH_4^+]$	4.8±1.0				10.3±1.4			

991

992 *Note:* Parameters are summarized as the mean ± standard error for all replicate aquaria over the

993 course of the experiments. Temperature, salinity, and dissolved oxygen were measured daily in

994 all experimental aquaria. pH_T, pCO_2, TA, and nutrient concentrations were determined from

995 discrete water samples taken in aquaria at the beginning, middle, and end of each experiment.

Figure Captions

Figure 1: Relative growth rates (RGR_{mass}; mean ± SE) of three kelp species exposed to different treatment combinations of ocean acidification (OA) and warming (OW) within month-long laboratory experiments in winter and summer (N= 18 individuals species^{-1} treatment^{-1}).

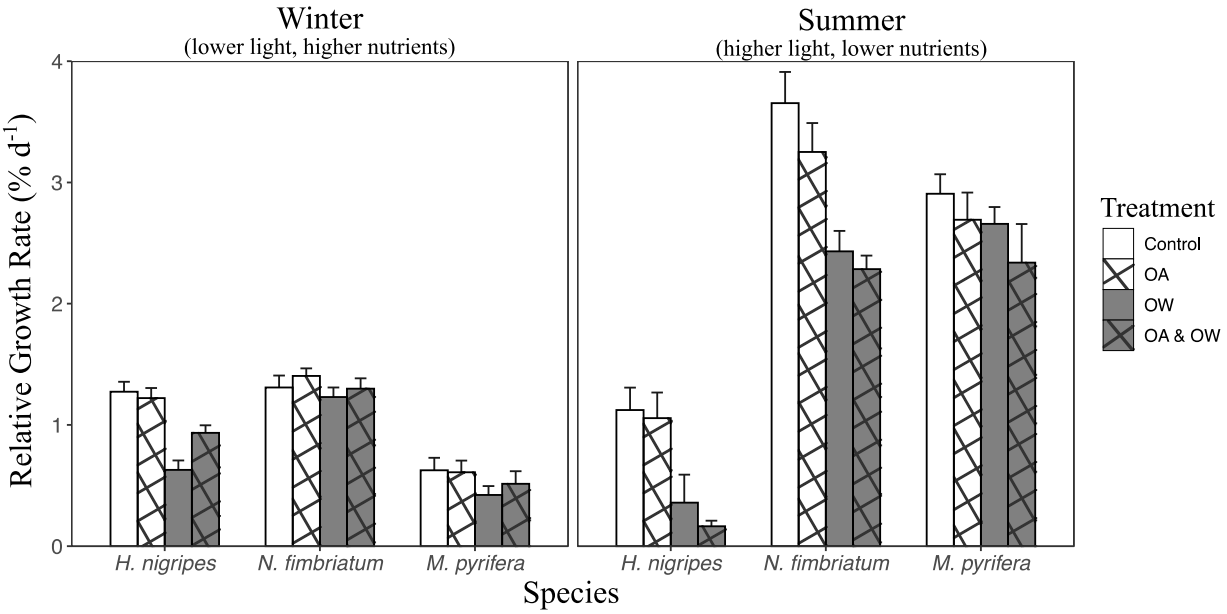
Figure 2: Tissue nitrogen content (%N; mean ± SE) of three kelp species exposed to different treatment combinations of ocean acidification (OA) and warming (OW) within month-long laboratory experiments in winter and summer (N= 18 individuals species^{-1} treatment^{-1}).

Figure 3: $\delta^{13}C$ values (‰; mean ± SE) of three kelp species exposed to different treatment combinations of ocean acidification (OA) and warming (OW) within month-long laboratory experiments in winter and summer (N= 18 individuals species^{-1} treatment^{-1}). The dotted line at a $\delta^{13}C$ value of -30 ‰ is the putative threshold below which macroalgae exclusively rely on diffusive uptake of CO_2 and no longer invest energy in carbon concentrating mechanisms (Raven et al. 2002).

Figure 4: Relative consumption (mean ± SE) of experimentally grown *H. nigripes* tissue in feeding assays used to test the seasonal effects of pH and temperature treatment on the palatability of algal tissue to a common kelp forest grazer. Lower case letters denote statistically significant differences among algal treatments.

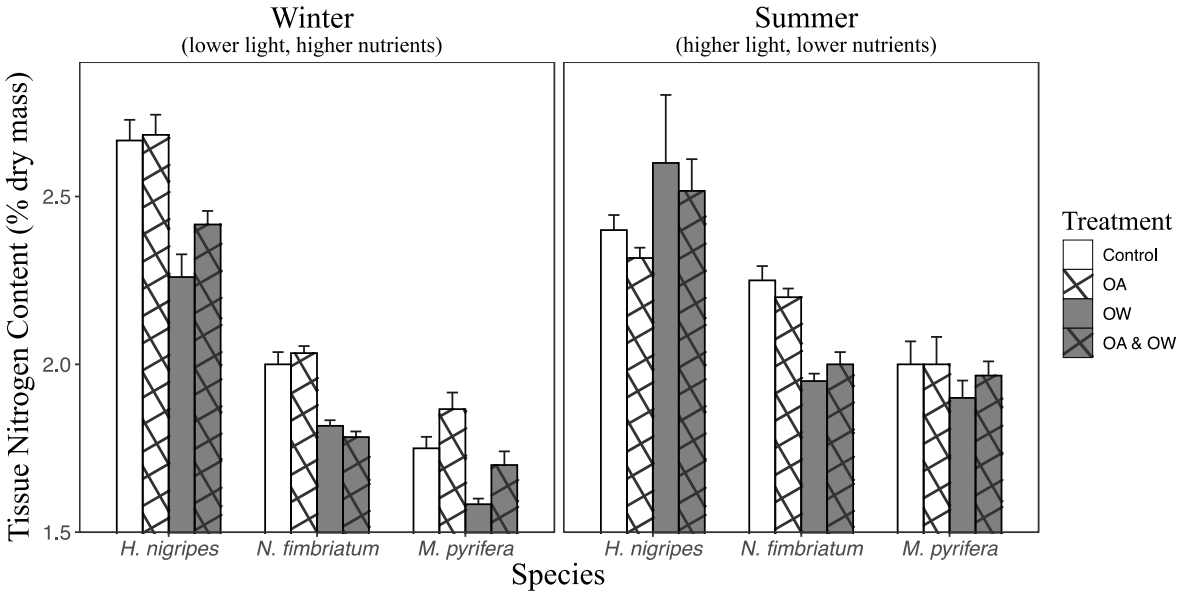
1016 **Figures**

1017 Figure 1

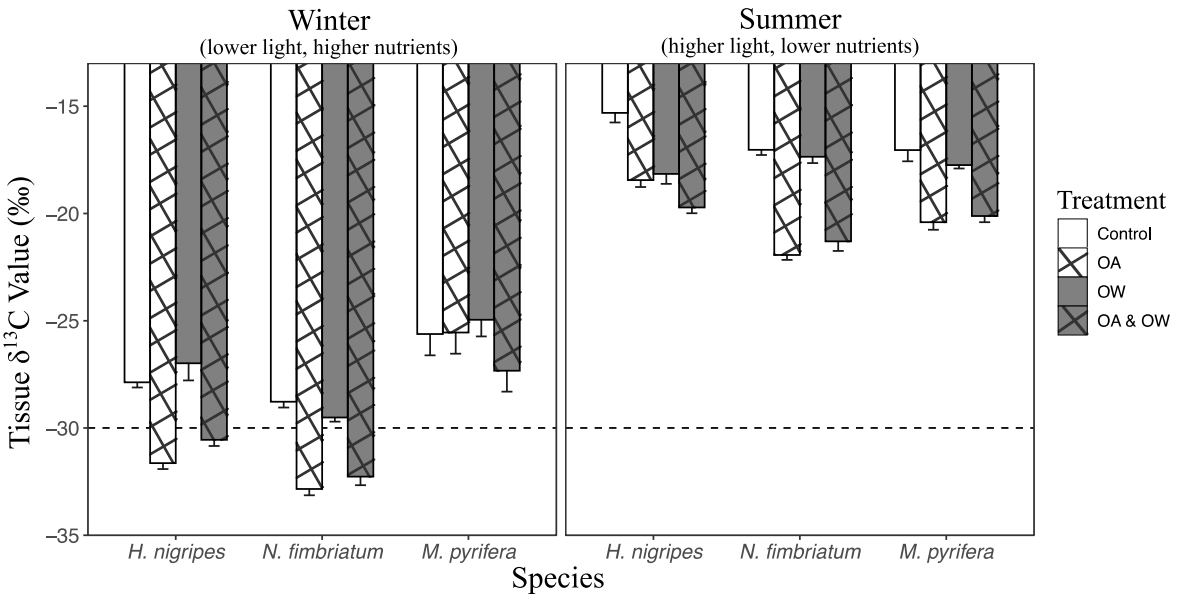


1018

Figure 2

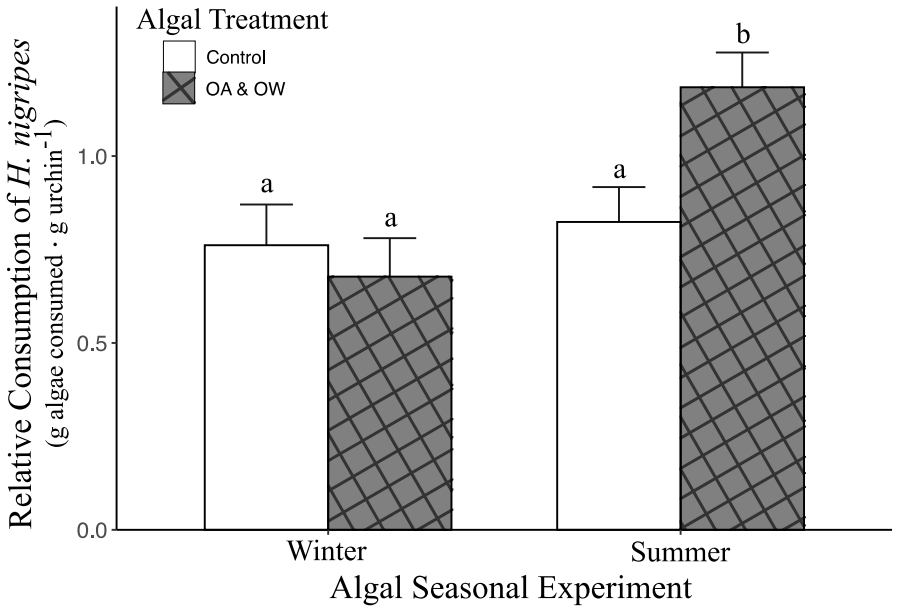


1021 Figure 3



1022

1023 Figure 4



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Appendix S1
Bell, L. E., L. Westphal, E. O'Brien, J. A. Toy, H. Damron, K. J. Kroeker, "Season Influences Interspecific Responses of Canopy-Forming Kelps to Future Warming and Acidification at High Latitude", *Ecosphere*

Figure S1. Linear blade extension rates of understory kelp species by treatment in seasonal experimental conditions (this study) compared to seasonal growth rates observed in situ at kelp forest sites in Sitka Sound (data from Bell and Kroeker 2022). Boxplots represent the data median, interquartile range, and any outliers for each group.

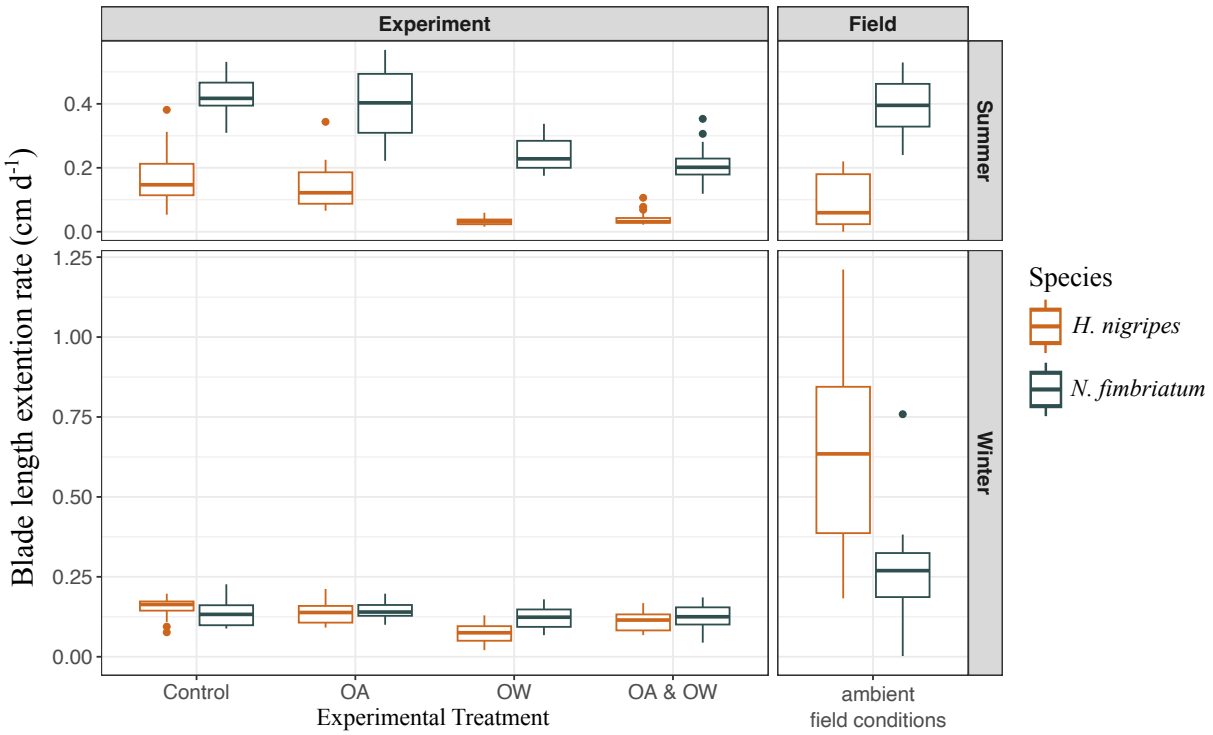

Figure S2. Relative consumption (mean ± SE) of experimentally grown *N. fimbriatum* tissue in feeding assays used to test the effects of seasonal pH and temperature treatment on the palatability of algal tissue to a common kelp forest grazer.

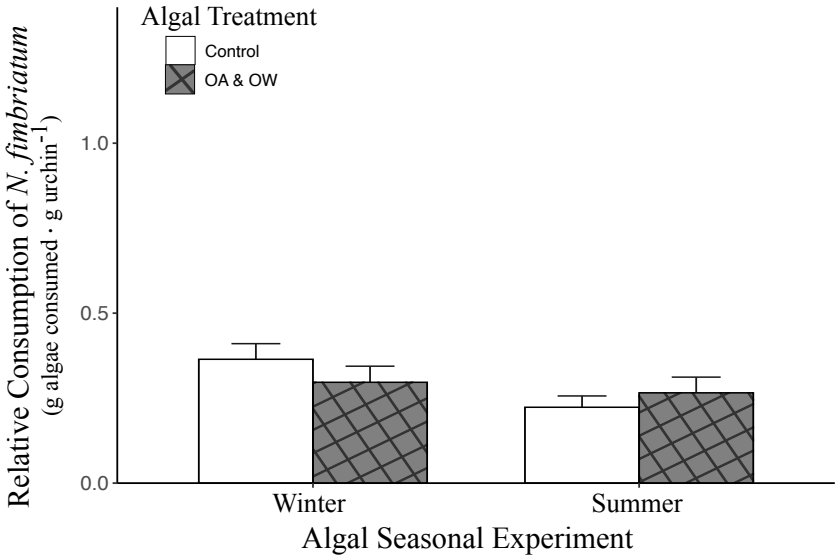

Table S1. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' relative growth rate as wet mass (% d^{-1}) by treatment in winter season experiment. Formula: *H. nigripes* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	Variance	Std. Dev.
aquaria:header	0.013	0.113
header	0.000	0.000
residual	0.092	0.303

Number of observations: 69
Groups: aquaria:header, 24; header, 8

ii. *ANOVA results from the mixed linear model*

Source	SS	MSE	numDF	denDF	F value	Pr(>F)
pH	0.187	0.187	1	18.87	2.038	0.170
temperature	2.601	2.601	1	18.87	28.42	**< 0.001**
pH:temperature	0.377	0.377	1	18.87	4.116	**0.057**

iii. Post-hoc pairwise contrasts among treatment levels

Treatment Contrasts	Estimate	SE	df	t ratio	p value
Control – OA	0.052	0.120	17.8	0.433	0.972
Control – OW	0.636	0.123	19.3	5.173	**< 0.001**
Control – OA & OW	0.338	0.122	18.5	2.777	**0.054**
OA – OW	0.584	0.123	19.3	4.750	**< 0.001**
OA – OA & OW	0.286	0.122	18.5	2.349	0.122
OW – OA & OW	-0.299	0.124	19.9	-2.404	0.109

Table S2. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' relative growth rate as wet mass (% d^{-1}) by treatment in summer season experiment. Formula: *H. nigripes* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
aquaria:header	0.000	0.000
header	0.000	0.000
residual	0.585	0.765

Number of observations: 68
Groups: aquaria:header, 24; header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.289	0.289	1	64	0.495	0.485
temperature	11.59	11.59	1	64	19.83	**< 0.001**
pH:temperature	0.069	0069	1	64	0.118	0.732

Table S3. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s % change in wet mass (% d^{-1}) by treatment in winter season experiment.
Formula: *N. fimbriatum* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
aquaria:header	0.000	0.000
header	0.000	0.000
residual	0.124	0.352

Number of observations: 72
Groups: aquaria:header, 24; header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.121	0.121	1	68	0.979	0.326
temperature	0.152	0.152	1	68	1.228	0.272
pH:temperature	0.003	0.003	1	68	0.026	0.873

Table S4. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s relative growth rate as wet mass (% d^{-1}) by treatment in summer season experiment.
Formula: *N. fimbriatum* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
aquaria:header	0.000	0.000
header	0.000	0.000
residual	0.739	0.860

Number of observations: 63
Groups: aquaria:header, 21; header, 7

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	1.089	1.089	1	59	1.472	0.230
temperature	17.25	17.25	1	59	23.33	**< 0.001**
pH:temperature	0.235	0.235	1	59	0.317	0.575

Table S5. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s relative growth rate as wet mass (% d^{-1}) by treatment in winter season experiment. Formula: *M. pyrifera* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	Variance	Std. Dev.
aquaria:header	0.000	0.000
header	0.013	0.114
residual	0.138	0.371

Number of observations: 60
Groups: aquaria:header, 24; header, 8

ii. *ANOVA results from the mixed linear model*

Source	SS	MSE	numDF	denDF	F value	Pr(>F)
pH	0.212	0.212	1	4.219	0.154	0.714
temperature	0.196	0.196	1	4.219	1.420	0.296
pH:temperature	0.032	0.032	1	4.219	0.229	0.656

Table S6. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s relative growth rate as wet mass (% d^{-1}) by treatment in summer season experiment. Formula: *M. pyrifera* RGR_{mass} ~ pH * temperature + (1|header/aquaria)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
aquaria:header	<0.001	0.013
header	0.000	0.000
residual	0.853	0.924

Number of observations: 70
Groups: aquaria:header, 24; header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	1.248	1.248	1	20.69	1.462	0.240
temperature	1.580	1.580	1	20.69	1.851	0.188
pH:temperature	0.049	0.049	1	20.69	0.060	0.812

Table S7. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' tissue nitrogen content (as % dry mass) by treatment in winter season experiment.
Formula: *H. nigripes* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.0002	0.014
residual	0.019	0.138

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.042	0.042	1	4.180	2.196	0.210
temperature	0.628	0.628	1	4.180	33.18	**0.004**
pH:temperature	0.027	0.027	1	4.180	1.432	0.295

Table S8. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' tissue nitrogen content (as % dry mass) by treatment in summer season experiment.
Formula: *H. nigripes* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.009	0.096
residual	0.057	0.238

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.023	0.023	1	3.191	0.401	0.569
temperature	0.145	0.145	1	3.191	2.561	0.203
pH:temperature	0.0002	0.0002	1	3.191	0.003	0.957

Table S9. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s tissue nitrogen content (as % dry mass) by treatment in winter season experiment.
Formula: *N. fimbriatum* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.002	0.049
residual	0.002	0.046

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.000	0.000	1	4	0.000	1.000
temperature	0.064	0.064	1	4	30.73	**0.005**
pH:temperature	0.002	0.002	1	4	0.727	0.442

Table S10. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s tissue nitrogen content (as % dry mass) by treatment in summer season experiment.
Formula: *N. fimbriatum* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.003	0.057
residual	0.005	0.068

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.000	0.000	1	4	0.000	1.000
temperature	0.121	0.121	1	4	26.47	**0.007**
pH:temperature	0.005	0.005	1	4	1.059	0.362

Table S11. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s tissue nitrogen content (as % dry mass) by treatment in winter season experiment.
Formula: *M. pyrifera* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.000	0.000
residual	0.008	0.087

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.092	0.092	1	19	12.04	**0.003**
temperature	0.140	0.140	1	19	18.42	**<0.001**
pH:temperature	0.001	0.001	1	19	0.075	0.787

iii. Custom post-hoc contrast between responses of algae grown in the control treatment versus the combined OW & OA treatment

Treatment Contrast	**Estimate**	**SE**	**df**	**t ratio**	**p value**
OW & OA – Control	-0.03	0.053	19	-0.568	0.577

Table S12. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s tissue nitrogen content (as % dry mass) by treatment in summer season experiment.
Formula: *M. pyrifera* tissue %N ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.005	0.069
residual	0.021	0.144

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	0.004	0.004	1	4	0.191	0.685
temperature	0.016	0.016	1	4	0.762	0.432
pH:temperature	0.004	0.004	1	4	0.191	0.685

Table S13. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' tissue $\delta^{13}C$ values by treatment in winter season experiment.
Formula: *H. nigripes* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.000	0.000
residual	1.023	1.011

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	76.78	76.78	1	19	75.07	**<0.001**
temperature	5.589	5.589	1	19	5.465	**0.031**
pH:temperature	0.056	0.056	1	19	0.055	0.817

Table S14. Summary statistics from mixed linear model analysis of *Hedophyllum nigripes*' tissue $\delta^{13}C$ values by treatment in summer season experiment.
Formula: *H. nigripes* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.006	0.080
residual	0.825	0.908

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	30.82	30.82	1	3.870	37.45	**0.004**
temperature	23.73	23.73	1	3.870	28.75	**0.006**
pH:temperature	3.417	3.417	1	3.870	4.140	0.114

Table S15. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s tissue $\delta^{13}C$ values by treatment in winter season experiment.
Formula: *N. fimbriatum* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.208	0.456
residual	0.404	0.635

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	27.50	27.50	1	4	68.10	**0.001**
temperature	0.015	0.015	1	4	0.037	0.858
pH:temperature	1.019	1.019	1	4	2.523	0.187

Table S16. Summary statistics from mixed linear model analysis of *Neoagarum fimbriatum*'s tissue $\delta^{13}C$ values by treatment in summer season experiment.
Formula: *N. fimbriatum* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.236	0.486
residual	0.454	0.674

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	45.94	45.94	1	4	101.1	**<0.001**
temperature	0.056	0.056	1	4	0.123	0.744
pH:temperature	0.539	0.539	1	4	1.186	0.337

Table S17. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s tissue $\delta^{13}C$ values by treatment in winter season experiment.
Formula: *M. pyrifera* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.000	0.000
residual	4.927	2.168

Number of observations: 23
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	8.779	8.779	1	19	1.868	0.188
temperature	2.386	2.386	1	19	0.508	0.485
pH:temperature	9.799	9.799	1	19	2.085	0.165

Table S18. Summary statistics from mixed linear model analysis of *Macrocystis pyrifera*'s tissue $\delta^{13}C$ values by treatment in summer season experiment.
Formula: *M. pyrifera* $\delta^{13}C$ ~ pH * temperature + (1|header)

i. *Variance components for random effects*

Groups	**Variance**	**Std. Dev.**
header	0.297	0.545
residual	0.591	0.769

Number of observations: 24
Groups: header, 8

ii. *ANOVA results from the mixed linear model*

Source	**SS**	**MSE**	**numDF**	**denDF**	**F value**	**Pr(>F)**
pH	19.68	19.68	1	4	33.31	**0.004**
temperature	0.103	0.103	1	4	0.174	0.698
pH:temperature	0.584	0.584	1	4	0.989	0.376

Table S19. Summary statistics from analysis of the relative consumption of *H. nigripes* by pH and temperature treatment and seasonal experiment.

i. Two-way ANOVA results for relative consumption

Source	**SS**	**MSE**	**DF**	**F value**	**Pr(>F)**
Treatment	0.831	0.831	1	4.571	**0.036**
Season	1.245	1.245	1	6.848	**0.011**
Treatment:Season	0.720	0.720	1	3.964	**0.051**

ii. Tukey's post-hoc tests comparing the effects of seasonal experiment and combined pH and temperature treatment on relative consumption

Condition1	**Condition2**	**Mean diff**	**95% CI lower**	**95% CI upper**	**P_{tukey}**
Summer OW+OA	*Summer Control*	0.360	0.036	0.685	**0.024**
Winter Control	*Summer Control*	-0.062	-0.485	0.361	0.980
Winter OW+OA	*Summer Control*	-0.146	-0.556	0.263	0.782
Winter Control	*Summer OW+OA*	-0.423	-0.846	0.000	**0.050**
Winter OW+OA	*Summer OW+OA*	-0.507	-0.916	-0.098	**0.009**
Winter OW+OA	*Winter Control*	-0.084	-0.575	0.407	0.969

Table S20. Summary statistics from analysis of the relative consumption of *N. fimbriatum* by pH and temperature treatment and seasonal experiment.

i. Two-way ANOVA results for relative consumption

Source	**SS**	**MSE**	**DF**	**F value**	**Pr(>F)**
Treatment	0.001	0.001	1	0.011	0.915
Season	0.163	0.163	1	3.475	0.067
Treatment:Season	0.067	0.067	1	1.421	0.238

References

Bell, L. E., and K. J. Kroeker. 2022. "Standing Crop, Turnover, and Production Dynamics of *Macrocystis pyrifera* and Understory Species *Hedophyllum nigripes* and *Neoagarum fimbriatum* in High Latitude Giant Kelp Forests." *Journal of Phycology* 58(6): 773–788. https://doi.org/10.1111/jpy.13291