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Biological Sciences

Impacts of ocean acidification on the palatability of two Antarctic macroalgae and the consumption of a grazer

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Abstract

Increases in atmospheric CO_2 have led to more CO_2 entering the world's oceans, decreasing the pH in a process called 'ocean acidification'. Low pH has been linked to impacts on macroalgal growth and stress, which can alter palatability to herbivores. Two common and ecologically important macroalgal species from the western Antarctic Peninsula, the unpalatable *Desmarestia menziesii* and the palatable *Palmaria decipiens*, were maintained under three pH treatments: ambient (pH 8.1), near future (7.7) and distant future (7.3) for 52 days and 18 days, respectively. Discs of *P. decipiens* or artificial foods containing extracts of *D. menziesii* from each treatment were presented to the amphipod *Gondogeneia antarctica* in feeding choice experiments. Additionally, *G. antarctica* exposed to the different treatments for 55 days were used in a feeding assay with untreated *P. decipiens*. For *D. menziesii*, extracts from the ambient treatment were eaten significantly more by weight than the other treatments. Similarly, *P. decipiens* discs from the ambient and pH 7.7 treatments were eaten more than those from the pH 7.3 treatment. There was no significant difference in the consumption by treated *G. antarctica*. These results suggest that ocean acidification may decrease the palatability of these macroalgae to consumers but not alter consumption by *G. antarctica*.

Keywords: Chemical defence; climate change; herbivory; ocean acidification; seaweed

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Introduction

Human-derived emissions from the combustion of fossil fuels, the production of cement and deforestation have led to a drastic increase in atmospheric CO_2 (Malhi *et al.* 2002, Heede 2014, Paraschiv & Paraschiv 2020). In 2019 alone, ~98.2 Mt CO_2 were added to the atmosphere daily (Liu *et al.* 2020). The culmination of decades of emissions since the Industrial Revolution has increased atmospheric CO_2 concentrations by ~50% from 280 ppm in 1750 to a peak of 420 ppm in 2024 (Joos & Spahni 2008, Lan & Keeling 2024).

One consequence of increased atmospheric CO_2 concentrations is ocean acidification (OA). Approximately a third of atmospheric CO_2 enters the ocean (Sabine *et al.* 2004, Gruber *et al.* 2019), where it reacts with seawater in a series of steps that ultimately release free hydrogen ions, thereby lowering pH. As a result of this gaseous uptake, the average ocean's surface pH has decreased by 0.1 pH units and is predicted to decrease a further 0.4 pH units over the next 80 years (IPCC 2022).

Changes in abiotic factors from climate change, particularly decreased ocean pH, can have a direct impact on the physiology and behaviour of marine organisms (Kroeker *et al.* 2013, Kindinger *et al.* 2022). These changes not only impact species individually but also impact the interactions between species, such as macroalgae-herbivore interactions. For example, OA can affect the growth rate (Johnson *et al.* 2014), tissue strength (Kinnby *et al.* 2021), nutritional quality (Duarte *et al.* 2016, Fieber & Bourdeau 2021) and putative chemical defences of macroalgae (Swanson & Fox 2007, Fieber & Bourdeau 2021, Kinnby *et al.* 2021). Similarly, OA can impact herbivores by altering growth (Sheppard Brennand *et al.* 2010, Bhuiyan *et al.* 2022), survival (Lopes *et al.* 2019, Park *et al.* 2020), development (Kurihara & Shirayama 2004, Watson *et al.* 2009, Place & Smith 2012) and reproduction (Kurihara & Shirayama 2004, Morita *et al.* 2010, Borges *et al.* 2018) and by shifting energy demands (Melzner *et al.* 2011, Saba *et al.* 2012, Ramajo *et al.* 2016, Lim & Harley 2018).

The consequences of OA on one species can impact the relationship between macroalgae and herbivores. For example, grazing pressure from invertebrates can become greater if energy demands on invertebrates increase from compensatory strategies in response to changing pH (Saba *et al.* 2012, Leung *et al.* 2018). Alternatively, grazing pressure could be altered from changes in the macroalgae, but the specific type of change is heavily dependent on the species and how the macroalga is being affected. For example, changes in nutritional quality or qualitative or quantitative changes in the production of chemical defences have been documented (Swanson & Fox 2007, Duarte *et al.* 2016, Fieber & Bourdeau 2021).

A significant portion of previous OA work has focused on calcifying species and communities (e.g. Andersson *et al.* 2011, Leung *et al.* 2022, Page *et al.* 2022), mainly due to the negative impacts of OA on the availability of carbonate and the alteration

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of seawater chemistry (Doney *et al.* 2009, Hurd *et al.* 2009) that reduce these organisms' ability to calcify. However, focusing on one functional group of macroalgae cannot provide a full picture of OA consequences on algae. Macroalgae are taxonomically and metabolically diverse (Li-Beisson *et al.* 2019, Tully 2019, Schubert *et al.* 2023, Guiry 2024), making it difficult to generalize regarding how they will respond as a whole to climate change based on a few studied species.

Fleshy macroalgal species are expected to be more resilient to increased CO_2 concentrations compared to calcified species because the former do not experience dissolution and have access to more CO_2 for photosynthesis (Koch *et al.* 2013), which has been supported by modelling (Schlenger *et al.* 2021). However, experiments have shown that the consequences of OA appear to be species-specific. Previous studies have found increases in net growth for some, but not all, of the fleshy macroalgae held under different conditions of OA (Johnson *et al.* 2014, Kram *et al.* 2016, Paine *et al.* 2023). In some cases, there have been contrasting results in net growth with OA conditions. For example, Swanson & Fox (2007) found that CO_2 levels predicted for 2100 resulted in a positive effect on the growth of the kelp *Nereocystis luetkeana* but a negative effect on the growth of the kelp *Saccharina latissimi*.

In addition to changes in net growth, shifts in chemical composition and photosynthesis as a response to lowered pH have also been observed in macroalgae (Garcia-Sanchez *et al.* 1994, Mercado *et al.* 1999, Gordillo *et al.* 2001, Duarte *et al.* 2016). Changes in chemical composition can alter the overall nutritional quality of macroalgae and can impact herbivore preference (Duarte *et al.* 2016). Furthermore, these changes in nutritional content can impact the consumers of algae (Urabe *et al.* 2003, Schoo *et al.* 2013, Sudo & Yoshida 2021, Sepúlveda *et al.* 2024). For example, the amphipod *Ampithoe tarasovi*, the sea urchin *Tetrapygus niger* and the sea snail *Tegula atra* experience reduced growth when fed a diet of lower-quality macroalgae (Sudo & Yoshida 2021, Sepúlveda *et al.* 2024).

High-latitude environments, such as the those of the western Antarctic Peninsula region (WAP; including islands to the west and north of the continental peninsula), are particularly vulnerable to decreased seawater pH due to the low buffering capacity associated with cold waters (Sabine *et al.* 2004, Nissen *et al.* 2024). The WAP is characterized by its large macroalgal forests that dominate shallow (< 70 m) benthic communities (Wiencke *et al.* 2014). These macroalgal communities contribute standing biomass levels comparable to temperate kelp forests, often covering more than 80% of the ocean benthos (Wiencke *et al.* 2014), and they play a vital role in nutrient cycling, nutrient retention and benthic food webs (Dunton 2001, Quartino & Boraso de Zaixso 2008, Wiencke & Amsler 2012, Iken *et al.* 2023). The dominant macroalgae in these communities are large, perennial browns from the family Desmarestiaceae, while the understory is dominated by smaller red macroalgae (Wiencke *et al.* 2014). In addition to producing large amounts of biomass, many of the macroalgae in these nearshore communities also produce chemical defences that protect them from herbivory (Amsler *et al.* 2020). Most of this macroalgal community is chemically defended, including all of the large browns and many of the common reds, with the notable exception of *Palmaria decipiens* (Amsler *et al.* 2005, Aumack *et al.* 2010). Despite their chemical defences, these macroalgae can serve as a food resource after they die and their former chemical defences break down (Wiencke & Amsler 2012).

One unique aspect of the WAP is the incredibly large number of mesograzers found in the macroalgal communities. Macroalgae shelter large mesograzer assemblages that mostly consist of amphipods with large numbers of gastropods and smaller numbers of isopods, copepods and ostracods (Iken 1999, Huang *et al.* 2007, Schram *et al.* 2016, Amsler *et al.* 2022). The density of amphipods on macroalgae in this region can be extremely abundant, with densities reaching as high as 300 000 and 26 000 individuals m^2 on the benthos in stands of *Desmarestia menziesii*, a dominant brown macroalga, and the red macroalga *Plocamium* sp., respectively (Huang *et al.* 2007, Amsler *et al.* 2008). These densities are approximately one to three times higher than reported amphipod densities in tropical and temperate regions (Amsler *et al.* 2014).

In the present study, we assessed how the palatability of two common macroalgae, *Desmarestia menziesii* J. Agardh and *Palmaria decipiens* (Reinsch) R. W. Ricker, is impacted by reduced seawater pH. These two species represent a chemically defended macroalga (*D. menziesii*) and a palatable macroalga (*P. decipiens*) that occur commonly in the community. Thalli of both species were exposed to three different pH treatments simulating ambient conditions (approximately pH 8.1), near-future conditions for 2100 (pH 7.7; IPCC 2022) and distant-future conditions (pH 7.3; IPCC 2022) and then used in a feeding assay with the common amphipod *Gondogeneia antarctica* (Chevreux). Additionally, we also conducted a feeding assay with *G. antarctica* exposed to the same pH treatments to determine whether there is an impact of pH on the amphipod's total consumption. *Gondogeneia antarctica* was selected because it is one of the most common amphipod species in this region (Huang *et al.* 2007) and is a very commonly studied WAP amphipod (e.g. Amsler *et al.* 2020, Park *et al.* 2020, Ahn *et al.* 2021). We hypothesized that the palatability of *P. decipiens* would increase while the palatability of *D. menziesii* would either increase or decrease due to reported increases in photosynthetic capacity and growth in several fleshy macroalgae species. Furthermore, we hypothesized that *G. antarctica* would demonstrate higher consumption at lowered pH due to a possible increase in energetic demands from compensatory strategies.

Materials and methods

Collection of macroalgae and amphipods

The shallow-water brown macroalga *D. menziesii* was collected from five sites near the US Antarctic Research Program's Palmer Station on Anvers Island on the WAP. Scuba divers collected *D. menziesii* from Palmer Station pier (S64°46.477', W64°03.274'), Hero Inlet (S64°46.569', W64°02.874'), Bonaparte Point (S64°46.745', W64°02.559'), Gamage Point (S64°46.432', W64°03.368') and Hermit Island (S64°47.880', W64°00.438'). *Desmarestia menziesii* samples were collected between 4 and 11 m on 19–27 December 2019 (Year 1) by cutting a ~85 g or larger section from an individual of *D. menziesii* with a knife and then placing the section into a fine mesh bag. *Palmaria decipiens* was collected between 2 and 8 m from Amsler Island (S64°46.487′, W64°03.262′) on 14 March 2023 (Year 2) by collecting small rocks with macroalgae attached and placing them in a mesh bag.

The collection bags were immediately placed in a 19 l bucket filled with seawater and transported to Palmer Station. *Desmarestia menziesii* was rinsed repeatedly with seawater in a series of fine mesh bags submerged in a tank of seawater to dislodge associated grazers. After the final rinse, the macroalgae were inspected to remove any remaining grazers by hand. The sections of *P. decipiens* were placed in a sorting tank. Each macroalga was visually inspected for grazers. Any grazers found were removed.

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Amphipods for the experiments were collected between 9 January 2023 and 18 February 2023 (Year 2) from multiple locations in the near vicinity of Palmer Station using the methods described by Huang *et al.* (2007). Briefly, macroalgal-associated crustaceans were collected by gently prying *D. menziesii* off the substrata with a knife then carefully floating the macroalga into a fine mesh bag to avoid disturbing the associated grazers. After being transported back to station, the grazers were removed from *D. menziesii* as described above. Then, the mesograzers were placed in a sorting table aquarium to separate *G. antarctica* from the rest of the mesograzers. A haphazard subset of these amphipods was used in the OA experiment. Another subset of the amphipods was held in an ambient flow-through tank in groups of ~200 individuals in bottles fitted with mesh windows to allow for water flow until they were used in the macroalgae feeding experiments.

Experimental set-up

A nearly identical experimental set-up was created for the Year 1 and Year 2 experiments. The experimental set-up consisted of 24 white plastic buckets of 19 l in volume placed on a submerged platform in two adjacent aquarium tanks (2.5 m diameter and 1 m depth; 3800 l) in the aquarium facility at Palmer Station (see Fig. S1). The facility was maintained on a 24 h light cycle in Year 1 and an ambient light cycle in Year 2, consistent with light availability at the time of collection. Both tanks were plumbed with ambient flow-through seawater to create a flow-through seawater bath to maintain an ambient temperature in all replicates. The tops of the buckets were elevated above the water level of the flow-through seawater.

Filtered seawater collected and flowed out of a common, constant head tank into a water distributor located in the centre of each water bath. Water flowed from the distributor to 12 mixing reservoirs arranged in a circle around the distributor. Along with an inflow water pipe, mixing reservoirs also contained a pH probe, a tube with mixed air and compressed CO_2 and a tube with compressed air alone to monitor and control the pH. After the seawater was adjusted to the desired pH in the mixing reservoirs (as described below), the seawater flowed into the experimental buckets. Finally, water flowed out of the bucket into the flow-through seawater bath.

There were eight buckets per pH treatment (ambient (8.1), 7.7 and 7.3). Seawater pH treatment levels were based on the average pH recorded for Palmer Station during collection (~8.1) and levels for the predicted near and distant future (IPCC 2022). The pH of the buckets was monitored throughout the experiment. Buckets in both decreased pH treatments were individually regulated with an automated pH monitoring system (AquaMedic, USA; Schoenrock *et al.* 2016, Schram *et al.* 2016). The target pH for each bucket was maintained by bubbling an air-CO_2 mixture or air alone into the mixing reservoirs as needed. The air-CO_2 mixture was created by combining ratios of air and CO_2 with a Multi-tube Gas Proportioning rotameter (Omega Engineering, Inc., Stamford, CT, USA) connected to a CO_2 cylinder and multiple air pumps.

The eight buckets for each pH treatment were randomly assigned within each water bath. Each water bath contained half of the replicates for each treatment to control for differences in light availability due to water bath location. The buckets had clear Plexiglass covers to reduce gas exchange with the atmosphere (Schram *et al.* 2016). In Year 2, some of the bucket lids were outfitted with screen mesh to equalize light levels inside of the buckets. The control seawater pH replicates received ambient air only.

Seawater samples from a quarter of the experimental buckets were collected for pH measurements (determined spectrophotometrically) and total alkalinity (TA; determined by potentiometric titration; Dickson *et al.* 2007) daily. This sampling method resulted in all buckets being tested over a 4 day cycle. In addition, the pH in all buckets was monitored at least once daily with a calibrated pH electrode.

In Year 1, seven thalli of *D. menziesii* were cut into three parts (one additional individual died and could not be used as planned). Each part of the macroalga was distributed into each of the pH treatments so that one individual was placed in the ambient, near-future and far-future treatments for comparison. After the macroalgae were placed in the buckets, the pH was slowly decreased in the lower pH treatments over a 28 h period. The experiment ran for a total of 52 days. At the end of the experiment, *D. menziesii* were removed from the experimental buckets and rinsed with seawater to remove epiphytes and grazers. Each macroalga was visually inspected to ensure epiphytes and grazers were fully removed. Each sample was then frozen in a −20°C freezer until processed.

In Year 2, individuals of *P. decipiens* were split into three parts. One third of each macroalga was distributed to each of the pH treatments. The macroalgae were placed inside clear plastic beakers with window screening mesh secured to the top of the beaker. This allowed for water flow while also protecting the macroalgae from grazing from amphipods in a concurrent experiment. The macroalgae were exposed to their respective pH treatments for 18 days. This macroalga had a shorter exposure period compared to *D. menziesii* because it is a pseudoperennial species with a relatively short-lived upright blade portion (Wiencke 1990, Weykam *et al.* 1997) and needed to be exposed to the treatments and used in the feeding assay before it started to senesce.

One hundred *G. antarctica* were placed into each of the experimental buckets in Year 2 to be used in a feeding rate assay. The amphipods were allowed to acclimatize to the experimental buckets for a few days before the pH in the non-ambient treatments was slowly decreased over the course of 52 h. The amphipods were fed small scrap pieces of *P. decipiens* and were also provided with plastic artificial plants seeded with diatoms from an outdoor tank and replaced with new, diatom-seeded artificial plants regularly. The amphipods were exposed to their respective pH treatments for 55 days.

Carbonate chemistry determination

Seawater pH was determined on the total hydrogen scale (pH_T) using a Perkin Elmer UV/VIS Spectrometer Lambda 40P in Year 1 and a Perkin Elmer UV/VIS Lambda 365 in Year 2 after the addition of the pH-sensitive indicator dye m-cresol purple (SOP 6b; Dickson *et al.* 2007). Seawater TA for the samples was determined with open-cell potentiometric titration (SOP 3b; Dickson *et al.* 2007) using a Mettler-Toldeo T50 open-cell titrator equipped with a pH probe (Model DGi 115-SC). Samples were siphoned into a jacketed beaker plumbed to a water bath (Neslab RTE-7 Circulating Bath, Thermo Scientific, USA) to maintain a constant temperature during titration (20°C). Mettler-Toledo *LabX* ® software was used to record titrant volumes in real time.

Carbonate chemistry parameters were calculated based on pH, TA, temperature and salinity data. In Year 1, *CO2calc* software (Robbins *et al.* 2010) with CO_2 constants provided by Roy *et al.*

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(1993) and a $KHSO_4$ acidity constant from Dickson (1990) was used for carbonate calculations as directed by Roy *et al.* (1993). In Year 2, the *R* package (R Core Team 2020) *seacarb* by Gattuso *et al.* (2022) with constants from Lueker *et al.* (2000) and Perez & Fraga (1987) was used for carbonate calculations as directed in *seacarb*. The temperature was recorded during sample collection and the salinity was measured with a Seabird 45 MicroTSG from the Palmer Station Waterwall (Palmer Station Instrument Technician 2023).

Preparation of Desmarestia menziesii *discs*

The chemical defences from each sample of *D. menziesii* from Year 1 were extracted using three changes of 1:1 CH_2Cl_2:methanol. The resulting extracts from each solvent change were combined and then filtered. The solvents were removed by evaporation using a rotary evaporator. The resulting dry lipophilic extracts were weighed to calculate the extract yield.

Artificial food was created using 2.2% alginate with 5% *Cladophora repens* powder, a palatable, sympatric green alga (Amsler *et al.* 2005). Macroalgal extracts were dissolved in a minimum volume of methanol and dried on the algal powder with a rotary evaporator (Hay *et al.* 1994).

The extracts from *D. menziesii* are strongly unpalatable at their natural concentrations. A preliminary feeding trial was run to determine what concentration of extract would deter feeding but also allow feeding rates to be measured. Extracts from several different *D. menziesii* were combined and then diluted to 50% of natural concentration. The extract-coated *C. repens* powder was placed in a 30 mm plastic Petri dish and mixed thoroughly with a cold alginate solution and food colouring (to help visually distinguish each treatment). Then, the mixture was gelled using cold 1 M $CaCl_2$. Finally, the artificial food rounds were cut into smaller discs with a cork borer to ~10 mm in diameter and 2 mm in thickness. Control artificial foods were created using the same methods without the addition of the *D. menziesii* extract. Artificial foods for the *D. menziesii* experiment were prepared using these methods. All experimental extracts were diluted to 50% of their natural concentrations.

To examine the palatability of the macroalgal extract concentration, *G. antarctica*, one of the most common species of amphipods in the macroalgal-associated community, was given a choice of artificial food discs in a feeding assay following the methods of Amsler *et al.* (2005). Twenty amphipods were haphazardly placed into nine 250 ml bottles filled with ambient seawater. The bottles contained an extract disc and a control disc. Paired bottles without amphipods served as autogenic controls for mass changes in the discs. Feeding preference was determined by calculating wet mass change between the paired discs from the experimental and control bottles at the end of assay.

Preparation of Palmaria decipiens *discs*

Two small discs were cut adjacent to each other from each section of *P. decipiens* from the experimental buckets. Each disc was labelled with a color-coded thread tied through the centre of the disc. The discs were allowed to soak in 250 ml plastic bottles for 4 h, then the water in the bottles was changed before the feeding assay to remove compounds released from the macroalgae when they were injured from the cutting of the discs (cf. McDowell *et al.* 2014).

Feeding assays

To examine the palatability of the macroalgal discs from each pH treatment, 20 non-treated amphipods were haphazardly placed into seven 250 ml bottles for *D. menziesii* and eight such bottles for *P. decipiens* filled with ambient seawater. The bottles contained a disc from each of the pH treatments (ambient, pH 7.7 and pH7.3) from the same initial individual that was split at the beginning of the experiment. Paired bottles without amphipods served as controls for autogenic changes in the discs. Feeding preference was determined by calculating wet mass change between the paired discs from the experimental and autogenic control bottles at the end of assay.

To test the feeding rate of amphipods exposed to lowered pH, 10 *G. antarctica* from each experimental bucket were placed in a 250 ml bottle filled with water from that bucket to maintain a constant pH. Two discs from one *P. decipiens* were cored from adjacent spots on the algal blade. One disc was placed in the bottle with the amphipods and the other was placed in a paired bottle without amphipods to serve as an autogenic control. The feeding assay ran for 12 h. Amphipods were returned to their experimental buckets and the discs were weighed. Consumption was determined by calculating wet mass change between the paired discs from the experimental and autogenic control bottles at the end of assay.

Statistical analyses

Statistical analyses were performed with *R* v4.0.2 (R Core Team 2020) using the *ez* (Lawrence 2016), *car* (Fox & Weisberg 2019) and *mvnormtest* packages (Jarek 2012). Normality and homogeneity of variance were tested using the Shapiro-Wilks test and Levene's test, respectively. The consumption amount from each assay was corrected using the autogenic controls. The consumption from the extract concentration experiment was compared using a *t*-test. Extract yields from the pH treatments were compared using an analysis of variance (ANOVA). A one-sample *t*-test was used to test whether amphipods were eating macroalgal discs with 50% extract concentration. The feeding assays comparing the pH treatments were compared using an ANOVA for the *G. antarctica* assay and a repeated-measures ANOVA for the three-choice feeding assays because the choices in such an assay are not independent of each other (Roa 1992). A Greenhouse-Geisser correction was utilized for *P. decipiens* because it did not meet the assumption of sphericity (Greenhouse & Geisser 1959, Armstrong 2017). Pairwise comparisons using a Bonferroni correction were utilized as a *post hoc* test for the repeated-measures ANOVA. The cut-off for statistical significance was set to $P \leq 0.05$.

Results

Seawater parameters during the experiments are summarized in Table I. Mean (± SD) pH values of the ambient and lowered pH treatments were very similar between Year 1 and Year 2. Data for each parameter (pH, TA, salinity, dissolved inorganic carbon (DIC), etc.) on each day of the experiment are available at the US Antarctic Program Data Center (see 'Details of data deposit' statement below). TA, temperature and salinity remained similar between the pH treatments across both years.

The amphipod *G. antarctica* showed a significant preference for the control artificial foods over the foods that contained 50% natural concentrations of *D. menziesii* extracts ($t_{16} = 2.4068$, $P = 0.0285$). On average, macroalgal discs containing *D. menziesii*

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Table I. Carbonate chemistry of the ambient and lowered pH treatments (mean ± SD). Seawater parameters (n = 8) are calculated from total alkalinity (TA; μmol kg^{-1} seawater, spectrophotometric pH_T (mean ± SD), temperature (°C) and salinity (ppt). Calculated parameters included pCO_2 (μatm) and saturation states of aragonite (Ω_{arg}) and calcite (Ω_{cal}).

	Year 1			Year 2		
	Ambient	pH 7.7	pH 7.3	Ambient	pH 7.7	pH 7.3
pH_T	8.07 ± 0.07	7.69 ± 0.11	7.32 ± 0.08	8.02 ± 0.06	7.73 ± 0.08	7.35 ± 0.08
TA	2284 ± 78	2261 ± 42	2245 ± 64	2243 ± 17	2248 ± 29	2247 ± 15
Temperature	2.45 ± 0.34	2.46 ± 0.34	2.46 ± 0.33	2.61 ± 0.40	2.65 ± 0.43	2.65 ± 0.42
Salinity	32.97 ± 0.29	32.96 ± 0.29	32.96 ± 0.29	33.46 ± 0.20	33.48 ± 0.21	33.48 ± 0.21
pCO_2	367 ± 48	947 ± 221	2245 ± 409	408 ± 48	856 ± 145	2123 ± 363
DIC	2145 ± 56	2243 ± 41	2343 ± 72	2121 ± 30	2218 ± 37	2334 ± 32
Ω_{arg}	1.62 ± 0.37	0.73 ± 0.21	0.32 ± 0.07	1.45 ± 0.22	0.79 ± 0.16	0.34 ± 0.08
Ω_{cal}	2.59 ± 0.58	1.17 ± 0.33	0.50 ± 0.11	2.31 ± 0.35	1.25 ± 0.26	0.54 ± 0.12

DIC = dissolved inorganic carbon.

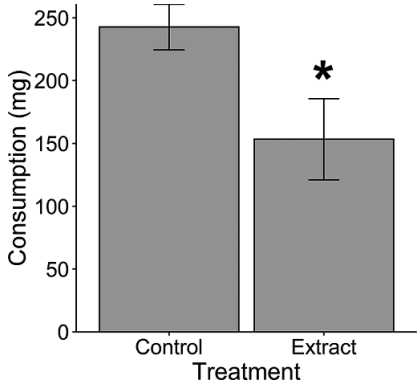

Figure 1. Feeding preference of *Gondogeneia antarctica* grazing on macroalgal discs containing ground tissue of the macroalga *Cladophora repens* and extract of the macroalga *Desmarestia menziesii* (n = 9). Bars correspond to mean consumption ± SE. The asterisk indicates a significant difference (P < 0.05) in a t-test.

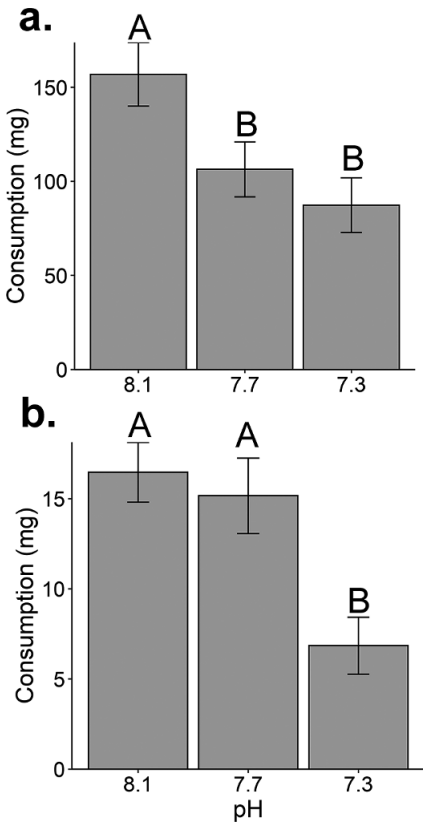

Figure 2. Feeding preference of the amphipod *Gondogeneia antarctica* grazing on macroalgae exposed to different pH treatments. **a.** Consumption of discs containing ground tissue of the macroalga *Cladophora repens* and extracts of the macroalga *Desmarestia menziesii* (n = 7). **b.** Consumption of discs of the macroalga *Palmaria decipiens* (n = 8). Bars correspond to mean consumption ± SE. Letters indicate significant groups (P < 0.05) in a repeated-measures analysis of variance.

extract were eaten 36% less than control discs (Fig. 1). The consumption of macroalgal discs with *D. menziesii* extract was found to be significantly higher than 0 using a one-sample t-test, meaning amphipods were eating discs with the extract (t_8 = 4.746, P = 0.0015).

Extract yields for *D. menziesii* ranged from 22.63 to 48.32 mg extract/g alga and did not significantly differ between the pH treatments. A preference for macroalgal discs containing extract from *D. menziesii* exposed to ambient seawater over extracts from macroalgae exposed to pH 7.7 and 7.3 was observed in *G. antarctica* (Fig. 2). A repeated-measures ANOVA showed a significant impact of pH on *D. menziesii* palatability ($F_{2,12}$ = 3.927, P = 0.0488). Artificial food pellets made with extracts from the ambient pH treatment were consumed ~38% more than those made with extracts from macroalgae maintained at reduced pH (Bonferroni pairwise comparison, P < 0.05).

Gondogeneia antarctica had a strong preference for *P. decipiens* kept under ambient pH or pH 7.7 compared to macroalgae exposed to pH 7.3 ($F_{1.132,7.924}$ = 6.839, P = 0.0286; Fig. 2). On average, pairwise comparisons revealed that consumption was two-fold lower in the pH 7.3 treatment compared to the other two treatments (P < 0.05).

Gondogeneia antarctica that were exposed to the different pH treatments for 8 weeks exhibited no significant difference in total consumption of untreated *P. decipiens* (Fig. 3). Amphipods in each of the treatments consumed ~25 mg of *P. decipiens* over the 12 h of the experiment.

Discussion

The macroalgae *D. menziesii* and *P. decipiens* and the amphipod *G. antarctica* were exposed to three pH treatments simulating

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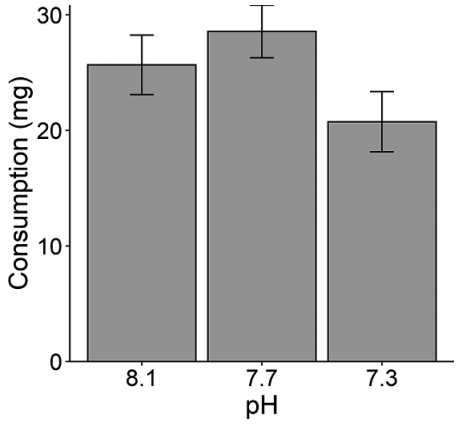

Figure 3. Total consumption of discs of the macroalga *Palmaria decipiens* by the amphipod *Gondogeneia antarctica* kept under different pH treatments for 8 weeks (n = 8). Bars correspond to mean consumption ± SE.

current ambient conditions (pH 8.1), end-of-the-century conditions (pH 7.7; IPCC 2022) and distant-future conditions (pH 7.3; IPCC 2022). These macroalgae were selected to represent a common unpalatable (*D. menziesii*) and palatable (*P. decipiens*) species (Amsler *et al.* 2005, Aumack *et al.* 2010). We found a reduction in palatability to (non-treated) *G. antarctica* in both *D. menziesii* extracts and *P. decipiens* discs when exposed to decreased pH. However, when pH-treated *G. antarctica* were offered untreated, identical foods we found no significant difference in total consumption between *G. antarctica* from any of the treatments.

Previous studies have shown that OA can have a direct impact on the physiology and behaviour of marine organisms (Ericson *et al.* 2010, Kroeker *et al.* 2013, Ramajo *et al.* 2016), especially in consumers (e.g. Kurihara & Shirayama 2004, Lim & Harley 2018, Park *et al.* 2020, Anand *et al.* 2021). In addition to these potential direct impacts on a species, the interactions between species, such as macroalgae-herbivore interactions, can also be altered. OA-induced changes in the growth and chemical composition of macroalgae can alter consumer preference for specific macroalgal species (Fieber & Bourdeau 2021). Additionally, differences in tolerance to low pH can shift entire ecosystem macroalgal composition, which can change the abundance of specific food items for consumers (Hall-Spencer *et al.* 2008, Harvey *et al.* 2021).

Fleshy macroalgae are generally more resistant to OA compared to calcifying species and can sometimes benefit from a decrease in pH (Hall-Spencer *et al.* 2008, Johnson *et al.* 2014, Kram *et al.* 2016). However, resistance to OA does not mean that these species are unaffected by this process. Changes in macroalgal palatability have been observed in several macroalgae when exposed to OA conditions (Swanson & Fox 2007, Poore *et al.* 2013, Duarte *et al.* 2016, Fieber & Bourdeau 2021). For example, the palatability of *Fucus vesiculosus* has been found to increase when exposed to low-pH treatments in summer through winter (Raddatz *et al.* 2017). Additionally, Poore *et al.* (2013) found that the palatability of *Sargassum linearifolium* was not impacted by decreases in pH alone. However, decreases in pH were able to mitigate reductions in palatability from increases in temperature.

Stress from changes in abiotic factors such as salinity, temperature and pH can alter secondary metabolite production in algae (Kolackova *et al.* 2023). Alterations in secondary metabolites used as chemical defences can impact the overall palatability of macroalgae. The response can range from decreased, increased or unaffected chemical defence production between different species (Swanson & Fox 2007, Rich *et al.* 2018, Fieber & Bourdeau 2021). The kelp *Laminaria setchellii* and several species of the green algal genus *Halimeda* experience a decrease in phenolic and terpene content, respectively, when exposed to decreased pH (Campbell *et al.* 2014, Fieber & Bourdeau 2021). However, the amount of phlorotannins, a putative chemical defence, have been shown to increase in some kelps when exposed to high-CO_2 treatments (Swanson & Fox 2007).

In our study, *D. menziesii* extracts from an ambient pH were preferred over extracts from the pH 7.7 and pH 7.3 treatments. Since the extracts were lipophilic and therefore did not contain other desirable components to consumers, such as proteins, this preference for ambient-treatment extracts demonstrates that the potency of the extracts increased with decreased pH. These results suggest that OA could delay when the carbon from *D. menziesii* would become available to consumers in macroalgal communities along the WAP. The brown macroalga *D. menziesii* commonly dominates or co-dominates shallow-water communities down to 20 m in this region of the WAP (Amsler *et al.* 1995, 2024). Although this macroalga is typically not consumed while it is living, this macroalga and other sympatric species are important food resources for grazers when their chemical defences break down after death (Wiencke & Amsler 2012). However, an increase in the amount or the potency of the chemical defences in *D. menziesii* could increase the amount of time for which the macroalga would need to be dead before the chemical defences would break down sufficiently to become palatable to consumers, lengthening the time for their carbon to become available to higher trophic levels. This concept is supported by the findings that high CO_2 exposure and larger putative chemical defence levels have both been correlated with longer decay times in other brown macroalgae (Swanson & Fox 2007).

In addition to changes in chemical defences, shifts in chemical composition that lower nutritional quality have also been observed in OA experiments (e.g. Gordillo *et al.* 2001, Duarte *et al.* 2016). Decreases in protein and fatty acid concentrations have been observed in several macroalgal species when exposed to CO_2 enrichment (Garcia-Sanchez *et al.* 1994, Mercado *et al.* 1999, Gordillo *et al.* 2001, Rossoll *et al.* 2012, Duarte *et al.* 2016). However, these changes in composition vary with corresponding photosynthesis or growth changes for particular species. For example, decreases in protein content and increases in C:N ratios are correlated with lower growth and photosynthesis rates in *Porphyra leucostricta* and *Gracilaria tenuistipitata* (Garcia-Sanchez *et al.* 1994, Mercado *et al.* 1999). Gordillo *et al.* (2001), however, found similar composition changes but increases in growth and photosynthesis in *Ulva rigida* with CO_2 enrichment. These reductions in nutritional quality can result in lower palatability to consumers. Duarte *et al.* (2016) found that exposure to high CO_2 reduced protein content and organic matter in the brown macroalga *Durvillaea antarctica*. As a result, the amphipod *Orchestoidea tuberculate* preferred *D. antarctica* from the ambient CO_2 treatment three-fold more than macroalgae from the higher CO_2 treatment (Duarte *et al.* 2016).

Our study found that the palatability of *P. decipiens* decreases by half when exposed to a pH 7.3 treatment for 18 days. This decrease in palatability could be attributed to a decrease in nutritional quality of the macroalga or to the production of an unpalatable metabolite as a response to stress. The nutritional quality of primary producers can influence ecosystem trophic structure by determining herbivory pressure, consumer to producer biomass

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ratios and the rate at which energy is cycled through the food web (Cebrian *et al.* 2009). *Palmaria decipiens* is one of the few palatable macroalgae in these communities (Amsler *et al.* 2020). A reduction in nutritional quality could lead to heavier herbivory pressure on this macroalga if grazers must consume more macroalgae to compensate for low-nutrition food items (Duarte *et al.* 2016). Furthermore, reductions in nutritional quality can impact consumers through shifting biochemical compositions, decreasing egg production and reducing growth rates in some invertebrates (Urabe *et al.* 2003, Rossoll *et al.* 2012, Schoo *et al.* 2013).

Previous studies have shown that invertebrates can be susceptible to OA through alterations in reproduction (Kurihara & Shirayama 2004, Ericson *et al.* 2010, Morita *et al.* 2010), development (Kurihara & Shirayama 2004, Watson *et al.* 2009, Place & Smith 2012) and growth (Sheppard Brennand *et al.* 2010). In addition to these changes, the energy demands of invertebrates can also shift as organisms reallocate available energy to different processes as a response to low pH exposure (Pan *et al.* 2015). One common response of invertebrates to higher energy demands is increasing food intake (Saba *et al.* 2012, Ramajo *et al.* 2016). Saba *et al.* (2012) found that Antarctic krill increase their feeding rates greater than three-fold and increase their metabolic rates when exposed to high CO_2 concentrations. In some situations, having access to greater food amounts can mitigate some of the negative effects of OA exposure. For example, Melzner *et al.* (2011) found that inner-shell corrosion in the mussel *Mytilus edulis* was not observed in moderate CO_2 treatments when given a high volume of food. Similarly, the hard coral *Acropora cervicornis* can utilize increased feeding to mitigate decreases in calcification and growth from high CO_2 exposure (Towle *et al.* 2015). In contrast to other studies, Ramajo *et al.* (2016) found that juvenile scallops exposed to high CO_2 had significantly higher metabolic, growth, calcification and feeding rates compared to when exposed to ambient CO_2. However, scallops with a low food supply exposed to the same pCO_2 altered the composition of their shell-periostracum layer.

Amphipods utilize calcium carbonate to create their exoskeletons (Luquet 2012), making them susceptible to increased energetic requirements under OA to maintain their calcification. However, in the present study, we found no significant difference in the total consumption of *G. antarctica* of food discs with decreasing pH. This result aligns with the reported robustness of arthropod feeding, as a whole, to OA compared to more susceptible groups, including echinoderms and molluscs (Clements & Darrow 2018). Other OA studies found that the larvae of the Dungeness crab, *Metacarcinus magister*, and the Pacific green shore crab, *Hemigrapsus oregonensis*, showed no difference in feeding rates on prey items when exposed to lowered pH (Christmas 2013). Similar trends in feeding rates on algae have also been observed in some krill, shrimp, amphipods and copepods (Arnberg *et al.* 2013, Poore *et al.* 2013, Li *et al.* 2015, Cooper *et al.* 2016, Glandon & Miller 2017, McLaskey *et al.* 2019). However, while measuring feeding responses can be a tool for estimating energy acquisition (Clements & Darrow 2018), feeding cannot measure all processes that might be impacted by OA. For example, there can be changes in respiration, fatty acid accumulation efficiency and development rates that are not reflected in consumption rates (Arnberg *et al.* 2013, Li *et al.* 2015, McLaskey *et al.* 2019). Consequently, any such impacts on *G. antarctica* could have gone undetected in our study. In addition, *P. decipiens* is one of the most protein-rich macroalgae in this region (Peters *et al.* 2005), making it possible that the untreated *P. decipiens* used as food in the experiment could have provided enough nutrition to mask possible differences in energy demands of *G. antarctica*.

The results of the present study show that OA negatively affected the palatability of the unpalatable *D. menziesii* and the palatable *P. decipiens* but did not impact the feeding of *G. antarctica*. These changes in palatability are probably occurring because of changes in either nutritional quality or secondary metabolite production. Alterations in either of these components could lead to major impacts for the WAP food web, such as delaying when an unpalatable macroalga enters the detrital food web or decreasing the nutritional quality of a palatable macroalga for consumers. Overall, our results suggest that the indirect effects of OA on food items can be more impactful than the direct effects on amphipods along the WAP.

Supplementary material. To view supplementary material for this article, please visit http://doi.org/10.1017/S095410202400052X.

Details of data deposit. Data are available at the US Antarctic Program Data Center: https://www.usap-dc.org/view/project/p0010193.

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Competing interests. The authors declare none.

Author contributions. HEO, CDA, JBM and JBS designed the study. HEO, MOA, CDA and JBS collected the macroalgae. HEO, MOA and CDA collected the amphipods. All authors conducted the experiment. HEO analysed the data, prepared the figures and wrote the first draft of the manuscript. All authors contributed to editing the final manuscript.

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