Feeding preferences and the effect of temperature on feeding rates of the graceful kelp crab in the Salish Sea

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Abstract

Graceful kelp crabs (*Pugettia gracilis*) are abundant consumers in shallow subtidal ecosystems of the Salish Sea. These dynamic habitats are currently experiencing multiple changes including invasion by non-native seaweeds and warming due to climate change. However, little is known about *P. gracilis'* foraging ecology, therefore we investigated their feeding preferences between native and invasive food sources, as well as feeding rates at elevated temperatures to better assess their role in changing coastal food webs. To quantify crab feeding preferences, we collected *P. gracilis* from San Juan Island, WA and conducted no-choice and choice experiments with two food sources: the native kelp, *Nereocystis luetkeana,* and the invasive seaweed, *Sargassum muticum*. In no-choice experiments, *P. gracilis* ate equal amounts of *N. luetkeana* and *S. muticum*. However, in choice experiments, *P. gracilis* preferred *N. luetkeana* over *S. muticum*. To test effects of warming on these feeding rates, we exposed *P. gracilis* to ambient (11.5 ± 1.3°C) or elevated (19.5 ± 1.8°C) temperature treatments and measured consumption of the preferred food type, *N. luetkeana.* Crabs exposed to elevated temperatures ate significantly more than those in the ambient treatment. Our study demonstrates the diet flexibility of *P. gracilis*, suggesting they may be able to exploit increasing populations of invasive *S. muticum* in the Salish Sea. Warming ocean temperatures may also prompt *P. gracilis* to increase feeding, exacerbating harmful impacts on *N. luetkeana,* which is already vulnerable to warming and invasive competitors.

Introduction

Crabs play significant ecological roles in coastal food webs. In a variety of coastal ecosystems, crabs can play an important trophic role as grazers capable of modulating populations of foundational primary producers. In kelp habitats, crab herbivory mediates kelp growth and survival (Dobkowski 2017), kelp forest density (Jofré Madariaga et al. 2013), and kelp community structure and productivity (Lubchenco & Gaines 1981; Dobkowski et al. 2017; Dobkowski 2017). In salt marshes, shore crabs also serve as key consumers and regulators of salt marsh vegetation and biomass (Beheshti et al. 2021).

Kelp crabs (genus *Pugettia*), often feed on brown macroalgae and occur in the same longitudinal range as bull kelp (*Nereocystis luetkeana*), Alaska to California (Morris et al. 1980). They are common residents of *N. luetkeana* beds in the Salish Sea, which range from rocky shallow subtidal areas to 30 m depth (Kruckenberg 1991; Duggins et al. 1989). The graceful kelp crab, *Pugettia gracilis*, and the Northern kelp crab, *Pugettia producta*, are significant consumers of *N. luetkeana* (Dobkowski 2017; Dobkowski et al. 2017), along with sea urchins (genus *Strongylocentrotus* and *Mesocentrotus;* Paine & Vadas 1969) and snails (*Lacuna vincta*; Chenelot & Konar 2007). Although *P. gracilis* is known to be found in kelp beds in the Salish Sea (Dobkowski 2017), little has been quantified about their actual feeding preferences. Understanding these effects on *N. luetkeana* is important as it is a foundational species that provides habitat and serves as a food source for many marine fishes, mammals, and invertebrate species in the Pacific Northwest of North America (Steneck et al 2002; Carney et al. 2005; Daly & Konar 2010). Although an important part of the ecosystem, grazers and herbivores are not the only pressure being placed on native kelps.

Sargassum muticum is an invasive species and a potential competitor to native kelps, including *N. leutkeana* (Britton-Simmons 2004; Gaydos et al. 2008). On the west coast of North America, *S. muticum* is now found from Alaska to Mexico, overlapping in range with the distributions of *N. leutkeana* and *P. gracilis*. In the early 20th century, *S. muticum* was introduced to Washington State and the Salish Sea (Britton-Simmons 2004; Seebach et al. 2010). Along the west coast, invasive *S. muticum* has demonstrable negative impacts on native seaweeds through direct competition and inhibition of recruitment (Ambrose & Nelson 1982; DeWreede 1983; Stæhr et al. 2000). In the Salish Sea specifically, *S. muticum* populations have been shown to reduce light and nutrient concentration availability for native kelp species, reducing the native canopy by 75% and the understory by 50% (Britton-Simmons 2004). Increased populations of *S. muticum* have also been documented to influence grazers within subtidal ecosystems. Experiments demonstrate that *S. muticum* serves as an additional food supply, shelter, and spawning habit for many crab and snail species (Seebach et al. 2010; Britton-Simmons 2011), while for other species such as the green sea urchin, *Strongylocentrotus droebachiensis*, are deterred by *S. muticum* (Marks et al. 2020).

Coastal food webs of the Salish Sea are experiencing both short-term and long-term warming due to climate change. The annual mean water temperature in the Salish Sea is 10°C, fluctuating between 6.5°C to 11.5°C seasonally (Khangaonkar et al. 2019). Climate models predict that by 2100 global ocean temperatures will increase by 1.57°C and estuarine and intertidal ecosystems, the ecosystems in which kelp crabs are found, warming more intensely by 3.94°C (Khangaonkar et al. 2019; Berry et al. 2021). Short-term, intense periods of warming due to heat waves are also becoming more common and have created large-scale shifts in the structure of kelp forests (Berry et al. 2021; Khangaonkar et al. 2021; McPherson et al. 2021). In 2014–2016, Salish Sea estuarine temperatures were warmer by an average of 2.3°C (Khangaonkar et al. 2021). Nearshore intertidal sea surface temperatures increased by 6.2°C during this heat wave (Gentemann et al. 2017).

Food web interactions and the organisms within them have been influenced by warming temperatures in a variety of ways. Many herbivores, including crabs, have shown increased feeding at high temperatures due to an increase in metabolic requirements (Hill 1980; McPherson et al. 2021). For example, in laboratory studies the mud crab, *Scylla serrata*, increased feeding at elevated temperatures of 20°C and 25°C (Hill 1980). The same trend of consuming more at higher temperatures has also been shown in king crabs, *Paralithodes camtschaticus*, (Siikavuopio & James 2015) and shore crabs, *Carcinus maenas* (Elner 1980). In simulations based on the 2014–2016 northeast Pacific marine heatwave, there was an increase in biological activity due to ocean temperatures (Khangaonkar et al. 2021). Thus, understanding the effects of herbivores like *P. gracilis*, warming, and interactions on both *N. luetkeana* and *S. muticum* is especially critical.

As ocean temperatures increase on both long-term and episodic timescales in the Salish Sea, it is of particular importance to understand how ecologically significant organisms and the food webs they comprise may respond. The sensitivity of adult *N. luetkeana* to ocean warming has been well documented and linked to recent declines in many Pacific northwest and Salish Sea populations (Schiel

et al. 2004; Supratya et al. 2020; Berry et al. 2021). In laboratory studies, the growth and development of healthy *N. luetkeana* spores had reduced success when incubated in temperatures of 17°C or above (Schiltroth et al. 2018). It remains unclear how ocean warming affects the ability for *N. luetkeana* to respond to other environmental factors, such as invasive species like *S. muticum.* Increased *S. muticum* populations have been correlated with rising seawater temperatures and increased nutrient enrichment (Norton 1977; Wang et al. 2019). Increasing populations of *S. muticum* may influence the distribution and abundance of *N. luetkeana* and consequently associated food web interactions. If this continues, *N. luetkeana* populations could experience this additional stressor in parallel to their already documented vulnerabilities to warming (Schiel et al. 2004; Supratya et al. 2020).

Our first objective in this study was to understand the relationship between *P. gracilis* and both native and invasive food sources. We asked: 1) Can *P. gracilis* consume both *N. luetkeana* and S. *muticum*? And if so, 2) Does *P. gracilis* have a preference between these two food sources? We hypothesized that *P. gracilis* would be able to consume both seaweeds but would prefer the native *N. luetkeana* over the invasive *S. muticum* because similar feeding preferences have been demonstrated by the closely related Northern kelp crab (*Pugettia producta*) (Dobkowski et al. 2017). We conducted choice and no-choice feeding trials to determine what seaweeds *P. gracilis* can eat as well as quantify which food sources they prefer to eat when given two options. By studying these feeding preferences, we can better understand the future impacts of invasive species on *P. gracilis* and the ecological pressures that potentially affect *N. luetkeana*.

Our second objective was to assess how *P. gracilis* feeding is affected by elevated and episodic temperatures characteristic of short-term warming and longer-term future subtidal ocean conditions. We hypothesized that *P. gracilis* would increase feeding rates at higher temperatures similar to observed trends in other invertebrate species (Elner 1980; Carr & Bruno 2013; Siikavuopio & James 2015). To do this, we conducted feeding trials (using the preferred food option, *N. luetkeana*) at two temperatures, ambient (11.5 ± 1.3°C) and elevated (19.5 ± 1.8°C), to determine the differences among feeding rates between temperatures.

Methods

No Choice and Choice Experiments

We collected 12 *P. gracilis* (3.5 ± 1.8 g) from 0 to 2 m depth from four sites (Reuben Tart County Park, Deadman's Bay, Friday Harbor Labs, and Eagle Cove; Fig. I). We did not assess crab sex because our crabs were randomly collected in the field without preference for males or females. Once collected, we housed the crabs in sea tables in flow-through seawater tanks at Friday Harbor Labs (FHL). Crabs resided individually in plastic tanks (28 cm x 15 cm x 11 cm) with plastic mesh lids and consumed a mixed diet of local seaweeds prior to, and in between, experiments. We used a block experiment design, treating the crabs as the blocking factor, to examine the feeding preferences of *P. gracilis*.

We conducted two sets of experiments: (1) no-choice feeding experiments, where crabs were offered only one food type (*N. luetkeana* or *S. muticum*), and (2) choice feeding experiments, where crabs were offered both food types simultaneously. No-choice experiments enabled us to quantify food consumption of each food type individually while the choice experiments enabled us to assess food preference between the two food types. Each crab participated in three independent feeding trials in a randomized order: *N. luetkeana* only, *S. muticum* only, and choice of *N. luetkeana* and *S. muticum*, leading to a total of 36 trials.

To prepare food for these experiments, we collected *N. luetkeana* and *S. muticum* from detached, floating "drift" sources near FHL. All food sources were harvested from the same drift patch and we used only non-reproductive kelp blades to standardize for freshness of the food source and environmental factors such as drift time. The wet mass of food items was determined prior to every trial using an Ohaus Navigator XT scale. We offered similar sized pieces of *N. luetkeana* (5.52 ± 0.33 g) and *S. muticum* (5.55 ± 0.43 g) to avoid biasing the crabs toward the visibly larger food item.

Each crab was starved for 24 hours prior to each independent trial. The starvation period was followed by a 48-hour test period which took place in the same flow-through seawater tanks holding the crab. Pilot experiments showed 48 hours to be sufficient time for crabs to eat a quantifiable amount of the food sources offered. We used a short feeding time to minimize effects of nutrient enhancement due to crab excretion on seaweed mass. We measured blotted wet mass before and after each experiment to calculate how much each crab consumed. Thirty-six controls used the same experimental design, which included no crabs, to account for natural mass loss or gain of seaweed not due to crab consumption over a 48-hour period. Each control was run following the crab trial and subtracted from the corresponding trial.

To analyze these data, we used an unpaired t-test for the no-choice experiments and a paired t-test for the choice experiments to determine if there were significant differences in food consumption between the two food types. All analyses were conducted in R version 1.2.1335 (R Foundation for Statistical Computing Platform 2020).

Temperature Experiments

We collected 18 additional *P. gracilis* (mean and SD: 3.3 ± 1.2 g) from Friday Harbor Labs (Fig. I). We did not reuse crabs between feeding preference experiments and temperature experiments. We maintained crabs in the lab using the same set up described for the experiments above, and seaweeds were collected using the same procedure as in the feeding experiments.

Each of the crabs were randomly assigned to a temperature treatment: ambient (twelve *P. gracilis*; mean: 11.5 ± 1.3°C) or elevated (six *P. gracilis*; mean: 19.5 ± 1.8°C). Temperature in tanks was regulated using aquarium heaters. Temperature was monitored using a DS18B20 temperature probe which logged temperature every 10 minutes to a ESP8266 microcontroller running MicroPython. Crabs were acclimated to the temperature treatment for 48 hours while feeding normally, then starved for 24 hours before the feeding trial. All crabs were given *N. luetkeana* only during feeding rate trials to control for food type.

To compare the amount of *N. luetkeana* consumed between the two temperature treatments, we utilized a Welch's t-test to accommodate our unequal sample sizes. This analysis was conducted in R version 1.2.1335 (R Foundation for Statistical Computing Platform 2020).

Results

No Choice and Choice Experiments

P. gracilis successfully consumed both *N. luetkeana* (mean and SD: 0.85 ± 0.17 g) and *S. muticum* (0.84 ± 0.12 g) during the 48-hour feeding period. Crabs displayed no significant difference in their consumption of *N. luetkeana* versus *S. muticum* when given no choice between the two food types (t = 0.075, df = 11 p = 0.941; Fig. II).

Conversely, *P. gracilis* consumed significantly more *N. luetkeana* (0.64 ± 0.09 g) than *S. muticum* (0.35 ± 0.06 g) when given a choice between the two food types (t = 3.132, df = 11 p = 0.011; Fig. III).

Temperature Experiments

Crabs in the ambient temperature treatment consumed 0.4 ± 0.4 g of *N. luetkeana*, while crabs in the elevated temperature treatment consumed 1.9 ± 1.4 g over 48 hours. Crabs exposed to elevated temperature ate significantly more *N. luetkeana* than those exposed to ambient temperature (Welch's t-test: t = 4.3118, df = 17, p < 0.001; Fig. IV).

Discussion

Our results show that *N. luetkeana* is the preferred food type of *P. gracilis* but also suggest that the crabs can modify their diet to exploit the invasive food source, *S. muticum*. This suggests *P. gracilis* has a more generalist diet beyond just the kelp for which the crabs are named. Generalist feeding strategies are common among crabs, including *Acanthonyx scutiformis*, a coastal crab and seaweed generalist, and *Uca annulipes*, another coastal crab and omnivore (Milner et al. 2009; Vasconcelos et al. 2009). Our finding that *P. gracilis* can eat equally as much *S. muticum* as *N. luetkeana* when given no choice is significant for their continued success in response to changing food availability which may be characteristic of future conditions. However, further research is needed to determine if both food types confer the same nutritional value. As a generalist consumer, *P. gracilis* is well-positioned to take advantage of an increasingly available invasive food source.

Our study is realistic of field food conditions because co-occurring *N. luetkeana* and *S. muticum* beds in the Salish Sea have been observed, emulating our choice experiments. As *S. muticum* populations increase, food conditions recreated in our choice experiments may become more common, creating more opportunities for crabs to choose their food type. We have determined that *N. luetkeana* is the preferred food source of *P. gracilis* so in scenarios where *N. luetkeana* and *S. muticum* beds are co-occurring, even though *P. gracilis* can consume both, they may choose to consume *N. luetkeana*. Despite the increasing *S.*

muticum populations and changing ocean temperatures, this feeding alone puts pressure on *N. luetkeana*.

Our results suggest that at higher temperatures, *P. gracilis* consumes greater amounts of *N. luetkeana* than at ambient ocean temperatures. This response is consistent with increased consumption rates measured in other coastal invertebrates in response to increased temperatures. Green sea urchins, *Strongylocentrotus droebachiensis*, (Carr & Bruno 2013), king crabs, *Paralithodes camtschaticus*, (Siikavuopio & James 2015) and shore crabs, *Carcinus maenas* (Elner 1980) have also exhibited increase consumption and metabolic rates at higher temperatures (Carr & Bruno 2013). As ocean temperatures rise, our work demonstrates that *P. gracilis*, will increase the amount of food consumed, placing pressure on their preferred food source, *N. luetkeana*. Further research is needed to understand if *P. gracilis* increases consumption of their non-preferred food type, *S. muticum* at elevated temperatures as well, and if these trends are consistent across closely related crabs.

N. luetkeana and other native kelp populations have demonstrated negative responses to elevated temperatures, whereas invasive *S. muticum* populations have demonstrated positive responses to similar elevated temperatures (Ambrose & Nelson 1982; DeWreede 1983; Stæhr et al. 2000; Britton-Simmons 2004). In one study, high temperatures decreased growth and performance of native seaweeds, such as *Fucus serratus* and *Chondrus crispus*, but enhanced growth and performance of *S. muticum* (Atkinson et al. 2020). In the San Juan Islands, Washington, *S. muticum* survived in temperatures up to 28°C, whereas *N. luetkeana* survived only until 18°C (Lüning & Freshwater 1988). The future quantity and quality of *N. luetkeana* beds has been shown to, and is predicted to continue to, decrease with increasing ocean temperatures (Simonson et al. 2015; Schiel et al. 2004; Supratya et al. 2020). If *P. gracilis* consumes more *N. leutkeana* at higher temperature, and *S. muticum* populations proliferate in warmer waters, future *N. luetkeana* survival may be threatened by these combined impacts.

Elevated temperatures used in our experiments have relevance to short term, episodic warming events that have become increasing more prevalent and longer-term warming characteristic of future predictions. Our elevated temperature conditions are aligned with the already established intertidal and shallow subtidal ecosystem warming predictions and mirror acute and episodic temperature stress due to the increasing prevalence of warming events like marine heat waves (Lüning & Freshwater 1988; Khangaonkar et al. 2019). For example, in the central Strait of Georgia, *N. luetkeana* has been exposed to sea surface temperatures of 15–21°C in the summer months (Schiltroth et al. 2018). In 2014 and 2021, there were marine heat waves with increased temperatures from 2.5°C to upwards of 6°C that impacted the Pacific Northwest which prompted a massive die-off of over 90% of *N. luetkeana* along the Pacific coast of North America (Rogers-Bennett & Catton 2019; Kuroda & Setou 2021). Since 1925, there has been a 54% increase in annual marine heatwave days (Kuroda & Setou 2021). Therefore, the short-term elevated temperature conditions in our experiment have the most near-term field relevance in the context of these episodic and extreme temperature stresses. With the short duration of temperature stress, the temperature experiments closest resemble the time scale of heat waves and show the effects of a short temperature anomaly on food web interactions during these periods.

Many studies on ecological effects of warming and invasive species have been conducted independently, but recent evidence has shown that climate change and invasive species can act together to alter marine communities (Stachowicz et al. 2002; Sorte et al 2010; Strayer 2010; Miranda et al. 2019; Atkinson et al. 2020). As waters warm, *S. muticum* may be increasingly able to outcompete *N. luetkeana* in the Salish Sea due to its increased productivity and growth rates in warmer waters (Norton 1977; Wang et al. 2019). Therefore, both ocean warming and competition from invasive seaweeds each place separate stress on native seaweeds such as *N. luetkeana*. These stresses could be compounded by *P. gracilis'* preference for the native seaweed, *N. luetkeana*, over the invasive seaweed, *S. muticum* and increased consumption of *N. luetkeana* at elevated temperature. If this trend occurs in the field, *N. luetkeana* populations may experience compounding stressors in warming conditions from increased herbivory in addition to higher levels of competition from invasive seaweeds.

Graceful kelp crabs will likely be able to modify their diets as nearshore algal communities and food availability change in response to warming temperatures and invasive species. Our results show that *P.gracilis* eats more at higher temperatures but generalist feeding strategies make them well-positioned to manage changing ecosystems. Though we found that *S. muticum* was not the preferred food source of *P. gracilis*, it is a competitor of *N. luetkeana* which proliferates at high temperatures, suggesting it is also well-positioned to thrive under future ocean conditions. Conversely, *N. luetkeana* is likely to experience compounding negative effects of competition by increasing populations of *S. muticum*, decreased survival due to warming, and increased grazing by *P.gracilis* thus making them the most vulnerable of the three organisms we studied. Our study helps to identify relative vulnerabilities of interacting species within coastal food webs in the face of changing community structure and climate change.

Declarations

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Katrina Johnson, Katie Dobkowski and Sasha Seroy contributed to the study conception and design. The material preparation, data collection, and data analysis were performed by Katrina Johnson. The manuscript was written by Katrina Johnson and all authors commented and edited the manuscript drafts. All authors read and approved of the final manuscript.

Data Availability

Data are available from the authors upon request.

Ethics Approval

All applicable institutional guidelines for working with organisms were followed.

References

1. Atkinson, J., N. G. King, S. B. Wilmes, and P. J. Moore (2020) Summer and Winter Marine Heatwaves Favor an Invasive Over Native Seaweeds. Journal of Phycology

2. Ambrose, R. F., and B. V. Nelson (1982) Inhibition of Giant Kelp Recruitment by an Introduced Brown Alga. Botanica Marina 25:265-268

3. Beheshti, K. M., K. Wasson, C. Angelini, B. R. Silliman, and B. B. Hughes (2021) Long-term study reveals top-down effect of crabs on a California salt marsh. Ecosphere 12

4. Berry, Helen D., T. F. Mumford, B. Christiaen, P. Dowty, M. Calloway, L. Ferrier, E. E. Grossman, and N. R.

5. VanArendonk (2021) Long-term changes in kelp forests in an inner basin of the Salish Sea. PLoS ONE 16(2): e0229703

6. Britton-Simmons, K. H. (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. Marine Ecology Progress Series 277:61-78

7. Britton-Simmons, K. H., B. Pister, I. Sánchez, and D. Okamoto (2011) Response of a native, herbivorous snail to the introduced seaweed *Sargassum muticum*. Hydrobiologia 661:187-196

8. Carney, L. T., J. R. Waaland, T. Klinger, and K. Ewing (2005) Restoration of the bull kelp *Nereocystis luetkeana* in nearshore rocky habitats. Marine Ecology Progress Series 302:49-61

9. Carr, L. A., and J. F. Bruno (2013) Warming increases the top-down effects and metabolism of a subtidal herbivore. PeerJ 1:e109

10. Chenelot, H., and B. Konar (2007) *Lacuna vincta* (*Mollusca, Neotaenioglossa*) herbivory on juvenile and adult *Nereocystis luetkeana* (*Heterokontophyta, Laminariales*). Hydrobiologia 583:107-118

11. Daly, B., and B. Konar (2010) Temporal trends of two spider crabs (*Brachyura, Majoidea*) in nearshore kelp habitats in Alaska, U.S.A. Crustaceana 83:659-669

12. DeWreede, R. E. (1983) *Sargassum muticum* (*Fucales*, *Phaeophyta*): regrowth and interaction with *Rhodomela larix* (*Ceramiales*, *Rhodophyta*). Phycologia 22:153–160

13. Dobkowski, K. (2017) The role of kelp crabs as consumers in bull kelp forests-evidence from laboratory feeding trials and field enclosures. PeerJ

14. Dobkowski, K. A., J. Kobelt, S. Brentin, K. L. Van Alstyne, and M. N. Dethier (2017) Picky Pugettia: a tale of two kelps. Marine Biology 164

15. Duggins, D. O., C. A. Simenstad, and J. A. Estes (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173

16. Elner, R. W. (1980) The influence of temperature, sex and chela size in the foraging strategy of the shore crab, Carcinus maenas (L.). Marine Behaviour and Physiology **7**:15-24.

17. Gaines, S. D., and J. Lubchenco (1982) A unified approach to marine plant- herbivore interactions. II. Biogeography. Annual review of ecology and systematics. Volume 13:111-138

18. Gaydos, J. K., L. Dierauf, G. Kirby, D. Brosnan, K. Gilardi, and G. E. Davis (2008) Top 10 principles for designing healthy coastal ecosystems like the Salish Sea. EcoHealth 5:460-471

19. Gentemann, C. L., M. R. Fewings, and M. García-Reyes (2017) Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophysical Research Letters 44:312-319

20. Hill, B. J. (1980) Effects of temperature on feeding and activity in the crab *Scylla serrata*. Marine Biology 59:189-192

21. Hollarsmith, J. A., A. H. Buschmann, C. Camus, and E. D. Grosholz (2020) Varying reproductive success under ocean warming and acidification across giant kelp (*Macrocystis pyrifera*) populations. Journal of Experimental Marine Biology and Ecology 522:151247

22. Jofré Madariaga, D., M. Ortiz, and M. Thiel (2013) Demography and feeding behavior of the kelp crab *Taliepus marginatus* in subtidal habitats dominated by the kelps *Macrocystis pyrifera* or *Lessonia trabeculata*. Invertebrate Biology 132:133-144

23. Khangaonkar, T., A. Nugraha, W. Xu, and K. Balaguru (2019) Salish Sea Response to Global Climate Change, Sea Level Rise, and Future Nutrient Loads. Journal of Geophysical Research: Oceans 124:3876-3904

24. Khangaonkar, T., A. Nugraha, S. K. Yun, L. Premathilake, J. E. Keister, and J. Bos (2021) Propagation of the 2014–2016 Northeast Pacific Marine Heatwave Through the Salish Sea. Frontiers in Marine Science 8

25. Kuroda, H., and T. Setou (2021) Extensive marine heatwaves at the sea surface in the northwestern Pacific Ocean in summer 2021. Remote Sensing 13

26. Levitus, S., J. I. Antonov, T. P. Boyer, and C. Stephens (2000) Warming of the world ocean. Science 287:2225-2229

27. Lüning, K., and W. Freshwater (1988) Temperature Tolerance of Northeast Pacific Marine Algae. Journal of Phycology 24:310-315

28. Marks, L. M., D. C. Reed, and S. J. Holbrook (2020) Niche Complementarity and resistance to grazing promote the invasion success of *Sargassum horneri* in North America. Diversity 12

29. McPherson, M. L., D. J. I. Finger, H. F. Houskeeper, T. W. Bell, M. H. Carr, L. Rogers-Bennett, and R. M. Kudela (2021) Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. Communications Biology 4:298

30. Milner, R. N. C., T. Detto, M. D. Jennions, and P. R. Y. Backwell (2009) Hunting and predation in a fiddler crab. Journal of Ethology 28:171

31. Miranda, R. J., M. A. Coleman, A. Tagliafico, M. S. Rangel, L. T. Mamo, F. Barros, and B. P. Kelaher (2019) Invasion-mediated effects on marine trophic interactions in a changing climate: positive feedbacks favour kelp persistence. Proceedings. Biological sciences 286:20182866

32. Morris, R. H., D. N. Abbott, E. C. Haderlie (1980) Intertidal Invertebrates of California. Stanford University Press, Stanford

33. Norton, T. A. (1977) The growth and development of *Sargassum muticum* (Yendo) Fensholt. Journal of Experimental Marine Biology and Ecology 26:41-53

34. Paine, R. T., and R. L. Vadas (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography 14:710-719

35. Rogers-Bennett, L., and C. A. Catton (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific Reports 9

36. Schiel, D. R., J. R. Steinbeck, and M. S. Foster (2004) Ten years of-induced ocean warming causes comprehensive changes in marine benthic communities. Ecology 85:1833-1839

37. Schiltroth, Braeden, S. Bisgrove, and B. Heath (2018) Effects of warm ocean temperatures on bull kelp forests in the Salish Sea. Salish Sea Ecosystem Conference. 515

38. Seebach, A., A. M. Colnar, and W. G. Landis (2010) Ecological Risk Assessment of the Invasive *Sargassum Muticum* for the Cherry Point Reach, Washington

39. Siikavuopio, S. I., and P. James. 2015. Effects of temperature on feed intake, growth and oxygen consumption in adult male king crab *Paralithodes camtschaticus* held in captivity and fed manufactured diets. Aquaculture Research **46**:602-608.

40. Simonson, E. J., R. E. Scheibling, A. Metaxas (2015.) Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. Marine Ecology Progress Series 537: 89-104

41. Sorte, C. J. B., S. L. Williams, and J. T. Carlton (2010) Marine range shifts and species introductions: Comparative spread rates and community impacts. Global Ecology and Biogeography 19:303-316

42. Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the United States of America 99:15497-15500

43. Stæhr, P. A., M. F. Pedersen, M. S. Thomsen, T. Wernberg, and D. Krause-Jensen (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Marine Ecology Progress Series 207:79-88

44. Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner (2002) Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.

45. Strayer, D. L. 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55:152-174

46. Supratya, V. P., L. J. M. Coleman, and P. T. Martone (2020) Elevated Temperature Affects Phenotypic Plasticity in the Bull Kelp (*Nereocystis luetkeana*, *Phaeophyceae*). Journal of Phycology 56:1534-1541

47. Vadas, R. L., R. W. Elner, P. E. Garwood, and I. G. Babb (1986) Experimental evaluation of aggregation behavior in the sea urchin *Strongylocentrotus droebachiensis* - A reinterpretation. Marine Biology 90:433-448

48. Vasconcelos, M. A., T. C. Mendes, W. L. S. Fortes, and R. C. Pereira (2009) Feeding and decoration preferences of the epialtidae crab *Acanthonyx scutiformis*. Brazilian Journal of Oceanography 57:137-143

49. Wang, M., C. Hu, B. B. Barnes, G. Mitchum, B. Lapointe, and J. P. Montoya (2019) The great Atlantic *Sargassum* belt. Science 364:83-87

Figures

Figure 1

Location of four *P. gracilis* collection sites on San Juan Island, Washington. 1: Rueben Tart County Park (48°36'45" N, 123°05'53" W), 2: Deadman's Bay (48°30'46" N, 123°08'47" W), 3: Friday Harbor Labs (48°32'43" N, 123°00'44" W), 4: Eagle Cove (48°27'39" N, 123°01'57" W)
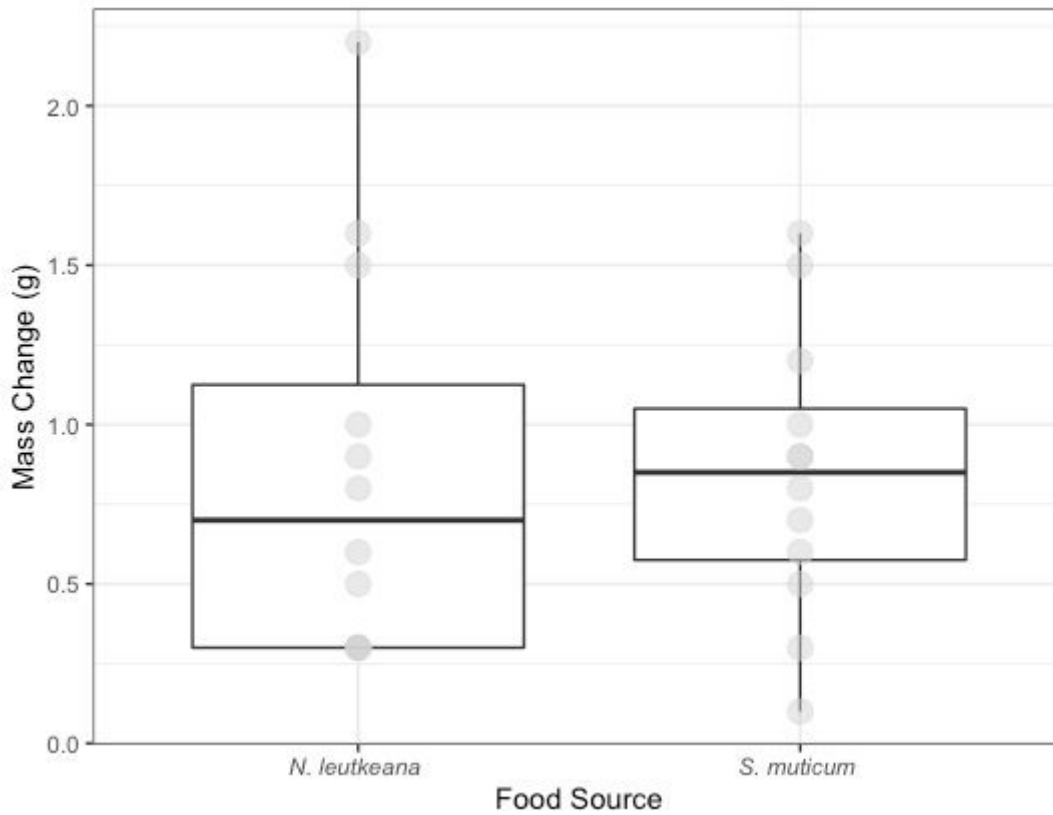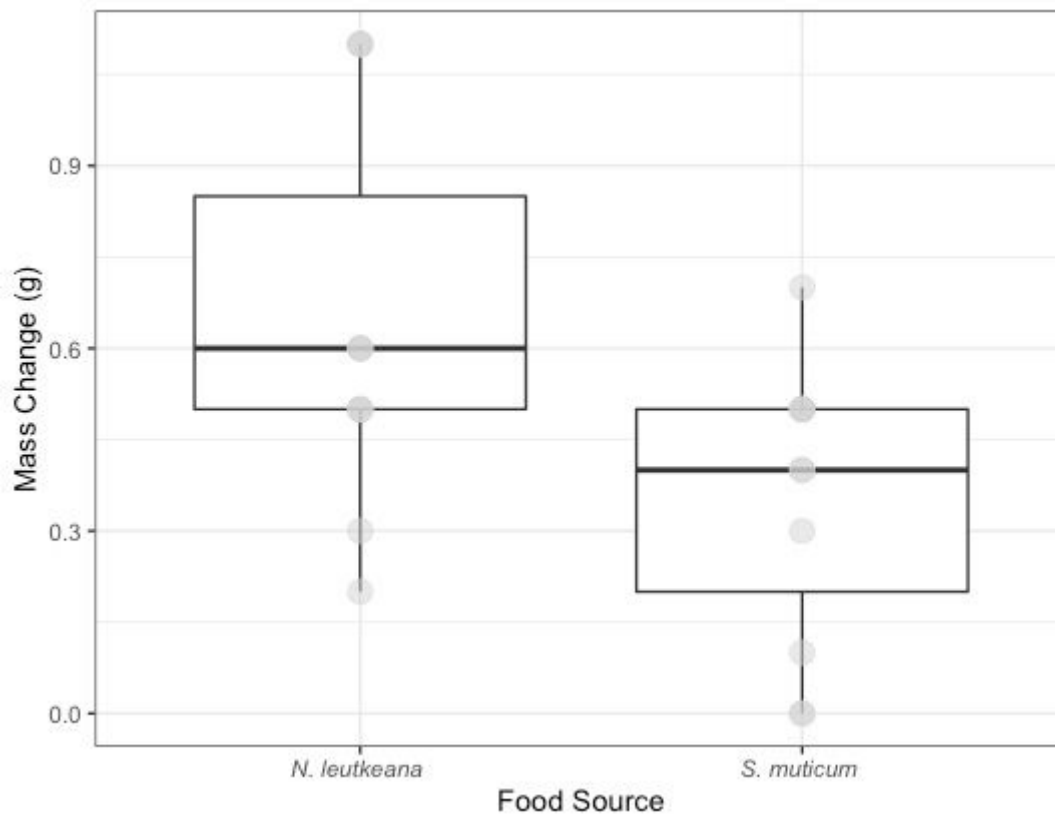
Figure 2

Medians and interquartile ranges of mass of seaweeds consumed (adjusted for the controls) by *P. gracilis* (n=12) in no choice experiments. Crabs consumed both types of food equally when they were not given options (unpaired t-test: t= 0.075, df=11 p-value=0.941)

Figure 3

Medians and interquartile ranges of mass of seaweeds consumed (adjusted for the controls) by *P. gracilis* (n=12) in choice experiments. P. gracilis consumed significantly more *N. luetkeana* than *S. muticum* when given the choice between the two food types (paired t-test: t=3.132, df=11 p-value=0.011)
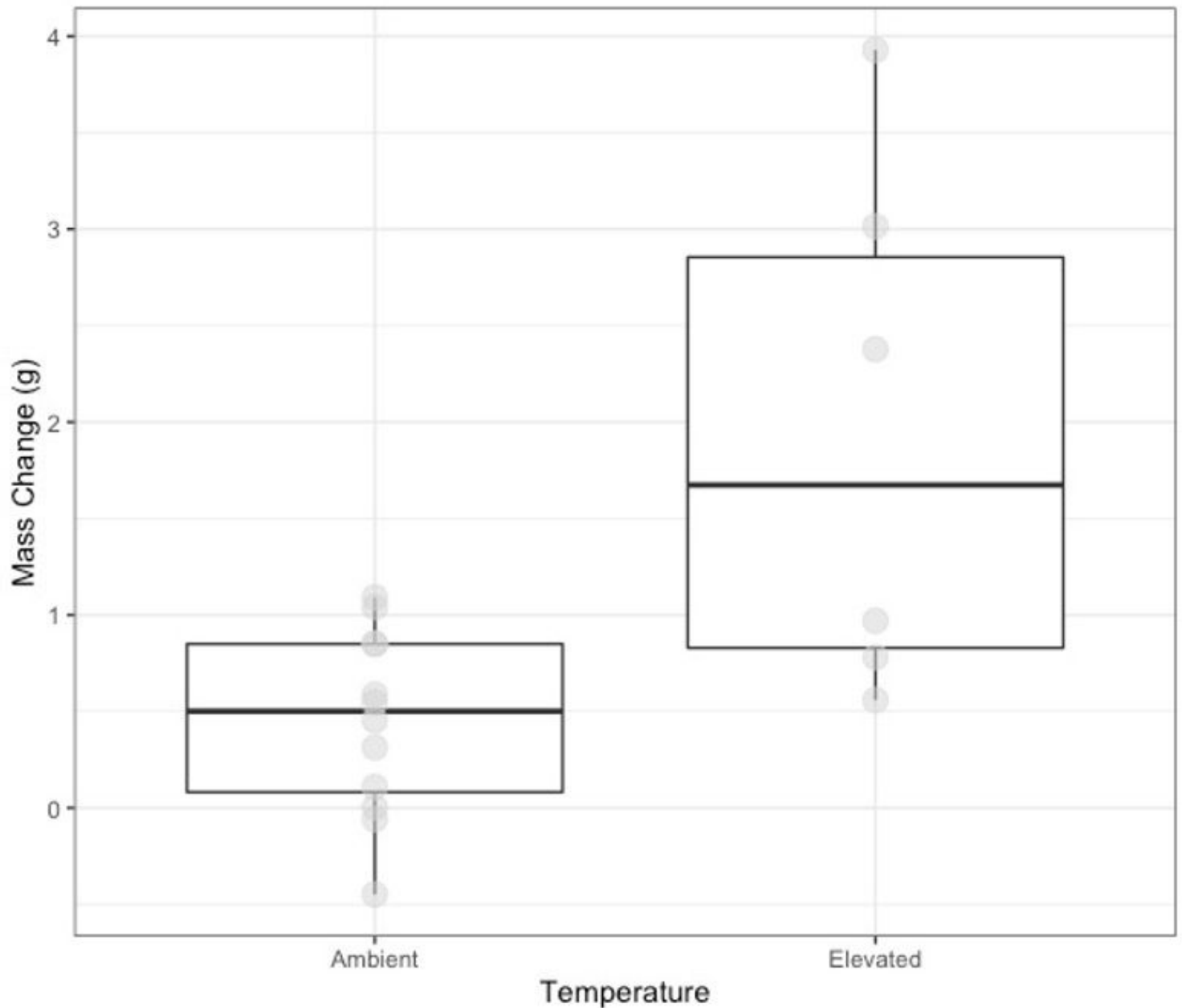
Figure 4

Medians and interquartile ranges of mass of *N. luetkeana* consumed by *P. gracilis* (n=18) in temperature treatments. The ambient temperature treatment had a mean of 11.5 ± 1.3°C and the elevated temperature treatment had a mean of 19.5 ± 1.8°C. (Welch's t-test, T= 4.3118, df= 17, p-value= 0.0002817)

Supplementary Files

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- SupplementaryTableI.png
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