Feeding preferences and the effect of temperature on feeding rates of the graceful kelp crab, *Pugettia gracilis*

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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 ocean warming. 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 temperature 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.

1 **Feeding preferences and the effect of temperature on feeding rates of the graceful kelp crab, *Pugettia gracilis***

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15 **Abstract**

16   Graceful kelp crabs (*Pugettia gracilis*) are abundant consumers in shallow subtidal ecosystems of the

17 Salish Sea. These dynamic habitats are currently experiencing multiple changes including invasion by non-native

18 seaweeds and ocean warming. However, little is known about *P. gracilis'* foraging ecology, therefore we

19 investigated their feeding preferences between native and invasive food sources, as well as feeding rates at elevated

20 temperatures to better assess their role in changing coastal food webs. To quantify crab feeding preferences, we

21 collected *P. gracilis* from San Juan Island, WA and conducted no-choice and choice experiments with two food

22 sources: the native kelp, *Nereocystis luetkeana,* and the invasive seaweed, *Sargassum muticum*. In no-choice

23 experiments, *P. gracilis* ate equal amounts of *N. luetkeana* and *S. muticum*. However, in choice experiments, *P.

24 gracilis* preferred *N. luetkeana* over *S. muticum*. To test effects of temperature on these feeding rates, we exposed *P.

25 gracilis* to ambient (11.5 ± 1.3°C) or elevated (19.5 ± 1.8°C) temperature treatments and measured consumption of

26 the preferred food type, *N. luetkeana*. Crabs exposed to elevated temperatures ate significantly more than those in

27 the ambient treatment. Our study demonstrates the diet flexibility of *P. gracilis*, suggesting they may be able to

28 exploit increasing populations of invasive *S. muticum* in the Salish Sea. Warming ocean temperatures may also

29   prompt *P. gracilis* to increase feeding, exacerbating harmful impacts on *N. luetkeana,* which is already vulnerable to

30   warming and invasive competitors.

31

32   **Introduction**

33   Crabs play significant ecological roles in coastal food webs. In a variety of coastal ecosystems, crabs can

34   play an important trophic role as grazers capable of modulating populations of foundational primary producers. In

35   kelp habitats, crab herbivory mediates kelp growth and survival (Dobkowski 2017), kelp forest density (Jofré

36   Madariaga et al. 2013), and kelp community structure and productivity (Lubchenco & Gaines 1981; Dobkowski et

37   al. 2017; Dobkowski 2017). In salt marshes, shore crabs also serve as key consumers and regulators of salt marsh

38   vegetation and biomass (Beheshti et al. 2021).

39   Kelp crabs (genus *Pugettia*)*,* often feed on brown macroalgae and occur in the same range in latitude and

40   longitude as bull kelp (*Nereocystis luetkeana*), from Alaska to California (Morris et al. 1980). They are common

41   residents of *N. luetkeana* beds in the Salish Sea, which range from rocky shallow subtidal areas to 30 m depth

42   (Kruckenberg 1991; Duggins et al. 1989). The graceful kelp crab, *Pugettia gracilis,* and the Northern kelp crab,

43   *Pugettia producta,* are significant consumers of *N. luetkeana* (Dobkowski 2017; Dobkowski et al. 2017), along with

44   sea urchins (genus *Strongylocentrotus* and *Mesocentrotus;* Paine & Vadas 1969) and snails (*Lacuna vincta*;

45   Chenelot & Konar 2007). Although *P. gracilis* is known to be found in kelp beds in the Salish Sea (Dobkowski

46   2017), little has been quantified about their actual feeding preferences. Understanding these effects on *N. luetkeana*

47   is important as it is a foundational species that provides habitat and serves as a food source for many marine fishes,

48   mammals, and invertebrate species in the Pacific Northwest of North America (Steneck et al 2002; Carney et al.

49   2005; Daly & Konar 2010). Although an important part of the ecosystem, grazers and herbivores are not the only

50   pressure being placed on native kelps.

51   *Sargassum muticum* is an invasive species and a potential competitor to native kelps, including *N.*

52   *leutkeana* (Britton-Simmons 2004; Gaydos et al. 2008). On the west coast of North America, *S. muticum* is now

53   found from Alaska to Mexico, overlapping in range with the distributions of *N. leutkeana* and *P. gracilis*. In the

54   early 20th century, *S. muticum* was introduced to Washington State and the Salish Sea from the Western Pacific

55   (Britton-Simmons 2004; Seebach et al. 2010). Along the west coast, invasive *S. muticum* has demonstrable negative

56   impacts on native seaweeds through direct competition and inhibition of recruitment (Ambrose & Nelson 1982;

57 DeWreede 1983; Stæhr et al. 2000). In the Salish Sea specifically, *S. muticum* populations have been shown to

58 reduce light and nutrient concentration availability for native kelp species, reducing the native canopy by 75% and

59 the understory by 50% (Britton-Simmons 2004). Increased populations of *S. muticum* have also been documented to

60 influence grazers within subtidal ecosystems. Experiments demonstrate that *S. muticum* serves as an additional food

61 supply, shelter, and spawning habitat for many crab and snail species (Seebach et al. 2010; Britton-Simmons 2011),

62 while other species such as the green sea urchin, *Strongylocentrotus droebachiensis*, are deterred by *S. muticum*

63 (Marks et al. 2020).

64   Coastal food webs of the Salish Sea are experiencing both short-term and long-term warming due to

65 climate change. The annual mean water temperature in the Salish Sea is 10°C, fluctuating between 6.5°C to 13°C

66 seasonally (Khangaonkar et al. 2019). Climate models predict that by 2100 Salish Sea surface temperatures will

67 increase by approximately 1.57°C and estuarine and intertidal ecosystems, the ecosystems in which kelp crabs are

68 found, warming more intensely by 3.23°C (Khangaonkar et al. 2019; Berry et al. 2021). Short-term, intense periods

69 of warming due to atmospheric heatwaves are also becoming more common and have created large-scale shifts in

70 the structure of kelp forests (Berry et al. 2021; Khangaonkar et al. 2021; McPherson et al. 2021; Raymond et al.

71 2022). Atmospheric heatwaves are short time periods (2+ days) of elevated air temperatures, based on historical

72 averages for a given area, that influence shallow nearshore environments (Raymond et al. 2022). Atmospheric

73 heatwaves are most influential and relevant in intertidal and nearshore ecosystems (Raymond et al. 2022). In 2014-

74 2016, Salish Sea estuarine temperatures were warmer by an average of 2.3°C (Khangaonkar et al. 2021). Nearshore

75 intertidal sea surfaces were warmer by a maximum of 6.2°C (Gentemann et al. 2017). Intertidal organisms often

76 experience a wide range of temperatures with short term high temperature exposures within the range of elevated

77 temperatures tested within this experiment. Temperature changes are often accompanied by other abiotic changes,

78 like changes in salinity or acidification that may also influence biological responses to environmental stress.

79   Food web interactions and the organisms within them have been influenced by warming temperatures in a

80 variety of ways. Many herbivores, including crabs, have shown increased feeding at high temperatures due to an

81 increase in metabolic requirements (Hill 1980; McPherson et al. 2021). For example, in laboratory studies the mud

82 crab, *Scylla serrata*, increased feeding at elevated temperatures of 20°C and 25°C (Hill 1980). The same trend of

83 consuming more at higher temperatures has also been shown in king crabs, *Paralithodes camtschaticus*,

84 (Siikavuopio & James 2015) and shore crabs, *Carcinus maenas* (Elner 1980). In simulations based on the 2014-2016

85   northeast Pacific heatwave, there was an increase in biological activity due to ocean temperatures (Khangaonkar et

86   al. 2021). Thus, understanding the effects of herbivores like *P. gracilis*, warming, and interactions on both *N.*

87   *luetkeana* and *S. muticum* is especially critical.

88   As ocean temperatures increase on both long-term and episodic timescales in the Salish Sea, it is of

89   particular importance to understand how ecologically significant organisms and the food webs they comprise may

90   respond. The sensitivity of adult *N. luetkeana* to ocean warming has been well documented and linked to recent

91   declines in many Pacific Northwest and Salish Sea populations (Schiel et al. 2004; Supratya et al. 2020; Berry et al.

92   2021). In laboratory studies, the growth and development of healthy *N. luetkeana* spores had reduced success when

93   incubated in temperatures of 17 °C or above (Schiltroth et al. 2018). It remains unclear how ocean warming affects

94   the ability for *N. luetkeana* to respond to other environmental factors, such as invasive species like *S. muticum.*

95   Increased *S. muticum* populations have been correlated with rising seawater temperatures and increased nutrient

96   enrichment (Norton 1977; Wang et al. 2019). Increasing populations of *S. muticum* may influence the distribution

97   and abundance of *N. luetkeana* and consequently associated food web interactions. If this continues, *N. luetkeana*

98   populations could experience this additional stressor in parallel to their already documented vulnerabilities to

99   warming (Schiel et al. 2004; Supratya et al. 2020).

100   Our first objective in this study was to understand the relationship between *P. gracilis* and both native and

101   invasive food sources. We asked: 1) Can *P. gracilis* consume both *N. luetkeana* and S. *muticum*? And if so, 2) Does

102   *P. gracilis* have a preference between these two food sources? We hypothesized that *P. gracilis* would be able to

103   consume both seaweeds but would prefer the native *N. luetkeana* over the invasive *S. muticum* because similar

104   feeding preferences have been demonstrated by the closely related Northern kelp crab (*Pugettia producta*)

105   (Dobkowski et al. 2017). We conducted choice and no-choice feeding trials to determine what seaweeds *P. gracilis*

106   can eat as well as quantify which food sources they prefer to eat when given two options. By studying these feeding

107   preferences, we can better understand the future impacts of invasive species on *P. gracilis* and the ecological

108   pressures that potentially affect *N. luetkeana*.

109   Our second objective was to assess how *P. gracilis* feeding is affected by elevated temperatures

110   characteristic of short-term warming subtidal ocean conditions in the Salish Sea. We hypothesized that *P. gracilis*

111   would increase feeding rates at higher temperatures similar to observed trends in other invertebrate species (Elner

112   1980; Carr & Bruno 2013; Siikavuopio & James 2015). To do this, we conducted feeding trials (using the preferred

113 food option, *N. luetkeana*) at two temperatures, ambient (11.5 ± 1.3°C) and elevated (19.5 ± 1.8°C), to determine the

114 differences among feeding rates between temperatures.

115

116 **Methods**

117 *No Choice and Choice Experiments*

118   We collected 12 *P. gracilis* (3.5 ± 1.8 g) from 0 to 2 m depth from four sites in June and July of 2020

119 (Reuben Tart County Park, Deadman's Bay, Friday Harbor Labs, and Eagle Cove; Supplemental 1, Supplemental

120 Tbale 1). Crabs were collected randomly without bias towards sex or size. We did not use ovigerous females and all

121 crabs were adult crabs. Once collected, we housed the crabs in flow-through seawater tanks at ambient water

122 temperature (11-12°C) at Friday Harbor Labs (FHL). Crabs resided individually in plastic tanks (28 cm x 15 cm x

123 11 cm) with mesh lids and consumed a mixed diet of local seaweeds prior to, and in between, experiments. We used

124 a block experiment design, treating the crabs as the blocking factor, to examine the feeding preferences of *P.*

125 *gracilis*. Two of the twelve crabs molted during the experiment and therefore we have only utilized the data from

126 before the molting event.

127   We conducted two sets of experiments: (1) no-choice feeding experiments, where crabs were offered only

128 one food type (*N. luetkeana* or *S. muticum)*, and (2) choice feeding experiments, where crabs were offered both food

129 types simultaneously. No-choice experiments enabled us to quantify food consumption of each food type

130 individually while the choice experiments enabled us to assess food preference between the two food types. Each

131 crab participated in three independent feeding trials in a randomized order: *N. luetkeana* only, *S. muticum* only, and

132 choice of *N. luetkeana* and *S. muticum*, leading to a total of 36 trials (Supplemental 2).

133   To prepare food for these experiments, we collected *N. luetkeana* and *S. muticum* from detached, floating

134 "drift" sources near FHL. All food sources were harvested from the same drift patch and we used only non-

135 reproductive kelp blades to standardize for freshness of the food source and environmental factors such as drift time.

136 The wet mass of food items was determined prior to every trial using an Ohaus Navigator XT scale. We offered

137 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

138 the visibly larger food item.

139   Each trial lasted three days (Supplemental 2). Crabs spent the same amount of time in the flow-through

140 tanks prior to the experiment. Crabs were starved for 24 hours prior to each independent feeding period. The

141 starvation period was followed by a 48-hour feeding period which took place in the same flow-through seawater

142 tanks holding the crab. Pilot experiments showed 48 hours to be sufficient time for crabs to eat a quantifiable

143 amount of the food sources offered. We used a short feeding time to minimize effects of nutrient enhancement due

144 to crab excretion on seaweed mass. We measured blotted wet mass before and after each experiment to calculate

145 how much each crab consumed. Thirty-six controls used the same experimental design, which included no crabs, to

146 account for natural mass loss or gain of seaweed not due to crab consumption over a 48-hour period. Each control

147 was run and subtracted from the corresponding trial.

148   We conducted a Shapiro Test for normalcy (choice: p = 0.4126; no-choice: p = 0.9729) and therefore

149 proceeded with a Bartlett Test for normally distributed data to test for equal variances across test groups (choice: p =

150 0.463; no-choice: p = 0.5846). All conditions were met to proceed with a t-test for differences in means. To analyze

151 these data, we used an unpaired t-test for the no-choice experiments and a paired t-test for the choice experiments to

152 determine if there were significant differences in food consumption between the food types. We calculated algal

153 mass consumed (g) per crab mass (g) for comparability purposes. We did not assess effects of sex or size because of

154 the small sample size and limited power to include these factors as covariates. All analyses were conducted in R

155 version 1.2.1335 (R Foundation for Statistical Computing Platform 2020).

156

157 *Temperature Experiments*

158   We collected 18 additional *P. gracilis* (mean and SD: 3.3 ± 1.2 g) from Friday Harbor Labs in November

159 of 2020 and trials were run from November 2020 to February 2021 (Supplemental Table 2). We did not hold or

160 reuse crabs between feeding preference experiments and temperature experiments and ambient water temperatures

161 where the laboratory seawater pump is located does not change appreciably throughout the year. We maintained

162 crabs in the lab using the same set up described for the experiments above, and seaweeds were collected using the

163 same procedure as in the feeding experiments.

164   Each of the crabs were randomly assigned to a temperature treatment: ambient (twelve *P. gracilis* mean and

165 SD: 3.2 ± 1.1 g; temperature mean and SD: 11.5 ± 1.3°C) or elevated (six *P. gracilis* mean and SD: 3.6 ± 1.3 g;

166 temperature mean and SD: 19.5 ± 1.8°C). Temperature in tanks was regulated using aquarium heaters. Temperature

167 was monitored using a DS18B20 temperature probe which logged temperature every 10 minutes to a ESP8266

168 microcontroller running MicroPython. Crabs were placed in their own individual tanks with heaters. The unbalanced

169   sample size was due to some elevated treatment crabs experiencing a significantly high temperature shock because

170   of unstable heaters; thus those crabs were removed from the experiment. For elevated temperature treatments, the

171   water began at ambient temperature and was slowly raised to reach the target temperature over the course of 24

172   hours, a temperature increase that the study organisms could be exposed to in their natural environments on the same

173   time scale. Crabs were acclimated to the elevated temperature treatment for another 48 hours while feeding normally

174   prior to trials. As in the no-choice and choice experiments described above, crabs were then starved for 24 hours

175   before a 48 hour feeding period (Supplemental 3). All crabs were given *N. luetkeana* only during feeding rate trials

176   to control for food type. Eighteen controls (12 in ambient water conditions, six in elevated water conditions)

177   followed the same experimental design, which included no crabs, to account for natural mass loss or gain of

178   seaweed not due to crab consumption. Each control was run and subtracted from the corresponding trial.

179   To compare the amount of *N. luetkeana* consumed between the two temperature treatments, we utilized a

180   Welch's t-test to accommodate our unequal sample sizes. For analysis, we calculated algal mass consumed (g) per

181   crab mass (g). This analysis was conducted in R version 1.2.1335 (R Foundation for Statistical Computing Platform

182   2020).

183

184   **Results**

185   *No Choice and Choice Experiments*

186   *P. gracilis* successfully consumed both *N. luetkeana* (mean and SE: 0.26 ± 0.04 g) and *S. muticum* (0.22 ±

187   0.03 g) during the 48-hour feeding period. Crabs displayed no significant difference in their consumption of *N.*

188   *luetkeana* versus *S. muticum* when given no choice between the two food types (t=0.075, df=10 p-value=0.464; Fig.

189   I).

190   Conversely, *P. gracilis* consumed significantly more *N. luetkeana* (0.23 ± 0.03 g) than *S. muticum* (0.15 ±

191   0.04 g) when given a choice between the two food types (t=3.038, df=11 p-value=0.013; Fig. II).

192

193   *Temperature Experiments*

194   Crabs in the ambient temperature treatment consumed 0.14 ± 0.05 g of *N. luetkeana,* while crabs in the

195   elevated temperature treatment consumed 0.58 ± 0.10 g over 48 hours. Crabs exposed to elevated temperature ate

196 significantly more *N. luetkeana* than those exposed to ambient temperature (Welch's t-test: t= -2.564, df= 5.95, p-

197 value=0.04; Fig. III).

198

199 **Discussion**

200   Our results show that *N. luetkeana* is the preferred food type of *P. gracilis* but also suggest that the crabs

201 can modify their diet to exploit the invasive food source, *S. muticum*. This suggests *P. gracilis* has a more generalist

202 diet beyond just the kelp for which the crabs are named. Generalist feeding strategies are common among crabs,

203 including *Acanthonyx scutiformis,* a coastal crab and seaweed generalist, and *Uca annulipes,* another coastal crab

204 and omnivore (Milner et al. 2009; Vasconcelos et al. 2009). Our finding that *P. gracilis* can eat equally as much *S.*

205 *muticum* as *N. luetkeana* when given no choice is significant for their continued success in response to changing

206 food availability which may be characteristic of future conditions. We did not assess effects of sex or size due to the

207 small sample size but recognize that this is a variable to be considered in future studies. Further research is also

208 needed to determine if both food types confer the same nutritional value. As a generalist consumer, *P. gracilis* is

209 well-positioned to take advantage of an increasingly available invasive food source.

210   Our study is realistic of field food conditions because co-occurring *N. luetkeana* and *S. muticum* beds in the

211 Salish Sea have been observed, emulating our choice experiments. As *S. muticum* populations increase, food

212 conditions recreated in our choice experiments may become more common, creating more opportunities for crabs to

213 choose their food type. We have determined that *N. luetkeana* is the preferred food source of *P. gracilis* so in

214 scenarios where *N. luetkeana* and *S. muticum* beds are co-occurring, even though *P. gracilis* can consume both, they

215 may choose to consume *N. luetkeana.* Despite the increasing *S. muticum* populations and changing ocean

216 temperatures, this feeding alone puts pressure on *N. luetkeana*.

217   Our results suggest that at higher temperatures, *P. gracilis* consumes greater amounts of *N. luetkeana* than

218 at ambient water temperatures. This response is consistent with increased consumption rates measured in other

219 coastal invertebrates in response to increased temperatures. Green sea urchins, *Strongylocentrotus droebachiensis*,

220 (Carr & Bruno 2013), king crabs, *Paralithodes camtschaticus*, (Siikavuopio & James 2015) and shore crabs,

221 *Carcinus maenas* (Elner 1980) have also exhibited increased consumption and metabolic rates at higher

222 temperatures (Carr & Bruno 2013). As ocean temperatures rise, our work demonstrates that *P. gracilis,* may increase

223 the amount of food consumed, placing pressure on their preferred food source, *N. luetkeana*. Further research is

224   needed to understand if *P. gracilis* increases consumption of their non-preferred food type, *S. muticum,* at elevated

225   temperatures as well, and if these trends are consistent across closely related crabs. Though we only examined

226   temperature as an abiotic effect on P. *gracilis* feeding, future studies should examine the effects of multiple co-

227   occurring abiotic stressors.

228   *N. luetkeana* and other native kelp populations have demonstrated negative responses to elevated

229   temperatures, whereas invasive *S. muticum* populations have demonstrated positive responses to similar elevated

230   temperatures (Ambrose & Nelson 1982; DeWreede 1983; Stæhr et al. 2000; Britton-Simmons 2004). In one study,

231   high temperatures decreased growth and performance of native seaweeds, such as *Fucus serratus* and *Chondrus*

232   *crispus,* but enhanced growth and performance of *S. muticum* (Atkinson et al. 2020). In the San Juan Islands,

233   Washington, *S. muticum* survived in temperatures up to 28°C, whereas *N. luetkeana* has decreased performance and

234   fitness starting at 18°C (Lüning & Freshwater 1988). The future quantity and quality of *N. luetkeana* beds have been

235   shown to, and is predicted to continue to, decrease with increasing ocean temperatures (Simonson et al. 2015; Schiel

236   et al. 2004; Supratya et al. 2020). If *P. gracilis* consumes more *N. leutkeana* at higher temperature, and *S. muticum*

237   populations proliferate in warmer waters, future *N. luetkeana* survival may be threatened by these combined

238   impacts.

239   Elevated temperatures used in our experiments have relevance to short term, episodic warming events that

240   have become increasing more prevalent in intertidal ecosystems. Our elevated temperature conditions are aligned

241   with the already established intertidal and shallow subtidal ecosystem warming predictions and mirror acute and

242   episodic temperature stress due to the increasing prevalence of warming events like atmospheric heatwaves

243   (Raymond et al. 2022). The short-term elevated temperature conditions in our experiment have the most near-term

244   field relevance in the context of these episodic and extreme temperature stresses. With the short duration of

245   temperature stress, six days, the temperature experiments closest resemble the time scale of recent atmospheric

246   heatwaves and may predict the effects of a short temperature anomaly on food web interactions during these periods.

247   Many studies on ecological effects of warming and invasive species have been conducted independently,

248   but recent evidence has shown that ocean warming and invasive species can act together to alter marine

249   communities (Stachowicz et al. 2002; Sorte et al 2010; Strayer 2010; Miranda et al. 2019; Atkinson et al. 2020). Our

250   results show that in warmer waters, *S. muticum* may be increasingly able to outcompete *N. luetkeana*, supported by

251   its increased productivity and growth rates in warmer waters (Norton 1977; Wang et al. 2019). Therefore, both

252   ocean warming and competition from invasive seaweeds each place separate stress on native seaweeds such as *N.*

253   *luetkeana*. These stresses could be compounded by *P. gracilis'* preference for the native seaweed, *N. luetkeana*, over

254   the invasive seaweed, *S. muticum* and increased consumption of *N. luetkeana* at elevated temperature. If this trend

255   occurs in the field, *N. luetkeana* populations may experience compounding stressors in warming conditions from

256   increased herbivory in addition to higher levels of competition from invasive seaweeds.

257   Graceful kelp crabs will likely be able to modify their diets as nearshore algal communities and food

258   availability change in response to warming temperatures and invasive species. Our results show that *P.gracilis* eats

259   more at higher temperatures but generalist feeding strategies make them well-positioned to manage changing

260   ecosystems. Though we found that *S. muticum* was not the preferred food source of *P. gracilis*, it is a competitor of

261   *N. luetkeana* which proliferates at high temperatures, suggesting it is also well-positioned to thrive under warmer

262   ocean conditions. Conversely, *N. luetkeana* is likely to experience compounding negative effects of competition by

263   increasing populations of *S. muticum*, decreased survival due to warming, and increased grazing by *P.gracilis* thus

264   making them the most vulnerable of the three organisms we studied. Our study helps to identify relative

265   vulnerabilities of interacting species within coastal food webs in the face of changing community structure and

266   atmospheric heat waves.

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Figure 1

No Choice Experiment Feeding Levels of *P. gracilis*

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=0.464).
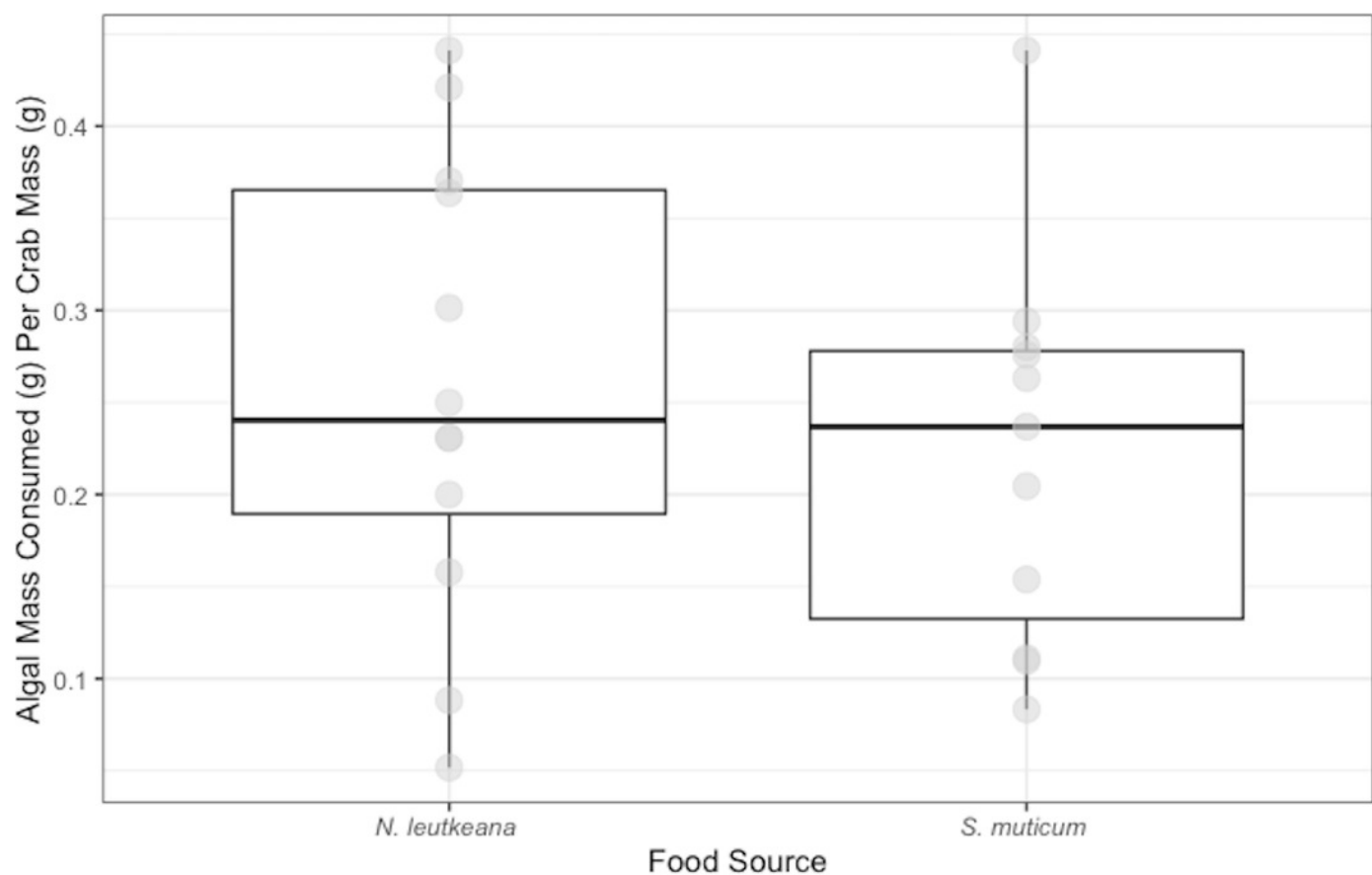
Figure 2

Choice Experiment Feeding Levels of *P. gracilis*

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=3.038, df=11 p-value=0.013).
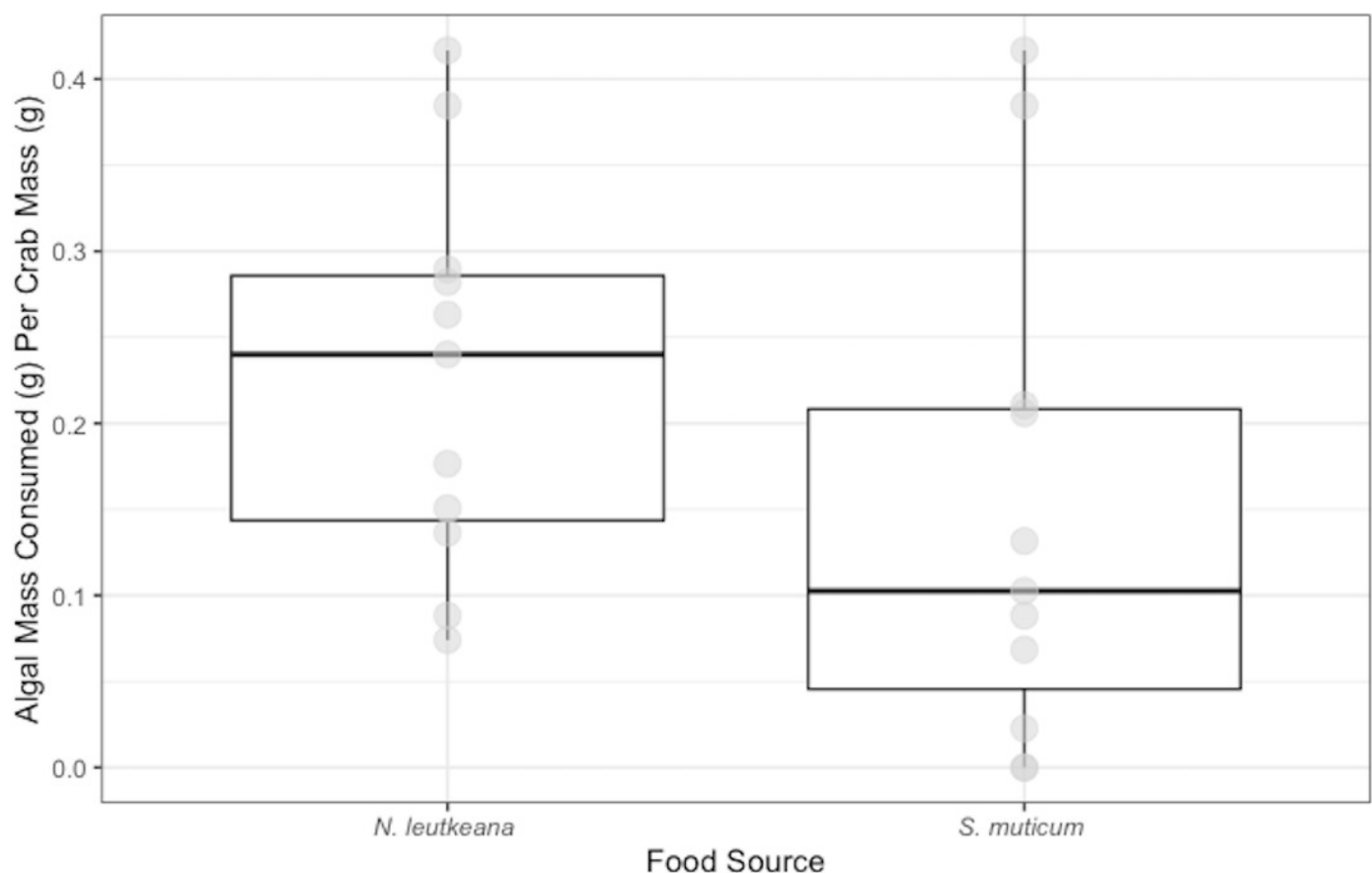
Figure 3

Temperature Experiment Feeding Levels of *P. gracilis*

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= -2.564, df= 5.95, p-value=0.04)