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Morphological and trophic differences between kelp crabs (Pugettia producta) inhabiting kelp and pilings”\

Sarah Mueller

Morphological and trophic differences between kelp crabs (*Pugettia producta*) inhabiting kelp and pilings

Sarah Mueller*, Mairan Smith, and Kaitlyn Carney

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Abstract

Individuals within a species may specialize on fine-scale habitats, allowing them to exploit different opportunities for foraging, resting and refuge, and reproduction. Kelp crabs (*Pugettia producta*) in Puget Sound can be observed on both bull kelp (*Nereocystis luetkeana*) and dock pilings, with unknown implications for function and behavior. In this study, we investigated how the morphology and diet of kelp crabs living on bull kelp and on pilings differs. We collected 30 kelp crabs from each habitat and measured their carapace width, leg length, and color. Additionally, we performed stable isotope analysis to determine possible diet sources of the crabs in each habitat. We found distinctions between individuals using different habitats in carapace width and leg length but not color. Kelp-dwelling crabs had greater carapace width and shorter legs relative to their body size than piling-dwelling crabs, but the crabs in different habitats did not vary in redness. We also observed sexual dimorphism: male crabs had smaller carapaces and longer legs relative to their body size and were more red than females. Varying leg length between habitats could be due to grasping ability: longer legs may be better to grab wide pilings, while short legs may be beneficial for holding narrow bull kelp stipes. Differences in size between habitats could be due to variations in pressures including food availability, predation, and human disturbance that could impact the growth and mortality rates of crabs. There were no conclusive differences in diet between kelp- and piling-dwelling crabs.

Introduction

Individuals within a species may specialize on fine-scale habitats, which has implications for the ecology and evolution of a species (Hultgren and Stachowicz 2010). Variation in resource use, including habitats, between conspecific individuals of the same stage class, age, sex, or at the same site is known as individual variation (Fodrie et al. 2015). Factors in the selection of habitats by organisms include color, habitat structure, temperature, and predation intensity. These differences in habitat characteristics ultimately have fitness consequences such as impacts on growth, mortality, and mating success (Hultgren and Stachowicz 2010). Additionally, different habitats may support distinct food resources and varying structural complexity (Fodrie et al. 2015). Habitat specialization likely allows individuals to exploit different opportunities for foraging, resting and refuge, and reproduction (Fodrie et al. 2015).

Kelp crabs (*Pugettia producta*) are a common species of spider crab in the Pacific Northwest that demonstrate habitat specialization. In California, *P. producta* is a kelp specialist (Hines 1982) and has been found to have distinct size and color distributions in kelp forests (Hultgren and Stachowicz 2010; Iampietro 1999). In the intertidal zone, crabs are small and maroon or dark olive and inhabit surf grass and foliose red algae, while in the shallow subtidal crabs are small, maroon, and primarily inhabit foliose red algae (Iampietro 1999). Farther from shore in the deep subtidal, larger, amber-colored crabs are found on giant kelp, *Macrocystis pyrifera* (Iampietro 1999). In general, carapace color of the crabs match their substrate (Iampietro 1999), and mismatching colors—a red crab on kelp, for instance—have been found to result in higher mortality rates (Hultgren and Stachowicz

2010). *P. producta* has the ability to change its color, which is produced by pigments such as carotenoids and phycobilins, to match its substrate via molting (Iampietro 1999). The crabs sequester pigments from the algae they consume in order to camouflage with their habitat (Hultgren and Stachowicz 2010). In the Puget Sound, *P. producta* can be observed on both bull kelp (*Nereocystis luetkeana*) and pilings. However, no research exists on the drivers of this pattern in habitat use, so functional and behavioral implications remain uncertain.

One potential driver of individual variation in habitat use is differences in food resources between habitats. *P. producta* is primarily herbivorous, consuming various types of algae. On the Central California coast, (Iampietro 1999) found that crabs occupying all depth zones primarily consume giant kelp, *M. pyrifera*. Deep subtidal crabs fed exclusively on kelp, while shallow subtidal and intertidal crabs additionally consumed small amounts of red and other brown algae, surf grass, and other food sources (Iampietro 1999). Kelp crabs may also be omnivorous if sufficient algae is not available (Leighton 1966).

We investigated how the morphology—carapace width, leg length, and color—and diet of kelp crabs living on kelp and pilings differs. We predicted that kelp crabs living on bull kelp would be kelp-colored and larger than piling-dwelling crabs, potentially due to higher food availability and lower density. Additionally, we predicted that crabs living on pilings and on kelp may have morphological differences due to the varying requirements of climbing on and grasping different substrates. We also expected diets to differ, with kelp-dwelling crabs consuming more kelp.

Materials and Methods

Data Collection

In October and November 2016, we collected 30 kelp crabs from two sites: bull kelp (*Nereocystis luetkeana*) beds near the shore of Point Defiance Park in Tacoma, WA, and pilings of docks near the Point Defiance ferry terminal in Tacoma, WA. Immediately after collection, we measured carapace width and leg length and took images of the dorsal and ventral sides of each crab using a digital camera. The sex of the crab was also recorded. Additionally, for stable isotope analysis, we took a rear leg tissue sample from three male crabs of approximately equal size from each habitat and a sample of bull kelp. All samples were dried, weighed and sent to the University of California Santa Cruz Stable Isotope Lab and analyzed using an isotope ratio mass spectrometer (IRMS)

The color of each crab was calculated from the digital photographs. After calibrating each photograph to neutral gray, the red, green, and blue channels of the ventral side photograph were measured using RGB Measure in ImageJ. We used ventral-side photographs because the ventral surfaces of the crabs showed the most prominent color difference. We defined "redness" as the red channel measurement.

Data Analysis

Leg length was standardized to carapace width to better account for the crabs' leg length relative to their body size with the following equation:

$$\text{Standardized leg length} = \frac{\text{Leg length (cm)}}{\text{Carapace width (cm)}}$$

To determine relative contributions of possible diet sources to each individual and population, we used isotopic values in a dietary mixing model in Stable Isotope Analysis in R (SIAR). We included isotopic values for intertidal invertebrates and algae from previous student research, our kelp crab tissue samples, and published trophic enrichment factors as model inputs (Hoeinghaus and Davis III 2007; Fantle et al. 1999). Model-derived estimates of proportions of algae and invertebrates in crabs' diets were tested for significant differences.

Carapace width (n = 60 crabs), standardized leg length (n = 60 crabs), and redness (n = 39 crabs) were analyzed using a 2-way ANOVA, with sex and habitat type (kelp or piling) as explanatory variables. Assumptions of normality and equal variance of residuals were met for all tests. Tukey post-hoc tests were used for pairwise comparisons.

Results

Morphological Parameters

Carapace width was greater in kelp-dwelling crabs than piling-dwellers (2-way ANOVA; $F_{1,56} = 4.74$, $p = 0.034$; Figure 1) and greater in female crabs than in males ($F_{1,56} = 7.16$, $p = 0.010$). Habitat type had no significant effect on the difference in carapace width between males and females ($F_{1,56} = 0.02$, $p = 0.903$). Female, kelp-dwelling crabs had the largest carapace size, while male, piling-dwelling crabs had the smallest carapace size.

Leg length standardized to carapace width was greater in piling-dwelling crabs than kelp-dwellers (2-way ANOVA; $F_{1,56} = 10.21$, $p = 0.002$; Figure 2) and males had longer legs than did females ($F_{1,56} = 117.72$, $p < 0.001$). Habitat type had no significant effect on the difference in leg length between males and females ($F_{1,56} = 0.58$, $p = 0.448$).

Redness was not significantly different between kelp-dwelling crabs and piling-dwellers (2-way ANOVA; $F_{1,35} = 1.04$, $p = 0.314$; Figure 3). However, male crabs were significantly redder than were females ($F_{1,35} = 18.29$, $p < 0.001$). Habitat type had no significant effect on the difference in redness between males and females ($F_{1,35} = 0.88$, $p = 0.356$). Female, kelp-dwelling crabs were the least red, while male crabs in both habitats were the most red.

Dietary Analysis

Stable isotope data resulted in no conclusive differences in diet source (barnacles, mussels, green algae, red algae, bull kelp, or stringy green algae; Figure 4) between kelp-dwelling and piling-dwelling crabs. In both habitats, kelp crabs appeared to be consuming similar proportions of each of the various diet sources.

Discussion

Morphological Parameters

Our results indicate that individuals differing in some morphological characteristics such as carapace width and relative leg length, though not color, did show variation in habitat use. As we predicted, kelp-dwelling crabs were larger and had different leg morphology, with greater carapace width and shorter legs relative to their body size than piling-dwelling crabs. However, contrary to our hypothesis, the crabs in different habitats did not vary in redness. Additionally, we observed significant sexual dimorphism: male crabs had smaller carapaces and longer legs relative to their body size and were more red than females.

The differences we observed in leg length relative to body size between crabs using the two habitats could be due to structural differences between pilings and kelp and the crabs' ability to grasp their substrates. The longer legs of piling-dwelling crabs may be better to grab wide pilings, while the relatively short legs of kelp-dwelling crabs could be beneficial for holding narrow bull kelp stipes.

The lack of difference in redness observed between habitats could be due to the limited difference in algae diets between habitats. Because crabs sequester pigments from the algae they consume, individuals using kelp and piling habitats would have similar colors if the algal composition of their diets was similar. However, though there were no habitat-specific differences in redness, male crabs were much more red than females. In crabs, color differences among individuals may be due to behavioral interactions between sexes and variations in mating success, in addition to factors such as growth stage, season, stress levels, circadian rhythm, and temperature (Silbiger and Munguia 2008). In the kelp crabs we studied, behavioral interactions seem to be the most likely driver of color difference as few environmental variables would be expected to differ between males and females occupying the same areas.

Kelp and piling habitats likely have varying severity of pressures including food availability, predation, and human disturbance that could impact the growth and mortality rates of crabs, leading to differences in size and age distributions between the two habitats. Piling-dwelling crabs were smaller and therefore likely younger. They probably experience high anthropogenic disturbance on the pilings, which were located in a marina, and may also experience other factors including lower resource availability and higher predation. Kelp-dwelling crabs were larger and likely older. On kelp, they may experience higher resource availability because they are living on their food source, lower predation, and/or lower disturbance, as the kelp beds are farther from centers of human activity. Hultgren and Stachowicz (2010) found that small, maroon kelp crabs had higher mortality on kelp (although growth rates on kelp and red algae were equal) and hypothesized that small crabs may be less abundant on kelp due to higher mortality rates or could be avoiding the kelp because of the risk of mortality. Large crabs also grew faster on kelp with only slightly higher mortality, so may preferentially inhabit kelp (Hultgren and Stachowicz 2010). Additionally, for larger but not for smaller crabs, prior feeding on kelp increased habitat preference for it, a process known as positive preference induction (Hultgren and Stachowicz 2010). An ontogenic shift in habitat use likely occurs in these crabs, with small, younger individuals inhabiting red algae and larger, older individuals moving to kelp (Hultgren and Stachowicz 2010). A similar pattern could be occurring between kelp and pilings, with younger, smaller individuals on pilings moving to bull kelp beds as they age and grow, though more research tracking crabs would be required to determine whether crabs migrate between pilings and kelp.

Dietary Analysis

We found no clear difference in diet between kelp-dwelling and piling-dwelling crabs based on our stable isotope results. This is contrary to our prediction that crabs living on bull kelp would consume more of it, while the crabs living on pilings would need to rely on other food sources such as other types of algae or marine invertebrates. Additionally, our results did not indicate that bull kelp was the majority of the crabs' diet, contrary to previous studies that have found that kelp crabs primarily consume kelp

(Iampietro 1999) or even strictly specialize on kelp (Hines 1982). There does seem to be a carbon shift between the two groups of crabs, but a larger sample size would be required to confirm this. Additionally, our diet sources do not appear to fully explain all individuals' $\delta^{13}C$ and $\delta^{15}N$ ratios, with two individuals falling far to the bottom right, suggesting we may be missing a diet source. A more in-depth analysis including a more crab samples and additional diet sources could further clarify whether or not there are dietary differences between crabs on pilings versus kelp.

Conclusion

We observed morphological differences but similar diets between kelp crabs living on pilings and on kelp. However, our study did not address the ecological patterns driving these trends, which could include competition, predation, or temporal patterns. For instance, a competition study between kelp-dwelling and piling-dwelling crabs could determine whether competitive ability is driving habitat use. Individual habitat use could also vary temporally because in Puget Sound, bull kelp senesces in fall, detaching from the substrate and eventually degrading. Because of this, kelp-dwelling crabs lose their habitat every winter, but it remains unknown whether these crabs migrate to pilings or to another habitat.

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Tables and Figures

Table 1. Adjusted $\delta^{13}C$ and $\delta^{15}N$ values for individual kelp crabs

Crab #	Habitat	$\delta^{13}C$	$\delta^{15}N$
1	Piling	-13.91	7.33
2	Piling	-15.89	9.14044
3	Piling	-13.56	7.31767
4	Kelp	-16.92	7.97502
5	Kelp	-16.69	7.8683
6	Kelp	-15.92	7.77922

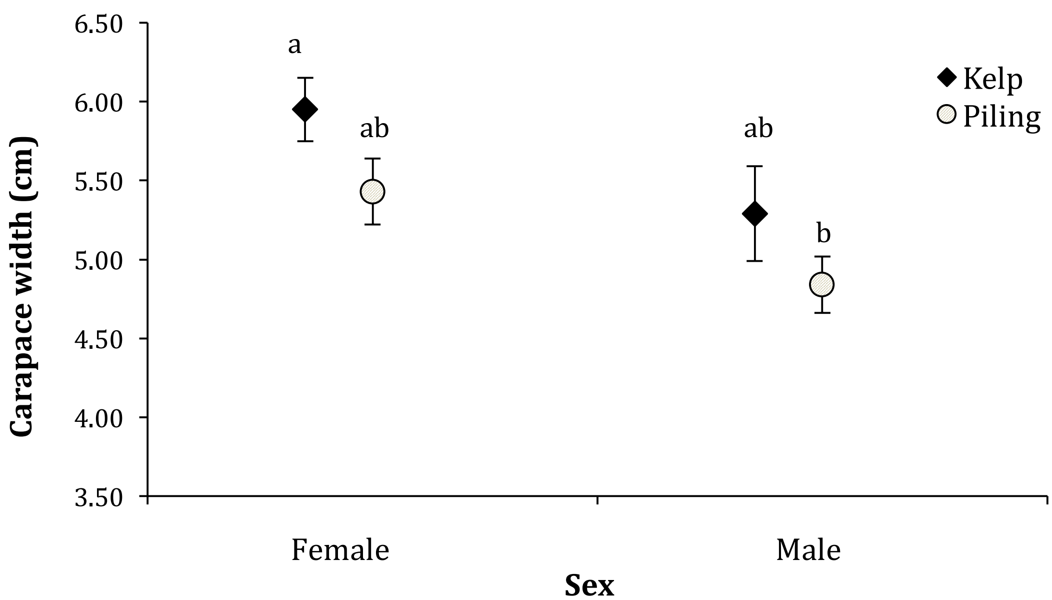

Figure 1. Mean (± SE) kelp crab carapace width by sex and habitat (kelp or piling). Carapace width was greater in kelp-dwelling crabs than piling-dwellers (p = 0.034) and greater in female crabs than in males (p = 0.010). The difference in carapace width between males and females was similar between habitats (p = 0.903). Letters indicate statistical significance.

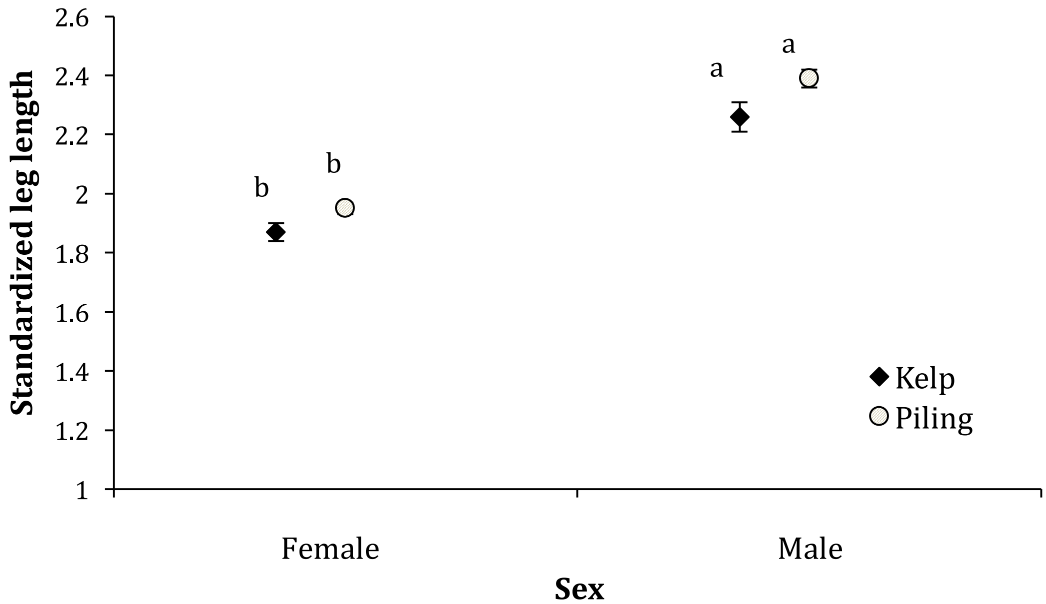

Figure 2. Mean (± SE) kelp crab leg length standardized to carapace width by sex and habitat (kelp or piling). Piling-dwelling crabs had longer legs relative to their carapace width than did kelp-dwellers ($p = 0.002$), and males had longer legs than did females ($p < 0.001$). Habitat type had no significant effect on the difference in leg length between males and females ($p = 0.448$). Letters indicate statistical significance.

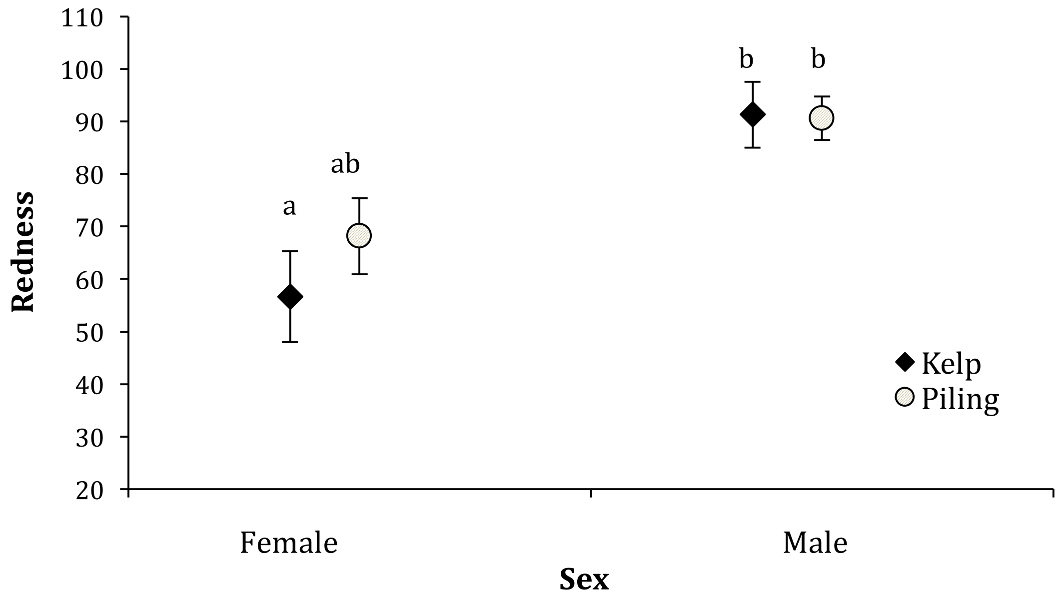

Figure 3. Mean (± SE) kelp crab redness by sex and habitat (kelp or piling). Letters indicate statistical significance. Redness was not significantly different between kelp-dwelling crabs and piling-dwellers ($p = 0.314$), but male crabs were redder than females ($p < 0.001$). Habitat type had no significant effect on the difference in redness between males and females ($p = 0.356$). Letters indicate statistical significance.

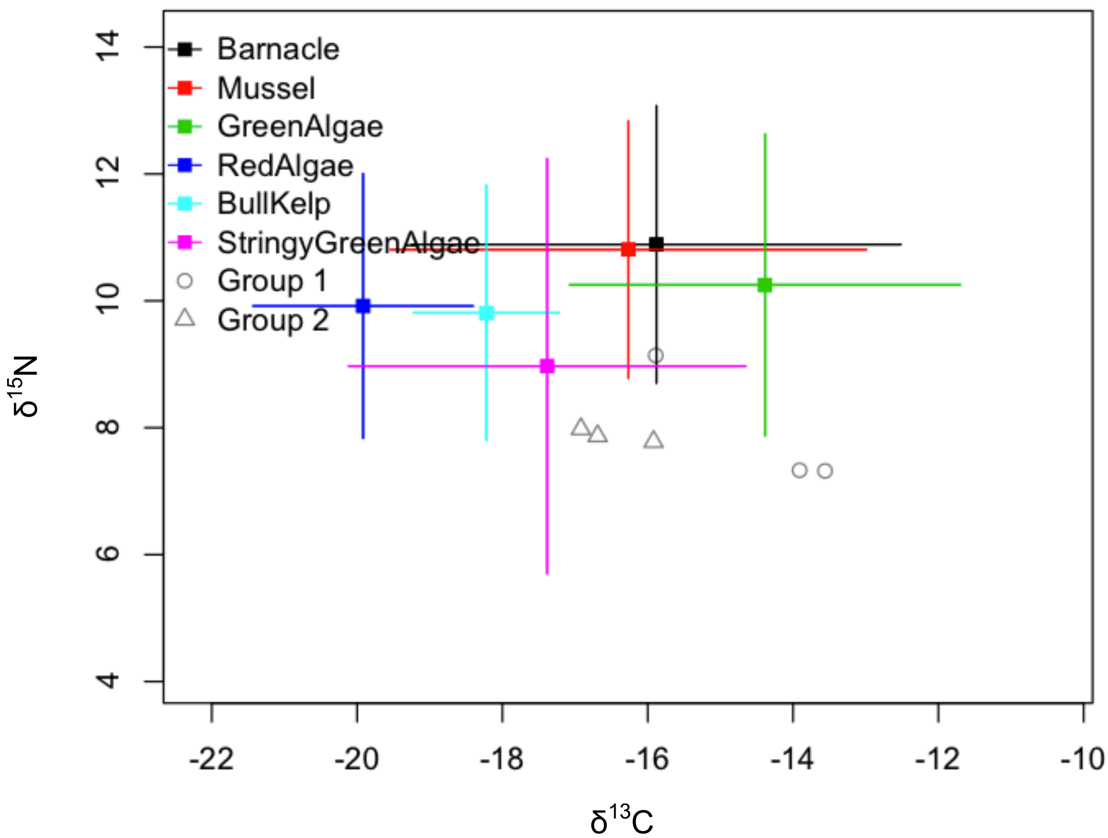

Figure 4. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of muscle tissue from individual kelp crabs. Values have been corrected by subtracting 1% and 2.5% respectively from the measured $\delta^{13}C$ and $\delta^{15}N$ presented in Table 1. Potential diet sources have been grouped into barnacles, mussels, green algae, red algae, bull kelp, and stringy green algae. Group 1 (open circles) are the piling-dwelling crabs and Group 2 (open triangles) are the kelp-dwelling crabs. There were no conclusive differences in diet source between kelp-dwelling and piling-dwelling crabs.

Appendix: R output

2-way ANOVA: Carapace width vs. Habitat and Sex

```
Analysis of Variance Table

Response: Carapace
            Df Sum Sq Mean Sq F value   Pr(>F)
Habitat      1  3.825  3.8254  4.7385 0.033726 *
Sex          1  5.781  5.7807  7.1607 0.009754 **
Habitat:Sex  1  0.012  0.0121  0.0150 0.902864
Residuals   56 45.208  0.8073
```

Tukey pairwise comparisons

```
       trt    means  M
1 F:Kelp   5.946429  a
2 F:Piling 5.430769 ab
3 M:Kelp   5.293750 ab
4 M:Piling 4.835294  b
```

2-way ANOVA: Standardized leg length vs. Habitat and Sex

```
Analysis of Variance Table

Response: Leg.std
            Df  Sum Sq Mean Sq  F value    Pr(>F)
Habitat      1 0.22026 0.22026  10.2144  0.002291 **
Sex          1 2.53862 2.53862 117.7247 2.188e-15 ***
Habitat:Sex  1 0.01258 0.01258   0.5836  0.448129
Residuals   56 1.20759 0.02156
```

Tukey pairwise comparisons

```
      trt    means M
1 M:Piling 2.393120 a
2 M:Kelp   2.259524 a
3 F:Piling 1.950102 b
4 F:Kelp   1.874760 b
```

2-way ANOVA: Redness vs. Habitat and Sex

```
Analysis of Variance Table

Response: Red
            Df  Sum Sq Mean Sq F value   Pr(>F)
Habitat      1   379.5   379.5  1.0439 0.313924
Sex          1  6649.8  6649.8 18.2942 0.000139 ***
Habitat:Sex  1   318.6   318.6  0.8764 0.355611
Residuals   35 12722.2   363.5
```

Tukey pairwise comparisons

```
       trt    means  M
1 M:Kelp   91.31314  a
2 M:Piling 90.54756  a
3 F:Piling 68.14980 ab
4 F:Kelp   56.65300  b
```