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Fast Kelp Crab Consumption: Implications for Washington State Sea Otters

**ABSTRACT**

Estimating the energy intake rate of an animal population can provide information on the status of the population and can serve as a proxy for estimating growth rate. Direct observation of sea otter (*Enhydra lutris spp.*) foraging allows researchers to collect data on key foraging behavior variables such as prey handling time, type, and size that is then assembled into a Monte Carlo model to estimate the energy intake rates of sea otter populations. In order to generalize this model to populations throughout the sea otter’s range, the energy intake model assumes that the same prey type of a given size is equivalent across regions, and as a result, the energetic benefit to a sea otter when consuming that prey is also assumed to be equivalent. Despite the assumption that sea otter foraging behavior and prey characteristics are largely independent of geography, a deviation has recently been observed. Average handling time of kelp crabs (*Pugettia spp.*) by sea otters (*Enhydra lutris kenyoni*) in Washington is approximately 1.5- 2 times faster than in California or British Columbia. In an attempt to understand what is driving this difference, we tested 1) whether kelp crabs are equivalent sea otter prey items in Washington and California by comparing biomass to width ratios of kelp crabs collected in Washington and California and 2) whether sea otters in Washington may be exhibiting diet specialization on kelp crabs by comparing the handling times of sea otters who specialize in eating kelp crabs in California to sea otters in Washington and British Columbia. Results of our kelp crab morphometric analysis suggest that Washington kelp crabs may have a larger biomass to width ratio than kelp crabs in California. We found that the handling times of small crabs by Washington sea otters and handling times by California kelp crab specialists were equivalent (*p* = 0.313), and Washington sea otters were faster than California kelp crab specialists in handling large kelp crabs (*p* = 0.007). Given that we would expect a lower biomass per width if a difference in kelp crab biomass were driving the difference, our finding that Washington kelp crabs appear to have a higher biomass per width than California kelp crabs suggests that a difference in individual kelp crab biomass is not driving the faster handling times in Washington. Our results also suggest that Washington sea otters may be specializing in kelp crabs, as evidenced by their similar, and even faster, handling times when compared to kelp crab specialists in California. Importantly, the faster kelp crab handling times in Washington result in energy intake rate estimates as much as one third higher than in any other region. While it is possible that Washington otters do have much higher energy intake rates, further investigation of the assumptions of the model may be warranted, and give researchers further insight into the ecology of sea otters throughout their range.

**INTRODUCTION**

Sea otters (*Enhydra lutris*) are intermittently distributed along the coasts of the northern Pacific Ocean. Three subspecies are currently recognized and are separated geographically: *Enhydra lutris lutris* in Japan and Russia; *Enhydra lutris kenyoni* in Alaska, British Columbia, and Washington; and *Enhydra lutris nereis* in California. The maritime fur trade resulted in sea otters in Washington and British Columbia being hunted to local extinction in the early 1900s, and sea otters from Alaska were translocated to both locations in 1969-72 (Jameson et al. 1982) in the hopes of reestablishing populations. Though a population of sea otters remained in California through the fur trade (Kenyon 1969), their numbers were significantly reduced and have suffered from slow population growth well past the end of the fur trade (Estes et al. 2006).

Sea otters lack insulating blubber and instead rely on thick fur and a fast metabolism to regulate their body temperature, consuming as much as a third of their body mass per day to support their metabolic needs (Kenyon 1969). Unlike other diving marine mammals, sea otters return to the surface after each foraging dive to consume their prey and typically forage close to shore (Kenyon 1969, Riedman 1991), allowing for direct observation. A standardized protocol for collecting sea otter foraging data has been developed and is used by research groups throughout the sea otter’s North American range (Kvitek et al. 1998, Laidre and Jameson 2006, Tinker et al. 2008, Hessing-Lewis et al. 2017). In this protocol, researchers on land use high-powered telescopes to observe a foraging sea otter for a continuous sequence of foraging dives, referred to as a foraging bout. For each foraging dive, observers recorded key variables, including: dive duration (time underwater searching for prey), surface duration (time on surface between dives, usually spent consuming prey), and dive outcome (whether or not prey was successfully captured). For each successful foraging dive, observers record prey handling time (times spent handling and consuming prey) and identify prey type to the lowest possible taxonomic level, number of prey items, and prey size. Prey size is estimated in relation to average sea otter forepaw width. The average width of a sea otter’s paw has been measured in both northern sea otters (*E. lutris kenyoni*; 50mm) and southern sea otters (*E. lutris nereis*; 42mm), and is used to estimate the size of a prey item visually, where a “size 1” ≤ 1 sea otter paw, “size 2” > 1 sea otter paw but ≤ 2 sea otter paws, and so on (Kvitek et al. 1993, Tinker 2015). Prey size categories (1, 2, 3, and 4) are further split into size category qualifiers a, b, and c, where “a” is the smallest 1/3 of the size class, “b” is the middle 1/3 of the size class, and “c” is the largest 1/3 of the size class.

The sea otter’s unique foraging behavior allows researchers to estimate energy intake rates based on observed foraging behavior and previously assembled information on diameter-biomass relationships and calorific densities for each prey type (Oftedal et al. 2007). Studies of sea otter foraging patterns have been used to infer sea otter population status (Estes et al. 2003, Laidre and Jameson 2006, Tinker 2015). For instance, diet diversity has been shown to increase with increasing density of sea otter populations (Tinker et al. 2008). Similarly, a negative relationship between sea otter density and biomass intake rate has been observed in populations throughout their range (Newsome et al. 2015). Utilizing these relationships and measuring the energy intake rates of sea otter populations can help identify the status of a population and whether it is at or approaching carrying capacity.

To account for the biases associated with observational data collection (e.g. larger prey being identified more accurately, difficulty in observing foraging otters that are far off shore, etc.) researchers have used a Monte Carlo simulation model to account for the non-random nature of missing data (Tinker 2015). This simulation model outputs estimated energy and mass intake rates, and diet composition. Standardized protocol for sea otter foraging data collection and some assumptions of uniformity of sea otter foraging behavior and prey allow for the simulation model to be generalized across regions and for foraging data to be compared across regions. A key assumption made when calculating sea otter energy intake rates with the simulation model is that a prey type of a given size is equivalent across regions, and as a result the energetic benefit to a sea otter when consuming that prey type is also assumed to be equivalent. Energy contents of common sea otter prey used in the simulation model were measured for invertebrates collected in California (Oftedal et al. 2007), the results of which are used for modeling the energy intake of sea otters throughout their North American range. Oftedal et al. (2007) produced power functions for prey items to estimate the edible biomass of a prey item based on the width— the metric that is observable from shore. The kilocalorie contents of common prey items were also measured using bomb calorimetry to determine kilocalories of energy per gram of edible biomass. When combined with observational foraging data, the information gathered by Oftedal et al. (2007) can be used to accurately model sea otter energy intake rates.

Despite the assumption that sea otter foraging behavior and prey characteristics are largely independent of region, a deviation has recently been observed. The average handling time of kelp crabs (*Pugettia spp.*) by sea otters in Washington is about 1.5- 2 times faster than that of California and British Columbia sea otters (Hale et al. 2018, in review). This pattern is consistent across decades of sea otter foraging observations in Washington State (Laidre and Jameson 2006), as well as across different observers (Hale et al. 2018, in review). It is currently unclear what may be driving this difference in observed kelp crab handling time. One hypothesis is that Washington kelp crabs have a lower edible biomass than equally sized kelp crabs from California or British Columbia, resulting in faster handling times. A second hypothesis is that there is a learned ability of Washington sea otters to handle and consume kelp crabs faster than in other areas. This kind of learned ability is known as diet specialization, and has been widely documented in sea otter populations (Estes et al. 2003, Tinker et al. 2008). Individual diet specialization is frequently observed in sea otter populations that are high density (~3-7 otters/ km2), where high sea otter densities lead to low food availability (Tinker et al. 2012, Newsome et al. 2015). Kelp crabs (*Pugettia spp.*) make up a substantial portion of sea otter diets in North America, comprising 8-20% of their diet in some locations (Tinker 2004) and up to 28% (based on grams/minute intake rate) in Washington State at sites where they are the primary prey item (Hale et al. 2018, in review). Due to the ubiquity of kelp crabs in sea otter diets, any changes to the accepted energy content of kelp crabs or energy intake rates associated with them could produce a marked effect in the overall estimates of sea otter energy intake rates.

The objectives of this study were to 1) test whether kelp crabs in Washington have a different maximum biomass to width ratio than kelp crabs in California and 2) test whether California kelp crab specialist sea otters exhibit different kelp crab handling times than Washington or British Columbia sea otters.

**METHODS**

**Kelp crab morphometric data collection**

We collected kelp crabs (*Pugettia producta*) from the Washington coast and compared their width-to-total-biomass ratio to California kelp crabs measured by Oftedal et al. (2007). Kelp crabs (*Pugettia producta*) were collected in April 2018 on the outer Washington coast at Sand Point (48.128347°N, 124.712291°W). This site was selected because it is a sea otter foraging observation location where kelp crabs are an important prey item in sea otter diets (19% of diet) and because of considerations concerning ease of access. Collections were performed by hand by removing kelp crabs from *Macrocystis pyrifera* mats (WDFW Permit no. 17-343a). Specimens were kept on ice and covered with towels dampened with seawater and transported back to a lab on the University of Washington Seattle campus. Kelp crabs were separated into individual plastic bags and euthanized via freezing at -20°Cbefore processing. Maximum carapace width was measured from outside edge to outside edge of the anterolateral teeth in millimeters using digital calipers (Mitutoyo Corporation) to the nearest 0.01 mm. Specimens were weighed using a digital scale (Ohaus Corp., Florham Park, NJ) to the nearest 0.01 g.

**Kelp crab morphometric data analysis**

We used a power function of the form [biomass] = a·[diameter]b to estimate biomass from maximum carapace width. In this function [biomass] was the unprocessed wet biomass (grams) of each individual crab and [diameter] was the maximum carapace width (millimeters) for each individual crab. We created four models to examine the data and found the maximum likelihood estimates (MLE) by minimizing the negative log likelihood (NLL) using Microsoft Excel.

Model 1 treated California and Washington kelp crabs as one population with one power function and estimated parameters *a*, *b*, and *σ* (3 total parameters); Model 2 treated California and WA kelp crabs as two independent populations with two power functions and estimated parameters *a*, *b*, and *σ* for each population (6 total parameters); Model 3 treated California and Washington kelp crabs as one population with one power function and estimated parameters *a* and *b* but with independent *σ* values for each population (4 total parameters); and Model 4 treated California and Washington kelp crabs as two independent populations with two power functions and estimated parameters *a* and *b* for each region and with a single global *σ* value (5 total parameters). All NLL’s were calculated using a lognormal distribution. We compared the corrected Akaike Information Criteria (AICc) values of the four models to determine the best-fit model.

**Sea otter foraging observations**

Observations of tagged southern sea otters (Tinker et al. 2007, 2008) allowed us to compare the handling times of known kelp crab specialists in California to kelp crab handling times of sea otters in Washington and British Columbia. Foraging data from the central coast of British Columbia were collected by researchers at the Hakai Institute (Rechsteiner, unpublished); California data was collected in Monterey, CA (Tinker, unpublished); and Washington foraging data was collected on the Washington coast (Hale et al. 2018, in review). Sea otter foraging data was gathered using a standardized protocol (Ostfeld 1982) by observers on land using high-powered telescopes.

Only dives where a single kelp crab was captured or where multiple kelp crabs of the same size were included in our analysis. For dives where multiple kelp crabs of the same size were captured, the total handling time was divided by the number of crabs on the dive. Additionally, dives that were missing information on prey size, prey quantity, or handling time were omitted, and only dives where the entire kelp crab was consumed were included in our analysis.

**Sea otter foraging data analysis**

As northern and southern sea otter paw sizes are different (50mm for northern, 42mm for southern), it was not possible to compare the handling times of qualitative size classes (1a, 1b, etc.) directly across regions. Handling times for each region - California (CA), Washington (WA), and British Columbia (BC) - were summarized for two groups based on the size of the kelp crab captured: “small” (prey sizes 1a, 1b, and 1c for Northern sea otters; prey sizes 1a, 1b, 1c, and 2a for Southern sea otters) and “large” (prey sizes 2a, 2b, 2c, and 3a for Northern sea otters; prey sizes 2b, 2c, and 3a for Southern sea otters). These size classifications correspond to “small” being ≤ 50mm wide for Northern sea otters and ≤ 60 mm wide for Southern sea otters, and “large” being > 50mm for Northern sea otters and > 60 mm for Southern sea otters. To test for a difference in kelp crab handling times between regions, the average kelp crab handling times for each of the three study regions (British Columbia, Washington, and California) were compared using two one-way ANOVA tests— one for “small” kelp crabs and one for “large.” Results of the ANOVA tests were examined using Tukey HSD (honest significant difference) post-hoc tests.

We used a second pair of one-way ANOVA tests to compare the kelp crab handling times of Washington otters, British Columbia otters, and kelp crab specialist otters in California. Handling times for each region were grouped into the same “small” and “large” sub-groups. Results of these ANOVA tests were also examined using Tukey HSD post-hoc tests. All sea otter handling time data analysis was performed using R (RStudio Team 2016).

**RESULTS**

**Kelp crab morphometrics**

We collected a total of *n* = 60 kelp crabs of various sizes (10-42 mm) and sexes (*n* female = 27, *n* male = 33) and compared them to *n* = 50 kelp crabs collected by Oftedal et al. (2007). Parameter estimates of all four models are summarized in Table 1. Of the four models that we tested to fit the morphometric data (Figure 2), the model that estimated separate power function parameters *a*, *b*, and *σ* for California and Washington kelp crabs (Model 2, Figure 1B) had the lowest AICc value (Table 2).

**Regional handling time comparison**

We found that small kelp crab handling time was significantly faster in Washington than in both California and British Columbia (*p* = 5.88E-11, *p* = 2.19E-12, respectively; Figure 1A). We also found that large kelp crab handling time was significantly faster in Washington than in both California and British Columbia (*p* = 0.00E0, *p* = 7.04E-3, respectively; Figure 1B). Interestingly, we also found that large kelp crab handling times in British Columbia were significantly faster than large kelp crab handling times in California (*p* = 4.33x10-6).

**California kelp crab specialist handling time comparison**

We found that small kelp crab handling times by Washington otters and California kelp crab specialists were not significantly different (*p* = 0.313; Figure 3A). Conversely, sea otter handling times of small kelp crabs in British Columbia were significantly slower than average handling time in Washington (*p* = 2.02x10-12) and significantly slower than the average handling time of California kelp crab specialists (*p* = 3.33x10-7). Average sea otter handling time of large kelp crabs in Washington (Figure 3B) was significantly faster than both California kelp crab specialists (*p* = 0.007) and British Columbia sea otters (*p* = 0.003). However, there was no significant difference in the average handling time of large kelp crabs by California specialists and British Columbia otters (*p* = 0.313).

**DISCUSSION**

**Sea otter handling time comparison**

The results of our comparison of sea otter handling times of kelp crabs confirmed findings outlined in Hale et al. (2018, in review) that Washington otters have significantly faster average handling times than otters in both California and British Columbia, for both small and large crabs. When compared to kelp crab specialists in California, handling times of small kelp crabs in Washington did not differ and were significantly faster than specialists in their handling of large kelp crabs. Furthermore, as there are very few tagged and individually identifiable otters in Washington, and the handling time averages we present include data from all otters (specialists and non-specialists), it is possible that Washington specialists are even faster than the population-wide average suggests. This difference in kelp crab handling times may stem from differences in the kelp crabs themselves or a difference in the sea otters.

Like any model, a number of assumptions are made when estimating the energy intake rates of sea otters using foraging data, including assumptions of equivalent prey items and sea otter foraging behavior. Under these assumptions, the energy intake rate estimates of Washington otters are as much as one third higher than anywhere else where data has been collected (Hale et al. 2018, in review). Given that energy intake rates are a key metric used to predict the status of a sea otter population, a difference this large could dramatically change projections for the Washington population. The energy intake rates of other sea otter populations— from Bering Island, Russia to southern California— have a very consistent range of ~20 kcal/min in areas with virtually unlimited prey, down to ~6-7 kcal/min in highly food limited areas (Tinker 2015), whereas Washington sea otter intake rates range from ~30kcal/min down to only ~15 kcal/min. Because the intake rates in other areas are relatively uniform, the higher intake rate estimates in Washington are especially notable.

While it is entirely possible that Washington otters are experiencing higher energy intake rates than other regions, it is important to examine other factors that could be causing the faster handling times but that may not be changing the true energy intake rates. If Washington sea otters do not actually have higher energy intake rates, then some other factor may be in violation of the assumptions of the energy intake model. One possible explanation is that Washington otters are not as thorough when handling kelp crabs as sea otters in other regions. Our comparison of California kelp crab specialist handling times indicated that Washington otters had significantly faster times than specialists for large crabs, an unexpected result given that Washington otters exhibited similar handling times to specialists for small crabs. The sample size for large kelp crab handling times of California specialists was noticeably smaller (*n* = 17) than for British Columbia or Washington (*n* = 139 and *n* = 119, respectively), indicating that sea otters in California may encounter large kelp crabs less frequently. Interestingly, in our comparison of handling times of large kelp crabs (Figure 1B), not only were Washington kelp crab handling times significantly faster than the other regions, but British Columbia kelp crab handling times were significantly faster than California times. Southern sea otters that occur in low density populations— where food is not limiting— have been observed consuming prey items less efficiently, leaving a larger proportion uneaten (Tinker, personal obs.). Similarly, groups of sea otters in British Columbia have exhibited the same behavior upon arriving to a previously unoccupied site (Rechsteiner, personal obs.). Based on these observations, if Washington sea otters are less food-limited than otters in other regions, they may be consuming kelp crabs less thoroughly, reducing the overall handling time. Similarly, the faster handling times of large kelp crabs in both British Columbia and Washington could be driven by the same principle; if sea otters in these regions experience large kelp crabs more often than otters in California, they may be consuming them less thoroughly.

In our sample of sea otter handling times from Washington, 78% of kelp crab handling time observations were of small kelp crabs, compared to 84% in California and 61% in British Columbia. Based on these proportions, it does appear that California otters may experience larger kelp crabs less often than otters in California or Washington. However, as these handling times only reflect kelp crabs that were completely consumed and could be sized confidently, future studies to explore the size distributions of kelp crabs across their distribution may be needed to indicate if the observed proportions of small and large crabs in sea otter diet reflect the proportions that sea otters are encountering.

Currently, sea otter foraging observation protocols do attempt to correct for unfinished prey items, as observers note when an otter does not a finish a prey item and visually estimates the proportion that was uneaten (Kvitek et al. 1998, Laidre and Jameson 2006, Tinker et al. 2008). But if otters that exhibit faster kelp crab handling times are somehow discarding an undetected portion of their prey, observation methods may need to be revised. Future research that more closely examines Washington sea otter processing of kelp crabs through video analysis and observation of captive otters could address the possibility that the handling time anomaly is coming from handling differences that cannot be observed from shore.

**Kelp crab morphometrics**

The results of our kelp crab morphometric analysis suggested that Washington kelp crabs have a greater biomass than kelp crabs from California of the same width. Of the models that we tested, the best (Model 2) was a model that utilized two separate power functions to describe the biomass per width relationship and treated the California and Washington populations independently. However, Model 2 predicted a higher biomass per width ratio in Washington kelp crabs than in California crabs, the opposite of what we would expect if a difference in kelp crab morphology were driving the difference in sea otter kelp crab handling times.

While there was more variation in the California kelp crabs sampled by Oftedal et al. (2007) than in kelp crabs sampled in our study, the comparison of models with a single *σ* (Model 1 vs. Model 4) where variation was treated as independent of region, still indicated that the better model was the one that treated the population samples as distinct using two separate power functions, suggesting that the variation alone did not account for CA and WA being considered different populations in the best-fit model. Several factors could explain the higher variation in the California kelp crab sample. The kelp crab *Pugettia producta* is known to range in size based on the habitat that it occupies (Hultgren and Stachowicz 2010) and like most decapods, exhibits seasonal molting. In the study by Oftedal et al. (2007), kelp crabs were collected over multiple seasons, in multiple geographic areas, and with a range of methods while the kelp crabs in the present study were collected over a single month span and from a single location. The range of collection methods and timing of collection by Oftedal et al. (2007) has the potential to introduce additional variation in the sizes and masses of crabs that were collected. The kelp crabs from each region also differed in their size ranges, with California kelp crab maximum carapace widths ranging 16-69 mm and Washington crabs ranging 10-43 mm. These possible sources of variation may account for the observed variability in the samples. Additionally, while variation in the samples did drive model selection to some degree— the better overall models were the ones that allowed for independent *σ* values— variability was not the dominant force.

Sea otters typically eat smaller kelp crabs whole, but remove the carapace of larger kelp crabs before consuming the rest of the crab (Tinker, personal observation). It is therefore possible that a difference in the proportion of edible biomass could be the crucial difference between kelp crabs in Washington and California. If kelp crabs in Washington of the same size have a lower proportion of edible biomass than kelp crabs in California, they may be able to handle and consume them faster. It is also possible that Washington kelp crabs differ purely in their energy content (kilocalories/gram of tissue). If this were the case and Washington kelp crabs had a lower energy density, then faster handling times would not translate into a higher kilocalorie intake rate. Calorimetric analysis of Washington kelp crabs (comparable to that of Oftedal et al. 2007) could shed light on whether differences in the kelp crabs themselves are driving the faster handling times in Washington.

**Implications and future research**

Through the results of this study we were able to explore several hypotheses to explain the faster kelp crab handling times in Washington sea otters, an anomaly shown to have a strong influence on the estimated energy intake rates of the Washington population. Understanding the energy intake rates of sea otter populations is crucial to managing them effectively. If the assumptions are accurate that sea otter foraging behavior and prey are independent of region, and energy intake rates of Washington sea otters are truly higher than in other areas, the carrying capacity of the Washington population could be higher than previously thought. Moreover, if energy intake rates are not actually higher in Washington, diagnosing the forces that are driving the faster handling times could provide insight to aid in management of the species, not only for the Washington population, but for sea otters across their range.

**REFERENCES**

Estes, J. A., B. B. Hatfield, K. Ralls, and J. Ames. 2006. Causes of mortality in California sea otters during periods of population growth and decline. Marine Mammal Science 19:198–216.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. Journal of Animal Ecology 72:144–155.

Hale, J. R., K. L. Laidre, M. T. Tinker, R. J. Jameson, S. J. Jeffries, S. E. Larson, and J. L. Bodkin. 2018. Influence of Occupation History and Habitat on Washington Sea Otter Diet. Manuscript in review.

Hessing-Lewis, M., E. U. Rechsteiner, B. B. Hughes, M. Tim Tinker, Z. L. Monteith, A. M. Olson, M. M. Henderson, and J. C. Watson. 2017. Ecosystem features determine seagrass community response to sea otter foraging. Marine Pollution Bulletin.

Hultgren, K. M., and J. J. Stachowicz. 2010. Size-related habitat shifts facilitated by positive preference induction in a marine kelp crab. Behavioral Ecology 21:329–336.

Jameson, R. J., K. W. Kenyon, A. M. Johnson, and H. M. Wight. 1982. History and Status of Translocated Sea Otter Populations in North America. Wildlife Society Bulletin (1973-2006) 10:100–107.

Kenyon, K. 1969. The Sea Otter in the Eastern Pacific Ocean. North American Fauna 68:1–352.

Kvitek, R. G., C. E. Bowlby, and M. Staedler. 1993. Diet and foraging behavior of sea otters in Southeast Alaska. Marine Mammal Science 9:168–181.

Kvitek, R. G., P. Iampietro, and C. E. Bowlby. 1998. Sea otters and benthic prey communities: a direct test of the sea otter as keystone predator in Washington state. Marine Mammal Science 14:895–902.

Laidre, K. L., and R. J. Jameson. 2006. Foraging patterns and prey selection in an increasing and expanding sea otter population. Journal of Mammalogy 87:799–807.

Mitutoyo Corporation. (n.d.). Mitutoyo Absolute Digimatic CD-6" CS Digital Caliper manual.

Newsome, S. D., M. T. Tinker, V. A. Gill, Z. N. Hoyt, A. Doroff, L. Nichol, and J. L. Bodkin. 2015. The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. Oecologia 178:45–59.

Oftedal, O. T., K. Ralls, M. T. Tinker, and A. Green. 2007. Nutritional constraints on the southern sea otter in the Monterey Bay National Marine Sanctuary and a comparison to sea otter populations at San Nicolas Island, California and Glacier Bay, Alaska. Monterey Bay National Marine Sanctuary.

Ohaus Corp., Florham Park, NJ. (n.d.). Ohaus Scout SC2020 Portable Balance.

Ostfeld, R. S. 1982. Foraging Strategies and Prey Switching in the California Sea Otter. Oecologia 53:170–178.

Riedman, M. 1991. The sea otter (Enhydra lutris) : behavior, ecology, and natural history. Washington, D.C. : U.S. Dept. of the Interior, Fish and Wildlife Service, Washington, D.C.

RStudio Team. 2016. RStudio: Integrated Development Environment for R. RStudio, Inc., Boston, MA.

Tinker, M. T. 2004. Sources of variation in the foraging behavior and demography of the sea otter, Enhydra lutris. PhD Dissertation, University of California, Santa Cruz.

Tinker, M. T. 2015. The use of quantitative models in sea otter conservation. Sea otter conservation.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. Food Limitation Leads to Behavioral Diversification and Dietary Specialization in Sea Otters. Proceedings of the National Academy of Sciences of the United States of America 105:560–565.

Tinker, M. T., D. P. Costa, J. A. Estes, and N. Wieringa. 2007. Individual dietary specialization and dive behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging strategies. Bio-logging Science: Logging and Relaying Physical and Biological Data Using Animal-Attached Tags 54:330–342.

Tinker, M. T., P. R. Guimarães, M. Novak, F. M. D. Marquitti, J. L. Bodkin, M. Staedler, G. Bentall, and J. A. Estes. 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. Ecology Letters 15:475–483.

**TABLES & FIGURES**

**Figure 1:** Average sea otter handling times of small (Figure **1A**) and large (Figure **1B**) kelp crabs (*Pugettia producta*) by region. Kelp crabs less than 50 mm wide in British Columbia and Washington were defined as “small” and kelp crabs less than 60 mm wide were defined as “small” in California. Sample sizes (number of kelp crab captures) for small kelp crab handling times in British Columbia, California, and Washington were n = 221, n = 639, and n = 422, respectively. Sample sizes for large kelp crab handling times in British Columbia, California, and Washington were n = 139, n = 126, and n = 119, respectively. Error bars represent standard error. Average handling times were compared using a one-way ANOVA. Letters above bars correspond to statistically different groups. (BC = British Columbia, CA = California, WA = Washington).



**Figure 2:** Maximum likelihood estimation (MLE) of four power function models fit to kelp crab morphometric data from California (triangles) and Washington (circles): **(A)** Model 1 treating CA and WA kelp crabs as one population and estimated using parameters *a*, *b*, and *σ* (3 total parameters); **(B)** Model 2 treating CA and WA kelp crabs as two independent populations and estimated using *a*, *b*, and *σ* for each population (6 total parameters); **(C)** Model 3 treating CA and WA kelp crabs as one population estimated with *a* and *b* but with independent *σ* values for each population (4 total parameters); and **(D)** Model 4 treating CA and WA kelp crabs as two independent populations estimated with *a* and *b* values for each region but with a single global σ value (5 total parameters). All MLE’s used a lognormal distribution and models were fit to data using an equation of the form [biomass]=*a*[width]*b*.

**Figure 3:** Average sea otter handling times of small (Figure **3A**) and large (Figure **3B**) kelp crabs (*Pugettia producta*) by region, comparing kelp crab handling times for all otters for British Columbia and Washington and only kelp crab specialists from California. Kelp crabs less than 5 cm wide in British Columbia and Washington were defined as “small” and kelp crabs less than 6 cm wide were defined as “small” in California. Sample sizes for small kelp crab handling times in British Columbia, California, and Washington were n = 221, n = 227, and n = 422, respectively. Sample sizes for large kelp crab handling times in British Columbia, California, and Washington were n = 139, n = 17, and n = 119, respectively. Error bars represent standard error. Average handling times were compared using a one-way ANOVA. Letters above bars correspond to statistically different groups. (BC = British Columbia, CA = California, WA = Washington).



**Table 1:** Maximum likelihood estimates for parameters of four different models to predict wet mass from carapace width of kelp crabs (*Pugettia producta*) in California and Washington. All models were based on a power function of the form [biomass]=*a*[width]*b*. The lognormal parameter *σ* was used to calculate the negative log-likelihood of each model.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Parameter a (Coefficient)** | | | **Parameter b (Exponent)** | | | **σ (Lognormal parameter)** | | |
|  | **global** | **WA** | **CA** | **global** | **WA** | **CA** | **global** | **WA** | **CA** |
| **Model 1** | 0.0011845 |  |  | 2.7747 |  |  | 0.2284 |  |  |
| **Model 2** |  | 0.0006393 | 0.0026097 |  | 2.9819 | 2.5487 |  | 0.0892 | 0.3070 |
| **Model 3** | 0.0007198 |  |  | 2.9409 |  |  |  | 0.0902 | 0.3465 |
| **Model 4** |  | 0.0006390 | 0.0026074 |  | 2.9821 | 2.5489 | 0.2172 |  |  |

**Table 2:** Summary of kelp crab morphometric power function model selection results. Models were compared using the sample size-corrected Akaike information criterion (AICc). Model parameters were estimated by minimizing the negative log-likelihood (NLL).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Hypothesis** | **NLL** | **Parameters** | **AICc** | **ΔAICc** | **w*i*, weight** |
| Model 1 | 256.12 | 3 | 518.48 | 76.38 | 2.57E-17 |
| Model 2 | 214.64 | 6 | 442.09 | 0.00 | 9.92E-01 |
| Model 3 | 221.68 | 4 | 451.75 | 9.66 | 7.93E-03 |
| Model 4 | 250.74 | 5 | 512.06 | 69.97 | 6.34E-16 |