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RAPID CONSUMPTION OF KELP CRAB: IMPLICATIONS FOR SEA OTTERS IN WASHINGTON STATE

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ABSTRACT—As animal populations approach environmental carrying capacity, competition for food increases, generally leading to decreased individual energy intake rate. Energy-intake rate can therefore be used as one metric of population status relative to carrying capacity. Focal observations of Sea Otter (*Enhydra lutris*) foraging behavior have been used throughout their range to estimate energy-intake rates and infer population status. In Washington State, previous research has demonstrated that handling times for Kelp Crabs (*Pugettia* spp.) by Sea Otters are 1.5 to 2 times faster than those observed in California and British Columbia, resulting in higher energy-intake rate estimates for Sea Otters in Washington. We investigated potential causes for the difference in handling time by: (1) comparing Sea Otter handling times of Kelp Crab and non-Kelp Crab prey items in Washington, California, and British Columbia; (2) comparing the handling times of Kelp Crabs by a subset of Sea Otters in California, which are Kelp Crab specialists (2003–2012, $n = 244$ Kelp Crab captures) to those of Sea Otters in Washington (2015–2018, $n = 541$ captures) and British Columbia (2013–2017, $n = 359$ captures); and (3) comparing the biomass-to-width ratios of Kelp Crabs from Washington and California. We did not observe consistent differences between regions in Sea Otter handling times of non-Kelp Crab prey. Mean Sea Otter handling time of small Kelp Crabs (carapace ≤ 1 Sea Otter paw width) in Washington (32.7 s) was significantly faster than in British Columbia (52.0 s, $P < 0.0001$) and all of California (40.6 s, $P < 0.0001$), but was not significantly different from that of Kelp Crab-specialist Sea Otters in California (31.7 s, $P = 0.313$). Mean Sea Otter handling time of large Kelp Crabs (≥ 1 Sea Otter paw) in Washington (64.7 s) was significantly faster than in British Columbia (87.7 s, $P = 0.003$), in all of California (104 s, $P < 0.0001$), and in the subset of Kelp Crab-specialist Sea Otters in California (91.6 s, $P = 0.007$). Kelp Crabs in Washington had a larger biomass-to-width ratio than Kelp Crabs in California: in Washington, a Kelp Crab with a 20-mm maximum carapace width had a 3.8% greater predicted biomass than a Kelp Crab in California of the same width, and a 27.1% greater biomass for a 60-mm carapace. Our results suggest that Sea Otters in Washington are Kelp Crab specialists with behavioral differences

allowing them to consume Kelp Crabs faster, a difference that may affect the inference of Sea Otter population status from energy-intake rates in Washington.

Key words: British Columbia, California, energetics, *Enhydra lutris*, foraging behavior, Kelp Crab, *Pugettia producta*, Sea Otter, Washington

Sea Otters (*Enhydra lutris*) historically occupied the coasts of the North Pacific from Japan to Baja California, but were hunted extensively during the maritime fur trade in the 18th and 19th centuries, resulting in a loss of approximately 99% of their original numbers (Kenyon 1969). The maritime fur trade resulted in Sea Otters in Oregon, Washington, and British Columbia being hunted to local extinction in the early 1900s. Sea Otters from Alaska were translocated to Washington from Amchitka Island in 1969 and 1970, to Oregon between 1970 and 1971, and between 1969 and 1972 to British Columbia from Amchitka Island and Prince William Sound (Jameson and others 1982) in the hope of reestablishing populations. After the maritime fur trade, a remnant population of Sea Otters remained in California (Kenyon 1969), though their numbers were significantly reduced (Estes and others 2006). Sea Otters are now intermittently distributed along the north Pacific coasts, with 3 subspecies recognized owing to geographic separation and genetics: *Enhydra lutris lutris* in Japan and Russia; *Enhydra lutris kenyoni* in Alaska, British Columbia, and Washington; and *Enhydra lutris nereis* in California.

The translocation and subsequent population growth and range expansion of Sea Otters in some areas (British Columbia, Southeast Alaska, and Washington) and the recovery of extant populations in other areas (California and Southwest Alaska) has resulted in a patchwork of populations throughout the Sea Otter range. Evaluating the status of a population is a fundamental aspect of the management and recovery of a species. A range of life-history and demographic metrics have been used to infer the status of marine mammal populations, including individual body condition, time spent foraging, age at maturity, reproductive rate, and survival rate (Estes and others 1982; Bengtson and Laws 1985; Fowler 1990; Frie and others 2012; Williams and others 2013). In order to better understand Sea Otter population recovery post-fur trade, researchers have collected extensive data on Sea Otter diet and foraging behavior (Estes and others 1982; Tinker and

others 2008; Tinker 2015; Hale and others 2019; Rechsteiner and others 2019). Unlike other diving marine mammals, Sea Otters must return to the surface after each foraging dive to consume their prey, and typically forage close to shore, allowing for direct observation (Kenyon 1969; Riedman and Estes 1990). A standardized protocol for collecting Sea Otter foraging data has been developed and is used by research groups throughout much of the Sea Otter's range (Kvitek and others 1998; Laidre and Jameson 2006; Tinker and others 2008; Hessing-Lewis and others 2018; Hale and others 2019; Rechsteiner and others 2019).

Sea Otters are a keystone species, exerting top-down control on ecosystem structure (Estes and Palmisano 1974; Garshelis and others 1986; Riedman and Estes 1990; Estes and Duggins 1995). As a result, the rate at which Sea Otters consume prey, the prey species they consume, and their population dynamics can all create cascading effects through an ecosystem. In addition to estimates of diet composition and prey-capture rates, researchers have used observational data to estimate energy-intake rates, allowing for more powerful inferences about Sea Otter prey selection and population status relative to carrying capacity (Estes and others 2003; Laidre and Jameson 2006; Tinker 2015). Because of known biases associated with observational data collection (for example, larger prey being identified more accurately, difficulty in observing foraging otters that are far offshore, and so forth), energy-rate estimates are calculated using a Monte Carlo simulation model that accounts for the non-random nature of missing data (Dean and others 2002; Tinker and others 2008, 2012). This "Sea Otter foraging analysis" (SOFA) provides unbiased estimates of energy and biomass intake rates and diet composition, which can be compared within and between regions provided methods of data collection are standardized. A key assumption required for comparisons of SOFA estimates across regions is that a prey type of a given size is equivalent everywhere, in both its edible biomass and in its caloric density. Size-specific estimates of edible

biomass and caloric density of common Sea Otter prey were measured for invertebrates collected in California and Alaska (Oftedal and others 2007), and power functions were fit to these data to estimate the edible biomass of a prey item based on the maximum linear dimension—the metric that is observable from shore when making Sea Otter foraging observations. The prey data gathered by Oftedal and others (2007) provide a common basis for estimates of energy-intake rates calculated using the SOFA model.

Despite the assumption that foraging behavior and prey characteristics for Sea Otters are largely independent of region, a deviation has recently been observed. Hale and others (2019) found that the average handling time of Kelp Crabs (*Pugettia* spp.) by Sea Otters in Washington was 1.5 to 2 times faster than that of Sea Otters in California and British Columbia. This pattern is consistent across decades of foraging observations of Sea Otters in Washington State (Laidre and Jameson 2006), as well as across different observers (Hale and others 2019). Preliminary analyses suggest that the consistently faster handling times in Washington are only exhibited with Kelp Crabs and not with other Sea Otter prey items, however a formal comparison has not yet been published, and it is also unclear what may be driving the regional difference in observed Kelp Crab handling time (Hale and others 2019). One hypothesis is that Kelp Crabs in Washington have a lower edible biomass than equally sized Kelp Crabs from California or British Columbia, resulting in faster handling times. A 2nd hypothesis is that there is a learned ability of Sea Otters in Washington to handle and consume Kelp Crabs faster than in other areas. This kind of learned ability can result from individual diet specialization, where individuals spend time consuming a small number of prey types, thereby increasing their efficiency, and decreasing their handling time, when consuming those prey types (Tinker and others 2008). Individual diet specialization has been widely documented in Sea Otter populations (Estes and others 2003; Tinker and others 2008) and is commonly observed in long-established Sea Otter populations where high Sea Otter densities (>3 otters km^{-2}) deplete preferred prey types, leading individuals to specialize on less-preferred species (Newsome and others 2015; Tinker and others 2012). Although individual diet

specialization can be indicative of high-density Sea Otter populations, population-level specialization can occur independently of population density as a result of different driving forces in which bottom-up changes in prey composition cause more profitable prey types to suddenly become available (Watt and others 2000; Smith and others 2021). Kelp Crabs make up a substantial portion of Sea Otter diets in Washington and California, comprising 8 to 20% (percent occurrence) of their diet in some locations (Laidre and Jameson 2006; Tinker 2004) and up to 35% (based on grams/minute intake rate) in Washington State at sites where they are the primary prey item (Hale and others 2019). Owing to the ubiquity of Kelp Crabs in Sea Otter diets in Washington and elsewhere, differences in the energy content of Kelp Crabs or energy intake rates associated with Kelp Crabs could produce a marked effect on the overall estimates of Sea Otter energy-intake rate.

The objectives of this study were to: (1) compare the handling times of Kelp Crab and non-Kelp Crab prey items by Sea Otters in Washington, California, and British Columbia in order to confirm that Kelp Crabs are the only consistently anomalous prey item; (2) compare the handling times of Kelp Crabs by a subset of Sea Otters in California (Kelp Crab specialists) to those of Sea Otters in Washington and British Columbia to investigate the possibility of Kelp Crab specialization in the Washington Sea Otter population; and (3) test whether Kelp Crabs in Washington have a different biomass-to-width ratio than Kelp Crabs in California.

METHODS

Sea Otter Foraging Observations

To accomplish our first objective of comparing handling times of Kelp Crab and non-Kelp Crab prey items between regions, we used observations of Sea Otters foraging on Kelp Crabs, Cancer Crabs, clams, and Razor Clams (*Siliqua patula*) in Washington, British Columbia, and California. For our second objective of comparing the handling times of Kelp Crabs from a subset of Kelp Crab-specialist Sea Otters in California to the handling times of Sea Otters in Washington and British Columbia, we used observations of tagged southern Sea Otters (Tinker and others 2007, 2008) in California and untagged northern Sea Otters in British

Columbia and Washington. We were not able to directly examine specialist handling times for Sea Otters in Washington or British Columbia because there are not currently tagged Sea Otters in either of these regions that can be repeatedly observed to confirm individual diet specialization. Foraging data from the central coast of British Columbia were collected by researchers at the Hakai Institute between 2013 and 2017 (Rechsteiner and others 2019); California data were collected in Monterey, CA, between 2007 and 2012 (Tinker and others 2019), and Washington foraging data were collected on the Washington coast between 2015 and 2018 (Fig. 1B; Hale and others 2019). Data collections at all locations occurred over all seasons and followed established field methods (see Tinker and others 2008, 2012). Prey item sizes were estimated using these established methods in which size 1 prey are <1 Sea Otter forepaw width; size 2 are <2 forepaw widths but >1 ; size 3 are <3 forepaw widths but >2 ; and size 4 are >3 forepaw widths. Each size category (1, 2, 3, and 4), is further split into qualifiers (*a*, *b*, and *c*) where *a* represents the smallest 3rd of the category, *b* represents the middle 3rd, and *c* represents the largest 3rd.

Northern Sea Otters are larger than Southern Sea Otters, both in body size and in paw size (Riedman and Estes 1990). To investigate whether this size difference introduced bias into our groupings of Sea Otter prey items, we used a two-sample t-test to compare average paw widths of captured Southern Sea Otters from California ($n = 535$) and Northern Sea Otters from Washington ($n = 30$). We found that the average Northern Sea Otter ($\bar{x} = 50.4$ mm, $s = 3.5$ mm) and Southern Sea Otter paw widths ($\bar{x} = 44.2$ mm, $s = 3.5$ mm) were significantly different, regardless of sex ($t = 9.4716$, $df = 563$, $P < 0.0001$). However, the difference was less than 1 cm (6.2 mm), and as prey size classes (size 1, 2, 3, and 4) are subdivided into thirds (*a*, *b*, and *c*), the effective level of precision for prey size estimates is one-third of a Sea Otter paw width (16.8 mm for Northern Sea Otters and 14.7 mm for Southern Sea Otters). Because this level of precision is greater than our measured difference between subspecies paw sizes, when determining how to separate prey item size groups for our analysis (for example, “small” and “large” Kelp Crabs), we did not adjust the prey size estimate based on the subspecies of Sea Otter.

Only dives in which a single prey item was captured or multiple prey items of the same size and type were captured were included in the analysis. For dives in which multiple prey items of the same size and type were captured, the total handling time was divided by the number of prey items captured on the dive to calculate handling time per item, then each prey item from the dive was treated as a replicate data point—the same method used to deal with multi-prey dives in the SOFA model. Additionally, dives that were missing information on prey size, prey quantity, or handling time were omitted, and only dives for which the entire prey item was consumed were included (for example, dives where females shared prey with their pup were excluded).

In addition to our above analysis of Sea Otter foraging data, we also sought to explore the relative availability of Kelp Crabs to Sea Otters in each region. Owing to a lack of data on Kelp Crab abundance in our study regions, we instead examined the percent occurrence of Kelp Crabs in Sea Otter diet from each region as an index of relative availability to Sea Otters. For this analysis, we calculated the number of dives that included at least one Kelp Crab as a percent of the total number of successful dives for each region, regardless of the proportion of prey consumed.

Sea Otter Foraging Data Analysis

In order to test for differences in Sea Otter handling times of prey classes between regions, we compared the average handling times for each of the 3 study regions (British Columbia, Washington, and California) and prey size groups using one-way ANOVA tests. We summarized Kelp Crab handling times for each region into 2 groups based on the size of the Kelp Crab captured: “small” (prey sizes 1*a*, 1*b*, and 1*c*) and “large” (prey sizes 2*a*, 2*b*, 2*c*, and 3*a*). Clams, which included unidentified clams and Butter Clams (*Saxidomus giganteus*), were grouped into 2 size groups for each of the 3 regions: “small” (prey sizes 1*a*, 1*b*, and 1*c*) and “large” (prey sizes 2*a*, 2*b*, 2*c*, 3*a*, 3*b*, 3*c*, and 4*a*). Cancer Crabs—which included unidentified Cancer Crabs, Dungeness Crabs (*Metacarcinus magister*), and Red Rock Crabs (*Cancer productus*)—were grouped into 3 size groups for each of the 3 regions: “small” (prey sizes 1*a*, 1*b*, and 1*c*), “medium” (prey sizes 2*a*, 2*b*, and 2*c*), and

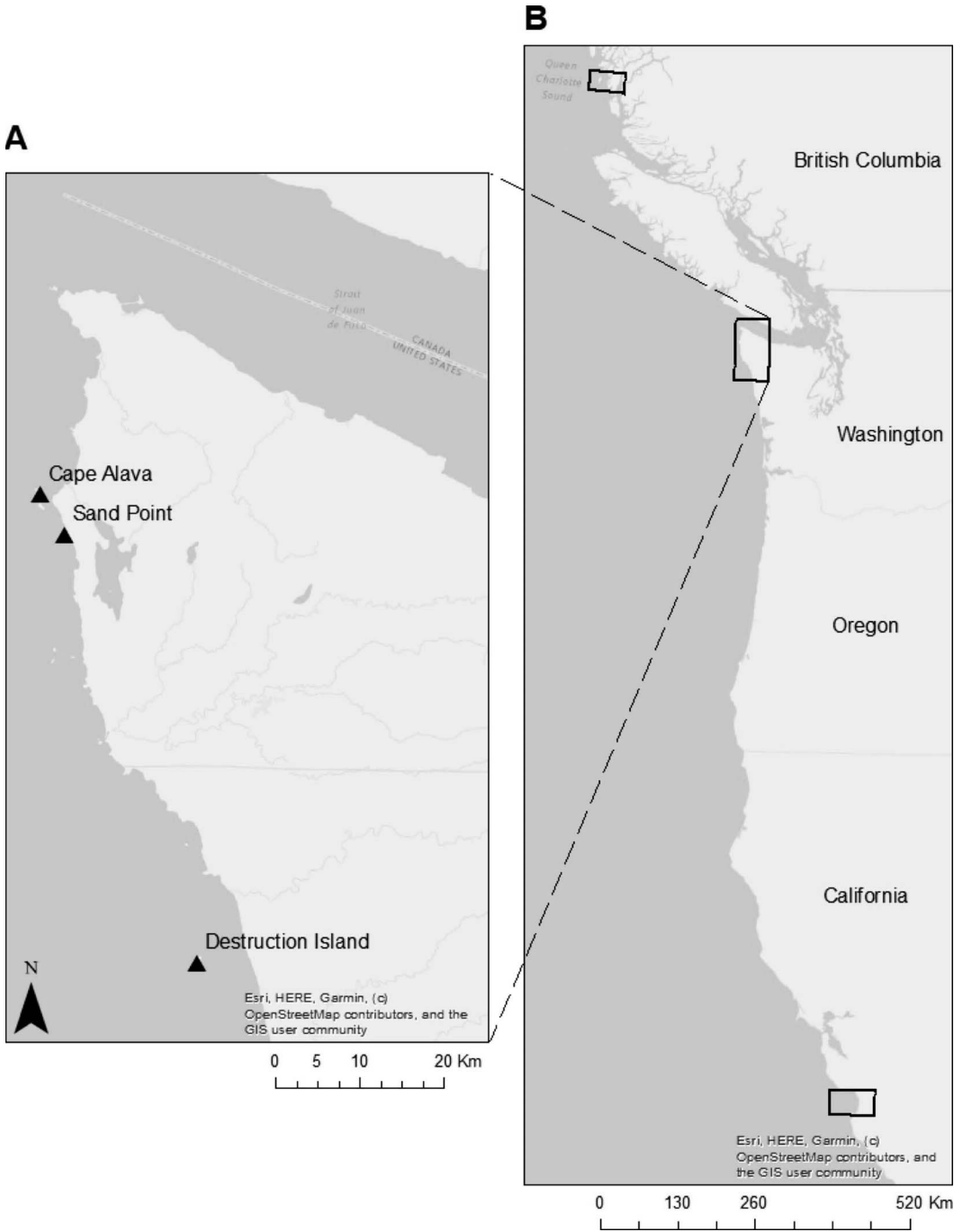


FIGURE 1. (A) The Olympic Peninsula of Washington State. Triangles mark Kelp Crab collection positions. (B) The west coast of the United States and Canada. Boxes indicate study regions where Sea Otter foraging data, including Kelp Crab handling times, were collected.

TABLE 1. Power functions of 4 different models predicting wet mass, [biomass], from maximum carapace width, [width], of Kelp Crabs (*Pugettia* spp.) in California (CA) and Washington (WA). The lognormal parameter σ was used to calculate the negative log-likelihood of each model. Model variables with a subscript “WA” or “CA” were estimated based on data from the corresponding Kelp Crab population; model variables with a subscript “all” were estimated based on data from both Kelp Crab populations combined.

Model	Functions	Variables	Total variables
Model 1	[biomass] = $a_{(all)}[width]^{b_{(all)}}$ } $\sigma_{(all)}$	$a_{(all)}, b_{(all)}, \sigma_{(all)}$	3
Model 2	[biomass] = $a_{(WA)}[width]^{b_{(WA)}}$ } $\sigma_{(WA)}$ [biomass] = $a_{(CA)}[width]^{b_{(CA)}}$ } $\sigma_{(CA)}$	$a_{(WA)}, b_{(WA)}, \sigma_{(WA)},$ $a_{(CA)}, b_{(CA)}, \sigma_{(CA)}$	6
Model 3	[biomass] = $a_{(all)}[width]^{b_{(all)}}$ } $\sigma_{(WA)}, \sigma_{(CA)}$	$a_{(all)}, b_{(all)}, \sigma_{(WA)}, \sigma_{(CA)}$	4
Model 4	[biomass] = $a_{(WA)}[width]^{b_{(WA)}}$ } $\sigma_{(all)}$ [biomass] = $a_{(CA)}[width]^{b_{(CA)}}$ } $\sigma_{(all)}$	$a_{(WA)}, a_{(CA)}, b_{(WA)}, b_{(CA)}, \sigma_{(all)}$	5

“large” (prey sizes 3a, 3b, 3c, 4a, 4b, and 4c). Results of the ANOVA tests were examined using Tukey HSD (honest significant difference) post-hoc tests. Because of a lack of occurrence of Razor Clams in the foraging data from British Columbia, Razor Clam handling times were only compared between Washington and California and were grouped into 2 groups; “small” (prey sizes 1a, 1b, and 1c) and “large” (prey sizes 2a, 2b, and 2c); and were compared using Welch two-sample t-tests. All Sea Otter handling-time data analyses were performed using R (R Core Team 2022).

Kelp Crab Morphometric Data Collection

We collected Kelp Crabs (*Pugettia producta*) from the Washington coast (Fig. 1) and compared their width to total biomass ratio to Kelp Crabs from California measured by Oftedal and others (2007). These data from the Kelp Crabs collected by Oftedal and others (2007) are the data currently input into SOFA, the model used to estimate energy-intake rates for Sea Otter populations in Washington, California, British Columbia, and other areas. Kelp Crabs were collected during 2018 on the outer Washington coast in April at Sand Point and July at Cape Alava and Destruction Island. Sites were primarily selected because they correspond to Sea Otter foraging observation locations where Kelp Crabs are the primary prey item in Sea Otter diets (up to 35% of diet by grams/minute intake rate), with Kelp Crabs being collected opportunistically at Destruction Island. Collections were performed by hand by removing Kelp Crabs from the kelp species *Macrocystis pyrifera* and *Nereocystis luetkeana* in kelp beds that occurred in the same areas utilized by foraging Sea Otters. Kelp Crabs were kept on ice and covered with

towels dampened with seawater until they could be separated into individual plastic bags and euthanized via freezing at -20°C before processing. Following the protocol of Oftedal and others (2007), 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 and specimens were weighed using a digital scale (Ohaus Corp) to the nearest 0.01 g.

Kelp Crab Morphometric Data Analysis

To test whether Kelp Crabs in Washington have a different biomass to width ratio than Kelp Crabs in California, we compared four models (Table 1) fit to Kelp Crab biomass and width data from Washington and California. We used a power function of the form:

$$[\text{biomass}] = a[\text{diameter}]^b,$$

where [biomass] was the unprocessed wet biomass (grams) of each individual crab, [diameter] was the maximum carapace width (millimeters) for each individual crab, a was a coefficient, and b was the power variable of the function. We fit 4 models to the biomass and width data by minimizing the negative log likelihood (NLL) using the “optim” function in R (R Core Team 2022). All NLLs were calculated using a lognormal distribution. Model 1 treated Kelp Crabs from California and Washington as 1 population with 1 power function and estimated parameters a , b , and σ (3 total parameters), where σ represents the standard deviation from the lognormal in the NLL equation; Model 2 treated Kelp Crabs from California and Washington as 2 independent populations with 2 separate power functions and estimated parameters a , b , and σ for each population (6 total

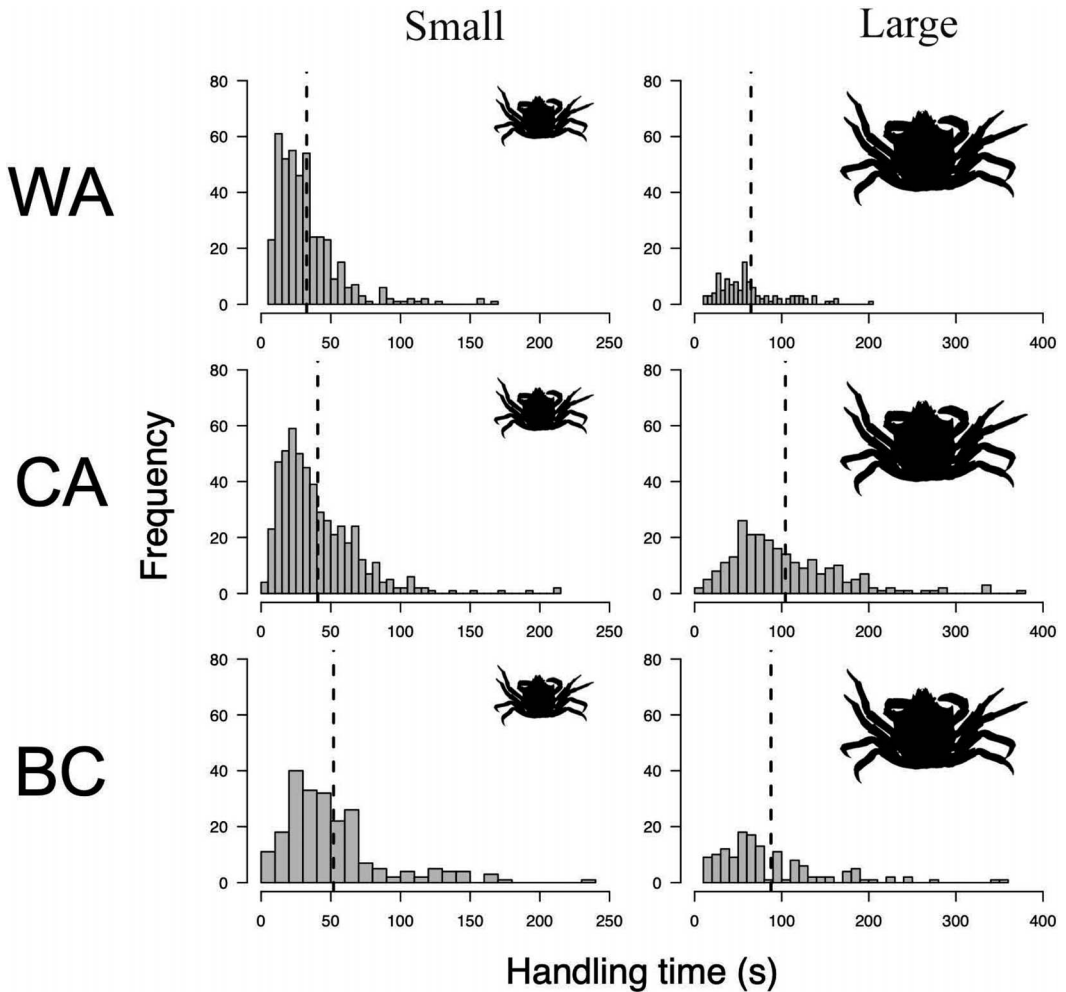


FIGURE 2. Sea Otter handling times of small (left column) and large (right column) Kelp Crabs (*Pugettia* spp.) in Washington (WA), California (CA), and British Columbia (BC). Kelp Crab size groups were defined using Sea Otter foraging observation method of estimating prey size relative to Sea Otter paw width where “small” Kelp Crabs are ≤ 1 Sea Otter paw width (prey sizes 1a, 1b, and 1c) and “large” Kelp Crabs are > 1 Sea Otter paw width (prey sizes 2a, 2b, 2c, and 3a). Vertical dashed lines represent average handling time. Sample sizes for small Kelp Crab handling times in Washington, California, and British Columbia were $n = 422$, $n = 520$, and $n = 220$, respectively. Sample sizes for large Kelp Crab handling times in Washington, California, and British Columbia were $n = 119$, $n = 245$, and $n = 139$, respectively. The Kelp Crab silhouette was created by Carter Johnson.

parameters); Model 3 treated Kelp Crabs from Washington and California as 1 population with 1 power function and estimated parameters a and b but with independent σ values for each population (4 total parameters); and Model 4 treated Kelp Crabs from California and Washington as 2 independent populations with 2 separate power functions and estimated parameters a and b for each region and with a single

global σ value (5 total parameters). We compared the corrected Akaike Information Criteria (AICc) values of the 4 models to determine the best-fit model.

RESULTS

Handling Time Comparison of Kelp Crabs

Sea Otter handling times of both small and large Kelp Crabs (Fig. 2) in Washington were

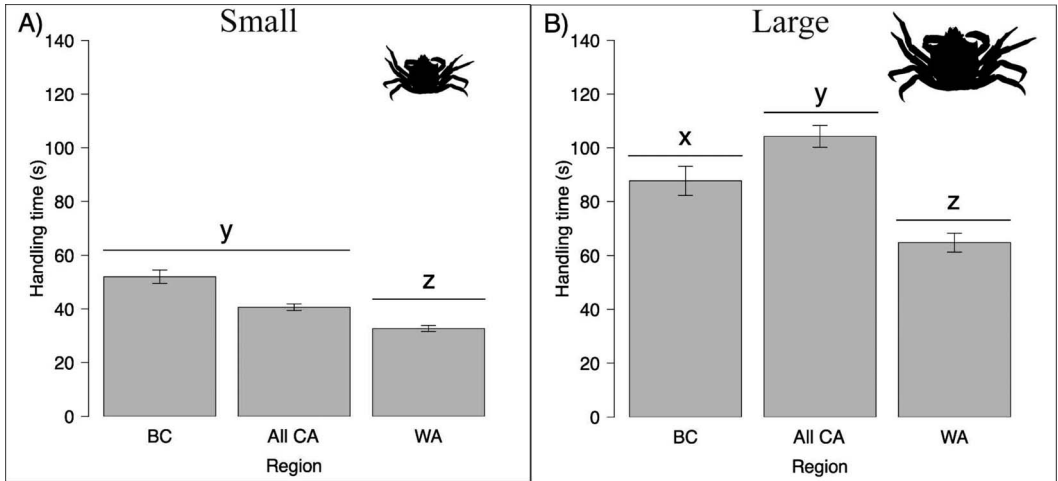


FIGURE 3. Average Sea Otter handling times of small (A) and large (B) Kelp Crabs (*P. producta*) by region. Kelp Crab handling times for each region (California [CA], Washington [WA], and British Columbia [BC]) were summarized into 2 groups based on the size of the Kelp Crab captured: “small” (prey sizes 1a, 1b, and 1c) and “large” (prey sizes 2a, 2b, 2c, and 3a). Sample sizes (number of Kelp Crab captures) for small Kelp Crab handling times in British Columbia, California, and Washington were $n = 220$, $n = 520$, and $n = 422$, respectively. Sample sizes for large Kelp Crab handling times in British Columbia, California, and Washington were $n = 139$, $n = 245$, and $n = 119$, respectively. Error bars represent standard error. Average handling times of “small” ($F = 33.66$, $df = 2$, $P < 0.0001$) and “large” ($F = 18.42$, $df = 2$, $P < 0.0001$) Kelp Crabs were compared using one-way ANOVAs. Letters above bars correspond to statistically different groups. (BC = British Columbia, CA = California, WA = Washington). The Kelp Crab silhouette was created by Carter Johnson.

faster than the respective handling times in both California and British Columbia. When we compared Sea Otter handling times of small Kelp Crabs, we found a significant difference between regions ($F = 33.66$, $df = 2$, $P < 0.0001$). We found that small Kelp Crab handling time in Washington was 24% faster than in California and 59% faster than in British Columbia (both with $P < 0.0001$; Fig. 3A). Similarly, we found a significant difference between regions ($F = 18.42$, $df = 2$, $P < 0.0001$) when comparing average Sea Otter handling times of large Kelp Crabs. We found that handling time in Washington was 61% faster than in California ($P < 0.0001$) and 35% faster than in British Columbia ($P = 0.007$; Fig. 3B). Interestingly, we also found that the average large Kelp Crab handling time in British Columbia was 19% faster than the average large Kelp Crab handling time in California ($P < 0.0001$).

When we compared Sea Otter handling times of Kelp Crabs in Washington to the Kelp Crab handling times of a subset of Sea Otters in California that specialize in consuming Kelp Crabs (Kelp Crab specialists) and to the Kelp

Crab handling times of Sea Otters in British Columbia, we found a significant difference between regions for small Kelp Crab handling times ($F = 42.18$, $df = 2$, $P < 0.0001$). Average handling times of small kelp crabs by Sea Otters in Washington were not significantly different than handling times by Kelp Crab specialists in California ($P = 0.313$; Fig. 4A). Conversely, average handling time of small Kelp Crabs by Kelp Crab specialists in California was 4% faster than Kelp Crab handling times in British Columbia ($P < 0.0001$). Our comparison of large Kelp Crab handling times by Kelp Crab specialists in California and handling times in Washington and British Columbia found a significant difference between regions ($F = 6.848$, $df = 2$, $P = 0.0012$). Average handling time of large Kelp Crabs by Sea Otters in Washington was 41% faster than Kelp Crab specialists in California ($P = 0.0211$; Fig. 4B). There was no significant difference in the average handling times of large Kelp Crabs between specialists in California and British Columbia otters ($P = 0.918$).

Our analysis of the percent occurrence of Kelp Crabs in all successful dives for each region

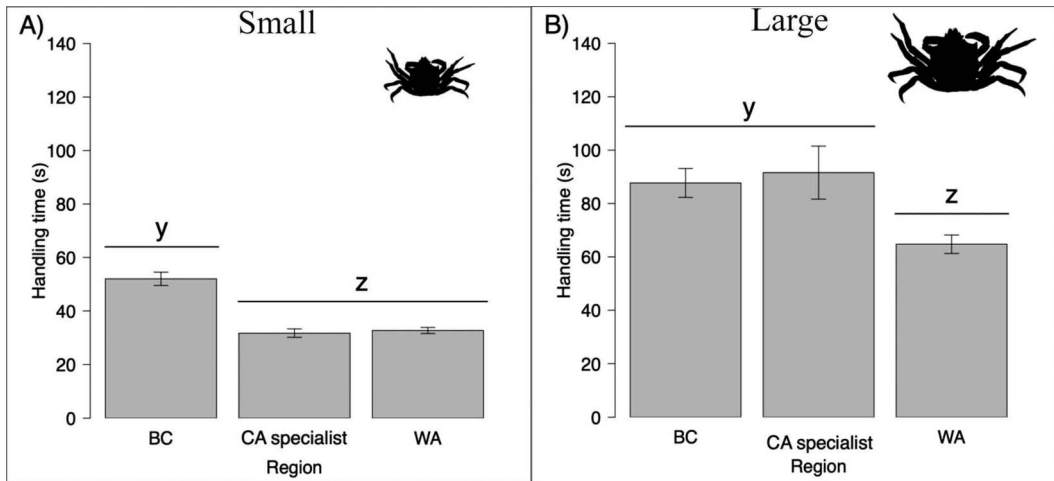


FIGURE 4. Average Sea Otter handling times of small (A) and large (B) Kelp Crabs (*P. producta*) by region, comparing Kelp Crab handling times for all otters for British Columbia and Washington and only Kelp Crab specialists from California. Kelp Crab handling times for each region (California [CA], Washington [WA], and British Columbia [BC]) were summarized into 2 groups based on the size of the Kelp Crab captured: “small” (prey sizes 1a, 1b, and 1c) and “large” (prey sizes 2a, 2b, 2c, and 3a). Sample sizes for small Kelp Crab handling times in British Columbia, California, and Washington were $n = 220$, $n = 204$, and $n = 422$, respectively. Sample sizes for large Kelp Crab handling times in British Columbia, California, and Washington were $n = 139$, $n = 40$, and $n = 119$, respectively. Error bars represent standard error. Average handling times of “small” ($F = 42.18$, $df = 2$, $P < 0.0001$) and “large” ($F = 6.848$, $df = 2$, $P = 0.0012$) Kelp Crabs were compared using one-way ANOVAs. Letters above bars correspond to statistically different groups. (BC = British Columbia, CA = California, WA = Washington). The Kelp Crab silhouette was created by Carter Johnson.

found that 12.8% ($n = 468$) of all dives made by Sea Otters in Washington ($n = 3666$ total), 9.2% ($n = 427$) of dives in British Columbia ($n = 4626$ total), and 7.3% ($n = 1461$) of dives in California ($n = 20,076$) included at least one Kelp Crab.

Handling Time Comparison of Non-Kelp Crab Prey

Our handling-time comparisons of non-Kelp Crab prey yielded few consistent patterns across prey sizes and between regions. We found, when we compared the handling times of Sea Otters for Cancer Crabs (Fig. S1), a significant difference between groups in the average handling time of small Cancer Crabs ($F = 5.213$, $df = 2$, $P = 0.0058$), medium Cancer Crabs ($F = 7.1$, $df = 2$, $P = 0.0009$), and large Cancer Crabs ($F = 5.436$, $df = 2$, $P = 0.0049$). Handling time of small Cancer Crabs by Sea Otters in California was 32% faster than Sea Otters in Washington ($P = 0.0115$), and 33% faster than Sea Otters in British Columbia ($P = 0.0141$). However, average handling time of medium Cancer Crabs by Sea Otters in Washington was 25% faster than for Sea Otters in British Columbia ($P = 0.0007$), and 18% faster

than Sea Otters in California ($P = 0.0295$). Similarly, average handling time of large Cancer Crabs by Sea Otters in Washington was 53% faster than for Sea Otters in California ($P = 0.0037$), and 52% faster than Sea Otters in British Columbia ($P = 0.0200$). We also found when we compared the average handling times of clams (Fig. S2) that the average handling time of small clams ($F = 40.97$, $df = 2$, $P < 0.0001$) by Sea Otters in British Columbia was 60% faster than Sea Otters in Washington ($P < 0.0001$), and 26% faster than Sea Otters in California ($P < 0.0001$). Average handling time of small clams by Sea Otters in California was also 27% faster than for Sea Otters in Washington ($P = 0.0004$). Average handling time of large clams ($F = 3.753$, $df = 2$, $P = 0.0236$) was not significantly different between Sea Otters in Washington and California ($P = 0.165$) or between Sea Otters in British Columbia and Washington ($P = 0.961$); however, average handling time of large clams by Sea Otters in British Columbia was 13% faster than California ($P = 0.0171$). Finally, we found when we compared the average handling times of Razor

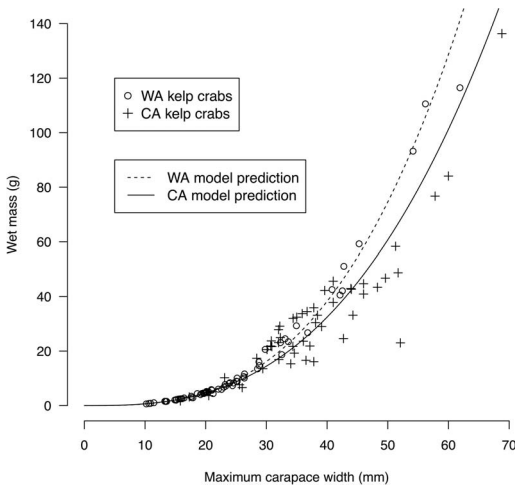


FIGURE 5. Maximum likelihood estimate (MLE) of the best-fit model of Kelp Crab morphometric data from Washington ($n = 66$) and California ($n = 50$) Kelp Crabs (*P. producta*), fit to data using an equation of the form $[\text{biomass}] = a[\text{width}]^b$. The best fit model (Model 2, see Table 2) treated California and Washington Kelp Crabs as 2 independent populations and estimated using a , b , and σ for each population (6 total parameters).

Clams (Fig. S3) that the average handling time of small Razor Clams was 53% faster for Sea Otters in Washington than in California ($t = -2.5701$, $df = 69.251$, $P = 0.0123$), and the average handling time of large Razor Clams was 72% faster for Sea Otters in Washington than in California ($t = -6.2197$, $df = 108.7$, $P < 0.0001$).

Kelp Crab Morphometrics

We collected a total of $n = 66$ Kelp Crabs (*P. producta*) of various sizes (10 to 62 mm) and sexes (female $n = 28$, male $n = 38$) along the Washington coast between Neah Bay and Destruction Island and compared them to $n = 50$ Kelp Crabs (16 to 69 mm) collected by Oftedal and others (2007) in California. Of the 4 models

fit to the morphometric data, the model that estimated separate power function parameters a , b , and σ for Kelp Crabs from California and Washington (6 parameters; Model 2, Fig. 5) had the lowest AICc value (Table 2). The parameter estimates (Table 3) for Model 2 found a greater biomass-to-width ratio in Kelp Crabs from Washington ($a = 0.00062$, $b = 2.99094$, $\sigma = 0.09220$) than in Kelp Crabs from California ($a = 0.00103$, $b = 2.80678$, $\sigma = 0.34113$).

DISCUSSION

Our results suggest that Sea Otters in Washington may be specializing on Kelp Crabs, with behavioral differences allowing them to consume Kelp Crabs faster than Sea Otters in British Columbia and California. This difference in handling time may affect the understanding of Washington’s Sea Otter population status.

The results of our Kelp Crab morphometric analysis did not show that a difference in Kelp Crab morphology is driving the handling time difference for Sea Otters in Washington. Our results suggest that Kelp Crabs from Washington have a larger biomass than Kelp Crabs from California of the same width. This higher predicted biomass-to-width ratio in Kelp Crabs from Washington was the opposite relationship we would have expected if a difference in Kelp Crab morphology was driving the difference in Kelp Crab handling times by Sea Otters, because higher biomass per width would not be expected to result in faster average handling times. We would expect that a crab with a greater biomass and more tissue would take longer to process than a crab with less biomass, even if both had the same width. We found that there was more variation in the biomass/width relationship for Kelp Crabs from California sampled by Oftedal and others (2007) than for Kelp Crabs from Washington sampled in our study. Several factors could explain this. Kelp Crabs can vary

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) using the “optim” function from the R package “stats” (R Core Team 2022).

Hypothesis	NLL	Parameters	AICc	Δ AIC	w_i , weight
Model 1	279.36	3	564.94	78.72	7.07E-18
Model 2	236.73	6	486.22	0.00	8.76E-01
Model 3	240.89	4	490.13	3.91	1.24E-01
Model 4	272.92	5	556.39	70.16	5.09E-16

TABLE 3. Maximum likelihood estimates for parameters of 4 different models predicting 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 $[\text{biomass}] = a[\text{width}]^b$. The lognormal parameter σ was used to calculate the negative log-likelihood of each model.

	Parameter <i>a</i> (coefficient)			Parameter <i>b</i> (exponent)			σ (lognormal parameter)		
	global	WA	CA	global	WA	CA	global	WA	CA
Model 1	0.00112	—	—	2.79405	—	—	0.22521	—	—
Model 2	—	0.00062	0.00103	—	2.99094	2.80678	—	0.09220	0.34113
Model 3	0.00074	—	—	2.93323	—	—	—	0.09092	0.34534
Model 4	—	0.00067	0.00326	—	2.96503	2.48646	0.21337	—	—

in size based on the type of habitat they occupy. For example, individual Kelp Crabs (*P. producta*) living in intertidal algae have been shown to be smaller than individuals found in kelp forests (Hultgren and Stachowicz 2010). Kelp Crabs also, like other decapods, exhibit periodic molting throughout their life cycle, ending their growth after a terminal molt (Strathmann 1987), so can vary in their morphology throughout their life cycle. In the study by Oftedal and others (2007), Kelp Crabs were collected over multiple seasons, over a breadth of geographic areas, and using several different methods, whereas the Kelp Crabs in the present study were collected over a shorter time span and from only 3 locations (Fig. 1A). The range of timing and location of collection by Oftedal and others (2007) has the potential to introduce additional variation in the sizes and masses of crabs that were collected. Kelp Crabs from each region also differed slightly in their size ranges, with Kelp Crabs from California having maximum carapace widths ranging from 16 to 69 mm ($\bar{x} = 37.3$, $s = 10.7$ mm) and Kelp Crabs from Washington ranging from 10 to 62 mm ($\bar{x} = 24.7$, $s = 11.0$ mm), and Kelp Crabs from California showing higher variability at sizes above 30 mm (Fig. 3). Although we observed higher variability in the biomass/width relationship in Kelp Crabs from California compared with Kelp Crabs from Washington, the comparison of models with a single shared σ (Model 1 vs. Model 4), still indicated that the better model was the one that treated Kelp Crabs from California and Washington as distinct using 2 separate power functions, suggesting that the variation in biomass/width relationship in Kelp Crabs from California alone did not account for California and Washington being considered different populations in the best-fit model. In other words, despite the variability in the California

Kelp Crab biomass/width relationship, the Washington and California populations were still distinct enough from one another to drive the best-fit model selection. Additionally, although there were some differences in the timing and location of collection, Kelp Crabs that we collected in Washington can still be reasonably compared to the Kelp Crabs collected by Oftedal and others (2007) for our purposes, as collections in both studies occurred in the same habitats used by foraging Sea Otters.

Sea Otters typically eat small Kelp Crabs whole, but often remove the carapace of large Kelp Crabs before consuming the remainder of the crab (Tinker, pers. obs.; Hale, pers. obs.). It is therefore possible that a difference in the proportion of “edible biomass”, rather than total biomass, could be the crucial difference between Kelp Crabs in Washington and California, leading to faster Kelp Crab handling times in Washington. Oftedal and others (2007) established a protocol of processing Kelp Crabs to estimate edible biomass in which small crabs (carapace < 4 cm) were weighed whole and large crabs (carapace > 4 cm) had their carapace removed before weighing, mimicking the typical processing performed by a Sea Otter. In addition to maximum carapace width, we also measured the edible biomass of Kelp Crabs collected for our study using the same method as Oftedal and others (2007). However, Oftedal and others (2007) only reported a single value for edible biomass across all Kelp Crab sizes and did not publish edible biomass data for different Kelp Crab sizes. We were therefore unable to compare edible biomass between the 2 populations. In addition to biomass to width relationships, it is assumed that Kelp Crabs in Washington have the same energy content per mass as Kelp Crabs in California, and therefore faster handling times lead to increased energy intake rate estimates.

Further research is needed to determine if Washington Kelp Crabs are energetically equivalent to California Kelp Crabs, and therefore if the faster observed handling times translate into increased energy intake rates as currently assumed. Calorimetric analysis of Kelp Crabs from Washington comparable to that of Oftedal and others (2007) could shed light on whether faster Kelp Crab handling times in Washington result in higher energy intake rates.

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 Sea Otters in Washington are up to a third higher than expected based on the current population growth rates and densities (Hale and others 2019). Given that energy-intake rates are a key metric used to infer the status of a Sea Otter population, a difference this large could have significant implications for understanding Sea Otter population regulation in Washington, as high energy-intake rates but slow population growth and low population density can indicate that something other than resource abundance is limiting a population, like top-down predation (Tinker 2015). The energy-intake rates of other Sea Otter populations from the Russian Commander Islands to southern California have been shown to vary consistently with Sea Otter population density and population growth rate (Tinker 2015). Typical energy-intake rates range from 12 kcal min⁻¹ to 21 kcal min⁻¹ in recently established and rapidly growing populations, compared to energy-intake rates ranging from 7 kcal min⁻¹ to 11 kcal min⁻¹ in long established, stable, or slowly increasing populations where resource abundance is thought to be limiting further growth (Tinker and others 2012; Tinker 2015; Coletti and others 2016). Meanwhile, Sea Otter energy-intake rates in Washington decreased with increasing Sea Otter cumulative density from approximately 28 kcal min⁻¹ in recently established and rapidly growing populations to approximately 16 kcal min⁻¹ in long established, stable or slowly increasing populations (Hale and others 2019).

The results of our comparison of Sea Otter handling times of Kelp Crabs confirmed findings in Hale and others (2019), where it was documented that Sea Otters in Washington have

significantly faster average handling times for both small and large Kelp Crabs than Sea Otters in both California and British Columbia. Without the ability to confirm individual diet specialization in Washington through observation of tagged Sea Otters, we instead compared Sea Otter handling times of Kelp Crabs in Washington to the handling times of known Kelp Crab specialists in California, as a key feature of individual diet specialization in Sea Otters is a faster handling time of the specialists' preferred prey (Tinker and others 2008, 2009). When compared to Kelp Crab specialists in California, handling times of small Kelp Crabs in Washington were not significantly different and were significantly faster than specialists in their handling of large Kelp Crabs, suggesting that diet specialization on Kelp Crabs may be occurring in Washington's Sea Otter population. However, tagging and observing individual Sea Otters is the only known way to measure individual diet specialization, and currently the Washington Sea Otter population does not include any tagged individuals.

Individual diet specialization in Sea Otter populations (Estes and others 2003; Tinker and others 2008) is commonly observed in long-established Sea Otter populations where increased Sea Otter densities deplete preferred prey types, leading individuals to specialize on less-preferred species (Newsome and others 2015; Tinker and others 2012). Conversely, population-level diet specialization occurs independently of population density when bottom-up changes in prey composition cause more profitable prey types to suddenly become available (Watt and others 2000; Smith and others 2021). The population of Sea Otters in Washington State has yet to reach its predicted carrying capacity within much of its current range (Hale and others 2022), suggesting that prey abundance may not be a limiting factor for the Washington population, and therefore that individual diet specialization may not be driving faster handling times of Kelp Crabs by Sea Otters in Washington. Instead, population-level specialization may be driving the observed faster handling times in Washington. This hypothesis is further supported by the fact that faster Sea Otter handling times of Kelp Crabs were observed in both 1993–1999 and 2010–2017 (Hale and others 2019), two time periods with different population statuses. Species diversity

of benthic communities decreases at higher latitudes (Witman and other 2004), suggesting that available prey for Sea Otters in Washington may be less diverse than for Sea Otters in California. If Kelp Crabs are sufficiently abundant in Washington and there are fewer alternative prey items than in other areas, Sea Otters that would typically take advantage of a range of prey items will instead turn to Kelp Crabs in higher proportions than in areas where there is greater prey diversity, such as California. Stable isotope analysis of Sea Otter whiskers during a time where Sea Otter density was below the expected carrying capacity in Washington showed higher individuality in diet than in regions with similarly low Sea Otter density (Newsome and others 2015), suggesting that Sea Otters in Washington may exhibit characteristics of individual specialization despite not being close to carrying capacity.

To explore whether Kelp Crabs are more abundant in Washington, we examined the percent occurrence of Kelp Crabs in all successful dives for each region and found that 12.8% of all dives made by Sea Otters in Washington included at least one Kelp Crab, compared to 9.2% of dives in British Columbia and 7.3% of dives in California. Additionally, when examining all dives in which Kelp Crabs were captured, Washington Sea Otters had a higher proportion of multi-capture dives (61%) compared to Sea Otters in British Columbia (33%) and California (12%). Although these analyses do not replace a formal survey of Kelp Crab abundance, they do suggest that Kelp Crabs may be more abundant where Sea Otters forage in Washington than in British Columbia or California. If this is the case, Sea Otters in Washington may encounter Kelp Crabs more frequently, allowing them to increase their efficiency at handling Kelp Crabs, resulting in population-level specialization of Kelp Crabs in Washington. Subtidal SCUBA surveys have been conducted on the Washington coast (Shelton and others 2018; Kvitek and others 1989, 1998, 2000), but Kelp Crabs are observed at very low densities and are likely underrepresented in these surveys. Typically, only conspicuous prey are counted during SCUBA surveys, thus cryptic prey such as Kelp Crabs may be overlooked (Kvitek and others 1998; Shelton and others 2018). This may be especially true for Kelp Crabs (*Pugettia* spp.), as Kelp Crabs inhabit and consume several differ-

ent species of algae and sequester pigment from the algae they consume in order to camouflage themselves (Hultgren and Stachowitz 2010). Kelp Crabs therefore have a three-dimensional distribution in which they are available to Sea Otters (Ostfeld 1982), most of which is not included in quadrat and transect SCUBA surveys. As a result, we are not able to robustly investigate how the abundance of Kelp Crabs may be related to Sea Otter handling efficiency of Kelp Crabs in Washington.

In general, our handling time comparisons of non-Kelp Crab prey yielded no consistent patterns across all prey sizes or between regions. One pattern that we did observe was in the average handling times of Cancer Crabs, where Sea Otters in Washington exhibited faster average handling times than Sea Otters in California or British Columbia of medium and large Cancer Crabs, but were not faster in their handling of small Cancer Crabs. Although the faster handling was not consistent across all sizes of Cancer Crabs, this pattern may suggest a conflation of behavior, in which a learned ability to handle Kelp Crabs (a prey item morphologically similar to Cancer Crabs) faster is leading to faster handling times in some size classes of Cancer Crabs for Sea Otters in Washington. We also observed a pattern in the handling times of Razor Clams, in which average handling times in Washington were 53% faster than in California for small Razor Clams and 72% faster for large Razor Clams. One possible explanation for this pattern is that the foraging data that we collected for Washington (2015–2018) coincided with exceptionally high Razor Clam recruitment (Hale 2022), increasing the availability of Razor Clams to Sea Otters, potentially leading to population-level specialization and faster subsequent handling times. However, despite these handling-time differences, Razor Clams are not a common prey item outside of the sandy habitat on the southern portion of the Washington coast, suggesting that the faster handling of Razor Clams by Sea Otters in Washington would not have as large of an impact on population-wide foraging analysis than the difference in handling times of Kelp Crabs that are a ubiquitous prey item.

Our comparison of Kelp Crab handling times by Sea Otters in Washington and Kelp Crab specialist Sea Otters in California found that Sea Otters in Washington had significantly faster

handling times (64.7 s) than Kelp Crab specialists (91.6 s) for large Kelp Crabs. This result was unexpected given that Sea Otters in Washington exhibited similar handling times to California Kelp Crab specialists for small crabs. A possible explanation for this is that Sea Otters in California may encounter large Kelp Crabs less frequently, spending more time on each individual large crab than a Sea Otter in Washington might. However, when we examined all foraging dives with at least 1 Kelp Crab, regardless of proportion consumed, this did not appear to be the case. We found that Sea Otters in California captured a higher proportion of large crabs (39% large) than Sea Otters in Washington (21% large), but a similar proportion of large crabs in British Columbia (38% large). Though these percentages only represent the size occurrences of captured Kelp Crabs and not necessarily the size distribution of the Kelp Crab populations, it does not suggest that Sea Otters in California encounter large Kelp Crabs less frequently than Sea Otters in Washington.

Although it is entirely possible that Sea Otters in Washington are experiencing higher than expected 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 affect the true energy-intake rates. One possible explanation for the faster handling times is that Sea Otters in Washington are not as thorough when handling Kelp Crabs as Sea Otters in other regions. Sea Otter foraging observation protocols attempt to correct for obviously unfinished prey items, with observers visually estimating the proportion of each item that was uneaten (Kvitek and others 1998; Laidre and Jameson 2006; Tinker and others 2008). Our handling time estimates were limited to dives for which the observer recorded “no portion uneaten”; however, subtle differences in the proportion of meat extracted from the carapace may be difficult to reliably determine using current methods. Along the Washington coast, the 40-m depth contour (considered to be usable Sea Otter foraging habitat) extends as much as 15 km offshore, but the maximum viewing distance of spotting scopes averages approximately 1 km (Hale and others 2019). With usable Sea Otter foraging habitat extending past the viewable distance of a spotting scope, it is likely that our ability to accurately record subtle characteristics of Sea Otter foraging behavior is limited to

nearshore habitats and likely decreases with distance from shore. Future research that more closely examines Sea Otter behavior when processing Kelp Crabs through video analysis and observation of captive otters could address the possibility that the handling time anomaly is coming from behavioral differences that cannot be easily observed from shore.

Context-specific differences in prey handling behavior are one of the central predictions of theoretical models collectively known as “optimal foraging theory” (Stephens and Krebs 1986). For example, for a Sea Otter handling a particular prey item there may be a point where it is more energetically beneficial to terminate handling and begin searching for another prey item than extract a diminishing amount of meat from the current item. Consistent with this prediction, Southern Sea Otters in California that occur in low-density populations (for example, San Nicolas Island), where food is not limiting, have been observed consuming prey items less efficiently, leaving a larger proportion uneaten (Tinker and others 2008; Tinker, pers. obs.). Similarly, groups of Sea Otters in British Columbia have exhibited the same behavior upon arriving to a previously unoccupied site (Foster, personal obs.). Based on these observations, if Sea Otters in Washington encounter Kelp Crabs more frequently than Sea Otters in other regions, they may be consuming Kelp Crabs less thoroughly, reducing the overall handling time. However, this hypothesis would require further exploration using different methods, as the current field protocol is unable to distinguish such subtle differences in prey consumption.

In this study we were able to explore several possible explanations for the faster observed Kelp Crab handling times by Sea Otters in Washington, an anomaly shown to have a strong influence on the estimated energy-intake rates of Washington’s Sea Otter population (Hale and others 2019). Our results suggest that a difference in Kelp Crab morphology is unlikely to be driving the faster observed handling times, and instead that population-level specialization on Kelp Crabs may be reducing the handling time of Kelp Crabs across the Washington Sea Otter population. Currently, the accepted Sea Otter foraging model (SOFA) assumes that Sea Otter foraging behavior and prey are independent of region, however our results suggest that there

can be significant geographic variability in foraging behavior. Our results also suggest that there may be geographic variation in Kelp Crab morphology, evidence that supports the development of more regionally specific foraging models. Future work towards creating more regionally specific foraging models as well as the use of multiple metrics—both population and foraging models—to make inferences about Sea Otter population status will improve the understanding of Sea Otter population dynamics and provide insight to aid in management of the species throughout their range.

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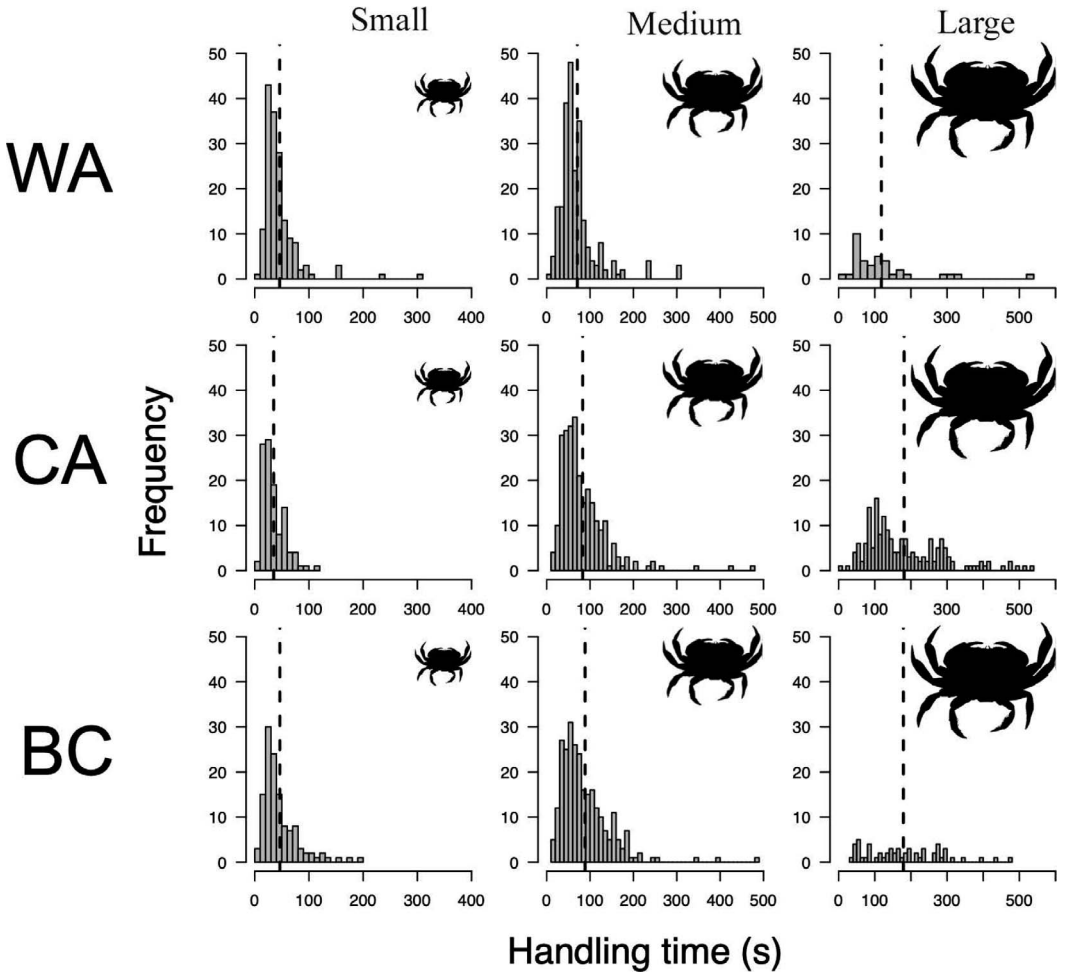


FIGURE S1. Sea Otter handling times of small (left column), medium (center column), and large (right column) Cancer Crabs (*Metacarcinus magister*, *Cancer productus*, and *Cancer* spp.) in Washington (WA), California (CA), and British Columbia (BC). Cancer Crab size groups were defined using the Sea Otter foraging observation method of estimating prey size relative to Sea Otter paw width where “small” Cancer Crabs are ≤ 1 Sea Otter paw width, “medium” Cancer Crabs are >1 Sea Otter paw width, but <2 paw widths, and “large” Cancer Crabs are >3 Sea Otter paw widths. Vertical dashed lines represent average handling time. Sample sizes for small Cancer Crab handling times in Washington, California, and British Columbia were $n = 161$, $n = 111$, and $n = 124$, respectively; medium Cancer Crabs were $n = 235$, $n = 264$, and $n = 266$, respectively; and large Cancer Crabs were $n = 36$, $n = 176$, and $n = 57$, respectively. The Cancer Crab silhouettes are from Eyster (2021), unaltered.

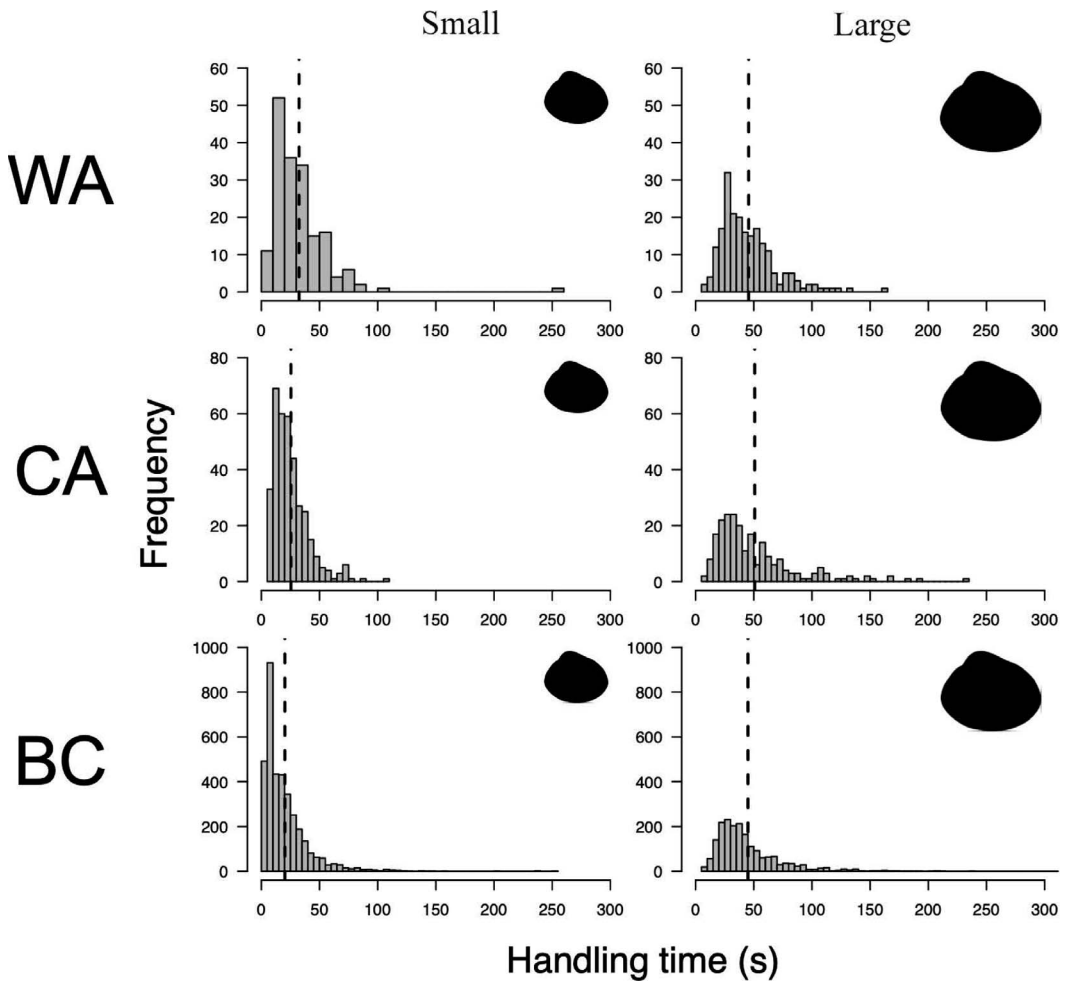


FIGURE S2. Sea Otter handling times of small (left column) and large (right column) clams (*Saxidomus giganteana* and unidentified clams) in Washington (WA), California (CA), and British Columbia (BC). Clam size groups were defined using the Sea Otter foraging observation method of estimating prey size relative to Sea Otter paw width where “small” clams are ≤ 1 Sea Otter paw width and “large” clams are > 1 Sea Otter paw width. Vertical dashed lines represent average handling time. Sample sizes for small clam handling times in Washington, California, and British Columbia were $n = 178$, $n = 363$, and $n = 3595$, respectively. Sample sizes for large clam handling times in Washington, California, and British Columbia were $n = 211$, $n = 224$, and $n = 1896$, respectively. The clam silhouettes are from Collins (2021), unaltered.

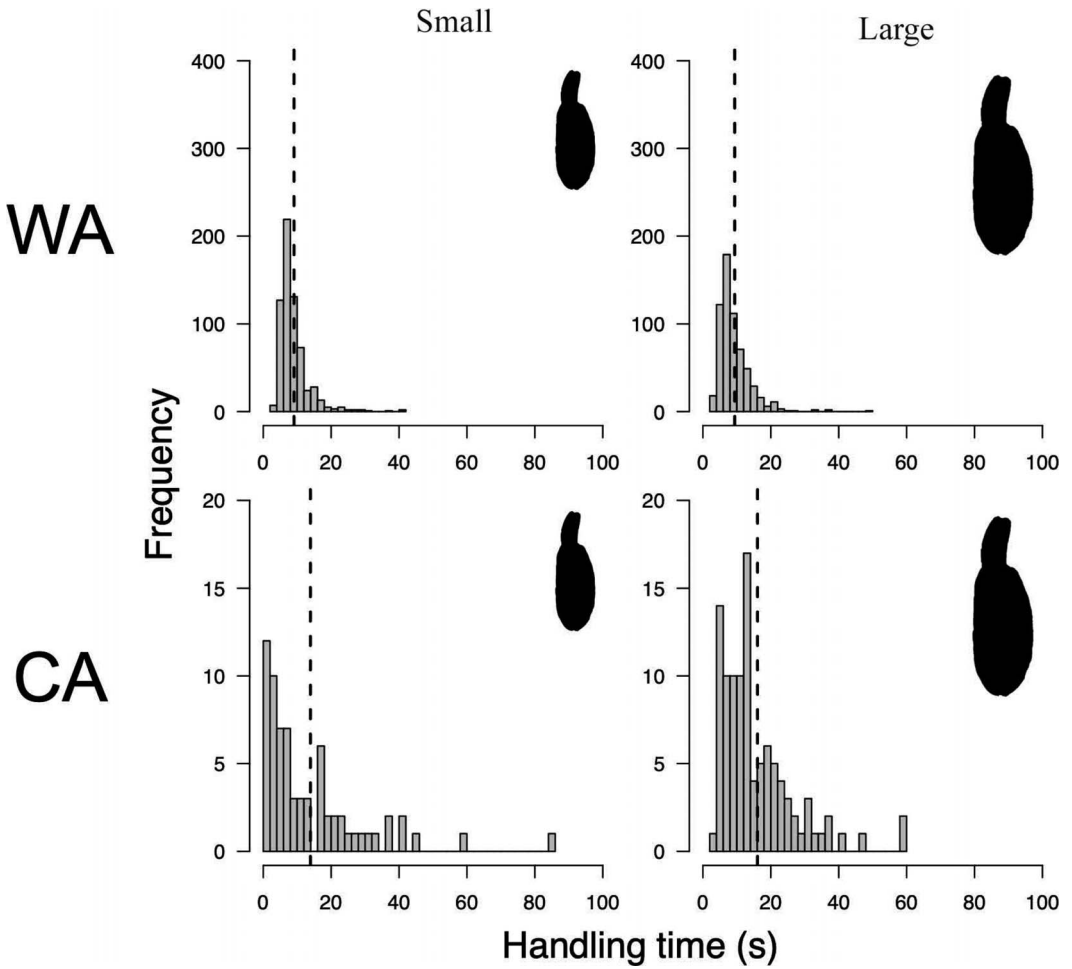


FIGURE S3. Sea Otter handling times of small (left column) and large (right column) Razor Clams (*Siliqua patula*) in Washington (WA) and California (CA). Razor Clam size groups were defined using the Sea Otter foraging observation method of estimating prey size relative to Sea Otter paw width where “small” razor clams are <1 Sea Otter paw width, and “large” Razor Clams are >1 paw width. Vertical dashed lines represent average handling time. Sample sizes for handling times of small Razor Clams in Washington and California were $n = 645$ and $n = 69$, respectively. Sample sizes for handling times of large Razor Clams in Washington and California were $n = 623$ and $n = 103$, respectively.