Doctoral Dissertation

Study on a recolonizing population of sea otters (*Enhydra lutris*) in eastern Hokkaido: feeding habits and the effects of a major environmental disturbance upon them (北海道東部におけるラッコ（*Enhydra lutris*）の再定住個体群に関する研究：食性と大きな環境撹乱の影響)

By

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Abstract

Sea otters (*Enhydra lutris*) are keystone species throughout most of their range alongside the western coasts of North America and the Eastern coast of Russia, and they exert a disproportionately large influence on the ecosystem to their population numbers or biomass. They are also opportunists and dietary generalists, with a well-documented ability to adjust their diets in response to prey availability changes. Therefore, sea otter feeding behavior is an excellent indicator of the health and lower trophic makeup of a marine ecosystem. After sea otters were extirpated from several regions worldwide due to the fur trade, recolonizations have shown a potential to transform local ecosystems and associated fisheries, altering the availability of benthic invertebrates for predators and extraction by humans. For example, across the western coast of North America, the rapid recolonization of sea otters resulted in conflicts with fisheries that developed during the absence of sea otters. In eastern Hokkaido, sea otters were extirpated before 1900 due to intensive hunting, and the first confirmed sighting of a live individual occurred in 1973, although subsequent sightings have been sporadic. In 2014, a mother and pup were observed for the first time and the population has shown gradual growth. Accordingly, concerns have arisen about potential conflicts between sea otters and fisheries. In fall 2021, a massive red tide event (*Karenia selliformis*) created a major environmental disturbance with wide-ranging impacts, including die-offs of sea urchins, which are valuable fisheries resources, and common prey items for local sea otters. This environmental disturbance provided a unique opportunity to assess how this sea otter population's feeding ecology changed in response. This study aims to indicate how ecosystem health and resource viability may be impacted by this relatively new piece in the ecosystem and potentially coexist going forward.

Sea otter population trend relates to the carrying capacity, and comparison with Alaska situation will provide suggestions for predicting the future in Hokkaido population. Rapidly recolonized sea otter populations across Alaska had demonstrated the capacity to disrupt local ecosystems, often resulting in overexploitation of prey resources, and required dietary and behavioral shifts, such as deeper feeding depths and longer duration. In Chapter 1, feeding dive behaviors in eastern Hokkaido were compared to previous studies in North American populations to assess potential ecosystem impacts and evaluate whether observed behaviors indicate sustained prey availability. To place Hokkaido's sea otter feeding behaviors in the context of other populations, I compiled feeding dive behavior observational data from 2019 to 2023, feeding dive duration and dive depth. The otters in Hokkaido exhibited shallower feeding dives and shorter dive durations than other populations, most similarly resembling the foraging behaviors observed in the first report of Northern Chichagof Island, Alaska, and the outer coast of the Olympic Peninsula, Washington State. These populations existed under many of the same recolonization situations and environmental conditions observed in Hokkaido, including primarily feeding on bivalves, within mixed sediment benthic substrates. However, in the second report of Chichagof Island, otters depleted primary prey items and began foraging for alternative prey at deeper depths. Whereas the absence of significant changes in dive depth, duration, or dietary composition suggests Hokkaido's population had not yet experienced substantial prey depletion. Shorter feeding dive durations in Hokkaido compared to bivalve-favoring populations in Alaska were most likely a result of shallower feeding depths, and the lack of change in dive depth or prey composition was characteristic of a population with adequate prey availability and no need to forage deeper.

In Chapter 2, I aimed to determine the impacts of a red tide algal bloom of *Karenia selliformis* dinoflagellates on the benthic community of invertebrates and sea otter diets, providing a framework to prepare for future red tide events. The red tide spreading along the eastern coastal side of Hokkaido in the fall of 2021 resulted in widespread mortalities of sea urchins. In this study, SCUBA surveys sampling benthic invertebrates were conducted in 2020, 2022, and 2023 to track impacts on the benthic community. Focal observations of feeding dive behavior of sea otters were conducted from 2020 through 2023. In 2022, the year after the red tide, a significant decrease in benthic sea urchins was observed, resulting in

their disappearance from sea otter diets. The benthic bivalve population increased in this year, alongside a doubling of the percentage within diets. In 2023, densities of sea urchins within the benthic environment showed a slight increase, while bivalves displayed a slight decrease. Dietary sea urchin and bivalve percentages immediately returned to pre-red tide levels in 2023, indicating a temporary shift. The lack of impact on bivalves overall or an observed sea otter population decrease also suggests minimal changes in the health of the local population.

In Chapter 3, I aimed to observe how sea otter feeding behaviors changed in response to regularly changing environmental conditions such as seasonal life cycles of marine canopy covering plants which modify the habitat the sea otters live in, or to the stochastic red tide event and its associated sea otter dietary composition shifts. Throughout their range, sea otters are associated with habitats containing dominant canopy-covering marine plants. In the study area, the main composition of the canopy was sargassum and eelgrass, and less kelp. Canopy cover appeared to decline gradually between June 5th and July 8th, and then drastically by September 3rd. Sea otters did not exhibit a change in distance from feeding location to canopy cover across seasons, typical of other sea otter populations in California and Alaska that do not also experience major environmental shifts in temperature or wave condition concurrently, indicating that the otters do not seasonally alter distance and association with canopy covering plants, even as the location and distribution of those canopy plants do change. If this is indeed the case, it may prove a useful tool in predicting sea otter foraging patterns throughout eastern Hokkaido in areas with similar canopy covering communities. The red tide event did not affect feeding dive duration; however, handling time per prey item and number of prey items per dive significantly increased after the red tide. This shift is likely tied to increasing dietary percentages of bivalves and small prey items. Percentages of dives where tool use was present also displayed a decrease after the red tide, which may have been due to the increase in bivalve percentage within the diet and a reduction of sea urchins. These shifts indicate that the dietary changes, in turn, influenced sea otter foraging behaviors.

This thesis indicates that feeding behavior tendencies in eastern Hokkaido were similar to newly recolonizing sea otter populations that forage primarily on bivalves in mixed sediment seafloors across the west coast of North America. I also revealed how this sea otter population displayed resilience to environmental disturbance, temporarily shifting away from sea urchins to a higher reliance on more preferred bivalve prey. Dietary plasticity could benefit the population in the future as the likelihood of environmental disturbances increases due to climate change. However, if more red tides and marine heatwaves occur, there is also the possibility that prey availability is impacted differently. Generally, this research would ideally play a role in informing mediation between the economic needs of vital local fisheries industries and communities of eastern Hokkaido and the emerging interests and health of a growing sea otter population, valuable members of the ecosystem that has long been missing.

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Chapter 1: General Introduction

1.1 Sea Otter Ecology

Sea otters (*Enhydra lutris*) are the largest members of the weasel family (Mustelidae), yet they are the smallest marine mammals in terms of body size (Riedman and Estes, 1988). Along with polar bears, sea otters have the shortest evolutionary history of marine adaptation compared to pinnipeds, sirenians, and cetaceans (Davis and Bodkin, 2021). Currently, 3 subspecies of sea otters have been delineated. Southern sea otters (*E. l. nereis*) can currently be found along the coast of California in several locations. Northern sea otters (*E. l. kenyoni*) are located in the Aleutian Islands (Alaska, USA), Prince William Sound (Alaska, USA), Southeast Alaska (USA), and down the coast of British Columbia (Canada) and Washington State (USA). Asian sea otters (*E. l. lutris*) can be found from the Kamchatka Peninsula (Russia) and the Commander Islands (Russia) down through the Kuril Islands (Russia) and Eastern Hokkaido, Japan (Davis and Bodkin, 2021). Compared to marine mammals of a similar size, sea otters need to consume significantly more food, as they do not store fat in large quantities or in blubber, and rely on their thick insulating layer of fur and rapid metabolism of food (Kenyon, 1969).

Sea otters are dietary generalists, consuming a wide variety of different organisms. The predominant diet of a sea otter population can vary greatly based on location (Fujii et al., 2015), however, they mostly feed upon larger invertebrates, such as sea urchins, marine snails, bivalves, and crustaceans throughout their range (Kvitek et al., 1993; Fujii et al., 2015). There are rare reports of feeding on fish and certain fish eggs (Davis and Bodkin, 2021). In contrast with other marine mammal carnivores, sea otters need to surface to consume their prey above water, after collecting it from the seafloor with their front paws (Davis and Bodkin, 2021; Bodkin et al., 2004). Their powerful bite force (Davis and Bodkin, 2021) allows them to crack hard-shelled prey

organisms to reach the nutritious insides. These animals occasionally use stones to crack hard-shelled prey organisms that they cannot do so with their teeth, such as several species of bivalves (Fujii et al., 2015).

1.2 Sea Otter Decline and Recovery

Historically, sea otter populations extended from Hokkaido (Japan), through the Kuril Islands/ Kamchatka Peninsula (Russia), through Aleutian Islands and along the west Coast of North America to Baja California (Canada and USA) (Larson et al., 2002; Kenyon, 1969). However, otters were driven and extirpated from most of that range through extensive hunting associated with the fur trade (Larson et al., 2002), which proved to be an incredibly lucrative venture for several colonial nations (Lensink, 1960). The sale of the Alaskan territories to the United States from Russia in 1867 intensified the widespread extirpation of sea otters, as the United States imposed far fewer limitations on the harvesting of sea otters (Lensink, 1960).

The declining population trends only began to reverse following the North Pacific Fur Seal treaty of 1911, which functioned as a turning point in international conservation of several marine mammal species (Chapman, 1973). In many of these remnant populations, the number of animals recovered to pre-overharvesting levels; however, throughout much of their historical range, they remained a non-presence (Larson et al., 2002). In North America, there were several successful efforts to reintroduce sea otters to parts of their historical range during the 1960s and 1970s.

The Asian sea otter used to be found from the Russian Kamchatka peninsula down through Hokkaido before heavy exploitation (Riedman and Estes, 1991). Like their North American counterparts, these sea otter populations also experienced depletions and completely dissapeared

from large parts of their range, including complete extirpation from Hokkaido, where was never likely an area where sea otters occurred in high densities, and it can be surmised that the population was extirpated prior to the commercial hunting era (Hattori et al., 2005).

The sea otter populations of the Kuril Islands, which had been decimated by the fur trade, have made a substantial recovery since the early 1900s. The Nemuro Peninsula in Hokkaido is only 3.7 km away from the southern tip of the Kuril Islands. However, with the Asian sea otter in Japan, the recovery has been delayed in comparison to their North American counterparts. In 1996, sea otters were first reported being regularly seen along eastern Hokkaido, at Cape Nosappu (Hattori et al., 2005). The main hindrance to further sea otter expansion may bes anthropogenic disturbance, from local fisheries in particular (Hattori et al., 2005).

1.3 Wider Impacts of Sea Otter Recolonizations and Response of Local Communities

When reintroduced into an ecosystem, sea otters have displayed an ability to greatly alter their surrounding ecosystem (Bodkin et al., 2004; Watt et al., 2000). It has been revealed that sea otters limit the number of sea urchins by feeding, thereby suppressing the destruction of rocky-shore denudation caused by overgrazed the kelp forest by sea urchins (Estes et al., 1998). Whereas throughout their range, sea otters have come into conflict, or perceived conflict, with several commercial fisheries due to their diet overlapping (Boustany et al., 2021; Carswell et al., 2015; Hattori et al., 2005). In southern California, many of those within the local fisheries industries associate the decline of the abalone populations with the recovery and re-establishment of sea otters (Boustany et al., 2021). More concretely, in a McDowell Group survey and report (2005) conducted in the 1990s and 2000s, it was determined that an estimated 11.2 billion USD loss to

fisheries occurred from 1996-2005 due to the re-emergence of sea otters as an industry resource competitor (Carswell et al., 2015). Although, it is worth noting that this survey directly considered all California sea cucumbers, geoduck, and Dungeness crabs consumed by sea otters as losses to fishermen's incomes (Carswell et al., 2015).

However, human-otter relations have not always been characterized by an antagonistic relationship between otter foraging habits and fisheries industries yields. It is worth noting that indigenous peoples around the world had long-standing coexisting relationships with sea otters before colonization, such as in the case of the Tlingit in Southeast Alaska and the Ainu in Hokkaido (Ibarra, 2021; Tezuka, 2009). Even in the modern era, sustainable, indigenous community sea otter hunting has been permitted in Alaska for the last two decades (Carswell et al., 2015).

1.4 Environmental Changes and Sea Otters

Even after ceasing the overhunt, sea otters are subject to the same environmental changes and disturbances, both natural and anthropogenic, that all marine life encounter. The most famous environmental disruption upon a sea otter population would have to be the Exxon Valdez oil spill in Prince William Sound, Alaska, where the over 10 million gallons of oil had catastrophic impacts on a wide variety of local wildlife, taking years to recover from (Dean et al., 2002).

There are also changes that indirectly affect sea otters, such as changes in their feeding habits due to changes in their food environment, rather than direct environmental changes that lead to their death. Such was the case in Amchitka Island, Alaska, where a shift away from kelp forest fish was preceded by a reduction in kelp forest habitat due to extensive grazing from rising sea urchin populations (Watt et al., 2000).

As dietary generalists and opportunists (Davis and Bodkin, 2021), sea otters are relatively well-positioned to accommodate shifts in prey type availability. However, stochastic environmental disturbances, such as red tide, have been observed to impact sea otter feeding behaviors and dietary preferences. Paralytic shellfish poisoning, often the result of exposure to harmful red tide algal blooms (MacQuarrie and Bricelj, 2008), has the potential to alter sea otter feeding behaviors (Davis and Bodkin, 2021). Additionally, red tides have recently been observed to directly negatively impact the health of sea otters by facilitating exposure to domoic acid toxicosis (Miller et al., 2021).

In October 2021, a massive red tide (*Karenia selliformis*) HAB event swept across the eastern coast of Hokkaido, resulting in mass die-off of marine organisms, notably sea urchins, and millions of dollars' worth of damage to the fisheries industry (Kuroda et al., 2021; Iwataki et al., 2022; Yamaguchi et al., 2022). The loss of sea urchins, which make up a portion of the Hokkaido sea otter's diet, had the potential to result in changes within the dietary percentages of this population. Any dietary compositional changes could further alter general foraging behaviors such as dive duration and handling time, as such behaviors are often linked heavily to prey type and or size (Maldini et al., 2010; Ostfeld, 1982).

1.5 Seasonal Change and Sea Otters

The vast majority of sea otter prey items throughout their range are benthic invertabrates, which rarely experience the same seasonal shifts. However, in some cases, otters have occasionally been observed to shift diets seasonally, and this is typically due to differential prey availability caused by phenomena such as annual fish spawning in the Aleutian Islands (Watt et al., 2000).

Even within the Aleutian population, the seasonality of sea urchin consumption (favored during the summer months) was more so likely a result of being favored during months when seasonally spawning fish were not available (Watt et al., 2000).

In Hokkaido, it is also possible that the kelp harvest in summer is affecting the behavior of sea otters. Oftentimes, sea otters forage in the vicinity of high densities of marine plant canopy cover, usually various kelps, which they also utilize as resting habitat (Nicholson et al., 2018). However, the yearly kelp harvest during the summer season in Eastern Hokkaido presents may produce environmental changes in this area. On the other hand, the impacts of which I have not had the opportunity to observe in their easternastern counterparts, which primarily reside in habitats where kelp is has not historically been harvested in the United States and Canada. Only relatively recently, with trial farming only beginning in Alaska and British Columbia in the 1980s and 1990s, have the United States and Canada begun to pursue larger scale kelp harvesting operations (Stekoll et al., 2020).

In contrast to the kelp-dominated ecosystems in which many sea otters reside, in eastern Hokkaido is also home to a different and diverse canopy covering plant community, mainly consisting of sargassums (*Sargassum* spp.) and eelgrasses (*Zostera* spp.). Both seagrasses and sargassums exhibit seasonal variation in spatial distribution and vertical distribution in the water column throughout Japan (Hamana and Komatsu, 2021; Hayashida, 2000).

1.6 Research Goals

The recently re-established status of the Eastern Hokkaido population of sea otters allowed me and the research team to monitor and compare sea otters exposed to different environmental

and anthropogenic conditions with other well-documented examples of recolonizing sea otters from along the western coast of North America. The decades of research and information that are available regarding the short and long term changes sea otter experienced during various stages of recolonization in the U.S. and Canada provide a variety of potential outcomes that could be mirrored in Japan. Information gained from observing the sea otters of eastern Hokkaido and how they relate to their North American counterparts may prove useful in informing stakeholders in the region on what may be expected as the sea otter population grows and spreads further throughout the region.

The rare cold weather red tide event of October 2021 also offered a novel opportunity to see how sea otters respond to such a stochastic environmental disturbance in this region, and to observe whether the dietary plasticity seen throughout the species' range allowed the Hokkaido Sea otters to withstand the event and shift dietary composition and feeding behavior without significant damage to the health of the population. The unique changing seasonal conditions within this area, along with the seasonal changes brought on by the kelp harvest, allowed me to monitor how sea otters would respond. The overall goal of this thesis research was to observe how this newly recolonizing population of sea otters influences an industry and ecosystem that developed in their absence, and how they responded to both stochastic and seasonal environmental changes.

In chapter 2, I drew upon the wealth of knowledge avaialble with North American populations to ascertain what stage in recolonization the Hokkaido population most resembled. In chapter 3, I compared the dietary preferences of sea otters in Hokkaido before and after a massive red tide harmful algal bloom event to determine if the mass environmental depletions of marine invertebrates within the region had any effect on sea otter dietary composition. In chapter 4, I wanted to investigate whether the foraging behaviors, that I determined were characteristic of the

population in chapter 2, experienced any seasonal changes or alterations in response to the environmental and potential dietary changes brought on by the red tide covered in chapter 3.

Chapter 2: Sea Otter Foraging Behaviors of Recolonizing Hokkaido population, a review and comparison with North American populations

2.1. Introduction

The historic, pre-fur trade distribution of sea otters was far more extensive than it is today. Due to overexploitation from the international fur trade, they experienced a prolonged period of decline between the 1700s and early 1900s (Lensink, 1960). The heart of the sea otter range, Alaska, experienced multiple periods of fur harvesting, which appeared to greatly increase when the Russian traders were later joined by British, American, French, and Spanish traders, who seemed to be much more prolific in their collection of otter pelts (Lensink, 1960; Sturgis, 1805). Following the 1911 international fur seal treaty, and at a point by which otter pelt harvesting ceased being a profitable endeavor, sea otters received protected status, and it is around one of the first designated protected areas (the Aleutian Islands National Wildlife Refuge, declared in 1913) where some of the first signs of recovery and population expansion could be seen (Estes, 1990; Lensink, 1960; Watt et al., 2000). Highly successful translocations of sea otters from the Aleutian Islands to eastern Alaska and the Pacific Northwest region of the United States between 1965 and 1970 led to strong population recoveries that were heavily studied over the ensuing half-century (Bodkin et al., 2004; Laidre and Jameson, 2006; Laidre et al., 2009; Jameson, 1995; Kvitek et al., 1993; Pitcher, 1989; Wolt et al., 2012). In addition to the protected Aleutian population, a small, isolated population of sea otters in northern California had remained, which began to recolonize previously occupied areas in the region (Kiekhefer et al., 2004). The majority of these areas were sites where sea otters had not been present for an extended period, and the local ecosystems and fisheries had developed in their absence, resulting in conflicts with the economic interests of the fisheries industries (Carswell et al., 2015). Newly, rapidly recolonizing sea otter populations have demonstrated an

ability to alter the ecosystem around them, such as overexploiting and heavily depleting preferred prey items early on in the recolonization, before reaching carrying capacity (Garcia, 2012).

Carrying capacity (k) is broadly defined as the highest number of individuals of a species or population that their habitat or environment can support, typically based on availability of resources and habitat space (Chapman and Byron, 2018). As sea otters are still relatively recently returning residents to many of the historic parts of their range, the true carrying capacity of these regions has not been observed; however, Tinker et al. (2019) applied a stastical model in order to project that the carrying capacity for all of southeast Alaska is approximately 75,000 individuals.

Kvitek et al. (1992) revealed that sea otters initially foraged for prey in shallower waters, and later on foraged at deeper depths and for less profitable prey items after the more profitable prey and easier to reach areas have been depleted. One unifying trend found across sea otter populations, particularly in Alaska, is the close link between foraging dive depths and durations, with deeper dives correlating strongly with longer dive durations (Kvitek et al., 1993; Wolt et al., 2012). Alterations in these foraging behaviors can also be indicative of changing environmental conditions surrounding them. However, a variety of different environmental and behavioral factors appear to be influential on sea otter foraging dive depth and duration. In certain populations, in particular those otters in Elkhorn Slough, dive durations appeared to differ greatly across prey item size than prey item type (Maldini et al., 2010), whereas sea otters near Santa Cruz, California, were shown to display high variability in foraging depth depending on prey type (Ostfeld, 1982).

Regarding the foraging behavior of sea otters, not only do their prey and diving behavior differ depending on the region, but their use of tools also varies. Along with dolphins, sea otters are some of the most heavily studied aquatic organisms that use tools (Mann and Patterson, 2013). Sea otter tool use is classified as the behaviors that occur when an individual collects a rock (or

other hard object) and uses it to break open prey (Perry, 2012). Tool use amongst sea otters has been shown to produce positive benefits for otters that utilize them to a higher degree, often allowing greater access to larger and harder-shelled prey items, and reducing tooth damage (Law et al., 2024). Variations in tool usage can at times be attributable to different environmental conditions. Sea otter populations in North America tended to utilize tools on a higher percentage of foraging dives that were primarily snails or bivalves than those that were primarily sea urchins (Fujii et al., 2015). Tool-using species exposed to similar environmental conditions have, in some cases, still exhibited variation in tool usage, which may be attributable to socially learned behaviors (Perry, 2012). However, unlike many such species, sea otters' tool use is more widespread across the species, and not limited to specific individuals or populations (Kenyon, 1969; Perry, 2012). Genetic differences are also not strong indicators of tool use (Perry, 2012). It is theorized that the lower frequency of tool use in the northern subspecies could be due to the larger size and strength of individuals (Kenyon, 1969), dietary composition (Riedmen and Estes, 1990), and difficulty of access to the nutritious part of prey items (Perry, 2012). One clear dietary difference among Aleutian Sea otters when compared to more southern populations is that sea otters in this part of the world consume considerably more fish (Watt et al., 2000) and other non-shelled prey items such as sea stars (Fujii et al., 2015), which do not tend to require tool use in the way that shelled benthic invertebrates often do (Kenyon, 1969; Perry, 2012). The predator defenses of prey items in the local ecosystem may also drive greater tool use, as has been hypothesized with the California sea otters, potentially requiring more tool use to accommodate the more armored snail species (Perry, 2012). Differences or similarities in tool usage between the Hokkaido sea otters and other, more established populations could also be indicative of certain similarities or differences in surrounding environments. Differential utilization of tools for different prey items

could also indicate whether the unifying trends observed across North American populations (Fujii et al., 2015) also apply to this population.

By comparing the behavior and ecology of Kuril sea otters, about which little information has been accumulated, with those of Alaska and California sea otters, which have been extensively studied, it may be possible to clarify whether they are reaching environmental carrying capacity and what kind of culture they have. My hypothesis was was as follows;

1) sea otter dive depths and dive durations in Eastern Hokkaido would be shallower and shorter, respectively, than other sea otter populations that have had longer periods to re-establish, and most closely resemble examples of populations during early periods of recolonization.

2) foraging dive depths and durations in Hokkaido would also be similar to populations of sea otters found to favor the same prey items (Bivalves), and within similar habitats.

3) similar to sea otters in Alaska (Wolt et al., 2012), dive duration would be most highly correlated with foraging dive depth, with the exception of shallower dives within the first 20 meters of the surface.

4) due to the small size of the population (Suzuki et al., unpublished), dive depth and duration would not change significantly.

5) sea otters in Hokkaido, which have been established to favor bivalves more highly (Johnstone et al., 2024), will utilize tools more so on dives where the dominant prey items were either bivalves or snails.

The objective of this chapter was to examine how the foraging behaviors of the newly recolonizing population of sea otters in Hokkaido compared to those in previously studied populations across the western coast of North America.

2.2 Materials and Methods

2.2.1 Study area

The study area I surveyed was the sea around Moyururi and Yururi Islands in Eastern Hokkaido, located 3 km from the port at the Nemuro Peninsula (Figure 2-1). Commercial fisheries for sea urchins, crabs, and kelp drive the predominant coastal economy in this region (Andrew et al., 2002; Ito et al., 2024). Previous study locations used for the comparison ranged from Northern California, Washington State, Southeast Alaska, to the Aleutian Islands, with surveys dating back from the early 19th century to the 2020s (Figure 2-1).

2.2.1 Foraging Behaviors

Foraging behavior observations were conducted from a small chartered local vessel, Dai 65 Koeimaru, using binoculars (Nikon StabilEyes 16 x 32, Nikon, Minato City, Tokyo, Japan) during instances where sea otters were confirmed to be feeding (foraging dive events) from September 2019, June to August 2020, and June to September 2021 (Table 2-1a). Instances where a sea otter was observed to complete a full dive event include an observed dive, observed surface, and observed handling of prey items (indidcation of a successful dive). Locations of observed foraging dives were recorded using GPS (Garmin, Olathe, Kansas, USA). Dive duration (the

elapsed seconds between a sea otter diving and surfacing with prey) and handling time (the time between dives where sea otters were processing prey) were recorded following confirmation of successful foraging. For analysis, I estimated handling time per one prey by dividing handling time by the number of prey handled to account for dives where different numbers of prey items are collected, and to prevent bias. Dive depth was later estimated by comparing recorded GPS locations with a local topographical map (with precision of 1 meter per contour line) provided by the Japan Hydrographic Association Marine Information Research Center on GIS (QGIS, Open Source) software because it is known that sea otter dive depth typically matches the depth of the seafloor (Tinker et al., 2007), as they primarily prey upon benthic organisms (Bodkin et al., 2004). Dietary composition of diet was determined through limited analysis to focal follows within 5-10 foraging dives (defined as a dive bout), to avoid sampling bias (Laroche et al., 2021; Watt et al., 2000). Prey item size was determined in comparison to sea otter paw size (i.e., 5 cm; Kvitek et al., 1993). Prey items smaller than one paw (<5cm) were classified as small, larger than one paw and smaller than two (5-10cm) were classified as medium, and larger than two paws (>10cm) were classified as large (Kvitek et al., 1993). For comparison of prey types and sizes of foraging dives, the first observed dives where a single prey type and size were collected were evaluated.

Tool usage was determined through visual and auditory observations of sea otters utilizing rocks to crack open prey items made from the research vessel. Tool use was evaluated for comparison with North American populations by calculating the percentage of dives within bouts where tool use was present from a sample of 15 foraging dive bouts where a main prey item could be identified between September 2019, June to August 2020, and June to September 2021 (Table 2-1b). Following Fujii et al. (2015), when tool use was observed at any point in a foraging dive, then that dive would be counted as a tool use dive, and the number of those out of the total dives

within the bout would constitute the percentage of tool use. Dives were classified under a particular prey type if they constituted the majority of prey consumed during a dive (Fujii et al., 2015). For comparison of prey item type and tool utilization, tool use was evaluated over the entirety of the survey, including the years after the red tide of October 2021, due to the small sample size of bouts recorded pre-red tide. With the inclusion of May to September 2022, and May to September 2023, there was a total of 43 foraging dive bouts recorded.

2.2.2 Data Analysis and Comparison

Sea otter dive duration data collected from the Hokkaido population were compared to various studies conducted on American sea otter populations in the Alaskan Aleutian Islands, Prince William Sound, Alaska, Southeast Alaska, the Olympic Peninsula, Washington State; and California (Table 2-2). Several of these studies tracked sea otter foraging behaviors following various stages of recolonization and included valuable information regarding the conditions of the environments in which these sea otters reside. The elapsed time since initial recolonization varied across these populations from 6 years to above 70 years (Table 2-2). The average foraging dive durations and foraging dive depths of sea otter populations in Amchitka Island (AK), Simpson Bay (AK), Chichagof Island (AK), Barrier Islands (AK), Olympic Peninsula (WA), Strait of San Juan de Fuca (WA), and Elkhorn Slough (CA) were compared to the averages found in the Hokkaido population between 2019-2021. The percentage of dives within a foraging bout where sea otters were observed using tools were used to approximate frequency of tool use within the population. The average sea otter foraging dive bout tool utilization was compared to sea otter populations from the Aleutian Islands (AK), Southeast Alaska (AK), and California. Shapiro-Wilks normality tests would confirm normal distributions of the data. Foraging dive behavioral correlations were

evaluated utilizing Pearson's correlation test, where r represents the correlation coefficient (Masello et al., 2010). Significant difference between tool use presence within foraging dive bouts with different primary prey items was determined with a Tukey's difference test (Almeida et al., 2012; Estes et al., 1995; Johnson et al., 2020; LaRoche et al., 2021; Patel et al., 2023). All statistical analysis tests were conducted with RStudio software (Posit PBC, Boston, Massachusetts, USA).

2.3 Results

2.3.1 Dive duration and depth

Dive duration and depth were extrapolated from 46 foraging dive events recorded between 2019 and 2021 (Table 2-1). Nearly all foraging dives (93.5%) were within 5 meters of the surface, with an average foraging dive depth of 2.8±1.9 m, with a range between 1 and 11 meters (Figure 2-2). The average dive duration was 40.5±0.4 s. Neither dive depth nor duration significantly changed between 2019 and 2021 (Appendix 1). Compared to the previously studied North American sea otter populations, the Hokkaido population appears to forage at shallower depths and for shorter durations (Table 2-2). The Hokkaido population appeared to display the greatest similarity with the feeding behaviors of Northern Chichagof Island, Alaska, in 1989 and the Olympic Peninsula, Washington State, in 1993. The populations in Hokkaido, Chichagof Island, and the Olympic Peninsula were all increasing, displayed a preference towards bivalves as prey items, and resided in habitats characterized by a mixed rocky and sandy benthos (Table 2-2). No significant correlation ($p=0.144$) could be shown that sea otter dive durations were strongly correlated with foraging dive depths. Prey type and size also did not seem to be highly influential on average dive durations (Figure 2-3), with perhaps the exception of large-sized sea urchins (76.5%), which was much higher than the average for medium sea urchins (34%) and of any of

the other prey items (28.8 – 52.8%). The number of prey items collected per dive appeared to be more indicative, as foraging dives where larger numbers of prey had noticeably higher dive durations than foraging dives where lower numbers of prey items were collected (Figure 2-4), and the significant Pearson's correlation ($r=0.29$, $p<0.05$) I observed between the number of prey items per dive and dive duration (Figure 2-5).

2.3.2 Tool Use

Sea otter tool use percentage per bout appeared to be slightly higher than populations overall (1.1±4.7%) and for most prey items than that of Amchitk Island Sea otters, and slightly lower than Adak Island. However, tool use per bout was much lower than in Southeast Alaska and California, the other two populations where bivalves were favored (Table 2-3). It is difficult to draw definitive conclusions based on the small sample size for this comparison, however the preliminary data including an additional 42 bouts from 2022 and 2023 surveys (6.2±15.9; Johnstone et al., unpublished) indicate that this may be a persistent characteristic of this population. Sea otters appeared to utilize tools on a higher percentage of dives where sea urchins (13.3±9.0%) were the dominant prey item, compared to dives favoring other prey items, such as bivalves (5.5±15.6%), crabs (3.8±6.6 %), and snails (2.0±4.5%) (Figure 2-6).

2.4 Discussion

2.4.1 Comparison of sea otter dive duration and depths in Hokkaido with other recolonizing populations

My comparison of foraging dive behaviors revealed that sea otters in the newly recolonizing Hokkaido population foraged primarily at shallower depths and for shorter periods than the majority of other populations in North America (Table 2-2). There did not appear to be significant differences in dive durations or depths between subspecies of sea otters, despite the morphological differences in body size, paw size, and skull type (Campbell and Santana, 2017), allowing for the current assumption that there may be little differences among sea otter subspecies of foraging dive behaviors. However, due to the lack of information regarding the Asian Sea otters (*E. l. lutris)*, this information may be subject to change in the future as more data about this subspecies is gathered. The populations that appeared to exhibit the most similar behaviors to recolonizing sea otter populations in the Olympic Peninsula, Washington State (Laidre and Jameson, 2006), and the North of Chichagof Island, Southeast Alaska (Kvitek et al., 1993). Both populations shared several similar characteristics with the sea otters in Hokkaido. The mixed rocky and sandy benthic conditions in each of these regions may have had an impact on the similar foraging behaviors. Preferred prey items (bivalves) likely affected these similarities, as prey type has been an indicator of dive durations within other sea otter populations (Estes and Duggins, 1995; Kvitek et al., 1993; Ostfeld, 1982). The location of these populations may have also had an impact, where all three were located in areas where otters could be in proximity to the open Pacific Ocean, as well as shallow protected areas that were relatively limited near the coast (Bodkin et al., 2004; Hale et al., 2019). Northern Chichagof Island (58.16°N), the Olympic Peninsula (47.79°N), and eastern Hokkaido (43.42°N) are all from middle latitudes, between 30°to 60°North and South. Invertebrate sizes (Pardal et al., 2021), bivalves in particular, have been shown to have a direct relationship with increasing latitudes (Roy et al., 2000). The similar latitudes of these three populations might account for similarities in prey types and even potentially the sizes of those prey

items. However, in a comprehensive comparative study, Wolt et al. 2012 revealed that the most important factor influencing the length of sea otter feeding dives was dive depths. for dives under 20 meters deep. While the dive duration and dive depth seemed to both fall within the short and shallower ends of observed foraging dive behaviors in other populations, there is little to suggest that there is a significant correlation between the two.

With the lack of an observable significant correlation between dive depth and duration within the population, likely as a result of how shallow the dives were as shown in Wolt et al. (2012) I investigated what factors might most directly influence sea otter dive durations within this population. The lack of a correlation between prey type and prey size with dive duration (Figure 2-3) contrasts with many North American populations where either or both factors appeared to have a strong impact (Kvitek et al., 1993; Maldini et al., 2010; Ostfeld, 1982). The correlation found between the number of prey per dive and dive duration (Figure 2-5) indicates that prey per dive is the most impactful factor. This is logical, as it takes a longer time to collect prey items if otters are collecting more of them.

The Olympic Peninsula (WA), Chichcagof Island (AK), and Hokkaido populations' foraging behavior studies were performed within the first 25 years of initial recolonization, and during periods where the populations appeared to be increasing and not yet reaching carrying capacity.

The record of Chichagof Island, an additional 10 years after the highly similar observed foraging dive behaviors, might provide insight into what could lie in store for the future of the Hokkaido Sea otters. By 1999, sea otters were observed foraging 3 times deeper, and for nearly double the amount of time as in 1989 (Bodkin et al., 2004; Kvitek et al., 1993). There appears to be precedent for continued expansion within this population, given the increasing population and

lack of increase in dive depth or duration during the study period, where sea otters may eventually need to conduct deeper, longer foraging dives as they begin to approach carrying capacity.

2.4.2 Tool Use in Hokkaido Sea Otter Populations

The higher tool usage of sea otters on foraging dives preferring sea urchins (Figure 2-6) was unexpected given the previous studies indicating both bivalves (in particular in populations where bivalves are favored) and snails tended to require higher tool usage across several populations, likely due to the thickness of the shells of both mollusks and bivalves necessitating more tool usage for access to the nutritious innards (Fujii et al., 2015). One potential explanation could be differences in the type of sea urchins and bivalves that are primarily preyed upon in these populations. Fujii et al. (2015) revealed that thicker-shelled bivalves (Oftedal et al., 2008), horse mussels (*Modiolus modiolus*), giant rock scallops (*Crassadoma gigantea*), and Washington/ butter clams (*Saxidomus* spp.) were the bivalves most often observed being preyed upon with tool use. In Hokkaido, the most common identifiable observed bivalve prey items were Sakhalin surf clams (*Spisula sachalinensis*) and エゾワスレ/Venus clams (*Callista brevisphonata*). As clams generally have thicker shells, this would likely discount shell thickness as the cause. Another potential cause could be the subspecies of sea otter and size (Campbell and Santana, 2017), however, the differences in tool use percentage between Aleutian and Southeast Alaskan populations (otters which had been translocated from the Aleutian Islands in the 1960s), would seem to indicate that genetic differences do not account for tool use variation (Fujii et al., 2015). Going forward, it may be beneficial to test the shell hardness of the prey items in eastern Hokkaido and see if they vary greatly from prey items in the North American sea otter populations' ranges.

These same potential differences in morphology and prey may also be related to the lower percentage of tool utilization within this population overall, when compared with other populations where bivalves were favored in North America (Table 2-3).

2.4.3 Conclusions

Shorter dive durations within this population, even when compared to bivalve-favoring populations in Alaska and California, are likely tied to shallower foraging dive depths. It appears that the Hokkaido sea otter population is still not being driven to forage in more difficult to access areas (Appendix 1), and has not yet reached carrying capacity. However, the population did not increase in research years (Suzuki et al., unpublished); it is still uncertain whether this population will continue to grow and expand. However, it may indeed reach carrying capacity, and even sooner reach a size in which competition with local fisheries would be more apparent, in a similar manner observed in Northern California and Southeast Alaska (Carswell et al., 2015). There is also precedent for otters to continue to forage at deeper depths, for longer periods of time, after depletions of prey occur in these shallower and more accessible areas (Bodkin et al., 2004; Kvitek et al., 1993). However, an increasing sea otter population offers opportunities for ecotourism revenue, which has been confirmed to tangibly benefit this economic sector in locations with more advanced sea otter recolonizations (Fujii et al., 2023).

2.5 Tables and Figures

Table 2-1: Number of foraging dive events (*a*), and dive bouts with an identifiable main prey item (*b*) per year and month between 2019 and 2021 (incuding 2022-2023 for tool use comparison between preferred prey items).

a

Year/Month	May/Jun	Jul	Aug/Sep	Total
2019	**0**	**0**	**4**	**4**
2020	**1**	**18**	**10**	**29**
2021	**2**	**6**	**5**	**13**
Total	**3**	**24**	**19**	**46**

b

Year/Month	May/Jun	Jul	Aug/Sep	Total
2019	**0**	**0**	**2**	**2**
2020	**0**	**5**	**3**	**8**
2021	**2**	**1**	**2**	**5**
Total pre red tide	**2**	**6**	**7**	**15**
2022	**5**	**5**	**0**	**10**
2023	**7**	**5**	**5**	**17**
Total post red tide	**12**	**10**	**5**	**27**

Table 2-2: Number of years between when recolonization began to the time of the research study, average dive duration (s), dive depth(m), subspecies, population trend, habitat benthic conditions, preferred prey items, and reference studies of sea otter populations in North America and Hokkaido, Japan. This order is based on the time elapsed since recolonization at the time of the study, starting with the longest time period, and ending with the shortest. Subspecies Northern*: E. l. kenyoni* ; Southern*: E. l. nereis;* Asian*: E. l. lutris.*

Population Location	**Years since recolonization**	**Foraging Dive Depth (m)**	**Dive Duration (s)**	**Subspecies**	**Population Trend**	**Benthic Habitat**	**Preferred Prey Item Type**	**Reference**
Amchitka Island (AK)	70	11	Unable to confirm	Northern	Increase, decrease (carrying capacity exceeded), and stabilization	Rocky	Sea Urchins	a, b, c
North of Chichagof Islands (AK) – 1999	30	18.9±4.6	85±8.8	Northern	Increasing	Rocky and sandy	Bivalve	d
Olympic Peninsula (WA)	<24	12.5	46.9±1.17	Northern	Increasing	Rocky and sandy	Bivalve	e, f
North of Chichagof Island (AK) – 1989	20	6	42±14	Northern	Increasing	Rocky and sandy	Bivalve and Sea Urchins	g
Prince William Sound (AK)	20	27±19.5	113.4±52.8	Northern	Increasing	Soft and mixed sediment	Bivalve	h
Hokkaido (Japan)	<20	2.8±1.6	40.5±0.4	Asian	Increasing	Rocky and sandy	Bivalve	i
Maurelle Islands (AK)	19	>20	89±38	Northern	Increasing	Rocky and sandy	Bivalve	g
Barrier Islands (AK)	19	18.5	103.7±31.3	Northern	Increasing	Rocky and sandy	Bivalve	g
Elkhorn Slough (CA)	<19	<15	51.0	Southern	Increase then decrease	Soft sediment	Bivalve	j, k, l
Strait of San Juan de Fuca (WA)	<6	12.5	54.5±0.7	Northern	Increasing	Rocky, sandy, and muddy	Sea Urchins	f

a: Estes, 1990; b: Lensink, 1960; c: Watt et al., 2000; d: Bodkin et al., 2004; e: Jameson, 1995; f: Laidre and Jameson, 2006; g: Kvitek et al., 1993; h; Wolt et al., 2012; i: This study; j: Garcia, 2012; k: Kieckhefer et al, 2004; l: Maldini et al., 2010

Table 2-3 Mean (SD) frequency of tool use per foraging bout among sea otter populations in North America and Japan. Data compared with findings of Fujii et al., 2015.

Sea Otter Population Location	Frequency tool use	Preferred Prey Item	Reference
Amchitka (Alaska)	0.28 ± 0.06	Sea Urchins	Fujii et al., 2015
Adak (Alaska)	1.45	Sea Urchins	Fujii et al., 2015
Monterrey (California)	16.6 ± 0.2	Crab	Fujii et al., 2015
Other California and Southeast Alaskan Populations	9.8 - 16.5	Bivalve	Fujii et al., 2015
Hokkaido, pre red tide (Japan)	1.1 ± 4.7	Bivalve	This study
Hokkaido, post red tide (Japan)	7.9 ± 15.4	Bivalve	This study

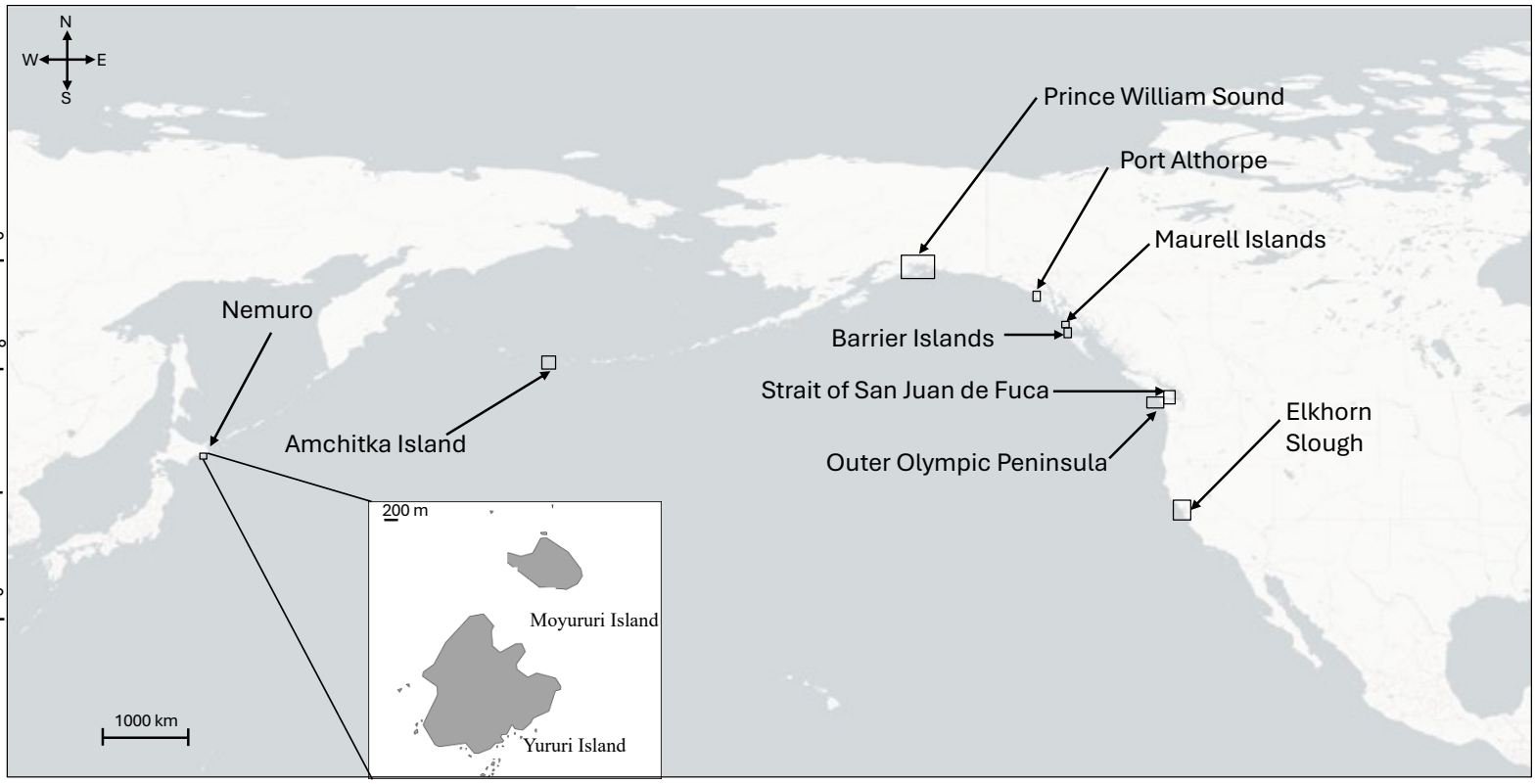

Figure 2-1: Locations of surveys compiled for the feeding behavior comparison.

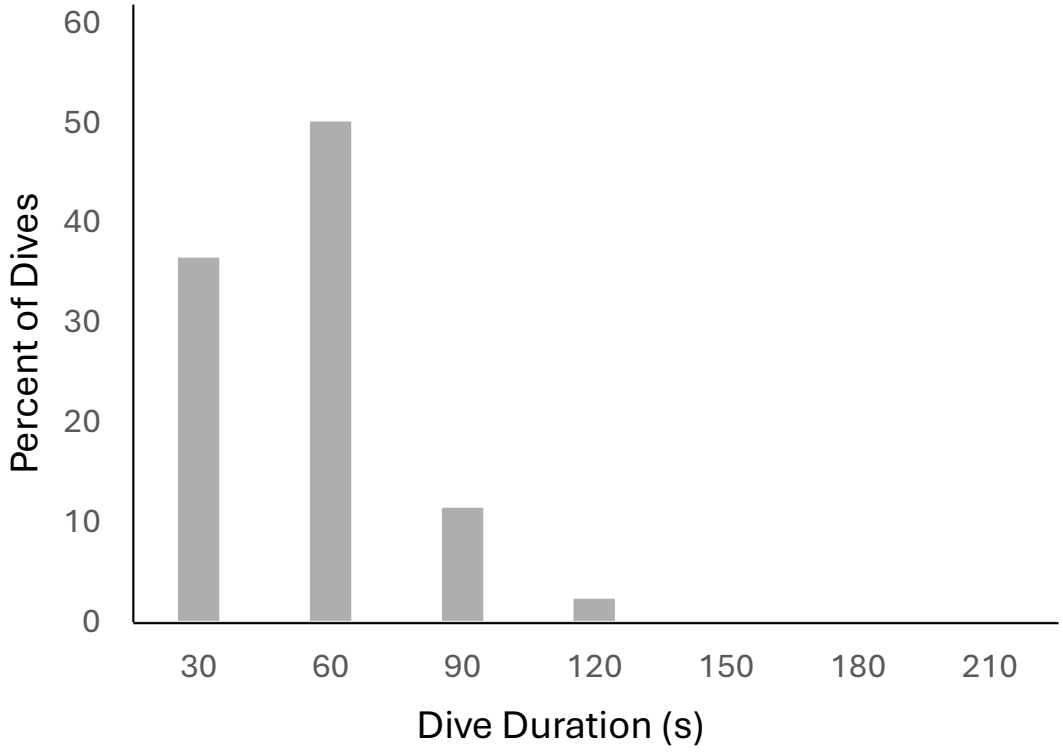

Figure 2-2: Percentage of sea otter foraging dives between 2019-2021 at different durations.

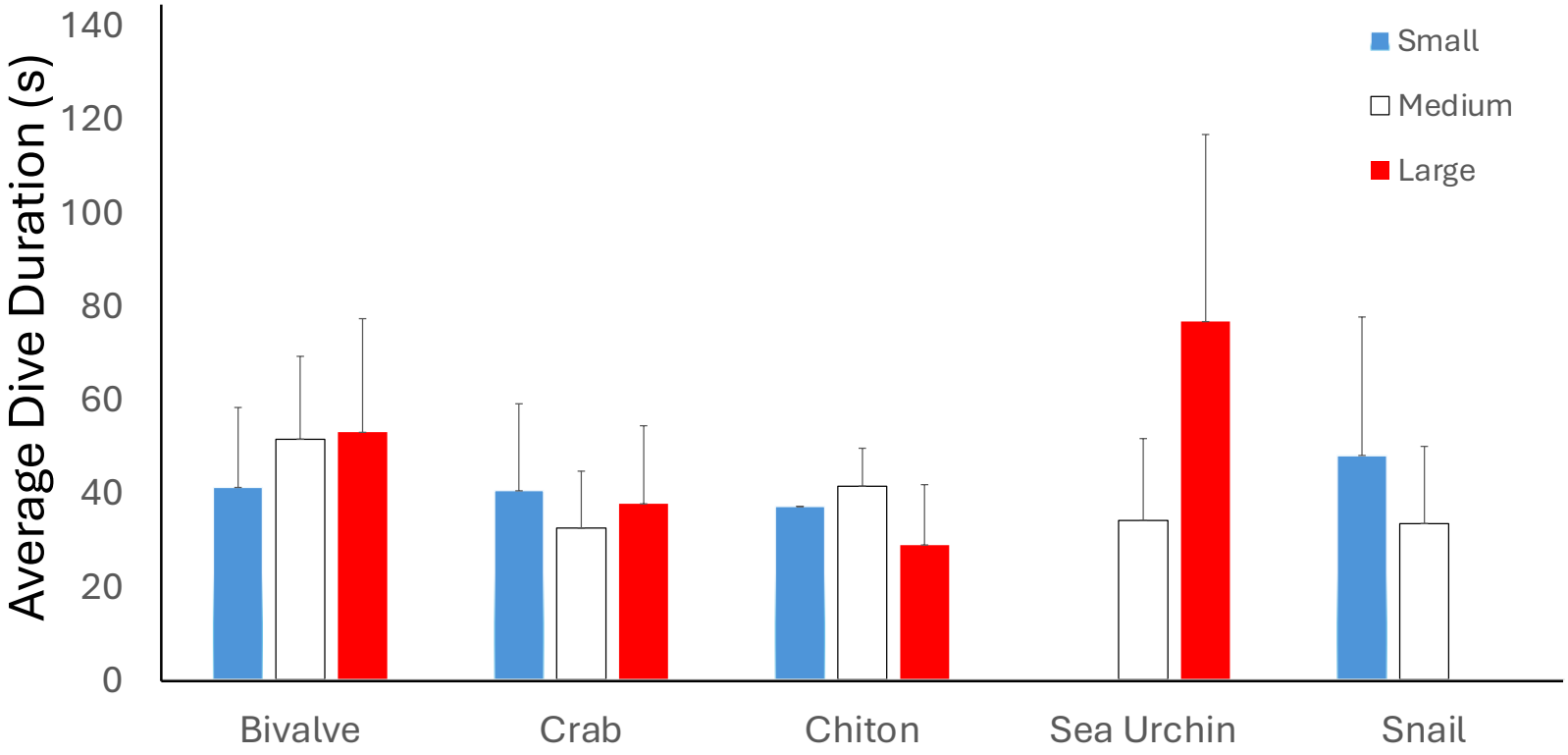

Figure 2-3: Average dive durations for major prey items (Bivalves, Crabs, Chitons, Sea Urchins, and Snails) of different size classes (small, medium, and large) of sea otter foraging dives within the Hokkaido population. Error bars represent one standard deviation.

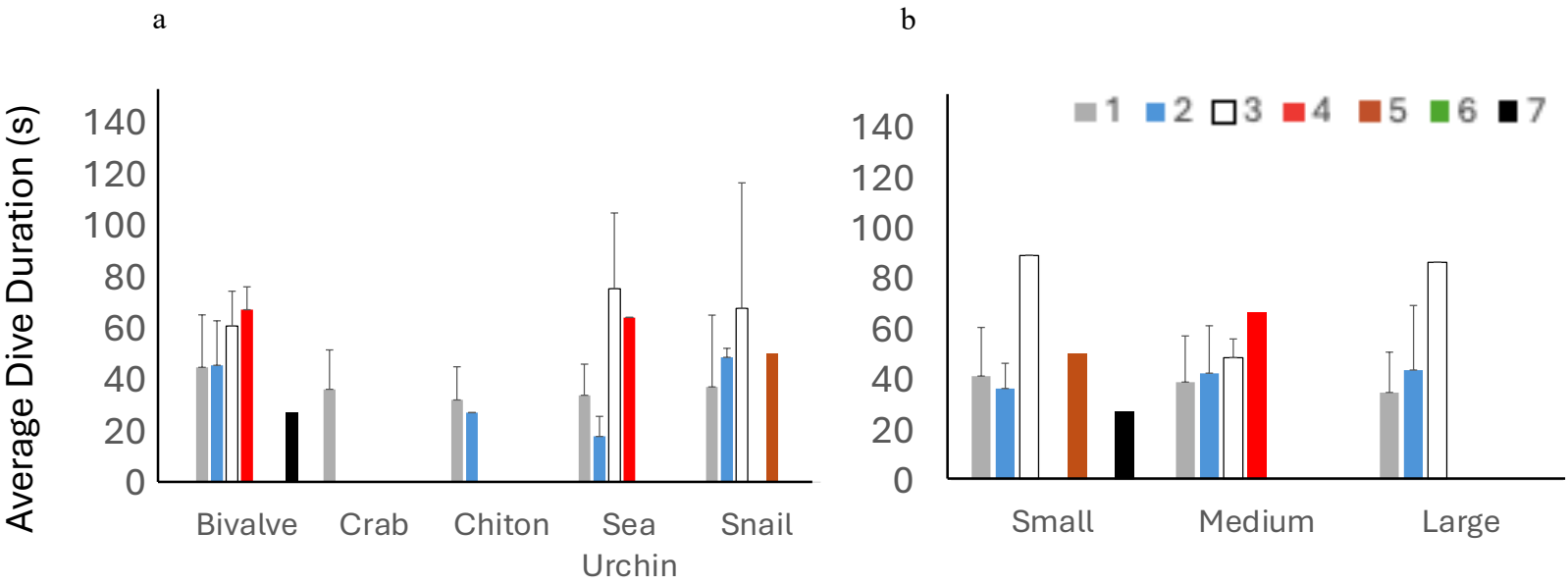

Figure 2-4: Average dive durations for major prey items *a*, and three size classes *b*, of foraging dives containing different numbers of prey. Error bars represent one standard deviation.

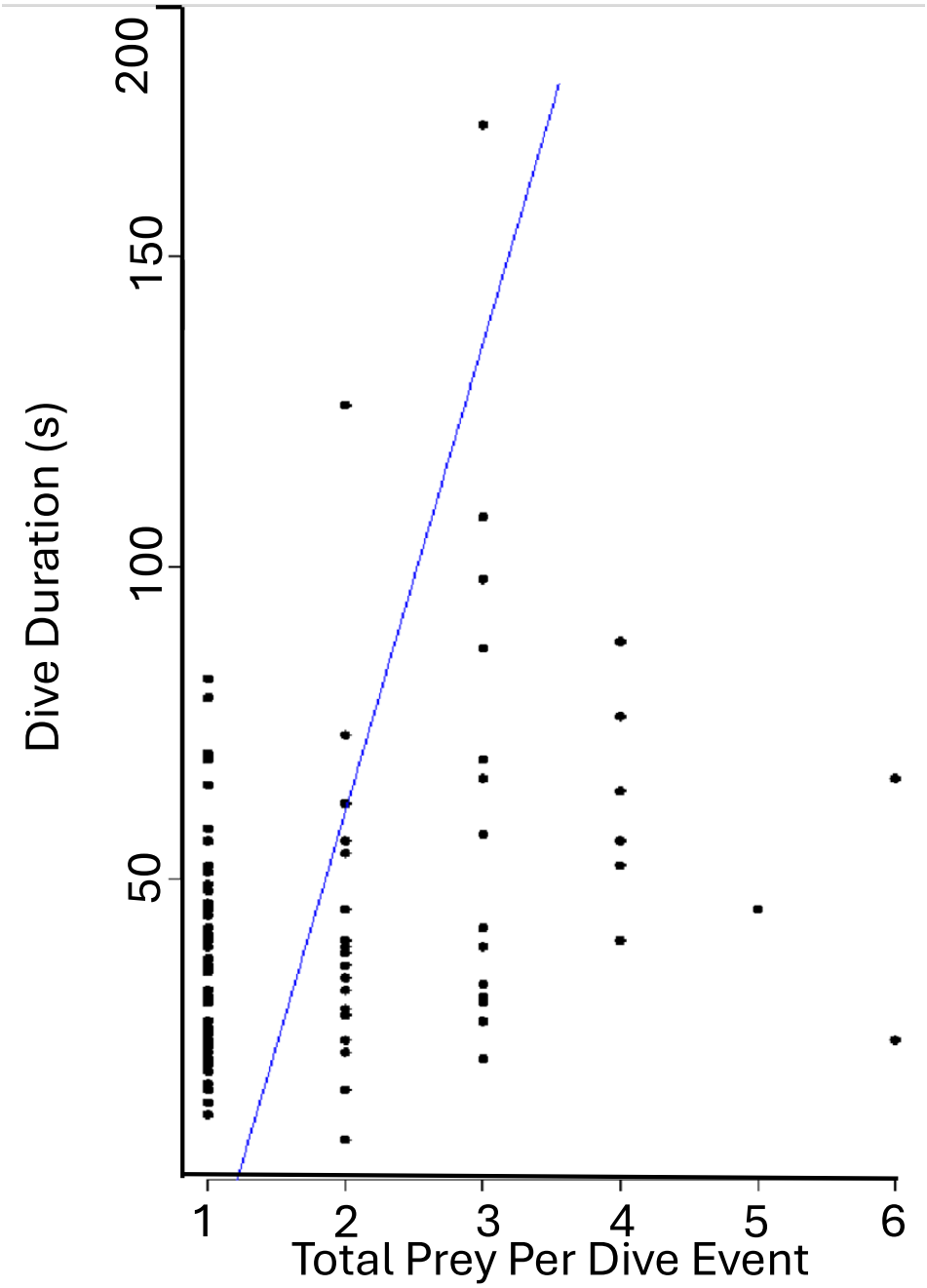

Figure 2-5: Pearson's correlation between total prey items per sea otter dive event and dive duration (s).

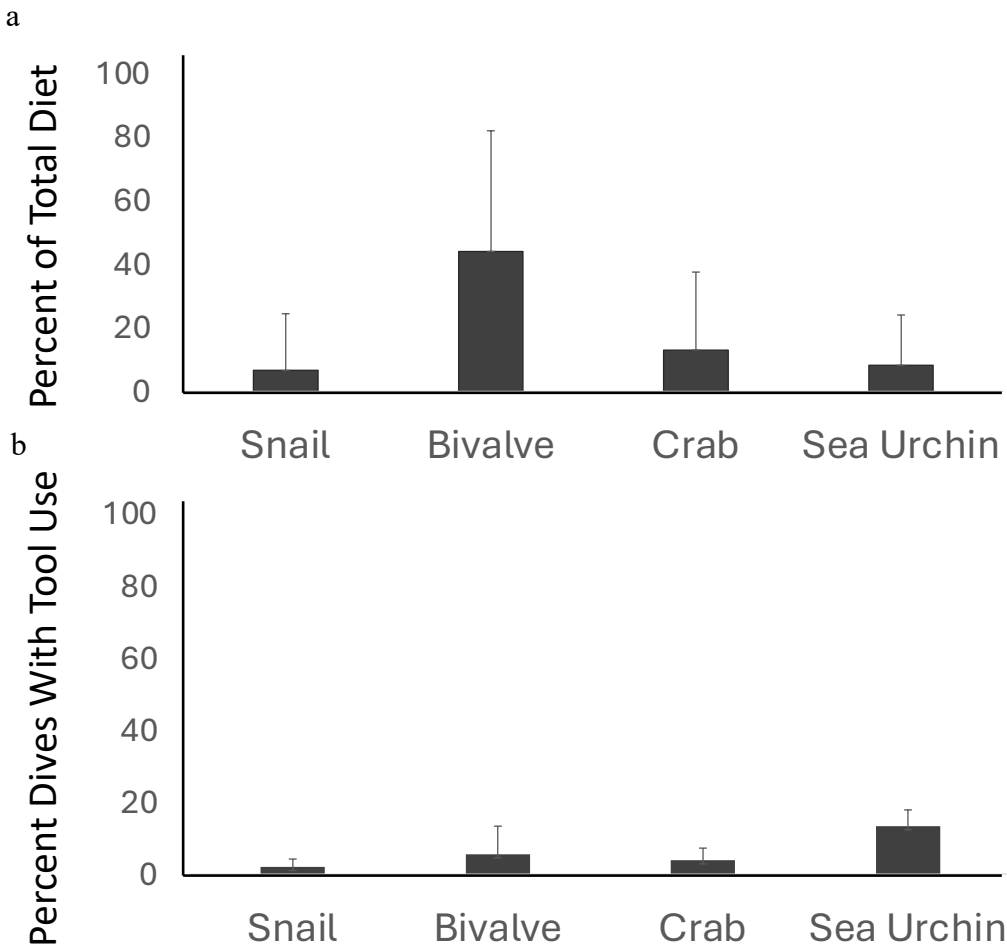

Figure 2-6: Average percent of: *a* prey items within sea otter foraging dive bouts, and *b* percent of tool use of dive bouts favoring major prey item types (Sea Urchins, Bivalves, Crabs, Snails).

Chapter 3: The effect of a harmful algal bloom (*Karenia selliformis*) on the benthic invertebrate community and the sea otter (*Enhydra lutris*) diet in eastern Hokkaido. (Published in PLOSOne as Johnstone et al., 2024)

3.1 Introduction

Red tides, or harmful algal blooms (HABs), are generated by the proliferation of specific phytoplankton varieties, such as dinoflagellates or diatoms. They result in a reddish or brownish tint to the water and produce toxins that can lead to extensive mortality among marine organisms, including fish and shellfish. Warm water dinoflagellates, such as Karenia brevis, can have long-term effects on ecosystems and the economies of local fisheries. K. brevis events have been linked to the mortality of fish and invertebrates in the Gulf of Mexico for over 50 years. The west coast of Florida has experienced several HABs, resulting in the mortality of various marine species. Higher-trophic organisms, such as dolphins and manatees, are also vulnerable to the effects of these toxins. Consequently, HABs have been extensively investigated over the past several decades, often serving as the focus of national and international environmental policy discussions. Commercial and artisanal fisheries rank among the most crucial industries in the Japanese economy, directly or indirectly impacting millions of Japanese citizens. HABs can profoundly disrupt local fisheries, resulting in considerable economic losses. In severe instances, such events may necessitate the complete closure of fisheries in affected areas.

HABs have been documented in Japan for centuries, with records dating back to 731 CE (Fukuyo et al., 2002). Many of these occurrences have been observed in southern Japan, particularly in regions like the Seto Inland Sea (Oghaki et al., 2019). The heightened frequency of HABs over the last 50 years, extending to higher latitudes, correlates with increasing global temperatures (Imai et al., 2006; Zohdi and Abbaspour, 2019). Historically, open ocean HABs have

been rare in the cold waters around Hokkaido, with occurrences primarily concentrated in shallow coastal waters and bays. (Iwataki et al., 2022; Shimada, 2021). However, in 2021, a HAB linked to ocean temperatures 1-3°C above average occurred in eastern Hokkaido, resulting in extensive fish and sea urchin mortality (Kuroda et al., 2021; Iwataki et al., 2022; Yamaguchi et al., 2022). This event significantly affected the sea urchin fishery, which relies on hatchery production for reseeding coastal habitats (Hasegawa et al., 2022; Iwataki et al., 2022; Kuroda et al., 2022).

I used the HAB in 2021 to study the ecosystem-level effects in eastern Hokkaido. Sea otters in this area were extirpated during the 19th-century Maritime Fur Trade but began recolonizing the area in the 1980s (Hattori et al., 2005; Kenyon, 1969; Tezuka, 2009). While there is limited information regarding the diet of sea otters in Hokkaido, I have observed them eating bivalves (*Clinocardium californiense*, *Callista brevisiphonata*, and others), sea urchins (*Strongylocentrotus intermedius*), crabs (*Paralithodes brevipes* and *Telmessus cheiragonus*), snails, and chitons (*Cryptochiton stelleri*) (Mitani et al., 2021). Bivalves are the predominant prey for sea otters in my study area, but sea urchins and crabs are also important. In response to the HAB, my null hypothesis was that sea otters would accommodate to the reduced abundance of sea urchins by shifting to other prey, with minimal effects on health and behavior. The alternate hypothesis was that the HAB would severely affect sea otters, including decreased food consumption, emaciation, and possibly death. I also hypothesized that any dietary shifts would depend on the recovery of benthic invertebrates, especially sea urchins. The objective of this paper was to examine the impact of a red tide on the feeding behaviors of sea otters and their associated environments. The sea otter population's response to the red tide provided a unique opportunity to observe the effects of a significant environmental event on sea otters in Hokkaido for the first time. Additionally, this research encompasses the first comprehensive and long-term observation of feeding behavior in

this newly recolonizing sea otter population in Hokkaido. The study addresses critical gaps in knowledge regarding this expanding population, which is expected to become increasingly relevant as it continues to grow and interact more frequently with human activities and the fisheries industry. The aim of this paper was to reveal the effect of red tide on the feeding habits of sea otters and their feeding environment. The response to the red tide by the sea otter population represents the first opportunity to observe the impacts of a major environmental event on sea otters in Hokkaido. My research also includes the first extensive and long-term observation of sea otter feeding behavior in this new recolonizing population in Hokkaido. My study also fills in some of the substantial gaps in knowledge in this growing population, which will only become more important as it grows and comes into increasing contact with humans and the fisheries industry.

3.2 Materials and Methods

3.2.1 Study Area

My study area was the Moyururi and Yururi Islands (43.2219°, 145.6244°), about 4 km from the coast and 12 km from Nemuro in Eastern Hokkaido (Figure 3-1). This area has commercial fisheries for sea urchins, crabs, and various species of kelp.

3.2.2 Benthic Survey

Benthic surveys were conducted using SCUBA in September 2020, 2022, and 2023 in an area of concentrated sea otter foraging activity along the west coast of Moyururi Island. The sea area was divided by twenty 200 m x 200 m grids, and each grid was designated one point .one

point each grid was set. Quadrats used were 50 cm x 50 cm in size, as were used in Kvitek et al. (1993), and I deployed them randomly four times at each point. Random placement of quadrats and collection of benthic invertebrates within was conducted by a hired professional diver. A professional diver sampled benthic invertebrates in four randomly selected 50 cm x 50 cm quadrats around each point. Crabs were counted but not collected, so morphometrics (length, width, and mass) were not recorded. They are also significantly more mobile than other benthic organisms collected, so it would be difficult to confirm the number of crabs in the survey area. All other specimens were frozen at -20°C until species identification and morphometrics were recorded later. Specimens were divided into three size classes: small (2-5 cm), medium (5-10 cm), and large (>10 cm), following Kvitek et al. (1993). The number of specimens counted or collected was used to estimate each species' average seafloor density (number m-2).

3.2.3 Sea Otter Diet

I conducted observations of sea otter foraging behavior using binoculars (Nikon StabilEyes 16x32, Nikon, Minato City, Tokyo, Japan) during 30-minute focal follows from June to August 2020, June to September 2021, and May to September 2022 from a small boat. The location of each focal follow was recorded using GPS (Garmin, Olathe, Kansas, USA). When a sea otter began feeding, I documented dive duration, prey type (to the highest specificity possible), prey number, prey size, and inter-dive interval. Only focal follows with 5-10 foraging dives were included in my analysis to avoid sampling bias (Watt et al., 2000; LaRoche et al., 2021). Prey size was estimated relative to the width of a sea otter paw (i.e., 5 cm; Kvitek et al., 1993).

3.2.4 Data Analysis

I compared the seafloor densities for bivalves, sea urchins, snails, chitons, and crabs pre- (2020) and post-HAB (2022, 2023). Additionally, I compared sea otter prey compositions (percentage of dietary bivalves, crabs, sea urchins, chitons, and snails) before (2020-2021), immediately after (2022), and one year after (2023) the HAB. Prey species that could not be identified were categorized as unknown and excluded from the analysis. Other prey items that were anecdotally observed, such as sea cucumbers and hermit crabs, were also excluded from the analysis. A Shapiro-Wilks normality test confirmed normal distributions for both benthic organism number and sea otter dietary percentage data. Tukey's HSP tests were conducted to identify differences (Almeida et al., 2012; Estes et al., 1995; Johnson et al., 2020; LaRoche et al., 2021; Patel et al., 2023).

3.3 Results

3.3.1 Benthic Surveys

On average, 235 benthic specimens were collected from 20 grids (Table 1) during each survey. Before the HAB (2020), sea urchins (6.7 per m^2) had the highest seafloor density, followed by snails (1.5 per m^2), chitons (0.6 per m^2), and bivalves (0.3 per m^2). Immediately after the HAB (2022), sea urchins (1.2 per m^2) decreased significantly (82%) from pre-HAB levels (Tukey's HSD test, $p < 0.05$), while bivalves (1.8 per m^2) displayed a 6-fold increase ($p = 0.066$) (Figure 3-2). No significant differences were observed for chitons (0.4 per m^2) and snails (2.8 per m^2) between 2020 and 2022 (Chitons $p = 0.845$, Snails $p = 0.364$). One year after the HAB (2023), the density of bivalves (1.3 per m^2, $p = 0.712$) declined 28% from levels immediately after the HAB but remained elevated by 4.3-fold compared to pre-HAB densities. Likewise, snails (2.0 per m^2, $p = 0.645$) decreased by 29%, sea urchins (2.3 per m^2, $p = 0.115$) increased by 2-fold, and chitons (0.5 per m^2, $p = 0.959$) remained unchanged.

3.4.2 Sea Otter Diet

From 2020-2022, 265 foraging dives during 34 focal follows were monitored, and 508 prey items were recorded (Table 2-2). Before the HAB (October 2021), there were no significant differences in the percentages of prey captured during focal follows (Table 3-2). The predominate prey were bivalves ($\bar{x} = 34.8\%$; range 31.8-36.5%), crabs ($\bar{x} = 13.7\%$; range 12.9-15.3%), and sea urchins ($\bar{x} = 7.8$; range 4.7-13.7%). The average percentages for chitons and snails were less than 5%. Immediately after the HAB in 2022, the percentage of dietary bivalves increased significantly (2-fold) to 67.3% (Tukey's HSD test, $p < 0.05$), while sea urchins completely disappeared from

the diet (Figure 3-3). One year after the HAB (2023), the percentage of sea urchins increased significantly to 13.9% ($p < 0.05$), and the percentage of bivalves returned to near the pre-HAB level of 37.5% ($p < 0.05$). The percentages of chitons, snails, and crabs in the diet were not significantly different across the entire survey period.

3.4 Discussion

My benthic surveys revealed an 82% decrease in sea urchin density and a 6-fold increase in the number of bivalves immediately after the HAB in 2022 (Table 3-1). By the following year (2023), the average sea urchin density showed partial recovery, while clam density remained elevated compared to 2020. However, my surveys were not comprehensive and susceptible to interannual sampling bias. Nevertheless, my data indicated a pronounced decrease in sea urchin density after the HAB, with a partial recovery one year later. Additionally, clam density appeared to increase post-HAB and remain elevated.

An earlier study showed that the HAB caused mass mortality of sea urchins and moderate effects on chitons and snails throughout the coastal waters of eastern Hokkaido, similar to HABs in other regions (Friligos and Gotsis-Skretas, 1989; Jin et al., 2008; Backer, 2009; Ohgaki et al., 2019; Iwataki et al. 2022; Orlova et al., 2022). Consequently, the HAB likely caused the decrease in sea urchin density and distribution around the Moyururi and Yururi Islands. Reseeding with hatchery-raised sea urchins did not occur in my study area after the HAB, so the partial recovery represents a natural process that may take about three years before sea urchins reach the size consumed by sea otters (Ochiishii Fisheries Cooperative, pers. comm.).

I observed an increase in the density of bivalves after the HAB. Bivalves filter phytoplankton from the water column for nutrition and may exhibit higher growth rates during HABs (Foe and Knight, 1985). Certain algal blooms, such as brown tide algae (*Aureococcus anophagefferens*) along the northeastern coast of the United States, can adversely affect bivalves by inhibiting larval growth (Rolton et al., 2014; Przeslawski et al., 2008). However, some bivalves are not affected by the brevetoxin-producing algae Karenia selliformis (Yao & Takashi, 2023). Generally, more intense planktonic blooms are associated with higher water temperatures (Peeters et al., 2007; Visser et al., 2016), and such conditions were observed before the HAB in my study area (Yamaguchi et al., 2022). My results may indicate enhanced bivalve growth, as small (2-5 cm) bivalves significantly increased abundance (Tukey's HSD Test, $p < 0.05$). However, I cannot rule out interannual sampling bias. Chitons and snails did not significantly change in abundance over the three years.

I observed a shift in the sea otter diet immediately after the HAB and during the recovery period one year later. Before the HAB, sea urchins accounted for 9.2% (range 4.7-13.7%) of the diet. However, following the HAB, sea urchins disappeared from the diet (Table 2-2), reflecting their diminished abundance. Despite this, the number of sea otters in the study area remained constant (Suzuki et al., in prep). Bivalves were the predominant prey (34.1%) before the HAB, with their contribution to the diet doubling to 67.3% after the HAB (Table 3-2). The likely cause for this increase was prey-switching when sea urchins decreased in abundance. This switch may have been facilitated by the enhanced growth of bivalves, leading to increased abundance in larger size classes. My results suggest that as generalists (Davis and Bodkin, 2021), sea otters responded to the shifting benthic community structure by consuming prey that became more abundant because of the HAB.

Sea otter populations in California and the Aleutian Islands, Alaska, show a greater preference for sea urchins compared with those in eastern Hokkaido (Estes et al., 1978; Estes et al., 1980; LaRoche et al., 2021; Watt et al., 2000). Sea otter dietary preference correlates with prey abundance, and they do not necessarily require a wide range of prey to thrive (Ostfeld 1982; Tinker et al. 2008; Wolt et al. 2012; Davis et al. 2021). The unusual HAB (Gail, 1950; Orlova et al., 2002) in eastern Hokkaido provided an opportunity to observe the ecosystem effects at two trophic levels (Hasegawa et al., 2022; Iwataki et al. 2022; Kuroda et al. 2021; Kuroda et al., 2022). Because of the dietary adaptability of sea otters (Davis and Bodkin, 2021), the HAB had no obvious effect on the health and abundance of sea otters in my study area. As sea urchins recover, their dietary contribution may return to pre-HAB levels, especially with the reseeding of small, hatchery sea urchins.

3.6 Tables and Figures

Table 3-1: Seafloor densities (per m^2) of invertebrates sampled during surveys before (2020) and after (2022 and 2023) the HAB.

	Density (number m^2)				Total number collected
	Urchin	Chiton	Bivalves	Snail	
Pre-HAB					
2020	6.7	0.6	0.3	1.5	257
Post-HAB					
2022	1.2	0.4	1.8	2.8	230
2023	2.3	0.5	1.3	2.0	219

Table 3-2: Mean (±1 SD) percentage of prey in focal follow pre-HAB (2020, 2021) and post-HAB (2022 and 2023).

	Urchin	Chiton	Bivalve	Snail	Crab	Unknown	Bouts	Successful Dives
Pre-HAB								
2020/2021	7.9 ± 14.5	3.8 ± 6.4	34.9 ± 34.4	4.5 ± 9.4	13.8 ± 27.5	35.2 ± 32.9	20	150
Post-HAB								
2022	0 ± 0	2.0 ± 3.4	67.3 ± 34.2	7.0 ± 26.1	10.7 ± 23.5	12.6 ± 22.8	14	115
2023	13.9 ± 19.7	1.5 ± 6.3	37.5 ± 37.0	8.7 ± 18.4	11.8 ± 21.1	25.4 ± 23.1	24	201

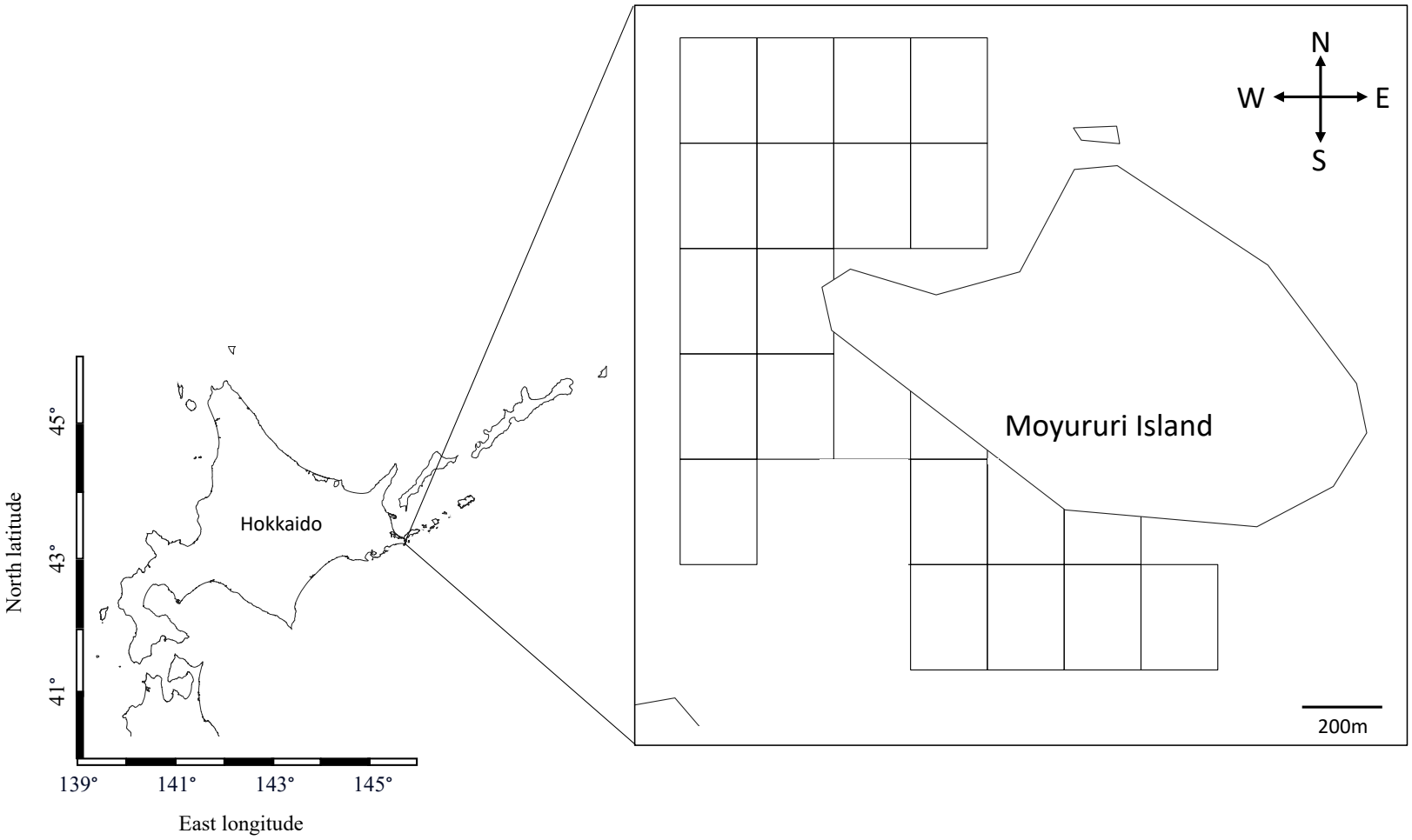

Figure 3-1: The study area for the benthic surveys at Moyururi Island in Eastern Hokkaido. Square blocks show the 200 m^2 quadrats surveyed utilizing random quadrat sampling.

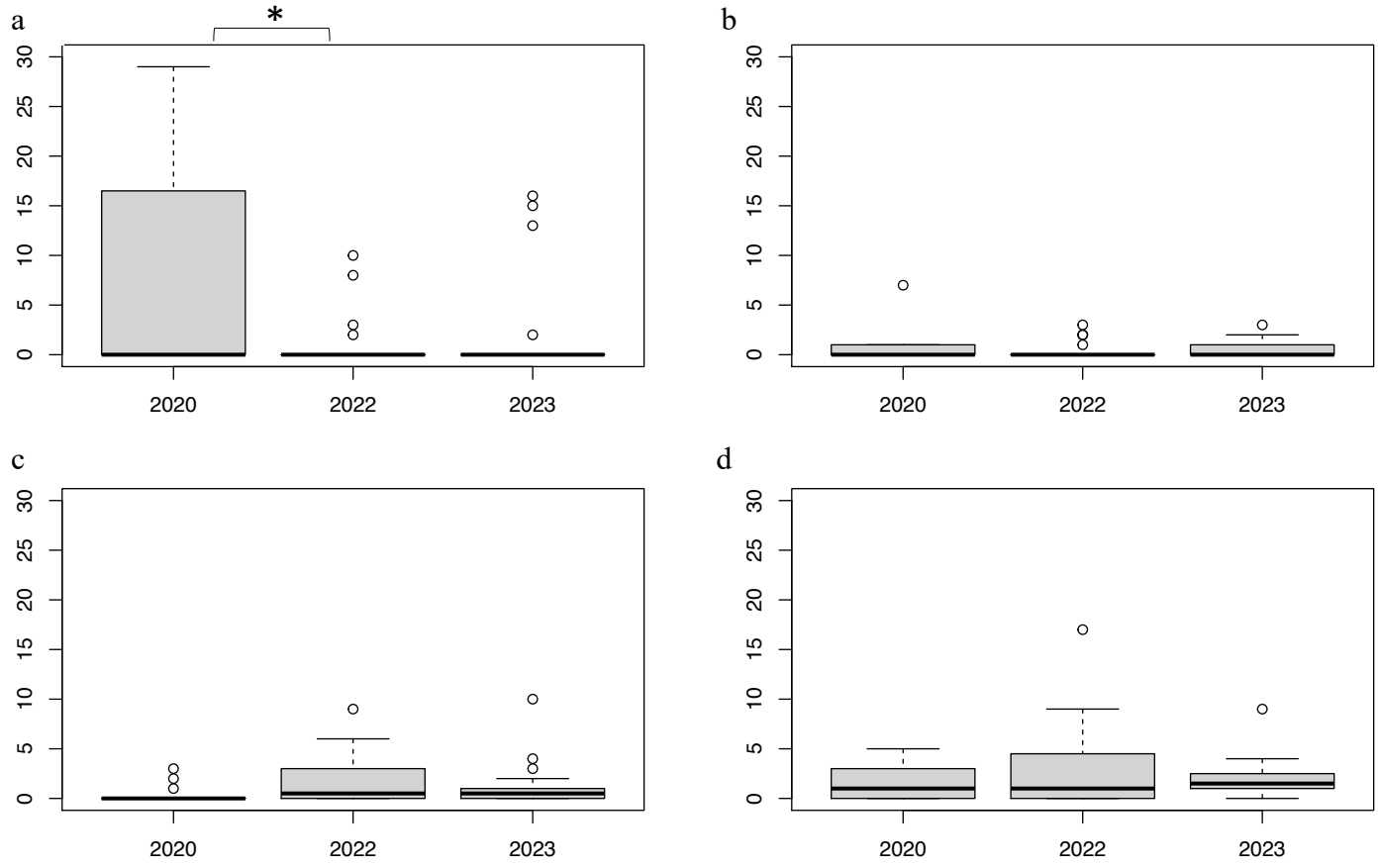

Figure 3-2: Number (per m^2) of major sea otter prey items sampled from SCUBA survey: *a* (Sea Urchins), *b* (Chitons), *c* (Bivalves), *d* (Snails) retrieved during benthic quadrat surveys of 2020, 2022, and 2023. Asterisks (*) above the graph display a significant difference ($p < 0.05$) between two years.

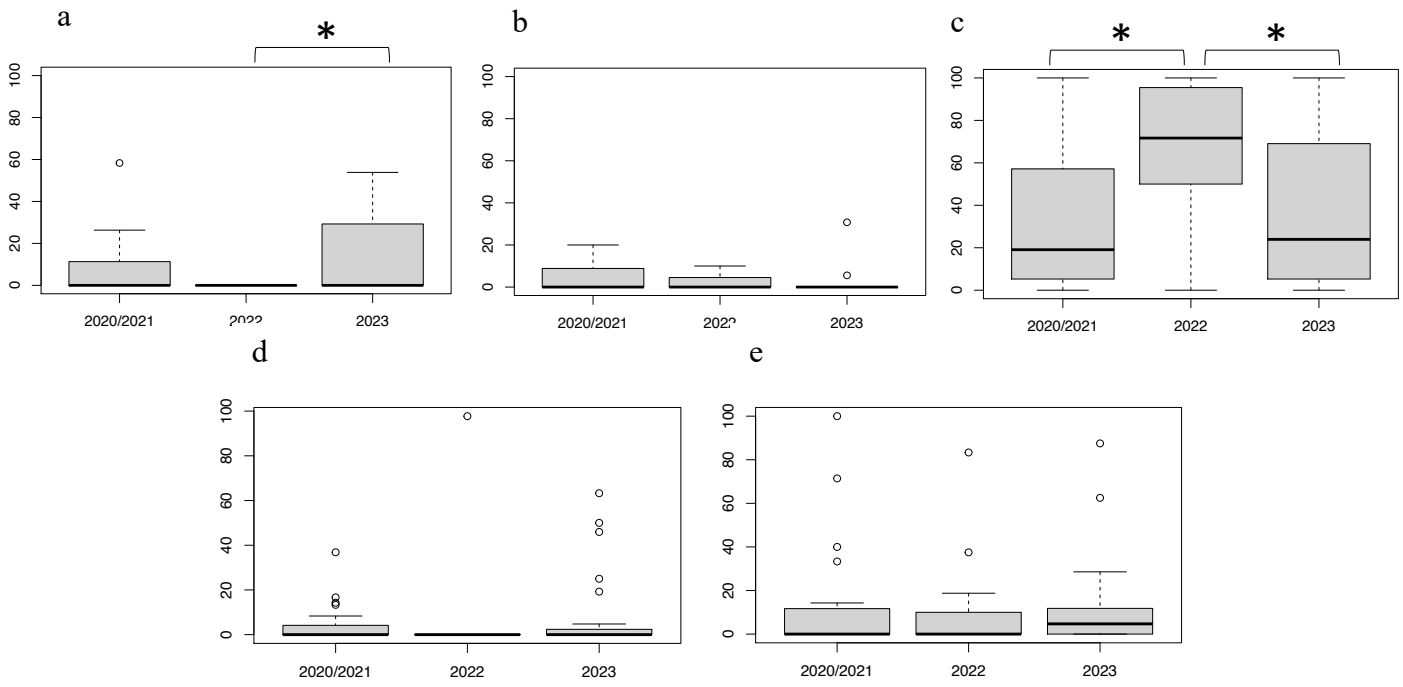

Figure 3-3: Observed average proportion of major prey items of sea otters: *a* (Sea Urchins), *b* (Chitons), *c* (Bivalves), *d* (Snails), and *e* (Crabs) per bout in the Sea Otter diets at Moyururi and Yururi Islands from 2020/ 2021, 2022, and 2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$) between two or more years.

Chapter 4: Impacts of changing environmental conditions on sea otters in eastern Hokkaido

4.1 Introduction

Sea otters primarily live in habitats that experience seasonal changes in environmental conditions such as temperature (Bodkin et al., 2001). Individuals and groups have been observed to favor different locations in response to changing seasons, oftentimes also connected with sex of the animal, and the dynamics within the local population (Garshelis and Garshelis, 1984). Sea otters also have been observed to exhibit multiple behavioral changes in response to seasonal fluctuations (Esslinger et al., 2014). Seasonally changing conditions, such as an increase in the intensity of rough seas, may also influence sea otter feeding location, which can therefore have an impact on sea otter diet (Doroff et al., 2012). Sea otters that reside in areas that are further north, and thus are exposed to a greater variation in temperature and daylight than those at lower latitudes, it logically follows that their behaviors have greater seasonal fluctuations (Esslinger et al,. 2014). Sea otters have, in certain cases, been observed to exhibit seasonal shifts in their diets which can primarily be attributed to shifts in prey availability (LaRoche et al., 2023; Watt et al., 2000). On Amchitka Island, Alaska, the diets of sea otters varied significantly across seasons due to the seasonal spawning migrations of various fish prey species (Watt et al., 2000). A primary example of this is how smooth lumpsuckers went from one of the dominant prey species within Aleutian otters' diets during winter and spring to being completely absent from the diet in summer and fall (Watt et al., 2000). Nutritional characteristics, such as lipid content, can even vary amongst prey items consumed across seasons (LaRoche et al., 2023). Changes in the environment have the potential to cause changes in dietary behavior, and one of the major changes that occurs is within the plant community surrounding them. In large swaths of their range, sea otters have been

associated with canopy-level marine plant species (usually kelp, in particular giant kelp), utilized as both a refuge and foraging area (Estes and Duggins, 1995). Giant kelp (*Macrocystis*), is the largest benthic organism on earth, and most widely distributed of the kelp genera, and can be found in a wide range of different habitats (Graham et al., 2007). At higher latitudes, it has been shown that kelps exhibit seasonal changes in growth rate in response to warmer temperatures (Hamilton, 2004), whilst kelps closer to the equator growth variabilility is more linked with changes in resource availability (Graham et al., 2007). Giant kelp recedes during the autumn when the upwhellings of nutrients that they sustain growth with begin to decline (Kurman and terHorst, 2023).

In eastern Hokkaido, in the study area of focus, canopy covering plants show a seasonal shift in both location and makeup throughout the summer (Figure 4-4). Rather than giant kelp, the majority of canopy covering plants in the Nemuro region of Hokkaido are either Sargassums (*Sargassum* spp.) or eelgrasses (*Zostera* spp.), both of which experience spatial and vertical distribution shifts across seasons in Japan (Hamana and Komatsu, 2021; Hayashida, 2000). Sargassums, a type of brown algae, have benthic holdfasts, and certain species are lined with gas vesicles that allow for the majority of the plant to float at the surface (Amaral-Zettler et al., 2016). Eelgrasses exist in a wide variety of habitats, of varying temperatures and salinities. The onset of eelgrass seed and flower development season can vary based on latitude, occurring later in more northern parts of the North American Pacific coast (Blok et al., 2018). The kelps in this region, which lie below the canopy covering plants, are seasonally harvested, which could also influence sea otter foraging behaviors. In eastern Hokkaido, the ナガコンブ kelp (*Saccharina longissima*) is the most harvested species in the region, and is vital to the local economy (Ito et al., 2022). In Nemuro city, the nearest large municipality to my research area, the kelp harvest has consistently

made up to 40% of the landing value of fisheries (Ito et al., 2024). During my research periods, there were two notable kelp harvests, of different varieties of kelp, the ハルクキナガコンブ, which began on 05/25/2023 and ended on 06/01/2023, and the ナガコンブ, which began in late July (approximated to be 07/20/2023) and ended on 08/01/2023.

In chapter 3, I established how the changes in prey item availability in the benthic environment had significantly impacted sea otter dietary composition. However, given how dietary composition has been shown to be associated with characteristics of certain foraging behaviors, it was also therefore important to investigate the further impacts of these changes. Handling time and dive duration are generally correlated with prey item type (Bodkin et al., 2004; Johnson et al., 2023; Maldini et al., 2010; Ostfeld et al., 1982), and oftentimes with prey item size (Maldini et al., 2010), both of which displayed changes following the HAB event. In Northern California, sea otters exhibited significantly longer handling times for abalone than any other prey items and took significantly longer to handle sea urchins than clams (Ostfeld et al., 1982). Johnson et al. 2023 also theorized that sea otter populations display faster handling times for prey items when they tend to favor that prey item within their diet. In other words, sea otter populations and individuals may be more efficient at processing prey items when they are more dietarily specialized for that prey item. Sea otters have been observed to forage deeper when prey in shallower areas becomes more scarce (Bodkin et al., 2004; Leach et al., 2024). These changes often coincide with depletions of preferred prey items caused by overconsumption by rapidly growing populations (Leach et al., 2024). Feeding dives also exhibit greater variation amongst individuals where prey resources are less abundant (Tinker et al., 2008). Shifts in prey availability and therefore dietary composition, may also result in diving at different depths (Leach et al., 2024).

By comparing the behaviors of sea otters at different points during the summer season, as well as before and after the red tide, it may be possible to determine if sea otters in Hokkaido exhibit foraging behavior seasonal variations or changes following a harmful algal bloom. My hypothesis was as follows:

1) due to a lack of seasonally shifting or migratory prey items, sea otter dive durations, dive depths, and handling times would not change throughout the summer season.

2) handling times would decrease after the red tide as a result of the increase in the dietary percentage of smaller bivalves described in chapter 2.

3) due to an overall decrease in prey availability revealed by chapter 2, sea otters would need to forage at deeper depths, which would require longer dive durations in order to retrieve prey items.

4.2 Materials and Methods

4.2.1 Study area

The same area around two eastern Hokkaido Islands (Yururi and Moyururi) discussed in chapters 1 and 2 was surveyed for chapter 3.

4.2.2 Kelp Canopy Cover

I conducted 3 drone (MAVIC Air 3, SZ DJI Technology Company, Nanshan, Shenzen, Guangdong, China) photography surveys across the study area along the coasts of the two islands, where canopy cover could be identified. Tidal variation, determined from Tides4Fishing, a website that aggregates tidal data from a variety of sources, including the American National Oceanic and Atmospheric Administration (NOAA), did not vary throughout the 2023 drone survey season, and therefore would have had a negligible impact on canopy estimation (Appendix 2). Photographs were stitched together utilizing METASHAPE (Agisoft LLC, St. Petersburg, Russia) software and converted into a KMZ layer that could be uploaded into a GIS (QGIS, Open Source) map. Kelp canopy cover was estimated by detecting canopy points with KeLpy software (Barnacle Foods, Juneau, Alaska, USA) and quantified within the GIS file. 100 x 100 meter grids were generated across the study area to quantify differences in canopy cover and compare with foraging dive location. Proximity to canopy cover was also calculated with GIS software.

4.2.3 Kelp Harvesting Seasons

Kelp harvesting seasons were determined through information accessed through inquiries with the research team boat captain, who is also a fisherman and (part of the Ochiishi fisheries cooperative network). My research surveys included 2 separate kelp harvesting periods, which for this study were designated as Harvest 1 (ハルクキナがコンブ) and Harvest 2 (ナガコンブ).

4.2.4 Foraging Behaviors

Foraging behavior observations were conducted from a small chartered local vessel using binoculars (Nikon StabilEyes 16 x 32, Nikon, Minato City, Tokyo, Japan) during 30-minute focal follows from June to August 2020, June to September 2021, May to September 2022, and May to September 2023. Locations of observed foraging dives were recorded using GPS (Grin, Olathe, Kansas, USA). Dive duration and handling time were recorded during these focal following periods. Dive depth was later estimated by comparing recorded GPS locations with a local topographical map on GIS software. Sea otter dive depth typically matches the depth of the seafloor (Tinker et al., 2007), as they primarily prey upon benthic organisms (Bodkin et al., 2004). For comparisons of handling times and dive depths of foraging dives containing different prey item types, only foraging dives where prey a single prey item type was collected were considered. Dive location in relation to kelp canopy cover was estimated by comparing recorded GPS locations with the GIS layer created with the Metashape and KeLpy software. Dietary composition of diet was determined through limited analysis to focal follows within 5-10 foraging dives, to avoid sampling bias (Laroche et al., 2021; Watt et al., 2000). Prey item size was determined in comparison to sea otter paw size (i.e., 5 cm; Kvitek et al., 1993). Classification of sea otters as mother-pup pairs or single otters was determined by observed presence of a pup associated with the adult otter being focally followed.

4.2.5 Dive Survey

SCUBA Dive Surveys were conducted in the same way as discussed in Chapter 2. Kilojoules per prey item were determined through calculations based on kilojoules per gram averages provided to us by Japan Food Inspection Corporation (Appendix 3).

4.2.6 Data Analysis

Correlation between 100 x 100 grids with varying amounts of canopy cover and number of foraging dives observed within the grids was evaluated using a Pearson's correlation coefficient. Significant differences in foraging dive behaviors across seasons and before and after the red tide were compared using a Tukey's difference test (Almeida et al., 2012; Estes et al., 1995; Johnson et al., 2020; LaRoche et al., 2021; Patel et al., 2023).

4.3 Results

4.3.1 Seasonal Change

I initially found that dive depth significantly decreased from the early summer (May/June) to late summer (August/ September) ($p<0.05$), while both dive duration and handling time of prey items did not significantly change seasonally (Figure 4-1). Seasonally, the sea otter dietary composition of bivalves, the preferred prey item, did not change significantly between May/June (49.4%), July (46.6%), and August/ September (32.9%) (Figure 4-2). Dietary percentage comprised of sea urchins likewise did not exhibit significant changes across the summer seasons (May/June: 0.3%, July: 5.2%, August/ September: 7.7%), while they did appear to disappear from

the May/June survey periods. While average foraging dive depth was slightly deeper amongst single sea otters (4.2) than mothers with pups (4.0), both displayed similar decreases as the summer season progressed (Table 4-1).

4.3.2 Canopy Cover

I established that there was indeed a correlation between sea otters and areas of kelp canopy cover within this study area ($r= 0.22$, $p<0.05$, Figure 4-3). The average number of points of canopy cover per 100 X 100 m grids was reduced from May/ June to July to August/ September (Figure 4-4). As foraging dive depths decreased across the summer, the distance between sea otter foraging dive locations and canopy cover did not significantly change over the same period (Figure 4-5). There did not appear to be any significant difference between foraging dives favoring different prey types and distance from canopy cover (Figure 4-5). Both dive duration ($p<0.05$) and foraging dive depth ($p<0.05$) displayed a high correlation with distance of the dive to canopy cover.

4.3.3 Kelp Harvest

The composition of prey items appeared to change across the kelp harvesting seasons. In 2023, the percentage of sea urchins within the diet appeared at its highest during the first kelp season, whilst the percentage of bivalves appeared to be at its highest during the time period between the first and second kelp seasons (Figure 4-6).

4.3.4 Red Tide and Foraging Behaviors

Handling time per prey item decreased significantly between 2020/2021 and 2022 ($p<0.05$) and 2023 ($p<0.05$) (Figure 4-7). Dive duration, conversely, displayed a significant decrease between 2020/2021 and 2023 ($p<0.05$) (Figure 4-7). Average handling times per prey item appeared to decrease across all prey item types between 2020/2021 and 2022, while all increased aside from bivalves in 2023 (Table 4-2). Average foraging dive depths increased for all prey items after the red tide, while they continued to do so in 2023, aside from Bivalves (Table 4-2). The average number of bivalves per dive for each bout increased significantly ($p<0.05$) between 2020/2021 (0.5 ± 0.6) and 2022 (1.4 ± 0.8) (Figure 4-8). Average bivalve handling times decreased significantly ($p<0.05$) from 2019-2021 (32.8 ± 20.9 s) and 2022/2023 (25.8 ± 19.1 s) (Figure 4-9). The KJ per bivalve individual collected during the benthic dive surveys decreased significantly ($p<0.05$) between 2020 (275.0 ± 107.1) and 2022 (83.5 ± 151.3) (Figure 4-10). Foraging dive depths reduced considerably between 2020/2021 (2.8 ± 1.9) and 2022 (4.0 ± 1.9; $p<0.05$) and 2023 (4.0 ± 1.8; $p<0.05$) (Figure 4-11). Prey item availability did not appear to factor into this, as most losses in available prey occurred at deeper depths. The percentage of tool use within dive bouts mirrored the disappearance and reappearance of sea urchins within sea otter diets in 2022 and 2023, respectively (Figure 4-12).

4.4 Discussion

4.4.1 Seasonal Change

The significant change in foraging dive depth across the different sampling periods across the summer is an indication that sea otters may be modifying foraging location or behavior as the summer season progresses. However, the lack of observed significant change in dietary

composition, dive duration, and handling time was an indication that some other external factor might be influencing this change in dive depth.

4.4.2 Canopy Covering Marine Plants

The decrease in canopy cover as the summer continued displayed how the plant community in my study area underwent notable changes throughout the growing season. This change, along with the lack of significant change in the average distance of sea otter foraging dives to canopy covering plants, indicates that sea otters are maintaining the same proximity to the sargassum and eelgrass. Along with the high correlation between depth and canopy cover, this tendency may explain the aforementioned changes in foraging dive depth, as the retraction of canopy covering plants in July and August/ September necessitated the otters to forage in shallower, closer to shore areas, as the summer progressed. The lack of an observable difference in the changes in dive depth between single otters and pup-rearing females would indicate that this maintenance of proximity to canopy cover is a behavior observed amongst all individuals. With sea otter population carrying capacity being, in part, determined by marine plant (typically kelp) canopy cover (Tinker et al., 2019), it is possible that sea otter foraging is impacted by it to some degree as well. The maintence of proximity to canopy cover across the summer season, would seem to indicate that it does.

4.4.3 Kelp Harvesting Season

The amount of data I currently have is possibly too little to draw a correlation between dietary preferences composition and kelp harvesting season. However, the nearly two-fold increase in bivalve percentage and a near fivefold decrease in sea urchin percentage between the first kelp

season and the time period after it concludes before the second kelp season begins might indicate that otters forage differently in response to anthropogenic activities. Further years of monitoring of the kelp harvest and foraging behaviors in order to determine if there is a significant correlation.

4.4.4 Red tide and foraging behaviors

Dive duration increasing after the red tide as prey size decreased may initially appear contradictory as it is often linearly correlated with dive duration (Maldini et al., 2010), and was contrary to my initial hypothesis. These differing trajectories can therefore be tied to the decrease in prey caloric value. This, along with the previously described increase in small bivalves within the benthic environment and dietary consumption of bivalves indicates that the red tide resulted an increase in predation on smaller, less calorically valuable, bivalves which, in turn, necessitated sea otters to conduct longer foraging dives in order to collect more of this less valuable prey. The dietary shift may also be the cause of the decrease in handling time, which has been observed to be linked to both prey type (Maldini et al., 2010; Osfteld, 1982) and prey size (Maldini et al., 2010). The need to forage longer for more, less calorically prey items per dive could potentially prove more harmful to this sea otter population in case of more severe red tides that exert even greater depletions of larger calorically valuable prey items. The increase in dive depth cannot yet be explained, as bivalves were more concentrated in shallower areas. It could also be related to the increase in dive duration, but I established in chapter 1 that dive depth and duration could not be proven to be significantly correlated. The decrease in the percentage of tool use in foraging dives after the red tide may likely be tied to the disappearance of sea urchins from otter diets during this time. The persistence of the majority of these foraging behavior changes in 2023, with the exception of tool use, are an indication that perhaps these behavioral changes resulting from the

red tide are more long-lasting that the dietary changes that appeared to return to the norm one year on. Further monitoring of these trends will be key to see to what extent the behavioral changes are long-lasting.

4.4.5 Conclusion

Foraging dive depth seasonal changes may be a novel phenomenon, even if the cause for this requires further investigation. The changes in dive duration, handling time, and prey utilizations were consistent with environmental changes often linked to sea otter foraging behavior, in this instance, closely associated with the shifts in dietary composition that had previously been observed in Chapter 2.

4.5 Tables and Figures

Table 4-1: Average foraging dive depths (±SD) of pup-rearing mother and single Sea otters in May/ June, July, and August/ September.

Month of Survey	Mother/ Pup Pair Foraging Dive Depth (m)	Single Otter Foraging Dive Depth (m)
May/ June	4.3 ± 1.6	4.6 ± 2.0
July	3.8 ± 2.0	4.2 ± 1.8
August/ September	2.4 ± 1.1	3.2 ± 1.7

Table 4-2: Average handling time (±SD) per prey ttem and dive depth for foraging dives comprised of Sea Urchins, Bivalves, Chitons, Crabs, and Snails.

Prey type of foraging dive	2020/2021 Average Handling Time Per Prey Item (s) * Average Depth (m)	2022 Average Handling Time Per Prey Item (s) * Average Depth (m)	2023 Average Handling Time Per Prey Item (s) * Average Depth (m)
Sea Urchin	36.7 ± 0.9 * 3.7 ± 3.8	No Dives Recorded	48.1 ± 26.1 * 5.3 ± 0.6
Bivalve	38.1 ± 25.7 * 2.5 ± 1.3	33.8 ± 22.8 * 4.5 ± 1.2	26.2 ± 22.4 * 3.6 ± 1.4
Chiton	64 ± 12.3 * 2.7 ± 1.5	28.5 ± 9.2 * 6.0 ± 0.0	No Dives Recorded
Crab	72.1 ± 41.1 * 2.3 ± 0.9	47.3 ± 11.9 * 3.0 ± 0.8	61.8 ± 65.8 * 4.0 ± 1.8
Snail	14.0 ± 0.0 * 1.0 ± 0.0	No Dives Recorded	17.5 ± 3.5 * 5.0 ± 0.0

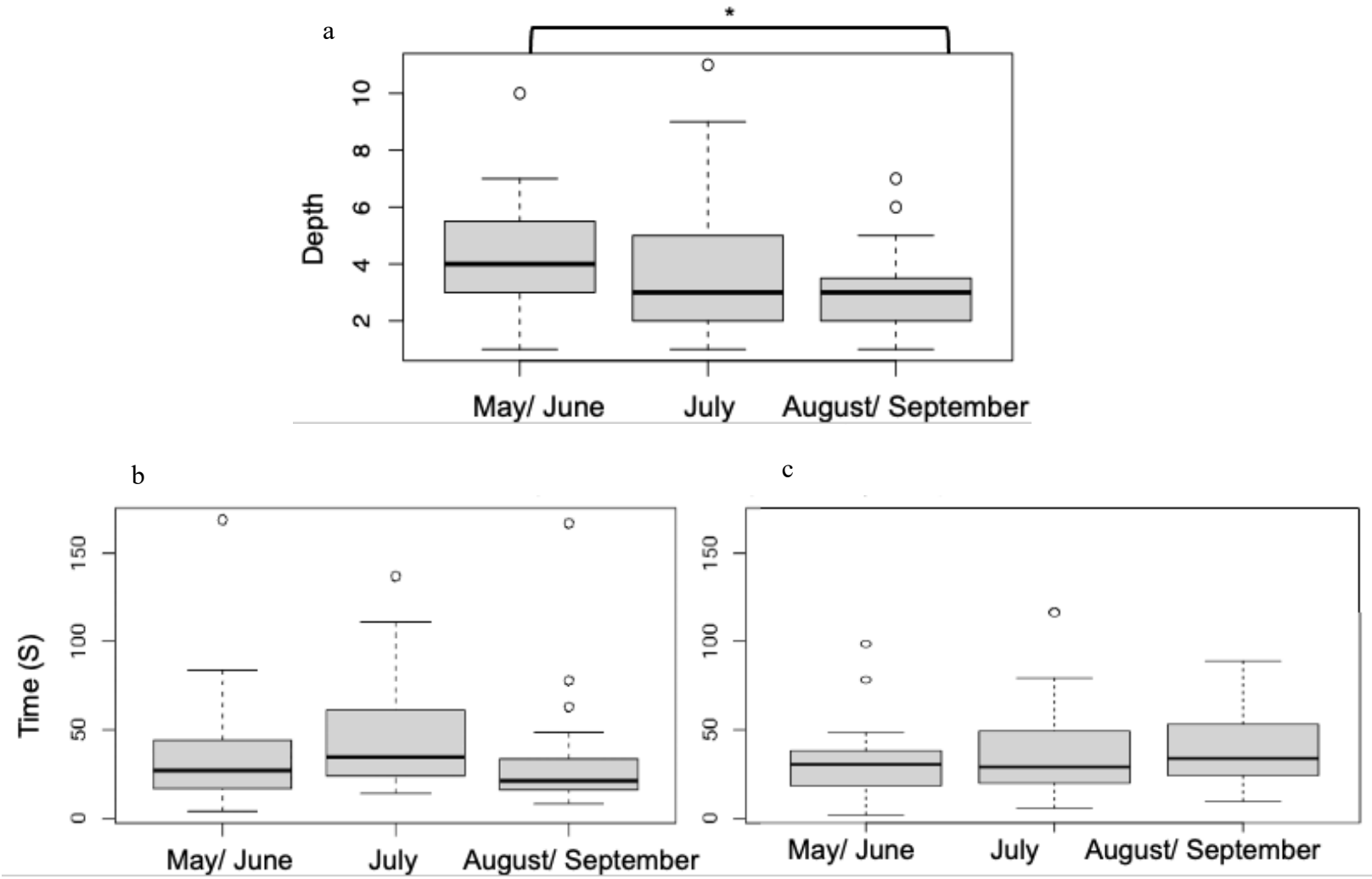

Figure 4-1: (*a*) Foraging dive depth, (*b*) handling time, (*c*) dive duration across the summer research periods from 2019-2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$).

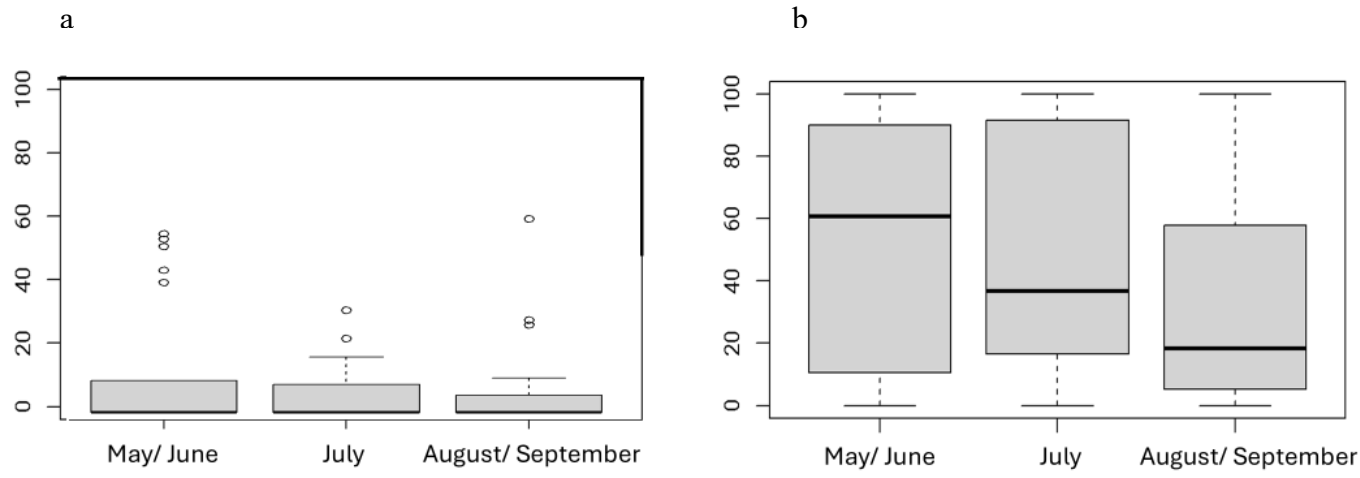

Figure 4-2: Sea Urchin (*a*), and Bivalve (*b*) percentages within sea otter diet during the summer survey periods.

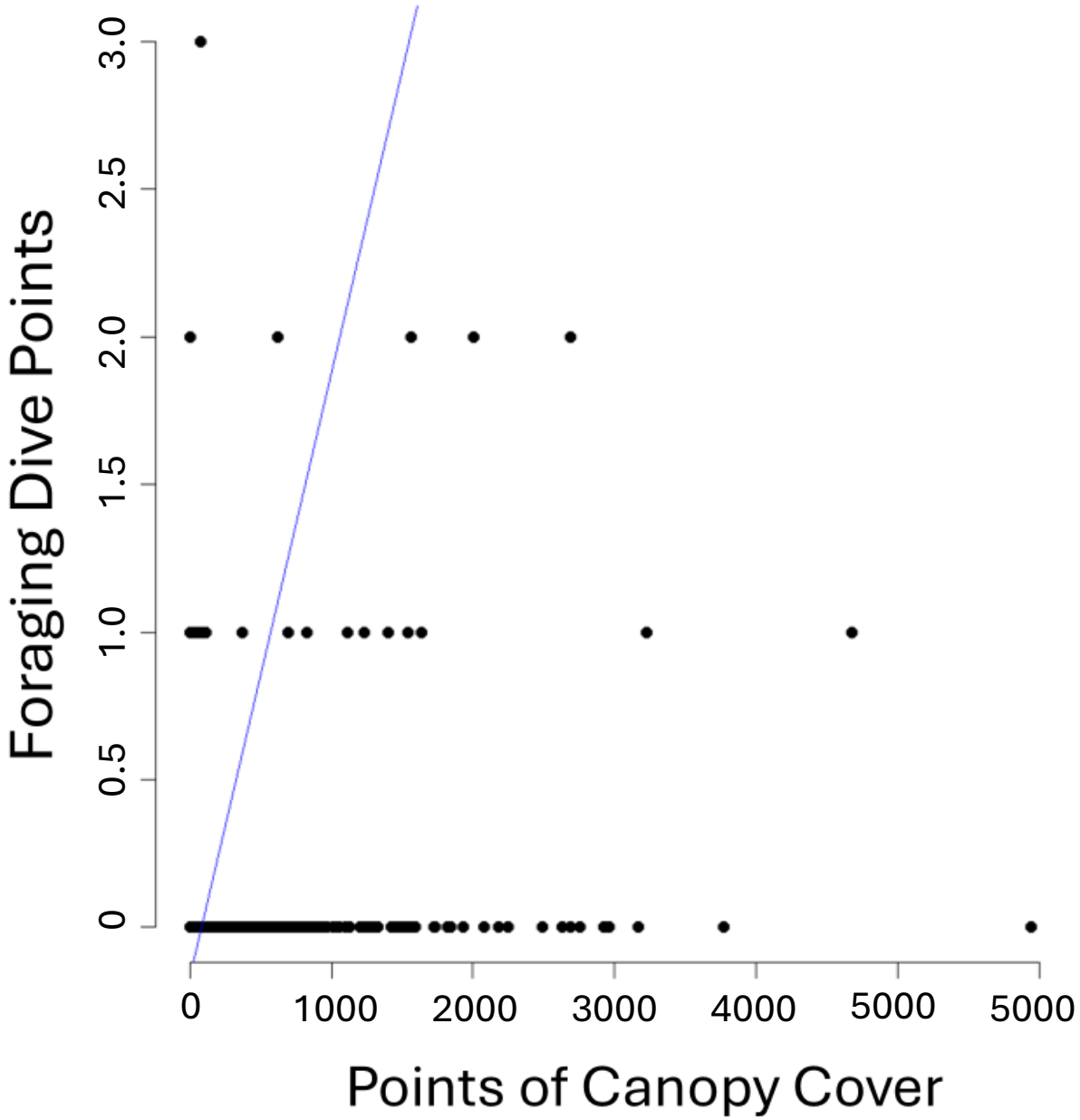

Figure 4-3: Correlation between points of canopy cover within 200 x 200 grids and number of foraging dives observed within the grids.

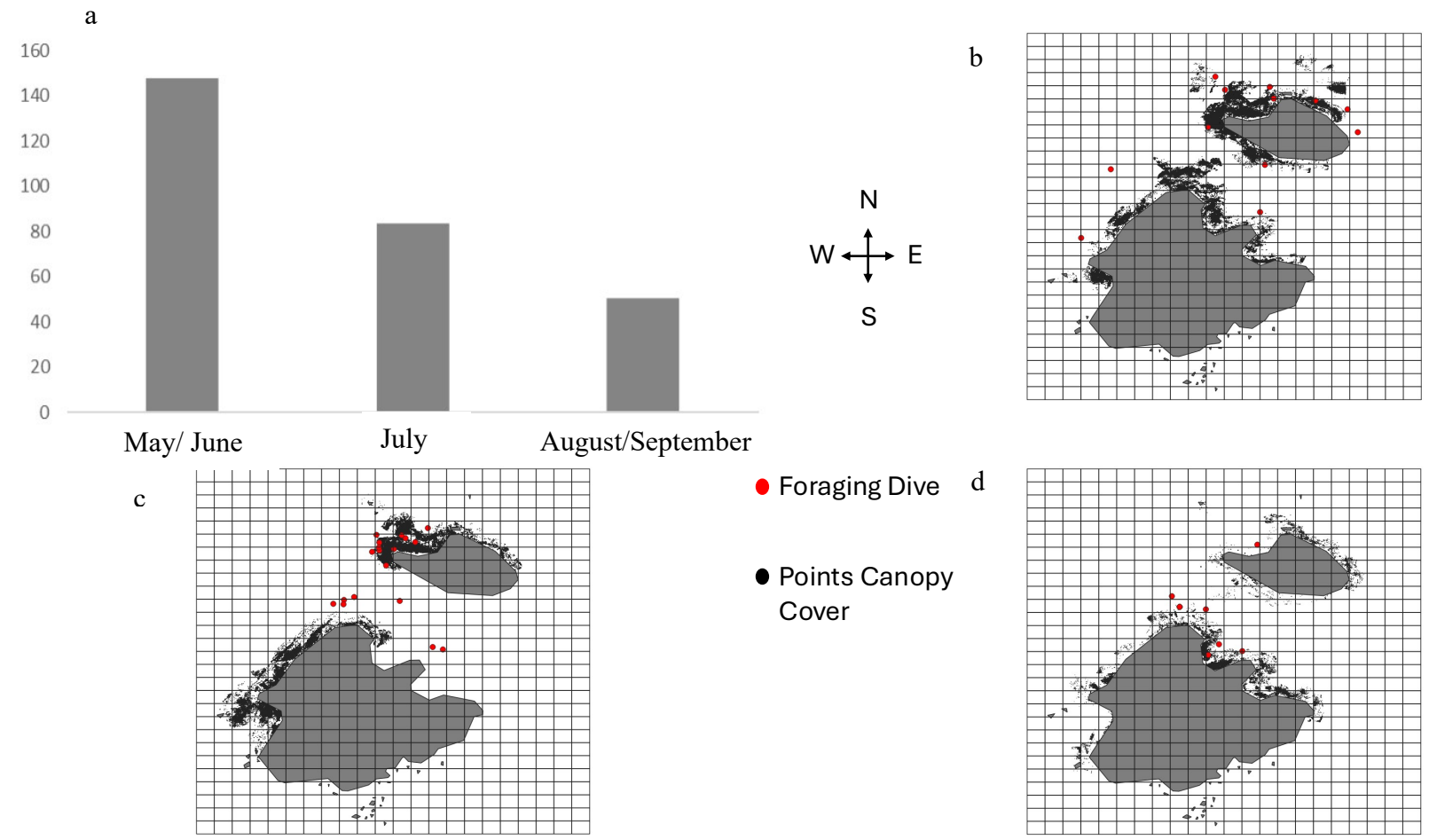

Figure 4-4: (*a*) Average number of points of canopy cover per 100 X 100 m grid across seasons, Maps of points of canopy cover and foraging dive locations in (*b*) May/ June, (*c*) July, and (*d*) August/ September.

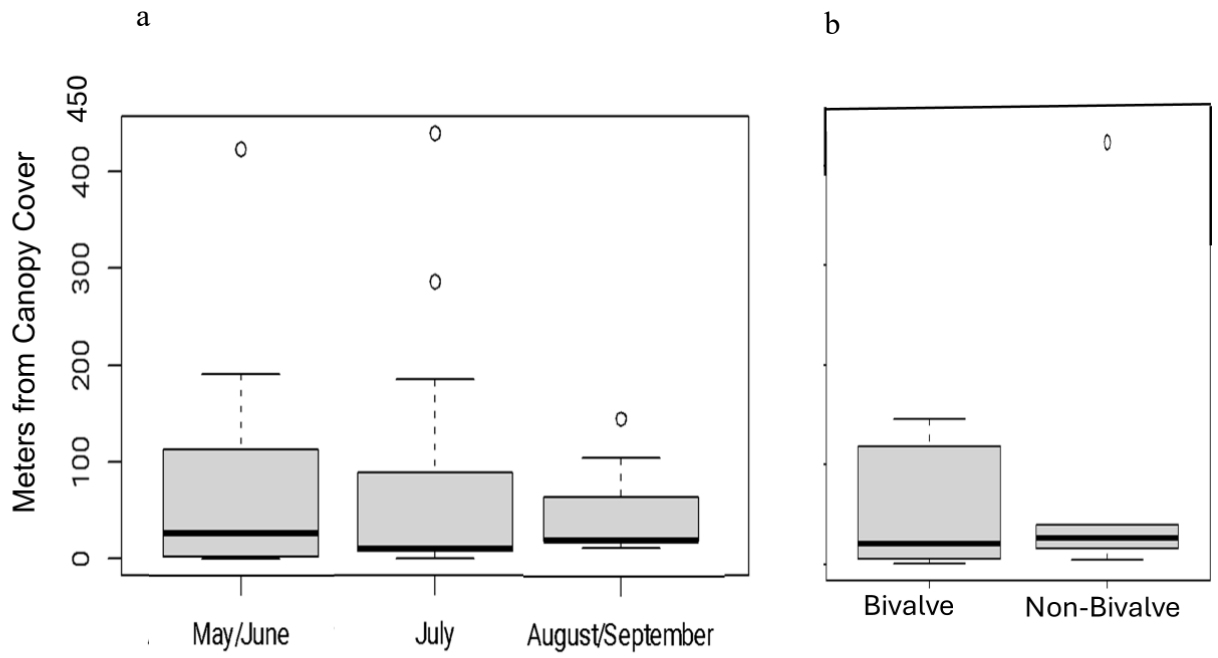

Figure 4-5: Distance of Sea otter foraging dives from Canopy covering marine plants (*a*) across May/June, July, and August/ September and (*b*) for foraging dives where bivalves were retrieved or other prey items were retrieved.

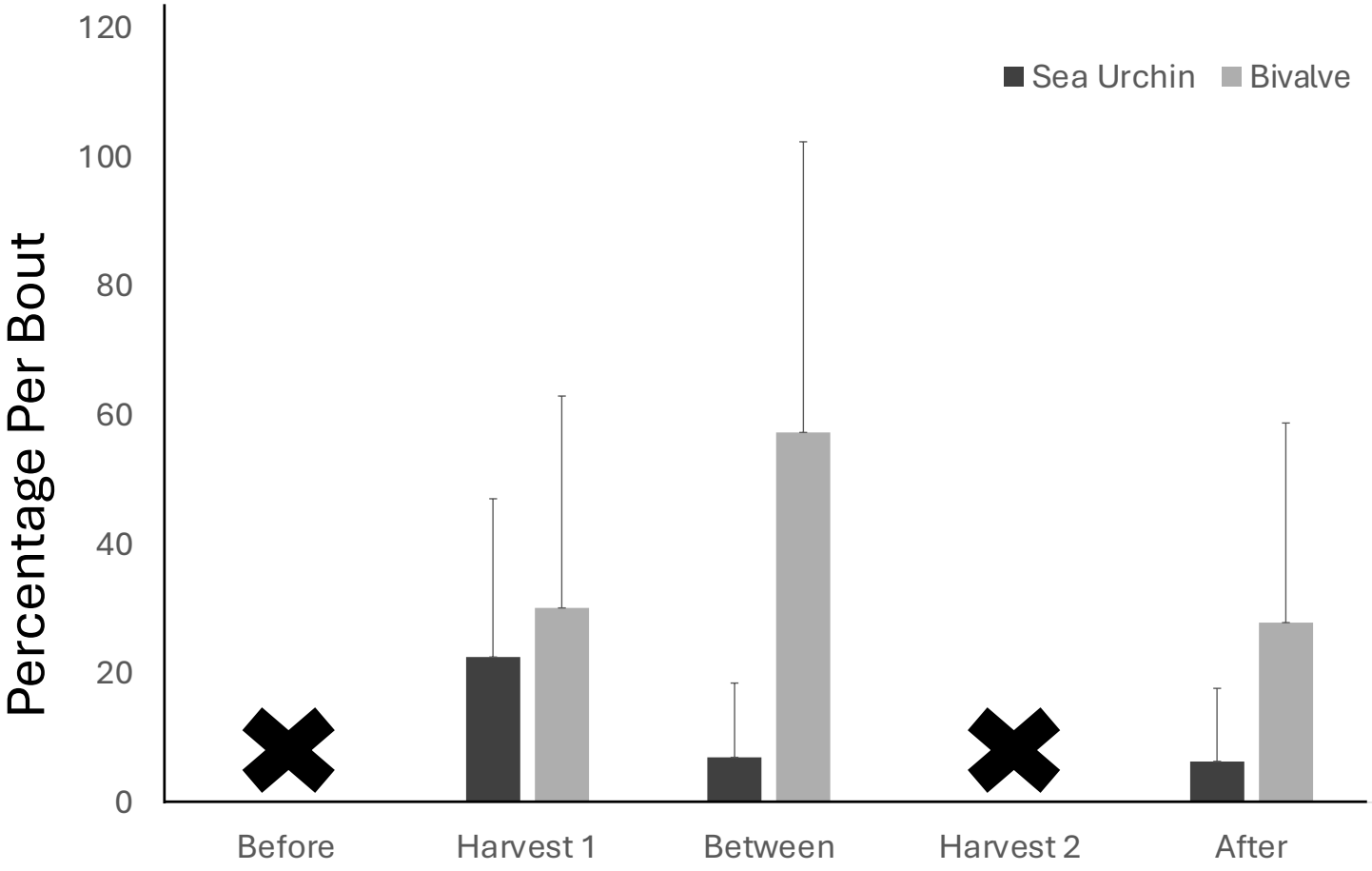

Figure 4-6: Average Percentage per bout of Sea Urchins and Bivalves across Kelp Harvesting Seasons in the Summer of 2023. Large X symbols denote a lack of foraging behavior survey data from this period.

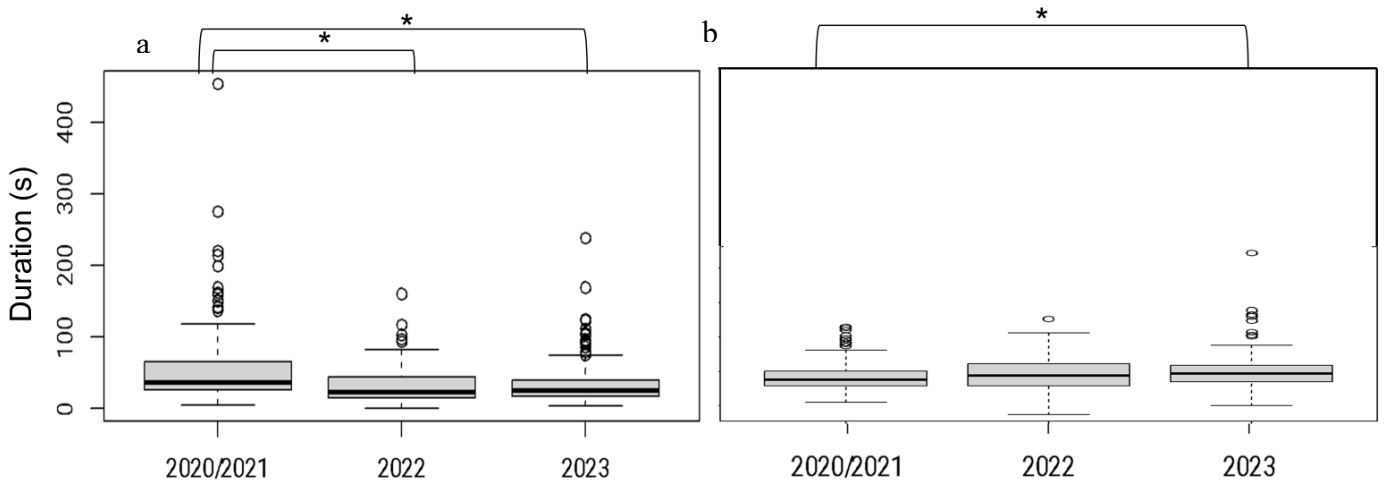

Figure 4-7: Duration (s) of sea otter (*a*) handling times and (*b*) foraging dives in 2020/2021, 2022, and 2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$).

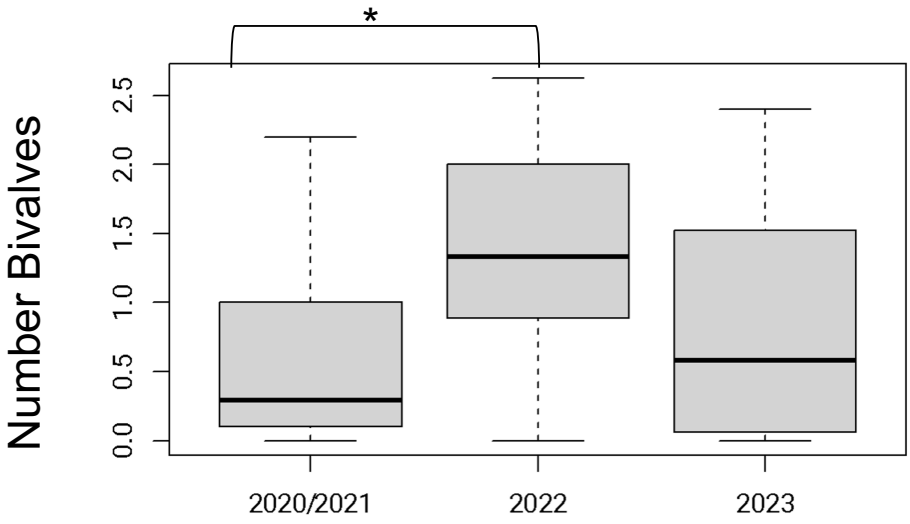

Figure 4-8: Number of bivalves per foraging dive bout in 2020/2021, 2022, and 2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$) in the number of bivalves per foraging bout between year categories.

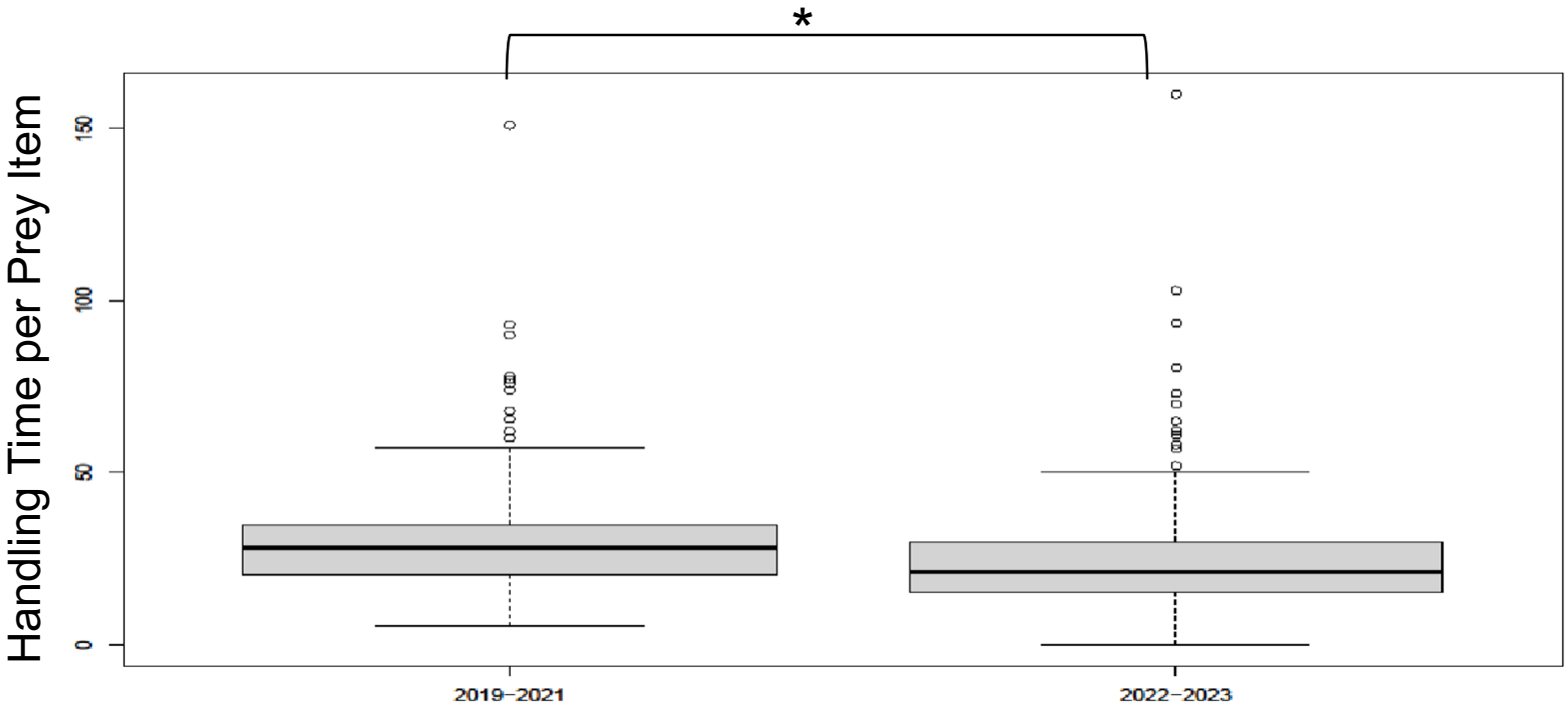

Figure 4-9: Average handling time per prey item before the red tide (2019-2021) and afterwards (2022-2023). *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$).

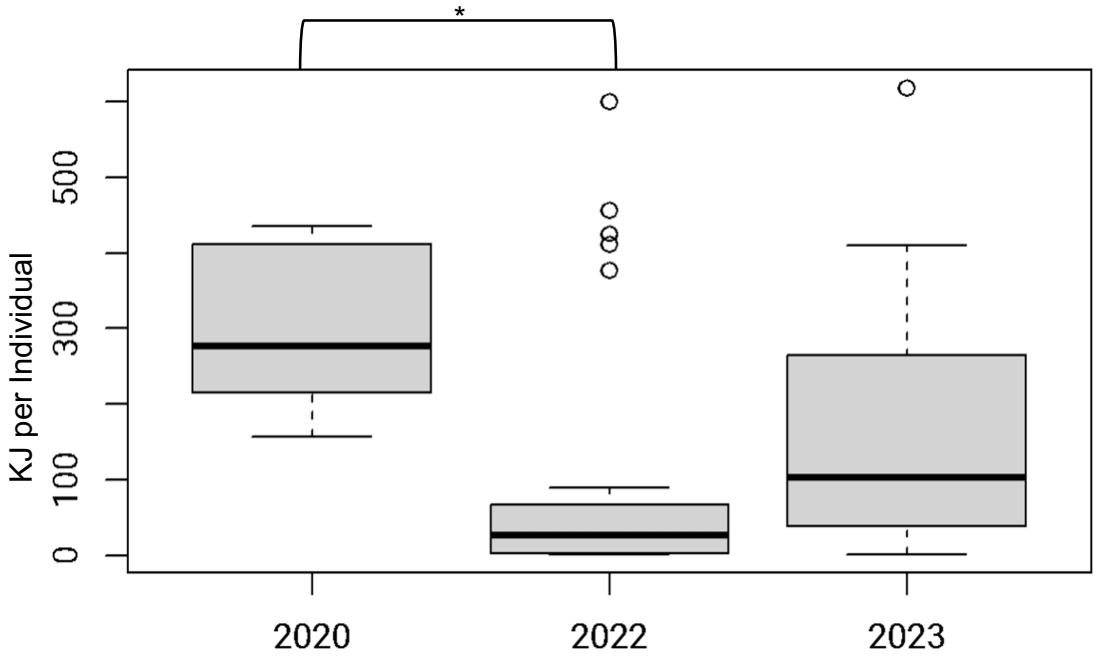

Figure 4-10: Kilojoules per benthic bivalve individual in 2020, 2022, and 2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$).

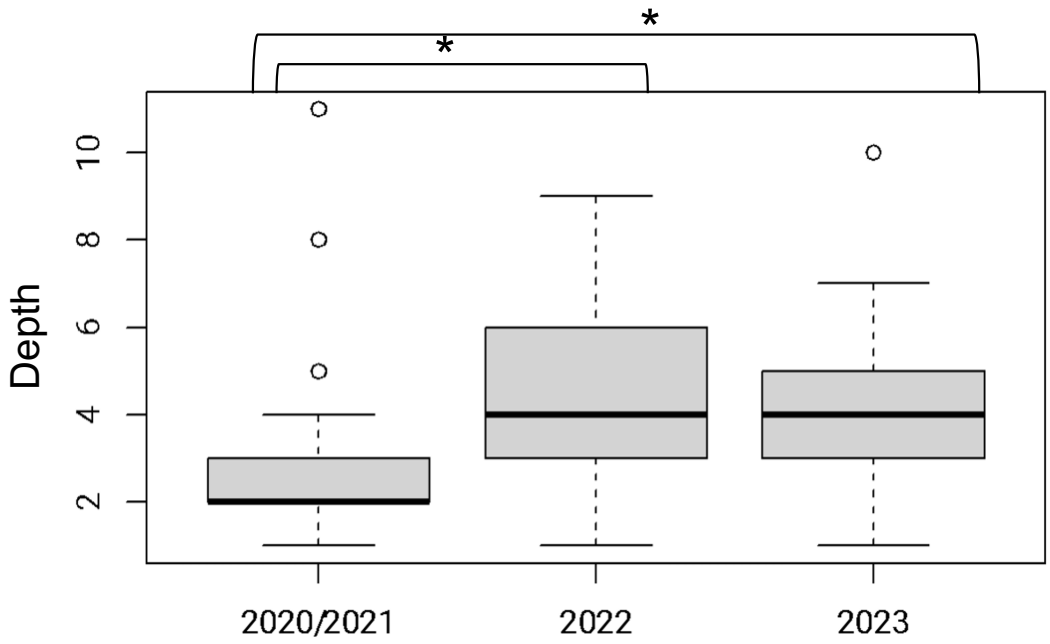

Figure 4-11: Foraging dive depths in 2020/2021, 2022, and 2023. *Error bars* represent ±1 SE. Asterisks (*) above the graph display a significant difference ($p < 0.05$).

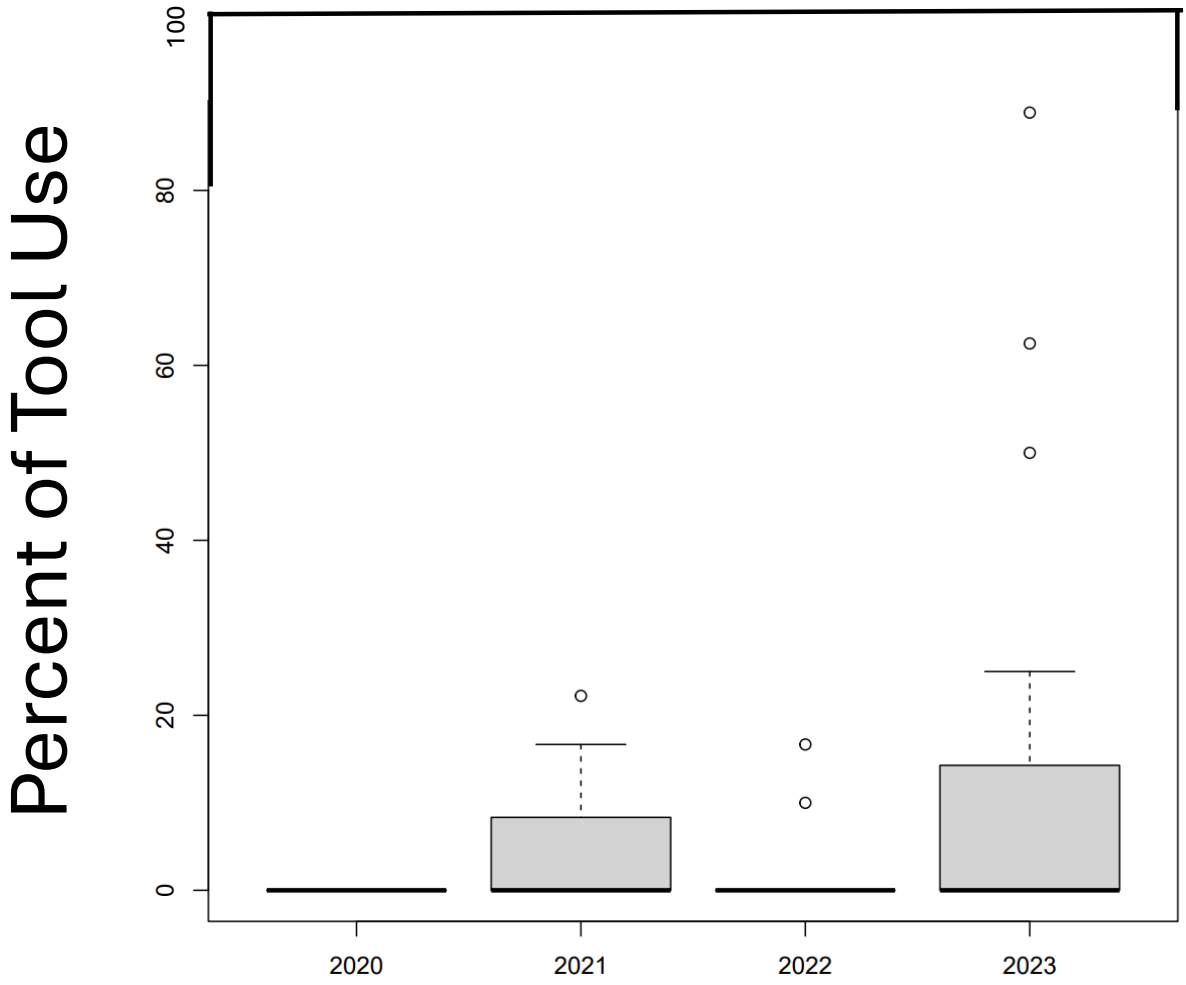

Figure 4-12: Percent of tool use in foraging dive bouts in 2020, 2021, 2022, and 2023.

Chapter: 5 General Discussion

My results indicate that sea otters in Hokkaido (*Enhydra lutris lutris*), that have arrived from the Kuril Islands, display similar feeding behavioral tendencies to populations that have returned to portions of their historic range, through natural recovery and inflow from nearby populations or anthropogenic translocations, along the west coast of North America (*E. l. kenyoni*; *E. l. nereis*) that most resemble their situation in both habitat type and recolonizing situation. The lack of information on recolonizing populations in eastern Russia, along with the long history of sea otter research across the North American Pacific coast, were the primary reasons that the populations that were used for the comparison were selected. Foraging behavior tendencies of this population appear to be typical of newly recolonizing sea otter populations that forage primarily on bivalves in mixed sediment seafloors (Bodkin et al., 2004; Kvitek et al., 1993; Laidre and Jameson, 2006; Laidre et al., 2009). The similar populations in Washington State and Alaska may provide some insight into what can be expected from the Hokkaido otters in the future, as I expect the population to expand and increase. The results, along with the population number (Suzuki et al., unpublished), also indicate that the Hokkaido sea otters are still not at or approaching carrying capacity, and that perhaps the carrying capacity of sea otters that this habitat can support is limited by factors other than prey carrying capacity. Other factors that have been shown to influence sea otter population carrying capacity include seafloor depth, kelp canopy presence, and the type of marine habitat; in particular whether it is an estuary or not (Tinker et al., 2021). Rapid recolonizations have often resulted in depletions of prey (Garcia, 2012) and shifts in dietary behavior in both prey type and potentially depth. One area in which this population differed greatly from their North American counterparts, however, was in utilizing tools to a lesser degree than other populations where bivalves are the most common prey items (Fujii et al, 2015). The cause

of this major difference is yet to be determined, but further research may give insight into whether factors such as physiological differences or prey species differences are related to this unexpected behavioral observation. While there is some precedent for rising sea otter populations to come into conflict with local industry (Carswell et al., 2015), it is important to recognize the opportunities offered by such an increase, namely in ecotourism (Fujii et al., 2023), some of which are starting to be seized by local residents (Murayama, 2023). The existing infrastructure to accommodate ecotourism for sea otters is relatively small, meaning there is the relatively open market in which local stakeholders can capitalize on a new natural resource.

My results indicated that sea otters in Hokkaido may display a tendency to utilize tools on a higher percentage of foraging dives where sea urchins were the preferred prey item. This would run contrary to the prevailing existing research, where sea urchins typically utilized tools more so with harder-shelled prey items such as bivalves and snails (Fujii et al., 2015). The higher tool utilization for sea urchins might indicate that the species of urchins in Hokkaido are more difficult to access for otters, which might also provide insight as to why they are not one of the main prey items in the region. However, further research is needed to confirm the causes of this phenomenon regarding both sea urchins and bivalves in Eastern Hokkaido within my study site. A greater understanding of why these sea otters employ greater rates of tool utilization for sea urchins might provide insight into why they may or may not pose a threat to the sea urchin mariculture industry in Hokkaido going forward, even as prey depletions may occur as the population increases.

My red tide investigation allowed for an opportunity to observe the impacts of a stochastic and disruptive environmental event across multiple levels of the trophic cascade within eastern Hokkaido, with greater implications for the local fisheries industries as well. The benthic surveys conducted prior to and after the red tides confirmed the extent to which the massive red tide event

impacted the local ecosystem at the study site, in particular observing the 82% drop in benthic sea urchin density. Focal observational surveys, and the complete absence of sea urchins, combined with a doubling of the percentage of bivalves within otter diets in 2022, indicated altered sea otter dietary shifts in response to the changes brought on by the red tide. Due to the lack of sea urchin reseeding occurring within the study site, it will require a longer time of monitoring to determine if the benthic population of sea urchins recovers within the area. However, the lack of population decline and the immediate recovery of the dietary percentage of sea urchins within otter diets provides an encouraging sign of the resilience of this population, as well as gives an indication that sea otters may have selectively avoided sea urchins in 2022 in the aftermath of the red tide, but were no longer doing so in 2023. Sea otters have been observed avoiding contaminated prey, however the mechanism for this is still not fully understood (Coletti, 2021). One issue that remains yet to be seen is how sea otters in this region would respond to red tides or environmental disturbances that more heavily impact their preferred prey items, bivalves. As climate change continues, and oceans continue to warm, the likelihood of more red tide events will increase, and the knowledge gained from the research I conducted may be useful in being more prepared for what to expect the next time such a disturbance occurs.

My results displaying the lack of change in distance to canopy cover, along with the seasonal change in foraging depth, indicate that sea otters maintain a similar association with canopy-covering plants even as the distribution of these plants changes. Sea otters have displayed a strong association with canopy-covering kelp in many parts of their range, even benefiting the overall health of the ecosystem due to exerting control on sea urchin densities (Duggins, 1980; Hale, 2022; Kenner and Tinker, 2018; Paine and Vadas, 1969; Watson, 1993; Watson and Estes, 2011). The results revealed by my research indicate that they will maintain an association with

canopy covering plants, even when the main canopy cover is a mix of sargassum and eelgrasses, and the sea urchin population is heavily anthropogenically managed. Possessing knowledge of where sea otters may likely forage in relation to canopy covering plants may help inform future resource harvesting practices, and reduce future potential conflicts with sea otters throughout the region as they continue to recolonize. Further insights gained into foraging behaviors and dietary preferences in relation to kelp harvesting seasons may also prove beneficial towards a future coexistent relationship between nature and industry, however, more research and data will be required in order to draw sufficient conclusions regarding this topic.

The subsequent shifts in handling time and number of prey per foraging dive indicate that the red tide event had a greater impact on sea otter foraging behavior beyond simply dietary composition. While this change was likely a result of the dietary increase in bivalves, the persistence of foraging behavioral differences a year after the dietary percentages returned to pre-red tide conditions indicates that the red tide may have had a greater impact on this population of sea otters than it initially appeared.

In the future, as the Hokkaido population continues to be monitored by local stakeholders who stand to be impacted by probable continued growth, the information collected during this research, and in particular what I know of similar populations, may be highly useful in developing a sustainable compromise model between fisheries and sea otters, as well as provide information useful in developing a fruitful ecotourism industry that still supports the local economy. The dietary plasticity and lack of negative health impacts as a result of the harmful red tide indicate strong resistance to stochastic change, an essential characteristic for organisms to have in a rapidly changing climate and anthropogenically modified ecosystem. However, the heavy bivalve reliance of this population might make them more susceptible to bivalve die-offs. More extensive red tides

may eventually negatively impact a population in ways I have not yet been able to observe. The persistence of certain behavioral changes may provide future insight into what long-lasting negative impacts this population could experience in the future. Therefore, continued tracking of longer-lasting impacts of the red tide is imperative. Local stakeholders should likewise remain prepared to act should behavioral changes persist and lead to tangible alterations in population health or resource availability.

Knowledge of similar populations, seasonal preferences, and responses to environmental disturbances such as the red tide, marine heat wave, and avian flu will be invaluable in developing sustainable conservation for all of the pressures that are highly likely to be exerted upon the recolonizing sea otter population, as well as the local fisheries industries.

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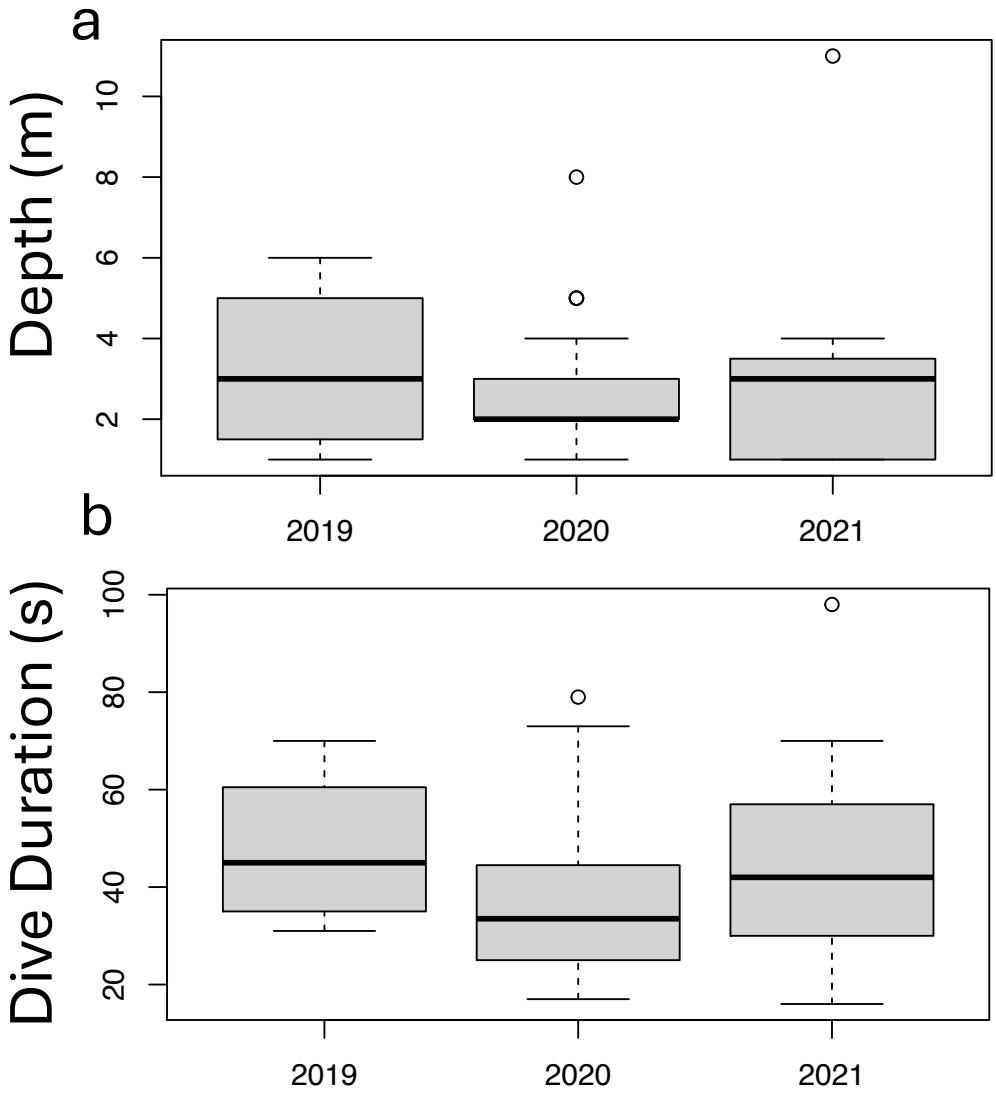
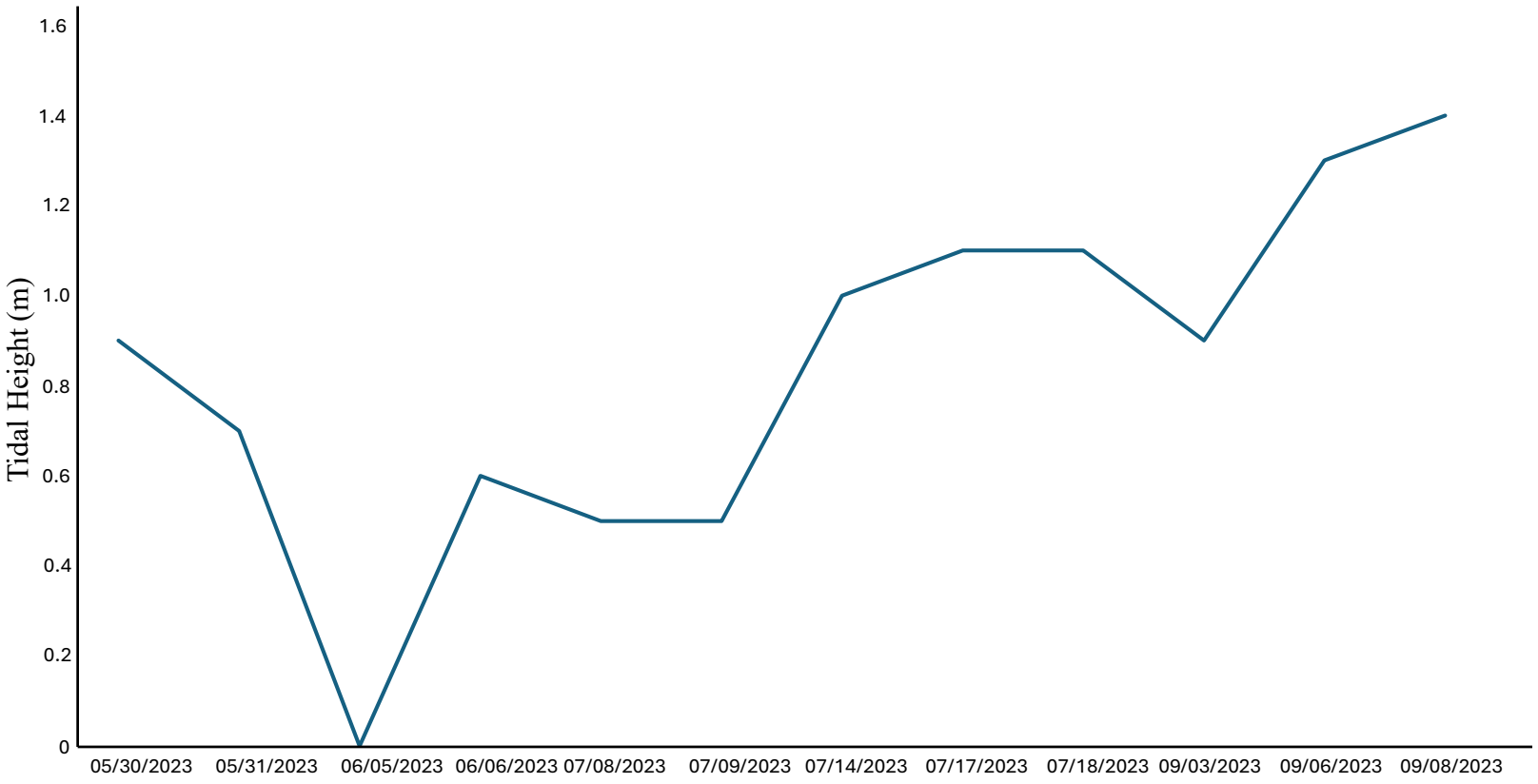


Appendix 1: Sea otter dive (a) depths (m) and (b) duration (s) in 2019, 2020, and 2021.



Appendix 2: Estimated tidal heights (m) at the time of the survey on all dates in the 2023 research season where drone photography was conducted.

Appendix 3: Prey type and size, prey average kilojoules per gram (kj/g), average weight of prey item (from samples collected in 2020, 2022, and 2023 benthic SCUBA surveys), and prey kilojoules per individual (kj/ind.). * Most sea urchins in the region (えぞばフンウニ) are around 5 centimeters (cm), therefore there were no large sea urchins to be measured.

Prey type	Prey Size	kj/g	Weight (g)	kj/ind.
Sea Urchin*	Medium	2.6	13.0	34.2
Sea Urchin	Small	2.6	6.2	16.0
Sea Cucumber	Large	3.0	138.7	415.5
Sea Cucumber	Medium	3.0	68.8	205.3
Sea Cucumber	Small	No Estimate	No Estimate	No Estimate
Chiton	Large	2.9	234.6	674.0
Chiton	Medium	2.2	47	102.9
Chiton	Small	No Estimate	No Estimate	No Estimate
Crab	Large	No Estimate	No Estimate	No Estimate
Crab	Medium	2.7	15.4	41.2
Crab	Small	2.7	15.4	41.2
Sea Star	Large	2.5	23	56.8
Sea Star	Medium	2.7	16.9	42.4
Sea Star	Small	No Estimate	No Estimate	No Estimate
Hermit Crab	Large	No Estimate	No Estimate	No Estimate
Hermit Crab	Medium	2.8	3.0	8.4

Hermit Crab	Small	2.8	3.0	8.4
Bivalve	Large	3.1	83.8	247.4
Bivalve	Medium	2.6	84.2	214.9
Bivalve	Small	No Estimate	No Estimate	No Estimate
Snail	Large	No Estimate	No Estimate	No Estimate
Snail	Medium	3.9	75.8	297.9
Snail	Small	3.9	75.8	297.9