*Journal of Mammalogy*, XX(X):1–13, 2022
https://doi.org/10.1093/jmammal/gyac095



# Brown bear–sea otter interactions along the Katmai coast: terrestrial and nearshore communities linked by predation

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Sea otters were extirpated throughout much of their range by the maritime fur trade in the 18th and 19th centuries, including the coast of Katmai National Park and Preserve in southcentral Alaska. Brown bears are an important component of the Katmai ecosystem where they are the focus of a thriving ecotourism bear-viewing industry as they forage in sedge meadows and dig clams in the extensive tidal flats that exist there. Sea otters began reoccupying Katmai in the 1970s where their use of intertidal clam resources overlapped that of brown bears. By 2008, the Katmai sea otter population had grown to an estimated 7,000 animals and was likely near carrying capacity; however, in 2006–2015, the age-at-death distribution (AADD) of sea otter carcasses collected at Katmai included a higher-than-expected proportion of prime-age animals compared to most other sea otter populations in Alaska. The unusual AADD warranted scientific investigation, particularly because the Katmai population is part of the Threatened southwest sea otter stock. Brown bears in Katmai are known to prey on marine mammals and sea otters, but depredation rates are unknown; thus, we investigated carnivore predation, especially by brown bears, as a potential explanation for abnormally high prime-age otter mortality. We installed camera traps at two island-based marine mammal haulout sites within Katmai to gather direct evidence that brown bears prey on seals and sea otters. Over a period of two summers, we gathered photo evidence of brown bears making 22 attempts to prey on sea otters of which nine (41%) were successful and 12 attempts to prey on harbor seals of which one (8%) was successful. We also developed a population model based on the AADD to determine if the living population is declining, as suggested by the high proportion of prime-age animals in the AADD. We found that the population trend predicted by the modeled AADDs was contradictory to aerial population surveys that indicated the population was not in steep decline but was consistent with otter predation. Future work should focus on the direct and indirect effects these top-level predators have on each other and the coastal community that connects them.

Key words: brown bear, camera trap, *Enhydra lutris*, harbor seal, predation, *Phoca vitulina*, sea otter, terrestrial–marine interaction, *Ursus arctos*

Sea otters (*Enhydra lutris*) became the target of the maritime fur trade in the Pacific Northwest following Vitus Bering's second Kamchatka Expedition (1741–1742). After this initial period of Russian exploitation of sea otters, multinational fur traders continued to commercially harvest sea otters until the early 1900s when sea otters had been nearly extirpated across most of their range from Russia to California, including the Katmai coastline in the Gulf of Alaska (Kenyon 1969; Bodkin 2015). By the time the Katmai National Park and Preserve was created (Fig. 1) in 1980, sea otters had begun to reoccupy the area, and by 1989, the estimated population was ~900 animals (DeGange et al. 1995). The source of animals for this recovery likely came from a remnant group that survived north of Katmai near Augustine Island in Kamishak Bay (Lensink 1960;

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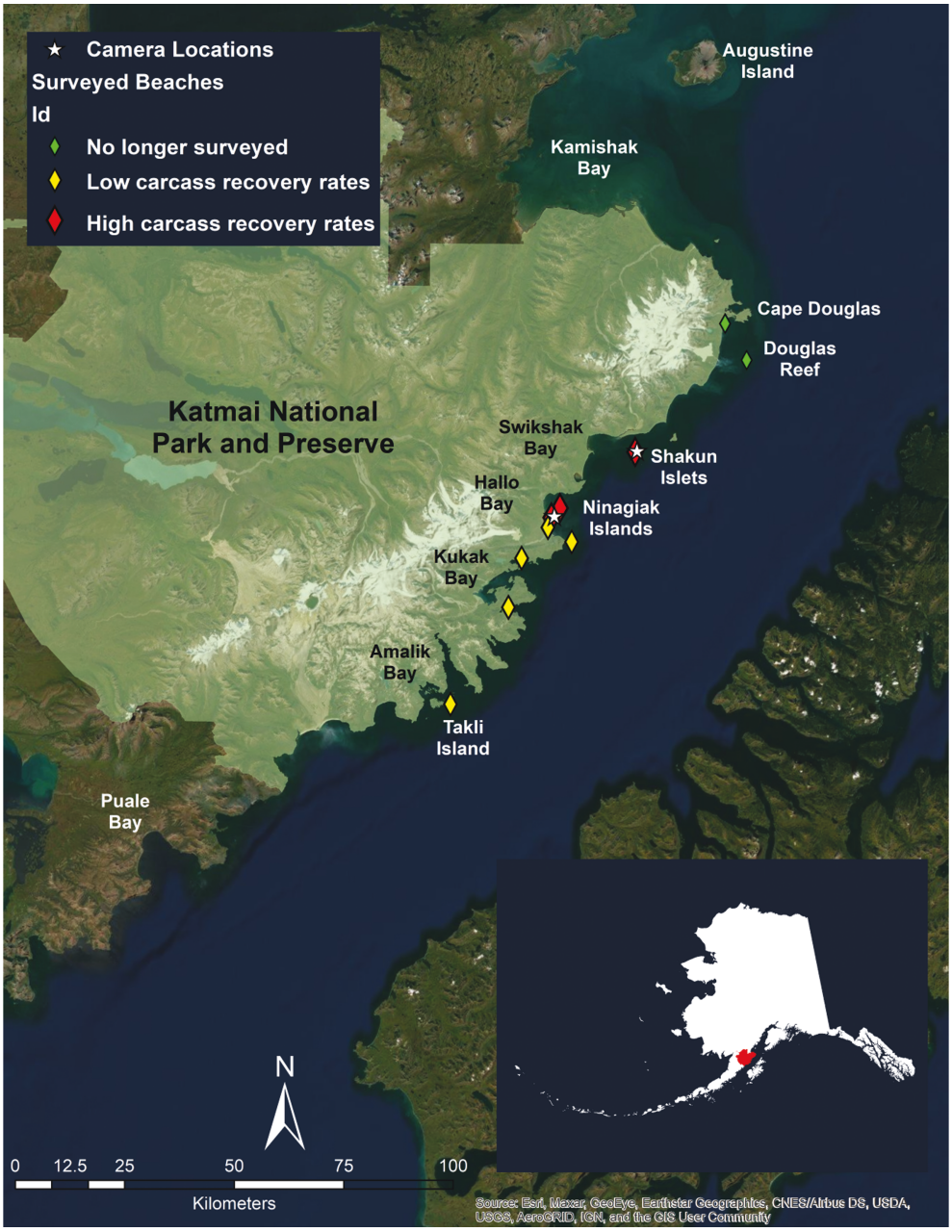



**Fig. 1.**—Locations of sea otter carcass surveys and marine mammal haulout sites where remote cameras were deployed in Katmai National Park and Preserve, Alaska.

Kenyon 1969; Flannery et al. 2021). By 2008, the Katmai sea otter population continued to grow and was estimated at ~7,000 animals, which likely approached carrying capacity (*K*; Coletti et al. 2016; Tinker et al. 2021). This assessment was based on several metrics including energy intake rates (kcal/min) derived from direct foraging observations and body condition derived from morphometric data collected during live captures (Monson and Bowen 2015). Since 2008, researchers have estimated 6,000–8,000 animals in the area, potentially peaking in 2012 (Coletti et al. 2016). Research suggests that energy intake rates have declined by about half and are now similar to intake rates from other sea otter populations considered at or near *K* (Coletti et al. 2016; Tinker et al. 2021).

Many long-lived mammals are characterized by variable survival rates among juvenile age classes (depending on population status), high survival among prime-age adults, and low survival among old-age classes. Furthermore, populations of long-lived mammals can experience density-dependent changes in age-specific survival rates as their populations near *K*. Juvenile survival typically exhibits the greatest change (i.e., relatively high rates below *K* and relatively low rates near *K*), prime-age adult survival remains high (especially for reproductive females), and old-age survival declines from low rates below *K* to even lower rates near *K* (Eberhardt 2002; Bonenfant et al. 2009). These age-specific survival patterns have been observed for terrestrial (Caughley 1966) and marine mammals (Barlow and Boveng

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1991), and sea otters are no exception (Kenyon 1969; Udevitz and Ballachey 1998; Monson et al. 2000a; Zagrebel'nyi 2004). Regardless of population status, the age-at-death distribution (AADD) of long-lived species is generally characterized by low percentages of prime-age animals. An AADD that includes a high percentage of prime-age animals is unusual for a long-lived mammal and suggests the population is subject to a source of age-independent mortality external to density-dependent mechanisms. This unusual pattern could be a conservation concern, as even small declines in prime-age female survival can negatively affect population dynamics (Tinker et al. 2006, 2016; Bodkin and Ballachey 2010).

"Prime-age" for sea otters ranges from 2 to 8 years old. These adult otters typically exhibit high survival rates and low proportions (~20%) of the AADD (Monson et al. 2000a). In 2006–2015, a study collected sea otter carcasses in Katmai and found that ~50% of the AADD was comprised of prime-age animals (Coletti et al. 2016). If the carcasses collected by Coletti et al. (2016) were representative of the dying population, then the abnormal death rate of prime-age otters in Katmai would be a management concern because the Katmai population is part of the Threatened Southwest Alaska stock (USFWS 2013). In 2005, the stock was protected under the auspices of the Endangered Species Act based on overall population declines of >90% since the early 1990s, in an area stretching from the western Aleutian Islands to the western end of the Alaska Peninsula (Estes et al. 1998, 2005, 2009; Doroff et al. 2003; Springer et al. 2003; Tinker et al. 2021). Understanding the factors that led to the AADD findings in Coletti et al. (2016) is of keen interest to researchers, managers, and conservation groups alike because results from the study suggest a decline in the Threatened sea otter stock in Southwest Alaska.

In this study, we explored the possibility that brown bears and other predators contribute to the high proportions of prime-age sea otters found dead in Coletti et al. (2016). When carcasses collection began in 2006, we assumed that terrestrial predators including brown bears rarely targeted sea otters as prey and mostly scavenged marine mammals opportunistically after they washed ashore. Most sea otter carcasses recovered at Katmai were found on islands that are both accessible to coastal predators including brown bears (Erlenbach 2020) with some also accessible to wolves, and include locations where sea otters and harbor seals (*Phoca vitulina*) often haul out. In addition to the high proportion of prime-age sea otter carcasses found at Katmai, a cache containing the remains of six recently killed harbor seals was found on one island during bear tagging operations in 2015 (Erlenbach 2020). We believe these seals were likely killed and cached by one bear, as it seems unlikely that this many seals would die of other causes at this location in such a short time. These seal mortalities, as well as observations of brown bears preying on sea otters on the Kamchatka Peninsula, Russia (Bednykh et al. 1986) and Kodiak Island, Alaska (Monson and DeGange 1995), suggested that brown bears may have hunted sea otters at haulout sites in Katmai, which in turn influenced the AADD found in Coletti et al. (2016). Implicit in this hypothesis is that predator-killed prime-age otters are overrepresented in the AADD because predated animals are more likely to be found than animals that die of other causes whose carcasses would be more widely dispersed.

Other predators are unlikely candidates for age-independent mortality at Katmai. Marine predators such as white sharks (*Carcharodon carcharias*; Tinker et al. 2016) and killer whales (*Orcinus orca*; Estes et al. 1998, 2004) do prey on sea otters but the former are rare in Alaska (Martin 2004) and the latter do not leave behind carcasses (Monson 2021). Bald eagles (*Haliaeetus leucocephalus*) also prey on sea otters, but take only small pups (Sherrod et al. 1975; Gelatt 1996). Gray wolves (*Canis lupus*) could be contributing to the inflated AADD of prime-age otters as they have been observed carrying dead sea otters along mainland beaches at Katmai (Griffin K., NPS, personal communication), and sea otters have been identified as a primary alternate prey for coastal wolves on at least one island in southeast Alaska (Roffler et al. 2021).

We conducted a preliminary field study to investigate sea otter predation by brown bears and wolves on Katmai islands and simulated the effects of an abnormal AADD on otter population dynamics. Our objectives included: (1) installing camera traps at sea otter and harbor seal haulout sites to collect direct evidence that brown bears, wolves, or other predators hunt otters and other marine mammals; and (2) developing a population model based on the sea otter AADD to estimate the rate of population decline that would occur if the AADD was representative of population-wide sea otter mortality.

## Materials and Methods

*Study area description.*—Katmai National Park and Preserve lies to the southwest of Cook Inlet along the Alaska Peninsula in southcentral Alaska (Fig. 1). The coastal section of the park is characterized by a rugged coast overlooked by a line of volcanic peaks. Numerous islands and rocky outcrops are scattered along the coast from immediately offshore (sometimes connected to the mainland at low tides) to more distant reefs and islands located up to 7 km from the mainland. Extensive intertidal mud flats occur at the outflow of major glacier-fed rivers that are habitat for razor clams that have long attracted foraging brown bears (Smith and Partridge 2004). Open exposed stretches of coast are rocky, with jagged outcrops and sea stacks formed by the stormy ocean conditions typical of Shelikof Strait in winter. Sea otters raft (i.e., resting in groups while floating on their back) and haul out at multiple locations along the coast, primarily on offshore islands and reefs.

We collected sea otter carcasses during fieldwork associated with the Gulf Watch Alaska monitoring program (https://gulfwatchalaska.org); thus, the carcasses described and analyzed in this study are the same as used in Coletti et al. (2016). Camera work was supported by Katmai National Park's Changing Tides Program (https://www.nps.gov/katm/learn/changing-tides.htm).

*Remote cameras.*—Our first goal was to photograph predator–marine mammal interactions on islands where some of the

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sea otter and harbor seal carcasses were collected. We installed motion-sensing/time-lapse cameras (PC900 – HyperFire Camera Trap, Reconyx Inc., Holmen, Wisconsin) at two haulout sites in Katmai: Shakun Island (outside of Swikshak Bay approximately 3.9 km offshore) and West Ninagiak Island (within Hallo Bay, approximately 2.4 km offshore; Figs. 1 and 2).

The physical characteristics of these two field sites differed. The Shakun site is an extensive rocky intertidal bench that may be entirely connected to the island at low tides but with many rocky outcrops (where sea otters and seals often haulout) that may be surrounded by shallow water at low to mid-tides and are completely covered at high tide (Fig. 3A). In contrast, the haulout site at West Ninagiak is a gradually sloping gravel beach with some rock outcrops at the top, where hauled out sea otters are never separated from the island and harbor seals were never seen hauling out. Neither haulout site is particularly unique nor are they the only haulout sites used by otters at Katmai.

Each camera was housed in a factory-built steel case with spikes welded to the face to prevent bears from destroying the camera. We mounted the camera, steel case, and an auxiliary power source (Duracell DURA 12-10F2, 12 Volt, 10 Ah AGM sealed battery) inside a second custom-built aluminum case supported by a tripod bolted into bedrock or large boulder (Fig. 3B). The cameras had the ability to record in low light but not total darkness. They also had an infrared-light source that allowed image capture at night, but the haulouts were located too far from the camera for it to be effective in complete darkness.

At each site, we used two cameras that had overlapping, but different views of the haulout site. The motion-sensing trigger was set to take pictures at any time during a 24-h day. Time-lapse images were scheduled at 1- or 2-min intervals beginning an hour before sunrise and ending an hour after sunset of the longest day within each recheck period. Memory storage capacity of the cameras was limited to ~105,000 images, so we set the time-lapse rate to the length of time between rechecks, so the camera would take the maximum number of images possible without running out of storage before the next check. That is, we used a rate of 60/h if recheck interval was short so that <105,000 images would be taken before the next recheck, or a rate of 30/h if recheck interval was longer and >105,000 images would have been taken at the 60/h rate before the next recheck. Most usable images came from the time-lapse mode because activity at the marine mammal haulouts was too far away to trigger the motion sensor. We left cameras in place year-round and visited the camera installations to replace memory cards and batteries.

We defined "potential bear-days" for each site as all days during which at least one camera operated, and we knew bears could be active. Potential bear-days began the first calendar day and ended the last calendar day; an image of a bear was collected by a camera on an island in any one season. Wolves are active year-round, so all days the cameras operated were a "potential wolf-day." In contrast, we defined predator-days (e.g., "bear-days" or "wolf-days") as specific days when a predator was documented by one or both cameras at a site. We defined a predator–otter or predator–seal interaction (e.g., "bear–otter interaction" or "bear–seal interaction") when a predator was documented as deliberately approaching animals that were hauled out and caused them to enter the water. We looked for evidence in photos of a confirmed kill, which included either identification of an otter or seal in the mouth of a predator or the predator staying on site for some time (generally >15 min) after its approach to the haulout with its head down and the appearance of eating. Additional evidence included eagles flocking to the kill site after a predator left the area (if the predator did not carry the carcass away), as well as eagles returning to the kill site for several days whenever the kill site was above the water line.

*Age-at-death distributions.*—Our second goal was to quantify the effect of elevated prime-age mortality of sea otters on the Katmai sea otter population if our AADD accurately reflected overall population survival rates. To do so, we carried out two objectives: (1) we compared the proportion of prime-age individuals in the Katmai AADD to those in other sea otter populations; and (2) we estimated the population growth rate based on the Katmai AADD (Table 1). We derived AADDs from ages of sea otters found dead along the Katmai coast during fieldwork conducted for the Gulf Watch Alaska monitoring program in late June to early July from 2006 to 2015. Ideally, we conduct carcass surveys in the spring before the growth of new beach grasses and other vegetation, which can hide sea otter remains (Monson et al. 2000a, 2011). Due to remoteness of the Katmai coast, however, most of our survey effort coincided with other Gulf Watch Alaska fieldwork during summer. We surveyed mainland beaches for carcasses starting in 2006 and began carcass collections on islands in 2007. Most years, survey efforts continued at the mainland beaches of Hallo Bay and opportunistically along the beaches just south of Cape Douglas. We found that carcass recovery rates (number of carcasses recovered per linear kilometers of beach searched) were much lower on mainland beaches compared to island beaches; as a result, after 2007 we modified our survey to focus on searching the beaches on the Shakun Islets off Swikshak Bay, the Ninagiak island complex within Hallo Bay, and a series of islands east of Takli Island off Amalik Bay (Fig. 1).

Carcass surveys involved one or more observers walking beaches, searching below and up to the strand line, which is the area of debris deposition from the previous winter. Because bears often drag sea otter and harbor seal carcasses off the beach, we also searched into the upland grasses above the strand line. Observers recorded the location of each carcass, its condition, and sex, if possible. Observers collected the skull if present, and removed a tooth (preferentially a premolar) for age analysis at Matson's Laboratory (Manhattan, Montana; Bodkin et al. 1997). Staff at Matson's Laboratory decalcified longitudinal sections of the tooth for cementum annuli readings, which provided age estimates ±1 year (Bodkin et al. 1997). Observers identified pups by open skull sutures and deciduous teeth (Nicholson et al. 2020). Observers also noted evidence of carcass consumption by predators (e.g., crushed skull and remains spread over a large

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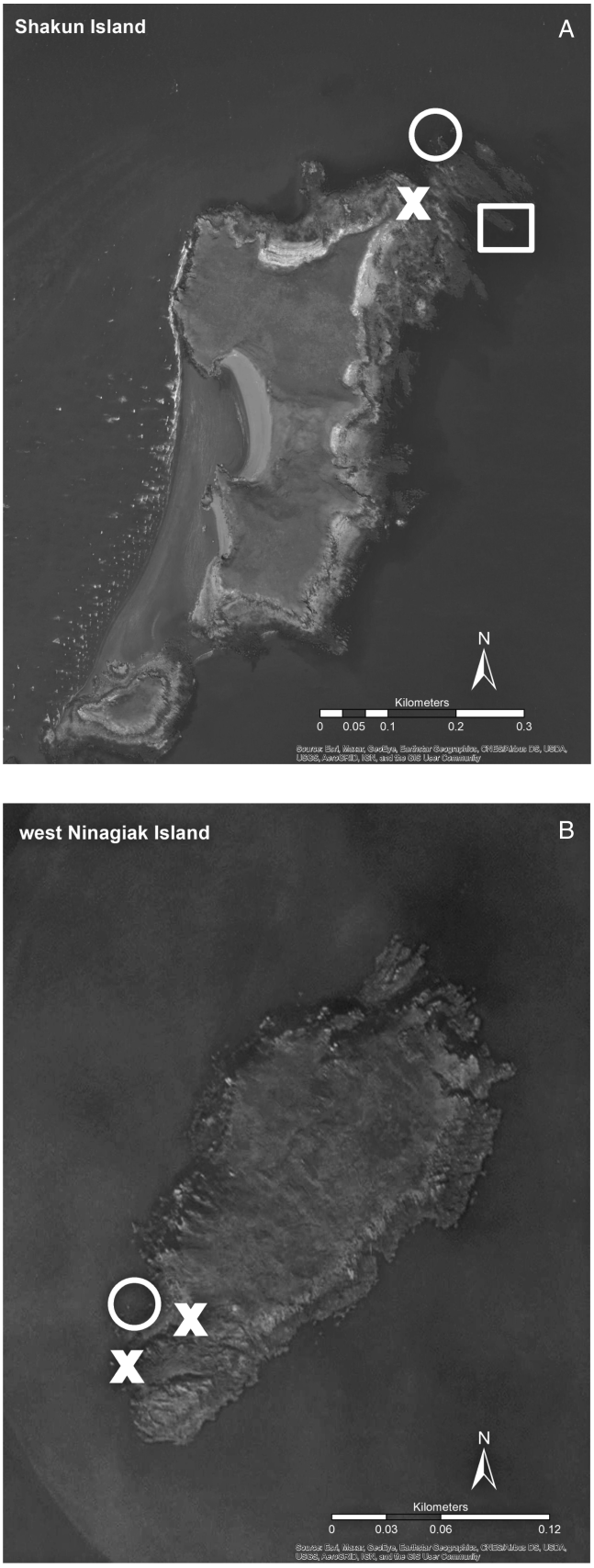



**Fig. 2.**—(A) Remote camera locations (X), sea otter haulout (circle), and the harbor seal haulout (rectangle) on Shakun Island in Katmai National Park and Preserve, Alaska, in 2016–2017. Cameras at Shakun were located ~50 m apart but installed with one focused on the sea otter haulout and the other focused on the harbor seal haulout. (B) Remote camera locations (X) and sea otter haulouts (circle) on West Ninagiak Island along the coast of Katmai National Park and Preserve, Alaska, in 2016–2017. Cameras at West Ninagiak were ~100 m apart but both focused on the same sea otter haulout location.

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**Fig. 3.**—(A) A brown bear with a recently killed sea otter taken at the Shukun sea otter haulout site in Katmai National Park and Preserve, Alaska, in 2016. The reef at the far left (enclosed in oval) is the primary sea otter haulout location where most bear–sea otter interactions were photographed. (B) Custom-built aluminum case and tripod mount for trail cameras set up to photograph animals at each marine mammal haulout site.




Fig. 3.—Continued

area), although there was no way to know definitively if consumption was related to scavenging or predation or whether it was done by bears or wolves. Bald eagles also scavenge marine mammal carcasses but tend to leave mainly intact skeletal remains on the beach largely devoid of soft tissue and the skinned out hide turned inside out often still attached at the nose and tail. Data from these carcass surveys are publicly available in Kloecker and Monson (2020).

For our first objective, we compared the proportions of carcasses in young (0–1 years old), prime-age (2–8 years old), and old (9+ years old) age classes in the Katmai collection to those in collections from western Prince William Sound (WPWS), during two periods when that population was considered near *K*: 1976–1989 (before the *Exxon Valdez* oil spill), and 2010–2015, after the population was considered recovered from the spill (Monson et al. 2000a, 2011; Ballachey et al. 2014). We defined "prime-age" for sea otters as ages 2–8 years old when they typically have high survival rates (Monson et al. 2000a, 2000b), although we recognized there are other ways to define "prime-age" based on reproductive maturity and senescence (Bodkin et al. 2000). We used a product multinomial likelihood ratio test (LRT; Agresti 2013) to test for differences between proportions in the two WPWS samples, and then between pooled data from WPWS and Katmai. These comparisons assume proportions in the three age groups are stable over time and a random sample of the true population AADDs, or at least that the bias is the same among populations. The KATM data in the form of the three age classes did not exhibit changes over years (two-tailed Fisher's exact test, $P = 0.25$; Agresti 2013). Although carcass collections are usually biased for young of the year (age 0; Kenyon 1969; Van Sickle et al. 1987) because their remains are more difficult to recover due to their small size, there is no reason to expect that this bias differs among otter populations.

For our second objective, we estimated the population growth rate by combining the Katmai AADD with reproductive rate estimates, relying on assumptions required for a female-only model with a stable age structure (Van Sickle et al. 1987). Because sex in our carcass collections was indiscernible, we assumed observed AADDs were representative of female AADDs. While male otters tend to have a shorter life expectancy than female otters, both sexes have generally high prime-age survival and similar AADDs (Zagrebel'nyi 2004). We also assumed a maximum age of 16, as only one individual was older than 16 in any of the 9 years of Katmai carcass collections. The KATM age structure (individual year classes 1–16) did not change over time (two-tailed Fisher's exact test, $P = 0.26$). This allowed us to pool all years into a single age structure and assume stability. Since pups <1 year old are underrepresented, we used an estimate of first-year survivorship (the probability at birth of surviving to age 1) in place of a category for animals <1 year old in the AADD (Van Sickle et al. 1987).

Although reproductive rate estimates are not available for the Katmai population, reproductive rates differ little among sea otter populations regardless of status relative to food availability (Jameson and Johnson 1993; Monson et al. 2000b). Reproductive rates of 2- to 3-year-old females ranged from 0.32 to 0.37 (male and female) pups per year (pooled average of 0.34), and reproductive rates for females ≥4 years ranged from 0.75 to 0.82 pups per year (pooled average of 0.81) among

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**Table 1.**—Age-at-death distributions (AADDs) based on sea otter carcasses recovered during beach surveys in Katmai National Park and Preserve, Alaska, in 2006–2015, and in western Prince William Sound (WPWS) before (1974–1989) and after the recovery (2010–2015) of sea otters from the *Exxon Valdez* oil spill. The bottom three rows denote the proportion of sea otters recorded in each age class: juveniles (0–1 years), prime-age (2–8 years), and old-age (≥9 years). [a]We did not include age 0 in our Katmai population model because of low recovery rates of pups on beaches due to scavengers.

| | Number of sea otter carcasses by survey year | | | | | | | | | | WPWS | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age | 2006 | 2007 | 2008 | 2009 | 2010 | 2012 | 2013 | 2014 | 2015 | Total | 1974–1989 | 2010–2015 |
| 0[a] | 2 | 0 | 3 | 2 | 1 | 0 | 8 | 10 | 3 | 29 | 85 | 91 |
| 1 | 9 | 5 | 4 | 0 | 3 | 2 | 5 | 4 | 4 | 36 | 13 | 33 |
| 2 | 6 | 2 | 2 | 0 | 0 | 1 | 3 | 1 | 1 | 16 | 2 | 7 |
| 3 | 7 | 3 | 1 | 1 | 1 | 2 | 5 | 2 | 1 | 23 | 5 | 7 |
| 4 | 1 | 1 | 0 | 1 | 2 | 2 | 3 | 2 | 1 | 13 | 7 | 5 |
| 5 | 2 | 2 | 2 | 2 | 3 | 3 | 6 | 3 | 0 | 23 | 4 | 11 |
| 6 | 0 | 5 | 4 | 4 | 2 | 3 | 5 | 2 | 0 | 25 | 2 | 5 |
| 7 | 0 | 4 | 4 | 2 | 3 | 2 | 3 | 3 | 0 | 21 | 11 | 7 |
| 8 | 3 | 4 | 2 | 4 | 1 | 0 | 6 | 3 | 3 | 26 | 11 | 11 |
| 9 | 2 | 1 | 6 | 0 | 3 | 0 | 8 | 4 | 2 | 26 | 13 | 24 |
| 10 | 0 | 2 | 0 | 2 | 1 | 1 | 3 | 3 | 2 | 14 | 18 | 17 |
| 11 | 2 | 3 | 0 | 0 | 4 | 3 | 4 | 2 | 2 | 20 | 14 | 11 |
| 12 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 8 | 6 | 16 |
| 13 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 7 | 7 | 7 |
| 14 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 4 | 5 | 5 |
| 15 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 4 | 3 |
| 16 | 0 | 3 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 7 | 3 | 2 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 |
| Annual total | 36 | 39 | 30 | 21 | 27 | 23 | 63 | 43 | 20 | 302 | 215 | 263 |
| Juvenile | 0.30 | 0.13 | 0.23 | 0.09 | 0.15 | 0.09 | 0.21 | 0.33 | 0.35 | 0.21 | 0.46 | 0.47 |
| Prime-age | 0.53 | 0.54 | 0.50 | 0.67 | 0.44 | 0.56 | 0.49 | 0.37 | 0.30 | 0.49 | 0.20 | 0.20 |
| Old-age | 0.17 | 0.33 | 0.27 | 0.24 | 0.41 | 0.35 | 0.30 | 0.30 | 0.35 | 0.30 | 0.35 | 0.33 |

three separate Alaskan sea otter populations that varied in status from well below to near *K* (Bodkin et al. 1993; Monson and DeGange 1995; Monson et al. 2000b). Our LRTs confirmed no difference among the three populations (2- to 3-year-olds: test statistic = 0.26, d.f. = 2, $P = 0.88$; and ≥4-year-olds: test statistic = 0.64, d.f. = 2, $P = 0.73$), so we employed the age-specific reproductive rates of 0.34 (95% CI: 0.24, 0.43) and 0.81 (95% CI: 0.76, 0.86) in our AADD-based estimation of population growth rate. We assumed a 50:50 sex ratio at birth.

We estimated first-year survivorship by multiplying preweaning and postweaning pup survival rates. Like reproductive rates, we must apply pre- and postweaning survival rates from the literature. A preweaning pup survival rate of 0.47 (95% CI: 0.33, 0.61) appears typical of a sea otter population near *K* (Monson et al. 2000b); however, Monnett and Rotterman (2000) suggest a possibly higher preweaning survival rate in a study of a sea otter population near *K* in eastern Prince William Sound (0.63, 95% CI: 0.53, 0.73, LRT-based test statistic = 3.32, d.f. = 1, $P = 0.07$); thus, we did not pool these data. We estimated population growth rate separately for each estimate of preweaning pup survival and took the geometric mean of the growth rate estimates. We accounted for uncertainty in this procedure in our bootstrapping (see below.) We used a postweaning survival rate of 0.76 (95% CI: 0.63, 0.90) based on survival to 6 months postweaning in Prince William Sound, Alaska (Ballachey et al. 2003).

We estimated population growth rate by solving the equation $a_n\lambda^n + a_{n-1}\lambda^{n-1} + \ldots + a_1\lambda + a_0 = 0$ (Van Sickle et al. 1987) for population growth rate ($\lambda$), where the coefficients, $a$, are defined in terms of the AADD ($f$), the reproductive rate schedule ($m$), pup survivorship ($l_1$), and the maximum age ($n$). In particular, $a_n = f_n$, $a_i = f_i - l_1 \sum_{k=i+1}^{n} f_k m_{k-i}$, $i = 1, 2, \ldots, n-1$, and $a_0 = -l_1 \sum_{k=1}^{n} f_k m_k$.

We estimated confidence intervals on $\lambda$ and $\lambda^{10}$ (population growth rate for the duration of the carcass collections) by parametric bootstrapping of the above process. We assumed the AADD was multinomially distributed and the following were binomially distributed based on estimated rates and sample sizes from previous studies: number of pups born to 2- to 3-year-old females (33 of 97) and number of pups born to ≥4-year-old females (173 of 214; both pooled across studies as noted above from Bodkin et al. 1993, Monson and DeGange 1995, Monson et al. 2000b), number of pups surviving to weaning (24 of 51, Monson et al. 2000b or 59 of 94, Monnett and Rotterman 2000, not pooled, as noted above) and number of pups surviving postweaning (29 of 38, Ballachey et al. 2003). These distributions account for uncertainty without an additional error term because binomial and multinomial variances are completely determined by sample size and outcome frequencies. In each bootstrap sample, we drew randomly from each distribution, and decided randomly from which of the two preweaning pup survival distributions to retain the value. We constructed 10,000 bootstrap samples and obtained the 95% CI by ordering the resulting estimates and extracting the 250th and 9,750th values. We obtained the probability the population was decreasing as the proportion of population growth rate estimates <1 and the

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probability the population was increasing or stationary as the proportion of population growth rate estimates ≥1.

We estimated "excess deaths" within the prime-age class based on the logic that we would not have found these animals had they not been killed by bears or other predators. That is, we determined how many prime-age animals would need to be removed from the collections to make the proportion prime-age ~0.20, which is typical of other sea otter populations. This is a minimum estimate of predator-related mortalities as bears and other predators would also take animals from the young and old-age classes; however, it gives a reasonable estimate of the magnitude of animals likely taken by predators. To accomplish this we solved for excess deaths ($x$) in the equation $(147 - x)/(65 + (147 - x) + 90) = 0.2$, where 65, 147, and 90 are the original numbers of young, prime-age, and old animals in the AADD, respectively (Table 1).

## Results

*Remote cameras.*—We first deployed cameras in March 2016 at the Shakun and West Ninagiak sites before bears emerged from winter dens, and at least one camera at the West Ninagiak site continued to function after bears left for hibernation the following fall. We first recorded a bear at an island site on 27 April 2016, and the last day a bear was documented at a site was 19 October 2016. As a result, we knew bears could be active during this time, and the 175 days that included these dates were considered potential bears days in both 2016 and 2017 when bears could swim to an island (Fig. 4). We did not document any wolf activity at either site at any time during this study, so we do not consider potential wolf-days further except to acknowledge that wolves are still potential predators on the mainland and some close-to-shore islands and reefs where we did not deploy cameras.

At the Shakun site, at least one camera operated for 275 days from 21 March 2016, to 14 August 2017 (190 days in 2016, 85 days in 2017; Fig. 4), during which time we obtained 661,828 images (Table 2). Cameras operated for 231 potential bear-days (147 days in 2016, 84 days in 2017), and we documented bear presence on 31 of these days (21% of potential days). We examined sea otter-specific haulout patterns from a subset of 103 days (21 March 2016 to 1 June 2016; 21 May 2017 to 20 June 2017) and found they hauled out on all but five of these days (95% of potential bear-days). During this 103-day period, we observed otters hauled out, on average, for 6:20 h ± 3:52 (max = 16:40 h), split between a morning and evening low tide period.

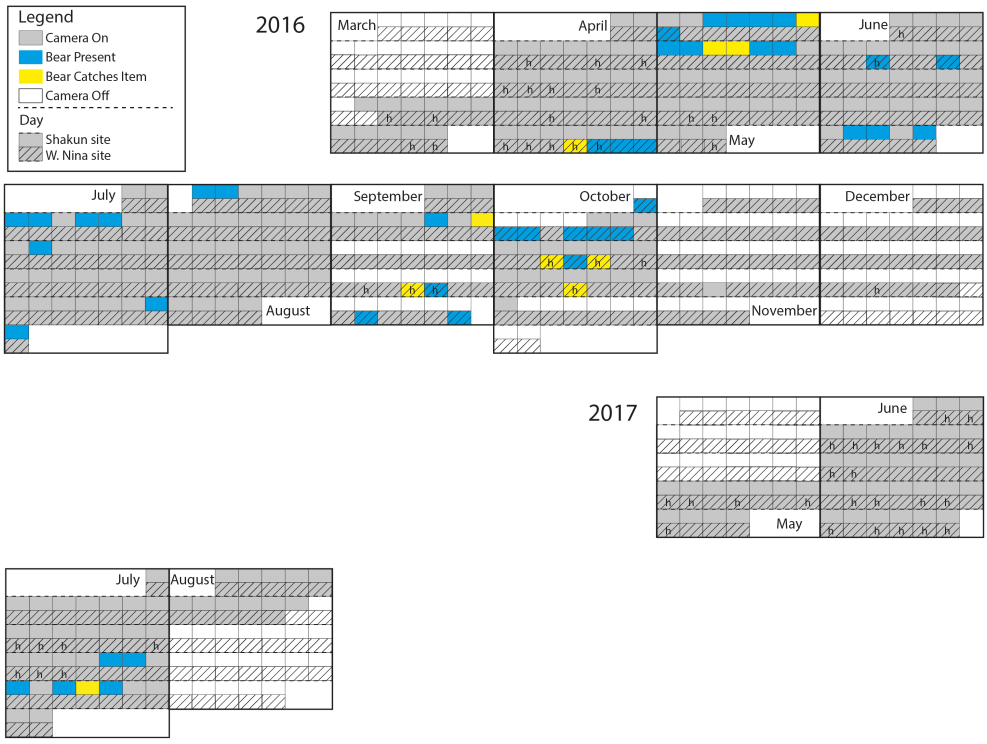



**Fig. 4.**—Schedule of remote camera operations at two marine mammal haulout sites along the coast of Katmai National Park and Preserve, Alaska from 2016 to 2017. The upper half of each calendar day (no cross hatching) represents camera operations at the Shakun Island site while the lower half of each calendar day (cross hatching) represents camera operations at the West Ninagiak Island site. Color of each calendar day by site (upper and lower halves) represents the camera operational condition (white = cameras off, gray = cameras operational) and bear activity (blue = bear present at the site sometime during that calendar day, yellow = evidence of a bear predation event at the site during that calendar day). The green arrow denotes the first day of the year a bear was documented on an island and the red arrow denotes the last day a bear was documented. All days in between these dates are "potential bear-days" unless no camera is operational at the site. Sea otters and/or harbor seals were observed hauled on all camera operational days at the Shakun site. Only sea otters were seen hauled out at the West Ninagiak site, and only on the days denoted by an "h."

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**Table 2.**—Details of remote cameras operating at two marine mammal haulout sites (two cameras per site) along the Katmai coast, Alaska, in 2016 and 2017. Potential bear-days were defined as days when cameras were operational and include only days between the first and last day a bear was documented on an island (27 April to 19 October). Numbers in parentheses denote the number of potential bear-days when sea otters (seot) and/or harbor seals (hase) were hauled out. Bear-days are days a bear was recorded by either camera at a site. Interactions indicate incidents where bears deliberately approached hauled out animals and caused them to enter the water. [a]Camera in motion-sensing mode only - did not take time-lapse images.

| Site | Cam. # | Start date | End date | Photo rate (#/h) | Total photos | Pot. bear-days | Bear-days | Interactions | Pred. events |
|---|---|---|---|---|---|---|---|---|---|
| Shakun | 1 | 21MAR16 | 23MAY16 | 60/h | 74,684 | 26 (26) | 11 | 7 seot | 3 |
| Shakun | 1 | 24MAY16 | 30JUN16 | 30/h | 28,651 | 37 (37) | 3 | 2 seot | 0 |
| Shakun | 1 | 1JUL16 | 10SEP16 | 60/h | 103,376 | 71 (71) | 11 | 5 seot | 1 |
| Shakun | 1 | 6OCT16 | 23OCT16 | 60/h | 24,771 | 13 (13) | 0 | 0 | 0 |
| Shakun | 1 | 21MAY17 | 20JUN17 | 60/h | 41,703 | 30 (30) | 0 | 0 | 0 |
| Shakun | 1 | 21JUN17 | 14AUG17 | 60/h | 66,903 | 54 (54) | 6 | 3 seot, 2 hase | 0 |
| Shakun | 2 | 21MAR16 | 23MAY16 | 60/h | 74,269 | 26 (26) | 11 | 5 hase | 0 |
| Shakun | 2 | 24MAY16 | 30JUN16 | 0/h[a] | 0 | 37 (37) | na | na | na |
| Shakun | 2 | 1JUL16 | 10SEP16 | 60/h | 105,890 | 71 (71) | 11 | 2 hase | 0 |
| Shakun | 2 | 6OCT16 | 23OCT16 | 60/h | 38,767 | 13 (13) | 0 | 0 | 0 |
| Shakun | 2 | 21MAY17 | 20JUN17 | 60/h | 39,684 | 30 (30) | 0 | 0 | 0 |
| Shakun | 2 | 21JUN17 | 11AUG17 | 60/h | 63,130 | 51 (51) | 6 | 3 hase | 1 |
| W. Nina. | 1 | 22MAR16 | 23MAY16 | 0/h[a] | 90 | 26 (3) | 5 | na | na |
| W. Nina. | 1 | 24MAY16 | 7JUL16 | 30/h | 32,229 | 44 (2) | 2 | 0 | 0 |
| W. Nina. | 1 | 8JUL16 | 24AUG16 | 60/h | 68,372 | 47 (0) | 8 | 0 | 0 |
| W. Nina. | 1 | 6OCT16 | 23DEC16 | 60/h | 77,958 | 13 (4) | 6 | 1 seot | 1 |
| W. Nina. | 1 | 21MAY17 | 28JUN17 | 60/h | 48,976 | 38 (22) | 0 | 0 | 0 |
| W. Nina. | 1 | 29JUN17 | 20JUL17 | 60/h | 26,202 | 21 (5) | 0 | 0 | 0 |
| W. Nina. | 2 | 22MAR16 | 23MAY16 | 60/h | 72,500 | 26 (3) | 5 | 1 seot | 1 |
| W. Nina. | 2 | 24MAY16 | 7JUL16 | 30/h | 32,186 | 44 (2) | 2 | 0 | 0 |
| W. Nina. | 2 | 8JUL16 | 5OCT16 | 30/h | 64,514 | 89 (3) | 8 | 1 seot | 1 |
| W. Nina. | 2 | 6OCT16 | 16NOV16 | 60/h | 40,825 | 13 (4) | 6 | 2 seot | 2 |
| W. Nina. | 2 | 21MAY17 | 28JUN17 | 60/h | 48,996 | 38 (22) | 0 | 0 | 0 |
| W. Nina. | 2 | 29JUN17 | 10AUG17 | 60/h | 53,434 | 42 (8) | 0 | 0 | 0 |

The average number of visibly hauled out otters in images each day was 7 ± 9.7 (mean daily maximum = 13 ± 14.5) with the maximum number >100. We documented hauled out seals and sea otters on all 31 days bears were present, and on these days, we documented 17 bear–otter interactions and 12 bear–seal interactions (29 bear–marine mammal interactions) and five predation events (four on sea otters and one on a harbor seal; Table 2, Figs. 3A and 4).

At the West Ninagiak site, at least one camera operated for 357 days from 22 March 2016, to 10 August 2017 (276 days in 2016, 80 days in 2017; Fig. 4), during which time we obtained 566,282 images (Table 2). Cameras operated on 252 potential bear-days (172 days in 2016, 80 in 2017). Only sea otters used this site, and in 2016, sea otters hauled out on 16 of 35 days (46%) before bear activity began, but on only 14 of the 172 potential bear-days (8%) when bears were active (Fig. 4). In 2017, we documented hauled out otters on 31 potential bear-days (39%), including during June and July, which were months with very few haulout events in 2016 (Fig. 4). During the days when sea otters were hauled out, they hauled out, on average, for 5:00 h ± 5:22; (max = 22:10 h) split between a morning and evening low tide period. The average number of visibly hauled out otters was 11 ± 19.9 (mean daily maximum = 20 ± 37.4) with the maximum >120. Bears were present on 21 (12%) of potential bear-days in 2016, but we did not document any bears at the West Ninagiak site 2017. Otters hauled out on only eight (38%) of the days when bears were present. When both bears and otters were present, we documented five bear–otter interactions, all of which resulted in predation events (Table 2).

We could not identify individual bears at either site; however, most sightings were single animals that appeared in photos for 3–10 consecutive days once they appeared (Fig. 4). We documented a female with two 2-year-old cubs on West Ninagiak in the spring of 2016, which was likely a female with yearling cubs that had been collared and tracked the previous summer, when 23% (1,472/6,318) of her locations were on islands (Erlenbach 2020).

*Age-at-death distributions.*—Age-at-death distributions in WPWS did not differ before and after the oil spill (test statistic = 0.25, d.f. = 2, $P = 0.88$; Table 1); thus, we pooled them to compare to the Katmai AADD. We found that the pooled WPWS AADDs were different than Katmai's (test statistic = 48.88, d.f. = 2, $P < 1e\text{-}10$; Table 1). We estimated predator-related mortality (i.e., $x$ = excess deaths in the carcass collections) was a minimum of 108 prime-age animals (74% of the 147 in the prime-age class; Table 1), assuming none of the juvenile or old-age animals were killed by bears or other predators, which is unlikely. For example, if we assume 25% of the animals in young and old-age classes were also excess deaths, then we would have to remove another 10 from the prime-age class for a total of 157 predator-related deaths (16 young + 118 prime-age + 23 old-age). If we assumed our carcass collections (Table 1) represented the true Katmai AADD (Table 1), the estimated annual population growth rate was 0.92 (95% CI: 0.71, 1.03). A population declining at that rate for the decade encompassing the carcass collections would be 0.42 (95% CI: 0.03, 1.37) the size of the population when carcass collections began. Eighty-nine percent of simulated

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populations were declining, and 11% were stationary or increasing.

## Discussion

We investigated the potential reasons the AADD documented by Coletti et al. (2016) consistently included ~50% prime-age animals over the decade spanning 2006–2015. We hypothesized brown bears may be disproportionately influencing our AADDs and evidence from our island-based camera traps supported this idea. Over a period of two summers, we gathered photo evidence of brown bears making 22 attempts to prey on sea otters of which nine (41%) were successful. If our Katmai carcass collections had been representative of the population's AADD, our population model suggested prime-age sea otter survival at Katmai would have been lower than most other sea otter populations where survival has been assessed (Kenyon 1969; Udevitz and Ballachey 1998; Monson et al. 2000b; Zagrebel'nyi 2004; Tinker et al. 2006) and the population should have experienced an almost 60% decline from 2006 to 2015. Contrary to these model predictions, aerial population surveys indicate that the sea otter population at Katmai was stationary or growing until at least 2012 when it may have peaked and then declined modestly (Coletti et al. 2016).

The mismatch between the AADD-predicted and survey-based population trends suggests that the carcass collections were biased toward a mortality source linked to the islands where we collected most of the carcasses. Sea otters regularly haul out on these islands and thus are exposed to predation, and our two camera sites documented bears (but not wolves) actively hunting sea otters and harbor seals. Brown bears are capable of killing animals much larger than sea otters and likely kill otters regardless of size and age. We therefore hypothesize that: (1) many carcasses we discovered on Katmai's offshore islands were there because they were killed by bears; (2) predation-related mortality reflects the age structure of the animals that were present on these islands; and (3) the observed AADD was biased toward predator-killed mortalities because density-dependent nonpredation-related mortalities were underrepresented as the carcasses of animals that die of other causes are much more widely dispersed.

Other nonpredation-related mortality factors are not viable explanations for the high proportion of prime-age carcasses in our collections because, unlike predation, factors such as disease, contaminants, and harmful algal blooms (HABs) should not cause a biased sample of the dying population to land on island beaches. In addition, our Gulf Watch program found no major contamination in mussels sampled along the Katmai coast (Rider et al. 2020), and living sea otters in this area showed no indication of health issues such as disease or high contaminate loads (Estes et al. 2010; Tinker et al. 2021). Oil from the 1989 *Exxon Valdez* oil spill did land on Katmai beaches (Irvine et al. 1999, 2006); however, remaining oil at Katmai would not have a larger or longer lasting effect than in Prince William Sound, which was much more heavily oiled yet was beginning to recover by 2006 (Ballachey et al. 2014). Finally, sea otters are capable of detecting and avoiding clams laden with paralytic shellfish poisoning, one of the most prevalent HABs in this area (Kvitek et al. 1991; Kvitek and Bretz 2004), and we have no evidence to suggest algal toxins were more prevalent at Katmai than other locations where sea otters also feed primarily on clams and have growing or stationary populations.

It is possible that the sea otter population at Katmai peaked in 2012 and declined modestly after reaching carrying capacity, as noted by Coletti et al. (2016), based on both the aerial population size survey data and information on energy intake rates. As a result of this process, the population's AADD may have shifted through time. An example of this occurred on Bering Island, Russia, which is a relatively closed population that appeared to reach or surpass $K$ and peak in 1990, after which it declined by 41% in a single year and then equilibrated (Bodkin et al. 2000). In the winter of 1990–1991, Bodkin et al. (2000) observed a massive mortality pulse dominated by males (81% of 742 carcasses collected), of which 75% were adults aged 4–10 years old. Females comprised only 19% of the total mortalities, and only 26% of these were adults. Following this event, the carcass collections displayed an AADD more typical of otter populations: the proportion of adults (4–10) dropped to an average of ~24% for both males and females, whereas old-age classes again predominated, averaging ~50% and ~56% for males and females, respectively (Fig. 4 from Zagrebel'nyi 2004).

If the driver of our unusual sea otter AADD at Katmai was simply the population reaching $K$, we could predict a sequence of changes in the AADD similar to what was observed by Bodkin et al. (2000). Prior to 2012, when the Katmai population was still growing and approaching $K$, juvenile and prime-age classes should have constituted the smallest fractions of the AADD, with older age classes dominating. Around 2012, we might expect an increase in prime-age mortality, but over time see the proportion of juveniles and old animals again dominating the AADD (Kenyon 1969; Eberhardt 2002), with prime-age animals constituting perhaps 20–25% of the AADD (Monson et al. 2000a, 2011; Zagrebel'nyi 2004). Contrary to this expected pattern, we found AADDs consistently comprised of ~50% prime-age otters for more than a decade (Table 1).

It appears that some brown bears at Katmai prey on sea otters. With the assumption that predators killed only prime-age animals, we calculated ~110 sea otter carcasses recovered at Katmai from 2006 to 2015 were excess deaths due to predation by bears and other carnivores. This is simply the number of prime-age animals that would need to be removed from the carcass collection to obtain 20% prime-age in the AADD, which is typical of other sea otter populations. If we make the more reasonable assumption that some young and old animals are also depredated, our calculations of excess deaths suggest half or more of the ~300 carcasses we collected from 2006 to 2015 may be predation-related. Furthermore, it is highly unlikely we recovered all available carcasses because (1) bears and other carnivores often drag carcasses off the beach where they are difficult to find, and because (2) we conducted carcass surveys in summer instead of spring, when remains of many otters could

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be hidden in beach or island vegetation. As a result, the total number of otters to be found, and thus the total number killed by bears and other carnivores, would have been even higher than the ~110–150 reported here. However, deaths due to predation appear to be overrepresented in the carcass collections and aerial survey data do not support the precipitous decline suggested by the AADD; therefore, we believe terrestrial carnivore predation has little influence on the overall population dynamics of the living Katmai sea otter population.

Sea otters may learn to avoid haulouts frequented by bears and other predators. It is plausible that sea otters are regularly frightened off the haulout by approaching predators and learn to avoid haulout locations targeted by bears and other carnivores; if true, this would be an excellent example of a nonconsumptive predator effect (Brown et al. 1999; Frid et al. 2007; Willems and Hill 2009; Atkins et al. 2019; Srinivasan 2019). Sea otters may avoid otherwise desirable habitat simply because they perceive risk of predator attack in that habitat (Wirsing et al. 2007, 2008; De Vos et al. 2015). It is likely that sea otters and other marine mammals rarely haul out on mainland locations along the Katmai coast where bears and other predators such as wolves are more abundant because they have learned about the potential lethal risk of doing so. This may also explain why otters hauled out less often at the West Ninagiak site when bears are active (<10% of bear-days) compared to days when bears were not as active (over 40% of potential bear-days when bears were not seen) because the beach geomorphology of this site is similar to mainland beaches. On the other hand, sea otters at the Shakun site, which has a geomorphology more typical of less predator-accessible reefs, showed no avoidance to hauling out when bear activity was consistently high. Harbor seals, which tend to be much more attentive and responsive to the presence of terrestrial activity than sea otters, never hauled out at the mainland-type beach at West Ninagiak but hauled out daily at the reef-type Shakun site.

We concluded that the carcass collections on the Katmai coast did not represent population-level mortality rates based on the mismatch between the AADD-predicted and survey-based population trends. We documented brown bears actively hunting sea otters and harbor seals on islands at Katmai and estimated ~⅓ to ½ of the ~300 carcasses we collected over 10 years were depredated by bears and other predators and this depredation was not age-specific. This resulted in predator-killed sea otters being overrepresented in the carcass collections. This work demonstrates that even with a biased carcass collection, utilizing and interpreting multiple data sets allowed us to identify an otherwise cryptic interaction between sea otters and coastal carnivores. Future studies at Katmai and other areas where terrestrial carnivores and sea otters coexist should continue to assess predator–otter interactions to quantify the effect that predators may have on the sea otter population and the importance of sea otters and other marine mammals to the terrestrial carnivores that prey on them. Furthermore, we suggest examining the extent of nearshore community effects, both direct and indirect, that arise from the linkage between these terrestrial and nearshore marine predators.

## Acknowledgments

Funding for this research was provided by the Exxon Valdez Oil spill Trustee Council (project number 16120114-R from 2012-2017) through the Gulf Watch Alaska program. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. The National Park Service (NPS) and the US Geological Survey Alaska Science Center also supported this work in part through the NPS Changing Tides project. We greatly appreciate the support of Brenda Ballachey, Dan Esler, Kelsey Griffin, Brian Robinson, Carissa Turner, James Walton, Benjamin Weitzman, Dave Gustine, Troy Cambier, Buck Mangipane, Lindsey Mangipane, and numerous others who have assisted on Gulf Watch Alaska field trips over the years as well as the exceptional cooperation by the NPS staff of Katmai National Park and Preserve and the Southwest Alaska Network. We thank Courtney Amundson for her thoughtful comments on an earlier draft of this manuscript, and two anonymous reviewers for additional comments. This manuscript has been approved for publication consistent with USGS Fundamental Science Practices (http://pubs.usgs.gov/circ/1367/). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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