Aquatic Mammals 2010, *36*(2), 129-137, DOI 10.1578/AM.36.2.2010.129

Observation of Steller Sea Lion (*Eumetopias jubatus*) Predation on a Harbor Seal (*Phoca vitulina richardii*) in the Glacier Bay Region of Southeastern Alaska

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Abstract

Pinnipeds prey primarily on fish and invertebrates; however, several species are known to prey upon other pinniped species. Herein, we document an observation of a Steller sea lion (*Eumetopias jubatus*) attacking and partially consuming a juvenile harbor seal (*Phoca vitulina richardii*) in Johns Hopkins Inlet in Glacier Bay National Park, Alaska. Population trends for Steller sea lions and harbor seals contrast dramatically in the Glacier Bay region. Although other marine predators are known to attack harbor seals, it is possible that Steller sea lions could potentially have both a direct and indirect influence on harbor seals in the Glacier Bay region.

Key Words: Steller sea lion, *Eumetopias jubatus*, harbor seal, *Phoca vitulina richardii*, pinniped, predation, feeding, Glacier Bay National Park, southeastern Alaska

Introduction

Predation may have direct and indirect effects on prey populations and can influence the distribution, abundance, and evolution of a species (Polis et al., 1989). Interspecific predation occurs in many foraging guilds (Burger, 1979; Creel & Creel, 1996); however, the ultimate mechanisms may vary and may be a result of competition for space or food, overt aggression, or predation as a source of food. Interspecific killing among mammalian carnivores is relatively common and may account for a substantial proportion of known mortalities in some species (Palomares & Caro, 1999).

Although pinnipeds prey primarily on fish and invertebrates, several species, including southern sea lions (*Otaria byronia*) (Majluf, 1987; Harcourt, 1993), New Zealand sea lions (*Phocarctos hookeri*) (Bradshaw et al., 1998; Robinson et al., 1999), leopard seals (*Hydrurga leptonyx*) (Siniff & Bengtson, 1977; Shaughnessy & Goldsworthy, 1990; Boveng et al., 1998; Walker et al. 1998; Hiruki et al., 1999), walrus (*Odobenus rosmarus*) (Fay, 1960; Lowry & Fay, 1984; Fay et al., 1990), and Steller sea lions (*Eumetopias jubatus*) (Gentry & Johnson, 1981; Pitcher & Fay, 1982; Byrnes & Hood, 1994; Calkins, 1998; Mathews & Pendleton, 2006) are known to prey upon other pinniped species. Naïve pups or smaller individuals are often targeted; and in some cases, interspecific predation by pinnipeds may limit population growth of other pinniped species (Boveng et al., 1998).

Although it can be difficult to quantify predator-prey interactions in diving mammals (Bertilsson-Friedman, 2006), the influence of predation on the behavior of individual prey (Frid et al., 2007) and on population trajectories of prey species has recently received substantial attention (Springer et al., 2003; Williams et al., 2004). In the North Pacific Ocean, Steller sea lions and harbor seals (*Phoca vitulina richardii*) are sympatric throughout much of their ranges, and both species have undergone substantial declines in some areas (Merrick et al., 1987; Pitcher, 1990; Small et al., 2008; Mathews & Adkison, 2010). In Alaska, Steller sea lions are primarily piscivorous (Pitcher, 1981; Sinclair & Zeppelin, 2002; Womble & Sigler, 2006; Trites et al., 2007; McKenzie & Wynne, 2008; Sigler et al., 2009); however, there have been observations and diet studies that have documented Steller sea lions attacking and feeding upon other pinniped species. Pinniped species that have been attacked or consumed by Steller sea lions include northern fur seal neonates (*Callorhinus ursinus*) (Gentry & Johnson, 1981), California sea lions (*Zalophus californianus*) (Byrnes & Hood, 1994), ringed seals (*Phoca hispida*) (Tikhimriov, 1959), harbor seals (Pitcher & Fay, 1982; Mathews & Adkison, 2010), spotted seals (*Phoca largha*), and bearded seals (*Erignathus barbatus*) (Calkins et al., 1999).

Herein, we present a detailed description of a Steller sea lion actively attacking and consuming a harbor seal and a postmortem examination of the remaining carcass of the harbor seal. This observation is of interest given that population trends for the two species in the Glacier Bay region contrast dramatically. Harbor seals in Glacier Bay National Park declined by up to 75% from 1992 through 2002 (Mathews & Pendleton, 2006), and the most recent data through 2008 indicate the decline has not abated or reversed with pups declining at 5%/y from 1992 through 2008 (Womble et al., 2010). In contrast, the number of Steller sea lions has increased throughout southeastern Alaska, particularly in the Glacier Bay and Icy Strait region (Calkins et al., 1999; Pitcher et al., 2007).

Materials and Methods

The observation was made by JNW and SC in Johns Hopkins Inlet (JHI) (58° 51.42 N, 137° 05.41 W) in Glacier Bay National Park in southeastern Alaska (Figure 1). Glacier Bay is a recently deglaciated fiord that has undergone rapid landscape change over the last 225 y due to the dramatic retreat of tidewater glaciers (Cooper, 1937; Field, 1947; Hall et al., 1995). JHI (12 km long × 2.5 km wide) is located in the upper West Arm of Glacier Bay and is the primary glacial ice site used by seals in Glacier Bay (Mathews & Pendleton, 2006). Approximately, two-thirds of the seals are found in JHI (Mathews & Pendleton, 2006) with peaks in seal numbers occurring in June (pupping season) and August (molting season) and with substantially fewer seals in July and September. Seals are also found at terrestrial sites throughout Glacier Bay and at two smaller glacial ice sites in McBride and Tarr Inlets (Figure 1) (Womble et al., 2010).

Observations of the predation event were made using binoculars (Swarovski 10 × 42), and photographs were taken using a Nikon D1X camera with a 80-300 m Nikkor lens. The primary observation was made from the *R/V Steller* (21 m) and a Boston Whaler (6 m) during a harbor seal capture trip.

Results

On 29 April 2006, at 1245 h, JNW observed two adult male Steller sea lions swimming in JHI (58° 51.42 N, 137° 05.41 W) in water approximately 330 m deep. An estimated 300 to 400 harbor seals were present in JHI, primarily hauled out upon drifting glacial ice emanating from Johns Hopkins and Gilman glaciers. Approximately 15 min later, at 1300h, JNW and SC observed a group of 10 to 15 gulls (*Larus* spp.) and black-legged kittiwakes (*Rissa tridactyla*) focused above one of the adult male Steller sea lions. The sea lion repeatedly moved aggressively through the water in the same general area and was holding a large object in its mouth. Closer visual inspection revealed that the object in the sea lion's mouth was a harbor seal as evidenced by the presence of fore flippers, spotted pelage, blubber layer, and size (Figure 2a). Large amounts of blood were observed in the water in the vicinity of the sea lion. The sea lion repeatedly tossed the harbor seal into the air and continued to swim aggressively with the seal in its mouth. On several occasions, the sea lion thrashed the harbor seal at the surface of the water (Figure 2a) and then dragged the seal beneath the surface for 25 to 30 s each time. The behavior of the sea lion was similar to behavior exhibited by sea lions when they are consuming large fish at the surface such as Pacific salmon (*Oncorhynchus* sp.) and halibut (*Hippoglossus stenolepis*). Throughout the predation event, gulls and kittiwakes were present above the sea lion and repeatedly dove into the water to retrieve small pieces of seal tissue. At 1340 h, the sea lion left the immediate area, and the remains of the harbor seal carcass were recovered.

Although the sea lion was observed actively consuming the harbor seal (Figure 2b), the entire seal carcass was not consumed by the sea lion. A substantial portion of the body of the harbor seal remained after the attack (Figure 3), and a necropsy was conducted on the remains of the harbor seal. The carcass was fresh, not scavenged, and was that of a juvenile harbor seal. The carcass was severed anterior to the axillary region and posterior to the pelvic region. No internal organs remained with the exception of the upper portion of the trachea. Only a small portion of the skull and the lower mandible, which was broken at the midline cartilaginous juncture, were present from the cephalic region of the body. Both fore flippers were intact, including the scapula, humerus, radius, ulna, and digits as well as surrounding superficial skeletal muscles, triceps brachii, and deltoid. The hind flippers were not present. The blubber layer (~4 cm thick) was intact and had not been consumed, but it was turned inside out and faced outwards. There were several (3 to 4) canine puncture wounds located on the dorsal surface of the pelage in the thoracic region (Figure 3). Two more puncture wounds were located on the ventral surface just posterior of the lower mandible. All puncture wounds were 2 cm in length and triangular in shape.

The canine puncture wounds found on the harbor seal carcass in JHI were very similar in shape and size to wounds observed on two other harbor seals found in Glacier Bay. First, on 22 August 2005, the carcass of a juvenile male harbor seal was found in Bartlett Cove in lower Glacier Bay. A necropsy

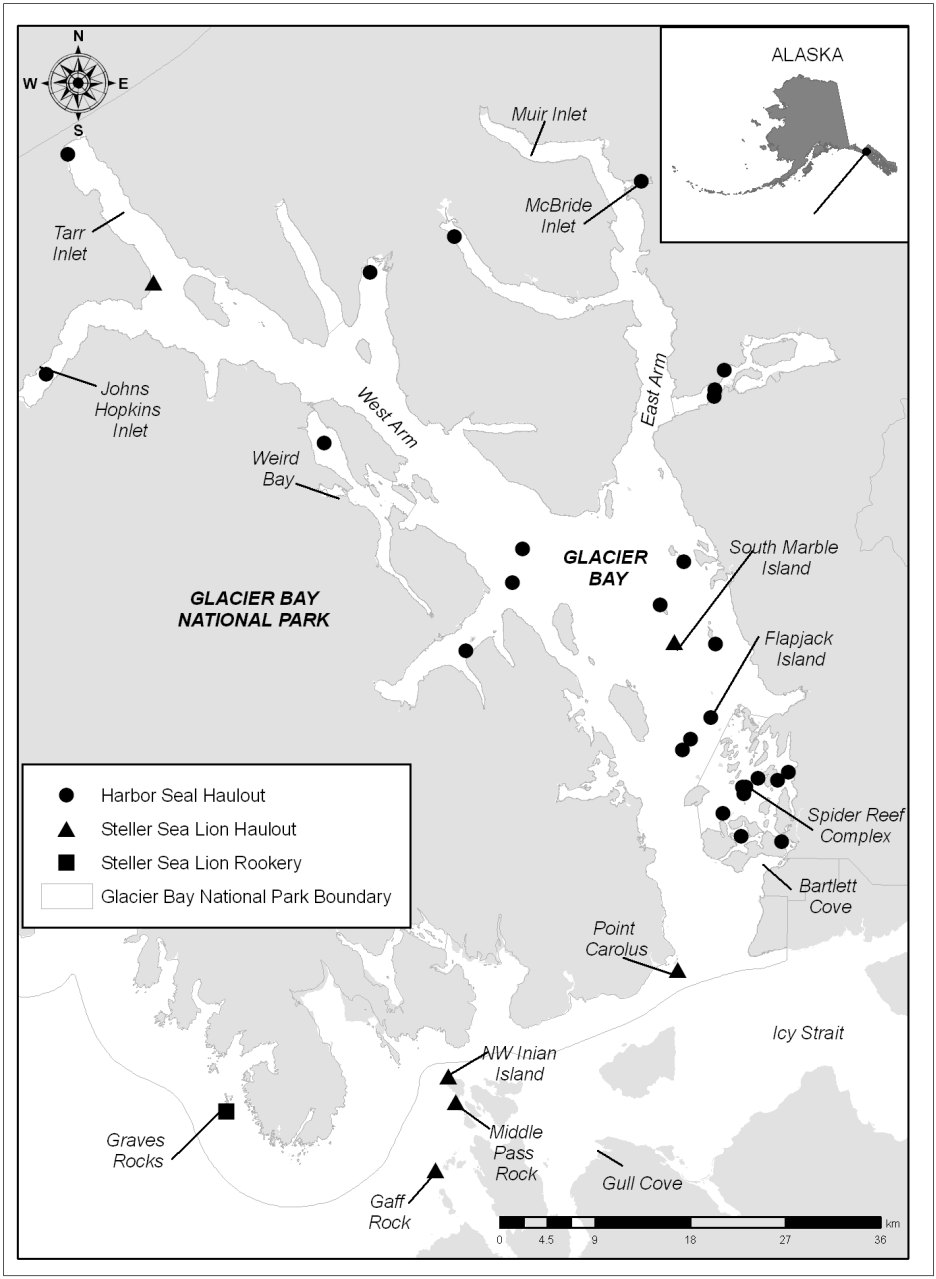

Figure 1. Locations of harbor seal and Steller sea lion haulouts and a Steller sea lion rookery in the Glacier Bay region of southeastern Alaska

of the harbor seal revealed paired puncture lesions on the posterior right hip. The puncture wounds were approximately 6 cm apart and 3 cm deep to the muscle depth. There was extensive damage to the underlying tissue in the left lumbar area, with linear areas of hemorrhaging underlying and connecting the puncture wounds.

Second, on 15 September 2008, a young-of-year female harbor seal was live-captured in JHI as part of a study aimed at quantifying movement patterns and habitat use of seals. The 3- to 4-mo-old seal had a large granulated open wound along her mid-dorsal area. The wound was approximately 13 cm in length, 3 cm in width, and 0.3 cm

in depth. There was a smaller, healed puncture wound, approximately 2.5 cm in length, anterior to the larger wound. Inspection of images of the wounds from the live-captured seal suggested that the wounds were likely not inflicted by other potential marine predators such as a killer whale (*Orcinus orca*). In addition, the partial remains of a harbor seal pup were found on Spider Island on 27 June 2006. Only the pelage of the seal pup remained; it was turned inside out and faced outwards. Although attack and/or predation was not directly observed in either of these three cases, the similarity in the size and intercanine distance of the puncture wounds and condition of the remains suggests an interaction with a large predator. Furthermore, as recently as 8 August 2009, observations of predatory behavior by a sea lion were also observed in Icy Strait near Gull Cove, just outside of Glacier Bay. The predatory attack involved an adult male Steller sea lion attacking and consuming a harbor seal pup (Gregory P. Streveler, Icy Strait Environmental Services, Gustavus, Alaska, pers. obs.). In addition to the aforementioned observations, several observations of Steller sea lion predation or suspected predation upon harbor seals have been opportunistically documented in the Glacier Bay region (Mathews & Adkison, 2010).

Discussion

The observation described occurred in Glacier Bay National Park in southeastern Alaska in an area where population trajectories for harbor seals and Steller sea lions contrast dramatically. Over the 17-y period from 1992 to 2008, population trend estimates for the number of harbor seals counted in Glacier Bay were negative at both glacial ice and terrestrial sites (Mathews & Pendleton, 2006; Womble et al., 2010). In contrast, the Steller sea lion population in southeastern Alaska has increased at approximately 3.2%/y (Pitcher et al., 2007). In addition, a new Steller sea lion rookery was established at Graves Rocks (Gelatt et al., 2007; Pitcher et al., 2007), and several new haulout sites (Tarr Inlet, Middle Pass Rock, Rocky Island, and Gaff Rock) have been recently colonized by sea lions in the Glacier Bay and Icy Strait region (Womble et al., 2009; J. N. Womble, pers. obs.).

It is possible that the growth and expansion of the Steller sea lion population in the Glacier Bay region could potentially influence the harbor seal population via direct and/or indirect mechanisms. First, direct predation on juvenile harbor seals by sea lions could result in an increase in harbor seal mortality which could directly influence juvenile recruitment. Although direct predation of harbor seals by Steller sea lions has been opportunistically observed on several occasions in the Glacier Bay region (Mathews & Adkison, 2010), there have not been systematic studies aimed at quantifying predation rates by Steller sea lions on harbor seals. Second, Steller sea lions could indirectly influence the distribution and foraging behavior of harbor seals through behaviorally mediated impacts on prey (e.g., Lima & Dill, 1990), competitive exclusion, and/or interspecific competition for prey (e.g., Bowen et al., 2003). Steller sea lions and harbor seals exploit similar prey species in the Glacier Bay region, including walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), herring (*Clupea pallasii*), sandlance (*Ammodytes hexapterus*), and salmon (*Oncorhynchus* spp.) (Gelatt et al., 2007; Herreman et al., 2009); thus, it is likely that some degree of dietary overlap may occur between these two species. Although, overlap in the distribution of ecologically similar species could result in competitive exclusion and potential competition for prey species, the potential impact of sympatric species on one another's food supply can be difficult to quantify (Orians & Willson, 1964). Such indirect interactions could lead to negative population-level effects on harbor seals (e.g., Mathews & Pendleton, 2006; Herreman et al., 2009); however, few data exist with which to evaluate this hypothesis.

Similar predatory behavior by Steller sea lions has been reported in other areas of the North Pacific Ocean and suggests that this behavior is not specific to the Glacier Bay region. For example, juvenile Steller sea lions have been observed killing and eating northern fur seal neonates at St. George Island in the Bering Sea (Gentry & Johnson, 1981), and a territorial male Steller sea lion was observed attacking and eating a California sea lion at Año Nuevo Island in California (Byrnes & Hood, 1994). Aggressive behavior by Steller sea lions toward harbor seals was also observed at Tugidak Island in the Gulf of Alaska in April of 1978 (Pitcher & Fay, 1982). In addition, pinniped remains have been found in the stomachs of Steller sea lions collected in the Gulf of Alaska and in the Russian Far East waters (Pitcher & Fay, 1982; Calkins, 1998). However, extensive diet studies of Steller sea lions throughout southeastern Alaska document that sea lions forage primarily on fish, invertebrates, and occasionally seabirds (Womble & Sigler, 2006; Trites et al., 2007; Sigler et al., 2009) and suggest that harbor seals are not a primary component of the diet of sea lions in the region.

The observed predatory attack on a harbor seal was made by an adult male Steller sea lion, and it is possible that this behavior may be limited

Figure 2a. Steller sea lion (*Eumetopias jubatus*) attacking juvenile harbor seal (*Phoca vitulina richardii*) in Johns Hopkins Inlet (JHI) in Glacier Bay National Park, Alaska, on 29 April 2006 (Photograph by Jamie N. Womble)

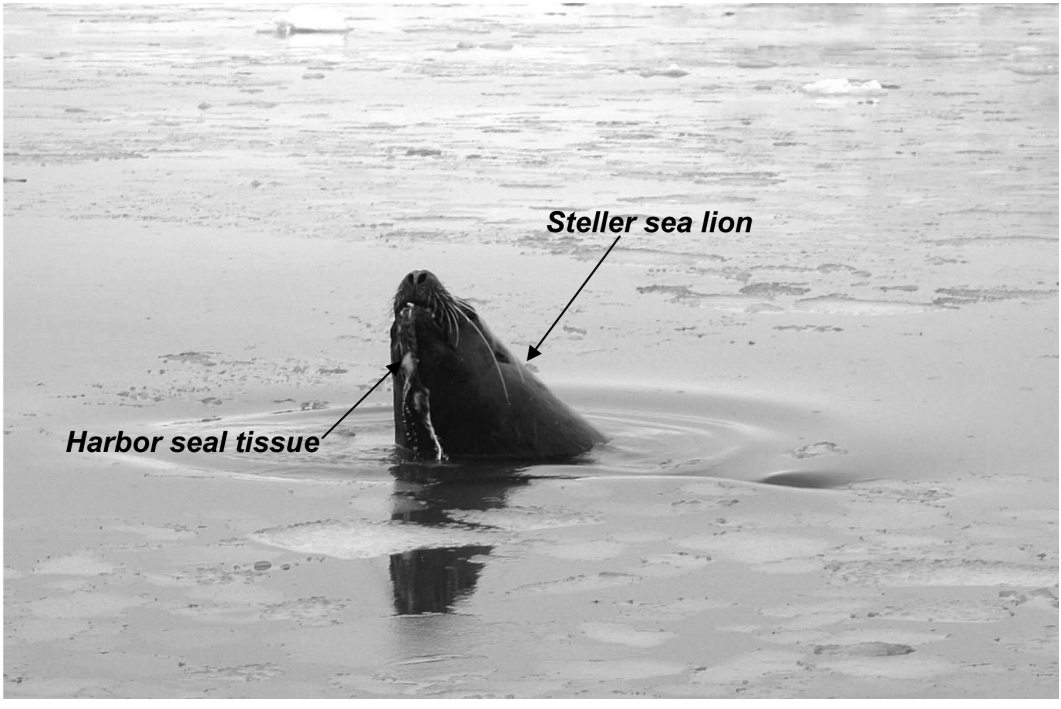

Figure 2b. Steller sea lion with harbor seal tissue in mouth in JHI in Glacier Bay National Park, Alaska, on 29 April 2006 (Photograph by Jamie N. Womble)

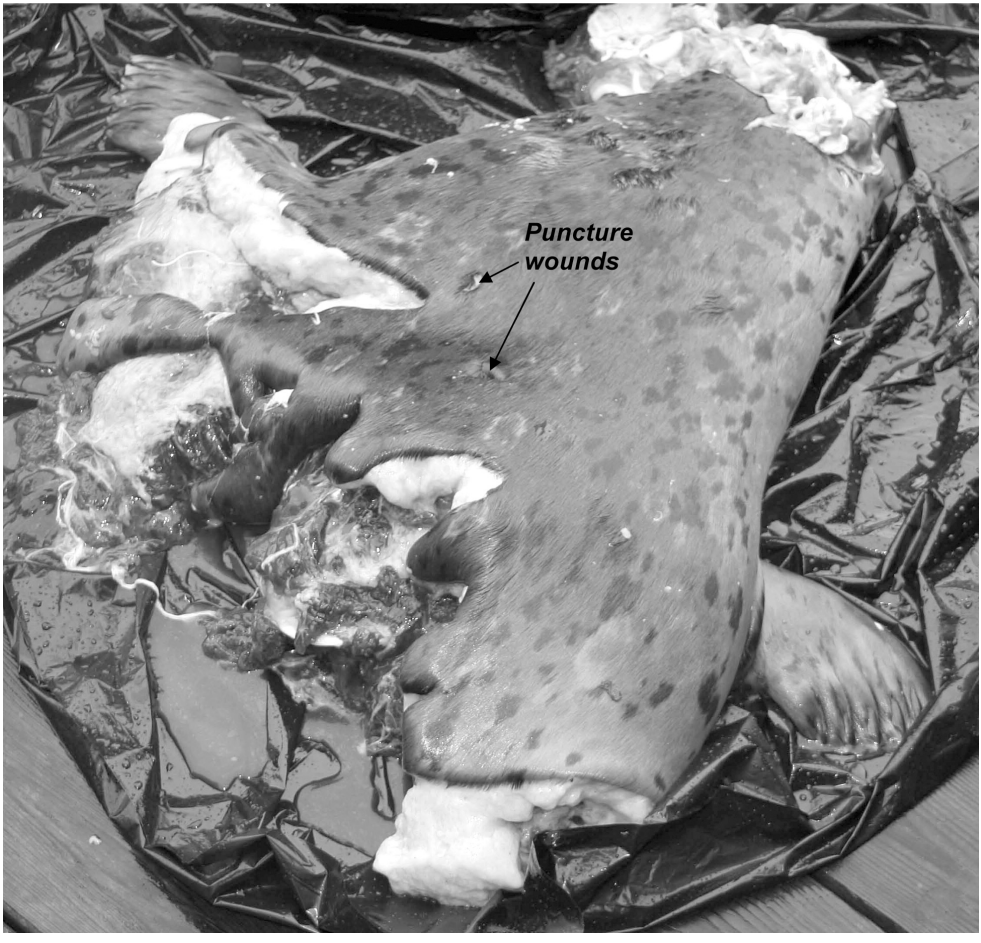

Figure 3. Carcass of harbor seal that remained after a predatory attack by a Steller sea lion in JHI in Glacier Bay National Park, Alaska, on 29 April 2006 (Photograph by Jamie N. Womble)

to a few individual sea lions that may specialize in attacking and killing harbor seals. For example, one subadult male New Zealand sea lion is believed to have been responsible for up to 43% of the mortalities of fur seal pups from 1996 to 1997 on Macquarie Island in the Southern Ocean (Robinson et al., 1999). In addition, at Seal Island, near the Antarctic Peninsula, only a few leopard seals were responsible for most of the observed predation events on Antarctic fur seal (*Arctocephalus gazella*) pups, and the same individual leopard seals were observed hunting fur seal pups in multiple years (Hiruki et al., 1999).

Steller sea lions may target young seals due to naïve behavior and small body size. Young seals, particularly recently weaned pups, may be ecologically naïve and, thus, less sensitive to signs and behavior of unfamiliar predators. After pups are weaned and begin to forage on their own, they may be particularly vulnerable and may fail to exhibit anti-predator behavior, such as evasive maneuvers or extended dive durations (e.g., Womble et al., 2007). In addition, the timing of the migratory movements of young seals out of JHI and Glacier Bay in autumn may also increase the likelihood of encounters with Steller sea lions as some juvenile seals travel near Steller sea lion haulout sites (J. N. Womble, unpub. data). Similarly, other studies have suggested that Antarctic fur seal pups may be particularly vulnerable to predation by leopard seals during the first few months of life as the fur seal pups are small in body size and old enough to enter the water, yet likely still naïve to the presence of leopard seals (Boveng et al., 1998; Hiruki et al., 1999).

In addition to Steller sea lions, other marine predators prey on harbor seals in the Glacier Bay region. Transient killer whales are a primary predator of

harbor seals in Glacier Bay (Calambokidis et al., 1989; Matkin et al., 2007) as well as in other areas of Alaska and British Columbia (Baird & Dill, 1995; Saulitis et al., 2000). From 1986 to 2003, harbor seals were documented as prey in at least 40% of transient killer whale kill incidents in Glacier Bay (Matkin et al., 2007). Transient killer whales occur throughout the waters of southeastern Alaska, with the highest numbers observed during summer, particularly in the Glacier Bay/Icy Strait region (Dahlheim et al., 2009). The seasonal occurrence of transient killer whales in the Glacier Bay region is likely influenced by the seasonal availability of marine mammal prey (Deecke et al., 2006), particularly recently weaned harbor seals that are likely vulnerable to predation. In addition to killer whales, it has been suggested that Pacific sleeper sharks (*Somniosus pacificus*) may also be potential predators of harbor seals in Glacier Bay. Harbor seal tissue was found in the stomach of one sleeper shark in Muir Inlet in the East Arm of Glacier Bay, and harbor seals and sleeper sharks co-occur in some areas of Glacier Bay (Taggart et al., 2005). Harbor seal tissue has also been found in the stomachs of Pacific sleeper sharks in other areas of Alaska (Bright, 1959; Sigler et al., 2006).

Conclusions

The opportunistic observation presented herein documents that Steller sea lions are a predator of harbor seals in the Glacier Bay region and that aggressive interactions do occur between the two species. Although opposing population trajectories are apparent for the two species, such opposing trajectories alone do not imply a direct link with the decline of harbor seals. Determining if predation by sea lions may have population-level consequences for harbor seals will require systematically (1) quantifying predation rates by sea lions on harbor seals, (2) quantifying predation rates by other harbor seal predators such as transient killer whales, (3) determining whether or not predation is compensatory or additive (e.g., Errington, 1946), and (4) quantifying which individuals and age classes in the population are preyed upon.

Acknowledgments

We thank the vessel (*R/V Steller*) and scientific crew, including G. Blundell, R. Dziuba, D. Foley, S. Gende, J. Herreman, D. Holcombe, S. Karpovich, L. Polasek J. Prewitt, and J. Wells for their assistance. Research was performed under MMPA Permit No. 358-1787-00 and 782-1676-01.

Editors' Addendum

At the time this article was in press, the authors brought to our attention an article titled "The Role of Steller Sea Lions in a Large Population Decline of Harbor Seals" by Elizabeth A. Mathews and Milo D. Adkison, published online (Early View) by *Marine Mammal Science*, doi: 10.1111/j.1748-7692.2010.00375.x. Both articles discuss observations of Stellar sea lion attacks on harbor seals in the Glacier Bay area and the possible influence these attacks may have on harbor seal population trends. The editors would like to direct readers to the Mathews and Adkison article, which expands on the discussion topics found in this article.

Literature Cited

Baird, R. W., & Dill, L. M. (1995). Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging behaviour, and prey handling. *Canadian Journal of Zoology*, *73*, 1300-1311.

Bertilsson-Friedman, P. (2006). Distribution and frequencies of shark-inflicted injuries to the endangered Hawaiian monk seal (*Monachus schauinslandi*). *Journal of Zoology*, *268*(4), 361-368.

Boveng, P. L., Hiruki, L. M., Schwartz, M. K., & Bengtson, J. L. (1998). Population growth of Antarctic fur seals: Limitation by a top predator, the leopard seal? *Ecology*, *79*, 2863-2877.

Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2003). Maternal and newborn life-history traits during periods of contrasting population trends: Implications for explaining the decline of harbor seals, *Phoca vitulina*, on Sable Island. *Journal of Zoology London*, *261*, 155-163.

Bradshaw, C. J. A., Lalas, C., & McConkey, S. (1998). New Zealand sea lion predation on New Zealand fur sea lions. *New Zealand Journal of Marine and Freshwater Research*, *32*, 101-104.

Bright, D. B. (1959). The occurrence and food of the sleeper shark, *Somniosus pacificus*, in a central Alaska bay. *Copeia*, *1*, 76-77.

Burger, J. (1979). Competition and predation: Herring gulls versus laughing gulls. *Condor*, *81*, 269-277.

Byrnes, P. E., & Hood, W. R. (1994). First account of Steller sea lion (*Eumetopias jubatus*) predation on a California sea lion (*Zalophus californianus*). *Marine Mammal Science*, *10*, 381-383.

Calambokidis, J., Taylor, B. L., Carter, S. D., Steiger, G. H., Dawson, P. K., & Antrim, L. D. (1987). Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology*, *65*, 1391-1396.

Calkins, D. G. (1998). Prey of Steller sea lions in the Bering Sea. *Biosphere Conservation*, *1*, 33-44.

Calkins, D. G., McAllister, D. C., Pitcher, K. W., & Pendleton, G. W. (1999). Steller sea lion status and

trend in southeast Alaska: 1979-1997. *Marine Mammal Science*, *15*, 462-477.

Creel, S., & Creel, N. M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, *10*, 526-553.

Cooper, W. S. (1937). The problem of Glacier Bay, Alaska: A study of glacier variations. *Geographical Review*, *27*, 37-62.

Dahlheim, M. E., White, P. A., & Waite, J. M. (2009). Cetaceans of southeast Alaska: Distribution and seasonal occurrence. *Journal of Biogeography*, *36*, 410-426.

Deecke, V. B., Straley, J. M., Matkin, D. R., & Gabriele, C. M. (2006). The mammal-eating killer whales of Glacier Bay National Park and Preserve: Hunting with the strong silent types. *Alaska Park Science*, *5*(2), 5-9.

Errington, P. L. (1946). Predation and vertebrate populations. *The Quarterly Review of Biology*, *21*, 144-177.

Fay, F. H. (1960). Carnivorous walrus and some Arctic zoonoses. *Arctic*, *13*, 111-122.

Fay, F. H., Sease, J. L., & Merrick, R. L. (1990). Predation on a ringed seal, *Phoca hispida*, and a black guillemot, *Cepphus grylle*, by a Pacific walrus, *Odobenus rosmarus divergens*. *Marine Mammal Science*, *6*, 348-350.

Field, W. O. (1947). Glacier recession in Muir Inlet, Glacier Bay, Alaska. *Geographical Review*, *37*, 369-399.

Frid, A., Heithaus, M. R., & Dill, L. M. (2007). Dangerous dive cycles and the proverbial ostrich. *Oikos*, *116*, 892-902.

Gelatt, T. S., Trites, A. W., Hastings, K. K., Jemison, L. A., Pitcher, K. W., & O'Corry-Crowe, G. (2007). Population trends, diet, genetics, and observations of Steller sea lions in Glacier Bay National Park. In J. F. Piatt & S. M. Gende (Eds.), *Proceedings of the Fourth Glacier Bay Science Symposium, October 26-28, 2004* (pp. 145-149). Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047. 246 pp.

Gentry, R. L., & Johnson, J. H. (1981). Predation by sea lions on Northern fur sea lion neonates. *Mammalia*, *45*, 423-430.

Hall, D. K., Benson, C. S., & Field, W. O. (1995). Changes of glaciers in Glacier Bay, Alaska using ground and satellite measurements. *Physical Geography*, *16*, 27-41.

Harcourt, R. G. (1993). Individual variation in predation on fur sea lions by southern sea lions (*Otaria byronia*) in Peru. *Canadian Journal of Zoology*, *71*, 1908-1911.

Herreman, J. K., Blundell, G. M., & Ben-David, M. (2009). Evidence of bottom-up control of diet driven by top-down processes in a declining harbor seal *Phoca vitulina richardsi* population. *Marine Ecology Progress Series*, *374*, 287-300.

Hiruki, L. M., Schwartz, M. K., & Boveng, P. L. (1999). Hunting and social behavior of leopard seals (*Hydrurga leptonyx*) at Seal Island, South Shetland Islands, Antarctica. *Journal of Zoology London*, *249*, 97-109.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619-640.

Lowry, L. F., & Fay, F. H. (1984). Seal eating by walruses in the Bering and Chukchi Seas. *Polar Biology*, *3*, 11-18.

Majluf, P. (1987). South American fur seal, *Arctocephalus australis*, in Peru. In J. P. Croxall & R. L. Gentry (Eds.), *Status, biology, and ecology of fur seals* (NOAA Technical Report #51) (pp. 33-35). Silver Spring, MD: National Marine Fisheries Service.

Mathews, E. A., & Adkison, M. D. (2010, in press). The role of Steller sea lions in a large population decline of harbor seals. *Marine Mammal Science*. doi: 10.1111/j.1748-7692.2010.00375.x

Mathews, E. A., & Pendleton, G. W. (2006). Declining trends in harbor seal numbers at glacial ice and terrestrial haulouts in Glacier Bay National Park, 1992-2002. *Marine Mammal Science*, *22*, 167-189.

Matkin, D. R., Straley, J. M., & Gabriele, C. M. (2007). Killer whale feeding ecology and non-predatory interactions with other marine mammals in the Glacier Bay region of Alaska. In J. F. Piatt & S. M. Gende (Eds.), *Proceedings of the Fourth Glacier Bay Science Symposium, October 26-28, 2004* (pp. 155-158). Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047. 246 pp. Retrieved 19 April 2010 from www.nps.gov/glba/naturescience/upload/Matkin_etal2007_KillerWhaleInteractions.pdf.

McKenzie, J., & Wynne, K. M. (2008). Spatial and temporal variation in the diet of Steller sea lions in the Kodiak Archipelago, 1999-2005. *Marine Ecology Progress Series*, *360*, 265-283.

Merrick, R. L., Loughlin, R. R., & Calkins, D. G. (1987). Decline in the abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. *Fishery Bulletin*, *85*, 351-365.

Orians, G. H., & Willson, M. F. (1964). Interspecific territories of birds. *Ecology*, *45*, 736-745.

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, *153*, 492-508.

Pitcher, K. W. (1981). Prey of the Steller sea lion (*Eumetopias jubatus*) in the Gulf of Alaska. *Fishery Bulletin*, *79*, 544-549.

Pitcher, K. W. (1990). Major decline in number of harbor seal, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science*, *6*, 121-134.

Pitcher, K. W., & Fay, F. H. (1982). Feeding by Steller sea lion on harbor seals. *The Murrelet*, *63*, 70-71.

Pitcher, K. W., Olesiuk, P. F., Brown, R. F., Lowry, M. S., Jeffries, S. J., Sease, J. L., et al. (2007). Status and trends in abundance and distribution of the eastern Steller sea lion (*Eumetopias jubatus*) population. *Fishery Bulletin*, *107*, 102-115.

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, *19*, 297-330.

Robinson, S., Wynen, L., & Goldsworthy, S. (1999). Predation by a Hooker's sea lion (*Phocarctos hookeri*)

on a small population of fur seals (*Arctocephalus* spp.) at Macquarie Island. *Marine Mammal Science*, *15*, 888-893.

Saulitis, E., Matkin, C., Barrett-Lennard, L., Heise, K., & Ellis, G. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound. *Marine Mammal Science*, *16*, 94-109.

Shaughnessy, P. D., & Goldsworthy, S. F. (1990). Population size and breeding season of the Antarctic fur seal *Arctocephalus gazella* at Heard Island—1987/88. *Marine Mammal Science*, *6*, 292-304.

Sigler, M. F., Hulbert, L. B., Lunsford, C. R., Thompson, N. H., Burek, K., O'Corry-Crowe, G., et al. (2006). Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the north-east Pacific Ocean. *Journal of Fish Biology*, *69*, 392-405.

Sigler, M. F., Tollitt, D. J., Vollenweider, J. J., Thedinga, J. F., Csepp, D. J., Womble, J. N., et al. (2009). Steller sea lion foraging response to seasonal changes in prey availability. *Marine Ecology Progress Series*, *388*, 243-261.

Sinclair, E. H., & Zeppelin, T. K. (2002). Seasonal and spatial differences in diet of the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy*, *83*, 973-990.

Siniff, D. B., & Bengtson, J. L. (1977). Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. *Journal of Mammalogy*, *58*, 414-416.

Small, R. J., Boveng, P. L., Byrd, G. V., & Withrow, D. W. (2008). Harbor seal population decline in the Aleutian Archipelago. *Marine Mammal Science*, *24*, 845-863.

Springer, A. M., Estes, J. A., vanVliet, G. B., Williams, T. M., Doak, D. F., Danner, E. M., et al. (2003). Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences*, *100*, 12223-12228.

Taggart, S. J., Andrews, A. G., Mondragon, J., & Mathews, E. A. (2005). Co-occurrence of Pacific sleeper sharks, *Somniosus pacificus*, and harbor seals, *Phoca vitulina,* in Glacier Bay. *Alaska Fishery Research Bulletin*, *11*, 113-117.

Tikhimriov, E. A. (1959). The question of use of warm blooded animals as food by sea lions. *Izvestiia TINRO*, *47*, 185-186.

Trites, A. W., Calkins, D. G., & Winship, A. J. (2007). Diets of Steller sea lions (*Eumetopias jubatus*) in southeast Alaska, 1993-1999. *Fishery Bulletin*, *105*(2), 234-248. Retrieved 19 April 2010 from http://fishbull.noaa.gov/1052/trites.pdf.

Walker, T. R., Boyd, I. L., McCafferty, D. J., Huin, N., Taylor, R. I., & Reid, K. (1998). Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science*, *10*, 75-81.

Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). Killer appetites: Assessing the role of predators in ecological communities. *Ecology*, *85*, 3373-3384.

Womble, J. N., & Sigler, M. F. (2006). Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion. *Marine Ecology Progress Series*, *325*, 281-293.

Womble, J. N., Gende, S. M., & Blundell, G. M. (2007). Dive behavior of a harbor seal (*Phoca vitulina richardii*) in the presence of transient killer whales (*Orcinus orcas*) in Glacier Bay National Park, Alaska. *Marine Mammal Science*, *23*, 203-208.

Womble, J. N., Sigler, M. F., & Willson, M. F. (2009). Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. *Journal of Biogeography*, *36*, 439-451.

Womble, J. N., Pendleton, G. W., Mathews, E. A., Blundell, G. M., Bool, N. M., & Gende, S. M. (2010, in press). Harbor seal decline continues in the rapidly changing landscape of Glacier Bay National Park, Alaska, 1992-2008. *Marine Mammal Science*, *26*.