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# Harbor seal (*Phoca vitulina richardii*) decline continues in the rapidly changing landscape of Glacier Bay National Park, Alaska 1992–2008

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Across Alaska, an estimated 10% or more of harbor seals (*Phoca vitulina richardii*) depend, at least seasonally, on glacial ice calved from tidewater glaciers as a haul-out substrate for resting, pupping, nursing, and molting (Bengtson *et al.* 2007). Some glacial ice sites, such as Icy Bay near Yakutat, Alaska, currently support in excess of 5,000 seals (Jansen *et al.* 2006). However, over the last few decades, counts of seals have steeply declined at two glacial ice sites in Aialik Bay in south-central Alaska and at Glacier Bay in southeastern Alaska (Hoover-Miller 1994, Mathews and Pendleton 2006). Declines in the number of harbor seals at some glacial ice sites are of particular concern for several reasons. First, glacial ice sites may serve as a refuge from predation for young pups during the pupping season and glacial ice habitat may facilitate the avoidance of both terrestrial and marine predators (Calambokidis *et al.* 1987). Second, harbor seals from glacial ice sites may function as source populations for surrounding regions due to the unusually high proportion of mother–pup pairs found at glacial ice sites. Third, harbor seals at glacial ice sites rely upon glacial ice calved from tidewater glaciers as a haul-out substrate and the rate of thinning of tidewater glaciers in Alaska is forecasted to continue at an unprecedented rate (Arendt *et al.* 2002, Larsen *et al.* 2007).

Glacier Bay (58°40′N, 136°05′W; Fig. 1) is one of the only two glacial ice sites in Alaska where long-term monitoring efforts for harbor seals have occurred during the pupping and molting periods since the 1970s (Hoover 1983, Hoover-Miller 1994, Mathews and Pendleton 2006). Based on surveys conducted from 1972 to 1978 (Streveler 1979[1]) and from 1982 to 1984, Calambokidis *et al.* (1987) concluded that Glacier Bay supported one of the largest breeding aggregations of harbor seals in Alaska. Between 1973 and 1986, Muir Glacier, in the East Arm of Glacier Bay, retreated more than 7 km. The dramatic retreat and subsequent grounding of the Muir Glacier resulted in the cessation of calving of the Muir Glacier in 1993 (Hall *et al.* 1995). As a result, the availability of floating glacial ice as a haul-out substrate for harbor seals in Muir Inlet was reduced (Calambokidis *et al.* 1987) and eventually resulted in the abandonment of upper Muir Inlet by harbor seals (Mathews 1995). Prior to the grounding of Muir Glacier, up to 1,347 seals were counted in upper Muir Inlet in the East Arm of Glacier Bay in the 1970s (Streveler 1979[1]). In 2008, fewer than 200 seals were counted in McBride Inlet near the terminus of the McBride Glacier, the only remaining tidewater glacier in the East Arm of Glacier Bay. As of 2004, McBride Glacier had retreated more than 2 km from the mouth of McBride Inlet (Molnia 2007).

In the early 1990s, E. A. Mathews established systematic methods to count seals (1) on floating icebergs in Johns Hopkins Inlet (JHI) (58°53′N, 137°05′W), the primary glacial ice site in West Arm, Glacier Bay where up to two-thirds of the seals are found, and (2) at terrestrial sites and at McBride Inlet (Fig. 1) (Mathews and Pendleton 2006). Mathews and Pendleton (2006) reported declines in non-pup counts in JHI during both the pupping (−39%/8 yr) and molting periods (−63%/11 yr); however, declines in seal counts at terrestrial sites (−75%/10 yr) were steepest. In August 1992, 6,189 seals were counted at glacial ice and terrestrial sites in Glacier Bay, but only 2,551 seals were counted at the same sites in August 2001. In contrast to the observed declines in non-pups, average pup counts remained stable in JHI from 1994 to 1999 (Mathews and Pendleton 2006).

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[1] Streveler, G. 1979. Distribution, population ecology and impact susceptibility of the harbor seals in Glacier Bay, Alaska. Unpublished report. Available from Glacier Bay National Park, P. O. Box 140, Gustavus, AK 99826.

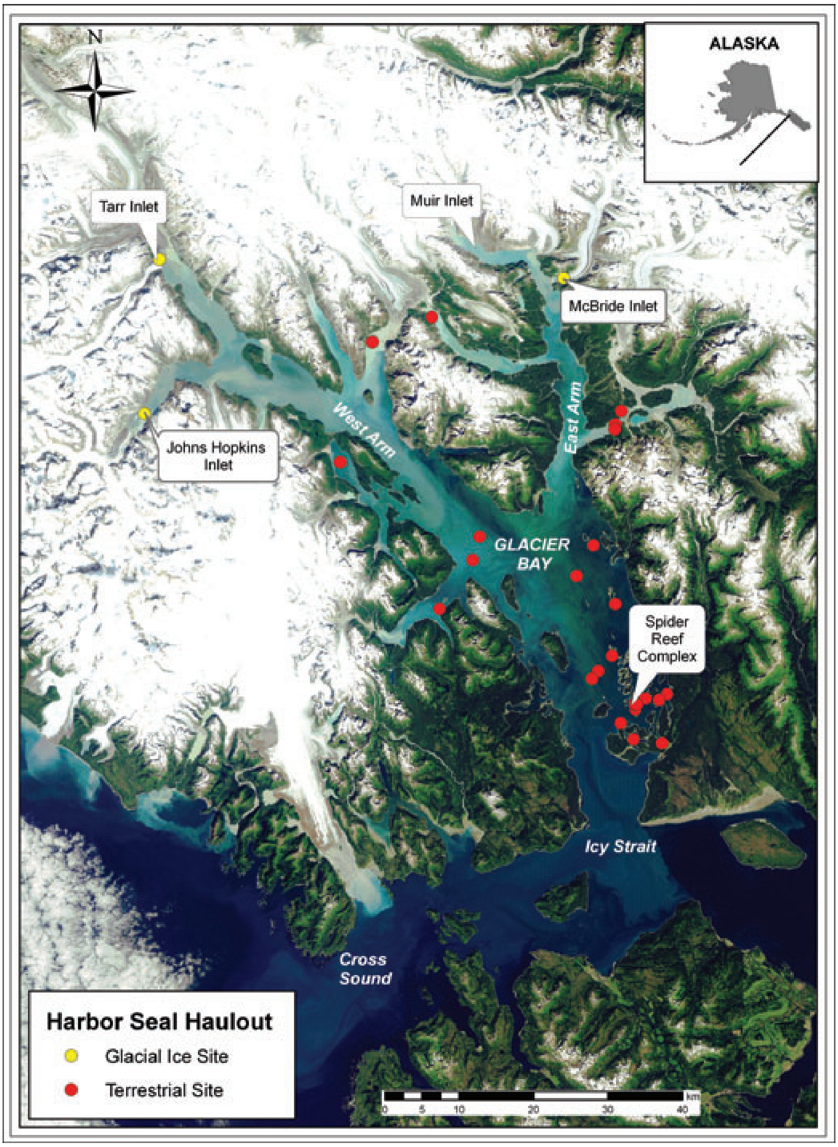

*Figure 1.* Harbor seal study area in Glacier Bay National Park (58°40′N, 136°05′W), southeastern Alaska including glacial ice and terrestrial sites used by harbor seals as of 2008.

Given the importance of glacial ice sites to harbor seals, the expected changes to glaciers due to global climate change, and the need to understand whether the declining trend in the number of harbor seals has continued, we reinitiated monitoring efforts at terrestrial sites in 2004 and at JHI in 2007, using the same methods used by Mathews and Pendleton (2006). Herein, we report (1) trend estimates for harbor seals in Glacier Bay over a 17-yr period from 1992 to 2008, (2) compare recent trends (2004–2008) in seal counts with trend estimates from 1992 to 2002 (Mathews and Pendleton 2006), (3) describe within-summer patterns of abundance in JHI (June–September 2007–2008), and (4) discuss the importance of Glacier Bay as a regional long-term monitoring site for harbor seals in Alaska.

Glacier Bay is a recently deglaciated fiord in southeastern Alaska (Fig. 1) that has undergone rapid landscape change over the last 250 yr due to the dramatic retreat of tidewater glaciers (Cooper 1937, Field 1947, Hall *et al.* 1995). Seals in Glacier Bay use two distinct habitat types for hauling out (glacial ice and terrestrial sites), which require two different monitoring methods. At terrestrial haul-out sites and at glacial ice sites in McBride Inlet and Tarr Inlet (Fig. 1), seals were surveyed from fixed-winged aircraft (Cessna 206). Each year from 2004 to 2008, we conducted replicate aerial surveys during late July and August at an altitude of approximately 300 m and ±2 h from the low tide over a 5–8 d cycle of very low tides. Photographic images were taken using a digital camera (Nikon D1X and Nikon D2X with 80–300 mm lens) and images were imported into ArcView 3.2a (ESRI Inc., Redlands, CA, U.S.A.). Seals in the digital images were counted twice by an experienced counter.

In JHI the numbers of seals on icebergs were counted from an elevated shore-based observation site (~35 m above sea level) by two observers. We conducted paired counts using tripod-mounted 20× binoculars (Mathews and Pendleton 2006) two to three times daily during survey periods from June through September of 2007 and 2008. During the pupping period (June), seals were classified as either pups or non-pups. During the molting period (August), all seals were classified as non-pups due to the difficulty in distinguishing pups and juveniles at a distance (Mathews and Pendleton 2006). Due to the expansive area of JHI (12 km long × 2.5 km wide), pups at a distance may be obscured by their mother, undetected altogether, or misclassified and thus may be underestimated. Therefore, in addition to counting the total number of pups we also estimated the proportion of pups from counts of 100 nearby seals multiple times throughout the day (Mathews and Pendleton 2006).

We used the same statistical methods as Mathews and Pendleton (2006) for estimating population trends, including the effects of covariates on counts, and analyzing factors affecting the proportion of pups. Specifically, we used over-dispersed Poisson regression (Link and Sauer 1997) to estimate trends in (1) the number of seals counted on icebergs in JHI (in June and August) and (2) the number of seals counted at terrestrial sites and at glacial ice sites in McBride Inlet and Tarr Inlet during late July and August. In addition to the data from Mathews and Pendleton (2006), we used data from shore-based counts of seals in JHI from 21 d in June, 20 d in July, 36 d in August, and 21 d in September from 2007 and 2008. Counts spanned 12 June through 1 July for the pupping period and 8 August through 30 August for the molting period in JHI. For terrestrial sites, we included data from aerial surveys on 21 different days between 31 July and 24 August from 2004 to 2008.

Covariates included in the analyses differed between the glacial ice and terrestrial habitat types because the same factors affect seal behavior differently depending upon habitat type. For example, tide height affects the proportion of seals hauled out at terrestrial sites (Small *et al.* 2003), but tides have little effect on seals using floating glacial ice (Mathews and Pendleton 2006). Date, time relative to solar noon (hereafter, time), time relative to low tide (hereafter, tide-time), and tide height were included as covariates for terrestrial sites. In addition, quadratic effects were included for date, the two-time variables, and we included an interaction between tide height and site, which allowed the effect of tide to vary among sites. For JHI analyses, covariates included date, time, weather variables (sky, precipitation), observer level (based on experience), and a subjective assessment of count quality. For JHI, quadratic effects were included for date and time.

Other aspects of the analyses, including producing model averaged estimates of trend (Burnham and Anderson 1998) and using logistic regression (Hosmer and Lemeshow 2000) to investigate patterns in the proportion of pups in the subset counts of seals in JHI, were the same as described by Mathews and Pendleton (2006), with a few exceptions. For JHI analyses, we used three levels of weather variables rather than the two levels used by Mathews and Pendleton (2006) and we excluded a variable that accounted for longer-term observer experience.

Over the 17-yr period from 1992 to 2008, population trend estimates for the number of seals counted in Glacier Bay were negative both at glacial ice and terrestrial sites (Fig. 2, 3). Trend estimates for seals in JHI were similar to those of Mathews and Pendleton (2006) with one primary exception: pup counts in JHI in June had a significant negative trend (−5.0%/yr; −6.0, −4.0 CI) for the 15-yr period from 1994 to 2008 (Fig. 2A). In contrast, from 1994 to 1999, the number of pups was stable (3.6%/yr; −1.0, 8.1 CI) (Mathews and Pendleton 2006). Long-term trend estimates for non-pups in June and August in JHI were also negative (Fig. 2B, 3A). In addition, the long-term trend estimate (−12.4%/yr; −13.7, −11.1 CI) for seals at terrestrial sites (Fig. 3B) was also similar to those reported by Mathews and Pendleton (2006). In all cases, the adjusted mean counts from the most recent data (2004–2008) are less than those for the years (1992–2002) reported by Mathews and Pendleton (2006), which suggests that declines in the number of seals have not abated or reversed.

The estimated pup proportion in JHI increased more slowly (year coefficient = 0.0148; 95% CI 0.0107–0.0188) for our longer-term analysis (1994–2008) compared with the estimate from 1994 to 1999 (year coefficient = 0.0539; 0.0394–0.0683) (Mathews and Pendleton 2006) with the proportion again related to date. Based on Wald chi-square statistics ($P < 0.05$), the final logistic regression model included year, date and date, time, sky, and precipitation. We assumed that the date of the peak pup proportion (estimated peak was 16 June) was constant across years. Although a long series of surveys was not available for all years, most years seemed to follow the predicted date pattern fairly well. One exception was in 2008, when the date of peak pup proportion was later than in most years (26 June–1 July).

Seasonal variation in seal counts in JHI followed the expected bimodal pattern for harbor seals in Alaska with peaks in June and August and substantially lower counts in July and September (Jemison *et al.* 2006). In addition, there was substantial within- and between-day variation in the number of seals counted. For example, on the afternoon of 12 August 2007 the maximum mean paired count of seals (mean = 378, SD = 33.94) in JHI was 81% less than the maximum mean paired count

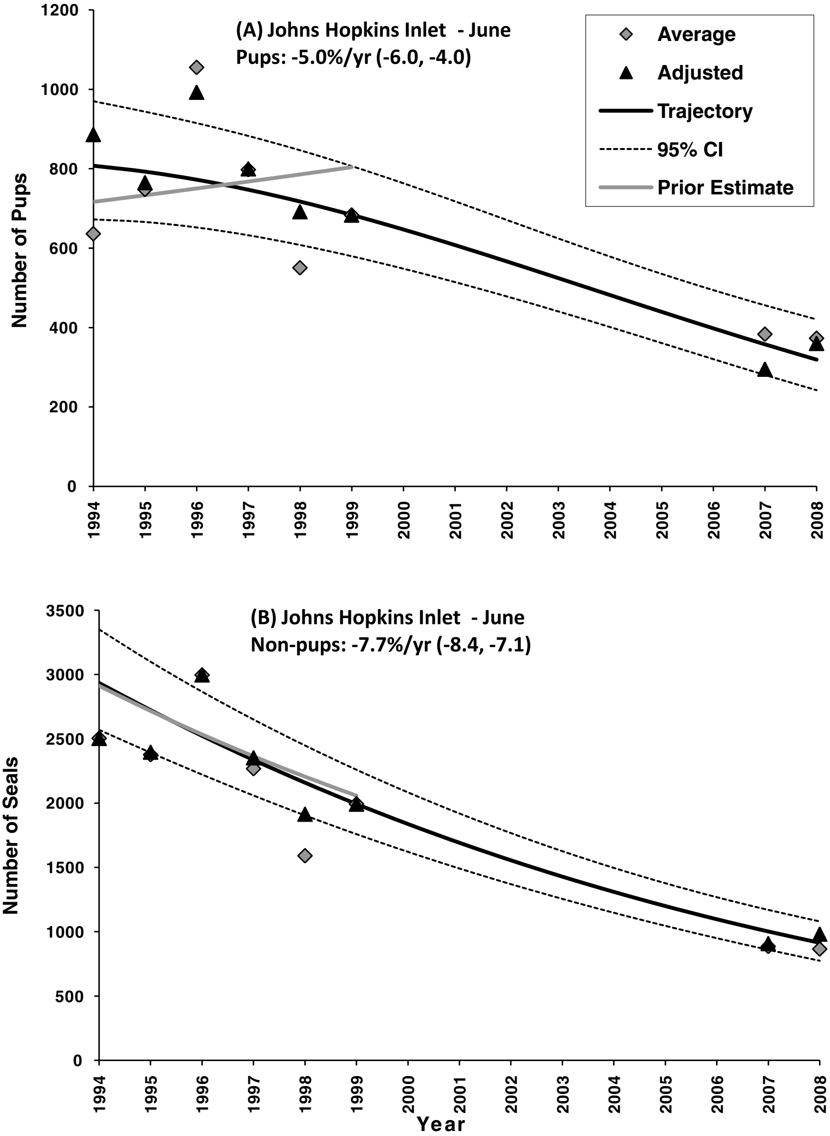

*Figure 2.* Trajectory (*i.e.*, the smoothed pattern of population change over time) of the number of (A) pups and (B) non-pups counted in June in Johns Hopkins Inlet, Glacier Bay from 1994 to 2008. Average counts were from field counts and adjusted counts were functions of the field counts adjusted for the effects of the other covariates in the model (*e.g.*, survey date, time, tide height).

(mean = 1961, SD = 183) 10 d later on 22 August 2007. The dramatic difference between the counts was attributed to a temporary reduction in the amount of glacial ice in JHI on 12 August 2007. Extreme temporal variation in the number of seals counted between August and September in JHI was previously documented with

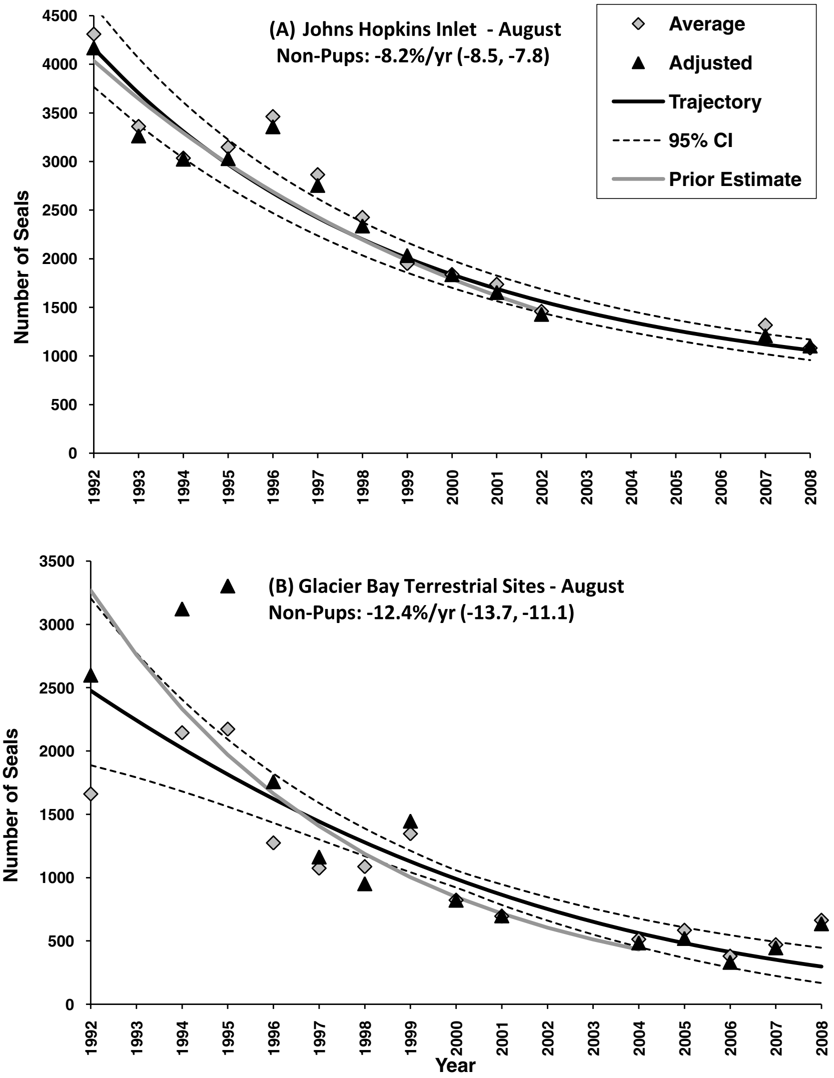

*Figure 3.* Trajectory (*i.e.*, the smoothed pattern of population change over time) of the number of seals counted in August in (A) Johns Hopkins Inlet and (B) in late July and August at terrestrial sites throughout Glacier Bay from 1992 to 2008. Average counts were from field counts and adjusted counts were functions of the field counts adjusted for the effects of the other covariates in the model (*e.g.*, survey date, time, tide height).

85% fewer seals counted in September than three weeks earlier in August 1993 (Mathews and Kelly 1996). These more recent data reinforce the notion that changes in survey timing, of even a few days or weeks, could influence seal counts and hence, trend estimates (Simpkins *et al.* 2003, Small *et al.* 2003, Jemison *et al.* 2006).

The number of seals in Glacier Bay continues to decline based on the most recent data through 2008 (Fig. 2, 3). In contrast to previous results, pup counts in JHI in June had a significant negative trend (−5.0%/yr) for the 15-yr period from 1994 to 2008 (Fig. 2A). Although the number of pups has declined in recent years, the proportion of pups has not, suggesting that productivity (pups/adult female) might not have declined. Mathews and Pendleton (2006) speculated that the pattern in JHI could be caused by the differential age- and sex-specific mortality, similar to Sable Island, Nova Scotia, where pup counts eventually declined with declines in adult females (Bowen *et al.* 2003). This pattern is similar to what appears to have taken in place in JHI, where the longer-term analysis (1994–2008) now estimates a decline in pups.

It is still unclear why seals are declining in Glacier Bay. Harbor seal population trajectories at other terrestrial sites (Ketchikan and Sitka) in southeastern Alaska have been increasing or stable (Small *et al.* 2003) and vary substantially from the continuous long-term declines documented in Glacier Bay. The opposing trends for harbor seals in the different regions create considerable difficulty in determining an overall trend for the southeastern Alaska stock of harbor seals (Angliss and Outlaw 2007). Elsewhere in the Gulf of Alaska, steep declines in the number of seals occurred at Tugidak Island from 1976 to 1988 (Pitcher 1990); however, recent data from the 1990s show increasing trends in the number of seals but with counts still far less than in the 1970s (Jemison *et al.* 2006). Although the declines in some areas appear to have abated (Jemison *et al.* 2006), harbor seal abundance in other areas, such as the western Aleutian Archipelago, declined by up to 86% between the 1970s and the late 1990s and mirrors similar declines in Steller sea lions (*Eumetopias jubatus*) in the same region (Small *et al.* 2008).

The similar declines in harbor seals and Steller sea lions in the Aleutian Archipelago (Small *et al.* 2008) are in sharp contrast to population trajectories for the two sympatric species in the Glacier Bay area. While harbor seals have declined substantially in Glacier Bay from 1992 to 2008, the trend in the number of Steller sea lions counted in the Glacier Bay/Icy Strait region has increased by 10.1%/yr from 1976 to 2009.[2] Steller sea lions occupy South Marble Island, the primary sea lion haul-out site in Glacier Bay, throughout the year (Womble *et al.* 2005, 2009) and a new sea lion rookery was recently established at Graves Rocks along the outer coast near Glacier Bay (Gelatt *et al.* 2007, Pitcher *et al.* 2007). Likewise, the median population growth rate for humpback whales (*Megaptera novaeangliae*) in northern southeast Alaska region has been 8.7%/yr from 1994 to 2002.[3] Steller sea lions, harbor seals, and humpback whales use similar foraging habitat and prey on similar prey species including walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), Pacific sandlance (*Ammodytes hexapterus*), and herring (*Clupea pallasii*) in the Glacier Bay area (Krieger and Wing 1984, Gelatt *et al.* 2007, Herreman *et al.* 2009*b*). Such prey overlap could

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[2] Personal communication from Grey W. Pendleton, Alaska Department of Fish & Game, Division of Wildlife Conservation, P. O. Box 110024, Juneau, AK 99811, 7 November 2009.

[3] Personal communication from A. Noble Hendrix, R2 Resource Consultants, Inc., 15250 NE 95th Street, Redmond, WA 98052, 31 August 2009.

lead to direct and indirect interactions and result in negative population-level effects on harbor seals (*e.g.*, Mathews and Pendleton 2006, Herreman *et al.* 2009*a*). Increased predation, consistent with observed demographic changes, has also been proposed as a factor in the ongoing harbor seal declines (Taggart *et al.* 2005, Mathews and Pendleton 2006).

Given the continued declines in the number of seals counted in Glacier Bay and the paucity of long-term monitoring data that exist for glacial ice sites in Alaska, we suggest that monitoring of seals during the pupping and molting periods continue for several reasons. First, Glacier Bay is one of only two glacial ice sites in Alaska where long-term monitoring efforts have occurred during both the pupping and molting periods since the 1970s (Streveler 1979,[1] Calambokidis *et al.* 1987, Mathews and Pendleton 2006). Alaska-wide estimates of harbor seal abundance have traditionally been conducted only during the molting period in August (Boveng *et al.* 2003). Monitoring seals during the pupping period at a few index sites, such as Glacier Bay, can provide data on pup production, an important variable for understanding population dynamics and interpreting rates of population change. In addition, count data collected at index sites can also provide data on the effects of environmental covariates on seal counts and can provide useful information for interpreting counts of seals from aerial surveys (Jemison *et al.* 2006).

Second, glacial ice sites may be particularly important habitat for harbor seals during the pupping season and may provide a refuge from predation for young seals. The proportion of pups in JHI ranges from 34% to 37% compared to 10%–25% reported for terrestrial haul-out sites (Calambokidis *et al.* 1987, Mathews and Pendleton 2006). However, the regional extent of the influence of pup production in Glacier Bay is unclear. Genetic analysis based on mitochondrial DNA suggests finer-scale population structure of harbor seals in Alaska (Westlake and O'Corry-Crowe 2002); however, Herreman *et al.* (2009*b*) suggest wider patterns of male-biased dispersal and less genetic differentiation based on the analysis of microsatellite data from seals in Glacier Bay and Prince William Sound. Furthermore, recent satellite telemetry data from juvenile and adult female seals tagged in JHI in September of 2007 and 2008 demonstrate that seals may exhibit strong site fidelity to Glacier Bay during the breeding season, particularly to the glacial ice site in JHI. Although individuals ranged extensively throughout the inner and outer waters of northern southeastern Alaska and the eastern Gulf of Alaska during the post-breeding season (September–April), 92% (22 of 24) of seals whose tags transmitted until the next breeding season (defined as 1 June), returned to Glacier Bay, and primarily to the glacial ice site in JHI.[4]

Finally, rapid and dramatic thinning and loss of glaciers in Alaska has occurred over the last 200 yr (Arendt *et al.* 2002, Larsen *et al.* 2007) and will likely influence the ecology of harbor seals that are dependent upon glacial ice as a resting substrate. Specifically in Glacier Bay, the dramatic retreat of tidewater glaciers of over 100 km over the past 250 yr represents one of the most rapid glacial

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[4] Unpublished data, Jamie N. Womble, National Park Service, Glacier Bay Field Station, 3100 National Park Road, Juneau, AK 99801.

retreats on record (Cooper 1937, Field 1947, Hall *et al.* 1995). From 1974 to 1982, 12 tidewater glaciers were actively calving icebergs into Glacier Bay (Molnia 2007); however, as of 2008, only five glaciers (Johns Hopkins, Gilman, Margerie, Lamplugh, and McBride) were actively calving icebergs into Glacier Bay. If the loss of ice-associated habitat continues as predicted, seals may use terrestrial haul-outs, spend more time in the water, or move to other areas outside of Glacier Bay. Each of these potential responses by seals to the loss of ice-associated habitat could have both local and regional demographic consequences, particularly if seals from glacial ice sites serve as source populations for surrounding regions. Ultimately, the loss of ice-associated habitat in conjunction with a declining population could limit the population recovery of seals in Glacier Bay. Given the reliance of seals on glacial ice habitat in Glacier Bay coupled with the rapidly changing extent of tidewater glaciers, we suggest that future monitoring efforts should include quantifying the availability of glacial ice relative to harbor seal abundance and distribution.

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## Literature Cited

Angliss, R. P., and R. B. Outlaw. 2007. Alaska marine mammal stock assessments, 2007. NOAA Technical Memorandum NMFS-AFSC-180. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center. 252 pp.

Arendt, A. A., K. A. Echelmeyer, W. D. Harrison, C. S. Lingle and V. B. Valentine. 2002. Rapid wastage of Alaska glaciers and their contribution to rising sea-level. Science 297:382–386.

Bengtson, J. L., A. V. Phillips, E. A. Mathews and M. A. Simpkins. 2007. Comparison of survey methods for estimating abundance of harbor seal (*Phoca vitulina*) in glacial fiords. Fishery Bulletin 105:348–355.

Boveng, P. L., J. L. Bengtson, D. E. Withrow, J. C. Cesarone, M. A. Simpkins, K. J. Frost and J. J. Burns. 2003. The abundance of harbor seals in the Gulf of Alaska. Marine Mammal Science 19:111–127.

Bowen, W. D., S. L. Ellis, S. J. Iverson and D. J. Boness. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: Implications for explaining the decline of harbour seals, *Phoca vitulina*, on Sable Island. Journal of Zoology, London 26:155–163.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretical approach. Springer, New York, NY.

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

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

Field, W. O. 1947. Glacier recession in Muir Inlet, Glacier Bay, Alaska. Geographical Review 37:369–399.

Gelatt, T., A. W. Trites, K. Hastings, L. Jemison, K. Pitcher and G. O'Corry-Crowe. 2007. Population trends, diet, genetics, and observations of Steller sea lions in Glacier Bay National Park, Alaska. Pages 145–149 *in* J. F. Piatt and S. M. Gende, eds. Proceedings of the Fourth Glacier Bay Science Symposium: U.S. Geological Survey Scientific Investigations Report 2007-5047. US Department of the Interior, US Geological Survey, Reston, Virginia.

Hall, D. K., C. S. Benson and W. O. Field. 1995. Changes of Glaciers in Glacier Bay, Alaska using ground and satellite measurements. Physical Geography 16:27–41.

Herreman, J. K., G. M. Blundell and M. Ben-David. 2009*a*. 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.

Herreman, J. K., G. M. Blundell, D. B. McDonald and M. Ben-David. 2009*b*. Asymmetrical male-mediated gene flow between harbor seal (*Phoca vitulina*) populations in Alaska. Canadian Journal of Zoology 87:498–507.

Hoover, A. A. 1983. Behavior and ecology of harbor seal (*Phoca vitulina richardsi*) inhabiting glacial ice in Aialik Bay, Alaska. M.S. thesis, University of Alaska, Fairbanks, AK. 133 pp.

Hoover-Miller, A. A. 1994. Harbor seal (*Phoca vitulina*) biology and management in Alaska. Marine Mammal Commission. Contract #T75134749. Washington, DC. 45 pp.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. John Wiley and Sons, Inc., New York, NY.

Jansen, J. K., J. L. Bengtson, P. L. Boveng, S. P. Dahle and J. Ver Hoef. 2006. Disturbance of harbor seals by cruise ships in Disenchantment Bay, Alaska: An investigation at three spatial and temporal scales. AFSC Processed Report 2006-02, Alaska Fisheries Science Center, National Marine Fisheries Service, Department of Commerce. 75 pp.

Jemison, L. A., G. W. Pendleton, C. A. Wilson and R. J. Small. 2006. Long-term trends in harbor seal numbers at Tugidak Island and Nanvak Bay, Alaska. Marine Mammal Science 22:339–360.

Krieger, K. J., and B. L. Wing. 1984. Hydroacoustic surveys and identification of humpback whale forage in Glacier Bay, Stephens Passage, and Frederick Sound, southeastern Alaska, summer 1983. NOAA Technical Memorandum NMFS F\NWC-66. U.S. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska. 60 pp.

Larsen, C. F., R. J. Motyka, A. A. Arendt, K. A. Echelmeyer and P. E. Geissler. 2007. Glacier changes in southeast Alaska and northwest British Columbia and contribution to sea level rise. Journal of Geophysical Research 112:F01007, doi:10.1029/2006JF000586.

Link, W. A., and J. R. Sauer. 1997. Estimation of population trajectories from count data. Biometrics 53:488–497.

Mathews, E. A. 1995. Longterm trends in the abundance of harbor seals (*Phoca vitulina richardsi*) and development of monitoring methods in Glacier Bay National Park, Southeast Alaska. Pages 254–263 *in* D. R. Engstrom, ed. Proceedings of the Third Glacier Bay Science Symposium, U.S. National Park Service, Glacier Bay National Park & Preserve, P. O. Box 140, Gustavus, AK.

Mathews, E. A., and B. P. Kelly. 1996. Extreme temporal variation in harbor seal (*Phoca vitulina richardsi*) numbers in Glacier Bay, a glacial fiord in Southeast Alaska. Marine Mammal Science 12:483–488.

Mathews, E. A., and G. W. Pendleton. 2006. Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. Marine Mammal Science 22:170–191.

Molnia, B. F. 2007. Late nineteenth to early twenty-first century behavior of Alaskan glaciers as indicators of changing regional climate. Global and Planetary Change 56:23–56.

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., P. F. Olesiuk, R. F. Brown, M. S. Lowry, S. J. Jeffries, J. L. Sease, W. L. Perryman, C. E. Stinchcomb and L. F. Lowry. 2007. Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. Fishery Bulletin 107:102–115.

Simpkins, M. A., D. E. Withrow, J. C. Cesarone and P. L. Boveng. 2003. Stability in the proportion of harbor seals hauled out under locally ideal conditions. Marine Mammal Science 19:791–805.

Small, R. J., G. W. Pendleton and K. W. Pitcher. 2003. Trends in abundance of Alaska harbor seals, 1983–2002. Marine Mammal Science 19:344–362.

Small, R. J., P. L. Boveng, G. V. Byrd and D. E. Withrow. 2008. Harbor seal population decline in the Aleutian Archipelago. Marine Mammal Science 24:845–863.

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

Westlake, R. L., and G. M. O'Corry-Crowe. 2002. Macrogeographic structure and patterns of genetic diversity in harbor seals (*Phoca vitulina*) from Alaska to Japan. Journal of Mammalogy 83:1111–1126.

Womble, J. N., M. F. Willson, M. F. Sigler, B. P. Kelly and G. R. VanBlaricom. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. Marine Ecology Progress Series 294:271–282.

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

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