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## Natural and human effects on harbor seal abundance and spatial distribution in an Alaskan glacial fjord

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### ABSTRACT

Tidewater glacial fjords support the largest populations of harbor seals (*Phoca vitulina richardii*) in Alaska and are a prime destination for tour ships. Chronic disturbance from ships, however subtle, could impact long-term population stability. We examined variation in abundance and distribution of harbor seals on floating ice in Disenchantment Bay, Alaska, a tour ship destination for over a century with near daily visitation by ships in the spring/summer over the last decade. Counts of seals by aerial transect showed a sharp decline in May, prior to pupping and the first ships arriving; counts rebounded by the end of June remaining high until August. Seal distribution and abundance peaked in 5–7 tenths ice cover; total area of ice cover showed no effect. Despite regular flushing of seals by ships, we found no broad-scale patterns in seal abundance and distribution that could be explained by ship presence. We cannot rule out mechanisms of long-term disturbance, difficult to detect and that might explain notable differences with other, similar sites. Population declines at disturbed glacial sites and the still rising popularity of vessel-based tourism indicate a need for individual-based studies on how seals respond to the dynamics of glacial ice environments and human-caused stresses.

Key words: harbor seal, spatial distribution, seasonal abundance, human disturbance, glacial fjords, cruise tourism, ice habitat, aerial survey, space-time model, zero-inflated counts.

Tidewater glacial fjords are high-priority stops on the itineraries of large cruise vessels in Alaska. Ice emanating from these glaciers supports some of the largest seasonal aggregations of harbor seals (*Phoca vitulina*) in the world (>5,400 animals at Icy Bay, Alaska; Jansen *et al.* 2006). These seal aggregations compose a significant portion of the statewide abundance (10%–15%; Boveng *et al.* 2003, Bengtson *et al.* 2007). They may also have higher than average productivity and thus be important source popula-

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tions (Womble *et al.* 2010). Glacial haul-out sites offer advantages over terrestrial sites during the physiologically demanding periods of pup rearing and molting, such as: (1) the availability of floating ice as a haul-out platform that does not vary with the tide; (2) fjords are largely protected from ocean swell and waves promoting reliable haul-out conditions; (3) there are milder, drier conditions at the head of fjords where seals haul out, due to offshore air flow across glaciers and topographical shielding of storms (Papineau 2000, National Ocean Service 2010); and (4) ice fields may provide protection from both land and marine predators (Calambokidis *et al.* 1987, Nordstrom 2002, Blundell *et al.* 2011, Hoover-Miller *et al.* 2011). Moreover, the estuarine nature of tidewater-glacier systems has been shown in some Alaskan fjords to promote relatively high primary productivity, which supports secondary consumers that are believed to provide foraging opportunities for upper predators (Arimitsu *et al.* 2012).

The environmental effects of cruise tourism in Alaska have gone largely untested despite the dramatic increase in such tourism since the 1980s (Alaska Department of Community and Economic Development 2004, Alaska Department of Environmental Conservation 2004). The number of visitors traveling on cruise ships surpassed 1 million in 2007—up from 140,000 in 1985 (Alaska Department of Commerce and Economic Development 1993, McDowell Group Inc. 2012). In the first published study of vessel effects on seals in glacial fjords, Jansen *et al.* (2010) documented flushing of seals by cruise ships when approached closer than 500 m, which occurred for 85% of the ships used as observation platforms. Despite a cruise-industry policy to avoid seals, in their study area (Disenchantment Bay, Alaska) ships regularly disturbed harbor seals at least in part because the seals were not spotted until at close range. In 2013, about 723 vessel-visits were scheduled at the six tidewater glacier fjords that cruise lines regularly visit in Alaska: Endicott Arm, Glacier Bay, Disenchantment Bay, Tracy Arm, Collette Fjord, and Columbia Bay (Cruise Line Agencies of Alaska 2013)—each with known populations of harbor seals.<sup>2</sup> Currently in the United States, only Glacier Bay has regulations that restrict the movement of vessels (including cruise ships) near harbor seals (36 Code of United States Federal Regulations 13.65). Increases of ship-based tourism at glacial fjords are among the factors being considered to explain dramatic declines in seals, especially as adjacent terrestrial populations have been stable or increasing (Small *et al.* 2003, Mathews and Pendleton 2006, Womble *et al.* 2010, Hoover-Miller *et al.* 2011). Uncertainty regarding the causes of these and other longer-standing declines of harbor seals in Alaska (*e.g.*, western Gulf of Alaska and Glacier Bay) underscores the need to differentiate natural from human-caused effects on populations and their use of a habitat (Pitcher 1990; Frost *et al.* 1999; Small *et al.* 2003, 2008; Mathews and Pendleton 2006; Womble *et al.* 2010).

Studies of harbor seals hauled out on land show that human disturbance can cause seals to abandon haul-out areas temporarily, long-term, or permanently, or shift their haul-out timing (Sullivan 1980, Allen *et al.* 1984, Henry and Hammill 2001, Grigg *et al.* 2002, Edrén *et al.* 2010, London *et al.* 2012). Suryan and Harvey (1999) found increased levels of tolerance among harbor seals to repeated disturbance by small boats, but increased vigilance and response to disturbance at sites with more pups. Pregnant and postpartum females have been noted to be more sensitive to disturbance (Newby 1973, Lawson and Renouf 1985, Suryan and Harvey 1999), particularly as they tend to haul out at the edges of mixed groups or at separate nursery sites (Allen *et al.* 1988, Thompson 1989). Successful weaning and pup

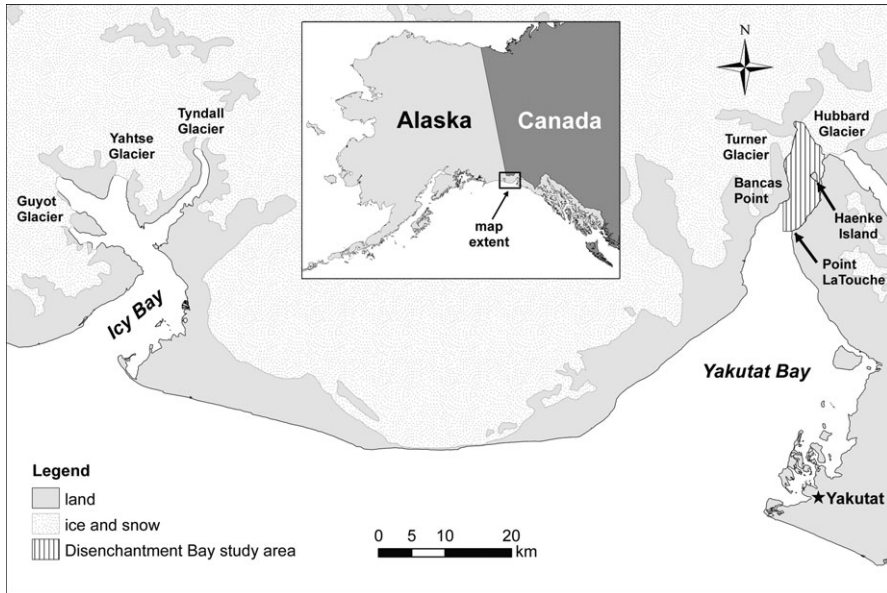
<sup>2</sup>Unpublished data (NMML/AFSC).

production can also be reduced by chronic disturbance (Thiery and Kiszka 2005). Less is known about the long-term response of seals to disturbance, though Montgomery *et al.* (2007) showed that haul-out locations of harbor seals in Cook Inlet, Alaska occur more distantly from human communities than expected on the basis of natural habitat features. With increasing human disturbance, historically profitable areas for seals (*e.g.*, where they rest or target prey; Brown and Mate 1983, Bayer 1985, Thompson *et al.* 1991) are likely to be degraded and show a decline in use as seals pioneer new habitat (Harris *et al.* 2003, Womble *et al.* 2010, Cordes *et al.* 2011). It has not yet been feasible to estimate effects of disturbance on harbor seal survival but models of energetics have shown that thermal stress on young seals repeatedly flushed into the water is a possible source of mortality, an effect particularly relevant in the near-freezing water of glacial areas (Harding *et al.* 2005, Jansen *et al.* 2010). Despite decades of harbor seal surveys throughout their range, most studies have focused on annual seal counts to examine long-term trends as opposed to more frequent counts of seals paired with habitat data to examine the effects of environmental factors. For managers to respond appropriately to decreasing populations, it is critical to know how seals over the course of a year strike a balance between their habitat requirements *vs.* what resources a habitat provides, and particularly whether human factors influence this equilibrium.

The aim of this study was to assess the factors that influence the number and location of harbor seals hauling out on ice in Disenchantment Bay, and in particular to test the effects of a dynamic ice environment and the cruise ships that regularly move through this habitat. Ships began visiting Disenchantment Bay sporadically in the 1880s and continued at low levels through most of the 20th century (USDA Forest Service 2001). Since the 1980s, ship visits in Disenchantment Bay per annum have risen from fewer than 15 to a peak of 170 in 2005 and are currently 130–150, resulting in near-daily visits of up to four cruise ships from mid-May to September (Cruise Line Agencies of Alaska 2013). Following from Jansen *et al.* (2010), who showed that ships regularly caused seals in Disenchantment Bay to flush off the ice, we hypothesize that chronic and proximate disturbance by ships elicits behavioral reactions over days to weeks that alter seal abundance and spatial distribution. We tracked vessel movements in conjunction with counts and locations of seals sampled *via* aerial transects to test whether seals avoided areas used most intensively by vessels, and ultimately, whether ships were likely to cause seals to avoid the ice haul-out area altogether. By accounting for environmental factors in a quantitative framework, we present findings that robustly define the glacial ice habitat and thus show its importance for these populations.

### *Study Area*

We studied the seal population in Disenchantment Bay (DB), a tidewater glacier fjord in the eastern Gulf of Alaska (Fig. 1). The study area was defined as the region within DB bounded to the south approximately by a line drawn between Point La Touche and Bancas Point (Fig. 1). During the spring and summer, floating ice is prevalent throughout the bay, emanating from two tidewater glaciers: Hubbard and Turner. Although calved ice can be >15 m across and >5 m above water (termed icebergs), the vast majority of ice in the study area was considerably smaller, termed bergy bits (<15 m across), growlers (<5 m), and brash (<2 m). The presence of floating ice suitable as haul-out platforms indicated active, daily glacial calving since bergy bits are believed to melt completely in about 1–3 d (Long 1992).



*Figure 1.* Map of Disenchantment Bay study areas near Yakutat, Alaska. Major tidewater glaciers are labeled. The location of the terminus of Hubbard Glacier was mapped in early June 2002 as part of this study. The extent of snow and ice-covered terrain (stippled area) was derived from a NOAA Coastal Service satellite photo taken in 1993. Icy Bay, an adjacent tide-water glacial fjord with a seal population (see Discussion), is shown for reference.

## METHODS

### *Aerial Surveys of Seals and Ice in Disenchantment Bay*

Aerial surveys of seals' relative abundance and distribution were conducted 1–4 times weekly from 2 May to 4 August 2002, beginning 12 d prior to the first entry of cruise ships into DB. Surveys were conducted almost daily from 12 to 16 May immediately preceding and following the first cruise ship visit of the year on 14 May. Subsequent surveys were timed to facilitate a comparison between periods of low and high ship visitation. Surveys were flown from 1300 to 1600 (ADT) to coincide with the daily peak in numbers of seals hauled out (Hoover 1983, Calambokidis *et al.* 1987). A single engine aircraft (Cessna 206; Yakutat Coastal Airways Inc., Yakutat, AK) was flown at 100 knots (185 km/h) and an altitude of 1,000 ft (305 m). We flew a standard grid of 14 transects, oriented along the longest axis of the bay and separated by 400 m. Seal locations and ice coverage were recorded by a video camera (Sony TRV900) mounted vertically in a housing on the starboard wing strut with the zoom lens preset to record a 70 m strip directly beneath the plane.

Videotapes were played back and analyzed on a 13 in. video monitor (Sony Trinitron, Model PVM1344Q) by a single observer (SPD). Harbor seals hauled out on ice were counted as they passed a horizontal line drawn across the bottom third of the screen. This ensured that the virtual width of the survey strip (70 m) was kept nearly constant even though the plane (and camera) may have rocked side to side and thus

recorded, if only briefly, seals that were just outside the intended strip. This method also standardized the position on the screen, and thus the survey time, at which seals were sighted. Pups were identified based on their relative size (smaller) and proximity (less than one body length away) to an adjacent seal. This likely underestimates the incidence of pups because mothers are known to leave pups unattended during the nursing period (Boness *et al.* 1994).

Locations of seal groups along transects were determined by matching the times of seal sightings to the GPS coordinates from a recorded track. For each video frame containing seals, at the point when the seal passed the horizontal line, the observer estimated visually the proportion of ice coverage to the nearest tenth for ice considered large enough to support at least one seal (*i.e.*, >2 m at its longest axis). When seals were not present, ice coverage was estimated at 15 s intervals which, depending on the speed of the plane, provided a measure of ice cover at least every 0.75–1 km. Hoover (1983) found that seals in Aialik Bay hauled out in peak numbers on ice that was 1–3 m across; parturient females preferred ice that was >5 m. In referring to ice cover, we used three types (or zones): scattered ice (1–3 tenths ice cover), intermediate ice (4–6 tenths), and dense ice (7–10 tenths).

### GIS Analyses

Seal counts and ice cover densities were mapped into a geographic information system (GIS) as separate point layers. To accommodate the statistical model, the ice and seal point data were each summarized into a grid of  $400 \times 400$  m cells for the entire study area ( $41 \times 19$  cells). Ice cover was averaged when multiple observations fell within a single cell's boundaries; seal counts were summed. GPS navigation tracks from cruise ships were converted to line layers in the GIS, and indices of potential cruise ship exposure to harbor seals were calculated on the basis of number of ship visits, ship distance, and time at closest approach (TACA; see below). The number of ship visits was summed for the 3 d leading up to and including the day of an aerial survey, which was then assigned to all cells (*i.e.*, a global variable). Low statistical power prevented us from testing effects using a finer temporal resolution of ship presence leading up to a survey. Ship distance was defined as the closest approach of a cruise ship to the centroid of each cell containing seals (*i.e.*, a cell-specific variable), and TACA was defined as the amount of time that ships spent within a 1 km radius of the point of closest approach to a cell. To get an adequate sample for these measures we used the tracks of cruise ships that entered the study area on the day of an aerial survey and the day prior. Ships' tracks were used to calculate ship activity for a given survey provided they reached their turn-around point prior to the end of the aerial survey. One ship that visited on 3 August, one day prior to the final aerial survey, was not tracked but we assumed that it followed a path similar to the most recent ship on 1 August. From 23 July to 1 August, reduced ice conditions allowed ships to follow nearly identical routes through the middle of the bay to within about 1 km of Hubbard Glacier.

### Time Series of Relative Abundance

Because the daily sampling coverage was standardized, the total observed seals provided an index of seasonal changes in abundance. We modeled temporal changes in abundance by fitting generalized additive models (GAM; Hastie and Tibshirani 1995) to counts of all seals and pups. GAMs are semiparametric



methods that allow the data to suggest flexible functional forms in response to explanatory variables, which is often necessary for ecological data where complicated functions may be expected (Barry and Welsh 2002). The GAM used a log-link function with a negative binomial distribution to allow for overdispersion. Following recommendations by Wood (2006), we tried variable numbers of knots but settled on six because beyond this the estimated degrees of freedom changed little. The smoothing and overdispersion parameter in the negative binomial were estimated using generalized cross-validation. Models were fit using the “gam” function in the “mgcv” package (Wood 2006) in the statistical program R (R Development Core Team 2006). We evaluated the effect of date separately because the space-time models (described below) sought to remove date effects that could have confounded the effects of weather and vessel covariates that also varied by date.

### *Space-Time Modeling of Covariate Effects on Seal Counts*

Based on local knowledge related by the Yakutat Tlingit Tribe, we expected harbor seals in DB to be spatially clustered. The tendency for seal counts in adjacent cells to be more similar than distant cells, termed spatial autocorrelation (SAC), presents challenges for inference from conventional statistical tests that assume samples are independent. Assuming independence when SAC exists overestimates the degrees of freedom, biases the coefficients and their standard errors, and can cause the coefficients to be considered significantly different from zero when they are not. It was, therefore, necessary to model the pair-wise correlations between all seal cell counts to account for the effects of SAC while simultaneously testing for covariate effects on those counts. Accounting for SAC reduces power to detect differences but also reduces the chances of falsely declaring significant effects. The spatial autocorrelation of the random errors was modeled using a conditional autoregressive model (CAR; Besag 1974).

Observations can also be correlated in time. As with SAC, assuming temporal independence of serial observations can inflate the degrees of freedom resulting in a higher risk of concluding a significant effect when one does not exist. The temporal autocorrelation of the random errors was modeled using a first-order autoregressive model (AR1).

Seals counts were modeled with global covariates (wind, rain, and number of ship-visits, which varied temporally but not spatially) and local covariates (ice cover, ship distance, and ship activity [TACA], which varied spatially and temporally). The effects of ice were modeled as 10 discrete classes of the percent cover from 1 to 10 tenths.

A frequent characteristic of large-scale survey data is a large number of zero observations. Seals in DB occupied less than a third, on average, of the cells containing ice on a given day. Such zero-inflated count data, a form of overdispersion (McCullagh and Nelder 1989), if modeled conventionally can also lead to incorrect inference and biased parameters. We modeled the zero-inflated data in two steps: (1) model the presence/absence component of the data (using a Bernoulli distribution), and (2) model the observed abundance conditional on seals being present (using a Poisson distribution; Mullahy 1986, Heilbron 1994, Welsh *et al.* 1996). Ver Hoef and Jansen (2007) favored a type of hurdle or two-stage spatio-temporal model (P1B) over simple zero-inflated Poisson (ZIP) spatio-temporal models because it allowed them to completely specify and separate the binary and count distributions. This nonmixture model was appropriate because seals were unlikely to be missed from the high contrast video and thus we had high confidence that an observed count of zero meant

seals were not present. We use only the P1B model, which accounts for spatio-temporal autocorrelation and zero-inflation. The zero-inflated, space-time P1B regression was fitted using Markov Chain Monte Carlo (MCMC) in WinBUGS software (Version 1.4, Imperial College & MRC, U.K.).

Using this model, we examined the empirical relationship between the distribution (presence) and abundance (counts) of seals and key habitat features, natural and anthropogenic. To display the model outputs for ice, our cover categories were used to estimate standardized resource selection coefficients (Manly *et al.* 2010), which when applied to logistic regression are odds ratios that sum to one. Thus the coefficients can be viewed as probabilities of habitat use by seals with the null hypotheses being equal probabilities of use across all ice categories. Credibility intervals for the standardized resource selection coefficients were obtained from the posterior distributions of the P1B regression parameters (Ver Hoef and Jansen 2007). For other habitat features, we report the 95% confidence intervals of the regression coefficients; if these included zero we concluded there was no statistical evidence of an effect (*i.e.*,  $P > 0.05$ ).

### *Meteorology*

Weather conditions (air temp, barometric pressure, relative humidity, and wind speed) in DB were measured using a HOBO weather station (Onset Computers, Bourne, MA) installed on Haenke Island (Fig. 1). We used precipitation data from the Yakutat Airport (NOAA-NCDC 2002), located 53 km to the south, as a proxy for rainfall in DB. Data on hourly precipitation and wind speed were summed or averaged, respectively, for the 6 h preceding each aerial survey for input to statistical models. Increased levels of rain and wind are known to reduce the propensity of seals to haul out (Hoover 1983, Boveng *et al.* 2003).

### *Cruise Ship Movements*

Cruise ships ventured as far into the bay as ice and visibility allowed, to give passengers close views of the glaciers. Navigation tracks from 56 cruise ships were recorded using portable global positioning system (GPS) receivers. This sample of ships represents those that visited on the day of, or day before, one of our aerial surveys. A schedule of all ship visits that occurred during the study was obtained from Cruise Line Agencies of Alaska (2013).

## RESULTS

### *Seasonal Changes in Seal Abundance and Distribution*

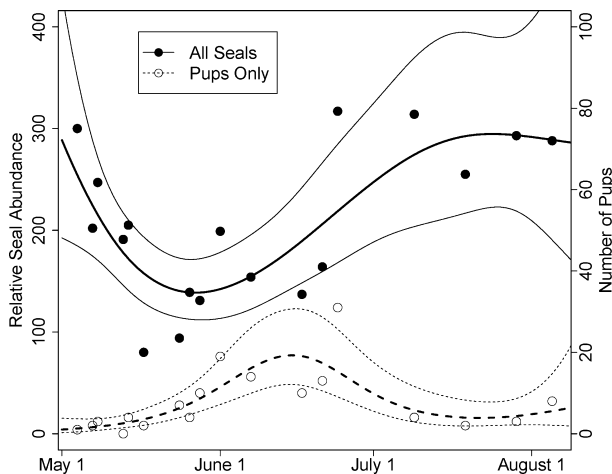
The modeled seal counts showed that relative abundance varied by date (estimated  $df = 3.44$ ,  $P = 0.011$ ; Fig. 2) with several pronounced shifts occurring during the study. On 3 May, relative abundance was near peak levels but then declined sharply to a minimum by mid-May. Counts increased slowly until late June when they rebounded and remained high until the last survey on 4 August. The number of pups also rose sharply in late June (estimated  $df = 3.73$ ,  $P = 0.002$ ; Fig. 2), suggesting that the rise in all seals resulted partly from an increase in pregnant and postparturient mothers; at the peak, mothers and pups combined contributed about 20% of the total (10% each). The subsequent decline in pup numbers in early July, despite high

numbers of all seals, was likely due to pups weaning and no longer associating with moms, which was a criteria for identifying an animal as a pup.

Seals hauled out in the highest numbers north and west of Haenke Island with smaller groups scattered to the south (Fig. 3). Distinct aggregations of seals were almost always apparent, but their spatial extent and location varied in conjunction with abundance. Prior to and during the decline in early May, seals were located in a relatively small area to the northwest of Haenke Island (Fig. 3). In late May, however, as abundance was increasing, seals occupied areas to the south and were more dispersed. During June, when ice cover was more extensive, seals were scattered almost equally north and south of Haenke Island, mostly in the western half of the bay. As ice cover steadily declined from late June through early August, seals were increasingly aggregated in areas closest to the Hubbard Glacier (Fig. 3).

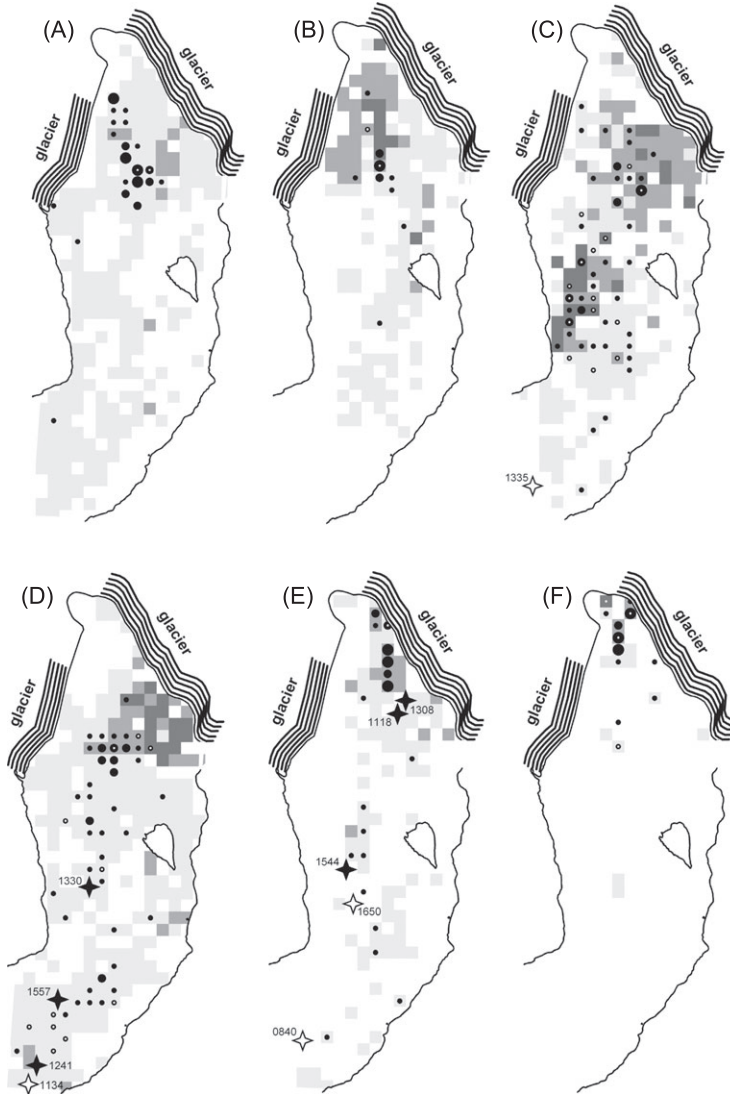
#### *Seal Distribution and Abundance in Relation to Ice, Weather, and Ships*

Even after accounting for strong positive temporal and spatial autocorrelation (see Ver Hoef and Jansen 2007), the effect of ice cover was significant and was the dominant factor explaining the distribution of harbor seals (Bernoulli model,  $P < 0.05$ ; Fig. 4). The standardized resource selection coefficients for individual classes of ice cover showed that all seals tended to use intermediate ice cover with a significant preference for ice with five-tenths cover ( $P < 0.05$ ; Fig. 4). Seals exhibited a lesser preference for scattered ice (1–3 tenths) and denser ice (8–9 tenths), with a lesser preference being significant for one-, two-, and eight-tenths ice cover ( $P < 0.05$ ; Fig. 4). Mothers and pups showed a similar preference for intermediate ice cover but tended to occur more often in denser ice cover; this preference was significant for



*Figure 2.* Counts of all seals and pups along video sampling transects (relative abundance) in Disenchantment Bay, May to August 2002. Raw counts for all seals are shown as solid circles, and raw counts for pups are shown as open circles. The thick solid curve is the fitted GAM model for all seals, with the 95% prediction intervals shown by the thinner solid lines. The thick dashed curve is the fitted GAM model for pups, with the 95% prediction intervals shown by the thinner dashed lines.





*Figure 3.* Spatial distribution of harbor seals, ice cover zones, and maximum penetration of cruise ships on the day of surveys ( $\diamond$ ) and the previous day ( $\star$ ) in Disenchantment Bay, Alaska, on (A) 6 May, (B) 16 May, (C) 31 May, (D) 20 June, (E) 18 July, and (F) 4 August 2002 (figures for all 18 survey dates are available as supplemental material online). The time of day that ships reached their maximum penetration appears near the location symbol. The range of seal counts summed per grid cell is shown in three levels: small dot (<5 seals), medium dot (5–20 seals), and large dot (>20 seals). A small, overlying white dot indicates the presence of at least one mother-pup pair within that grid cell. Ice cover is represented by a gradient in cell-color shading: light gray (scattered), medium gray (intermediate), dark gray (dense). For this graphic, if cells with no ice data were bounded on three sides by cells with ice measures, the average of neighboring cells was used as an estimate. Refer to Figure 1 for geographical points and scale.

seven-tenths cover ( $P < 0.05$ ; Fig. 4). Mother and pups showed a similar low preference for scattered and denser ice (Fig. 4), but with statistical significance only for one-tenth cover ( $P < 0.05$ ; Fig. 4).

There was no indication that the number of ship visits over the previous 3 d had an effect on the overall distribution of seals in DB (97.5% regression confidence interval [-4.59, 2.61]; see Methods). The closest approach distance of ships was negatively related to the incidence of seals ( $P < 0.05$ ; [-5.08, -1.17]), so that closer approaches were associated with a higher incidence of seals. This is likely the result of ships traveling near favorable seal habitat, which, based on our observations, included using leads of open water bordered by denser ice, transiting along a consolidated edge of ice, and turning around when bordering dense ice. We saw no evidence that ships were navigating to promote viewing of seals by passengers. There was no apparent effect of ship TACA on the distribution of harbor seals (-0.95, 0.14).

Similar to all seals, the distribution of mothers and pups was negatively related to the ships' closest approach distance (-2.22, -0.26), suggesting a spatial overlap in the preferred range of mother-pup pairs and ships. Neither ship TACA (-0.12, 0.58) nor presence (-2.45, 0.21) explained significant variance in mother-pup distribution. Our results suggest that mothers and pups respond similarly to the pooled population, though we note our sample was small.

The actual counts where seals occurred (abundance) confirmed a preference by seals for intermediate ice cover in five- to seven-tenths range (Fig. 5), with a significance preference for six-tenths ice cover (Poisson model,  $P < 0.05$ ; Fig. 5). This further

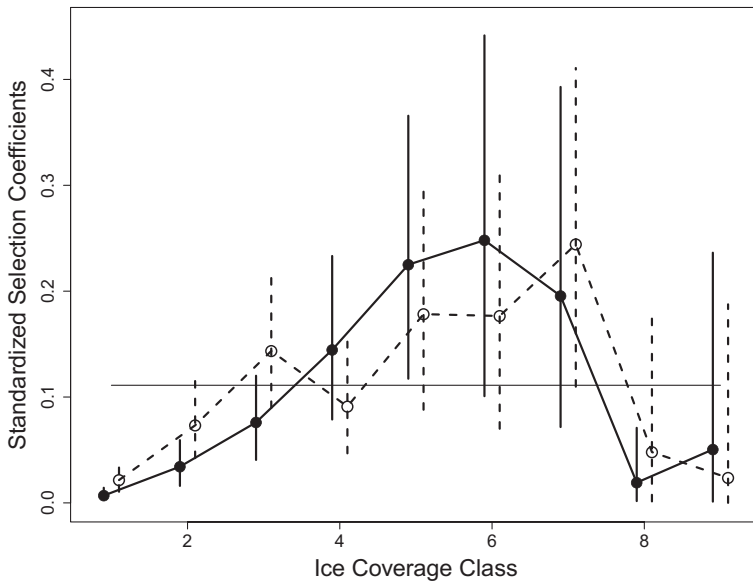


Figure 4. Standardized resource selection coefficient by harbor seals for ice cover class in Disenchantment Bay, Alaska, 3 May to 4 August 2002, for the Bernoulli part of the PIB model (*i.e.*, for the cell-based spatial distribution of seals). The solid circles and lines are for all seals, and the open circles and dashed lines are for mother-pup pairs. Confidence intervals (95%) are shown by the vertical bars. The thin horizontal line represents equal selection for all ice cover classes.

supports seals actively selecting this segment of the ice habitat. A significantly lesser preference was found for the one-tenth and nine-tenths ice cover ( $P < 0.05$ ; Fig. 5). In contrast to the first stage of the regression, the distance of ships' closest approach was not related to seal abundance ( $-1.12, 0.77$ ), showing that despite a spatial overlap in the general range of ships and seals, actual peak counts of seals did not consistently coincide with closest approaches of ships. TACA and ship presence were unrelated to seal abundance ( $[-0.30, 0.40]$  and  $[-1.56, 0.82]$ , respectively).

The abundance of mothers and pups showed more variability in relation to ice cover compared to the first stage of the model, which is again likely a function of our small sample of mothers and pups. Although there appeared to be a slight tendency for higher counts in intermediate ice, large confidence intervals around the coefficients obscured any preference for ice cover. Only four-tenths ice cover showed a significantly lower preference ( $P < 0.05$ ; Fig. 5). This suggests a broader preference for ice habitat compared to the results from the first stage of the model, a tendency that may be based on mothers cueing on factors other than ice cover such as the proximity of other seals (*e.g.*, mother may avoid nonbreeding seals and prefer habitat with other mothers). Mothers nursing pups may also drift on ice for longer periods (as surrounding ice cover changes) which may confound any initial preference for ice cover. Counts of mothers and pups were not statistically related to any of the measures of ship distance or activity (distance:  $[-4.58, 0.79]$ ; TACA:  $[-1.11, 0.88]$ ; and presence:  $[-2.57, 1.22]$ ). At least on short time scales, mother-pup attendance and distribution in DB were not seemingly influenced by cruise ships.

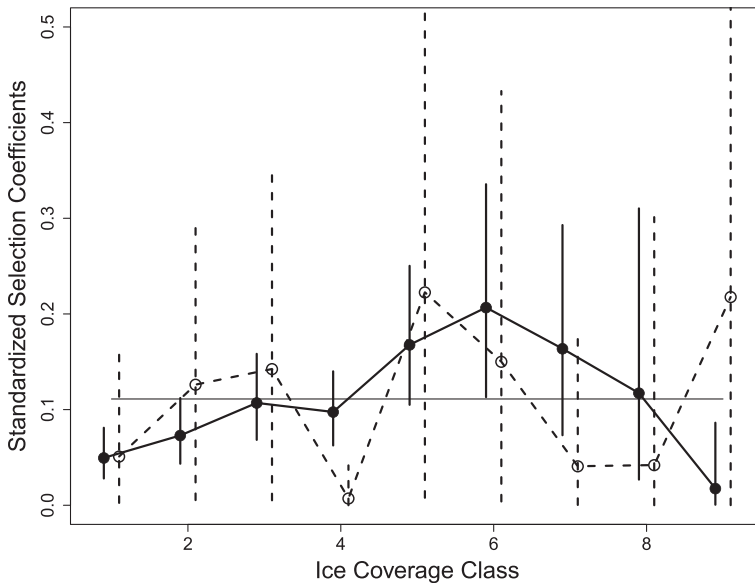


Figure 5. Standardized resource selection coefficient by harbor seals for ice cover class in Disenchantment Bay, Alaska, 3 May to 4 August 2002, for the Bernoulli part of the PIB model (*i.e.*, for the cell-based abundance of seals). The solid circles and lines are for all seals, and the open circles and dashed lines are for mother-pup pairs. Confidence intervals (95%) are shown by the vertical bars. The thin horizontal line represents equal selection for all ice cover classes.

Ice coverage in DB varied dramatically during the study. In May, the total ice-covered area (ICA) for scattered, intermediate, and dense ice combined varied between 28 and 56 km<sup>2</sup> (40%–80% of the total 70 km<sup>2</sup> study area; Fig. 6). During June, ICA peaked at 64 km<sup>2</sup> (~90%) and then declined to a minimum of about 5 km<sup>2</sup> (~7%) on the last survey on 4 August. In general, ICA was dominated by scattered ice, representing 25–45 km<sup>2</sup> (~70%–80% in proportion); intermediate ice ranged 10–20 km<sup>2</sup> (~15%–30%); dense ice was typically less than 3 km<sup>2</sup> (<1%). Patterns in the total ICA were driven largely by variation in the area covered by scattered ice.

Despite localized ice cover having a prominent effect on seal distribution and abundance, both stages of our model showed that the ICA was unrelated to both distribution and abundance of all seals and mothers and pups. Seal numbers were near maximum in early May when the ICA was intermediate. During the steep decline in counts of all seals in the first half of May, the total ICA varied widely with no discernible pattern. By 23 May, the ICA reached its highest level to that point and seal counts remained low. Moreover, as seal numbers increased later in the season, the ICA steadily declined. By July, with ice cover at less than half of the maximum, declining to the lowest level by August, seal abundance had mostly stabilized at higher levels.

Precipitation and wind speed did not have a significant effect on the distribution or abundance of all seals or mothers and pups. This was not surprising since extreme wind and rain events would have precluded aerial surveys and limited the variability in these measures.

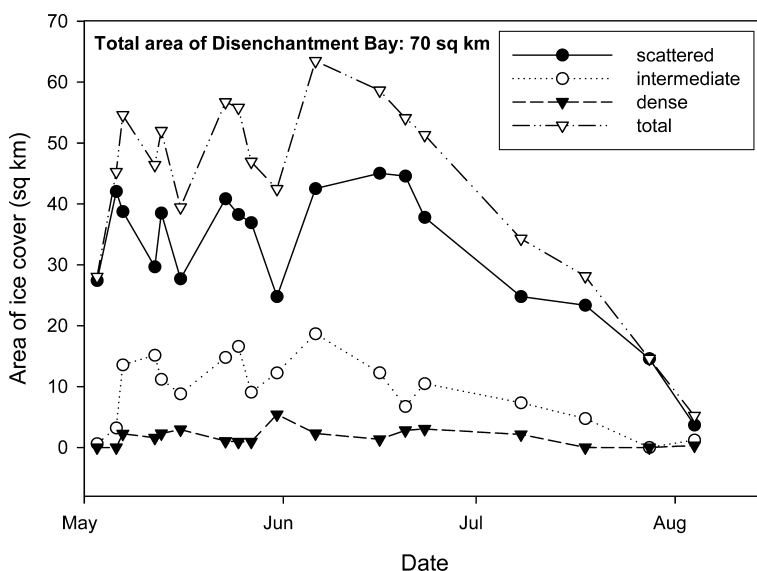


Figure 6. Estimated area of Disenchantment Bay (km<sup>2</sup>) containing three different ice cover types: scattered (1–3 tenths), intermediate (4–6 tenths), and dense (7–10 tenths), and all types combined (*i.e.*, ice-covered area [ICA]) from 3 May to 4 August 2002. Estimates of ice cover were averaged within grid cells (when  $n > 1$ ) and the areas of cells with each type of ice cover were summed (Jansen *et al.* 2006) and then scaled upward (proportionately) based on the percent of the study area that was sampled on a given day.

### *Cruise Ship Presence and Movement*

About half of the visits by cruise ships to DB (46%) were without other ships present; 42% overlapped with one other cruise ship (for an average of 1 h) and the remaining overlapped with two (11%) or three (1%) other vessels. As ships approached the study area (*i.e.*, Point LaTouche) from the south, they typically reduced speed from 12 to 6 knots, or lower if ice was in the immediate area. Vessel speed within the study area ranged from 0–6 knots depending on visibility and ice which varied considerably across the bay.

The durations of visits varied widely and were dependent partly on ice conditions and visibility. Vessels had various criteria for the type and size of ice they would negotiate to afford passengers closer views of Hubbard and Turner glaciers. Vessel captains and pilots were less inclined to enter DB when larger, denser ice spanned the mouth of the bay, usually resulting in shorter visits. Reduced visibility also shortened visit durations, especially if Hubbard Glacier was obscured. Under such conditions, ships would rarely venture north of Point LaTouche. Based on GPS tracks collected on cruise ships from 14 May to 1 August 2002 ( $n = 56$ ), the average period that vessels were within the study area was 2.17 h (range: 0.25–3.98 h). On average, ships arrived at 1141 (range: 0721–1541) and departed at 1353 (range: 0904–1721). Summarizing the frequency of cruise ship visits by time of day revealed that overall visitation was centered on the early afternoon. Studies at glacial sites show that numbers of harbor seals hauling out also peak in the early afternoon (between 1200 and 1600) (Hoover 1983, Calambokidis *et al.* 1987).

Cruise ships entered DB while favoring the eastern shoreline, but once north of Point LaTouche they typically used the middle of the bay (Fig. 7). In the early season (*i.e.*, May and June), ships would sometimes travel up the bay closer to the eastern shoreline, where open water persisted, and then turn around in the area around Haenke Island. Later in the season, as ice coverage diminished, cruise ships took more direct routes northward, often traveling in the middle of the bay and approaching Hubbard Glacier to within 1 km (Fig. 7). Ships would usually rotate a few times at their northernmost point to offer passengers a variety of views. Most ships exited using the same route.

## DISCUSSION

### *Seasonal Variation in Seal Counts*

The abundance of hauled-out harbor seals in Alaska is thought to peak both during pup-rearing and molting, with molting counts usually being higher and thought to have a broader mix of age and sex classes (Calambokidis *et al.* 1987, Frost *et al.* 1999, Jemison and Kelly 2001, Boveng *et al.* 2003, Ver Hoef and Frost 2003, Jemison *et al.* 2006). In contrast, our estimates of abundance showed near peak levels *prior* to pupping, a sharp decline at the onset of pupping, and then a more gradual increase to a peak during molting. The cause of the decline in seal counts in DB just before pupping is unknown. Wind speed and precipitation, particularly on survey days, were below the levels observed in other studies where there was a reduction in the number of seals hauled out (Hoover 1983, Boveng *et al.* 2003). Despite seasonal variation in ice cover, there were no marked changes early in the season to explain the decline of seals, and overall ice cover did not seemingly limit use of the area. In Glacier Bay,

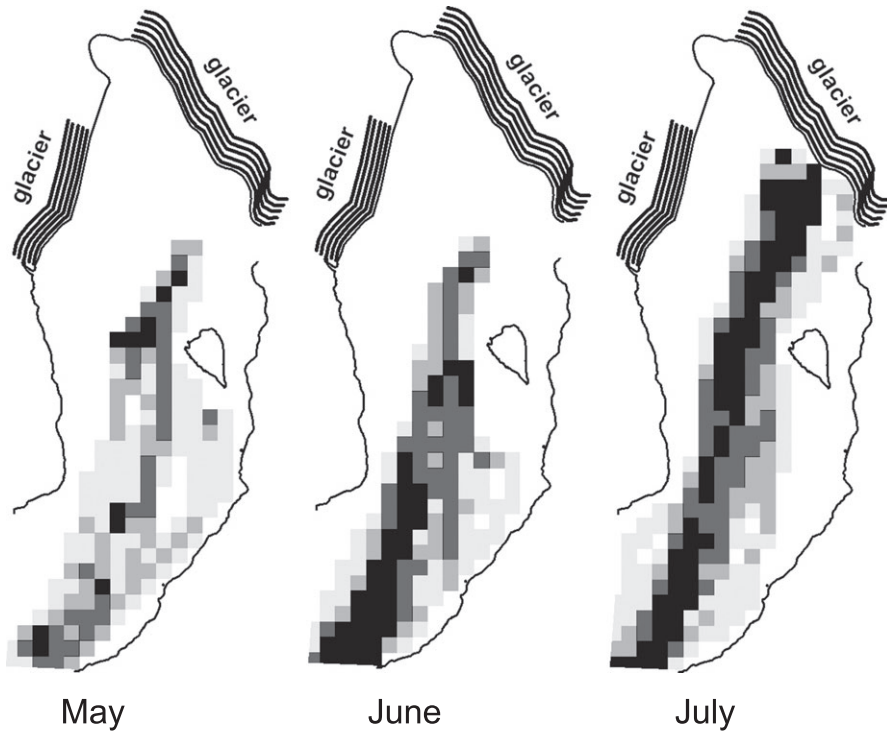


Figure 7. Patterns of ship movement and visitation time in Disenchantment Bay, Alaska, in 2002 ( $n = 56$  cruise ships of 105 total during study). Shading of cells represents the cumulative time that visiting ships spent within that cell for each of three months: May, June, and July (including early August). Four distinct shades, from gray to black, reflect increasing residence:  $<5$  min, 5–10 min, 10–20 min,  $>20$  min, respectively. Refer to Figure 1 for geographical points and scale.

declining use of ice habitat by seals was attributed to the declining ice cover in the years just prior to the retreating Muir Glacier's eventual grounding (Calambokidis *et al.* 1987). In contrast, Hubbard Glacier—which calves the vast majority of ice in Disenchantment Bay—is advancing, contrary to all but a few Alaskan tidewater glaciers (51 total) (Molnia 2007, Motyka and Truffer 2007, Krimmel 2008, Post *et al.* 2011). Floating ice cover is linked to seasonality in glacial calving, which is a complex function of other seasonal factors, including the glacier's advance/retreat cycle and speed, sea-surface temperature, subglacial freshwater runoff, and ice melt (Ritchie *et al.* 2008). Interestingly, in our study, maximum ice cover was centered on the peak pupping period when mothers have been shown to be increasingly selective in finding suitable ice for birthing and nursing (Hoover 1983).

The sharp decline in seal counts also appears unrelated to cruise ships, a conclusion supported by our space-time models (see below). To our knowledge, the first cruise ship entered DB on 14 May, at the midpoint in the overall decline in seal abundance. Due to thick ice and fog, this ship stopped barely within the study area and before any seals were within spotting range (*ca.* 1 km). According to ship schedules, we believe the next ship entered DB on 18 May, after declining seal counts had



stabilized. If the distribution of seals on 14 May was similar to that on adjacent dates when aerial surveys were conducted (13 and 16 May), the nearest seals to the ship (cell total > 1) would have been at a distance of more than 12 km. Only at distances less than 500 m to ships have harbor seals been shown to flush from the ice (Jansen *et al.* 2010). If the subsequent decline in seal numbers was a response to single vessel at 12 km, it would be difficult to reconcile the steady increase in seal counts later in the season when ship encounters also increased, in terms of ships per day (up to four), number of ship-days per week (up to five), and deeper penetration into the bay with diminishing ice cover.

Alternatively, seals could have left the bay (or spent more time in the water) in response to other factors not measured in this study, such as the abundance and distribution of prey. Diet studies of harbor seals near Yakutat Bay showed the dominant prey to be walleye pollock (*Theragra chalcogramma*) and a variety of smelt (Pitcher 1980). During peak smelt runs, harbor seals are commonly seen milling in river systems (Marston *et al.* 2002), including in the mouths of the Situk (70 km from DB), Lost (70 km) and Alsek Rivers (140 km).<sup>3</sup> In these river systems near DB, transient smelt runs reportedly occur from March to mid-June (Estes 1994). Capitalizing on these ephemeral prey resources may be key in building fat reserves for periods of fasting associated with rearing young, breeding, and molting (Bowen *et al.* 1992, Womble *et al.* 2005, Willson and Womble 2006). During our study, on 14 May 2002, when seal numbers in DB were near minimum, spawning smelt were reported in the Situk Estuary, as indicated by large feeding flocks of seabirds.<sup>4</sup> This elevated abundance of prey nearby may have been an incentive for harbor seals to leave DB. Grigg *et al.* (2009) posited that despite high fidelity by harbor seals for haul-outs within San Francisco Bay, seasonal movements to the outer coast occur more often during periods of upwelling there, and when there was lower prey availability inside the bay. It is also noteworthy that local maxima in seal counts that occurred around the first of each month (Fig. 4) correspond approximately to the fullest phase of the moon. Similar propensity of seals hauling out (and foraging less) around the full moon have been observed in other studies (Trillmich and Mohren 1981, Watts 1993, Cronin *et al.* 2009), and are thought to reflect reduced food availability (i.e., deeper prey) and thus less efficient foraging (Horning and Trillmich 1999, Lea *et al.* 2010).

The reduced abundance of seals in DB at the onset of pupping is similar to that of ice-associated harbor seals in Aialik Bay, Alaska. Hoover's (1983) first seasonal counts of Aialik seals in mid-May occurred at an apparent minimum in seal counts. Seal numbers then steadily increased until peak pupping in mid-June, but then, unlike at DB, counts declined and did not rebound until early August. Seal numbers at DB rebounded to maximum levels by the end of June. At Aialik, increasing abundance during pupping coincided with a pronounced decline in juveniles present, a seasonal pattern supported by earlier unpublished work on ice-associated harbor seals at DB.<sup>5</sup> This exodus of juveniles at Aialik was offset by an influx of adults which caused a peak in abundance near the time of peak pupping. Though little is known of the factors that influence local abundance and composition of harbor seal populations during the breeding season, we believe that movement of juveniles—which are not

<sup>3</sup>Personal observation of JKJ.

<sup>4</sup>Personal communication from D. Russell, pilot, Yakutat Coastal Airways, PO Box 163 Yakutat, Alaska 99689, 18 May 2002.

<sup>5</sup>Unpublished data (NMML/AFSC).

constrained by breeding/whelping requirements, *i.e.*, they are more transient, and can compose up to half of the population (Hoover 1983)—explain much of the rapid change in counts at DB. Other observations in glacial fjords point to an important role for social dynamics in this pattern, with breeding males supplanting juveniles in order to maintain underwater territories near nursing females (Hoover 1983). Harbor seals regularly show seasonal patterns in haul-out abundance and habitat use though often with unexplained anomalies (Brown and Mate 1983, Bayer 1985, Rosenfeld *et al.* 1988, Mathews and Kelly 1996, Harris *et al.* 2003, Grigg *et al.* 2012).

#### *Comparison with Other Sites*

The timing of pupping is comparable between DB and other glacial sites, peaking in June, but there are apparent differences in productivity. At peak pupping at DB, the proportion of pups relative to the total abundance was 10%, a figure less than half that observed at other glacial haul-outs (Icy Bay: 23%, Mathews 1995; Aialik Bay: 21%–34%, Hoover 1983, Hoover-Miller *et al.* 2011; John Hopkins Inlet and Muir Inlet: 34%–36%, Mathews and Pendleton 2006; 37%–40%, Calambokidis *et al.* 1987; and one terrestrial haul-out, Tugidak Island: 23%–27%, Jemison and Kelly 2001). Despite possible biases related to differences in the criteria for classifying mothers and pups, we believe these contrasting figures to be consistent and large enough to not likely be attributed to bias or sampling error. In all studies to date, proximity to the mother has been required for classifying a small seal as a pup. Because mothers are known to forage during lactation (Boness *et al.* 1994), unaccompanied pups get lumped with the nonpups, resulting in an overall underestimation of productivity.

#### *Effect of Modeled Covariates*

Ice cover was a key factor affecting abundance and distribution with seals tending to haul out in areas of intermediate rather than scattered or dense ice coverage. We believe this pattern results from seals selecting greater than some minimum density of ice to facilitate sociality and provide protection from predators such as killer whales (*Orcinus orca*); and to avoid the densest ice for ease in breathing and swimming at the surface, and spy-hopping to find aggregations of animals. Denser ice may also not represent optimal habitat because it tends to occur near the glaciers where waves from calving often crash over ice, sometimes causing them to overturn.

Our results suggest that areas close to ships were regularly occupied by seals. This appears to conflict with the finding that seals increasingly escape into the water when approached within 500 m by cruise ships (Jansen *et al.* 2010). Still, the majority of seals in our study (during a given ship visit) likely were not approached closer than 500 m and thus continued drifting on the ice. At the same time, ships favored traveling through areas with less ice, usually within leads near more consolidated ice. This created spatial overlap, with most seals tolerating passing ships and remaining on the ice. It is also worth noting that seals and ships were not mapped simultaneously and thus a temporal discordance could have confounded any avoidance of ship corridors by seals (see below). So, contrary to our expectations, seals did not appear to actively avoid areas where cruise ships traveled. Similarly, Grigg *et al.* (2012) found that harbor seals in San Francisco Bay, California, occurred most often in areas of high human activity. The authors suggested that prey availability was a greater constraint than the cost of tolerating disturbance. Harbor seals in Danish waters exhibited weaker

and shorter-lived reactions to disturbance during the breeding season, a pattern also thought to reflect a cost trade-off (Andersen *et al.* 2012). For seals in DB, unless disturbed closely by ships causing them to flush, the advantages of resting and staying dry on a stable piece of ice in areas frequented by ships (particularly for nursing moms) may outweigh the costs of more time traveling in the water to remain in less disturbed areas.

Though we did not detect an overt avoidance of areas used by ships, it is important to note that spatial scales, and distance effects, are likely to be obscured in glacial fjords where currents, ice, and relative locations of seals on the ice are constantly shifting over time. Seals also relocate without being disturbed, in response to ice drifting into less desirable areas, breaking up, turning over, or dispersing. To effectively filter out this variability would require greater transect coverage within short time periods of cruise ship presence and absence, or studies involving tracking of individual seals' behavior in relation to ships. The necessarily coarse quality of our data over these large fjords reflects more medium-term spatial processes (*e.g.*, seals aggregating and drifting on the ice) and less short-term (*e.g.*, seals flushing into the water).

#### *Hypothesized Mechanism of Long-term Disturbance*

Recent findings from multi-year studies have documented shifts in habitat use by seals believed to be driven by human disturbance (Cordes *et al.* 2011, Skeate *et al.* 2012). Our findings suggest that seals do not abandon the DB haul-out area as an immediate response to the number, proximity, or visit duration of cruise ships, despite seals being regularly flushed into the water. In the absence of data on seal abundance and distribution prior to the 1980s, before cruise ships entered DB in appreciable numbers, our study cannot address directly the long-term effects of vessel disturbance. However, clues regarding possible long-term effects can be drawn from existing, comparative counts at a neighboring, undisturbed area. Monthly counts of total seal abundance (by high-altitude aerial photogrammetry) from Icy Bay, a similar fjord with floating glacial ice (115 km away by water; Fig. 1), revealed a steady increase in numbers from May (1,011) to August (5,435) in contrast to counts at DB which showed an increase from May (1,544) to June (2,149) but then a modest decline to August (1,778; Jansen *et al.* 2006). Differences in seasonal use of these areas could arise from natural factors such as prey or ice conditions. We expect the tidewater glaciers at the two sites to have similar seasonal cycles of advance (winter/spring) and retreat (summer/fall), as supported by the seasonality in ice calving (*i.e.*, ice cover) documented in our study. The timing and magnitude of peak ice cover could be different, as the transition to retreat (and increase in calving) expected during late spring is influenced by the rates of warming in seawater and freshwater discharge which may vary between sites (Ritchie *et al.* 2008). Observations in Aialik Bay support some consistency in ice-cover seasonality, exhibiting a pattern similar to what we found for DB (Hoover 1983). Interestingly, on the scale of decades, predictions of ice availability at the two sites may indeed be different, as glaciers calving into Icy Bay are rapidly thinning and retreating, whereas Hubbard Glacier in DB is slowly advancing (Molnia 2008).

From a theoretical standpoint, contrasting habitat use by seals at neighboring sites with striking differences in vessel use, combined with low productivity at DB, point to possible mechanisms that may have, over decades, led to differences in habitat desirability for seals. We hypothesize that a significant factor was the rapid expansion of cruise ship visitation to DB since the 1980s, which could have initiated a spatial

shift in use away from DB and toward less disturbed areas, such as Icy Bay. Our observations of the occurrence and behavior of cruise ships, especially in relation to ice, document distinct seasonal intrusions into the seals' habitat at DB that may have differentially affected age-sex classes: (1) in May and June, ships regularly traveled through areas in south and central DB where we observed up to two-thirds of the mother-pup pairs (potentially diminishing habitat for pregnant and postpartum females and pups); (2) at the same time, denser ice cover further north and closer to the glaciers precluded ships from approaching the densest seal aggregations (potentially leaving undisturbed habitat for nonbreeders); and (3) declining ice cover in DB later in the summer allowed cruise ships access to the northern part of the bay where seals were previously isolated (potentially diminishing habitat for molting seals). Habitat displacement or abandonment in the presence of disturbance has been shown for several species of pinnipeds and other marine mammals (Grigg *et al.* 2004, Kirkman 2010, Kirkman *et al.* 2013), with new habitats believed to be lower quality and cause demographic impacts (Gerrodette and Gilmartin 1990, Stevens and Boness 2003, Bejder *et al.* 2006, Cartwright *et al.* 2012). Human disturbance can cause relatively rapid abandonment of traditional habitat with recolonization (post disturbance) taking much longer (Bartholomew 1949, Gerrodette and Gilmartin 1990, Skeate *et al.* 2012). In our study, the nearest alternative haul-outs to DB of more than a few seals are the ice field of Icy Bay and sandbars in the estuaries of the Dangerous and Alsek Rivers (approximately 500–1,000 seals in August<sup>6</sup>), 100–140 km to the southeast. Except for these sites, the *ca.* 500 km of outer coast between Cape Suckling and Cape Spencer—with DB and Icy Bay in the center—is completely exposed with only a few tens of seals hauling out at a given time (based on August surveys; NMML, unpublished data).

Seasonal patterns of ice cover mediated ship access to DB and to particular haul-out areas within the bay. We posit that denser ice cover provided a buffer that minimized disturbance for some seals during pup rearing but not for the majority during molting. During pup rearing, mothers and pups were likely at greater risk to disturbance because they tended to occur in areas to the south where there was greater overlap with ships. We argue that greater spatial overlap with ships means a higher frequency of flushing and thus greater energetic costs (Jansen *et al.* 2010), which could influence seals' longer-term decisions to reduce their seasonal use of DB. Those subjected to habitat degradation *via* chronic disturbance may decide over years to move entirely to a different area. Because seals rely on fat reserves to more efficiently nurse pups and molt out of the water (Pitcher and Calkins 1979), uninterrupted periods on a dry, stable platform promote energy savings and enhance fecundity and survival (Feltz and Fay 1966, Ashwell-Erickson *et al.* 1986, Boily 1995). Though we hypothesize that ship traffic contributed to reduced productivity and seasonal use of DB, we cannot rule out seasonal availability of ice, prey, or other features as factors in seals' decisions about where to pup and molt.

## CONCLUSIONS

Ice cover is a key factor affecting space use by harbor seals in glacial fjords, and it may be equally important in defining space use by vessels and their potential to disturb and ultimately displace seals. Complex mechanisms of direct and indirect

<sup>6</sup>Unpublished data (NMML/AFSC).

impacts on seals that may reduce vital rates or shift habitat use over many years are virtually unstudied. To better understand the mechanisms requires multi-year studies to connect the behavior and site fidelity of individuals affected by disturbance to effects on their reproduction and survival. However, results and ultimately predictions about the fate of ice-associated harbor seal populations exposed to disturbance may be equivocal because we are unaware of studies on pristine, comparison populations without exposure to vessel-based tourism. Lacking actual baseline data, the challenge of protecting seals lies in distinguishing altered behaviors that have become prevalent after chronic exposure to ships from those that are real-time responses to this relatively new feature of the environment. High priority should be placed on measuring seal behavior in areas where ship traffic has only recently expanded or has been precluded altogether. In the face of ever-increasing tourism in Alaska, and after more than a century of unrestricted use of glacial breeding and molting areas, we believe conservation requires measures to reduce overlap between vessels and ice-associated harbor seal populations.

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#### SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12140/supinfo>.

*Figures S1–S3.* Spatial distribution of harbor seals, ice cover zones, and maximum penetration of cruise ships on the day of surveys (↔) and the previous day (➔) in Disenchantment Bay, Alaska, by date. The time of day that ships reached their maximum penetration appears near the location symbol. The range of seal counts summed per grid cell is shown in three levels: small dot (<5 seals), medium dot (5–20 seals), and large dot (>20 seals). A small, overlying white dot indicates the presence of at least one mother-pup pair within that grid cell. Ice cover is represented by a gradient in cell-color shading: light gray (scattered), medium gray (intermediate), dark gray (dense). For this graphic, if cells with no ice data were bounded on three sides by cells with ice measures, the average of neighboring cells was used as an estimate. Refer to Figure 1 for geographical points and scale.