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Reaction of Harbor Seals to Cruise Ships

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ABSTRACT The largest aggregations of harbor seals (*Phoca vitulina*) in Alaska, USA, haul out on floating ice in tidewater glacial fjords. Seals use these fjords in peak numbers during the critical periods of pupping, breeding, and molting when visits by tour ships also peak. Documented and suspected declines of harbor seals in fjords with rising vessel traffic underscore the need to better understand possible impacts, particularly in areas where ship visits have risen substantially in the past 2 decades. We examined the interruption of haulout bouts of harbor seals due to approaching cruise ships in Disenchantment Bay, Alaska. We conducted observations from cruise ships and focused on disturbance of seals as evidenced by seals flushing into the water from the floating ice on which they rested. We investigated rate of flushing in relation to vessel distance, approach angle, group size, and seal type (mother, pup, or other). Using a survival-regression analysis, we found that the risk of disturbing harbor seals increased when ships approached within 500 m; seals approached as close as 100 m were 25 times more likely to enter the water than seals 500 m from a ship. Seals were 4 times more prone to enter the water when ships were approaching directly rather than passing abeam. Seals responded similarly regardless of group size or seal type. Energetic models indicated a potential to disrupt energy balance and cause thermal stress in disturbed pups if they spent >50% of their time in ice-chilled water. Studies at non-glacial sites suggest that pups spend 40–70% of their time in the water. Voluntary guidelines for approaching seals in Alaska recommend that cruise ships approach ≥ 91 m (100 yards), a distance at which we show 90% of seals would flush into the water. Our findings indicate a need to develop regulations to maintain a 500-m separation between cruise ships and seals in all Alaskan glacial fjords.

KEY WORDS Alaska, cruise ships, disturbance, energetics, harbor seal, haul-out behavior, *Phoca vitulina*, predation, survival analysis, thermoregulation.

Alaska, USA, is a major cruise tourism destination, with the third highest share (8%) of the total world capacity, ranking only behind the Caribbean (36%) and the Mediterranean (16%; Cruise Lines International Association [CLIA] 2007). The cruise ship capacity allotted to Alaska has nearly quadrupled since 1987, and mean annual growth (8%) is tracking industry growth internationally (CLIA 2007). More than half of summer visitors to Alaska, which in 2007 surpassed 1.7 million, embark on a cruise (Alaska Department of Community and Economic Development 2007, Alaska Department of Environmental Conservation 2007). These statistics, combined with a growing interest globally in nature-based and cultural tourism, point to Alaska's growing popularity among cruise ship tourists (Reynolds and Braithwaite 2001, World Tourism Organisation 2001). In particular, tidewater glacial fjords in southeastern and central Alaska are major attractions, with ≥ 1 of them on the itinerary of every cruise to Alaska (National Park Service 2001).

Ice emanating from tidewater glaciers provides habitat for pup-rearing, breeding, and molting for the largest aggregations of harbor seals (*Phoca vitulina*) in Alaska (Streveler 1979, Hoover 1983, Calambokidis et al. 1987), which can number >5,000 animals (e.g., Guyot and Yahtse glaciers, Icy Bay; Jansen et al. 2006). After major seal population declines in the Gulf of Alaska (85%; Pitcher 1990, Mathews and Kelly 1996, Frost et al. 1999, Jemison and Pendleton 2001, Small et al. 2001), and most recently at ice and terrestrial haul-out sites in Glacier Bay National Park, Alaska (63% and 75%, respectively; Mathews and Pendleton 2006), it has become increasingly important to understand the factors that affect seal survival and recruitment. Recent attention has focused on Disenchantment Bay, near Yakutat, because Alaska Native subsistence hunters from the local Tlingit Tribe have perceived a decline in seal numbers during the period when annual cruise ship traffic increased from 15 to 170 ship-visits per year (from approx. 1989 to 2007; K. Kozie, Wrangell-St. Elias National Park, unpublished report). Other fjords in Alaska that support large aggregations of harbor seals have experienced similar increases in vessel traffic from low numbers in the 1980s to the present, including College Fjord (167 ship visits scheduled for 2008), Glacier Bay (225), and Tracy Arm (295; Cruise Line Agencies of Alaska 2008). Broadly applicable techniques for estimating seal abundance in glacial fords have only recently been developed, so there is currently no time series for most of these fjords (except Glacier Bay) from which to assess population trajectories and impacts of increasing vessel traffic (Bengtson et al. 2004, Jansen et al. 2006). There are no published findings on effects of cruise ships on harbor seals. Our objectives were to determine whether harbor seals in a glacial fjord interrupt their haul-out time by flushing into the water in response to approaching cruise ships and to assess whether prematurely entering the water has energetic consequences for the population.

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Figure 1. Map of the study area in Disenchantment Bay, Alaska, USA, showing the 2 tidewater glaciers, Turner and Hubbard. The thin dashed line over water marks the southern boundary of our study area; the thicker dashed line over land marks the boundary between Wrangell-St. Elias National Park and Tongass National Forest. The inset shows the study area (arrow) where we observed harbor seals, 2002, in relation to Alaska and Canada. The stippled areas show glaciated terrain.

STUDY AREA

The marine environment of Disenchantment Bay comprises some 70 km², reaches depths of 260 m (850 feet) and is bounded by steeply sloping shorelines and a complex system of submarine moraines that extend south into Yakutat Bay (Fig. 1). At the surface, the bay is dominated by floating ice emanating southward from 2 tidewater glaciers. During our study, ice coverage was non-uniform and varied widely, from solidly packed areas with no open water, as often occurs in the north in front of and between the glaciers, to single floes surrounded by expanses of open water. Our study area was geographically defined as the region north of Point LaTouche, which essentially marks the boundary between Yakutat and Disenchantment bays (Fig. 1). Although some ice floes were scattered to the south of this boundary, the densest patches were nearly always north, especially in the upper reaches of the bay where most harbor seals were located. We sometimes observed elevated concentrations of ice and seals in Yakutat Bay, and thus shipboard observations sometimes occurred there.

Cruise ships visited Disenchantment Bay from May to September, venturing into the bay several kilometers north of Egg (Haenke) Island, ice and visibility conditions permitting, to afford passengers a close (1 km) view of Hubbard and Turner glaciers (Fig. 1). These ships could be nearly 305 m long and 32 m wide. As many as 5 ships visited the bay on peak traffic days.

METHODS

We conducted shipboard observations from 14 May 2002, when the first cruise ship entered Disenchantment Bay (when harbor seal pupping just began), to 1 August 2002 (when most pups had weaned and adult seals were starting to molt). The peak of pupping occurred on 23 June, although we observed pups with mothers throughout the study (Jansen et al. 2006). We identified pups as smaller seals in proximity to, and often interacting with or suckling from, an adult-sized animal that we assumed to be the mother. Their clean, light gravish color (compared with adult and subadult seals' dark gray or brownish color) was also helpful in distinguishing pups. We made observations of seals hauled out on ice when the ship was within a reliable viewing range, which was typically out to approximately 1,000 m, depending on visibility. We made observations from near the bow on the starboard or port sides of the vessel or from both sides simultaneously when 2 observers were available. Observers noted whether ships were inbound toward Hubbard Glacier, stopped, rotating in place, or outbound toward Yakutat Bay. We only used data recorded while the ship was inbound or outbound in our analyses. We attempted to first locate seal groups at various distances and bearings from the ship to provide a behavioral contrast between near and distant animals. We defined a seal group as ≥ 1 seals hauled out on one ice floe.

We recorded behavioral observations during 15-second intervals on data forms or by using a hands-free digital voice recorder. We later downloaded digital voice files, played them back via sound editing software that allowed observers to assign times to their observations, and transcribed the observations into a database. For each 15-second sample, we recorded distance and bearing (relative to the ship's course in 15° increments) to the seal group, total number of seals in the group, and number of mothers, pups, or other seals that entered the water during the interval. We measured distances from the shipboard observers to seals using laser rangefinder binoculars (Leica Vector[™] [with 12× magnification] and GeovidTM [with $7 \times$]) or an inclinometer. Once we chose a seal group for observation, we observed it continuously until the group either passed abeam of the ship or all seals entered the water. Details of our sampling protocol are presented in Jansen et al. (2006).

Analyses of Shipboard Observations

Our focus was on seals entering the water, as such behavior was 1) unmistakable, even at the limit of our visual range; 2) expected to have energetic costs with possible impacts on the seals' vital rates (Harding et al. 2005); and 3) the culminating behavior in a series that typically progressed from resting to alert, to active, to flushing into the water. Although the intermediate stages in this progression may impact a seal's energy budget, it was not feasible in our study to estimate or predict this impact. Using water entry as the response involved just one transition, from hauled out to in the water and thus allowed assignment of unique identifiers to all seals in the data set (i.e., we assumed seals were not able to swim ahead of the vessel and be counted again). We gave seals individual identifiers by numbering individuals within a group; we numbered the first to enter the water as 1, the second as 2, and so on. We could arbitrarily number remaining seals that did not enter the water while under observation because they all had identical behavior records (considering only the water-entry response). Each record included the seal and group identifiers, start and stop times

of the 15-second interval, the response (0 if the seal stayed on the ice, 1 if the seal entered the water), and the explanatory variables (covariates) distance from the ship to the group, bearing from the ship's course to the group, seal group size, and seal type (mother, pup, or other).

Our data were time-to-event data with censoring. Censoring occurred whenever a seal was lost to observation before entering the water, which occurred, for example, when the seal passed abeam of the ship or when the ship stopped its forward progress while we were observing a seal. For censored time to event data, we used the Cox proportional hazards model, a natural and widely used technique for estimating effects of covariates on a response variable (Therneau and Grambsch 2000). Although the basic Cox model assumes linear relationships and timeconstant covariates, we used semi-parametric extensions of the Cox model that allowed the data to suggest the functional form of covariate effects and that allowed for time-dependent covariates such as distance from the seal to the approaching vessel (Therneau and Grambsch 2000). We used S-Plus® version 6.1 for Windows (Insightful Corp., Seattle, WA) for all Cox regression modeling.

Because of the potential that the response to distance may have varied with the bearing of the ship, we investigated the shape of the response surface over the 2 variables simultaneously. This was not possible to do within the Cox regression framework alone. Instead, we fit a Cox regression with no explanatory variables and then used a generalized additive model (Hastie and Tibshirani 1990) to explore the relationship between distance, bearing angle, and residuals from the Cox regression.

To provide a measure of the risk of disturbance, we computed the proportions of seals under observation entering the water for each of 10 distance bins of 100 m from the ship as an approximate measure of absolute risk. We derived these estimates from the 526 seals (279 groups) that either entered the water during observation or passed abeam of the ship while still on the ice; we did not include seals that were lost to observation for other reasons (e.g., ship stopped moving). We calculated each proportion as the simple ratio of the number of seals that entered the water at distances that fell within the 100-m-wide bin divided by the total number of seals that we observed at distances within the bin.

Energetic Modeling of Heat Loss in Pups

Because cruise ships visited Disenchantment Bay almost daily during peak pup-rearing, and because newborn pups are the most likely to be thermally stressed, we modeled energy balance and thermoregulation to assess the impact to disturbed pups that flush into the water. We assumed heat production to be equal to field metabolic rate (e.g., Lavigne 1982, Harding et al. 2005). Thus, the energy balance for thermoregulation (E) is equal to heat production (P) minus heat loss to the environment (H), which are functions of body mass (w) and water temperature (t; Harding et al. 2005). When heat loss exceeds heat production pups must boost energy turnover an equal amount to maintain body

$$E(w,t) = \begin{cases} P(w) - H(w,t) & \text{if } H(w,t) > P(w) \\ 0 & \text{if } H(w,t) \le P(w) \end{cases}$$
(1)

where we assumed seals were not prone to overheating so that energy balance would be zero if they were not cold stressed (Harding et al. 2005).

We estimated heat loss (H) using a general function (Harding et al. 2005), as modified by Worthy (1991) and Kvadsheim and Folkow (1997):

$$H(w,t) = \frac{c \cdot A(w) \cdot (T - t_s)}{d(w)}$$
(2)

where *c* is thermal conductivity of blubber at 0.19 W/m/K (Kvadsheim and Folkow 1997), $T - t_s$ is the difference between body core (*T*) and ambient water temperature (t_s ; \emptyset rtisland and Markussen 1990), A(w) is body surface area (m²), and d(w) is blubber thickness (m), with A(w) and d(w) as functions of body mass w (kg). Mean body temperature of harbor seals is 38° C (Hedd et al. 1995, Hind and Gurney 1998). We calculated body surface area according to Meeh's equation: $A(w) = kw^{0.67}$, where k = 0.08 (Meeh's constant for harbor seal pups; Lavigne 1982). We assumed blubber thickness of pups was uniform and calculated it as $d(w) = [(10.23)\ln(w) - 10.74]/1,000$ (Rosen and Renouf 1997, Harding et al. 2005). We used mass at birth as 9.97 kg and a linear growth rate of 0.6 kg/day (Pitcher and Calkins 1979, Bowen et al. 2001; Table 1).

Based on different methods of estimating metabolic rates from the literature, we developed 2 models of energy turnover for harbor seal pups. Model A was a general model that used the relationship between field metabolic rate and body size generalized for free-ranging marine mammals (Boyd 2002). Model A assumed a normal mix of activities including resting, calm swimming, migratory swimming, and feeding, while incorporating specific thermal costs that vary with time spent in the water, body size, growth (e.g., increasing surface area), and blubber thickness (Harding et al. 2005). Model B was a more detailed model that used specific estimates of resting and active metabolic rates from captive studies of harbor seals to parse out the particular energy demands during resting (out of the water) and swimming for small pups (Davis et al. 1985, Rosen and Renouf 1998). In model B, we used metabolic rates (i.e., heat production) for a 10-kg pup at 3 levels of swimming activity (velocities of 0 m/sec, 0.5 m/sec, and 1.0 m/sec), resting metabolic rates when not submerged, estimated heat loss for time submerged (eq 2), and a range of time submerged from 40% to 70% (Davis et al. 1985, Rosen and Renouf 1998). Implicit in model B was that seal pups are thermally neutral when hauled out (Hind and Gurney 1998).

We used water temperatures of 3° C, 4° C, and 5° C as representative of the range in surface temperatures in icecovered areas of water typically found along the coast. We compared model outputs using these low temperatures with

Table 1. Input parameters for models of energy balance in ice-associated harbor seal pups during weaning (May to Jun) in Disenchantment Bay, Alaska, USA.

| Seal parameter | Value | Used in model A or B | Location | Source |
|-------------------------------|---------------------------------|----------------------|---|---|
| Pup birth wt | 9.97 kg | А, В | Icy and Disenchantment bays, AK, USA | Pitcher and Calkins 1979 |
| Pup growth rate | 0.6 kg/day | A, B | Sable Island, NS, Canada | Bowen et al. 2001 |
| Seal body temp | 38° Č | А, В | Captive | Hedd et al. 1995 (pup); Hind and Gurney 1998 (adult) |
| Lactation duration | 24 days | A, B | Sable Island, NS, Canada | Bowen et al. 2001 |
| Field metabolic rate | Mass dependent | А | Generalized | Boyd 2002 |
| Resting metabolic rate | Mass dependent | В | Captive | Rosen and Renouf 1998 |
| Swimming metabolic rate | Activity dependent ^a | В | Captive ^a | Davis et al. 1985 |
| % time in water (newborn) | 40 | А, В | Sable Island; Svalbard Archipelago, Norway | Bowen et al. 1999, Jørgensen et al. 2001 |
| % time in water (weaning age) | 70 | А, В | Prince William Sound, AK, USA; Svalbard Archipelago, Norway | Rehberg and Small 2001, Jørgensen et al. 2001 |
| Blubber thermal conductivity | 0.19 W/m/K | A, B | Captive | Kvadsheim and Folkow 1997 |
| Blubber thickness | Mass dependent | A, B | Generalized | Harding et al. 2005 |
| Body surface area | Mass dependent | А, В | Generalized | Lavigne 1982 |

^a We scaled swimming metabolic rate (SMR) to a hypothetical 10-kg pup using the same mass scaling as observed in studies of resting metabolic rate of captive seals (Rosen and Renouf 1998). This mass scaling could underestimate SMR, because there may be increased drag in pups who are less efficient swimmers, mostly at the surface (Williams and Kooyman 1985). This possible error is likely offset by assuming a higher average swimming speed than has been observed in free-ranging pups (0.5 m/sec vs. 0.2 m/sec). We calculated heat loss of captive seals by taking accounting for seal-water temp difference during trials (38 - 16.5 = 21.5° C) vs. temp inputs for the 2 models.

output from using water of 12° C, which is typical along the coast and in bays of the Gulf of Alaska in the summer (University of Alaska 2005). It is likely that water temperature in the upper 30 m in Disenchantment Bay rarely exceeds 7° C, and in areas of intermediate to dense ice it is likely \leq 3° C year-round, as shown by conductivity-temperature-depth sampling at another glacial fjord (Tracy Arm, AK, USA; J. K. Jansen, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration [NOAA], unpublished data) and measurements of seasurface temperatures (SSTs) near Yakutat (University of Alaska 2005). Even in Yakutat Bay, south of the haul-out area (Fig. 1) where little ice persists, summer SSTs rarely exceed 12° C and are commonly <10° C (University of Alaska 2005).

RESULTS

Observers boarded and recorded data on 76 of 105 cruises (73%) scheduled to visit Disenchantment Bay during our study. We observed 772 seal groups consisting of 6,008 15-second observations across 207 observer-hours. When the ship was moving, we made 5,344 15-second observations from 584 seals in 307 groups.

Neither group size nor seal type (mothers, pups, or others) was related to the risk of seals entering the water. However, distance and bearing from the ship were significant explanatory variables for that risk (Figs. 2, 3). Specifically, for approach distances decreasing from approximately 500 m, the effect curve increased steeply, corresponding to a risk of $e^{0.5} = 1.6$. At short distances (e.g., <100 m), the curve had a value of approximately 25 times more likely to enter the water than a seal approached at 500 m. Beyond approximately 600 m, there seemed to be little effect of the ship's approach, although confidence intervals expanded rapidly

because of the few observations at large distances. These findings are similar to estimates of absolute proportions of seals entering the water in relation to distance (Table 2).

Relative to a base risk of $e^0 = 1$ when a seal was directly abeam of the observer (90° from the ship's course), risk of a seal entering the water when approached at the same distance dead ahead of the vessel was approximately 3.7 times greater (Fig. 3). We found no significant interaction between distance and bearing. That is, the increase in the risk of a seal entering the water with decreasing bearing (from 90° [abeam] to 0° [ahead]) was the same across the range of distances (from 0 m to 1,000 m).

In general, there seemed to be few water-entry responses by seals to vessels at distances greater than approximately



Figure 2. Relative risk, expressed as the logarithm of the hazard, of a harbor seal entering the water (abandoning its ice haul-out platform) in response to various distances of approach by cruise vessels in Disenchantment Bay, Alaska, USA, 14 May to 1 August 2002. Approximate 95% confidence limits are shown by the thin curves. Observation distances are marked by the rug fibers plotted at the bottom.

Table 2. Proportion of ice-associated harbor seals entering the water in response to various approach distances (in 100-m bins) by cruise ships in Disenchantment Bay, Alaska, USA, 14 May to 1 August 2002. Approximate 95% confidence limits are shown (Agresti and Coull 1998). Note that a given proportion represents only the fraction of seals that entered the water (of those observed) within the relevant distance bin.^a

| Distance bin (m) | Proportion of seals that entered water | Lower 95% CI | Upper 95% CI | Total n |
|---------------------|--|-----------------|-----------------|---------|
| 1-100 | 0.89 | 0.69 | 0.97 | 19 |
| 101-200 | 0.77 | 0.66 | 0.85 | 74 |
| 201-300 | 0.44 | 0.36 | 0.52 | 158 |
| 301-400 | 0.24 | 0.19 | 0.31 | 182 |
| 401-500 | 0.06 | 0.03 | 0.11 | 154 |
| 501-600 | 0.05 | 0.03 | 0.10 | 133 |
| 601-700 | 0.03 | 0.01 | 0.09 | 115 |
| 701-800 | 0.04 | 0.01 | 0.10 | 80 |
| 801-900 | 0.03 | 0.01 | 0.11 | 62 |
| 901-1,000 | 0.00 | 0.00 | 0.09 | 39 |

^a Proportions are approximations because they do not account explicitly for the censored nature of the proportion data (i.e., seals that passed abeam of the ship and those that were lost to observation do not contribute to the measure), they do not adjust for the simultaneous effect of bearing angle, and they do not account for the amount of time the seals were exposed to the ship in each distance bin. Despite this approximation, estimates in this table were qualitatively similar to results of the Cox regression for distance.

500 m, but there was an increase in probability that a seal would enter the water when approached at distances of <400 m. That the absolute response by seals seemed to occur at smaller distances than the relative response may be a reflection of the smoothing parameter we used in the Cox regression, as well as a reflection of the limitations for approximating absolute risks (see Table 2). We conclude that most (77%) seals approached by vessels within 200 m were sufficiently disturbed to flush into the water.

Results of model A suggest that a typical harbor seal pup that spends 40% of its time in the water, even in ice-chilled glacial water (3° C), liberates enough heat via metabolism to



Figure 3. Relative risk, expressed as the logarithm of the hazard, of a harbor seal entering the water (abandoning its ice platform) in response to varying bearing angles during approach by cruise ships in Disenchantment Bay, Alaska, USA, 14 May to 1 August 2002. Approximate 95% confidence limits are shown by the thin curves. Observation bearings are marked by the rug fibers plotted at the bottom, which we jittered to better illustrate relative sampling densities at the 15° measurement increments.



Proportion of time pup is in water

Figure 4. Modeled net energy balance (MJ/day) for ice-associated harbor seal pups during nursing (May to Jun) in conditions typical within and near the study area, Disenchantment Bay, Alaska, USA, 2002. Energy values represent the remaining net energy (MJ) after accounting for metabolism and heat loss to water, which ranged from 3° C to 5° C in areas of ice cover. We present heat loss in 12° C water, typical along coastal Alaska for comparison. The top panel (A) shows results of model A, which used a generalized regression for marine mammals to estimate metabolic rate based on body mass (converted to pup age [days] given birth wt and growth rates). The bottom panel (B) shows results of model B, which used activity-dependent metabolic rates from experimental studies scaled to the mass of a newborn pup (10 kg).

support normal body temperature. However, if younger pups (<5-15 days old) were to increase the proportion of time in the water to >50%, they would need to increase metabolism (e.g., consume more energy via milk or prey) to remain thermally neutral and not incur an energy deficit. The steady increase in daily energy requirements for seal pups relative to increasing age is a combined function of growth and increased maintenance on a larger body (Fig. 4A).

Model B also indicated the likelihood of an energy deficit as a 10-kg harbor seal pup spends increasing time in the water (Fig. 4B). Using activity-specific metabolic rates, newly born pups apparently cannot meet their energy demands if they spend >50% of their time in water as cold as 3° C, especially if their typical activity (to which their energy budget would be adapted) involves traveling at the slowest speed tested in captive studies of 0.5 m/second, twice as fast as actually observed in free-ranging newborn pups (Jørgensen et al. 2001). Thus, similar to our conclusions from model A, for pups to increase their daily time in the water to >12 hours per day (50%) in ice-chilled water, they would have to increase metabolism above normal predicted levels to remain thermally neutral.

DISCUSSION

Previous studies on how seals on glacial ice respond when approached by vessels have shown that vessel type and size are factors in the strength of the response. In Muir Inlet, Glacier Bay, more harbor seals entered the water in response to smaller boats, such as kayaks, than to cruise ships, although the latter disturbed seals at greater distances (J. Calambokidis, Cascadia Research Collective, unpublished report). In Johns Hopkins Inlet, Glacier Bay, harbor seals vacated ice floes at greater distances in response to cruise ships than to boats approximately one quarter the size of cruise ships (B. Mathews, Glacier Bay Park and Reserve, unpublished report). Most vessels that enter Disenchantment Bay are cruise ships, although smaller charter or private boats reportedly traverse the eastern coastline (away from the main concentration of seals) infrequently to view the Hubbard Glacier, fish, hunt, or visit Egg (Haenke) Island (Jansen et al. 2006).

Sensitivity of seals to disturbance may also depend on previous experience and their breeding or molting status. Survan and Harvey (1999) found increasing levels of tolerance among harbor seals to repeated disturbance by small boats, yet those authors found increased vigilance and disturbance when pups were present. Although our study showed that mothers and pups were not more sensitive to cruise ships than other seals, other studies at terrestrial sites have noted a heightened alertness among pregnant and postpartum females and that they tend to haul out at the edges of mixed groups or at separate nursery sites altogether (Newby 1973, Jeffries 1982, Lawson and Renouf 1985, Allen et al. 1988, Thompson 1989). Although separation of mothers and pups via disturbance can be a significant source of mortality, we generally observed close mother-pup coordination when disturbed, as the mother entered the water first and waited for the pup to follow (Johnson 1977, Streveler 1979).

Our results are consistent with findings of J. Calambokidis (unpublished report) who found that an increasing proportion of harbor seals in Muir Inlet vacated ice floes when cruise ships approached closer than 500 m. On average, >50% of seals in Muir Inlet entered the water at distances to ships of approximately <300 m, surpassing 90% disturbance at <100 m, similar to our results. Speed of cruise ships and weather showed no obvious effect, although seals seemed to respond to ships at greater distances on clear, sunny days. We also found relative ship bearing to be an important determinant of disturbance, with a greater sensitivity of seals approached directly despite ships appearing smaller when viewed head-on.

We show that ice-associated harbor seal pups are likely to incur an energy deficit if they spend >50% of their time

submerged. As in most phocid pups, most mass gained during nursing is fat that serves to store energy and reduce heat loss as activity in the water increases (Bowen et al. 1992, Harding et al. 2005). Studies on free-ranging harbor seals show that newborn pups spend an average 40% of their time in the water (10 hr/day; Bowen et al. 1999 [Sable Island, 6-12° C], Jørgensen et al. 2001 [Svalbard Island, 4-5° C]). Pups nearing weaning age (approx. 19 days old) are in the water up to 70% of the time (17 hr/day; Jørgensen et al. 2001, Rehberg and Small 2001 [Tugidak Island, 5-10° C]). According to our model, for a newborn pup to increase time submerged to >50%-and still maintain a positive energy balance-would require an extra 4-10% (1.3-3.0 MJ/ day, respectively) of expected energy delivered daily via nursing (31 MJ; Bowen et al. 1992, 2001). To boost aquatic activity even higher, to 60-70%, even assuming a liberal 0.5 m/second swimming output, would require that a pup expend an extra 0.8-1.6 MJ/day (3-5% of its mother's estimated milk energy output of 31 MJ; Bowen et al. 2001) to maintain an energetic balance and thus normal growth. These percentage estimates are conservative, because daily milk energy output for mother seals reported in Bowen et al. (2001) represents an average across the entire nursing period; newborn pups would require <31 MJ per day and nearly weaned pups would require more. When the energy delivered by the mother does not meet energy required to maintain core body temperature, low-temperature stress occurs (Watts 1992, Watts 1996, Harding et al. 2005). A recent study of weaned harbor seal pups at terrestrial sites indicates that low-temperature stress is unavoidable when water temperature falls below 4° C, an effect likely to impact smaller seals during winter (Harding et al. 2005). The smallest pups with the least insulation faced low-temperature stress at $<10^{\circ}$ C. Temperature varied seasonally between 3° C and 17° C during the study by Harding et al. (2005). At the coldest temperatures, a 17-kg seal would have to consume 0.5 kg more prey daily than would a 32-kg seal to maintain an energetic balance. Researchers documented an approximately 30% decrease in over-winter survival in the lightest pups compared to the heaviest.

Low-temperature stress is particularly relevant to seals of tidewater glacial fjords because glacier calving and runoff in the warmer months, and freezing air temperature in winter, causes the water temperature to remain low throughout the year. Based on our energetic modeling and studies showing links between survival and low-temperature stress, we believe that even a modest increase in time that harbor seal pups spend submerged in ice-chilled glacial fjords is likely to upset energy balance. Any energy deficit would be compounded if flushing into the water was coupled with interruptions of nursing.

Alternatively, a mother whose pup was at risk of lowtemperature stress may choose to haul out in areas with warmer water, either on ice or land, or where there are fewer disturbances. For seals in Disenchantment Bay, the closest haul-out sites with more than just a few seals are at the Alsek River mouth (a land haul out 140 km away) and Icy Bay (a tidewater glacial fjord 115 km away), where hundreds to thousands of seals have been counted (Jansen et al. 2006). Icy Bay has a considerably larger area of dense ice cover and no regular vessel traffic due to a shallow moraine near the mouth of the bay. It is unlikely that mothers (with dependent pups) would relocate to either of these locations within the lactation period, a journey that would take ≥ 6 days at average swimming speeds, but translocating across years is certainly feasible (Jørgensen et al. 2001). Interestingly, pup productivity in Disenchantment Bay, measured as the ratio of pups to the entire population (10%; Jansen et al. 2006), was <50% that observed at other glacial haul-out areas (Aialik Bay: 26% [Hoover 1983]; Johns' Hopkins Inlet: 25–31%; Muir Inlet: 22–30% [Streveler 1979]; Johns' Hopkins Inlet: 34–36% [Mathews and Pendleton 2006]).

Given that apparently subtle behavioral responses could have population-level impacts, and considering the actual guidelines and regulations pertaining to vessel approaches, is there an appropriate level of protection against disturbance for harbor seals in glacial fjords? The United States Marine Mammal Protection Act (MMPA) of 1972 (Amended 2004, 50 CFR [Code of United States Federal Regulations] 216), and its implementing regulations, prohibits any take of marine mammals, which means in part it is unlawful for a vessel to conduct any act, negligent or intentional, that results in disturbing or molesting a marine mammal in waters under the jurisdiction of the United States. Voluntary guidelines in Alaska stemming from the MMPA advise that vessels maintain minimum distances from seals of 91 m (100 vards; NOAA 2006). The 91-m approach guideline from NOAA, which has responsibility for managing pinniped and cetacean populations in United States waters, applies without distinction to all species of marine mammal in Alaska (NOAA 2006). Accordingly, cruise ships entering Disenchantment Bay are advised not to approach seals \leq 91 m, a distance at which we showed approximately 90% of seals would already flush into the water. Chronic close approaches increase the likelihood of repeated disruption to individual seals' normal behavior and in turn their daily and seasonal energy budgets. Other studies indicate that such disruptions may cause seals to avoid haul-out areas over short or long time scales (Allen et al. 1984, Survan and Harvey 1999). The only enforceable regulation in United States waters that protects harbor seals from vessel disturbance is at Glacier Bay National Park, where cruise ships are excluded from Johns Hopkins Inlet during seal pupping (1 May to 30 Jun) and molting (1 Jul to 31 Aug; National Park Service 1996). Where cruise ships are permitted in the Park, they are not allowed to approach seals at <403 m (0.25 miles; 36 CFR 13.65).

In Disenchantment Bay, cruise ships whose companies are members of the NorthWest CruiseShip Association (NWCA, Vancouver, BC, Canada), which represents virtually all ships that entered the study area, have a stated policy to avoid approaching seals closer than 500 m. However, approaches closer than 500 m occurred on 85% of vessels that entered Disenchantment Bay (this study; based on ships with observers), which suggests that despite ships' best efforts to avoid seals it is difficult for large, slow-turning vessels to negotiate ice fields while also anticipating possible seal approaches. We expect that the main limitation is that vessel maneuvering to avoid ice must be initiated before ship personnel first become aware of seals ahead. Ship personnel serving as lookouts seemed to be primarily concerned with preventing collisions with large ice, and in most cases were not able, or not attempting, to identify seals until within close range by which time there were few options to avoid them.

MANAGEMENT IMPLICATIONS

Our findings point to the need for regulations requiring cruise ships to maintain minimum approach distances to harbor seals of 500 m, particularly during pupping when young seals seem prone to thermal stress. To facilitate separation between ships and seals on ice, we recommend using trained, dedicated observers and a formal sighting protocol to increase sighting distance to ≥ 1 km as we achieved in our study, which will aid ships in selecting a route not likely to disturb seals and to determine when the likelihood of disturbance dictates an area should be avoided. In areas of floating ice where seals are known to occur, confining travel to open water leads would allow ships to maximize the distance to potential ice habitat for seals. In Disenchantment Bay, even under the densest ice conditions there is often clearer water within 1 km of the eastern shoreline due to tidal currents to and from Russell Fjord (Fig. 1; Jansen et al. 2006), a potential corridor apart from the typically densest aggregations of seals. Marine pilots serving aboard cruise ships should be encouraged to consider this as the default path into Disenchantment Bay. At other glacial fjords, similar topography and ice conditions (i.e., open leads distant from seal aggregations) may similarly make it feasible for cruise ships to avoid seals. In these areas, we recommend a more adaptive approach to cruise ship management, using observers and an established navigation corridor when ice conditions permit. Still, in narrow fjords (<2 km) with more uniformly dense ice and widely scattered seals (such as Johns Hopkins Inlet), our findings support a blanket exclusion of cruise ships during seal pupping and molting because we believe disturbing seals in these areas is probably unavoidable.

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