

Beluga, *Delphinapterus leucas*, Ethogram: A Tool for Cook Inlet Beluga Conservation?

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Introduction

An ethogram is a catalogue of mutually exclusive and objective behaviors or actions exhibited by an animal that avoids subjectivity and functional inference as to their possible purpose. It is a key tool that helps to quantify species-specific behaviors by describing the discrete, basic motor patterns that form the behavioral repertoire of a given species (Kikkawa and Thorne, 1971; Martin and Bateson, 2007). By describing and defining the behavioral inventory of a species as an ethogram, behaviors among different populations may be compared more thoroughly

and accurately (Müller et al., 1998), as well as understood in terms of their causative and functional bases (Purton, 1978). The establishment of a basic ethogram is essential to the pursuit of further behavioral analyses of any given species (Scheer et al., 2004).

Despite the potential value of an ethogram to behavioral studies, only a few are available for a select number of species (Scheer et al., 2004). For marine mammals, the behavior of which has been studied extensively, the lack of ethograms cataloging their behaviors is surprising (a complete list of studies that include cetacean ethograms is given in Appendix A). The majority of cetacean ethograms focus on *Tursiops* (e.g., Mann and Smuts, 1999; von Streit et al., 2011), including perhaps the most comprehensive marine mammal ethogram, developed by Müller et al. (1998), who built upon previous observations to describe over one hundred behaviors of the bottlenose dolphins, *Tursiops truncatus*, observed along the San Diego coastline.

Some of the behaviors described in the cetacean ethograms, such as leaping, are shared among different species (Norris and Dohl, 1979; Dudzinski, 1996; Müller et al., 1998), while other behaviors, such as spray-

ing displayed by orca, *Orcinus orca* (Martinez and Klinghammer, 1978), are specific to only that species. Even though an ethogram based on the behaviors of one population is widely accepted as not representative for the species as a whole, that ethogram can serve as a reference and standard to understand basic species traits and to inform species management decisions.

Utilizing an ethogram to study a species of concern will provide a valuable tool to the emerging field of “conservation behavior,” which uses the proximate and ultimate aspects of animal behavior to aid conservation decisions and reduce the loss of biodiversity (Buchholz, 2007). The conservation of cetacean species may benefit from ethogram use, as cetaceans are known to exhibit behavioral changes in response to a wide variety of anthropogenic disturbances including navy sonar, aircraft overflight, ship traffic, ice breaking, and marine construction (Richardson et al., 1995; Southall et al., 2007). In addition, the response of bowhead whales, *Balaena mysticetus*, and possibly other cetaceans to these anthropogenic disturbances varies with behavioral activity (Beale and Monaghan, 2004; Ellison et al., 2012). A complete catalog of behaviors for

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ABSTRACT—We present the first peer-reviewed wild beluga, *Delphinapterus leucas*, whale ethogram, a comprehensive description and definition of behavioral states and events exhibited by the endangered stock of Cook Inlet beluga whales (CIBWs). The ethogram can be used to help quantify beluga behaviors and increase the utility of future and ongoing beluga behavioral studies, in Cook Inlet and for other populations. We tested the applicability of the ethogram by quantitatively examining spatial, temporal, and environmental effects on the probabil-

ity of observing specific beluga behaviors in Eagle Bay and Eagle River (Knik Arm, Cook Inlet). Behaviors were observed and recorded from 2007 to 2011 between May and December when belugas are known to forage in the study area. We found that CIBWs are generally more likely to travel than mill in Eagle Bay, except when the tide is ebbing and above its midpoint, and that traveling occurred more frequently in Eagle River than in either the north or south sections of the bay. The results of our quantitative behavioral analysis can be compared

with anecdotal observations of whale activity in the bay, and we encourage further investigation to more fully explain our results. The explicit language used to define this beluga ethogram will facilitate a more standard approach to behavioral studies of CIBWs, provide a means to quantify the response of CIBWs to anthropogenic activities, and allow comparison among multiple populations. Thus, this CIBW ethogram will potentially promote innovative approaches to help manage the endangered CIBW population.

a cetacean may thus help researchers quantify changes in observed behavior due to different levels and types of disturbance for a cetacean population inhabiting an anthropogenically-altered environment and assist in directing management efforts.

One endangered stock that may benefit from a behavior-based management approach is the Cook Inlet stock of beluga whales (*Delphinapterus leucas*). This small population has been geographically isolated from other beluga populations for over 10,000 years and is also the most genetically distinct of the species (O’Corry–Crowe et al., 1997; Laidre et al., 2000). The size of the Cook Inlet beluga whale (CIBW) population decreased by half between 1994 and 1998, primarily due to unsustainable subsistence harvests, and has continued to decrease by 1.6% annually since 1999 (Hobbs et al., 2000; Hobbs et al., 2015).

The geographic range of CIBWs has also contracted substantially over the last several decades, with very few whales observed in lower Cook Inlet during the summer months and the area of highest concentration in the upper inlet near Anchorage, the largest city and port in Alaska (Rugh et al., 2010). The CIBW was federally listed as an endangered species in 2008, primarily because of the lack of population recovery after regulation of the Alaska Native subsistence hunt, a relatively small geographic distribution, and concerns about long-term population viability (Hill and DeMaster, 1998; NMFS¹). Because very little research was conducted on CIBWs prior to their endangered listing, a dearth of literature exists on their basic ecology and behavior, and factors currently impeding recovery are unknown.

In this paper we present an ethogram of CIBW behaviors observed from May to December 2007 to 2011 in Eagle Bay and Eagle River in Knik Arm in the upper Cook Inlet, a frequent fall gathering area for the whales (Hunting-

ton, 2000; Hobbs et al., 2005; Rugh et al., 2010). It is our hope that this beluga whale ethogram will serve as a reference for future behavioral studies of CIBWs and other beluga populations. We also describe how CIBW behaviors vary by tide state and location within Eagle Bay, demonstrating how the application of our ethogram can increase both ecological and behavioral knowledge of CIBWs over varying temporal and spatial scales. Such knowledge will help direct future studies of CIBWs concerning their response to human disturbances within their critical habitat.

Methods

Study Area

Cook Inlet is a tidal estuary located in south-central Alaska and covers an area of approximately 20,000 km² with 1,350 km of coastline (Rugh et al., 2005). Extreme tidal fluctuations with a 9 m range result in strong currents up to 9–10 knots and tidal bores, which constantly alter the shoreline (Moore et al., 2000). Our CIBW behavioral studies were conducted in Eagle Bay and Eagle River, which are located in Knik Arm, upper Cook Inlet (Fig. 1).

Glacially-fed Eagle River flows through Eagle River Flats, a 866 ha estuarine marsh on Joint-Base Elmendorf-Richardson, before emptying into Eagle Bay. A complex interaction of physical forces influences the marine system of Cook Inlet, including those exerted by a high tidal range, glacial-fluvial effects from multiple river inputs, high degree of sedimentation, and the subarctic coastal climate of southcentral Alaska (Lawson et al.²). Direct anthropogenic influences on the study area are largely centered on the flats and include military training, both historic (Army artillery impact area since 1949) and current (winter firing of artillery into flats), as well as

activities associated with the remediation of white phosphorus residues.

Ethogram

We developed our ethogram opportunistically from a U.S. Army monitoring project of CIBWs in Eagle Bay and Eagle River. Observations of CIBWs were carried out from 2007 to 2011 between the months of May and December when belugas gather in Eagle Bay (Huntington, 2000) and feed in Eagle River. Observations were conducted by two or three experienced observers using 12x45 power binoculars and high-powered spotting scopes from the north shore at the mouth of Eagle River, an advantageous survey location to view whales throughout Eagle Bay and in the mouth of the river.

During the 2007 field season, beluga observation protocol followed the ad libitum sampling technique (Altmann, 1974), with general field notes recorded when belugas entered Eagle Bay. From these observations, multiple beluga behaviors were initially defined and described. Beginning in 2008, a more systematic sampling approach was employed, which consisted of a group follow protocol and focal group sampling method (Altmann, 1974).

Observers tracked a group of whales over the course of a 20-min sampling period and defined the activity of the group based on the behavioral state of the majority of whales during the period. A “group” of whales was defined as the number of estimated animals sufficiently close in proximity to potentially be confused with each other (Mann and Smutts, 1999). A behavior that occurred over an extended period of time, such as milling, was considered a “state” (Martin and Bateson, 2007).

Within each sampling period, we estimated the number of whales using instantaneous scans over the 20-min period, though estimates were usually made within the first 10 min of the round after counting all of the individuals in a group(s), trying to minimize double counting. Whales were also classified as white, gray, or calf,

¹NMFS (National Marine Fisheries Service) 2008. Conservation plan for the Cook Inlet beluga whale (*Delphinapterus leucas*). NMFS, Office of Prot. Res., Juneau, AK, 122 p.

²Lawson, D. E., L. E. Hunter, S. R. Bigl, B. M. Nadeau, P. B. Weyrick and J. H. Bodette. 1996. Physical system dynamics, white phosphorus fate and transport, 1994, Eagle River Flats, Fort Richardson, Alaska. CRREL Rep. 4 p. prep. for U.S. Army Alaska, Fort Richardson.

and the location of whale groups at the start of each sampling round was approximated, based on a 8 x 6 cell grid superimposed on a map of Eagle Bay and Eagle River (Fig. 1). Each cell represented a 1 km² area. At the end of each day, an estimate of the total number of whales was made by adding up the total number of individuals counted across all independent whale observations per the study protocol.

During the 2011 field season, the beluga observation protocol was expanded for whales that entered Eagle River. Specifically, we included a fine-scale behavioral component, or “event,” which we defined as a discrete behavior, such as flapping, that occurs at a certain point in time (Martin and Bateson, 2007). When an individual whale performed an event in the river, observers recorded the type of event, the time, and the state of the majority of the whales in the river at that time. Events were only recorded for whales in Eagle River up to the first turn in the river (Fig. 1) because of their proximity to observers, while states continued to be recorded for whales in both Eagle River and Eagle Bay.

Systematic observations were made on the Cook Inlet whales between 2008 and 2011. As our knowledge of the beluga behavioral repertoire has expanded, we constructed an ethogram of beluga behaviors frequently viewed in Eagle Bay and Eagle River and have added to it as new behaviors are described. Between 2008 and 2011 we also continued to refine and edit descriptions of the behaviors to be included in the ethogram. We present the ethogram in two categories, states and events, with video and photographs compiled for each behavior.

Testing the Applicability of the Ethogram

This ethogram was developed to provide standard definitions so that beluga behaviors could be quantified and to standardize future studies involving Cook Inlet beluga life history and ecology, thus enhancing our overall understanding of their biology. We used the ethogram to describe the be-

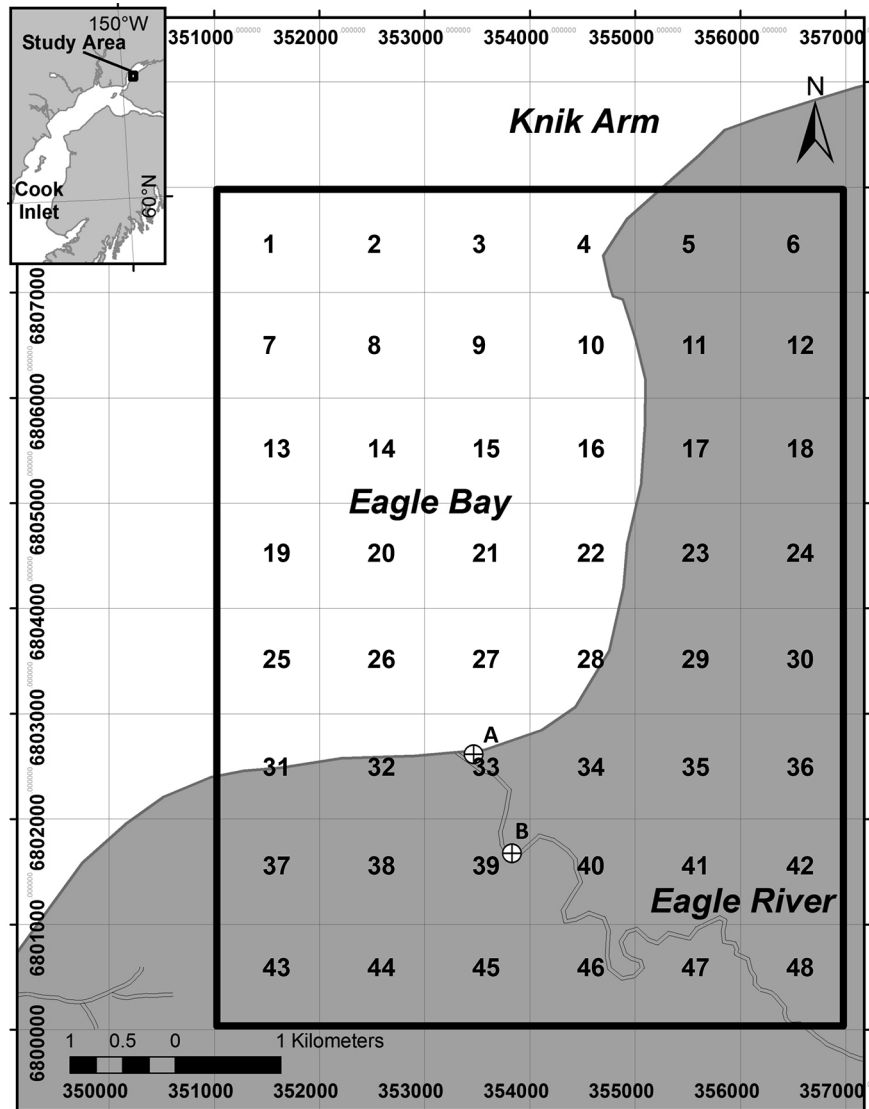


Figure 1.— Location of Eagle River and Eagle Bay in Knik Arm, Cook Inlet, Alaska, and superimposed grid for recording beluga whale visual locations. 1 cell=1 km² area. CIBWs only found in cells 1, 2, 3, 4, 7, 8, 9, 10, 13, 14, 15, 16, 19, 20, 21, 22, 25, 26, 27, 28, 31, 32, 33, and 39. Observations of whales in Eagle River conducted in mark “A” location and up river to mark “B”. Map projection in WGS 84, UTM Zone 6 North (meters), declination 19° E.

havior of belugas in Eagle Bay and Eagle River and analyze the frequency of behaviors to corroborate the apparent relationship between tidal fluctuations and beluga movements and behaviors in the study site.

On a large temporal scale, beluga distribution within Cook Inlet is based primarily on proximity to rivers with Chinook salmon, *Oncorhynchus*

tshawytscha, runs, rivers with medium flow accumulation, tidal flats, and areas with sandy coastlines (Moore et al., 2000; Goetz et al., 2007; Goetz et al., 2012). Daily beluga movement patterns, however, are largely determined by tides, and in upper Cook Inlet, it is believed that beluga travel is associated with tidal currents and direction (Ezer et al., 2008). Specific-

ly, with a flooding tide belugas move up Knik Arm to utilize typically inaccessible mudflats and river mouth areas for foraging (Ezer et al., 2008).

In Eagle Bay, during the ice-free months the belugas seem to move and behave in a fairly predictable pattern relative to the tide cycle, though these conclusions have been based solely on anecdotal evidence collected from 2007 to 2011 in conjunction with the beluga monitoring project around Eagle River Flats.

After about a half of the ebb cycle, belugas travel south from areas north of the bay with the outgoing tide. Some bypass Eagle River, but usually at least one group enters the river and mills or travels up and down the river until about three-quarter ebb. Those that entirely bypass the river seem to move west and mill along the shore until they reach the sandbar at the southern end of the bay, where they remain to mill or leave the bay. When the tide begins to flood, the whales actively travel, following the flooding current across the mudflats to the north end of Eagle Bay. By three-quarters flood, the whales have disappeared around the north point of the bay on their way to upper arm areas that are probably only accessible at or near high tide.

Whereas these anecdotal patterns seem to be typical of the belugas in Eagle Bay in the ice-free months, their actual probability and frequency had not yet been documented. The ethogram provides a method to classify these behaviors by time period so that the probability of seeing a behavior can be related to the environmental variables, thus allowing quantification of beluga movement patterns.

For this analysis, we consider the two most frequently observed behavioral states, milling and traveling, as they were easily assessed across the entire study area compared to individual behavioral events, which generally require close proximity to the whale. Eagle Bay was separated into three areas (Fig. 1): “North Bay” (grid areas 4, 10, 16, 22, 28, 34), the “River” (areas 33, 39, 40), and “South Bay” (areas 31, 32, 25, 26), which is located

adjacent to the previously referenced sandbar. For each 20-min period, tidal information from the Port of Anchorage tide station maintained by the National Oceanic and Atmospheric Administration was corrected with a half hour delay to account for the distance between the Port of Anchorage and Eagle Bay.

The tide cycle was divided into six categories: flood tide upper half and lower half, ebb tide upper half and lower half, at high tide or at low tide. Belugas were not observed in the bay during high tides, so we combined the remaining tide cycles into five categories: EbbAbove, EbbBelow, FloodAbove, FloodBelow, and Low.

Finally, behavior differences were thought to occur between August and the later months based on anecdotal observations made from Eagle River Flats so two time periods, “August” and “months other than August,” were considered. Only data from 2011 were used, as observations from only 2011 provided sufficient information to determine tide states for each 20-min observation period. Each 20-min observation period from 2011 with whales present and either milling or traveling in these grid areas was included in the analysis. Periods without beluga sightings were omitted.

With the probability of the logged behavior as the dependent variable, and location, tide categories, and month as the independent variables, we used logistic regression (glm) in the statistical computing language and environment R version 2.13.1 (<http://cran.r-project.org/>) and the code editor Tinn-R version 1.16.1.4 (<http://www.sciviews.org/Tinn-R/>) to estimate the probability of observing traveling as a behavior for a given 20-min interval in each area, under different tide categories and during August vs later months. We consider an additive model:

$$\text{Probability}(\text{traveling behavior}) \sim \text{tidequarter, \# + Bay.Location + Augustday,}$$

with all categories initially represented

individually and then combined into similar tide categories. We then used Akaike Information Criterion (AIC) in R in a stepwise elimination to identify the most parsimonious model.

Results

Ethogram

The ethogram described here follows the standard structure suggested by Martin and Bateson (2007) including events and states. Video sequences of all the definitions below can be found at <https://www.youtube.com/watch?v=4x7N0NoHgnU>. Images of feeding behavior provided by Stacy DeRuiter.

States

- 1) Milling: Whales surfacing in a more or less constantly varying direction, especially in relation to each other. They may remain in the same area or drift/move with the tide or current.
- 2) Traveling: Whale or whales moving in a consistent, unidirectional fashion relative to other individuals in a group. Traveling whales typically appear to move in a purposeful, coordinated manner, most often with the direction of the tidal current. An exception to this rule is that when traveling in rivers, whales may travel against the water flow. A single traveling whale moves forward with few to no lateral deviations in course.

Events

- 1) Bubbling: A whale blows underwater or near the surface and creates a cloud of bubbles that splash at the surface. This definition does not include the normal exhalation that sometimes occurs immediately prior to surfacing.
- 2) Fast Dive: Similar to the diving behavior state but more rapid and always accompanied by significant surface disturbance from the beating tail fluke. The acute downward angle bending may be absent or less dramatic.
- 3) Feeding: Whale usually observed in the “prey pursuit” (no. 7 below) behavioral event just prior to feeding. The distinction between the two events

is that a prey item is observed in the whale's mouth during feeding but not during prey pursuit. Visual observation of prey in a whale's mouth is extremely rare, owing to the turbid waters of Knik Arm combined with the tendency for belugas to ingest prey whole. To capture instances when prey was not observed in a whale's mouth, yet feeding had likely occurred, we added the following language to the definition of a feeding event: a prey-pursuit event which includes a whale driving a prey item onto land or into the air, followed by observation of a whale or pursuit wake at the point of prey re-entry into the water, and the observer has more than 50% confidence that the prey item was captured (e.g., as indicated by a violent surface disturbance at the point of reentry followed by an immediate cessation of observable activity); note that all three conditions must be met for this secondary definition to apply.

4) Flapping: Pectoral or caudal fin slams the surface and creates splash. Multiple flapping in sequence is considered a single event, unless another event is observed between flapping.

5) Floating: Whale observed at the surface with some portion of its body visible for an extended period of time (typically 10 sec or more) and with little to no directed movements. The whale moves passively with the current and does not transition into prey pursuit as often seen in side-scanning (no. 8 below).

6) Normal Dive: Surfacing whale bends its dorsal surface at an acute downward angle, slipping beneath the surface of the water with the tail flukes usually emerging completely out of the water and being the last part of the whale seen prior to complete submergence; this action is slow, almost casual.

7) Prey Pursuit: Whale exhibits sudden or explosive movements, often forward but may include rapid changes in direction and depth, always resulting in a fast-appearing linear wake, violent disturbance of water, or a combination of the two. No interactions between whales are observed prior to

or during this event to avoid confusion with social interactions.

8) Side-scanning: Whale swims (often very slowly) at the surface with the lateral aspect of its body visible. The pectoral flipper, lateral surface of the body, tail fluke, or a combination of these parts, is visible, often for 30 sec to several minutes. This behavioral event is often followed by explosive movements of the tail as the animal moves rapidly forward in pursuit of prey.

9) Snorkeling: A surfacing whale lifts its head gently to the surface in such a manner that only the melon, blowhole, and a small portion of the dorsal surface just posterior to the blowhole are visible. After gas exchange has occurred, the whale then gently lowers its head below the surface. The dorsal ridge is never seen during a snorkeling event. Note that this behavior often makes detection of whales difficult from a distance as it reveals only a small portion of the whale and leaves a rapidly dissipated, relatively small (several feet diameter), concavity at the surface of the water.

10) Social Interaction: Typically two, but sometimes more, whales engage in physical contact, chasing each other, or tail flapping each other, always followed by one of the individuals moving away from the other. This event does not apply to mother-calf interactions.

11) Spy Hopping: Whale emerges from the water with its head held vertically above the water, to at least eye level, but without the pectoral flippers being above the water's surface, and remains in this position for at least several seconds before submerging vertically with its head submerging last. The eyes are usually observed in a spy-hopping beluga.

12) Tail up: Caudal fin and sometimes part of the peduncle is observed above the surface, as if the whale is diving, but these remain in the air for an extended period of time (5 sec or more).

13) Other: Behavior exhibited by whale does not fall into one of the established event categories.

14) Unknown: Behavior not fully observed; observer cannot confidently place behavior into one of the established event categories.

Testing the Applicability of the Ethogram

A total of 659 h 40 min of observations from 3 June until 14 Dec. 2011 were collected. From these, 64 h 20 min were made in the presence of belugas and were included in the analysis.

In the initial analysis we found that EbbBelow (estimate = 1.53 (SE = 0.56), $z = 2.76$, $p < 0.01$), FloodAbove (estimate = 2.36 (SE = 0.83), $z = 2.83$, $p < 0.01$), FloodBelow (estimate = 1.90 (SE = 0.60), $z = 3.18$, $p < 0.01$), and Low tide (estimate = 1.92 (SE = 0.78), $z = 2.45$, $p < 0.01$) categories were statistically different from EbbAbove, but not from each other, and so they were grouped together for further analysis so that the tide quarter variable was either EbbAbove or not. The stepwise process removed the Augustday variable, as date was not found to have any effect on the probabilities, leaving the probability to be determined by the location and whether or not the tide was in the EbbAbove category.

The final logistic regression model was used to calculate the probabilities of observing travelling behavior when the tide was ebbing and was above half for that cycle (EbbAbove) for each bay location. Across all locations, traveling is more frequently observed during the grouped tide quarters than during the EbbAbove tide quarter (Fig. 2A). During the grouped tide quarter, traveling is significantly more likely to occur in Eagle River than either north or south Eagle Bay, while milling is significantly more likely to occur in the north section of the bay than in the river. During the EbbAbove tide quarter, belugas are in general more likely to be milling (Fig. 2B), but when traveling, the belugas are more likely to be found in the river than any other area of the bay.

Discussion

In total we cataloged two behavioral states and thirteen behavioral events

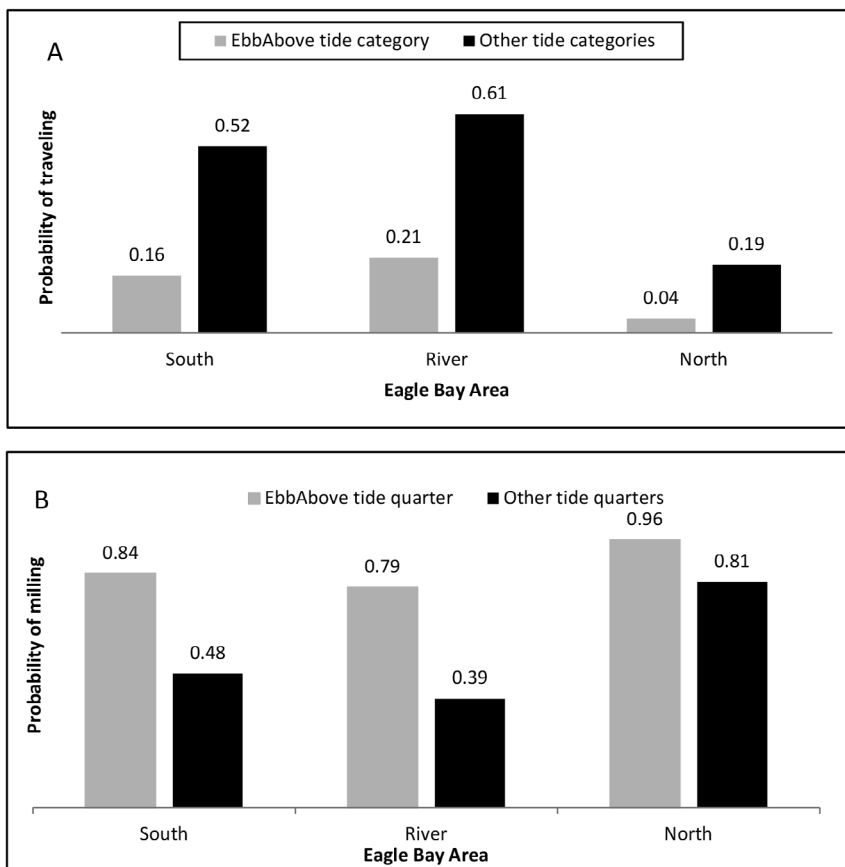


Figure 2.—The probabilities of observing belugas in the behavioral state of traveling (A) and milling (B) at above half tide level during an ebb tide versus all other tide stages combined, in three different areas of Eagle Bay and Eagle River, Knik Arm, Alaska, 2011.

displayed by the Cook Inlet beluga whales in Eagle Bay and Eagle River to establish the first peer-reviewed ethogram for wild beluga whales. In contrast with the extensively described behaviors for *Tursiops* (Müller et al., 1998) and *Stenella longirostris* (Norris and Dohl, 1979), the range of behaviors shown by CIBWs is quite small, which is explained, in part, by the lack of aerials in the beluga behavioral repertoire and by the turbid water present in Cook Inlet, which prevents identification of behavior occurring below the immediate surface layer.

We also demonstrated one application of the ethogram, the quantification of behavioral patterns exhibited by CIBWs, in relation to location within Eagle Bay and tide stage and level.

CIBW behavioral patterns were found to significantly vary with these variables within the study area. Other cetaceans, such as the bowhead whale, also exhibit behaviors that correlate with naturally varying factors including season and water depth (Würsig et al., 1984; Richardson et al., 1995). We found a relatively high probability of observing whales traveling during the majority of the tide cycle, which in general supports previous anecdotal observations. This result makes logical sense, as average current velocity in Cook Inlet is around 3 kn but can extend up to 12 kn (Moore et al., 2000); thus the whales will expend less energy traveling with the current than milling potentially against the current.

However, some of the results of

the tidal analysis contradicted the expected movement and behavioral patterns of the whales in Eagle Bay. For example, the data analysis shows that CIBWs more frequently mill than travel in the bay only when the tide is ebbing and above its midpoint. As the whales will move as far up the arm as possible during the high tide (Ezer et al., 2008), it may be that the majority of CIBWs traveled up Knik Arm and out of sight with the incoming tide and had not yet returned to the bay during that tide quarter. There was a small group of whales during the study period that was noted to swim against the tide at times and to enter Eagle Bay when the majority of whales were not present. It is possible that the behavior of these outliers influenced this result.

The other major finding of the analysis was that CIBWs more frequently travel in Eagle River during all tide stages than in any other area of Eagle Bay. In general, we observed more milling in the north and south areas of the bay as compared to the river. In contrast, anecdotal observations have suggested that the whales travel down from the north in Eagle Bay during the ebbing tide with some whales stopping to mill in Eagle River. The higher probability of observing milling in the north and south regions may be due to the fact that milling inherently occurs over a greater temporal scale whereas traveling through an area occurs more quickly; thus as the analysis was a function of duration of beluga observation, the chances of observing milling in a given area were greater than those of traveling.

It is less clear why CIBWs appear to travel more in the river than any other area. One possible explanation is that the current of Eagle River forces the whales to continually travel with or against the direction of the river current. The current at the mouth of the river is slower and may be more conducive to milling, and thus the whales would likely expend less energy milling just outside Eagle River than within the river itself. Another possible explanation that may operate in conjunction with the previous reasoning

is that the primary foraging grounds in Eagle River for CIBWs may be upriver and out of sight of observers on Eagle River Flats. Hence, the whales would frequently be observed traveling in the river in order to access their foraging sites. Further investigation using the ethogram of the specific events exhibited by CIBWs in Eagle River will provide a more complete explanation of these behavioral patterns.

We also acknowledge that certain sources of error may have affected our tidal analysis. Some of the unexpected behavioral results, such as frequent milling in the north bay, may stem from unknown, uncontrollable variables in Knik Arm, such as variations in local bathymetry or the size and timing of upper Cook Inlet salmon runs. Observer bias may have also played a role, as six different observers documented CIBW states, and there may have been discrepancies between their categorizations of states and events.

Furthermore, it is widely admitted that individual differences in the behavior of wildlife should be considered when analyzing a population. Individual differences in age, sex, size, aggressiveness, learning ability, past experience, heterozygosity, and a myriad of other variables can all affect how an animal reacts to a given situation and may determine the success or failure of a management strategy or a conservation initiative (Festa-Bianchet and Apollonio, 2003).

In addition, the use of both the focal group sampling method and the fine-scale behavioral sampling has several limitations in the development of our ethogram. First, behavioral sampling in the study area is limited to activities above the water line due to the extreme turbidity of Knik Arm. In the future, greater integration of DIDSON sonar imaging (Sound Metrics Corp.³) into the monitoring project may provide a better understanding of subsurface CIBW behaviors. It is also possible that the

³Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

whales may exhibit behaviors further out in Eagle Bay that would not be entirely visible to observers stationed at the mouth of Eagle River.

Furthermore, CIBWs may exhibit different behaviors in other areas of Cook Inlet, as unusual events have been recorded for whales observed in the Little Susitna River (Easley-Appleyard et al.⁴). Because of these limitations, our ethogram may underrepresent the total number of behaviors displayed by CIBWs and thus the catalog may be expanded to include new behaviors observed in the future; however, we believe that the present ethogram provides a general illustration of behaviors one might observe in this population.

Conservation Implications

The goal of this study was to develop an ethogram for CIBWs and demonstrate its quantitative use to enhance understanding of CIBW behavioral patterns. Facilitating cooperation among scientists studying CIBW behaviors is of particular importance due to the whales' endangered status. Moreover, the integration of visually observed behaviors with acoustic behavior can further expand knowledge of CIBW life history and ecology. Several recent and ongoing CIBW monitoring projects in Cook Inlet, including a remote photo-based monitoring study (Easley-Appleyard et al.⁴) and a photo-identification project (McGuire et al.⁵) incorporate a behavioral component. We hope that our ethogram will enable greater collaboration among these various groups and encourage more behavioral studies by

⁴Easley-Appleyard, B., L. Pinney, L. Polasek, J. P. Easley-Appleyard, B., L. Pinney, L. Polasek, J. Prewitt, and T. McGuire. 2011. Alaska SeaLife Center Cook Inlet beluga whale remote monitoring Pilot Study. Final Rep. from Alaska SeaLife Center, Seward, 49 p. (http://www.fakr.noaa.gov/protectedresources/whales/beluga/survey/cib_susitna093011.pdf).

⁵McGuire, T., and C. Kaplan. 2009. Photo-identification of beluga whales in upper Cook Inlet, Alaska. Final rep. of field activities in 2008. Rep. prep. by LGL Alaska Res. Assoc., Inc., Anchorage, for Nati. Fish and Wildl. Found., Chevron, and ConocoPhillips Alaska, Inc.

standardizing the behavioral language of CIBWs.

In addition, we show with our ethogram a correlation between CIBW behavioral state and environmental variables. Future studies should focus on whether CIBW behavioral states are influenced by anthropogenic disturbances such as seismic operations in Cook Inlet. Studies on bowhead whales demonstrate that traveling whales spend less time near the surface when in the vicinity of seismic operations, while feeding and socializing whales were more tolerant of such activities (Robertson et al., 2013). Recent seismic activities in Cook Inlet have included requirements to suspend operations when protected marine mammals, like CIBWs, are observed entering a defined activity zone.⁶ However, if CIBWs' sensitivity to this disturbance increases under a certain behavioral state, like travelling for instance, observers may miss CIBWs during their surveys (e.g., Miller et al. 2005; Harwood et al. 2010), as might happen if the whales spent more time underwater. Thus, with continued development in Cook Inlet, understanding and quantifying how human activities alter CIBW response in the context of a given behavioral state will result in more accurate density and population estimates near these operations (Robertson et al., 2013).

In Eagle River and Eagle Bay specifically, military activities may influence CIBW behavior, yet without objective and definitive descriptions of behavioral states and events, there has been no way to quantify the level of behavioral changes caused by these activities. Our study demonstrates the frequency of CIBW behavioral patterns relative to naturally occurring factors, which provides a CIBW behavior baseline in the absence of direct human disturbances. Further standardized behavioral observations of CIBW in Eagle Bay and Eagle River concurrently with military operations will al-

⁶Editorial, 2012. Responsible seismic operations in Cook Inlet, Alaska. Accessed 22 Aug. 2013. http://www.apachecorp.com/News/Articles/View_Article.aspx?Article.ItemID=2480

low for a comparison of the observed CIBW behavior with and without human disturbances, and thus enabling researchers to quantify the responses of CIBWs to these operations.

Finally, with the likely development of a hydroelectric dam in the Little Susitna River in the next few years, and its potential impacts on CIBW anadromous prey (Alaska Energy Authority⁷), the ability to unambiguously define CIBW foraging behaviors around construction events, may provide insight into changes in the behavior of belugas in response to changes in prey distribution and availability, or changes in the Susitna Delta itself resulting from changes in hydrology or siltation.

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Literature Cited

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49(3-4):227-267.

Beale, C. M., and P. Monaghan. 2004. Behavioural responses to human disturbance: a matter of choice? *Anim. Behav.* 68:1065-1069.

Buchholz, R. 2007. Behavioral biology: an effective and relevant conservation tool. *Trends Ecol. Evol.* 22(8):401-407.

Dudzinski, K. M. 1996. Communication and behavior in the Atlantic spotted dolphins (*Stenella frontalis*): relationships between vo-

cal and behavioral activities. Ph.D. Dissertat., Texas A&M Univ. Coll. Stat., 215 p.

Ellison, W. T., B. L. Southall, C. W. Clark, and A. S. Frankel. 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conserv. Biol.* 26:21-28.

Ezer, T., R. Hobbs, and L. Oey. 2008. On the movement of beluga whales in Cook Inlet, Alaska. *Oceanography* 21(4):186-195.

Festa-Bianchet, M., and M. Apollonio. 2003. *Animal behavior and animal conservation*. Island Press, Wash. D.C., 394 p.

Goetz, K. T., D. J. Rugh, and R. C. Hobbs. 2007. Habitat use in a marine ecosystem: beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Mar. Ecol. Prog. Ser.* 300:247-256.

_____, R. A. Montgomery, J. M. Ver Hoef, R. C. Hobbs, and D. S. Johnson. 2012. Identifying essential summer habitat of the endangered beluga whale *Delphinapterus leucas* in Cook Inlet, Alaska. *Endang. Spec. Res.* 16:135-147. Doi: 10.3354/esr00394

Harwood, L., T. Smith, A. Joynt, D. Kennedy, R. Pitt, S. Moore, and P. Millman. 2010. Potential for displacement of whales and seals by seismic and exploratory drilling activity in the Canadian Beaufort Sea - what have research and observations revealed to date? *In Proceedings of the Canada-U.S. Northern Oil and Gas Research Forum*. November 30 to December 2, 2010 in Calgary, Alberta, p. 30-31.

Hill, P. S., and D. P. DeMaster. 1998. Alaska marine mammal stock assessments, 1998. U.S. Dep. Commer., NOAA Tech. Memo. NMFS AFSC-97, 166 p.

Hobbs, R. C., D. J. Rugh, and D. P. DeMaster. 2000. Abundance of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska, 1994-2000. *Mar. Fish. Rev.* 62(3):37-45.

_____, K. L. Laidre, D. J. Vos, B. A. Mahoney, and M. Egleton. 2005. Movements and area use of belugas, *Delphinapterus leucas*, in a subarctic Alaskan estuary. *Arctic* 58:331-340.

_____, K. E. W. Shelden, D. J. Rugh, C. L. Sims, and J. W. Waite. 2015. Estimated abundance and trend in aerial counts of beluga whales, *Delphinapterus leucas*, in Cook Inlet, Alaska, 1994-2012. *Mar. Fish. Rev.* 77(1):11-31.

Huntington, H. P. 2000. Traditional knowledge of the ecology of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. *Mar. Fish. Rev.* 62(3):134-140.

Kikkawa, J., and M. J. Thorne. 1971. The behaviour of animals. Jacaranda Press, Milton. 223 p.

Laidre, K. L., K. E. W. Shelden, D. J. Rugh, and B. A. Mahoney. 2000. Beluga, *Delphinapterus leucas*, distribution and survey effort in the Gulf of Alaska. *Mar. Fish. Rev.* 62(3):27-36.

Mann, J., and B. Smuts. 1999. Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136(5):529-566.

Martin, P., and P. Bateson. 2007. *Measuring behavior: an introductory guide*. Camb. Univ. Press, Lond., 186 p.

Martinez, D. R., and E. Klinghammer. 1978. A partial ethogram of the killer whale. *Carnivore* 1:13-27.

Miller, G. W., V. D. Moulton, R. A. Davis, M. Holst, P. Millman, A. MacGillivray and D. Hannay. 2005. Monitoring seismic effects on

marine mammals - southeastern Beaufort Sea, 2001-2002. *In* S. L. Armsworthy, P. J. Cranford, and K. Lee (Editors), *Offshore Oil and gas environmental effects monitoring: approaches and technologies*, p. 511-542. Battelle Press, Columbus, Ohio.

Moore, S. E., K. E. W. Shelden, L. K. Litzky, B. A. Mahoney, and D. J. Rugh. 2000. Beluga, *Delphinapterus leucas*, habitat associations in Cook Inlet. *Mar. Fish. Rev.* 62(3):60-80.

Müller, M., H. Boutière, A. Weaver, and N. Candelon. 1998. Ethogram of the bottlenose dolphin (*Tursiops truncatus*) with special reference to solitary and sociable dolphins. *Vie Milieu* 48(2):89-104 [Engl. transl.].

Norris, K. S., and T. P. Dohl. 1979. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull.* 77(4):821-849.

O'Corry-Crowe, G. M., R. S. Suydam, A. Rosenberg, K. J. Frost, and A. E. Dizon. 1997. Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Neartic revealed by mitochondrial DNA. *Mol. Ecol.* 6:955-970.

Purton, A. C. 1978. Ethological categories of behaviour and some consequences of their conflation. *Anim. Behav.* 26:653-670.

Richardson, W. J., C. R. Greene, Jr., C. I. Malme, and D. H. Thomson. 1995. *Marine mammals and noise*. Academic Press, San Diego, Calif., 576 p.

Robertson, F. C., W. R. Koski, T. A. Thomas, W. J. Richardson, B. Würsig, and A. W. Trites. 2013. Seismic operations have variable effects on dive-cycle behavior of bowhead whales in the Beaufort Sea. *Endang. Species Res.* 21:143-160.

Rugh, D. J., K. E. W. Shelden, and R. C. Hobbs. 2010. Range contraction in a beluga whale population. *Endang. Species Res.* 12:69-75.

_____, C. L. Sims, B. A. Mahoney, B. K. Smith, L. K. Litzky, and R. C. Hobbs. 2005. Aerial surveys of belugas in Cook Inlet, Alaska, June 2001, 2002, 2003, and 2004. U.S. Dep. Commer., NOAA Tech Memo NMFS AFSC 149, 71 p.

Scheer, M., B. Hofmann, and I. P. Behr. 2004. Ethogram of selected behaviors initiated by free-ranging short-finned pilot whales (*Globicephala macrorhynchus*) and directed to human swimmers during open water encounters. *Anthrozoös* 17(3):244-258.

Southall, B. L., A. E. Bowles, W. T. Ellison, J. J. Finneran, R. L. Gentry, C. R. Greene, Jr., D. Kastak, D. R. Ketten, J. H. Miller, P. E. Nachtigall, W. J. Richardson, J. A. Thomas, and P. L. Tyack. 2007. Marine mammal noise exposure criteria: initial scientific recommendations. *Aquat. Mamm.* 33:411-522.

Würsig, B., E. M. Dorsey, M. A. Fraker, R. S. Payne, W. J. Richardson, and R. S. Wells. 1984. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: surfacing, respiration, and dive characteristics. *Can. J. Zool.* 62:1910-1921.

von Streit, C., G. Udo, and L. von Fersen. 2011. Ethogram of two captive mother-calf dyads of bottlenose dolphins (*Tursiops truncatus*): Comparison with field ethograms. *Aquat. Mamm.* 37(2):193-197.

**Appendix:
Cetacean Ethograms by Species**

**Atlantic spotted dolphin
(*Stenella frontalis*)**

- Dudzinski, K. M. 1996. Communication and behavior in the Atlantic spotted dolphins (*Stenella frontalis*): relationships between vocal and behavioral activities. Ph.D. Dissertat., Texas A&M Univ. Coll. Sta., p. 196–204.
- Herzing, D. L. 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquat. Mamm.* 22:61–79.
- Miles, J. A., and D. L. Herzing. 2003. Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquat. Mamm.* 29(3):363–377.

Bottlenose dolphin (*Tursiops* spp.)

- Chechina, O. N., and N. L. Kondratieva. 2009. Formation of probabilistic structure of motor behavior in bottlenose dolphins in captivity. *Zhurnal Vyshei Nervnoi Deyatelnosti Imeni I P Pavlova* 59(5):587–592.
- Mann, J., and B. Smuts. 1999. Behavioural

- development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136(5):529–566.
- Müller, M., H. Boutière, A. Weaver, and N. Candelon. 1998. Ethogram of the bottlenose dolphin (*Tursiops truncatus*) with special reference to solitary and sociable dolphins. *Vie Milieu*. 48(2):89–104, [Engl. trans.].
- von Streit, C., G. Udo, and L. von Fersen. 2011. Ethogram of two captive mother-calf dyads of bottlenose dolphins (*Tursiops truncatus*): Comparison with field ethograms. *Aquat. Mamm.* 37(2):193–197.
- Weaver, A. C. 1987. An ethogram of naturally occurring behavior of bottlenose dolphins (*Tursiops truncatus*) in southern Californian waters. Masters thesis, San Diego State Univ., San Diego, Calif. 360 p.

Tucuxi (*Sotalia guianensis*)

- do Nascimento, L. F., P. I. A. P. Medeiros, and M. E. Yamamoto. 2008. Description of the surface behavior of marine tucuxi, *Sotalia guianensis*, at Pipa Beach. *Psicologia: Reflexão & Crítica* 21(3):509.

Orca (*Orcinus orca*)

- Martinez, D. R., and E. Klinghammer. 1978. A partial ethogram of the killer whale. *Carnivore* 1:13–27.

- Salden, D. R. 1979. Supplementary observations concerning an ethogram of the killer whale (*Orcinus orca* L.). *Carnivore* 2(3):17–18.

**Short-finned pilot whale
(*Globicephala macrorhynchus*)**

- Hofmann, B., M. Scheer, and I. P. Behr. 2004. Underwater behaviors of short-finned pilot whales (*Globicephala macrorhynchus*) off Tenerife. *Mammalia* 68(2–3):221–224.
- Scheer, M. 2010. Review of self-initiated behaviors of cetaceans directed towards human swimmers and waders during open water encounters. *Interact. Stud.* 11(3):442–466.
- _____, B. Hofmann, and I. P. Behr. 2004. Ethogram of selected behaviors initiated by free-ranging short-finned pilot whales (*Globicephala macrorhynchus*) and directed to human swimmers during open water encounters. *Anthrozoös* 17(3):244–258.

**Spinner dolphin
(*Stenella longirostris*)**

- Norris, K. S., and T. P. Dohl. 1979. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull.* 77(4):821–849.