Physical–biological interactions in a subarctic estuary: How do environmental and physical factors impact the movement and survival of beluga whales in Cook Inlet, Alaska?

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1. Introduction

Cook Inlet, Alaska, is a subarctic estuary that extends about 250 km from the Gulf of Alaska in the south into the city of Anchorage in the northeast where it branches into two shallower extensions, the Knik Arm north of Anchorage and the Turnagain Arm southeast of Anchorage (Fig. 1). The hydrodynamics and the associated ecosystem in CI are dominated by one of the largest tidal ranges observed in coastal regions of the world’s oceans. Water levels and currents in Cook Inlet are predominantly driven by the semi-diurnal tides coming from the Gulf of Alaska; the tidal ranges are amplified from about 1–2 m near the Gulf of Alaska to 8–10 m in the northern Inlet near Anchorage (Fig. 2). The large tides produce strong currents and tidal bores (especially in the Turnagain Arm) with tidal currents of up to 5 m s⁻¹. Analysis of remote sensing data indicated that as much as 500 km² of mud flats are flooded and exposed twice daily by the large tides (Ezer and Liu, 2010). In addition to tidal currents, other forcing mechanisms of energetic flows include buoyancy-driven flows from melting ice and rivers, and to lesser extent wind-driven currents (for more details on the ocean dynamics, see the numerical simulations of CI presented in Oey et al., 2007 and Ezer et al., 2008).

The upper inlet reaches temperatures of over 15 °C during the summer (Fig. 3), but is partly frozen during the winter months from about December to early April (Mulherin et al., 2001). Therefore, marine mammals in the inlet have to adapt to unique environmental conditions with large daily and seasonal changes.

Cook Inlet is the habitat of the Cook Inlet beluga whales (CIBW; Delphinapterus leucas); the CIBW have been the most isolated group of belugas, since they have been separated for several thousand years from other populations of beluga whales found in the Bristol Bay, the eastern Bering Sea, the eastern Chuckchi Sea and the Beaufort Sea (Hobbs et al., 2005). Population estimates based on aerial surveys indicate that abundance of CIBW has declined from over 1300 individuals in the late 1970s to about 650 in the mid 1990s to around 300 today (Hobbs et al., 2000, 2005, 2008). In comparison, the other populations of belugas around Alaska are stable and include about 60,000 animals. The decline in population estimates of CIBW between
1994 and 1998 was attributed to hunting (about 67 whales per year were harvested). However, following regulation of Native subsistence harvest of belugas in 1999, the estimates continued to show large cyclic interannual variation with no evidence of recovery. In 2008, the CIBW stock was declared as endangered under the Endangered Species Act and in 2011 parts of CI were designated as beluga whale critical habitat areas.

To survive in the harsh and unique environment of CI, the CIBW need to maximize their use of resources within CI such as salmon and other anadromous fishes in river mouths and avoid dangerous conditions such as stranding on tidal mudflats, fast moving floating ice, tidal bores and attacks by killer whales (Shelden et al., 2003). The movement and population dynamics of the CIBW can be divided into four different time-scales: daily, seasonal, interannual, and decadal and longer trends; preliminary studies of the first two time scales have been started, while very little is known on the longer time scales. During the summer and fall the CIBW have been observed to move some 30 km per day (Ezer et al., 2008; Hobbs et al., 2005; Rugh et al., 2000, 2004, 2005). It is believed that this daily movement takes advantage of the large tides, which allows the beluga to swim over flooded mudflats to reach river mouths in the upper CI (Ezer et al., 2008); these shallow regions are only accessible a few hours a day during high tide. There are also indications of seasonal preferences; the CIBW are often concentrated near river mouths in the upper CI during summer and fall, but disperse throughout the middle and lower inlet during the winter (Hobbs et al., 2005), when the upper inlet and rivers are frozen (Mulherin et al., 2001). Studies of the upper inlet (in particular over the Turnagain Arm mudflats) are difficult, since this area is not readily accessible to boats and lacks direct hydrodynamic observations. Therefore, results from numerical hydrodynamic inundation models (Ezer et al., 2008; Oey et al., 2007) and from satellite remote sensing data (Ezer and Liu, 2009, 2010) have been used in the past to study the dynamics of the tides there and map the tidal flats.

The goal of this study is to obtain a better understanding of the relation between physical environmental factors in CI and the CIBW population. Such knowledge may help to explain the variation in CIBW population estimates and how the CIBW population may adapt to future changes, either man-made (e.g., shore construction, dredging, energy resources, etc.) or environmental (e.g., global or regional climate). The paper is organized as follows. First, in Section 2, the beluga and environmental data collection and analysis are described, then the results of the analysis are presented in Section 3, focusing on seasonal and interannual time scales. Finally, conclusions and discussion are offered in Section 4.

2. Data collection and analysis

2.1. Beluga data: satellite tracking, annual counting and stranding reports

The satellite-tracked beluga whale data were initially described by Hobbs et al. (2005) and later, a short subset data of 2 whales over a period of a few weeks were used by Ezer et al. (2008) to show how the belugas move up and down the upper Knik and Turnagain Arms.
using the tides for their advantage. Since the daily movement in the upper CI has been described by Ezer et al. (2008), here the analysis is focused on seasonal to decadal time scales and on the spatial distribution of the CIBW; to do that, the area of interest in the mid- and upper CI was divided into 4 sub-regions (Fig. 1). Raw data obtained from NOAA/Fisheries includes total of some 20 animals, tracked between May-1999 to May-2003. The data are exploratory with small sample sizes of beluga selected opportunistically, and the distribution of tracking data was uneven. The number of tracked whales was 1, 2, 10 and 7 for 1999, 2000, 2001 and 2002–2003, respectively, with

![Anchorage Water Level and Beluga Stranding Events](image)

Fig. 2. Hourly tidal water level in Anchorage (blue line) and time of reported beluga stranding events (red stars) during June to October, 2009.

![Water temperature in Anchorage (weekly averaged)](image)

Fig. 3. The seasonal cycle of water temperature near Anchorage during the years of CIBW tracking (1999–2003). The data were weekly averaged to remove the daily variations.
much more data in late summer and fall (August–November) and less data in winter and spring. Some days have multiple tracking points while another period has no data for several weeks. Moreover, the accuracy of each location (within hundreds of meters) and bad data points required challenging quality control. Therefore, first we mapped all the raw data points for each animal on top of a map of low and high tide shorelines obtained from satellite imagery (Ezer and Liu, 2009, 2010). Then we manually identified the points that clearly fell outside the high water-level shoreline of the inlet and removed them from the data set. We also checked for cases where the same animal was tracked traveling too great a distance within too short a time interval (Ezer et al., 2008), found that the movement of the CIBW when swimming with the tidal currents is over 2 m s$^{-1}$. Typically, between tens to a few hundred data points were removed from each animal file (5–10% of data points).

Abundance estimates of the beluga population have been obtained annually since 1993 using aerial surveys and video photography during 6–7 days each early summer (Rugh et al., 2000, 2004, 2005). The accuracy of these estimates depends on complete coverage and corrections that account for observer error and detectability. For example, water with high turbidity means that beluga are only visible when close to the surface. These estimates indicate a long-term decline in the beluga population as well as interannual variations that will be discussed later.

Reports on beluga stranding events (Vos and Shelden, 2005) are sparse and the exact location is not always indicated in the reports. Moreover, some reports may include animals that have been dead for some time before being observed and reported, while some live stranded belugas may have survived and escaped with the next high tide. We mapped the stranding locations from the few reports that were digitized and provided to us by NOAA on top of the satellite derived shorelines. Initial analysis shows that stranding events happened more often after the highest peak in the Spring tide (Fig. 2); during this period the tidal range decreases from day to day, requiring the CIBW to daily adjust the distance they can safely swim over the flooded mudflats. Further studies of particular “stranding danger zones” are underway with the help of the remote sensing data analysis of Ezer and Liu (2009, 2010), but here, only the annual number of stranding events will be considered.

2.2. Environmental data

Water level (Fig. 2) and temperature (Fig. 3) data are recorded by the NOAA station in Anchorage. During the time when the CIBW are active in the upper CI, the interannual changes in water temperatures for 1999–2003 (when CIBW were tracked) varied by as much as 2 °C during the summer and 4 °C during the fall (Fig. 3). Note that in the spring (early April to mid May) of 1999 and 2002 the water was relatively colder than during the other years, but during the fall (October to December) 1999 was one of the coldest years while 2002 was one of the warmest, the result is that the ice-free period in the upper CI may have been longer by about 1.5 months in 2002 compared with 1999 and 2001 (based on the time when temperatures are below freezing). Our study will try to see if those interannual changes affect the CIBW behavior. The long-term changes in water temperature and their impact on potential ice formation are shown in Fig. 4. Between 1995 and 2004, the average water temperature during summer increased (Fig. 4b) and the freezing season became shorter (Fig. 4a). These changes are likely to affect the CIBW environment. Some of the long-term variations may relate to large-scale climate variations over the Pacific Ocean, such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008); these indices represent large-scale atmospheric pressure patterns and sea surface temperature variations over the North Pacific Ocean. The PDO index has been connected to salmon production in the North Pacific and river flow into C1 (Mantua et al., 1997), ecosystem productivity in the Bering Sea (Jin et al., 2009), and fisheries catches in the Gulf of Alaska (Litzow, 2006). Therefore, it is reasonable to hypothesize that the ecosystem of C1 may also be affected by the PDO variations.

Monthly averaged river discharge data is available from the USGS; the location of several major rivers is shown in Fig. 1. Note however, that stream flow is often measured farther upstream, not in the location where the flow reaches the inlet. We focused our analysis on 7 major rivers with good data, 2 rivers are located in the mid and lower CI (subregion A in Fig. 1), 2 in each of the upper Arms (subregions C and D) and one, the Susitna River, in the mid–north inlet (subregion B). The river data were previously used in the hydrodynamic model of CI (Ezer et al., 2008; Oey et al., 2007); the model shows how salinity fronts move with the tidal currents and create “rip tides” with strong vertical motion. The impact of river discharge on CIBW may relate to the impact of rivers on fish runs (Mantua et al., 1997).

Remote sensing data, such as from MODIS and Landsat satellites were used to map the changing coastlines and morphology of the upper inlet (Ezer and Liu, 2009, 2010); the strong tidal currents transport large amounts of sediment from one place to another which can impact the accessibility of particular regions to CIBW. These changes could lead to beluga stranding if the whales do not learn to adjust to the new morphology of the mudflats.

The analysis method used here involves a standard linear regression method to look for statistically significant correlations between the numbers of CIBW found at a particular region (defined in Fig. 1) during a particular time window, and environmental data such as river flows into the same region. Other qualitative assessments will compare the trends in the CIBW population to time-series of environmental parameters.

3. Results

3.1. The seasonal movement of the belugas and its relation to river runoffs

Because of the uneven distribution of the CIBW tracking data, the analysis combines tracking data by month and by region (see definition of regions in Fig. 1), rather than looking at the movements of an individual whale (as was done for a few animals in the study of Ezer et al., 2008). Fig. 5 shows the distribution of all the beluga tracking locations during each month (for brevity, only every other month is shown); different animals are marked by different colors and symbols. The results provide more details and a larger data set than previous descriptions of the seasonal trends (Hobbs et al., 2005). The general seasonal pattern of the beluga movements is clearly seen, as is the complexity of the CIBW distribution. During the winter months, when the upper inlet is partly ice covered, the CIBW disperse throughout the upper inlet from Point Possession and North Foreland south, to Kalgin Island in the lower inlet (Fig. 5a,b). Then, in late spring and early summer, when the snow and ice melt and the river discharges are at their peak, the CIBW move first to the area near the Susitna River delta (Fig. 5c,d), and later in the fall to the Turnagain and Knik Arms (Fig. 5e,f).

The seasonal variations in water and air temperatures can impact the CIBW by affecting the timing of snow melt, the amount of river discharge, and possibly the amount of fish availability at river mouths; therefore, we test the hypothesis that a relation exists between belugas location and river discharge. The preferred region (out of the 4 sub-regions shown in Fig. 1) of the CIBW at each month is compared with the monthly river discharges that flow into each region of CI (Fig. 6). To prevent a statistical bias due to the uneven counting of belugas during the year (Fig. 6a), we do not consider the number of animals, but rather the relative percentage in each region, i.e., we ask the following question: of the belugas seen in each month, what is their preferred location? During January
to March, while not many belugas are tracked (Fig. 6a), 70%–100% of them spent time in the lower/mid inlet (subregion A, Fig. 6b). During April to July 60%–90% of the CIBW are found near the Susitna River delta (subregion B, Fig. 6c); the Susitna River has the maximum relative discharge in May, accounting for about 50% of all the total discharge analyzed, i.e., it has as much flow as the combined flow of the other 6 rivers (Fig. 6h). In late summer and early fall (August to November) the CIBW move first to Knik Arm (subregion C, Fig. 6d) and then (September to December) to Turnagain Arm (subregion D, Fig. 6e). The CIBW preference between the two Arms is correlated with the relative decrease of river discharge into Knik Arm (Fig. 6i) and the increase of discharge into Turnagain Arm (Fig. 6j) during the fall.

Table 1 summarizes the correlation between the preferred region of the CIBW and the relative flow of each river; $R$ is the correlation coefficient of linear regression, and significance level in % is defined as $S = 100(1 - p)$, where $p$ is the statistical p-value. Though correlation does not necessarily imply causation, it suggests which rivers have the most influence on the motion of the belugas. The highest positive correlation, $R = 0.69$ ($S > 98\%$), is between the Susitna River discharge and the percentage of belugas found nearby (subregion B in Fig. 1). The highest negative correlation, $R = -0.88$ ($S > 99\%$), is between the rivers that flow into the lower inlet (mostly the Kenai River) and the percentage of belugas found in subregion B. The latter result can be seen also in Figs. 6b, c, g and h, whereas the inferred trigger of the belugas to start moving from subregion A to subregion B around April is the relative reduction of Kenai River discharge and the relative increase of Susitna River discharge. Another potential trigger is that water temperatures start warming (Fig. 3), so sea ice is retreating from the upper CI at that time. For example, the mean date of ending ice during 1969–1986 was April 7 ± 18 days (Mulherin et al., 2001). The fact that the number of belugas in Turnagain Arm is positively correlated with the Kenai River flow ($R = 0.67$, $S > 98\%$) could be coincidental or related to unknown reasons, since the plume of the Kenai River does not extend that far. The preference of the belugas to move to Knik Arm is least affected by the local rivers compared to the other regions, so they may be driven by other parameters, such as water temperature and ice coverage. The results suggest that the CIBW learned to optimize their movements within the inlet to follow the different timing of peak river discharges in different rivers.

### 3.2. Interannual and long-term variations in the beluga population

While similar seasonal patterns seem to repeat in different years, there are considerable variations between the movements of one animal to another, and between the movements in one year and another. Although the sample sizes were very small, there seem to be larger variations in the movements of the tagged CIBW during the fall compared with other seasons. However, there are also many more tracking data during the fall, which could create a bias in the analysis. Therefore, we looked closely at weekly composites of the tracking data in each year and the relation of the CIBW location to water temperatures (Fig. 7). This figure suggests that changes in water temperature between one year and another, as seen in Figs. 3 and 4, may cause changes in the beluga behavior. For example, in the first week of March, the water was below freezing in 2002, but slightly warmer in 2003 (and free of ice at that year, according to remote sensing data, not shown). As a result, the belugas in 2003 started moving to the upper inlet earlier than they did in 2002 (Fig. 7a). During the fall and early winter (early September to late December), the water temperature in 2002 was higher than the temperature in other years (Fig. 3), and thus the belugas in 2002 (blue diamonds in Fig. 7) spent more time in the upper Knik Arm (Fig. 7b,c) and then in Turnagain Arm (Fig. 7d). In particular, during the third week of December, the water temperature in Anchorage during 2002 was still slightly above freezing, while the temperature in 1999, 2000, 2001 and 2003 was already below freezing at that time (Figs. 3 and 7d); this difference in environmental conditions influenced the CIBW, so they started moving towards the lower
Fig. 5. The location of all the belugas tracking data found in each month (only every other month is shown for clarity). In each panel, different colors or shapes represent different animals. The number of belugas and the number of data points are indicated in each panel. The black and gray lines are satellite-derived shorelines for very high and very low water levels, respectively (see Ezer and Liu, 2009, 2010, for details). The area of the exposed tidal mudflats between the black and gray lines can change, depending on the tidal range at each tidal cycle.
inlet in 2000, but remained in Knik Arm, Turnagain Arm and near the Susitna River at the same time of the year in 2002.

The annual averaged PDO index and 2 major river discharges over 15 years are compared with the CIBW population counts and stranding (Fig. 8). Besides the declining trend in estimates of the beluga population from 1994 (Fig. 8b), quite striking is the fact that all those data sets apparently show a cycle of about 4 years, which may connect to large-scale climatic variations over the northeast Pacific Ocean as indicated by the PDO index (Fig. 8a). Long-term climatological changes (local and regional) may have impacted the CIBW population over the years, and one parameter that represents the changing climate over the Northeastern Pacific is the PDO index, as discussed before. For example, a statistically significant correlation was found between the water level at Anchorage and the annual PDO index ($R = 0.7, S > 99\%$). It is interesting to note that while global sea level is rising, one of the few regions in the world oceans where a distinct sea level decline over the past decade is seen is the Gulf of Alaska (see Fig. 1 in Willis et al., 2010). Water level decline may affect the ability of the CIBW to reach shallow tidal flats in the upper CI, or affect the number of stranding events (Fig. 8c). River discharge and Salmon production was also found to be affected by the PDO (Mantua et al., 1997), so based on our previous findings it is not unreasonable to assume that the PDO is affecting the CIBW behavior. For example, the watershed regions of the Kenai River (Fig. 8d) and the Susitna River (Fig. 8e) are very different, so climate variations may affect them differently. The Kenai River watershed includes the Kenai Peninsula area between CI and the coastal mountains bordering the Gulf of Alaska in the southeast, while the Susitna watershed stretches north of CI from the Susitna Glacier at the Alaska Range. As a result of those differences, the correlation between the two river discharges is $R = 0.76$ for their monthly flow, but only $R = 0.52$ for their annual flow; these interannual differences are seen in Fig. 8d and e, and could affect the behavior of the CIBW in each year. The Kenai River had maximum annual flow in 2002, while the Susitna River had maximum annual flow in 2005. Note that the Susitna River increase in flow from 2000 to 2005 and decrease

<table>
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<tr>
<th>Belugas in:</th>
<th>Low-CI (A)</th>
<th>Mid-CI (B)</th>
<th>Knik Arm (C)</th>
<th>Turnagain (D)</th>
</tr>
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<tbody>
<tr>
<td>Rivers in A:</td>
<td>+0.36 (94%)</td>
<td>-0.88 (99%)</td>
<td>+0.18 (42%)</td>
<td>+0.67 (98%)</td>
</tr>
<tr>
<td>Rivers in B:</td>
<td>-0.31 (67%)</td>
<td>+0.69 (98%)</td>
<td>-0.32 (70%)</td>
<td>-0.52 (92%)</td>
</tr>
<tr>
<td>Rivers in C:</td>
<td>-0.49 (89%)</td>
<td>+0.46 (87%)</td>
<td>-0.28 (62%)</td>
<td>-0.46 (86%)</td>
</tr>
<tr>
<td>Rivers in D:</td>
<td>+0.19 (44%)</td>
<td>-0.11 (27%)</td>
<td>-0.38 (78%)</td>
<td>+0.41 (81%)</td>
</tr>
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Fig. 6. Comparison of the monthly distribution of the tracked belugas (left panels) and the monthly river flows (right panels). The top panels show the total numbers of (a) tagging data and (f) the total river discharges of 7 rivers (in m$^3$ s$^{-1}$). The other panels show (b-e) the percentage of beluga seen in each of subregions A-D and (g-j) the relative river flow (in %) into each subregion.
thereafter between 2005 and 2008 resembles the change of water temperature in Anchorage (Fig. 4b). If water temperatures reflect air temperatures in the region, warmer years may result in faster mountain ice melt that feed the Susitna River. The Kenai River discharge, on the other hand, is not correlated with the water temperature in Anchorage.

For the beluga population estimates (Fig. 8b), it is difficult to explain the strong cyclicity by sampling error, or by changes in births and deaths. Instead, rather than changes in the total population, the fluctuations may reflect changes in spatial distributions that 1) are not covered in the sampling design, or 2) are linked to changes in observer error and detectability of CIBW during the survey. Two facts may support this hypothesis. First, during years with higher population estimates one notices that high numbers of stranding events occur (2000, 2003, 2007; Fig. 8c). This may indicate that during those years, larger numbers of CIBW are found in the upper tidal flats where they are more easily seen and also prone for stranding. Second, during years with lower population estimates (1995, 1998, 2002 and 2005) the rivers in subregions A and B have maximum discharge. However, as seen before (Fig. 6), a larger river flow will be advantageous for the CIBW population (peak fish runs are associated with river flow), so why are their numbers declining in those years? One explanation is that during those years, more belugas stay offshore where coverage is partial and remain uncounted in those deeper waters.

To further look if there are interannual variations in the preferred location of the CIBW during the period when the aerial surveys are conducted, Fig. 9 shows the count index from the aerial surveys from 1993 to 2011 (before correction for observer error and detectability) for three regions, the Susitna Delta, Knik Arm and Turnagain Arm (including the Chickaloon Bay area in the lower part of the Turnagain Arm, south of Anchorage; see Fig. 1). It is quite clear that the CIBW are not evenly distributed each year during the survey period; their preferred location is likely related to the changing environmental conditions described above. For example, between 1993 and 1996, the number of belugas counted in the Susitna delta increases significantly (Fig. 9), while few belugas were seen in Knik and Turnagain Arms; does this trend correspond to the increase in the Kenai and Susitna river flow which peaked in 1995? (Fig. 8). Also, the unusually large number of belugas counted in Turnagain Arm in 2004 (more than any other year since 1995, Fig. 9) may relate to the warmer than usual water temperatures during this year (the warmest year of the record shown in Fig. 4b). In any case, the large interannual changes of the CIBW distribution may have a confounding effect on estimates of population abundance.

4. Conclusions

The goal of the study was to get a better understanding of the physical and environmental conditions that may affect the movement and survival of the endangered beluga whales in Cook Inlet. Such understanding could help explain the declining numbers of belugas and offer future conservation strategies.

CI is a subarctic estuary with unique environmental conditions to which the CIBW must adjust. The inlet is a closed ecosystem for the belugas, which are believed to have been separated from other Alaskan stocks of belugas for thousands of years. Our study thus suggests that the CIBW optimize their movements and behavior to changing physical parameters such as extremely large tides (up to 10 m range) and large seasonal variations in water temperatures.
and river runoffs. Previous studies (e.g., Ezer et al., 2008) focus on the daily movement of the CIBW with the tides, while here the focus is on seasonal movements (extending the studies by Hobbs et al., 2005, and others), as well as preliminary analysis on potential long-term interannual variations in the beluga population. The most critical factor besides temperatures and ice coverage that appears to influence the seasonal motion of the CIBW was the pattern of river flow.

The rivers which flow into CI have different watershed regions and are affected by different environmental and climatic conditions, so their peak discharges occur at different times. For example, rivers on the north and west side of CI (e.g., Susitna River) are fed by spring-time glacier and snow melt along the Alaska Range mountains, while rivers flowing from the east (e.g., Kenai River) depend on watersheds over the Kenai Peninsula; the latter may be influenced by similar climate that affects the Gulf of Alaska. Peak river flow may be related to increases in the numbers of salmon and other fish species that the CIBW feed on (which is the subject of a follow up research now underway). The study thus shows how the movement of the CIBW follows the relative discharge pattern of different rivers. For example, between August and December the river flow into Knik Arm decreases while the river flow into Turnagain Arm increases; this pattern coincides with more belugas moving from Knik to Turnagain Arm at that period (Fig. 6). The dispersion of the CIBW to the middle–lower CI (subregion A) in the winter is likely affected by the formation of ice in the upper inlet. The study suggests that small temperature differences from one year to another can impact the CIBW behavior: the belugas stay longer in the northern upper CI during warmer years and move earlier towards the lower inlet during colder years (Fig. 7); this could have implications if long-term climatic changes occur over the next decades and centuries.

One of the most intriguing and least understood issues is the pattern of the CIBW population count, which includes a declining long-term trend, as well as an apparent 4-year cycle (Fig. 8b); the former may represent a real decline of the population, but the latter cycle, which resembles the PDO index (Fig. 8a), may require a different explanation. The study suggests a possible hypothesis that may explain the interannual cycle in the number of CIBW counted each year: The variations from year to year represent preferred beluga

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**Fig. 8.** The annual mean values of (a) PDO index, (b) CIBW population count, (c) CIBW stranding death reported and annual river flows for (d) Kenai and (e) Susitna rivers.
locations (Fig. 9) that may influence observer error and detectability rather than interannual variations in the total number of CIBW. The data suggest that in years when the population estimate is low, a larger proportion of the CIBW may go undetected and thus the number of animals may be undercounted. Several findings support this hypothesis:

1. With the slow rate of replacement of the belugas and the estimated numbers of death by stranding (approximately 5–20/year) and predation (a few individuals/year), there is no clear explanation how the number of belugas can change cyclically by about 100 animals (20–30% of the total population) from one year to the next.

2. The years of minimum CIBW counts (1995, 1998, 2002 and 2005) coincide with increase in PDO index (warming northeast Pacific) and maxima in relative river flow into subregions A and B. Thus following our finding of correlation between CIBW location and river flow, one expects the belugas to spend more time in subregions A and B and less time in the upper two Arms.

3. Comparing the distribution of CIBW in 2000 (high count) and 2002–2003 (low count; Fig. 8b), one finds that the population estimate was reduced by about 28%. During this time, the number of beluga tracking data points in Turnagain Arm was reduced from 44% of the total in 2000, to 32% in 2001 and 13% in 2002–2003; at the same time the percentage of beluga tracking points in subregions A and B was increased from 36% in 2000 to 51% in 2002–2003.

4. The number of dead stranding belugas (Fig. 8c) peaked in years with relatively higher population numbers (2000, 2003 and 2007), so mortality by stranding does not seem the cause of the reduction in the CIBW population in 2002 and 2005 (Fig. 8b). A possible explanation for the stranding pattern is that in years in which the CIBW spend more time in the shallow upper CI, the CIBW are more likely to be detected, and more likely to be stranded.

In summary, further studies are needed to explain the year-to-year fluctuations in the CIBW population and improve the accuracy of the population estimates. In additional to the environmental data used here, hydrodynamic models (Ezer et al., 2008; Oey et al., 2007), remote sensing data (Ezer and Liu, 2009, 2010) and ecosystem models (e.g., Jin et al., 2009) can be helpful for future studies of the CIBW. Ongoing research in collaboration with a quantitative fisheries study will evaluate the availability of CIBW feeding sources. Remote sensing and geospatial analysis will study morphology and coastline changes that may create areas of high risk for CIBW stranding.

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**References**


