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ORIGINAL PAPER

River discharge predicts spatial distributions of beluga whales in the Upper Cook Inlet, Alaska, during early summer

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Abstract In the Cook Inlet, a subarctic estuary in Alaska, the endangered population of beluga whales (*Delphinapterus leucas*) has not recovered despite regulation of hunting and the reason is not well understood. To examine the potential roles of habitat and food availability, we compared spatial data on distribution and abundance from aerial surveys undertaken during the seasonal transition into early summer, with corresponding data for river discharge and salmon abundance. Principal component regression indicated strong relationships with rates of river discharge that explained over 90 % of the inter-annual variability of beluga abundances recorded in the Susitna Delta. Belugas moved away from the Susitna Delta when flow rate from the Susitna River was low relative to rivers draining into the Knik Arm and Turnagain Arm. Using only three principal components describing shape, river discharge during May explained 86 % of the inter-annual variability in abundances recorded in the Susitna Delta. In years of reduced abundance in the Susitna Delta, movement was toward the Knik Arm until 2003, transitioning thereafter to the Turnagain Arm including Chickaloon Bay. In contrast, escapements of Chinook salmon in the Deshka River (a tributary of the Susitna River) showed an inverse relationship with beluga abundance in the Susitna Delta, suggesting that escapements were dependent on beluga abundance. These results demonstrated the influence of highly dynamic habitat availability on the distribution of belugas and the importance of the physical environment in structuring the activity of higher predators on prey species.

Keywords Cook Inlet · Beluga whales · River discharge · Physical–biological interactions · Spatial structuring

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Introduction

Building evidence of physical–biological interactions and the relationships that organisms have with their environment has renewed interest in managing resources within an ecosystem context. The focus has often been on the role of the physical environment in controlling production (e.g., Malone et al. 1996), but the environment can also structure distributions of higher predators at high latitudes (e.g., Thiele et al. 2004; Hofmann et al. 2008; Ribic et al. 2008), generating spatially intricate ways in which physical processes influence the distribution and abundance of individual populations. Understanding how these complex spatial relationships operate is vital to developing the predictive capability to manage populations within their ecosystem context.

In Cook Inlet (Fig. 1), beluga whales (*Delphinapterus leucas,* hereafter CIBW) are geographically isolated and genetically distinct from other beluga stocks around Alaska (O'Corry-Crowe et al. 1997; Hobbs et al. 2005). Unlike the other stocks, which are large and stable, population estimates for CIBW declined from the late 1970s to ~300 whales (Hobbs et al. 2000a, 2005, 2008; Ezer et al. 2008, 2013). As a result, CIBW were listed as endangered under the US Endangered Species Act in October 2008. Annual population estimates based on aerial surveys from 1994, while indicating a substantial decline during the period when hunting was allowed, nevertheless showed little evidence of a recovery in abundance following regulation in 1999. Several biological explanations have been suggested, like mortality through predation by killer whales or stranding, reduced recruitment, and limited food availability.

However, recent evidence suggests a prominent role for environmental and climatic influences through the dynamic structuring of habitat. CIBW show strong variation in their seasonal distribution around the Cook Inlet. Historic records and satellite-tracking studies, as well as aerial surveys, indicate that the whales disperse during winter to mid-Inlet waters near Kalgin Island, and sightings have been reported in the southern Inlet as well. In the mid-Inlet, strong oscillatory tidal currents in deepwater channels are associated with rip tides (Oey et al. 2007). Buoyancy and wind forcing also contribute, resulting in a partially mixed estuarine system with a weak counterclockwise circulation and tidally dominating currents. This transports water entering through the Kennedy-Stevenson entrances from the Alaska Current northeastward along the eastern side of the Inlet, resulting in a more oceanic environment with salinities close to those in the Gulf of Alaska. Although information on the winter diet of CIBW in Cook Inlet is sparse, the whales are capable of feeding throughout the water column and taking a wide variety of mesopelagic and groundfish species. By contrast, in summer and fall, CIBW are concentrated in the northern Cook Inlet where tides are significantly amplified ($\sim$10 m tidal range), producing strong currents with speeds up to 4 m/s during the flood, and exposing extensive mudflats during the subsequent ebb (Ezer and Liu 2009). The belugas are thought to feed most efficiently during this period, focusing their foraging efforts at streams and rivers in the Susitna River delta, Chickaloon Bay, Knik Arm, and the Turnagain Arm (Fig. 1), where anadromous fish are concentrated during their seasonal runs (e.g., Anonymous 2006). Anecdotal evidence indicates an increase in blubber from 2 to 3 inches in April–May to 12 inches in fall as a result of this seasonal feeding.

These changes in the movement and distribution of CIBW suggest biological responses that are linked to variation in the physical environment. Ezer et al. (2008) have connected beluga behavior to physical parameters such as tidal dynamics, comparing data from a circulation and inundation model with satellite tracking of two whales over a 5-day period. This was followed by a study in which the authors compared data from satellite tracking of more than 20 animals, annual population counts, and stranding reports, with environmental observations over annual and decadal timescales (Ezer et al. 2013). At the annual scale, water temperature, ice coverage, and river flow were implicated in seasonal movements of CIBW, in particular the timing of peak river flows during summer.

As a result, identifying the important factors impeding population recovery of CIBW may rely on better understanding of the physical–biological interactions within the complex spatial environment of the northern Cook Inlet. As suggested by the low blubber reserves in April–May, the change in spatial distribution from winter into summer reflects a critical transition for beluga as early runs of Chinook salmon and eulachon up rivers of the Cook Inlet begin. Because the aerial surveys are targeted for the period from late May to early June, they provide important information not only of beluga abundances between years,

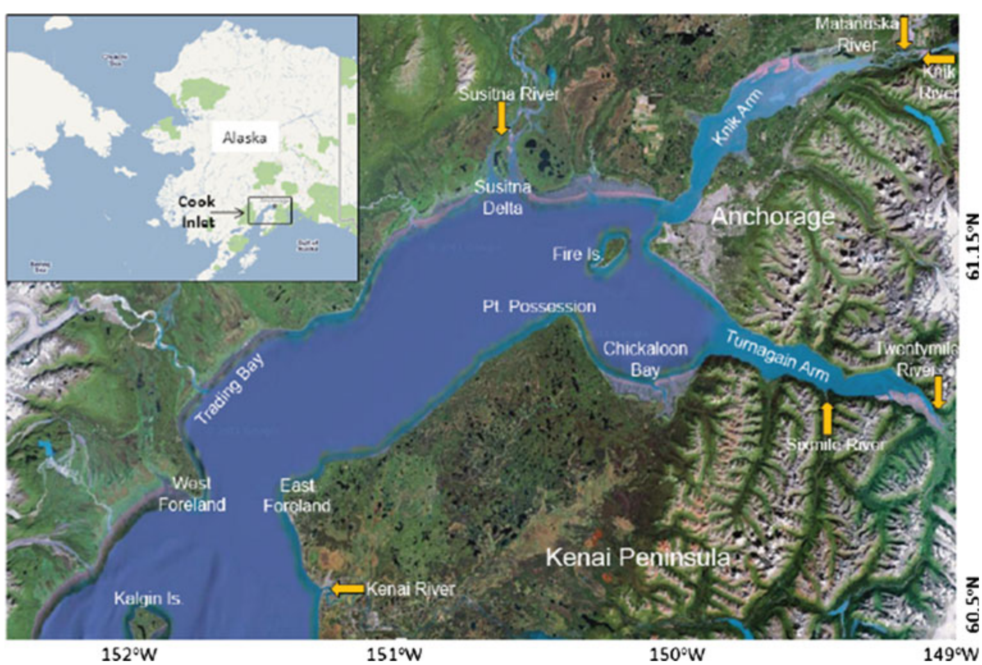

Fig. 1 The study area of northern Cook Inlet (large image based on Google maps) and its location in Alaska and the larger region (*inset* at the *top-left corner*). The locations where rivers enter the Cook Inlet are shown by *yellow arrows*; USGS flow data are taken upstream of the river mouths

but also of spatial distributions around the Upper Cook Inlet following this transition. Based on the evidence implicating river discharge (Ezer et al. 2013), we compared spatial data from the aerial surveys for the sectors of the Upper Cook Inlet where belugas are found, with corresponding flow data from rivers discharging into each sector, and examined these for relationships with salmon abundance indices available for the Susitna River system.

Methods

Data sources: aerial survey, river discharge, and Chinook escapements

The National Marine Fisheries Service began annual aerial surveys of CIBW in 1993, including the upper and lower sections of the Cook Inlet (e.g., Rugh et al. 2000, 2005). Sampling effort is allocated based on past distributions of beluga and the spatial coverage possible in a day's flying. Several days (e.g., seven in 2008) are allocated to the surveys of the upper Inlet to as far south as East Foreland and West Foreland. On each of these days, a complete survey is conducted, with 100 % coverage of the coastal margin out to 3 km including lower parts of rivers. A series of non-randomized transects along and across the Inlet are also flown. In this way, most of the upper Inlet is covered over the sampling period (e.g., 88 % in 2008). In the lower Inlet, two survey days are allocated to 100 % coverage of the west and east coastal margin, respectively, with non-randomized transects along and across the Inlet. A lower proportion of the lower Inlet is covered over the 2 days (e.g., 23 % in 2008). On encountering a group of belugas, the aircraft makes several passes during each of which at least two samplers make independent counts of the number in the group, generating a set of multiple observations for each group.

Count data are presented in annual reports by sampling day and by sector within the lower and upper Inlet. In the lower Inlet, belugas have been counted very infrequently: only 4 % of the count in 1994, 4 % in 1995, and 1 % in 2001 were found south of East Foreland and West Foreland; otherwise, there have been no sightings. In the upper Inlet, the sectors are: the Turnagain Arm not including Chickaloon Bay, Chickaloon Bay to Point Possession, Point Possession to East Foreland, Trading Bay, the Susitna Delta, Fire Island, the Knik Arm, and the mid-Inlet east of Trading Bay (Fig. 1). CIBW are commonly found in the Turnagain Arm, Chickaloon Bay, Susitna Delta, and Knik Arm, but only rarely in other sectors. As opposed to the population estimates, which incorporate corrections for detectability bias and observer error (e.g., Hobbs et al. 2000b), the count data represent the median of the multiple counts of each whale group encountered, summed for each sector within a single day, and by day. The highest sum observed on any 1 day during the sampling period is used as an annual Abundance Index. In this way, the survey obtains an empirical observation, assuming that at least this many belugas are in the population and the discrepancy between days is because of differences in the proportion undetected or missed by observers. Since in any 1 day some CIBW are likely not to be detected, the index can be seen to represent a lower bound of beluga abundance for each year. For the same reasons, variation in counts for each sector is large between days; as a consequence, the highest daily sum in each sector over the sampling period is used for comparing between sectors (Rugh et al. 2005). In this study, we used the highest median counts from the Susitna Delta, Knik Arm, Turnagain Arm, and Chickaloon Bay for the years 1993–2011 and compared the sector and index counts with variation in the rate of discharge of indicator rivers, representing the drainage into each sector.

Monthly averaged river flow data are available from the USGS. We used discharge data for six major rivers (Fig. 1) targeted by Ezer et al. (2013); note that stream flow is often measured farther upstream, not in the location where the flow reaches the Inlet. The Susitna River is the major system in the Upper Cook Inlet, discharging into the Susitna Delta. In the Knik Arm, the Matanuska River drains meltwater from the same region as the Susitna, whereas the Knik River drains from the east side of the Knik Arm. The Twentymile River drains from the same geological range into the north side of the Turnagain Arm. In contrast, the Sixmile River drains from the south side of the Turnagain Arm above Chickaloon Bay; the Kenai River also drains from this southeastern region and forms a good proxy for river discharge into Chickaloon Bay. Discharge from the two rivers draining each of the northwest, northeast, and southeast regions followed a similar pattern that varied between regions. We examined discharge data for the month of May, leading up to and overlapping the sampling period for the beluga survey.

To explore whether prey availability influenced beluga abundance in the Susitna Delta sector during the period of the survey, we also examined daily escapement data for adult Chinook salmon available from the Alaska Department of Fish and Game (ADFG) Web site, taken during annual counts from 1995 located at river mile seven on the Deshka River. The Deshka River is a tributary that joins the Susitna River $\sim$30 miles north of the Susitna Delta and is the most productive Chinook salmon system in the northern Cook Inlet Management Area (e.g., Deshka River king salmon white paper, 2009. Yanusz R and Rutz D, Dept. of Fish and Game, State of Alaska). Raw count data per day for salmon runs each year were downloaded from the ADFG Web site, summed for the period of the run, and compared with beluga sector counts for the Susitna Delta and river discharge data.

Statistical analysis

Exploring the beluga sector counts for spatial structuring, we used principal component analysis (PCA) to reduce the dimensionality of the data (Khattree and Naik 2000; Quinn and Keough 2002). For each year of the aerial survey ($n = 19$), we had a $p \times 1$ random vector consisting of the counts from each sector of interest ($x_1,\ldots x_p$, where $p = 4$) giving a $n \times p$ matrix $\mathbf{x}$. So that large differences in the variances between sectors did not influence the analysis, we constructed a $p \times p$ correlation matrix ρ based on Pearson's correlation coefficient between x_i and x_j. The first principal component is the linear combination $\mathbf{a_1}'\mathbf{x} = a_{11}x_1 + \cdots + a_{1p}x_p$, where $\mathbf{a_1} = (a_{11}\ldots a_{1p})'$, such that var ($\mathbf{a_1}'\mathbf{x}$) is the maximum among all linear combinations of $\mathbf{x}$. The second principal component is uncorrelated with the first and has maximum variation among all linear combinations uncorrelated with $\mathbf{a_1}'\mathbf{x}$ and so on for the remaining components. We obtained the eigenvalues of the correlation matrix, which represent the variances of the principal components, and the eigenvectors for the coefficients of their elements. We used the cumulative proportion of total variance to select the number of principal components, with the minimum percentage of total variance to be explained specified at 90 %.

Similarly, to study the differences between rivers, we applied PCA to the discharge data and analyzed the size and shape of the flow rates. For each year in which data were recorded during May ($n = 9$), we had a $p \times 1$ random vector consisting of the flow rates from each river ($\mathbf{x_i}' = x_1,\ldots x_p$, where $p = 6$) giving a $n \times p$ matrix $\mathbf{x}$. Again, because variance was much higher for the Susitna River, we constructed a $p \times p$ correlation matrix ρ to avoid large differences in the variances between rivers influencing the analysis and obtained the corresponding eigenvalues and eigenvectors. We then applied a principal component regression to explore how well linear combinations of principal components serve as predictor variables of beluga abundances. We selected the set of components giving maximum predictive ability using the sum of squares of the predicted residuals for the observations, the predicted residual sum of squares (PRESS) (Khattree and Naik 2000), comparing values under alternative models for predicting (1) sector counts for the Susitna Delta and (2) the beluga Abundance Index.

Finally, examining the relationship between beluga abundance and prey availability, we compared escapements of Chinook salmon sampled from the Deshka River against the sector counts for the Susitna Delta. Because these unexpectedly showed an inverse relationship that suggested escapements were dependent on beluga abundance, we used the latter as an indicator of predation pressure on the Chinook run and applied another principal component regression to explore how well river discharge and predation pressure predicted escapements. Again, the set of components giving maximum predictability was assessed using PRESS.

Results

Beluga abundances

Compared to the population estimate, the beluga Abundance Index showed a stable count of ~300 belugas from 1993 to 1996, before declining to less than 200 in 1998, the year after hunting was reduced (Fig. 2). After 1998, the index continued to trend downward, until 2006, but more slowly than the population estimate. However, the index then peaked above 300 belugas in 2009 and 2010, and the discrepancy between the population estimate and the index decreased considerably between 2003 and 2009–2010.

The measures incorporated considerable variation in the spatial distribution of the belugas, with variability in the Abundance Index tracking fluctuations in the Susitna Delta sector. Thus, the highest median counts for each sector showed belugas concentrated in the Susitna Delta from 1993 to 1996 (Fig. 3a), but at a minimum in 1997 when numbers in the Knik Arm peaked. A partial recovery of numbers in the Susitna Delta over the next 2 years corresponded to declines in the Knik Arm, and this inverse relationship appeared to persist into 2001. Numbers in the Susitna Delta then declined to a second minimum in 2003 while those in Knik Arm stayed stable but numbers in Chickaloon Bay increased rapidly. Following 2003, Susitna

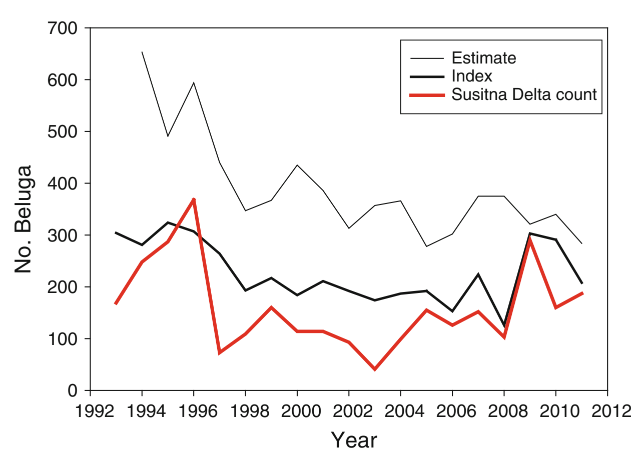

Fig. 2 Aerial survey of beluga whale population in the Cook Inlet: (1) Population estimate, (2) Abundance Index, (3) sector count for Susitna Delta

Delta abundance increased slowly for 2 years, while Chickaloon Bay peaked dramatically in 2004 with a secondary peak in Turnagain Arm (Fig. 3a); however, no belugas were found in the Knik Arm that year. Corresponding to a rapid fluctuation in the Abundance Index, numbers in the Susitna Delta peaked again in 2009 with a count of 290 whales, higher than any year except 1996, but largely disappeared in the other sectors. In the following year, a decline in the Susitna Delta coincided with a peak in Chickaloon Bay; no belugas were found in the Knik Arm that year.

Exploring these data using PCA (Table 1), the first principal component, which represented differences between the northern (Susitna Delta and Knik Arm) and eastern (Turnagain Arm and Chickaloon Bay) sectors, explained 40 % of the variability. The second component measured differences between the Susitna Delta and Knik Arm, and explained 38 % of the remaining variability; the third component seemed to measure differences between Chickaloon Bay and the upper Turnagain Arm. In all, the first three principal components accounted for 92.5 % of the total variation. The scaling plot for the first and second PCs (Fig. 4) showed years of high abundance in the Susitna Delta clustered in one group (red), another group of years (blue) when as many or more belugas were counted in the Knik Arm as the Susitna Delta, and a third group when activity in the Turnagain Arm and Chickaloon Bay was important. The Susitna Delta group included only years when the Abundance Index was high. The second principal component was also high in 2010; only in 1993, did a negative value correspond to a year when the Abundance Index was high.

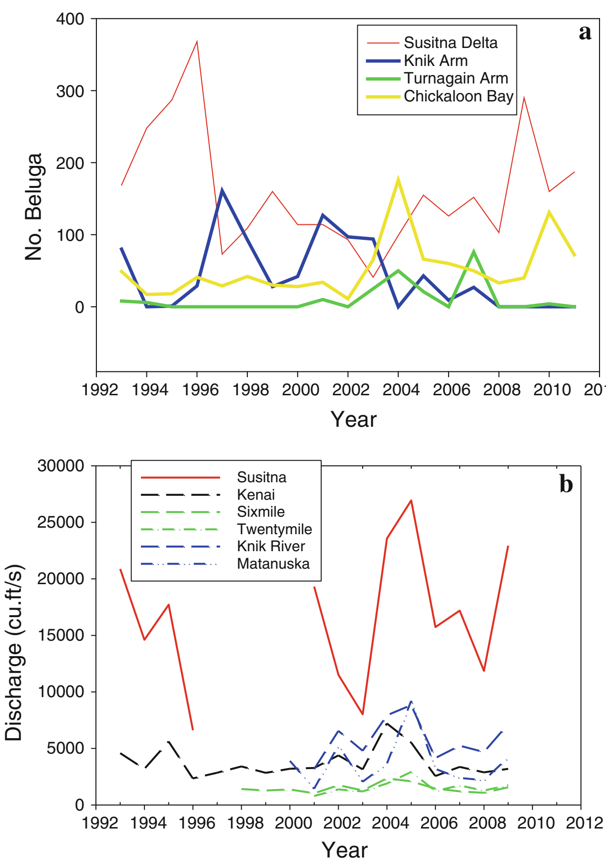

Fig. 3 **a** Aerial survey counts of beluga from 1993 to 2011 in sectors of the northern Cook Inlet: Susitna Delta, Knik Arm, Turnagain Arm, Chickaloon Bay. **b** Discharge during May 1993–2009 from indicator rivers for drainage areas around the Upper Cook Inlet: Susitna River, Matanuska River, Knik River, Twentymile River, Sixmile River, Kenai River. *Colors* correspond to rivers feeding beluga sampling sectors: Susitna Delta (*red*), Knik Arm (*blue*), Turnagain Arm including Chickaloon Bay (*green*)

River discharge

Despite gaps prior to 2001, data for river discharge in May demonstrated the considerable flow from the Susitna River relative to all other rivers, and the small flow from the Sixmile and Twentymile Rivers relative to those feeding into the Knik Arm (Fig. 3b). They also demonstrated large inter-annual variability in flow, especially for the Susitna River. The increase in beluga numbers in the Susitna Delta from 1993 to 1996 corresponded to an increase in discharge from the Susitna River from 6,100 cu ft/s in 1992 to a maximum over 20,000 cu ft/s ($\sim$560 $m^3\ s^{-1}$) in 1993.

Table 1 Principal component analysis for counts of beluga whales between 1993 and 2011 from sectors delineated in the northern Cook Inlet

Sector	No. years	Mean	SD
(a) Summary statistics			
Susitna Delta	19	160.42	83.70
Knik Arm	19	43.74	50.02
Turnagain Arm	19	10.53	20.35
Chickaloon Bay	19	52.21	40.25

Component	Eigenvalue	Percentage variance	Cumulative
(b) Eigenvalues			
1	1.594	39.9	39.9
2	1.526	38.2	78.0
3	0.579	14.5	92.5
4	0.300	7.5	100.0

Sector	PC1	PC2	PC3	PC4
(c) Eigenvector coefficients				
Susitna Delta	−0.270	0.684	0.331	0.590
Knik Arm	−0.221	−0.717	0.153	0.643
Turnagain Arm	0.640	−0.076	0.763	−0.046
Chickaloon Bay	0.684	0.111	−0.533	0.485

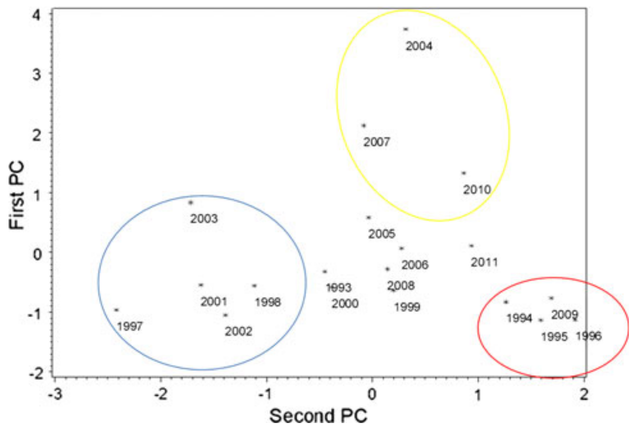

Fig. 4 First two principal components for counts of beluga whales between 1993 and 2011 from sectors delineated in the northern Cook Inlet. *Red circle* highlights years of peak abundance in the sector count for the Susitna Delta and the Abundance Index for the Cook Inlet; *blue circle* indicates years when the sector count for the Knik Arm was equal or more than the Susitna Delta; *yellow highlights* years when sector counts peaked in the Turnagain Arm and Chickaloon Bay

Beluga abundance fell dramatically in 1997, the year after discharge fell back to 6,600 cu ft/s. Discharge from the Kenai River, the only other river for which there are data available for this period, also declined by half in 1996 suggesting that flow rates in other areas were affected. From 2001, when data for the Susitna River were available again, discharge minima in 2003 and 2008 correspond to low points in beluga counts for the Susitna Delta sector, whereas peaks in flow during 2005 and 2009 correspond to maxima. The damped response in 2004 occurred in the same year as a dramatic increase in beluga numbers in Chickaloon Bay, when discharge from the Kenai River increased to 7,200 cu ft/s from 3,100 cu ft/s, while discharge from the Sixmile River increased to 2,340 cu ft/s from 1,280 cu ft/s. Similarly, the small peak in 2007 in beluga numbers in the Turnagain Arm in 2007 corresponded to a small peak in discharge from the Twentymile River.

Exploring these data using PCA (Table 2), the first principal component was a measure of the size of river discharge and explained 76 % of the total variability. The second principal component accounted for 11 % but measured the shape and seemed to reflect differences between the southwest drainage area and those northwest and northeast of the Cook Inlet. The third component measured differences between the Susitna River and those feeding into the Knik Arm, and to a lesser extent the Turnagain Arm. The first three principal components explained 95.5 % of the total variability.

Examining their relationship to beluga abundance using principal component regression, we found that the size variable represented by the first component was not useful

Table 2 Principal component analysis for discharge from indicator rivers between 2001 and 2009 into sectors delineated in the northern Cook Inlet

River	years	Mean	SD
(a) Summary statistics			
Susitna	9	17,451	6,320
Matanushka	9	3,724	2,372
Knik	9	5,831	1,882
Twentymile	9	1,571	610
Sixmile	9	1,526	458
Kenai	9	3,946	1,516

Component	Eigenvalue	Percentage variance	Cumulative
(b) Eigenvalues			
1	4.57	76.2	76.2
2	0.65	10.8	87.0
3	0.51	8.5	95.5
4	0.14	2.3	97.8
5	0.09	1.5	99.3
6	0.04	0.7	100.0

Sector	PC1	PC2	PC3	PC4	PC5	PC6
(c) Eigenvector coefficients						
Susitna	0.352	0.221	0.880	0.180	−0.122	0.071
Matanushka	0.400	0.458	−0.378	0.599	0.277	0.228
Knik	0.447	−0.001	−0.227	−0.367	−0.588	0.518
Twentymile	0.427	0.389	−0.066	−0.592	0.312	−0.462
Sixmile	0.428	−0.406	−0.142	0.341	−0.372	−0.614
Kenai	0.387	−0.652	0.082	−0.083	0.572	0.290

for predicting abundances in the Susitna Delta. Instead, the best variables were the second, third, and fifth principal components, where the fifth seemed to represent differences in the flow between rivers within drainage area. Accordingly, in year i, the number of beluga y_i in the Susitna Delta is best predicted by:

$$y_i = 130.3 + (46.3)\mathrm{PC}_{2i} + (41.3)\mathrm{PC}_{3i} - (140.8)\mathrm{PC}_{5i} + \varepsilon_i$$

where PC_{2i}, PC_{3i} and PC_{5i}, $i = 2001,\ldots2009$, are the principal component scores of the second, third, and fifth principal components. Thus, in the scaling plots for the second versus third principal component (Fig. 5a), years of high flow in the Susitna River in 2001, 2004, 2005 separated from other years, whereas 2009 separated along the fifth principal component. In 2002 and 2003, flow into both the Susitna Delta and Knik Arm decreased substantially, giving negative values along PC2 and PC3.

In this way, we were able to separate variability due to size of flow and select predictor variables based on the remaining variability due to shape of the flow, to predict beluga abundance in the Susitna Delta (Fig. 6). The

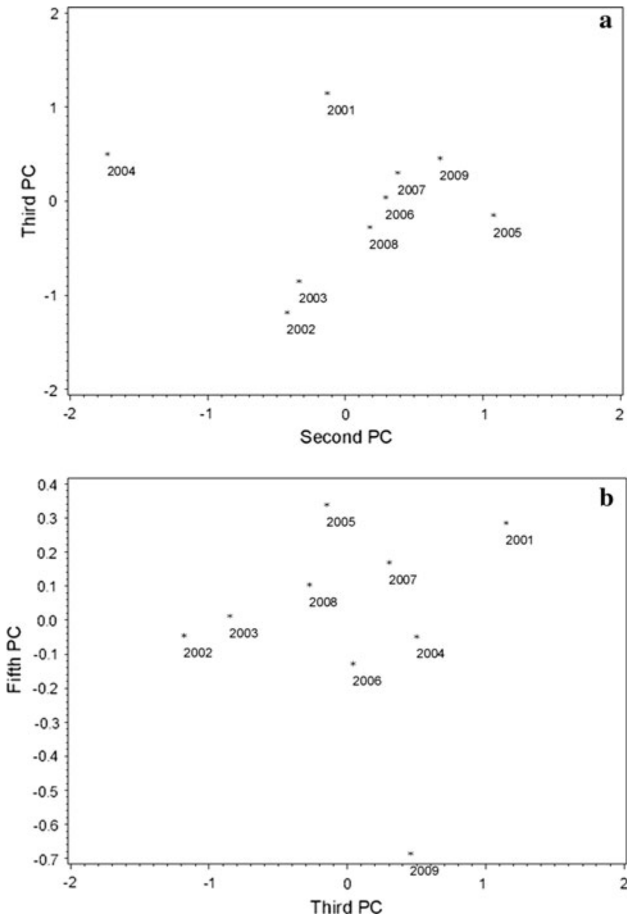

Fig. 5 Principal components (PC) for shape of discharge from indicator rivers during May 2001–2009 into sectors delineated in the northern Cook Inlet. **a** Third versus Second PC **b** Fifth versus Third PC

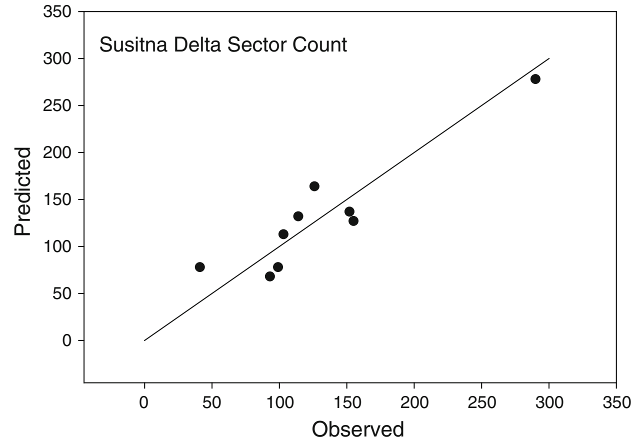

Fig. 6 Principal component regression predicting beluga abundance in the Susitna Delta sector between 2001 and 2009 using river discharge data. *Line shows* the 1:1 relationship

Table 3 Predictive ability of selected principal components from principal component regressions for river discharge

Procedure	Variables	R^2	PRESS
(a) Susitna Delta sector counts			
Best two variables	PC2, PC5	0.67	76,081
Best three variables	PC2–PC3, PC5	0.86	35,177
Best four variables	PC1–PC3, PC5	0.94	38,871
Best five variables	PC1–PC3, PC5–PC6	0.97	33,677
Procedure	Variables	R^2	PRESS
(b) Beluga Abundance Index			
Best two variables	PC3, PC5	0.47	42,436
Best three variables	PC3, PC5–PC6	0.58	39,286
Best four variables	PC2–PC3, PC5–PC6	0.64	81,617
Best five variables	PC1–PC3, PC5–PC6	0.70	139,786

PRESS predicted residual error sum of squares

resulting model had PRESS = 35,177 and R-square of 0.86. Although an alternative model gave a slightly lower PRESS and yielded an R^2 of 0.97, this demanded the use of five principal components, including the first (Table 3). When used to predict the beluga Abundance Index, the best three variables were PC3, PC5, and PC6 giving PRESS = 39,286; R^2 was lower at 0.58. Using a model with five components sharply reduced predictive ability, even though it yielded an R^2 of 0.70.

Chinook salmon escapements

Unexpectedly, escapements of Chinook salmon in the Deshka River showed evidence of an inverse relationship with beluga abundance in the Susitna Delta sector (Fig. 7b). Thus, total Chinook counts (Fig. 7a) showed an increasing trend from 1995 when data were first available until a peak in 2004, after which the number fell to reach a minimum in 2008 with some recovery thereafter, and there was no evidence of any relationship between Chinook escapements and discharge from the Susitna River during May or June. These results suggest that escapements were dependent on beluga abundance rather than the reverse. As a result, we treated the number of beluga as an indicator of predator pressure.

Exploring these data by PCA incorporating river discharge and beluga data (Table 4), the first principal component was again a measure of size, this time of river flow and predation pressure. It explained 67 % of the total variability. The second principal component accounted for 19 % and measured the shape, reflecting differences between the southwest drainage area and both Susitna River flow and Susitna Delta predation pressure. The third component seemed mostly to measure differences in flow between the Susitna and Kenai Rivers on the one hand, and the Matanushka and Twentymile Rivers on the other. The first three principal components explained 94 % of the total variability.

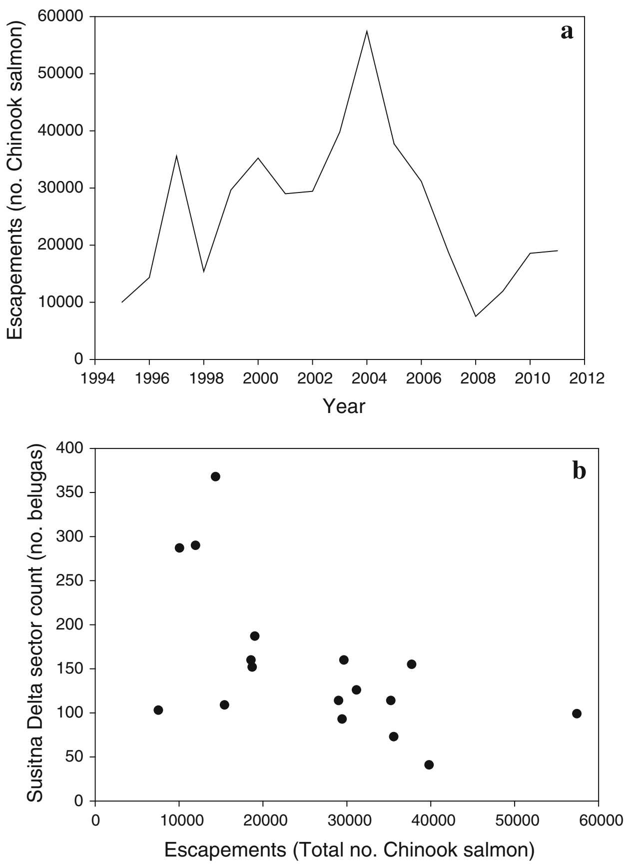

Fig. 7 Total escapements of Chinook salmon along the Deshka River **a** during years 1995–2011 **b** compared to beluga counts for the Susitna Delta sector

Examining their relationship to escapements using principal component regression, we found that the size variable represented by the first component was in this case useful for predicting Chinook abundances in the Deshka River. Moreover, the first three principal components were the best variables, explaining 76 % of the total variability. Adding PC6 to the model reduced predictive ability dramatically, even though it improved R-square by 8 %.

Discussion

River discharge predicts beluga abundance in the Susitna Delta

Comparing spatial data from annual surveys of the Cook Inlet, we found evidence of an important association between beluga distributions and rates of river discharge, as previously suggested by Ezer et al. (2013). However, whereas Ezer et al. used year-round satellite-tracking data of few belugas to connect river flows to seasonal movements, we used data from aerial surveys of the CIBW population during early summer to study inter-annual variation in the whales' distribution. During the seasonal transition into early summer, CIBW responded to changes in the discharge of the Susitna River by moving away from the Susitna Delta when flow rate was low relative to rivers draining into the Knik and Turnagain Arms. Using only three principal components, river flow rates during May explained 86 % of the inter-annual variability in abundances recorded during surveys in the Susitna Delta sector. This was not simply due to the effect of a single influential year in which discharge and abundances were high: even leaving out data for 2009, flow rates explained 80 % of the variability in beluga abundance in the Susitna Delta.

Moreover, river discharge also predicted 56 % of the variability in the beluga Abundance Index, again using only three principal components. Including more components raised prediction capability further. In years when the beluga Abundance Index was high, activity appeared to be concentrated in the Susitna Delta. In years when movement away from the Susitna Delta was high, the Abundance Index tended to be lower, suggesting that detectability of CIBW may change considerably between sectors. This movement was weighted toward the Knik Arm initially, transitioning in 2003 to the Turnagain Arm including Chickaloon Bay, in a year when flow rates into the Susitna Delta and Knik Arm dropped considerably. The survey reports indicated that CIBW in the Susitna Delta were in shallow water, whereas they occupy deeper channels elsewhere, in the Knik Arm especially, so the variability in the Abundance Index may be the result of divergence in diving behavior between sectors.

PCA is often criticized because it relies on the interpretations of the principal components that are subjective, guided only by the coefficients of each eigenvector. Similarly, grouping of data points involves subjective interpretation. However, when used to construct hypotheses, it offers a rigorous, quantitative method to explore data that reduces dimensionality and can be used to separate out size and shape effects. When used in principal component regression, it is also a way to manage variability by extracting only those components that maximize predictability, using the dependent variable to select the appropriate model. Even though interpretations are subjective, the approach provides a rigorous way to predict future observations. In our case, even though data were available for 19 years of beluga surveys, there were only 9 years in which flow had been monitored from all six rivers. As a result, the predictive models so far do not incorporate environmental oscillations on cycles of more than a few years and may contain biases when applied to predict outside the period 2001–2009.

Nevertheless, the strong association between CIBW counts and river discharge, and the models based on selected principal components, represent a powerful

Table 4 Principal component regression predicting total annual Chinook salmon escapements between 2001 and 2009 using river discharge and Susitna Delta sector counts of belugas (SDSB)

Predictor	Years	Mean	SD
(a) PCA summary statistics			
Susitna	9	17,451	6,320
Matanushka	9	3,724	2,372
Knik	9	5,831	1,882
Twentymile	9	1,571	610
Sixmile	9	1,526	458
Kenai	9	3,946	1,516
SDSB	9	130	69

Component	Eigenvalue	Percentage variance	Cumulative
(b) PCA eigenvalues			
1	4.68	66.8	66.8
2	1.31	18.8	85.6
3	0.56	8.0	93.6
4	0.26	3.7	97.3
5	0.14	2.0	99.3
6	0.04	0.6	99.9
7	0	0	100.0

Sector	PC1	PC2	PC3	PC4	PC5	PC6	PC7
(c) PCA eigenvector coefficients							
Susitna	0.363	0.335	0.514	−0.565	−0.166	−0.036	−0.379
Matanushka	0.396	0.025	−0.604	−0.223	0.562	0.306	0.131
Knik	0.442	−0.048	−0.141	0.451	−0.292	0.291	−0.639
Twentymile	0.425	0.080	−0.325	−0.314	−0.636	−0.368	0.261
Sixmile	0.414	−0.288	0.159	0.361	0.385	−0.662	0.051
Kenai	0.367	−0.429	0.450	0.004	−0.130	0.488	0.472
SDSB	0.170	0.782	0.129	0.445	0.028	0.085	0.370

Procedure	Variables	R^2	PRESS
(d) Predictive ability of selected principal components			
Best two variables	PC1, PC2	0.66	1.1×10^9
Best three variables	PC1–PC3	0.76	1.4×10^9
Best four variables	PC1–PC3, PC6	0.84	4.2×10^9
Best five variables	PC1–PC3, PC5–PC6	0.87	5.9×10^9
Best six variables	PC1–PC3, PC5–PC7	0.89	8.7×10^9

approach for generating predictions that can be compared to empirical distributions and abundances of CIBW. In comparison, we found little evidence of any association with food availability. There was no direct relationship between flow rate for the Susitna River in May and the data available for runs of Chinook salmon in the Deshka River upstream. Nor did the belugas appear to be positioning themselves in anticipation of food availability later in the season: in other data examined for the later large runs of sockeye salmon, high numbers of escapements in the lower Inlet did not translate into beluga counts, and there was little evidence of a relationship between beluga numbers sampled in the Susitna Delta and subsequent escapements recorded in tributaries of the Susitna River. In any case, beluga movements indicate responses on daily (Ezer et al. 2008) and monthly (Ezer et al. 2013) timescales suggesting distributions are more likely to reflect current or shorter-term indicators. Indeed, the inverse relationship between beluga numbers in the Susitna Delta and Chinook escapements in the Deshka River implied that belugas were not so much responding to prey abundance, as that escapements were shaped by predation during the run.

Predicting physical–biological interactions within an ecosystem

The evidence that belugas respond to the relative rates of river flow around the northern Cook Inlet strongly

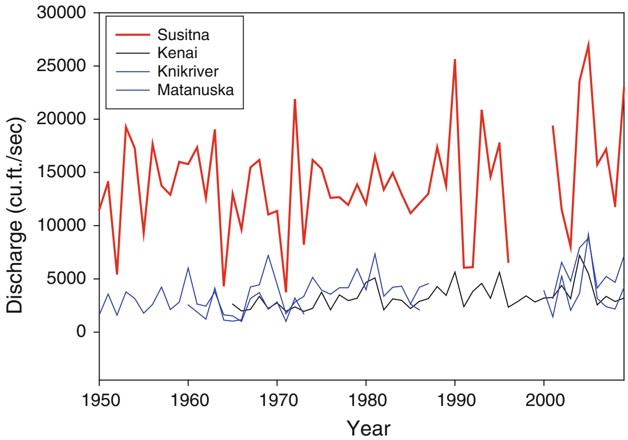

Fig. 8 Historic discharge rates during May from the Susitna, Kenai, Knik, and Matanuska Rivers

implicates the availability of suitable habitat in structuring their abundance and distribution, and potentially in the population dynamics governing their recovery. Variability in habitat, mediated by river discharge, may in turn be controlled by physical processes operating on longer timescales. Thus, historic discharge data for May (Fig. 8) indicate periods of extreme variability in the Susitna River since 1950, with peaks in 1953, 1963, 1972, and 1990. Notable lows occurred in 1952, 1964, 1971, and 1991–1992. The results presented here suggest these oscillations may have been associated with rapid changes in the corresponding beluga distributions between years.

Based on the historic flow data for the Susitna River, the annual aerial survey appears to have coincided with a period of volatility from 1990 onwards when mean flow rates during May varied within a range of ~20,000 cu ft/s between years. This followed a stable period from 1974 when the same flow indices varied by only ~5,000 cu ft/s, during which beluga distributions may not have changed much. Because discharge reflects meltwater from changes in precipitation and heating, periods of volatility may be linked to climate cycles like the Pacific Decadal Oscillation, implicated by Ezer et al. (2013) to help explain beluga distributions obtained from satellite tracking. Better understanding of the physical–biological interactions underlying the relationship with river discharge may further enhance predictive capability, and predictions can be tested against future survey data to assess model performance, eventually incorporating data series that cover longer environmental cycles.

On shorter timescales, the models offer a way to impute beluga distributions and abundance in other months of the year not covered by the survey. Compared against other sources of empirical data, the predictions can be tested to assess performance beyond the temporal limits of inference. Fine-tuning the models in this way holds promise for forecasting over shorter timescales, for instance to facilitate efficient spatial allocation of sampling effort in the aerial surveys. The models can also be used to assess the impact of projected changes in flow rates from developments like the Cook Inlet Tidal Energy Project and the hydroelectric project currently planned for the Susitna River basin and to develop mitigation measures that address anticipated exposure of belugas to high risk areas.

Moreover, the effects are not restricted to the interaction between CIBW and river discharge. Thus, the inverse relationship between beluga numbers in the Susitna Delta and escapements in the Deshka River suggests an approach to predict the number of Chinook salmon reaching rivers in the Susitna system. Moreover, it implies not only a way in which physical processes in the Cook Inlet can regulate local abundance of resource populations through the control exerted on predator distributions, but also potentially a mechanism over longer temporal scales by which regional cycles can influence ecosystem dynamics at a local level. Examining the complex spatial relationships generated by interactions between physical and biological processes can help us better understand how populations are regulated within an ecosystem context.

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