Predicting physical-biological interactions in high-latitude marine ecosystems.

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Abstract

Managing the biological consequences of rapid environmental change in polar regions fundamentally relies on accurate prediction, particularly in generating expectations of shifts in patterns of abundance and distribution. Yet quantitative approaches remain elusive. Quantifying the effects of physical-biological interactions in systems that already reflect projected future change, and are often more accessible, may help predict ecosystem consequences with greater precision. In Cook Inlet, a subarctic estuary in Alaska, movement and distribution of beluga whales are linked to variation in physical processes, notably rates of river discharge. We examined relationships between river discharge and beluga abundance indices for Chickaloon Bay, the upper Turnagain Arm, and Knik Arm; between river discharge and escapements of Chinook salmon in the Susitna River system; and compared spatial distributions of killer whale sightings with beluga whales and salinity data from a circulation model. Principal Components Regression indicated strong relationships with rates of river discharge that explained over 90% of the inter-annual variability of beluga abundances recorded in the Chickaloon Bay; and over 70% of escapements of Chinook salmon. Killer whale sightings, concentrated on the eastern side of the lower Inlet, followed the inflow of water through the Kennedy-Stevenson entrances; interactions were associated with surface salinities in the approximate range of 24-30 ppt. These relationships hold promise for an approach in which precise quantitative predictions can be compared to empirical observations to gauge the performance of hypotheses concerning ecosystem responses to climate change.

Key words: Spatial distributions, river discharge, beluga whales, killer whales, Chinook salmon, river discharge, Cook Inlet.
The biological consequences of rapid environmental change are generally considered difficult to predict. Changes currently under way in polar regions are particularly difficult because of the logistical exigencies in conducting research in remote regions under harsh conditions. Despite this, considerable progress has led to consistent themes, expressed in this symposium, that focus on the remarkable declines in the extent and duration of sea ice cover (e.g. Moore et al. 2013*, Carmack 2013*) associated with changes in the abundance and spatial distribution of fish and tertiary predators (e.g. Dunmall et al. 2013*, Divoky and Tremblay 2013*, Imrie and Tallman 2013*). Some species identified as particularly vulnerable (Boveng 2013*) contrast with others likely to take advantage by moving north into the Arctic Sea from the Subarctic (Hollowed et al. 2013*). Yet there are few approaches that hold promise for quantitatively predicting the extent of the expected changes in abundance and distribution, and the consequent impact on high-latitude ecosystems.

In the case of beluga whales (*Delphinapterus leucas*), populations in the Arctic Ocean showed extensive migrations into ice-covered regions (Hauser et al. 2013*) and to considerable distances offshore. In Hudson Bay, recent changes in sea-ice associated with increased sightings of killer whales suggested a shift to a marine-based ecosystem (Hammill 2013*). Belugas within the bay currently show large movements offshore, in contrast to other populations further east where, in a marine-based ecosystem, distributions are restricted to coastal areas to avoid killer whale predation. Quantifying the effects of these physical-biological interactions in systems that already reflect
projected future change, and are often more accessible, offers an approach that may help predict the ecosystem consequences of climate change with greater precision.

In Cook Inlet (Fig. 1), a subarctic estuary in Alaska, beluga whales (hereafter CIBW) are geographically isolated from other populations in the Arctic and adjacent seas (Hobbs et al. 2005; O’Corry-Crowe et al. 1997). Following earlier declines, annual population estimates based on aerial surveys from 1994 have shown little evidence of a recovery in abundance following regulation of hunting in 1999. However, strong variation in seasonal distributions around the Cook Inlet has been documented in historic records and by satellite tracking studies, that are related to the physical environment (Ezer et al. 2008, 2013). Thus during winter, the whales disperse to mid-Inlet waters near Kalgin Island. There, 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 counter-clockwise circulation and tidally dominating currents. This transports oceanic water entering through the Kennedy-Stevenson entrances from the Alaska Current north-eastward along the eastern side of the Inlet. By contrast in summer and fall, CIBW are concentrated in the northern Cook Inlet associated with streams and rivers in the Susitna River Delta, Chickaloon Bay, Knik Arm and the Turnagain Arm (Fig. 1). In this region, tides are significantly amplified (~10 m tidal range), producing strong currents with speeds up to 4m/s during the flood and exposing extensive mudflats during the subsequent ebb (Ezer and Liu 2009).

Movement and distribution of CIBW are linked to variation in physical processes. Ezer et al. (2008) showed that beluga behavior is connected to physical parameters such as tidal dynamics by comparing data from a circulation and inundation model with
satellite-tracking of two whales over a five-day period. Data from satellite tracking of
more than 20 animals, annual population counts, and stranding reports, with
environmental observations over annual and decadal time scales (Ezer et al. 2013),
implicated water temperature, ice distribution and river flow in seasonal movements of
CIBW. Recently, Principal Components Regression indicated strong quantitative
relationships with rates of river discharge, which explained 86% of the inter-annual
variability of beluga abundances recorded in the Susitna Delta (Ashford et al. 2013).
Thus, in year $i$, the number of beluga $y_i$ in the Susitna Delta could be predicted by:

$$y_i = 130.3 + (46.3)PC_{2i} + (41.3)PC_{3i} - (140.8)PC_{5i} + \varepsilon_i$$ (1)

where $PC_{2i}$, $PC_{3i}$ and $PC_{5i}$, $i=2001,\ldots,2009$, are the principal component scores of the
second, third and fifth principal components from a Principal Components Analysis of
discharge from six indicator rivers. Belugas moved away from the Delta when flow rate
from the Susitna River was low relative to rivers draining into the Knik Arm and
Turnagain Arm. In years of reduced abundance in the Susitna Delta, movement was
towards the Knik Arm until 2003, transitioning thereafter to the Turnagain Arm including
Chickaloon Bay. Moreover, escapements of Chinook salmon in the Deshka River, a
tributary thirty miles from the mouth 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 demonstrate the influence of physical processes and habitat
availability on the distribution of belugas, and the importance of the physical
environment in structuring predation pressure on prey species in the Cook Inlet
ecosystem. However, they did not provide a mechanistic explanation for the habitat relationship. Instead, interactions with killer whales have also been implicated (Shelden et al. 2003). Dead belugas have been documented with telltale rake marks. Although the incidence of interactions was low, the rate of negative impacts was high: during 15 observed interactions, 11 included reports of beluga injuries or mortalities. Most interactions occurred in the upper Inlet; in contrast, most killer whale sightings occurred in the lower Inlet where few belugas have been recorded. Although potentially biased by changes in activity with season and near centers of population around Anchorage and the Kenai Peninsula, these results suggested habitat partitioning between belugas and killer whales that may in turn be structured by the physical environment.

In this contribution to the symposium proceedings, we examined movement of CIBW away from the Susitna Delta during periods of low relative flow rate, quantifying relationships between river discharge and CIBW abundance indices for Chickaloon Bay, the upper Turnagain Arm, and Knik Arm recorded during the aerial surveys in early summer. Based on the inverse relationship found by Ashford et al. (2013) between beluga distributions in the Susitna Delta and chinook salmon escapements in the Deshka River, we examined how well river discharge predicted escapements. Finally, in light of these data, we compare the spatial distributions of killer whale sightings documented by Shelden et al. (2003) with those of beluga whales and salinity data from a circulation model of the Cook Inlet (Oey et al. 2007), and discuss our results in the context of a potential shift from an ice-based to a marine-based ecosystem in the Arctic Ocean and adjacent seas (Hamill 2013*).
**Methods**

Annual aerial surveys of CIBW by the National Marine Fisheries Service include the upper and lower sections of the Cook Inlet (e.g. Rugh et al. 2000, 2005). Several days (e.g. seven in 2008) are allocated to a series of full surveys of the upper inlet as far south as East Foreland and West Foreland, with 100% coverage of the coastal margin out to 3 km including lower parts of rivers. Non-randomised transects are also conducted offshore, so that 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; non-randomized transects are carried out offshore, but a lower proportion of the lower inlet is covered overall (e.g. 23% in 2008). At least two samplers make independent counts of the number of belugas in each group encountered, generating a set of multiple observations for each group. CIBW are commonly found in the Turnagain Arm, Chickaloon Bay as far west as Point Possession, the Susitna Delta, and Knik Arm, but only rarely in other sectors. For each sector, the median of the multiple counts of each whale group are summed by day. Variation in counts for each sector is large between days and the discrepancy is assumed to be because of differences in the proportion undetected or missed by observers. As a consequence, the highest daily sum in each sector over the sampling period is used for comparing between sectors (Rugh et al. 2005). For this study, we used the highest median counts from the Knik Arm, Turnagain Arm and Chickaloon Bay for the years 2001-2009 for which we had full data on 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 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 south-eastern region and forms a good proxy for river discharge into Chickaloon Bay.

Discharge from the two rivers draining each of the north-west, north-east and south-east regions followed a similar pattern that varied between region. We examined discharge data for the month of May, leading up to and overlapping the sampling period for the beluga survey.

Data for annual counts of escapements of adult Chinook salmon from 2001-2009 at the Deshka River weir are from the Alaska Department of Fish and Game (ADFG) website. Full details can be found in Ashford et al. (2013). The Deshka River is a tributary that joins the Susitna River ~30 miles north of the Susitna Delta, and is the most productive Chinook salmon system in the northern Cook Inlet Management Area. The run commences in late May, approximately coinciding with the start of the NMFS survey. We examined whether relative flow between the indicator rivers predicted escapements using data from Ashford et al. (2013) and comparing these with the river discharge data.
Hydrographic and circulation data are from the Cook Inlet ocean circulation and inundation model described in details in Oey et al. (2007). This is a three-dimensional numerical model with 0.5-1km horizontal grid and 16 vertical layers; the model is forced by tides, winds and 6 river flows, and simulates water level, currents, temperature and salinity. In particular, the spatial and daily salinity distribution were used to determine the range of salinities occupied within the Cook Inlet by belugas (Ezer et al., 2013) and killer whales (Shelden et al., 2003).

*Statistical analysis*

We used Principal Components Regression to predict beluga distributions away from the Susitna Delta, based on principal components presented in Ashford et al. (2013), that reduced the dimensionality of the data (Khattree and Naik 2000) to analyze the size and shape of the river discharge rates. Full details are presented in Ashford et al. (2013). Because variance was much higher for the Susitna River than other rivers, a $p \times p$ correlation matrix $\rho$ was constructed to avoid large differences in the variances between rivers influencing the analysis. We applied a regression using the same principal components to explore how well linear combinations of principal components served as predictor variables of beluga abundances in Chickaloon Bay, the upper Turnagain Arm, and Knik Arm. 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 the sector counts. We applied the same procedure to
examine the relationship of river discharge with Chinook salmon escapements in the Deshka River.

**Results**

**River discharge and beluga distributions away from the Susitna Delta**

Despite gaps prior to 2001, data for river discharge in May demonstrated the considerable flow from the Susitna River relative to all other rivers; the small flow from the Sixmile and Twentymile Rivers relative to those feeding into the Knik Arm; and the large inter-annual variability in flow, especially for the Susitna River (Fig. 2). From Ashford et al. (2013), 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 abundances using Principal Component Regression (Table 1), we found that, similar to Ashford et al. (2013) for the Susitna River Delta, the size variable represented by the first component was not useful for predicting abundances in the upper Turnagain and Knik Arms. The best variables were the fourth and fifth principal components, where the fourth represented differences between discharge from the northeastern and other two drainage areas, while the fifth principal
component represented differences in the flow between rivers within drainage area. The resulting models had a PRESS = 5589 for upper Turnagain Arm and PRESS = 24777 for Knik River. However, they yielded R-squares of 0.53 and 0.35 respectively, much lower than Ashford et al. (2013) showed for the Susitna Delta. Although models with three components gave a PRESS only slightly higher, R-squares improved only marginally.

In contrast, for Chickaloon Bay, we found that the size variable represented by the first component was useful for predicting beluga abundance. The best variables were the first, second, third and sixth principal components, where the sixth seemed largely to represent differences in the flow between rivers within the Turnagain and Knik Arms. The resulting model had a PRESS = 29012 and yielded an R-square of 0.91, higher even than for the Susitna Delta (Ashford et al. 2013). Accordingly, in year \(i\), the number of beluga \(y_i\) in the Chickaloon Bay can be predicted by:

\[
y_i = 59.4 + (11.1)PC_{1i} - (37.3)PC_{2i} - (18.7)PC_{3i} - (97.6)PC_{6i} + \epsilon_i
\]

Where \(PC_{1i}\), \(PC_{2i}\), \(PC_{3i}\) and \(PC_{6i}\), \(i=2001,\ldots,2009\), are the principal component scores of the first, second, third and sixth principal components. Although dropping the third principal component gave only a slightly higher PRESS, this yielded a lower R-square of 0.83.

**Chinook salmon escapements**

For the Principal Components Regression comparing river discharge with Chinook salmon escapements in the Deshka River (Table 1d), we found that the size
variable represented by the first component was useful for predicting Chinook
abundances. The first, second and sixth principal components were the best variables,
giving the lowest PRESS and explaining 74% of the total variability. Accordingly, in
year $i$, the number of Chinook salmon escapements $y_{iCS}$ in the Deshka River can be
predicted using river discharge by:

$$y_{iCS} = 29190 + (3367)PC_{1i} - (11999)PC_{2i} - (26452)PC_{6i} + \varepsilon_i$$  (3)

Where $PC_{1i}$, $PC_{2i}$, and $PC_{6i}$, $i=2001,\ldots,2009$, are the principal component scores
of the first, second, third and sixth principal components.

Salinity and killer whale distributions

Across the lower reaches of the Turnagain and Knik Arms, where tides are
amplified, salinities did not supersede 25 ppt (Section A in Oey et al 2007). Salinity of <
21 ppt dominated across the Knik Arm at the end of the ebb tide; more saline water
intruded on the western side at the end of the flood, but in a core deeper than 10 m. In the
Turnagain Arm, higher salinity persisted through the tidal cycle, with salinities > 22 ppt
reaching 40 km up the Arm at the end of the ebb tide, and 60 km at the end of the flood
(Fig 3a,b). Comparing with killer whale sightings (Shelden et al. 2003), the Knik Arm
had only a single anecdotal report, and this was located in its lower reaches. Six reports
were located in the Turnagain Arm, of which five were in its upper reaches. Nevertheless,
all reports of interactions with belugas occurred in water north of the Forelands and, of 11
observed beluga deaths caused by killer whales in the upper Inlet between 1991-2000, eight occurred in the Turnagain Arm.

In the mid-inlet at the latitude of Kalgin Island (bottom panels of Fig. 3), fresher water occupied the water column along the eastern boundary and the eastern coast of Kalgin Island, while salinities > 31.4 ppt were concentrated in a deep core. Fresher water also occupied the water column along the western boundary, with more saline waters (but less so than the eastern core) in the trench and along the western shore of Kalgin Island. Salinities of < 31.4 ppt persisted within 20 m of the surface across the section, and killer whale sightings were restricted to a few anecdotal reports along the eastern shore near Kenai and Nikiski. Farther south (not shown), salinities > 32 ppt occurred along the whole of the eastern side of Cook Inlet as far west as the bank south of Kalgin Island. Mixing to depth ensured that the salinity gradient was horizontal, and concentrated in a narrow zone south of Kalgin Island. Killer whale sightings were concentrated on the eastern side of the Inlet, north into Kachemak Bay, following the inflow of water through the Kennedy-Stevenson entrances.

* Discussion

Similar to the relationship found by Ashford et al. (2013) for beluga abundances in the Susitna Delta, river discharge explained over 90% of the variation in numbers of CIBW in Chickaloon Bay during annual surveys of the Cook Inlet. This corroborated CIBW responses to relative freshwater inputs, even in years when they moved away from the larger flows feeding the Susitna Delta. Moreover, not only did river discharges
predict beluga spatial distributions, they also predicted escapements of Chinook salmon
in the Deshka River, explaining over 70% of the variation between years. As shown by
Ashford et al. (2013), a strong inverse relationship between escapements and beluga
abundances downstream in the Susitna Delta indicated that river discharge drives
escapements through its effect on predation pressure. In turn, the spatial distributions of
beluga appeared consistent with a response to killer whales: although reports indicated
that a high proportion of interactions result in mortality or injury, spatial partitioning
along salinity gradients would account for the low incidence and mortality rate estimated
by Shelden et al (2003). Interactions were associated with surface salinities in the
approximate range of 24-30 ppt, suggesting that CIBW use areas characterized by lower
salinities as refugia from killer whale predation.

Nevertheless, salinity may not directly control spatial partitioning, or be the only
factor involved. Ezer et al. (2013) showed that shallow mudflats and strong tidal currents
in the upper CI are important, and may give CIBW a survival advantage over larger killer
whales. Alternatively, differential use of visual cues in foraging behavior may restrict
killer whales to clearer water, away from more turbid freshwater from glacial melt.
Moreover, the low incidence of interactions may be influenced by killer whale social
behavior: features of the pods sighted in the upper inlet suggested they were not
residents, but transients with a much larger hunting range (Shelden et al. 2003). Ice
distributions may also be important on seasonal time scales (Ezer et al. 2008). These
processes may all contribute, creating refugia in space and time, yet they are highly
correlated and linked to river discharge and circulation. As a result, salinity represents a
useful measure to predict partitioning, even if it is not exclusive as a controlling parameter.

However, distributions are susceptible to sampling bias. Thus, detectability of CIBW in the aerial surveys may change considerably between sectors as a result of changes in diving behavior (Ashford et al. 2013), whereas biases in killer whale sightings can arise due to higher urban densities near Anchorage and towns on the Kenai Peninsula. Even so, while important to take into consideration, these biases did not fundamentally affect our conclusions. The analyses of CIBW abundances were made between years within sector, avoiding confounding by spatial changes in behavior. Urban densities near Anchorage are higher than on the Kenai Peninsula, arguing that if anything the discrepancy in incidence of killer whale sightings between the upper and lower inlet is under-estimated. Biases in observer effort may influence west-east differences, but interactions between belugas and killer whales occurred in the upper inlet where observer effort is high, supporting a generally low rate of incidence.

Large differences in the variances between rivers can also influence the analysis. However, principal components regression provides a rigorous way to predict future observations that avoids this problem by using a correlation matrix. With a longer series of data, the predictive models can incorporate environmental oscillations on cycles of more than a few years, allowing them to be applied to longer time scales. The Cook Inlet is characterized by extreme physical conditions, including tidal bores in the upper inlet, rip currents in channels in the mid inlet, fast moving salinity fronts and large spatial variations in salinity, and floating ice in winter (Oey et al. 2007, Ezer et al. 2008, Ezer et al. 2013) that may all respond to climate cycles. Yet these conditions may be key to
CIBW persistence where they create habitats in which belugas are at an advantage over killer whales.

Results from Ashford et al. (2013) and this study indicate that the strongest association of CIBW with river discharge occurred in the Susitna Delta and Chickaloon Bay where killer whale sightings were among the lowest. Beluga abundances appeared to shape escapements in the Deshka River; suggesting on the one hand that killer whale interactions constrain CIBW responses to variation in food availability; and on the other hand, extending the scope of prediction to lower trophic levels in the Cook Inlet ecosystem. In the light of these relationships, evidence of poleward expansion in killer whale sightings in the Arctic Ocean as sea-ice retreats indicates that northern beluga populations, which currently show extensive migrations into ice-covered regions and to considerable distances offshore (Hauser et al. 2013*), can be projected to shift to more coastal distributions, with refugia linked to sources of freshwater influx from rivers and estuaries. An example is the Mackenzie River, which empties into the Beaufort Sea through multiple channels in a large delta that, like the upper Cook Inlet, has extensive mudflats and complex circulation. Based on our results, as beluga become restricted to coastal areas, relative discharge through these channels is likely to structure their distributions. In consequence, predation pressure exerted by belugas in the Beaufort Sea would shift from offshore areas to shape projected anadromous fish runs (e.g. Kline 2013*). Changing population structure, with beluga populations more narrowly defined by the geographical extent of their system, would be governed by connectivity defined by the size and extent of river plumes discharging along the coast.
However, the limits of inference of the quantitative relationships found for the Cook Inlet need careful consideration. Depending on how closely northern systems converge on that in the Cook Inlet, spatial partitioning may similarly occur along salinity gradients between 24-31 ppt, and river discharge have comparably sized effects on beluga and fish distributions. But differences between systems will mean that these relationships will vary: bathymetry, configuration and drainage basin effects on meltwater will all contribute. Nevertheless, the relationships offer an alternative approach to constructing hypotheses concerning ecosystem responses to climate change, which can provide precise quantitative predictions with measures that can be compared against empirical observations to gauge performance. In this way, field data can guide the creation of further hypotheses in an iterative process of fine-tuning. Quantitatively examining the complex spatial relationships generated by interactions between physical and biological processes can help us better understand how high-latitude marine ecosystems respond to climate change.

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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.
Fig 2 a) Aerial survey counts of beluga from 1993-2011 in sectors of the northern Cook Inlet: Susitna Delta, Knik Arm, Turnagain Arm, Chickaloon Bay (from Ezer et al. 2013). 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) (from Ashford et al. 2013) c) Total escapements of Chinook salmon along the Deshka River compared to beluga counts for the Susitna Delta sector (from Ashford et al. 2013)
Fig 3  The salinity in the upper (top panels) and mid (bottom) CI during low (left) and high (right) tides; the strong vertical flow in the deeper channels of the mid-CI are also shown in contours (from model simulations by Oey et al., 2007). The location of one tagged beluga which was tracked by satellite in Turnagain Arm in September 2000, is also shown (from Ezer et al., 2008).
Table 1. Predictive ability of selected principal components from Principal Component Regressions for river discharge on: sector counts of beluga for a) Chickaloon Bay b) upper Turnagain Arm and c) Knik Arm; and on d) Chinook salmon escapements in the Deshka River. PRESS, predicted residual error sum of squares.

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