

# Trend in aerial counts of beluga<sup>1</sup> or white whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, 1993-2005

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## ABSTRACT

Thirty-eight aerial surveys of beluga or white whales (*Delphinapterus leucas*) were conducted in Bristol Bay, Alaska, during six different years between 1993 and 2005. Belugas were sighted mainly close to shore in the upper parts of Nushagak and Kvichak bays, as well as along the coast between these bays and in the lower parts of major rivers. Data from 28 complete counts made in good or excellent survey conditions were analysed for trend. Counts ranged from 264 to 1,067. The estimated rate of increase over the 12-year period was 4.8%/year (95% CI = 2.1%-7.5%). Such a rate of increase suggests that either the population was below the environmental carrying capacity in the early 1990s or, alternatively, that factors that had been limiting population increase were alleviated after that time. A review of possible changes in human-caused mortality, predation and prey availability did not reveal a single likely cause of the increase. Among the factors that could have played a role are recovery from research kills in the 1960s, a modest decline in subsistence removals and a delayed response to increases in Pacific salmon (*Oncorhynchus* spp.) abundance in the 1980s. The positive growth rate for this population shows that in recent years there has been no substantial negative impact of human or natural factors, acting either alone or in combination, and there is no need for changes to the current management regime.

KEYWORDS: BELUGA WHALE; WHITE WHALE; INDEX OF ABUNDANCE; MONITORING; SURVEY-AERIAL; TRENDS

## INTRODUCTION

Beluga whales (*Delphinapterus leucas*) are common in coastal and offshore waters of western Alaska. During summer months they congregate predictably at certain coastal locations; that distribution pattern was used to identify provisional management stocks (Frost and Lowry, 1990). Subsequent studies of mitochondrial DNA confirmed that three beluga stocks occur in waters off western Alaska during summer, the Bristol Bay stock, the eastern Bering Sea stock and the eastern Chukchi Sea stock (O’Corry-Crowe *et al.*, 1997). Those stocks are considered to be separate management units (Angliss and Outlaw, 2007).

The Bristol Bay region (Fig. 1) supports an abundance of fish and wildlife, and beluga whales are present in this area throughout the year. They are seen most commonly in Kvichak and Nushagak bays, especially in the months from April to August (Chythlook and Coiley, 1994; Frost and Lowry, 1990; Frost *et al.*, 1984). Kvichak and Nushagak bays also support large runs of anadromous fishes, especially red salmon (*Oncorhynchus nerka*), which are a major prey item of the belugas in this region (Brooks, 1955; Frost *et al.*, 1984). Scientific studies conducted in the region in the 1950s and in 1982-1983 provided information on beluga distribution and abundance, movements and diving patterns, food habits and entanglements in fishing nets (Brooks, 1955; Frost *et al.*, 1984; Frost *et al.*, 1985; Lensink, 1961).

The Alaska Beluga Whale Committee (ABWC) was formed in 1988 to conserve beluga whales and manage beluga subsistence hunting in western Alaska in cooperation with the National Oceanic and Atmospheric Administration

(Adams *et al.*, 1993; Fernandez-Gimenez *et al.*, 2006). Aerial surveys to estimate the abundance and trends of western Alaska beluga stocks have been a part of the ABWC research program since the early 1990s. This paper presents the results of ABWC surveys flown in Bristol Bay during 1993-2005, and estimates the trend in counts of belugas over that period.

## METHODS

### Aerial surveys

Aerial surveys were flown using a high-wing, twin-engine *AeroCommander* with oversized bubble windows. The survey crew included the pilot, a data recorder and two observers (from a group of three individuals) seated behind the pilot on the left and right sides of the aircraft. The survey was designed to cover all of Kvichak and Nushagak bays (Fig. 1), which includes the region where essentially all reported June-July sightings of belugas in Bristol Bay have occurred (see fig. 3 in Frost and Lowry, 1990). The standard survey track followed the entire coast of both bays 0.9km off shore, including the lower parts of major rivers. In the wider portions of the bays we also flew east-west transects at 1.8km intervals to cover the entire area. On those lines, observers counted whales in a strip 0.9km wide on each side. Strip widths were measured by inclinometers and angles were marked on the aircraft windows with grease pencils. Survey altitude was 305m except that when surveying rivers it was 91m. Airspeed was maintained at approximately 222km hr<sup>-1</sup> during all surveys. Years in which surveys were conducted were determined by availability of funding and needs to conduct other activities of the ABWC. For each year the objective was to complete five replicate surveys of the entire area known to be used by belugas.

<sup>1</sup> The common name agreed for *Delphinapterus leucas* by the Scientific Committee of the International Whaling Commission is the white whale. However, ‘beluga’ is commonly used in several parts of the world, including Alaska, and is used in this paper.

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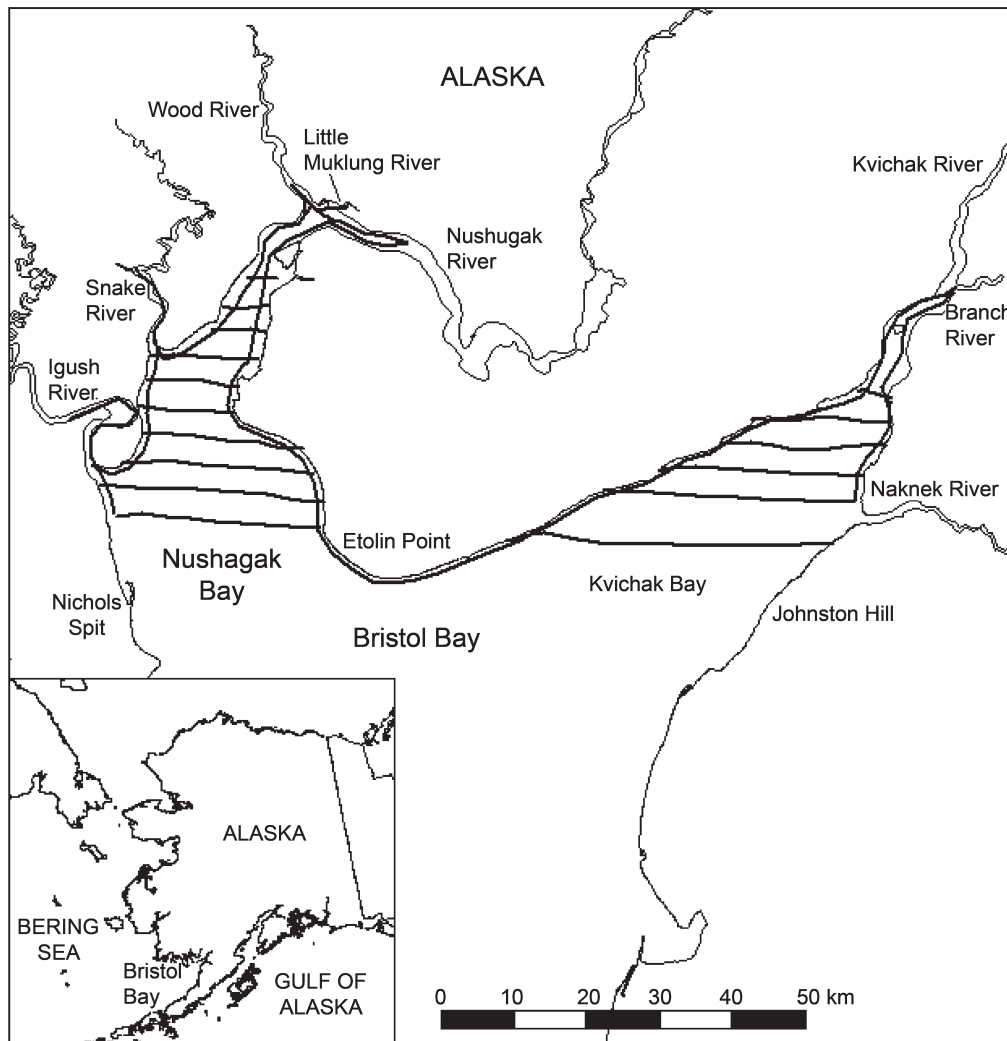


Fig. 1. Map of the Bristol Bay study area showing representative survey flight lines (heavy dark lines).

All belugas visible at the surface along the survey track were counted and counts were recorded either on datasheets by the observers or on a computer by the recorder. When large groups were encountered two or more counts were made. In those situations the aircraft circled after passing by the group and flew past again on a line oriented to provide one observer the clearest view of the entire group. Multiple counts, usually by both observers, were recorded individually, and observers identified which count was best (e.g. minimum glare and no whales in the blind area directly under the plane) and that single count was used in analysis of the data.

A computerised data logging system recorded the time and position determined by the global positioning system at the beginning and end of each transect, at 60 second intervals along the transect, and at every beluga sighting. Beluga counts, weather, sea state, glare, overall sighting conditions and other potentially relevant observations were also entered into the database.

#### Data analysis

As soon as possible after the survey, computer records were checked for accuracy and edited as necessary. Later all data were entered into a geographic information system (GIS; ArcInfo and ArcView). All sightings and survey tracklines were plotted in the GIS, and the results were examined to

identify any possible duplicate sightings which, when found, were removed from the database. Duplication occurred only when cross-bay lines intersected coastal transects, and duplicate sightings were identified based on location, timing and group size.

Sea state (DeMaster *et al.*, 2000) and glare (pers. obs.) can have a great effect on counts of belugas. Those and other environmental factors (e.g. low clouds or fog) were integrated in the parameter 'sighting conditions', which was recorded as 'excellent', 'good', 'fair' or 'poor.' The GIS was used to examine the relationship between sighting conditions on individual surveys and beluga counts. This examination revealed that counts were much lower when conditions on the shoreward-looking side of coastal transects were recorded as fair or poor – within years, the means of counts made under fair or poor conditions were 48%-79% lower than those made under good or excellent conditions. Therefore, it was decided to include in the analysis only those surveys for which the entire study area was surveyed with good or excellent sighting conditions on the shoreward side of alongshore transects (which is where nearly all sightings occurred, see below).

The rate of increase for the period 1993-2005 was estimated by fitting an exponential model to the individual counts assuming a normal error distribution. In this model, the instantaneous rate of increase ( $r$ ) in the population ( $N$ ) is

constant over time ( $t$ ):  $N_t = N_0 * e^{rt}$ . The rate of increase can be estimated in a linear regression framework ( $\ln[N_t] = \ln[N_0] + rt$ , where  $r$  is the slope of the regression). Confidence intervals of the estimated rate of increase were calculated as:  $95\% \text{ CI} = r \pm t_{0.025, \text{df}} * \text{SE}(r)$ . The instantaneous rate ( $r$ ) was converted into an annual rate of increase as  $e^r - 1$ .

**RESULTS**

Thirty-eight aerial surveys were conducted during 1993-2005. Belugas were sighted mainly close to shore in the upper parts of Nushagak and Kvichak bays, as well as along the coast between these bays and in the lower parts of major rivers (Fig. 2).

Three of the 38 surveys were incomplete due to weather that precluded counting in parts of the study area, and 7 failed to meet the criterion of good or excellent sighting conditions. The dataset used to analyse for trend therefore included 28 counts, with 3 to 6 counts in each year (Table 1). The number of belugas counted per survey ranged from 264 to 1,067. The annual counts showed an increase over time, with the 2005 average count being 76% greater than the average count in 1993.

The estimated rate of increase from the linear regression model for the period 1993-2005 was 4.8%/year (95% CI=2.1%-7.5%). The fit of the model through the count data is illustrated in Fig. 3.

Table 1

Aerial survey counts of beluga whales in Bristol Bay, Alaska, 1993-2005.

Survey date	Flight	Total count	Mean count	CV
29/06/93	1	311		
30/06/93	1	415		
03/07/93	1	269		
17/07/93	1	452		
18/07/93	1	362		
<b>1993 combined</b>			<b>362</b>	<b>0.21</b>
06/07/94	1	473		
07/07/94	1	391		
07/07/94	2	264		
<b>1994 combined</b>			<b>376</b>	<b>0.28</b>
14/07/99	1	287		
15/07/99	1	441		
15/07/99	2	454		
16/07/99	1	349		
17/07/99	1	690		
<b>1999 combined</b>			<b>444</b>	<b>0.35</b>
10/07/00	1	284		
11/07/00	1	531		
11/07/00	2	432		
12/07/00	1	496		
12/07/00	2	361		
<b>2000 combined</b>			<b>421</b>	<b>0.24</b>
06/07/04	1	362		
08/07/04	1	674		
08/07/04	2	674		
09/07/04	1	556		
09/07/04	2	779		
10/07/04	1	794		
<b>2004 combined</b>			<b>609</b>	<b>0.16</b>
13/07/05	1	393		
13/07/05	2	480		
14/07/05	1	1,067		
14/07/05	2	607		
<b>2005 combined</b>			<b>637</b>	<b>0.47</b>

**DISCUSSION**

**Distribution of belugas within Bristol Bay**

Mitochondrial DNA analyses indicate that the belugas inhabiting Bristol Bay are demographically distinct from other belugas in western Alaska (O’Corry-Crowe *et al.*, 1997), and they are considered by the National Marine Fisheries Service (NMFS) to be a management stock separate from other western Alaska beluga stocks (Angliss and Outlaw, 2007). The total range occupied by this population throughout the year is not well described, but compilations of sightings (Frost and Lowry, 1990), recent surveys (this study) and satellite-linked telemetry (L. Quakenbush, pers. comm.) indicate that essentially all the animals are in the Kvichak Bay-Nushagak Bay region during the months of June and July.

Within Kvichak and Nushagak bays several concentration areas have been used consistently during the summer since at least the mid-1950s (Brooks, 1955; Frost and Lowry, 1990; Frost *et al.*, 1984) and this study. In fact, the specific sites (e.g. certain portions of rivers) occupied by concentrations of belugas in June and July were essentially identical over the 24-year period in which we (LFL and KJF) have surveyed the area. Belugas occurred mostly very near shore in the upper portions of Kvichak and Nushagak bays and along the intervening coastline. The vast majority of sightings made during this study were within 0.9km of the shoreline. Although the sightings shown in Fig. 2 suggest a fairly broad onshore-offshore distribution, this actually reflects the large tidal range and gently sloping topography which, in combination, cause the location of the shoreline in some places to vary by three kilometres or more during a tidal cycle. Their predictable distribution pattern, which is apparently stable over time, makes beluga whales in Bristol Bay relatively easy to locate and count.

**Trend in counts**

With an annual rate of increase of 4.8% per year, we estimate that the abundance of Bristol Bay belugas increased by 65% over the 12-year period. This result is quite similar to the 76% increase in the mean of counts over this same period. Our results are consistent with the observations of long-time residents and Alaska Native beluga hunters who report that more belugas are present in Kvichak and Nushagak bays now than there were 10-20 years ago.

Prior to this study there had been no rigorous effort to estimate the number of belugas in Bristol Bay. Brooks (1955) studied belugas in Kvichak and Nushagak bays, and estimated their abundance as 1,000 in 1954 and 525 in 1955 ‘...based on surface observations, aerial observations, and fishermen and pilot reports’. Lensink (1961) continued the work of Brooks in the late 1950s and concluded that ‘...accurate counts are impossible in the turbid waters of this area, but the population probably numbers between 1,000 and 1,500 animals’. It is not possible to compare these earlier estimates to one another or to our recent counts, therefore we cannot say how the population size may have changed since the 1950s.

Frost *et al.* (1984) studied belugas in Kvichak and Nushagak bays in 1982-1983, and one aerial survey of the entire study area in good sighting conditions on 29 June 1983 resulted in a count of 334 belugas. The 1983 count was only slightly lower than the mean counts for 1993 and 1994, suggesting that there was little population growth over that 11-12 year period. It appears therefore that the period of rapid growth of this population probably began in the early 1990s.

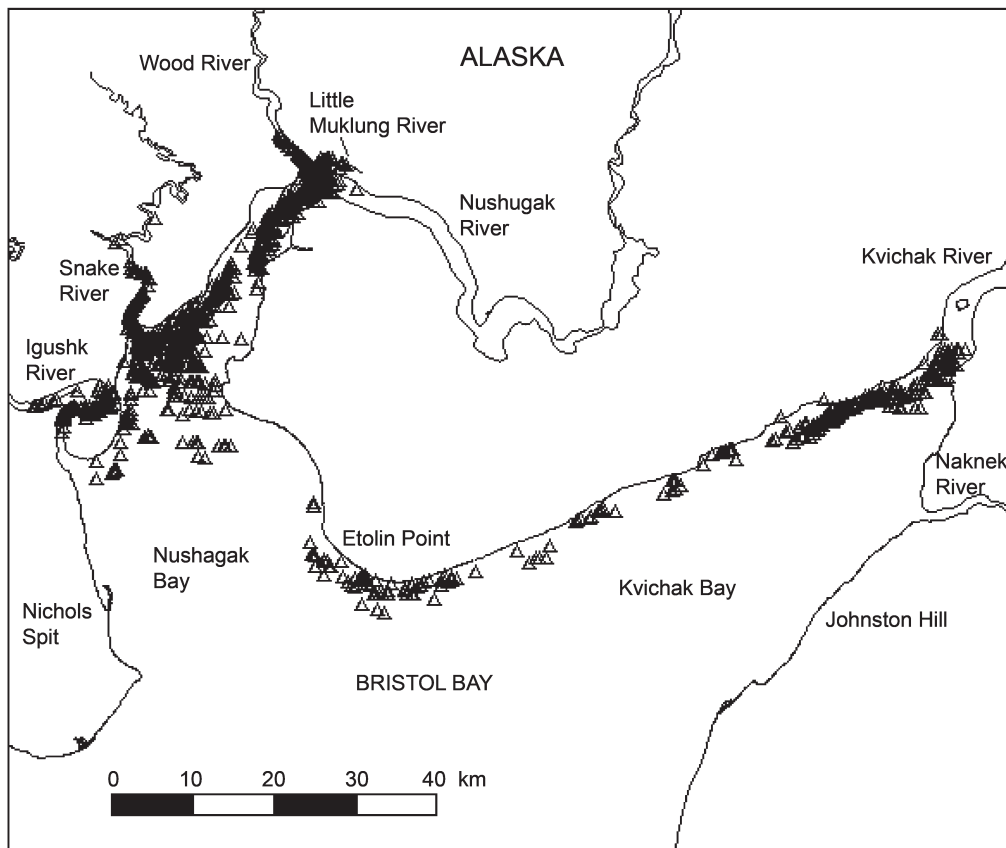


Fig. 2. Map of Bristol Bay showing all sightings of beluga whales made during aerial surveys in 1993-2005 (triangles).

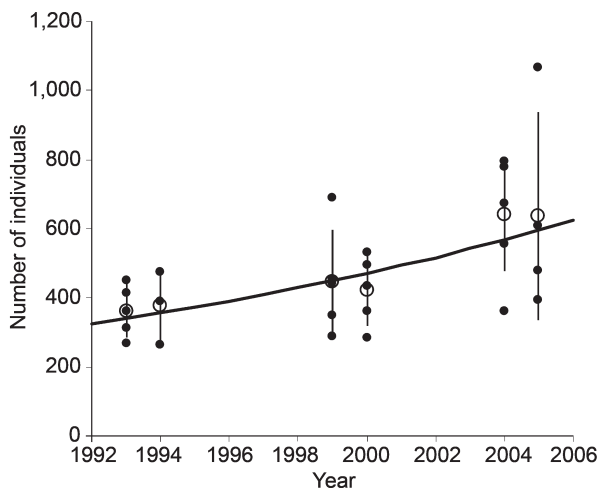


Fig. 3. Fit of the exponential model to Bristol Bay beluga count data (black dots=individual counts, white circles=mean counts, vertical bars=standard deviations, heavy black line=predicted counts).

Within year counts made in good and excellent sighting conditions in 1993-2005 were reasonably consistent and the coefficients of variation associated with those counts were relatively low. However, more whales were counted on some surveys than on others. Possible explanations include: (1) on some surveys some groups of belugas may not have been counted because they were absent from the area surveyed; (2) some whales at the surface within the survey area may have been missed because of sighting conditions or some other factor; and (3) belugas may have behaved differently at different times (e.g. spent more or less time at the surface). As discussed above, all available information

indicates that Bristol Bay belugas are restricted to the surveyed area during June-July so the first possible explanation is unlikely. Undoubtedly some animals are missed during any given survey but no attempt was made to quantify that bias since the main objective was to estimate population trend. Missed animals should not bias our estimate of trend provided that the bias is consistent over time. Several measures were taken to ensure consistent bias, including eliminating surveys flown in fair or poor sighting conditions and using a limited pool of experienced observers and identical techniques in all the surveys. The third factor, variation in beluga behaviour, probably explains most of the variability in counts for two reasons. First, data collected on surfacing patterns of belugas in Bristol Bay show considerable variation, including long periods when whales rest or feed in water so shallow that they are at the surface essentially all the time (Frost *et al.*, 1985). Second, substantial differences have been seen in counts of specific whale groups over relatively short periods of time. The best example of this was on 14 July 2005, the day when the highest count of the entire series was obtained. On that day a large group of whales was located in western Kvichak Bay at about 13:30 hours, with a best count of 638 animals. Approximately 2.5 hours later, during the second survey of the day, another count was made of the same group in the same area, and the best count that time was 163, just 25% of the number seen earlier on the same day. Sighting conditions were excellent during both counts, and when the second count was so much lower it was decided to fly additional lines covering the entire adjacent area but no more whales were found. This within-day difference was probably due entirely to behaviour, with the higher count occurring when essentially all animals were at the surface and the lower one when many of them were diving. Dive data from five

satellite-tagged belugas in Bristol Bay corroborate that there is considerable variation in surfacing behaviour (J. Citta, pers. comm.).

**Why has the Bristol Bay beluga population increased?**

Other than the counts and estimates described above, there are no historical data on the number of belugas in Bristol Bay. However, the apparently steady increase in the population over the 12 years of our study indicates that it was below the environmental carrying capacity (K) during that period. For this to be true, either something was acting previously to keep the population from growing toward K, something changed causing K to increase, or both.

Human activities have caused both intentional and unintentional removals of belugas from this population. During 1954-1966, 127 belugas were killed for research (Brooks, 1957; Vania and Klinkhart, 1967) and 8 were live-captured for oceanaria (Lensink, 1958; Ray, 1962; Reeves and Leatherwood, 1984). Belugas are hunted by Alaska Natives for subsistence, and since 1987 the ABWC and the Bristol Bay Marine Mammal Council have compiled beluga harvest data for Bristol Bay. The reported average annual landed catch during 1987-2006 was 20 belugas. Average catch was highest for the 5-yr period 1987-1991 (mean=25, range=13-36) and somewhat lower during the subsequent three 5-yr periods (1992-1996 mean=20, range=6-35; 1997-2001 mean=17, range=6-31; 2002-2006 mean=20, range=13-23) (Frost and Suydam, in prep.). These figures do not include the number of whales that were struck but not retrieved, but that number is believed to be 'quite low' in this area (ABWC, pers. comm.).

Belugas also have been taken incidentally in gillnet fisheries for salmon but data on the numbers killed in Bristol Bay are incomplete. Frost *et al.* (1984) found 27 dead belugas during their studies in May-July 1983, at least 12 of which had died in nets. The Bristol Bay salmon gillnet fisheries have never been monitored by observers, but during the period between 1990 and 2000 fishermen reported one beluga death in 1990, one in 1991 and none thereafter (Angliss and Outlaw, 2005). It is uncertain whether the number killed in nets has declined since 1983; in general, self-reported data on incidental takes in fisheries are negatively biased (Credle *et al.*, 1994). There have been no major changes in fishing effort or methods in the Bristol

Bay salmon fishery over the past 25 years that would be expected to result in a decline in the incidental take, although the total number of actively fished permits has declined by about 10% (Westing *et al.*, 2006). It is likely that some belugas die each year as a result of interactions with the gillnet fishery.

Killer whales (*Orcinus orca*) are natural predators of belugas. Frost *et al.* (1992) documented a number of killer whale sightings in Bristol Bay in 1989-1990, including instances where they chased and killed belugas. Those authors considered such events to be very unusual based on historical observations of biologists and local residents. However, Bristol Bay area residents report that killer whales have been seen quite frequently in the Nushagak side of Bristol Bay in recent years, and that they affect the distribution of belugas when they are present (Molly Chythlook, pers. comm.). Since there have been no directed studies of killer whales in this area it is impossible to assess whether or not they have had an influence on abundance of Bristol Bay belugas.

It is possible that the environmental carrying capacity for Bristol Bay belugas has changed due to an increase in availability of food for them. The prey species of belugas in Bristol Bay during the late spring and summer are relatively well known (Brooks, 1955; Frost *et al.*, 1984; Lensink, 1961). In May and early June they feed mostly on smelt (*Osmerus mordax*) and red salmon smolt migrating out of the rivers. From mid-June through mid-August they feed primarily on salmon, with red salmon dominant but other species (chum, *Oncorhynchus keta*; pink, *O. gorbuscha*; and silver *O. kisutch*) becoming more important later in the season. From mid-August through September salmon are seldom eaten and prey items found in beluga stomachs have included flatfishes, sculpins, lampreys (*Lampetra japonica*) and shrimps (*Crangon* spp.). There are no published data on diet during the autumn and winter months.

There are no programmes for assessing or monitoring the abundance of potential beluga prey other than salmon, but there are extensive data for salmon (Fig. 4). Red salmon returns to Bristol Bay streams are strongly cyclical, with peaks in abundance about every five years and smaller runs in intervening years. From the late 1950s through the 1970s, Bristol Bay run cycles were regular and quite consistent, with an average run size of about 18 million (Hare and

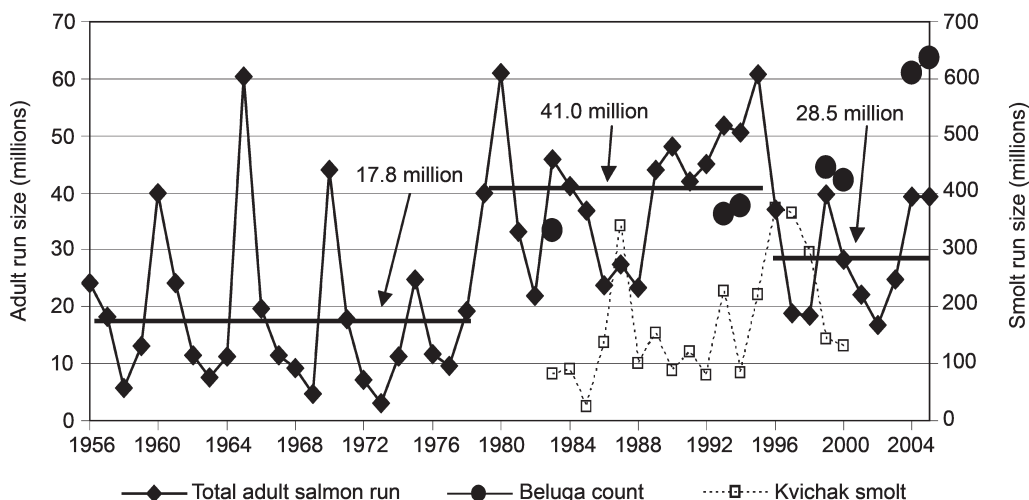


Fig. 4. Beluga counts from aerial surveys and estimated run size (in millions) of salmon smolts and adults in Bristol Bay, Alaska, 1956-2005. Horizontal lines and numbers on the figure show the average adult salmon run for three time periods.

Mantua, 2000; Hyun, 2002; Sands, 2006; Westing *et al.*, 2006). Salmon abundance increased markedly during 1979-1995, with less regular cyclical peaks and average run size of 41 million. From 1996-2005, average runs declined to 28.5 million, but were still substantially higher than prior to 1980. While thresholds of prey abundance needed for belugas to thrive and increase are not understood, the larger size of red salmon runs before and during the period covered by the aerial surveys may be a partial explanation for the increased beluga numbers. Salmon stocks in Bristol Bay were greatly reduced by overfishing in the 1940s and early 1950s. By the mid-1950s, resource agencies were attempting to control salmon predators because of their perceived negative effect on salmon abundance (Brooks, 1955; Fish and Vania, 1971). Certain of the actions taken were specifically intended to reduce beluga predation on salmon smolts by displacing them from river mouths during the outmigration of smolt. Efforts began in 1956 and included harassment by motorboats and small dynamite charges (Lensink, 1961), followed later by acoustic devices that transmitted killer whale calls underwater (Fish and Vania, 1971). The 'beluga spooker' program was discontinued in 1978 and organised efforts to displace belugas no longer occur (Frost *et al.*, 1984).

Although there is no clear single explanation for the apparent increase in beluga numbers in Bristol Bay since 1993, it is possible that several factors have played a role, either alone or in combination. These include recovery from research kills in the 1960s, a modest decline in the rate of subsistence harvest since the early 1990s and a delayed response to increases in salmon abundance in the 1980s. It is also conceivable that killer whale predation has lessened over this period although there are no data currently to support or refute that possibility. In the absence of *inter alia* information on how the body condition of individuals in the population may have changed over time, it is not possible to make firm inferences as to why this population has increased. Simultaneous indexing of both population abundance and condition of individuals in the population may provide managers with a much more complete understanding of the status of a population compared to a situation where only information on absolute abundance or change in abundance is available (Gerrodette and DeMaster, 1990).

### Management implications

In the United States, the Marine Mammal Protection Act requires use of the 'potential biological removal' (PBR) system to evaluate whether human 'taking' of marine mammals is excessive relative to the goals of that Act, and if it is steps must be taken to reduce the number of animals incidentally removed (killed or seriously injured) in commercial fisheries. The basic population data required to support the PBR system are a minimum estimate of population size and an estimate of the maximum net productivity rate ( $R_{max}$ ). Using those data and an assumed recovery factor, an upper limit on removal levels consistent with management goals is calculated (Wade, 1998) for comparison with the number of animals being killed or seriously injured by various human activities. While PBR was first articulated in legislation passed in the US, it has also been used by managers in other countries to calculate safe removal levels for marine mammals (e.g. Butler *et al.*, 2008; Marsh *et al.*, 2004).

The PBR process produces an informative threshold for managers regarding anthropogenic removals (Read and Wade, 2000). However, the process requires a considerable

amount of data that can be expensive and difficult to collect. Serious problems that may arise include: (1) inadequate resources to survey populations with sufficient precision and frequency (Taylor *et al.*, 2007); (2) problems with developing methods to correct survey data for detection and availability biases; (3) a lack of data for estimating  $R_{max}$ ; (4) a lack of data on total anthropogenic removals; and (5) insufficient data to adequately describe population structure. For  $R_{max}$  so little is known that in 2007 default values were used in the stock assessments produced by NMFS for 147 of the 156 stocks that were evaluated (<http://www.nmfs.noaa.gov/pr/sars/draft.htm>). The result is that in many situations, for example for 13 of the 36 Alaskan stocks evaluated in 2006 (Angliss and Outlaw, 2007), a valid PBR cannot be calculated. Furthermore, there are situations where populations have shown major declines in spite of the fact that estimated human takes have been well below PBR (Angliss and Outlaw, 2007) e.g. western stock of Steller sea lions, *Eumetopias jubatus*; eastern Pacific stock of northern fur seals, *Callorhinus ursinus*; southwest Alaska stock of northern sea otter, *Enhydra lutris kenyoni*. Presumably such situations mean that those populations are declining for reasons other than direct take by humans, and therefore the PBR system is poorly suited for evaluating actions needed to allow the populations to recover.

Compared to the cost of acquiring the data required to implement the PBR management regime for a given population (i.e. a conservative estimate of current absolute abundance, an estimate of  $R_{max}$ , and an estimate of current total anthropogenic removals), basing management actions on monitoring trends in abundance can be less expensive and more effective for some populations in some areas, providing adequate data can be collected. More importantly, a series of index counts may detect population responses in situations where factors other than direct taking by humans are impacting the status of a population, and also could account for cumulative effects.

We believe that is the case with this study, which has shown that the Bristol Bay beluga stock has increased at a rate of 2.1%-7.5% per year during 1993-2005. This evidence of increase in population size indicates that the aggregate effects of direct takes (e.g. subsistence hunting, entanglement in fishing gear), indirect interactions with humans (e.g. competition for food resources, habitat alteration), and other factors (e.g. predation, changing climate) over that 12-year period were 'acceptable' in the sense that they did not prevent the population from increasing. Therefore, we conclude that there is no need for a change in the *status quo* with regard to management of this stock.

There are two other beluga whale populations that are (or have been) of generally similar size to Bristol Bay and that occur in similar sub-arctic environments, Cook Inlet (Alaska) and the Saint Lawrence estuary (Canada). The trend in abundance is being closely monitored for both, with results showing that the Cook Inlet population is declining (Hobbs *et al.*, 2000; Lowry *et al.*, 2006) while the St. Lawrence population is most likely stable (Gosselin *et al.*, 2001; Hammill *et al.*, 2007). Results from this study suggest that once factors limiting those populations have been identified and mitigated, it would be reasonable to expect them to increase at a similar rate to the Bristol Bay population. To adequately protect and manage these small populations, it is essential that trend monitoring programmes be continued in those regions. In addition, to the extent possible, it would be useful to collect data on the body condition of animals in these populations. It is also

important to continue to monitor human activities so that if changes in trends are detected, potential causes can be examined.

## ACKNOWLEDGEMENTS

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