Evaluation of the Potential to Use Capture-recapture Analyses of Photographs to Estimate the Size of the Eastern Canada — West Greenland Bowhead Whale (Balaena mysticetus) Population

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Abstract

The summering areas of the Eastern Canada-West Greenland (EC-WG) population of Bowhead Whales (Balaena mysticetus) are large and remote, making it difficult to conduct a systematic aerial survey of the entire range in a short period of time. Surveys conducted in different parts of the Bowhead Whales’ summer range at different times or in different years cannot be used to obtain a robust estimate of population size because whales may move among summering areas within and between years. We suggest an alternative approach to estimate the size of the EC-WG population using photographic surveys of spring and summer aggregation areas. With two years of photographic surveys, capture-recapture estimates can be made of the number of marked whales in the population, and the proportion of the population that has recognizable marks can be estimated using data from the Bering-Chukchi-Beaufort (BCB) population of Bowhead Whales. These two populations appear to be increasing at near their maximum possible rate, based on estimates of age at sexual maturity and calving interval for the BCB population, and this justifies using the proportion that is marked from the BCB population for analyses of the EC-WG population. Confidence intervals for the photograph-based population estimate are likely to be narrower than those from systematic aerial surveys. A major side-benefit of the photographic surveys is that life history information, which is sparse for the EC-WG population, would be obtained.

Key Words: Aerial survey, Atlantic, Arctic, Bowhead Whale, Balaena mysticetus, photo-identification, population estimation.
INTRODUCTION

Between about 1915, when commercial whaling for Bowhead Whales (Balaena mysticetus) ended, and the 1970s, there was only sporadic hunting of these whales by Inuit in eastern Canada (Mitchell and Reeves 1982) and West Greenland (Reeves and Heide-Jørgensen 1996). Authorized annual hunts of small numbers of Bowhead Whales for subsistence began in eastern Canada in 1996 (DFO 2008; Koski and Ferguson 2012) and in West Greenland in 2009 (Heide-Jørgensen et al. 2012). To confirm that authorized harvest levels will not adversely affect the Bowhead Whale population, more reliable estimates of population size and reproduction and mortality rates are needed.

Until recently, Bowhead Whales in Baffin Bay and Davis Strait were considered to be separate from those in Hudson Bay and Foxe Basin, and the two putative populations were assessed and managed separately (COSEWIC 2005). Satellite telemetry data, in combination with genetic analyses, catch history, and evidence of population segregation, have recently shown that Bowhead Whales off eastern Canada and West Greenland likely belong to a single population, the Eastern Canada – West Greenland (EC-WG) population (Ducek et al. 2006; Heide-Jørgensen et al. 2006; IWC 2008). The recognition of a single relatively larger population rather than two small populations lessens concerns that even small harvests could lead to conservation concerns.

Scientists from the Canadian Department of Fisheries and Oceans (DFO) conducted aerial transect surveys during 2002-2004 to estimate the size of the EC-WG Bowhead Whale population in its summering areas. However, all such areas could not be surveyed in one year and different parts of the range were surveyed in different years, thus confounding the combined results (IWC 2009a). The data, as presented by Ducek et al. (2008), were re-analysed at the 2008 IWC Scientific Committee meeting (IWC 2009a) and a putatively negatively biased abundance estimate of 6344 (95% Confidence interval 3119-12906) was agreed for management advice (IWC 2009b). Independent estimates for part of the EC-WG population that occurs off West Greenland have been made from spring aerial surveys in 2006 (1229; 95% CI 495-2393: Heide-Jørgensen et al. 2007) and from mark-recapture analyses of genetic samples taken off West Greenland in 2010 compared with samples taken off West Greenland and in Canadian waters from 2000 to 2009 (1410 ± Standard Error 320 whales of which 999 ± SE 231 were females: Wig et al. 2011). These estimates of Bowhead Whales off West Greenland would not account for whales in the EC-WG population that do not, or at least did not during the survey period from 2000-2009, pass through Greenland waters.

The large summer range of the EC-WG Bowhead Whale population and the remoteness of much of that range make conducting a systematic aerial survey of the entire region in a short period of time in summer very difficult. An alternative approach to estimate the size of this population would be to use capture-recapture analyses of photographs obtained from aerial photographic surveys. Capture-recapture estimates of abundance based on photographs have been made for several populations of large whales (Best et al. 2001; Stevick et al. 2003; Calambokidis and Barlow 2004; Bradford et al. 2008; Carroll et al. 2011). In particular, photographic capture-recapture analysis has been used to estimate the size of the Bering-Chukchi-Beaufort Seas (BCB) population of Bowhead Whales (da Silva et al. 2000; Schweder 2003; da-Silva et al. 2003; da-Silva and Tiburcio 2010; Koski et al. 2010a; Schweder et al. 2010) and these estimates have been similar to those provided by the ice-based visual count surveys (da Silva et al. 2000; Schweder 2003; George et al. 2004; Koski et al. 2004; Schweder et al. 2010). In this paper, we evaluate the potential for photographic studies to provide data that would permit estimation of the size of the EC-WG Bowhead Whale population and provide ancillary life-history information that is useful for the management of Bowhead Whale harvests.

METHODS

Bowhead Whales acquire permanent scars from encounters with ice, Killer Whales (Orcinus orca), Polar Bears (Ursus maritimus), ropes, fishing gear and other sources (Rugh et al. 1992a, 1998; George et al. 1994; Higdon and Ferguson 2010). Vertical aerial photography generally provides the best view of these markings and has been used during numerous studies of the BCB Bowhead population (Koski et al. 1993, 2006a, 2008; Angliss et al. 1995) and a few studies on the EC-WG population (Finley 1990; Cosens and Blouw 2003). Vertical photographic studies should follow the methods of Angliss et al. (1995) and Koski et al. (1992, 2006a, 2008). Photographs are taken through a camera port in the floor of a suitable aircraft such as a Twin Otter using a medium format, hand-held camera or high-resolution digital 35 mm camera which is held vertical to the water surface. A radar altimeter is used to determine the altitude above sea level at the instant that a picture is taken and a Global Positioning System records the precise location. Calibration targets are used to scale the whale images to actual whale size (Koski et al. 2006a; Mocklin et al. 2010).

In addition to aerial photography, photographs have been taken during vessel-based surveys that can contribute to re-sighting histories of EC-WG Bowhead Whales (Finley 1990; Higdon and Ferguson 2008a, b). The vessel-based photographs do not provide consistent imagery of most regions of a whale, but if particular regions of the whale that are frequently captured in photographs are used for determining whether a whale is marked or not, then they can be used to provide sighting histories that supplement the vertical aerial photographs.

The best opportunities to photograph EC-WG Bowhead Whales are in (a) the spring staging areas (April to early July) where they concentrate along ice edges or in the pack ice before moving to the summering areas, and (b) the mid-to-late summer feeding areas (August to mid-September). An ideal survey design would incorporate
sampling in both of these settings each year.

Aerial Photographic Surveys in Spring Staging Areas

Three spring concentration areas have been documented where EC-WG Bowhead Whales could be photographed successfully. The first is along the ice edge near Igloolik where large numbers of Bowhead Whales congregate in late spring to early summer (early June to early July) before they gain access to summering areas in the central High Arctic through Fury and Hecla Strait (Figure 1) (Dueck et al. 2006; Higdon and Ferguson 2008a). This location is near logistics centres at Igloolik and Hall Beach and large numbers of vertical aerial photographs could be obtained during a study based there. Unlike vessel-based surveys, which could not be conducted during heavy ice conditions, aerial photography would be minimally affected by ice cover, provided that the ice edge remains intact to prevent Bowhead Whales from dispersing farther north through Fury and Hecla Straits. In fact, presence of ice tends to result in better-quality photographs because ice dampens waves, thus lowering the sea states.

The second spring concentration area is in the pack ice at the entrances of Pond Inlet and Lancaster Sound. Bowhead Whales congregate in the pack ice in that area during June before they enter Lancaster Sound or move south to summering areas along eastern Baffin Island (Davis and Koski 1980; Koski 1980; Heide-Jørgensen et al. 2006). The logistics base for photography in this area would be Pond Inlet.

The third spring aggregation area is Disko Bay, West Greenland, where during some spring seasons up to 1200 Bowhead Whales, but more commonly 150-200, are observed during April and May (Heide-Jørgensen et al. 2007). The Bowhead Whales that occur in and around Disko Bay are primarily adult females (Laidre et al. 2007; Heide-Jørgensen et al. 2010), which tend to be well marked (Miller et al. 1992; Rugh et al. 1992b, 1998) and so are particularly valuable for capture-recapture studies. The logistics base for this area would probably be either Ilulissat or Kangerlussuaq.

Figure 1. Areas where concentrations of Bowhead Whales are known to occur during spring and late summer (from various sources of published and unpublished data).
Aerial Photographic Surveys in Summing Areas

Aerial photographic surveys of the main summering areas of the EC-WG Bowhead Whale population could also provide large numbers of photographs. The weather conditions tend to be favourable for conducting photography during the mid-to-late summer and summering areas are relatively well known from surveys conducted in the 1970s (Koski 1980; Davis and Koski 1980) and in 2002-2004 (Dueck et al. 2008). One or two aircrafts could move between the areas shown in Figure 1. These photographs could be supplemented with photographs taken during other marine mammal surveys such as Narwhal (Monodon monoceros) and Beluga (Delphinapterus leucas) surveys in the Canadian Arctic (Richard et al. 1994, 2010; Innes et al. 2002).

There are two main summering areas where photography is recommended because large numbers of Bowhead Whales are regularly present, and three secondary summering areas where smaller numbers of whales are present. Photographs could be obtained in all of these areas from August to mid-September.

The first main summering area is in Prince Regent Inlet and the Gulf of Boothia where large numbers of Bowhead Whales were seen during the 2002-2004 surveys. The second area is the nearshore area along southeastern Baffin Island at and south of Isabella Bay, which was identified by Koski (1980) and Finley (1990). Large numbers of adult Bowhead Whales are seen there.

The secondary summering areas are (a) Admiralty Inlet, (b) Eclipse Sound and Milne Inlet, and (c) Cumberland Sound. The use of these areas is more variable than the main summering areas and numbers of Bowhead Whales present is usually smaller, but in some years, large numbers of them can be found. For example, Dueck et al. (2008) estimated that more than 2000 Bowhead Whales were present in Eclipse Sound and Milne Inlet in 2002, but they saw none in 2004.

Boat-based Photographic Surveys

Boat-based photographic studies were conducted in northern Foxe Basin in the 1990s (Weins 1998) and in 2007 and 2008 (Higdon and Ferguson 2008a, b). Large numbers of photographs were obtained but the number of images of matchable quality was relatively small because the same region of the whale was not visible on all of them. Nonetheless, photographs from boat-based surveys conducted during the same year as an aerial photographic survey could contribute “capture” histories for use in generating the population estimate. Boat-based photographic studies with the help of people from the local communities have the added advantage of incorporating local and traditional knowledge and giving the resultant abundance estimates more credibility at the local level.

Collecting and Processing Images

The methods for analysing the photographs would be the same as those used in studies of the BCB population (Koski et al. 1992, 2006a; Rugh et al. 1998; Zeh et al. 2002). All photographs would be cropped to a uniform size (12.5×17.5 cm), labelled, and stored on hard drives. Calibration targets would be photographed in the field to scale digital images to true body length as described by Koski et al. (1992, 2006a) and Mocklin et al. (2010). Whale measurements would be taken from uncropped Tag Image Files (TIFFs) created from the raw digital files. All photographs taken each year would be examined to identify within-season duplicate images. All images would be scored for identifiability and image quality as described by Rugh et al. (1998) and Zeh et al. (2002). Between-year matches would be identified with the aid of a computer-assisted matching program (Hillman et al. 2008). The data for each image would be entered into a standard database in the same manner as has been done for the BCB photographs, with each image having a unique identifier and all images of a given Bowhead Whale having the same whale number.

Number of Photographs Needed

The precision of a capture-recapture estimate of the EC-WG Bowhead Whale population would depend on the number of photographs that are obtained and the size of the population. Thus, in order to estimate the number of photographs required in each year of the study, a range of plausible population sizes must be assumed.

Several estimates of population size can be made using the existing estimates even though many are estimates of only part of the population. Using a strip transect survey, and accounting for detection and availability bias, Koski et al. (2006b) estimated that there were 1549 Bowhead Whales in areas surveyed in Hudson Strait and off West Greenland in late March of 1981, and noted that 92% of Bowhead Whales sighted during an extensive survey effort in the winter of 1981, which covered most of the potential Bowhead Whale wintering habitat, were in those two areas. Allowing for the sightings made outside Hudson Strait and West Greenland gives a total population estimate of 1684 whales. Assuming a rate of increase of 1.034 as has been reported by Zeh and Punt (2005) for the BCB population gives a 2012 estimate of 4747 whales in the EC-WG population. This estimate is likely biased low because the BCB population was experiencing an offtake rate of 0.5% per year from hunting and the EC-WG population was not hunted regularly until 1996 and recent removal rates of zero to about seven whales per year (e.g., IWC 2012) have probably been much lower than 0.5%.

A second estimate of population size can be made by assuming
Table 1. Expected recaptures in Year 2 given the actual population size in 2012 with 50, 100, 150 and 250 photographs of marked whales being obtained in each of Year 1 and Year 2. The estimated number of marked whales and the 95% CI are calculated using the method of Chapman (1951). It is assumed that 0.2897 of the whales photographed would be marked based on the proportion from the BCB Bowhead Whale population (Koski et al. 2010a). The numbers in parenthesis in the last column are negative.

<table>
<thead>
<tr>
<th>Actual 2012 population size</th>
<th>Number of marked Bowhead Whales photographed each year (2 years)</th>
<th>Expected recaptures in Year 2</th>
<th>Estimate of number of marked Bowhead Whales</th>
<th>95% CI of estimate</th>
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<td>4750</td>
<td>50</td>
<td>2</td>
<td>866</td>
<td>66 - 1666</td>
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<td>100</td>
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<td>1274</td>
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<td>2600</td>
<td>(934) - 6134</td>
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<tr>
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<tr>
<td></td>
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<td>4559</td>
<td>1031 - 8087</td>
</tr>
<tr>
<td></td>
<td>250</td>
<td>11</td>
<td>5249</td>
<td>2532 - 7967</td>
</tr>
</tbody>
</table>

Figure 2. Estimates of the number of marked whales in the EC-WG Bowhead Whale population and their confidence intervals in relation to the number of photographs obtained. Numbers above the confidence intervals are expected number of recaptures. See Table 1 for derivation of these estimates.

that the 999 adult female Bowhead Whales estimated by Wiig et al. (2011) to have used spring concentration areas along West Greenland represents the entire adult female segment of the population. Koski et al. (2006a) estimated that adult Bowhead Whales make up 0.3975 of the BCB population. If one assumes that the EC-WG population is at a similar point on its recovery trajectory towards equilibrium (and thus has essentially the same age composition as the BCB population) and the sex ratio is 50:50, then adult females would make up 0.1988 of the EC-WG population, which would have been 5026 Bowheads in 2010. Allowing for an assumed 3.4% rate of increase from 2010 to 2012 results in a 2012 population size of 5374.

As mentioned earlier, the IWC (2009b) currently uses an estimate of population size of 6344 (95% CI 3119 – 12906) for interim management decisions based on data from aerial surveys conducted in summer 2002. If that estimate were incremented by 1.034 per year, then the 2012 population size would be 8863. The Scientific
Committee considered it likely that the 6344 estimate was negatively biased, so presumably the same would apply to estimates derived from it.

Dueck et al. (2008) provided the highest estimate to date of the EC-WG population, which was 14400 (95% CI 4811 – 43105). Although that estimate was rejected by the IWC Scientific Committee (2009b) for a number of reasons (see IWC 2009a, page 179), it needs to be considered when setting upper bounds on the options for assessing the number of marked Bowhead Whales that would need to be photographed to get a reliable mark-recapture estimate. Accounting for assumed population increase from 2002 to 2012 gives an estimated central estimate of population size of about 20100 whales which has been rounded to 20000 in Table 1. In addition, a 2012 population estimate of 13500 Bowhead Whales has been included in Table 1 to represent an approximately midpoint compromise between the IWC-accepted estimate and Dueck et al.’s (2008) estimate.

The data in Table 1 show that by increasing the number of marked Bowhead Whales photographed, a more precise population estimate, or one with a tighter confidence interval, will be obtained and that a larger actual population size will require a greater number of photographs of marked individuals to obtain a reliable estimate of population size (Figure 2). Table 1 also shows that a low number of recaptures tends to produce a negatively biased population estimate and that a minimum of about 5-7 recaptures is required to avoid seriously biased estimates. Given the range of uncertainty in the population size, the survey should attempt to obtain at least 150 marked whales, or about 500 photographs of different whales, each year. This number of photographs should be achievable because we obtained photographs of 77 different marked Bowhead Whales during 2 days of photography in Isabella Bay in 1986 and 21 photographs of different marked whales during 2 days of photography in Isabella Bay in 1987 (Finley 1990). Since then, the population is believed to have more than doubled. Also, whales are more concentrated and more consistently found in their spring staging areas.

**Computing Population Estimates**

Population estimates would be calculated using the methods of Koski et al. (2010a). An estimate of the number of marked whales would be made using a closed population model for capture-recapture data (Huggins 1989, 1991) as implemented in Program MARK (White and Burnham 1999). A simple model with no covariates would likely produce the most precise estimate unless a very large number of photographs and recaptures were obtained (Koski et al. 2010a). However, other models would be investigated to find the best model for the data.

To estimate the size of the EC-WG population from the number of marked Bowhead Whales in the population, one must divide the estimated number of marked whales (N =) by the estimated proportion of the population that is marked (p*). Bowhead Whales acquire their markings throughout their life. Young or small whales are rarely marked whereas most large, old mature whales have some distinguishing marks (Rugh et al. 1992a, 1998). These marks are added at a very low rate (Koski et al. 1992, 2010a) and so whales classified as marked during the first sampling occasion, when the marked sample is defined, can readily be identified during the second when recaptures are sought. Because of the slow accumulation rate of scars, the proportion of the population that is marked is related to the population structure. Both the BCB and EC-WG populations of Bowhead Whales were severely reduced during the commercial whaling period (Bockstocoe and Burns 1993; Ross 1993; Woody and Botkin 1993; Zeh et al. 1993), and therefore, it is reasonable to assume that both populations have been increasing since the cessation of commercial whaling at rates at or near the theoretical maximum. The proportions of these two populations that are made up of immature and mature animals are likely similar. Given the large geographical range of the EC-WG population and the difficulty and cost of achieving complete survey coverage of that range in a single year, the photographic effort is, like the aerial transect survey effort, unlikely to obtain a fully representative sample of the population. Therefore, we propose to use the same value of p* that has been obtained for the BCB population (0.2897 in Koski et al. 2010a) to represent the proportion of marked whales in the EC-WG population. Although the BCB and EC-WG populations may be at different stages of recovery from commercial whaling, the BCB population, which Brandon and Wade (2007) suggested may be approaching carrying capacity, appears to be closer to its pre-whaling size than the EC-WG population, although admittedly the pre-whaling size of the EC-WG population is not well known. Thus the true p* for the EC-WG population, if it differs significantly from that of the BCB population, would probably be lower and population estimates made using the higher BCB value of p* would be conservative (negatively biased). The uncertainty in the estimate of p* is likely to be much smaller than the uncertainty associated with aerial surveys of different parts of the population’s range at different times.

Two values of p* have been calculated by Koski et al. (2010a) from BCB photographic data collected over several years. These multi-year values are considered more reliable than any single-year value because the Bowhead Whale migration past Barrow in spring is size- (age-) structured, and gaps in coverage due to weather and other factors may bias calculation of the proportion of marked whales using data from a single year. Biases are minimized by using data from several years. The proportion of the BCB Bowhead Whale population estimated to have been marked during 1984-1987 was 0.33937 (SE 0.01225) and during 1989-2004 it was 0.28968 (SE 0.0070) (Koski et al. 2010a). There is a non-significant negative correlation in yearly values of p* from 1984 to 2004 (r = -0.057, P<0.01). A declining value of p* is consistent with an
increasing population size (i.e., more young unmarked animals are being added to the population).

To quantify the potential range of values of $p^*$ for the EC-WG population, we used the photographic data from the 1984-2004 BCB studies near Barrow to create a time series of estimates of $p^*$ with 95% confidence intervals using the bias-correcting procedures described in Koski et al. (2010a) and data from each year separately (Figure 3). This approach produces wider confidence intervals for $p^*$ since an estimate of $p^*$ based on several years of photographs is likely to be more accurate as well as more precise: year-to-year biases average out when several years of data are used.

The methodology of Koski et al. (2010a) would be followed to

<table>
<thead>
<tr>
<th>Problems</th>
<th>Photography</th>
<th>Aerial surveys</th>
</tr>
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<tbody>
<tr>
<td>Whales move between areas during survey</td>
<td>Samples of photographs are nearly random if there are movements of whales between areas within or between sampling periods. Individuals moving between areas will be identified and accounted for.</td>
<td>Reduces reliability of estimate because some whales may be missed and others could be counted more than once if movements occur during the survey period.</td>
</tr>
<tr>
<td>Weather is bad</td>
<td>Reduced number of photographs but population estimate still possible by continuing the survey longer or by continuing the survey the following year.</td>
<td>If the survey is not completed within a short period of time, the estimate is a partial estimate and cannot be combined with later surveys because whales move among areas.</td>
</tr>
<tr>
<td>Ice cover is high</td>
<td>Whales are more difficult to find when ice is heavy but seas are dampered and quality of photographs is good. Once whales are found they tend to be easier to photograph in ice than in open water.</td>
<td>Whales are difficult to see in heavy ice, reducing the number of sightings and widening confidence intervals of estimates. Correction factors are very different for whales in ice and open water and are often not available or sample size is reduced when different correction factors are required for different habitats and age classes.</td>
</tr>
<tr>
<td>Cannot cover entire range of the population during the survey</td>
<td>Not a serious problem if there is mixing between sampling periods.</td>
<td>Results in negative bias in estimate. Cannot be accounted for.</td>
</tr>
<tr>
<td>Whales are segregated by age and sex classes and by reproductive state</td>
<td>An estimate of the proportion of population that is marked is needed. The probability of an animal being marked depends on its size (age). If the proportion marked comes from the survey photographs, then photographic effort must be proportional to the number of animals in each area. If that number is generated from outside data, then there is less concern about proportional sampling</td>
<td>Survey effort must be uniform throughout the range to avoid biased estimate. An alternative is to have separate survey designs for each area but the CV tends to be larger then because small numbers of sightings go into each individual estimate. Correction factors should be established for different age and sex classes from satellite tagged whales.</td>
</tr>
<tr>
<td>Qualified scientists are required to conduct the study</td>
<td>The required skill level is higher for conducting photographic surveys, but a much smaller crew (2-3 people, 1 photographer and 1-2 data recorders/observers) can conduct the entire survey</td>
<td>A large number of experienced observers are needed for a short period of time because all parts of the range need to be surveyed during a short time period</td>
</tr>
</tbody>
</table>
calculate population estimates $N = N^* / p^*$ and their estimated variances. The estimated variances can be obtained via either a delta method calculation or a bootstrap procedure. In the former case, confidence intervals can be obtained as recommended by Burnham et al. (1987) and Buckland (1992), and, in the latter case, from percentiles of sorted bootstrap values of $N$ (Buckland and Garthwaite 1991). The bootstrap confidence limits may be more reliable because they do not depend on the simplifying assumptions used to obtain the delta method variance for $N$ and the corresponding confidence limits.

**DISCUSSION**

Two years of aerial photographic surveys in the major spring aggregation areas and summering areas of the EC-WG Bowhead Whale population could provide an unbiased estimate of population size. This is something that aerial transect surveys are unlikely to be able to provide because (a) the large size of the summer range of this population, and (b) the poor weather conditions, which frequently interrupt surveys before they are completed, preclude complete coverage in a single year. In addition, confidence intervals of estimates from photographic surveys are likely to be narrower than those of estimates from transect surveys. For example, the 2002–2004 transect surveys of the EC-WG population were conducted over three seasons and the estimate of 14400 whales had lower and upper 95% bounds of 4811 and 43105 (Dueck et al. 2008) while the estimate of 12631 for the BCB population based on photographic surveys (Koski et al. 2010a) had lower and upper bounds of 7900 and 19700. However, Table 1 indicates that the level of precision of photographic mark-recapture estimates may not be better than that of transect survey estimates if they are only two years of photographic survey effort and the number of recaptures is small because the population is larger than expected. On the other hand, Koski et al. (2010a) showed that the precision of their 2004 estimate for the BCB population increased by including surveys in a third season, even though the effort in the third season was much lower than the first two seasons. The increased precision was a result of an increased number of different “captured” and “recaptured” whales when the third season was included. Inclusion in the analysis of photographs from vessel-based survey effort and from other researchers can also increase precision of the mark-recapture population estimate. Thus co-ordination and co-operation among the various researchers working in Canada and Greenland would be expected to improve estimates from dedicated aerial photographic surveys.

Aerial and vessel-based photographs of EC-WG Bowhead Whales have been obtained during previous studies (Finley 1990; Heide-Jørgensen and Finley 1991; Cosens and Blouw 2003; Higdon and Ferguson, 2008a, b) and during recent surveys in the Disko Bay area in the spring, such as those reported by Heide-Jørgensen et al. (2007). After the first few photographic surveys have been completed and the catalogue of EC-WG Bowhead Whale photographs has grown in size, it would be possible to obtain a future estimate of population size from a single survey using the models developed by Schweder et al. (2010). Other key population parameters such as rates of population increase and survival could also be estimated from the Schweder et al. (2010) modelling approach. The precision of population estimates and other life history parameters estimated using Schweder et al.’s (2010) model increases as the number of photographs in the overall database increases (Schweder and Sadykova 2009). Unlike aerial transect surveys, which are useful only for estimating the number of animals present in the survey area at the time of the survey, each photographic survey contributes to future estimates and results in improved precision.

Table 2 summarizes some of the benefits and shortcomings of using aerial photographic studies compared to aerial transect surveys for estimating the size of the EC-WG Bowhead Whale population. An additional benefit of conducting aerial photographic studies rather than aerial transect surveys to estimate population size is that life history information can be obtained from analyses of photographs. The life history information is not obtained from transect surveys. Photography projects conducted in the Beaufort and Chukchi Seas intermittently from 1981 to 2005 have provided much of the life history information that is available on the BCB Bowhead Whale population. This includes estimates of individual growth rates, adult survival, length-frequency distribution of the population, year-to-year timing of migration by individual whales, calving intervals, proportion of calves in the population, and first-year calf survival (Nerini et al. 1984; Koski et al. 1992, 1993, 2006a, 2008, 2010a, b; Miller et al. 1992; Rugh et al. 1992b, 2009; Zeh et al. 1993, 2002; Angliss et al. 1995; da-Silva et al. 2007).

The widely reported observation of a Gray Whale (Eschrichtius

![Figure 3. Time series of values of $p^*$ showing forward projected values and 95% probability limits using the method of da-Silva et al. (2011) based on 1984-2004 data reported in Koski et al. (2010a). No surveys were conducted in 1988, 1993, and 1995-2002, and the data shown are the forward projected values based on the previous and next year with data.](image)
robustus) in the Mediterranean Sea in 2010 has been interpreted as an indication that reduced sea ice in high latitudes is allowing more frequent inter-basin movements by whales (Scheinin et al. 2011). Heide-Jørgensen et al. (2011) showed that satellite-tagged Bowhead Whales from the BCB population have entered an area previously thought to be visited only by EC-WG Bowheads, and George and Bockstoce (2008) documented a likely case of a whale that was originally struck in Baffin Bay and later killed in the southern Chukchi Sea. Since Bowhead Whales are considerably more “ice-adapted” than Gray Whales, the movement of Bowheads in either direction through the Northwest Passage may be more common now than it was historically and it is likely to become more so with the expected ongoing climatic amelioration. Thus, it will be important at some stage to compare photograph catalogues of Bowhead Whales from the Pacific and Atlantic sectors of the Arctic to estimate the rate of exchange. If such comparisons are not made, estimates of the EC-WG population could be overestimated because at least part of the survey area contains individuals from the BCB population. The studies proposed in the present paper would add a large number of new photographs to the relatively small existing collection of EC-WG photographs, and thus improve estimates of exchange rate and reduce any positive bias introduced by overlap in the ranges of the two populations.

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