Bowhead Whales in the Eastern Arctic, 1611–1911: Population Reconstruction with Historical Whaling Records*

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ABSTRACT

As early as 1611 Bowhead whales resident between the east coast of Greenland and the island of Spitzbergen were the subject of intensive commercial hunting effort by Dutch, German and British whalers. By 1911 there was no significant, permanent population of Bowhead whales living in these waters. To understand the relationship between the commercial exploitation of the Bowhead and their eventual extinction we must determine the chronology of their decline, starting with an estimate of the initial, pristine stock size. In this paper we compare and contrast four methodological approaches that can be used to estimate the Greenland–Spitzbergen Bowhead stock size prior to, and during, commercial exploitation. Using species-specific biological parameters, a delayed-difference recruitment model, and historical whaling records, we reconstruct the Greenland–Spitzbergen Bowhead population throughout the period of human predation. We estimate that there were approximately 52,500 adult Bowhead whales resident in the waters between the east coast of Greenland and the island of Spitzbergen in 1611.

KEY WORDS

Bowhead whales, historical whaling records, marine mammal population estimation

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1. INTRODUCTION

The estimation of marine mammal stock sizes prior to human predation, and the chronological pattern of their decline, is of more than historical interest. For the purposes of modern policy assessment the identification of species 'at risk', 'threatened', or 'endangered' is often a function of current population size, recent changes in population size, and current population size as a proportion of the pristine population size. As a result, there has been considerable research effort directed towards the derivation of pristine population estimates using historical data for a wide variety of marine mammal species.[1] The Bowhead whale (Balaena mysticetus), also known as the Arctic Right whale, or the Greenland Right whale, has been of particular interest in this regard due to its long history of commercial exploitation, its relatively small current stock sizes, and the persistence of a debate surrounding the International Whaling Commission's sanction of an aboriginal subsistence hunt, despite the maintenance of a ban on all commercial exploitation. The objective of this paper is to map out the pattern of decline in the Greenland–Spitzbergen eastern Arctic Bowhead whale population from its pristine level in 1611, to virtual extinction in 1911. In an effort to accomplish this objective we compare and contrast four methodological approaches that can be used to estimate whale populations using historical whaling records. We consider models based on exponential, logistic, and Schaefer growth functions. To derive our population estimates we use species-specific biological parameters taken from studies of the current stock of Bowhead whales resident in the Bering Sea, with a comprehensive annual series of nation specific harvest figures, and a delayed-difference recruitment model with a slightly adapted Schaefer growth function. In contrast to the relatively low pristine population estimates generated with models using variants of the exponential growth function, we estimate that the initial adult population of Greenland–Spitzbergen stock of Bowhead whales was approximately 52,500.

Bowhead whales were one of the first whale species to face intense commercial exploitation by European hunters. The Bowhead were prized by commercial whalers because they were relatively slow and docile, their bodies floated when killed, and they frequented narrow stretches of open water between ice flows. These features made this species relatively easy to capture. In addition, Bowhead whales are baleen, rather than toothed, whales. As such, during the seventeenth, eighteenth and nineteenth centuries the capture of a Bowhead whale produced two marketable products: whale oil and whale bone.[2] Prior to human predation there were five geographically distinct, permanent, and robust Bowhead stocks: the Sea of Okhotsk stock, the Bering Sea stock, the Hudson's Bay stock, the Davis Strait stock and the Greenland–Spitzbergen stock.[3]

For more than 300 years a substantial proportion of European whale products were extracted from eastern Arctic Bowhead stocks. As early as 1536 Basque whalers pursued the Bowhead whale in the waters of Grand Bay and the Strait of Belle Isle, off the coast of Labrador. During the first two decades of the seventeenth century Dutch, German, French, Basque and British whalers began to hunt Bowhead whales from shore based stations on the island of Spitzbergen. By 1650 all other European nations had abandoned the industry, leaving the Dutch to maintain the only significant commercial whaling industry in Europe. Dutch vessels participated in a seasonal pelagic hunt along the east coast of Greenland and in the north Atlantic between Greenland and Spitzbergen. In 1719, with the Dutch enjoying a virtual monopoly in the production of whale products for the European market, effort was diversified towards the west coast of Greenland and into the Davis Strait. Thirty years later Dutch whalers were beginning to face increasing competition from British, and to a lesser extent, US vessels. By 1780 the British had assumed the dominant position in the eastern Arctic Bowhead hunt, and by 1803 the Dutch abandoned the industry altogether. 1828 marked the end of regular, large scale hunting effort by commercial whalers in the eastern Arctic.[4] We can identify 1911, the year a British whaling vessel spent an entire season off the east coast of Greenland and did not sight, much less land, a single Bowhead whale, as the date of 'virtual extinction' for this stock.[5] Today, there is no substantial, permanent population of Bowhead whales in the waters between Greenland and Spitzbergen.[6]

In Section 2 we briefly discuss the available historical data on European commercial whaling that can be used to derive annual population estimates for the Greenland–Spitzbergen stock of Bowhead whales. In the third section we review and comment on methodological approaches that may be used to estimate pristine marine mammal population levels, including the models that have been used to derive estimates for the Greenland–Spitzbergen Bowhead stock. Section 4 contains a more detailed description of the delayed-difference recruitment model that we use to derive annual estimates of the Greenland–Spitzbergen Bowhead stock size between 1611 and 1911. In Section 5 we discuss the chronological pattern of decline in the stock and we briefly comment on the relationship between the observed changes in stock size and changes in the economic environment in which commercial exploitation was occurring. Section 6 includes a report on the results from sensitivity tests we have performed on exponential, logistic, and Schaefer population reconstruction models. The final section concludes.

2. HISTORICAL WHALING RECORDS

Throughout the seventeenth, eighteenth and nineteenth centuries European governments relied to a considerable extent on the taxation of ships and products that moved in and out of their domestic ports. As a result, harbour masters were required to keep careful records listing the ships and cargo that moved through the port facilities under their supervision, including whaling vessels and whale products. In addition, whaling ships' captains maintained logbooks that contain extremely detailed information, including the number of sailors employed, the number of whales captured, the location of whale captures, the value and quantity of products extracted from these whales and the routes travelled by the vessels.[7] We also have access to a substantial body of literature that reports prices for whale products throughout the 1611–1911 period from a wide variety of European markets. There is, therefore, a considerable amount of raw data describing early European commercial whaling. These raw data have been collected and published in a wide variety of sources and used to support an equally wide variety of research activities. Of interest to us here is the use of these data to estimate the size of the Greenland–Spitzbergen stock of Bowhead whales prior to, and during commercial exploitation.

It would be ideal if we had information on the age and gender of the Greenland–Spitzbergen Bowhead whales captured in each year, the quantity of food available for the whales in each year, information on environmental conditions that might have had an impact on the rate of natural increase in the population, and annual estimates indicating the density of other predators, such as Orcas or aboriginal hunters, and the presence of other competitors for the whales' food supplies. Unfortunately, we have none of this information. We must, therefore, construct our population estimates with the only information available to us – biological parameters taken from studies of the current stock of Bowhead whales resident in the Bering Sea, and information about the number of Greenland–Spitzbergen Bowhead whales captured by whaling vessels from the Netherlands, Germany, Britain and the United States (with some sporadic information from other nations) between 1611–1911.

To compile a comprehensive list of all Bowhead whales taken from the Greenland-Sptizbergen stock in each year we have used published figures documenting catch by nation, augmented with estimated figures to interpolate nation-specific catch information across missing years. Our estimates are based on information that is closely and positively correlated with the number of whales captured, including the number of ships participating in the hunt and the quantity of whale products brought to market.[8]

Between 1661 and 1803 we have used information on Dutch harvests from de Jong (1983) and Ricard (1787). For the first 50 years of commercial harvests from the Greenland–Spitzbergen stock (1611–1660) the Dutch industry was almost exclusively shore based, with whaling stations operating on the islands of Spitzbergen and Jan Mayen. Our catch figures for this earliest era are not as complete as they are for the post-1661 period, but where necessary we have estimated the number of whales caught by Dutch whalers based on the quantity of whale oil brought to the Amsterdam market.

For German harvest numbers we have again relied on de Jong (1983), who reported the number of whales captured by Hamburg vessels from 1661–1780, and all German vessels from 1780–1803. Assuming the relative size of the German whaling fleet outside of Hamburg was similar before and after 1780, we have scaled up the German catch figures to account for whales taken by vessels sailing from ports other than Hamburg prior to 1780.

Like the German catch figures, those available for the British industry are port specific during the earliest period. Lists of the number of voyages and total catch are available for the port of Hull from as early as 1733, but not for other British ports until 1814.[9] However, the British statement of trade specifically identifies products from the eastern Arctic whaling grounds (the 'fisheries'). During the period prior to 1814 the harvest information for whaling vessels from Hull has been scaled up in proportion to the national production of domestic whale products. On average, approximately 37 per cent of the total British production of whale oil originated in Hull during these years.[10]

In contrast to British effort, which became insignificant after 1828, US whalers did not begin to hunt intensively from the Greenland–Spitzbergen Bowhead stock until the stock was severely depleted late in the nineteenth century.[11] As a result, US harvest figures, taken from Ross (1979) and Starbuck (1964), are small through virtually all of the period of human predation.

After 1870 there was very little commercial extraction from the Greenland–Spitzbergen stock. Unfortunately, we have no catch figures for this period, and we have, therefore, estimated harvests using information on the number of voyages to the eastern Arctic by US and British whaling vessels. During the years for which they are available, we have also included harvest figures for other nations, such as Norway, Iceland, Spain and France.

Our aggregate harvest series (illustrated in Figure 1) sums our best estimate of total catch in each year for all participating nations throughout the period of commercial exploitation, 1611–1911. In addition to all of the available published catch figures, the series includes estimated catch figures for at least one nation during the years 1611–1660, 1733–1803, 1803–1813, and 1870–1911. According to our series, between 1611–1911 the Dutch accounted for approximately 65 per cent of the aggregate harvest taken from the Greenland–Spitzbergen Bowhead stock. We estimate that German whalers took approximately 14 per cent of the catch, British whalers 16 per cent, U.S. vessels captured less than one per cent, and all other nations accounted from the remaining five per cent of the aggregate harvest.

To determine if our aggregate harvest series is reasonable, we can compare it to the only other comprehensive series of catch figures for the Greenland–Spitzbergen Bowhead stock that is available. By decade between 1660–1911 Ross (1993, Table 13.1) reports raw catch figures for Dutch, German and British harvests from the Greenland–Spitzbergen Bowhead stock based on sources that are similar, but not identical to those we have used. In general, Ross's figures, which do not contain estimates to cover gaps in the series, reveal a chronological pattern of extraction that is very similar to the pattern in our series. More specifically, Ross identifies peak harvest decades for the Dutch, Germans and

British that are identical to our peak harvest decades for these nations: 1680–1689, 1670–1679 and 1810–1819, respectively. However, because Ross begins his series in 1660, after 50 years of commercial exploitation, and because Ross makes no effort to estimate missing harvest figures, his cumulative total catch from the Greenland–Spitzbergen stock is only 90,740. Our cumulative total catch is 32.8 per cent higher (120,507) over the entire 1611–1911 period, and 18 per cent higher (107,070) over the matching 1660–1911 years.

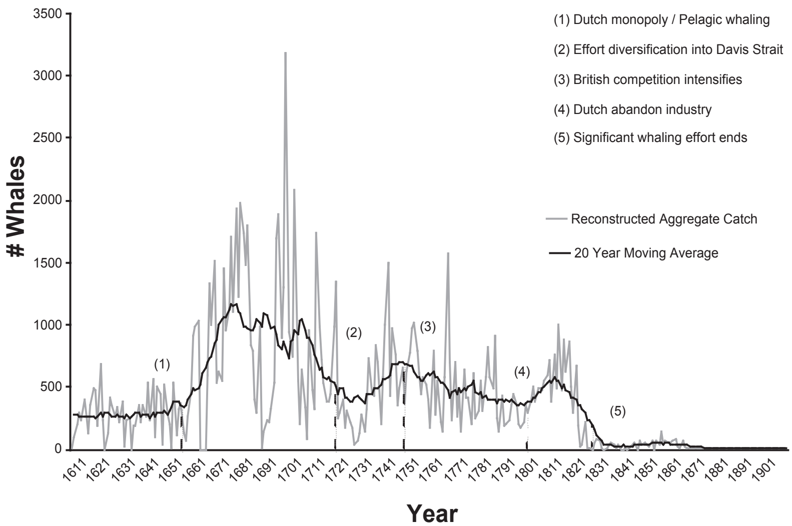

FIGURE 1. Reconstructed aggregate harvest from Greenland–Spitzbergen stock

In Figure 1 we have included a 20-year moving average of our harvest series to emphasise the long run trends in the catch figures. The smoothed series facilitates the identification of five distinct changes in the pace of commercial extraction. These changes coincide with changes in the economic environment in which the commercial industry based on the Greenland–Spitzbergen Bowhead operated. During the first phase of exploitation the industry was shore based and harvest figures were relatively low and stable. After 1650 the Dutch established a virtual monopoly in the production of whale products for the European market and they began large-scale pelagic whaling. During this phase harvest figures rose and became considerably more volatile. After diversification into Davis Strait in 1719 catch figures from the Greenland–Spitzbergen stock remained volatile, but fell on average. Although increased competition from British whalers pushed up harvest numbers after 1750, there was an even more dramatic increase in harvests as the British came to dominate the hunt between 1780 and 1828. It appears that something significant happened to the stock in the late 1820s when catch figures dropped precipitously and never recovered.

3. METHODOLOGICAL APPROACHES AND PRISTINE STOCK ESTIMATES

It is possible to derive estimates of pristine marine mammal populations that do not rely on historical catch records. Recently Roman and Palumbi (2003) have used models based on genetic diversity and the rate of mitochondrial DNA sequence variation to estimate initial population sizes for Humpback, Fin, and Minke whales in the north Atlantic. Their estimated pristine population sizes are considerably larger than other published estimates for these stocks. We cannot contrast our population estimates with figures derived using these rapidly evolving genetic models because no estimates using these techniques have yet been published for eastern Arctic Bowhead whale populations. Even if estimates using Roman and Palumbi's approach were available for the Greenland–Spitzbergen stock, it is not clear that the calibration of their genetic models is any more reliable than the calibration of even fairly complicated reconstruction models that rely on historical whaling records. It seems likely that future pristine population estimates using these genetic modelling techniques in support of research based on historical whaling records may be of considerable value. However, at this time marine mammal population reconstruction based on basic species-specific biological parameters, simple growth models, and the abundant historical information on harvests remains both a dominant and a desirable approach.

There are a number of techniques that rely on a historically intensive, but biologically sparse approach to derive estimates of pristine whale populations – that is, the population size immediately before commercial exploitation by Europeans. For the Greenland–Spitzbergen Bowhead stock the range in these estimates is both large and dependent on methodological choice. Mitchell (1977) estimates that the pristine Greenland–Spitzbergen Bowhead stock size was approximately 26,000. This estimate has been accepted by the International Whaling Commission and by other authors studying the eastern Arctic ecosystem from a biological, ecological, and economic perspective.[12] Using a more transparent model Woodby and Botkin (1993) confirmed Mitchell's estimate when they reported a pristine population figure of approximately 24,000. The most recent estimate, by Hacquebord and Leinenga (1994), raised the pristine population figure to 46,000 using an approach similar to Woodby and Botkin's with a much longer harvest series. In this paper we argue that the pristine Greenland–Spitzbergen Bowhead population was even higher still – approximately 52,500 adult whales in 1611.[13] Because the basic data used to derive these pristine population estimates are very similar, the differences are primarily a result of the choice of methodology and the exploitation period considered when constructing the estimates.

The first estimate of the pristine population of the Greenland–Spitzbergen Bowhead stock was made by Mitchell for the International Whaling Commission. He explains his methodology as follows:

> I propose to make a *first approximation* of initial population size in the following manner. First, to identify published statistics covering the peak of the fishery in the stock area, then sum the 10 peak years. Second, to examine the published information bearing on the estimation of loss rates in the fishery, especially for the peak period, and add to the 10 year sum of catches the additional number of animals estimated to have been struck but lost and presumed killed. This gives a *minimum estimate* of initial population size.[14]

Mitchell identified the peak period as 1679–1688, during which he calculated that 10,599 whales were taken by the Dutch. He estimated that an additional 2,553 whales were taken by Hamburg ships during this decade, resulting in a total of 13,152 whales captured. Allowing a further 20 per cent mortality for whales that died from harpoon wounds but were lost at sea (the loss rate), implies a total hunting mortality of 15,782 whales during the years 1679–1688. In addition, Mitchell (1977, 20) reasoned that, '…there must have been a substantial residual population on the order of 10,000 or more whales in 1689…' to account for the whales killed over the next two centuries. Mitchell's total estimate of the pristine stock was the sum of these two figures: 25,782. If we use our harvest figures and Mitchell's methodology, the estimate of the pristine stock would be only slightly lower: 25,001. It does not appear, therefore, that Mitchell's estimate depends critically on the harvest series used.[15]

The emphasis in Mitchell's procedure should be placed on 'first approximation' and 'minimum estimate'. His methodological approach relies on assumptions regarding biological parameters, but these assumptions are implicit in the choice of a residual population level in 1689. Indeed, such a small residual population, only 10,000 whales, could not account for the survival of the stock and the commercial industry into the twentieth century under any of the other, more transparent methodological approaches considered in this paper.[16] Any explicit discussion of the relationship between the biological characteristics of the Greenland–Spitzbergen Bowhead and the stock's ability to support 230 years of human predation must be conditional on the specification of a more transparent biological model.

In general, population reconstruction using historical whaling records cannot rely on stock-specific biological parameters because the stocks in question have often never been exhaustively studied, they may be small and difficult to study, or in many cases the stocks may be extinct. This implies that for most marine mammal population reconstruction we must rely on the most basic biological growth functions, with the fewest and least controversial parameters. There are three basic modelling procedures that may be used with historically intensive, but biologically sparse evidence: the exponential growth model, the logistic model, and the Schaefer model.

Woodby and Botkin (1993), and Hacquebord and Leinenga (1994) both use an exponential growth function in the construction of their pristine population estimates for the Greenland–Spitzbergen Bowhead. This modelling approach requires only one biological parameter – a constant rate of natural increase (the birth rate minus the death rate: $r = b - d$) that is independent of the size of the whale population. With an exponential model population (p_t) in year t increases to population p_{t+1} in the next year:

$$p_{t+1} = p_t + r\,p_t \qquad (1)$$

This model presupposes that all mortality is natural. To apply it to the history of a hunted species, hunting mortality h_t must also be subtracted:

$$p_{t+1} = p_t + r\,p_t - h_t \qquad (2)$$

Woodby and Botkin assume a rate of natural increase of 5 per cent[17], they use Ross's (1993) harvest series (augmented to allow for a loss rate of 20 per cent) covering the years 1660–1719. They then assume that in 1719, the year the Dutch diversified effort into Davis Strait, there were 1,000 whales remaining in the Greenland–Spitzbergen stock, and they iterate Equation (2) backwards from 1719 to 1660. They conclude that there were 23,973 Bowhead whales in the Greenland–Spitzbergen stock in 1660. If we use our harvest figures and Woodby and Botkin's methodology the pristine stock estimate would fall slightly to 19,134.

Woodby and Botkin do not explain why they only consider the years 1660–1719, nor do they justify their assumption that there were only 1,000 whales remaining in 1719. Ross's harvest series indicates that in the decade following 1719 there were 3,846 whales taken from the Greenland–Spitzbergen stock by Dutch and German vessels. Our harvest series indicates that there were 4,603 whales taken from this stock between 1720 and 1729. These post-1719 catch figures imply that the rate of natural increase after 1719 must have been far higher than 5 per cent if a residual stock of 1,000 whales supported a commercial hunt over the next 192 years.

Hacquebord and Leinenga further developed the exponential model by solving for the growth rate of the population:

$$\{(p_{t+1} - p_t) / p_t\} = r - (h_t / p_t) \qquad (3)$$

If the growth rate of the population is zero, then Equation (3) can be solved for p_t:

$$p_t = h_t / r \qquad (4)$$

This is the equation that Hacquebord and Leinenga use to calculate the pristine stock of Greenland–Spitzbergen Bowhead whales. They estimate that between 1669 and 1800 103,973 whales were taken from the stock. At the start of their period they report that the average annual catch was 925.2 whales, but this average annual harvest fell by approximately 60 per cent between 1669 and 1800, such that by the end of their period the average annual catch was only 369.3 whales. Using these two figures to represent h_t in 1669 and 1800, with an assumed rate of natural increase equal to 2 per cent (r = 7 per cent birth rate less 5 per cent death rate), Hacquebord and Leinenga calculate that the pristine 1669 population must have been $p_t = 925.2 / 0.02 = 46{,}260$ whales, with a residual 1800 population equal to $p_t = 369.3 / 0.02 = 18{,}464$ whales.[18] Again, the harvest series does not seem to be a key determinant of their pristine population estimate – if our harvest series is used with Hacquebord and Leinenga's methodology the initial population estimate falls by only 2,332, to 43,928.

TABLE 1. Pristine Population Estimates

Author	Using Raw h_t	Using Allen and Keay h_t
Mitchell (1977)	25,782	25,001
Woodby and Botkin (1993)	23,973	19,134
Hacquebord and Leinenga (1994)	46,260	43,928
Allen and Keay	43,731	52,477

Note: Mitchell (1977) and Hacquebord and Leinenga (1994) derive their pristine population estimates using raw harvest figures that are very similar to Ross's (1993) series. Woodby and Botkin (1993) derive their pristine population estimate using Ross's (1993) harvest series. The Allen and Keay pristine population estimate reported under 'Raw h_t' uses the methodological approach described in Section 4 with Ross's (1993) harvest series.

It is not clear why Hacquebord and Leinenga assume that the commercial hunt ceased in 1800. According to our harvest series an additional 14,717 Bowhead whales were captured from the Greenland–Spitzbergen stock after 1800. There is also a more fundamental conceptual difficulty with Hacquebord and Leinenga's calculation. As the derivation makes clear, Equation (4) indicates the harvest that can be taken each year without a change in the stock. Hacquebord and Leinenga, therefore, have estimated the population level that can sustain an average harvest of 925 whales per year into perpetuity, rather than a pristine stock level.

This difficulty emphasises an unappealing feature of the exponential growth model used by both Woodby and Botkin, and Hacquebord and Leinenga. Because both birth and death rates are independent of population size, the exponential growth model predicts perpetual growth at the rate of natural increase in the absence of hunting. Unlimited growth is clearly inconsistent with the existence of a biological equilibrium within the Arctic ecosystem in which the pristine whale population is stable over the long run.[19] In his review of a selection of biological growth models Clark (1976) specifies, among other things, the mathematical conditions required for the presence of a stable pristine stock. These conditions are violated by the exponential growth models used by Woodby and Botkin, and Hacquebord and Leinenga.

The simplest model that can imply biological stability uses a logistic growth function, in which the rate of natural increase varies as the stock size varies.[20] Like the exponential growth function, the logistic growth function requires only one biological parameter – the rate of natural increase. With the logistic model the rate of population growth declines as the population approaches a maximum value:

$$\{(p_{t+1} - p_t) / p_t\} = r\,(1 - p_t / p_{max}) \qquad (5)$$

The left hand side of this equation is the growth rate of the whale population, while r on the right hand side is the rate of natural increase at the pristine population level, also known as the maximum environmental holding capacity (p_{max}). The actual growth rate drops to zero as the population approaches this maximum. The conventional representation of this relationship is obtained by multiplying Equation (5) by p_t :

$$p_{t+1} - p_t = r\,p_t - r\,p_t^2 / p_{max} \qquad (6)$$

Unlike the exponential model, the logistic model accommodates a stable pristine population, however, it also embodies peculiar assumptions about vital rates. To see the oddities substitute birth and death rates (b – d) for r in Equation (5):

$$\{(p_{t+1} - p_t) / p_t\} = b\,(1 - p_t / p_{max}) - d\,(1 - p_t / p_{max}) \qquad (7)$$

The left-hand side of this equation is again the population growth rate. The first term on the right side is the birth rate, the second term is the death rate. Each of these follows the logistic pattern with the rates at their highest values when the population is near zero. As the population expands to its maximum size, the rates fall to zero. But why should the rates follow this pattern? It is strange that natural mortality should be at its highest when the population is low and should then decline as the population expands and resource pressure increases. It is also strange to imagine that the birth rate would be at its highest when the population is small and then fall as the population expands and potential mates become more abundant. At the cost of a small increase in the number of required biological parameters the Schaefer delayed-difference recruitment model, and its variants, reinterprets and reorganises the variables in the logistic growth function such that these peculiarities are removed.

4. A DELAYED-DIFFERENCE RECRUITMENT MODEL

In a standard delayed-difference recruitment model, first employed in a fisheries context by Schaefer (1957), the difficulties associated with the logistic model are addressed by treating the death rate (d) as independent of population size, and the population (p_t) is explicitly interpreted to be the adult population. The death rate then becomes the natural mortality rate of adults, and births are 'recruits', that is the number of young reaching sexual maturity, assumed to be τ years of age. Recruitment can now be defined as births ($b\ p_{t-\tau}$) minus infant mortality ($b\ p_{t-\tau}^2 / p_{max}$), which increases with the population pressure on the resource.

$$p_{t+1} = p_t + b\ p_{t-\tau}\ (1 - p_{t-\tau} / p_{max}) - d\ p_t \qquad (8)$$

The changes involved in moving from the logistic model to the delayed-difference recruitment model produce an approach to population measurement with a long pedigree. This model is a 'Malthusian positive check model', in which the positive check arises from pressure on the resource base and operates through the infant mortality rate. Given the vulnerability of the young, this is an attractive simplification with which to approach the analysis of population growth. The cost associated with acquiring the more intuitively appealing features of Schaefer's delayed-difference recruitment model is the introduction of additional biological parameter requirements. To use this modelling approach we must identify birth and death rates separately, rather than simply knowing the rate of natural increase, and we must know the average age at which Greenland–Spitzbergen Bowhead whales reached sexual maturity.[21]

For most marine mammal species that require historically intensive population reconstruction methods the additional biological parameters needed for the Schaefer approach are not available. However, because the stock of western Arctic Bowhead whales has been studied in such detail, we have access to species-specific biological parameters. In fact, because we have access to this species-specific biological research, we may quite confidently move beyond the standard Schaefer delayed-difference recruitment model and add just slightly more complexity.

We have followed Conrad (1989) in making an adaptation to Schaefer's standard model prior to reconstructing the chronology of decline for the Greenland–Spitzbergen Bowhead population. Studies of large marine mammal populations indicate that recruitment functions are not symmetric parabolas with maximum growth achieved when population equals one half of the environmental holding capacity, but instead they are skewed, reaching peak recruitment closer to p_{max}. Studies of the Bering Sea stock confirm that this is the case for Bowhead whales. In particular, Equation (8) becomes:

$$p_{t+1} = p_t + b\ p_{t-\tau}\ (1 - (p_{t-\tau} / p_{max})^{\alpha}) - d\ p_t \qquad (9)$$

The recruitment term ($b\ p_{t-\tau}\ (1 - (p_{t-\tau} / p_{max})^{\alpha})$) and natural mortality term ($d\ p_t$) from this equation are graphed in Figure 2.[22] The new recruit function is almost symmetric – the skew introduced by the exponent α is apparent, but not prominent. The natural mortality function is a straight line that intersects the new recruit function at the pristine population size. This pristine population is stable because the number of new adults equals the number of natural adult deaths. It should be noted that the population of 107,000, at which the new recruit function intersects the horizontal axis, corresponds to p_{max} in Equation (9). p_{max} therefore, does not correspond to a population level that is ever realised – it is merely a parameter governing the position of the new recruit function.

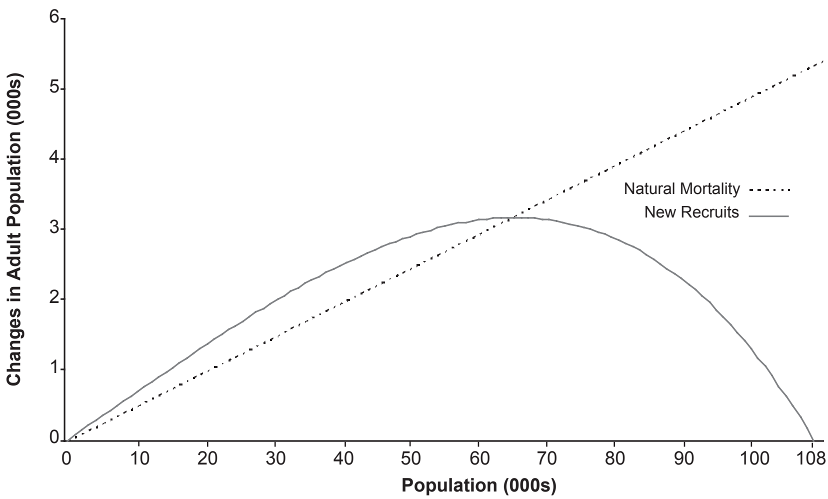

FIGURE 2. Delayed difference recruitment model

We can see from Figure 2 that the maximum sustained yield (the largest difference between the new recruit and natural mortality functions) is approximately 535 whales per year with the stock level equal to 38,000. This peak natural increase in the population is less than the average of 544 whales that were taken per year over the entire era of intensive exploitation (1611–1828) and considerably less than the 1,500 whales per year that were killed, on average, during the peak harvest decade (1680–1689).

The introduction of hunting mortality into our adapted Schaefer delayed-difference recruitment model is simply a reduction in population size in addition to natural mortality. Following other studies of the eastern Arctic Bowhead hunt, we assume a loss rate (Ω) in excess of the number of whales captured to allow for the 'ones that got away', but nonetheless died. The adapted Schaefer delayed-difference recruitment model we have used to reconstruct the Greenland–Spitzbergen Bowhead stock between 1611 and 1911, therefore, takes the form:

$$p_{t+1} = p_t + b\, p_{t-\tau}\, (1 - (p_{t-\tau} / p_{max})^{\alpha}) - d\, p_t - \Omega\, h_t \quad (10)$$

The biological parameters we employ in our population reconstruction have been compared to similar parameter estimates from a fairly wide range of northern whale stocks and species.[23] More specifically, we have assumed that b = 0.07, d = 0.05, α = 2.40, τ = 15, and Ω = 1.20. In Section 6 we discuss the results from sensitivity tests, in which we have derived pristine stock estimates using our delayed-difference recruitment model, the standard Schaefer model, the logistic model, and the exponential model under various assumptions regarding the rate of natural increase, the age at sexual maturity, the skewness parameter, the loss rate, the number of whales remaining in 1911, and the construction of the harvest series.

To produce annual population estimates we began in 1610 with an assumed pristine stock in long run biological equilibrium – determined by our choice of p_{max}. We then used our parameter estimates from the Bering Sea Bowhead stock and our comprehensive Greenland–Spitzbergen harvest series in Equation (10) to generate stock levels for every year until 1911. Under the assumption that there were 1,000 Bowhead whales remaining in the Greenland–Spitzbergen stock in 1911, we have calculated that prior to commercial exploitation by European whalers there were 52,477 adults in the pristine stock.

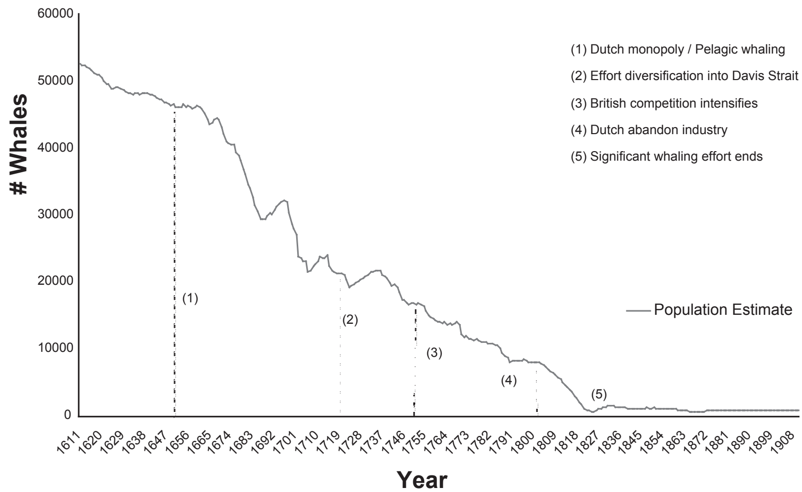

FIGURE 3. Greenland–Spitzbergen stock estimates

5. THE CHRONOLOGY OF DECLINE

Figure 3 plots our reconstruction of the Greenland–Spitzbergen stock of Bowhead whales from 1611–1911. We can see that the population faced depletion through virtually the entire period of human predation. We find that the only sustained period of stock expansion came immediately after the Dutch diversified effort into Davis Strait, but before the introduction of substantial British competition (1719–1737). This suggests that the commercial industry never entered a 'bio-economic equilibrium', in which the size of the stock, the whaling fleet, and economic profits could have been relatively stable. Similar to our exercise illustrated in Figure 1, we have noted five transition points on Figure 3 that indicate significant changes in the economic environment in which commercial exploitation was occurring.

During the period of shore based whaling (1611–1660) the stock fell relatively slowly. However, as the Dutch assumed a dominant position in the European industry and pelagic whaling became more common (1660–1719) catch levels rose and stock levels fell more rapidly. During this phase in the commercial hunt the stock was able to recover periodically as a result of disruptions in Dutch exploitation caused by military and naval conflicts in Europe: 1665–1667, 1691 and 1710, for example. The next commercial phase (1719–1750) was characterised by continued Dutch dominance of the European market for whale products and effort diversification that divided the Dutch fleet between the Greenland–Spitzbergen stock and the Davis Strait stock. This era includes the only extended period of positive growth for the Greenland–Spitzbergen stock, and more generally, depletion rates were considerably lower than their long run average. Unfortunately, the introduction of international competition for the Greenland–Spitzbergen stock (1750–1803) signalled a return to rapid stock reductions and the eventual demise of the Dutch commercial industry. After the Dutch abandoned commercial whaling in 1803, British, and to a lesser extent, US vessels continued to hunt from the Greenland–Spitzbergen stock. During this phase (1803–1828) the stock collapsed, falling from 7,888 adults to just over 1,134 in only 25 years. The final era of commercial exploitation (1828–1911) saw very few vessels pursuing the last remaining whales from the stock. During this period Bowhead whales were often taken as by-catch when commercial whalers were in pursuit of other whale species, walrus, and seals in the waters between the east coast of Greenland and the island of Spitzbergen.

6. SENSITIVITY TESTS

Our estimate of the pristine population of Greenland–Spitzbergen Bowhead whales is considerably larger than the other estimates available in the literature. To produce this estimate we have used an adapted Schaefer delayed-difference recruitment model that requires more biological parameters than the exponential, logistic, or standard Schaefer models. Because the Greenland–Spitzbergen stock has been virtually extinct for almost 100 years we cannot empirically verify that our parameters – derived from the current Bowhead stock resident in the western Arctic – accurately reflect the biological characteristics of the eastern Arctic Bowhead. Therefore, a potential weakness in our approach is the reliance on additional, untested parameter assumptions. Fortunately, relative to the other methodological approaches our pristine stock estimate is fairly robust to reasonable changes in the assumed parameters, the construction of the harvest series, and the assumed residual 1911 stock size. To illustrate the relative robustness of our pristine stock estimate, we have performed a series of sensitivity tests on our model, the exponential model, the logistic model, and a standard Schaefer model by varying the harvest series, each biological parameter, and the residual 1911 stock size, and recalculating pristine population levels.[24]

Because we have sought to construct a comprehensive harvest series for the Greenland–Spitzbergen stock, we have been forced to estimate the number of whales caught by some nations in some years over the 1611–1911 period. It may be that the estimates in our harvest series are an inaccurate representation of the number of whales actually taken from the stock during the relevant years. Because of the importance that the harvest series plays in all methodological approaches, this is potentially a serious concern. However, if we use the only other relatively comprehensive harvest series available, constructed by Ross (1993), then the pristine stock estimate derived using our adapted Schaefer growth function falls by only 16.7 per cent, from 52,477 to 43,731. To put this decrease in our 1611 stock estimate into context, if we derive pristine population figures for the Greenland–Spitzbergen Bowhead stock using the exponential, logistic or standard Schaefer models, then a switch from our comprehensive harvest series to Ross's series leads to a 82.6 per cent increase, 18.4 per cent decrease, and 20.4 per cent decrease, respectively, in the pristine stock estimates produced by these models.[25]

A further concern regarding our estimate of the number of whales taken from the stock in each year is the loss rate we employ. We have assumed that for every ten whales landed by Dutch, German, British and American whalers, two were killed but never recovered. Woodby and Botkin (1993, 393 and 401) report that for the Bering Sea stock the loss rate during the nineteenth century was approximately 24 per cent, but for the Greenland–Spitzbergen stock the loss rate over the years 1791–1822 was no more than 15 per cent. Our assumption of a 20 per cent loss rate lies between these two extremes. If we assume a loss rate of 25 per cent, our pristine stock estimate increases by only 4.2 per cent, to 54,659. If we assume a loss rate as low as 15 per cent, our stock estimate falls by 4.2 per cent, to 50,296. Again, our approach appears no more sensitive to changes in the loss rate than the exponential, logistic, or standard Schaefer approach, which experience increases in their pristine stock estimates of 3.3

per cent, 3.3 per cent, and 4.2 per cent, respectively, if we assume a 25 per cent loss rate. If we assume a 15 per cent loss rate, these models experience decreases in their pristine stock estimates of 4.2 per cent, 4.2 per cent, and 4.2 per cent, respectively.

Perhaps the most arbitrary assumption that all population reconstruction methods must make prior to the calculation of pristine stock estimates involves the residual stock size remaining at the end of the period of study. We have no way of knowing how many whales remained in the Greenland–Spitzbergen Bowhead stock when we assume 'virtual extinction' in 1911. Moore and Reeves (1993, Table 9.2) report that between 1940 and 1990 there have been only 37 confirmed Bowhead sightings east of Greenland and west of Spitzbergen. If we alter our assumption regarding the residual stock remaining in 1911 from 1,000 to 5,000, our pristine stock estimate increases by less than 1 per cent to 52,993. A reduction in the assumed end point from 1,000 adults to only 100 adults reduces our pristine stock estimate by 0.001 per cent to 52,424. If we use the exponential model, the difference in pristine population estimates resulting from a change in the assumed residual population from 5,000 to 100 is just 13 individuals. The difference for the logistic model is only 242, and the difference for the standard Schaefer model is 1,016.

The parameter that has the greatest impact on all of the methodological approaches used to estimate pristine stock levels is the rate of natural increase (r = b – d). This is not surprising given that the rate of natural increase determines the population's ability to recover quickly from human predation. For our delayed-difference recruitment model we assumed that the maximum birth rate was 7 per cent and the rate of natural mortality among adults was 5 per cent, for a maximum rate of natural increase of 2 per cent. This assumption is fairly standard in studies of northern whale species. However, Tillman, Breiwick and Chapman (1983) reconstruct the Bering Sea stock of Bowhead whales using assumed rates of natural increase between 0 and 4 per cent, and Woodby and Botkin (1993) assumed a 5 per cent rate of natural increase for their reconstruction of the Greenland–Spitzbergen stock. If we increase the rate of natural increase in our model from 2 per cent to 5 per cent, then our pristine population estimate falls by 36.4 per cent to 33,382. This pristine population estimate is still considerably higher than the figures reported by Woodby and Botkin, and Mitchell (1977). To reduce our pristine population estimate as low as 24,000 (approximately the pristine population estimates reported by Woodby and Botkin, and Mitchell) we would have to assume a rate of natural increase greater than 9 per cent. This rate of natural increase far exceeds any reasonable estimates available in the literature on the reproductive abilities of northern whale species. If we assume a rate of natural increase of only 1 per cent our pristine stock estimate increases by 24.7 per cent, to 65,417. Again, the adapted Schaefer delayed-difference recruitment model does not appear to be considerably more sensitive to changes in the rate of natural increase than the other models we consider – the pristine population figures derived using an exponential growth model fall by 72.9 per cent and increase by 107.0 per cent when we move to a rate of natural increase of 5 per cent and 1 per cent, respectively. For the logistic and standard Schaefer growth functions, the pristine population levels drop by 38.2 per cent and 29.9 per cent when we assume a 5 per cent rate of natural increase, and increase by 26.3 per cent and 16.7 per cent when we assume a 1 per cent rate of natural increase.

The exponential and logistic approaches do not distinguish between adult and immature whales in their population reconstruction. This implies that these two models do not require any explicit assumption regarding the age of sexual maturity (τ), and as a result their pristine stock estimates are unaffected by changes in our assumption regarding this biological parameter. The standard Schaefer, and our adapted Schaefer model, on the other hand, do explicitly distinguish between adult and immature whales, and therefore, do depend on τ. Although there is accumulating evidence indicating that Bowhead whales are remarkable for their longevity, there is still some controversy regarding the estimation of their typical life-span and the proportion of a typical population that has yet to reach adulthood. Conrad (1989, 983) assumes that western Arctic Bowhead whales enter adulthood at age five. Woodby and Botkin (1993, 397) report that Bowhead whales may not reach the age of sexual maturity until 10 years of age. Zeh et al. (1993, 476) increase this estimate to 14 years, and George et al. (1999, 577) identify an even higher age for sexual maturity; '…at least 15 years…with values favored by the data in the range of 15–24 years of age'. We have assumed that on average the Bowhead resident off the east coast of Greenland entered the adult population at age 15. If we increase the delay from birth to adulthood from 15 years to 25 years our pristine stock estimate falls by 13.2 per cent to 45,542. A decrease in τ in our model from 15 to five years raises our pristine stock estimate by 20.3 per cent, to 63,146. To put these figures into context, for the standard Schaefer model the pristine stock estimate decreases by 16.9 per cent if we increase the age of sexual maturity to 25, and increases by 25.5 per cent if we decrease the age of sexual maturity to five.

The final biological parameter we employ in our population reconstruction is the skewness parameter (α) on the new recruit function. This parameter is not used in the exponential, logistic or standard Schaefer models. It is, therefore, unique to our reconstruction approach, and as such, it is reassuring to find that our pristine population estimate is quite insensitive to fairly substantial changes in α. If we increase the skewness parameter from 2.40 to 2.80, our pristine stock estimate falls by only 1,387 individuals, or 2.6 per cent. If we decrease the skewness parameter from 2.40 to 2.00, our pristine stock estimate increases by 1,740, or 3.3 per cent.

TABLE 2. Sensitivity Testing

	Pristine Stock Estimate			
Parameters	Exponential	Logistic	Schaefer	Allen and Keay
h_t = Allen-Keay	**26,352**	**86,088**	**61,586**	**52,477**
= Ross (1993)	48,123	70,247	49,052	43,731
Ω = 15 per cent	25,254	82,503	59,028	50,296
= 20 per cent	**26,352**	**86,088**	**61,586**	**52,477**
= 25 per cent	27,230	88,956	64,144	54,659
p_{1911} = 100	26,349	86,046	61,586	52,424
= 1,000	**26,352**	**86,088**	**61,586**	**52,477**
= 5,000	26,362	86,288	62,424	52,993
r = 0.01	54,537	108,694	71,858	65,417
= 0.02	**26,352**	**86,088**	**61,586**	**52,477**
= 0.05	7,134	53,165	43,162	33,382
τ = 5	•	•	77,309	63,146
= 15	•	•	**61,586**	**52,477**
= 25	•	•	51,212	45,542
α = 2.00	•	•	•	54,217
= 2.40	•	•	•	**52,477**
= 2.80	•	•	•	51,090

Note: Parameters in **bold** have been used to construct our best estimate of the pristine stock of Greenland–Spitzbergen Bowhead whales.

The results from these six sensitivity tests indicate that our adapted Schaefer delayed-difference recruitment model is not sensitive to changes in the harvest series, residual population assumption, or biological parameters employed, relative to the other three methodological approaches considered in this paper. Under all sensitivity tests the ordering of the pristine population estimates from all four models remains unchanged, and in all but two cases (r = 0.05 and τ = 25 years) our pristine population estimate remains considerably larger than any of the other estimates available in the literature.

7. CONCLUSIONS

Our objective in this paper has been to provide a detailed description of our reconstruction of the Greenland–Spitzbergen stock of Bowhead whales throughout the period of commercial exploitation by European whaling vessels (1611–1911). At this point we simply wish to reiterate and emphasise the conclusions we have already reported in the sections above. First, based on our adapted Schaefer delayed-difference recruitment model, we believe that there were approximately 52,500 adult Bowhead whales resident in the waters between the east coast of Greenland and the island of Spitzbergen prior to intensive hunting by European commercial whalers in 1611. Given that there do not appear to have been any more than 1,000 Bowhead whales resident in these waters by 1911, it is evident that this stock faced nearly constant depletion during the period of commercial exploitation. Our annual population estimates indicate that the chronology of stock decline matches changes in the economic environment in which the extractive industry operated. In particular, the stock appears to have collapsed after the Dutch abandoned the industry and the British became the dominant participants. We have also argued that our pristine stock estimate is relatively insensitive to reasonable changes in our assumptions regarding harvest figures, species-specific biological parameters, and the residual 1911 population level. Our pristine stock estimate is considerably larger than the other estimates available in the literature, and this difference appears to be the result of methodological differences and differences in the period of exploitation considered in the reconstruction models.

As a final point, it seems appropriate to comment briefly on the implications that arise as a result of our upward revision of the accepted pristine population estimate for the Greenland–Spitzbergen Bowhead whale. Although there are many questions that may need reexamination two issues seem to stand out. First, the impact that human predation had on the eastern Arctic ecosystem must have been even more dramatic than previously reported. One cannot remove well over 52,000 large marine mammals from an ecosystem in a fairly short time period without serious disruption. Second, the absence of co-operation among whalers, or intervention by government regulators, despite persistent economic and biological depletion suggests a significant illustration of the impact that unfettered economic incentives may have on both species and industry sustainability.

NOTES

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1 For just a few examples from the north Atlantic see Leatherwood and Reeves 1983, Reeves, Stewart and Leatherwood 1992, Weslawski, Hacquebord, Stempniewicz and Malinga 2000, or Roman and Palumbi 2003.

2 See Davis, Gallman and Gleiter 1997, 28–31, and Ross 1993, 516–17.

3 See Braham 1984, Moore and Reeves 1993, and Shelden and Rugh 1995.

4 For a discussion of the Bowhead whale hunt in the eastern Arctic from its earliest incarnation see Ross 1993, or Proulx 1986. A history of Dutch whaling can be found in de Jong 1983, or de Vries and van der Oude 1997. For a discussion of the history of British whaling in the eastern Arctic see Scoresby 1820, or Munroe 1854. For more general historical discussion of early whaling see Jenkins 1921, Jackson 1978, or Bockstoce 1986.

5 Ross (1979) identifies 1911 as the extinction date for the Bowhead in the eastern Arctic. Reeves (1980) claims that periodically individual Bowhead whales were captured in the eastern Arctic as by-catch until 1939.

6 See Vibe 1967, 81–2, de Jong 1983, 90, and Shelden and Rugh 1995, 3.

7 See Hacquebord 2001, 172–3.

8 A similar comprehensive list of Bowhead harvests from the Davis Strait stock is available from the authors. If we use our methodological approach with this comprehensive series for the Davis Strait, we estimate that the pristine adult population of Bowhead whales resident off the west coast of Greenland was just over 18,000 in 1719.

9 See de Jong 1983, and Munroe 1854.

10 No information on British whaling voyages is available between 1803 and 1813, but we have again estimated harvests using oil consumption to interpolate across the missing years.

11 During the early nineteenth century US whaling vessels were much more commonly found hunting from the Davis Strait and Hudson's Bay stocks of eastern Arctic Bowhead.

12 For examples see International Whaling Commission 1978, and de Vries and van der Oude 1997, 263.

13 Although it is not clear from their descriptions of the estimation procedures, we assume that Mitchell, Woodby and Botkin, and Hacquebord and Leinenga refer to the pristine adult population of Greenland–Spitzbergen Bowhead whales. If they were referring to the total population, then the difference between our pristine population estimate and these earlier estimates is even larger. According to Zeh et al. 1993, between 40–60 per cent of the total population of western Arctic Bowhead whales is under the age of sexual maturity. If this age distribution applied to the pristine population of the Greenland–Spitzbergen Bowhead population, then our estimate of the total pristine population increases to approximately 105,000.

[14] Mitchell 1977, 17 (emphasis added).

[15] Using the same methodology Mitchell and Reeves (1981) slightly revised this estimate when constructing a pristine population figure for all three eastern Arctic Bowhead stocks.

[16] Our harvest series indicates that almost 79,000 Bowhead whales were removed from the Greenland–Spitzbergen stock between 1689 and 1911.

[17] Although 2 per cent is a more typical value for the rate of natural increase in a population of sexually mature baleen whales, estimates for large marine mammals can range between 0–7 per cent. See Woodby and Botkin 1993, 398.

[18] Hacquebord (2001) reiterates and expands on Hacquebord and Leinenga's (1994) pristine population estimate in a detailed discussion of the impact that the removal of 46,000 Bowhead whales must have had on the eastern Arctic ecosystem.

[19] The presence of a long run biological equilibrium would not necessarily imply that the eastern Arctic Bowhead stock was constant prior to the introduction of human predation. This was clearly not the case. However, if we hold all determinants of the Bowhead population that are not described by the biological model fixed, then it would seem reasonable to expect the stock size to move towards a stable long run mean. Biological models that are dependent on the exponential growth function are unstable, such that even if we hold all exogenous determinants of the Bowhead population fixed, the population would still grow at the constant rate of natural increase into perpetuity.

[20] There are no published estimates of the pristine population of Greenland–Spitzbergen Bowhead whales using the logistic model. However, variants of this model have been used with historical catch records for Canadian beavers by Carlos and Lewis 1993, 478, and for north Pacific seals by Paterson 1977, 105.

[21] The Schaefer model, like all population models based on a logistic growth function, imposes a smooth parabolic shape on the growth dynamics. At very high and very low stock levels population growth among most marine mammal species, including whales, does not follow a smooth parabola. Therefore, models that use a logistic growth function do a very poor job describing population expansion and contraction where there are sharp discontinuities near the maximum environmental holding capacity, and near extinction.

[22] We have constructed fig. 2 with the parameter values used in our estimation of the pristine Greenland–Spitzbergen Bowhead population.

[23] See Conrad 1989, table 1, Chapman 1981, 283, Clark and Lamberson 1982, 109, Amundsen, Bjorndal and Conrad 1995, 173, Mitchell 1977, 20, Ross 1979, 91, and Davis, Gallman and Gleiter 1997, 140.

[24] It is interesting to note that the pristine stock estimates derived using our model are very similar to the estimates derived using the logistic and standard Schaefer models, but the exponential model – a variant of which was used by both Woodby and Botkin, and Hacquebord and Leinenga – produces considerably smaller pristine population estimates.

[25] The substantial increase in the pristine stock estimate resulting from the switch from our comprehensive harvest series to Ross's series when we use an exponential growth function highlights the problem associated with the absence of a biological equilibrium in this approach. The increase in the pristine stock size when using the exponential model

is entirely due to the increase in the population level between the year our harvest series begins (1611) and the year Ross's harvest series begins (1660).

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