GROWTH, MORPHOLOGY AND ENERGETICS OF BOWHEAD WHALES
(*BALAENA MYSTICETUS*)

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GROWTH, MORPHOLOGY AND ENERGETICS OF BOWHEAD WHALES (*BALAENA MYSTICETUS*)

A

THESIS

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John Craighead George

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Abstract

This thesis describes investigations on bowhead whales (*Balaena mysticetus*) specifically on age, growth, morphology and energetics. The examined whales were harvested by Inupiat whale hunters primarily in Barrow, Alaska since the 1970s. Bowheads are robust cetaceans reaching 19m in length and inhabit most of the ice-covered waters of the circumpolar Arctic. They have the thickest blubber ($\geq$ 35 cm) of any cetacean and the longest and most extensive baleen apparatus. Bowheads grow rapidly from 4 to ~8 m in their first year, after which they experience a 2-3 year growth pause in both body length and mass. However, the baleen continues to grow during this period. Sex differences are minimal but adult females tend to grow longer than males and have smaller pectoral limbs. Several lines of evidence, including the recovery of 19th century stone weapons from recently harvested whales, suggest bowheads are the longest-lived mammals. Age was estimated using the aspartic acid racemization technique which suggests that sexual maturity occurs in the mid-20s with maximum ages to 200 years. All harvested whales examined showed strong thermal gradients through their blubber and through the muscle, the latter being atypical of most mammals. The deep body temperature averaged 33.8° C which is lower than in other non-hibernating eutherian mammals. An elevation of body temperatures in pursued whales was not noted. Resting metabolic rates for whales were estimated using a heat-loss technique. The thermal conductivity of the blubber averaged 0.23 $Wm^{-1}K^{-1}$, similar to that of other whales and marine mammals. Heat flux rates were highest for the palatal rete, flukes, and tongue, and lowest for the thorax. The estimated metabolic rates were considerably lower than predicted by the Kleiber regression. These investigations suggest that bowhead whales are unique among mammals in several respects including: their extensive baleen rack, massive head, great longevity, lower resting metabolic rates and body temperatures than in other cetaceans, and an approximately 3 year growth pause following weaning. Their thick blubber likely buffers bowheads against high variability in primary and secondary productivity in arctic seas.

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This thesis is a tribute to them all. I dedicate it to them.

Chapter 1 General Introduction

Life history studies track an animal from early development to its natural death. The investigations in this dissertation have similarities to life history studies conducted over a century ago on other large mammals. This is because the bowhead whale was poorly known to science until the last three to four decades in part due to their isolated habitat in remote Arctic seas. Basic information such as population size, migration routes, reproductive rates, age at maturity, and fundamental anatomy and physiology have only recently been studied in detail.

Studies of detailed aspects of bowhead whale (*Balaena mysticetus*) anatomy and physiology would be nearly impossible if not for the Native whale hunt which currently takes place in 11 villages spread across Alaska's Arctic coast. The willingness of the whaling captains and crews to allow us to examine their whales provides a rare opportunity to inspect freshly killed animals over a range of ages, size and sex, reproductive condition, and seasons. The information analyzed in this thesis focuses mainly on postmortem and field examinations of landed bowhead whales from 1980 to 2007. These studies included sampling tissues, taking morphometric measurements, weighing entire whales and their organs, age estimation, measuring post-mortem body temperatures, inspecting scars and injuries, documenting hunting statistics and conditions, and other aspects.

General Description of the bowhead

The bowhead whale is a large pagophylic or "ice-loving" member of the *Balaenidae* which inhabits the ice-associated regions of the Arctic and sub-Arctic seas (Tomilin, 1957; Moore and Reeves, 1993). *Baleana* is whale in Latin, and *mysticetus* is derived from two Greek words "mystakos" (mustache) and "ketos" (sea monster) (Montague, 1993). Bowheads begin life in sub-zero sea water in spring within the ice-lead systems of northwest Alaska - they are the only mysticete that gives birth in Arctic waters, and the only mysticete that spends its entire life in polar regions. Bowheads are an important subsistence species for many coastal native communities in Russia, Alaska and Canada. They may exceed 19 m in body length and 80 metric tons in body mass. The bowhead whale exhibits a number of superlatives among Cetacea. These include: the thickest blubber, greatest longevity, longest baleen, low body core temperatures, and large head-to-body length ratios (George *et al.*, 1999; Haldiman and Tarpley, 1993).

In systematic nomenclature, the bowhead's cranial features and baleen rack are among the most highly *derived* (modified version of the primitive condition) in cetacea. Referring to the nineteenth century name of the bowhead, Charles Darwin wrote in his revolutionary work On the Origin of Species (Darwin, 1859),

"*The Greenland Whale is one of the most wonderful animals in the world, and the baleen, or whale-bone, one of its greatest peculiarities.*"

Without ever seeing a bowhead, he identified the baleen, I think correctly, as one of its most unusual and important features. Arguably, it is their highly developed baleen apparatus that allows the bowhead to thrive in the unpredictable low-density prey fields of the Arctic seas (Neibauer and Schell, 1993). Bowheads have about 640 baleen plates in their mouth, divided between two equal-sized racks. The longest baleen blade in our dataset was 409 cm for a female with an estimated body length of 19 m. Yankee whalers reported baleen to 487 cm in length.

Another luminary, Herman Melville, wrote in his famous novel Moby Dick,

"*What would become of a Greenland whale, say, in those shuddering, icy seas of the North, if unsupplied with his cozy surtout?*"

The blubber of the bowhead is considered the thickest in cetacea. A reliable maximum blubber measurement of 37 cm was taken in our studies. It composes up to 50% of the body mass of some whales. Thus, Darwin and Melville identified two of the most important characters of the bowhead whale.

A considerable body of literature exists on bowhead population size and trend, distribution, and basic anatomy (Marquette, 1977; Nerini *et al.*, 1984; Schell *et al.*, 1993, George *et al.*, 2004; Haldiman and Tarpley, 1993; Burns *et al.*, 1993; Gerlach *et al.*, 1994; Zeh *et al.*, 1993). Much less has been published on bowhead whale energetics, physiology, morphometrics, and age-growth relationships (Burns *et al.*, 1993).

Characteristics of cetaceans

A number of species spanning several orders of mammals have adapted to a partial or fully aquatic life. While only the Sirenians and Cetaceans are fully aquatic, many species of mammals including shrews, seals, primates and elephants have adaptations that allow them to live, swim and feed in or near ponds, rivers and oceans in varying degrees (Reynolds *et al.*, 1999). Whales are superb swimmers and occupy all the deep oceans and seas and at times enter freshwater systems. They can migrate across entire ocean basins and therefore exhibit the longest migrations of any mammal, and all while fasting.

Water presents many challenges for homoeothermic mammals due to its unique physical properties. Water has a thermal conductivity 25 times higher than air, its volume specific heat capacity is 3000 times higher, it is far more viscous, 800 times denser and maximum oxygen content is 1/30 that of air (Schmidt-Nielsen, 1997). Bowheads also contend with near-freezing water temperatures throughout life which subjects them to thermal demands that relatively few marine mammal species can withstand. Cetaceans solved the problem of low oxygen concentrations by continuing to breathe air and the greater drag and thermal demands by streamlining, developing a thick blubber layer, using flukes for propulsion, having paddle-like limbs, becoming hairless and other adaptations.

Large body size in mysticetes is one of the key traits that allow cetaceans to range throughout the world's oceans. That is, the physical and energetic properties associated with exceptionally large body size offer some advantages. Their surface-to-volume ratio is low, which greatly reduces size-specific heat loss, and they carry a large quantity of fat compared to their maintenance metabolism. Large mysticetes can fast for over half the year following a relatively brief summer feeding period in some cases. They can extensively nurse while fasting which is rare among mammals (Costa and Williams, 1999). In physical terms, fat stores accumulate proportionally faster ($mass^{1.0}$) than maintenance metabolism ($mass^{0.75}$) as a function of body weight; hence large animals have proportionately larger reserves available. When mammals reach the mass of a bowhead, basal metabolic rates per kilogram are less than 1% of a mouse-sized mammal (Schmidt-Nielsen, 1997) and their fasting endurance is roughly 1000 times longer.

Due to the elevated heat transfer properties of cold Arctic water and the uncertainty of annual primary production, bowheads and other cetaceans that inhabit Arctic seas have evolved behavioral and morphological adaptations to further reduce heat loss and energetic demands. In bowheads, this includes the highly developed blubber layer (epidermis, dermis and hypodermis) for both storing lipids and reducing heat loss. This also presents a challenge to bowheads as they require highly developed mechanisms for losing heating during exercise.

Blubber is composed mainly of fats and is thereby an effective insulator, but it is not nearly as effective as fur (in air). Furthermore, if blubber is perfused with blood its properties change and conductivity increases considerably. The thermal conductivity (TC) of whale blubber is about 0.25 $Wm^{-1}K^{-1}$ while arctic fox (*Vulpes lagopus*) and caribou (*Rangifer tarandus*) fur has a value of 0.04 $Wm^{-1}K^{-1}$ (Kvadsheim, 1998). This means that a fox would need a blubber coat six times thicker (~30 cm) to provide the same thermal resistance as its fur. Blubber has several advantages over fur in that it is effective in water, is buoyant and serves as a caloric storage organ. In addition blubber has the distinct advantage in that its insulative properties can be adjusted via blood perfusion (Kvadsheim, 1998). The ability to regulate the TC of its coat offers an advantage to an animal when it is heat-stressed. Furthermore, they do not need to shed their coats during summer. Body temperatures of grizzly bears (*Ursus arctos*) become elevated as much as 2°C when chased such as during radio collaring operations. They risk hyperthermia if pursuit continues particularly in combination with anesthesia (E. Follmann, pers. comm.).

Heat loss models

An approach to estimating metabolic rates, sometimes referred to as the "heat-balance" method first advanced by Kleiber a half century ago, has been applied to seals, whales and other species (Kleiber 1961; Brodie, 1975; Brodie and Paasche, 1985; Kvadsheim, 1998). We applied this approach to bowhead whales. It is based on the principle that at rest, ultimately heat loss from an endothermic animal must equal its heat production. Expressed as a simple equation:

$$H_P = H_c + H_e + H_s$$

Where H_P = internal heat production or metabolism, H_c = the combined conductive and convective heat loss, H_e = evaporative heat loss, and H_s = heat storage which intermittently is positive or negative (Elsner 1999). Radiative heat exchange is considered insignificant for whales immersed in cold water. Evaporative heat loss is low but has been estimated for some whales and can be added to the equation. Therefore, conductive and convective heat loss is responsible for most heat transfer in whales, in particular those that live in cold seas. If heat loss can be calculated or measured accurately, one can estimate the metabolic rate of an animal at rest.

Fossil history and evolution

That cetaceans descended from terrestrial mammals was apparent even in Darwin's time or earlier; however, the precise ancestry has been somewhat controversial. Thewissen *et al.*,

(2007) provide strong evidence for an artiodactyl origin in the Eocene epoch about 50 million years ago. A definitive character for cetacea is the *involucrum* or characteristic fold in the tympanic bone. It is found in all fossil and recent cetaceans and in no other mammals. This synapomorphy (shared trait) has undoubtedly helped paleontologists trace the various intermediate and transitional forms of whales from quadrupeds to fully aquatic whales (Thewissen *et al.,* 2007).

Cetaceans evolved in south Asia. The fossil record tracing the transition of cetaceans from land-dwelling quadrupeds into fully aquatic whales is now among the best known in Mammalia. As a group, cetaceans are a dramatically derived group of mammals compared with their terrestrial counterparts. The adaptations for life in water include telescoping skulls, movement of nares to a dorsal position, development of flukes, isolation of the hearing apparatus, shortened necks, complete loss of hind limbs, and addition of caudal vertebrae (Thewissen *et al.*, 2007). Balaenids date from the Oligocene with considerable radiation during the Miocene (Vaughan *et al.*, 2000). With regard to bowheads, seasonal and/or permanent sea ice apparently developed much later during the early Pleistocene. Therefore, we speculate that the bowheads' sea ice-related adaptations, such as the arched head and extensive baleen apparatus may have evolved relatively recently in geological time, i.e., in the last 1 to 2 million years (George *et al.*, 1999).

Inupiat and Yupik Subsistence Whale Hunting

One of more intriguing aspects of the bowhead whale is that several indigenous cultures evolved around hunting them and using their products for food, fuel and building materials. Consequently, the bowhead provides both cultural and nutritional sustenance (Harritt *et al.*, 1995). Inupiat and Yupik Eskimos of North America and eastern Asia have hunted bowheads for at least the last 2000 years. Hunting enormous animals like the bowhead whale requires a large coordinated group of people, sophisticated tools and complex hunting strategies (Harritt *et al.*, 1995; Stoker and Krupnik, 1993). Anthropologists speculate that the bowhead whale hunt served to create cohesive social structures and division of labor in the coastal Inupiat communities during the pre-contact period. This was necessary because many of the able men would leave the village for long periods during the hunt. Inter-family and even inter-village alliances were also needed to make bowhead whale hunting possible (Stoker and Krupnik, 1993). These communities developed in coastal areas which had good access to the spring lead systems (e.g., Sireniki, Wales, Kivalina, Point Hope, Icy Cape, and Point Barrow) through which bowhead whales migrated, and to coastal areas along the fall migration route, such as Shingle Point in the Mackenzie Delta area (Canada), Kaktovik, Point Barrow, and numerous villages along the Chukotka coast (Freeman *et al.*, 1998).

Currently about 40 whales are harvested annually among 11 villages with Barrow taking about half the harvest in some years. For over 40 years, Native hunters in these villages have allowed biologists to sample the animals they harvest, and this collaboration has produced a considerable body of literature on the biology of the animal. Hundreds of reports and publications have resulted from these investigations. We are grateful to hunters for allowing us to examine their animals – none of this work would be possible without them. We also have benefited from the Inupiat traditional knowledge about bowhead whales. Many of the scientific studies that have been conducted by the North Slope Borough Department of Wildlife Management have stemmed from observations by senior Inupiat whale hunters (Albert, 2000).

Objectives

Objectives of this study were to:

1. Quantify the natural variability in the external morphology by length, age, and sex in the bowhead whale;
2. Estimate the age of bowhead whales using aspartic acid racemization;
3. Estimate the body mass and develop a length, girth mass model;
4. Document regional heterothermy in bowhead whales, and
5. Estimate resting metabolic rates for bowhead whales of different size and body mass.

Chapters

Chapter 1. Introduction (above).

Chapter 2: External Morphology of the Bowhead Whale (*Balaena mysticetus*) with Emphasis on the Development of the Head. This chapter summarizes morphometric examinations of 320 bowhead whales harvested by Alaskan Eskimos for years 1989 to 2007. The external morphological relationships as a function of body length and sex were quantified. Allometric changes are described in particular those associated with the development of the head and feeding apparatus. A hiatus in growth and body mass in the first years of life is described.

Chapter 3: Body Mass of Bowhead Whales (*Balaena mysticetus*) of the Bering Chukchi Beaufort Seas. Eight bowhead whales harvested by Eskimos at Barrow, Alaska were weighed using a combination of direct and indirect methods. Length-mass models were fit to the data and described. Body mass was also estimated independently using an approximation of volume based on a series of girth measurements.

Chapter 4. Age and Growth Estimates of Bowhead Whales (Balaena mysticetus) via Aspartic Acid Racemization. The age of 48 bowhead whales was estimated using the aspartic acid racemization technique developed by Jeffery Bada at Scripps Institute of Oceanography. This work was subsequently published in 1999 in the Canadian Journal of Zoology (George *et al.*, 1999). The method is based on measuring the ratio of the optical isomers of aspartic acid in the eye lens. Growth curves were estimated which agreed well with other estimates. Four whales exceeded 100 yr in age and one was about 200 years old. The recovery of 19th century whaling tools from living bowheads also suggests that their lifespan exceeds 100 years.

Chapter 5. Regional Heterothermy in the bowhead whale (*Balaena mysticetus*). Postmortem temperatures were measured at several locations on freshly harvested bowhead whales. Regional differences in the temperature of various body sections were found along with temperature gradients from the skin to 1 m deep at all sites examined.

Chapter 6. Low Metabolic Rates of Bowhead Whales (*Balaena mysticetus*). This chapter examines some aspects of heat transfer in bowhead whales to the environment and uses a heat-loss model to estimate resting metabolic rate. The average deep body temperature was estimated at 33.8° C (N = 28; SD = 0.83; range 32.4° - 35.3° C) which is lower than other eutherian mammals. The resting metabolic rate was estimated to be lower than in other cetaceans and lower than the Kleiber prediction. Mechanisms for conserving and dissipating heat from various parts of the body were described. Reasons whey bowheads might carry such a large energy store in the form of thick blubber are discussed.

References

Albert, T. F. 2001. The influence of Harry Brower, Sr., an Inupiaq Eskimo Hunter, on the bowhead whale research program conducted at the UIC-NARL faculty by the North Slope Borough. In: D. Norton, ed. Fifty more years below zero: tributes and mediations for the Naval Arctic Research Laboratory's first half century at Barrow, Alaska. University of Alaska Fairbanks, 2001 xvi. 576 p., ill., maps, 20 cm. ISBN 0-919034098-5.

Brodie, P.F. 1975. Cetacean energetics, an overview of intraspecific size variation. Ecology 56:152-161.

Brodie, P. and Paasche, A. 1985. Thermoregulation and energetics of fin and sei whales based on postmortem, stratified temperature measurements. Can. J. Zool. 63:2267-2269.

Costa, D.P, and Williams, T.M. 1999. Marine Mammal Energetics. *In*: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution, pp. 578.

Darwin, C. R. 1859. On the origin of species. John Murray. London.

Elsner, R. 1999. Living in water: solutions to physiological problems. In: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution. pp. 73-116.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Can. J. Zool. 77:571-580.

Harritt, R.K., Jolles, C.Z., McCartney, A.P. 1995. Introduction. Allen P. McCartney, *Ed.* In: Hunting the largest animals. Native whaling in the western arctic and subarctic. Studies in Whaling No. 3 Occasional Publication No. 36, The Canadian Circumpolar Institute, University of Alberta, Canada.

Freeman, M.R., Bogoslovskaya, L., and R. Caulfield. 1998. Inuit, whaling, and sustainability. Altamira Press. 208 pp.

George, J. C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978-2001) of western arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20 (4):755-773.

Gerlach, C., George, J.C., Suydam, R. 1993. Bowhead whale (*Balaena mysticetus*) length estimations based on scapula measurements. Arctic 46: 55-59.

Haldiman, J.T. and Tarpley, R.T. 1993. Anatomy and Physiology. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. 787 pp.

Kleiber, M. 1961. The fire of life, an introduction to animal energetics. Wiley & Sons Inc., New York, USA. 454 pp.

Kvadsheim, P.H. 1998. Blubber as Insulation: A study in heat balance in harp seals (*Phoca groenlandica)* and minke whales (*Balaenoptera acutorostrata*). Ph.D dissertation at the Department of Arctic Biology and Institute of Medical Biology, Univ. of Tromso, Tromso, Norway. 26 p + appendices.

Marquette, W.M. 1977. The 1976 catch of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos with a review of the fishery 1973-1976, and a biological summary of the species. Unpublished report. US Dept of Commerce, NOAA, NMFS, Seattle , WA .Ohsumi S. 1980a. Population study of the Bryde's whale in the Southern Hemisphere under scientific permit in the three seasons, 1976/77–1978/79. Report International Whaling Commission 30:319–331.

Montague, J. 1993. Introduction. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. 787pp.

Neibauer, H.J. and Schell, D.M. 1993. Physical environment of the Bering Sea population. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. 787pp.

Nerini, M.K., Braham, H.W., Marquette, W.M., and Rugh, D.J. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). Journal of the London Zoology Society 204:443-468.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whales. Rep. int. whal. Commn 29: 397-406.

Reynolds, J. E., Odell D.K., and Rommel, S.A. 1999. Marine mammals of the world. *In*: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution, pp. 578.

Schell, D.M., and Saupe, S.M. 1993. Feeding and growth as indicated by stable isotopes. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Schmidt-Nielsen. 1997. Animal physiology: adaptation and environment. Cambridge University Press. Cambridge, England. 611 pp.

Stoker, S.W., Krupnik, I.I. 1993. Subsistence whaling. In: J.J. Burns, J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. 787 pp. Allen Press, Lawrence, Kansas.

Thewissen, J.G. M., Cooper L, N., Clementz, M.T., Bajpai, S., Tiwari, B.N. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature 450: 1190-1194.

Tomilin, A.G. 1957. Mammals of the U.S.S.R. and adjacent countries. 9. Cetacea. Translated by the Israel Program for Scientific Translations, Jerusalem, 1967. 717 pp.

Vaughan, T.A., Ryan, J.M., Czaplewski, N.J. 2000. Mammalogy. Saunders College Publishing, Orlando, FL. 565 pp. + Appendices.

Chapter 2 External Morphology of the Bowhead Whale (*Balaena mysticetus*) with Emphasis on the Development of the Head[1]

Abstract

We assembled records of 1,060 bowhead whales of the Bering-Chukchi-Beaufort Sea stock landed between the 1960s and 2007. Of these, 874 records had at least a body length measurement which ranged from 460 cm to 1950 cm. Morphometric data recorded by North Slope Borough biologists were available for 320 whales for years 1989 to 2007. We quantified the external morphological relationships as a function of body length and sex. Bowheads have more rotund bodies, larger heads, highly arched rostrums, thicker blubber and larger flukes than other mysticetes. Following rapid growth to age 1, the skull and rostrum grow disproportionately faster than the postcranial body. Growth nearly ceases after weaning (age 1) to about age 4 . Similarly the baleen grows disproportionately faster as a function of body length in the first years of life until the animal reaches about 9-10 m at age 3-7 yr. Following this, baleen growth slows while the skull continues to grow proportionally larger through life. The balaenids may be the only mammal to exhibit this growth trait. This differential growth likely serves to maximize feeding efficiency on small low-density prey as quickly as possible. Sex differences in morphometric measurements as a function of body length were significantly different for the pectoral limbs (M>F), and genital slit length (F<M). Umbilical girth in pregnant females is significantly greater than non-pregnant females, but blubber thickness was not significantly different. Blubber thicknesses for whales captured in spring and autumn was <u>not</u> significantly different, while <u>girths</u> at the axilla and umbilicus were significantly greater in autumn presumably as a consequence of summer feeding.

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[1] J. C. George, J. E. Zeh, R. Suydam, and E. H. Follmann. External Morphology of the Bowhead Whale (*Balaena mysticetus*) with Emphasis on the Development of the Head. In Prep. Formatted for Journal Arctic.

Introduction

The bowhead whale (*Balaena mysticetus*; Inupiaq - *Aġviq*) or Greenland right whale is the only member of Suborder Mysticeti that lives entirely within the Arctic sea ice and that does not migrate to temperate seas to calve. Bowheads are one of four living species in the Family Balaenidae and sister taxa to all other mysticete families (Sasaki et al, 2005; Rychel *et al.,* 2004). Bowheads of the Bering-Chukchi-Beaufort Seas stock-(BCBS) are an important subsistence species both culturally and nutritionally for coastal Inupiat and Yupik Eskimos of Northwest Alaska (Stoker and Krupnik, 1993; Reeves and Leatherwood, 1985).

The external morphology of an organism is a reflection of its phylogeny and selection pressures through time. The cetaceans are characterized by smooth skin, fusiform body, development of flukes, paddle-like pectoral limbs, and lack of external pelvic limbs from ancient chronic selection for an aquatic environment (Pabst *et al.*, 1999). Bowhead characters include a rotund body, thick blubber (to ~40 cm), long baleen and a heavy skull. The latter presumably supporting their extensive baleen apparatus and for breaking through sea ice to breathe.

Quantitative analyses of the external morphology and age of small cetaceans have been published by several researchers (e.g., Amano and Miyazaki, 1993; Yonekura et al., 1980; Kasuya and Shiraga, 1985). The classic literature for large mysticetes includes analysis of external morphological relationships (Ohmura *et al.*, 1969; Ohsumi, 1979; Tomilin, 1957; True, 1904). Relatively little quantitative analysis has been published on the external morphology of the bowhead whale but a few publications provide basic morphometric data and analysis (Durham, 1980; Eschricht and Reinhardt, 1866; Tomilin, 1957; Tarpley *et al.* 1995; Marquette, 1977). External morphology has been used to differentiate between breeding populations in other cetaceans and to identify possible sub-species (Christensen *et al.*, 1990; Best 1985).

Cetaceans are sexually dimorphic. In the Suborder Mysticeti, females typically grow longer than males while the opposite is true for the Suborder Odontoceti. Growth patterns vary among cetaceans reflecting differing life histories and adaptations to environmental factors. Amano and Miyazaki (1993) found that Dall's porpoise (*Phocoenoides dalli*) contrast with other delphinids in post-natal growth of the posterior portion of the body. They speculate that this is an adaptation for fast swimming. Woodward *et al.* (2006) applied hydrodynamic models to whale morphological data to compare life history strategies of some large cetaceans. For balaenids they concluded that "*the rotund right whale has large high aspect ratio flukes for efficient slow speed cruising that is optimal for their continuous filter feeding technique.*" Ohmura *et al.* (1969) made an exhaustive analysis of several aspects of right whale morphology, anatomy, osteology and described allometric changes in body proportions with size and age.

In this paper we present quantitative descriptions of the external morphology of bowhead whales along with some aspects of the osteology. We examine the development and allometric variation of the head as a function of body size and age because of the obvious importance and emphasis on the development of a large head in this species. A primary purpose is to provide detailed quantitative descriptions of bowhead morphology to: 1) establish a baseline of morphological variability in bowheads, 2) estimate body length from incomplete data such as rostrum or fluke or flipper measurements, 3) compare the morphology of BCBS bowheads with those of other stocks, 4) interpret and elucidate data from old commercial harvest records such as baleen lengths, body lengths, oil yields, etc., and 5) provide comparative data for use in other studies, such as aerial photogrammetry and archeological investigations (e.g., Gerlach *et al.*, 1993).

Methods

Morphometric data for bowhead whales were obtained from animals harvested by Alaskan Eskimos during their subsistence hunt. These data were recorded by National Marine Fisheries Service (NMFS) personnel dating from the 1960s and by North Slope Borough (NSB) biologists since 1981. For many whales harvested since ~1974, a series of standard cetacean measurements were taken during the butchering process similar to those in Geraci and Lounsbury (1993) (Figure 2.1). Measurements are taken with a 30 m surveying tape to the nearest centimeter. Girth or circumference measurements at the axilla, umbilicus, and anus were taken as half-measurements and doubled. The peduncle girth was taken as a complete circumference. Measurements of anterior and posterior pectoral fins were taken as straight-line measurements to the distal tip of the limb, which differs slightly from standard protocols which are taken parallel to the long axis (e.g., Geraci and Lounsbury 1993). Flipper width was taken at its widest breadth at a slight angle to the long axis.

Most, but not all, measurements were taken on each animal, therefore sample sizes vary for specific analyses. The location and description of the measurements used in our analyses are summarized in Table 2.1 and sample sizes for each measurement are listed in Table 2.2.

Statistical Analysis

Statistical analyses were conducted using SPSS PC 11.5. Least squares linear regression was used for morphometric data that showed strong linear relationships. For morphometric relationships that showed clear non-linear relationships (such as girth v body length), quadratic models were fitted. The morphometric data were not log-transformed since the estimated untransformed models fitted the data well (many R^2 values > 0.85) and the relationships are more easily interpreted. The residuals from these fits did not exhibit any severe non-constant variance. Sex differences were tested ($\alpha = 0.05$) using multiple regression with sex as a binary variable (0 = females, 1= male).

The full model with sex differences is

$$y = \beta_0 + \beta_1 x + \beta_2 \cdot \text{sex} + \beta_3 x \cdot \text{sex} + \beta_4 x^2$$

where 'y' represents the morphometric variable to be modeled.

Model for slope differences in sex:

interaction model

$$y = \beta_0 + \beta_1 x + \beta_2 \cdot \text{sex} + \beta_3 x \cdot \text{sex}$$

Model for intercept differences in sex:

quadratic model

$$y = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 \cdot\text{sex} + \beta_4 x \cdot\text{sex}$$

In all these models, x is the morphometric variable of interest (e.g., fluke width in cm) and sex is scored as female=0 and male=1.

The full model was run initially on all data to test for slope and intercept differences. If the interaction term was not significant ($p < 0.05$) then the simpler model was fitted. The p-values were tabled with the equations accordingly. Model terms were consolidated where possible to simplify the final model expression.

For morphometric measurements that clearly showed a curved function with body length such as girth, a quadratic model was initially fit.

Data Quality and Sample Selection

Morphometric data quality was scored for all whales on a 1-5 scale, with 1 being the best. The score reflects the reliability of the measurements based on whether the measurement landmarks (e.g., midlines) were accessible, whether a complete suite of measurements was made, the position of the animal, and on the expertise of the biologists who made the measurements. George (JCG) and Suydam standardized their techniques and collected the majority of the data used here. Only data quality *scores 1 and 2* were used. Data quality scores of 3 and higher included measurements made by untrained observers, of animals in ventral recumbency, or due to other factors (e.g., partially butchered whales, bloated or "stinker whales", flippers removed, etc.).

For the analysis we used a subset of the master dataset as follows:

1) For the basic morphology, we used data from 1989 to 2007. Most whales were landed and examined at Barrow. Calves and yearlings or "*ingutuks*" were included; fetuses were excluded. The reason for these filters is that by 1989, JCG had standardized the methods for taking the measurements and trained other members of the necropsy team. Prior to that, measurements were not made consistently among observers.
2) For the analysis of the development of the head (rostrum and skull) the same dataset for the morphometrics (1) above was used. Age was estimated for young whales using baleen carbon cycle models from Lubetkin *et al.* (2008). Baleen ages were limited to whales with baleen < 250 cm, since the estimated age for larger whales is imprecise. Ovarian corpora and aspartic acid racemization ages were estimated using equations from various sources (Lubetkin *et al.* 2008; Rosa *et al.* 2004; George *et al.*, 2004). Relatively few cranial (condylo-basal) measurements (N = 32) were available for analysis compared with the external measurements such as "snout-to-blowhole" length .
3) For the blubber *thickness* analysis, we limited the dataset to whales landed from 2003 to present (2007) because prior to 2003, blubber thickness measurements often included

both dermis and hypodermis and were made both on and off the animal which affects the measurement. This problem was not identified until the bowhead health assessment workshop in 2001 (Willetto *et al.,* 2002). We began switching to the new protocols in 2002 and had our techniques standardized by 2003. Technically, the blubber is "dermis" and excludes the epidermis and hypodermis (Haldiman and Tarpley, 1993). In this analysis, we defined blubber thickness as the straight-line measurement of the thickness of the epidermis and dermis combined.

4) Sample sizes were limited for certain specific measurements: skull length, mandible length, skull width, and in particular analyses involving age estimates. Thus to increase the sample size, we used all available data in these cases.

Growth of the baleen and rostrum (snout-to-blowhole) as a function of body length was examined in more detail than other parameters. To determine the body length at which the slope inflected (L), we applied the following model:

$$y = \beta_0 + \beta_1 * BL + (\beta_2 * I_{LBL})$$

where L is the inflection point interaction term; $I_{LBL} = 0$ if $BL <= L$ and $I_{LBL} = BL$ if $BL > L$

This approach was used because the *P*-value of the snout-body length regression was consistently $P < 0.001$ and not useful for comparisons between models. We used an iterative approach to maximize the *t*-statistic for body length groups and to determine the inflection point in the snout to body length relationship; i.e., the body length where *t* was maximized.

Results and Discussion

We found records for 1,060 bowhead whales landed between 1940 and 2007 from NSB and NMFS files. Of these, 874 records had at least a body length and ranged from 460 cm to 1950 cm. After screening, reliable morphometric data were available for 320 whales for years 1989 to 2007. Of these, 162 and 158 had data quality scores of 1 and 2, respectively. Sample sizes vary for each measurement because not all measurements were obtained on all whales. Results of the regression analyses and sample sizes for the basic morphological relationships are listed in Table 2.2.

General Description

The bowhead is typified by a highly arched rostrum, black skin, and rotund profile (Figure 2.2). The blubber is the thickest, baleen longest and relative head size the largest in cetacea (Eschricht and Reinhardt, 1866; Tomilin, 1957; Reeves and Leatherwood, 1985). Its robust body and thick blubber are likely adaptations to the Arctic seas they inhabit year-round. The baleen is black, long (to 410 cm in our study) with fine hairs (to ~50 cm) on the lingual side. The rostrum lacks callosities of the right whales (*Eubaleana glacialis*). The flukes are large, broad, and triangular - tapering distally to a narrow blunt apex. They are divided by a broad median notch.

The skin is black but mottled steel-gray in neonates. The epidermis is 2.5- 3.0 cm thick in sub-adults and adults and 4.5 cm in neonates – both of which appear to be maxima in cetacea. The chin is typically non-pigmented (often termed the "chin patch") along its distal, ventral, and lateral surfaces. However, about 5% of the whales examined had no detectable chin patch. The longest patches were 4.8 m in length along the lateral surface. Generally, the patch is longer on the ventral surface than the lateral surface of the chin. The presence and relative size of the chin patch appears to be unrelated to body length and age. Extensive pigmentation on the body ventrum occurs rarely (1-2 %) where it forms striking patterns more characteristic of right whales. Large whales develop white areas around the eye and peduncle, presumably as a function of age. Some immature whales (< 13 m) show some light "peppering" around the eye, however, nearly all whales > 13 m have at least some white around the eye.

White scars from injuries from sea ice scrapes, ship propellers, fishing gear, killer whales and other causes are common, especially on adults. Nearly all whales, particularly those > 13m, have some white scarring primarily on the dorsal surface along the rostrum and back. The anterior edge of the flippers and flukes often has scars as well.

The head is large and the condylo-basal length averages ~34% of the animals' total length for both sexes combined (Hillmann *et al.*, 1997; NSB data). The rostrum is strongly arched with the nares at the apex. Biologists have presumed that the "bowed" shape of the head is an adaptation to living in sea ice and is used to break through ice, but also for supporting their large baleen apparatus (Hillmann *et al.*, 1997; Nerini *et al.*, 1984; Lambertson *et al.*, 2005). Native hunters have reported bowheads breaking ice up to 1 m in thickness; we have witnessed such behavior in ice 20 cm (George *et al.*, 1989). The lips form a curved arch and enclose the baleen rack; the ventral portion of the upper jaw seats within the lower lips. The eye (~4 cm in diameter) is located just ventral to the lateral midline above the commissure of the mouth gape and approximately 0.32 (SD = 0.03; N=53; NMFS data) of the distance from the tip of the rostrum to the fluke notch.

Regarding the bowhead's evolutionary history, the question arises as to when they split off from their sister taxa and developed ice-associated adaptations, such as the bowed rostrum, finless condition, and thick blubber. Balaenids date from the Oligocene with considerable radiation during the Miocene (Vaughan *et al.*, 2000) and were much more diverse than now in the Pliocene. However, seasonal and later permanent sea ice apparently developed only during the Pleistocene. Therefore, one might speculate that the bowheads' cold water and sea ice-related adaptations such as the arched head, may have evolved relatively recently in geological time, i.e., in the last 1-2 million years. Bowheads are unusual in that they are likely the longest-living cetacean probably reaching 150 yr or older and have the latest age at sexual maturity of any known cetacean. (George *et al.*, 1999). Their long generation time could have implications for their adaptability to rapid environmental change (i.e., global warming).

Morphometric and allometric relationships

With the exception of the girth and blubber measurements, most of the measurements reported here show strong linear correlations with body length. While highly correlated, some relationships such as the snout-to-blowhole and baleen length show inflections with body length which are likely associated with allometric growth of the head. These morphometric data appear sufficiently robust for investigating regional morphological differences between populations or "stocks" (Christensen *et al.*, 1990).

Body Length

The longest whales in our dataset were females. We have three records of females 19.0, 19.2, and 19.5 m in length from villages other than Barrow, Alaska. We also have a reliable measurement of an 18.3 m female bowhead (05S7) landed in Savoonga, Alaska, but for all four of these whales other morphometric data were not available and were not included in this analysis. After filtering for data quality, the longest whale in this analysis was an unusually large 17.37 m male.

Aerial photogrammetric measurements from a single photograph indicate the longest bowhead based on a high quality measurement was 17.27 m . A larger whale photographed in 1981 was 17.57 m (sex unknown) but the calibration was questionable (NMFS, LGL, NSB photogrammetry database; Bill Koski pers. comm., 2008). Photogrammetric lengths are generally lower than those for landed whales suggesting some stretching or postural change occurs during hauling (George *et al.*, 2004).

In mysticetes, females tended to be larger than males. However there is enough variability in body size by sex that a simple *t*-test of mature adults did not show a significant difference. However, von Bertalanffy growth models in Lubetkin *et al.* (2008) suggest asymptotic lengths for males of about 18.0 m and females about 21.2 m.

Aerial photogrammetry of newborn bowhead calves indicates a birth length of 360 – 450 c m (Koski *et al.*, 1993). Our measurements of term fetuses range from 390 to 410 cm (mean = 393.0, SD = 17.7, N = 8) which is consistent with the aerial photogrammetry. Term fetuses have been recovered only during the spring harvest. Ice-based and aerial surveys indicate that parturition peaks in mid-May. Durham (1980) reported the length of two neonates harvested in the 1970s at Barrow, at 450 and 460 cm in length. Our data includes a large spring calf mistakenly harvested at Barrow on 24 May; it measured 530 cm.

Growth of bowheads is rapid in the first year. After birth at ~400 cm, bowheads grow to an average length of 819 cm (SD = 40; range = 745 – 907 cm) based on the lengths of yearling whales landed the following spring (~12 months old) where the age was determined by baleen length (Lubetkin and Zeh 2006; Lubetkin *et al.*, 2008). Thus, growth during the first year of life averages ~1.1 cm/day. As in other mysticetes, weaning probably takes place at 6-7 months and feeding is uncommon in spring, so the rapid growth to age 1 is almost entirely supported by the mother's milk (Boyd *et al.*, 1999). After the first year, growth in body length slows or may cease entirely for about four years (Schell and Saupe, 1993; George *et al.*, 1999; Lubetkin *et al.*, 2004; Lubetkin, 2008) (Figure 2.3) – which is unusual among mammals.

Longevity and Physical Maturity

Longevity in bowheads appears to be at the mammalian extreme. Direct and circumstantial evidence suggest that they live over 100 yr and likely to 150 yr (George *et al.*, 1999; Rosa *et al.*, 2004). Growth rates for whales past the length at maturity (~13.5 m) is slow (<10 cm/yr). The onset of physical maturity occurs at about 40 and 50 yr for males and females, respectively; however, it is not clear when growth ceases or if bowheads continue growing as some age/length models suggest (George *et al.*, 1999). Native hunters have remarked that bowheads live "two human lifetimes" (pers. com., Arnold Brower, Jr.).

Ingutuk

Native whale hunters of Northern Alaska recognize at least five morphological phenotypes of bowhead whales one of which is the *ingutuk* (Braham *et al.*, 1980). In the early 1980s, some hunters contended that they were not bowheads at all and should not be counted in the harvest quota. The traits that hunters use to distinguish the *ingutuk* from "classic" bowhead whales are: (1) greater girth, (2) short, thin and light baleen, (3) better meat quality, (4) thicker blubber, (5) denser bone, (6) thicker skin, and (7) gum tissue extending further down the baleen length. Braham *et al.* (1980) cited anthropologist F. Rainey who noted that some of these characters were also found in some immature female "classic" bowhead whales. Whales with a combination of *ingutuk* and "classic" bowhead features have also been described (Braham *et al.*, 1980) who also found a disproportionate number of females among *ingutuks* suggesting that this phenotype might be a sex-related trait.

Early biochemical, allozyme, and chromosomal studies, suggest that *ingutuks* cannot be distinguished from the "classic" bowhead whales (Braham *et al.*, 1980), although these investigations were limited to only one *ingutuk* individual. More recently, Rooney *et al.* (2002) conducted a phylogenetic analysis of molecular sequence data collected from both "classic" bowhead whale and *ingutuk* morphotypes. They also re-evaluated morphological evidence using discriminant analysis that putatively sets the *ingutuk* apart from other bowhead whales. They concluded that while the *ingutuk* does have some distinct morphological features (such as small heads and short baleen) that these are most likely juvenile characters and it is not a distinct taxon.

Development of the Head and Feeding Apparatus

Rostrum (snout-to-blowhole) vs. body length

The snout-to-blowhole measurement is an index of the length of the pre-maxillary bones of the rostrum. Rostrum (snout-to-blowhole) length and body length are highly correlated ($R^2 > 0.9$) in bowheads (Table 2.2, Figure 2.4). Using an iterative approach to maximize *t*-statistics, the relationship of body length to rostral length suggests a weak inflection at 9 m and a strong inflection at about ~11.5 m. Whales 11.5 m in length are usually > 10 years old (Lubetkin *et al.*, 2004; Lubetkin *et al.*, 2008; Schell and Saupe, 1993). Both the rostrum and baleen grow disproportionately faster as a function of body length for whales < 10-11 m. This growth pattern likely accommodates rapid baleen growth in younger animals. There is a suggestion in our data that baleen length is different for males and females over 11.5 m ($p = 0.045$) (Table 2.2).

Because bowheads and right whales feed on relatively small zooplankton such as copepods and small euphausiids, the baleen apparatus must grow as quickly as possible to accommodate the baleen rack and allow the animal to feed effectively. Ohmura *et al.* (1969) report that rapid baleen growth follows weaning in right whales and continues until the animals are about 13.5 m in length. By contrast, the baleen of gray whale (*Eschrichtius robustus*) is short and can reach maximum size within a year or two. For a bowhead baleen growth may take 20 years and perhaps half that long for right whales to approach a maximum. It follows that the rostral bones must also grow accordingly to accommodate the expanding baleen rack.

Baleen

Bowheads have considerably longer baleen than other mysticetes. The longest baleen we are aware of is 487 cm (15.98 ft) from a whale taken during the Yankee whaling period in the western Arctic (Bockstoce and Burns, 1993). The longest blade in our dataset is 409 cm (02B3) for a female with an estimated length of 19 m. There was no significant difference in baleen length by sex as a function of body length ($p = 0.65$).

In Arctic seas, such as the Beaufort Sea, prey densities are often relatively low (< 1 gm/m^3) so bowheads must filter enormous volumes of water to meet their nutritional needs (Richardson and Thomson, 2002). The extensive baleen apparatus of the bowhead is probably an adaptation to feeding on small prey species in areas of relatively low density. By contrast, the maximum length of right whale baleen is about 250 cm for large (17 m) animals which is just over half the baleen length for the largest bowheads (Ohmura *et al.*, 1969).

Lambertson *et al.* (2005) described the bowhead feeding apparatus and baleen in great detail but did not describe its growth as a function of age and body length. Baleen growth is rapid in the first year of life (~ 70 cm/yr) and eventually slows to ~15 cm/yr in adults (Lubetkin *et al.*, 2004; Lubetkin *et al.*, 2008) (Figure 2.5a). There is an inflection in the baleen-to-body-length-ratio at ~9-10 m when the baleen length is approaching 200 cm and most of the whales are less than 10 years old. Slope comparisons suggest the baleen growth rate for whales < 10 m is about twice that for whales greater than 10 m (Figure 2.5b). Therefore, it appears that baleen growth slows (inflects) at a shorter body length than the rostrum.

Growth of the head as a function of age

Growth in bowhead body length slows markedly in young whales (most dramatically age 2-4 yr; Lubetkin *et al.*, 2008) while the baleen continues to grow and the skull length to body length ratio increases during the growth pause. This finding and our skull measurements suggest that skull length increases during this growth pause, further supporting the idea that the head grows disproportionately faster during the first ~5 years of life (Figure 2.6).

Skull and mandible

Eschricht and Reinhart (1866) mention the disproportionate size of the head stating that in terms of relative head size among cetaceans "*first place must be assigned to the Greenland whale*". Reeves and Leatherwood (1985) also reported that bowheads have a larger head to body length ratio than other whales. Condylo-basal skull length in adult bowheads can reach 0.37-0.38 of the body length in adults (this study; Eschricht and Reinhart, 1866) and forms the bulk of the skeletal mass (Chapter Body Mass; Tomilin, 1957). Eschricht and Reinhart (1866) further noted that the head grows proportionately *larger* in adults which we confirmed in our analysis (Figure 2.7).

For analysis of the skull size, we used all available data and did not limit it to the morphometric dataset which excluded some animals caught before 1989. Skull to body length ratios for 33 whales (excludes calves) averaged 0.34 (range = 0.30-0.37; SD = 0.21; n = 31) with sub-adults < 8 m at the lower end of the range. We found no statistical differences between sexes

($p = 0.69$) in these ratios. Thus, as noted above, the head to body length ratio increases through life, which is opposite other mammals. In fact, balaenids may be the only mammal to show this unusual allometric growth trait.

Mandible length is highly correlated (> 0.95) with body length and appears to be a strong linear relationship. Like the cranium (skull), the mandible is also proportionately longer than in other cetaceans. The longest reliable measurement of a mandible (of a prepared specimen) in our dataset was 569 cm for a 16.8 m female (87B4) which is 0.33 of its body length. As one might expect, the mandible grows in proportion to the rostrum and maxillary bones (Figure 2.8).

Post Cranial Morphology

Fluke Width

The fluke width or span averages about 34% of the body length (Figure 2.9). Fluke span, as a function of body length, (34.2%, SD=0.025, Range 0.26 - 0.41, $n = 182$) is at the cetacean maximum, and nearly identical to that of the right (*Eubalaena glacialis*) and humpback whales (*Megaptera novaeangliae*) (Woodward *et al.*, 2006; Moore *et al.*, 2004). The relationship appears linear in bowheads; however Moore *et al.* (2004) fitted an exponential function to their data for right whales. In neonates, the caudal edge is somewhat pleated but becomes nearly straight in adults with a slight (graceful) concavity lateral to the fluke notch (Durham 1980). The fluke to body length relationship was not significantly different between sexes ($p > 0.05$). The largest fluke span we measured was 716 cm for a large female (whale 02B3). Unfortunately a reliable body length was not available for this giant whale, as it had to be hoisted from the water in sections (hence, it was not included in our morphometric analyses). Hunters estimated the whale's length at 19.3 m. Regression analysis suggests the length would be 18.9 m (Table 2.2).

Flukes are large in Balaenids probably to maximize low-speed swimming ability and thermoregulatory functions. The vasculature of the flukes is highly developed and is an effective means of both circumventing and conserving heat. When necessary, the flukes provide an effective means of circumventing the thick blubber of the thorax to dissipate heat (Elsner *et al.*, 2004). Woodward *et al.* (2006) noted that similar to other balaenids "*the rotund right whale has large, high aspect ratio flukes for efficient slow speed cruising that is optimal for their continuous filter feeding technique*".

Pectoral Fins

The pectoral fins or flippers of the bowhead are blunt and paddle shaped. The blubber is relatively thin on the flippers at about 2 cm. The pectoral fin inserts at 0.36 (SD= 0.04, N = 51; source: NMML and NSB raw data) posterior to the anterior tip of the rostrum. Pectoral fin length averages about 20% of the body length in males and 18% in females (Figure 2.10 and 2.11). They appear to be proportionally the same size as North Pacific right whales (Ohmura *et al.*, 1969).

Males had significantly larger pectoral fins than females. The difference was highly significant ($p < 0.001$) across all 3 measurements - anterior length, posterior length and width. The largest pectoral limb we measured (ant. length = 325 cm) was for a large 17.4 m male (95B9) with an estimated age of 174 yr.

Similarly, there was a significant difference in the size of scapula where males have significantly longer scapulas (along the long axis) than females. The larger scapula is likely needed to accommodate the larger muscle mass to articulate the bigger limbs. The larger pectoral limb in males may be associated with copulatory activity to aid in restraining or orienting themselves or the female during copulation. There may be a selective advantage for males with larger limbs. Interestingly, the size of the limb for a male pseudohermaphrodite described by Tarpley *et al.* (1995) was intermediate between male and female flipper size (it was not included in this analysis).

Blubber Thickness

The term "blubber" is used rather loosely in the cetacean literature. By recent definitions, the blubber is considered "dermis" and excludes the epidermis and hypodermis (Haldiman and Tarpley, 1993). As noted in the methods, we define blubber thickness here as the linear thickness of the epidermis + dermis. Bowheads are considered to have the thickest blubber of any cetacean, but the blubber thickness of North Pacific Right whales (*Eubalaena japonica*) is not much less. Two ~14 m female right whales had a ventral blubber thickness of 23 cm, while the blubber thickness for a 14 m female bowhead averages about 27-28 cm near the same location (ventral midline near the umbilicus).

Blubber thickness is somewhat difficult to measure because of its flexible nature. When hauled ashore, the blubber of a whale is under tension, and measurements differ between those taken on and off (i.e., blubber removed) of the animal. Furthermore, the fatty hypodermis attached to the blubber (particularly young animals) can lead to positive bias in the blubber thickness measurement if not excluded (Willetto *et al.*, 2002). Therefore, we chose to analyze only blubber thickness data taken from 2003 to 2007 (Figure 2.12a, 2.12b and 2.13) where we controlled for this problem.

Blubber thickness was not well correlated with body length except for adult animals. This could reflect measurement error but natural variation between animals also must explain some of the scatter in the data. Dorsal blubber thickness (1 m posterior to blowhole) ranged from 13 cm for a neonate to 38.5 cm for a large female and a maximum of 37 cm in the filtered dataset (2003-2007). Ventral thicknesses were similar, however, using the filtered dataset (2003-2007), a paired sample *t*-test indicated that dorsal blubber thickness was significantly greater than ventral thickness (dorsal = 22.65, SD 5.06, n = 61; ventral = 20.88 SD = 4.10, n = 61). Blubber thickness appears to be slightly greater for animals in the 8-9 m length range and suggests a "J" shaped function with increasing length (Figure 2.12a, 2.12b, and 2.13). After the animal reaches about 10 m, blubber thickness appears to increase as a linear function of body length (Figure 2.12a and 13). Pregnant females tend to have thicker blubber but the difference is not significant ($p > 0.05$). However, their girth at umbilicus was significantly greater (see below).

Seasonal differences in blubber thickness Inspection of plots indicates a slight difference between spring and fall blubber thickness but were they not statistically different when tested but only barely so ($p = 0.052$) (Figure 2.12b). Note that spring animals had thicker blubber in this analysis. However, as discussed below axillary and umbilical girth are significantly greater in autumn. Hence fattening is likely occurring in the hypodermis, viscera and perhaps muscle more than the blubber itself (C. Rosa, pers. comm.). This pattern is consistent with the classical work by Rice and Wolman (1971) for Eastern Pacific gray whales where girth changed seasonally but blubber thickness did not.

Girth

Four girth measurements were routinely taken at the axilla, umbilicus, anus and peduncle. The respective girth measurements are located at 0.39, 0.56, 0.75 and 0.92 of the body length (Table 2.3). With the exception of the peduncle, the girths all showed a "J" shaped function with body length (Figures 2.14-17). Year-1 animals (often called *Ingutuks*) carry a large maternal investment of fat from nursing and had the greatest girth to body length ratio (mean = 0.79). Axillary girths on some young whales were nearly equal to their body lengths (Figure 2.14). Once a body length of about 10 m is reached, the girths scale fairly consistently with body length.

Pregnant females had significantly greater umbilical girths than non-pregnant females where whales over 1250 cm in length were analyzed (Figure 2.18). (Note: the length of the smallest mature female was 1260 cm). However, the axillary girth was not different for pregnant and non-pregnant whales perhaps because the fetus is carried in the abdomen. However, as mentioned earlier blubber thickness was not significantly different between pregnant and non-pregnant females which some find confusing (see Blubber Thickness).

Woodward *et al.* (2006) defined a "maximum girth statistic" for right whales as (Girth_{max}/body length). The mean for right whales was 0.686 (SEM=0.036) which is identical to our mean measurement of 0.680 (SEM=0.004) for all bowheads. However, yearling bowheads had a much higher mean girth ratio (0.79) than adult right and bowhead whales.

Seasonal differences (spring vs. autumn) in girth vs body length were significant for both axillary and umbilical girth (e.g., Figure 2.15) but not anus and peduncle girths (Figures 2.17 and 2.19). Pregnant and yearling whales were removed from the analysis since the girth of yearlings reflects the maternal investment from nursing and not seasonal fattening. Similarly pregnant females are rotund from carrying their fetus and do not reflect seasonal changes accurately.

Girth data have proven useful for analysis of environmental variation. George *et al.* (2005) analyzed whale girth data grouped by "heavy" and "light" ice years in the Eastern Canadian Beaufort Sea. Results indicated that bowheads have a higher girth/length index during light ice years probably due to greater primary productivity.

Peduncle girth is highly correlated with body length (R^2~0.9). We found no statistical differences in peduncle circumference by sex (Figure 2.19). Peduncle girth is a relatively easy measurement to make and is highly repeatable. For strandings and decomposed whales where peduncle girth is the only measurement available, it can be used to estimate body length with reasonable accuracy.

Genital groove size

As in most cetaceans, there are marked differences in the relative size of the genital groove between sexes. The mean length of the genital groove for females was 32.0 cm (SD = 10.0, n = 131) and for males 125.8 cm (SD = 29.2, n = 116). Both the direct measurement and the ratio of genital groove length as a function of body length are significantly different between sexes, and can serve as an excellent means for sex determination without formal training in cetacean biology (Figure 2.20).

Fluke to anus and umbilicus

We investigated the fluke notch to umbilicus and fluke notch to anus length as a function of body length. The slope of the fluke to umbilicus regression was twice that to the anus. This suggests that growth in the lumbar region (fluke to umbilicus) is more rapid than the caudal region (fluke to anus). In both cases the relationships were linear and highly correlated (R^2 = 0.98) with body length (Figure 2.21). The fluke to umbilicus slopes were significantly different between sexes but the reason is not immediately obvious. It appears that much of the difference is driven by a single large female (07B9) so additional measurements are needed to confirm this finding. However, this whale was pregnant with a term fetus and it could be that adult females had slightly larger abdomens to accommodate carrying these relatively large (4+ m) fetuses.

Ohmura *et al.* (1969) investigated these relationships as well as the "position" of the eye as a proportion of body length for North Pacific right whales. They noted an inflection in all these relationships at a body length of 13 m but the change in relative position of the eye in relation to body length was most dramatic. They interpreted these findings as follows: "The *proportional position of the eye moves posteriorly according to the growth of the body, and its movement becomes rapid after the body length of 13 m is attained. The proportional position of the umbilicus and anus and anterior fluke margin shows almost the same tendency of that of the eye. This means that the head becomes proportionately larger and the tail becomes proportionately shorter according to the growth of [the] body.*" Therefore, it appears that in both bowhead and right whales, growth of the head is disproportionally greater than the posterior region and that the growth spurt begins at a shorter length (but probably not a younger age) for bowheads than right whales.

Problems with Measurements and Analysis

We tested the accuracy of some measurements by taking multiple readings by different observers. Because of the round body shape, straight-line measurements of body length are made lateral to the animal on the ice or ground. The measuring tape is held parallel to the long axis of the animal, and can be as much as a meter from the tip of the rostrum or flukes in some cases (due to the bulging abdomen or protruding blowhole). We do not use a pole or square to make the length measurements since they must be made quickly before (or most commonly while) the animal is being butchered. Nevertheless, the accuracy of the measurements is better than expected; the coefficient of variation for the body length measurements was ~1 % based on multiple trials (9 independent length measurements of 3 different whales). We also tested a large carpenters square (made from 2"x4"s) and a carpenter's electronic distance measurement tool to more accurately measure body length of a bowhead, and found it agreed within a few cm of the survey tape measurement in two trials.

George *et al.* (2004) reported on the effect of animals stretching when hauled from the water during the harvest. This was based on measurements of three whales made in the water and after being hauled onto the ice. Based on this small sample, they cautiously concluded that body length may increase by about 9% during the hauling process. Therefore, the analyses reported here should be applied mainly to landed whales.

Girth measurements are among the most challenging measurements to take. Only half-girth measurements can be obtained during postmortem examinations because the animal is laying on its lateral surface. Locating the dorsal and ventral midline is difficult as there are few good landmarks and the whale can become distorted once hauled ashore. Still measurement accuracy appears to be acceptable. We found differences of only ~1% between multiple measurements of girth (on the same animal) by different observers. This is surprising considering the difficulties in making the measurement but it may reflect the small sample size used in this brief experiment.

As noted earlier, blubber thickness measurements are difficult to make due to its labile nature. Following the health assessment workshop (Willetto *et al.*, 2002) in which problems with blubber thickness measurements were identified, we have tried (since 2003) to carefully exclude the hypodermis in the measurements which should give a more realistic picture of true blubber thickness over a range of body lengths. Blubber thickness data will be reanalyzed when sufficient samples are collected.

Conclusions

Bowhead whales are morphologically adapted to life in the cold ice-covered seas of the Arctic. They have raised rostrums for breathing in sea ice, lack dorsal fins, and have thick blubber and large heads with extremely long baleen. They are morphologically similar in many respects to their close relatives the right whales. The large head and broad flukes are needed for high-drag filter feeding on small patchy aggregations of euphausiids and copepods. Bowheads however appear to differ from right whales somewhat in that bowheads put greater emphasis on growth of the head and baleen rack early in life, and briefly, at the expense of increasing body length (Ohmura *et al.*, 1969). Blubber thickness generally increases as a function of body length. The thick blubber is probably more important for energy storage than thermoregulation since other cetaceans and pinnipeds remain thermoneutral in 0° C water with much thinner blubber (Pabst *et al.*, 1999).

The data provided here should provide a good basis for describing normal variability in the bowhead and for comparative studies with other cetaceans (e.g., Figure 2.22). These might include: morphometric comparisons between stocks, investigations of climate change and sea ice density, sex differences, seasonal effects, analysis of morphometric and genetic data. More complex statistical approaches should be applied to these data to choose the best models and assess process error associated with different biologists, years, and whale sizes.

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References

Amano, M. and Miyazaki, N. 1993. External morphology of Dall's porpoise (*Phocoenoides dalli*): growth and sexual dimorphism. Can. J. Zool. 71: 1124-1130.

Best, P. B. 1985. External characters of southern minke whales and the existence of a diminutive form. *In*: The scientific reports of the whales research institute, vol. 36, p 1-34. The Whales Research Institute, Tokyo, Japan.

Bockstoce, J.R. and Burns, J.J. 1993. Commercial whaling in the North Pacific sector. In The Bowhead Whale. Edited by J.J. Burns, J.J. Montague, and C.J. Cowles. Allen Press, Lawrence. pp. 563-576.

Boyd, I.L., Lockyer, C. and Marsh, H.D. 1999. Reproduction in marine mammals. In: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (*eds*). Smithsonian Institution, pp. 578.

Braham, H. W., F. E. Durham, G. H. Jarrell, and S. Leatherwood. 1980. Ingutuk: A morphological variant of the bowhead whale, *Balaena mysticetus*. Mar. Fish. Rev. 42: 70-73.

Christensen, I., Haug,T., and Wiig, O. 1990. Morphometric comparison of minke whale (*Balaenoptera acutorostrata*) from different areas of the North Atlantic. Marine Mammal Science 6 (4): 327 - 339.

Durham, F.E. 1980. External morphology of bowhead fetuses and calves. Marine Fisheries review. 42 (9-10): 74-80.

Elsner, R. George, C. O'Hara, T. 2004. Vasomotor responses of isolated peripheral blood vessels from bowhead whales: thermoregulatory implications. Marine Mammal Science 20 (3): 546–553.

Eschricht, D.F., and J. Reinhardt. 1866. On the Greenland right-whale (*Balaena mysticetus*), with special reference to its geographic distribution and migration in times past and present, and to its external and internal characteristics. Pages 1-150 in W. H. Flower, ed. Recent memoirs on the Cetacea. The Ray Society, London.

George, J.C., Clark, C., Carroll, G.M. and Ellison, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. Arctic 42: 24-30.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Can. J. Zool. 77:571-580.

George, J. C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978-2001) of western arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20 (4):755-773.

George, J.C., Nicolson C., Drobot, S., and J. Maslanik.. 2005. Progress Report: Sea Ice Density and Bowhead Whale Body Condition. Paper SC/57/E13 presented to the IWC Scientific Committee, Ulsan Korea.

Geraci, J.R. and Lounsbury, V.J. 1993. Marine mammals ashore: a field guide for strandings. Texas A&M University Sea Grant College Program, Galveston, TX.

Gerlach, C., George, J.C., Suydam, R. 1993. Bowhead whale (*Balaena mysticetus*) length estimations based on scapula measurements. Arctic 46: 55-59.

Haldiman, J.T. and Tarpley, R.J. 1993. Anatomy and Physiology. In: The bowhead whale. J.J. Burns, J.J Montague, and Cowles, C. J. (eds). Allen Press., Lawrence, Kansas.

Hillmann, D.J., Henk, W.G, and Nader, P. 1997. Initial observations on the skull and mandibles from Eskimo harvested bowhead whales (*Balaena mysticetus*). Report to the NSB Department of Wildlife Management, Box 69, Barrow, AK. August 1997.

Kasuya, T. and Shiraga, S. 1985. Growth of Dall's porpoise in the western north pacific and suggest geographical growth differentiation. *In*: The scientific reports of the whales research institute, vol. 36, p 139-142. The Whales Research Institute, Tokyo, Japan.

Koski, W.R, Davis, R.A., Miller, G.W., and Withrow, D.E. 1993. Reproduction. In: Burns, J.J., Montague, J. and C.J. Cowles (eds.). The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

Lambertson, R.H., Rasmussen, K.J., Lancaster, W. C., and Hintz, R. J. 2005. Functional morphology of the mouth of the bowhead whale and its implications for conservation. Journal of Mammalogy 86 (2) 342-352.

Lubetkin, S.C., Zeh, J.E., Rosa, C., and George, J.C. 2004. Deriving von Bertalanffy age-length relationships for bowhead whales (*Balaena mysticetus*) using a synthesis of age estimation techniques. Paper SC/56/BRG3 Report to the International Whaling Commission, Sorrento, Italy.19 pp.

Lubetkin, S.C. and Zeh, J. 2006. Deriving age-length relationships for bowhead whales (*Balaena mysticetus*) using a synthesis of age estimation techniques. Paper SC/58/BRG14 presented to the IWC SC.

Lubetkin, S.C., Zeh, J. E., Rosa, C., and George, J. C. 2008. Age estimation for young bowhead whales (*Balaena mysticetus*) using annual baleen growth increments. Can. J. Zool. 86(6): 525–538.

Marquette, W.M. 1977. The 1976 catch of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos with a review of the fishery 1973-1976, and a biological summary of the species. Unpublished report. US Dept of Commerce, NOAA, NMFS, Seattle , WA .Ohsumi S. 1980a. Population study of the Bryde's whale in the Southern Hemisphere under scientific permit in the three seasons, 1976/77–1978/79. Report International Whaling Commission 30:319–331.

Moore, M.J. Knowlton, A.R., Kraus, S.D., Mclellan, W.A., and Bonde, R.K. 2004. Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002). J. CETACEAN RES. MANAGE. 6(3):199–214.

Nerini, M.K., Braham, H.W., Marquette, W.M., and Rugh, D.J. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). Journal of the London Zoology Society 204:443-468.

Ohmura, H., Ohsumi, S., Neomoto, T., Nasu, K, Kasuya, 1969. Black right whales in the North Pacific. T. The Scientific Reports of the Whales Research Institute. No. 21. 78 pp + appendices.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whales. Rep. int. whal. Commn 29: 397-406.

Pabst, D.A., Rommel, S.A., and McLellan, W.A. 1999. The functional morphology of marine mammals. In: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution, pp. 578.

Reeves, R.R. and Leatherwood, S. 1985. Bowhead whale (*Balaena mysticetus*). *In*: Handbook of marine mammals. Edited by S.H. Ridgeway and R. Harrison. Academic Press, London.

Rice, D.W., and Wolman, A.A. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). Special Publication No. 3. U.S. Fish & Wildlife Service, Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, WA. Copies available from: the Secretary-Treasurer of the Society, Dr. Bryan P. Glass, Department of Zoology, Oklahoma State University, Stillwater, OK 74074.

Richardson, J. and Thomson, D. (eds.). 2002. Bowhead whale feeding in the Eastern Alaska Beaufort Sea: update of scientific and traditional information. OCS Study MMS 2002-012; LGL Rep. TA 2196-7. Rep. From LGL Ltd., King City, Ont., for U.S. Minerals Management Serv., Anchorage, AK, and Herdon, VA. Vol. 1, xliv + 420 p; Vol. 2; 277 p.

Rooney, A.P., George, J.C. And Tarpley, R.J. 2002. Phylogenetic and morphometric analyses of the ingutuk, a morphological variant of the bowhead whale (*Balaena mysticetus*). Paper SC/54/BRG19 presented to the IWC Scientific Committee, Shimonoseki, Japan.

Rosa, C., George, J.C., Zeh, J., O'Hara, T. Botta, O. and Bada, J. 2004. Update on age estimation of bowhead whales using aspartic acid racemization. Paper SC/56/BRG6 presented to the 56th Scientific Committee of the International Whaling Commission, June 2004, Sorrento, Italy.

Rychel, A.L., Reedera, T.W., Bertaa, A. 2004. Phylogeny of mysticete whales based on mitochondrial and nuclear data. Molecular Phylogenetics and Evolution 32 (3): 892-901.

Schell, D.M., and Saupe, S.M. 1993. Feeding and growth as indicated by stable isotopes. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Sasaki, T., M. Nikaido, H. Hamilton, M. Goto, H. Kato, N. Kanda, L. A. Pastene, Y. Cao, R. E. Fordyce, M. Hasegawa, and N. Okada. 2005. Mitochondrial phylogenetics and evolution of mysticete whales. Syst Biol 2005 54: 77-90.

Stoker, S.W., Krupnik, I.I. 1993. Subsistence whaling. In: J.J. Burns, J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. 787 pp. Allen Press, Lawrence, Kansas.

Tarpley, R.J., Jarrell, G.H., George, J.C., Cubbage, J. and Stott, G.G. 1995. Male pseudohermaphroditism in the bowhead whale, *Balaena mysticetus*. Journal of Mammalogy 76 (4): 1267-1275

Tomilin, A.G. 1957. Mammals of the U.S.S.R. and adjacent countries. 9. Cetacea. (Translated by the Israel Program for Scientific Translations, Jerusalem, 1967). 717 pp.

True, F.W. 1904. The whalebone whales of the western North Atlantic. Smithsonian Institution, No. 1414; Washington, D.C.

Vaughan, T.A., Ryan J.M., Czaplewski, N.J. 2000. Mammalogy. Saunders College Publishing, Orlando, FL. 565 pp. + Appendices.

Willetto, C. E., O'Hara, Todd M., and Rowles, T. 2002. Bowhead Whale Health and Physiology Workshop. Published by the North Slope Borough, Barrow, Alaska.

Woodward, B.L., Winn, J.P., and Fish, F.E. 2006. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. Journal of Morphology 267:1284–1294 (2006).

Yonekura, J., Matsui, S. and Kasauya, T. 1980. On the external characters of *Globicephala macrorhynchus* off Taiji, Pacific coast of Japan. The scientific Reports of the Whales Research Institute. The Whales Research Institute, Tokyo, Japan.

Table 2.1. Standard cetacean measurements used in the analysis of bowhead whale morphology.

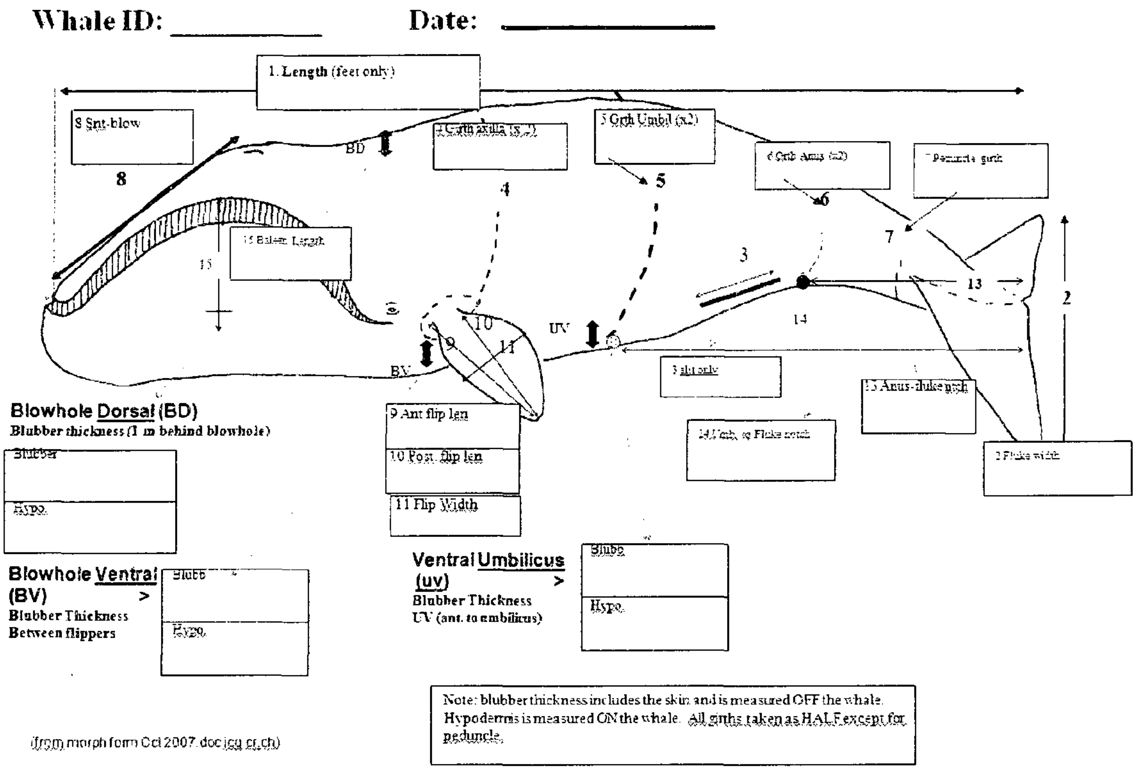
External Morphometric	Comment
1. whale_id	Year + village code + series number (NMFS code)
2. data quality	Morphometric measurement score 1-5; 1 is best; 1&2 used in this analysis
3. sex	Male, female, pseudohermaphrodite (0,1,2)
4. ingutuk?	Was the whale an *ingutuk*? (i.e., a yearling)
5. harvest date	Date of harvest
6. season	Season of harvest
7. body length	Body length to the nearest cm
8. Snout to blowhole	Straight line measurement from tip of rostrum to center of blowhole (cm)
9. Fluke	Straight line fluke width (cm)
10. Anterior flipper length	Straight line from axilla to anterior flipper length (cm)
11. Posterior Flipper length	Straight line from post-axilla to posterior Flipper length (cm)
12. Flipper width	Breadth of pectoral fin from distal digit I to digit (cm)
13. Girth at Axilla	Girth at axilla taken as a half-girth (cm)
14. Girth at umbilicus	Girth at the umbilicus taken as a half-girth(cm)
15. Girth at anus	Girth at the anus taken as a half girth(cm)
16. Girth at Peduncle	Girth at peduncle- usually taken as a complete circumference
17. Fluke to anus	Straight line measurement from fluke notch to anus
18. Fluke to umbilicus	Straight line measurement from fluke notch to umbilicus
19. Length genital groove	Length of genital grove (cm)
20. Baleen length	Straight line length of longest baleen plate (cm)
21. Dorsal Blubber thickness	Dorsal blubber thickness taken on ground after being removed from the animal (hypodermis excluded) (cm)
22. Ventral Blubber thickness	Ventral blubber thickness taken on ground after being removed from the animal (hypodermis excluded) (cm)
23. pregnant?	Was the animal pregnant?
24. skull length	Straight line condylo-basal measurement (cm)
25. mandible length	Straight line length of mandible (cm)
26. scapula length	Average longitudinal length of both scapula (cm)

Table 2.2 Summary of regression results of various morphometric characters as a function of body length. In cases where sex differences were not significant, the regression equation was estimated from the reduced model excluding the insignificant sex effect indicated by the Sex Diff *P*-value. The * indicates significance at the 0.05 level; and ** indicates significance at the 0.01 level. ψ indicates significant difference between body length groups but not when all lengths are used. For dorsal and ventral blubber thickness, only regressions for whales caught since 2003 were analyzed. Regressions with low R^2 have greater uncertainty, e.g., girths.

Body Length vs:	**Reg. Eq. Males**	**N**	**R^2**	**Females**	**P-Values**		
					Sex Diff.	**Sex Int.**	**Model**
Snt - blowhole (≤11.5m)	$y = 0.375x - 111.929$	192	0.875	$y = 0.375x - 114.029$	p = 0.387	p = 0.720	p<0.001
Snt. -blowhole (>11.5m)Ψ	$y = 0.324x - 80.730$	121	0.826	$y = 0.324x - 73.378$	p = 0.045*	p = 0.147	p<0.001
Fluke width	$y = 0.388 x - 46.446$	182	0.943	$y = 0.388 x - 45.992$	p = 0.844	p = 0.073	p<0.001
Ant. Flip length	$y = 0.182x - 26.97$	311	0.974	$y =.0.209x - 48.13$	p = 0.000**	p = 0.000**	p<0.001
Post. Flipper length	$y = 0.145x - 19.154$	310	0.924	$y = 0.176x - 46.889$	p = 0.000**	p = 0.000**	p<0.001
Flipper width	$y =0.101x - 26.104$	311	0.951	$y = 0.120x - 42.056$	p = 0.000**	p = 0.000**	p<0.001
Girth axilla	$y = 0.089x + 0.000193x^2 + 392.23$	306	0.819	$y = 0.089x + 0.000193x^2 + 392.23$	p = 0.466	p = 0.284	p<0.001
Girth umbilicus	$y = -0.282x + .00032x^{2+} 582.52$	222	0.659	$y = -0.335x + 0.00034x^2 + 618.07$	p = 0.090*	p = 0.049*	p<0.001
Girth anus	$y = -0.121x +0.00019x^2+ 283.47$	109	0.697	$y = -0.613x + 0.0004x^2 + 557.35$	p = 0. 998	p = 0.631	p<0.001
Girth peduncle	$y = 0.100x + 23.468$	298	0.904	$y = 0.100x + 23.645$	p = 0.858	p = 0.326	p<0.001
Baleen (≤ 9 m) Ψ	$y = 0.362x - 188.83$	90	0.455	$y = 0.362x - 187.679$	p = 0.880	p = 0.575	p<0.001
Baleen (> 9 m)	$y = 0.240x - 56.232$	159	0.848	$y = 0.240 x - 55.955$	p = 0.934	p = 0.858	p<0.001
Dorsal blubber (≥ 2003)	$y = -0.010x + 0.0000114x^2 + 19.926$	70	0.699	$y = -0.010x + 0.0000114x^2 + 19.346$	p = 0.407	P = 0.407	p<0.001
Ventral blubber (≥ 2003)	$y = -0.013x + 0.0000114x^2 + 20.359$	64	0.658	$y = -0.007x + 0.0000099x^2 + 20.915$	p = 0.376	P = 0.376	p<0.001
Scapula length	$y = 0.079x - 12.40$	59	0.949	$y = 0.103x - 33.86$	p = 0.003**	p = 0.000**	p<0.001
Mandible length	$y = 0.378x - 43.840$	54	0.962	$y = 0.376x - 39.476$	p = 0.498	p = 0.504	p<0.001
Skull width	$y = 0.149x - 15.256$	18	0.967	$y = 0.149x + 21.061$	p = 0.324	p = 0.147	p<0.001
Skull Length	$y = 0.366x - 30.122$	32	0.969	$y = 0.366x - 21.176$	p = 0.650	p = 0.447	p<0.001
Fluke-umbilicus	$y = 0.498x - 41.547$	21	0.980	$y = 0.421x - 33.753$	p = 0.053	p = 0.030**	p<0.001
Fluke --anus	$y = 0.238x + 24.332$	33	0.953	$y = 0.238x + 16.187$	p = 0.123	p = 0.172	p<0.001

Table 2.3. Body position of girth measurements for bowhead whales. Snt-axilla= distance from snout to axilla; snt-umb= snout to umbilicus; snt-anus = snout to anus; snt-ped= snout to peduncle; BL=body length.

		Ratios			
sp#	**BL**	**snt-axilla**	**snt-umb**	**snt-anus**	**snt-ped**
87B3	1099	0.45			0.91
98B10	1328	0.40	0.54	0.73	0.92
98B15	845	0.40			
98B16	915	0.36	0.56	0.75	
98B18	1150	0.41	0.57	0.77	0.95
98B19	952	0.34	0.54	0.74	
98B20	1180	0.42	0.58	0.78	0.92
98B21	1516	0.35	0.55	0.74	
98B24	1029	0.36	0.58	0.74	0.90
Mean		**0.39**	**0.56**	**0.75**	**0.92**



Whale ID: ____________ **Date:** ______________

1. Length (feet only)

8 Snt-blow

4 Grth axilla (x 2)

5 Grth Umbil (x2)

6 Grth Anus (x2)

7 Peduncle girth

15 Baleen Length

3 alt only

13 Anus-fluke notch

14 Umb. to Fluke notch

2 Fluke width

9 Ant flip len

10 Post. flip len

11 Flip Width

Blowhole Dorsal (BD)
Blubber thickness (1 in behind blowhole)

Blubber
Hypo.

Blowhole Ventral (BV) >
Blubber Thickness
Between flippers

Blubb
Hypo.

Ventral Umbilicus (uv) >
Blubber Thickness
UV (ant. to umbilicus)

Blubb
Hypo.

Note: blubber thickness includes the skin and is measured OFF the whale. Hypodermis is measured ON the whale. All girths taken as HALF except for peduncle.

(from morph form Oct 2007.doc jcg cr.ch)

Figure 2.1. Measurement schedule for landed bowhead whales, Alaska. Girths are taken as half-measures from the dorsal to ventral midlines and doubled. Flipper measurements are non-standard; they are taken from the axilla to the distal apex of the flipper.

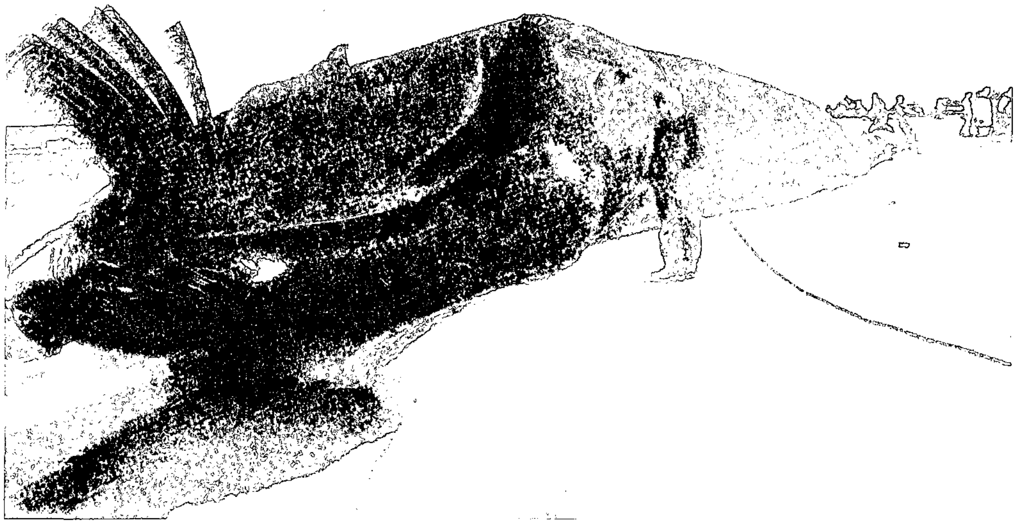
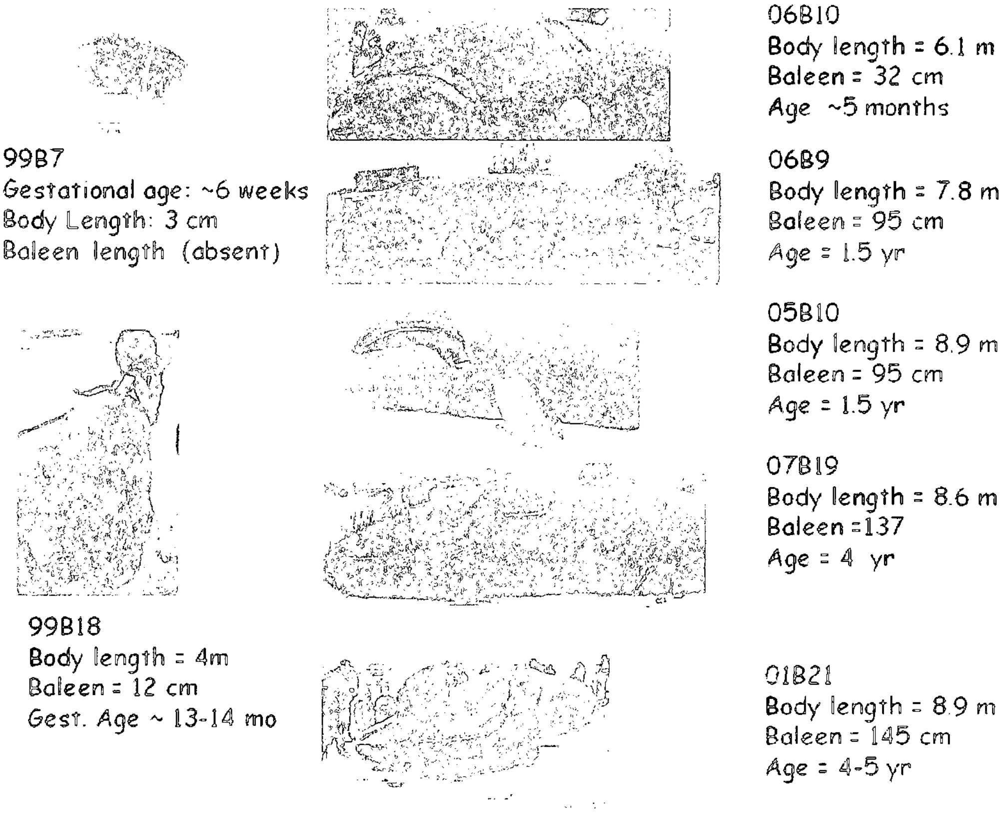


Figure 2.2. Overview photograph of a large bowhead whale. Note the long baleen and protruding rostrum. The animal is finless, the skin is black except for white scars, the white chin patch and age-related whitening of the peduncle, eye and base of the flipper.



99B7
Gestational age: ~6 weeks
Body Length: 3 cm
Baleen length (absent)

99B18
Body length = 4m
Baleen = 12 cm
Gest. Age ~ 13-14 mo

06B10
Body length = 6.1 m
Baleen = 32 cm
Age ~5 months

06B9
Body length = 7.8 m
Baleen = 95 cm
Age = 1.5 yr

05B10
Body length = 8.9 m
Baleen = 95 cm
Age = 1.5 yr

07B19
Body length = 8.6 m
Baleen =137
Age = 4 yr

01B21
Body length = 8.9 m
Baleen = 145 cm
Age = 4-5 yr

Figure 2.3. Photographs of bowhead whales in various growth phases for animals less than 10 yrs of age.

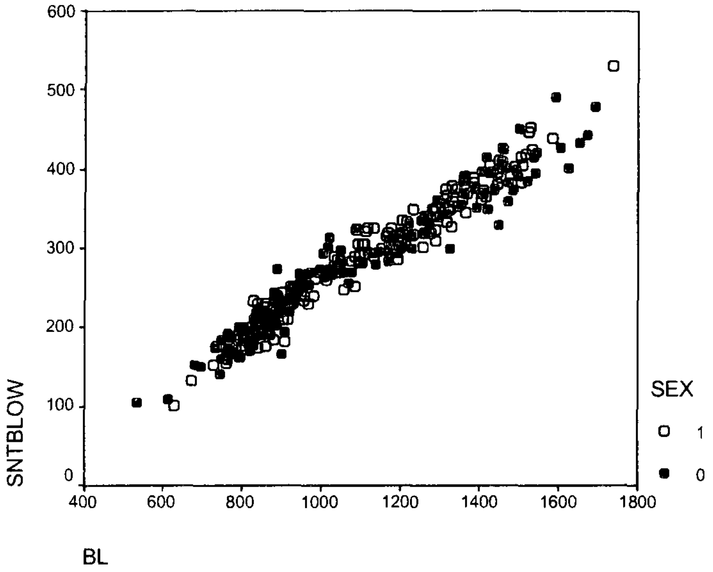
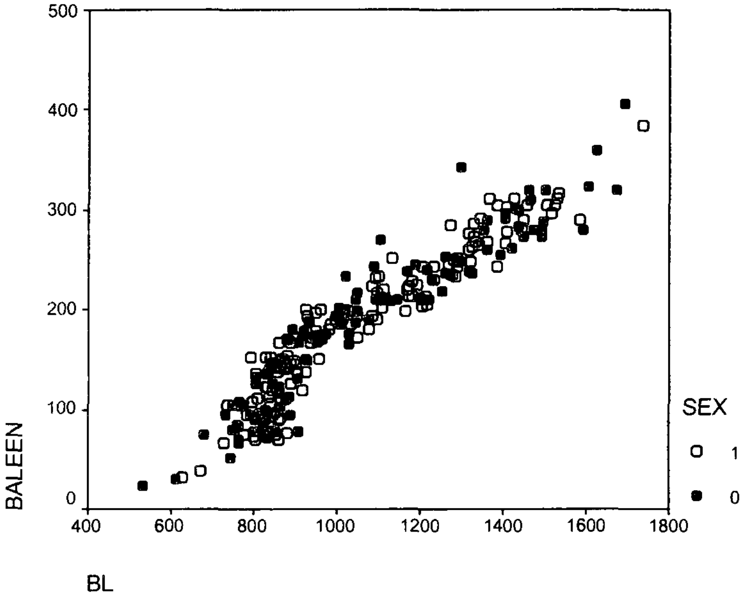
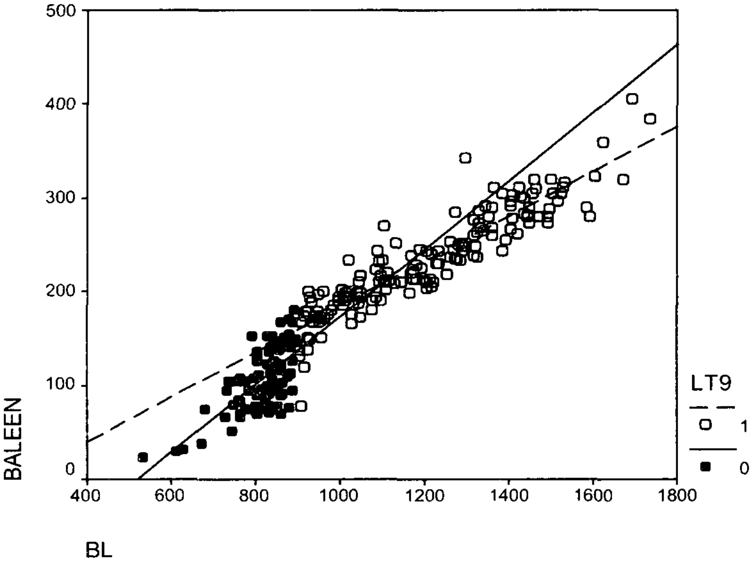


Figure 2.4. Body length (BL, cm) vs. snout-to-blowhole (SNTBLOW, cm) length for bowhead whales landed in Alaska. Females = 0, males = 1. Note the inflection in the data at ~10 m which also occurs for baleen vs. body length. All measurements are in cm.



a



b

Figure 2.5 a) Baleen length (BALEEN, cm) vs body length (BL cm) for bowhead whales, Alaska. Note the inflection at about 9-10 m. Females = 0, males = 1. b) Body length (BL, cm) vs. baleen length (BALEEN, cm) for bowhead whales ≤ 9 (0) and >9 m (1), Alaska. Note the inflection in baleen growth at 9-10 m. Least squares regression lines are fit to the data.

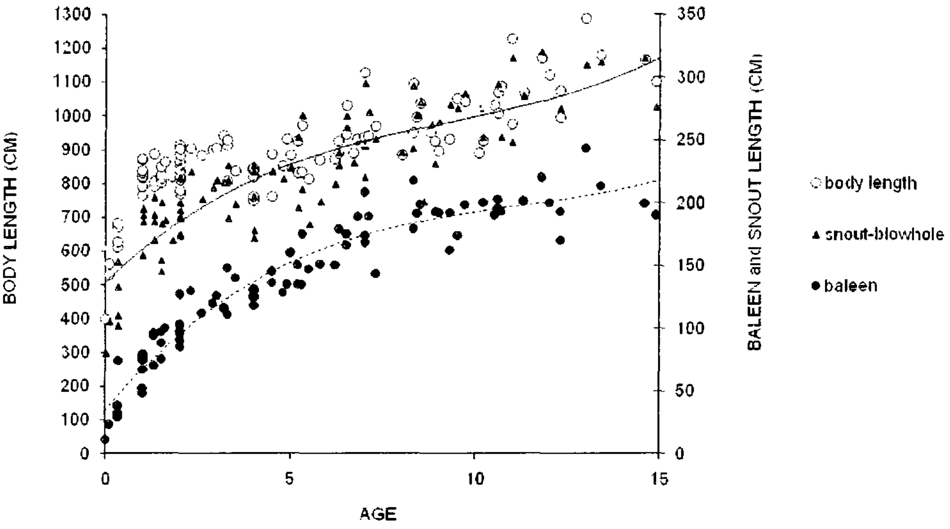


Figure 2.6. Bowhead whale body length (cm), snout-to-blowhole length (cm) and baleen length data plotted as a function of age, Alaska. All data were fit with a 3rd order polynomial regression.

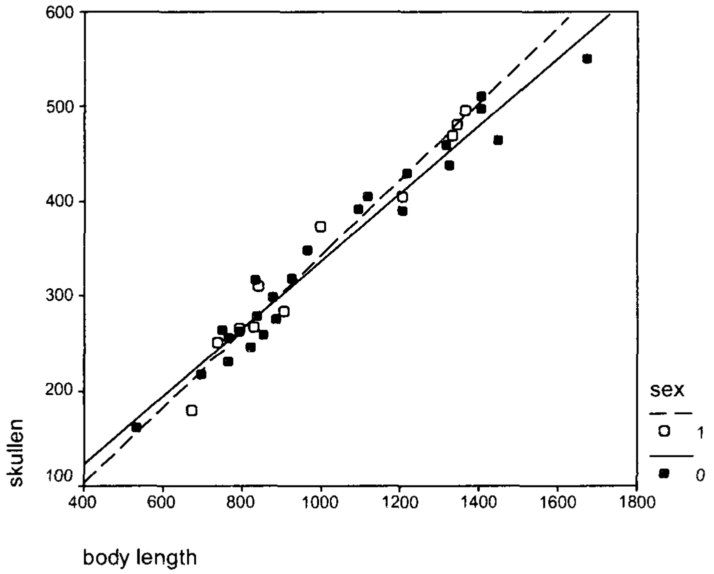


Figure 2.7. Bowhead whale condylo-basal skull length (SKULLEN) vs body length (BL), Alaska. The correlation is high ($R^2 > 0.9$) and there is no difference between sex. Linear regression lines are shown. Females = 0, males = 1.

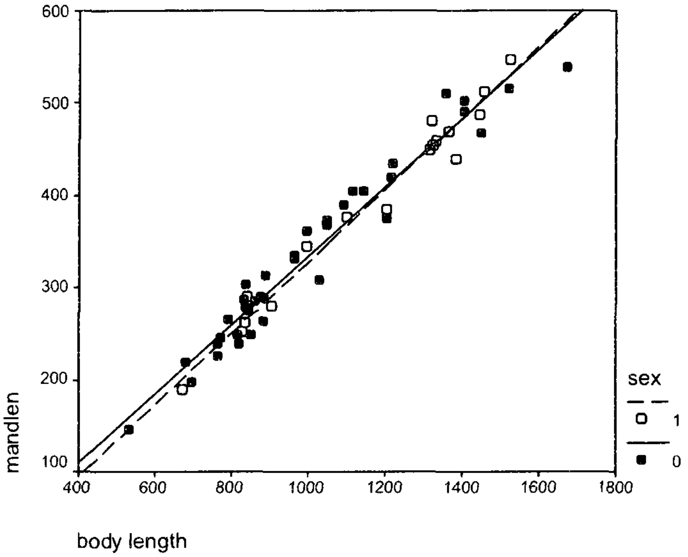


Figure 2.8. Mandible length (MANDLEN, cm) vs body length (BL, cm) for bowhead whales, Alaska. The correlation ($R^2 = 0.97$) is high; therefore mandible length can be used to accurately estimate body length. Females = 0, males = 1.

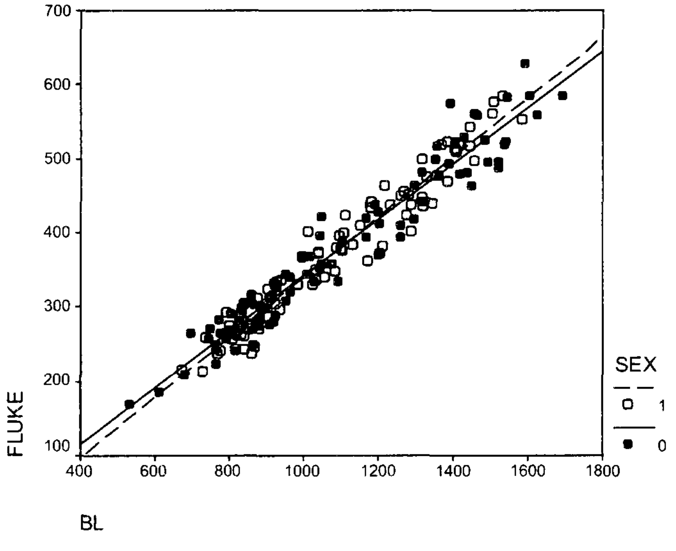


Figure 2.9. Plot of body length (BL, cm) vs. fluke width (FLUKE, cm) for bowhead whales, Alaska. These variables are highly correlated ($R^2 > .90$) with no significant difference between sexes. Thus, fluke width can be used to estimate body length fairly accurately. Females = 0, males = 1.

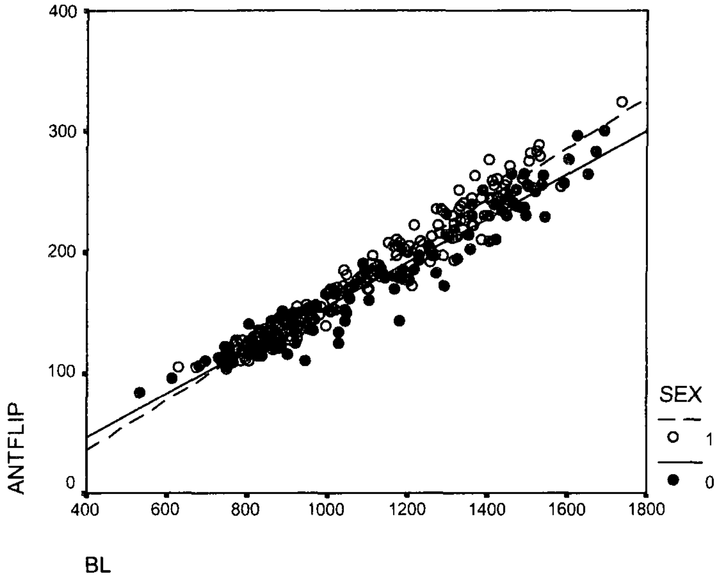


Figure 2.10. Body length (BL; cm) vs. anterior flipper length (ANTFLIP, cm) for bowhead whales, Alaska. There was a significant difference in anterior flipper length vs body length between sexes. Males have larger and longer pectoral appendages than females. Females = 0, males = 1.

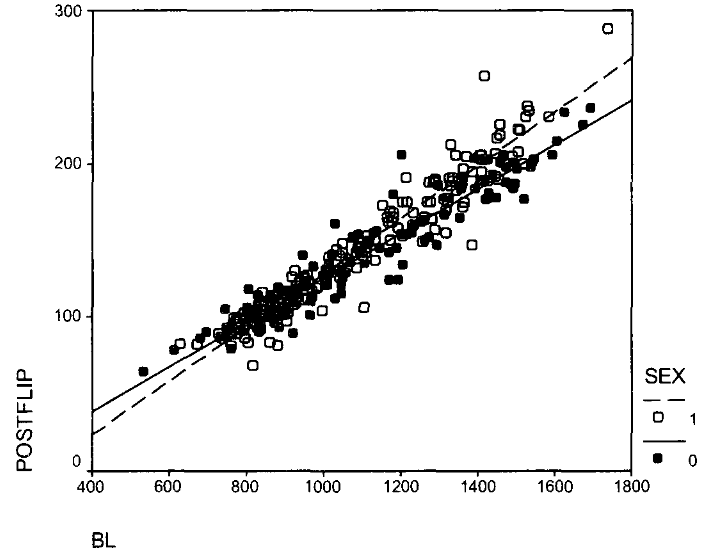


Figure 2.11. Body length (BL, cm) vs. posterior flipper length (POSTFLIP, cm) for bowhead whales, Alaska. As with the anterior flipper length, males had significantly longer pectoral appendages than females, particularly for large males (>14 m). Females = 0, males = 1.

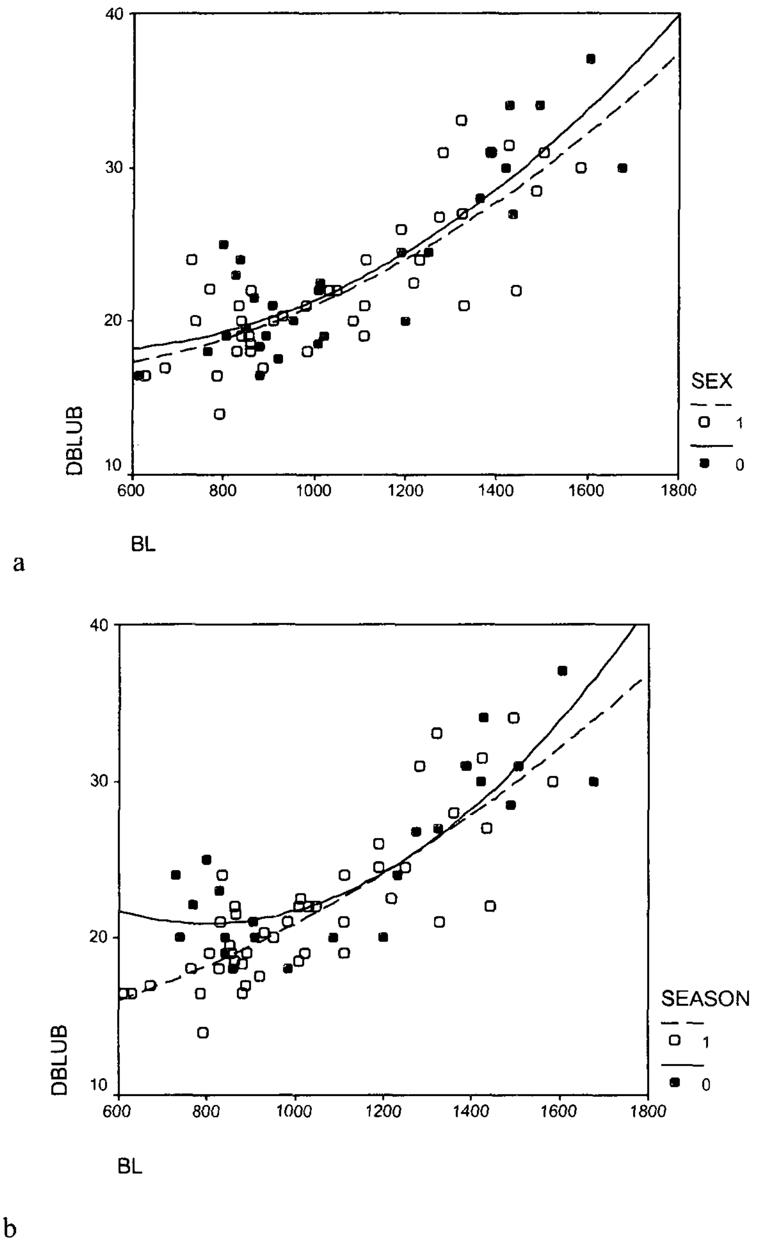


Figure 2.12 a) Dorsal blubber (DBLUB, cm) thickness vs body length (BL, cm) for bowhead whales, Alaska. Ingutuks (yearlings) are included in plots. Females = 0, males = 1. b) Dorsal blubber thickness (DBLUB, cm) by body length (BL, cm) by season (spring = 0, fall = 1), Alaska. Data for both plots were restricted to the years 2003 to 2007 due to inconsistencies in how blubber thickness was measured prior to that period. A quadratic model is fit to the data in both plots.

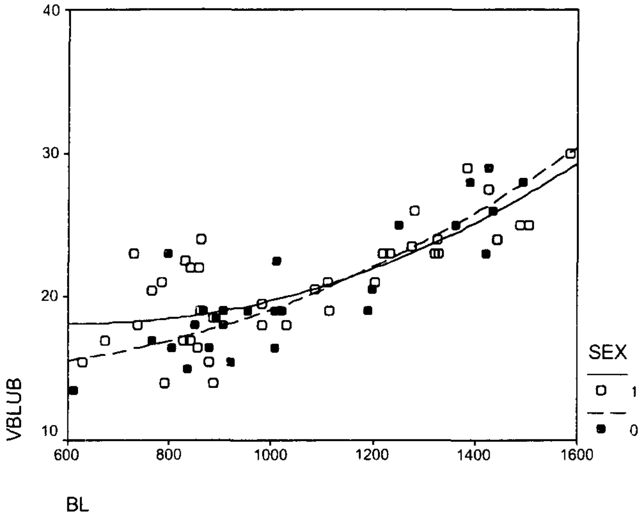


Figure 2.13. Ventral blubber thickness (VBLUB,cm) by body length (BL, cm) season (spring=0, fall=1), Alaska. Data were restricted to the years 2003 to 2007 due to inconsistencies in how blubber thickness was measured prior to that period. A quadratic model is fit to the data. Females = 0, males = 1.

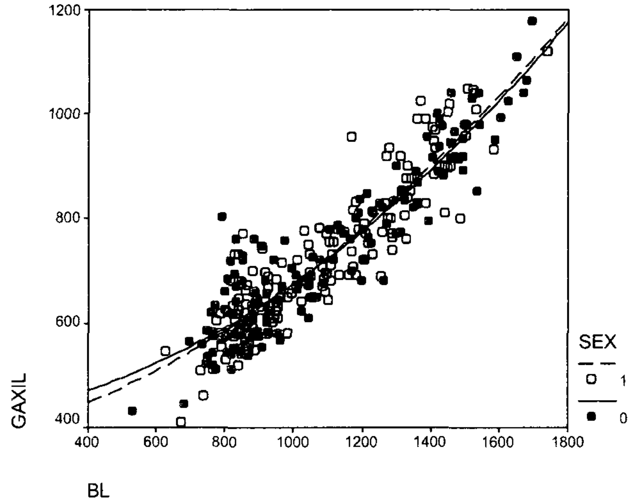


Figure 2.14 Girth at axilla (GAXIL) by body length (BL, cm) for males and females for bowhead whales, Alaska. Ingutuks are included in this plot and explain the rotund animals in the 8-9 m range. Females = 0, males = 1.

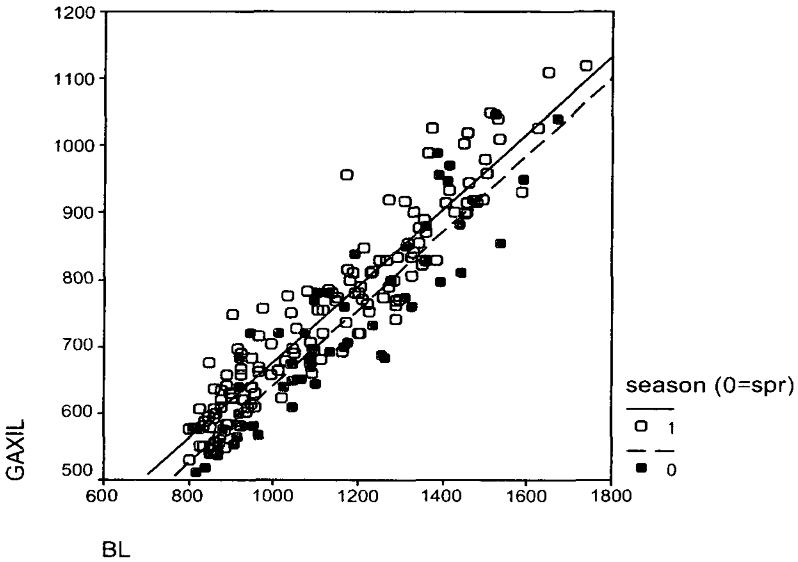


Figure 2.15 Girth at axilla (GAXIL, cm) by body length (BL, cm) for spring vs autumn animals for bowhead whales, Alaska. *Ingutuks* (yearlings) were removed from this analysis since spring yearlings are quite rotund from nursing rather than seasonal feeding. The girth at axilla is significantly different between seasons. Spring = 0, fall = 1.

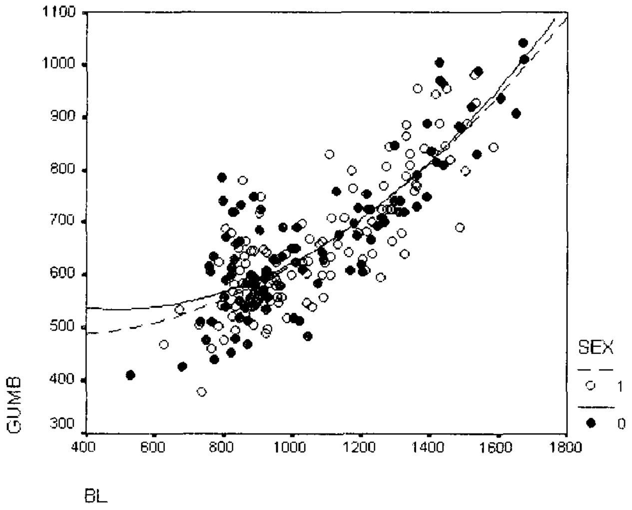


Figure 2.16. Girth at umbilicus (GUMB, cm) vs body length (BL, cm) for bowhead whales, Alaska. Yearlings or *Ingutuks* were included in this plot and form the group of whales with a large proportional girth in the 8 m range. There was a marginal difference between males and females. Females = 0, males = 1.

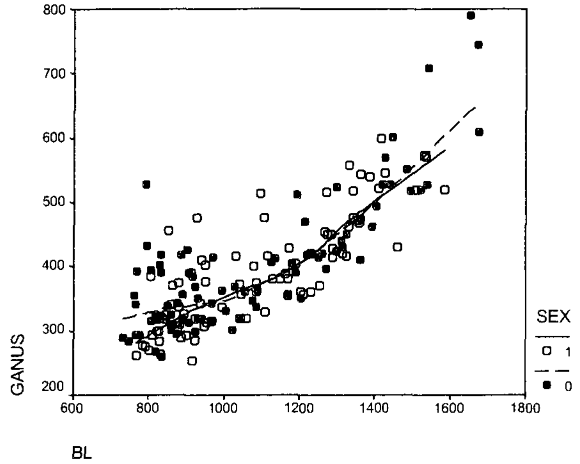


Figure 2.17. Girth at anus (GANUS, cm) vs body length (BL, cm) for bowhead whales, Alaska.. There was no significant difference between females (0) and males (1). The plot show Lowess (locally weighted scatter plot smoothing) curves fitted to 50% of the data. The 7.9 m female with the girth at anus over 500 cm appears to be a reliable measurement and was reported as a "very fat whale".

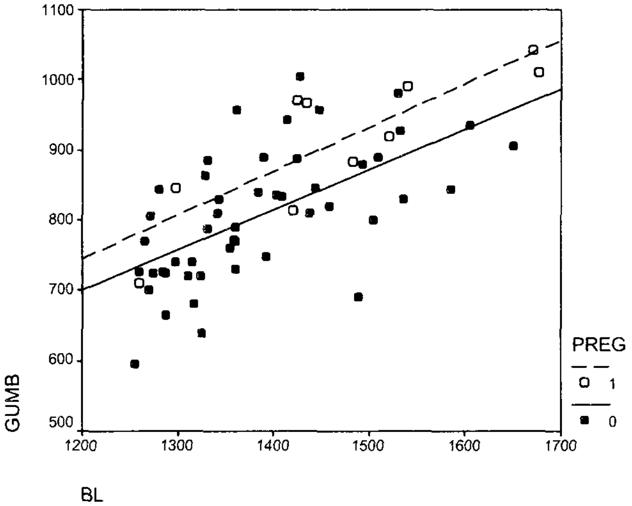


Figure 2.18. Bowhead whale body length (BL, cm) vs. girth at axilla (GUMB; cm) for pregnant (1) and non-pregnant (0) females over 1250 cm (the smallest pregnant whale as 1260 cm), Alaska. While there was no clear significant difference in girth at axilla, the girth at umbilicus for pregnant and non-pregnant whales was significantly different (p = 0.035).

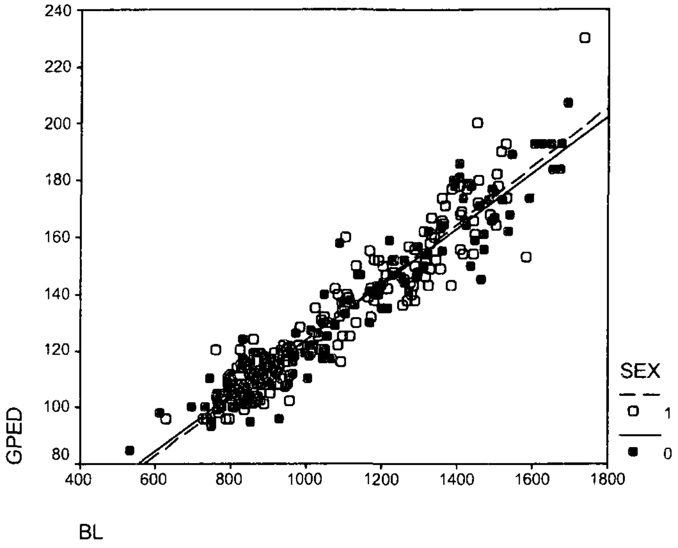


Figure 2.19. Bowhead girth at peduncle (GPED; cm) vs. body length (BL, cm), Alaska. There were no statistically significant differences between sexes. However, the largest measurement was for a male. Females = 0, males = 1.

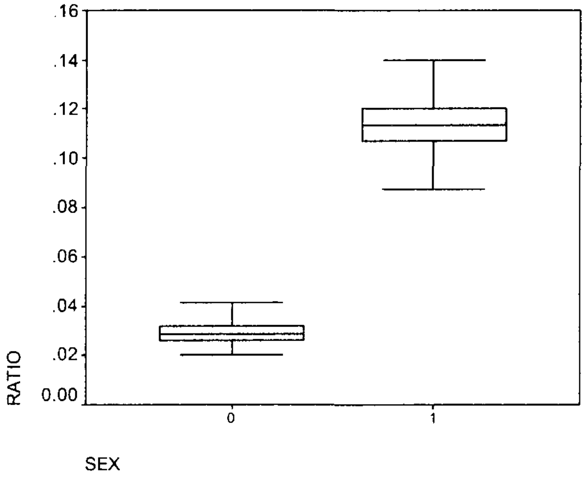


Figure 2.20. Box plot of the genital groove to body length (RATIO) by sex for bowhead whales, Alaska. Note that there is no overlap between the two sexes thus the ratio can be used to definitively sex a bowhead whale. Females = 0, males = 1.

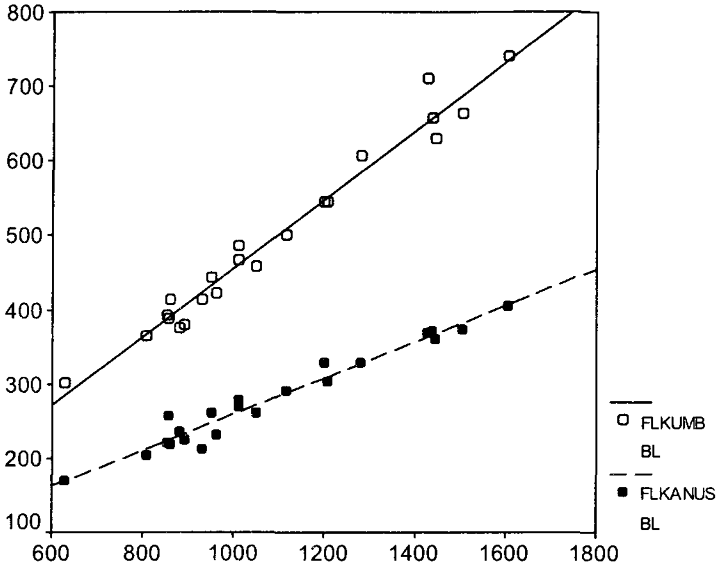


Figure 2.21. Fluke notch to anus (FLKANUS; cm) and to umbilicus (FLKUMB; cm) vs. body length (BL) (0=female, 1 = male) for bowhead whales, Alaska. Note that the growth in the lumbar or fluke notch to umbilicus section is more rapid (i.e., a steeper slope). In both cases the relationship is strongly correlated and appears linear.

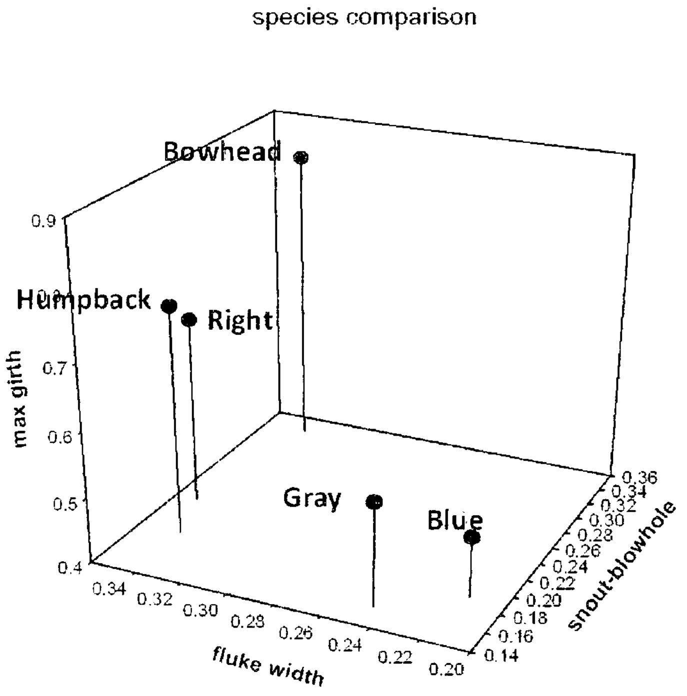


Figure 2.22. A 3-D scatter plot of three morphometric characters as a function of average body length in five species of baleen whales. Data for non-bowhead species are from Woodward *et al.* (2006). In this comparison, the bowhead whale sits apart from other baleen whales in the maximum girth and rostral length (snout-blowhole) ratios.

Chapter 3 Body Mass of Bowhead Whales (*Balaena mysticetus*) of the Bering Chukchi Beaufort Seas [1]

Abstract

Body mass estimates of large whales are useful in a number of applications such as energetic studies, ecosystem modeling, and estimating subsistence harvest food production. We weighed eight bowhead whales harvested by Alaskan Eskimos at Barrow, Alaska using direct and indirect methods. The three smaller specimens (< 4 m) and the largest (12.87 m) specimen were weighed directly, others were weighed using a combination of direct and estimation procedures. These small whales were fetuses but we included them in the analysis since their length/girth ratios were not significantly different from the other (sub-adult) whales ($p > 0.05$) in this study, and because their complete mass could be determined exactly on a scale. Three models were fit to the data: Shultz model: $W = aL^b$; Rice and Wolman $W = aLG^2$; modified Rice and Wolman $W = aL^{b1}G^{b2}$ (where W=weight (kg), L=length (m), Girth (m)). Based on AIC scores, the best fit model is the Rice and Wolman standard model ($R^2 = 0.987$). The modified Rice and Wolman model had a higher R^2 of 0.995, and an AIC score only slightly larger. The estimated body mass of a whale using the Rice and Wolman model matched well with body mass values estimated independently using a series of girth measurements ($R^2 = 0.983$; absolute difference 1.2%) to estimate the volume of the whale and subsequent mass assuming their density was 1.0 gm/cm^3.

Introduction

The bowhead whale (*Balaena mysticetus*) is a rotund pagophylic cetacean with a circumpolar distribution inhabiting most high latitude seas (Moore and Reeves, 1993). They have served a vital cultural and nutritional role in coastal Alaskan Eskimo societies for at least 1,000 years (Stoker and Krupnik, 1993; Nelson, 1969). Bowheads are distributed in five putative stocks, all of which were greatly reduced in the 1700s and 1800s by commercial whaling (Bockstoce and Botkin, 1983; Ross, 1993). The Bering-Chukchi-Beaufort Seas stock (BCBS) has the largest

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[1] J. C. George, M. Philo, R. Suydam, and G. Carroll. Body Mass of Bowhead Whales (*Balaena mysticetus*) of the Bering Chukchi Beaufort Seas. Formatted for Journal Arctic.

population size (estimated in 2001 at 10,470 whales 95% CI = 8,100 - 13,500) and is subject to an aboriginal hunt in 11 Alaskan villages (George *et al.*, 2004).

Bowhead body mass data are useful for energetic and feeding habitat research as well as nutritional studies of coastal Eskimos (George *et al.*, 1988; Braund and Associates, 1993; Lockyer *et al.*, 1985; Thomson 1987, 2002). Eskimo whale hunters harvest whales during their spring and fall hunt. During the spring hunt, whales are hauled onto the shorefast ice and butchered from 5 to 40 km from the nearest village. During the fall hunt the whales are pulled onto the beach where they are butchered. The whales are then divided into crew shares. Crews use a precise and complex process to divide and distribute equal proportions of the animal among the active whaling crews (e.g., George, 1981). The number of crew taking part in the butchering typically ranges from 20 to 50 people. Since the crews reduce the whales to manageable sections, we were able to use the butchering process as an opportunity to weigh animals (Figure 3.1).

We found it difficult to obtain complete and reliable mass estimates without interfering with butchering and distribution processes. Therefore, a combination of direct weights together with weight estimation techniques was used to weigh animals. Thus, the analysis of these bowhead whale mass data involves unique error issues.

Length-mass models have been estimated for a variety of whales, mainly using historical commercial harvest data, and then used to make inferences about other species (Lockyer, 1976). Beginning as early as 1907, simple formulae were used to estimate mass from the length of whales to approximate commercial whale yield (Shultz, 1938). George *et al.* (1988, 1991, 1992) provide preliminary mass estimates of some of the whales reported here. They do not, however, consider length-mass models in any detail. The mass estimates and models presented here are the only estimates based on direct measurements of bowhead whales that we could find in the literature.

Methods

Tallied Weights

The weights for whales 88B8, 88B4, 90B1, and 87B3 were estimated by tallying the weights of sections of the whale as they were removed during the butchering process. The weights of the sections were either: a) measured directly using a spring scale[2], b) estimated using the volumes of the sections (for blubber), or c) estimated visually for some muscle sections. Weights of the sections were sometimes estimated because butchering proceeds rapidly and there was not time to weigh every piece. Blubber with attached skin (blubber/skin) was flensed in approximately rectangular pieces so volume could be calculated from length, width and height measurements. To assess the accuracy of this technique, the weight/volume relationship (density) of a series of samples was compared. Whale 90B8 and term fetuses were weighed directly using a Phillips 2,268 kg x 0.5 kg electronic scales.

The Eskimo crew cuts the muscle into sections to divide the whale evenly among the crews during the butchering process. The muscle was cut into roughly 30-50 kg sections that were irregularly shaped, making volume estimates difficult using linear measurements. After weighing several pieces, we found that weight could be visually estimated quite accurately since the chunks were so uniform. The weights of several pieces of muscle were estimated in this way. Individual organs were weighed as they were removed from the whale. Skeletal elements were reduced to manageable sections using a chainsaw and then weighed with a spring scale suspended from a portable tripod on the ice in spring or using heavy equipment during the autumn hunt.

The weight for an animal was estimated as follows: a) the weights of all muscle pieces were tallied[3], b) the volume of the sections of blubber with attached skin were calculated, converted to weight estimates and tallied, c) weights of paired structures (kidney, lung, side of baleen, etc.) were calculated by weighing one and doubling the weight, d) blood was estimated to be 6 % of total weight (Lockyer, 1976) the skeletal sections were weighed and tallied, and e) the weights of all sections were summed to produce an estimate.

We estimated the blubber and skin or *maktak* mass by estimating its density and estimating the volume of the numerous *maktak* sections. Eskimo crews cut the blubber into roughly rectangular pieces, and measurements of length, width and depth were used to calculate the volume of each piece. Using results from laboratory experiments and field measurements (see below) we estimated the density of blubber as approximately 0.95 kg/l. The total mass of the blubber piece may be calculated as the product of its volume and its density. The volume of

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[2] All weights less that 90.7 kg were made with the Hanson 90.7 x 1 kg scale; measurements over 90.7 kg were made with a 136 kg x 2 kg or a 227 kg x 2 kg scale.

[3] Muscle sections were estimated visually in most cases. However, whale 88B8 was nearly entirely weighed in sections (even the *maktak*) since it was a small whale with thin blubber.

maktak strips was determined by measuring their length, width and height to nearest cm. We also weighed 42 of these sections to the nearest 0.5 kg.

Direct weights were calculated for four whales (three fetuses and one large subadult) (Table 3.1). We used the fetuses in this analysis since they could be accurately weighed and because their length/girth proportions were not significantly different than the sub-adult whales in this study. Whale 90B1 was directly weighed in sections using a certified 2,268 kg x 0.5 kg digital crane scale. The sections were summed to estimate the total mass of the animal and then corrected upwards for blood loss by 6% (Lockyer, 1976). Term fetuses were weighed using a 2,268 kg x 0.5 kg electronic platform scale.

Body length is taken as a straight line from the anterior tip of the rostrum to the notch between the tail flukes. For whales harvested before 1995, only an axillary half-girth was taken. Scales large enough to weigh large whales in one piece were not available, so the larger whales were weighed in pieces. Because whales must be butchered quickly to prevent spoilage, not all pieces removed from a whale were weighed directly due to time constraints. Each mass measurement technique contributes error to the total estimated mass of the whale. The uncertainty in these measurements was quantified and used to estimate statistical weights for each of the animals (Thompson, 1996).

Body mass data were then fit to three different models using SPSS PC 11.5. The models were as follows:

Shultz (1938) model	$W = aL^b$
Rice and Wolman (1971) (RW1)	$W = aLG^2$
Modified Rice and Wolman (RW2)	$W = aL^{b1}G^{b2}$

Where, W = Weight (or body mass, kg); L= Length (m) , G= axillary girth (m); "a" and "b" are fitted parameters.

The AIC scores for each model were calculated as follows:

$$AIC = n \cdot \log(RSS/n) + 2K + \text{constant}$$

Where n = 8 is the number of data points (whales), RSS is the residual sum of squares, and K is the number of fitted parameters.

Body mass was also estimated by a volumetric method. Since 1995, a series of four half-girth measurements were routinely made during postmortem examinations of whales (axilla, umbilicus, anus and peduncle). The locations of these girth measurements was measured along the whales' long axis so that the proportional length of each section could be determined. Then we divided the whale into a series of four frustums, summed them, and estimated the volume of the animal (see equation 1). Since bowhead whales are only slightly positively buoyant, the density of sea water (~1 gm/cc) was used to estimate mass from its volume. Body mass was determined using the two methods for 147 randomly chosen whales, and these masses were compared using least squares regression.

Whale volume[4] was calculated as follows:

Equation 1:

$$\text{Whale Volume} = \sum_{i=1}^{4} \frac{\pi * p \cdot BL}{3}\left(r_i^2 + r_i \cdot r_{i+1} + r_{i+1}^2\right) + \text{VF}$$

Where:

BL = body length

p = body section proportion of total length

r = radius of section *i, j* (snout, axilla, umbilicus, anus, peduncle)

VF = volume of flukes (omitted as negligible)

Proportion of total body length

Snout to axilla = 0.39

Axilla to umbilicus 0.17

Umbilicus to anus = 0.19

Anus to peduncle = 0.17

Peduncle to fluke notch = 0.07

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[4] The flukes were not included in the body mass estimate for the volume technique

Results and Discussion

Sufficient data were gathered for four whales to estimate body mass; direct weights were measured for four others (Tables 3.1, 3.2, Figure 3.1). The correlation coefficient for the rectangular blubber and epidermis (or *maktak*) sections (those cut evenly) was higher (r^2=0.93) than those for the non-rectangular pieces (r^2=0.45; Figure 3.2). Approximately 10-15% of the blubber/skin strips were asymmetrical. The high correlation coefficients in both cases confirm that linear measurements of blubber/skin sections can be used to accurately determine their weight. A mean *maktak* density of 0.95 gm/cc was estimated based on field measurements of 27 symmetrical *maktak* sections that were weighed. The "volume method" for estimating blubber mass made weighting whales on the sea ice manageable.

The visual estimation method amounted to roughly guessing the mass of a piece of the whale, usually muscle, by picking up the piece and comparing the mass to the previously lifted pieces. This method was the least precise but still gave surprisingly accurate results. An independent experiment with replicated trials on 14 test pieces of muscle provided an estimate of the standard error associated with this visual measurement process. The measured mean mass for 14 sections was 140.0 kg (SD = 40.4) versus 144.1 kg (SD = 51.1) for the visual estimation approach.

The number of sections with estimated weights varied for each whale. For example, whale 90B8 was weighed without using estimation techniques (all 69 pieces were weighed on scales) so its weight was more accurate than other whales weighed using mostly visual and volume estimation techniques. For whale 88B4, approximately one third of the sections were estimated using the volume method, one third using the visual method, and one third was weighed on scales. Since each whale was weighed in pieces, blood loss was considerable. Lockyer (1976) estimated blood loss due to flensing for baleen whales at 6% of body mass. We adjusted our total mass by this amount.

The fitted models were as follows:

The Schultz (1938) model (S1) is the simplest, least accurate and does not account for changes in girth. This model is useful for estimating mass where girth is not available.

$$W = aL^b$$

The resulting parameter estimates and 95% confidence intervals were:
$a = 50.33$ (95% CI -64.43 – 165.09; $b=2.45$ (95% CI = 1.51 – 3.38)

The Rice and Wolman (1971) models are more general and were originally developed for gray whales. In statistics, general models are those with more parameters and so, in this case, fit a broader range of body shapes. We fit the model RW1:

$$W = aLG^2$$

The resulting parameter estimates and 95% confidence intervals were:
$a = 38.53$ (95% CI = 35.85 – 41.21)

We also fit the model RW2,

$$W = aL^{b1}G^{b2}$$

and obtained parameter estimates and 95% confidence intervals of:
$a = 28.97$ (95% CI = 4.29 - 53.66), $b_1 = 0.028$ (95% CI = -0.81 - 0.87), $b_2 = 3.38$ (95% CI = 2.16 - 4.61).

The general RW1 model had the lowest AIC score of the models fitted to the data and appears to have good predictive capability (Table 3.2, Figure 3.3). The RW2 model had a similar AIC score and slightly higher R^2. Because the girth of bowhead whales varies between animals and seasons and the RW2 model is the most sensitive to this variation, it could be a better model but this could not be confirmed with so few data (Table 3.2). For obvious reasons, the S1 model is rather insensitive to morphologic differences and is useful only for whales in which girth data are lacking.

For sub-adult whales and those near the length at maturity, both the RW1 and RW2 models are adequate. The RW2 model has three parameters and the standard errors of the coefficients suggest it may be over parameterized since there was only 8 whales in the data set. For adult whales (> 13 m) it is difficult to determine which model is best, and estimating mass of a whale beyond the data is statistically unadvisable. However, we realize that mass estimates of large whales are needed for many applications and suggest either RW model is suitable for extrapolation.

Whale 90B1 was unusually heavy and its predicted mass was above the RW1 model-estimated weight (Figure 3.1). The whale was described by hunters as an "*ingutuk*" which is an Inupiat term for a fat young whale. Statistical diagnostics confirm that this whale was unusually heavy compared to the fitted model (Thompson, 1996).

Comparison with the volume method

We also compared the estimated weights of whales using the RW1 method with the mass of whales using an entirely independent method we call the "Volume Method" (VM). In this approach the volume of the animal was estimated from a series of girths (at the axilla, umbilicus, anus and peduncle). The flukes were omitted since it is almost impossible to estimate their volume and they contribute less than 1% to the total mass based on direct measurements. However, an adjustment for fluke mass could easily be added. We did not have all four girth measurements for the whales which we weighed (only a single axillary girth was taken in the years before 1995). Instead, we compared masses for 84 whales estimated using VM and RW1 models. Agreement between the models was excellent ($R^2 = 0.982$; N=84) further suggesting the RW1 method provides a good approximation of a bowhead whales' actual mass (Figure 3.4).

Large body size and comparisons with other cetaceans

Large body size in mysticetes is one of the key traits that allow cetaceans to range throughout the world's oceans. That is, the physical and energetic properties associated with exceptionally large body size offer some advantages. Their surface-to-volume ratio is low, which greatly reduces size-specific heat loss, and they carry a large quantity of fat compared to their maintenance metabolism. Large mysticetes can fast for over half the year following a relatively brief summer feeding period in some cases. They can extensively nurse while fasting which is rare among mammals (Costa and Williams, 1999). In physical terms, fat stores accumulate proportionally faster (mass$^{1.0}$) than maintenance metabolism (mass$^{0.75}$) as a function of body weight; hence large animals have proportionately larger reserves available. When mammals reach the mass of a bowhead, basal metabolic rates per kilogram are less than 1% of a mouse-sized mammal (Schmidt-Nielsen, 1997) and their fasting endurance is roughly 1000 times longer.

We compared the relative length/mass relationship of bowheads with other large cetaceans in four cetacean families to examine their general length-weight relationships (Figure 3.5). Bowheads and their close relatives, the right whales, were the most rotund at a given length. The balaenopterids (fin (*Balaenoptera physalus*), blue (*B. musculus*), sei (B. *borealis*), minke (*B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*) had much lower body mass at the same length. These differences probably reflect the general niche and life history of these species. The balaenopterids or rorquals are powerful, fast swimming whales with a slender, but heavily muscled body shape that is adapted to gulp feed and migrate across large ocean expanses. They typically feed at higher latitudes and migrate to low latitudes in winter. Bowhead whales, on the other hand, are slow growing and slow swimming cetaceans that live in circumpolar waters throughout the year feeding on low density prey (George *et al.*, 1999). Natural selection has produced a more rotund body shape, large head, thicker blubber and a greater mass at length in the bowhead compared with other cetaceans.

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References

Bockstoce, J.R. and Botkin, D.B. 1983. The historical status and reduction of the western arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry, 1848-1914. Report of the International Whaling Commission (Special Issue 5): 107-141.

Bockstoce, J.R. and Burns, J.J. 1993. Commercial whaling in the North Pacific sector. In The Bowhead Whale. Edited by J.J. Burns, J.J. Montague, and C.J. Cowles. Allen Press, Lawrence. pp. 563-576.

Braund, S.R. and Associates. 1993. North Slope Subsistence Study: Barrow, 1987, 1988 and 1989. Prepared by Stephen R. Braund and Associates with the Institute of Social and Economic Research, UAA, Anchorage, AK. Report to U.S. Dept. of the Interior, Minerals Management Service, Alaska OCS Region, Anchorage, AK.

Costa, D.P, and Williams, T.M. 1999. Marine Mammal Energetics. *In*: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution, pp. 578.

George, J.C. 1981. Current procedure for allocating the bowhead whale, *Balaena mysticetus*, by the Eskimo whalers of Barrow, Alaska. In: Tissue Structural Studies and Other Investigations on the Biology of Endangered Whales in the Beaufort Sea, T.F. Albert (ed.), pp. 789-804. Report to the Bureau of Land Management from the Department of Veterinary Science, University of Maryland, College Park, Md. 20742.

George, J. C., Philo, L. M., Carroll, G. M., and Albert, T. F. 1988. Subsistence Harvest of Bowhead Whales, *Balaena mysticetus*, by Alaskan Eskimos. Report of the International Whaling Commission 38: 389-392.

George, J.C., Philo, L.M., Suydam, R., Tarpley, R. and Albert, T.F. 1992. Summary of the 1989 and 1990 subsistence harvests of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos. Rep. int. Whal. Commn 42:479-483.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Can. J. Zool. 77:571-580.

George, J.C., Philo, L.M., and Carroll, G.M. 1991. Observations on weights of subsistence-harvested bowhead whales. *In*: Fifth Conference on the Biology of the Bowhead Whale, *Balaena mysticetus*: Extended Abstracts and Panel Discussions. T.F. Albert (ed.). North Slope Borough, Barrow, AK. 244 pp.

George, J. C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978-2001) of western arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20 (4):755-773.

Lockyer, C. 1976. Body weights of some large whales. *J. Cons. Int. Explor. Mer* 36(3):259-73

Lockyer, C.H., McConnell, L.C., and Waters, T. D. 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Can. J. Zool. 63:2328-2338.

Moore, S.E. and Reeves, R.R. 1993. Distribution and movement. In: J.J. Burns, J.J. Montague and Cowles, C.J. (eds.) The Bowhead Whale. Special publication No. 2 of the Society for Marine Mammalogy. 787 pp.

Nelson, R.K. 1969. Hunters of the northern ice. University of Chicago Press. 429 pp.

Rice, D.W. and Wolman, A.A. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). The American Society of Mammalogists, Special Publication 3. 142 pp.

Ross, W.G. 1993. Commercial whaling in the North Atlantic sector. pp 511-561. In: J.J. Burns, J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Schmidt-Nielsen. 1997. Animal physiology: adaptation and environment. Cambridge University Press. Cambridge, England. 611 pp.

Schultz, L.P. 1938. Can the weight of whales and large fish be calculated? *J. Mammal.*, 19: 480-87

Stoker, S.W., Krupnik, I.I. 1993. Subsistence whaling. In: J.J. Burns, J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. 787 pp. Allen Press, Lawrence, Kansas.

Thomson, D.H. 1987. Energetics. *In*: W.J. Richardson, Ed. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-1986. Report from LGL Ecological Research Associates, Inc. Bryan TX., for US Minerals Management Service, Reston, VA 22091. OCS Study 87-0037, Contract No. 14-12-0001-30233.

Thomson, D.H. 2002. Energetics of bowhead whales. p. 22-1 to 22-40. In: W.J. Richardson and D.H. Thomson. (eds.). Bowhead Whale Feeding in the Eastern Alaska Beaufort Sea: Update of Scientific and Traditional Information. For OCS Study MMS 2002-012; LGL Rep. TA 2196-7. Rep. From LGL Ltd., King City, Ontario Department of Interior, Mineral Management Service. Anchorage, AK 99598 and Herdon, VA. Vol. 1, xliv + 420 p; Vol. 2; 277 p.

Thompson, S. E. 1996. Two bowhead whale projects: historic catch uncertainty, and length, girth, mass modeling. Master's thesis, Colorado State University, Department of Statistics. Fort Collins, Colorado.

Table 3.1. Weights of bowhead whales used in this analysis. All data were collected from whales harvested during the annual subsistence hunt in northern Alaska, 1987-1990. Codes for the method of weighing are: D = direct weight, E = Estimated weight, D,E = a combination of direct and estimated weights.

Whale	**Mass (kg)**	**Length (m)**	**Girth (m)**	**Method**
87N1F	64	1.65	1.1	D
90B4F	928	3.9	2.3	D
89B2F	1047	4.01	2.6	D
88B8	4816	7.5	4.6	D,E
88B4	11551	9.04	5.9	D,E
90B1	13443	8.38	5.9	D,E
87B3	14800	10.99	6.1	D,E
90B8	27346	12.87	7.4	D

Table 3.2. Statistical data for the models fitted to harvested whales (1987-1990).

Model ID	**Model**	**R^2**	**AIC**
Shultz	$W= aL^b$	0.945	57.0
RW1	$W= aLG^2$	0.987	49.9
RW2	$W = aL^{b1}G^{b2}$	0.995	50.4

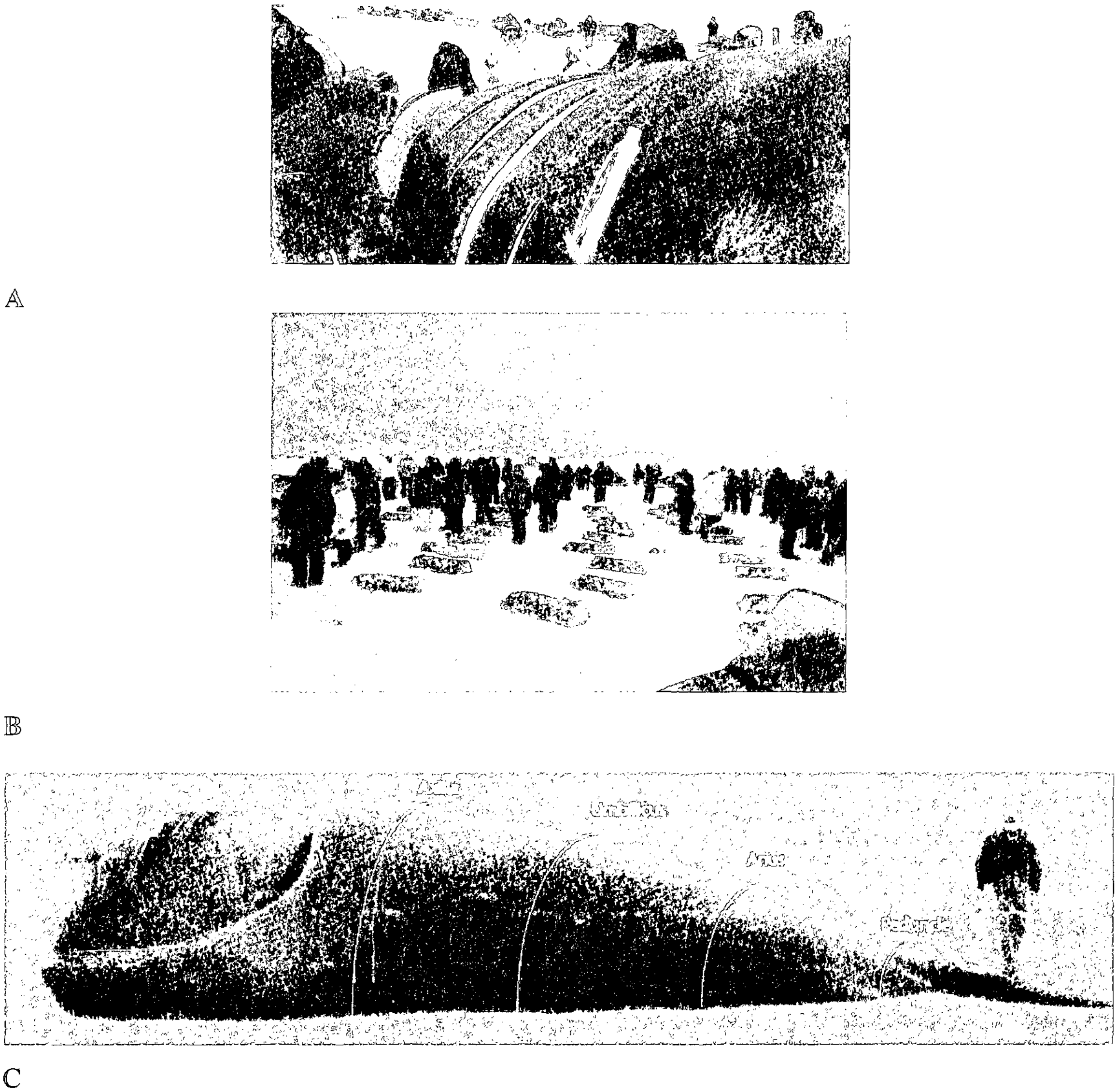

Figure 3.1 (A) During the whale butchering process, Eskimo hunters remove symmetrical sections of blubber, in part to allow consistent sharing of the animal. Virtually the entire animal is divided amongst the assisting crews and then further distributed to the community in a series of ceremonies and festivals. (B) For the first whale taken each season, the whale is divided among crews for all registered captains. Here whale 07B1, the first of the season, is being divided amongst all the crews. (C) Bowhead whale image showing locations of girth measurements for estimating volume.

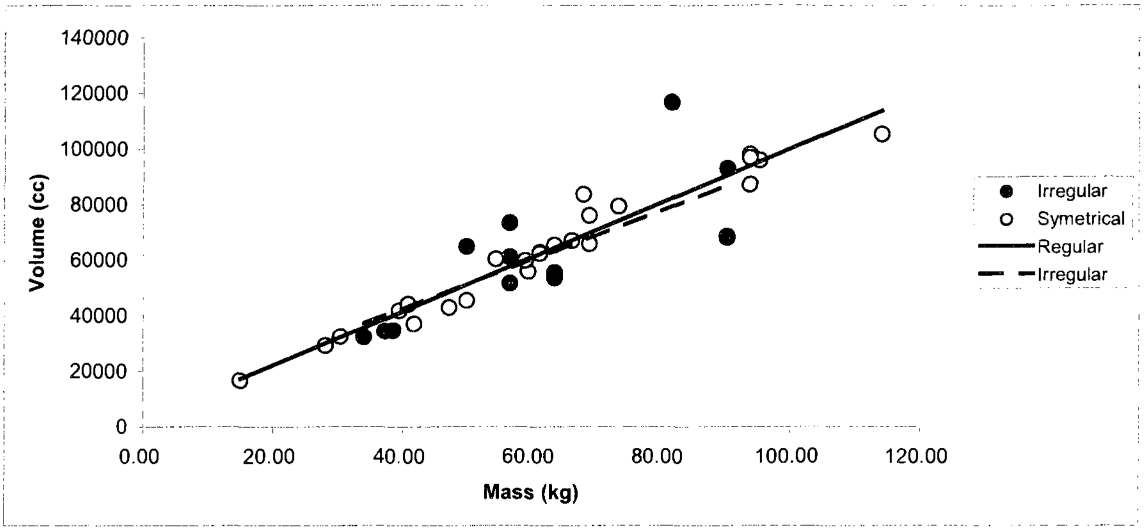

Figure 3.2. Estimated volume and measured mass (kg) of the *maktak* or blubber strips from bowhead whales, Alaska, 1987-1990. The highly predictive capability of the "volume method" for estimating blubber mass essentially made weighing the whales on the ice possible. In the short period during the butchering process, it was not possible to weigh all of the *maktak* sections.

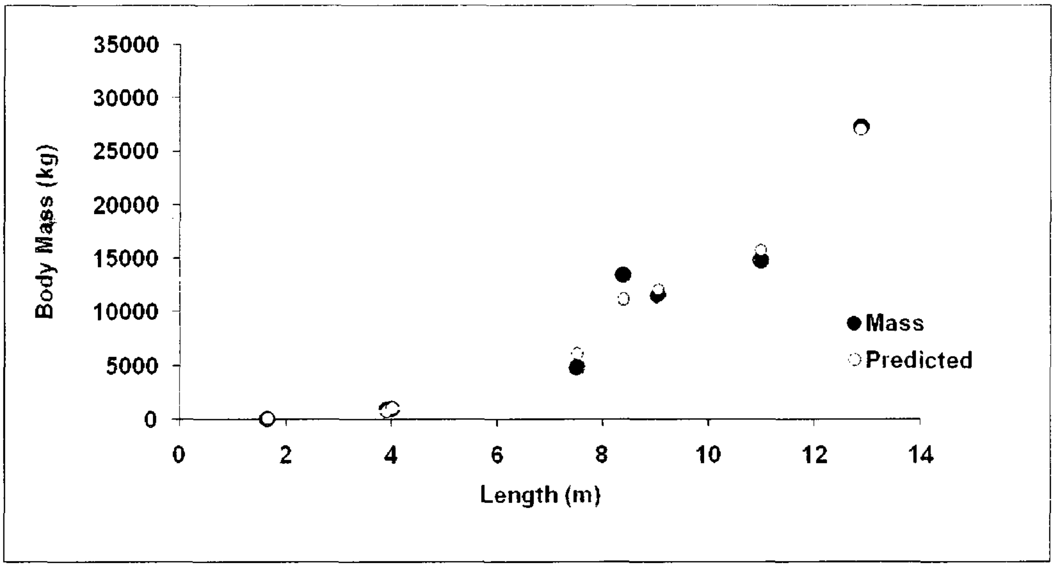

Figure 3.3. Body mass (kg) of bowhead whales (solid circles) weighed in this study by body length (m). Estimated body mass (open circles) using the Rice and Wolman-1 model.

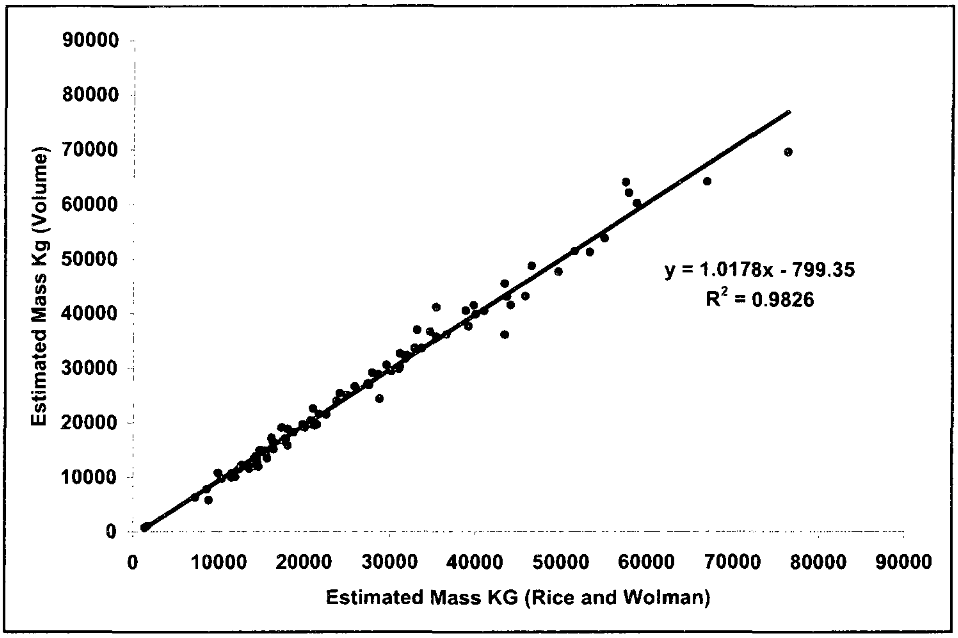

Figure 3.2. Bowhead whale body mass predicted by model RW1 and from a completely independent volumetric method. The correlation between the two methods is high ($R^2 = 0.81$) suggesting that the RW1 model is reasonably accurate even for mature bowhead whales. Alaska, 1987-1990.

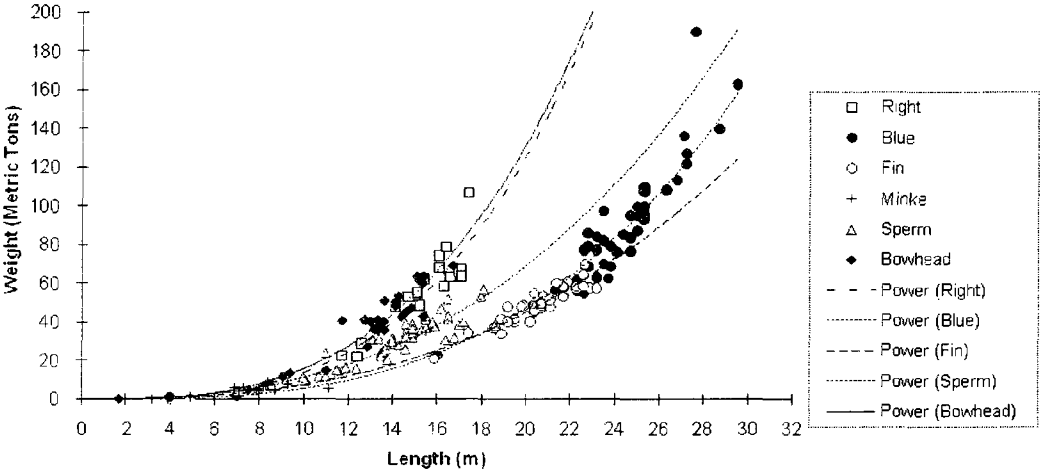

Figure 3.3. Comparative plot of power curves fit to body mass data for five species of cetaceans. Note that the bowhead and right whales are nearly identical in their length/mass curves.

Chapter 4 Age and Growth Estimates of Bowhead Whales (*Balaena mysticetus*) via Aspartic Acid Racemization[1]

Abstract

A total of 48 eye globes was collected and analyzed to estimate ages of bowhead whales using the aspartic acid racemization technique. In this technique, age is estimated by intrinsic changes in the D and L enantiomers of aspartic acid in the nucleus of the eye lens. Age estimates were successful for 42 animals. Racemization rate (Kasp) for aspartic acid was based on data from earlier studies of humans and fin whales; the estimate used was $1.18 \times 10^{-3} \times yr^{-1}$. The D/L ratio at birth (D/L_0) was estimated using animals ≤ 2 yr (n=8) since variability in the D/L measurements is large enough that differences among ages in this range are unmeasurable. The D/L_0 estimate was 0.0285. Variance of the age estimates was obtained using the delta method. Based on these data, growth appears faster for females than males. Age at sexual maturity (age at length 12 -13 m for males and 13 - 13.5 m for females) occurs at ages of around 25 yr. Growth slows markedly for both sexes at roughly 40-50 yr. Four individuals (all males) exceeded 100 yr in age. Standard error increased with estimated age, but the age estimates had lower coefficients of variation for older animals. Recoveries of "traditional" whale hunting tools from five recently harvested whales also suggest lifespans in excess of 100 yr for some whales.

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[1] J. C. George, J. Bada, J. Zeh, L. Scott, S. E. Brown, T. O'Hara, and R. Suydam. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via Aspartic Acid Racemization. Canadian Journal of Zoology 77: 571-580.

Introduction

Estimating the age of cetaceans has been the subject of considerable research (Perrin and Myrick 1980; Christensen 1981; Hohn *et al.,* 1989). Age is a key variable in all aspects of wildlife research. For odontocetes, age can be determined by sectioning a tooth and "reading" or counting the growth layer groups (GLGs). GLGs are considered to be annual in many odontocetes (Hohn *et al.* 1989). In some cases, well marked whales (both odontocetes and mysticetes) can be reidentified from photographs. If the animal was first marked as a neonate or the age was known then the age of the animal can be determined (Payne *et al.* 1990). A routine method for determining the age of mysticetes is through analysis of tissues collected during postmortem examination. In many mysticetes, growth layers (horny epithelium) called 'ear plugs' form on the external surface of the tympanum in the external auditory meatus (Slijper 1962). These can be counted to give an indication of age, however, such laminations do not form in bowhead whales (*Balaena mysticetus*). Schell *et al.* (1989) demonstrated that the age of bowhead whales could be estimated by counting oscillations in the stable carbon isotopes in the baleen, however, this technique is limited to ≤ 11 yr due to wear at the distal end of the plate. Christensen (1981) demonstrated the usefulness of tympanic bullae in estimating age. His work indicated a highly significant correlation with ear plug laminae (slope 1.01; $r = 0.89$) suggesting growth layers in bullae give a reliable estimate of age. Furthermore, Christensen (1981) reported that bullae were more often readable than ear plugs.

Determining age by measuring the degree of racemization of aspartic acid, an amino acid in the eye lens and teeth, has been applied to several species of marine mammals including bowhead whales (Bada and Brown 1980; Bada *et al.* 1980; Bada and Brown 1981; Bada *et al.* 1983; Bada 1984; Nerini 1983a,b). We will refer to the technique used in this analysis as the aspartic acid racemization technique (AAR). The technique is based on the fact that aspartic acid can exist in two different isomeric forms called the D and L enantiomers (optical isomers). In the last century, Pasteur demonstrated that living organisms produce only L-enantiomer (Bada *et al.*. 1980). Living organisms maintain the disequalibrium state metabolically. In the absence of such maintenance, a process called "racemization" begins. In the racemization reaction, the L amino acids are converted interchangeably into the D enantiomer until there are equal proportions of both enantiomers or a D/L ratio of 1.0. The rate at which racemization occurs is different for each amino acid and is affected by temperature. The greater the temperature, the faster the reaction.

Since the nucleus of the eye lens and tooth enamel are metabolically inactive tissues, changes in the D/L ratio are mostly temperature controlled. In most mammals, the proteins are "incubated" at about 37°C. Since the racemization rates have been measured, the age of these tissues can be estimated from the D/L ratio (Bada *et al.* 1980). The D/L value when the animal is born (D/L_0) is another variable that must be determined in order to use this technique. This value is slightly greater than 0 and therefore must be subtracted from the tissue measurement.

Nerini (1983a) explored two techniques for aging bowhead whales including tympanic bullae lamina and AAR of the eye lens. Following initial studies, Nerini concluded that due to (a) the large variability in the age estimates for the AAR technique compared with ear plug laminae in fin whales and (b) the implied delayed age at sexual maturity, the technique was of little use for aging bowhead whales.

Schell *et al.* (1989) independently estimated ages of bowhead whales using the "baleen aging" approach. Their estimates supported the advanced age at sexual maturity suggested by the AAR technique.

Other independent approaches at aging bowhead whales and estimating survival rates all suggest slow growth, great longevity and high survival rates.

- Koski *et al.* (1992) used photographic recaptures to estimate growth rates of bowhead whales. Their analysis suggested advanced age at sexual maturity of "late teens to mid-twenties".
- Whitcher *et al.* (1996) reported high survival rates (ca 0.99) based on analysis of photographic recaptures.
- The discovery of several traditional (pre-contact) whaling tools in living whales suggests advanced longevity (George *et al.* 1995; Krupnik 1998).
- Posterior distributions from Bayesian population assessments favor values for age at sexual maturity from 15 to 24 (Givens *et al.* 1995).

Population assessment models used for managing the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Givens *et al.* 1995; Punt and Butterworth 1997) require information about maximum age and/or adult survival. Currently the upper bound of adult survival rate, a model input, is based on "weight of evidence" rather than a truly data-based calculation. Hence, data on longevity are useful for setting a reasonable bound on this rate (IWC 1997).

This paper reassesses the AAR technique and reports the results of new analyses using the technique to gain new information on longevity, growth and other natural history parameters for bowhead whales.

Methods

Sample Collection and Estimation of D/L Ratio

North Slope Borough (NSB) and NOAA National Marine Mammal Laboratory (NMML) personnel carefully collected a series of bowhead eyes from animals taken between 1978-1981 and 1993-1997 during the annual harvest of whales by Alaskan Eskimos. The eyes were immediately frozen, returned to the laboratory and dissected to recover the intact lens nucleus. Any lens samples in which the nucleus was not easily visible or was contaminated with blood were discarded. Following a six hour hydrolysis in 6 M HCl to break down lens nucleus proteins to free amino acids, the (average) extent of aspartic acid racemization (D/L ratio) in each lens nucleus sample was determined using either ion exchange or high performance liquid chromatography (HPLC) based methodologies (Bada 1984; Zhao and Bada 1995). The D/L ratios for the samples obtained in the 1978-1981 harvest were determined using ion exchange chromatography (Nerini, 1983a; Bada, 1984); all other D/L ratios were determined using the HPLC based method (Zhao and Bada, 1995).

Estimating the Racemization Rate for Aspartic Acid

The racemization rate (Kasp) for aspartic acid is determined by regressing the natural log of (1+D/L)/(1-D/L) for a sample on the animals' ages (Masters *et al.* 1977). The slope of the regression line estimates 2Kasp. In the case of humans and fin whales, the relationship appears to be linear. Masters *et al.* (1977) reported 2Kasp for humans, with body temperature 37°C, as $2.50\text{x}10^{-3}\ \text{yr}^{-1}$ with a standard error of $0.29\text{x}10^{-3}\text{yr}^{-1}$ based on a sample of 17 normal human eye lenses. We estimated 2Kasp for fin whales based on the sample of 16 whales given in Nerini (1983b) (with average D/L used when two lenses were available) as $2.209\text{x}10^{-3}\text{yr}^{-1}$ with a standard error of $0.716\text{x}10^{-3}\text{yr}^{-1}$. Note that the maximum deep body temperature of fin whales (36.1° C) is lower than humans, and one would expect Kasp to be lower (Brodie and Paasche 1985). However, ages of the fin whales, based on ear plug data, are less precisely determined than human ages, increasing the variability of the estimate of 2Kasp for fin whales and perhaps leading it to be negatively biased. The human and fin whale estimates are not significantly different, and if we were convinced that both were estimating the same quantity, we would use a weighted average of the two, which would be close to the more precise human estimate. We opted instead to use an unweighted average ($2.35\times10^{-3}yr^{-1}$) to give some weight to the possibility that whale 2Kasp is lower than human. The estimated variance of this average is $V_k = 0.149\times10^{-6}$, and the standard error 0.39×10^{-3} yr^{-1}.

Estimating Age and the Relationship of Length to Age

The ratio of L to D aspartic acid was determined by the method of Zhao and Bada (1995). Ages were calculated using the unweighted average estimate of 2Kasp given in the previous section as follows:

$$\text{age} = [\ln((1+D/L)/(1-D/L)) - \ln((1+D/L_o)/(1-D/L_o))]/[2Kasp]$$

Growth rates were estimated by fitting the von Bertalanffy growth curve model to the data using non-linear least squares. The fitted model was:

$$\text{length (y)} = (Lmax + I_F \bullet Ldiff)\ (1.0\text{-}\exp(-k(t-t_o))$$

where t = age, Lmax = average maximum length for males, I_F is coded as 0 for males and 1 for females, Ldiff = average difference between female and male maximum length, k = rate constant, and t_o= age at length 0. Note that t_o is not really an age but rather a constant analogous to the intercept in a linear model which permits the growth curve to be fit even if some of the age estimates are negative and the smallest lengths are much greater than zero.

Determining the D/L_o (age 0) Value

The D/L_o estimate is a critical variable in calculating the age estimates. The D/L_o value for the term fetus was 0.027; however, this single sample may not be representative and has no error term. The variability in the D/L measurements is large enough that age differences between ages 0 and 2 are unmeasurable. Therefore, we used all the animals assumed on the basis of their baleen length (<110 cm) to be age 2 or less in calculating the D/L_o term and its associated variance. This baleen length for animals age 2 or less is based on data in Table 4.4 of Schell (1992). We used the mean of $\ln((1+D/L)/(1-D/L))$ for all animals with baleen less than 110 cm in length (n=8), including the term fetus (4.1 m; 95B8f), as the D/L_o term in the equation for age. The sample variance V_o was used as the estimated variance of the D/L_o term.

D/L Ratio Measurement Error

To estimate the variance of a D/L measurement, four "blind" tests were conducted. Paired eye globes from four animals were analyzed without prior knowledge that they were from the same animal. The D/L ratio was estimated for each. These data, together with three similar paired fin whale samples from Nerini (1983b), were used to obtain an estimated variance V of a single measured value of $\ln((1+D/L)/(1-D/L))$ from an analysis of variance.

Standard Error for Age Estimates

We applied the delta method (Seber 1982, pp. 7-8) and a formula of Goodman (1960) for an estimate of the variance of a product of two independent random variables to calculate standard errors for the age estimates. This approach is necessary to treat the multiple sources of error in the estimates discussed above: measurement errors in the D/L ratios of the samples, variability in the D/L ratio at age 0, and error in the estimate of 2Kasp.

The equation for age given above can be written as the product of two independent random variables: age = xy where $x = [\ln((1+D/L)/(1-D/L))-\ln((1+D/L_o)/(1-D/L_o))]$ and $y = 1/[2Kasp]$. These quantities are clearly independent since x is estimated from bowhead data and y from human and fin whale data. Since the two terms in x are independent for all the sampled whales except the eight young ones used to estimate the D/L_o term, an estimate of the variance of x is given by $V_x = V+V_o$. The delta method gives us $V_y = V_k/[2Kasp]^4$ as an estimate of the variance of y. Then formula (5) of Goodman (1960) gives

$$V(age) = x^2V_y + y^2V_x - V_xV_y$$

where V(age) is the estimated variance of the age estimate with the appropriate measured and estimated quantities used in computing x and y. The standard error (SE) is just the square root of V(age).

Calibration of HPLC Analysis

Five standards were made from Fisher determined 100% L aspartic acid and 1:1 D/L (racemic mixture) aspartic acid and doubly distilled water. These known D/L ratios were used to test the accuracy of the HPLC at slightly different ratios. A calibration model was obtained by regressing "known" on "measured" D/L ratios where the constant was set to 0. The model was then used to correct the measured D/L of the samples run on that particular day. The correlation coefficients were all at least 0.99.

Different buffers, different columns, different concentrations of the sample, insufficiently cleared columns, and just plain touchiness of the machine all cause random error. The need for this calibration is because the HPLC may measure different concentrations at different levels of accuracy, so the standards span likely sample D/L ratios.

Each lens sample was run at an approximate concentration of 10^{-4} molar, and on low attenuation, meaning that their resulting integrated peaks would be large so as to increase the accuracy of the measurement. The D and L peaks of aspartic acid were identifiable by their retention times and their relative sizes and shapes, and the ratio calculated from the areas given by the integrator.

Results and Discussion

Eye lenses were collected from 48 bowhead whales. Of these whales, 24 (50%) were female and 24 were male, 24 were >13 m and presumably mature. Of these 48 animals, racemization age was estimated for 42 animals (Table 4.1; Figure 4.1 and 4.2); again the sex ratio was 50:50. In six cases, samples were excluded due to problems associated with dissecting out the eye lens nucleus and from samples damaged during handling. If the sample is contaminated with "modern" tissue during dissection (e.g. blood) then it cannot be used. The von Bertalanffy growth model was fit to the age-length data (Table 4.2, Figure 4.1).

The estimated ages varied considerably for a given length class. This is expected for young animals (<10 m) based on work by Schell *et al.* (1989) and others. However, variability in Kasp estimates, measured D/L ratio, and D/L_0 values also produce substantial error (Table 4.1). Uncertainty in the Kasp rate is a major contributor to uncertainty in the estimated ages, especially the older ones. Errors in the D/L measurements appear to be relatively small, although there appear to be outliers, perhaps caused by sample contamination. Error in T_0 estimates and possible sample contamination account for most of the variability in the age estimates at the younger ages. Taken together, these sources of error lead to large coefficients of variation (CV) for the age estimates, particularly for young animals. Standard errors increased with age while CV decreased; thus older animals have greater precision in a relative sense (Figure 4.2).

Estimate of D/L_o

The mean value of the $\ln((1+D/L_0)/(1-D/L_o))$ term for the eight animals with baleen less than 110 cm was 0.05692, corresponding to $D/L_o = 0.0285$. The sample variance of the $\ln((1+D/L_0)/(1-D/L_o))$ term among these animals was $V_o = 0.9809 \times 10^{-4}$.

D/L Ratio Measurement Error (HPLC machine)

The residual mean square from an analysis of variance of $\ln((1+D/L)/(1-D/L))$, with each whale with paired data constituting a group, was $V = 0.7946 \times 10^{-4}$. A paired t-test between left and right globes for the bowhead whales indicated no significant differences in D/L ratio ($p = 0.48$), and there was no significant difference when the fin whale pairs were also included ($n=7$; $p=0.91$). A sample of seven whales gives an imprecise estimate V; more paired samples run blind would improve the estimate.

Representativeness of Sample

We did not use a random sampling scheme to obtain the eyes used in this analysis. Eye globes were collected as whales were available. Twenty animals (48% of the 42 with age estimates) were greater than 13 meters which roughly agrees with the proportion of mature animals (41%) estimated from aerial photogrammetry at Barrow (Angliss *et al.* 1995a).

Growth, Age at Sexual Maturity and Longevity

Figure 4.1 is consistent with the published literature in suggesting interrupted growth following weaning (at age 1), with a wide range of ages in animals up to 10 m (Koski *et al.* 1993; Schell *et al.* 1989). Of course, this is partly a consequence of the high CV of the estimates at young ages. Following this period, growth for both sexes appears steady up to physical maturity. The age at sexual maturity at length 12 - 13 m for males and 13 - 13.5 m for females (Koski *et al* 1993) is in the mid twenties according to the von Bertalanffy growth curves (Figure 4.1, Table 4.2) .

The curves suggest that females grow more quickly than males, though the difference is not statistically significant. The accepted onset of sexual maturity is late teens to mid twenties

(Schell *et al.* 1989; Schell 1992; Koski *et al.* 1992; IWC 1995) although Koski *et al.* (1992) noted that growth rates computed from photogrammetric data on males and females combined indicated an age range of 22 to 31 for a 13m bowhead. Schell (1992) projected growth rates of subadults for which he had determined ages using the baleen aging approach to estimate ages of 15 - 17 yr for 13 - 14 m bowheads, updating the estimate of 18 - 20 yr given by Schell *et al.* (1989). The AAR estimates of Table 4.1 and the smoothed version of them provided by the von Bertalanffy growth curves are consistent with the range of estimates, though they point to the high rather than the low end of the range.

It is of interest to compare the growth rates suggested by the von Bertalanffy curves with those obtained from photogrammetric measurements of identified whales photographed in more than 1 yr. Koski *et al.* (1992) estimated growth of whales approximately 10 m long at 0.2 to 0.4 m/yr, slowing to 0.15 m/yr at 12 m, 0.1 m/yr at 13 m, and less than 0.1 m/yr at longer lengths. The curves based on the AAR ages indicate growth of 0.2 m/yr at 10 m length, 0.15 m/yr at around 12 m, 0.1 m/yr at 13 m, and less than 0.1 m/yr after 13.3 m for males and 14.3 m for females, at ages in the mid thirties. The von Bertalanffy curves suggest that physical maturity occurs much later. While we do not put great emphasis on results of a fit of a somewhat unrealistic model to noisy data, the agreement between the AAR and photogrammetric growth estimates is encouraging.

A particular objection to the von Bertalanffy model as a model for bowhead growth is that it may be inappropriate for a species that shows a pause in growth following weaning. However, when we omitted the animals judged on the basis of their baleen length to be age 2 or less, set the age of all other animals less than 6 yr to 6, and fit the model for growth from size at age 6 on, we obtained results that did not differ significantly, with virtually identical estimates of age at sexual maturity.

It can also be argued that the growth constant k may differ by sex, so the von Bertalanffy model should be fit separately to males and females. A larger sample would allow this to be done, but it cannot be done with the present sample because we lack females at old ages to determine maximum length for females. A fit that allows k to differ by sex fits the available data better but gives less realistic maximum lengths (15.5 m for males and 21.8 m for females, compared to 16 m and 17 m when k is assumed to be the same for both sexes.) Among the 216 males and 250 females with measured lengths harvested between 1980 and 1998, 4.2% of the males exceeded 16 m and 4.4% of the females exceeded 17 m, but no reliably measured whale longer than 17.8 m was harvested. The photogrammetry data of Angliss *et al.* (1995b) show no bowheads exceeding 18 m in length in over 1800 photographs, and fewer than 1% of the photographed whales exceeded 17 m in length.

The baleen aging technique is probably a better method for estimating growth of young whales and age at sexual maturity given the large standard errors of AAR ages for young animals. However, lack of definition of cycles in the baleen contributes some uncertainty to baleen ages in young animals, and wear at the tip means that extrapolation is involved in estimating ages of animals older than 11 years or so. The AAR technique is the only one that has provided "direct" data on ages of mature animals.

These data also suggest that some animals (4/42) live over 100 yr. The age for whale 95WW5 was estimated at 211 yr (SE = 35). We did not collect the eye globe from this animal (provided by hunter); however, the whale hunters reported that the eye globe was quickly frozen and that the whale appeared old with "tough" meat and blubber. The eye globes for the other old males (78WW2, 95B7, 95B9) were either collected by ourselves or a biologist. The postmortem handling of these specimens was not different than the other animals and is therefore is not a likely reason for the large estimated age. If these ages are accurate, then the presence of animals of advanced age in this small sample suggests older animals may be in the population. It is interesting to note that each of the bowhead lenses with high D/L ratios had a yellow, amber colored lens nucleus. In investigations of pigmented lenses in humans (of the same age) it has been found that the extent of aspartic acid racemization was the same in both yellow colored and normal lens nuclei, i.e., it did not affect age estimates. Nonetheless, yellowing of the lens is associated with advanced age (Masters *et al.* 1977).

An obvious feature of the data is the abrupt decline in the number of animals over age 70 (Figure 4.1). This break roughly coincides with the end of commercial whaling (Bockstoce 1986; Bockstoce and Burns 1993). Thus, if these ages are correct, it could be that the current age distribution is skewed due to intensive hunting during the period 1848 to 1915. While such speculation is enticing, we have a small sample of old animals that are imprecisely aged, thus the above is little more than conjecture.

The extreme longevity reported here is greater than for other cetaceans where age data exist (Ohsumi 1979; Lockyer 1984). Other cetaceans appear to occasionally exceed 100 yr in age (Ohsumi 1979). Ohsumi (1979) reported ages of 110 and 114 yr for a southern hemisphere blue and fin whale based on a count of ear plug laminae. The maximum ages for bowhead whales reported here agree somewhat with the estimated age of a stone harpoon point taken from a Wainwright whale 93WW5 in 1993. Unfortunately an eyeball was not collected from the Wainwright animal but, nevertheless, the recovery of this point did prompt this re-examination of the AAR technique. Whale 95B9 exhibited a spondalitic lesion on the vertebra which suggests advanced age and is not reported elsewhere in the literature. We should also note the curious observation that few of the 150 or more bowhead whales that we have examined display any obvious pathology at all. Philo *et al.* (1993) summarized the relatively few cases of pathology described for bowhead whales. All of these observations tend to suggest that longevity in excess of 100 yr is not improbable.

Indirect Evidence of Longevity in Bowhead Whales

Six "traditional" whaling tools have been recovered from five bowhead whales landed since May 1981 (Philo *et al.* 1993, George *et al.* 1995, Weintraub 1996). In 1981, an ivory harpoon head with a metal point was recovered from the blubber of a whale (81WW2; 17.7 m) taken in Wainwright, Alaska (Philo *et. al.* 1993). A triangular metal blade (about 3 x 3 cm) similar to a walrus harpoon point was recovered from an unknown whale taken in Wainwright, AK in either 1992 or 1993 (it was found in some blubber stored in an ice cellar). A slate whale point was recovered from whale 92B2 (15.7m, female) taken in Barrow in May 1992; and two stone points were recovered from whale 93WW5 (a 16.7 m, male) taken at Wainwright on 27 May 1993. In 1997, a 16.1 m male also taken at Wainwright (97WW3), carried a triangular slate harpoon tip similar to that found in whale 92B2 and 93WW5. In all cases, the points were recovered from the blubber in the dorsal thoracic region. By matching these points with collections at the Smithsonian Institution, researchers suggested that these points may have been placed by Eskimo whale hunters 100-130 yr BP (Weintraub 1996). Researchers at the University of Alaska Museum evaluated the ivory/metal point recovered from 81WW2. They suggested that points with this manufacture style were similar to some collected on St. Lawrence Island in the 1920s and may have been made as late as the 1970s (walrus harpoons) (Philo *et al.* 1993). However, Krupnik (1998) notes that ivory harpoons with metal end-blades were in use as early as 1791 in the Chukotka region. None of the recovered traditional points were associated with any modern whaling equipment (Yankee harpoons or projectiles) suggesting that the strike was made with entirely traditional gear. After the 1880s when the most hunters made the transition to

Yankee weaponry, they may have still used traditional tools for religious reasons to strike the animal and then a shoulder gun to dispatch it.

Age information has also been inferred from commercial whaling irons. Yankee whalers aboard the *Beluga* recovered a whaling iron embedded in the blubber of a bowhead whale in 1890 that was likely placed by the *Montezuma* which last cruised in 1854 (Dall 1899). Thus, this whale carried the iron for a minimum of 36 years.

Lifespan vs Age at Sexual Maturity

Age at sexual maturity (asm) for bowhead whales is still somewhat controversial. However it is generally accepted to initiate around at least 15 yr (Schell *et al.* 1989; Schell 1992). Estimates discussed by the International Whaling Commission Scientific Committee (IWC, 1995) ranged from low teens to high 20s. Givens *et al.* (1995) used a Bayesian population assessment to determine a posterior distribution for asm of 10 to 30, with values favored by the data in the range of 15 to 24 yr. It is well documented in the scientific literature on mammals that age at sexual maturity and longevity are correlated (Stearns 1992). Caswell *et al.* (1996) tabled data on age at first reproduction (afr) and maximum lifespan (mls) for a number of species (Table 4.3). The purpose of the exercise was to construct a life table for use in estimating incidental mortality of harbor porpoise (*Phocoena phocoena*). The criteria for inclusion in the table were: a) the population had to be unexploited b) only a single offspring at a time produced, and c) only one species per genus could be included.

The resulting linear model regressing asm on lifespan yields: $y = 5.96x + 2.90$ ($R^2=0.91$); where y = maximum lifespan and x = age at first reproduction. We will assume for this discussion that asm = afr-1 (IWC 1995:148). It is important to note that these data were compiled independently, since the model will be affected by the criteria used and the species chosen. If the lower limit of 15 years in the range of values for age at sexual maturity currently believed plausible for bowheads represents the true age at sexual maturity for this species (so afr=16), then bowheads, which fit the criteria for listing in Table 4.3, would be expected to have a maximum life span of about 98. If, on the other hand the AAR and photogrammetric estimates of age at sexual maturity in the twenties hold, the regression equation predicts a maximum lifespan exceeding 100. If afr is around 25, mls is predicted to be around 150. Although Caswell's data are consistent with the AAR age estimates for bowheads, we do *not* wish to suggest that use of this regression equation is a suitable approach for estimating maximum lifespan. Obvious weaknesses with this approach include: mostly non-marine mammal species were used, there may be errors in the estimates of maximum lifespan, the asm for bowheads forces extrapolation beyond the Table 4.3 data, and bowheads are "exploited" although at a low level. Nevertheless, it is comforting that the bowhead AAR age estimates of asm, afr and mls appear to fit the Table 4.3 data, and fit the general pattern for mammals where sexual maturity and lifespan are positively correlated.

Problems with AAR Age Estimates

AAR age estimates (based on the nucleus of the lens) will over-estimate age if the animal has cataracts (brunnescent group IV)(Masters *et al.* 1977). Cataracts have not been reported in bowhead whales (Philo *et al.* 1993). We are currently involved in a cooperative project describing the anatomy of the eye and associated musculature . Thus far, over 50 eyeballs have been dissected but none have been observed to have obvious cataracts (Zhu 1996).

Another factor that could result in AAR-based ages being over-estimates would be the presence of more asparagine residues (in comparison to humans and other mammals, including several marine species) in the eye lens nucleus proteins of bowhead whales. Asparagine racemizes several times faster than aspartic acid (Geiger and Clarke, 1987; Brinton and Bada, 1995). Thus, if there is extensive replacement of aspartic acid residues with asparagine residues in the bowhead lens proteins, this would generate an overall apparent faster rate of racemization of aspartic acid (during acid hydrolysis, asparagine is converted to aspartic acid). The extent of aspartic acid racemization in the bowhead whale eye lens nucleus samples would thus be greater than in eye lens nucleus samples from other mammals of similar age. Using the human and fin whale based racemization rates would then give age estimates for bowhead whales that were too old. It seems unlikely that asparagine would replace aspartic acid in bowhead whales eye lens nucleus proteins and not in other cetacean species.

We recognize that specific aspartic acid residues in αA and αB-crystallin (lens proteins) racemize at different rates in humans which could lead to inaccuracies in age estimates (Fujii *et al.* 1994a, Fujii *et al.* 1994b). However, since the approach of Zhao and Bada (1995) measures the overall D/L value, the racemization rates should not differ significantly between animals.

The AAR age estimates would be biased *downwards* if: a) the eyeglobe was held at a lower temperature than humans or fin whales, or b) the samples were contaminated with blood or "modern" tissue. The cornea is in contact with cold water throughout the year and it is possible that the internal temperature of the globe is lower than deep body temperature. Sub-normal temperatures would slow racemization and subsequently the AAR aging technique would *under*-estimate age to some degree. If surrounding tissue or blood contaminates the sample (lens nucleus) during dissection, the D/L ratio could be dramatically lowered resulting in a gross underestimate.

Ages for young animals (<10 yr) have large SE and associated CV since the resolution of the technique for bowheads is at best ± roughly 12 yr (Table 4.1). For bowhead whales, however, which appear to have a long lifespan, errors of this order are probably acceptable for making life history assumptions.

Some Thoughts on Longevity in Bowhead Whales

In our discussion of extended longevity in bowhead whales, we begin with a brief discussion of mammalian life history and allometry. Means by which mammals respond to environmental change include evolutionary modifications of their life history parameters (e.g., birth size, number of offspring, growth rate, body mass, age at sexual maturity, longevity) (Stearns 1992). These factors tend to be highly correlated - changes in one parameter affects the others. Extant members of the order Cetacea exhibit the most extreme body mass ever achieved in Nature. Presumably, since the appearance of mysticetes in the late Oligocene (ca 25 m.y.), greater body size gave individuals a competitive advantage (for many reasons) and thus continued to increased to their modern size little restrained by habitat size and gravitational limitations (Colinvaux 1979; McLeod *et al.* 1993). The energetic and skeletal requirements of attaining great body mass demand an extended lifespan simply because growing large takes time. Extended lifespan is a shared life history trait of all large mammals; the strong positive correlation between longevity and body mass in vertebrates is well established in the biological literature (Stearns 1992; Petters 1989). Stearns (1992) provides convincing arguments (based on a synthesis of pertinent literature) that environmental and reproductive variability selects for longer reproductive lifespans. Nevertheless, bowhead whales appear to be at the upper range for Cetacea and mammalia as a whole, which poses the question: why might bowhead whales exhibit unusually long lifespans?.

We identified two environmental forces which may have been the principal selective forces in driving bowhead whale life history and specifically, longevity. These are: the cold marine environment (often ice covered), and relatively low density, patchy, and seasonally variable food supply. We propose a mechanism by which selective forces may have resulted in advanced longevity as follows. In order for a cetacean (homeotherm) to invade the high latitude polar seas, it must contend with a relatively low-density, seasonal food supply (Neibauer and Schell 1993) and extreme thermoregulatory problems. In response to thermoregulatory stress an arctic cetacean has relatively few options: maximize insulation (blubber layer), increase body mass (relative to length; "The Surface Law"), maximize food intake, and enhance its thermoregulatory mechanisms (physiological and anatomical adaptations). However, since prey densities are relatively low, bowheads exhibit slow growth rates, require many years to achieve sufficient skeletal development and blubber accumulation, and to attain sufficient size (mass) for reproduction and lactation. Such traits are evident in genus *Balaena*, these include: a) the most extreme development of the baleen apparatus (Lambertsen *et al.* 1989), b) the greatest development of the blubber layer, c) delayed age at first reproduction (about twice the age of right whales, *E. glacialis*), d) a long calving interval (ca 4 yr), d) complex (likely) thermoregulatory mechanisms (e.g., numerous vascular retes) (Albert 1980; Haldiman *et al.* 1985).

Note that the baleen apparatus of the bowhead is adapted to filter extremely small zooplankton (to 1 mm) and that they lack the ventral throat grooves typical of other mysticetes. Thus bowheads ingest food relatively slowly and can not quickly engulf large volumes of water and prey (Lowry 1993). These anatomical characters strongly suggest that these animals evolved to feed on low density prey. Thus, bowhead whales may have been "forced" to adjust their lifespan to respond to these physical, anatomical (e.g., body size) and reproductive challenges. One might speculate that at least some of these traits developed during the Pleistocene (5 m.y.) when the Arctic ocean became ice covered (Erickson 1990) and large portions of the highly productive shelf regions (e.g., Bering Sea) were above sea level. Another possible advantage to great size would be to assist in the bowhead's ability to break through sea-ice in order to breathe (George *et al.* 1989) and produce large calves capable of surviving in sub-freezing waters. As noted earlier, Stearns (1992) summarized earlier analysis which found that the correlation between age at first reproduction and life expectancy was high for (24) mammalian species representing several families. Implicit here is that life is extended to prolong the reproductive period which, again, appears to occur in bowhead whales. Tarpley and Hillmann (1998) examined reproductive materials from 27 mature female bowheads but did not see positive evidence of senescence, with the exception of a few animals that lacked large corpora albicantia (suggesting no recent ovulation). However, some animals had large corpora albicantia accumulations suggesting a long reproductive period (41 maximum for both ovaries). Similarly, we examined a large (15.2 m; 95B7) reproductively active male (semen exuding from the penis) with an estimated age of 159 yr SE = 27.

In summary, the harsh environmental conditions under which the bowhead whale evolved (cold water with relatively low prey densities) required great investment in lipid storage, body mass, thermoregulatory mechanisms, and a modification in reproductive strategy. These stressors may have led to slow growth, delayed maturity and subsequently extended longevity to ensure reproductive success.

Implications to Bowhead Whale Management

The longevity of bowhead whales has relatively minor implications in the management of the aboriginal hunt by Alaskan Eskimos. The subsistence harvest of bowhead whales is regulated at the international, national, and local levels. The harvest quota is established by the IWC (IWC 1982) based upon the nutritional and cultural needs of the Eskimo communities, and the annual replacement yield (RY) of the bowhead population. RY is estimated using population assessment models which require inputs such as: the population size, rate of increase, age at sexual maturity, and adult natural mortality. The models are most sensitive to the values used for population size and rate of increase, however low adult mortality rate does slightly elevate RY (Givens *et al.* 1995). Regardless, nutritional and cultural need is still considerably less than RY so there would be no change in management advice based on our results.

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References

Albert, T.F. 1980. Tissues (structure/function) (RU 280). In: Investigation of the Occurrence and Behavior Patterns of Whales in the Vicinity of the Beaufort Sea Lease Area. J. Kelley and G. Laursen (eds.), pp. 279-329. Final Report for the period October 1, 1978 through November 30, 1979 to the Bureau of Land Management, Department of the Interior, Anchorage, AK from the Naval Arctic Research Laboratory, Barrow, Alaska. 752 pp.

Angliss, R. P., Hobbs R. C., and DeMaster, D. P. 1995a. Determination of the sample size necessary to detect changes in length frequency distributions from a recovering population of bowhead whales. Rep. int. whal. Commn. 45:331-334.

Angliss, R.P., Rugh, D.J., Withrow, D.E. and Hobbs, R.C. 1995b. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). Rep. Int. Whal. Commn 45:313-324.

Bada, J. L., and Brown, S.E. 1980. Amino acid racemization in living mammals: biochronological applications. Trends in Biochemical Sciences, September 1980: p. 3-5.

Bada, J.L., Brown, S.E. and, P.M. Masters. 1980. Age determination of marine mammals based on Aspartic acid racemization in the teeth and lens nucleus. Rep. Int. Whal. Commn. (Special Issue 3):113-118.

Bada, J.L., and Brown, S.E. 1981. The amino acid aging method: dolphin studies, 1979-1980 report. Report No LJ-81-06C. Southwest Fisheries Center, La Jolla, CA

Bada, J.L., Mitchell, E., and Kemper, B. 1983. Aspartic acid racemization in narwhal teeth. Nature 303:418-420.

Bada, J.L. 1984. In vivo racemization in mammalian proteins. In: Posttranslational Modifications, K. Moldave and F. Wold (eds.), Methods in Enzymology 106:98-115, Academic Press.

Bockstoce, J.R. 1986. Whales, Ice and Men. University of Washington Press. Seattle, WA.

Bockstoce, J.R. and Burns, J.J. 1993. Commercial whaling in the North Pacific sector. *In* The Bowhead Whale. *Edited by* J.J.Burns, J.J. Montague, and C.J. Cowles. Allen Press, Lawrence. pp. 563-576.

Brinton, K. L. F. and Bada, J. L. 1995. Comment on "Aspartic acid racemization and protein diagenesis in corals over the last 350 years" by g. A. Goodfriend, P. E. Hare and E. R. M. Druffel. Geochim. Cosmochim. Acta 59: 415-416.

Brodie, P., and Paasche, A. 1985. Thermoregulation and energetics of fin and sei whales based on postmortem, stratified temperature measurements. Can. J. Zool. 63:2267-2269.

Burns, J.J. 1993. Epilog. *In*: Burns, J.J., Montague, J. and C.J. Cowles (eds.). The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

Caswell, H., Brault, S. Read, A., and Smith, T. 1996. Demography and incidental mortality of harbor porpoise in the Gulf of Maine: A Monte Carlo model life table analysis. SC/48/SM31.

Christensen, I. 1981. Age determination of minke whales, *Balaenoptera acutorostrata*, from laminated structure in the tympanic bullae. Rep. int. whal. Commn 31:245-253.

Colinvaux, P. 1979. Why big fierce animals are rare: an ecologists perspective. Princeton University Press, Princeton.

Dall, W.H. 1899. How long a whale may carry a harpoon. National Geographic Society Magazine. Vol. 10(4):136-137.

Erickson, J. 1990. Greenhouse Earth: tomorrow's disaster today. Tab Books, Blue Ridge Summit, PA.

Fujii, N., Ishibashi, Y., Satoh, K., Fujino, M., and Harada, K. 1994a. Simultaneous racemization and isomerization at specific aspartic acid residues in αA-crystallin from the aged human lens. Biochim. Biophys. Acta. 1204: 157-163.

Fujii, N., Satoh, K., Harada, K., and Yoshihiro, I. 1994b. Simultaneous stereoinversion and isomerization at specific aspartic acid residues in αA-crystallin from human lens. J. Biochem. 116: 663-669.

Geiger, T. and Clarke, S. 1987. Deamination, isomerization and racemization at asparaginyl and aspartyl residues in peptides. Succinimide-linked reactions that contribute to protein diagenesis. J. Biol. Chem. 262: 785-794.

George, J.C., Clark, C., Carroll, G.M., and Ellison, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, Spring 1985. Arctic 42:24-30.

George, J.C., Suydam, R.S., Philo, L.M., Albert, T.F, Zeh, J.E., and Carroll, G.M. 1995. Report of the spring 1993 census of bowhead whales, *Balaena mysticetus*, off Point Barrow, Alaska with observations on the 1993 subsistence hunt of bowhead whales by Alaska Eskimos. Rep Int. Whal. Commn 45:371-386.

Givens, G.H., Zeh, J.E., and Raftery, A.E. 1995. Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using the Baleen II Model in a Bayesian synthesis framework. Rep Int. Whal. Commn 45:345-364.

Goodman, L.A. 1960. American Statistical Association Journal 55:708-713.

Haldiman, J.T., Henk, W.G., Henry, R.W., Albert, T.F., Abdelbaki, Y.Z. and Duffield, D.W. 1985. Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). Anat. Rec. 211:391-402.

Hohn, A.A, Scott, M.D., Wells, R.S., Sweeney, J.C., and Irvine, A.B. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Marine Mammal Science 5(4): 315-342.

International Whaling Commission. 1982. Aboriginal Subsistence Whaling (with special reference to the Alaska and Greenland fisheries), Special Issue 4. *Edited by* G.P Donovan. International Whaling Commission, Cambridge.

International Whaling Commission. 1995. Report of the Scientific Committee, Annex F, Report of the Sub-Committee on Aboriginal Subsistence Whaling. Rep. int. Whal. Commn 45: 148.

International Whaling Commission. 1997. Report of the Sub-Committee on Aboriginal Subsistence Whaling. Appendix 2, Report of the *ad-hoc* Bowhead Assessment Group.

Koski, W.R, Davis, R.A., and Miller, G.W. 1992. Growth rates of bowhead whales as determined from low-level aerial photogrammetry. Rep. int. whal. Commn. 42: 491-499.

Koski, W.R, Davis, R.A., Miller, G.W., and Withrow, D.E. 1993. Reproduction. *In* The Bowhead Whale. *Edited by* J.J. Burns, J. Montague, and C.J. Cowles.. Allen Press, Lawrence. pp. 239-269.

Krupnik, I.I. 1998. Slate harpoon point reported in a Siberian bowhead whale in the 1950s. Report to the NSB Department of Wildlife Management by Arctic Studies Center, Smithsonian Institution, Washington, D.C., March 1998

Lambertsen, R., R. Hintz, W. Lancaster, A. Hirons, K. Kreiton and C. Moor. 1989. Characterization of the Functional Morphology of the Mouth of the Bowhead Whale, *Balaena mysticetus*, With Special Emphasis on Feeding and Filtration Mechanisms. Report to the Department of Wildlife Management, North Slope Borough, Box 69, Barrow, AK from Ecosystems, Inc., Institute for Environmental Medicine, University of Pennsylvania Medical Center, Philadelphia, PA 19104. 134 pp.

Lockyer, C. 1984. Age determination by means of the earplug in baleen whales. Rep. Int. Whal Commn. 34:692-696.

Lowry, L. 1993. Foods and Feeding Ecology. *In* The Bowhead Whale. *Edited by* J.J. Burns, J. J. Montague, and C.J. Cowles.. Allen Press, Lawrence. pp. 201-234.

Masters, P. M., Bada, J. L., and Zigler, J. S. 1977. Aspartic acid racemization in the human lens during ageing and in cataract formation. Nature 268, 71-73.

McLeod, S.A., Whitmore, F.C., and Barnes, L.G. 1993. Evolutionary relationships and classification. In The Bowhead Whale. Edited by J.J.Burns, J.J. Montague, and C.J. Cowles. Allen Press, Lawrence. pp. 45-66.

Neibauer, H.J. and Schell, D.M. 1993. Physical environment of the Bering Sea population. *In* The Bowhead Whale. *Edited by* J.J.Burns, J.J. Montague, and C.J. Cowles. Allen Press, Lawrence. pp. 23-44.

Nerini, M. K. 1983a. Age determination techniques applied to mysticete whales. MS Thesis. University of Washington, School of Fisheries, Seattle, WA.

Nerini, M.K. 1983b. Age determination of fin whales (*Balaenoptera physalus*) based upon Aspartic acid racemization in the lens nucleus. Rep. Int. Whal. Commn 34:447-448.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whales. Rep. int. whal. Commn 29: 397-406.

Payne, R., Rowntree, V., Perkins, J.S., Cooke, J.G., and Lankester, K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. Rep. Int. Whal. Commn (Special Issue 12):271-278.

Perrin, W.F., and Myrick, A.C. 1980. Age determination of toothed whales and sirenians: Special Issue 3. International Whaling Commission, Cambridge, England.

Peters, R. H. 1989. The ecological implications of body size. Cambridge University Press, Cambridge.

Philo, L.M., Shotts, E.B., Jr. and George, J.C. 1993. Morbidity and mortality. *In* The Bowhead Whale. *Edited by* J.J. Burns, J.J. Montague and C.J. Cowles (eds.). Allen Press, Lawrence. pp. 275-307.

Punt, A.E. and Butterworth, D.S. Assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) using maximum likelihood and Bayesian methods. Rep. Int. Whal. Commn 47:603-618.

Schell, D.M. 1992. Stable isotope analysis of 1987-1991 zooplankton samples and bowhead whale tissues. Report for US Minerals Management Service, Alaska OCS Region, 949 E. 36th Ave, Room 110, Anchorage, AK 99508. Contract no. 14-35-0001-30472. March 1992.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989. Bowhead (*Balaena mysticetus*) growth and feeding as estimated by $\delta\ ^{13}C$ techniques. *Mar. Biol.* 103:433-43.

Seber, G.A.F. 1982. The Estimation of Animal Abundance (2nd edition). Macmillan Publishing Co., Inc., New York.

Slijper, E.J., 1962. Whales. Hutchinson and Co. New York.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

Tarpley, R.J. and Hillmann, D.J. 1998. Observations on ovary morphology, fetal size and functinal correlates in the bowhead whale *Balaena mysticetus*. Report to the Department of Wildlife Management, North Slope Borough, Box 69, Barrow, AK.

Weintraub, B. 1996. Harpoon Blades point to long-lived whales (March, Geographica). National Geographic Society, 1145 17th St. NW, Washington, D.C. 20036.

Whitcher, B.J., Zeh, J.E., Rugh, D.J., Koski, W.R., Miller, G.W. 1997. Estimation of adult bowhead whale survival rates. Rep.int. whal. Commn 47: 388.

Zhao, M. and Bada, J.L. 1995. Determination of α-dialkylamino acids and their enantiomer in geological samples by high-performance liquid chromatography after derivatives with a chiral adduct of *o*-phthaldialdehyde. Journal of Chromatography A, 690:55-63.

Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M. and Koski, W.R. 1993. Current population size and dynamics. pp 409-489. *In*: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Zhu, Q. 1996. Studies on the eyes of the bowhead whale (*Balaena mysticetus*), ringed seal (*Phoca hispida*), and caribou (*Rangifer tarandus*). Ph.D. dissertation; Institute of Oceanology, Chinese Academy of Sciences, Qingdao, People's Republic of China.

Table 4.1. Basic data for bowhead whales using in this study with age estimates determined using aspartic acid racemization. Whale identification number indicates: year, village (B= Barrow, G= Gambell, WW = Wainwright, H = Pt. Hope, S = Savoonga) and sequential harvest number. The standard error (SE) is omitted for whales used in D/L_o calculations. The D/L ratios for the samples obtained in the 1978-1981 harvest were determined using ion exchange chromatography (Bada, 1984); all other D/L ratios were determined using the HPLC based method (Zhao and Bada, 1995).

Whale	**Body Length(m)**	**Sex**	**Baleen Length(cm)**	**D/L**	**Age**	**SE**
78B1	8.50	F	146	0.0308	2	6
78B3	8.40	M	95	0.0216	-6	NA
78G1	13.80	M	298	0.0540	22	7
78H1	9.30	F	150	0.0246	-3	6
78H2	9.70	M	164	0.0369	7	6
78WW1	16.30	F	322	0.1090	69	13
78WW2	15.20	M	319	0.1850	135	23
79B1	8.70	M	75	0.0270	-1	NA
79H3	9.10	M	105	0.0250	-3	NA
79WW1	17.20	F	316	0.0955	57	11
80G1	15.70	F	291	0.0590	26	7
80S1	14.70	M	229	0.0830	47	9
81G1	15.50	F	297	0.0680	34	8
81S1	16.80	F	NA	0.0724	38	8
81S2	14.20	F	361	NA	NA	NA
81WW1	16.20	F	NA	0.0615	28	7
93B18	9.30	M	200	0.0380	8	6
94B2	10.00	M	NA	NA	NA	NA
94B11	8.70	M	151	0.0300	1	6
94B12	8.30	M	123	NA	NA	NA
94B14	8.40	M	76	0.0270	-1	NA
95B4	8.60	F	102	0.0300	1	NA
95B7	15.20	M	305	0.2120	159	27
95B8	15.20	F	NA	NA	NA	NA

Table 4.1 cont.

95B8f	4.10	F	10	0.0270	-1	NA
95B9	17.40	M	384	0.2270	172	29
95B10	14.98	F	320	0.0510	19	6
95B11	13.00	M	263	0.0510	19	6
95B12	12.27	F	NA	0.0400	10	6
95B13	16.51	F	NA	0.0830	47	9
95B14	13.85	M	244	NA	NA	NA
95B15	14.80	M	289	0.0950	57	11
95B16	14.12	M	NA	0.1350	91	16
95WW5	14.60	M	NA	0.2700	211	35
96B1	8.46	F	126	0.0510	19	6
96B2	7.65	F	67	0.0380	8	NA
96B4	14.38	F	300	0.0770	41	9
96B6	12.70	F	235	0.0630	29	7
96B9	12.14	F	240	0.0650	31	8
96B10	13.40	F	320	0.0580	25	7
96B11	14.25	F	NA	NA	NA	NA
96B15	8.05	M	70	0.0320	3	NA
96B16	11.10	M	212	0.0590	26	7
96B17	13.31	M	269	0.0680	34	8
96B18	10.06	F	202	0.0540	22	7
96B19	13.10	M	249	0.0645	31	8
96B22	11.60	M	199	0.0535	21	7
96B24	10.87	F	243	0.0545	22	7

Table 4.2. Results of von Bertalanffy curve fit (Lmax = average maximum length for males, k = growth rate constant, t_o = age at length 0; Ldiff = average difference between female and male maximum length). Note: Lmax (female) = Lmax+Ldiff.

Parameter	**Value**	**SE**	***t*value**
t_0	-22.22	5.4	-4.10
Lmax(male)	16.02	0.802	19.97
k	0.032	0.008	3.84
Ldiff	0.997	0.823	1.21

Table 4.3. Species used in model life table construction (from Caswell *et al.* 1996). Age at first reproduction = afr, maximum lifespan = mls.

Species	**afr**	**mls**
African buffalo	4	18
Dall's Sheep	2.5	13
Elephant	11	60
Impala	2	11
Orca	15	91
Pilot Whale	8	65
Ringed Seal	4.5	40
Wildebeest	2.5	21
Zebra	3	20

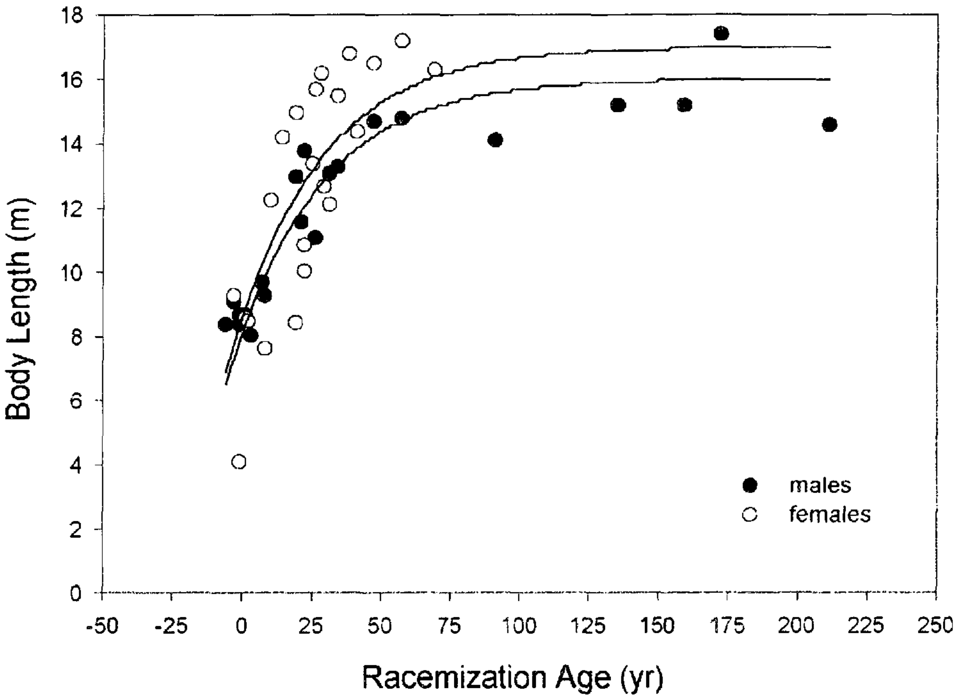

Figure 4.1. Estimated age-at-length for bowhead whales using the aspartic acid racemization technique. The von Bertalanffy growth curves are shown for females (upper curve) and males (lower curve).

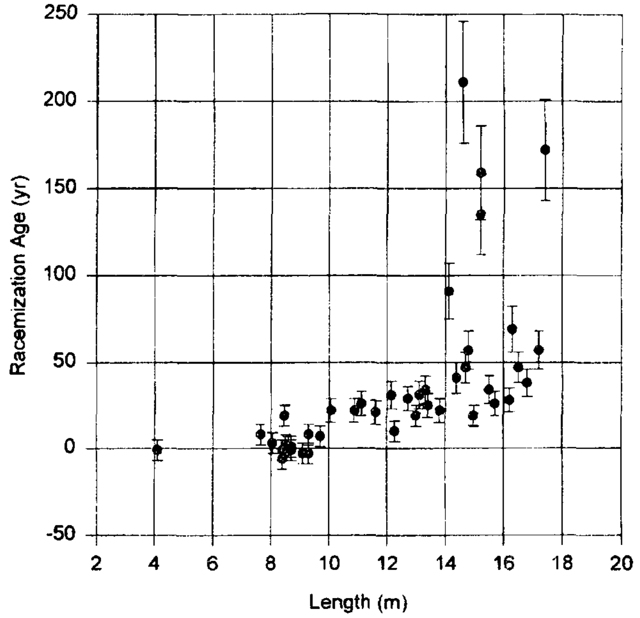

Figure 4.2. Age estimates (yr) by whale length (m) shown with estimated standard errors. Note that the standard error increases with age.

Chapter 5 Regional Heterothermy in the Bowhead Whale (*Balaena mysticetus*)[1]

Abstract

Postmortem temperatures were measured at several locations on freshly harvested bowhead whales. Strong temperature gradients were observed through the blubber at all sites examined. A gradient of ~ 1°C/cm was measured from the epidermis through the blubber at most sites on the abdomen and thorax. The temperature gradient was greatest through the dermis or blubber and inflected (or slowed) at the muscle-blubber interface; however, a temperature gradient persists through the muscle. We saw no strong evidence of a curved temperature gradient in blubber of the abdomen and thorax, which would suggest large active heat transfer via blood perfusion. This was not unexpected since the vessels in the blubber are small (< 0.5 mm) and subtle temperature curves in the blubber would probably fade within a few hours postmortem. There is anatomical data to suggest that active heat transfer occurs through the blubber of the abdomen and thorax.

Introduction

The bowhead (*Balaena mysticetus*) is a robust ice-adapted right whale (F: *Balaenidae*) that inhabits the ice-associated regions of the Arctic and sub-Arctic Seas (Tomilin, 1957). Bowheads are the only mysticetes that do not routinely migrate to temperate or tropical waters, and they exhibit anatomical and physiological adaptations associated with cold, ice-covered waters (George *et al.*, 1989; Tomilin, 1957; Haldiman and Tarpley, 1993; Chapter 6).

The circulatory system of cetaceans includes complex structures in appendages (flukes, dorsal fins, and flippers) (Elsner *et al.*, 2004a) and the tongue which are associated with temperature regulation (Heyning and Mead, 1997). While bowheads lack dorsal fins, they have circulatory structures common to other cetaceans. These include large arteries in the flukes surrounded by a venous network as well as arteriovenous anastomoses (AVA) separated from the arteries, which Scholander and Schevill (1955) postulated had both a heat-conservation and dissipation function. Elsner *et al.* (2004a) conducted experimental exposure of countercurrent arteries and AVA's from bowhead whales in the laboratory to the neurotransmitter (nor-epinephrine) and postulated on how they might function to dissipate and conserve heat.

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[1] J. C. George, E. Follmann, R. Elsner and T. Albert. Regional Heterothermy in the bowhead whale (*Balaena mysticetus*). Formatted for Journal Arctic.

Bowhead whales can grow extremely large (to 18 m), have thick blubber (maximum values 35-40 cm) and live in 0° C water much of the year. However, they make long migrations into summering areas where sea temperatures can exceed 5° C. This combination of stressors suggests that bowheads may require significant conservation and heat loss mechanisms, depending on season, behavior, and activity.

Temperature largely determines the distribution of animals (particularly mammals and birds) and their life-history strategies (Prosser, 1973; Marchand, 1996). Animals can be loosely separated into two groups based on their physiological strategies - poikilothermic (labile core temperatures) and homeothermic (regulated core temperature). In practice, temperature regulation in mammals represents a spectrum whereby the differences between these two conditions become somewhat arbitrary.

The International Union of Physiological Sciences (IUPS 1987) definition of warm-blooded animals is as follows: "the thermal state of an animal which maintains its core temperature considerably higher than that of the environment when subjected to a low ambient temperature". Homeothermy reflects a broad range of thermoregulatory strategies. It is characterized by metabolic thermogenesis coupled with feedback mechanisms for regulating temperature (Prosser, 1973). The IUPS (1987) further defines homeothermy as a "pattern of temperature regulation in an endotherm in which the cyclic variation in core temperature, either nychthermally or seasonally, is maintained within some arbitrarily defined limits (± 2°C) despite larger variations in ambient temperature". Core temperatures for some homeothermic species can drop much lower than during their normal state during heterothermy, hibernation, and torpor.

Regional heterothermy is a condition in which different regions (e.g., appendages, epidermis, thorax) are routinely held at different temperatures at the same time. It is a physiological strategy often used by mammals in cold regions to conserve energy. To some extent, all mammals exhibit some heterothermy but it is highly developed in Arctic and marine mammals (Schmidt-Nielsen, 1997; Elsner, 1999).

The purpose of this paper is to present temperature data from various regions of the bowhead whale, and determine the extent to which regional heterothermy exists in bowhead whales and the role it might play in thermoregulation for this highly adapted Arctic mammal.

Methods

We made temperature measurements on landed bowhead whales at several different locations within the body (Figure 5.1). The whales were harvested by Inupiat Eskimo whale hunters as part of their subsistence hunt (Stoker and Krupnik, 1993). The whales are killed, towed to either land or the ice edge (depending on season) and hauled ashore where they are butchered for food. Most of the work was conducted at Barrow, Alaska. Prior to the hunt, we sought permission to take measurements of landed whales. None of this work would be possible without the permission of the hunters. During the hunting season, when an animal was taken, we traveled to the harvest site to take measurements.

Deep Body Temperatures

The deep body temperature was taken with a sharpened 1 m stainless steel rod ~3 mm in diameter with the thermocouple embedded at the distal tip which we inserted into the animal during the butchering process. Temperature measurements were read to the nearest 0.1° C, with a Physitemp BAT-12 thermocouple reader.

Calibration

Calibration was conducted during each field season using distilled water and snow to achieve a 0° C bath. The bath temperature was measured using a certified calibrated mercury thermometer with 0.1° C gradations.

Deep body temperature time series

Prior to the hunting season, a whaling captain agreed to have a hunter place a temperature logger harpoon device into his whale after it was killed at sea. The probes used a HOBO H8 006-04 channel external data logger with H8 thermistor cable TMC6 HB (0-44° C); accuracy + 0.3° C at +20° C; resolution 0.2° at 20° C.

Thermistors were embedded into a 12 mm fiberglass rod at 4 intervals from 0 to 85.5 cm from the hilt as follows: 1) 83-85.5 cm; 2) 50.5-53.0 cm; 3). 27.0-29.5 cm; and 4) 1-4 cm. The temperature logger was housed within a sealed container attached to the rod. The hunter thrust the probe into the whale to its hilt. The hilt stopped the probe and served as the zero-depth calibration point for the thermistors.

Thermal gradients in the blubber

The thermal gradient was measured from the epidermis and inward towards the animals' center axis (or when bone was encountered) using the 1 m rod described earlier. After the animal was hauled ashore, temperatures were measured every 4 cm at specific landmarks along dorsal and ventral midlines (Figure 5.1, Table 5.1).

Forward Looking Infra-red Radiometer (FLIR)

FLIR images were made of whale 04B10, a 8 m male. The emmisivity was set at 0.96. The temperature scale was allowed to re-scale for each image. Many of the photos were taken in bright sunlight at mid-day. The air temperature averaged about -2^{0}C. Approximate tissue temperatures were estimated using the scale bar in the image mainly to confirm measurements made with the Physitemp BAT-12 thermocouple reader.

Results and Discussion

Regional Heterothermy

Postmortem temperature measurements at 33 locations across the bowhead whale suggest extreme regional heterothermy in this species (Figure 5.2). The deep body temperatures (T_b) within the viscera were fairly uniform among animals averaging 33.6° C (SD = 0.67, N=6) for the six animals examined in this study. We obtained a core temperature of 33.8° C (N = 28; SD = 0.83) for all T_b measurements which showed more variation (see Chapter 6). These are lower than in other placental mammals (Prosser 1973) and other cetaceans which range from ~35° to 38°C (Blix and Folkow, 1992; Vongraven *et al.*, 1990; Costa and Williams, 1999).

Nearly all of the temperature measurements outside the body core were below T_b (Table 5.2). Temperatures within the viscera (liver, kidney and intestines) appeared fairly consistent within one animal. Brain temperatures were not measured. The temperatures reported here were affected to some degree by postmortem time, however, they likely reflect real temperature differences in a *relative* sense. That is, the epidermis, the appendages (flukes and flippers), rostrum and lips are maintained at temperatures considerably lower than T_b. The exact temperatures of these structures on a living bowhead whale probably differ from those reported here.

Epidermis

The epidermis is probably held near ambient but cools quickly after death, therefore the true epidermis temperature in a living bowhead is unclear. Our measurements, aerial observations and some simple modeling suggest epidermal temperatures are maintained at or near the ambient water temperature. For about 9 months of the year, bowhead whales live in water ranging from 10° C to -1.8° C (the freezing point of sea water). During the brief Arctic summer in the Eastern Beaufort Sea, where most of the BCBS stock spends the summer months roughly June to early September (Moore and Reeves, 1993), water temperatures can reach >5° C or higher. This is largely dependent on the amount of sea ice present. Whale skin temperatures likely vary with water temperature. Since water has a high specific heat, and the surface area of the bowhead is so large, it is unlikely that the epidermis ever warms more than 1° C above the ambient water temperature. Heat loss to the water from the epidermis is predominantly from convective heat loss (if there is any water movement at all) and less so by conductive heat loss (to the water) as in the blubber.

For convective heat loss, power output (q") or heat loss can be calculated as:

$$q" = h * a* (Ts - Ta)$$

where h = conductive heat loss coefficient W/m^2 *C; a=area, Ts = epidermis temperature, Ta = ambient water temperature*

For fluids, convective heat loss coefficient values (*h)* range from 50 to 20,000. An approximate value for *h* in water flowing 0.6 m/s (or 2.2 km/h, a conservative bowhead swim speed) is 1,000 (White 1991). Using a value for q" of 100 W/m^2 at the flukes (Chapter 6) together with a value of h = 1,000, a fluke surface temperature of 0.16 C is achieved which is far more realistic.

In the epidermis of the thorax where the blubber exceeds 20 cm in thickness, estimated q" was low at 20 W/m^2 (Chapter 6). This observation suggests that the epidermis of the thorax, under rest conditions, is only a tiny fraction of a degree (~0.002° C) above ambient.

JCG took part in an aerial survey using ConocoPhillips Twin Otter fitted with a FLIR instrument out of Prudhoe Bay. FLIR film footage was taken of feeding bowhead whales near Cross Island. Although, the instrument can measure temperature differences of 0.1°C,; it could not detect bowhead whales at the surface which confirms that skin temperatures are essentially at ambient which astonished the technicians. The FLIR could easily pick up eiders (*Somateria spp.*) in the area of the feeding whales (NSB and LGL unpublished data).

Flippers

Measured postmortem temperatures of the flippers were near ambient from approximately the wrist to the distal tip but could be low due to postmortem cooling in the appendages (Table 5.2). These observations are consistent with the lack of large vessels in the flippers as compared with the flukes for instance. The flippers have counter current vessels similar in structure to those in the flukes but considerably smaller. Because the flippers are relatively thin and sparingly vascularized, they would cool more rapidly after death. It would be quite informative to know the deep flipper temperatures of live bowheads or within a few minutes postmortem. Regardless, given the paddle-like shape of the flipper and thin blubber layer (ca 1 cm), it seems likely that the internal temperature is low.

Flukes

The primary function of the flukes is to propel the animal through the water but they also serve as a heat-dissipation organ (Pabst *et al.*, 1999; Elsner *et al.*, 2004a). The blubber layer of the flukes is quite thin (~1 cm) and the vessels underlying it can be quite large (to ~ 0.5 cm in diameter; Figure 5.3). There are well-developed counter current vessels in the flukes as well as a considerable series of arterial venous anastamoses (AVA) (Elsner *et al.*, 2004) (Figure 5.3). Therefore, it seems reasonable that depending on their energetic condition, bowheads either conserve heat in the flukes or use them for heat dissipation. However, Hokannen (1990) suggests that heat production in bowheads routinely exceeds what can be passively lost through the blubber by conduction. If so, blood flow through the flukes' AVA system would be routine.

Tongue

The tongue is a large and complex organ in the bowhead whale consisting of fatty tissue interlaced with muscle bundles (Figure 5.4). The exterior of the tongue is cloaked in what Haldiman and Tarpley (1993) describe as a lamina propria-fatty submucosa layer, which serves as insulation. The fat layer is as much as 18 cm thick for whales ~ 10 m in length. The temperature at the center of the tongue was variable. The mean was 27.9° C (SD=3.37, N=8) at a depth of 64 cm into the tongue (Site 10) but several measurements slightly exceeded 30° C. The maximum temperature was 30.9° C. These measurements were made through the ventral portion of the chin (Site 10) into the center of the tongue partly because of the difficulty of consistently placing the probe into the anterior portion of the tongue through the mouth. However, temperature profiles made through the tongue's anterior tip on four whales showed a strong gradient. Also a 10-minute time series of temperature measurements made at sea for whale 99B19 (moments after death) indicated the tongue's core temperature remained constant at 30.3°C.

While cooler than the deep body, the tongue's temperature was surprisingly high considering its size and exposure to seawater. The bowhead tongue is likely to participate in thermoregulation as well as aiding in feeding (Heyning and Mead, 1997; Lambertson 2005). Heyning and Mead (1997) describe vascular rosettes running longitudinally through the tongue in gray whales (*Eschrichtius robustus*) which presumably serve a heat conservation function. We have noted similar structures in bowheads (Figure 5.4, see arrow).

Thermal gradients in the epidermis and dermis (blubber)

One of the more consistent findings of this study was that the blubber (dermis) showed strong thermal gradients for all the whales we measured (Figures 5.5, 5.6, and 5.7). Blubber thickness averaged 17-32 cm for the animals studied. The average temperature difference across the blubber was approximately 1°C/cm, which is consistent with passive heat flow through their blubber given a thermal conductivity of about 0.2 Wm/K (see Energetics Chapter).

The skin surface temperatures (epidermis) and deep body temperatures were similar between animals. However, the thermal curves between them differed by whale and region within the animal. These differences are likely due to a combination of factors including the postmortem time, *varying thickness* of the blubber between animals, activity state, and the thermal conductivity of the blubber. When the thermal gradients were calculated as a percentage of the blubber thickness, the temperature variations between animals was lower (Figure 5.8).

During activity, bowheads, like many mammals, probably encounter episodes of hyperthermia to some extent (Pabst *et al.*, 1999). In ice water, heat can be quickly dissipated to the environment via a number of structures (flukes, flippers, tongue) and their thick epidermis (Elsner *et al.*, 2004a). T. Albert (pers. comm.) speculated that the epidermis, which is 2.5 cm thick with strongly interdigitated dermal papillae containing capillaries, has a thermoregulatory function (Haldiman *et al.*, 1985; Haldiman and Tarpley, 1993; Pabst *et al.*, 1999). We are not aware of other literature that has speculated on the function of the greatly thickened epidermis of bowhead whales. As in other cetaceans, the blubber is bi-passed by small blood vessels which branch into small capillary beds at the base of the epidermis (Haldiman and Tarpley, 1993) where heat can be readily lost to the environment. The thermal conductivity of the epidermis is relatively high (0.5 $Wm^{-1}K^{-1}$, about that of muscle) and is typically near ambient, so blood perfused into the epidermis via dermal papilla would be cooled quickly. As a contrast, the epidermis of the minke whale is "paper thin" at about ~1 mm in thickness. Why minke (*Balaenoptera acutorostrata*) whale epidermis is so thin is unclear; however, Kvadsheim (1998) suggests that minke whales are often below their thermoneutral zone and may "never have metabolic rates as low as the BMR [basal metabolic rate]" (p.22). Therefore they would rarely need to transfer excessive heat through their epidermis, hence little need for a thickened epidermis and vascular bed. Another plausible explanation is that the thick skin of a bowhead is protection against abrasion when swimming in an ice field.

Active heat transfer through the blubber via blood flow to the epidermis would produce a curved (rather than straight) temperature gradient. We did not see strong evidence of a "curved" temperature gradient through the blubber although one measurement series of an animal chased for several hours showed a slight temperature curvature (Figure 5.9). For other animals, gradients in the blubber may have faded postmortem; so the question of active heat transfer through the blubber remains equivocal.

Temperature at Muscle-blubber Interface

The temperature at the muscle-blubber interface (MBI) was lower than that of the deep body viscera by several degrees. A thermal gradient was also evident through the muscle. These findings are consistent with those of Kvadsheim *et al.* (1997a) for harp seals. Heat loss models that used a core temperature for the muscle-blubber interface of minke whales overestimated heat loss and resting metabolic rates. The lower MBI temperature can result in a considerable reduction in energy loss to the animal (Kvadsheim *et al.*, 1997a). For example, the average temperature at the muscle blubber interface measured at the umbilicus (Site 8) for all the whales was 25.0° C (SD=5.0, n=7) while the mean deep body temperature for the same animals was 33.6° C (SD=0.67, n=6) (Figures 5.5 and 5.6).

Conclusions

We found evidence of extensive heterothermy in all regions of the bowhead whales we examined. Core temperatures were low averaging 33.6° C. Taken together we suspect that the bowhead is a "thermally labile" mammal and highly adapted to a cold environment in which food supplies are variable and seasonally limited. Reduced body temperatures and regional cooling both serve to reduce metabolic rates. Bowheads also have mechanisms that allow heat loss when necessary via blood flow to the flukes, tongue, and epidermis during periods when they are actively feeding, breeding, being hunted and during migration. Postmortem bacterial activity does take place and could increase the temperature of the animal's core. However, it probably does not elevate body temperatures until significant autolysis begins which is usually 12-24 or more hours after death based on our observations.

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References

Albert, T., Magaki, G., Casey, H.W., and Philo, L.M. 1980. Healed penetrating injury of a bowhead whale. Marine Fisheries Review 42:92-96.

Blix, A.S. and Folkow, L.P. 1995. Daily energy expenditure in free living minke whales. Acta Physiol Scand 153: 61-66.

Costa, D.P, and Williams, T.M. 1999. Marine Mammal Energetics. In: Biology of Marine Mammals. J.E. Reynolds III and S.A. Rommel, (eds.) Smithsonian Institution Press. 578 pp.

Elsner, B. 1999. Living in Water. In: Biology of Marine Mammals. J.E. Reynolds III and S.A. Rommel, (eds.) Smithsonian Institution Press. 578 pp.

Elsner, R. George, C. O'Hara, T. 2004a. Vasomotor responses of isolated peripheral blood vessels from bowhead whales: thermoregulatory implications. Marine Mammal Science 20 (3): 546–553.

Elsner, R., Meiselman, H.J., Baskurt, O.K. 2004b. Temperature-viscosity relations of bowhead whale blood: a possible mechanism for maintaining cold blood flow. Marine Mammal Science 20 (2): 339-334.

Folkow, L.P. and Blix, A.S. 1992. Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water. Scandinavian Journal of Physiology. 146: 141-150.

George, J.C., Clark, C., Carroll, G.M. and Ellison, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. Arctic 42: 24-30.

Haldiman, J.T., Henk, W.G., Henry, R.W., Albert, T.F., Abdelbaki, Y.Z. and Duffield, D.W. 1985. Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). Anat. Rec. 211:391-402.

Haldiman, J.T. and Tarpley, R.T. 1993. Anatomy and Physiology. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Heyning, J.E. and Mead, J.G. 1997. Thermoregulation in the mouths of feeding gray whales. Science 278:1138-1139.

International Union of Physiological Sciences Thermal Commission (IUPS Thermal Commission). 1987. Glossary of terms for thermal physiology. Pflugers Archiv 410:567-587.

Kvadsheim, P., Folkow, L., and Blix, A. 1995. Thermal conductivity of minke whale blubber.

Kvadsheim, P. H., Gotaas, A. R. L., Folkow, L. P., and Blix, A. S. 1997a. An experimental validation of heat loss models for marine mammals. Journal of Theoretical Biology. (184): 15-23.

Kvadsheim, P.H. 1998. Blubber as Insulation: A study in heat balance in harp seals (*Phoca groenlandica)* and minke whales (*Balaenoptera acutorostrata*). Ph.D dissertation at the Department of Arctic Biology and Institute of Medical Biology, Univ. of Tromso, Tromso, Norway. 26 p + appendices.

Lambertsen, R., K. J. Rasmussen, W. C. Lancaster, and R. J. Hintz. 2005. Characterization of the functional morphology of the mouth of the bowhead whale and its implications for conservation. Journal of Mammalogy 86(2):342-352.

Marchand, P. J. 1996. Life in the Cold: An introduction to winter ecology. University Press of New England, Hanover, NH. 305. pp.

Moore, S.E. and Reeves, R.R. 1993. Distribution and movement. In: J.J. Burns, J.J. Montague and Cowles, C.J. (eds.) The Bowhead Whale. Special publication No. 2 of the Society for Marine Mammalogy. 787 pp.

Pabst, A., Rommel, and McLellen. 1999. The Functional Morphology of Marine Mammals. In: Biology of Marine Mammals. J.E. Reynolds III and S.A. Rommel, (eds.) Smithsonian Institution Press. 578 pp.

Prosser, L. 1973. Comparative animal physiology. Volume 1. Environmental Physiology. C.L. Prosser, *Ed.* Saunders Company. 966pp + appendices.

Scholander, P.F., and Schevill, W.E. 1955. Counter-current vascular heat exchange in the fins of whales. Journal of Applied Physiology 8:279-267.

Schmidt-Nielsen. 1997. Animal physiology: adaptation and environment. Cambridge University Press. Cambridge, England. 611 pp.

Stoker, S.W., Krupnik, I.I. 1993. Subsistence whaling. *In:* J.J. Burns, J.J Montague and C.J. Cowles (eds.). *The Bowhead Whale.* 787 pp.

Tomilin, A.G. 1957. Mammals of the U.S.S.R. and adjacent countries. 9. Cetacea. (Translated by the Israel Program for Scientific Translations, Jerusalem, 1967). 717 pp.

White, F. M. 1991. Heat and Mass transfer. Addison-Wesley. Reading, MA. 718 pp.

Table 5.1. Sites on bowhead whales at which temperature measurements were made.

Site	Type	Site Description
1	Single measurement	Tip of rostrum down to bone
2	Single measurement	Center of dorsal rostrum down to bone
3	Single measurement	Posterior dorsal rostrum (to bone) just anterior to blowhole
4	Temp. Series; 4 cm increments	1 m posterior to the blowhole
5	Series; 4 cm increments	Dorsal opposite umbilicus
6	Series; 4 cm increments	Dorsal opposite anus
7	Series; 4 cm increments	Ventral near anus
8	Series; 4 cm increments	Near umbilicus
9	Series; 4 cm increments	Ventral midline between flippers
10	Series; 4 cm increments	Ventral midline into center of tongue
11	Series; 4 cm increments	Ventral midline anterior chin (not used)
12	Single measurement	Posterior mandible lateral surface
13	Single measurement	lateral mid-mandible lateral surface
14	Single measurement	lateral anterior tip of mandible (to bone)
15	Single measurement	lateral mid-lip
16	Single measurement	upper mid-lip
P	5 measurements equally spaced	Pectoral limb (flipper) measurements
F	5 measurements equally spaced	Fluke measurement series
T	Series; 4 cm increments	Anterior tongue (to about 20 cm depth)

Table 5.2. Temperature statistics for the bowhead flukes and flippers. Refer to Figure 5.1 for graphic representation of the locations. Measurements were taken down against the dense connective tissue of the flukes and to the bone on the rostrum and flippers. The Site 10 temperature is the center of tongue.

Flukes and Flippers

	Fluke1	Fluke2	Fluke3	Fluke4	Fluke5	Flip1	Flip2	Flip3	Flip4	Flip5
Mean	16.0	13.0	6.2	2.8	0.5	4.9	1.5	1.0	0.5	0.0
SD	4.4	4.5	4.2	0.6	1.1	3.7	1.2	0.7	1.3	1.0
N	9	7	7	6	6	7	7	8	8	8

Thorax and Rostrum

	Site 1	Site 2	Site 3	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16
Mean	15.9	18.3	23.6	27.9	17.4	25.0	14.3	11.4	2.5	0.1
SD	5.0	2.0	2.1	3.4	-	4.2	4.0	4.6	1.0	0.9
N	9	9	9	8	1	7	7	6	7	7

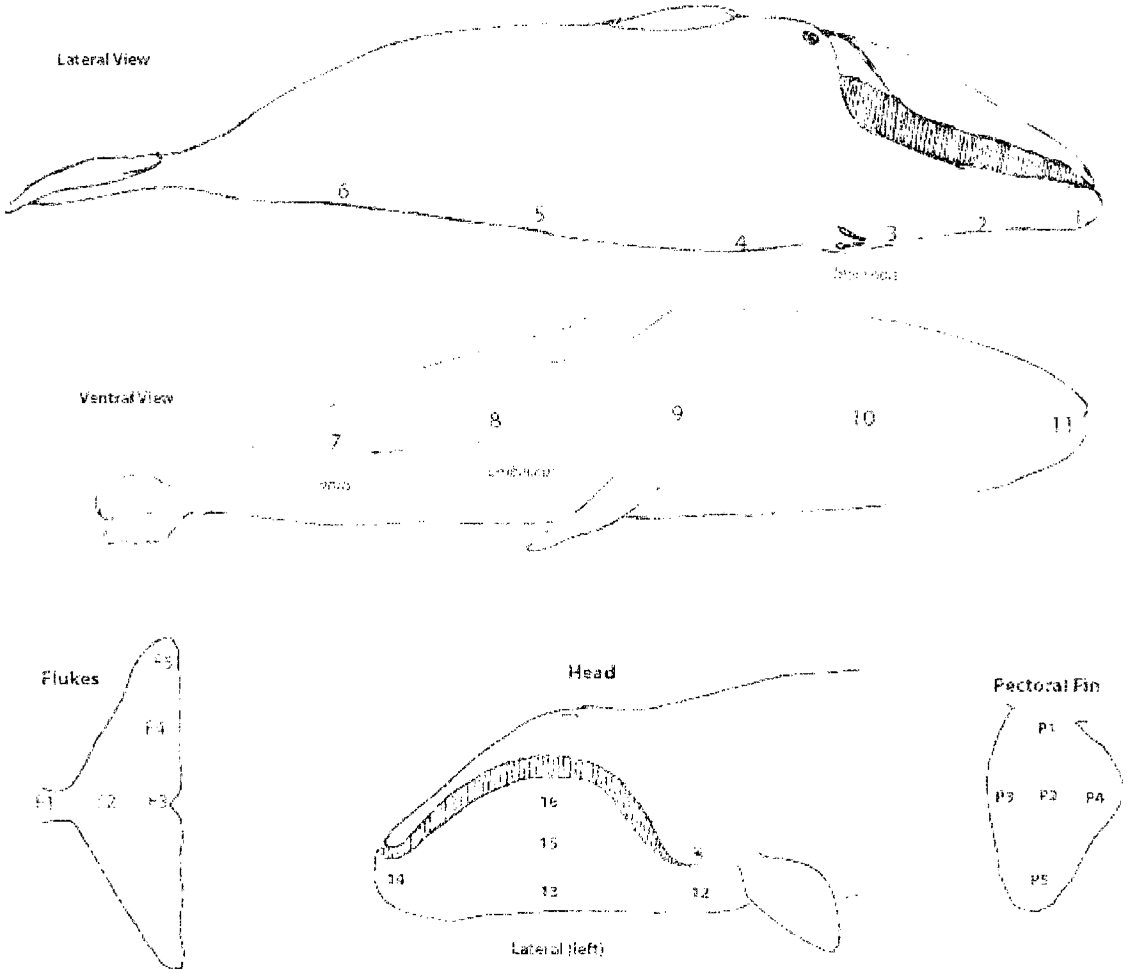

Figure 5.1. Temperature measurement sites on bowhead whales used in this study. Single temperature measurements were made against the bone or connective tissue in the flippers, flukes and rostrum. Thermal gradients were measured at 1 cm intervals in the thorax and abdomen.

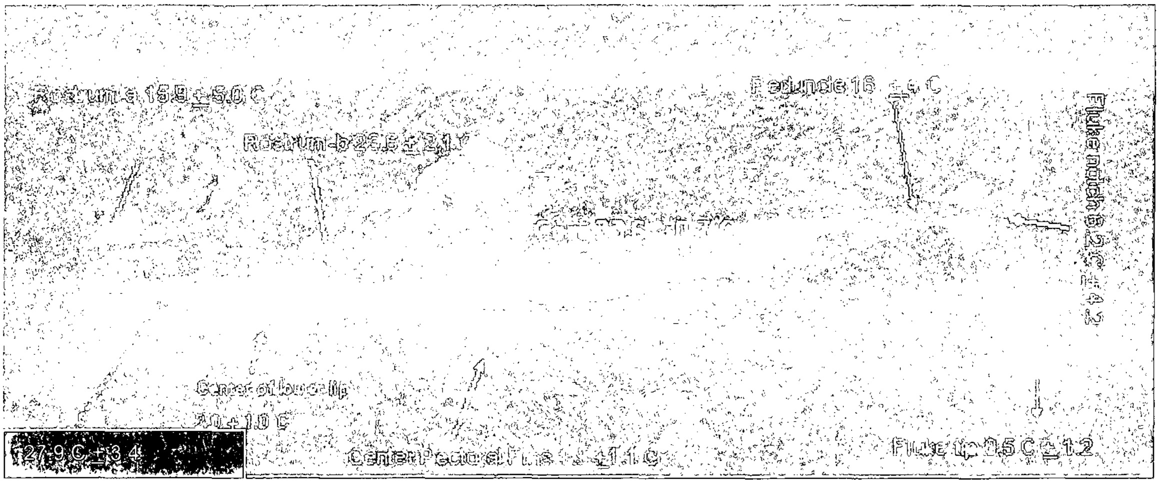

Figure 5.2. Mean temperature measurements for selected regions of the bowhead whale. Temperatures for the rostrum, lip, peduncle, and flipper where taken either against the bone or deep in the dense connective tissue (fluke and lip).

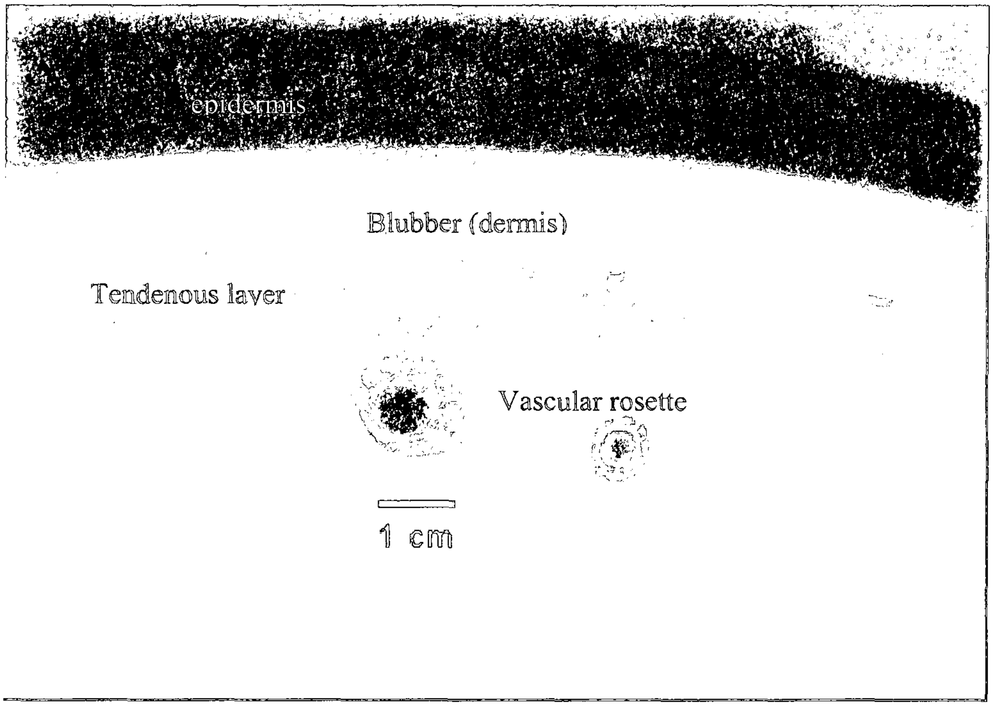

Figure 5.3. Photograph of a cross section of a bowhead whale fluke showing the vascular rosette arrangement, tendenous layer, blubber and epidermis (Haldiman and Tarpley, 1993; Pabst *et al.*, 1999).

Figure 5.4. Photograph of a transverse section of a bowhead tongue (whale 02B21) about mid-way along its length. Note the lamina propria-fatty submucosa layer which almost certainly serves as insulation. The fat layer can be 18 cm thick laterally. Inset: an artery with associated counter-current veins which runs longitudinally though the tongue is shown with a yellow arrow.

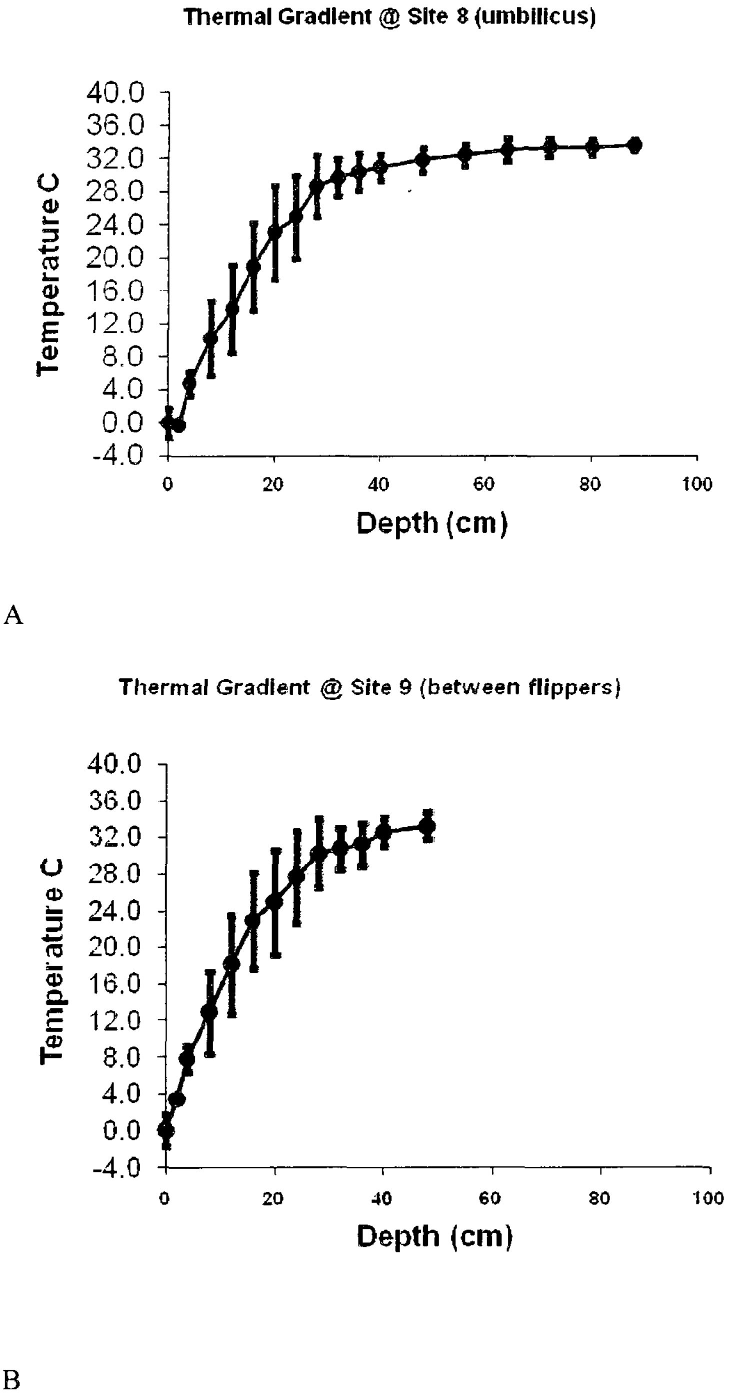

Figure 5.5. Thermal gradients through the blubber for 13 bowhead whales at Sites 8 and 9, Alaska. A) Site 8 (at the umbilicus) the measurements penetrate into the viscera at a depth of roughly 50 cm. B) Site 9, on the ventral midline between the pectoral limbs, the measurements end at the sternum (~ 50 cm depth) and do not penetrate through the peritoneum into the gut.

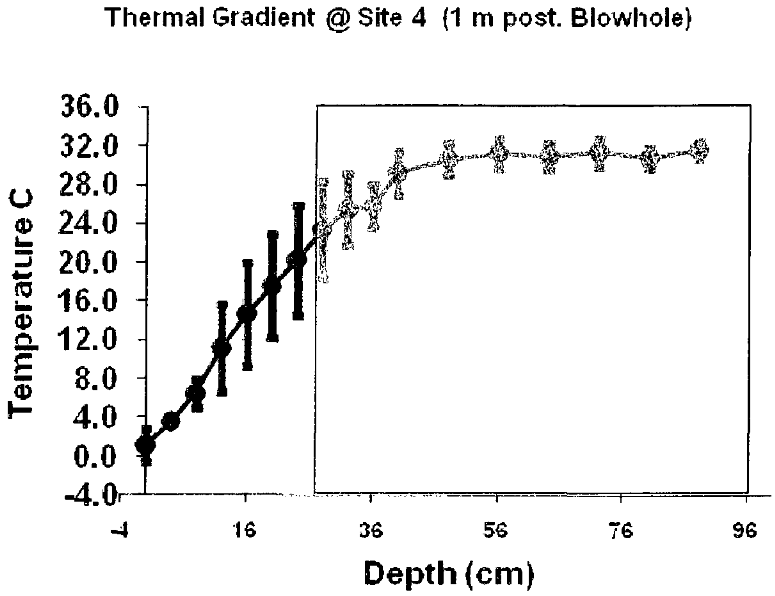

Figure 5.6. Temperature gradient plots for 13 bowhead whales taken 1 m posterior to the blowhole at Site 4. Note the temperature gradient extends through the muscle and into the gut which is indicated by the shaded area. The average depth of the muscle-blubber interface for the whales analyzed at this site was ~27 cm.

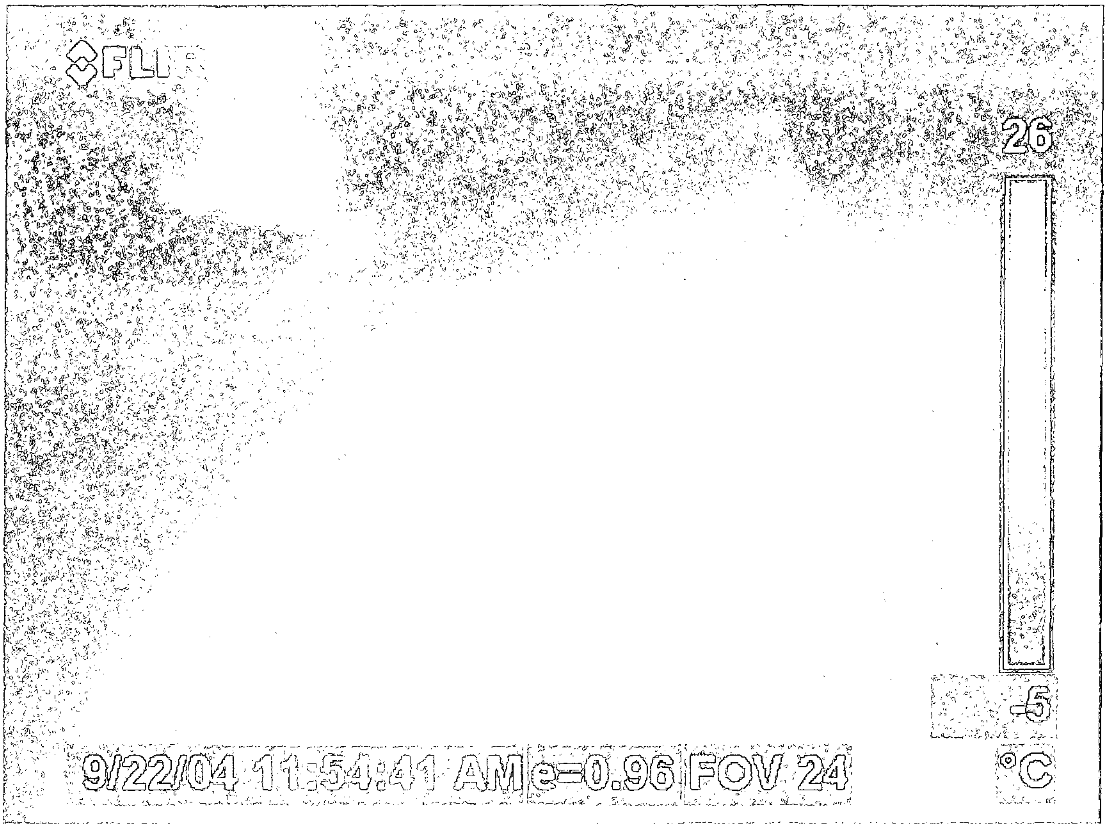

Figure 5.7. A FLIR image of the blubber of a bowhead whale being removed by hunters, Alaska. Note that the temperature at the muscle blubber interface is ~26° C which agrees well with measurements made using the temperature probe.

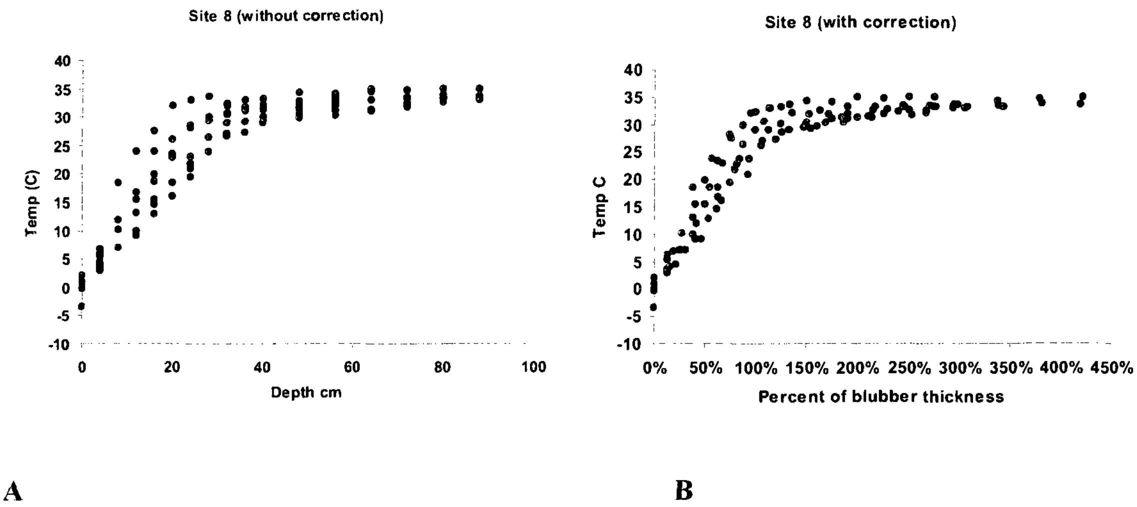

Figure 5.8. A) Scatter plot of temperature data for 13 bowhead whales by depth (cm) at Site 8 (umbilicus), Alaska. Note the dispersion of the data due, in part, to the different thickness of the blubber. B) The same data (Site 8) where depth is "dimensionless" and calculated as a percentage of the blubber thickness. Blubber thickness ranged from 17-32 cm for these whales. Note that the thermal gradient does not show an obvious curve in the blubber between 0 and 100%, suggesting that heat flow through the blubber layer (based on these measurements) is mainly conductive.

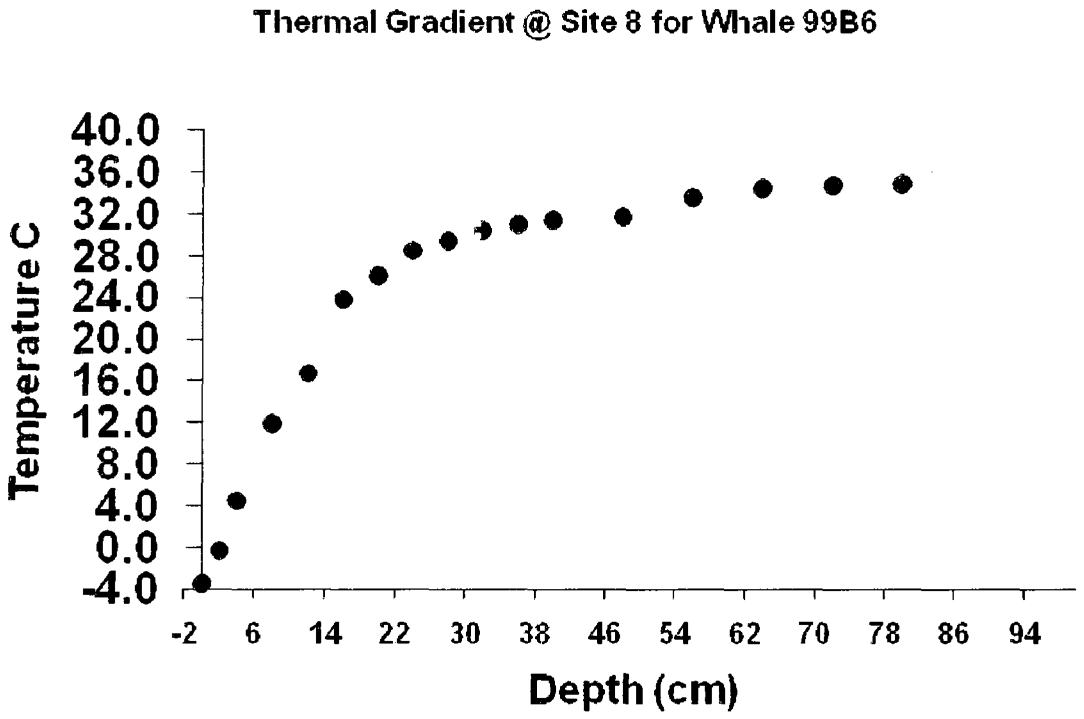

Figure 5.9. Temperature gradient through the blubber shown for a single animal (whale 99B6, 12.6 m female with 32 cm blubber) showing a non-linear temperature curve through the blubber. This animal was chased for several hours prior to being harvested. It had a thick (~5 cm) layer of hypodermal fat, which partially explains the "flat" temperature curve immediately ventral to the muscle-blubber interface. Note that for this animal, the muscle-blubber interface temperature is about 32° C, which is ~3° C lower than the deep body temperature (35.0° C). The temperature difference between the muscle-blubber-interface temperature and the body core was greater than 3° C for the other bowheads measured. There is a suggestion of a curved thermal gradient at Site 8 which suggests blood flow through the blubber.

Chapter 6 Low Metabolic Rates of Bowhead Whales (*Balaena mysticetus*)[1]

Abstract

The bowhead whale (*Balaena mysticetus*) is a highly derived cetacean adapted for life in ice-covered arctic seas. This paper uses a heat-loss model to estimate resting metabolic rate. We discuss and examine how adaptations such as thick blubber and low body temperatures may be related to longevity, reduced metabolic rates and other traits of bowheads.

We found deep body temperatures of recently killed bowhead whales to be lower than that reported for other eutherian mammals. The average deep body temperature was 33.8° C (N = 28; SD = 0.83; range 32.4° - 35.3° C). While lower, the variation in deep body temperatures is consistent with similar measurements for minke (*Balaenoptera acutorostrata*) whales. Body temperature was negatively correlated with body length ($p < 0.05$) and with the time (minutes) the whale was pursued by hunters. However, when both predictor variables were considered neither was significant, possibly because they are correlated. That is, larger whales require more time to land (i.e., more time is required).

The thermal conductivity (TC) of the combined epidermis and dermis often referred to simply as "blubber" was estimated using a "hot box" and a flash-heated needle probe. Both the hot-box and needle probe methods suggest thermal conductivities similar to those of other cetaceans, about 0.23 $Wm^{-1}K^{-1}$. The mean integrated TC value (epidermis and blubber) from the needle probe (for three juvenile whales, dorsal and ventral) was 0.230 (SD = 0.030) $Wm^{-1}K^{-1}$. The mean TC value for the epidermis and blubber using the hot-box was 0.230 (SD = 0.014) $Wm^{1}K^{-1}$. The TC of the epidermis (using the needle probe was 0.48 (SD = 0.022). While the mean TC values from the two methods are remarkably close, the needle probe results may be more accurate because some rendering of the blubber occurred in the hot-box during the long test periods. On the other hand, the needle probe may be affected by proximity to different tissues and boundary layers and give less accurate results.

A 5.6 and 9-hr time series of deep body temperatures made using a data logger placed in a whale soon after death indicated little change in the deep body temperature over these time

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[1] George, J.C., D. Goering, E. Follmann, R. Elsner, M. Sturm and H. Brower, Jr. Low Metabolic Rates of Bowhead Whales (*Balaena mysticetus*). Formatted for Journal Arctic.

periods. Whales that were pursued by hunters for long periods (up to 3 hr) did not have elevated body temperatures. These observations are consistent with observations for other large whales such as the humpback (*Megaptera novaeangliae*). This suggests they have effective mechanisms for circumventing their blubber to dissipate heat when necessary.

Resting metabolic rate estimates from heat loss models were 3,200 W (SD = 168) for a 13 m (31.6 metric ton) bowhead. This estimate is about a third of the Kleiber prediction (8,900 W; based on body mass) and for RMR estimates derived for minke whales scaled to the mass of a bowhead. Heat loss models by earlier researchers suggest that bowheads are in positive heat load even at rest due to their great size and thick blubber. However, they estimated RMR for bowheads using the "Kleiber curve" (derived mainly from smaller terrestrial mammals), and this may have led to an overestimate of power production. While Kleiber-based estimates are reasonable for some cetaceans (e.g., minke whales) and marine mammals such as seals, power output for bowhead whales appears to be lower than expected, based on the analysis reported here. A parsimonious interpretation of our data suggests that metabolic power production in bowheads is lower than in other similar-sized mammals and is not in positive heat-balance at rest. This interpretation is consistent with the distinctive bowhead characters such as low body temperatures, thick blubber, slow body growth, slow feeding rates, and great longevity.

Heat flux estimates from highest to lowest were the palatal rete, flukes, tongue and body. While these organs dissipate heat most readily, heat loss from the thorax and abdomen together was still slightly greater according to our model, because the surface area is five times greater.

Bowhead whales carry a large energy store in the lipids of their thick blubber. These fat stores coupled with low metabolic rates should allow bowheads to survive one or more summer seasons with poor feeding opportunities. Heat loss metabolic models provide only an approximation of the true condition of an animal in nature. Nonetheless, these models suggest boundaries for estimates of metabolic power and provide a tool for examining how the bowhead might dissipate heat from different sections of its body.

Introduction

Large cetaceans have unique energetic problems due to their massive size, the high thermal conductivity of water, variable and seasonal food supplies and other factors (Elsner 1999; Peters 1989). Variation in activity level and water temperature challenge a whale's ability to both maintain and dissipate body heat. Seasonal prey availability can contribute to thermoregulatory stress if the blubber coat becomes depleted from lack of food that results in a lower insulation value (Costa and Williams, 1999; Pabst *et al.*, 1999).

Because it is impractical to keep large cetaceans in captivity where researchers can make direct measurements, the energetics of large whales are not well understood (Elsner, 1999; Whittow, 1987; Costa and Williams, 1999). Only approximate estimates of metabolic rates for large whales are available with the exception of Wahrenbrock *et al.* (1974) who made direct measurements on two gray whale (*Eschrichtius robustus*) calves. Therefore, researchers have, by necessity, studied the energetics of large cetaceans using indirect approaches and mathematical models (Folkow and Blix, 1992; Hokkanen, 1990; Blix and Folkow, 1995; Thompson, 1987).

Until recently, energetic studies of marine mammals have been primarily of academic interest. However in recent years, resource agencies have used energetic models for critical management issues. The designation and exclusion of critical feeding habitat for Endangered Stellers sea lions (*Eumetopias jubatus*) within the billion-dollar pollock fisheries grounds along the Aleutian Islands by the US government (Ferrero and Fritz, 2002) is an example. Trophic dynamic models used to estimate interspecific competition and/or consumption rates in the Pollock fishery were used in decision making (Harvey *et al.*, 2003, Richardson *et al.*, 1987; Thomson, 1987 and 2002; Haug *et al.*, 1995; Blix and Folkow, 1995). Competition between cetaceans and desirable fisheries has repeatedly been raised by Japan at the International Whaling Commission (IWC) as a justification for whaling. While highly debated, these arguments are based on simulation models whose inputs include whale energetics, prey consumption rates, and the energy value of prey types (IWC, 2003: 336).

Since the 1970s, the Inupiat Eskimo people of the North Slope have had considerable concern about offshore petroleum leasing and development particularly in whale feeding regions and migratory paths (Albert, 1981; Ahmaogak, 1989). Their primary concerns are that industrial noise may displace bowhead whales from feeding areas or contaminate them or their feeding habitat by oilspills (National Research Council, 2003; NSB Science Advisory Committee, 1987). Energetic models were among the tools used to investigate this issue (Thomson 2002).

Various approaches have been used for cetacean energetic studies. Wahrenbrock *et al.* (1974) performed metabolic studies on two captive gray whale calves, one of which was held in captivity for one year. Although their research was conducted over 30 years ago, those estimates remain the only direct metabolic measurements on baleen whales.

Energetic estimates can be inferred from changes in body mass over time between feeding and fasting periods (Costa and Williams, 1999). This approach is based on the logic that the lipids gained during the summer feeding season must carry the animal through the subsequent fasting period. This approach is best applied to known seasonal feeders such as fin (*Balaenoptera physalus*), blue (*B. musculus*), sei (*B. borealis*) and gray whales. However, unlike other large mysticetes, bowheads do not migrate to temperate waters and likely feed to some extent in winter (Schell and Saupe, 1993; G. Sheffield, pers. comm.).

Blix and Folkow (1995) followed radio-instrumented minke whales (*B. acutorostrata*) and recorded their exhalations over a 24-hr period to estimate respiration rates for various behaviors. Respiration data together with estimates of swimming speed were used in a model to estimate metabolic rates. They suggest that the cost of swimming at slow speeds (~3 km/h) was "remarkably low". The authors noted that a problem with this approach is that values for the physiological parameters (i.e., tidal volume and extraction rates) were approximated from other mammals.

A method sometimes referred to as the "heat-balance" technique has been used to estimate resting metabolic rates of seals and whales (Kvadsheim *et al.*,1997a; Kvadsheim, 1998). This is the approach we used with bowhead whales. This approach is based on the principle that at rest, ultimately heat loss from an endothermic animal must equal its heat production. That is, if heat loss can be calculated or measured accurately, one can estimate the metabolic rate of an animal. If the animal is doing work then this must be added to BMR to estimate the power output. It is more correct to say that these approaches measure resting metabolic rates (RMR) since BMR estimates require the animal conform to several strict conditions (e.g., rest heart rate, fasted, thermoneutral, non-exercising, etc.) which is not often the case in nature. Estimating heat loss of a marine mammal using this approach requires, at a minimum, information on body shape and mass, the thickness and thermal conductivity of the blubber and deep body temperature. Researchers have applied this method, employing a range of simple to complex models (Kvadsheim *et al.*, 1997a; Hokannen 1990).

Kvadsheim *et al.* (1997a) is a key paper which provides verification of the heat loss estimation approach in estimating RMR. They provide a direct calibration of the heat-loss technique using harp seals (*Phoca groenlandica*), and as such, their work is an important scientific contribution. They measured the metabolic rates of live harp seals, and then euthanized the animals to make careful morphological measurements (blubber thickness, muscle mass, etc) needed for the heat-loss models. These data were used to test the performance of various heat loss models against their (direct) metabolic measurements. An important finding relative to our work, was that they found that the "dead blubber" of freshly killed seals had thermal conductivity properties close to the blubber of live animals in a vaso-constricted state. They found that a simple "flat-plate" model performed poorly for small marine mammals such as seals. However, models that accounted for cylindrical body shape and the asymmetrical distribution of blubber around the (heated) body core were satisfactory, varying from 3 to 18% of the measured values.

Hokkanen (1990) in his general modeling of temperature regulation in marine mammals posed many predictions regarding thermoregulation. His models suggest that it is energetically unnecessary for large cetaceans to migrate great distances to tropical seas to save on "heating bills" (p. 469). Hokkanen's calculations suggest that large whales would overheat during any activity if they were not able to dissipate significant amounts of heat via blood flow to the skin through peripheral vasodilation. The models suggest that bowhead whales could withstand a 200° C thermal gradient across the blubber and remain thermo-neutral. He states,

> "*The insulation of the bowhead is good enough to enable it to swim in liquid oxygen.*"
> (Hokkanen 1990: 469).

In a general review of cetacean physiology, Kanwisher and Ridgway (1983; 113) point out that a large fin whale "appears to be 100 times overinsulated" when compared with a small harbor porpoise (*Phoecena phoecena*) living in polar waters. They pointed out that blubber provides buoyancy and offers a large food store to cover the metabolic needs during long periods in food-poor tropical waters. Hokkanen's (1990) work also suggests that a primary function of whale blubber, particularly for bowheads, is for lipid storage and secondarily as insulation. However, he used RMR for large whales based on the Kleiber predictions, which our data suggest overestimates RMR for bowheads. Also, Hokkanen (1990) considered heat loss from whale appendages as minor and did not include these in his models. Research by several authors has shown that cetacean appendages are important for dissipating heat (Pabst *et al.*, 1999). Thus, this assumption probably caused Hokkanen to underestimate heat loss in large whales.

Bowhead whales lay at the mammalian extreme both morphologically and physiologically in several respects (Hokkanen 1990; Haldiman and Tarpley, 1993). Therefore, with regard to understanding energetics and heat loss of the bowhead, one must consider their: large mass and girth, extreme longevity, thick blubber layer (> 32cm), large flukes, thick epidermis, slow growth rates and low body temperature (George *et al.*, 1999; Koski *et al.*, 1993; Haldiman and Tarpley, 1993).

Considering that bowheads live in ice water much of the year, one might suspect bowheads to be constantly challenged with heat conservation. However, this may not be the case. Researchers have suggested that blubber serves several functions (buoyancy, streamlining, energy storage) in cetaceans, but primarily for thermoregulation (Pabst *et al.*, 1999). Nonetheless, for large whales, observations as early as the 1960s by Kanwisher and Sundnes (1965) suggested that blubber serves primarily as energy storage and secondarily for thermoregulation. As evidence, they pointed out that small cetaceans with thin blubber successfully inhabit the polar seas, and therefore suggest that thick blubber is unnecessary for thermoregulation.

Calculations by Hokkanen (1990) suggest that bowheads are over insulated and may need to dissipate heat even at rest. However, mammals are typically thermoneutral when at rest in their normal habitat (Schmidt-Neilson, 1997). An objective of this paper is to explore which of these explanations best approximates the bowhead condition.

The specific objectives of this paper are to: (1) present direct measurements of deep body temperatures for bowhead whales, (2) estimate the thermal conductivity of the epidermis, dermis (blubber), muscle, and tongue, (3) develop a heat loss model for bowhead whales, and (4) estimate resting metabolic rates for bowhead whales using a heat loss model.

Methods

Eskimo whale hunters harvest whales as part of a highly-regulated subsistence hunt. The whales are killed, towed to either land or the ice edge (depending on season) and hauled ashore where they are butchered for food. Prior to the hunt, we obtained permission to take samples and measurements from landed whales. During the hunting season, when an animal was taken, we traveled to the harvest site. During the butchering process, we took body temperatures, blubber samples, morphometric measurements and other data from these animals. Measurements were taken at different locations on the body (Figure 6.1). Most of the work was conducted at Barrow, Alaska.

Deep Body Temperatures and Calibration

Temperature Rod

Deep body temperature was taken from landed whales with a sharpened 1 m stainless steel rod with a thermocouple at the distal tip. Temperature measurements were read to the nearest 0.1° C with a Physitemp[2] BAT-12 thermocouple reader. Calibration was conducted during each field season using distilled water and ice to achieve a 0° C bath.

Data Logger

A data logging temperature probe was constructed. The probes used a HOBO[3] H8 006-04 channel external data logger with H8 thermistor cable TMC6 HB (0-44 C); accuracy + 0.3 C at +20° C; resolution 0.2° at 20° C. Thermistors were embedded into a 12 mm diameter fiberglass rod at 4 intervals from the hilt as follows: #1 83-85.5 cm; #2 50.5-53.0 cm; #3 27.0-29.5 cm; and #4 1-4 cm. The temperature logger was contained within a poly bottle taped to the rod. The probe was thrust into the whale to its hilt. The hilt stopped the probe at the skin and served as the zero-depth calibration point for the thermistors. The rod was thrust about 1 m deep into the abdomen near the umbilicus on 4 whales. Data from three of the whales exceeded 1 hour in length.

Thermal Conductivity (TC) of Blubber

Full thickness blubber samples approximately 30 x 30 cm, were removed from the whale from the area 1 m posterior to the blowhole and on the ventral midline between the flippers. Two

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[2] Physitemp Instruments, Inc., 154 Huron Avenue, Clifton, New Jersey 07013

[3] 470 MacArthur Blvd, Bourne, MA 02532

approaches were used to measure the TC of blubber in the laboratory: hot box and flash-heated needle probe.

Hot box

The "hot box" followed (approximately) the design of Kvadsheim *et al.* (1994). The box was built by the University of Alaska Fairbanks Engineering Department. The box has an open chamber surrounded by 25 cm of urethane foam. The floor of the box was heated with a 75 W heating pad attached to a 25 x 25 x 2.5 cm section of aluminum plate. The pad was heated using a power supply at 12.5 v. In the chamber over the heated plate a 25 x 25 x 6.86 cm section of UHMW plastic served as a 'standard' with known thermal properties (TC standard = 0.41 Wm^1K^{-1}). Thermocouples were set on both sides of the UHMW standard. The blubber specimen was set atop the standard within the chamber. Over the specimen a 20 kg brass plate (welded to a stainless steel ice-bucket) was suspended over the specimen. The brass plate provided a stable temperature at 0°C, and served to force a thermal gradient across the specimen. Thermocouples were used to measure the temperature difference across the blubber and across the standard. The TC of the blubber was estimated using the Fourier Equation as follows:

Equation 1

$$Q = k \cdot A \cdot \frac{\Delta T}{\Delta X}$$

where Q is the total heat (W) output through the sample; A is the area of the sample (m^2); k is the TC of a material (Wm/K), ΔT is the temperature difference across the sample and ΔX is the thickness of the sample.

Equation 2

Solving for k of bowhead blubber:

$$k = \frac{Q}{A \cdot \frac{\Delta T}{\Delta X}}$$

Because some heat (power) escapes into the foam box, a standard with known conductivity was added to accurately estimate *k* for the blubber. This allows a more precise estimate of the power emitted off the top of the standard and into the sample, thus *k* (of the sample) can be estimated as follows:

Equation 3

$$k_b = \frac{k_s * \frac{\Delta T_s}{\Delta x_s}}{\frac{\Delta T_b}{\Delta x_b}}$$

where ΔT_b is the temperature difference (C) across the blubber, and Δx_b is the thickness (m) of the blubber sample, ΔT_s is the temperature (C) difference across the standard, and Δx_s is the thickness (m) of the standard.

To integrate the TC measurements of the sections (layers) of blubber measured using the hot box, the following approach was used:

Equation 4

$$\frac{1}{k_t} = \sum_{i=1} \frac{\phi_1}{k_1} + \frac{\phi_{2'}}{k_2} + \ldots \frac{\phi_n}{k_n}$$

where: k_t = total effective TC of the entire blubber sample, and Φ is the fractional thickness of the i^{th} layer.

Flash-heated Needle Probe

The second method for estimating TC employed a flash-heated "needle probe". The needle is approximately 10 cm in length and includes both a heating coil and thermocouple, which is connected to a Campbell[4] data logger/power supply for power and data retrieval. The needle is inserted into the blubber and heated with a specific wattage for about 10 minutes and then allowed to cool. Since the rate of heating and cooling of the needle is a function of the TC of the material surrounding it, the TC of the tissue can be calculated. A data logger records time and

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[4] 815 West 1800 North, Logan, Utah 84321-1784 USA

temperature data. A series of computer programs written in Igor are used to analyze the resulting data whereby the TC of the material is estimated during both the heating and cooling cycle.

Bowhead Heat-loss Model

We devised a simple heat loss model in an Excel spreadsheet to estimate the overall power loss for whales of different body mass and length. Three different whale sizes (9 m, 13 m, and 16 m) were used to represent a sub-adult, pubescent, and adult bowhead, respectively. The whale was divided into 4 frustrums (truncated cones) based on the proportions of the whale (Fig. 1) and girth measurements (see Chapter 1). The blubber thickness and girth for each cone was estimated from measurements of landed whales. The average temperature at the muscle-blubber interface was estimated from temperature measurements of landed whales. We used an estimate for heat loss from respiration of 6.4% based on work by Folkow and Blix (1992).

Heat loss was estimated for each of the four sections. Heat loss from the flukes, flipper, tongue, and palatal rete were also computed. We used a "flat-plate" heat loss model since for large whales the heat loss difference between flat and curved surfaces (plate) is minimal. The total power output or heat loss was estimated as the sum of the various components, as follows:

Equation 5

$$TP = \sum_{i=1} F_1 + F_2 + F_3 + F_4 + FL + FP + PR + T + \mathrm{R}$$

where TP = total power output; F= body sections (frustrum), FL= flukes, FP = flippers, PR = palatal rete, T= tongue, R = respiratory loss.

Variance Estimation

The standard deviation on the metabolic rate estimates was calculated as follows. The thermal conductivity input to the model used the mean and standard deviation (SD) based on laboratory measurements. The temperature at the muscle-blubber interface was the mean and SD based on measurements from all whales. The model randomly sampled a normal distribution based on these statistics. The Monte Carlo sampling routine in software PopTools (Hood, 2003) was used to estimate a standard error by resampling 1000 times. The mean and variance were calculated from the results of the 1000 runs of the model.

Parameters for heat loss model

The model parameters are listed in Table 1.

Fluke, flipper and body surface area and temperature estimates

The internal temperature of the flukes was measured using the Physitemp probe at five different locations spaced along their length. The temperature was taken in the dense fibrous connective tissues at the fluke's core.

The area of the flukes and flippers was estimated by direct measurement of the appendages on a range of different whale sizes. A linear least squares regression model was used to analyze total body length by fluke and body length by flipper area as in the following equation:

$$y = \beta_o + \beta_1 x$$

where y = area, x = body length

The surface area (SA) of the entire body was calculated as a sum of the surface area for each of the frustrums. These surface area estimates were treated as constants in the calculations partly to reduce the number of parameters in the estimation. We used the following equation:

$$\mathrm{SA} = \pi \cdot (r_1 + r_2) \cdot \sqrt{(r_1 - r_2) + bl^2}$$

Where r_1 and r_2 are the radii at the ends of each of the body sections (frustrum) and bl = body length, (e.g., R-AG, AG-UG, etc., Figure 6.1)

Results and Discussion

Deep Body Temperature

The deep body temperature of landed (non-pregnant) bowhead whales was 33.8° C (N = 28; SD = 0.83; range 32.4° - 35.3° C). This is lower than reported for other cetaceans, and most other non-hibernating eutherian mammals (Schmidt-Nielsen, 1997; Kvadsheim *et al.* 1997a; Prosser 1991). Only Prototherian mammals such as the duck-billed platypus and spiny echidna, and perhaps some marsupials, have cooler average core body temperatures. Manatees of the Order Sirenia also have low body temperatures (34.4° C) (J. Reynolds, pers. comm., 2004). Schmidt-Nielsen (1997) notes that body temperature varies among species, individuals, time of day, etc. but as a "rule of thumb" suggests that most eutherian mammals maintain a body temperature of 38 ± 2° C.

Our bowhead body core measurements were lower than those reported for minke whales. Folkow and Blix (1992) reported mean deep body temperatures for minke whales of 34.7° C (SD = 0.8, N= 14). Their standard deviation or distribution in deep body temperatures was identical to the distribution of our measurements (i.e., SD = 0.8° C). Brodie and Paasche (1985) reported the deep body temperatures for fin whales at 36.1° C taken immediately after death, in the Icelandic commercial fishery. Morrison (1962) reported 490 temperature measurements (from F.H. Addison unpublished data) of commercially harvested humpback (*Megaptera novaengliae*) whales in Antarctica. Their mean temperature was 34.7° C (SD=0.9° C, Range = 31.7 to 38.3° C). The distribution (SD) of temperatures is large and similar to our measurements.

For humans, Guyton (1968) stated "no single [human] body temperature can be considered to be normal" and reports a range of 36.1 to ~37.2° C at rest. Temperature range from lows (for sleeping and cold-exposed humans) to highs (for individuals involved in strenuous exercise) was 35.6° to 40° C, respectively.

Body core temperatures were examined for the effects of body size, sex and the time the whale was pursued. Temperature differences between sexes showed no relationship ($p = 0.595$; independent *t*-test). Pursuit time and body length are statistically significant ($p < 0.05$) if regressed separately as predictors of body temperature. However, neither variable was significant in a multiple regression - body temperature vs. body length ($p = 0.08$) and pursuit time ($p = 0.276$). This suggests correlation between the two predictor variables – body length and pursuit time – which is not unexpected since larger whales often take more time to catch. The body temperatures for pursued whales, in some cases for over an hour, were not elevated. In fact, the lowest temperature was for the whale pursued the longest. Vongraven *et al.* (1990) reported that deep body temperatures in minke whales were not influenced by duration of pursuit. Brodie and Paasche (1985; p. 2268) found a similar result with fin whales and reported:

> "What was surprising here was the initially low deep core temperatures and, in particular, those of the two whales that had been intensively pursued. There is no evidence that excess heat, resulting from the increased propulsive activity, was stored within the core, at least near the monitoring sites, and surprisingly, the female fin whale that had not been pursued registered the highest temperature."

Possible explanations for lowered temperatures include directed heat loss in response to increased exercise, or that the animal had lost control of thermoregulation and peripheral circulation. Morrison (1962) also summarized Nishiwaki's unpublished data which showed no clear elevation of deep body temperatures for fin and blue whales with longer chase times. Cockrill (1951) described a 3-ton whale fillet towed in Antarctic (ice) water for 21 hours and only lost 0.5° C.

Based on the data reported here, and a review of several mammalian orders by Prosser (1991), bowhead whales appear to fall outside the temperature ranges of typical placental mammals. They agree more closely with deep body temperatures for some bat species and for non-eutherian mammals, and slightly below other large cetaceans.

Pregnant females were not considered in estimating body temperature. While body temperatures were not significantly different between groups, some of the coolest whales were pregnant. We questioned if the probe may have entered the uterus which may be cooler than the deep body temperature, however there is no evidence for this.

Body surface area

To model heat loss the surface area was estimated. The total surface area of the bowhead whale was estimated to be 36.7 m^2, 64.3 m^2, and 103.9 m^2 for 9, 13, and 16 m whales, respectively.

Fluke and flipper area

Flukes are relatively large in balaenids (Woodward *et al.*, 2006). Models resulting from regressing fluke area and flipper area against body length suggest a strong linear relationship (Figure 6.2). This is not unexpected since flipper and fluke length is highly correlated with body length in most cetaceans (Amano and Miyazaki, 1993; (Chapter 2). Results for the flipper were:

$$y = 24.9x - 17368 \ (R^2 = 0.95)$$

where y = area of the flipper (cm^2) and x = body length (cm)

Fluke area model

For the flukes, the resulting relationship between body length and fluke area was:

$$y = 45.4x - 25667 \ (R^2 = 0.91)$$

where y = area of the fluke (cm^2) and x = body length (cm)

Measured Heat Loss Rates

A time series of temperature measurements was made for 3 whales starting about 15 minutes postmortem and extending 0.8 hr, 5.8 hr and 8.3 hr, respectively. For the two whales with a time-series over 5 hrs in length, one cooled 0.39° C and the other warmed 0.84° C (Figure 6.3, Table 6.2). These data suggest that bowheads lose heat slowly (0.1° C/hr) even in cold water and may even warm from bacterial activity in the gut. Deep body temperatures of a dead bowhead whale appear to change little postmortem when the blubber layer is intact. In fact, the estimated thermal resistance of the thorax for our 16 m whale (blubber 30 cm) was 1.4 (m^2C/W) or roughly that of R = 1.4 or 4 cm of fiberglass.

These observations confirm those of Innes (1986) taken on a 13 m fin whale, which also cooled slowly. Our observations support the traditional knowledge of senior whale hunters at Barrow (Albert 2001). They know that unless the whale is butchered quickly, it will not cool and soon decompose becoming an "*avutianiq*" (meaning bloated whale). Regarding our study, Captain Edward Hopson, Sr. predicted before we started, "*you will find out that the bowhead whale is a thermos bottle.*"

Temperatures at several locations along the flukes were taken about 15-20 minutes postmortem for whale 98B10 (1298 cm female), after being removed for towing. The seawater was 3.3° C at the time. The temperature at the fluke's center where it joins the peduncle was 20.1° C and 5.6° C at the flukes' distal tip.

Flukes have a thin blubber layer (1.5 cm) sandwiched between the epidermis and a tendenous layer (Haldiman and Tarpley, 1993; Elsner *et al.*, 2004). The TC of the blubber was estimated at 0.26 $Wm^{-1}K^{-1}$ but these measurements may have been influenced by its proximity to the epidermis that has a high TC. The TC of the epidermis on the flukes was 0.53 $Wm^{-1}K^{-1}$, which is similar but slightly higher than the epidermis of the dorsal "trunk".

Thermal Conductivity of Epidermis, Dermis, and Tongue

The thermal conductivity of the fatty dermis or "blubber" is in the same range as other marine mammals (Kvadsheim *et al.*, 1996; Table 6.3; Figure 6.4). Mean TC values from the needle probe (0.23 $Wm^{-1}K^{-1}$, SD=0.009) (for paired samples) and the hot-box (0.231 $Wm^{-1}K^{-1}$, SD=0.14) gave almost identical results based on limited comparisons (Tables 6.2 and 6.3). For the thick blubber samples (>25 cm), the hot box required running the test over several days (up to 117 hrs) for the box temperatures to equilibrate. The long duration of the experiment period caused some rendering of lipids out of the blubber, which likely affected the TC measurements. Regardless, the TC estimates are quite consistent between the two techniques, and with those of other cetaceans.

The thermal conductivity of the epidermis averaged 0.48 (SE = 0.009) $Wm^{-1}K^{-1}$ or just over twice that of the blubber. Thus, the epidermis is a better conductor of heat than the blubber and likely aids in heat dissipation especially when the dermal papillae which penetrate into the epidermis are perfused with blood. The thermal conductivity of one sample of outer layer tongue from a 10 m whale using the needle probe was 0.22 $Wm^{-1}K^{-1}$.

Variation in blubber thermal conductivity and blubber density

We examined subsets of the thermal conductivity data to test for differences in TC values due to sex, position in blubber column, length, and dorsal vs. ventral orientation. While the data for these analyses were limited, we noted some interesting patterns in the TC and blubber densities described below (Figure 6.5).

The TC of the blubber (dermis) varied between the dorsal and ventral region of the thorax ($p = 0.8$). Kvadsheim *et al.* (1996), however, reported statistical differences in TC between different regions on minke whales. The lack of difference here could be due to the small sample size. The thermal conductivity of the blubber did however vary by location in the blubber column (Figure 6.4). TC was significantly higher in the lower portion of the blubber column and lowest in the center sections. This is consistent with measurements by Mau (2004) on the percent-lipid in the blubber by strata. Mau found the highest percent-lipid tended to occur in the middle of the blubber column.

Blubber density was positively (and significantly) correlated ($p = 0.028$) with TC. This is likely because higher lipid content results in a lower blubber density and thermal conductivity. The density and TC were lowest in the middle of the blubber layer (Figure 6.4). The mean thermal conductivity of the blubber was positively correlated with whale body length ($p = 0.038$). This finding is also consistent with those of T. Mau (pers. comm., 2004) in that larger whales had lower overall lipid content in the blubber and greater connective tissue content (Rosa, 2006).

Resting Metabolic Rates

Metabolic power production for a 9, 13, and 16 m bowhead in 0° C sea water was estimated to be 1,778 (SD= 92); 3,213 (SD= 168) and 5,112 SD =(238) W, respectively. These calculations assume the whale is at rest, the blubber is not circumvented by blood flow to the skin, and the tongue is exposed to cold water.

Based on these results, bowhead whales appear to fall well below the Kleiber curve in power production (Table 6.5). For instance, a 13 m bowhead produced power at approximately 30% of that predicted for most mammals based on the "Kleiber curve" (Kleiber, 1961). The Kleiber model is based on "basal metabolic rates" which are somewhat lower than RMR. For comparison, using published estimates from Blix and Folkow (1995) for minke whales (80 $\text{kJ}\cdot\text{kg}^{1}\cdot\text{day}^{-1}$), would suggest considerably higher RMR estimates for bowheads. For example, a 13 m bowhead with a body mass of 30 tons would produce about 28,000 W using their estimates. On the other hand, a minke whale scaled to the mass of a 13 m bowhead would have a somewhat lower power output per kilogram, but would still be greater than bowhead whales.

In our model we used the basic "flat plate" model for heat loss. Kvadsheim *et al.* (1997a) demonstrated that flat plate models over estimate heat loss by 5-10% compared with models that include body geometry ("curved plate"); however, this is most important for small mammals including small cetaceans such as porpoise and dolphins. For large cetaceans such as the bowhead, the blubber surface is effectively flat so the corrections would make little difference (< 5%). In fact, any curvature corrections would drop the already low RMR (power output) estimates.

Resting metabolic rate (RMR) is defined as the power output for an animal that is not engaged in activity. However, RMR is difficult to measure precisely and is affected by the age and physiological condition of an individual. An important consideration regarding metabolic rate is that it scales with body mass $^{0.75}$. This pattern is remarkably consistent across species within taxonomic groups (e.g., mammals). This relationship is sometimes referred to as the Kleiber curve or the "mouse to elephant" curve (Kleiber, 1961). This effect is partially attributable to the surface area to volume ratio effect which decreases with body mass and therefore reduces the heat flux per unit mass (Schmidt-Neilson, 1997).

Oxygen-stores and fat stores, however, scale directly (1.0 power) with body mass (Schmidt-Neilson, 1997). These conditions mean that there will be greater oxygen stores per kilogram of body mass for larger animals. For "huge" animals like whales, these trajectories diverge significantly. Much of the ability of large mammals to fast or dive for disproportionately longer periods than small mammals, is attributable to these scaling factors (Costa and Williams, 1999).

Low metabolic rates might explain the need for the unusually thick blubber of bowhead whales. That is, when resting, their thick blubber coat must remain thermoneutral. This may occur during the winter months when western Arctic bowheads linger within the pack ice margins of the Bering Sea. Also, during periods of food scarcity, bowhead whales may both be able to maintain low metabolic rates as well as use lipid stores. However, this logic is somewhat circular since our metabolic rate estimates are based on a heat loss technique which will undoubtedly be low because the animal is so well insulated.

Given the thick blubber and low metabolic rates, an obvious question is, how long could a bowhead whale survive during periods of prey failure with little or no feeding? Theoretically, bowheads should be able to survive longer than other cetaceans. To make this calculation, several assumptions need to be made regarding assimilation efficiency, percent lipid in the blubber, etc. A rough calculation (assuming a 90% efficiency rate in blubber catabolism; Lockyer *et al.* 1985) suggests a resting 13 m bowhead could survive ~2 years before it utilized 50% of its lipid reserves, and 4 years to use them entirely. Thus, Burns' (1993) hypothesis that the excessively thick blubber in the bowhead serves mainly as a buffer against multi-year prey failures has merit.

Because of the thin blubber in the flukes, the heat loss rates (W/m^2) are high despite the lower temperatures within the flukes (Figures 6.6 and 6.7). However, the body (tip of the rostrum to the peduncle (V1-V4) has a much larger surface area than the appendages and so, overall, more heat is lost through this region.

The model suggests that the palatal rete has the highest heat flux of any part of the whale because it is thermally undefended (Figure 6.7) with no blubber layer over it. However, the rete is small compared to other regions of the body, so the overall heat loss is relatively low. Of course, if the mouth is closed then heat loss would be reduced further.

Hypometabolism

The "triad of physiological responses" is known as the diving response which consists of: apnea, bradycardia, and peripheral vasoconstriction leading to reduced blood flow to most peripheral tissues. In addition, reduced metabolic rates, or hypometabolism, is also known or suspected in some species of diving marine mammals. Reduced metabolic rates and lowered core body temperatures during dives may be a key factor in extending the dive duration of marine mammals such as elephant (*Mirounga angustirostris*) and gray (*Halichoerus grypus*) seals (Andrews *et al.*, 1995; Elsner, 1999; Sparling and Fedak, 2004).

The relationship between body temperature and metabolic rates for poikilotherms or "cold blooded" vertebrates is well described in the literature (Schmidt-Nielson, 1997). However, its application to non-hibernating homeothermic mammals is not well studied and may be an important means of reducing energetic costs for some mammals (Elsner, 1999). The "Q_{10} effect" describes this relationship, whereby metabolic rate change by a factor of 2 to 3 for every 10° C increase or decrease in body temperature. The relationship is described by the following equation:

$$R_2 = R_1 \cdot Q_{10}{}^{(T_2 - T_1)/10}$$

Where, R_2 and R_1 are the metabolic rates at temperatures T_2 and T_1 (from Schmidt-Nielson, 1997).

Therefore, we should expect the metabolic rate of bowhead whales to be lower due to their lower body temperature. For example, a bowhead with a body temperature of 33.8° C would have a metabolic rate roughly 80% (using an average Q_{10} of 2) of a more typical mammal with a body temperature of 37° C (Elsner, 1999; Schmidt-Neilson, 1997). The Q_{10} effect applies to all metabolically active tissues. Thus dropping the temperature of the appendages and skeletal muscles will result in similar declines in oxygen requirements in those limbs and tissues.

Elephant seals exhibit an unusual strategy presumably to take advantage of this effect (Elsner, 1999; Andrews *et al.*, 1995). They can drop their body temperatures as much as 4° C during long dives. To "prepare" for a dive, they increase blood perfusion to their skin and increase its temperature. This heat is then quickly lost to the sea and the core temperature drops sharply. Once in the dive, they initiate the typical suite of physiological effects associated with the dive response such as vaso-constriction of the limbs and skeletal muscles. As noted, this drop in body temperature may result in a significant reduction in the metabolic rate and extend dive duration. Based on the unusual dive performance of the elephant seal alone, it seems reasonable that low body temperatures together with the Q_{10} effect may play a role in bowhead whales, and partially explain the low resting metabolic rates estimated here.

Blood flow

With its specific heat close to that of water, blood can transfer a considerable amount of heat to the skin (Hokkanen, 1990) and appendages of a whale (Pabst *et al.*, 1999) where it is subsequently lost to the environment. Consider a typical 5,000 W home hot water heater. A faucet running even at a moderate flow (~50 cc/s) can overwhelm the water heater's capacity to keep pace with the mass flow. The large arteries (1 cm diameter) in the flukes of large whales alone may be sufficient to accommodate a substantial portion of flow at this rate. Similarly, in the bowhead, if the blood moving to the flukes is ~34° C and is cooled to 14° C ($\Delta = 20$ C) with a specific heat ~3.22 kJ/kgC , a 50 cc/s flow rate would produce 4200 W.

It is not possible, however, for a bowhead to dissipate much heat unless the blubber is circumvented. Therefore, to dissipate heat, a bowhead must be able to shunt a significant amount of blood to the epidermis in the flukes, abdominal and lumbar regions, and perhaps to the flippers and tongue (Kvadsheim *et al.*, 1997b). The tongue of the bowhead is likely important for thermoregulation since it is extremely large, its core is relatively warm (~30°C) and it possess "vascular retial adaptations" (Heyning and Mead, 1997; Werth, 2007) (Figure 6.8).

Bowhead flukes have a sophisticated counter-current system of blood vessels whereby a central artery is surrounded by veins and an alternate arteriovenous anastomoses (AVA) system with vessels near the skin. In the vasoconstricted state, the counter-current system reduces heat loss from the flukes by returning blood through the counter-current system. Alternatively, in the relaxed state, Elsner *et al.*, (2004) speculated that the AVA system likely functions to dissipate heat when body temperatures are elevated (Figure 6.9) by shunting blood to vessels close to the skin. The thermal conductivity of the blubber increases when it is perfused with blood. In that case, it would not be necessary to move as much blood to the skin to lose heat if the TC of the blubber is significantly higher (Hokkanen, 1990). Bowhead dermis (including dermal papillae) of the abdominal and lumbar regions appears to be well vascularized. Therefore, it seems likely that, if necessary, a bowhead could augment heat loss by perfusing the "blubber" or fatty dermis, thereby *raising* its TC.

Life History Considerations and Synthesis

Our finding that metabolic rates of bowhead whales are low compared to that of similar sized whales is consistent with the unusual aspects of their life history, physiology and morphology. Their extreme baleen development allows them to feed on low-density zooplankton swarms in high Arctic seas (Thomson, 2002). The stomach is comparatively small (Tarpley *et al.* 1987) and feeding and energy accumulation is likely slower than in other baleen whales such as the balaenopterids (Kvadsheim, 1998; Haug *et al.*, 1995) which are "gulp" feeders. Its large flukes are needed for low-speed power required to push the whale through the water with its mouth agape, but they likely also help with heat dispersion. Average swim speeds for bowheads (mean ~4 km/h) are at the low end for cetaceans (Zeh *et al.* 1993; Woodward *et al.* 2006) but may be necessary to reduce the cost of swimming for this relatively non-athletic species (Costa and Williams, 1999). T. Albert (pers. comm.) has speculated that the thick epidermis and associated dermal papilla may be an adaptation for making heat loss more efficient (Haldiman *et al.*, 1985; Haldiman and Tarpley, 1993). Consider the following: (a) the epidermis is exceptionally thick and non-cornified, (b) the dermal papillae (and their vessels) are extensive and protrude into the epidermis, and (c) the epidermis has a thermal conductivity value over twice that of the blubber. Based on these traits, it is possible that the thickened skin has a heat dissipation function. Thus, heat moved near the skin via blood would be more quickly lost to seawater.

The bowhead's slow growth, low reproductive rate, late age at sexual maturity (~20 yr) and extreme longevity (Schell *et al.* 1989; Koski *et al.* 1993; George *et al*, 1999) could be the result of several factors including lowered body temperatures, i.e., a hypometabolic condition. Conti *et al.* (2006) found that mice genetically engineered to have lower core body temperatures (by only 0.5° C) lived 15% longer than "normal" mice. Growth rates of bowheads are slow compared with other cetaceans. Remarkably, Lubetkin and Zeh (2006) show evidence of a 2-3 year growth hiatus following weaning (at year 1). Because it is critical that the head and baleen rack grow sufficiently to feed effectively on small and typically low-density prey found in the high-arctic regions, there appears to be an allometric relationship in that the head grows disproportionately faster than body length in sub-adults (Chapter 2). Still, due to the slow rate of energy accumulation, body growth rates are slowed and sexual maturity is greatly delayed (George *et al.*, 1999; Koski *et al.*, 1993).

Bowhead whales appear to have resting metabolic rates that are lower than other similar-sized mammals falling below estimates of Kleiber. Their deep body temperatures are also low compared with other Eutherian mammals. Sub-normal body temperatures and relatively low metabolic rates can be partially explained by a hypometabolism condition via the Q_{10} effect. Hokkanen (1990) predicted that the high thermal resistance of bowhead whale blubber suggests they carry a heat load even at rest. However, the metabolic rate estimates he used in his models were based on the Kleiber curve and may be too high for bowheads. As noted above, bowhead whales may be hypometabolic compared with other mammals, but still may experience heat loading when exercising. At such times they likely produce more heat than can be lost through the blubber by conduction alone. Under these circumstances, dissipating heat by circumventing the blubber with blood flow to the skin or mouth is required. Due to this thick blubber coat, they may become heat stressed while migrating, actively feeding or when hunted. However, they appear to have effective mechanisms for dissipating heat as suggested by temperatures remaining constant in the body of chased whales (Whittow 1987).

Another possibility is that applying the Kleiber estimate using the full body mass of the bowhead leads to an overestimate. For five bowheads weighed in sections, an average of 44% of the body mass was blubber, which is mostly non-thermogenic (Kvadsheim, 1998; see Chapter 3). If only the lean body mass of the bowhead whale is used to estimate metabolic output, the estimate drops by 41%. When the lean mass power estimate is coupled to the Q_{10} correction, the power output agrees well with the power estimates from our model – and may explain the discrepancy between the Kleiber estimates and ours. For example, consider a 13 m whale with a power output based on the Kleiber model of 8,900 W. Assuming the thermogenic mass is 45% of the total mass (thermogenic mass = total mass – (muscle and bone); Chapter 2) the power estimate drops to about 4,900 W. Applying the Q_{10} correction lowers this figure to ~3,600 W, which is quite close to the estimate derived from the model (Table 6.5).

While low metabolic rates offer some disadvantages such as slow growth rates, they also offer advantages. When food is limited, as in winter, it may be possible for a bowhead to persist for long periods at a relatively low metabolic cost. Selection may have modified the bowhead to store huge amounts of lipid in the form of thick blubber, to survive periods (perhaps years) when "food is virtually lacking" as hypothesized by Burns (1993; p. 760). As noted earlier, a 13 m non-reproductive bowhead may take years to use just 50% of its lipid reserves. In nature, given stress from migration, reproduction, predation, etc, this time duration is unlikely, but does suggest that a bowhead may carry significant fat stores as a buffer. Kraus and Rolland (2007) nicely summarized the North Atlantic right whale strategy as "*survive the lean years, and reproduce in the good ones*."

Problems with the Analysis

The results reported here should be considered as preliminary estimates of bowhead whale metabolic rates. That is, while some of the model parameters are fairly well understood (TC of "dead" blubber, water temperature, body mass, surface area) many of the model parameters and assumptions are informed guesses. Variables such as the temperature inside the mouth when it is closed would obviously affect heat loss from the tongue. Another unknown is the degree to which blubber TC changes in live animals with blood perfusion. While bowheads live in water < 0° C much of the year, they may occasionally experience water temperatures in summer to 10° C which would greatly reduce heat loss.

While heat loss methods show promise, we suggest taking further body temperature measurements and making refinements to the heat loss models. We also suggest using other methods (e.g., lung volume and respiration rates) to estimate metabolic rate to compare to our results.

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References

Ahmaogak, G. 1989. Protecting the habitat of the bowhead whale. Proceedings of the Sixth Conference of the Comite Arctique International, 13-15 May 1985. pp. 593-597. L. Rey and V. Alexander (Eds.). E.J. Brill, New York, NY. 637 pp

Albert, T. 1981. Some thoughts regarding the possible effect of oil contamination on the bowhead whale, *Balaena mysticetus*. In: Tissue Structural Studies and Other Investigations on the Biology of Endangered Whales in the Beaufort Sea, T. Albert (Ed.), pp. 945-953. Report to the Bureau of Land Management, Anchorage, Alaska from the Department of Veterinary Science, University of Maryland, College Park, MD 20742. 953 pp.

Albert, T. F. 2001. The influence of Harry Brower, Sr., an Inupiaq Eskimo Hunter, on the bowhead whale research program conducted at the UIC-NARL faculty by the North Slope Borough. In: D. Norton, ed. Fifty more years below zero: tributes and mediations for the Naval Arctic Research Laboratory's first half century at Barrow, Alaska. University of Alaska Fairbanks, 2001 xvi. 576 p., ill., maps, 20 cm. ISBN 0-919034098-5.

Andrews, R. D., Jones, D. R., Williams, J. D., Thorson, Crocker, D.E., Costa, D. P. and Le Boeuf, B. J. 1995. Metabolic and cardiovascular adjustments to diving in northern elephant seals (*Mirounga angustirostris*). Abstracts, Tenth Biennial Conference, Biology of Marine Mammals, Galveston, TX, 22.

Amano, M. and Miyazaki, N. 1993. External morphology of Dall's porpoise (*Phocoenoides dalli*): growth and sexual dimorphism. Can. J. Zool. 71: 1124-1130.

Blix, A.S. and Folkow, L.P. 1995. Daily energy expenditure in free living minke whales. Acta Physiol Scand 153: 61-66.

Brodie, P. and Paasche, A. 1985. Thermoregulation and energetics of fin and sei whales based on postmortem, stratified temperature measurements. Can. J. Zool. 63:2267-2269.

Burns, J.J. 1993. Epilog. *In*: Burns, J.J., Montague, J. and C.J. Cowles (eds.). The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

Cockrill, W.R. 1951 Antarctic pelagic whaling; the role of the veterinary surgeon in the whaling industry, with special reference to standards of inspection in the production of whale meat for human consumption, and some notes on the pathology of the Baleen whales. Vet Rec., Vol. 63, Issue 7, 111-125

Conti, B., Sanchez-Alavez, M., Winsky-Sommerer, R., Morale, M.C., Lucero, J., Brownell, S., Fabre, V., Huitron-Resendiz, S., Henriksen, S., Zorrilla, E.P., de Lecea, L., Bartfai, T. 2006. Transgenic Mice with a Reduced Core Body Temperature have an Increased Life Span. Science 314, (5800): 825-828.

Costa, D. P. and Williams, T. M. 1999. Marine Mammal Energetics. In: Biology of Marine Mammals. Smithsonian Institution, Washington, D.C. p. 578.

Elsner, R. 1999. Living in water: solutions to physiological problems. In: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution. pp. 73-116.

Elsner, R., George, J. Craig, O'Hara, T. 2004. Vasomotor responses of isolated peripheral blood vessels from bowhead whales: thermoregulatory implications. Marine Mammal Science 20:546-553.

Ferrero, R. C., and L. W. Fritz. 2002. Stellers sea lion research coordination: a brief history and summary of recent progress. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-AFSC-129, 34 pp.

Folkow, L.P. and Blix, A.S. 1992. Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water. Scandinavian Journal of Physiology. 146: 141-150.

Guyton, A. G. 1968. Textbook of Medical Physiology. Saunders Company. Philadelphia, PA. 1194 p.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via Aspartic acid racemization. Can. J. Zool. 77:571-580.

Harvey, C J. Cox, S P. Essington, T E. Hansson, S. and Kitchell, J F. 2003. An ecosystem model of food web interactions and fisheries effects in the Baltic Sea. ICES Journal of Marine Science 60:1-12

Haldiman, J.T. and Tarpley, R.T. 1993. Anatomy and Physiology. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Haldiman, J.T., Henk, W.G., Henry, R.W., Albert, T.F., Abdelbaki, Y.Z. and Duffield, D.W. 1985. Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). Anat. Rec. 211:391-402.

Haug, T., Gjosaeter, H., Lindstrom, U., and Nilssen, K.T. 1995. Diet and food availability of north-east Atlantic minke whales (*Balaenoptera acutorostrata*), during the summer of 1992. ICES J. Mar. Sci., 52:77-86.

Heyning, J.E. and Mead, J.G. 1997. Thermoregulation in the mouths of feeding gray whales. Science 278:1138-1139.

Hokkanen, J.E.I. 1990. Temperature Regulation of Marine Mammals. J. theor. Biol. (1990) 145, 465-485.

Hood, G.M. 2003. PopTools version 2.5.8. Available on the internet http://www.cse.csior.au

International Whaling Commission. 2003. Annex J. Report of the standing working group on environmental concerns, competition between cetaceans and fisheries (p. 336). Journal of Cetacean Research and Management (5):333-361.

Kanwisher, J. and Sundnes, G. 1965. Physiology of small cetacean. Hvalradets Skrifter (48):45-53.

Kanwisher, J.W. and Ridgway, S.H. 1983. The physiological ecology of whales and porpoises. Sci. Amer. 248 (6): 111-120.

Kleiber, M. 1961. The fire of life, an introduction to animal energetics. Wiley & Sons Inc., New York, USA.

Koski, W.R, Davis, R.A., Miller, G.W., and Withrow, D.E. 1993. Reproduction. In: The Bowhead Whale. Edited by J.J. Burns, J. J. Montague, and C.J. Cowles.. Allen Press, Lawrence, Kansas. pp. 239-269.

Kraus, S.D. and Rolland, R. M. 2007. The Urban Whale. Harvard University Press. Cambridge, MA. 543 pp.

Kvadsheim, P.H., Folkow, L.P., Blix, A.S. 1994. A new device for measurement of the thermal conductivity of fur and blubber. J. Therm biol. 19:431-435.

Kvadsheim, P., Folkow, L.P., and Blix, A. 1996. Thermal conductivity of minke whale blubber. J. therm. Biol. Vol.21. No 2: 123-128.

Kvadsheim, P. H., Gotaas, A. R. L., Folkow, L. P., and Blix, A. S. 1997a. An experimental validation of heat loss models for marine mammals. Journal of Theoretical Biology. (184): 15-23.

Kvadsheim, P.H. and Folkow, L.P. 1997b. Blubber and flipper heat transfer in harp seals. Acta Physiol Scand 1997, 161, 385-295.

Kvadsheim, P. H. 1998. Blubber as insulation (Ph.D. Thesis). Tromso, Norway, University of Tromso. 34 p + appendices.

Lockyer, C.H., McConnell, L.C., and Waters, T. D. 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Can. J. Zool. 63:2328-2338.

Lubetkin, S.C. and Zeh, J. 2006. Deriving age-length relationships for bowhead whales (*Balaena mysticetus*) using a synthesis of age estimation techniques. Paper SC/58/BRG14 presented to the IWC SC.

Morrison, P. 1962. Body temperatures in some Australian mammals. III. Cetacea (Megaptera). Biological bulletin 123 (1):154-162.

National Research Council. 2003. Cumulative environmental effects of oil and gas activities on Alaska's North Slope. March 2003. The National Academies Press. 5000 Fifth Street, NW, Box 285, Washington, DC 20055

North Slope Borough, Science Advisory Committee. 1987. A review of the report "Importance of the Eastern Alaskan Beaufort Sea to Feeding Bowhead Whales, 1985-86". Review submitted to North Slope Borough, Barrow, AK (document NSB-SAC-OR-109). 53 pp.

Pabst, D.A., Rommel, S.A., and McLellan, W.A. 1999. The functional morphology of marine mammals. In: Biology of Marine Mammals. John E. Reynolds III and Sentiel A. Rommel (eds). Smithsonian Institution, pp. 578.

Peters, R. H. 1989. The ecological implications of body size. Cambridge University Press, Cambridge.

Prosser, C. Ladd. 1991 Editor. Environmental and metabolic animal physiology: Comparative Animal Physiology. 4th Edition. John Wiley and Sons.

Reynolds, J. 2004. Personal Communication. Mote Marine Laboratory, FL

Richardson, W.J., Wursig, B. and Miller, G.W. 1987. Bowhead Distribution, Numbers, and Activities. In: W.J. Richardson, *ed.* Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-1986. Report from LGL Environmental Research Associates, Inc. Bryan TX., for US Minerals Management Service. NTIS No. PB88-150271.

Rosa, C. 2006. Health assessment in the bowhead whale. Doctoral thesis, University of Alaska Fairbanks.

Schell, D.M., Saupe, S.M. and Haubenstock, N. 1989. Bowhead (*Balaena mysticetus*) growth and feeding as estimated by sigma 13C techniques. *Mar. Biol.* 103:433-43.

Schell, D. and Saupe, S. 1993. Feeding and growth as indicated by stable isotopes. *In*: J.J. Burns and J.J Montague and C.J. Cowles (eds.). *The bowhead Whale.* Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787pp.

Schmidt-Nielsen, K. 1997. Animal physiology: adaptation and environment. Cambridge University Press. Cambridge, England. 611 pp.

Sheffield, G. Personal communication. 2005. Alaska Department of Fish and Game, Nome Alaska.

Sparling, C.E. and Fedak, M.A. 2004. Metabolic rates of captive grey seals during voluntary diving. Journal of Experimental Biology (207): 1615-1624.

Tarpley, R.J., Sis, R.F., Albert, T.F., Dalton, L.M. and George, J.C. 1987. Observations on the anatomy of the stomach and duodenum of the bowhead whale, *Balaena mysticetus.* Am. J. Anat. 180:295-322.

Thomson, D.H. 1987. Energetics. In: W.J. Richardson, Ed. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-1986. Report from LGL Ecological Research Associates, Inc. Bryan TX., for US Minerals Management Service, Reston, VA 22091. OCS Study 87-0037, Contract No. 14-12-0001-30233.

Thomson, D.H. 2002. Energetics of bowhead whales. p. 22-1 to 22-40. In: W.J. Richardson and D.H. Thomson. (eds.). Bowhead Whale Feeding in the Eastern Alaska Beaufort Sea: Update of Scientific and Traditional Information. For OCS Study MMS 2002-012; LGL Rep. TA 2196-7. Rep. From LGL Ltd., King City, Ontario Department of Interior, Mineral Management Service. Anchorage, AK 99598 and Herdon, VA. Vol. 1, xliv + 420 p; Vol. 2; 277 p.

Vongraven, D., Ekker, M., Espelien, A.R., and Aarvik, F.J. 1990. Postmortem body temperatures in the minke whale, *Balaenoptera acutorostrata*. Canadian Journal of Zoology. 68: 140-143.

Wahrenbrock, E.A., Maruschak, G.F., Elsner, R., and Kenney, D.W. 1974. Respiratory function and metabolism in two baleen whale calves. Marine Fisheries Review 36:3-9.

Weingartner, T., K. Aagaard, R. Woodgate, S. Danielson, Y. Sasaki, D. Cavalieri. 2005. Circulation on the North Central Chukchi Sea Shelf, Deep-Sea Research, Pt. II, 52 (24-26): 3150 - 3174, 2005.

Werth, A.J. 2007. Adaptations of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. The Anatomical Record 290:546–568.

Whittow, G.C. 1987. Thermoregulatory adaptations in marine mammals: interactive effect of exercise and body mass: a review. Marine Mammal Science 3: 220-241.

Woodward, B.L., Winn, J.P., and Fish, F.E. 2006. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. Journal of Morphology 267:1284–1294 (2006).

Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M. and Koski, W.R. 1993. Current population size and dynamics. pp 409-489. In: J.J. Burns and J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. Special publication No. 2 of the Society of Marine Mammalogy. i-xxxvi + 787 pp.

Table 6.1 Parameters used in the heat loss model.

Parameter	**Description**	**Estimate and SD value**
Dx1	Blubber thickness (dermis); used the mean for 9,13,16 m whales.	9 m= 21 cm; 13 m= 24 cm; 16 m = 30 cm
Dx2	Epidermis thickness	2.5 cm
K_s	Thermal conductivity of the epidermis	0.48 ± 0.02 Wm/K
K_b	Thermal conductivity of blubber (dermis) Wm/K	0.23 ± 0.01 Wm/K
V1	Surface area for body volume from the head to the axilla	Units in cm^2
V2	Surface area for body volume from the axilla to the umbilicus	Units in cm^2
V3	Surface area for body volume from the umbilicus to the anus	Units in cm^2
V4	Surface area for body volume from the anus to the peduncle	Units in cm^2
T_w	Average annual temperature of the sea water (Weingartner et al., 2005).	For all estimates, we used 0° C assuming that Arctic Sea temperatures were ~ -1.8° C ~9 months of the year; (Weingartner *et al.* 2005)
$T_{b\text{-}m}$	Mean temperature of the muscle-blubber interface	25° ± 5 C
Fluke1,2,3	Mean measured fluke temperatures; proximal, medial, and distal sections	15,10, 5° C
R_t	Thermal resistance (m^2*C/W)	Estimated by model

Table 6.2. Summary of temperature data of bowhead whales from a time series of measurements made in the abdomen near the umbilicus soon after death, Barrow, Alaska. These were: A) Olemaun98[5] whale, an 8.3 hr time series, B) Whale 98B10, 5.82 hr time series, C) whale 99KK1, a 0.77 hr time series. *The temperature at 25 cm for whale 99KK1 appears quite different from similar measurements and may be from the probe partially pulling out from the whale.

A) Whale Olemaun98 (length estimated ~12 m)

Location	**Initial temp**	**Final temp**	**Δt**	**Rate (C/hr)**
Skin	5.4	4.15	-1.25	-0.15
25 cm	30.31	29.10	-1.21	-0.15
70 cm	34.01	34.85	0.84	0.10
85 cm	34.43	35.27	0.84	0.10

B) Whale 99B10 (body length: 942 cm, blubber thickness 20-22 cm)

Location	**Initial temp**	**Final temp**	**Δt**	**Rate (C/hr)**
Skin	7.56	3.5	-4.06	-0.70
25 cm	32.08	30.0	-2.08	-0.36
70 cm	34.04	34.63	0.59	0.10
85cm	34.43	34.04	-0.39	-0.07

C) Whale 99KK1 (body length: 770 cm, blubber thickness 23 cm)

Location	**Initial temp**	**Final temp**	**Δt**	**Rate (C/hr)**
Skin	1.6	1.6	0	0.00
25 cm*	10.6	10.2	-0.39	-0.50
70 cm	31.93	32.7	0.83	1.07
85 cm	33.59	33.17	-0.42	-0.54

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[5] The Olemaun 98 whale is listed as 'struck and abandoned' by the NSB and AEWC does not have a whale identification number for it. The Olemaun crew killed the whale and was towing it when a storm forced the crews to detach the whale for safety reasons.

Table 6.3. Thermal conductivity measurements of bowhead whale blubber using the hot box. The blubber was cut into two sections (Sect. 1 and 2)where TC (*k*) was measured independently and then a weighted average estimate (K tot) using equation (4). Rtot is the total thermal resistance.

Ventral blubber

Whale ID	**TC Sect 1. (w/skin)**	**TC sect 2**	**Sect. 1 (m)**	**Sect. 2(m)**	**Thick (m)**	**Rtot**	***k* tot**
98B10	0.247	0.226	0.095	0.10	0.195	0.827	0.236
98B13	0.248	0.208	0.093	0.09	0.183	0.808	0.228
mean	0.248	0.217					**0.232**

Dorsal blubber

Whale ID	**TC Sect. 1 (w/skin)**	**TC Sect. 2**	**Sect. 1(m)**	**Sect. 2 (m)**	**Thick(m)**	**Rtot**	***k* tot**
98B10	0.293	0.22	0.0889	0.1651	0.254	1.054	0.246
99B10	0.219	0.205	0.092	0.086	0.178	0.841	0.212
mean	0.256	0.213					**0.229**

Table 6.4. Subset of thermal conductivity (TC) measurements of bowhead whale blubber using the flash heated needle probe where paired dorsal and ventral samples were available. Region is where blubber was sampled; dorsal = blowhole dorsal, ventral= ventral midline opposite the blowhole. Upper, middle and lower refer to equal sections of the blubber sample where "upper" is near the epidermis. The k_{tot} statistic is the integrated *k* for the various layers.

Whale ID	**Region**	**Skin**	**Upper**	**Mid**	**Lower**	***k* tot**	**Blub. Thick. (cm)**
99B19	Dorsal	0.486	0.194	0.189	0.186	0.259	20
99B19	Ventral	0.488	0.190	0.188	0.187	0.261	20
99B20	Dorsal	0.449	0.181	0.176	0.190	0.217	25
99B20	Ventral	0.496	0.187	0.181	0.231	0.225	22
99B21	Dorsal	0.496	0.212	0.188	0.213	0.180	27
99B21	Ventral	0.450	0.207	0.193	0.222	0.238	20
mean		**0.478**	**0.195**	**0.186**	**0.205**	**0.23**	**22.33**
stdev		**0.022**	**0.012**	**0.006**	**0.020**	**0.03**	**3.01**

Table 6.5. Estimated heat loss of resting metabolic rates (Watts) estimated for an average 9, 13, and 16 m bowhead whale using the heat loss technique. The Kleiber estimate is also shown for comparison. Standard deviation was estimated by Monte Carlo sampling with 1000 repetitions. Whale lengths were chosen to represent a typical yearling or immature whale, a whale at the length of sexual maturity, and an average adult. The Q_{10} correction reduces the Kleiber prediction to 80% (of normal) reflecting the lower body temperature of the bowhead.

Method	**9 m whale**	**13 m whale**	**16 m whale**
Heatloss method[1]	1,764 ± 95	3,213 ± 168	5,070 ± 244
Kleiber Prediction:	3909	8,941	15,047
Kleiber with Q_{10} Correction	2,863	7,163	11,019

1. Based on a muscle-blubber interface temperature of 25° C

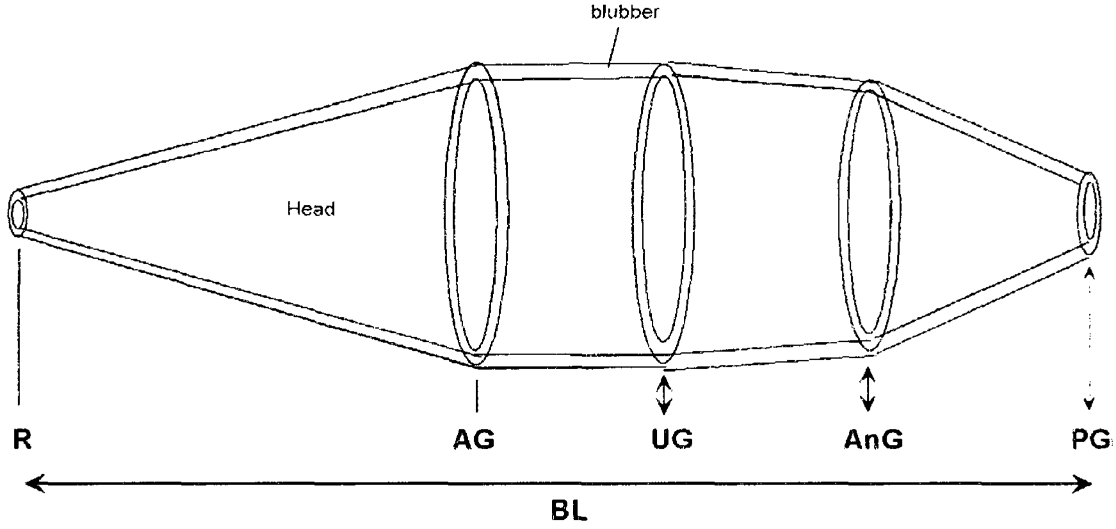
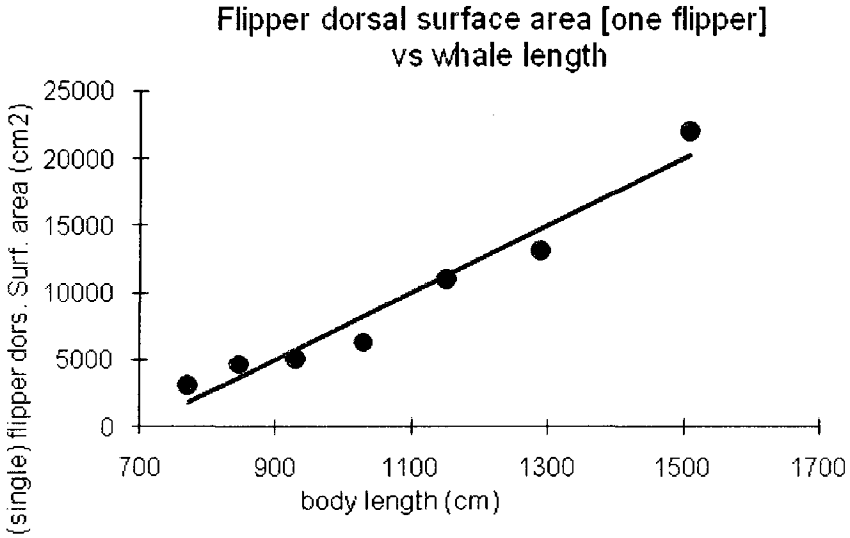
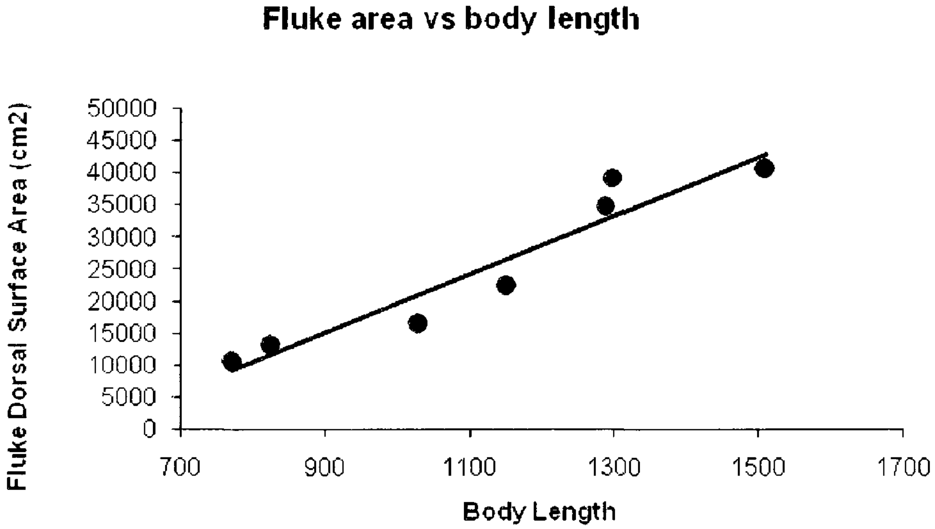


Figure 6.1. A schematic of the heat loss model for a typical bowhead whale. BL is the total body length (m), R is the rostral tip, AG = axillary girth, UG=umbilical girth, AnG=anal girth, PG=peduncle girth.



A



B

Figure 6.2. Regression model for flipper (A) and fluke area (B) on body length for bowhead whales. The high ($R^2 > 0.9$) correlation coefficients of the regression models suggest the models accurately approximate fluke and flipper area.

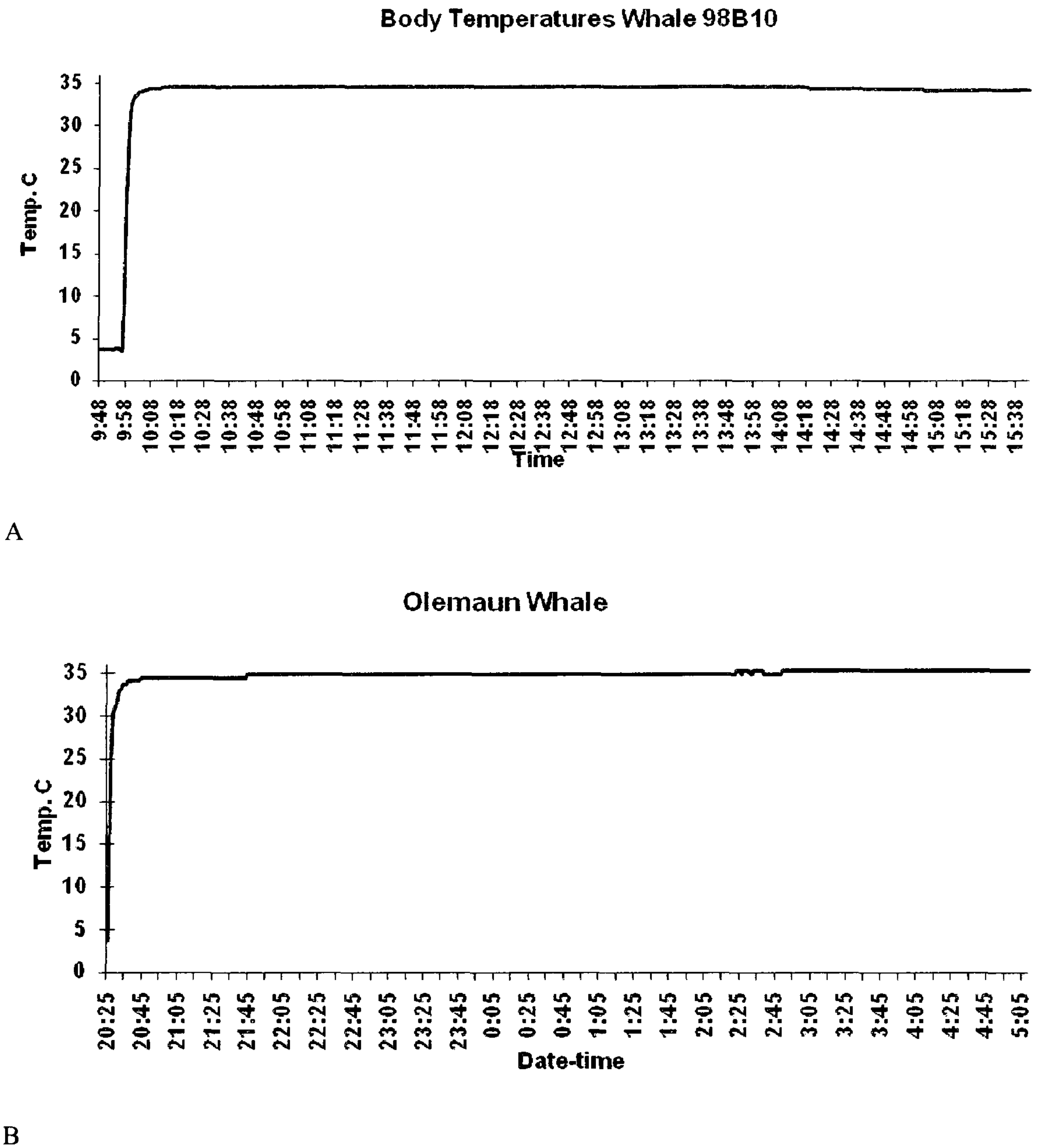
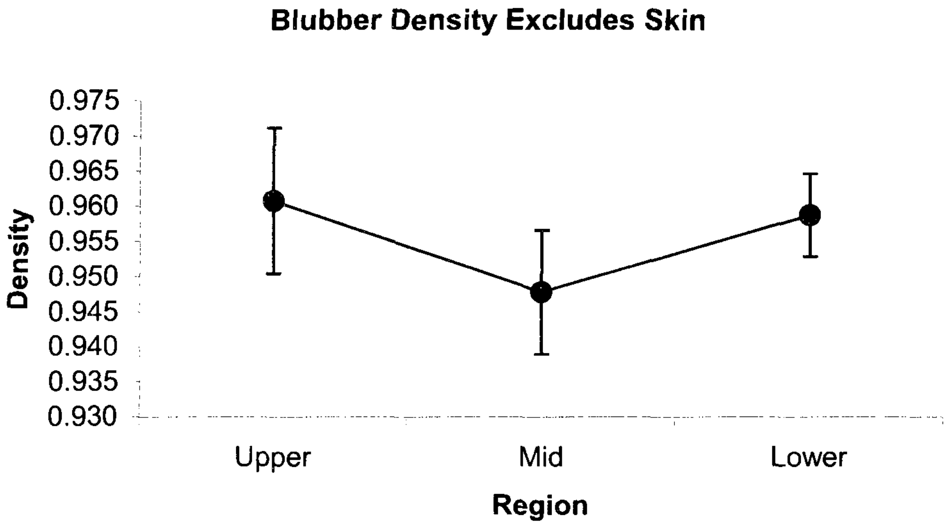
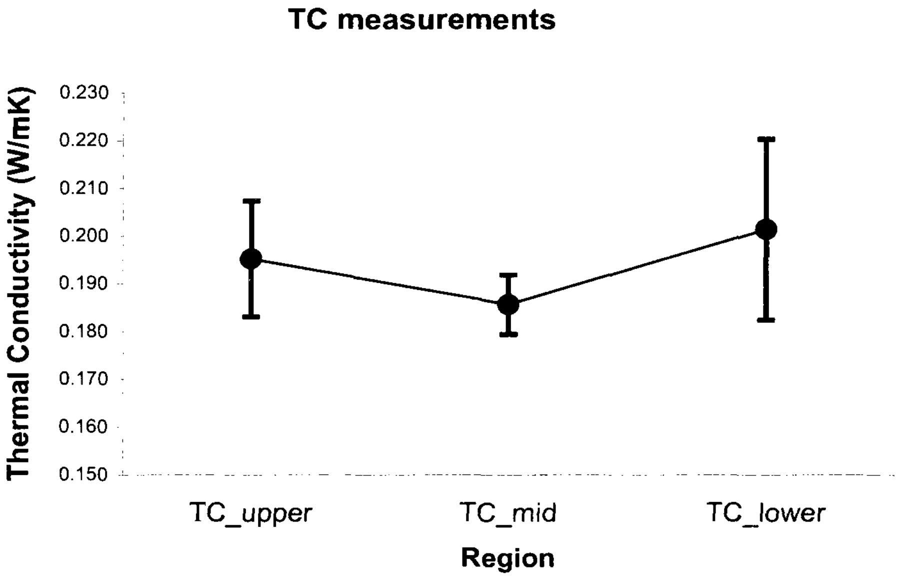


Figure 6.3. A time series of postmortem deep body (1 m depth into abdomen) temperatures taken at 1-minute intervals for two bowhead whales. The harpoon-type temperature sensor was linked to a data logger and was thrust into the whale about 20 minutes postmortem. For whale 98B10 (1298 cm female) in panel A, the deep body temperature dropped 0.39° C over a 5-hr period (n=325). For the "Olemaun" whale (whale was abandoned due to heavy seas but retrieved later) in panel B, the deep body temperature increased 0.84° C over a 9-hr period.



A



B

Figure 6.4. A) Bowhead whale blubber density (kg/l) measured in the upper, middle and lower region of the blubber layer. B) Thermal conductivity (TC) measured at the upper, middle and lower region of the blubber layer. Note that the TC is lowest in mid-layer but does vary between animals.

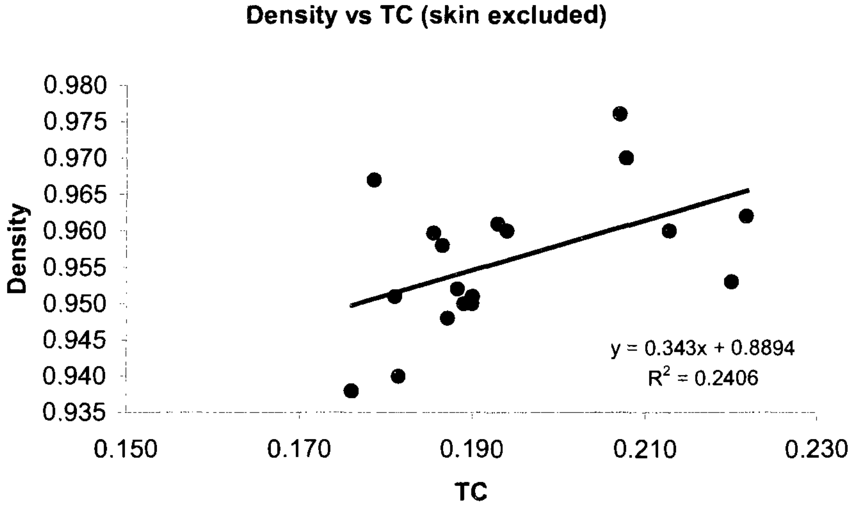


Figure 6.5. Linear regression of blubber density (kg/l) on blubber thermal conductivity for bowhead whales. There is a positive relationship between blubber density and thermal conductivity. The epidermis, excluded in this plot, has a TC value (~0.48 Wm/K) over twice that of blubber and a density > 1 gm/cc.

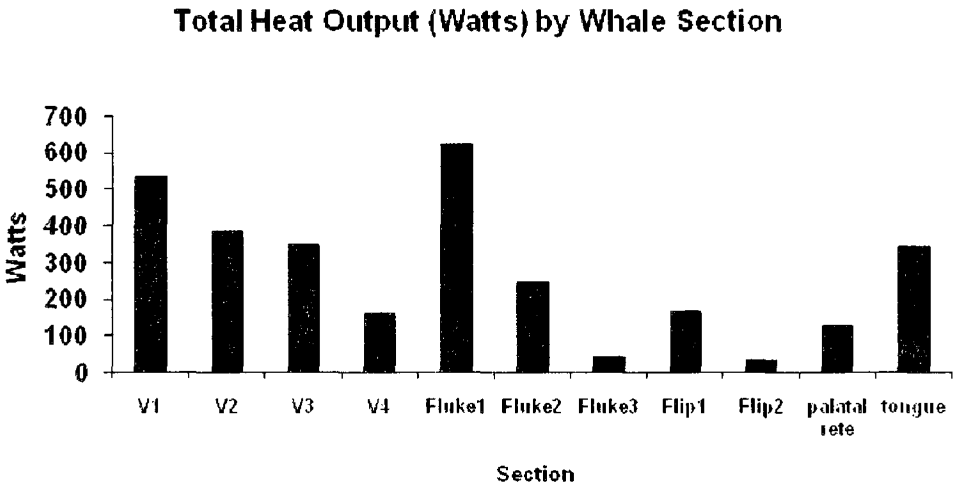


Figure 6.6. Total power output (watts) estimates for a 13 m bowhead whale by body portion. Sections V1-V4 refers to body sections from the head to the peduncle (see methods). Fluke 1-3 sections refer to the "inner, middle and outer" third of the fluke (see methods). Flip 1 and 2 are the proximal and distal half of the flipper.

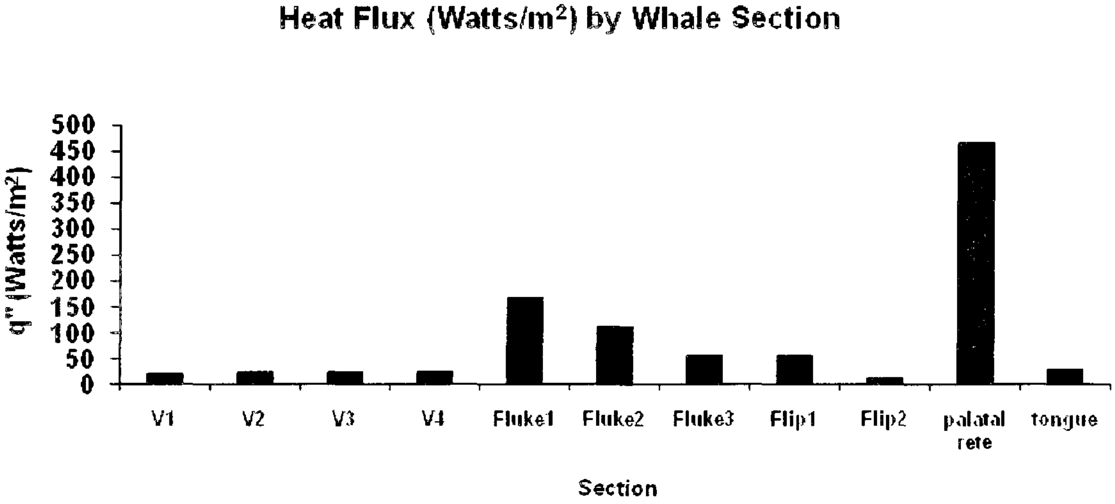


Figure 6.7. Estimated heat flux (W/m^2) from various portions of the bowhead whale. Note that the estimated heat flux is greatest from the flukes, tongue, and palatal rete mainly because the blubber layer is so thin (1.5 cm) in these regions, and absent over the palatal rete. The Fluke 1-3 sections refer to the "inner, middle and outer" third of the fluke (see methods). Flip 1 and 2 are the proximal and distal half of the flipper.

Figure 6.8. Photograph of the large tongue from bowhead whale 97B12, a 15.3 m male.

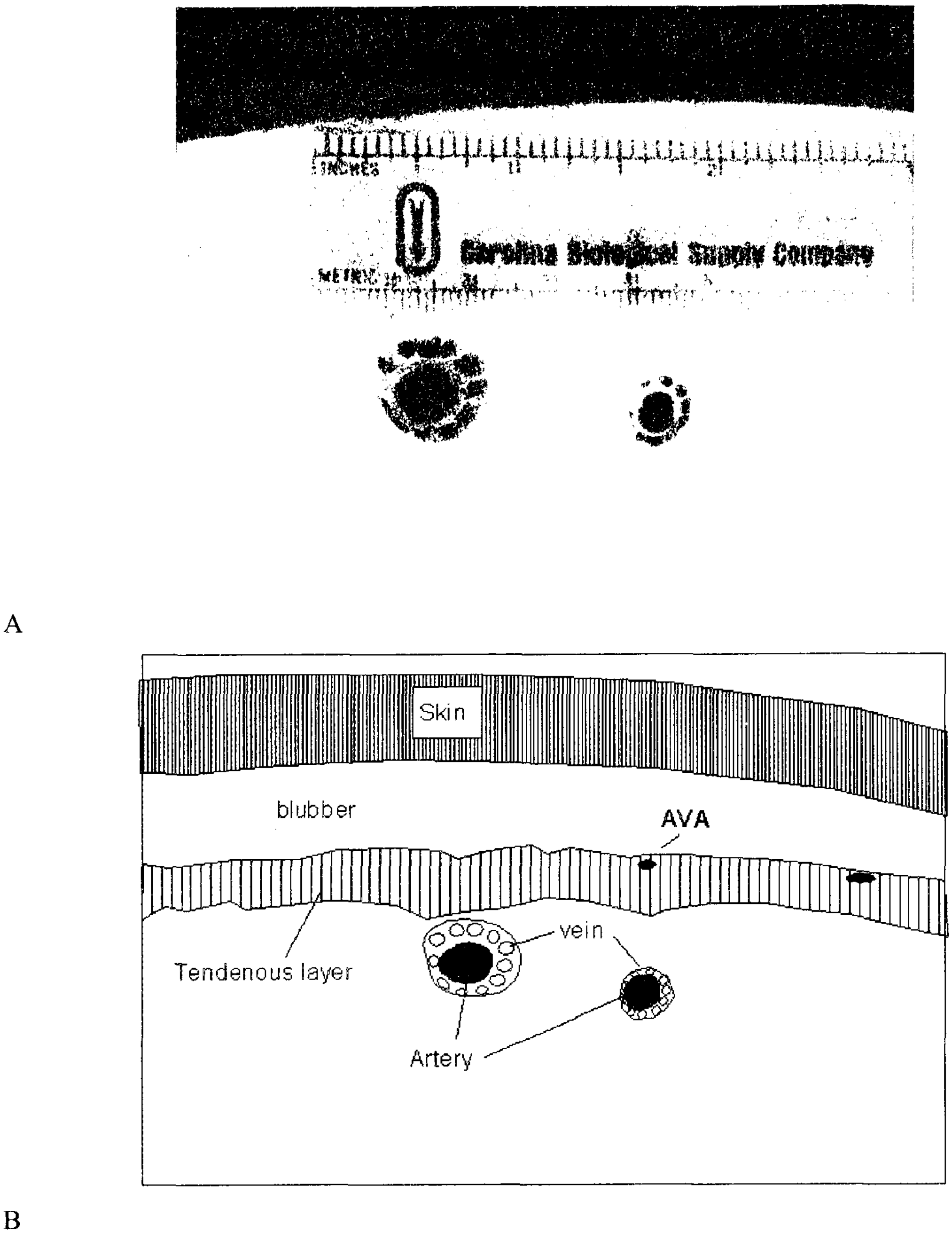


Figure 6.9. A) Photographic cross section of a bowhead whale fluke showing the counter-current heat exchange system (artery and surrounding veins), tendenous layer, blubber and epidermis. Note that the blubber layer is only about 1 cm thick on the flukes. B) Drawing labeling some aspects of the photograph (photo: J. George and E. Follmann).

Chapter 7 General Summary and Conclusions

These studies have clarified some basic life history characteristics of the bowhead and the selective pressures that have shaped the bowhead into its present form. These traits were found to be unique among cetaceans and other mammals in general. Traits include: exceptional longevity, large head and associated baleen development, unusually thick blubber, and low body temperatures.

Bowhead whales are important to native people of the circumpolar arctic. They have hunted the bowhead for at least 2000 years for food, heating fuel, transportation (dog teams), building materials (mandible, ribs, etc.) and cultural solidarity. Several circumpolar cultures (including the Inupiat) from Siberia to Greenland became almost singularly focused on bowhead whale hunting about AD 1000 during the expansion of the Thule culture. Many scholars associate this expansion with a period of climate warming AD 1000-1200 (Bockstoce, 1976; Stoker and Krupnik, 1993) which apparently had temperatures comparable to those of today. These traditions and a singular focus on bowhead whale hunting continue today as indicated by the fact that Barrow alone had over 55 registered whaling captains in 2008 and has increased over the past 20 years.

The basic external morphology of the bowhead is typical of other cetaceans in its fusiform body, paddle-like limbs, large flukes and similar features. What sets them apart from other cetaceans, however, is the extensive development of the baleen and blubber and large head. Also, bowheads experience a growth hiatus in body length and body mass after age one which can span three years. The baleen continues to grow throughout this period, however again indicating its importance. It is hypothesized that rapid growth of the baleen is a requirement for growth of the animal. An extensive baleen rack is of singular importance to a growing and to an adult bowhead for effective feeding in the relatively low prey densities of the Beaufort Sea and high-arctic regions. Bowheads require about 20 years to reach sexual maturity and to develop an adult-sized baleen rack and continue to grow in adulthood. By contrast, a young gray whale achieves adult-length baleen by its first year. This means that in the bowhead's first years of life, it is not yet an effective feeder and may be susceptible to nutritional stresses.

The head and specifically the skull has the unusual trait of growing proportionally larger as a function of body length throughout life. Balaenids are among the few mammals to exhibit this growth trait. Associated with the head, the baleen rack is more highly developed in the bowhead than other mysticetes. The fine fringe hairs along the lingual margin allow feeding on small copepods < 1 mm in length. Lambertson *et al.* (2005) provide evidence from physical models that the laterally convex shape of the baleen rack functions to accelerate water through the rack and generally increase feeding efficiency. The head and baleen rack comprises about 1/3 of the body length which is an indication of its importance to this animal.

Bowheads and right whales have thicker blubber than other cetaceans, however, the maximum dorsal blubber thickness of 37 cm is at least 10 cm greater than those reported for right whales. The epidermis is also unusually thick and may be the thickest of any mammal at 2.5-3.0 cm.

The bowhead whale appears to exhibit the greatest longevity of any existing mammal. In Chapter 4 (George *et al.,* 1999) the highest point estimate for age was 211 (SE= 34) years for a 14 m male; several other whales were over 150 years. These ages are greater than other mammals in the published literature. Reliable age estimates, based on ear plug lamina, for fin whales indicate maximum ages to 114 yr (Ohsumi 1979). Stearns (1992) provides convincing arguments based on a synthesis of pertinent literature that environmental variability, low reproductive rates and reproductive uncertainty selects for a longer lifespan. These characteristics are consistent with the condition for bowheads which spend much of their lives in highly variable ice-dominated seas with relatively low primary productivity. A recovery of six 19th century traditional harpoons from recently harvested whales also strongly suggests lifespans well in excess of 100 years (Figure 7.1).

Metabolic rates appear to be low, and body temperature among the lowest of the eutherian mammals. Steep thermal gradients through the blubber and muscle, differences between TC in the body regions and highly developed counter-current heat exchange systems in the flukes are consistent with efficient thermoregulation and heat conservation mechanisms. Bowheads also have effective and sophisticated mechanisms in the vascular system for circumventing the blubber when it is necessary to dissipate heat. These structures exist in the tongue, flukes, and epidermis (via dermal papilla) and dermis. Therefore, given our present understanding, it appears that bowhead whales are somewhat "over insulated" but are also in a relatively low-metabolic condition as compared with most mammals. These observations are not contradictory. An animal with a low metabolic rate must exercise during migration, feeding and avoiding predators. In doing so, they produce considerably more heat than can be lost by conduction through the blubber. Under these circumstances mechanisms for losing heat presumably through the flukes, tongue, and thorax are important. These studies seem to support Burns (1993) hypothesis that the "*extensive fat reserves of the bowhead temper this [extreme annual] environmental variability allowing individuals to survive much better than individuals of other species such as ringed seals.*" Similarly, other adaptations and modifications of the bowhead whale may be related to their ice-covered environment and the variability in food supplies in arctic waters.

References

Bockstoce, J.R. 1976. On the development of whaling in the Western Thule culture. Folk 18: 41-46.

Burns, J.J. 1993. Epilog. *In*: Burns, J.J., Montague, J. and C.J. Cowles (eds.). The Bowhead Whale. Society for Marine Mammalogy. 787 pp.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via Aspartic acid racemization. Can. J. Zool. 77:571-580.

Lambertson, R.H., Rasmussen, K.J., Lancaster, W. C., and Hintz, R. J. 2005. Functional morphology of the mouth of the bowhead whale and its implications for conservation. Journal of Mammalogy 86 (2) 342-352.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whales. Rep. int. whal. Commn 29: 397-406.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stoker, S.W., Krupnik,I.I. 1993. Subsistence whaling. In: J.J. Burns, J.J Montague and C.J. Cowles (eds.). The Bowhead Whale. 787 pp. Allen Press, Lawrence, Kansas.

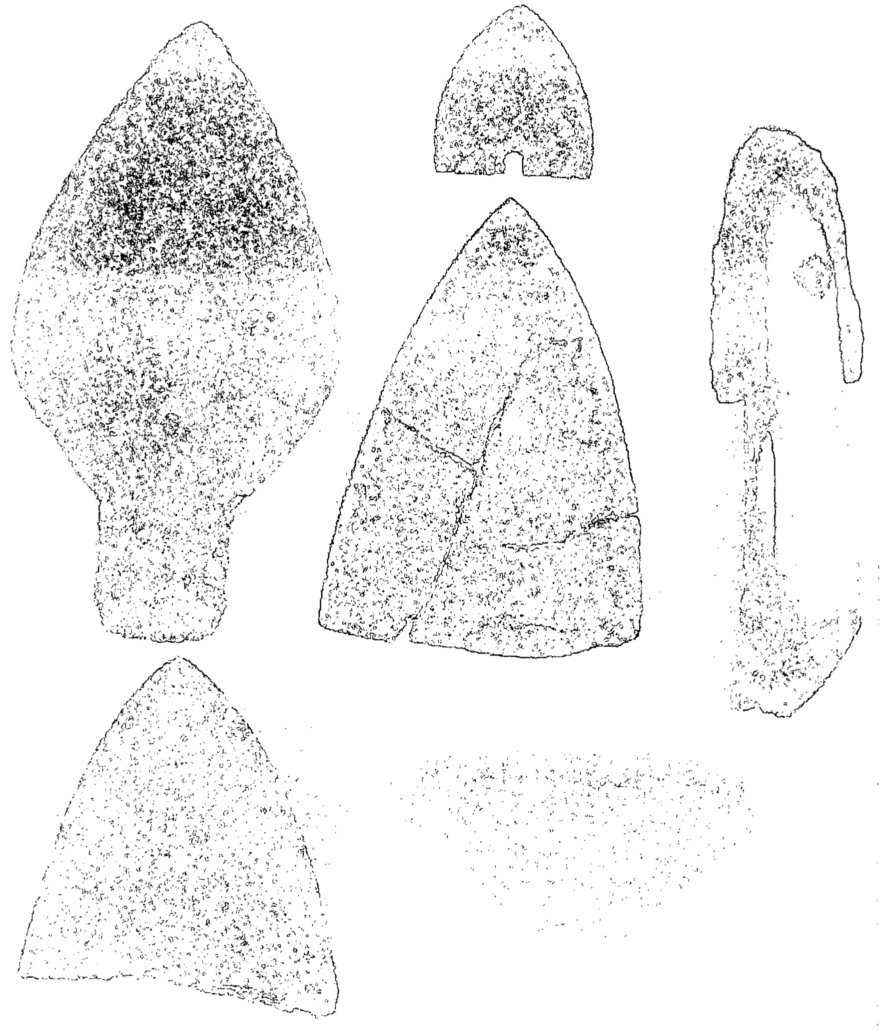


Figure 7.1 Photograph of six 19^{th} century traditional harpoons recovered from recently harvested whales. The presence of these weapons strongly suggests that bowheads have lifespans in excess of 100 years (photo J.C. George).