

Review

# History of polar whaling: insights into the physiology of the great whales<sup>☆</sup>

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## Abstract

The sheer size and pelagic nature of the great whales has effectively precluded detailed studies of most of their physiological processes. The vast majority of all data for these species have come from anatomical studies conducted on specimens that were caught in commercial and native whaling operations. In both the polar regions, an incredible number of whales were hunted, but anatomical studies were not usually conducted until relatively recent times. However, the anatomical data that do exist provide a valuable insight into some of the physiological demands placed on the animals by their marine habitat. These include information on blubber and nutrition; baleen and feeding ecology; contaminant chemistry and tissue samples; diving chemistry and acoustics. Taken together, these anatomical data provide the only substantial information on how these animals dive and hunt. Recent breakthroughs in chemical techniques however, are providing even greater details on function (for example, fatty acid signature methods). Coupled with advanced methods for tracking these whales at sea (acoustic and satellite), future studies should provide significant new information on the general physiology of these difficult to study species. © 2000 Elsevier Science Inc. All rights reserved.

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## 1. Introduction

Because of their pelagic nature and large body size, our knowledge of the physiology of the large whales comes mainly from our ability to work with harvested, hunted and stranded animals. I will confine myself here to the study of large, polar animals taken primarily in hunts, but will

make some references to the interesting studies of the few gray whales that have been in captivity (Marine Fisheries Review, 1974) and, as necessary, to the smaller toothed whales that have been studied in detail under captive scenarios.

The ultimate problem with this approach is that trying to study the physiology of animals that are not alive is somewhat difficult and thus, we have instead tended to infer physiology from anatomical structure. We have learned a great deal from hunted specimens of the large whales and much of this goes beyond diving physiology. Now, with the relatively recent ability to attach remote satellite sensors to some of the larger species and to

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track them acoustically, our knowledge of living cetaceans is increasing rapidly.

In this paper, I discuss the hunting of the great whales in polar waters and examine some of the current societal issues in this field. Next, I focus on how samples from hunted specimens have been used to build models of nutritional physiology, contaminant chemistry, feeding ecology, diving physiology and biochemistry. Finally, I will briefly cover how new methods and techniques allow scientists to track and monitor the great whales at sea.

## 2. History of whale hunting in polar regions

The great whales were hunted extensively at both poles, but on a different time scale and magnitude between subsistence and commercial operations. There are substantial archeological data showing that whales were hunted from shore in ancient times by native peoples (Slijper, 1979; Hofman and Bonner, 1985) but these were not the massive operations seen in the commercial fleets. Business oriented whaling began in the northern polar regions before 900 AD with Norwegian whalers. By the eleventh century, the Basques were taking an increasing number of whales for the lamp oil and whalebone industry and were working off of Newfoundland by 1600. The Dutch were whaling off Spitsbergen by the late 1500s and found the area to be "teeming with whales" (Slijper, 1979). By 1700, Holland had a fleet of over 250 whalers, 14 000 crew members and were taking almost 2000 whales (mostly the Greenland whale). Surprisingly, the anatomy of these animals was not of great interest beyond what was necessary to better understand how to hunt them. It was not until the late 1700s that J. Hunter provided one of the first 'modern' descriptions of the anatomy of the great whales (Slijper, 1979). By 1905, the industrialization of whaling had begun and the first factory ships arrived in the Arctic. The search for more profitable hunting areas began about this time and whalers turned south. The whaling station at Grytviken, South Georgia (Falkland Islands) was established in 1904 and by 1910, over 10 000 great whales were already being caught. Hunting in this area continued well into the 1900s and by 1960, a quota 15 000

'Blue whale units' had been established. World-wide, in 1953, over 43 000 whales were hunted.

Whaling products were originally sold for food and oil, but by the mid 20th century, it became no longer economical to capture most species. Also, in recent times, there has been an increased concern by humans for cetaceans and people have tried to protect whales by discouraging hunting through protest, political and economic sanctions. The creation of the International Whaling Commission in 1946 allowed for voluntary restrictions among countries, but with no enforcement ability, this commission has seen intense battles over whaling allowances. It is not my intention to support either side in this ongoing issue, but I do want to note that whaling continues at some level today in many locations in both northern and southern polar waters. Pedersen and Ruud (1946) provide an additional detailed bibliography of the scientific collections made during the Norwegian whaling programs.

In the Arctic regions, there are significant cultural and subsistence issues involved with whale hunting (Sergeant and Brodie, 1975). In Alaska, both bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales are taken for subsistence purposes in highly regulated hunts and the National Marine Fisheries Service, the Alaska Native Whaling Commission and the International Whaling Commission have worked together to establish control of the hunts. Through agreements with whaling villages, scientists have been allowed extensive access to these animals. However, cultural demands on the animals must always come first. These animals represent food, history and spiritual needs for these peoples. Detailed discussions on subsistence whaling and scientific studies conducted on bowhead whales are available (Burns et al., 1993).

It is not my purpose here to note every type of whaling or its location through which scientific samples have been collected. Rather, I wish to make the reader aware that there have been several different routes by which cetacean tissues have become available beyond those from stranded animals. Also, that there are native subsistence and cultural issues involved that must be respected and honored when dealing with subsistence hunting.

### 3. Nutritional physiology....the story of blubber

The most striking initial aspect of the anatomy of a great whale beyond its sheer body mass is the blubber layer that surrounds the animal. Cetacean blubber is not the familiar depot fat as seen in terrestrial mammals. It is a very structured material with a significant collagen matrix. In our laboratory, we commonly refer to the blubber as a type of dynamic spongy material where the collagen matrix is the structure of the sponge and the lipids move in and out of the matrix based upon metabolic demand. We can easily infer from the observed anatomy and behavior of the whale that blubber serves the multipurpose functions of an energy store, thermal insulator and a buoyancy regulator. These three functions are supported by both gross and microscopic anatomy.

Blubber can compromise from 15 to over 50% of the mass of a great whale depending on the species and season (Slijper, 1958, 1979; Rice and Wolman, 1971; Ackman et al., 1975; Lockyer et al., 1984; Lockyer and Waters, 1986; Lockyer, 1987). For example, Antarctic cetaceans will maximize their blubber content during the brief summer feeding period in polar waters to prepare for the breeding season in the more temperate, northern waters (Costa and Crocker, 1996). This separation in time and space between feeding/fattening and breeding/fasting is a critical behavior that can be exploited to identify the animals biochemically and will be discussed later. The combination of the great quantity of blubber along with its high lipid content provides a significant lipid store for energetic requirements. In phocid seals, we know that lipid metabolism can account for over 90% of the energetic requirements of the animal (Castellini et al., 1987). But, the isotope turnover techniques necessary to arrive at such values are not possible in whales. Rather, we infer that lipid metabolism provides the vast majority of energy in cetaceans based upon their total body lipid content, the seasonality of blubber quantity and the high lipid content of their prey.

Upon dissection, it becomes immediately obvious that cetacean blubber is not homogenous with either depth or position along the body (Ackman et al., 1975; Lockyer et al., 1984; Lockyer, 1987). The lipid content can vary significantly with depth such that the blubber next to the muscle in fin whales (*Balaenoptera physalus*) can have a high protein content while the blubber next to the skin

can be very high in lipid. Biochemical profiling of these layers provides some insight into the advantage of such layering, but since we cannot follow the in vivo changes in the blubber, we are left to infer the physiology from the anatomy.

Biochemical analysis of the lipids in these layers demonstrate differences in their lipid fatty acid composition (Ackman et al., 1975; Lockyer et al., 1984) with variances in chain length and saturation. The authors have proposed that the blubber layer near the skin in fin whales is more metabolically stable and acts as a long term storage site vs. the more dynamic base layer. There does not appear to be a consistent pattern in the fatty acid type, but we may infer that the lipids next to the muscle should be more liquid at core body temperatures than the lipids near the cooler skin layer. However, given logistical and theoretical constraints, it is not yet possible to test these hypotheses in living animals. Current studies on bowhead whale blubber layering are underway in our laboratory and suggest that the layering patterns may be different than seen in fin whales.

The ultimate end product of the quantity and quality analysis is that the energetic content of the blubber will vary with depth and position along the body of the whale. Because of the elevated lipid content, the gross calorimetry of the blubber can be very high with values approaching the theoretical limit of about 9 kcal/gm for pure oil. Here it is vital to remember the sponge analogy. The collagen matrix in the blubber is a constant. It is not metabolized and is either filled or emptied of lipid and only the lipid is oxidized for energy. The blubber itself is not metabolized as an entity — it is only the lipid that is extracted from the matrix that moves through metabolic catabolic pathways. Thus, the energy content of a section of blubber is best defined by the amount of lipid and the ability for that lipid to be mobilized.

Beyond the energetic profiles of blubber, the tissue has a clear role in thermoregulation as it is the only source of insulation for these mammals in polar, ice-laden waters. Interestingly, there is also a problem of how to dump heat when the animal is active, which is the opposite problem for smaller cetaceans that may need to conserve heat (Worthy and Edwards, 1990). The thermal mass of a large whale is such that cooling may be a significant problem and the adaptation to solve this problem is a series of rete mirabile (Scholan-

der and Schevill, 1955). These blood vessel networks act as heat exchangers and can be used to either dump heat to the environment or to shut off blood flow to conserve heat. These exchangers are not in the blubber layer itself and are found mainly in flukes and flippers. Again, these theories exist because of anatomical studies. No one has yet to conduct a whole body thermoregulatory study on a swimming, active large whale.

Finally, blubber also has a role in buoyancy regulation as the quantity of lipid in the animal will impact total body specific gravity. This impacts diving models at the level of the cost of diving and relative diving lung volumes. All of these factors are part of the hydrodynamic considerations for diving (Kooyman, 1989). Also, the large quantity of oil in the spermaceti organ of the sperm whale has been proposed as a factor in buoyancy regulation for this species (Clarke, 1978).

Taken together, these three defining characteristics of blubber (energy, insulation and buoyancy) are significant factors in determining diving efficiency and energetics.

There is one last aspect of blubber chemistry that is important to note even though it may not impact diving. Blubber acts as a significant site for lipophilic organochlorine contaminants (OC) such as the PCBs and DDTs (Borrell et al., 1995). Some species of whales show massive OC levels to the point of potential tissue and metabolic damage (De Guise et al., 1996). These compounds dissolve most readily in the blubber and since the blubber surrounds the outside of the animal, dart biopsies can be taken to conduct such studies on living animals. Future research will need to study how OC compounds distribute within the blubber layers and if there are preferential lipid classes where they sequester. These data must then be applied to our models of which lipids are mobilized for energy, and which remain in the blubber for long-term storage. At what point do these contaminants begin to harm the animal and what are the implications to human subsistence hunters who gather the animals for food? These are all important and critical issues that are not related to diving physiology, but may have a significant impact on the animals and humans associated with the whales. To that end, the North Slope Borough in Alaska is working with Native hunters and research scientists to better understand lipid chemistry and contaminant partitioning in bowhead whales.

#### 4. Feeding ecology

As noted earlier, many species of polar whales move towards temperate waters for breeding, but feed, possibly exclusively, in the Arctic and Antarctic regions. This behavior allows for an interesting biochemical identification of the animals. Because baleen whales collect tons of plankton for food, they act as perfect integrators of the oceanic conditions that are reflected in the biochemical profiles of the plankton. Stable isotope levels of carbon and nitrogen vary according to trophic level and are laid down in the baleen plates from the type of plankton consumed by the whale. Thus, along a baleen plate, annual cycles of  $^{13}\text{C}$  and  $^{15}\text{N}$  can easily be quantified and show the seasonal movements of bowhead whales in and out of the feeding areas (Schell et al., 1989). These data can then be further analyzed to look for long-term changes in the isotope ratios of the plankton, which in turn can be used to suggest changes in the oceanic carrying capacity. Using this method, Schell (2000) has analyzed bowhead baleen plates from samples collected decades ago. His data suggest a slow, but long term decline in the carrying capacity of the Bering Sea, which would be consistent with changes observed in that system within the last 30 years. While the carrying capacity argument is controversial, the annual feeding cycles are clearly obvious in the baleen plates and provide yet another link between anatomy and physiology.

A relatively new analytical approach is now being used to trace fatty acids from prey through to the blubber and lipids of marine mammals (Iverson et al., 1997). While these techniques are yet to be applied to large cetaceans, they are extremely powerful and could be a major breakthrough in describing ecology and feeding through physiology, biochemistry and anatomy. The technique is very sensitive and can be used to distinguish the diet of harbor seals groups living just a few kilometers apart.

#### 5. Diving physiology and biochemistry

We assume that the basic diving physiology of the great whales is similar to models that have been developed for seals, sea lions and smaller cetaceans that can more easily be studied. Under that paradigm, there are several anatomical patterns that would be predicted:

First, there should be an enhanced oxygen store in the muscle via increased myoglobin (Mb) concentrations. This has been documented in all the cetacean species examined to date with higher Mb levels seen in better divers and lower levels found in calves, poorer divers, etc (Slijper, 1979; Castellini et al., 1981; Kooyman, 1989). The presence of elevated Mb levels implies the use of muscle as an oxygen store, which supports the general model of oxygen partitioning in divers. While hematocrit (Hct) and blood volume have been determined in a captive gray whale (Gilmartin et al., 1974), there is no information in whales on the dynamic regulation of Hct and therefore blood oxygen carrying. However, we assume blood oxygen stores are critical to diving oxygen supplies.

The respiratory anatomy of cetaceans diverges however, from the general pinniped model. Our best data suggest that the phocid seals submerge upon exhalation with a small diving lung volume. The whales however appear to dive upon inhalation. We know that small dolphins and seals have extremely compliant chest walls that can allow lung compression at depth, which should minimize problems associated with nitrogen uptake at depth (Scholander, 1940; Irving et al., 1941). However, Leith (1989) points out that some cetaceans have extremely stiff airways that would seem counter-intuitive to the compression model. Small cetaceans can exchange over 80% of the total lung volume in a single breath, which allows for very short surface intervals during the blow at the surface (Kooyman and Sinnett, 1979). This requires reinforced airways to allow high flow rates, which seemingly offsets the advantage of having compliant airways that would allow collapse. How these two opposing demands are met in the large whales is not known. Some work on blow characteristics has been done with captive gray whales (*Eschrichtius robustus*) (Wahrenbrock et al., 1974). In this species, tidal volume was only 50% of total lung volume, as opposed to the 80% value noted earlier with small odontocetes. However, the dead space to tidal volume ratio was small, as seen in other diving species.

Another component of the mammalian diving response is a cardiovascular system adapted to exquisite control of blood flow at the micro-vessel level. As one would expect, this would be a difficult pattern to see in whales. However, recent experimental breakthroughs by Elsner have pro-

vided new insights into this area. Following field techniques established with ringed seals (Ostholm and Elsner, 1999), and working with the native bowhead whale hunters at Barrow and the North Slope Borough in Alaska, he has been able to remove arterial sections from the flukes of recently hunted whales and to keep the sections viable using in vitro methods. He can then infuse the media with a suite of vaso-dilator and vaso-constrictor pharmaceuticals and record the responses of the arterial vessels. His results suggest excellent chemical control of arterial wall diameter, which would be consistent with diving models.

Finally, diving theory predicts a suite of biochemical adaptations that should allow metabolism under hypoxic conditions. Some of these involve down-regulation of metabolic rate, the cessation of trans-membrane ionic transport during hypoxia and enzyme profiles consistent with enhanced anaerobic metabolism. Some of these tests have been conducted on whale tissues, with mixed results. While Shoubridge et al. (1976) concluded some tissue isozyme patterns were consistent with hypoxic tolerance in dolphins, Castellini et al. (1981) showed that these patterns were similar to those found in terrestrial sprinting mammals. However, on balance, no particular findings suggest enhanced hypoxia tolerance on the enzyme level. There should be some difference in these profiles between poor and excellent cetacean divers, but the samples have not been obtained to test these theories.

Taken together, these anatomical and biochemical data are consistent with our current models and theories about diving and provide our only insight into the diving physiology of these interesting mammals.

## 6. Future technologies

Recent electronic advances may provide us with new ways to investigate the biology of large cetaceans that were not possible in the past. Satellite linked dive recorders and positioning systems are now being placed on species have never been tracked before. These systems allow world-wide tracking and are robust enough to last for long time periods and to transmit great amounts of data. One of the problems has always been the attachment of such devices and current darting

techniques appear to have resolved some of those issues (Mate et al., 1997, 1998). As these new recorders become more powerful and smaller, they should provide even more information.

The last area to cover is the use of active and passive acoustic techniques to track and identify whales at sea. The recent release of U.S. Navy high quality underwater recordings has provided an incredible windfall of data that can be used to identify and track whales across great stretches of ocean or to identify different populations (Stafford et al., 1999). Animals can also be outfitted with acoustic tags that can be used to track them in more localized regions (Watkins et al., 1999). Modeling shows that the very powerful low frequency sounds of the large whales should allow them to communicate with one another across hundreds of kilometers of ocean. By using these new and exciting 'eavesdropping' techniques, we should be able to follow these animals as we have never been able to before. Acoustic tracking has been used for census counts of bowheads in Alaska and many of these new tracking concepts are reviewed in Costa (1993).

Finally, new biochemical and physiological techniques will allow even more powerful genetic identification, contaminant testing, nutritional assessment and health status examinations on living cetaceans or on cell cultures (De Guise et al., 1996; Matthews et al., 1988). However, from the days of simple anatomical descriptions of the great whales to modern techniques of molecular medicine and electronics, the goal has always remained the same: to describe how these mammals make their life in the sea and to quantify the impressive adaptations that allow them to do so. The study of polar physiology has been a major component of these studies and hopefully will continue to be so.

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