

Susceptibility of the great polar or bowhead whale to global warming

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ABSTRACT

The great polar or bowhead whale (*Balaena mysticetus*) is commonly believed to be pagophilic, or “ice-loving.” Given knowledge that the extent of ice cover in its Arctic habitat is decreasing, there is a need for improved knowledge of the susceptibility of this species to global warming. Here this question is approached by considering those evolutionary feedbacks which likely account for the divergent morphophysiological characteristics of balaenids and balaenopterids. Acknowledging first the very high concentrations of fluoride in krill, it is pointed out that the most plausible hypothesis explaining the evolutionary emergence of baleen whales is cladogenesis driven by toxic disease. Fluoride toxicosis is known to affect preferentially the enamel organ of tooth buds, which organ is essential for development of a durable dentition. When one then assumes a primordial mysticete population characterized by variation in individual densities to either side of that of seawater, a plausible and likely mechanism of disruptive selection is revealed. This in theory would have been linked to different levels of activity required for respiration. Natural selection for feeding power then predicts two radically different outcomes that conform to the distinctive morphophysiologicals of balaenids and balaenopterids. The presumptive balaenopterid evolutionary path involves maximization of feeding power through the attainment of high individual kinetic energies. The presumptive balaenid evolutionary path in contrast involves maximization of feeding power at low swimming velocities, and hence comparatively low individual kinetic energies. This difference notably explains the ability of the bowhead to flourish in shallow Arctic seas as a reflection of a feeding strategy not associated with a high probability of lethal collisions with solid substrate. It also explains the larger average body size of Southern Hemisphere balaenopterid races or variants as a manifestation of the greater probability of lethal collisions with solid substrate in the Northern Hemisphere. The paradoxically low pre-exploitation population size of the blue whale is then similarly explained by a comparatively high natural mortality rate causally related to extremely high individual kinetic energies during feeding, extremely large turning radii, and an associated higher probability of lethal collisions with solid substrate. Ubiquitous bacterial pathogens would be involved secondarily. Coupled with other lines of evidence, the empirical support for this novel hypothesis rejects theories to the effect that the interhemispheric size dimorphism in Earth’s largest whales is attributable to slightly lower ocean temperatures in the Southern Hemispheres. Further, in light of the rather shallow habitat of the bowhead, the same mechanism of mortality likely accounts in part for the bizarre morphology of that species. In the bowhead the propulsive action of the tail is constrained both by an extremely thick blubber layer and the fact that the body and tail themselves are foreshortened relative to the length of the head. It also is clear from measures of heat conductance through blubber that the thickness of its blubber greatly exceeds that required for thermal homeostasis. On these bases it is most reasonable to conclude that the bowhead whale is not in fact pagophilic, but rather thermophobic. It follows that amongst the Cetacea the bowhead probably should be viewed as comparatively extremely susceptible to global warming. One ecological threat to the bowhead to be anticipated with reduction in the extent of Arctic ice is a greater frequency of incursions into the Beaufort Sea by the humpback whale (*Megaptera novaeangliae*). Unlike other balaenopterids, the humpback whale is anatomically specialized for feeding in shallow water and carries weapons in the form of patches of barnacles on its chin and flippers. It also is well equipped to feed on euphausiids that comprise a component of the diet of the bowhead.

KEYWORDS: ARCTIC OCEAN, CLIMATE CHANGE, ENERGETICS, FEEDING, HABITAT, ICE, MORTALITY, PHYSIOLOGY, TRENDS

INTRODUCTION

Assessment of the susceptibility of the bowhead whale (*Balaena mysticetus*) to global warming should focus initially on the question of whether global warming will expand or contract the Arctic marine niche of this species. As Arctic ice is expected to continue to decrease, it will be tempting to infer that the size of the bowhead niche will expand, increasing carrying capacity. This would presume that the over-riding constraint on reproductive potential is imposed by wintertime expansion of ice in Arctic seas. Expansion of ice would limit feeding action, constraining reproductive power. Less ice would increase it. Although the bowhead is considered to be pagophilic (ice-loving), filter-feeding obviously requires a fluid, not frozen, habitat.

A critical biological issue, however, is whether the bowhead whale is in fact pagophilic. The diametrically opposite interpretation is that the bowhead whale, compared with other animals, is thermophobic: comparatively extremely heat intolerant. To avoid potentially major predictive errors, we therefore must first consider the enigmatic possibility that the bowhead whale is not adapted to very cold marine environments but has instead become restricted to cold environments by a process of evolutionary canalization. The most important of all the life-perpetuating features of the habitat of the bowhead in fact might exist only along the ice edge -- at or near freezing temperatures. Environmental carrying capacity for this species might fall, not increase, as Arctic ice decreases.

A bowhead whale entering its summer feeding grounds could be enjoying only temporary freedom from thermodynamic confinement to near-freezing water. Temporary freedom to move away from ice could stem from wintertime catabolism of fat and its anatomical consequence, seasonal reduction in the thickness of body insulation. Metabolic heat generated during active bouts of feeding in summer might be dissipated automatically via a fine blood vasculature found in both the dermal lamella and dermal papillae that penetrate each baleen plate (Lambertsen *et al.*, 1989 figs. 20-22). Thus an extremely heat intolerant nature in winter might still be followed by moderately energetic feeding activity in summer. As peripheral fat stores are replenished, absolute dependence on near-freezing conditions could develop.

In this light, analysis of the susceptibility of the bowhead whale to global warming must consider the reversibility of its evolved characters in response to climatic change. Classical evolutionary interpretation would hold that the bowhead of modern times is the result of a dispersal of ancestral mysticetes followed by adaptation to local conditions. Natural selection linked to various adverse influences accordingly would be said to have fixed genetic improvements that favored survival to adulthood and reproduction of individuals. And if we accept without question this classical view, we would have little to worry about the bowhead. For as environmental conditions change, morphophysiological character would change accordingly, would it not? The correct answer however appears rooted in those evolutionary feedback loops not taken into account by classical Darwinian theory.

This paper spells out the basic nature of feedback mechanisms apparently responsible for the extremely specialized nature of the bowhead whale. A system of self-reinforcing change is identified that, when operated, would "evolve" its principal morphophysiological traits. Positive feedbacks inherent to this system suggest that the bowhead whale is now trapped in an evolutionary dead end characterized both by self-encumberment and heat intolerance. These two problems do not appear to face other whales. On this basis it is concluded that, amongst Cetacea, the bowhead whale probably should be viewed as comparatively extremely susceptible to global warming.

BASIC CONSIDERATIONS

An array of three traits distinguishes the bowhead whale from virtually all other animals. This includes 1) extremely long baleen, 2) extremely thick blubber, and 3) extreme gigantism (with a maximal body mass perhaps second only to the blue whale [*Balaenoptera musculus*]). The bowhead whale, like other balaenids,

also is characterized by a body density less than that of seawater. It consequently floats when not actively diving. This combination of traits is the outcome of a balaenid evolutionary lineage dated on the basis of fossils to the early Miocene, 20-22 My bp (Fordyce, 1989; Fordyce and Barnes, 1994; Fordyce and de Muizon 2001).

FACTORS LEADING TO BALAENID-BALAENOPTERID DIVERGENCE

Complete mitogenomic analyses have confirmed the monophyly of Mysticeti (Árnason *et al.*, 2004; Sasaki *et al.*, 2005), as have analyses based on biochemical evaluation of short interspersed elements (SINE's) (Nikaïdo *et al.*, 1999). On both molecular and morphological grounds there is a consensus that all cetaceans ultimately were derived from the Artiodactyla (even toed ungulates) (Fordyce and de Muizon 2001). Fordyce (1989) has argued that the Early Oligocene radiation of odontocetes and mysticetes can be linked to opening of Drake's Passage and the full establishment of a Circum-Antarctic Current. In his view, that geophysical development promoted increasingly complex oceanic food chains and a rapid diversification of species marked by new feeding strategies.

However, we also have the studies of both Schneppenheim (1980) and Soevik and Braekkan (1981). Those workers demonstrated that euphausiids (krill) contain concentrations of fluoride an order of magnitude greater than those known to predispose agalactia in females and an occasional premature death in their progeny when fed to domesticated Bovidae (Landy *et al.*, 1991). That toxic effect of fluoride is relevant because bovids comprise a taxonomic family of the Cetartiodactyla. Further, the premature deaths that occasionally occur in the F₂ generation after chronic dietary exposure of the pregnant female to toxic concentrations of fluoride are attributable to accelerated attrition of teeth compromised by defective enamel (Krook and Maylin 1979). The occasional lethal effect of chronically high dietary exposure arises from a predisposition to starvation caused by impaired enamel formation (amelogenesis) during embryonic development (Krook and Maylin 1979). On this basis it can be suggested that the most plausible hypothesis explicating the origin of the bizarre feeding apparatus found in Mysticeti is cladogenesis driven by toxic disease. Population expansion of piscivorous marine mammals would increase pressure for utilization of smaller prey. Fluoride toxicosis then could well explain why primitive toothed mysticetes such as *Aetiocetus cotylalveus* Emlong, 1966 and their descendants lost their dentition in favor of baleen, inasmuch as its pathogenic effect is on the process of calcification, and in particular amelogenesis, not the formation of the hard keratin that comprises baleen. Consistent with this alternative hypothesis is the finding of Landy *et al.* (1991) that the highest natural concentrations of fluoride known in any vertebrate occur in the skeletons of fin whales, and the finding of Lambertsen *et al.* (unpublished) that high concentrations of fluoride also occur in the bones of bowhead whales. Those findings indicate that mysticetes actively assimilate fluoride from dietary sources, as also is the case in Bovidae.

EVOLUTIONARY OPTIONS FOR AMPLIFICATION OF FILTER FEEDING POWER

Consider the physics of filter-feeding. In very basic terms, the rate of filtration would be determined by the equation

$$\text{Filtration Rate} = [(\text{Driving Pressure} - \text{Back Pressure}) \times \text{Filter Area}] \div \text{Filter Resistance}$$

From this one can presume that the rate of prey capture could be increased by increasing the filtration driving pressure (inside the mouth); decreasing water pressure outside the baleen; decreasing the structural resistance per unit area of filter (provided its effectiveness is maintained); or increasing total filtration area. It follows that natural selection for feeding power as a result of competition for limited food resources could lead to a number of different filter-feeding specializations, or strategies.

With individual variation in success in capturing prey, it also is likely that diversification of a primordial population of mysticetes began with the emergence of morphophysiological heterogeneity, and in particular the appearance of individuals having body densities either less than or greater than seawater. The total body density of the first mysticetes, which might otherwise be indistinguishable, would largely depend on the

mass ratio of bone mineral to lipid in their bodies. Average body density likely would be that of seawater if one assumes that the specific energetic cost of both breathing and feeding originally was minimized by natural selection. As it turns out, variation on either side of that average value then suggests a mechanism of disruptive selection. A mechanism of disruptive selection based on opposing positive feedbacks would predict two distinct evolutionary pathways leading to what we now recognize as balaenids and balaenopterids (Fig. 1).

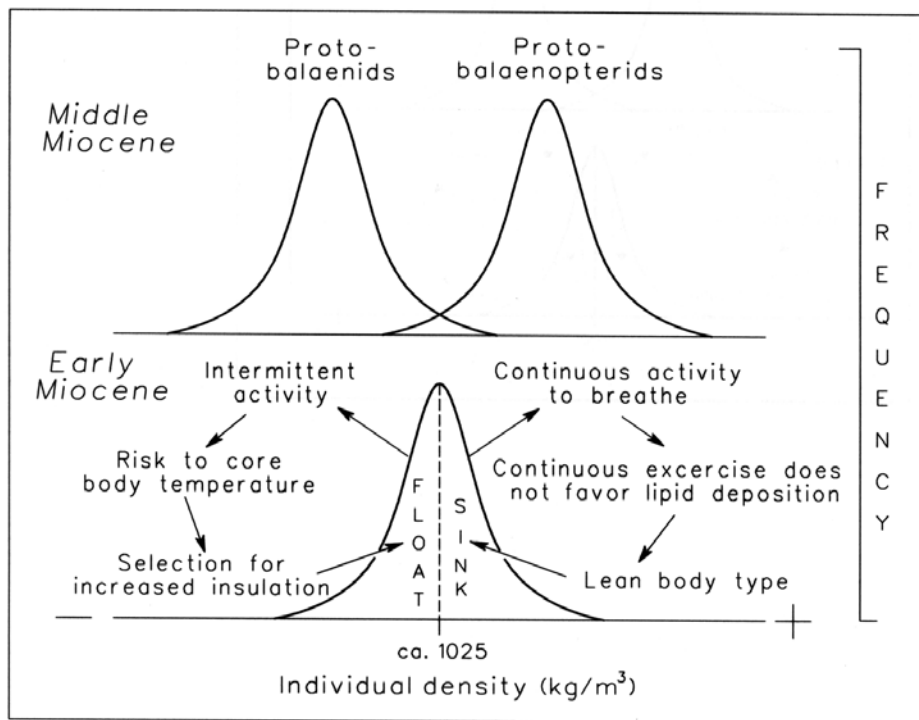


Fig. 1. Plausible and likely feedbacks giving rise to disruptive selection and evolutionary divergence of proto-balaenids and proto-balaenopterids. Paleontological dating follows that of Fordyce (1989) and Fordyce and Barnes (1994).

POSITIVE FEEDBACK IN PROTO-BALAENOPTERIDS AND ITS CONSEQUENCES

The primordial subpopulation most reasonably considered to comprise the proto-balaenopterids would have had whole body densities greater than seawater. Members of that subpopulation would tend to sink, as modern balaenopterids do when killed. This means that members of the presumptive proto-balaenopterid → balaenopterid lineage would have had to engage in continuous, if not constant swimming in order to breathe. That behavior is of predictive importance because a substantial flux of heat from core body tissues to the body periphery would be its immediate *and continuous* consequence. As a result core body temperature in proto-balaenopterids would tend to be protected. What is more, the continuous locomotor activity implied would tend to promote oxidation of lipid and mobilization of free fatty acids from body fat. This can be inferred from comparative biochemical studies that demonstrate that the energy requirements of moderate exercise in mammals typically are supplied by oxidation of lipids, not carbohydrates, and that moderate exercise stimulates lipolysis in body fat (Wolfe, 1998; Turcotte 1999; Horowitz and Klein, 2000; Spriet and Watt, 2003).

In summary, in the presumptive proto-balaenopterid population there would have been a positive feedback favoring a lean body type that would tend to sink. That body type would be characterized by a density greater than seawater and, therefore, high selective value associated with fine streamlining.

Moreover, with this positive feedback, selection for feeding power can be predicted to have preferentially increased swimming velocity over an increase in baleen length. This derives from the fact that, for any given swimming velocity, expansion of baleen area alone would increase filtration rate only arithmetically. In contrast, filtration driving pressure would tend to increase with the square of velocity, as in a Pitot tube. Furthermore, increasing feeding power by increasing baleen length would be less likely in the proto-balaenopterid → balaenopterid lineage because it would tend to work against fine streamlining of the head. For any population characterized by individual densities *greater* than seawater, the option of increasing baleen length would increase the cost of breathing while interfering with maximization of swimming speed and, therefore, the maximization of filtration driving pressure.

Assuming that the biomechanical problem of triggering the mouth at speed was overcome, selection for both large body size and fleetness therefore can be assumed to have operated in proto-balaenopterids. This would follow from the fact that in a dense fluid environment there would tend to be a net gain in propulsive efficiency with increasing body size. That gain is predictable because, for a given body shape and speed, drag tends to increase only with body surface area (a square function of some representative linear dimension, l) whereas the propelling muscle mass tends to increase with body volume (i.e., l^3).

The associated critical problem of triggering the mouth at speed is addressed by Lambertsen and Hintz (2004). In a close-range photogrammetric analysis of the craniomandibular system of the small minke whale (*B. acutorostrata*), which mitogenomic studies indicate to be a modern representative of the most ancient of all balaenopterid lineages (Árnason *et al.*, 2004; Sasaki *et al.*, 2005), those workers identify what might well be the mechanism that enabled the first true balaenopterid to open its mouth at speed in response to sensory stimuli. The problem that mechanism evidently solved relates to the fact that, at speed, maintenance of mouth closure depends both on a hydrostatic oral seal and negative oral pressures referable to hydrodynamic loading of lower jaw. Hydrodynamic loading would be derived from negative lift attributable to flow asymmetries over the head. Lambertsen (1983) in turn describes the anatomical modification of the tongue required for high speed engulfment feeding. The mechanical coupling of feeding and locomotion in balaenopterids that characterizes their engulfment feeding in turn is described by Lambertsen *et al.* (1995). With that anatomical coupling a positive feedback is automatically established between whole body kinetic energy and feeding power. The kinetic energy associated with body mass and the square of velocity is used to power the engulfment feeding mechanism that characterizes the entire family Balaenopteridae. The craniomandibular trigger mechanism suggested by the findings of Lambertsen and Hintz (2004) apparently was the root enabling cause of that family's adaptive radiation.

If at a minimum we assume intraspecific competition for food, it therefore follows from the principle of natural selection that the ultimate problem in the proto-balaenopterid → balaenopterid lineage would be a predisposition to self-destruction caused by high energy collisions with solid substrate. In that lineage, natural selection would tend to drive evolutionary increases in average body kinetic energy and, therefore, turning radius. Lethal collisions with Earth's solid substrate would be inevitable. This merely admits that matter consists of three phases: namely solid, liquid and gas; and basic planetary characteristics.

Empirical confirmation that this mechanism of mortality acts as the final limit on body size, and was the outcome of a body density less than that of seawater in a filter-feeding whale, now comes in the form of the larger average body masses of those balaenopterid races which inhabit the Southern Hemisphere. Inspection of any globe will show that the freedom for a whale to move is in fact substantially greater in the Southern Hemisphere. Hence the probability that a whale will sustain lethal collisions in the Southern Hemisphere must be substantially less than in the Northern Hemisphere. The prediction that at equilibrium those races or variants that inhabit the Southern Hemisphere should be significantly larger is, therefore, confirmed. With this simple explanation, the alternative theory of Tomilin (1946; 1967) and Mayr (1965) that the interhemispheric size dimorphism of rorquals is causally related to slightly lower water temperatures in the Southern Hemisphere can be rejected. That early theory notably is inconsistent with the

more recent analysis of Hakkanen (1990), who in the footsteps of Kanwisher and Sundnes (1966) demonstrated that heat dissipation is more of a problem for large whales than heat conservation.

Natural selection for feeding power also evidently explains both the gigantic size and the low pre-exploitation population abundance of the blue whale. The latter is a true paradox inasmuch as the blue whale, like most rorquals, has a two year reproductive cycle (Boyd *et al.*, 1999), a comparatively low average age at sexual maturity (Boyd *et al.*, 1999), extremely high body growth rates (Brown and Lockyer 1984); and almost certainly has the longest reproductive lifespan amongst balaenopterids (since lifespan tends to increase as a power function of body mass). On such bases one can say that the blue whale not only might well be the healthiest of all extant balaenopters, but therefore should have had a pre-exploitation population abundance at least as high as other species in its genus. The consensus that its pre-exploitation abundance was far lower than that of other extant balaenopters however indicates that it must suffer a disproportionately high natural mortality rate! Based on whaling statistics, for example, Croll and Kudela (in press) estimate that prior to exploitation by humans there only were about 4,900 blue whales in the North Pacific Ocean, compared with 43,500 fin whales (*Balaenoptera physalus*), 42,000 sei whales (*B. borealis*), 39,000 Bryde's whales (*B. brydei*), and 32,000 minke whales. The now evident solution to this paradox is simply to admit that collisions with solid substrate are responsible. They would not need to be instantaneously lethal. Ubiquitous bacterial forms would *secondarily* contribute to the comparatively high natural mortality rate of the blue whale through opportunistic infection of deep abrasions. The primary cause would be the collisions with solid substrate that would be inevitable under a selective regime maximizing feeding power.

Other aspects of whale zoogeography also can be explained quite readily by this mechanism. For example, it is not surprising that the gigantic blue whale in the Western Hemisphere now rarely if ever ventures north of the Aleutian archipelago (Nishiwaki 1966; Yochem and Leatherwood 1985; Moore *et al.*, 2002). The key observation in a mechanistic context is that the Aleutian archipelago marks a precipitous decrease in water depth from Pacific Ocean to Bering Sea.

I have seen fit here to emphasize the problem of lethal collisions faced by such giant mammals because this heretofore unrecognized natural limiting mechanism appears also to contribute to the current plight of the bowhead whale.

POSITIVE FEEDBACK IN PROTO-BALAENIDS AND ITS CONSEQUENCES

In comparison with the proto-balaenopterids, presumptive proto-balaenids are most simply defined as those primordial mysticetes which had a body density less than that of seawater. Here the most important physiological point is that, being lighter than seawater, such individuals would have been able to sustain long periods of locomotor inactivity while still being able to breathe. It follows that they would be predisposed toward inactivity. This strongly suggests, in addition, that they would be routinely exposed to the lethal threat posed by the high heat capacity of the aqueous marine environment. At the population level one therefore can expect evolution of the proto-balaenids type also to have been canalized by a positive feedback (Fig. 1). However, it would be one quite different from that which evidently gave rise to balaenopterids. The common driving factor nonetheless would be competition for food with natural selection for feeding power. Given the threat of hypothermia, this is most reasonably expected to have involved heightened selective pressure for both increased body size (which for a given body volume would conserve body heat by decreasing body surface area relative to volume) and increased blubber thickness (to reduce heat dissipation by increasing insulation).

Moreover, in the proto-balaenid → balaenid lineage, increasing blubber thickness would tend to increase the ratio of body lipid to bone mineral. As such the expected outcome over generations would be *enhanced* ability to float. Thicker blubber also would tend to damp the action of the tail, reducing the maximal speed that could be achieved for a given body mass. Hence with respect to the above equation the predictable outcome is that feeding power in this lineage would involve an increase primarily in the length, as well as number of baleen plates (Fig. 2).

Going one step further, we also can see that it would be unlikely for feeding power to have been increased in the proto-balaenid → balaenid lineage by maximization of swimming speed, since heat generated under high *intermittent* work loads would tend to be excessive compared with the insulative requirements imposed by prolonged periods of locomotor inactivity. Increasing the area of the baleen apparatus however would allow for increased feeding power at slow speed and, therefore, minimal risk of overheating. Further, inasmuch as the baleen laminae in fact are to some extent vascularized, increasing their length perhaps also would enhance the ability of the individual to dissipate heat during brief periods of high demand associated with feeding.

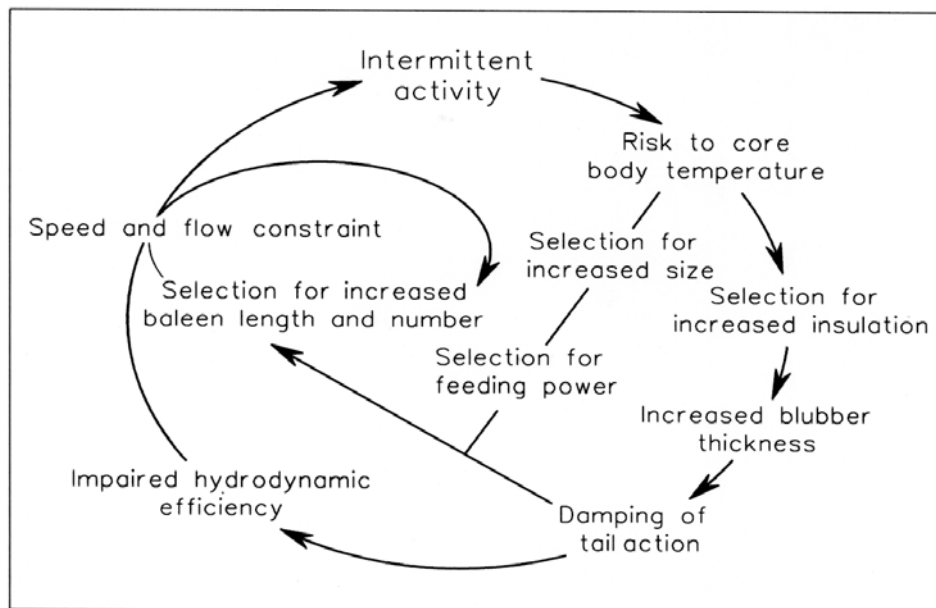


Fig. 2. Positive feedbacks leading to self-encumbrance of bowhead whale.

The expected outcome for the proto-balaenid → balaenid lineage therefore would be at least two phylogenetic constraints on movement; namely, extremely thick blubber and extremely long baleen. And it is this combination of traits that evidently favored modification of both the external surface curvature of the baleen apparatus and of individual baleen plates reported by Lambertsen *et al.* (1989) and Lambertsen *et al.* (2005) in the bowhead whale. Those modifications, which are peculiar to balaenids, in theory must reduce pressures external to the baleen apparatus during continuous feeding, thus simultaneously increasing flow through the baleen filter and reducing the amplitude of the pressure wave in front of the whale. As such they would help draw water out through the baleen while reducing the probability that actively mobile prey could sense and evade the oncoming predator. This prediction has been verified in tow tank experiments by Werth (2004), who used a scale model of the head and baleen apparatus of a bowhead based on the photogrammetric data reported by Lambertsen *et al.*, (1989) and Lambertsen (2005). It is important to note, however, that the magnitude of such a gain would depend on the baleen laminae having become both numerous and long. The evolutionary outcome we see today is a truly gigantic baleen whale that feeds at low velocities -- *and which therefore has comparatively low kinetic energies during its most critical behavior.*

I emphasize that the ability of the bowhead to avoid developing high body kinetic energies while feeding is the important outcome of the proto-balaenid → balaenid evolutionary path. For it is that ability which evidently enabled the bowhead as a species to flourish in shallow Arctic seas, including the Beaufort, where the fleet rorquals rarely if ever venture. I also emphasize that, by comparison, balaenopterids must develop high body kinetic energies to feed efficiently. This is because their feeding mechanism involves a

bounce phenomenon in which body momentum is automatically recaptured and used to complete the filtration process (Lambertsen *et al.*, 1995; Lambertsen and Hintz, 2004).

Given the comparatively shallow feeding habitat of the modern bowhead, a substantial selective pressure favoring limited rates of movement and further increase in baleen length moreover is to be expected. Indeed, the predictable evolutionary result of nonrandom mortality linked to high body kinetic energies would be *excessively* thick blubber (to constrain the tail) coupled with foreshortening of the body (to limit propulsive power). As such it is more than notable that both these “paradoxical” characteristics actually are seen in the bowhead whale when compared with the pelagic balaenopters. The blubber of the bowhead whale is about 2.5 times as thick as that of the blue whale, and far exceeds the animal’s requirement for insulation (Hokkanen 1990). At the same time its body and tail comprise only about 60% of its total length (Eschricht and Rheinart 1866), compared with about 77-78% in the blue whale (True 1904). A key point to be drawn from this combination of characters is that *the extremely thick blubber of the bowhead does not necessarily imply an expanded food reserve*. Its thickness must be interpreted in light of the fact that the body and tail has been foreshortened. From the point of view of comparative anatomy, the “glass” of the bowhead is half empty, not half full.

Another mechanism that might have contributed to the combination of characters noted is the problem of maintaining mouth closure at speed without the maxillomandibular cam articulation that evidently enabled the adaptive radiation of balaenopterids. Inasmuch as all balaenids lack a key mechanical component of that articulation (Lambertsen and Hintz 2004), they would face a greater risk of the mouth being forced open by negative hydrodynamic lift when or if they swam at high speed. What seems more than clear is that the morphology of the head in balaenids has evolved to minimize that particular problem, as there is a strong convergence of the maxillae toward the midline. For a given skull length, this well known feature of the balaenid skull minimizes the horizontal area of the mouth over which any negative hydrodynamic lift would act. In so doing the threat to the size of the food reserve individual balaenids carry probably was addressed to some extent.

THERMOPHOBIC NATURE OF BOWHEAD WHALE

The question at hand is whether the biophysical problems inherent in the evolutionary path of the bowhead now restrict the species to near-freezing habitats. This question appears to be answered by observations on the behavior of bowheads during the winter. According to the late Francis Fay, with whom I had the benefit of discussing this matter, bowheads in winter appear merely to loaf along the ice edge. On the basis of direct observation, Fay indicated that even in winter individual bowheads did not show signs of shivering or hyperactivity in response to cold.

The analysis of heat flow through blubber in large whales by Hokkanen (1990) moreover supports a conclusion that bowhead whales are, in actuality, thermophobic. Assuming a normal metabolic rate 1.5 times the *basal* metabolic rate predicted by the “mouse to elephant curve” of Kleiber (1975), Hokkanen (op. cit.) concluded that the thickness of the blubber in the average bowhead whale is so great that even in liquid oxygen it could maintain its body temperature within normal limits without any increase in metabolic rate. In accordance with the findings of Kanwisher and Sundnes (1966), Hokkanen assumed the heat conductance through live blubber to be $0.24 \text{ W m}^{-1} \text{ K}^{-1}$, about 20% greater than that of dead blubber, which is reasonable. The temperature drop across the 0.25 m thick blubber of the bowhead that would not require an increase in metabolism to maintain core body temperature was calculated to be 200 degrees!

It follows that there are now multiple lines of evidence supporting a conclusion that the bowhead whale is in fact comparatively extremely heat intolerant. Thus in all probability it is unable to venture into warm water. This restriction evidently reflects the distinct evolutionary path here identified. Taking that path, feeding power in the bowhead evolved to higher levels in parallel with anatomical changes that effectively limited whole body kinetic energies. The comparatively low maximum swimming speed of balaenids evidently is another manifestation of the same evolutionary path.

GLOBAL WARMING

With respect to global warming we can now attempt to address the important questions of 1) whether the morphophysiological outcomes of the evolutionary path of the bowhead could be reversed, and 2) if those outcomes could be reversed, what would be the cost? On the basis of the above analysis, it seems probable that the constraints on movement faced by the bowhead are causally related at least in part to the shallow depth of Arctic waters. Given the positive feedback loop attributable to a body density less than that of seawater, a long history of mortality events caused by collisions with the sea bottom provides a plausible explanation for much of its morphology, and in particular a blubber layer that far exceeds thermoregulatory requirements. Whether the bowhead could adapt to global warming involving a reduction of Arctic ice in this light is not clear. On the one hand, if average water temperature actually increases, there would be a decrease in dissolved oxygen and, therefore, decreased prey density. Under such conditions both intraspecific competition and foraging for food likely would increase per unit area of habitat. This would predict an increase in the level of activity of individual bowheads, with higher average kinetic energies and, therefore, higher rates of mortality related to collisions. If so one would predict that the species would be driven even harder down the evolutionary path that gave rise to its thermophobic nature. On the other hand, that outcome can not be considered especially likely in the foreseeable future inasmuch as ice by its very melting tends to prevent a change in water temperature. Further, the linear extent of the ice edge during winter, at least in the near term, would seem likely to be more than sufficient to maintain a large bowhead population. Such conceivably may change if the limit of ice in winter recedes to the narrow Bering Strait.

If there was no major increase in water temperature, reduction of ice coverage probably would have the effect of increasing the availability of prey by increasing the total habitable shallow area available for both breathing and feeding in summer. In the not-too-distant future it therefore probably will be most important to consider the impact of more frequent summertime incursions by the humpback whale (*Megaptera novaeangliae*), if not the killer whale (*Orcinus orca*) into the bowhead's obligatory Arctic habitat. Amongst the balaenopterids, the humpback whale is specialized for feeding in relatively shallow water. It also is well equipped to prey on euphausiids, which are known to comprise a portion of the bowhead diet (Lowry and Burns, 1980; Lowry and Frost, 1984). Further, unlike the small minke whale that might also successfully invade bowhead habitat owing to its comparatively low peak kinetic energies, the humpback carries armament. This occurs in the form of barnacle growths both under its chin and on the knobs of its flippers. Such is not a trivial matter as the bowhead whale, in contrast, is unarmed.

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