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Extreme physiological adaptations as predictors of climate-change sensitivity in the narwhal, *Monodon monoceros*

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ABSTRACT

Rapid changes in sea ice cover associated with global warming are poised to have marked impacts on polar marine mammals. Here we examine skeletal muscle characteristics supporting swimming and diving in one polar species, the narwhal, and use these attributes to further document this cetacean's vulnerability to unpredictable sea ice conditions and changing ecosystems. We found that extreme morphological and physiological adaptations enabling year-round Arctic residency by narwhals limit behavioral flexibility for responding to alternations in sea ice. In contrast to the greyhound-like muscle profile of acrobatic odontocetes, the *longissimus dorsi* of narwhals is comprised of 86.8% ± 7.7% slow twitch oxidative fibers, resembling the endurance morph of human marathoners. Myoglobin content, 7.87 ± 1.72 g/100 g wet muscle, is one of the highest levels measured for marine mammals. Calculated maximum aerobic swimming distance between breathing holes in ice is <1,450 m, which permits routine use of only 2.6%–10.4% of ice-packed foraging grounds in Baffin Bay. These first measurements of narwhal exercise physiology reveal extreme specialization of skeletal muscles for moving in a challenging ecological niche. This study also demonstrates the power of using basic physiological attributes to predict species vulnerabilities to environmental perturbation before critical population disturbance occurs.

Key words: narwhal, *Monodon monoceros*, sea ice, physiology, climate change, myoglobin, skeletal muscle, aerobic dive limit, slow twitch fiber.

Some of the most obvious and marked impacts associated with recent warming of the earth's lower atmosphere have occurred in polar marine environments. In both arctic and antarctic regions, alterations in climate have been linked to changes in sea ice cover, sea level, water temperature, and ocean currents (Rothrock *et al.* 1999, Parkinson and Cavalieri 2002, Comiso and Parkinson 2004, Walsh 2008). The rate of change within arctic ecosystems in particular exceeds trends recorded over the past several millennia (Root *et al.* 2003, Overpeck *et al*. 2005, Walsh 2008). These climate-related environmental events are poised to initiate population extinctions, range expansions and contractions, and serve as major driving forces behind evolution in natural populations of marine mammals (O'Corry-Crowe 2008). Despite this, such biological impacts often remain unrecorded due to the cryptic behaviors of oceanic mammals and the remote location of events.

As highly derived, long-lived (*i.e.*, K-selected) species, Arctic marine mammals are poorly equipped to respond quickly to sudden alterations in climate (Moore and Huntington 2008). Furthermore, the sensitivity to environmental perturbation is heightened for many specialized species due to small population size following centuries of commercial or subsistence harvest, slow reproduction rates, reliance on specific sea ice conditions for foraging, as well as their position at the apex of the food web (O'Corry-Crowe 2008). This is supported by recent evidence indicating that the observed changes in the arctic marine environment are already impacting marine mammals (Derocher *et al*. 2004, Ferguson *et al.* 2005, Laidre and Heide-Jørgensen 2005*a*, Laidre *et al.* 2008). Consequently, the three year-round cetacean occupants of arctic waters, the narwhal (*Monodon monoceros*), beluga whale (*Delphinapterus leucas*), and bowhead whale (*Balaena mysticetus*), have been listed by the International Whaling Commission (IWC 1997) as "vulnerable" to climate-induced disturbance.

As one of the three most vulnerable arctic marine mammal species (Laidre *et al.* 2008), the West Greenland narwhal populations have experienced significant declines (Heide-Jørgensen and Acquarone 2002, Heide-Jørgensen 2004). Reasons for this trend include limited geographical range and a relatively small worldwide population size. Exceptional site fidelity, dependence on predictable, seasonal changes in sea ice, and a geographically narrow and specialized feeding pattern (Heide-Jørgensen *et al*. 2003; Laidre *et al*. 2004; Laidre and Heide-Jørgensen 2005*a*,*b*; Thiemann *et al*. 2008) likely exacerbate the problem. For example, narwhal populations from Canada and Western Greenland rely on intense periods of foraging in localized wintering areas in Baffin Bay to meet annual energetic demands. While affording access to high prey densities at depth, these areas must also provide sufficient open leads and cracks to allow for breathing (Heide-Jørgensen *et al*. 2003, Laidre and Heide-Jørgensen 2005*a*), an enormous environmental challenge during the winter months.

With limited access to this species especially during the polar winter, it has been difficult to document the impact of recent, rapid environmental changes on narwhals or to predict future impacts. In this study, we approached this problem by examining the morphological (Table 1) and physiological characteristics required for supporting specialized winter foraging by the narwhal. Specifically, fiber type composition and myoglobin concentration were determined for the primary locomotory muscle, the *longissimus dorsi*, and used as indicators of swimming (Hulten *et al*. 1975, Costill *et al.* 1976) and diving (Blessing 1972, Kooyman 1989, Noren and Williams 2000) capability, respectively. These attributes were then used to examine the factors contributing to sub-ice range limits as well as the capacity of the narwhal to adapt to changing ice conditions.

Table 1. Morphological characteristics of adult narwhals in the present study. Length represents total body length from the rostrum to the fluke notch, excluding the tusk. Girths and diameters are for the maximum values recorded along the body. Sex is indicated by the ID (M = male, F = female). Age classification was based on overall size including body mass according to Hay (1984).

Animal ID	Length (cm)	Maximum girth (cm)	Maximum diameter (cm)	Estimated mass (kg)	Fineness ratio
1M	506.0	258	82.1	1,647	6.2
2M	320.0	228	72.6	529	4.4
3F	335.3	214	68.1	593	4.9

Methods

Field Site and Animals

Field research was conducted in the Pond Inlet coastal region of northern Baffin Island (Nunavut Territory, Canada) during August–September ($T_{\text{air}} = 1.7$–5.4°C, $T_{\text{water surface}} = 2.3$–$5.2$°C) to coincide with the narwhals' movements onto summering grounds within the local inlets. All animals were considered members of the Eclipse Sound subpopulation. Routine swimming behaviors (relative speed, maneuvering and predatory evasive movements) of individual narwhals and pods in Milne Inlet and western Eclipse Sound were recorded during this period by observers either in small skiffs or from surrounding cliff sites. The degree of ice cover ranged markedly during this period and depended on wind direction. Morphological measurements and tissue samples were collected opportunistically from three mature narwhals (Table 1) during a local Inuit subsistence hunt.

Body Morphology

Maximum girth and straight-line body length from maxilla tip to the notch of the tail flukes were recorded for each animal. Because of the large size of the animals, half of the girth (from mid-dorsal ridge to the ventral line) was measured and doubled for total girth. Body mass was calculated from length measurements using the equation of Hay (1984):

$$M = 0.0003231L^{2.48} \tag{1}$$

where M is body mass in kilograms and L is body length in centimeters. The fineness ratio, an index of body streamlining, was calculated according to Webb (1975):

$$FR = LD^{-1} \tag{2}$$

where FR is the fineness ratio, L is total body length in centimeters, and D is maximum body diameter in centimeters.

Tissue Samples

Samples of skeletal muscle and heart were collected within 30 min of death and placed in cooled, airtight containers on ice until fixation or freezing in liquid

nitrogen within 5 h. For each animal, samples of the *longissimus dorsi* were taken half way between the dorsal ridge and fluke from the mid belly of the muscle bundle after removal of the overlying tendon sheath (Howell 1930). In addition, samples of the left ventricle of the heart were obtained for one adult (1M). All tissue samples were divided into two sections for use in histochemical and biochemical analyses. The histochemical sample was cut, embedded in optimum cutting temperature (O.C.T.) compound, and frozen in isopentane cooled by liquid nitrogen according to the procedures of Dubowitz (1985). The remaining sample was frozen in a container immersed directly in liquid nitrogen. All samples were stored in airtight vials and shipped in a dry nitrogen container. Once at the laboratory, the vials were transferred to a freezer and stored at -70°C until analysis. To avoid dehydration of the samples, ice crystals were placed in the vials before transfer to the freezer.

Histochemistry

Details of the muscle analyses have been reported previously (Williams *et al.* 1997). Briefly, fiber typing was accomplished by staining 10 micron sections of the frozen muscle samples. Myofibrillar ATPase was determined at pH = 9.4 according to Ponganis and Pierce (1978). NADH was stained by the methods of Novikoff *et al.* (1961), and glycerophosphate dehydrogenase was stained following the procedures of Wattenberg and Leong (1960). Fibers were classified as slow twitch oxidative (SO), fast twitch glycolytic (FG), and fast twitch oxidative and glycolytic (FOG) according to Peter *et al*. (1972).

Myoglobin

Myoglobin content was determined using the procedure of Reynafarje (1963) in which each muscle is subdivided into duplicate samples, homogenized in low ionic strength buffer (40 mM phosphate, pH = 6.6), sonicated for 1–3 min (Branson Sonifier Cell Disrupter 185, Danbury, CT), and centrifuged (4°C; 13,000 × *g* for 90 min). The buffer to tissue ratio was 19.25 mL buffer per gram of tissue. The resulting clear supernatant was bubbled with pure CO for approximately 8 min; sodium dithionite ensured a complete reduction. Lastly, the absorbance of each sample was read at 538 and 568 nm on a desktop spectrophotometer (Beckman, Inc., Fullerton, CA).

Body Oxygen Store and Aerobic Dive Limit Calculations

To estimate the maximum dive duration supported by aerobic metabolic processes, the calculated aerobic dive limit (cADL) was determined by dividing the total body oxygen store (lung, blood, and muscle) by metabolic rate following the methods of Kooyman (1989) and described in detail in Noren *et al*. (2002). Briefly, muscular stores were determined from values measured in the present study, blood stores were determined from hematological values measured previously for narwhals (Vogl and Fisher 1982), and lung stores, which are negligible during diving, were estimated from an allometric regression for the lung volume of marine mammals (Kooyman 1989).

Metabolic rates for cADL assessments were calculated for each of the narwhals in this study using the total cost of transport for adult, swimming marine mammals from Williams (1999),

$$\mathrm{COT_{TOT}} = 7.79\mathrm{Mass}^{-0.29} \quad (3)$$

Here the total cost of transport ($\mathrm{COT_{TOT}}$) is in $\mathrm{J \bullet kg^{-1} \bullet m^{-1}}$ and body mass is in kilograms. $\mathrm{COT_{TOT}}$ was subsequently converted into metabolic rate by multiplying the value by the preferred speed of swimming reported for wild narwhals, and assuming a caloric equivalent of 4.8 kcal per liter of O_2 and a conversion factor of 4.187×10^3 $\mathrm{J \bullet kcal^{-1}}$. Under free-ranging conditions preferred swimming speeds generally correspond to the minimum cost of transport speed (Hoyt and Taylor 1981, Williams *et al.* 1992, Williams 1999) enabling the calculation of swimming metabolic rate for routine movements. The selected preferred speed for our calculations was 1.4 $\mathrm{m \bullet s^{-1}}$, and was based on the mean horizontal (Dietz and Heide-Jørgensen 1995) and vertical (Heide-Jørgensen and Dietz 1995) transit speeds of free-ranging narwhals. Whenever possible, speeds associated with directed movements over relatively short (<5 h) were used to avoid artifacts associated with nonlinear swimming performance. Admittedly, narwhals exhibit speeds that can range from 0.64 to 2.36 $\mathrm{m \bullet s^{-1}}$ (Dietz and Heide-Jørgensen 1995, Heide-Jørgensen and Dietz 1995, Laidre *et al.* 2002, Laidre *et al.* 2003). Because locomotor efficiency is reduced at speeds exceeding approximately ±10% of preferred speeds (see Williams *et al.* 1992 for a discussion pertaining to swimming dolphins), we based our model on the average speed that would maximize submergence time. To account for variation in underwater performance, we also calculated the metabolic consequence of altering speed ±10% of the mean value, and adjusted for potential energetic savings associated with stroke-and-glide swimming during diving (Williams *et al.* 2000).

Rather than maximum diving capabilities, these calculations provide submergence times and coincident sub-ice ranges for breath-holds that are based primarily on aerobic metabolic processes. Such aerobic dives represent 95%–99% of dives in a wide variety of diving vertebrates (Kooyman 1989), and permit an assessment of the match between morphological characteristics of an animal and its routine performance demands.

All results are presented as means ± 1 SD unless otherwise indicated.

Results

Body Morphology

Morphological characteristics and fineness ratios (FR) for three adult narwhals are presented in Table 1. Values for FR were within the range, 4.0–7.0, considered the ideal for streamlined bodies of rotation (Hertel 1966). The fineness ratio of the two smaller animals approximated the optimum value of 4.5.

Skeletal Muscle Morphology and Histochemistry

Muscle fiber type and mean fiber diameter for samples of the *longissimus dorsi* of mature narwhals are presented in Figure 1 and Table 2, respectively. Both slow twitch (SO) and fast twitch (FOG and FT) fibers were distinguished, with SO fibers representing the predominant fiber type. For all three animals, SO fibers accounted for over 79% of the total fiber population in each sample. Mean fiber diameters were 62.6 ± 20.0μ for slow twitch fibers and 60.3 ± 16.2μ for fast twitch fibers combined. When expressed as percentage area of the muscle, 87.8% ± 6.3% of the

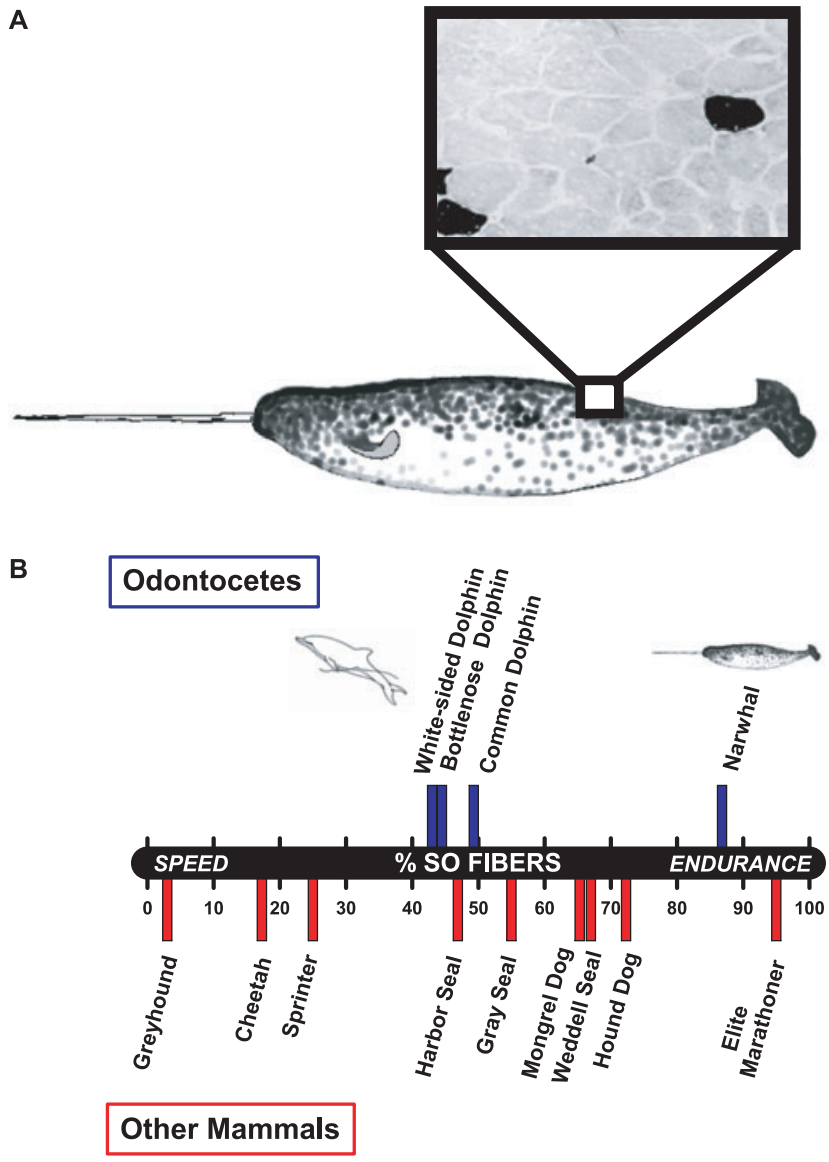

Figure 1. Skeletal muscle fiber profile of narwhals. Sample location and a photomicrograph of a thin section (10μ thick) of the *longissimus dorsi* muscle stained by the myosin ATPase method for fiber type is shown in the upper panel (A). Light areas denote slow oxidative (SO) fibers; dark areas are fast twitch (FG and FOG) fibers. Oxidative potential of these fibers was further differentiated by histochemical tests for NADH diaphorase and glycerophosphate dehydrogenase. The lower panel (B) compares the percentage of SO fibers in the major locomotory muscles of mammals. Values for narwhals in the present study are compared to those of similar muscles powering the flukes of other odontocetes (upper bars) as well as swimming and running skeletal muscles of pinnipeds and terrestrial mammals, respectively (lower bars). Data for fiber composition are from (1) odontocetes: Pacific white-sided dolphin

Table 2. Skeletal muscle characteristics of the *longissimus dorsi* for narwhals. Values are reported as mean ± 1 SD ($n = 3$ animals). Identification of muscle fiber type (Peter *et al.* 1972), population percentages, and percentage area of muscle is based on 450–600 individual fibers evaluated per sample. Duplicate samples were analyzed for each subject.

Muscle fiber type	SO	FOG and FT
Mean diameter (μ)	62.6 ± 20.0	60.3 ± 16.2
% Fibers	86.8 ± 7.7	13.2 ± 7.7
% Area of muscle	87.8 ± 6.3	12.2 ± 6.3
Myoglobin content (g/100 g wet muscle) = 7.87 ± 1.72		

cross-sectional area of the *longissimus dorsi* of narwhals is comprised of SO fibers while FT and FOG fibers account for only 12.2% ± 6.3% (Table 2).

Myoglobin

The average measured concentration of myoglobin (Mb) in the *longissimus dorsi* of narwhals is 7.87 ± 1.72 g/100 g wet muscle (Table 2). This level of Mb is among the highest recorded in any cetacean (Noren and Williams 2000), and provides an exceptionally large oxygen store in the locomotory muscle. In comparison, the myoglobin content for the left ventricle of the heart measured for one narwhal was considerably lower at 1.35 g/100 g wet muscle. Similar low levels for myocardial tissue were found for two other odontocetes, the false killer whale (*Pseudorca crassidens*) at 1.02 g/100 g wet muscle and common dolphin (*Delphinus delphis*) at 1.14 g/100 g wet muscle from T. M. Williams (unpublished data).

Body Oxygen Store and Aerobic Dive Limit Calculations

As found for other marine mammals (Kooyman 1989), the skeletal muscles and blood represented major oxygen stores for narwhals (Table 3). The largest store was found in the muscles, which comprised 44%–55% (mean = 51% ± 6%, $n = 3$ animals) of the total oxygen reserve for this cetacean. Summing the oxygen stores for muscle, blood, and lungs resulted in an estimated total body oxygen store of 41.6–106.5 L O_2 or 64.7–79.9 mL $O_2 \bullet kg^{-1}$ (mean = 74.5 ± 8.5 mL $O_2 \bullet kg^{-1}$)

←

(*Lagenorhynchus obliquidens*), *erector spinae* (epaxial) (Ponganis and Pierce 1978); bottlenose dolphin (*Tursiops truncatus*), *longissimus dors*i (Bello *et al.* 1985); common dolphin (*Delphinus delphis*), *longissimus dorsi* (Suzuki *et al.* 1983); narwhal (*Monodon monoceros*)- *longissimus dorsi* (present study); (2) pinnipeds: harbor seal (*Phoca vitulina*), *longissimus dorsi* (Reed *et al*. 1994, Watson *et al*. 2003); Weddell seal (*Leptonychotes weddellii*), *longissimus dorsi* (Kanatous *et al*. 2002); gray seal (*Halichoerus grypus*), *longissimus dorsi* (Reed *et al*. 1994); and (3) terrestrial mammals: greyhound (*Canis familiaris*), *semitendinosus* (Gunn 1978); African cheetah (*Acinonyx jubatus*), *vastus lateralis* (Williams *et al.* 1997); human sprinter (*Homo sapiens*), *gastrocnemius* (Wilmore and Costill 2004); mongrel dog (*Canis familiaris*), *tibialis anterior* (Kuzon *et al.* 1989); hound dog (*Canis familiaris*), *tibialis anterior* (Kuzon *et al.* 1989); human elite marathoner (*Homo sapiens*), *gastrocnemius* (Wilmore and Costill 2004).

Table 3. Estimated tissue oxygen stores of narwhals. Comparisons are provided for the three narwhals in this study (two male and one female). Details of the calculations are provided in the text and in Noren *et al.* (2002).

	Narwhal specimen		
	1M	2M	3F
Body mass (kg)	1,647	529	593
Lung volume (TLC) in L[a]	122.4	41.1	45.9
Diving lung volume 75% TLC (L)[b]	91.8	30.8	34.5
Alveolar [O_2] 15% diving lung volume[a]			
Total O_2 in lung (L)	13.8	4.6	5.2
Muscle mass = 36% body mass (kg)[b]	592.6	190.1	213.5
Myoglobin (g Mb/100 g muscle)[c]	5.89	8.74	8.97
Total body Mb (g)[c]	34,901.8	16,613.0	19,149.2
Mb O_2 combining capacity 1.34 mL $O_2 \bullet g^{-1}$[a]			
Total O_2 in muscle (L)	46.8	22.3	25.7
Blood volume = 126.5 mL $\bullet$ kg^{-1} (L)[d]	210.2	67.4	75.7
Arterial volume 33% total blood volume (L)[e]	69.4	22.3	25.0
Venous volume 67% total blood volume (L)[e]	140.8	45.2	50.7
Hemoglobin (g Hb/100 mL blood)[f]	22.5	22.5	22.5
Hb O_2 combining capacity 1.34 mL $O_2 \bullet g^{-1}$[a]			
Arterial O_2 store assumes 95%–20% saturation (L)[a]	15.7	5.0	5.7
Venous O_2 store less 5 volume % of arterial (L)[e]			
Assumes 95%–20% saturation[a]	30.3	9.7	10.9
Total O_2 in blood (L)	45.9	14.7	16.5
Total O_2 in Body (L)	106.5	41.6	47.4

[a]Kooyman (1989).
[b]Goforth (1986).
[c]Current study.
[d]Ridgway *et al.* (1984).
[e]Lenfant *et al.* (1970).
[f]Vogl and Fisher (1982).

for the narwhals in the present study (Table 3). These oxygen stores theoretically support 15–17 min (mean = 16 $\pm$ 1 min) of aerobic diving, assuming a metabolic rate of 3.8–5.2 mL $O_2 \bullet kg^{-1} \bullet min^{-1}$ (mean = 4.7 $\pm$ 0.8 mL $O_2 \bullet kg^{-1} \bullet min^{-1}$) at a constant swim speed of 1.4 $m \bullet s^{-1}$ (Fig. 2). Energetic savings associated with gliding on descent (Williams *et al.* 2000) increases the cADL to 21–24 min (mean = 22 $\pm$ 2 min) for these narwhals (Fig. 2).

Discussion

Based on histochemical and biochemical profiles, the major locomotory skeletal muscle of the narwhal, the *longissimus dorsi*, indicates an animal built for slow, endurance swimming. Mean fiber diameters for slow twitch fibers (62.6 $\pm$ 20.0μ) and fast twitch fibers combined (60.3 $\pm$ 16.2μ) were 19%–162% larger than that reported for the same muscle in harp seals (George and Ronald 1973), but were similar in size to the locomotory muscle (quadriceps) of humans (Dubowitz 1985). Although both fast twitch and slow twitch fibers were identified (Table 2, Fig. 1A), slow twitch

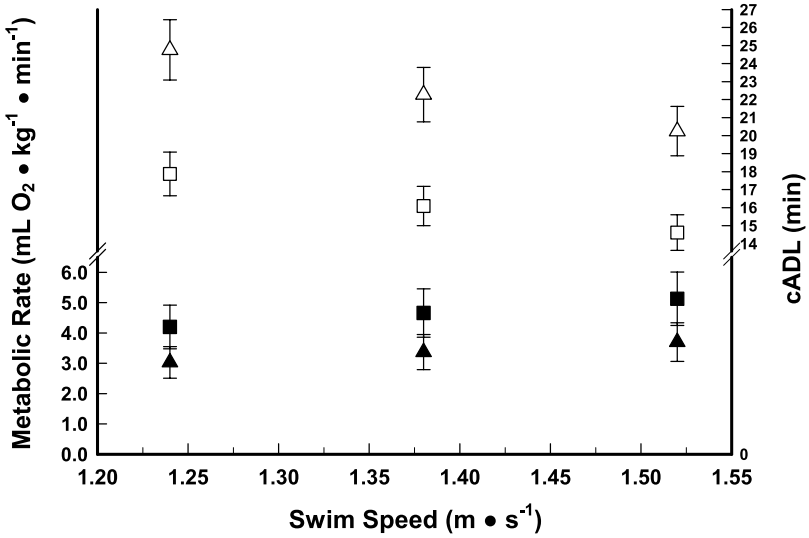

Figure 2. Metabolic rates (closed symbols) and aerobic dive limits (open symbols) in relation to routine swimming speed for narwhals. Symbols and lines represent mean ± 1 SD for the three narwhals in this study, and include a comparison for constant (squares) and stroke-and-glide (triangles) swimming styles. Note that increased gliding results is an energetic cost savings (Williams *et al.* 2000) that reduces overall diving metabolic rate, thereby increasing aerobic dive limits. The range of speeds evaluated included the minimum cost of transport speed (1.4 m • s^{-1}) ± 10% reported for free-ranging narwhals (Heide-Jørgensen and Dietz 1995). Aerobic dive limits were calculated from total body oxygen stores and metabolic rates as determined from the cost of transport for swimming by marine mammals (see Table 3).

fibers predominated and accounted for nearly 90% of the total fiber population. Such a fiber type profile represents the extreme end of the spectrum for locomotory muscles of mammals (Fig. 1B). Among human athletes, the *gastrocnemius*, a major skeletal muscle powering running, is comprised of 93%–99% SO fibers in elite distance runners and only 25% SO fibers in sprinters (Wilmore and Costill 2004). Even among marine mammals, the narwhal demonstrates the highest proportion of SO fibers for the *longissimus dorsi* for both pinnipeds and other odontocetes (Fig. 1B).

The characterization of the narwhal as a slow, aerobic swimmer based on the contraction times and metabolic properties of skeletal muscle (Hulten *et al.* 1975, Wilmore and Costill 2004) has been confirmed through behavioral observations (Vibe 1950, present study), and calculations of speed from movement patterns recorded by satellite-linked recorders (Dietz and Heide-Jørgensen 1995). Horizontal speeds of wild narwhals average only 1.4 m • s^{-1} (range = 0.81–2.36 m • s^{-1}); vertical speeds are within approximately 10% of this range (Heide-Jørgensen and Dietz 1995), and among the slowest reported for marine mammals (Williams 2009). Our observations of narwhals encountering killer whales (*Orcinus orca*) also suggest a deliberate moving, endurance athlete. Rather than burst activity, the major escape response involved prolonged submergence and/or swimming into nearby areas of dense, wind-blown pack-ice. Similar, slow movements by narwhals in the presence of killer whales have been reported by Laidre *et al.* (2006). This is in contrast to the energetic, high speed escape behaviors of other cetaceans such as Pacific white-sided

dolphins (*Lagenorhynchus obliquidens*), whose locomotory muscles are equally divided into slow twitch and fast twitch fiber types (Ponganis and Pierce 1978; Fig. 1B).

A benefit of slow oxidative muscle fibers is the associated high myoglobin levels (Wilmore and Costill 2004), which provide an advantage for prolonged diving. Oxymyoglobin generally represents an important on-board oxygen store for supporting aerobic metabolic processes in cetaceans during submergence (Kooyman 1989). Consequently, myoglobin concentration correlates with diving capacity (Noren and Williams 2000). With a myoglobin level that is among the highest reported for any cetacean (Table 2), the skeletal muscles of narwhals rival oxygen carrying capacities for deep divers including sperm whales (*Physeter macrocephalus*) and Northern bottlenose whales (*Hyperoodon ampullatus*; see Noren and Williams 2000 for a review).

The advantage of elevated myoglobin concentrations is also apparent when calculating the aerobic dive limit (cADL) of the narwhal (Table 3). Total body oxygen stores estimated for the narwhals in the present study ranged from 41.6 to 106.5 L O_2 (64.7 to 79.9 mL $O_2 \bullet kg^{-1}$), and depended on body size. Over 50% of the store was in the form of oxymyoglobin within skeletal muscle (Table 3). At a routine swim speed of 1.4 $m \bullet s^{-1}$ during diving (Heide-Jørgensen and Dietz 1995) and an associated metabolic rate of 3.8–5.2 mL $O_2 \bullet kg^{-1} \bullet min^{-1}$ (Fig. 2), these oxygen stores will theoretically support 21–24 min (mean = 22 ± 2 min) of aerobic diving by narwhals assuming the animals glide during the dive cycle (Williams *et al.* 2000). Average dive performance measured for wild narwhals wearing satellite-linked dive recorders from Laidre *et al.* (2002) is well below this limit, which is consistent with the expected pattern for aerobic diving by many marine mammal species (Kooyman 1989).

By combining the data for aerobic dive limits with the performance characteristics of wild narwhals, we can evaluate the physiological capacity for routine sub-ice travel for this cetacean. If we assume that narwhals swim constantly at a minimum cost of transport speed of 1.4 $m \bullet s^{-1}$, the associated cADL ranges from 15 to 17 min. This enables the 529–1,647 kg narwhals in the present study to move horizontally a distance of 1,252–1,430 m between two adjacent breathing holes or open water leads (Fig. 3A). In the vertical direction, these same capabilities allow the animals to travel back and forth to 626–715 m in depth. If the narwhal, as reported for other cetaceans (Williams *et al*. 2000), incorporates gliding periods during diving, metabolic costs are lowered. As a result cADL is increased to 21–24 min, which allows the animal to dive aerobically to depths of 867–990 m (Fig. 3A). Note that this aerobic advantage associated with gliding does not affect horizontal travel distances because the gliding behavior is linked primarily to lung compression and buoyancy changes with depth (Williams *et al.* 2000).

Because we assume straight line travel from a breathing hole to the benthos and back, or between breathing holes, these calculations represent the maximum range values for aerobic diving by narwhals. It would be expected that narwhals are capable of longer duration dives and attaining deeper depths with the incorporation of anaerobic metabolic pathways. Indeed, the maximum dive duration reported for free-ranging narwhals is 26.2 min (Heide-Jørgensen and Dietz 1995, Laidre *et al.* 2002) and the maximum depth is 2,355 m (Laidre *et al*. 2003), both of which exceed our estimated aerobic limits. Based on our calculations achieving such extended durations or depths is dependent on body mass and likely associated with an increased reliance on anaerobic processes for the narwhal. This is evident from the prolonged surface durations of narwhals following exceptionally long dive duration and depths

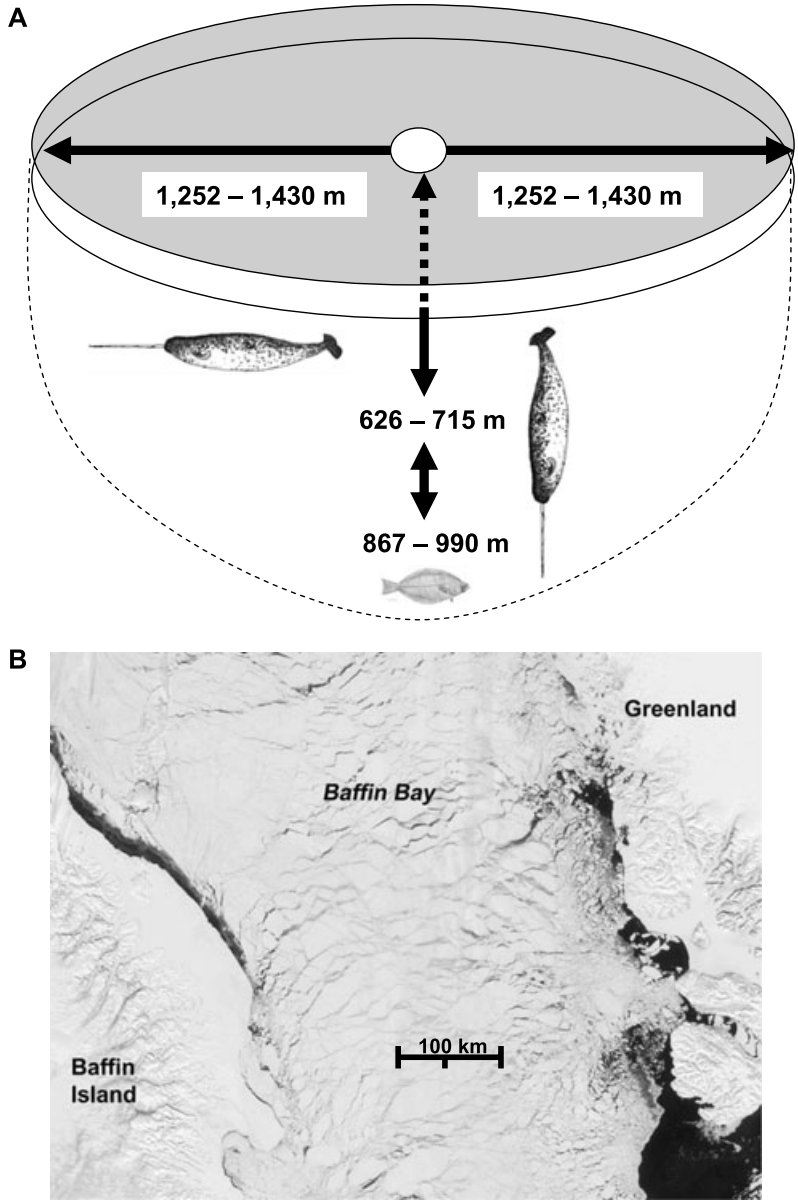

Figure 3. Predicted area available for routine sub-ice movements by adult narwhals. In the upper panel (A), horizontal and vertical dive distances from a central breathing hole (white circle) are shown by the arrows and based on muscle characteristics (Table 2), routine travel speeds (Heide-Jørgensen and Dietz 1995) and aerobic dive limits (Fig. 2) for the adult narwhals in this study. Gliding on descent results in an increase in dive distance compared to dives involving continuous swimming as shown by the vertical arrows. All transit distances assume a straight line path and account only for aerobic breath-holds. Values are ranges for the three narwhals in Table 1. The lower panel (B) presents a MODIS satellite image

(Laidre *et al.* 2002) that serve to accommodate the recovery from anaerobic byproducts. The implication is that these deep dives come at a cost for the narwhal.

In general, 92%–99% of dives performed by free-ranging narwhals on winter foraging grounds (Laidre *et al.* 2003) are within the cADL determined in the present study. However, one subgroup reported by Laidre *et al.* (2003) consistently surpassed 800 m, with approximately 13% of the dives exceeding the predicted aerobic dive limit. This suggests that narwhals, particularly during challenging winter ice conditions, may already be operating at their maximum performance levels. The result is little flexibility to extend dive durations or depths to compensate for the rapid changes in ice cover or prey availability associated with ongoing climate changes.

Similar physiological–environmental limitations constrain horizontal movements of foraging narwhals. This is obvious from the massive size of ice floes covering traditional foraging grounds of narwhals, which can exceed 50–100 times the maximum aerobic horizontal swimming distance of the animals (Fig. 3A, B). For example, the southern wintering grounds for narwhals from Canada and Western Greenland encompass an area of 23,125 km^2 in Baffin Bay of which 438 km^2 is open water during the late winter months (Laidre and Heide-Jørgensen 2005*a*). Body width and anatomical location of the blowhole (Table 1) require an ice opening of at least 0.5 m for an adult narwhal to breathe. Assuming a surrounding lead width sufficient for breathing, the largest ice floe allowing routine, full sub-ice access to an averaged-sized adult narwhal is 1.3 km wide (Fig. 3A). Access is markedly reduced with increasing size of the floe, with aerobic stores of the narwhal maximally allowing for underwater movements of 0.66 km back and forth along the floe periphery. Based on this, over 75.2% of the sub-ice area of a 10 km wide ice floe is inaccessible for routine exploring or foraging, 89.6% of the waters below a 25 km floe and 97.4% of a 100 km floe are inaccessible. Thus, depending on the time of year and pattern in ice fracturing only 2.6%–10.4% of the total wintering grounds may be accessible to the foraging narwhal subpopulation at any one time.

Admittedly, such calculations are complicated by ice movements and temperature, as well as the ability of narwhals to break through newly formed ice to exploit or create open water areas. Despite this, recognizing the physiological limits of the animals provides an understanding of the extreme challenge and potential constraint on movements currently encountered by narwhals particularly during critical periods of intense foraging in winter (Laidre and Heide-Jørgensen 2005*b*). As areas of open water within traditional winter feeding grounds decrease (Laidre and Heide-Jørgensen 2005*a*), it is not surprising that several narwhal populations in the waters surrounding Baffin Island are threatened (Heide-Jørgensen 2004) and that large-scale mortality events associated with ice entrapments have increased (Siegstad and Heide-Jørgensen 1994, Heide-Jørgensen *et al.* 2002). This is especially likely if the animals increasingly embark on risky exploratory dives to establish new feeding territories.

←

(250 m resolution) of sea ice conditions in Baffin Bay on 29 April 2002 at the end of the winter foraging period. Dark areas denote leads and open water; light areas are sea ice or land. The scale line is positioned at the lower edge of the Northern Wintering Ground and upper edge of the Southern Wintering Ground of Canadian and Western Greenland narwhal populations (Laidre and Heide-Jørgensen 2005*a*). The size of ice floes (B) relative to maximum sub-ice travel distance of narwhals (A) allows only peripheral penetration under the ice to forage. (Image courtesy of NASA/GSFC, MODIS Rapid Response, http://rapidfire.sci.gsfc.nasa.gov/).

In conclusion, historical behavioral patterns for high Arctic marine mammals have long been matched to evolutionarily honed physiological traits that support efficient movement and foraging patterns. The body morphology and skeletal muscle characteristics of the narwhal have enabled a pack-ice lifestyle through slow endurance swimming and prolonged diving. In comparing these physiological traits with current environmental conditions and behaviors recorded in the wild, we find that free-ranging narwhals appear to be approaching their physiological capacity. As a result, this distinctive Arctic cetacean may have little physiological flexibility to adjust swimming and diving behaviors in response to shifts in habitat and prey resources associated with ongoing trends in global climate change, a sensitivity reflected in the ecology of the narwhal (Laidre *et al.* 2008). Rather than a unique case, similar vulnerabilities to habitat disturbance may be predicted for other highly adapted species by using this physiological–environmental approach.

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