

REVIEW

Physiological consequences of Arctic sea ice loss on large marine carnivores: unique responses by polar bears and narwhals

Anthony M. Pagano^{1,*} and Terrie M. Williams²

ABSTRACT

Rapid environmental changes in the Arctic are threatening the survival of marine species that rely on the predictable presence of the sea ice. Two Arctic marine mammal specialists, the polar bear (*Ursus maritimus*) and narwhal (*Monodon monoceros*), appear especially vulnerable to the speed and capriciousness of sea ice deterioration as a consequence of their unique hunting behaviors and diet, as well as their physiological adaptations for slow-aerobic exercise. These intrinsic characteristics limit the ability of these species to respond to extrinsic threats associated with environmental change and increased industrial activity in a warming Arctic. In assessing how sea ice loss may differentially affect polar bears that hunt on the ice surface and narwhals that hunt at extreme depths below, we found that major ice loss translated into elevated locomotor costs that range from 3- to 4-fold greater than expected for both species. For polar bears this instigates an energy imbalance from the combined effects of reduced caloric intake and increased energy expenditure. For narwhals, high locomotor costs during diving increase the risk of ice entrapment due to the unreliability of breathing holes. These species-specific physiological constraints and extreme reliance on the polar sea ice conspire to make these two marine mammal specialists sentinels of climate change within the Arctic marine ecosystem that may foreshadow rapid changes to the marine ecosystem.

KEY WORDS: Arctic, Climate change, Marine mammals, *Monodon monoceros*, *Ursus maritimus*

Introduction

Over the millennia, wild species have evolved unique morphological and physiological characteristics to efficiently meet their energetic demands. Such evolutionary processes are especially notable for marine mammals that must balance extraordinarily high energetic costs of living in a challenging thermal environment (Costa and Williams, 1999; Rojano-Doñate et al., 2018; Williams et al., 2001) with exceptionally high metabolic rates and large intakes of prey (Costa and Williams, 1999). To support metabolic demands, many species of marine mammal radiated to polar regions to exploit the seasonally high availability of energy-rich prey (Bluhm and Gradinger, 2008; Huston and Wolverton, 2009; Sakshaug, 2004). Survival in these polar regions necessitated several unique adaptations that included the evolution of thick blubber layers for insulation and for the long-term storage of energy (Blix, 2016), as well as remodeling of the small intestines for food processing to meet elevated metabolic demands

(Williams et al., 2001). For many polar marine mammals, these processes must occur on short time scales due to the seasonal availability of energy-rich prey, which further increases the risk of energetic shortfalls from climatic perturbations (Pagano et al., 2018a).

Presently, the Arctic is warming more than twice as fast as the rest of the planet on average, a phenomenon known as Arctic amplification (Cohen et al., 2014; Screen and Simmonds, 2010). This amplification is driven by declines in sea ice cover, resulting in a sea ice–albedo feedback mechanism (Dai et al., 2019; Screen and Simmonds, 2010), but may also be driven by global atmospheric circulation changes that have shifted warm and moist tropical air into the Arctic (Clark and Lee, 2019; Lee, 2014). These phenomena have resulted in declines in September Arctic sea ice at a rate of 13.3% per decade since 1979 (Serreze and Stroeve, 2015) (Fig. 1). The current record low for September sea ice extent occurred in 2012, which was 49% less than the average extent between 1979 and 2000 (Overland and Wang, 2013). Additionally, there has been a 50% decrease in multi-year ice since 1999 (Kwok, 2018) and a 75% decline in sea ice volume since the 1980s (Overland et al., 2014). Increases in open water are resulting in greater absorption of solar radiation into the ocean, leading to increases in sea surface temperatures and delayed autumn freeze-up (Stroeve et al., 2014) as well as increases in atmospheric moisture content (Boisvert and Stroeve, 2015) and cloud cover (Jun et al., 2016). As a result, sea ice retreat is trending 3–9 days earlier per decade and sea ice advance is trending 3–9 days later per decade relative to 1979–2014 (Stern and Laidre, 2016). Additionally, winter sea ice extent has declined at a rate of 3.4% per decade since 2000 (Stroeve and Notz, 2018). Climate forecasts indicate that the Arctic may be largely ice-free (i.e. sea ice extent <1.0 million km²) in summer by mid-century (Laliberté et al., 2015; Massonnet et al., 2012; Overland and Wang, 2013). In addition to direct environmental impacts, the continued decline in Arctic sea ice may indirectly affect wild animals through increased anthropogenic activity in the Arctic including shipping, fisheries and resource extraction activity (Crépin et al., 2017; Melia et al., 2016; Pizzolato et al., 2016).

These environmental and anthropogenic changes are projected to have marked impacts on Arctic animals. Eleven species of marine mammals are ice associated, and thus depend on the Arctic marine ecosystem (Kovacs et al., 2011; Laidre et al., 2008). While forecasted climate change and sea ice declines are likely to eventually affect nearly all Arctic marine mammals, Laidre et al. (2008) identified the polar bear (*Ursus maritimus*) and narwhal (*Monodon monoceros*) as two of the three most sensitive to these environmental changes. This conclusion was based on the relatively small circumpolar abundance of both species, their dependence on sea ice, and their diet specialization (Laidre et al., 2008). Additionally, both species exhibit low genetic diversity, which may further hinder their ability to adapt to environmental change (Cahill et al., 2013; Hailer et al., 2012; Louis et al., 2020;

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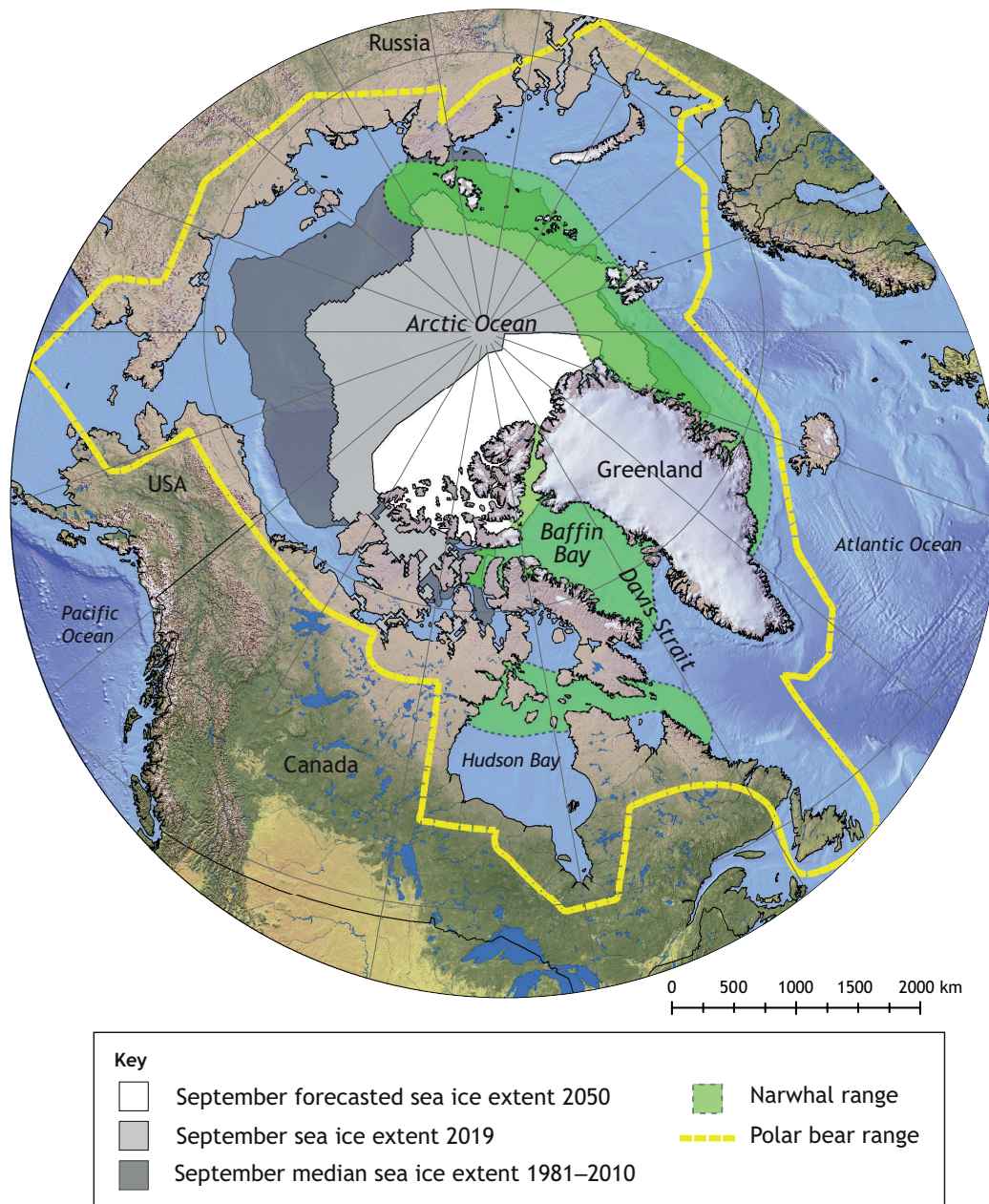


Fig. 1. Map of the Arctic sea ice in September and the current distribution of polar bears and narwhals. The circumpolar distribution of polar bears (Durner et al., 2018) and narwhals (Heide-Jørgensen, 2018) is shown with the September median sea ice extent between 1981 and 2010 (Fetterer et al., 2017), September sea ice extent in 2019 (Fetterer et al., 2017), and the forecasted September sea ice extent in 2050 based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) Geophysical Fluid Dynamics Laboratory Coupled Physical Model (GFDL-CM3; Griffies et al., 2011) using the 4.5 (moderate radiative forcing stabilization scenario) representative concentration pathway (RCP; van Vuuren et al., 2011).

Westbury et al., 2019; Palsbøll et al., 1997). As a result, narwhals and polar bears are considered important sentinel species of the impacts of climate change throughout the Arctic, particularly given their roles as apex predators (Estes et al., 2011, 2016; Moore and Reeves, 2018; Ripple et al., 2014).

In this Review, we examine the unique physiological attributes and limits of these two ice-dependent marine mammals and assess how these intrinsic characteristics may challenge their ability to adapt to an increasingly ice-free Arctic ecosystem. We evaluate the consequences of sea ice loss for polar bears that rely on a stable surface to catch their prey, and contrast this with narwhals that rely on predictable ice conditions and access to breathing holes to

replenish tissue oxygen stores following each dive. The increased presence of humans and killer whales (*Orcinus orca*) permitted by a new, ice-free Arctic adds another threat to these animals.

Energetic consequences of moving in a warming Arctic

One of the most obvious responses to deteriorating Arctic sea ice associated with environmental warming is a marked alteration in the movements of wildlife. This has resulted in increased energy expenditures for large, mobile mammals like polar bears and narwhals. Using the total cost of transport (COT_{tot}) as a common metric, Fig. 2A demonstrates the magnitude of the energetic impact when these animals switch from preferred to extreme

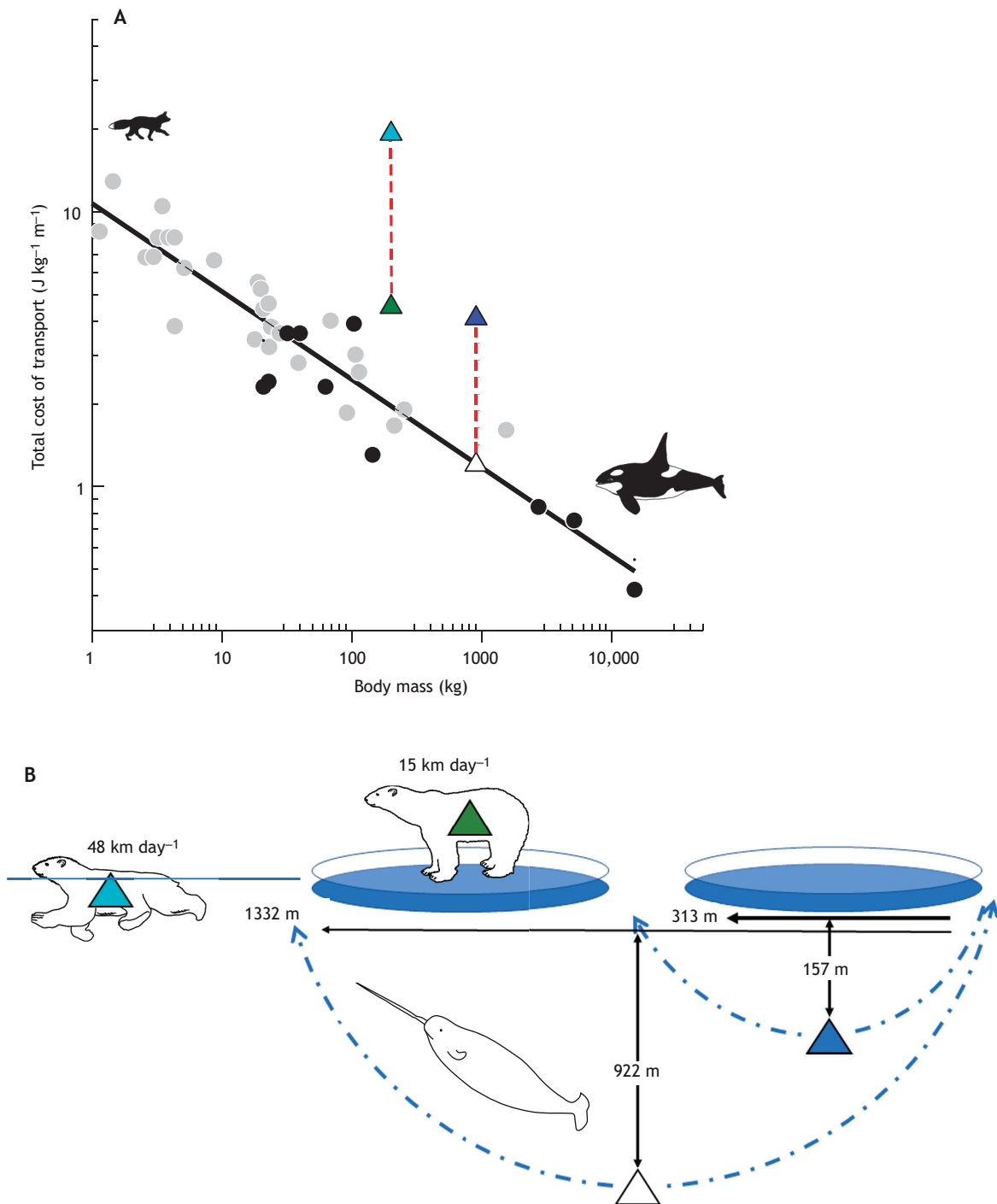


Fig. 2. Changes in total transport costs and movement patterns for polar bears and narwhals. (A) Total cost of transport (COT_{tot}) for terrestrial and marine mammals is plotted in relation to body mass (redrawn from Williams et al., 2015). Changes in COT_{tot} for walking (green triangle) and swimming (cyan triangle) polar bears and a routine (white triangle) and escape (blue triangle) dive in narwhals are presented. The solid line is the least squares regression as presented in the text; points represent individual species. Data for polar bears are from Pagano et al. (2018b) and Griffen (2018); data for narwhals are from Williams et al. (2011, 2017, 2020). (B) Maximum predicted distances moved under routine and escape conditions for narwhals and polar bears are compared. Symbols correspond to the total transport costs in panel A. The area available for sub-ice movements are shown for adult narwhals based on muscle characteristics (Fig. 5), routine travel speeds (Heide-Jorgensen and Dietz, 1995) and aerobic dive limits (Williams et al., 2011). Note that no gliding occurred during the escape dives. All transit distances assume a straight-line path and account only for aerobic breath-holds (redrawn from Williams et al., 2011, with additional unpublished dive data from T.M.W. of narwhals escaping from human-based threats). In polar bears, linear distances per day are based on the mean distance covered during long distance swims (Pagano et al., 2012) and mean drift-corrected movements of bears on the sea ice (Durner et al., 2017).

locomotor behaviors. Total transport costs for running and swimming mammals can be described by a single equation (Williams, 1999), $COT_{tot} = 10.7M^{-0.32}$ ($N=58$ species, $r^2=0.94$,

$P<0.001$), where COT_{tot} is in $J\ kg^{-1}\ m^{-1}$ and body mass (M) is in kilograms. The minimum total cost of walking is $4.5\ J\ kg^{-1}\ m^{-1}$ for a 200 kg adult polar bear (Pagano et al., 2018b); the predicted

cost for routine diving is $1.2 \text{ J kg}^{-1} \text{ m}^{-1}$ for a 900 kg narwhal. As detailed below, these transport costs increase 3- to 4-fold due to locomotor responses associated with climate-driven changes in the Arctic (Fig. 2).

Physiological integration for ice living

Polar bears: life on the ice

Polar bears are the most recently evolved marine mammal (Berta, 2012), physiologically and behaviorally adapted to feed on ice-dependent seals. The evolution of polar bears from brown bears approximately 479–343 thousand years ago (Liu et al., 2014) included physical adaptations to aid their carnivorous, semi-aquatic and high Arctic lifestyle. These adaptations included a larger body size, white fur, larger feet with shorter claws, a flattened cranium and an acute olfactory sense (Harington, 2008). Concurrently, polar bears became diet specialists, feeding almost exclusively on the blubber from ice-dependent seals, particularly ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald, 1977). Polar bear foraging success peaks in the spring and early summer when these seals are weaning their pups (Pilfold et al., 2012; Stirling and Archibald, 1977; Stirling and Øritsland, 1995; Stirling et al., 1999) and polar bears may acquire up to two-thirds of their annual energy requirements during this period (Stirling and Øritsland, 1995). Like other large carnivorous mammals, this diet specialization for carnivory has conferred a high metabolic rate necessitating greater prey requirements relative to other similarly sized mammals. This is driven primarily by higher basal metabolic rates relative to non-carnivorous mammals (Nagy et al., 1999; Pagano et al., 2018a; Williams et al., 2001). The average spring field metabolic rate (FMR) of adult female polar bears (Pagano et al., 2018a) is 20% greater than the predicted FMR of a similar-sized ungulate (Riek et al., 2019) (Fig. 3).

Historically, the ability of this large carnivore to catch energetically dense, fatty ice seals enabled it to meet its high metabolic demands. As ice conditions allow, polar bear movements are directed towards sea ice over continental shelf habitats with depths less than 300 m (Durner et al., 2009), which is thought to have the greatest abundance and access to seal prey. Like other large predators, polar bears are primarily ambush hunters, in which they wait at seal breathing holes and catch seals as they come up to

breathe (Pagano et al., 2018a; Stirling, 1974). This highly specialized hunting method reduces the need for chasing down prey and reduces activity and energy expended relative to more search-intensive hunting methods (Williams et al., 2014). Nevertheless, in most regions, polar bears exhibit larger home ranges than would be predicted based on their body mass (Ferguson et al., 1999) and move long distances in response to sea ice dynamics, exhibiting some of the greatest movement patterns of any quadrupedal mammal (Amstrup et al., 2000). These long-distance movements are facilitated by an economical cost of transport while walking at slow speeds, supported by their plantigrade foot posture, relative to their elevated cost of transport when moving at high speeds (Pagano et al., 2018b).

Given their reliance on the sea ice over shallow water habitats, the potential threat of climate change to polar bear energetic intake is apparent. As climate change results in progressively earlier sea ice break-up and retreat, polar bears are displaced from their primary foraging habitats earlier, with diminished opportunities for catching seals. Additionally, as the return of sea ice in the autumn becomes progressively later, the period of seal accessibility becomes further reduced. Ice seals represent a substantial energetic pay-off (Table 1), making other prey less profitable to energetic intake. The blubber from an adult ringed seal or adult bearded seal can sustain the energy demands of an adult female polar bear in the spring for approximately 11.7 or 60.1 days, respectively (Pagano et al., 2018a; Fig. 3).

Increased land use as a result of sea ice declines is occurring in some polar bear populations (Atwood et al., 2016; Cherry et al., 2013; Laidre et al., 2020; Rode et al., 2015), as is increased consumption of terrestrial food resources (Gormezano and Rockwell, 2013; Iverson et al., 2014; Prop et al., 2015). However, most terrestrial-based foods available to polar bears have considerably lower energetic densities and lower overall digestible energy (Table 1). For example, a polar bear would need to consume approximately 1.5 caribou (*Rangifer tarandus*), 37 Arctic char (*Salvelinus alpinus*), 74 snow geese (*Chen caerulescens*), 216 snow goose eggs (i.e. 54 nests with four eggs per clutch), or 3 million crowberries (*Empetrum nigrum*) to equal the digestible energy available in the blubber of one adult ringed seal (Best, 1985; Dyck and Kebreab, 2009; Gormezano and Rockwell, 2015; Stirling and McEwan, 1975). This disparity in energetic pay-off indicates that

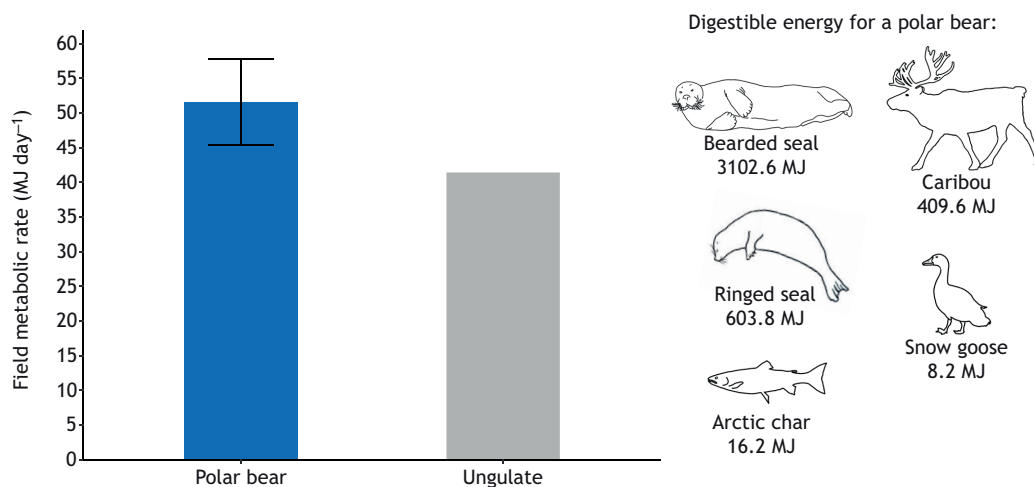


Fig. 3. Field metabolic rate of polar bears and the digestible energy in polar bear prey. Mean \pm s.e.m. daily field metabolic rate from nine adult female polar bears (mean mass=175.3 kg) on the spring sea ice in the Beaufort Sea (Pagano et al., 2018a) compared with the predicted daily field metabolic rate of a similarly sized ungulate (i.e. mass=175.3 kg) based on the equation from Riek et al. (2019). The digestible energy of potential polar bear prey on the sea ice and on land are also shown based on the digestible energy from the prey sources listed in Table 1.

Table 1. Digestible energy content of potential marine and terrestrial prey for polar bears

Species	Mass (kg)	Absolute digestible energy (MJ)	Absolute digestible energy relative to an adult ringed seal (%)	Digestible energy density (MJ kg ⁻¹)	Digestible energy density relative to an adult ringed seal (%)
Bowhead whale	29,832	641,804.9	106,294.28	21.5	164.12
Bearded seal	250	3102.6	513.85	12.4	94.44
Ringed seal	46	603.8	–	13.1	–
Caribou	87.4	409.6	67.84	4.7	35.80
Arctic char	2.1	16.2	0.03	7.7	58.64
Snow goose	2	8.2	1.36	4.1	31.23
Snow goose egg	0.1	0.7	0.12	7	53.31
Crowberries (10,000)	2.8	2.0	0.33	0.7	5.33

Based on the blubber and protein from an adult bowhead whale (Laidre et al., 2018), the blubber from an adult bearded seal (Best, 1985; Ryg et al., 1990; Stirling and McEwan, 1975), the blubber from an adult ringed seal (Best, 1985; Pagano et al., 2018a; Stirling and McEwan, 1975), the fat and protein from an adult caribou (Gerhart et al., 1996; Gormezano and Rockwell, 2015), the energy content of an adult Arctic char (Dyck and Kebreab, 2009), the fat and protein from an adult female lesser snow goose (Ankney and Macinnes, 1978; Gormezano and Rockwell, 2015), the fat and protein from a lesser snow goose egg (Badzinski et al., 2001; Gormezano and Rockwell, 2015), and the energy content of 10,000 crowberries (Dyck and Kebreab, 2009).

few resources exist on land within the polar bears' range that could compensate for declines in seal feeding opportunities (Rode et al., 2015). The limited energetic potential of terrestrial foods in the Arctic is evident in the low density and smaller body size of Arctic brown bears relative to their lower-latitude counterparts (Ferguson and McLoughlin, 2000; Kingsley et al., 1988; Rode et al., 2015).

In contrast, other marine-based prey such as walrus and cetaceans offer a significant energetic pay-off for polar bears (Table 1). The digestible energy from the blubber and protein of an adult bowhead whale (*Balaena mysticetus*) would equal the digestible energy from the blubber of 1063 adult ringed seals (Laidre et al., 2018) (Table 1). In fact, the historic availability of beached marine mammal carcasses along the Arctic coast has been proposed to have instigated the divergence of polar bears from brown bears (Harington, 2008). Contrary to past interglacial periods when whale carcasses may have enabled the persistence of polar bears, present whale abundances in the Arctic are unlikely to support large numbers of polar bears (Laidre et al., 2018). In recent decades in Alaska, polar bears on land in the autumn feed on the carcasses of bowhead whales that are subsistence-harvested by coastal residents (Atwood et al., 2016; Miller et al., 2006, 2015). On Wrangel Island, Russia, polar bears in the autumn have been observed to feed on walrus and other marine mammal carcasses and to occasionally kill walruses hauled out on land (Ovsyanikov, 2005). Hence, in some regions polar bears have access to marine mammal prey during the open water season. In other regions where polar bears come on land in the summer, particularly along the shores of Hudson Bay, most adult polar bears appear to either fast (Knudsen, 1978; Latour, 1981; Lunn and Stirling, 1985; Ramsay and Hobson, 1991) or consume vegetation with limited energetic benefit (Derocher et al., 1993; Knudsen, 1978).

Given potential declines in energetic intake of seal prey, any added locomotor costs will exacerbate the challenge of maintaining daily energetic balance. Thinning of the sea ice has resulted in increases in sea ice drift and correspondingly increased the movements and energy expenditure of polar bears to compensate for the change (Durner et al., 2017). Ice drift alone increased the annual energy expenditure of adult female polar bears in the Beaufort and Chukchi Seas by 1.8–3.6% in recent decades (Durner et al., 2017). Increases in sea ice fragmentation are also likely to increase the energetic costs of polar bear movements and increase polar bear swimming frequencies to reach stable sea ice (Sahanatien and Derocher, 2012). In some areas, polar bears have exhibited increasing rates of long-distance swimming (>50 km) as a result of

declines in Arctic sea ice (Pagano et al., 2012; Pilfold et al., 2017) (Fig. 4). On average, these swims last 3.4 days, ranging from 0.7 to 9.7 days (Pagano et al., 2012; Pilfold et al., 2017). Such long-distance swims are energetically intensive (Blanchet et al., 2020; Durner et al., 2011; Pagano et al., 2020) as polar bears are inefficient swimmers (Griffen, 2018; Pagano et al., 2019). Using internal temperature logger data from two adult female polar bears swimming in the Beaufort Sea, Griffen (2018) estimated the mean cost of swimming to be 2.75 ml O₂ g⁻¹ h⁻¹. This results in an estimated cost of transport while swimming that is 4.3 times the minimum total cost of transport while walking (Fig. 2).

The high energetic cost of swimming suggests that polar bears are poorly adapted for aquatic locomotion relative to other semi-aquatic and marine mammals. This is probably due to the greater drag incurred when swimming at the water surface, as well as the inefficiency of paddling locomotion (Fig. 4A) (Fish, 2000; Pagano et al., 2019). For example, an adult female polar bear swimming for 10 days, as occurred in 2012 in the Beaufort Sea (Fig. 4B), would have an energetic demand of 13.25 MJ kg⁻¹ which is 4.7 times greater than the 10 day mean FMR of adult female polar bears on the spring sea ice (2.87 MJ kg⁻¹; Fig. 4C) (Pagano et al., 2018a). To offset this 10 day energy demand, a 190 kg polar bear would need to consume the blubber from 4.3 adult ringed seals (Best, 1985; Stirling and McEwan, 1975), which is 3.4 more adult ringed seals than would need to be consumed relative to the average FMR of an adult female polar bear on the spring sea ice (Pagano et al., 2018a). This high energetic cost of swimming has been proposed to influence the habitat use decisions of polar bears in the Beaufort Sea (Pagano et al., 2020), potentially dissuading bears from swimming to land despite the energetic benefit available by feeding at bowhead whale carcasses on land in Alaska. Even though polar bears are capable of swimming long distances, instances of bears drowning have been documented (Monnett and Gleason, 2006).

Bears that move to land in the summer in the Beaufort Sea appear to swim more frequently than bears that remain on the sea ice (Pagano et al., 2020). Nevertheless, once on land, bears exhibit reduced energetic costs. The movement-based energy expenditure of polar bears on land in Alaska in September was 43% lower (5.07 MJ kg⁻¹ month⁻¹) than the mean energy expenditure while on the sea ice from May to July (8.88 MJ kg⁻¹ month⁻¹) and 18% lower than the mean energy expenditure while on the sea ice in September (6.21 MJ kg⁻¹ month⁻¹) (Pagano et al., 2020). This reduced energy expenditure is primarily driven by decreased activity rates while on land (Knudsen, 1978; Latour, 1981; Lunn

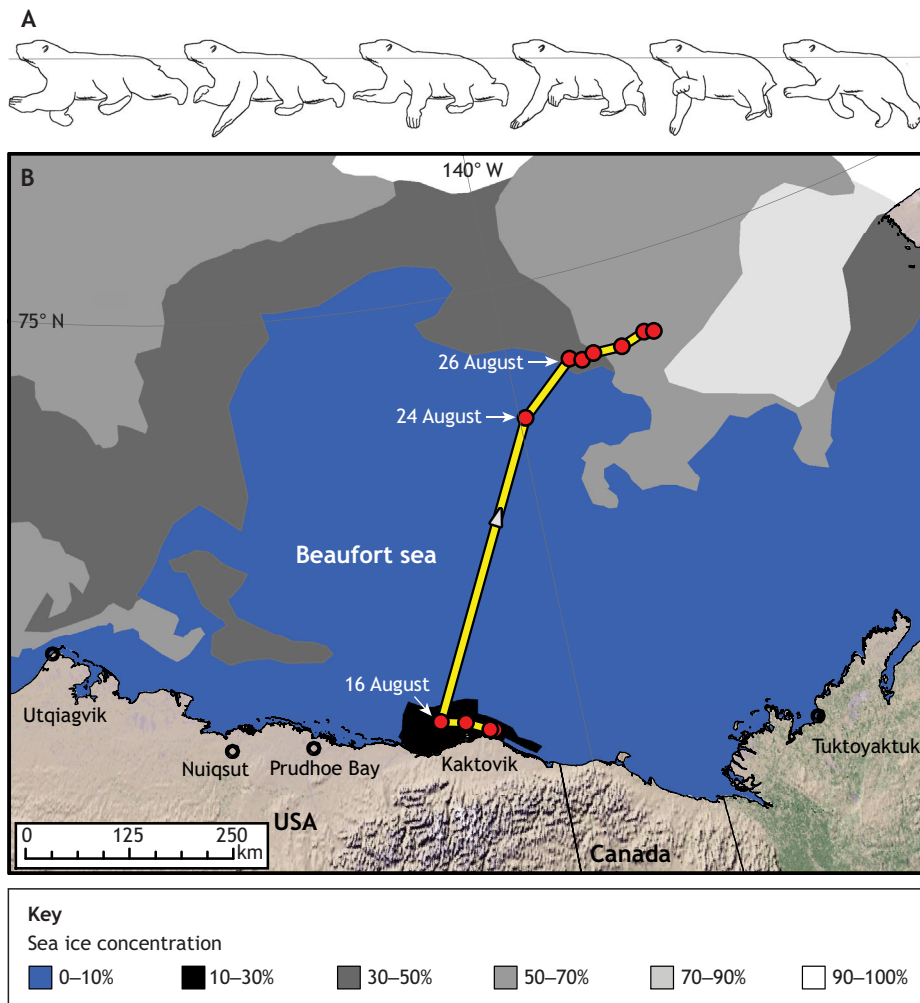
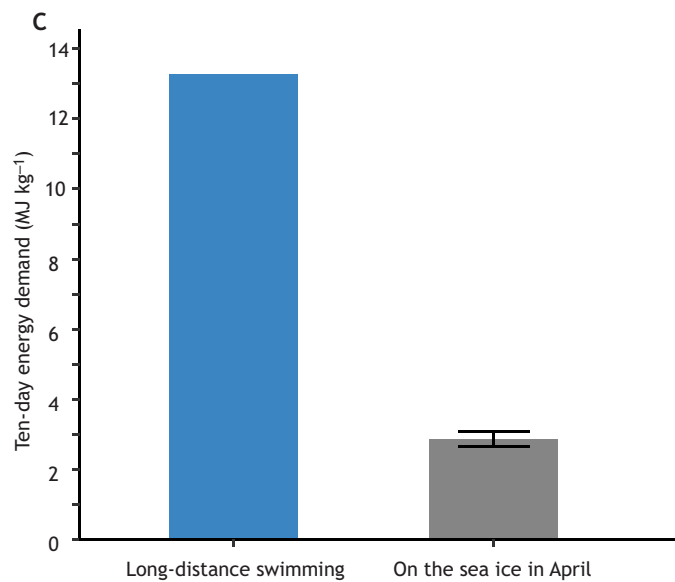


Fig. 4. An example of a long-distance swim in a polar bear and the corresponding energetic cost. (A) Pectoral paddling swimming motion of a subadult female polar bear (redrawn from Pagano et al., 2019). The first image shows the left forelimb at the beginning of the power phase of the stroke cycle. In the last image, the left forelimb is moved forward to return to the power phase. (B) GPS movements of an adult female polar bear in the Beaufort Sea that made a swim of 462 km between 16 and 26 August 2012 (Durner, 2019). GPS location data are shown over National Ice Center chart data from 13 August 2012 (National Ice Center, Suitland, MD, USA; <https://www.natice.noaa.gov/index.html>). Sea ice concentration refers to the percentage of area covered with sea ice. (C) Estimated mass-specific energetic cost of an adult female polar bear making a 10 day swim based on the mean estimate derived from two adult female polar bears (Griffen, 2018) compared with the mean±s.e.m. 10 day field metabolic rate of nine polar bears on the sea ice in April (Pagano et al., 2018a).



and Stirling, 1985; Pagano et al., 2020; Ware et al., 2017), although individuals in a prolonged fast will also experience reduced metabolic rates (Castellini and Rea, 1992; Rosen and Trites, 2002; Westerterp, 1977). Low ratios of urea and creatinine in the blood serum of polar bears on land near Hudson Bay during the

summer had led to the hypothesis that polar bears may be capable of reducing their metabolism and protein catabolism to hibernation-like levels during periods of limited food intake despite remaining active (Nelson, 1987; Nelson et al., 1983; Ramsay et al., 1991). However, subsequent research has since

disproven this hypothesis based on changes in body composition, rates of mass loss, and internal body temperature, all of which indicate that polar bears on land exhibit metabolisms and protein catabolism consistent with a prolonged fast rather than a hibernation-like state (Atkinson et al., 1996; Pilfold et al., 2016; Robbins et al., 2012; Whiteman et al., 2015).

While on land in the summer, on average, adult male polar bears lose 0.96–1.21 kg day⁻¹ (Atkinson et al., 1996; Polischuk et al., 2002) and adult females lose 0.73 kg day⁻¹ (Polischuk et al., 2002). This rate of mass loss is similar to the median rate of mass lost in captive adult male (1.40 kg day⁻¹) and female (1.10 kg day⁻¹) polar bears while fasting (Pilfold et al., 2016). Hence, as the summer ice-free period increases due to climate change (Stern and Laidre, 2016), polar bears on land without access to marine mammal prey are at an increased risk of starvation (Molnár et al., 2010, 2014, 2020; Pilfold et al., 2016) and reproductive failure (Molnár et al., 2011, 2020; Robbins et al., 2012). This is supported by model estimates which indicate that 9–24% of the adult males in western Hudson Bay would die of starvation if the summer fasting period increased to 180 days (Molnár et al., 2014; Pilfold et al., 2016). Similarly, Robbins et al. (2012) estimated that 16% of the adult males in western Hudson Bay would die of starvation if the summer fasting period increased to 162 days. In recent decades the amount of time bears have spent on land in this area has increased by 3 weeks, keeping bears on land for approximately 130 days, with bears arriving on land 2 weeks earlier than they did between 1980 and 1989 (Castro de la Guardia et al., 2017).

Overall, the energetic imbalance driven by reduced access to sea ice has been manifested in declines in body condition, survival and abundance of polar bears in Hudson Bay (Lunn et al., 2016; Obbard et al., 2016, 2018; Regehr et al., 2007; Sciullo et al., 2016; Stirling et al., 1999). Furthermore, pregnant adult females in Hudson Bay experience one of the longest reproductive fasts of any mammal, enduring up to 8 months of fasting (Atkinson and Ramsay, 1995). The reproductive success of these individuals is linked to their ability to enter dens with sufficient fat stores (Atkinson and Ramsay, 1995; Derocher et al., 1992). In view of this, reduced time feeding on the sea ice and increased fasting durations on land could further lead to reproductive failure (Derocher et al., 2004). In Baffin Bay, a similar pattern has been found: bears are now spending 30 more days on land in recent decades relative to the 1990s and exhibiting declines in body condition as well as cub production (Laidre et al., 2020). Given these threats to energetic balance, current models predict a global decline in polar bear abundance of one- to two-thirds by the end of the century (Amstrup et al., 2008; Molnár et al., 2020; Regehr et al., 2016).

Narwhals: the view from below

For air-breathing divers, like the narwhal, changes in ice cover with Arctic warming present a different energetic challenge than observed for polar bears. Narwhals evolved from warm-water ancestors that occupied the Mediterranean Basin, North Atlantic and North Pacific during the Miocene and early Pliocene epochs (Barnes et al., 1985; Bianucci et al., 2019; Lambert and Gigase, 2007). At this time, the tusked cetaceans diverged from beluga whales (*Delphinapterus leucas*) (Kellogg, 1928; Steeman et al., 2009) with gene flow largely ending between the two species approximately 1.25 million years ago (Westbury et al., 2019). Both of these high Arctic cetaceans share many unique physiological and morphological characteristics for polar living that differ from most other cetacean species. For example, both species lack a dorsal fin,

either as an adaptation for swimming under the sea ice (Harington, 2008) or for enhanced maneuverability for foraging along the benthos (Dietz et al., 2007; Werth and Ford, 2012).

Some of the most marked physiological adaptations for Arctic living by narwhals involve enhanced diving capacity that enables foraging to extreme depths exceeding 1500 m. Based on stomach contents and dive behavior, narwhals acquire much of their annual energy intake during the winter (Laidre et al., 2004), by diving for Greenland halibut (*Reinhardtius hippoglossoides*) along the benthos (Finley and Gibb, 1982; Laidre and Heide-Jørgensen, 2005a; Laidre et al., 2003). Laidre and Heide-Jørgensen (2005a) found Greenland halibut in 51% of the stomachs of harvested narwhals in the winter near West Greenland. In addition to halibut, narwhals chase, capture and eat Arctic cod (*Boreogadus saida*), squid (*Gonatus fabricii*), shrimp (*Pandalus* spp.) and capelin (*Mallotus villosus*) (Finley and Gibb, 1982; Laidre and Heide-Jørgensen, 2005a). These benthic prey account for a greater portion of their diet in the summer (Finley and Gibb, 1982; Laidre and Heide-Jørgensen, 2005a; Watt and Ferguson, 2015; Watt et al., 2013), although capelin and squid may also be an important prey source in the winter (Watt and Ferguson, 2015).

Given this deep-diving lifestyle, narwhals have evolved highly specialized locomotor skeletal muscles to support tissues during extended breath-holding (Fig. 5). Myoglobin concentration for the longissimus dorsi of the narwhal is one of the highest measured for any cetacean (7.87±1.72 g myoglobin per 100 g wet muscle), thereby providing a large oxygen store for prolonged diving (Fig. 5A; Williams et al., 2011). In comparison, myoglobin levels for the same muscle in beluga whales are 56% lower (mean=3.44±0.39 g myoglobin per 100 g wet muscle) (Noren and Williams, 2000). Both cetaceans are capable of dives exceeding 18 min (Noren and Williams, 2000), with oxygen stored primarily in the muscles of narwhals and in the blood of beluga whales. For the narwhal, this adaptation for elevated oxygen storage in the muscles is accompanied by an increase in the proportion of slow twitch muscle fibers, making narwhals comparatively slow, endurance swimmers unlike most small-bodied, athletic cetaceans (Fig. 5B; Williams et al., 2011). Hence, like polar bears, narwhals are built for slow-aerobic performance.

Despite their slow speed, the enhanced oxygen stores of narwhals enables the species to dive aerobically to depths and durations far exceeding those of smaller odontocetes (toothed whales). Comparing dolphins with narwhals, we find that the total oxygen stores of a 187 kg bottlenose dolphin (approximately 45 ml O₂ kg⁻¹) are equally divided between the lungs, blood and skeletal muscles (Fig. 5A); this supports aerobic diving for 6–8 min (Noren et al., 2002). In contrast, more than half of the oxygen stores of female narwhals and 44% of the oxygen stores of male narwhals are located in the myoglobin of muscles. For a 1400 kg male narwhal, on a mass-specific basis, the total store of oxygen is 65% greater than that of the dolphin, supporting an aerobic dive limit of 19–21 min depending on travel speeds (Williams et al., 2011).

The availability of large onboard stores of oxygen has enabled narwhals to winter in extreme polar regions where they dive for prey that accounts for the majority of their annual energetic input (Laidre et al., 2004). Able to remain in habitats with less than 3% open water, narwhals are considered the most polar of Arctic cetaceans (Kenyon et al., 2018; Laidre and Heide-Jørgensen, 2005b, 2011), overwintering at high densities around Baffin Bay and Davis Strait (Fig. 1) (Laidre and Heide-Jørgensen, 2011; Westdal et al., 2010). Key to survival under such extreme conditions is the ability to balance the parsimonious use of large oxygen stores with the use of reliable locations of breathing holes in the ice to replenish their

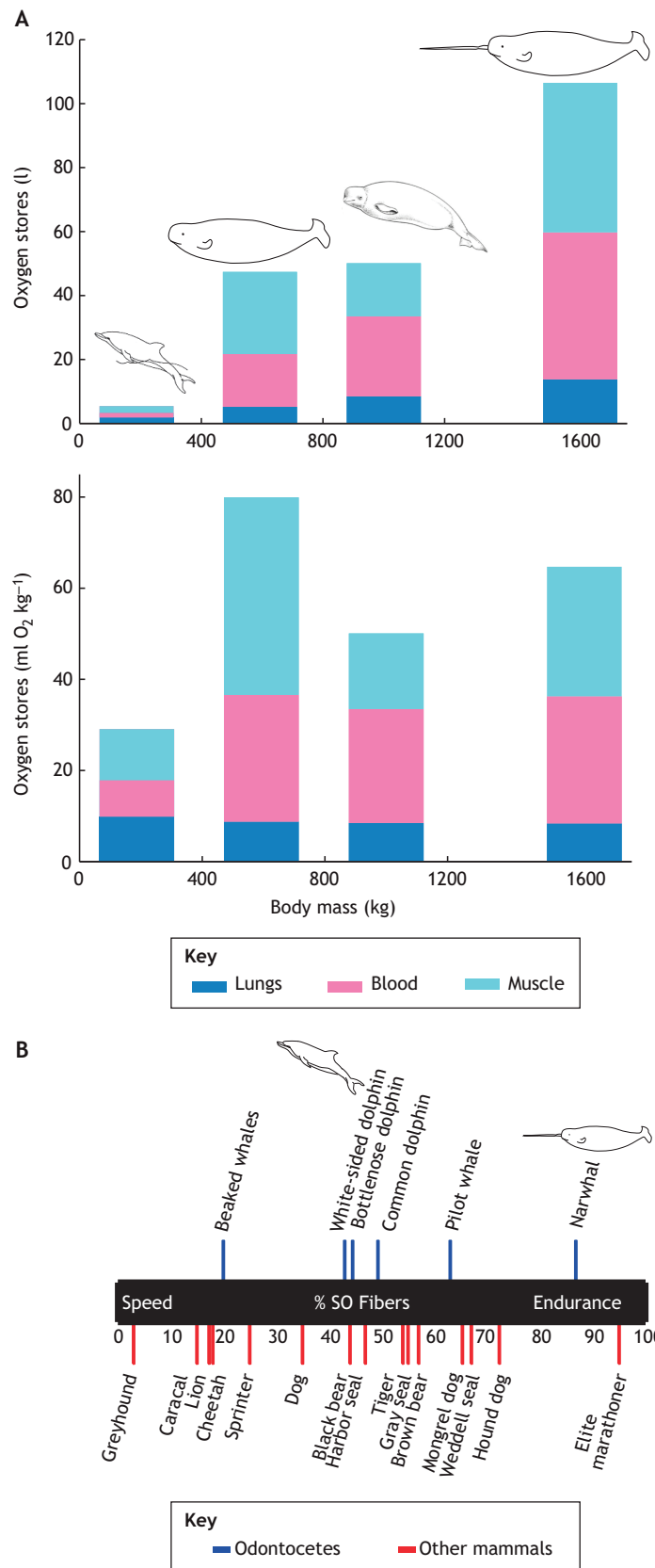


Fig. 5. Adaptations of the skeletal muscles of narwhals for diving and swimming. Body oxygen stores in the muscles and other tissues and proportion of slow-twitch fibers in the primary locomotory muscles are compared for the narwhal and other large mammals. (A) Bar height and color indicate the size of the on-board oxygen stores located in the lungs (dark blue), blood (pink) and skeletal muscle (cyan) for marine mammals varying in body mass; tissue values are compared for the total tissue stores (first) and mass-specific stores (second). Data are compared for bottlenose dolphins (Noren et al., 2002), female narwhals (Williams et al., 2011), beluga whales (Noren and Suydam, 2016) and male narwhals (Williams et al., 2011), as indicated by the icons. (B) Comparison of the percentage of slow oxidative (SO) fibers in the major locomotory muscles of narwhals with those of similar muscles powering the flukes of other odontocetes (upper blue bars) as well as swimming and running skeletal muscles of pinnipeds and terrestrial mammals, respectively (lower red bars). Data in panel B are redrawn from Williams et al. (2011), with new data on felids from Kohn et al. (2011), cetaceans from Sierra et al. (2015), and black bears (*Ursus americanus*) from Tinker et al. (1998).

oxygen stores at the termination of each dive. The presence and stability of breathing holes for diving narwhals has become less predictable as a result of climate-driven changes to the sea ice

(Laidre and Heide-Jørgensen, 2005b). Increased capriciousness of open holes and cracks in the ice has led to entrapment and death for these mammals (Heide-Jørgensen et al., 2002, 2013), often due to

starvation, coupled with human harvest and predation from polar bears (Heide-Jørgensen, 2018; Heide-Jørgensen et al., 2002; Siegstad and Heide-Jørgensen, 1994).

The loss of summer sea ice in the Arctic has resulted in an increased presence of killer whales representing a new apex predator within the Arctic marine ecosystem (Higdon and Ferguson, 2009; Stafford, 2019). Killer whales are one of the few aquatic animals known to attack and kill narwhals (Ferguson et al., 2010; Laidre et al., 2006), thus affecting narwhal behavior and distribution (Breed et al., 2017). In response to the presence of killer whales, narwhals will exhibit slow evasive movements towards areas of dense pack-ice, prolonged submergence times, or will move towards shallow waters (Laidre et al., 2006; Steltner et al., 1984; Williams et al., 2011), which conforms to their physiological and locomotor profile (Williams et al., 2011). Yet these slow movements may be insufficient in escaping killer whales, unlike the high-speed escape behaviors of other cetaceans (Williams et al., 2011). In an increasingly ice-free Arctic, narwhals are physiologically challenged in their ability to escape from perceived threats.

One such threat involves increased ice entrapments of narwhals that have occurred in their summering areas, potentially as a result of delayed migrations driven by later timing of autumn freeze-up with climate change (Laidre et al., 2012) or large-scale human disturbance such as seismic exploration (Heide-Jørgensen et al., 2013). Climate-induced changes in spawning and recruitment rates of the narwhal's preferred prey, along with increased depredation through commercial fishing in ice-free waters (Reeves et al., 2014), have also increased the risk of energetic shortfalls for this Arctic cetacean. Arctic cod also appear to be decreasing in abundance at the southern extent of their range (Provencher et al., 2012) and are likely to experience range-wide declines with continued loss of Arctic sea ice (Tynan and DeMaster, 1997).

The sudden increase in anthropogenic disturbance as humans progressively advance into areas that were historically ice-bound for much of the year is problematic for a naïve species like the narwhal that has lived in relative isolation from industrial activity in the Arctic (Heide-Jørgensen et al., 2002, 2013). Narwhals are sensitive to underwater ship noise and exhibit long-distance displacements particularly when pack-ice cover is absent (Finley et al., 1990; Heide-Jørgensen et al., 2013). Continental shelf areas in the Arctic contain the world's largest remaining petroleum hydrocarbon accumulations (Gautier et al., 2009). As a result, seismic explorations are expected to increase in the primary range of narwhals as sea ice declines facilitate commercial exploration (Reeves et al., 2014). Reeves et al. (2014) estimated that approximately 58% of the range in which narwhals occur overlaps with known petroleum hydrocarbon provinces and 8% overlaps with existing or possible future oil and gas lease areas. Additionally, shipping traffic has been found to have increased significantly in southern Baffin Bay and other regions of the Arctic between 1990 and 2015 as a result of declines in sea ice (Pizzolato et al., 2016).

Behavioral and physiological responses of narwhals to seismic activities and other anthropogenic disturbances reveal the limits of extreme adaptations that were necessary for deep diving in ice-covered areas (Fig. 2). Dives by adult narwhals exposed to seismic noise often forgo many of the cost-efficient behaviors (i.e. prolonged gliding descents, gait changes and low stroke frequencies) that allow prolonged diving. A consequence is a more than tripling of the cost per dive, complete depletion of oxygen stores and entry into anaerobiosis (Williams et al., 2020), and coincident reduction of under-ice movements (Fig. 2B). Ultimately, these elevated costs and physiological reactions during escape are not sustainable and require

prolonged recovery periods for the restoration of oxygen stores (Williams et al., 2017, 2020). These physiological costs, combined with displacement from primary habitats (Heide-Jørgensen et al., 2013), act to increase overall energy expenditure in narwhals while simultaneously reducing foraging efficiency and energetic intake. Thus, as observed for polar bears, these behavioral changes threaten overall energetic balance. Admittedly, this discussion has focused on short-term physiological limits on foraging and escaping in narwhals; additional research will be needed to translate these limits into long-term energetic impacts from anthropogenic disturbance that will occur as the ice continues to retreat. Population models that can account for these likely threats are clearly needed to better predict the effects of forecasted declines in Arctic sea ice on narwhal abundance.

Conclusions

Although species with specialized habitat and prey demands are generally known to be vulnerable to environmental change (Clavel et al., 2011; McKinney and Lockwood, 1999; Munday, 2004; Mykrä and Heino, 2017; Van Valkenburgh, 1999), it is clear that the extreme physiological adjustments required for polar living have compounded the effect of climate change on large mammalian Arctic species. This is due to the critical inter-relationships between physiological specialization and environmental and ecological stability. Polar bears and narwhals are extreme dietary specialists, reliant on acquiring most of their annual dietary intake within seasonally restricted periods. Both species exhibit unique suites of morphological and physiological adaptations that have enabled them to survive in an exceptionally challenging environment. In polar bears, continued warming and declines in Arctic sea ice are likely to challenge their ability to hunt seals in many regions while also increasing their annual movement patterns and swimming frequencies. In the absence of summer sea ice, polar bears will become increasingly reliant on the terrestrial ecosystem, which has limited energetically dense food resources relative to the marine environment. In narwhals, continued warming is likely to further disrupt the timing of migrations, reduce the predictability of winter sea ice conditions in their primary foraging habitats, and expose this naïve species to increased disturbance from industrial activity and predation from killer whales. The physiological specializations of these predators, whether hunting on top or below the sea ice, are ill suited for a rapidly warming Arctic. Declines in these species are likely to foreshadow declines in other ice-dependent marine mammals and some of their principal prey, such as Arctic cod that rely on sea ice-associated zooplankton (Tynan and DeMaster, 1997). In particular, due to their apex trophic position, the decline of polar bears and narwhals is likely to alter trophic dynamics (Estes et al., 2011, 2016) and thus lead to rapid changes in the entire Arctic marine ecosystem.

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Competing interests

The authors declare no competing or financial interests.

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