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Biology and Cultural Importance of the Narwhal

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Abstract

Though narwhal have survived multiple ice ages, including 2.5 Ma and the last interglacial period with warming temperatures, Arctic climate change during the Anthropocene introduces new challenges. Despite their evolutionary connection to Arctic Pleistocene fossils, narwhal archeocete ancestors from the Pliocene (*Bohaskaia monodontoides*) and Miocene (*Denebola* and Odobenocetopsidae) inhabited warm waters. Narwhal Arctic adaptation holds valuable insights into unique traits, including thin skin; extreme diving capacity; and a unique straight, spiraled, and sensory tooth organ system. Inaccessible weather, ice conditions, and darkness limit scientific studies, though Inuit knowledge adds valuable observations of narwhal ecology, biology, and behavior. Existing and future studies in myriad fields of physical, chemical, biological, and genetic science, combined and integrated with remote sensing and imaging technologies, will help elucidate narwhal evolution, biology, and adaptation. When integrated with *Qaujimajatuqangit*, "the Inuit way of knowing," these studies help describe interesting biologic expressions of the narwhal.

CULTURAL IMPORTANCE OF THE NARWHAL

Multiple epistemologies are useful and complementary in investigating the narwhal and the Arctic environment more broadly. Perceptions and descriptions of narwhal and Arctic biology benefit from the integration of Inuit-derived epistemology. Among these approaches to knowledge are *Qaujimajatuqangit*, "the Inuit way of knowing" (IQ), and *Isuma*, "wisdom, to think, or thinking." IQ is an oral tradition passed on through generations by keen observations of Inuit and are contextual, integrating multiple environmental variables, as Inuit are inextricably linked to their land, with knowledge created from decisions that are time dependent for survival. Mythology and dream interpretation may also be included in IQ. Because respect for the environment and gratitude for its offerings are at the core of IQ, knowledge is implemented with reverence for all animals, including the narwhal. Technologies used in narwhal hunting, such as the *qamutik*, Inuit sled, and *qajait* or *qayaq*, kayak, are designed to have minimal impact to transportation in a harsh environment. Kayaks are constructed specifically for individuals, with considerations of size, weight, and arm reach and including design elements tailored to the waters being used. The person and their relationship with the environment define the technology (1). Technology does not attempt to control the environment but is respectful of it (2).

Forced relocation, colonization, and language oppression, defined as "enforcement of language loss by physical, mental, social and spiritual coercion," interrupted the passage of knowledge between generations (3, p. 487). Revitalization of *Qaujimajatuqangit* continues, with postcolonial changes that are associated with a resurgence of Inuit culture and language. IQ is valuable and should be harnessed more for scientific advancement. Successful scientific collaboration depends on an appreciation of IQ; respect for Inuit values; and recognition of past colonial efforts to abolish Inuit culture, language, and wisdom. Though previous researchers have cited specific contributions on narwhal from IQ, more recent studies of narwhal anatomy, physiology, migration, and behavior have broadened the applications of how this knowledge can be used and valued even more in the future. Formal recognition is necessary through collaborative efforts or *Isumaqatigingniq* to continue Inuit–scientist collaborations in all forms of outreach, including scientific conferences and publications.

SCIENTIFIC APPROACHES TO IQ INTEGRATION

Scientists have taken various approaches to including IQ, ranging from none; to a communication citation; to full inclusion of perspective, contribution, and coauthorship. Though researchers are open to IQ's value, few take the initiative to fully appreciate and understand its potential importance. As a result, IQ integration more often is directed at a specific research question and acknowledged with a sentence or as a manuscript citation, rather than approaching the Inuit-derived epistemology with more open questions and full integration of unexpected or unanticipated observations with the recognition of an Inuit contributor as an author, equal, or expert. Suggested guidelines are helpful before, during, and after incorporating IQ (4).

Because Inuit postcolonial perceptions of scientists are understandably founded in mistrust, researchers may not be seen as sensitive to the same level of respect, reverence, and gratitude for the Arctic environment. Valued awareness of IQ, and recognition and acknowledgment of Inuit insights and observations, will help scientific investigators reinforce to their Inuit partners the importance of collaboration. Opportunities for discoveries of Arctic science and, specifically, narwhal biology are expanded greatly through the collaborative efforts of science and IQ (5–7).

IQ ADDS TO CULTURAL AND SCIENTIFIC STUDIES

IQ has benefited narwhal studies in multiple areas, including migration, aggregation, dive patterns, acoustics, integrative and organismal biology, evolution, ecology, conservation, and tusk function. Historically, publications from the 1700s to 1800s focused on the narwhal primarily as a curiosity due to its extraordinary and valuable tusk, which was worth more than 500 times its weight in gold. Tusks were also used as an antidote for potential poisoning of kings and rulers. Narwhal also held fascination for the art world, celebrated in works such as Flemish tapestries, including *The Lady and the Unicorn* at the Cluny Museum in Paris and *The Hunt of the Unicorn* at the Cloisters Museum in New York, which remain some of the most valuable art pieces in the world. Though Inuit contributions are mentioned rarely in the literature, early Norse experiences with the narwhal are surmised to be offered by Inuit hunters. Mentions of the narwhal in twentieth- and twenty-first-century literature switch attention to establishing whale harvest quotas to maintain sustainable populations. A wide array of publications focus on survey counts to establish population size. Studies of migration and aggregation, particularly through electronic tagging, help support overall narwhal population estimates. More recently, the biological literature has included genetic studies addressing biologic questions of diversity, evolution, climate science, COVID-19 (coronavirus disease 2019) transmission, and tusk sensory function.

NARWHAL MIGRATION AND POPULATION, SCIENCE, AND IQ PERSPECTIVES

The scientific literature cites a wide range for the global narwhal population. The current estimate of 177,230 is compiled from a Canadian Baffin Bay population total of 141,909 (8); 14,485 from the Northern Hudson Bay (9); and populations from Greenland (including Eastern Greenland) of 6,444 and from Western Greenland of 14,392 (10). Yet in 2010, the total number of narwhal was estimated to be 80,000, with variation between 58,000 and 86,000 (11). Population modeling currently projects declining future narwhal populations (12) due to environmental changes associated with climate change indicators such as sea ice decline and the associated increase in killer whale populations (13) and reduced prey availability (14).

Inconsistencies in survey counts have been noted in the literature; the Admiralty Inlet population in Canada was estimated at 18,000 in 2010 (15) but was documented at 35,000 just two years later (8). Population estimates have actually increased over time (16–19). However, decreasing narwhal population numbers were reported in Western Greenland (20, 21), along with studies showing signs of a species at risk (22). Results of the study affected Inughuit and Greenlandic hunting quotas, because overhunting was attributed as a potential cause. Uummannaq narwhal hunter Pavia Nielsen addressed the 2006 Inuit Circumpolar Conference in Barrow, Alaska (Utqiagvik), to present Inughuit hunters' observations about increasing narwhal populations that contradicted scientific results. A study several years later (23) concluded that low population numbers were attributable to survey methodology. Despite results from the Marine Mammal Commission report in 2005 showing that declining narwhal numbers translated to reduced hunting quotas for subsistence hunters, in 2012 the North Atlantic Marine Mammal Commission Scientific Committee and the Joint Commission on the Conservation and Management of Narwhal and Beluga confirmed that narwhal populations in Western Greenland were sustainable.

Reports on harvested narwhal from agencies in Canada and Greenland in 2015 indicated that 766 were harvested from Canadian Inuit communities (24), and 408 from communities reporting in Greenland (25). In Canada, a moratorium on narwhal hunting and a fishing limit set in 2015 by Fisheries and Oceans Canada and the Canadian Government were the result of disputed population estimates used in setting narwhal harvest quotas. The findings were challenged with threats of a lawsuit from Nunavut Tunngavik Inc. and the Nunavut Wildlife Management Board representing Inuit hunters in the High Canadian Arctic. Mixed results from scientific surveys were also questioned as a means to set harvest quotas.

Current difficulties with population estimates include (*a*) weather conditions prohibiting continuous surveys; (*b*) use of a fixed point of reference, usually with one plane, when whales may be appearing at multiple locations at the same time; (*c*) ice blocking or covered in the inlets; (*d*) killer whales scattering narwhal groupings; (*e*) population mixing or philopatry (narwhal returning to the same area); and (*f*) added calculations that cannot be estimated accurately from an aerial surface view, because narwhal swim in layers. There is thus a great potential benefit to integrating more IQ in the survey process including population, migration, and aggregation studies. Future research will benefit from the active participation of Inuit hunters, who can supply an additional source of population information that can influence the accuracy of scientific population estimates. Inuit hunters have the advantage of being spread out over the water and land in vast numbers and engaged in radio communication to monitor narwhal sightings. More active participation will enable instances of multiple populations appearing at the same time to be counted accurately, an issue that was presented at the Inuit Circumpolar Conference in 2005. The circumpolar Inuit are a vast wealth of IQ that can, and should, be more integrated into the scientific process (**Figure 1**). In many cases of environmental and animal management, the Inuit offer additional observations that can augment, assist, and direct scientific studies.

IQ–SCIENCE COLLABORATIVE BENEFITS

Knowledge of narwhal biology has benefited greatly from collaboration with Inuit from the High Arctic of Eastern Canada and Western Greenland (5, 26), including studies showing the significance of IQ in understanding Arctic climate and environmental change (27–30), Arctic wildlife management (31–38), and Arctic marine mammals (7, 39–41). More specifically, authors have used IQ to describe the narwhal and its behavior (6, 42–50), including hunters' observations of seasonal aggregations, migration, and population, as well as anatomic variations of narwhal in the Canadian Arctic and off Northwest Greenland (5, 6, 51, 52).

Examples showing the benefit of IQ–science collaborations include recognition studies of individual narwhal in a population through scientific observations of skin markings (53), because scientific observations have limited use in identifying narwhal returning to a specific geographical region. Inuit recognize individual narwhal and can identify geographical regions of individual narwhal by body, tusk morphology, and behavior. IQ is useful in better understanding population admixture. For example, during a large *sassat/sikujjivik/sikujjaujut* (an ice entrapment caused by the formation of fast ice) in Pond Inlet in 2008, when more than 1,000 narwhal were trapped, perished, or harvested, Inuit recognized many of the whales from a group in Clyde River, 410 km south, and which was recognized by scientists (54). Because seismic testing had occurred close to the time of this event, Inuit speculated that these whales were disoriented and traveled to Pond Inlet. Other factors contribute to migration and distribution changes, including climate change and global warming, with more open water over a longer period; more prevalent killer whale predation; and noise pollution from commercial development and shipping, including mining and tourism (55). Increased killer whale populations in ice-free regions over a longer time span cause increased consumption loss (13). Narwhal lose their evolutionary advantage of a dorsal ridge, which allows them to escape below the ice more easily or move to an area separated by a large area of ice, as compared to the orcas' large dorsal fin, which prevents them from such areas. Comparative dive times, with narwhal recorded at 20 min versus only 11 min for killer whales, are another factor in

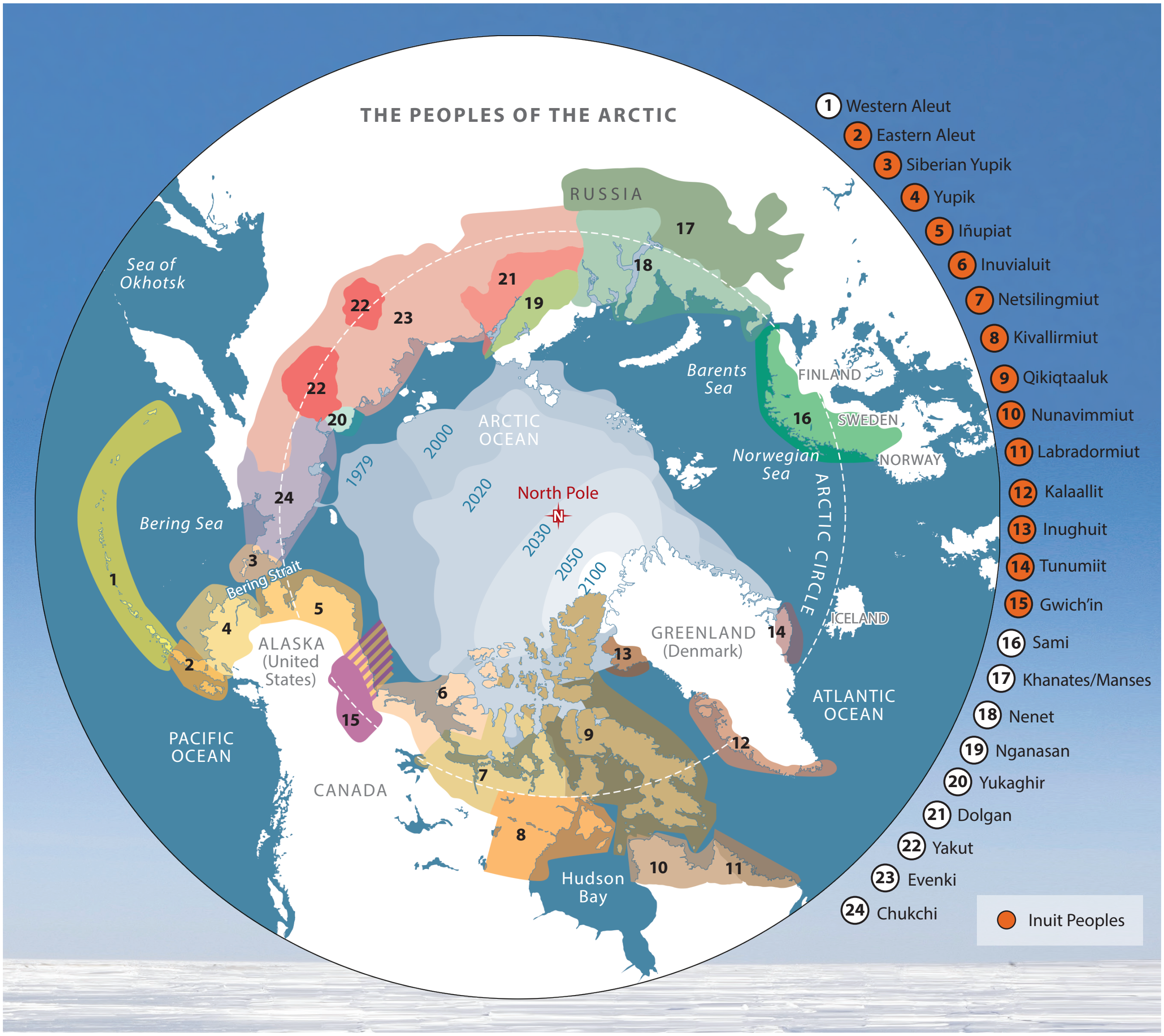

Figure 1

Inuit peoples of the Arctic, based on the book *Arctic: Culture and Climate*, published by Thames & Hudson for the English version and by Paulsen for the French version, in co-publication with the British Museum, as part of the exhibition Polar Mission at the Oceanographic Museum of Monaco.

narwhal survival. Future studies of migration and distribution of narwhal populations can and will be advanced by integrating facial recognition software with IQ to better monitor changing migration patterns affected by climate and other environmental factors (56). Inuit hunters are sensitive to these changes and can identify narwhal migratory patterns and groups to other communities. In the case of climate change, some communities long associated with narwhal hunting have seen their populations decrease or disappear, whereas others have observed new or increasing narwhal populations (57).

CONSERVATION AND ANTHROPOGENIC IMPACT ON ARCTIC ECOSYSTEMS

Additional environmental factors include the rapid detection and accumulation of plastics in the Arctic ecosystem. Approximately 360 million tons of plastics are produced globally each year (58), with 19–23 metric tons mismanaged and 90% transferred from land sources to water (59). The Arctic Ocean is the last stop of the North Atlantic Thermohaline circulation, and the North Pacific also carries plastics that originate from southern latitudes to the Arctic, eventually infiltrating Arctic food webs of aquatic and terrestrial systems (60). Microplastics, broadly defined as <5 mm, are ubiquitous, and their small size makes their source-to-sea impact dramatic in Arctic ecosystems, as they are incorporated easily into multiple trophic levels of the food web. Added risk comes from their ability to easily bind heavy metals and persistent organic pollutants. Studies that monitor and describe the impact of anthropogenic contaminants on narwhal through global transport of ocean currents, increased maritime activity in the Arctic, and mismanaged waste will continue to provide valuable insights to government oversight agencies and conservation scientists about impact, adaptation, and survival in this rapidly changing geographic region (61, 62).

Arctic fauna particularly are facing one of the most pressing conservation issues: increasing and sustained ocean noise pollution generated from human activity (anthrophony), which has come to the attention of the International Maritime Organization, the shipping industry, Inuit organizations, scientists, and conservation experts. Noise propagation sources include ocean commercial and tourism-based vessel engine cavitation, seismic testing, and increased Arctic Ocean vessel traffic, as ice-free passages open pathways for both commercial and tourism-related development. Statistical measurements of Arctic Ocean vessels can be misleading; the addition of 25% more vessels over a time period from 2013 to 2019 is described more accurately by the distance traveled. For example, bulk vessels defined by the Protection for the Arctic Marine Environment's Arctic Ship Traffic Data, established in 2019, showed an increase of 160% in the distance traveled and an overall 75% increase in all vessels (63).

Discoveries of rich mineral deposits and gas and oil reserves have focused more attention on harnessing Arctic resources, and thus have led to more offshore commercial development and additional transport shipping noise. Greenland is one example of rapid growth and environmental concern from both commercial and tourism-based interests. Greenland has an ecosystem with rich geo- and biodiversity. Its terrestrial and ocean environment (64) is home to 9,500 species (65), including narwhal, walrus, musk ox, caribou, Arctic hare, polar bear, and 253 bird species (66–68). With developing economic, social, and political interests, the country faces critical choices that impact the approach to maintaining this rich biodiversity.

Though the International Ecotourism Society defines ecotourism as "responsible travel to natural areas that conserves the environment, sustains the well-being of local people, and involves interpretation and education," Greenland's rich mineral deposits and rapidly developing tourism market have attracted economic investors overlooking these priorities, once again reminding the Inuit of past colonial interests and values. Greenland has ceased to be a formal Danish colony since 1953, though this autonomy still has its memories of past Danish colonization, including Inuit children being taken away from their homes and placed in an orphanage in Nuuk to integrate them into Danish society. Most were never reunited with their families (69). Hunting grounds were taken away, and even the Thule American airbase was built after an existing Inuit community was given just a few days to move (70). Interests in harvesting rich natural resources highlight ongoing economic incentives and alternative motives from cultural imperialism (71). For ecotourism to be seen as a potential economic opportunity, Greenlanders want to see these developments balanced with sensitivity and respect for Inuit, Inughuit, and Greenlandic values.

Otherwise, future collaborations between scientists and Inuit will be clouded by a lack of respect and the very premise set to "conserve the environment" and sustain Inuit values.

Using the UN Sustainable Development Goals as a politically established international guide, Goal 12 calls for "responsible consumption and production." This calls into question methods proposed and used to explore natural resources in the Arctic using seismic testing, for example, because clearly the noise produced impacts biodiversity, one of the necessary factors for Goal 14, to "conserve and sustainably use the oceans, seas and marine resources for sustainable development." What should be done? Both scientifically and IQ-agreed recommendations should be followed to protect the Arctic Ocean environment, so that species like narwhal can better survive, adapt, and thrive in their environment. An additional subtarget goal of reduced noise pollution would clarify the importance of this environmental concern among those already addressed.

Narwhal are recognized as one of the most extraordinary marine mammals on the planet, revered by the Inuit and the subject of fascination throughout history in art and science. Since the writings of Albertus Magnus in the 1500s, the whale, and particularly its unusual and unique tusk, has captivated both aristocracy, as a symbol of imperial recognition integrated in scepters and thrones, and science, as an evolutionary challenge to understand the functional significance of nature's only straight, spiraled, and asymmetric tusk, defying many of the principles of tooth expression and morphology. Studies of the narwhal tooth sensory organ system (5, 72) are thus a useful model for the continued research needed in other sensory organ systems. These include, but are not limited to, taste, smell, sight, sound, and touch. Combined with this approach are needed studies of narwhal physiology and anatomic systems, including the skeletal, muscular, nervous, renal and urinary, respiratory, endocrine, digestive, circulatory and cardiovascular, reproductive, and immune and lymphatic systems. Narwhal anatomy and physiology present extremes and outliers of evolutionary adaptation, and future studies will contribute valuable insights into cetacean, as well as human and mammalian, evolution. For example, elucidating the digestive system may provide links to why whales are carnivores when their evolutionary artiodactyl predecessors, including even-toed ungulates, ruminants, and other species, were herbivores. Why do narwhal possess the most directed high-frequency beam for echolocation? Why does their unique fluke design differ from those of other whales?

CETACEAN EVOLUTIONARY BACKGROUND

The remarkable evolutionary transformation of cetaceans is notable among all mammals. They originated from artiodactyl origins of even-toed ungulates more than 55 Ma, during the Eocene era (73), and underwent morphological adaptations that have provided a successful transition from land to ocean (74). The fossil record is equally astonishing in documenting the changes from the Eocene (56–34 Ma), including spine reorientation, hind limb reduction, posterior nostril movement, development and functional use of underwater hearing, and diverse pathways for feeding and expression of tooth organ systems (75–77). Cetaceans classified in the order Cetartiodactyla include other groups without true hooves and without true ruminants, e.g., camel, pig, and hippopotamus. Studies of molecular genetics show that hippopotamus and whales share this common ancestor (78), even with disparate diet, habitat, physiology, and behavior. Divergent parvorders of Odontoceti (toothed whales) and Mysticeti (baleen whales) have been established from the fossil record and supported by molecular genetic study. Toothed mysticetes had pre-baleen structures in the Oligocene Epoch, 24–34 Ma, and toothless mysticetes were prevalent dating back 30 Ma to the recent past. The evolutionary pathway for modern mysticetes progressed from toothed archeocetes and then to toothed plus baleen whales and extant baleen whales. Molecular genetic findings of inactive genes for ameloblastin and enamelin in extant mysticetes also partially support

Supplemental Material >

this. The narwhal evolutionary pathway proceeds more directly from ancestral toothed whales. Yet, when examining tooth evolution for odontocetes, narwhal have adapted an uncharacteristic tooth form (**Supplemental Figure 1**). Lineages leading to modern cetacean families were present by the Middle Miocene. Balaenopteridae, Ziphiidae, Monodontidae + Phocoenidae, and Delphinidae began to diversify in the Early-to-Middle Miocene; Delphinoidea (Monodontidae + Phocoenidae + Delphinidae) is well-supported, with Monodontidae related more closely to Phocoenidae, as noted in previous analyses (79–87) (**Supplemental Figure 2**). Crown delphinoids originated in the Early Miocene ($\bar{x}$ = 19.78 Ma; 95% CI: 18.81–20.76). Fossil lineages grouped in the Kentriodontidae have been tied to the early diversification of Delphinidae and Delphinoidea, but revision of this group is in process (88–90). Both crown Phocoenidae and crown Monodontidae originated in the Late Miocene. Additional investigation may link such diverse artiodactyl links of evolution as the discovery of Arctic camels (91, 92).

SYSTEMS APPROACH TO CETACEAN AND NARWHAL PHYSIOLOGY

Whales have some of the most interesting biological adaptations in anatomy, physiology, and functional use. The systems approach to whale anatomy is thus useful in addressing future studies of physiology and sensory function. Like those of other cetaceans, the narwhal digestive system is multichambered, similar to other herbivorous mammals including ruminant herbivores, despite the evolutionary dietary adaptation to carnivory. Preliminary examination of their digestive system from the three distinctly different populations concludes differing foraging patterns (93). East Greenland subspecies prey primarily on capelin from the pelagic ocean zone, whales from northern Hudson Bay on shrimp and halibut from the benthic, and narwhal from Baffin Bay on both benthic and pelagic prey. The reproductive system is composed of internalized organs including breasts, teats, and a penis. Whales and narwhal lack an internal bone in the penis to keep it rigid, a trait shared with sea cows and humans. Whales have elastic tissue and do not need blood flow to keep rigid. Of skeletal interest is the fact that whales retain a pelvis despite having no hind limbs, which functions to stabilize the penis, control the birthing canal, and assist in locomotion. Reproduction occurs tail first, equivalent to breach birth, so that the entire whale can emerge before taking a breath. Future studies may provide insight into the genetic shift to create this reverse. Whales do not have lips but rather wrap their tongue around a tube that dispenses milk. The musculoskeletal system includes adaptation of the artiodactyl limbs, such as variable flipper forms, being more paddle shaped on narwhal as opposed to square shaped on right and bowhead whales; falcate on porpoises, dolphins, and rorqual mysticetes; triangular on some river dolphins; elongated on finned pilot whales; and very long on humpback whales. Cetacean flippers can move in multiple planes and have the same humerus, radius and ulna, carpal, and phalange morphology as humans, with an added hyperphalangy for flipper extension (**Supplemental Figure 3**). Their hind limbs undergo a gradual reduction, as seen in the archeocete *Basilosaurus*, with rudimentary hind limb remnants; in contrast, narwhal have no evidence of hind limbs and a remnant pelvis. Cetacean spinal movements are complex and flexible, including circular movements around an axis yaw horizontal plane; pitch vertical plane-like yaw but rotated 90°; and roll over the long axis of body, tipping sideways on the transverse plane. Narwhal fluke design is consistent with that among most whales, with one acute departure: a concave leading edge without sweepback. Males have high efficiency at high speeds, and females have increased lift and thrust at low speeds. The lack of sweepback in males and increased efficiency may be associated with tusk drag, and female fluke design is more efficient during deeper dives, which are more common for them (94). Narwhal skeletal anatomy is best described through a series of anatomical plates (**Figure 2**) showing developmental and morphological adaptation with tusk expression and sexual dimorphism (95). The

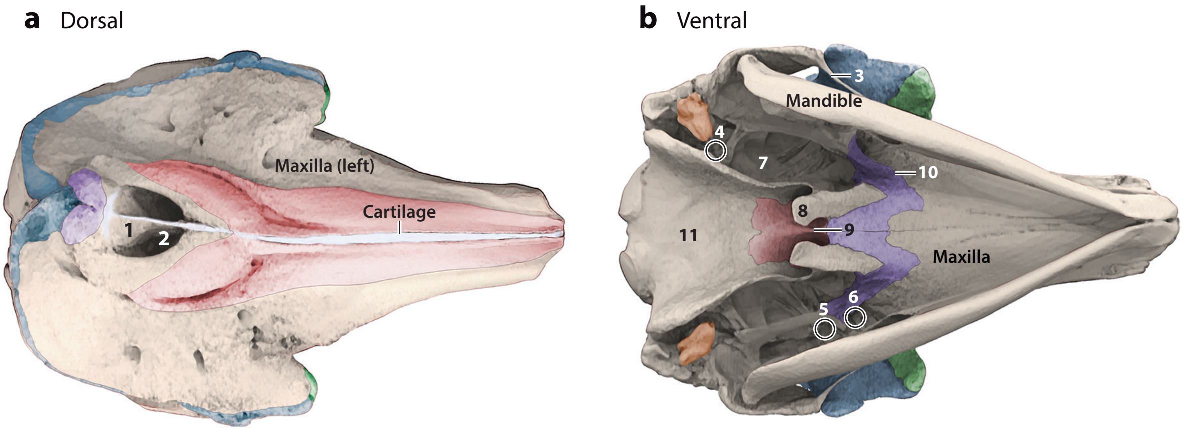

Figure 2

Anatomical plates of adult female skull of *Monodon monoceros* with (*a*) dorsal and (*b*) ventral views based on computerized tomography scans. Illustration credit: Ethan Tyler, from Martin Nweeia narwhal anatomical plate series.

circulatory and cardiovascular system are marked by veins that surround arteries at the periphery for warming; likewise, cooling veins close to arteries release cool temperatures for sperm mobility. Both veins and arteries can dilate or constrict for another layer of thermoregulation. Added thermoregulation is compensated for with thin blubber, a noncompressible insulator for whales, in the tail fluke, flipper, and genital areas to regulate heat, which can interfere with reproduction and sperm mobility. The odontocete respiratory system can be identified by its one blowhole, as compared with two in mysticetes. Blowholes in archeocetes are located more anteriorly, whereas those in more modern cetaceans migrate back dorsally. Blowhole shape is unique to each whale; thus, species can be identified based on blowhole breadth.

EVOLUTIONARY ADAPTATION OF SENSORY ORGANS

Narwhal sensory organs help to elucidate evolutionary adaptation by exploring the extremes and constraints of functional use. Limited vision and greatly expanded auditory function are examples of these extremes associated with cetacean sensory organs. The sense of sound is recognized as one of the most important sensory functions for narwhal. Mysticetes emit low-frequency sounds from the larynx, which are generated via vibrations caused as air rushes past the vocal folds and are associated with communication. Only odontocetes use sound for navigation and prey tracking. Tusked narwhal especially need echolocation to navigate thin leads in the ice. Sound vocalizations are produced and emitted from phonic lips and filtered through fat bodies in the melon. Returning sounds are received by fat in the lower jaw. Sound reception from bone conduction is not likely, as narwhal ears are separated from the skull. Narwhal have the most directional echolocation beam used for orientation and foraging of any cetacean (96). During a routine hydrophone recording in 2007 at Qakkiat Point in Arctic Bay, Nunavut, an investigator positioned in the water approximately 6 feet from the tip of a male narwhal being tagged for research experienced a

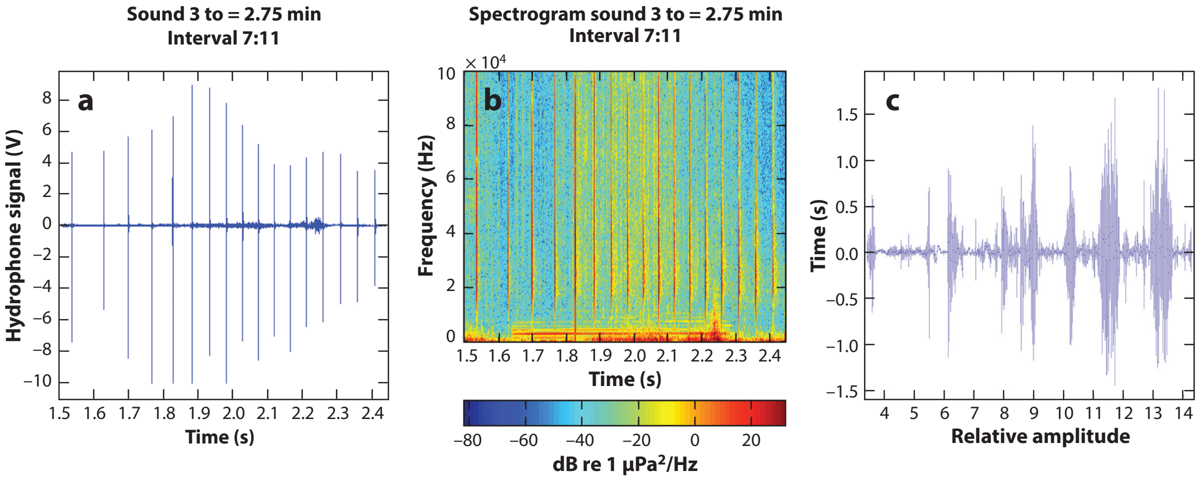

Figure 3

(*a*,*b*) Sound spectrograms show that the distance between clicks changes from 0.09 to 0.045 s, decreasing with time. If multiplied to 1,500 m/s (average sound speed in water) and probably divided by 2(136–68)/2 m = (68–34) m, the result gives the maximum distance at which the whale can check and measure if there is a target around. The signals begin soon after the noise. (*c*) Acoustic analysis to explain instant and abrupt leg-numbness results from a full 15-s period when there is a series of high-amplitude short pulses with deep modulation. The average envelope frequency is approximately 0.8–1 Hz, and the human body can be sensitive to it. This sound file may be an example of a nonlinear high-frequency sound that can explain a momentary numbness in an investigator's leg during acoustic recordings of a captive narwhal. Data acquisition was in 2007 at Kaqqiak Point, Arctic Bay, Canada, using two Brüel and Kjær 8103 hydrophones placed 1 m below the water surface on an anchored pole 2 m long positioned approximately 3 m directly in front of the narwhal's head, in line with the sound-producing nasal sacs. Recording was made using the Fostex FR-2 housed in a self-sustaining floating pelican case. Acoustic analysis of the recording and experience of Martin Nweeia, DMD, by Galina Morizov, PhD, and Andrey Morizov, PhD, Webb Research Inc.

momentary numbness in the right leg. Hydrophone recordings documented the directed beam and its characteristics (**Figure 3**). Hair is another mammalian trait that may be useful as a sensory stimulus between a calf's lips and a mother's genital area to extrude her teats for milking. Hair appearing near the narwhal eye may also be involved with sensory signal transmission regarding currents during resting periods. The most complete sensory organ system studied in the narwhal is the erupted tusk and tooth organ system (72) (**Figure 4**). Tusk function is primarily sensory and modeled after Brännström's hydrodynamic theory of tooth sensitivity. Evidence includes (*a*) high expression of the sensory genes *Dlx2*, *FAM134B*, *NGFR*, and *TFAP2A* in narwhal pulpal tissue when compared to surrounding tissues; (*b*) neuronal markers CGRP and substance P in pulpal tissue, with important physiological and pathological roles (73); (*c*) patent dentinal tubules and channels within cementum tusk covering formed by Sharpey's fibers, allowing direct communication between the tooth sensory system and the external ocean environment; and (*d*) in vivo neurophysiological tusk perception to detect differences in high salt- and freshwater solutions. By examining anatomy, histology, physiology, diet (97), genetics, and in vivo experiments for sensory confirmation, research has generated the most complete understanding of narwhal sensory function. Primary sensory function likely is linked to use in sexual selection and reproductive fitness, and most likely mate choice or intersexual selection (72, 98). Secondary considerations include establishing male hierarchy (72, 99–102). Other theories include male–male rivalry or intersexual selection (101). New studies of position-resolved structural and mechanical properties of narwhal dental tissues by Fourier-transform infrared reflectance microspectroscopy with 100 × 100-μm to 200 × 200-μm spatial resolution illustrate unusual properties of tusk strength and flexibility.

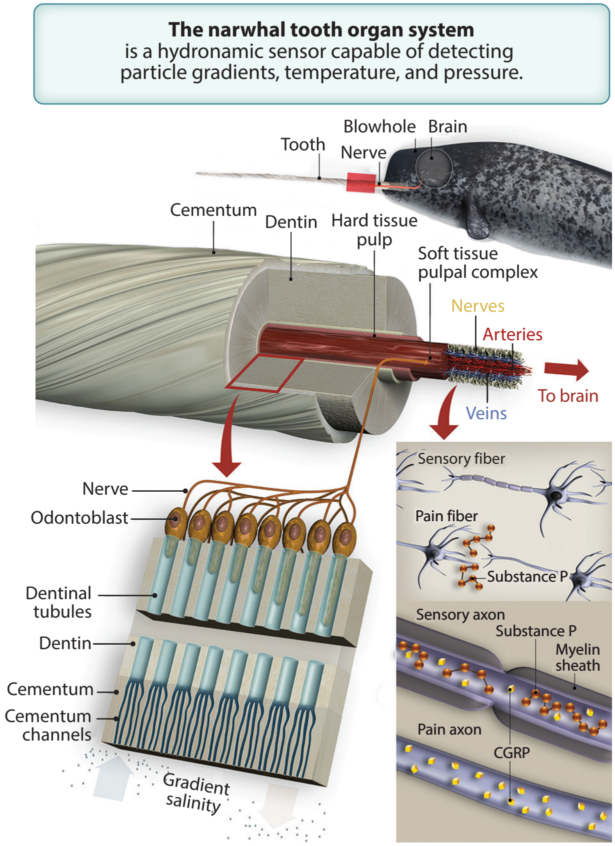

Figure 4

Sensory model of the erupted male narwhal tusk showing, from bottom left, the introduction of water gradients penetrating cementum channels connected to patent dentinal tubules through the full thickness of the dentinal layer, connecting to odontoblastic processes and cells at the base of the tubules and at the periphery of the pulp, which stimulate nerve tissue connecting the base of tusk tissue to the maxillary branch of the fifth cranial nerve to the brain. Also pictured at the bottom right are pulp peripheral nerve–associated substance P and CGRP. Illustration credit: Kevin Hand.

Young's modulus and microhardness were measured using nano indentation with 200×100-μm spatial resolution. Mineral-to-collagen ratios showed decreasing values from tip to base and from the inner pulpal wall to the external surface (103) (**Figure 5**; see also **Supplemental Appendix**). Results from this study help formulate an estimate that narwhal tusk flexibility in a 2.5-m length can bend in all directions by 12°. Additional studies will advance our understanding of unique narwhal evolutionary adaptation and functional tissue characteristics that may have biomimicry applications in modern medicine.

Supplemental Material >

Narwhal, and whales in general, are some of the most intelligent animals on the planet, as measured by comparing brain to body size. Their brains contain more gray and less white matter, which may relate to added information processing; future studies will help examine narwhal intelligence and processing.

Paleontological studies of biologic structures can guide phylogenetic analyses. For example, as early as 1937, investigation of fetal membrane and uterine structures determined the narwhal's artiodactyl origins (97). Synapomorphy, described as shared traits from a common ancestor,

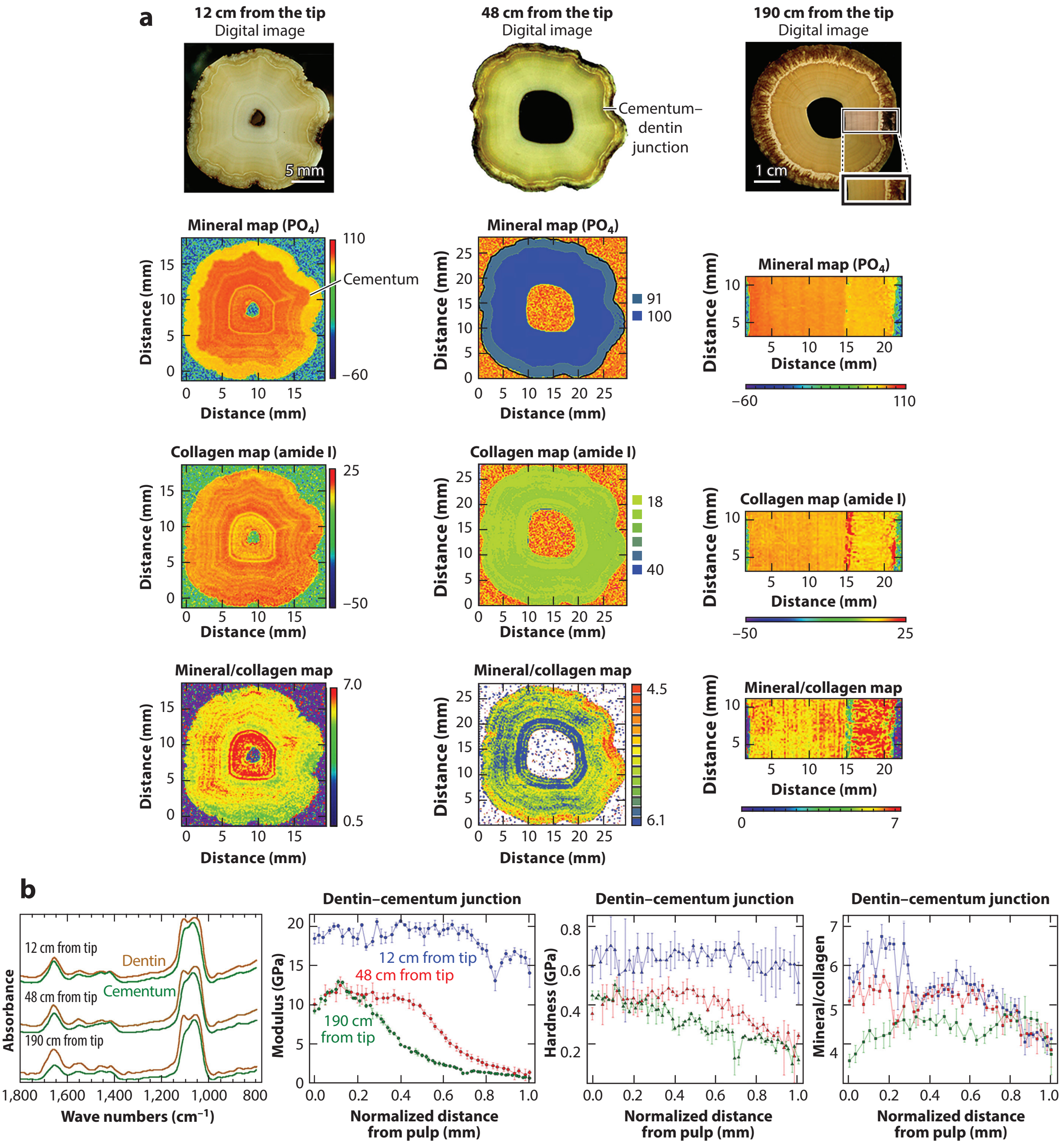

Figure 5

(*a*) Fourier transform infrared reflectance microspectroscopy position-resolved maps showing mineral PO_4, collagen amide 1, and combined mineral/collagen intensities at 12, 48, and 190 cm from the tusk tip. (*b*) Tusk structural properties. Position-resolved properties of modulus, microhardness, and mineral/collagen ratios from the pulp chamber to the outer cementum surface from tusk cross-sections at 12, 48, and 190 cm from the tusk tip. Illustration credit: N. Eidelman, F.C. Eichmiller, Y. Zhang, Y.G. Jung, A.A. Giuseppetti, and M.T. Nweeia.

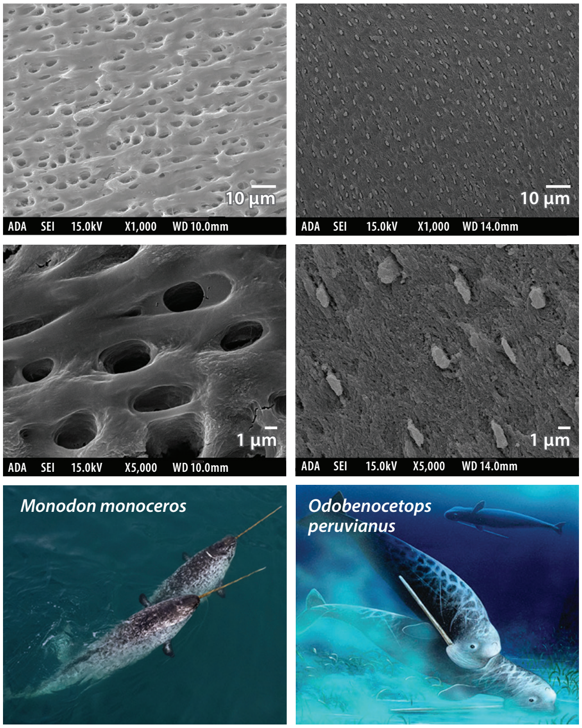

Figure 6

Scanning electron micrographs at 1,000× and 5,000× showing (*top row*) adult male *Monodon monoceros* tusk dentinal tubules and (*bottom row*) homologous tusk dentinal tubules of *Odobenocetops peruvianus*. Electron micrographs credit: Anthony Giuseppetti; narwhal photo credit: Nansen Webber; *Odobenocetops* illustration credit: Mary Parrish.

represents another method for understanding phylogeny. Evolutionary adaptation of mammals from different environments is illustrated by comparing the paraxonic foot of cetaceans, hippopotamus, and humans, all of which share the same axis between the third and fourth digits (104). Homologous structures also suggest synapomorphy. In the case of narwhal tusk microstructure, the unique patent dentinal tubules from the ocean environment to the dental pulp is present in *Odobenocetops* tusks (**Figure 6**). Integrating biological studies of organ systems with genetic analysis through studies of narwhal genomics, phenomics, transmission genetics, and phylogenetics will provide a better understanding of narwhal biology.

GENOMIC COMPARISONS IN CETACEAN PHYLOGENETIC STUDIES

Phylogenetic comparisons benefit from increased variable base pairs, so highly resolved narwhal and beluga genomes can improve determination of their inferred relationship and shared Monodontidae family. By analyzing whole genomes with an estimated 20,000 genes, sampling errors are less likely to be included in results. Among the proposed comparative studies of beluga and narwhal should be genome content, including gene order along chromosome linear length; gene orientation, or the direction in which the coding sequence is read compared with other genes; and the mere presence or absence of genes in the genome, as has been initiated in the studies by the Zoonomia Consortium at the Broad Institute (105). Elucidation of an ancestral genome (106) provides insight to specific markers for mammalian diversity. Examination of the sequence not containing genes or encoding proteins will also elucidate the evolutionary path, describing whether genes are evolving together and how changes can affect species biology. Portions of the genome that have no genes but contain regulatory elements and noncoding RNAs can help determine critical points of evolutionary adaptation.

Narwhal biology is strongly linked to the Arctic climate. Narwhal survived ice ages during the last 2.5 million years, including the cooling cycles of the little ice age during the Holocene, spanning the last 11,700 years. Narwhal sediment remains in the North Atlantic from this era indicate a similar distribution to today's populations. Molecular signals from narwhal and beluga show a common ancestor 6.3 million years before the onset of major cooling cycles. With global warming, narwhal should be able to adapt as they did during the last interglacial period associated with minimal ice and warming temperatures 125,000 years ago, though survival during the Anthropocene has the added element of human interaction.

LINKING GENETICS WITH NARWHAL DISEASE RISK

Genetic studies have predicted and will continue to predict viral infection rates for narwhal and other Arctic cetacean species. Collaborative efforts to engage Inuit hunters in monitoring unusual symptoms in cetaceans can assist early detection and diagnosis of water or airborne diseases. For example, studies of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) transmission to animals demonstrated high susceptibility of and potential transmission to cetaceans, as they share with humans most of the angiotensin-converting enzyme 2 (ACE2) spike protein binding sites for the virus. High Arctic communities were affected by SARS-CoV-2 transmission; thus, future viral transmissions for high-latitude communities and ecosystems remain concerning. Arctic mammals are integral components of high-latitude ecosystems and may become important in a chain of transmission with other Arctic mammals. Toothed whales appear uniquely vulnerable to developing illness from SARS-CoV-2. These species have a high binding propensity for the virus due to a very similar amino acid sequence of ACE2 (the receptor site for SARS-CoV-2 binding) compared to humans (107). Of the 25 amino acid residues associated with the viral spike protein binding site on ACE2 in humans, cetaceans share 22. At the same time, toothed whales have demonstrated a limited immune resistance to infection from viruses with functional loss of the GTPase genes myxovirus1 (MX1) and MX2, thus potentially manifesting severe disease outcomes (108). A Bronx Zoo tiger exhibited COVID-19 symptoms and disease (109), yet this species' predicted ACE2 binding capacity was only medium relative to humans (110). There is an urgent need to understand disease reservoirs and the possibility of infection in nonhuman species. Gammacoronavirus has already been found in a beluga whale (111) and bottlenose dolphins (112), and a suspected alphacoronavirus was found in harbor seals (113). All are associated with respiratory diseases, though the cellular receptor these viruses use to mediate cellular entry is unknown. Prior epidemics of phocine distemper virus in harbor seals in 1988 and 2002 accounted for more than 50,000 deaths, reminding us of viral impact in the ocean environment (114).

Beyond its role in mediating cellular entry of SARS-CoV-2, ACE2 is of special significance to the cardiovascular biology of toothed whales. ACE2 plays a role in controlling blood pressure by converting a vasodilatory peptide (AngI) into the vasodilatory AngII. Vasoregulatory peptides such as angiotensins act on smooth muscle in the vasculature to change artery diameter and regulate blood flow. The marine mammal dive response permits these animals to dive for extended durations and to extreme depths. A key element of the dive response is blood pressure regulation; heart rate falls during submergence and must be balanced by profound vasoconstriction in the peripheral vasculature to prevent a dangerous drop in central arterial pressure. Evidence for positive selection has already been noted in cetacean ACE2, and this has been linked to adaptation of the renin–angiotensin system, which is important for blood pressure control as well as salt balance in the marine environment. Genetic capabilities have generated a new pathway for understanding and predicting the changing ocean environment, anthropogenic variables, and their potential threat to narwhal and other Arctic species.

ADVANCING THE PROCESS OF DATA COLLECTION

The methodology and process of data acquisition have changed dramatically over the past 50 years, from traditional specimen collection to remote imaging and sensing. Remote technologies include those that are brought to observational sites and continue to gather data after one leaves the site, as well as fixed technologies like genetic sequencers or computerized tomography (CT) scanners that are now mobile and can be brought remotely to a sample site. Advances in these remote technologies have been transformational in data collection and onsite analysis. Many of the technologies used to gain observation and knowledge in the Arctic benefit most by being there over prolonged periods. Due to expense, remoteness, weather and ice conditions, darkness, and logistics, scientists can typically remain in base camps, boats, or other field sites for only limited time periods. Thus, remote technologies that can continue to collect data sets over more prolonged periods hold tremendous benefit. Examples of remote imaging and sensing include, but are not limited to, cameras (115), motion detection video, light scanners (116) (**Supplemental Figure 4**), advanced drones with longer programmable flight times (117, 118), mobile position emission tomography (PET)/CT scanners, augmented reality, and artificial intelligence. Whale tags and remote-sensing devices placed on whales have been used extensively and successfully in the Arctic and on narwhal to measure dive depths (119, 120); patterns, migration and distribution, and orientation (90); acceleration and sex-specific movement (121); seasonal diet selection and foraging behavior, seasonal habitat identification, salinity, temperature, sound recordings, navigation, and communication (122–124); and heart rate (125).

Supplemental Material >

Hospital-grade equipment, which typically requires returning samples to institutions for analysis, has also been housed in waterproof casings for onsite analysis of brain activity and heart rate on narwhal for the first time in the Arctic (72). These new technologies, and availability of traditionally large instrumentation in a mobile format for remote field use, provide scientists access, ease of analysis, and remote-sensing data collection abilities.

Inuit observers and the use of IQ are scientists' most valuable remote-sensing resource. As astute observers of the natural and physical world, Inuit observers are uniquely connected to their environment by survival (126). Because they hunt over a longer seasonal period, as a result of increasing ice-free areas and climate change, and live and observe extensively on the water, they are the most reliable remote-sensing collectors available to scientists and can provide invaluable information on narwhal behavior and habitat. For example, skin molting had not been reported as a potential reason for narwhal migration into freshwater inlets until Inuit hunters in Greenland witnessed the thin, gauze-like skin molting off summering narwhal off Qaannaaq, Greenland (127). Hunters also observe the extremes of survival; thus, dive duration times reported in the scientific literature of 25 min (120) are almost doubled at 45 min by Inuit observations during hunting.

CONCLUSION

Though many research efforts have focused on the narwhal, and more broadly on Arctic biology, management of Inuit hunting practices and quotas, and ecosystem studies, ongoing studies that combine IQ, social, political, conservation, remote-sensing, and scientific perspectives are needed. The "pristine" Arctic has already succumbed to environmental disruption during the

Anthropocene through pollutants and mismanaged waste, increased noise from seismic testing and natural resource harvesting, commercial and tourism-based boat traffic, longer shipping routes in an increasingly ice-free Arctic, microplastics, and climate change. Narwhal populations are currently stable and sustainable, but increasing environmental pressures and stressors are influencing and potentially disrupting their evolutionary path. The increased and rapid rate of these changes outweighs any political capacity to address them, and so we must engage the Inuit in active monitoring and observation that may prove useful to balance the environmental variables for survival so that narwhal can maintain their peaceful place in the Arctic ecosystem. Though scientists have new technologies to address remote sensing and imaging, as well as powerful analytic instruments, tools, and technologies, perhaps their most valuable remote-imaging and sensing instruments are the Inuit themselves, as careful, consistent, and accurate observers of nature. Large systems-based teams of researchers benefit from valuable new research tools combined with hundreds of years of observational information collected by Inuit and stored as IQ and Isuma.

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