The largest of August Krogh animals: Physiology and biomechanics of the blue whale revisited

J.A. Goldbogen a,*, P.T. Madsen b

a Hopkins Marine Station, Department of Biology, Stanford University, USA
b Zoophysiology, Department of Biology, Aarhus University, Denmark

ABSTRACT

The blue whale is the largest animal ever. This gigantism probably evolved to exploit seasonal krill blooms, where massive feasts allow for accumulation of large blubber reserves that can fuel their low mass specific metabolism during prolonged periods of fasting. Until recently, the physiology and biomechanics of blue whales could only be inferred from anatomical inspections, but the recent development of biologging tags now provide unique insights into how these ocean giants function and interact with their environment. Their mandibles, the largest bones ever to evolve, along with a highly expandable buccal cavity, enable an extreme and dynamic bulk feeding behavior. During a lunge feeding event, blue whales accelerate up to 5 m/s to engulf a volume prey laden water that is commensurate with the whale’s gigantic body size. Perhaps due to the costs of such extreme foraging, their dive times of 10-15 min are much shorter than scaling would predict for their size. Like other diving animals, blue whales display a dive response with heart rates down to 4 BPM to prolong dive times and perhaps mitigate decompression sickness. Blue whales make the lowest and most energetic calls of any mammal with ocean traversing potential under natural ambient noise conditions. However, communication space may be severely reduced due to pervasive shipping noise. We hope that an increasing ability to study the physiology and behavior of blue whales and other marine megafauna will enable informed decisions and ensure our permanent co-existence in the face of increasing human encroachment into marine habitats.

1. Introduction

In 1934, Nobel Laureate August Krogh, published an interesting and speculative paper entitled ‘Physiology of the Blue Whale’, in Nature (Krogh 1934). The paper appears to be motivated by the first edition of the Discovery Reports, reporting on the morphology of blue whales (Balaenoptera musculus) at the height of shore-based whaling (Mackintosh and Wheeler, 1929). The report included some of the first comprehensive data sets of body size in blue whales that are extraordinary in the context of comparative physiology and evolution, prompting Krogh (1934) to offer a novel treatise of the functional and physiological implications of such gigantism. The studies of blue whale biomechanics and physiology could well have ended with Krogh’s cohort of scientists, as blue whales were hunted so intensely that they were at the brink of extinction in the 1960’s. However, the whaling moratorium has allowed for a slow recovery of some populations, paving the way for the recent use of multisensor biologging tags (Fig. 1) to study the field physiology of blue whales to understand their biology and aid their conservation.

2. Engulfment of 100 tons of prey laden water

Blue whales are the largest animals ever to have existed on Earth. Body lengths can reach nearly 30 m (Figs. 1 and 2A) and body mass may exceed 100 t (Lockyer, 1976). Accordingly, the remains of these animals include the largest bones of any vertebrate, of both the present and the past, in the form of mandibles that are up to 6.8 m in curvilinear length (Fig. 2B, Pyenson et al. 2012). The mandibles form a key structural component of the feeding apparatus of rorqual whales (Balaenoptera), blue whales and their close relatives, such as fin whales (Balaenoptera physalus) and humpback whales (Megaptera novaeangliae). These whales rely on an extreme lunge feeding strategy where large volumes of prey laden water are intermittently engulfed and filtered (Goldbogen et al. 2017, Fig. 3). As noted by Mackintosh and Wheeler (1929), blue whales exhibit positive allometry of their engulfment apparatus whereby larger whales have relatively larger skulls and ventral grooves. Therefore, larger whales have relatively larger engulfment capacities that provides enhanced foraging capacity at larger scales (Kahane-Rapport et al. 2020). The calculated engulfment capacity of blue whales is larger than their own body, so blue whales temporarily double in size and moving mass during each lunge feeding event (Fig. 2).

* Corresponding author at: Hopkins Marine Station, Department of Biology, Stanford University, USA. E-mail address: jergold@stanford.edu (J.A. Goldbogen).

https://doi.org/10.1016/j.cbpa.2020.110894
Received 19 December 2020; Received in revised form 29 December 2020; Accepted 29 December 2020
Available online 5 January 2021
1095-6433/© 2020 Published by Elsevier Inc.
3. Short dive times despite large body mass

The high capacity foraging strategy in blue whales is specialized for a single prey type, krill (Euphausiacea), resulting in one of the highest predator:prey size ratios among marine vertebrates. The paradox of the extreme size difference between predator and prey was noted by Krogh (1934): how does one of the largest animals grow, survive and reproduce by feeding on such small prey? Despite the high energy density of krill (Clarke 1980), blue whales must find the densest aggregations of krill to forage successfully. Densely packed patches of krill tend to occur at
200–300 m depth (Friedlaender et al. 2019), and diving is therefore fundamental for foraging. Because larger animals have greater oxygen stores (assuming isometric scaling) and use oxygen at a lower mass-specific rate (assuming negative allometry of metabolic rate), they should be able to dive longer and enhance foraging efficiency (Berenbrink 2021; Williams and Davis 2020; Berenbrink 2020). Based on predicted oxygen stores and rates of oxygen consumption from Kleiber’s contemporary scaling analysis (Kleiber, 1932), Krogh (1934) calculated dive durations of 50 min for blue whales. Recently tagging of blue whales reveal that most dives are much shorter than Krogh’s prediction, with typical foraging dives being shorter than 15 min (Fig. 3) (Kahane-Rapport et al. 2020), suggesting short aerobic dive limits (Kooymen et al., 2020). It has been proposed that the high energetic cost of lunge feeding rapidly depletes oxygen stores during a breath-hold, thereby limiting foraging dive duration (Acevedo-Guitierez et al. 2002). Secondly, it may be that the evolutionary drivers for an extreme diving physiology that supports prolonged breath-holds of 40–60 min or longer (Tyack et al., 2006) only apply to truly deep-diving whales, such as beaked whales and sperm whales that forage at 500–2000 m depth (Madsen and Goldbogen 2018).

### 4. Extreme functional anatomy enable extreme bulk feeding

As Krogh (Krogh 1934) surmised, the biomechanics of swimming play a major role in the energetics of blue whales. Because swimming and feeding are integrated in blue whales, the swimming behavior associated with feeding underlie both the costs and benefits of lunge filter feeding in rorquals. The foraging behavior of blue whales is unsteady and non-linear (Friedlaender et al. 2017; Goldbogen et al. 2013), with foraging blue whales sometimes adopting complex 3D paths, including 360-degree barrel rolls (Fig. 3). During a lunge (Fig. 3), whales accelerate to high speed (up to 5 m/s) and open their large mouths to flow, thereby incurring high drag (Potvin et al. 2020). The dynamic pressure generated by an open mouth at high speed forces inversion of the tongue through an intermuscular space called the cavum ventral (Lambertsen 1983). The expansion of the ventrally located feeding pouch, the oropharyngeal cavity, is facilitated by specialized blubber that is reversible extendible up to several times its resting length. The inverted tongue becomes the lining of the expanded oropharyngeal cavity that contains the engulfed prey-laden water, and both the muscle-lined blubber and the tongue exhibit microstructural adaptations that allow muscle and nerve to extend without damage during feeding (Lillie et al. 2017; Shadwick et al. 2013; Vogl et al. 2015). The muscle within the ventral groove blubber likely plays a role in controlling the expansion of the oropharyngeal cavity, and by action-reaction the whale accelerates the water that is being engulfed.

As momentum is transferred to the engulfed water, blue whales slow to speeds of around 1 m/s or lower, thus each subsequent lunge requires that the whale accelerate again (Fig. 3). After the jaws close, a window of baleen is exposed between the upper and lower jaws through which the engulfed water must be purged during filtration. The medial side of the baleen rack contains a fibrous mat of fringes that act as the filter keeping prey inside the mouth as engulfed water is forced out of the mouth over a period of 30–100 s. Although it is not fully understood how baleen works as a filter in vivo (Werth 2013), this high-throughput filter is fundamental to foraging success and the ability of blue whales to feed en masse on krill. If krill density is high, blue whales can achieve high foraging efficiencies (energy consumption relative to expenditure). Thus, despite the high cost of lunge feeding, blue whales exhibit the morphological adaptations necessary to exploit a seasonally abundant resource at high rates. Such foraging success can not only support extreme body size and rapid growth of their calves as noted by Krogh, but it also allows blue whales to develop fat that may be needed to migrate to breeding grounds at lower latitudes and invest in reproduction during periods of prolonged fasting. Like most non-feeding travel in large marine vertebrates, migration is enabled by high energy reserves with respect to daily field metabolic rates, and powered by very slow swimming strokes (0.2 Hz) to attain steady speeds (~2 m/s) at a low cost of transport (Gough et al. 2019).
5. Heart rates down to 2 BPM

Krogh (Krogh 1934) also raised the pertinent question of how blue whales and other diving mammals can avoid decompression sickness. Breath-hold divers have the advantage over scuba divers in that they only dive on one lung full of air that eventually, if diving deep enough, will be compressed to provide functional lung collapse. However, breath-hold divers can suffer from decompression sickness if spending sufficient time at depths where a combination of high partial pressures of nitrogen and open alveoli enable high rates of nitrogen invasion to the blood and tissues (Paulev 1965). Indeed, blue whales spend significant time between 20 and several hundred meters where nitrogen invasion rates potentially are high. However, Krogh’s paper was published 6 years before Scholander’s seminal discovery of the “dive response” where peripheral vasoconstriction and bradycardia limits perfusion of most organs except for the brain and heart (Scholander 1940). The dive response also reduces perfusion of pressurized lungs, and the associated reduction in nitrogen uptake may alleviate decompression sickness (“the bends”). Researchers recently managed to use biologging technology to measure the heart rates of a feeding blue whale in the wild, showing that blue whales also have a dive response during submergence and reach bradycardia down to 4–8 bpm and as low as 2 bpm (Goldbogen et al. 2019). The heart rate increases during execution of feeding lunges and decreases during the filtration of engulfed water. Ascent back to the sea surface is associated with tachycardia, and subsequently heart rate maxima at the sea surface likely facilitate gas exchange during the brief ventilation bouts (Fig. 3). Despite the dive response, it still remains a conundrum how breath-hold diving marine mammals, such as blue whales, making repetitive dives within functional lung collapse depth, seemingly avoid problems of decompression sickness. Anti-bubble nucleation agents, re-enforced upper airways and functional lung shunts are viable working hypotheses, but experimentally difficult to test.

6. Can loud infrasonic calls overcome increasing vessel noise?

The physiological extremes of diving and feeding underlie an extreme life history in blue whales that is characterized by extensive migrations bookmarking concentrated foraging seasons and breeding seasons far from food resources. The transitions between, and coordination of individuals within, migration and breeding foraging seasons may be mediated by long-distance sound communication (Oestreich et al. 2020). Therefore, the physiology and functional ecology of communication is an important yet still understood feature of blue whale biology. Unlike other large baleen whales, blue whales and fin whales do not have fixed breeding grounds where elaborate vocal displays serve as song apparently to mediate social interactions and play a role in mating. Rather, completely unknown to Krogh and the rest of the world in 1934, blue whales emit the most energetic vocalizations (at source levels of more than 180 dB re 1 \( \mu \)Pa (rms)) at very low frequencies between 12 and 100 Hz (Fig. 4). Such omni-directional and partly infrasonic vocalizations have the potential to be heard by conspecifics over many hundreds of kms under natural noise conditions in deep water, perhaps explaining how blue whales have evolved to solve the problem of finding each other in large ocean basins (Payne and Webb 1971). We still do not understand how these sounds are produced and heard by blue whales, and it remains a mystery why they appear to have shifted the pitch of their calls down over the last 30 years (McDonald et al. 2009). However, it is clear that the dramatic increase in shipping over the last century has increased ambient noise by several orders of magnitude in many regions. This increased shipping noise overlaps in frequency with blue whale vocalizations, reducing the range over which whales can hear each other’s calls (Fig. 4). Because blue whales depend on vocal communication for both mating and socializing, this may negatively impact populations that are still recovering from whaling. We do not know if, or how, such increasing anthropogenic noise affects blue whale populations. This important for the conservation of blue whales, because the small population is still recovering from whaling, and both mating and socializing may depend critically on vocal communication. So, while the moratorium on whaling has highlighted blue whales as a prime example of how conservation efforts do make a difference to wild populations, another and much more complex problem than ending whaling is of how we can co-exist with these large animals as a growing human encroachment in all of the world’s oceans increase fishing, risks of vessel collisions, toxic loads on food chains and noise pollution.

7. The importance of marine megafauna field physiology

The perception of blue whales, the largest animals to have ever lived on Earth, has changed over the past century from being the prime source for the oil industry to a current appreciation of their roles as large charismatic predators facilitating top down energy cascades and nutrient recycling in marine ecosystems. Krogh (Krogh 1934) started the scientific fascination of the physiological repercussions of gigantism, but today such a mechanistic appreciation of marine megafauna is also highly relevant for understanding their ecological role in marine ecosystems, their sensitivity to human stressors and their resilience to global change to provide an informed basis for conservation measures and mitigation of human activity at sea. The conservation physiology of blue whales and other large animals at sea is severely hampered by their conservation status and the insurmountable impracticalities of studying them in captivity, but the recent advents and use of field physiological
techniques in the forms of drones and tags provide a promising avenue for new knowledge on the largest of August Krogh’s animals.

Declaration of Competing Interest

We declare no conflicts of interest.

Acknowledgements

The authors are grateful for support from the Danish Council for Independent Research (Det Frie Forskningsråd Natur og Univers) and Stanford University. We thank Tobias Wang and Ilias Foskolos for comments on earlier version of the ms. We also thank Brandon Southall and John Calambokidis for previously published data excerpts from the SOCAL-BRS project that formed the basis for figure schematics.

References


