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## From Small Beginnings to Giants: An Integrative Review of Cetacean Gigantism and its Ecological Implications for Aquatic Biology and Fisheries

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### Abstract

Blue whales (*Balaenoptera musculus*) are not only the most massive animals on earth, but their ancestors were small fry. How and why did some lineages of cetaceans cross the physiological, ecological, and evolutionary barriers necessary for achieving such extreme body size? In this synthesis I combine evidence from physiology, biomechanics, behaviour, paleo biology, genomics and macroecology with that of palaeo-oceanography to explore the processes which have facilitated gigantism in cetaceans and specifically in rorqual whales. What we find is no single cause, but a succession of “gatekeepers” (new innovations that make larger size possible) and “ratchets” (either ecological or genetic situations that favor the retention and amplification of large size). Key gates include: (i) transitions in feeding mode and head/neck specializations that scale prey intake faster than costs (ii) dive and locomotor physiology that support high throughput foraging while maintaining oxygen balance and (iii) genome architectures that ameliorate cancer risk and metabolic stress in long lived monstrous bodies [1-34]. Drivers are Plio–Pleistocene movements of ocean productivity and variance movement strategies that follow ephemeral prey and demographic genomic processes of shipping successful eco physiological packages [35-51]. Comparative information from other aquatic megafauna (ichthyosaurs, sharks) and non marine systems will help resolve broader rules and peculiarities of cetaceans [52-58]. Together, these bodies of evidence shed light on how the biggest animal on Earth “started small”, and why extreme size is not only a rare evolutionary outcome but also a fragile ecological accomplishment.

**Keywords:** Gigantism, Cetaceans, Rorqual whales, Genomics, Paleo-oceanography

### Introduction

#### Framing the Puzzle of Marine Gigantism

Whales are a frontier of biological design. Their time allocation for foraging, diving and commuting is size dependent, but their potential to extract high prey densities can increase with body size [1,2,5,15,16]. Extreme sizes in baleen whales (Mysticeti) are found only among rorquals (e.g., blue, fin), although bowheads and right whales also attained large size by another mode of feeding [59,60]. The key question is thus two-fold: what innovations and environmental regimes are needed for large size to be possible, and what conditions make large size beneficial and evolutionary stable over the long run [15,18,35-37,61]. Classic and recent work on mysticete feeding mechanics and physiology (covering aspects of kinematics, hydrodynamics, tissue properties and cardio respiratory limits) now quantify the margins and tradeoffs at large size [1-14,20,21].

#### A Macroecological Template: When the Ocean Favors Giants

Gigantism exists where energy is supplied in strong, predictable bursts while foraging mechanisms can process it effectively [54,58,61]. The models illustrate that energetic trade-offs establish upper limits to marine mammal body size with solutions depending upon prey densities and the scaling of foraging costs relative metabolic rate [36,37].

Baleen whale prey intake has been increased dramatically (up to 6-fold), which further ties basin scale productivity to possible apex body sizes using independent lines of evidence and may support the general pattern correlating maximum marine mammal size to productivity regimes [14-16,18-21,33-38,45,48-50]. In sharks, the route to gigantism is often associated with filter feeding or regional endothermy and macropredation, each of which access productive patches of ocean [56,58]. Ichthyosaurs (marine reptiles) attained colossal body sizes quickly in the Mesozoic during periods of ideal ocean conditions [52,55]. Vertebrate-wide rules of thumb, such as trends in the evolution of body size under ecological release (island-rule responses) emphasize how such general principles structure body-size evolution [53].

### **From Small Archaeocetes to Giant Mysticetes: The Fossil Record's Timeline and Tests**

The fossil record shows that increases in baleen whale size were episodic and that a number of lineages evolved into large size at different times [62-65]. Certain analyses have claimed that baleen whales became giants long before once believed, with a slow start to size increase during the Miocene while others link such individual occurrences of large bodiedness to the Plio-Pleistocene, when climate reorganized ocean circulation and stratification [35,59,66]. An interesting hypothesis is that gigantism preceded the full elaboration of modern filter feeding in some clades [67,68]. Functional discoveries—like a complex sensory organ that mediates lunge feeding—highlight how innovations in the head and throat could unlock new energetic “regimes” for crown rorquals whereas true giant early whales expand the range of “giant” morphologies [9,69].

### **Gatekeeper Innovations: Feeding Mechanics, Minimum Viable Sizes, and Neuromechanics**

#### **Packaging Energy: Engulfment vs. Skimming**

While lunge feeding is an evolutionary innovation allowing Rorquals to engulf tens of cubic meters of dense prey in seconds, inflows that can exceed the deteriorating cost of movement if body size exceeds mode specific thresholds [1,2,5-8,13,16]. Geometric and tagged data model how engulfment volume, jaw/ventral pouch mechanics and flow through the oral cavity set the profits while balaenid cross-flow filtration and baleen porosity reveal an alternative scaling pathway for continuous skim feeding [6-8,10–13]. On minke, recent work has shown a minimum size for functional engulfment filtration linking mechanisms at the micro-scale to macroevolutionary size distributions [4].

#### **The Soft Tissue and Neural Toolkit**

Lunge feeding demands exceptional tissue extensibility and coordination [2,3]. An organ of touch at the mandibular symphysis times and gauges force proffered during engulfment while high speed bouts take temporary power needs to the limits of what is possible [5,9,21]. Kinematic analyses record variability in gape timing, roll, and body posture among rorquals that serve to further expand the mechanical ‘design space’ for gigantism [13,14,70].

#### **Decoupled Trajectories in Head Evolution**

Fossil and developmental evidence indicates that tooth loss and baleen evolution were partially decoupled in early mysticetes leaving room for alternative feeding modes in stem groups [62,64,65,68]. Hydrodynamic analyses of baleen architecture reinforce the idea that filtration performance evolved along multiple functional axes [10-12,70].

#### **Diving, Power, and the “Krogh Problem” for Giants**

From August Krogh’s initial physiological truncation of the blue whale to contemporary integrative biomechanics, the margins around the metabolism of extremely large rorquals are small but sufficiently workable [2,71]. Dive time budgets and the scaling of cost per lunge limit depth time exposure; that is, the available time at a given depth (and therefore the foraging ‘profit window’ of each dive) [1,5,6,8,14,16,21]. Direct cardiac measurements demonstrate species of giants exhibit extreme bradyarrhythmias and tachyarrhythmias during dives, measuring how these species meet elevated oxygen demands in the midst of high power engulfment [20]. With increasing body size, the volume of prey engulfed scales more rapidly than drag penalties, but increased mass-specific cost and reduced dive capacity ultimately impose a constraint on returns [5,8,21].

### **Ratchets in the Seascape: Climate, Productivity, and Movement Strategies**

#### **• Pliocene and Pleistocene Oceanography as a Size Amplifier**

Independent origin of gigantism in several rorqual lineages matches shifts in upwelling, stratification, and nutrient delivery during the Plio-Pleistocene consistent with macroecological expectations for size ceilings and energy delivery [35,18,36-38].

#### **• Tracking Ephemeral Prey**

Recent telemetry and acoustics indicate that blue whales cue on annual windows when prey layers begin to %dvslhv,vwlxphgwkvh\vwhuivehdxwlrqlqwklugljjhurdg morzvwhpvrrinrqwfryhu [39,40]. Prey density and oxygen usage determine foraging efficiency [45]. Wind-upwelling-whale associations show fine scale spatial lags and temporal delays, pointing to memory or predictive behavior as essential in mediating variability [41,46].

#### **• Climate Extremes and Anthropogenic Overlays**

Marine heatwaves can concentrate or displace prey fields, which may affect foraging success and reproduction in blue whales [43]. The overlap with ship traffic in foraging hotspots generates collision risk, which intersects with ecology [72].

- **Listening to the Food Web**

We currently rely on animal borne and docked recorders: for instance, it has been shown that song occurrence and characteristics follow migration gradient or seasonal foraging condition becoming thus population scale bioindicators of trophic state [47,48 73-75].

## **Genomic and Molecular Enablers of Being Huge (and Living Long)**

- **Beating Peto's Paradox in Whales**

Comparative genomic analysis shows enrichment and adaptive evolution of pathways related to cell cycle regulation, DNA repair, apoptosis, and somatic maintenance—the candidate mechanisms of cancer suppression in large or long life mammals [22-24,49]. Gene losses during the land to water transition (e.g., in coagulation, skin, and olfaction) indicate genome level rewiring that is consistent with aquatic life at a minimum—possibly indirectly promoting larger sizes [34].

## **Genomes of Giants—and their Kin**

Focusing on high quality assemblies, blue whale investigations identified segmental duplications and demography bowhead genomes reveal longevity pathways while wider surveys discovered convergent signatures throughout marine mammals [22,33,49,50]. Conservation genomics refines population structure and questions subspecies designations in blue whales worldwide and pedigree based inference is revising mutation rates and historical abundance for baleen whales [30,32,51]. In orquals, reticulation is observable in genomes as some pairs show limited contemporary hybridization despite evidence of hybridization in other parts of the genome suggesting modern boundaries are maintained by selection, behavior or ecology [25,31].

## **Life Histories, Social Structure, and Ecosystem Context**

Characteristics of the life history that can dampen variation in fitness may evolve correlated with body size. Menopause in some toothed whales and kin selected benefits in long lived, social cetaceans [17]. Coevolution of predators and prey (e.g., killer whales ecomorphs) has lead to diverse predation regimes that feedback on the behavior and habitat use of baleen whales [76]. At the ecosystem-level, the evolution of gigantism in active marine predators and elasmobranchs supports the energy–foraging rule: mechanisms to harvest prey fields denser than a relaxed-catchability threshold lead to gigantism [44,54].

## **Synthesis: "Started Small," Crossed Gates, then Ratcheted up**

At least four steps help explain how Earth's biggest animal started small:

**Opportunity Landscape (Ratchet):** Marine systems periodically offered plentiful, predictable food surpluses in the upper water column during Plio–Pleistocene time increasing returns to body size [18,35-38].

**Functional Gates (Gatekeepers):** Head and neck innovations of mysticetes (baleen architectures; engulfment mechanics; extensible tissues and nerves) permitted prey intake to scale superlinearly with body size, but only above a size threshold allowed by the minimum viable size [3,4,6-13,68].

**Physiological Integration (Gatekeeper):** Dive capacity, locomotor efficiency, and transient high power performance remained within workable ranges with superlarge swallows and with high drag states [1,2,5,8,13-16,19-21].

**Genomic Reinforcement (Ratchet):** Natural selection on tumor suppression, DNA repair and regulatory networks decreased the relative fitness costs of large long lived bodies; demographic histories and partial reticulation promoted the purging and consolidation of successful phenotypes [22-34,].

Comparative studies (ichthyosaurs, sharks) demonstrate that once gatekeepers are established, favorable ocean states can drive size evolution [52,55,58]. That extant blue whales use memory and environmental cues to follow pulsed resources shows how behavior maintains the giant phenotype in an ice- age ocean [39-48].

## **Conservation and Future Directions**

The giants will remain as long these gates are left open, and the ratchets keep their teeth in place. Safeguarding migration pathways and foraging hotspots against ship strikes and noise, while monitoring climate driven variation of prey abundance, are key to the durability of the energetic balance of giant whales [41-44,72]. Revised prey consumption estimates and the impact of "whale pump" mechanisms, suggest that the ecophysiological relevance of restoring large whales may be even greater with respect to biogeochemistry [38,77,78].

Continuing to develop not only large scale foraging energetics under high resolution, which have made possible the calculations of Table 1, but also genomic maps of selection (including regulatory elements) and paleoceanographic reconstructions will enable sharper tests of causation within the gatekeeper–ratchet framework [15,16,18,22,24,26,30,33-35,49,50].

To date, scenario analyses now estimate climate risk to baleen whales and prioritize management levers supporting recovery with new pedigree methods improving estimates of mutation rates and abundance histories required to

calibrate demographic models [51,79].

### Conflict of Interest Declaration

The author declares that there is no conflict of interest related to this manuscript.

### Data Availability Statement

No new data were generated or analyzed in support of this review. All information discussed in this manuscript was derived from published sources cited in the reference list.

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### Authors' Contribution

The author conceptualized the review, conducted the literature synthesis, drafted the manuscript, and approved the final version.

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