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Parallels for cetacean trap feeding and tread-water feeding in the historical record across two millennia

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Abstract

Trap feeding and tread-water feeding are cetacean hunting strategies first recorded in the 2000s in two whale species at opposite sides of the globe. In both behaviors, whales sit motionless at the surface with their mouths open. Fish are attracted into the whale's mouth and are trapped when the jaw is closed. We identify striking parallels with the behavior of a sea creature named hafgufa in Old Norse sources. The hafgufa tradition can be traced back to the *aspidochelone*, a type of whale frequently described in medieval bestiaries, first appearing in the *Physiologus*, a 2nd century CE Alexandrian manuscript.

KEYWORDS
aspidochelone, hafgufa, history, rorqual, trap feeding, tread-water feeding

1 | INTRODUCTION

Since 2014, similar and apparently novel cetacean feeding strategies have been observed at coastal locations in two species of balaenopterid whales at opposite sides of the planet. In both cases, whales were observed to adopt a previously unknown strategy of waiting motionless at the surface of the water with their mouths open for a sustained period, before rapidly closing them to trap prey. In humpback whales (*Megaptera novaeangliae*) this behavior has been named as "trap feeding" and was observed in the Northeast Pacific (McMillan et al., 2018). In whales of the Bryde's whale complex (*Balaenoptera brydei*) a very similar but possibly distinct behavior has been observed in the Gulf of Thailand and named as tread-water feeding (Iwata et al., 2017).

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We describe a hitherto unidentified yet striking parallel in both the visual appearance and other characteristics of trap and tread-water feeding whales with sea creatures described in ancient and medieval sources. The strongest parallels appear in an Old Norse description of the hafgufa, one of several types of whales described around Icelandic waters. While postmedieval scholars have often confused the hafgufa with fantastical creatures such as the kraken and even mermaids, a close examination of earlier sources demonstrates that they refer to it explicitly as a "type" of whale. This raises the interesting and significant possibility that, rather than appearing for the first time in two species on opposite sides of the globe within the last two decades, these feeding strategies may have existed in the distant past. We will describe first the evidence for trap and tread-water feeding, then trace the historical evidence for the hafgufa tradition and its predecessors, before weighing the evidence for links between them.

2 | MATERIALS AND METHODS

2.1 | Marine biological background

Trap and tread-water feeding behaviors in whales were first reported by marine biologists less than a decade ago (Iwata et al., 2017; McMillan et al., 2018). These behaviors have been observed only in rorquals, a subgroup of baleen whales, distinguished by grooved throat pleats that expand to allow swallowing of large mouthfuls of fish in a single gulp. The only rorquals known to use these feeding strategies are the humpback whale and Bryde's whales, or the Bryde's whale complex, a term that encapsulates a number of as yet undefined species or variants within this group or complex. The complex includes the Sittang or Eden's whale (*B. edeni*) in the Indo-Pacific, Rice's whale (*B. ricei*) in the Gulf of Mexico and two smaller variants, the Indo-Pacific Bryde's whale (*B. brydei*) and Omura's whale (*B. omurai*) (Rosel et al., 2021).

The range of the humpback whale is nearly global, and that of the Bryde's whale complex is more restricted to subtropical and warm temperate waters (Figure 1). Until recently it was thought neither species occurred in the Mediterranean or the Red Sea (National Oceanic and Atmospheric Administration, 2022a, 2022b). However, humpbacks and members of the Bryde's whale complex have been reported in the Red Sea (Notarbartolo di Sciara et al., 2017),

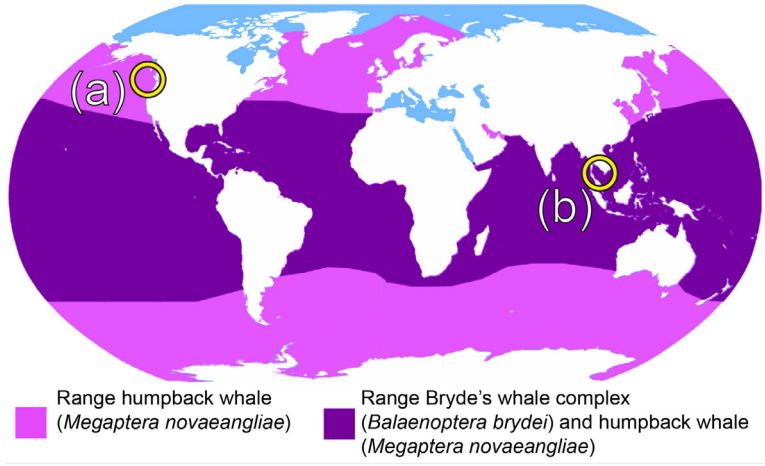


FIGURE 1 Range of Bryde's whale complex and humpbacks (after the NOAA Fisheries Species Directory 2022a, 2022b) and the locations of trap feeding behaviors by humpbacks off Vancouver Island (a) and tread-water feeding by Bryde's whales in the upper Gulf of Thailand (b).

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FIGURE 2 A digital reconstruction of a humpback whale trap feeding (J. McCarthy).

while a Bryde's whale was also stranded off the coast of Alexandria in 2018, demonstrating at least an occasional presence in the Mediterranean (Abo-Taleb et al., 2020).

Trap or tread-water feeding is a specialist hunting technique, where a rorqual whale positions itself vertically in the water with only the tip of its snout and mandible (jaw) protruding from the surface, or with its rostrum in a near vertical position and its mandible horizontally near the water's surface (Figure 2). In this respect it is somewhat similar to skim feeding, a strategy employed mainly by nonrorquals, including right whales and bowhead whales, where the mouth is held open, but the whale remains in constant motion as a filter feeder. Stationary mouth-open feeding behaviors in rorquals was first recorded in 2011, when a team of cetacean researchers observed it in humpback whales feeding primarily on herring off Vancouver Island (McMillan et al., 2018). Before that study was published, a similar feeding strategy was observed among Bryde's whales feeding primarily on anchovies in the Gulf of Thailand but was separately named tread-water feeding (Iwata et al., 2017). There, it was observed 58 times in 31 whales including eight adult–calf pairs, with the stationary position adopted by the whales for a maximum of 32 s. Iwata et al. (2017) interpreted the strategy as a unique reaction to pollution and eutrophication in the Gulf of Thailand, which had forced the whale's prey of anchovies near to the surface. However, they also considered this might simply be an energy-efficient method of feeding, an interpretation supported by the subsequent publication of the Canadian study, in an area where the waters are not eutrophic. McMillan et al. (2018) speculated that trap feeding is simply a strategy that works well when schools of fish are dispersed at low density, making them too low-return to catch using other high-energy feeding strategies like lunge feeding.

Iwata (2017, p. R1154) suggested that tread-water feeding whales may create a current with their jaws to draw in fish from a wide area of ocean surface and McMillan et al. (2018, pp. 13–14) have similarly suggested that the instinctive shoaling of fish toward the apparent shelter of the trap feeding whale's mouths may be a key element of the technique. Seabirds (rhinoceros auklets, *Cerorhinca monocerata*; common murres, *Uria aalge*; and other alcids) were present for every recorded instance of trap feeding in humpbacks to date, and their presence may be a necessary factor in the technique, driving fish to seek the shelter of the whale's mouth. In trap feeding there is evidence the pectoral fins are also used to push or flick prey into the humpback's mouth (McMillan et al., 2018). It is possible that tread-water feeding does not rely on seabird presence or the use of pectoral fins, but further observation will be required. Nevertheless, both behaviors, if not identical, share the key characteristic wherein the whale remains essentially motionless with mouth agape at the surface for a defined period.

These stationary feeding strategies take a place amongst a wide range of known rorqual feeding strategies, including lunge feeding, bubblenet feeding, flick feeding, bottom feeding and lobtail feeding. Lunge feeding, charging at a school of fish with mouth agape, is perhaps the most common tactic in humpbacks, and one for which rorqual

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whale anatomy is highly specialized (Shadwick et al., 2019). Bubble feeding involves first creating a circular curtain of bubbles to encircle and concentrate a shoal of fish, allowing the whale to charge into the center. Like trap feeding, lobtail feeding is a novel behavior first observed in the 1980s, sometimes described as "culturally transmitted" among associated groups of whales. The appearance of lobtail feeding has been interpreted as an adaptation by the whales to a crash in the availability of herring due to overfishing (Allen et al., 2013; Weinrich et al., 1992). McMillan et al. (2018) draw parallels between the emergence of trap feeding and lobtail feeding, as trap feeding off Vancouver Island also increased in frequency over time, from two recorded instances in 2011 to 16 in 2015. Iwata et al. (2017) also suggested tread-water feeding might also be culturally transmitted.

2.2 | Historical traditions

We identify a persistent tradition of sea creatures exhibiting strong parallels with trap/tread-water feeding, with the most detailed version appearing in the mid-13th century Old Norse didactic text *Konungs skuggsjá* (the King's Mirror). This manuscript was composed for the Norwegian King Hákon Hákonarson (reign 1217–1263). The full description of the sea creature, referred to as a hafgufa, given in the *King's Mirror* is as follows:

> "There is one fish yet to be accounted, and I am rather reluctant to tell of it because of its great size, which most people will find unbelievable. Few people can say anything clear about it, for it is seldom near land or in the sights of fishermen, and I do not expect that there are many such fish in the sea. We usually call it the hafgufa in our tongue. I do not know exactly how long it is in ells, because in those instances where it has appeared to men, it has looked more like an island than a fish. I do not know of it having been caught or found dead, and it seems to me that there are no more than two in the sea, which do not increase in number between themselves, because I suppose that it is the same two that are ever present. And it would not be good for other fish that they were as numerous as other whales, because of their great size and the vast sustenance they require. It is said of the nature of this fish that, when it goes to feed, it gives a great belch out of its throat, along with which comes a great deal of food. All sorts of nearby fish gather, both small and large, seeking there to acquire food and good sustenance. But the big fish keeps its mouth open for a time, no more or less wide than a large sound or fjord, and unknowing and unheeding, the fish rush in in their numbers. And when its belly and mouth are full, [the hafgufa] closes its mouth, thus catching and hiding inside it all the prey that had come seeking food" (Lárusson 1955, p. 33; M. Firth, Trans.).

Given that medieval observers do not have the benefit of modern technologies that allow close observation at a distance or modern scientific concepts to help interpret what they see, the *King's Mirror* is surprisingly accurate in its description of marine fauna. In his analysis of the *King's Mirror* as a source of marine biological information, Whitaker (1986) found clear correlations between 26 of these Old Norse descriptions and marine animals recognized by modern science. This echoes the view of earlier scholars who remarked that of the author of the *King's Mirror* that, "although well acquainted with much of the earlier mediæval literature, he has liberated himself to a surprising extent from its fabulous conceptions" (Nansen, 1911, p. 244). However, in the case of the hafgufa, Nansen could find no scientific match, and concluded that here the author "could not altogether avoid the supernatural in treating of the sea." Similarly, Whitaker, despite a more exhaustive study, was also forced to conclude that it "must be relegated to the world of the miraculous" (Whitaker 1983, p. 8).

The hafgufa appears in other Old Norse manuscripts, including *Qrvar-Odds saga*, an Old Norse *fornaldarsaga* (legendary saga) composed in the late 13th century, and an Old Norse *þula* (naming poem) that lists various types of whales, found appended to most redactions of Snorri Sturluson's 13th-century *Skáldskaparmál*. There are also earlier descriptions of similar creatures but referred to with different names. The earliest of these is in the *Physiologus* (The

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Naturalist), a Greek text compiled in Alexandria ca. 150–200 CE that preserves zoological information brought to Egypt from India and the Middle East by early natural historians like Herodotus, Ctesias, Aristotle, and Plutarch, as well as merchants and other travelers (Dorofeeva, 2017, p. 665). From ca. 300 CE, *Physiologus* was translated into Arabic, Armenian, Coptic, Ethiopian, Latin, and Syriac, and then, in the Middle Ages, was translated into various European vernaculars, including Old English (pre-975 CE) and Icelandic ca. 1200 CE.

Unfortunately, the original Greek text of *Physiologus* does not survive; however, one of the earliest extant redactions of the text, *Physiologus Latinus versio B*, ca. 400 CE, offers this account of a whale which, it says, the Greeks called the *aspidochelone*:

> "When it is hungry it opens its mouth and exhales a certain kind of good-smelling odor from its mouth, the smell of which, once the smaller fish have perceived it, they gather themselves in its mouth. But when his mouth is filled with diverse little fish, he suddenly closes his mouth and swallows them." (*Physiologus B*, *24*, pp. 11–13 in Carmody, 1939; E. Sebo, Trans.).

The description has the following elements, which appear in virtually all the texts based upon it, including most medieval *Bestiary* descriptions of whales: (1) the creature holds its jaws open, (2) emits a smell or scent, (3) attracting small fish to jump into its mouth, and (4) when enough have been gathered, it swallows. The *Physiologus Latinus versio B* redaction was immensely influential and most later versions are clearly drawn from it. However, the *Bern Physiologus* (Codex Bongarsianus 318, Burgerbibliothek, Bern), probably produced at Reims about 825–850 CE and believed to be a copy of a 5th-century manuscript (Woodruff, 1930), like *Konungs skuggsjá* above, adds the detail that the whale emits a strong, not a sweet, smell. This version also includes an illustration which is probably the earliest known from this tradition. Although damaged, the dark lines depicting the surface of the water show that the whale has its head above the water and holds a fish in its mouth, with others nearby (Figure 3).

The Icelandic version of *Physiologus*, which begins with the statement, *Es hualr i sǫ er heiter aspedo* (There is a whale in the sea called the *aspido*; AM 673 a II 4 to fol. 3r, Reykjavík), underlies later 13th-century Scandinavian depictions of the creature that became known as the hafgufa. This text also includes an illustration of the creature, depicting it as whale-like, with one or two fish in its mouth and others attempting to jump into its mouth. (Figure 4).

While the Icelandic *Physiologus* represents an intermediary stage between earlier *Physiologus* traditions and the description of the hafgufa in *Konungs skuggsjá*, it does adhere quite closely to the conventions of its predecessors.



FIGURE 3 An illustration from the Bern *Physiologus* labeled *De Ceto Magno Aspidohelunes* (on this great Aspidochelone) (Bern, Burgerbibliothek, Cod. 318 fol. 15v; https://www.e-codices.unifr.ch/en/list/one/bbb/0318; CC BY 4.0, color and contrast corrected).

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FIGURE 4 Icelandic *Physiologus* (ca. 1200) depiction of the Apsido feeding (Reykjavík AM 673 a II 4to fol. 3v; Public Domain; color and contrast corrected).

However, *Konungs skuggsjá*, (quoted above), adds new details to the description. It offers a clearer sense of how wide the whale opens its jaws and includes the detail that, rather than emitting some kind of perfume as bait, the whale regurgitates food as part of this feeding strategy. This detail is unique to this description. The last significant description of the hafgufa is in the 14th-century redaction of *Qrvar-Odds saga*. Here the width of its jaws is again described as immense, but uniquely this source describes its open mouth at the surface of the water as so large as to appear to be two rocks exposed from the sea that a ship can sail between.

Throughout its many versions, the hafgufa/aspidochelone tradition remains distinct from other ancient accounts of whales such as the biblical story of Jonah. Postmedieval texts that mention or describe the hafgufa tend to draw directly on either *Konungs skuggsjá* or *Physiologus*. The Ortelius map of Iceland of 1658 shows many fantastical sea monsters (Figure 5). None are named as the hafgufa, but one unnamed creature is described as an island-sized whale that, due to its bulk, cannot chase prey but must rather rely on artifice. While literary representations of the hafgufa retain the associations with whales up to the 17th century this may be the last iconographic representation that does so. From the 18th century, the hafgufa tradition only becomes further muddled as commentators seek to explain it through, or equate it with, other creatures, both real and fantastic.

2.3 | Comparing the evidence

The strongest argument in favor of a real link between trap/tread-water feeding and the hafgufa/aspidochelone tradition is the similarity of behavior and appearance. Although the historical tradition often appears exaggerated, with respect to the size of the creature and the length of time spent motionless, the descriptions are otherwise strikingly similar and generally straightforward. There is little similarity with other whale behaviors; skim feeding is similar in that the whale's mouth is held open, but the whale remains in constant motion while most historical sources describe a motionless creature that is often mistaken for an island or intertidal rocks. Early zoological texts are a mix of accurate observation with fantastical elements that are often failed attempts to explain nature in terms that are now unrecognizable to modern readers. Even animals which must have been well-known to ancient and medieval authors are not always described accurately. The tradition does include some fantastical elements such as the exaggerations mentioned above and the suggestion that mariners might have landed on and even lit fires on the creature, but otherwise the creature is shown as preoccupied with its signature behavior of trapping fish in its mouth. (Figure 6).

When new elements appeared in this tradition in medieval sources, the introduced details add to the already-strong parallels with trap and tread-water feeding already apparent from the *Physiologus*. This is particularly true with

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FIGURE 5 Above: Ortelius's 1658 map of Iceland showing various mythological sea creatures. Below, a detail of a sea creature labeled H, "the greatest of whales" which could not chase fish but caught them through cunning (Public Domain; color and contrast corrected).

the Old Norse-Icelandic tradition in the 13th century. The description of the hafgufa in *Qrvar-Odds saga* includes the detail that it swam to the surface, opened its mouth with its nostrils and lower jaw exposed from the sea, and patiently waited to feed (at least the length of one tide; Jónsson, 1954, pp. 280–6). Moreover, the added detail of the two giant rocks representing the creature's jaws and nostrils, can be said to match the appearance of the rostrum and jaw of a trap feeding whale seen from a distance (Figure 7).

Konungs skuggsjá also adds a detail not seen in previous descriptions. Rather than using a scent or perfume as a bait as it does in the aspidochelone tradition, here the hafgufa is said to expel its own bile as bait. For rorquals such as humpbacks and Bryde's whales, there is evidence of both regurgitation of food during feeding and of a distinct smell associated with feeding. As rorquals close their mouths during feeding, "an enormous, dense, slurry-like collection" composed of "prey (of all types and sizes)" is drawn back towards their narrow esophagus and compressed for swallowing (Werth et al., 2017, p. 2083). Excess water is ejected as the food is compressed and is likely to contain at least some remains of prey. A 2018 survey from the Gulf of Alaska described that "the remains of prey seen in the water and/or floating at the surface after a presumed foraging event" (Straley et al. 2018, p. 178). Although no test has been made of whether the release of this regurgitated material contributed to drawing more prey into a kill zone, many rorqual prey species such as herring and euphausiids (krill) are omnivorous and would undoubtedly be drawn to this ejecta.

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FIGURE 6 Details of known or suspected aspidochelones in selected medieval manuscripts. (a) British Library MS. Harley 3244, fol. 65r, 1236, ca. 1250, Public Domain; (b) Icelandic *Physiologus*, Reykjavík AM 673 a II 4to fol. 3v, ca. 1200, Public Domain; (c) British Library Sloane MS 3544, ca. 1225–1275, Public Domain; (d) Philippe de Thaon's *Bestiary*, Oxford Merton College MS. 249 fol. 8r, ca. 1200, CC BY-NC; (e) Bodleian Library MS. Laud Misc. 247 fol. 157r, ca. 1240, CC-BY-NC; (f) MS. Ludwig XV 3 (83.MR.173), fol. 89v, ca. 1270, Public Domain; (g) *Le Bestiaire Divin De Guillaume Clerc De Normandie*, Bibliothèque nationale de France Français 14969, fol. 42v, Public Domain, 13th century (all color and contrast corrected).

Separately, there is also evidence of a distinct smell associated with whale feeding. Marine biologists have noted the distinctive "rotten cabbage" smell of dimethyl sulfide released when large numbers of zooplankton or small fish feed on phytoplankton and demonstrated that whales and many other marine predators including fish, seabirds, turtles, and penguins are attracted to this smell over great distances (Owen et al., 2021). These factors may help to explain the characteristics of the hafgufa in the 13th-century *Konungs skuggsjá*. It seems entirely possible that that the now-proven association between feeding whales and the smell of dimethyl sulfide was interpreted by early

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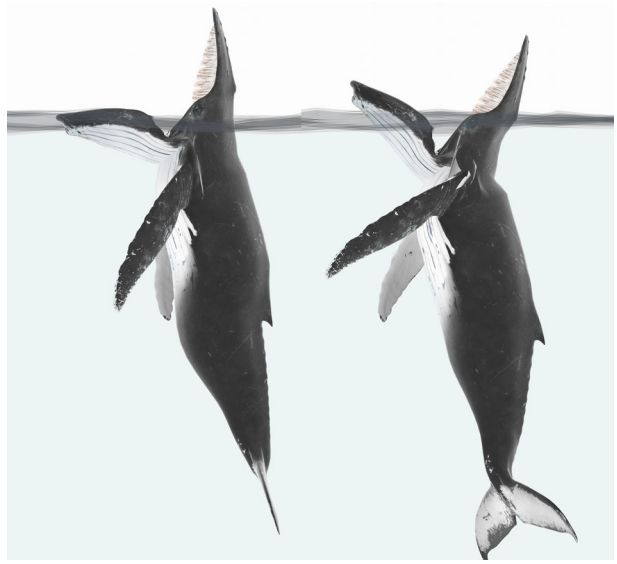


FIGURE 7 Diagram of humpback engaged in trap feeding; with a jaw either flush with the waterline or raised to a similar height to the rostrum (J. McCarthy).

mariners as a scent or perfume released by the whales themselves, and that remains of prey left behind by rorquals while feeding might be interpreted as deliberate regurgitation to draw in more prey.

3 | DISCUSSION

The search for observed natural phenomenon in medieval and ancient texts is not a new one. Numerous sea mammals have been suggested as the inspiration for mermaids (Lehn & Schroeder, 1981, 2003) and one study has even suggested that the penises of humpback, right, or gray whales breaching the surface might have inspired tales of sea serpents (Paxton et al., 2005). Alternative theories for the inspiration for hafgufa have occasionally been advanced in modern times, though these either lack detail or can be dismissed as mistaken readings of historical sources. One such theory proposed for the hafgufa is that it may have been inspired by submarine volcanic activity, presumably through large-scale disturbance of the water through bubbles or waves (Lehn & Schroeder, 1981, p. 365). Certainly, hot springs below the ocean's surface do occur in the North Atlantic, in some cases far from shore such as at the Strýtan hydrothermal chimney at Eyjafjörður in Iceland. However, while such features may have contributed to a general belief in gigantic sea creatures, this phenomenon bears little specific resemblance to detailed descriptions of the hafgufa.

Others have suggested that the hafgufa was inspired by giant squid, due to confusion with the kraken, a mythical sea creature commonly described as a colossal squid or octopus. The discovery of intact specimens of giant squid from the 1870s makes this idea seem plausible (Salvador & Tomotani, 2014) but it is incorrect, and the error arises partly from a confusion between the kraken and hafgufa traditions. In 1741 the Norwegian-Danish missionary, Hans Egede (1818, p. 87) stated that the kraken was the same creature known by the Icelanders as the hafgufa. This in turn led other scholars (e.g., Salvador & Tomotani, 2014, p. 972) to believe that the kraken appears in medieval texts. The kraken, however, is a modern sea monster, first appearing in the written record only in the early 1700s, and only coming to popular attention later that century. Egede's error subsequently led some to suggest that the hafgufa, like

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the kraken, is a giant squid (Nordgård, 1921, pp. 113–115). Later associations of the hafgufa with mermaids made by some scholars (e.g., Hermannsson, 1975; Zoega 1922, p. 182) result from similar misreadings of source material.

The possibility of a link between the hafgufa/aspidochelone tradition and trap or tread-water feeding cannot be easily dismissed. The tradition remained remarkably coherent and consistent over 1,500 years, with minimal embellishment or reinterpretation. Definitive proof for the origins of myths is exceedingly rare and often impossible, but the parallels here are far more striking and persistent than any previous suggestions. If the hafgufa tradition were linked to trap/tread-water feeding behavior, several interesting possibilities are raised. Firstly, the earliest written description of this whale behavior would not be from the 2000s but from at least ca. 300 CE in Egypt. Indeed, the observation that the Egyptian source is based on may have been made much earlier and perhaps far from Alexandria, anywhere from the Atlantic to the Indian Ocean. In this scenario, trap or tread-water feeding behavior would not be an animal kingdom "invention" of the 21st century, but rather an occasional strategy with much deeper roots. The lack of scientific observations prior to the last two decades might be explained by the relative rarity of this feeding strategy, or alternatively because the strategy was not being used. Niche hunting strategies like trap feeding and lobtail feeding may have been rendered largely unnecessary when whale populations crashed and competition for fish reduced. The rapid recovery of whale numbers has been driven by the evolving public attitudes to whales, through an early modern concept of them as a resource to be industrially exploited to the late 20th century in which they became a symbol for all endangered species (Mazzoldi et al., 2019). After just a few decades of legal protection it is hard to appreciate just how far is left to go in reaching a normal baseline population for whales. Rorqual whale populations prior to the emergence of industrial whaling in the 17th century are difficult to estimate for obvious reasons. Previous attempted to estimate past whale populations were made using archived logbooks of whaling vessels (Smith et al., 2012) but estimates from cetacean genetic diversity are likely to be more accurate. These suggest a pre-17th century North Atlantic population of humpbacks somewhere around 112,000, crashing to less than 1,000 individuals by 1955, but now estimated to have recovered to over 20,000 due to legal protection (Ruegg et al., 2013). Even now, modern rorqual whale populations in the North Atlantic remain less than a fifth of their natural level. With higher populations would have come fiercer competition between whales for fish. Niche survival strategies once more common before depletion of whale populations in the North Atlantic in the 17th century may be reemerging, either persisting in cultural knowledge despite the rare use of the method or reinvented. The sudden appearance of this behavior in two whale species seems to support this theory, as both whale populations are recovering from whaling pressure.

3.1 | Conclusions

Similarities between the hafgufa/aspidochelone traditions and cetacean trap feeding and tread-water feeding strategies have not been recognized despite several previous attempts to link the creature to a real sea creature. This is because trap feeding and tread-water feeding have only been recorded comparatively recently but the parallels are striking. The nature of ancient historical source material means that theories linking them to real scientific or biological phenomena are often impossible to prove or disprove definitively but the theory presented here highlights the potential value of applying ancient or traditional ecological knowledge to modern scientific enquiry. There may be much more to learn about ocean life from medieval and from historical documents that predate human pressures on the marine environment, such as biomass reduction, biodiversity loss, and climate change.

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AUTHOR CONTRIBUTIONS

John Kennington McCarthy: Conceptualization; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Erin Sebo:** Investigation; methodology; writing – original draft; writing – review and editing. **Matt Firth:** Investigation; methodology; writing – original draft; writing – review and editing.

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