

## Review



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# A behavioural framework for the evolution of feeding in predatory aquatic mammals

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Extant aquatic mammals are a key component of aquatic ecosystems. Their morphology, ecological role and behaviour are, to a large extent, shaped by their feeding ecology. Nevertheless, the nature of this crucial aspect of their biology is often oversimplified and, consequently, misinterpreted. Here, we introduce a new framework that categorizes the feeding cycle of predatory aquatic mammals into four distinct functional stages (prey capture, manipulation and processing, water removal and swallowing), and details the feeding behaviours that can be employed at each stage. Based on this comprehensive scheme, we propose that the feeding strategies of living aquatic mammals form an evolutionary sequence that recalls the land-to-water transition of their ancestors. Our new conception helps to explain and predict the origin of particular feeding styles, such as baleen-assisted filter feeding in whales and raptorial ‘pierce’ feeding in pinnipeds, and informs the structure of present and past ecosystems.

## 1. Introduction

Aquatic ecosystems are shaped by complex interactions between predators and prey, with changes in feeding behaviour often leading to significant downstream effects on ecosystem structure. The secondary adaptation of mammals to life in water provides a good example. Predatory aquatic mammals—i.e. otters and all marine mammals except sea cows—have infiltrated aquatic ecosystems ranging from the poles to the Equator, and from freshwater and coastal environments to the deep sea [1,2]. Across this diverse range of habitats, they act as consumers at almost every trophic level, from top predators [3,4] to planktivores [5,6]. While most species feed primarily at one trophic level, others (e.g. the leopard seal, *Hydrurga leptonyx*) can switch between prey types depending on their availability [7].

Understanding aquatic mammal feeding is essential both from a modern biological and a palaeobiological perspective. Extant aquatic mammals are large-scale consumers and play a key role as ecosystem engineers—for example, as bioturbators influencing the structure of infaunal invertebrate communities [8]; by maintaining kelp forests via the control of herbivorous invertebrates [9]; and as nutrient distributors influencing phytoplankton productivity [10]. Similar behaviours have likely contributed to the structure of aquatic ecosystems ever since mammals returned to the water, and are thus crucial in constructing an accurate picture of their evolution.

Key to these complex ecosystem functions is the diverse behavioural repertoire aquatic mammals use to capture and consume prey, which is usually classified into three distinct groups: raptorial, suction and filter feeding [1]. Raptorial feeders (also known as ‘pierce’ or ‘bite’ feeders) are thought to use

their teeth and jaws alone to capture prey, which is then typically swallowed whole [11–13]. This includes most seals and dolphins, although leopard seals and killer whales, *Orcinus orca*, are sometimes grouped as ‘grip and tear’ feeders, based on their ability to process large vertebrate prey [11,13]. Suction feeders (e.g. beaked whales) generate sub-ambient pressure inside their oral cavity to draw prey towards the mouth [14]. Finally, filter feeders (e.g. mysticete whales and crabeater seals, *Lobodon carcinophaga*) are species that use a specialized structure to filter small prey from seawater in bulk [1].

Overall, this subdivision of aquatic mammal feeding is intuitive, but has the drawback of focusing on a single, prominent behaviour, without explicitly acknowledging how different strategies interrelate or overlap. To consider an example, suction is framed mostly in terms of its use in prey capture (e.g. in beaked whales), when in reality suction capabilities are much more variable and often employed in conjunction with raptorial and filter feeding [7,15–18]. Likewise, describing non-filtering species as raptorial or suction feeders does not account for the way these animals deal with water ingested alongside the food, even though the need to remove excess water is widely acknowledged [19–21]. Both orquals and crabeater seals are typically described as specialist filter feeders, even though orquals capture prey primarily by ram engulfment [22] and crabeater seals by suction [23]. In both cases, sieving follows capture as prey is separated from seawater, but this filtering action is not the primary prey acquisition method.

Current perceptions of aquatic mammal feeding may therefore confuse different parts of the feeding cycle (e.g. prey capture versus water removal) and obscure the real breadth of behaviours employed by individual species. This may prompt misinterpretations of both feeding capabilities and the degree to which behaviour may vary in different foraging scenarios. In addition, by putting the emphasis on a single dominant behaviour, they hamper a better understanding of how aquatic mammal feeding evolved. Here, we introduce a new behaviour-based framework encompassing all major feeding styles, and argue that aquatic mammal feeding strategies can be seen as an evolutionary succession leading from terrestrial to increasingly more specialized, and obligately aquatic, habits. Our behavioural framework provides a firm basis for reconstructing the land-to-sea transition of feeding behaviour in predatory secondarily aquatic mammals, and furthermore helps to clarify the feeding ecology and functional morphology of their living relatives.

## 2. The aquatic mammal feeding cycle

The tetrapod feeding cycle is usually divided into four stages, namely, ingestion, transport, processing and swallowing [24,25]. While these stages hold for most terrestrial species, they do not account for the unique challenges faced by air-breathing tetrapods underwater. Unlike fish, aquatic tetrapods cannot expel water ingested alongside food via their respiratory organs, which has led most of them to require a dedicated water removal stage as part of their feeding cycle. Building on the established model of tetrapod feeding [24], we therefore here redefine the feeding cycle of aquatic mammals (and, more broadly, aquatic tetrapods in general) to include the following four consecutive functional stages:

(I) prey capture via movements of the jaws, forelimbs or the entire body; (II) prey manipulation & transport (IIa) and processing (IIb), which often occur in an alternating fashion, and mostly inside the oral cavity; (III) removal of water ingested with the food; and (IV) swallowing (figure 1). Each stage of the feeding cycle involves a variety of potential component behaviours (e.g. snapping, suction or chewing), which together combine into a distinct feeding strategy (e.g. suction or filter feeding). This basic division applies to all extant predatory aquatic mammals and describes a single feeding event, irrespective of which feeding strategy is followed. Below, each stage of the feeding cycle is explained in detail, and illustrated using relevant examples.

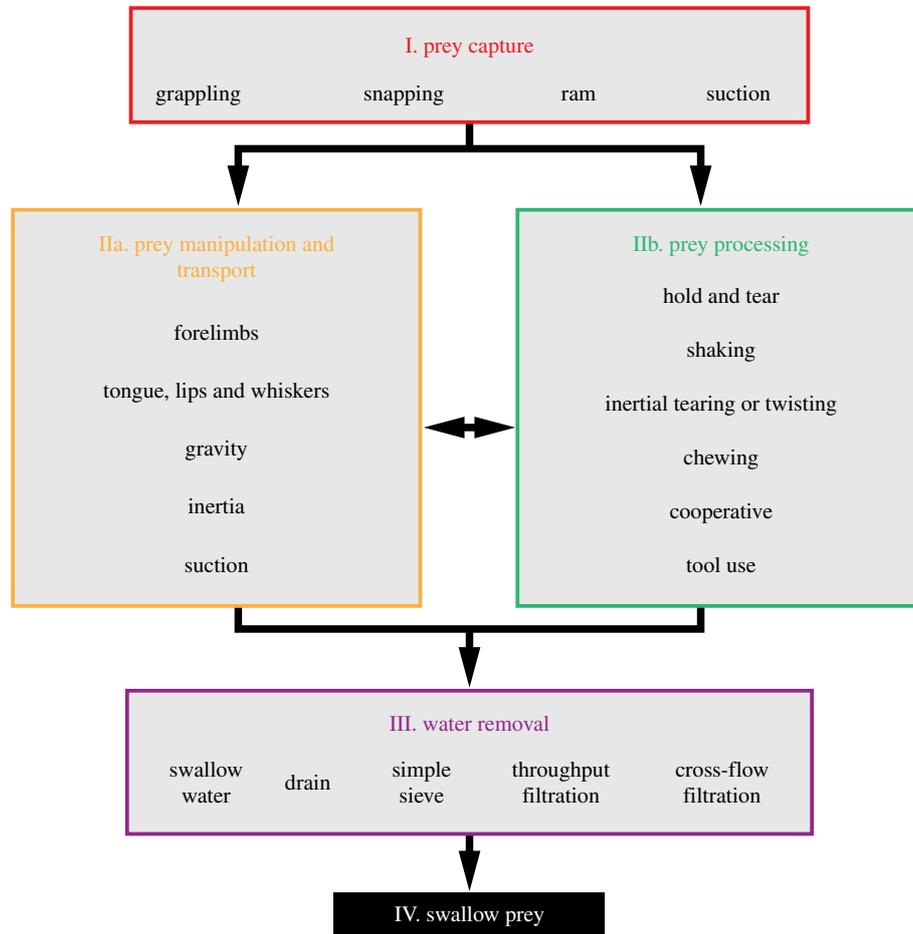
### (a) I. Prey capture

As in most carnivorous tetrapods, prey capture among aquatic mammals occurs mostly at the same time as ingestion [24]. Like their terrestrial ancestors, otters use their forelimbs to grapple with prey (figure 2a) [26]. By contrast, cetaceans and pinnipeds capture food with their jaws, usually via rapid movements of the head (snapping) and/or body (ram feeding) [1]. Whether animals are snappers depends directly on the structure and flexibility of the neck, with pinnipeds generally being considerably more mobile than cetaceans in this regard [27]. Where snapping occurs, it can be directed either anteriorly, as in many pinnipeds (figure 2b) [1,7,28]; or laterally, as in ‘river dolphins’ such as the Amazon river dolphin *Inia geoffrensis* [29] (figure 2c). To facilitate prey capture, cetaceans that employ lateral snapping have evolved elongate pincer-like jaws. Cetaceans with relatively short and inflexible necks use ram feeding to overtake and engulf prey (figure 2d), irrespective of whether the latter consists of an individual fish, as in the case of oceanic dolphins, or entire swarms/schools of krill, copepods and forage fish, as in most baleen whales [1]. Right whales and orquals are both ram feeders, but differ in employing this behaviour in a continuous (also known as skim feeding) and intermittent (lunge, gulp or engulfment feeding) fashion, respectively [22,30,31].

As an alternative to snapping and ram feeding, several marine mammals have evolved ways that effectively make their food come to them: by depressing their tongue and hyoid apparatus, they generate lower pressure inside the oral cavity, creating suction strong enough to draw prey into the mouth (figure 2e) [19–21]. For suction to be effective, the mouth opening needs to be relatively small, which in several odontocetes has resulted in a shortening of the rostrum, or else a partial closure of the lateral gape by adjacent soft tissue [14]. Suction for prey capture is common among odontocetes, such as beaked whales, monodontids and sperm whales [14,15,19] and pinnipeds, such as the leopard seal, the bearded seal, *Erignathus barbatus*, and the harbour seal, *Phoca vitulina* [7,32,33]. By contrast, the only living mysticete known to use suction is the grey whale, *Eschrichtius robustus*, which mostly uses this ability to suck up prey-laden sediment from the ocean floor [34]. Occasionally, however, grey whales have also been observed to feed on free-floating prey [35].

### (b) IIa. Manipulation and transport

Once caught, prey items frequently need to be reoriented and transported towards the back of the mouth for swallowing. Terrestrial mammals move food in two stages: first from the



**Figure 1.** Overview of the aquatic mammal feeding cycle, split into consecutive stages of prey capture, manipulation and processing, water removal and swallowing. Each stage (numbers I–IV) may involve one or more out of a range of component foraging behaviours. Because aquatic mammals may alternate between manipulation and processing as they feed, these are presented as two separate subsets of behaviours (IIa and IIb) that can be used interchangeably during the same stage in the feeding cycle. Functional definitions for each feeding behaviour are presented in table 1.

front of the snout towards the postcanines for mastication, and then towards the oropharynx for swallowing [25]. By contrast, aquatic mammals mostly no longer chew, and instead often need to reorient food intraorally so as to allow them to swallow prey items whole (e.g. [17]). Manipulation of prey can occur either directly, via the forelimbs (e.g. in otters and pinnipeds [26,36]) and the soft tissues inside and surrounding the mouth (tongue, lips and whiskers); or indirectly, through the use of gravity, inertia or intraoral suction. Transport through gravity occurs when an animal turns its rostrum upwards out of the water, and then partially opens its jaws to allow a captured prey item to fall towards the back of the mouth [28]. By contrast, transport by inertia involves a brief release of the prey item, followed by its recapture by a rapid forward movement of the snout. Intraoral suction is unique to aquatic feeding and, like the use of suction for prey capture, involves generation of lower pressure inside the oral cavity; however, in this case, it is only used to transport captured food items from the front of the mouth towards the pharynx [14].

### (c) IIb. Prey processing

Prey processing describes all actions that alter the size or consistency of a prey item prior to swallowing, and thus can be seen as the first step of the digestive process. In aquatic mammals, processing typically occurs only when food is too large or awkwardly shaped to be swallowed whole. In the vast

majority of terrestrial mammals, food processing is virtually synonymous with chewing, which, however, is thought to be largely absent in aquatic mammals. Notable exceptions are otters, which have a well-developed complex dentition; otariid pinnipeds, which use chewing to generate weak points in prey that make it more likely to tear during further processing [37,38]; and, possibly, the Amazon river dolphin, which is the only extant cetacean bearing weakly heterodont teeth [39]. Besides chewing, prey can be processed by tearing it between teeth and forelimbs [38]. Alternatively, a prey item can be dismembered using the jaws only, either by actively grabbing it with the teeth and shaking it (e.g. in leopard seals) or by working against the inertia of the floating corpse to tear and/or twist off manageable lumps of flesh [28]. More rarely, a similar outcome is achieved cooperatively (e.g. in the killer whale, *O. orca*), with two or more predators simultaneously pulling on prey in order to rip it apart [3]. Rarer still is use of stones as a tool to crack open shells, a behaviour that, among aquatic mammals, appears to be restricted to otters [40].

### (d) III. Water removal

Aquatic foragers almost invariably are forced to ingest water along with their food. The use of suction for capture or intraoral transport exacerbates this problem, as suction itself relies on the creation of water flow into the oral cavity. The simplest way of dealing with excess water is to swallow it

**Table 1.** Glossary of key terms and functional definitions for the behaviours used during aquatic mammal feeding.

<b>bulk feeding</b>	— any feeding strategy where multiple prey items are captured at once, irrespective of the prey capture method.
<b>chewing</b>	— modification of prey inside the oral cavity using repetitive movements of the jaw to pierce, cut or crush items using the teeth.
<b>component feeding behaviour</b>	— any feeding-related behaviour used during one of the four stages of the feeding cycle.
<b>cross-flow filtration</b>	— water removal method where prey is retained by a specialized filter oriented parallel to the flow of water out of the oral cavity.
<b>draining</b>	— water removal method where the head is lifted above the surface, allowing water to drain out of the oral cavity with gravity.
<b>feeding strategy</b>	— any series of component feeding behaviours combining into a complete feeding cycle.
<b>filtering</b>	— separation of small food items from water using a dedicated filtering structure, such as specialized teeth or baleen.
<b>forelimb (manipulation)</b>	— manipulation and transport of prey secured using the forelimbs.
<b>grappling</b>	— use of forelimbs to assist with securing prey during prey capture.
<b>gravity (manipulation)</b>	— intraoral transport of prey by lifting the head clear of the water, orienting the snout upwards, and allowing the captured item to fall towards the rear of the oral cavity.
<b>hold and tear</b>	— tearing prey by stretching it between the teeth and forelimbs.
<b>inertia (manipulation)</b>	— intraoral transport of prey involving the momentary release of a captured item, followed by a rapid forward movement of the head or entire body and, finally, recapture of the prey further posteriorly inside the oral cavity.
<b>inertial tearing/ twisting</b>	— tearing or twisting pieces off large prey by pulling directly against its inertial mass.
<b>prey capture</b>	— first stage of the feeding cycle involving any foraging behaviour that is used to capture or physically secure prey, typically, although not necessarily, inside the mouth.
<b>prey manipulation</b>	— second stage of the feeding cycle (along with prey processing), involving any foraging behaviour used to transport or manipulate prey prior to swallowing.
<b>prey processing</b>	— second stage of the feeding cycle (along with prey manipulation), involving any foraging behaviour used to physically prepare prey for swallowing (e.g. cutting, crushing or tearing).
<b>ram feeding</b>	— prey capture involving a rapid forward movement of the body aimed at engulfing prey. Can be used in either a continuous (skim feeding) or intermittent (raptorial, lunge feeding) fashion.
<b>shaking</b>	— tearing captured prey by shaking or flicking it from side to side.
<b>simple sieving</b>	— separation of small food items from water by sieving using jaws and/or simple teeth, rather than a specialised filtering structure.
<b>snapping</b>	— prey capture via rapid forward and/or sideways movements of the jaws using a flexible neck.
<b>suction</b>	— generation of lower intraoral pressure to draw prey into, or transport prey inside, the oral cavity.
<b>throughput filtration</b>	— water removal method where prey is retained behind a specialized filter oriented perpendicular to the flow of water out of the oral cavity.
<b>tool use</b>	— use of simple tools (e.g. anvil stones) during mechanical processing of prey.
<b>water removal</b>	— third stage of the feeding cycle, involving any behaviour used to remove water drawn into oral cavity along with prey.
<b>water swallowing</b>	— water removal method whereby ingested water is swallowed along with prey.

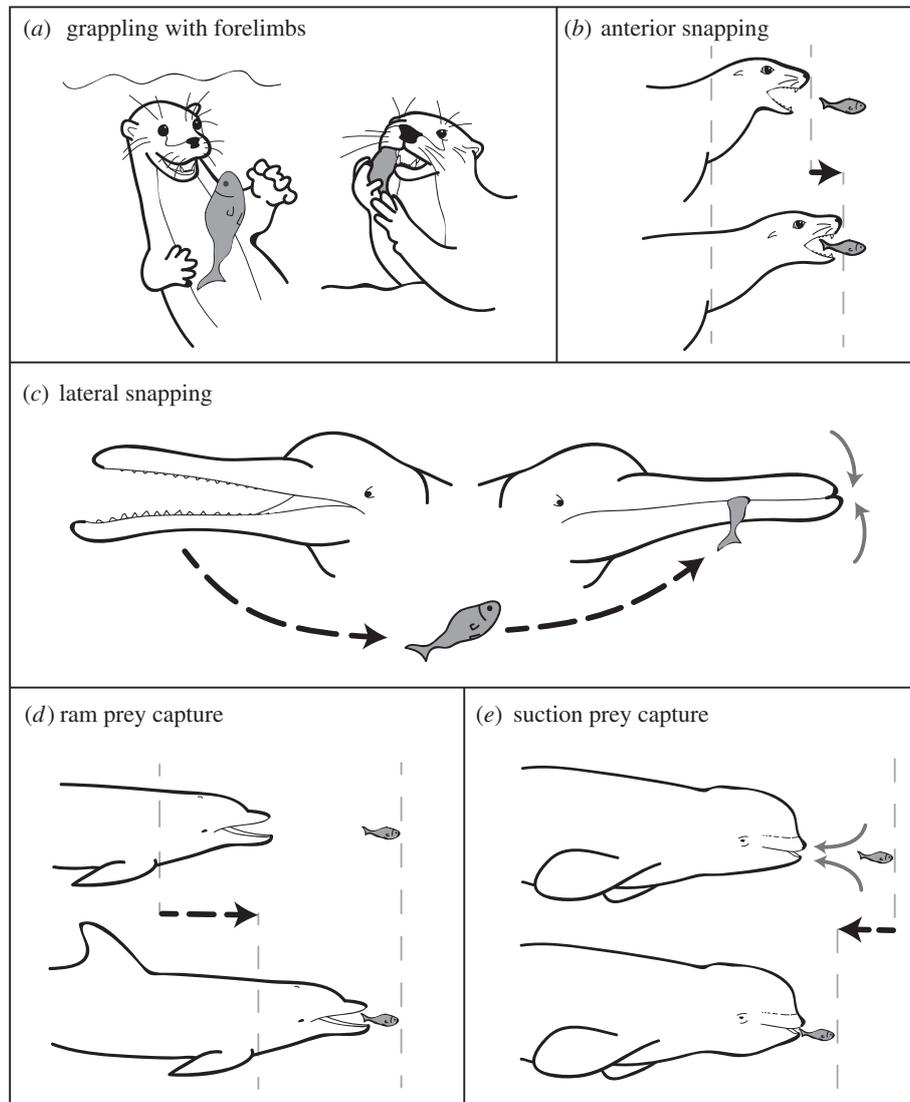
along with the food itself. This process may be relatively common, but seems costly in terms of the strain put on the excretory system and the impact that the additional volume is likely to have on locomotion and feeding performance. Thus, in general, the amount of swallowed water is likely to be small [41]. Alternative water removal strategies include both passive and active approaches. A relatively straightforward, passive way is to drain water from the oral cavity by lifting the rostrum above the water surface, so that water can flow out with gravity while the food is held between the teeth. This method may be common when prey is processed at the surface before swallowing [26,37].

When feeding beneath the surface, water does not passively drain out of the mouth and hence must be actively expelled. This can occur either by creating a constant flow through and out of the oral cavity (as seen in skim-feeding balaenids), or through muscular action [1]. As the water is expelled, food is prevented from leaving the mouth by the semi-closed jaws, teeth or a specialized filter. Where prey

items are relatively large, it is sufficient for the jaws, lips, gums and/or teeth to act as a simple sieve, or 'cage jaw' [18,42]. By contrast, small prey, such as krill or copepods, require the use of a specialized filter, such as the elaborate, interlocking teeth of leopard and crabeater seals, or the racks of comb-like, keratinous baleen plates found in mysticetes [5,7,43]. These two types of filter may work in different ways, with at least some mysticetes (e.g. right whales) employing longitudinal cross-flow, rather than transverse throughput filtration [22,44].

#### (e) IV. Swallowing

The final stage in the feeding cycle is swallowing (deglutition), where food passes from the oral cavity into the oropharynx and, finally, the oesophagus [25]. Unlike terrestrial mammals, which typically chew their food into a soft bolus, fully aquatic mammals often have to swallow prey items largely intact. Seals take large prey to the surface and



**Figure 2.** Overview of the prey capture behaviours employed by aquatic mammals, including (a) grappling, anterior and lateral snapping (b–c), (d) ram and (e) suction. Dashed arrows denote changes in the position of the predator or prey.

swallow via multiple ‘gulping’ actions, presumably with the aid of gravity [37,45]. Choking and suffocation are not uncommon, especially when the prey has sharp spines that cause it to become irretrievably lodged in the throat [46].

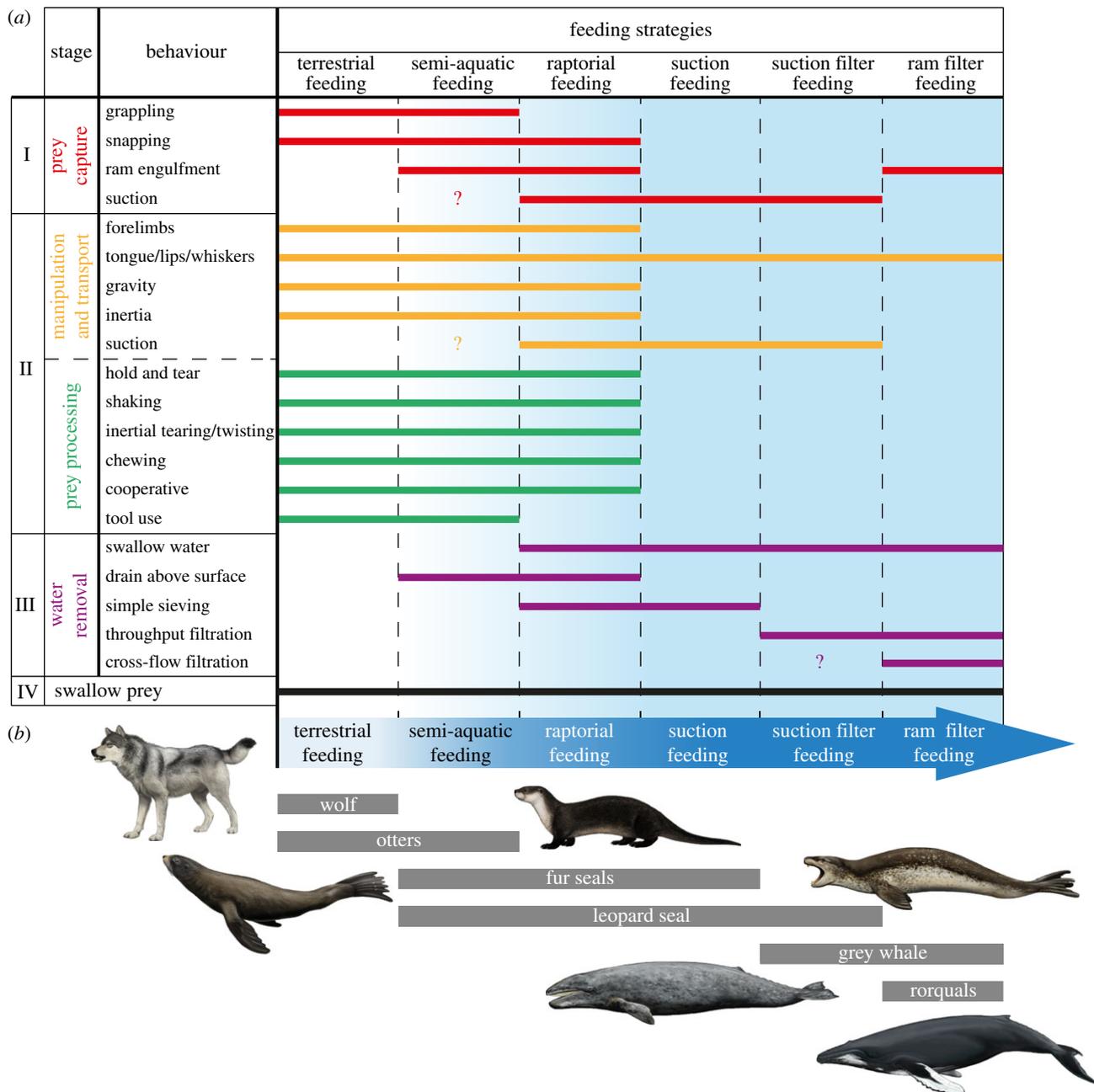
### 3. Feeding strategies

In theory, most of the behaviours used for capture, manipulation, processing and water removal are not mutually exclusive, and could be combined into a myriad of different feeding strategies. In reality, however, most aquatic mammals follow a relatively well-defined set of only five feeding strategies: (i) semi-aquatic feeding; (ii) aquatic raptorial feeding; (iii) suction feeding; (iv) suction filter feeding; and (v) ram filter feeding (figure 3). All of these strategies are flexible in that the animals employing them neither need to use every behaviour that may be part of the strategy, nor necessarily follow a single feeding strategy in all foraging scenarios. Thus, a leopard seal may use raptorial feeding when hunting penguins, but suction filter feeding when preying on krill [7]. Likewise, other pinnipeds are capable of semi-aquatic, raptorial or suction feeding when targeting different prey types [37], while grey whales—usually regarded as suction filter feeders—also

occasionally use ram filter feeding [47]. Nevertheless, any single feeding event will only follow one feeding strategy at a time: a leopard seal cannot filter a penguin, nor can a grey whale ingest benthic invertebrates via ram engulfment.

Within our new framework, semi-aquatic feeding describes any feeding events where some behaviours occur underwater (e.g. ram feeding or snapping during prey capture), while others occur in air at the surface, either while floating or treading water, or while hauled out on land (e.g. prey manipulation and processing). Both otters and pinnipeds use semi-aquatic feeding when consuming large prey, which is typically captured underwater before being processed at the surface [26,37]. Water ingested along with prey can generally be drained from the oral cavity while the head is held clear of the water.

In contrast to semi-aquatic feeding, aquatic raptorial feeding describes feeding events where all components of the feeding cycle occur underwater. Here, snapping and ram feeding are typically used for prey capture, although suction may facilitate the process by drawing prey within range of the teeth prior to biting [17]. Following initial capture, intraoral suction is used to transport prey to the back of the oral cavity, with any ingested water being expelled via simple sieving. Aquatic raptorial feeding is common among



**Figure 3.** Comprehensive overview of the feeding strategies employed by aquatic mammals. (a) Particular behaviours (rows) used during each stage (I–IV) of the feeding cycle combine into a limited number of feeding strategies (columns). A behaviour is listed as pertaining to a particular feeding strategy when it is used by at least some species when following that strategy. Question marks denote instances when the presence of a particular behaviour is uncertain. (b) All of the feeding strategies fall along a behavioural and evolutionary continuum leading from terrestrial to increasingly more specialized aquatic feeding styles, with each strategy being derived directly from the one preceding it. The presence of such a continuum is particularly evident in certain species that may switch between related (i.e. adjacent) strategies, depending on the foraging scenario. Examples of such taxa are shown at the bottom of the figure. Illustrations by Carl Buell.

pinnipeds and dolphins, both of which tend to capture and swallow small fish whole. In some cases, however, larger prey is also targeted and may be partly processed underwater by shaking or tearing [38].

Suction feeding describes events where prey capture occurs mainly via suction. For this mode of capture to be effective, targeted prey is typically small enough to be sucked entirely into the oral cavity, with minimal or no prey processing [37]. Prey can be either immobile (e.g. benthic invertebrates) or evasive (e.g. squid), with the latter sometimes requiring prolonged chases [48,49]. In cetaceans, specialization towards suction feeding tends to be accompanied by the loss of most or all of the teeth (e.g. beaked whales) [14]. Following suction, simple sieving is

used to retain individual prey items inside the oral cavity while water is expelled.

Suction filter feeding is effectively an extension of suction feeding, but, instead of simple sieving, uses a specialized filter to separate prey from ingested water. This filter consists of either highly elaborate teeth (in leopard and crabeater seals) [7,43] or baleen (in the grey whale) [34,47], and is capable of retaining smaller prey than simple sieving, thus enabling suction filter feeders to gather small prey in bulk. Finally, filtering and bulk feeding are also characteristic of ram filter feeding, which is arguably the most highly specialized of all aquatic mammal strategies. Ram filter feeding is only used by baleen-bearing mysticetes, and involves neither suction nor teeth to capture prey. Instead, prey is ingested via

continuous (skim feeding, as seen in right whales) or intermittent (lunge feeding, as seen in rorquals) ram movements, and then retained in the oral cavity via a specialized filter while excess water is expelled [5,50].

#### 4. Feeding strategies in context: an evolutionary continuum?

Viewed in an evolutionary context, the distribution of feeding strategies among extant aquatic mammals does not seem to follow any obvious phylogenetic pattern. Thus, for example, sperm whales and beaked whales, both of which diverged early from the other living odontocetes [51], appear to be obligate suction feeders [14,19], whereas platanistids (nested between sperm whales and beaked whales) and many late-diverging delphinids tend to feed raptorially [1,15,21]. Nevertheless, in terms of the anatomical and behavioural features that distinguish them, all of the strategies described here form a logical sequence leading from terrestrial to increasingly more aquatic foraging styles (figure 3*b*).

Thus, semi-aquatic feeding closely resembles terrestrial feeding, except for the presence of a distinct water removal stage (figure 3*a*). Aquatic raptorial feeding, in turn, is similar to semi-aquatic feeding, except that all behaviours occur underwater. Suction feeding likely evolved from raptorial feeding when suction, so far mainly used for intraoral transport, became the main tool for capturing prey. This strategy was then further modified into suction filter feeding, via the addition of a dedicated filter capable of separating small prey from ingested water in bulk. Finally, ram-based filter feeding retained the specialized filter but did away with suction, as baleen whales evolved new ways of maximizing food intake via oral cavity expansion (in rorquals) and skim feeding (in right whales) [5].

In line with the versatility of many aquatic mammals, the boundaries between the different strategies are frequently crossed—but only when those strategies grade into each other. For example, otters primarily use semi-aquatic feeding [26], yet can also capture and consume prey entirely on land [52]. Likewise, fur seals use semi-aquatic feeding when processing large prey, raptorial feeding for medium-sized fish and squid, and suction feeding when targeting extremely small prey [37]. Harbour seals also use both raptorial and suction feeding, depending on prey size [33]. Leopard and crabeater seals both use suction feeding to capture individual fish, but suction filter feeding when targeting krill [7]. Leopard seals, in addition, are capable of semi-aquatic and raptorial feeding when capturing and processing larger prey [4,45]. Finally, grey whales are primarily suction filter feeders, but occasionally also employ ram-based filter feeding [47].

Together, the gradational similarities between the various feeding strategies and the frequent occurrence of boundary-crossing taxa reveal a behavioural continuum that seems to emulate the evolution of aquatic mammal feeding (figure 3*b*)—a path that must be followed each time a lineage specializes to forage in water. Strikingly, the same sequence convergently arose in otters, pinnipeds and cetaceans irrespective of their different morphologies, which suggests that mammals may be constrained in their options as they specialize to feed in water: just as the evolution of powered flight in pterosaurs, bats and birds may have necessitated

the existence of intermediary gliding species, so too the evolution of filtering in mammals may in some way depend on a suction feeding ancestor. Our new evolutionary framework parallels a similar scheme devised for aquatic mammal locomotion [53], and can be employed to generate testable hypotheses about the evolution of predatory aquatic mammal feeding as a whole [14,16,18,54–56].

Thus, for example, we predict that suction could not have evolved from semi-aquatic feeding without a raptorial intermediate, and that ram-based filter feeding could not have evolved from raptorial feeding without suction and suction filter feeding intermediates. These predictions are borne out by the fossil record e.g. in the form of raptorial sperm and beaked whales preceding their suction feeding extant relatives [57,58], toothless suction feeders arising from within largely raptorial clades [59], and suction feeding archaic mysticetes [18,54]. Each of these occurrences represents an independent evolutionary event that supports the directionality of our model, and together they suggest that our framework applies irrespective of where, or how often, specializations for aquatic feeding have taken place.

#### 5. Evolutionary and ecological implications

Our new evolutionary framework, and the behavioural transitions it implies, invite a reinterpretation of extinct aquatic mammal feeding in light of the ecology of their extant relatives. Feeding represents the key interaction between a predator and its prey, and as such fundamentally contributes to ecosystem structure. Thus, identifying how and when novel feeding behaviours first arose provides insights into both evolution and, crucially, the role of aquatic mammals in past ecosystems. Unlike most previous attempts at reconstructing feeding evolution, our framework relies entirely on modern experimental or observational data, rather than fossils. This approach has three advantages: (i) it allows us to include behavioural data that do not fossilize; (ii) it removes the uncertainty inherent in predicting complex behaviour from fossil morphology; and (iii) it provides an entirely separate line of investigation against which inferences from the fossil record can be tested.

For example, it has been suggested that the evolution of baleen-assisted filter feeding in early mysticetes was derived directly from raptorial feeding, via a transition involving both functional teeth and baleen [55,60]. Our framework challenges this idea, and instead suggests that the ancestors of modern mysticetes passed through both a suction feeding phase and a suction filter feeding phase (as exemplified by the grey whale) prior to evolving ram-based filtering. This interpretation is further supported by recent fossil evidence for suction feeding in archaic mysticetes [18,54], as well as the development of baleen after the decay of the tooth buds in extant mysticete fetuses [61,62]. Filter feeding enabled the mass exploitation of fish and krill and, ultimately, allowed for the evolution of such giants as the blue whale, *Balaenoptera musculus*, as well as the highly abundant crabeater seal [63]. Ultimately, the evolution of filter feeding may therefore indicate when aquatic mammals first began to impact ocean productivity via introduction of micronutrients to surface waters [10].

Likewise, our framework provides a straightforward explanation for the repeated evolution of suction feeding.

As a natural extension of behaviour already present in raptorial feeders, suction for capture allowed aquatic mammals to target infaunal prey, leading to the independent evolution of benthic specialists such as the walrus, the grey whale, the bearded seal, and the extinct, walrus-like odontocete *Odobenocetops* [32,47,64,65]. Suction is also widespread among cephalopod-eating pinnipeds and cetaceans, such as sperm and beaked whales, many of which are deep divers [1,19]. Repeated specialization for suction in these ancestrally raptorial taxa likely marks the beginning of concurrent moves into deep-sea foraging grounds [57,58,66], and it is possible that without its appearance aquatic mammals would not have been able to exploit this niche.

In addition to exploring the origins of highly specialized strategies, our framework informs interpretations of the initial transition to aquatic feeding. Thus, for example, raptorial 'pierce' or 'bite' feeding, as performed by fur seals, has been cited as the likely ancestral feeding mode for pinnipeds [11,67]. Based on our framework, we instead predict that the earliest pinnipeds used a semi-aquatic strategy more similar to modern otters. Evidence for this is provided by the oldest fossil pinniped, *Enaliarctos mealsi*, which retained cutting carnassial teeth and trochleated interphalangeal articulations that would have enabled it to grasp food using its forelimbs during prey processing [68]. *Enaliarctos* may even have routinely brought prey on to land to perform processing [69]. This feeding mode is clearly distinct to raptorial biting underwater using the jaws alone, and illustrates how viewing fossils within the context of our framework can help to guide palaeoecological interpretations.

Finally, our new framework informs the contribution of foraging behaviours to the feeding success of aquatic mammals within modern ecosystems. By switching feeding strategies, aquatic mammals may be able to reduce their foraging costs, while simultaneously maximizing hunting success for a given target prey or foraging environment [17,37]. The specific behaviours used at each stage of the feeding cycle influence key feeding parameters like pursuit and capture success, and handling-and-eating time [70]. In addition, species with a wider behavioural repertoire are able to exploit more varied prey types [37], and hence are likely better at adapting to changes in prey distribution or diversity. This is important within the context of global environmental change and the recovery time of species previously exploited by humans [71]. By describing the full range of behaviours

displayed at all stages of the feeding cycle, we hope that our new framework will make it easier to account for varying foraging costs, especially those associated with switching feeding strategies. This will allow more accurate modelling of ecosystem interactions and energy flow, and thus provide a clearer picture of the role of aquatic mammals within modern ecosystems.

Overall, this review shows that mammals feeding in water face challenges beyond those experienced by their terrestrial relatives, and thus need to be modelled and studied separately. A similar situation likely exists in other marine tetrapods, including marine birds and various kinds of reptiles. Our study helps to conceptualize the feeding behaviour of such groups, and demonstrates how doing so may provide broader, independent insights into ecology and evolution. Besides feeding, fundamental differences between terrestrial and aquatic regimes have also emerged in terms of locomotion [53,72] and sensory capabilities [73,74], with downstream effects on morphology and development (e.g. [75]). Future research may reveal to what degree adaptations in such different functional systems interacted to shape aquatic mammal evolution.

One key example of such an interaction might be the potential interplay between feeding behaviour and adaptations for swimming. Thus, reducing the role of the forelimb in prey capture and/or processing may have facilitated the evolution of dedicated flippers, which consequently would have become largely unsuitable for feeding purposes. Greater agility and speed then might then have provided access to smaller prey types, in turn driving feeding evolution towards suction and, later on, filtration. Ultimately, the availability of small prey opened up the possibility of bulk feeding, and likely helped to spur the rise of the largest animals on Earth.

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