

Invited reply



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Reply to comment by Kienle *et al.* 2017

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Kienle *et al.* [1] suggest amendments to our framework for feeding in predatory aquatic mammals [2]. Below we reply to their suggestions and demonstrate that they are fundamentally flawed from both a mechanical (feeding cycle, strategies) and an evolutionary perspective. They do, however, inspire an important addition to the range and structuring of capture behaviours encoded in our framework.

Feeding cycle. Our framework groups feeding behaviours with similar functions, such as capture and processing, and thus clarifies how different species perform similar tasks during feeding. Kienle *et al.* [1] suggest that these groupings should be broken up, with capture, ‘external’ processing and manipulation behaviours instead being clustered into a single ‘ingestion’ stage. We question the biological justification for lumping behaviours as disparate as chasing, killing and dismembering. Capturing prey is unrelated to, and need not be followed by, processing. By contrast, ‘external’ and intraoral processing behaviours are functionally akin, with both aiming to dismember prey to start the digestive process. Lumping capture and processing furthermore deviates from the most recent conceptualization of the tetrapod feeding cycle by Schwenk & Rubega [3], which, *contra* [1], both explicitly includes a separate capture/subjugation stage (p. 12) and specifically associates ‘external’ with intraoral processing (p. 21).

Besides the inclusion of water removal, our model differs from [3] only in not recognizing a separate ‘ingestion’ stage. This is because we view ingestion as a *moment* in time—namely, when food enters the mouth [4]—that can occur during multiple stages, and be achieved and reversed several times during feeding. By contrast, capture, manipulation and processing reflect *periods* of time over which specific behaviours are performed.

Feeding strategies. Kienle *et al.* [1] criticize our use of a semi-aquatic strategy by suggesting it arises circumstantially from an animal’s position in the water. Rather, semi-aquatic feeding requires that certain behaviours are performed *entirely* in air—probably because it is more efficient, or perhaps even necessary, for an animal to do so. An obvious example is otters catching fish underwater before processing them ashore (figure 1a), but semi-aquatic feeding also includes processing in air while floating at the surface (figure 1b,c; electronic supplementary material, video S1). Semi-aquatic feeding explicitly excludes events that generally occur entirely underwater. For example, a humpback whale may indeed feed near the surface, but will normally only do so if prey happens to aggregate there, or to use the air/water interface as a trap. Exposure to air is incidental, and in no way an integral part of the feeding event.

Hierarchical subdivision and clustering of feeding strategies, as proposed by Kienle *et al.* [1], is counterproductive for three reasons. Firstly, it complicates comparisons between feeding strategies and their respective component behaviours. Secondly, it downplays the fluid and versatile nature of feeding strategies, which is particularly pronounced in pinnipeds [5], and instead reinforces a narrow and inaccurate view that ties individual species to just a single strategy. Finally, it creates groupings that are, ultimately, entirely



Figure 1. Examples of semi-aquatic feeding in wild aquatic mammals. (a) *Aonyx capensis* chewing aquatic prey while ashore; (b) *Phoca vitulina* performing hold and tear processing in air at the surface; (c) *Arctocephalus pusillus doriferus* performing shake processing at the surface.

(a)

		I. prey capture		
prey approach		head strike	ram/prey chasing	suction
		<hr/>		
prey prehension		forelimb prehension	jaw prehension	engulfment

(b)

stage	behaviour	feeding strategies					
		terrestrial feeding	semi-aquatic feeding	raptorial feeding	suction feeding	suction filter feeding	ram filter feeding
I	capture						
	approach						
	prehension						
	head strike						
	ram/prey chasing						
	suction		?				
	forelimb prehension						
	jaw prehension						
	engulfment						

Figure 2. Revisions to the prey capture stage to be incorporated into our behavioural framework. See electronic supplementary material for revised glossary definitions, and electronic supplementary material, figures S1 and S2, for a full overview of the revised feeding cycle and framework.

arbitrary. For example, there is no *a priori* reason to group suction filter feeding with ram filter feeding (based on their shared water removal mechanism), rather than with suction feeding (based on their chief capture behaviour).

Terminology and structure. We disagree that ‘biting’ should replace ‘raptorial’, as it simply describes the act of closing the jaws—often over food, but sometimes also during agonistic behaviour or courtship. Furthermore, ‘biting’ fails to describe raptorial behaviours involving the forelimbs. Most importantly, however, Kienle *et al.* [1] define biting, and its suggested sub-strategies, based on single behaviours, like ‘seizing prey with the jaws, beak, and/or teeth’. This approach is counterproductive, as it obscures the distinction between strategies and behaviours, fails to apply insights from the tetrapod feeding cycle, and ignores the behavioural diversity encoded in our original framework.

Nevertheless, we agree that the act of biting should be included in our framework as an additional behaviour. Specifically, we propose to adopt the terms ‘jaw prehension’ (seizing prey between the jaws) [3] and ‘engulfment’ (engulfing prey entirely within the oral cavity) in a new ‘prey capture’ substage. The latter may follow an initial ‘approach’ phase, during which prey is brought within the range of the feeding apparatus via ram, head strikes or suction (figure 2). Other changes to our glossary proposed by [1] are discussed in the electronic supplementary material.

Evolutionary sequence. Kienle *et al.* [1] criticize our proposed ‘evolutionary continuum’ by misconstruing it as a predetermined sequence. Rather, our framework describes an observed pattern based on the similarities between different strategies, and arranges them in such a way that disjunct distributions (i.e. disappearances and reappearances) of particular component behaviours are minimized ([2], fig. 3). The result is a parsimonious sequence, or transformation series, which can be tested against the range of strategies actually employed by living species. In particular, we hypothesize that switching between strategies is easier when the latter involve similar behaviours, and thus also similar morphological and physiological requirements. For example, semi-aquatic feeders can often also feed raptorially, and some suction feeding species are also capable of filter feeding. By contrast, there is no living species using raptorial feeding and filtering *without* also being capable of suction, and no species capable of both semi-aquatic and suction feeding that does not also feed raptorially (figure 3).

There are two reasons why our behavioural framework can plausibly be extended to aquatic mammal evolution.

- (i) Semi-aquatic and raptorial feeding inherently differ from suction and filter feeding both in the large number of behaviours they share, and in the role water plays in the feeding cycle (figure 3*a,b*). Raptorial

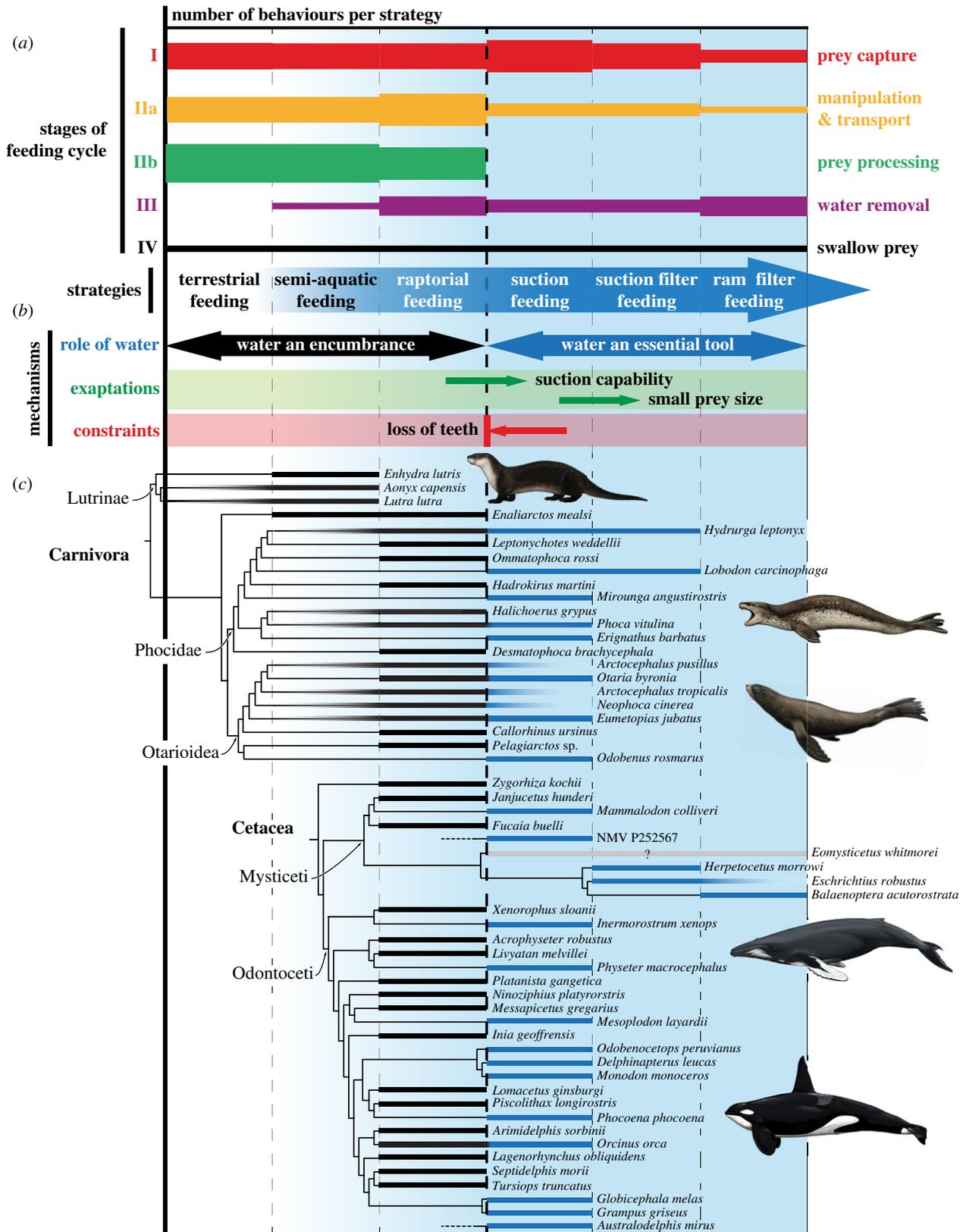


Figure 3. Sequence and directionality in the evolution of aquatic mammal feeding. (a) Relative importance of different parts of the feeding cycle for each strategy. The thickness of each bar reflects the number of component behaviours in our original framework ([2], fig. 3), including the new additions proposed in figure 2. (b) Mechanisms underlying the directionality of the evolutionary continuum implied by our framework. (c) Feeding strategies deployed by various aquatic mammals show the patterns expected from our framework when mapped on to a phylogenetic tree. Note the behavioural flexibility of most pinnipeds and the frequent emergence of suction feeding species from among raptorial clades. Data sources for (c) are listed in the electronic supplementary material, table S2. NMV, Museums Victoria (Melbourne, Australia).

feeding employs capture, manipulation and processing behaviours similar to terrestrial feeding, with water being mostly an encumbrance that needs to be dealt

with prior to swallowing. By contrast, suction and filter feeding specifically exploit the liquid properties of water to capture and retain prey (i.e. they are

inherently more 'aquatic'), and consequently offer access to areas of ecospace that are normally unavailable to terrestrial species [6]. This is analogous to locomotion in secondarily aquatic tetrapods, which displays repeated, convergent transitions from drag-based to lift-based swimming [7].

- (ii) Just like individual species may switch between related strategies, the evolution of a new feeding strategy is plausibly facilitated by relevant behavioural, morphological and physiological exaptations (figure 3*b*): the closer the ancestral feeding mode is to the new strategy, the more exaptations are likely to exist. Specifically, mammals are poised to cross the boundary between raptorial and suction feeding, given the prevalence of suction behaviour among raptorially feeding species [2,5]. Conversely, in cetaceans, a transition from suction back to raptorial feeding may be impeded—though not necessarily made impossible—by the loss of relevant capture and processing behaviours, as well as loss of functional teeth. A further, more subtle, exaptation may be related to prey size. For suction feeding to work, prey needs to be small enough to be drawn into the oral cavity, thus imposing smaller (relative) prey sizes than raptorial feeding [8,9]. Concurrently, suction allows the capture of much smaller prey than teeth or jaws alone can easily handle. Together, these prey size parameters create the basis for filter feeding, which can arise simply through the addition of a specialised filter (elaborate teeth or baleen).

Phylogenetics and the fossil record offer a chance to test predictions from our behavioural framework. For our hypothesis to be supported, our evolutionary sequence would have to occur whenever a lineage adapts to a new feeding strategy, irrespective of the frequency of such transitions across the tree. Given the exaptations and constraints described above, we furthermore expect a prevalence of transitions towards more aquatic feeding strategies, but do not rule out movements in the opposite direction. Current

evidence bears this out: suction feeding has arisen from seemingly raptorial ancestors in pinnipeds, sperm whales, beaked whales, delphinidans and archaic mysticetes (figure 3*c*). In both pinnipeds and mysticetes, this was followed by the emergence of (suction) filter feeding, although the feeding strategy of edentulous mysticetes is admittedly difficult to determine from fossil evidence alone. Finally, we are not aware of any purely raptorially feeding species arising from obligately suction feeding ancestors, supporting the presence of a backward constraint.

In summary, we conclude that the proposed amendments to our framework are unjustified. Feeding can, and should, be studied from a comparative point of view, rather than being forced into narrow and rigid hierarchies. Of course, our model is not absolute, and we cannot assert that the evolutionary continuum it entails applies in every case. Nevertheless, our framework is parsimonious, supported by observational data and grounded in evolutionary theory. Overall, it is perhaps best conceptualized as a 'path of least resistance' that most, or all, aquatic mammals have followed to some extent. Not all lineages have adopted suction and filtering, and nor do they need to, as their present strategies are obviously successful. Nevertheless, it is possible for particular species to be more specialized than others, and for specialization to follow well-trodden, convergent paths.

Data accessibility. Additional data and discussion are available as the electronic supplementary material.

Authors' contributions. All authors discussed the results and collaborated on writing the paper.

Competing interest. We declare we have no competing interests.

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