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Revisiting the behavioural framework of feeding in predatory aquatic mammals

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Hocking *et al*. [1] (hereafter HEA) present a framework for defining and evaluating feeding strategies in predatory aquatic mammals. While we appreciate the review, we address three difficulties with the framework: (i) the tetrapod feeding cycle needs minimal revision to accommodate aquatic mammals, (ii) the proposed feeding strategies need further clarification and (iii) evolution should not be described as a logical sequence. Our goal is to clarify and expand on HEA's feeding framework to ensure that predatory aquatic mammals can be examined in a comparative framework with other tetrapods.

First, HEA argue that the four stages of the tetrapod feeding cycle—ingestion, intraoral transport, processing and swallowing [2]—do not adequately address the problems faced by air-breathing aquatic mammals. HEA, therefore, propose an alternative feeding cycle: (I) prey capture, (IIa) prey manipulation and transport and (IIb) prey processing, (III) water removal and (IV) swallowing. These changes constrain our ability to compare feeding behaviour across tetrapod lineages. The tetrapod feeding cycle is already sufficiently flexible to accommodate behaviourally diverse clades, so we propose using the existing tetrapod feeding cycle [2] with some revisions based on HEA (figure 1).

In the tetrapod feeding cycle, ingestion encompasses all behaviours used to capture, subdue, kill and process prey before it enters the oral cavity [2]. Therefore, HEA's stages I, IIa and IIb are already included in ingestion and can distinguish between different behaviours prior to prey entering the mouth (figure 1). For example, sea otters (*Enhydra lutris*) dive to grab benthic prey (prey capture), move prey using their mouth/forepaws (prey manipulation) and use tools/teeth to open hard-shelled prey (external prey processing) [3]. Following the existing tetrapod feeding cycle, intraoral transport (movement of food inside the mouth towards the pharynx) occurs after ingestion and is followed by

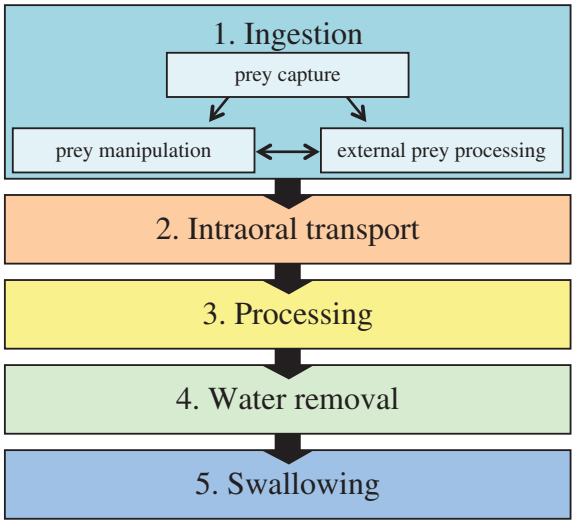

Figure 1. Modified feeding cycle of aquatic tetrapods based on Schwenk [2] and Hocking *et al*. [1]. (Online version in colour.)

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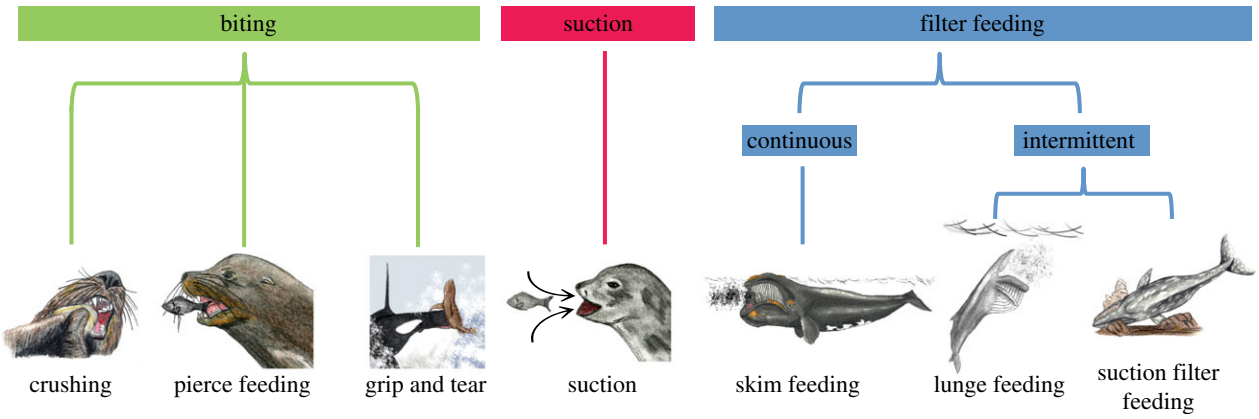

Figure 2. Overview of feeding strategies and subcategories in marine mammals. (Online version in colour.)

intraoral processing (mechanical breakdown of food inside the mouth) [2]. For most aquatic mammals, there is no intraoral processing [1,4,5]. However, there are exceptions, as a few species chew (some otariids) and others masticate (sea otters; electronic supplementary material, table S1) [1,6,7]. We agree with HEA's addition of a water removal stage, which is followed by swallowing (figure 1).

Under our revised framework, five stages—ingestion, intraoral transport, processing, water removal and swallowing—constitute the aquatic tetrapod feeding cycle (figure 1). This revision retains all tetrapod feeding cycle stages [2], subsumes HEA's stages I–II under ingestion and incorporates HEA's water removal stage. These changes allow aquatic mammals to be examined in the same framework as other tetrapods, while providing the flexibility to accommodate these behaviourally diverse lineages. These stages are not static; animals may not go through every feeding stage or follow this order during each feeding event, and each stage can encompass a range of behaviours.

Second, HEA describe five feeding strategies for predatory aquatic mammals: semi-aquatic, raptorial, suction, suction filter and ram filter feeding. The semi-aquatic strategy, defined as when some feeding behaviours are performed at the surface, does not follow the same convention as the other strategies because it is defined by an animal's position in the water column rather than the behaviour(s) used during the feeding cycle [1]. Under this definition, a humpback whale (*Megaptera novaeangliae*) lunge feeding would be classified as a filter feeder if underwater and as a semi-aquatic feeder if it surfaced during feeding. The classification of the same behaviour into two separate strategies leads us to conclude that semi-aquatic feeding is not valid and should not be used. The four other feeding strategies proposed by HEA are useful with some modifications. We have provided a revised glossary of terms (electronic supplementary material, table S1).

Based on the tetrapod literature, we suggest three feeding strategies for predatory aquatic mammals—suction, biting and filter feeding—accompanied by subcategories (figure 2). Suction is a common feeding strategy in aquatic mammals, and we agree with HEA's review.

We suggest that biting replace HEA's raptorial strategy because, while the terms are often used interchangeably, 'raptorial' is inconsistently defined; for example, raptorial refers to predatory behaviour [8], biting [1,5] or rapidly moving appendages [9]. We propose the addition of three subcategories under biting (figure 2): (i) crushing—prey are fragmented by the teeth during ingestion or intraoral processing. This is exemplified by sea otters using molars to break down hard-shelled prey [4,5]; (ii) grip and tear feeding—animals hold prey with the jaws/forelimbs, shake prey and/or rip off smaller pieces during ingestion. This category encompasses multiple behaviours, including shake feeding and hold and tear feeding [4,7,10], and has been documented in some odontocetes [11], pinnipeds [7,12], polar bears (*Ursus maritimus*) [13] and sea otters [6]; (iii) pierce feeding—animals bite prey during ingestion, often swallowing prey whole with little manipulation or external prey processing [10]. In pierce feeding, suction can be used in combination with biting to pull prey inside the mouth [14]; this has been described in some pinnipeds and odontocetes [5,15,16].

In filter feeding a specialized structure is used to trap prey in the mouth during water removal [5,17]. HEA define two separate strategies: suction filter feeding and ram filter feeding. We suggest nesting these terms under filter feeding and that the word 'ram' (engulfing prey via 'rapid acceleration of the whole body' [18]) be avoided when naming a feeding strategy because ram applies to most feeding strategies and is inconsistently used [1,16,17]. Under our framework, filter feeding is first subdivided into two types: continuous and intermittent (figure 2) [5,17,19]. Continuous filter feeders swim slowly and constantly through dense prey patches with their mouths open and the prey passively enters the oral cavity. Ingestion and water removal occur simultaneously [17]. This behaviour is also called skim feeding or continuous ram filter feeding and best exemplified by balaenid whales [1,5,17]. By contrast, intermittent filter feeders actively engulf a single mouthful of water during ingestion and remove water via filtering structures during a distinct water removal phase [17]. Intermittent filter feeding can be further subdivided into lunge and suction filter feeding based on the ingestion method (figure 2). Lunge feeding (also called intermittent ram filter feeding, gulping and ram gulping) is best exemplified by rorqual whales that swim rapidly at a prey patch while opening their mouths to draw in prey [5,17]. In suction filter feeding, animals such as gray whales (*Eschrichtius robustus*) [20] and some phocids [21,22] use suction to pull prey from the water or benthos into the mouth. These changes highlight the repeated evolution of a few feeding strategies in predatory aquatic mammals, while also emphasizing the diversity of behaviours within each strategy (figure 2).

Third, evolution is not a progression of linear events [23]. HEA use the phrases 'logical sequence' and 'evolutionary continuum' to describe the evolution of feeding strategies in

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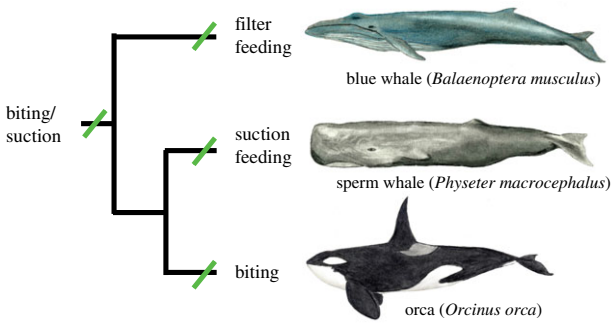

Figure 3. Example framework for understanding the evolution of feeding strategies in cetaceans under a tree-like process rather than a continuum. Biting, suction and filter feeding are contemporary feeding strategies in extant cetaceans. (Online version in colour.)

predatory aquatic mammals, as depicted in their figure 3. This incorrectly suggests that species have a tendency to become increasingly specialized or complex over time [23]. HEA state that filter feeding is the 'most highly specialized' aquatic feeding strategy, which falsely suggests that all aquatic mammals are predetermined to become filter feeders. This is not supported by the repeated evolution of biting and suction across these disparate aquatic mammal lineages (figure 3). Descriptions of individual feeding strategies as more or less aquatic should be avoided. All strategies used by aquatic mammals are aquatic and allow species to exploit different niches and prey densities (figure 3).

Our recommendations are to (i) adopt our revised tetrapod feeding cycle (figure 1), (ii) incorporate our revisions to the glossary (electronic supplementary material, table S1), (iii) use our feeding strategies and subdivisions (figure 2) and (iv) model the evolution of feeding as a tree-like process (figure 3). HEA's review and the comments that they have inspired provide a comprehensive framework that should be adopted to refine our understanding of predatory aquatic mammal feeding. Such a framework facilitates the investigation of ecological mechanisms and evolutionary processes in aquatic tetrapods.

Data Accessibility. Additional data are available as the electronic supplementary material.

Authors' contributions. All authors outlined the manuscript; S.S.K. drafted it; C.J.L. designed the figures; all authors edited the manuscript and gave final approval for publication.

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