Limb use by foraging marine turtles, an evolutionary perspective

Jessica A Fujii Corresp., [1], **Don McLeish** [2], **Andrew J Brooks** [3], **John Gaskell** [4], **Kyle S Van Houtan** [1,5]

[1] Monterey Bay Aquarium, Monterey, California, United States
[2] Hawaiian Hawksbill Conservation, Lahaina, Hawaii, United States
[3] Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California, United States
[4] Living Reef- Daydream Island, Whitsundays, Queensland, Australia
[5] Nicholas School of the Environment, Duke University, Durham, North Carolina, United States

Corresponding Author: Jessica A Fujii
Email address: jfujii@mbayaq.org

The exaptation of limbs for foraging is documented in both marine and terrestrial tetrapods. These behaviors are particularly unexpected in marine tetrapods due to the physical constraints of body plans adapted to locomotion in a fluid environment. Despite these obstacles, ten distinct types of limb-use while foraging have been previously reported in nine marine tetrapod families. Here, we add marine turtles to the diversity of marine tetrapods known to use limbs for foraging, and extend the evolutionary timeline of this behavior back 70 million years. Through direct observation and crowd-sourcing, we document a range of behaviors across habitats in three marine turtle species, suggesting its widespread occurrence. We argue the presence of these behaviors among marine tetrapods may be limited by limb mobility and evolutionary history, rather than foraging ecology or social learning. These behaviors may be remnant of ancestral forelimb use that have been maintained due to a semi-aquatic life history.

TITLE: Limb use by foraging marine turtles, an evolutionary perspective

AUTHORS: Jessica A. Fujii,[1] Don McLeish,[2] Andrew J. Brooks,[3] John Gaskell,[4] Kyle S. Van Houtan [1,5]

AFFILIATIONS:

[1] Monterey Bay Aquarium, Monterey, CA, USA;

[2] Hawaiian Hawksbill Conservation, Lahaina, HI, USA;

[3] Marine Science Institute, University of California, Santa Barbara, CA, USA;

[4] Living Reef - Daydream Island, Whitsundays, QLD 4802, Australia;

[5] Duke University, Nicholas School of the Environment, Durham, NC, USA.

Corresponding author: Jessica A. Fujii[1]

Email address: jfujii@mbayaq.org

Abstract.

The exaptation of limbs for foraging is documented in both marine and terrestrial tetrapods. These behaviors are particularly unexpected in marine tetrapods due to the physical constraints of body plans adapted to locomotion in a fluid environment. Despite these obstacles, ten distinct types of limb-use while foraging have been previously reported in nine marine tetrapod families. Here, we add marine turtles to the diversity of marine tetrapods known to use limbs for foraging, and extend the evolutionary timeline of this behavior back 70 million years. Through direct observation and crowd-sourcing, we document a range of behaviors across habitats in three marine turtle species, suggesting its widespread occurrence. We argue the presence of these behaviors among marine tetrapods may be limited by limb mobility and evolutionary history, rather than foraging ecology or social learning. These behaviors may be remnant of ancestral forelimb use that have been maintained due to a semi-aquatic life history.

Introduction.

Marine turtles, and most other marine tetrapods, have evolved body forms that are best suited to move, orient, and minimize drag in a fluid environment rather than using their articulating limbs to directly aid in prey capture or processing (Fish 2016). Due to the limitation of these evolved body plans and the constraints of the aquatic environment, Taylor (1987) predicted mouth-based filter, suction, or ram foraging to be the primary foraging mechanisms for all marine tetrapods. Although the evolution of foraging mechanisms generally coincides with associated morphological traits, such as filter feeding and baleen in Mysticete whales (Deméré et al. 2008), many species have been observed using innovative strategies counter to what their evolved body plans would predict. Following Gould & Vrba (1982) and Lloyd & Gould (2017), these traits would be considered exaptations; "traits that were adapted for one evolutionary function, but were later co-opted (but not selected) to serve a different role". Such exaptations can provide insight into an organism's current ecological dynamics (Gould & Vrba 1982) as well as the evolutionary conditions influencing these novel behaviors.

Given the predictions of Taylor (1987), a surprising number of marine tetrapods have been documented to use their limbs to directly aid in prey capture, manipulation, and processing (Iwaniuk & Whishaw 2000). Rudimentary limb-use for foraging is observed in a range of terrestrial and aquatic taxa. It likely evolved in ancestral tetrapods and was subsequently developed, maintained, or lost in different lineages over time (Iwaniuk & Whishaw 2000). For those lineages that lost the ability, the use of limbs to aid in foraging is often an exaptation – wherein limbs evolved for locomotion have been co-opted to be used in food handling (Gould & Vrba 1982). Such exaptations (hereafter limb exaptations) may improve foraging efficiency, expand ecological niches, and perhaps confer greater resiliency in dynamic or altered environments. Why these limb exaptations develop in some species, but not others, is not well understood. Hocking et al. (2017b) suggested less-specialized, semi-aquatic marine mammals (Mustelidae, Odobenidae, Otariidae, Phocidae) might retain the use of forelimbs to manipulate prey, but older and taxa more specialized for the aquatic environment like cetaceans would rely solely on suction, filter, or ram foraging.

Marine turtles (Cheloniidae) are the oldest extant line of marine tetrapods but some still maintain a semi-aquatic lifestyle for thermoregulation and breeding (Kelley & Pyenson 2015). Like many other marine tetrapods, marine turtles generally use suction or bite-and-tear foraging strategies to capture and process food (Moreno et al. 2016). To date, however, marine turtle foraging mechanisms have received little attention. While our knowledge of marine turtle diet has drastically improved over recent years with innovative technology (Arthur et al. 2007; Patel et al. 2016; Van Houtan et al. 2016) there are still many aspects of feeding behavior that are missed without direct observation. Here, we describe three marine turtle species – green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and loggerhead (*Caretta caretta*) – using limb exaptations in the wild, which have not been previously assessed. We set these observations in context with other marine tetrapods known to use their flippers, forelimbs, or tails as direct aids in obtaining or processing food and discuss the role of behavioral, morphological and ecological factors that may limit or promote this behavior.

Materials & Methods.

While viewing a fixed-station underwater video from a coral reef in Moorea, French Polynesia we opportunistically observed a hawksbill sea turtle use its limbs while foraging, prompting a broader survey for the occurrence and context of this behavior. We documented marine turtle foraging behavior from underwater surveys, web image and video searches (e.g., Google, YouTube, Vimeo, Flickr, Shutterstock), and the published literature. We aimed to document the presence of this behavior across marine turtle species, demographics, habitat, and prey types and to place it in the evolutionary context of other marine tetrapods.

For this study, limb-use for feeding was defined as the intentional use of flippers, paws, tails, or feet to directly aid in the capture, processing, or transport of the animal’s food while in the marine environment. We conducted web searches for video and images using the animal’s common name or common group (for example, “green turtle” or “sea turtle”) as well as feeding terms (e.g. “feeding”, “foraging”, “eating”). Once an initial record was found, we conducted more in-depth searches for that species or group to determine the ecological context of the behaviors. Feeding strategies were grouped into broad behavioral categories and feeding stages based previous study definitions (Hocking et al. 2017b), Table 1)

We defined marine tetrapods similar to previous studies (Kelley & Motani 2015; Kelley & Pyenson 2015). We excluded the polar bear (*Ursus maritimus*) as there is significant genetic admixture with a fully terrestrial species (Miller et al. 2012), and marine snakes as they lack external limbs. We initially included sea birds, yet limited observations to feeding occurring entirely in the marine environment. Foot-paddling, for example, is observed in a number of Laridae gulls, yet it occurs in terrestrial or mudflat habitats (Tinbergen 1962) and so was not included.

Due the difficulty of observing wild foraging behaviors for many marine tetrapods, the absence of limb-use while feeding documentation in this study does not indicate the behavior does not or cannot occur. In light of this, our intent was to be descriptive, not exhaustive, in comparing the occurrence of these behaviors. Due to the relative rarity of this behavior, we grouped marine tetrapods into families for comparisons. We broadly compared evolutionary, morphological, ecological, and behavioral factors to qualitatively determine if the presence of limb exaptations followed patterns across marine tetrapod families. Evolutionary relationships and divergence times are from Timetree.org (Hedges et al. 2006).

Results & Discussion.

Carr (1967) described hatch-year green turtles using the sharp claw on their foreflippers to swipe and tear food in captivity. Davenport & Clough (1985) similarly observed these behaviors in captive juvenile loggerhead turtles. However, both studies suggested these behaviors would be limited to juveniles due to undeveloped, weak jaws. Since these initial observations, there have been no additional study in wild juvenile or mature marine turtles. We documented limb exaptations in three species of marine turtle, and put these behaviors in a larger ecological and evolutionary context, with the knowledge that many more marine tetrapods may utilize similar strategies that have not yet been observed or documented. The diversity of limb exaptations observed and the conditions that appear to favor them suggests that using limbs to aid in feeding may be a more widespread strategy than previously believed.

In addition to the previously described digging observed in green turtles (Christianen et al. 2014), we found four types of limb exaptations by hawksbill, loggerhead, and green turtles. Hawksbill and green turtles were observed using corralling, leveraging, holding, and swiping to capture, process, or transport a variety of sponges, cnidarians, and macroalgae (figure 1a-d, f). We documented loggerhead sea turtles swiping to process benthic mollusks (figure 1e). Although these feeding strategies are not required to consume any of these prey items, they likely help improve feeding efficiency and niche breadth.

Limb-use while feeding has been previously reported in eight families of marine tetrapods including Balaenopteridae, Delphinidae, Trichechidae, Dugongidae, Mustelidae, Odobenidae, Otariidae, and Phocidae (figure 2). Within these families, ten types of limb-use for foraging has been observed: digging, striking, tossing, kerplunking, leveraging, swiping, holding, pounding, lobtailling, and corralling (Table 1). Holding and digging were the most common behaviors seen across families (Bowen et al. 2002; Hocking et al. 2017a; Kastelein & Mosterd 1989; Marshall et al. 2003; van Neer et al. 2015). Stunning prey included directly striking or tossing as well as indirect kerplunking and was seen only in Delphinids (Domenici et al. 2000; Gonzalez & Lopez 2000). Lobtail feeding is currently exclusive to humpback whales (Weinrich et al. 1992).

Some forms of limb use, while still noteworthy, would not be considered exaptations. Sea otters (*Enhydra lutris*) demonstrated the most diverse and complex forms of limb-use for foraging, including pounding prey against tools (Fujii et al. 2014). However, unlike other marine tetrapods, the use of forelimbs by sea otters is likely a true adaptation (Fabre et al. 2015). To our knowledge, limb exaptations have not been documented in any other marine tetrapods, but future studies may reveal currently undescribed behaviors.

Although flipper morphology and foraging ecologies likely evolved via convergent evolution across marine tetrapods (Kelley & Motani 2015; Kelley & Pyenson 2015) it is noteworthy that this exaptation has potentially developed repeatedly in marine tetrapods. Iwaniuk & Whishaw (2000) showed that rudimentary limb use likely first evolved in ancestral tetrapods but was subsequently maintained, developed, or lost in various lineages over time. It is, therefore, possible that the predisposition for this ancestral behavior was maintained as tetrapods returned to the marine environment and manifests under appropriate modern conditions.

Unlike other foraging strategies, that can be analyzed via skull structure in extinct and extant species (Motani et al. 2015), it is currently unknown if there are any detectible physical predictors of limb-use that could be used for studying the origin of this behavior. As marine turtles do not have opportunities for social learning, these behaviors either develop via independent trial and error, or are maintained as an innate behavior (Lutz et al. 2002). Several species of terrestrial or semi-aquatic turtles have also been documented using their forelimbs to assist in processing food (Davenport et al. 1984; Lutz et al. 2002), but the limbs of these species are not as specialized as marine turtle foreflippers. This does, however, support the suggestion that this behavior was present in an ancestral turtle. If this behavior was present when marine turtles evolved, approximately 120 million years ago, then these limb exaptations have been present in the marine environment almost 70 million years before all other extant marine tetrapods (Bowen et al. 1993; Kelley & Pyenson 2015).

We compared the prey type, relative prey size, and habitat across the marine tetrapods listed above to determine if distinct ecological factors promoted the development of limb exaptations (electronic supplemental material table S1). Surprisingly, limb exaptations were observed in a wide variety of conditions. Benthic feeders consumed bivalves, grasses, macroalgae, sponges, anemones, and hard corals. Pelagic feeders consumed fish, jellyfish, and small marine mammals. Prey size often exceeded gape size (precluding whole consumption) but relatively smaller prey were also consumed, and included both mobile and sessile species. These factors may still be important factors at the species level, but did not remain constant across marine tetrapod families.

Unlike prey and habitat type, limb mobility may play a larger role in the development of limb exaptations. Foreflipper mobility varies across marine tetrapods due to trade-offs for maneuverability, stability, or propulsion (Fish 2004). Taylor (1987) suggested that the constant need of foreflippers for locomotion and stability in the marine environment would limit their availability for other uses, including foraging. Although foreflippers used in propulsion have greater mobility compared to the foreflippers of taxa that use hindlimbs as the primary source of propulsion (Fish 2004; Kelley & Pyenson 2015), we found limb exaptations by species that used both forms of propulsion (electronic supplemental material, table S1). The limited mobility of foreflippers may prompt the use of tails for limb exaptations in Delphinidae and Balaenopteridae cases. The limited mobility of forelimbs may also explain the lack of limb exaptations by penguins and other cetacean families. Of the marine turtle foraging observations we report, all save one (figure 1b) involved foreflipper pronation movements. Figure 1b instead shows foreflipper supination while holding prey. Foreflipper pronations are the dominant mechanism marine turtles employ for swimming, crawling on land, excavating body pits for nesting, and aiding thermoregulation while basking (Van Houtan et al. 2015).

The regular use of limbs for tasks beyond swimming may also promote the development of limb exaptations. As noted in Hocking et al. (2017b), limb use was more common in semi-aquatic mammals who may also use forelimbs for locomotion on land. In marine turtles, although predominately aquatic, females must return to land for nesting. Additionally, terrestrial basking by marine turtles is considered a female-biased behavior (Van Houtan et al. 2015). The wider range of flipper-use by female marine turtles may also result in a female sex-bias in limb exaptations. From our observations, we identified all hawksbills to be females, but were unable to determine the sex of the other turtles due to visibility in photos or video.

Conclusions.

The use of limbs to directly aid in foraging *a priori* is an unexpected strategy used by a variety of marine tetrapods. Despite being the oldest extant line of marine tetrapods, this is the first time such a wide range of limb use has been described in marine turtles. We argue that these limb exaptations across marine tetrapods are limited by limb mobility and that the frequent use of forelimbs for other behaviors may promote the development of these feeding strategies. These observations provide additional insight into the diversity and possible evolution of this exaptated behavior.

Acknowledgements.

J. Goldbogen, J. Moxley, M. Staedler, T. Nicholson, M. Murray, A. Johnson, L. Henkel and two anonymous reviewers improved earlier versions of this manuscript. The Coonamessett Farm Foundation provided underwater video.

REFERENCES

Arthur KE, O'Neil JM, Limpus CJ, Abernathy K, and Marshall G. 2007. Using animal-borne imaging to assess green turtle (Chelonia mydas) foraging ecology in Moreton Bay, Australia. *Marine Technology Society Journal* 41:9-13.

Bowen BW, Nelson WS, and Avise JC. 1993. A molecular phylogeny for marine turtles: trait mapping, rate assessment, and conservation relevance. *Proceedings of the National Acadeny of Sciences USA* 90:5574-5577.

Bowen W, Tully D, Boness D, Bulheier B, and Marshall G. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* 244:235-245. http://www.jstor.org/stable/24866378

Christianen MJ, Herman PM, Bouma TJ, Lamers LP, van Katwijk MM, van der Heide T, Mumby PJ, Silliman BR, Engelhard SL, and van de Kerk M. 2014. Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proc R Soc London B: Biol Sci* 281:20132890. 10.1098/rspb.2013.2890

Davenport J, and Clough W. 1985. The use of limbscales of "pseudoclaws" in food handling by young loggerhead turtles. *Copeia* 1985:786-788. 10.2307/1444774

Davenport J, Munks SA, and Oxford PJ. 1984. A comparison of the swimming of marine and freshwater turtles. *Proceedings of the Royal Society of London Series B Biological Sciences* 220:447-475. 10.1098/rspb.1984.0013

Deméré TA, McGowen MR, Berta A, and Gatesy J. 2008. Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete whales. *Systematic Biology* 57:15-37. https://doi.org/10.1080/10635150701884632

Domenici P, Batty RS, Simila T, and Ogam E. 2000. Killer whales (Orcinus orca) feeding on schooling herring (Clupea harengus) using underwater tail-slaps: kinematic analyses of field observations. *Journal of Experimental Biology* 203:283-294.

Fabre A-C, Cornette R, Goswami A, and Peigné S. 2015. Do constraints associated with the locomotor habitat drive the evolution of forelimb shape? A case study in musteloid carnivorans. *Journal of Anatomy* 226:596-610. 10.1111/joa.12315

Fish FE. 2004. Structure and mechanics of nonpiscine control surfaces. *IEEE Journal of Oceanic Engineering* 29:605-621. 10.1109/JOE.2004.833213

Fish FE. 2016. Secondary Evolution of Aquatic Propulsion in Higher Vertebrates: Validation and Prospect. *Integrative and Comparative Biology* 56:1285-1297. https://doi.org/10.1093/icb/icw123

Fujii JA, Ralls K, and Tinker MT. 2014. Ecological drivers of variation in tool-use frequency across sea otter populations. *Behavioral Ecology* 26:519-526.

Gonzalez AF, and Lopez A. 2000. 'Kerplunking': Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science* 16:646-653. 10.1111/j.1748-7692.2000.tb00959.x

Gould SJ, and Vrba ES. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4-15. https://doi.org/10.1017/S0094837300004310

Hedges SB, Dudley J, and Kumar S. 2006. TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* 22:2971-2972. 10.1093/bioinformatics/btl505

Hocking DP, Ladds MA, Slip DJ, Fitzgerald EMG, and Evans AR. 2017a. Chew, shake, and tear: Prey processing in Australian sea lions (Neophoca cinerea). *Marine Mammal Science* 33:541-557. 10.1111/mms.12384

Hocking DP, Marx FG, Park T, Fitzgerald EMG, and Evans AR. 2017b. A behavioural framework for the evolution of feeding in predatory aquatic mammals. *Proceedings of the Royal Society B: Biological Sciences* 284. 10.1098/rspb.2016.2750

Iwaniuk AN, and Whishaw IQ. 2000. On the origin of skilled forelimb movements. *Trends in Neurosciences* 23:372-376. https://doi.org/10.1016/S0166-2236(00)01618-0

Kastelein RA, and Mosterd P. 1989. The excavation technique for molluscs of Pacific Walruses (Odobenus rosmarus divergens) under controlled conditions. *Aquatic Mammals* 15.
Kelley NP, and Motani R. 2015. Trophic convergence drives morphological convergence in marine tetrapods. *Biology Letters* 11:20140709. 10.1098/rsbl.2014.0709
Kelley NP, and Pyenson ND. 2015. Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* 348. 10.1126/science.aaa3716
Lloyd EA, and Gould SJ. 2017. Exaptation Revisited: Changes Imposed by Evolutionary Psychologists and Behavioral Biologists. *Biological Theory* 12:50-65. 10.1007/s13752-016-0258-y
Lutz PL, Musick JA, and Wyneken J. 2002. *The biology of sea turtles*. New York: CRC press.
Marshall CD, Maeda H, Iwata M, Furuta M, Asano S, Rosas F, and Reep RL. 2003. Orofacial morphology and feeding behaviour of the dugong, Amazonian, West African and Antillean manatees (Mammalia: Sirenia): functional morphology of the muscular-vibrissal complex. *Journal of Zoology* 259:245-260. 10.1017/S0952836902003205
Miller W, Schuster SC, Welch AJ, Ratan A, Bedoya-Reina OC, Zhao F, Kim HL, Burhans RC, Drautz DI, Wittekindt NE, Tomsho LP, Ibarra-Laclette E, Herrera-Estrella L, Peacock E, Farley S, Sage GK, Rode K, Obbard M, Montiel R, Bachmann L, Ingólfsson Ó, Aars J, Mailund T, Wiig Ø, Talbot SL, and Lindqvist C. 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. *Proc Nat Acad Sci USA* 109:E2382–E2390. 10.1073/pnas.1210506109
Moreno AF, Escalona VHC, Rguez-Baron JM, Ruiz MG, and Hart CE. 2016. Functional morphology in marine turtle skulls. In: Rquez-Baron JM, Lara-Uc M, and Rodriguez RR, eds. *Advances in research techniques for the study of sea turtles*. New York: Nova Publishers, 1-26.
Motani R, Chen X-h, Jiang D-y, Cheng L, Tintori A, and Rieppel O. 2015. Lunge feeding in early marine reptiles and fast evolution of marine tetrapod feeding guilds. *Scientific Reports* 5. 10.1038/srep08900
Patel SH, Dodge KL, Haas HL, and Smolowitz RJ. 2016. Videography Reveals In-Water Behavior of Loggerhead Turtles (Caretta caretta) at a Foraging Ground. *Frontiers in Marine Science* 3. 10.3389/fmars.2016.00254
Taylor MA. 1987. How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society* 91:171-195.
Tinbergen N. 1962. Foot-paddling in gulls. *British Birds* 55:117-120.
Van Houtan KS, Andrews AH, Jones TT, Murakawa SKK, and Hagemann ME. 2016. Time in tortoiseshell: a bomb radiocarbon-validated chronology in sea turtle scutes. *Proceedings of the Royal Society B: Biological Sciences* 283. 10.1098/rspb.2015.2220
Van Houtan KS, Halley JM, and Marks W. 2015. Terrestrial basking sea turtles are responding to spatio-temporal sea surface temperature patterns. *Biology Letters* 11. 10.1098/rsbl.2014.0744
van Neer A, Jensen LF, and Siebert U. 2015. Grey seal (Halichoerus grypus) predation on harbour seals (Phoca vitulina) on the island of Helgoland, Germany. *Journal of Sea Research* 97:1-4. https://doi.org/10.1016/j.seares.2014.11.006
Weinrich MT, Schilling MR, and Belt CR. 1992. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, Megaptera novaeangliae. *Animal Behaviour* 44:1059-1072. https://doi.org/10.1016/S0003-3472(05)80318-5

Table 1(on next page)

(on next page)

Functional definitions of observed types of limb use by feeding marine tetrapods.

ᶧFeeding behaviors fell in one of three categories of feeding stages: capture, processing, and transport based on Hocking et al. (2017b).

BEHAVIOR	FEEDING STAGE[ǂ]	DEFINITION
Digging	Capture	Using one or both flippers or paws to remove benthic sediment in order to access benthic food.
Striking	Capture	Using one or both flippers, or tail, to forcibly hit prey, usually to stun.
Tossing	Capture	Using flipper or tail to project prey into the air, usually used to stun prey.
Kerplunking	Capture	Slapping water surface with tail to cause a startle response in prey to aid in capture.
Leveraging	Processing	Placing one or both flippers against benthic substrate to create tension while pulling food from substrate with mouth.
Swiping	Processing	Moving one flipper against food to create tension while tearing food into smaller pieces with mouth.
Holding	Processing	Using both flippers to keep food in place, either by squeezing flippers or gripping with claws while pulling food apart with mouth.
Pounding	Processing	Using both flippers or paws to hold food while rapidly hitting against another object.
Corralling	Transport	Using one or both flippers to guide loose food in a directed manner toward mouth.
Lobtailing	Transport	Slapping water surface with tail during bubble-net feeding to corral prey together.

Figure 1

Limb use in marine turtle foraging

(*A*) A hawksbill sea turtle holding a lobe coral (*Porites lobata*) to eat the black-brown protein sponge (*Chondrosia chucalla*) clinging to its surface in Kahekili, Maui USA, taken March 2010. (*B*) A green turtle holding a mosaic jellyfish (*Thysanostoma thysanura*) in the water column near the ocean surface in the Similan Islands, Thailand, taken June 2017 (©Rich Carey/Shutterstock.com). (C) A hawksbill sea turtle leveraging against the reef substrate to pry away a magnificent sea anemone (*Heteractis magnifica*). This was a frame grab from a video in Cook's Bay, Moorea, French Polynesia from June 2013. (*D*) A green turtle leveraging against the reef substrate to pry away bites of red macroalgae (*Amansia glomerata*) in Kahekili, Maui, taken October 2016. (*E*) A loggerhead sea turtle swiping the shell of an Atlantic deep-sea scallop (*Placopecten magellanicus*) while it consumes the edible tissue. This is a frame grab from a video in the mid-Atlantic Bight USA taken on July 2009 and available courtesy of the Coonamessett Farm Foundation (Patel et al. 2016). (*F*) A green turtle swiping the stinging jellyfish (*Cyanea barkeri*) in the water column at Hook Island, Queensland, Australia, taken June 2017. Image credits by the authors, save (*B*) ©Rich Carey/Shutterstock.com and (*E*) Coonamessett Farm Foundation.

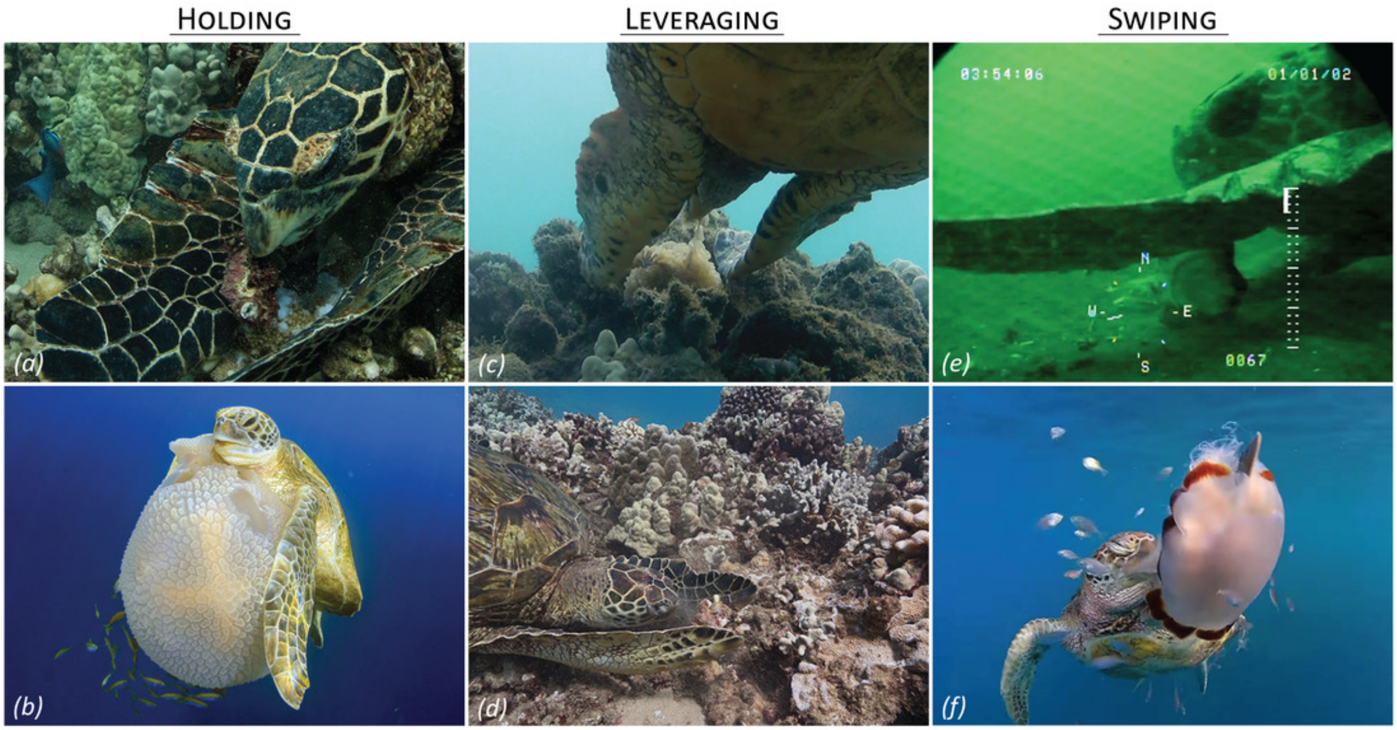
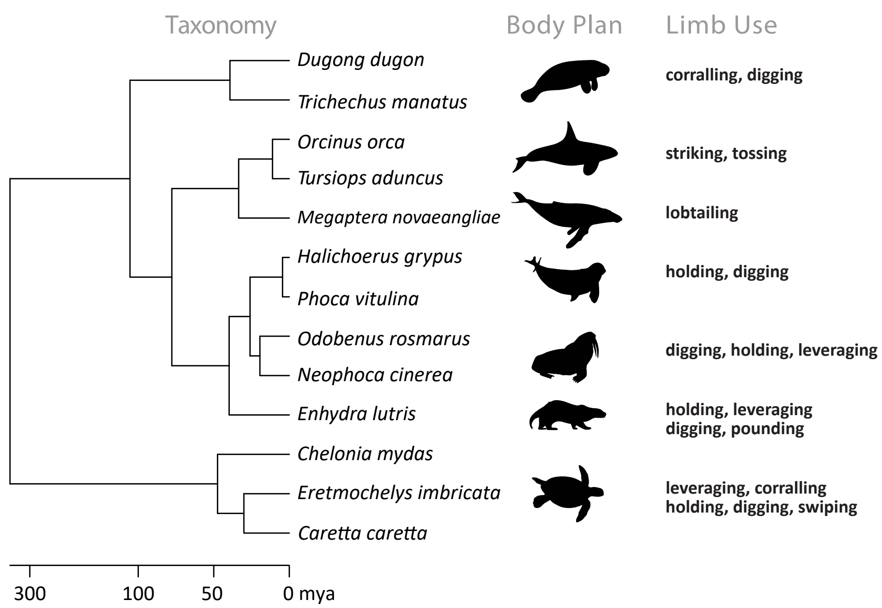

HOLDING
LEVERAGING
SWIPING
(a)
(b)
(c)
(d)
(e)
(f)
03:54:06
01/01/02
N
W
E
S
0067

Figure 2 (on next page)

Evolutionary links between marine tetrapods known to use limbs while feeding and the diversity of body plans and types of limb use

Silhouettes show a representative body plan for each family. Specific feeding behaviors are listed for each family.


Taxonomy
Body Plan
Limb Use
Dugong dugon
Trichechus manatus
corralling, digging
Orcinus orca
Tursiops aduncus
striking, tossing
Megaptera novaeangliae
lobtailing
Halichoerus grypus
Phoca vitulina
holding, digging
Odobenus rosmarus
Neophoca cinerea
digging, holding, leveraging
Enhydra lutris
holding, leveraging
digging, pounding
Chelonia mydas
Eretmochelys imbricata
Caretta caretta
leveraging, corralling
holding, digging, swiping
300
100
50
0 mya