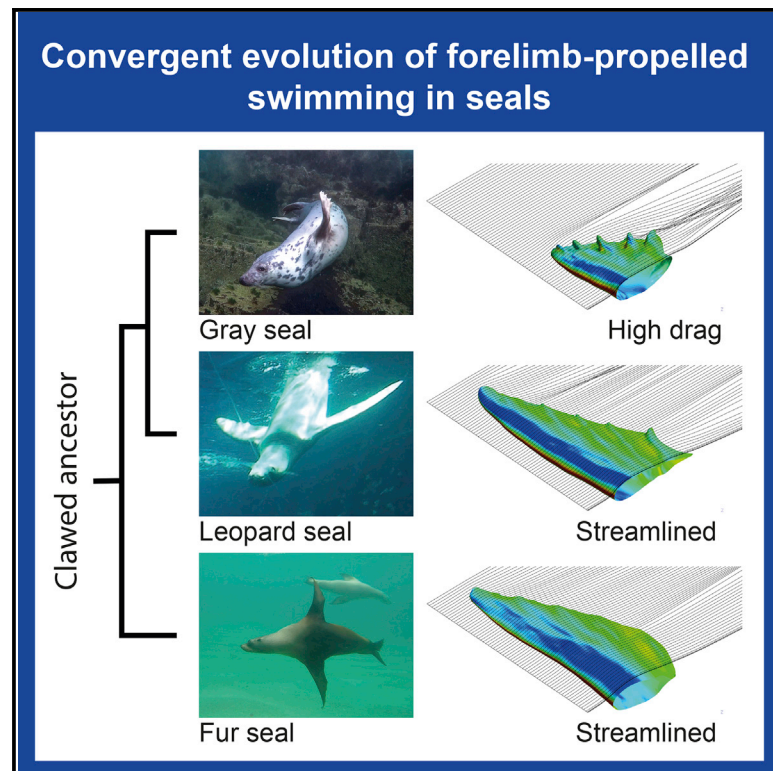


Current Biology

Convergent evolution of forelimb-propelled swimming in seals

Graphical abstract



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In brief

Hocking et al. combine 3D anatomy, behavior, and computational fluid dynamics to reveal how forelimb-propelled swimming evolved multiple times in pinnipeds (seals and sea lions). They show that all pinniped forelimb swimmers derive from foot-propelled ancestors, thus resolving a longstanding mystery at the heart of pinniped evolution.

Highlights

- The origin of forelimb swimming in fur seal and sea lions is an enduring mystery
- Southern true seals (Monachinae) independently evolved sea lion-like flippers
- Fluid dynamics modeling demonstrates convergence in both form and function
- Like monachines, fur seals and sea lions evolved from a hindlimb-propelled ancestor



Report

Convergent evolution of forelimb-propelled swimming in seals

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SUMMARY

Modern pinnipeds (true and eared seals) employ two radically different swimming styles, with true seals (phocids) propelling themselves primarily with their hindlimbs, whereas eared seals (otariids) rely on their wing-like foreflippers.^{1,2} Current explanations of this functional dichotomy invoke either pinniped diphyly^{3–5} or independent colonizations of the ocean by related but still largely terrestrial ancestors.^{6–8} Here, we show that pinniped swimming styles form an anatomical, functional, and behavioral continuum, within which adaptations for forelimb swimming can arise directly from a hindlimb-propelled bauplan. Within phocids, southern seals (monachines) show a convergent trend toward wing-like, hydrodynamically efficient forelimbs used for propulsion during slow swimming, turning, bursts of speed, or when initiating movement. This condition is most evident in leopard seals, which have well-integrated foreflippers with little digit mobility, reduced claws, and hydrodynamic characteristics comparable to those of forelimb-propelled otariids. Using monachines as a model, we suggest that the last common ancestor of modern seals may have been hindlimb-propelled and aquatically adapted, thus resolving the apparent contradiction at the root of pinniped evolution.

RESULTS

Flipper anatomy

Pinniped forelimbs show notably divergent degrees of adaptation for swimming (Figure 1). Northern true seals (phocines), here exemplified by gray seals (*Halichoerus grypus*), retain clawed paws resembling those of terrestrial carnivorans, like bears. Their fingers can spread out, curl, and are supported by robust bones with strongly trochleated joints. However, unlike in terrestrial carnivorans, the first digit is the longest and all the fingers are connected by thin webbing. Both these features increase the surface area of the paw and allow it to turn into a somewhat triangular paddle adept at pushing water.

Otariids like New Zealand fur seals (*Arctocephalus forsteri*) have diverged further from their ancestral bauplan. Their

forelimbs effectively lack claws and are stretched into a wing-like flipper with a high aspect ratio. The first metacarpal is notably elongate and straight, rather than curved as in gray seals. In addition, there is a marked decrease in length from the first digit to the fifth, causing the flipper to taper distally. The distal phalanges bear cartilaginous extensions that further lengthen the flipper and create a flexible trailing edge.⁹ The finger bones are flattened and connected by simplified joints with reduced mobility. Instead of webbing, the space between the digits is padded with thick connective tissue, which nearly locks the fingers in place and gives the flipper a smooth, teardrop-shaped cross section.

Southern true seals (monachines) fall along an anatomical gradient between these two extremes,^{10,11} corroborating an earlier quantitative study on pinniped limb proportions

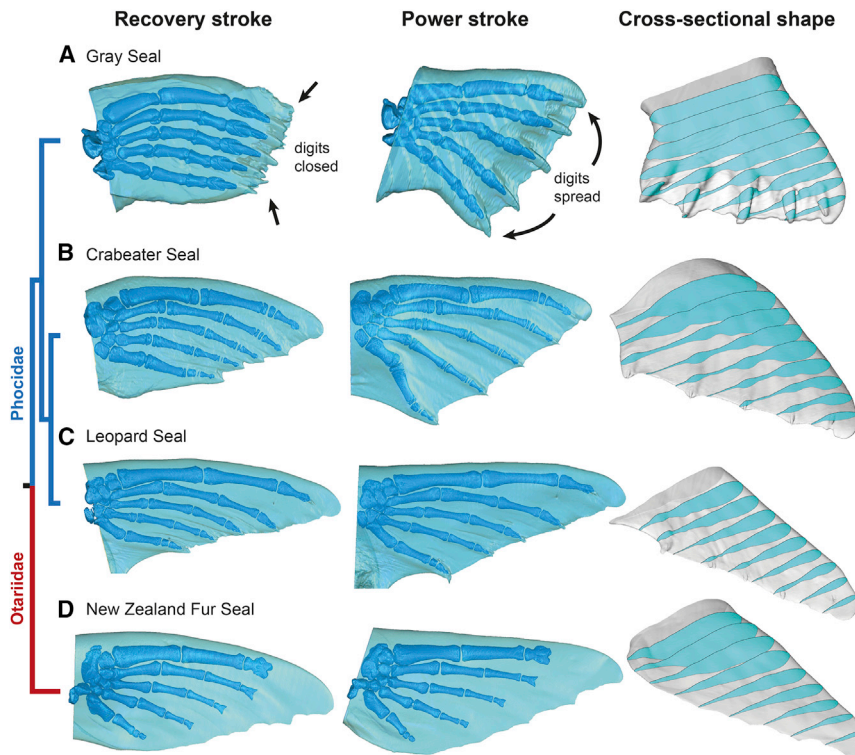


Figure 1. Variation in the anatomy and dexterity of seal flippers

Computed tomography (CT)-derived 3D flipper models of (A) a gray seal, *Halichoerus grypus* (NHMUK ZD.2018.144); (B) a crabeater seal, *Lobodon carcinophaga* (NMV C38154); (C) a leopard seal, *Hydrurga leptonyx* (NMV C39957); and (D) an NZ fur seal, *Arctocephalus forsteri* (NMV C40065). The flippers are shown with the fingers relaxed (left) and splayed out (center), both in dorsal view, reflecting the recovery and powered phases of a swimming stroke. The column on the right shows the flippers in posterodorsolateral view, with cross sections to highlight their different degrees of streamlining. Recovery stroke images of left flippers in (A), (B), and (D) are mirrored to provide a consistent orientation with the spread right flippers. For (C), a left flipper was scanned in both postures, and so all three images are mirrored.

(Figure S1).¹² Toward the phocine end of the spectrum, crabeater seals (*Lobodon carcinophaga*) retain the ability to spread the digits but have small claws, simplified finger joints, and a distally tapering flipper. The first metacarpal is elongate but curved, and the fingers gradually decrease in length, but not as much as in otariids. There are no cartilaginous extensions. In cross section, the surface of the flipper appears smoother than in phocines, but thin webbing means depressions between the digits remain evident.

Closer to the otariid extreme, leopard seals (*Hydrurga leptonyx*) have an even more elongate, wing-like flipper. Their fingers decrease in length far more strongly than in crabeater seals and are largely fixed in position by thick pads of interdigital soft tissue. The claws are small, the finger joints simple, and the first metacarpal is both elongate and straight. Distally, the first digit supports a flap of soft tissue that extends beyond the level of the claw. In cross section, there is almost no height difference between the finger bones and interdigital padding, resulting in a smooth, almost teardrop-shaped outline.

Swimming behavior

Phocids and otariids are thought to employ fundamentally different swimming styles, with phocids propelling themselves with their feet, whereas otariids rely on their foreflippers.¹ In both cases, the other pair of limbs is thought to help mostly with steering. Contrary to this traditional interpretation, our observations suggest that phocid and otariid swimming styles are part of a single behavioral continuum.

Propulsive forelimb strokes frequently form part of the behavioral repertoire of true seals, as evident from our footage of gray seals, harbor seals (*Phoca vitulina*), Hawaiian monk seals

(*Neomonachus schauinslandi*), and leopard seals (Figures 2A–2C; Video S1). They are used extensively during slow swimming (e.g., interactions with conspecifics, prey, or objects on the seafloor) to provide rapid acceleration out of a turn and to generate bursts of speed in conjunction with the feet.^{1,13–15} In addition, both phocids and otariids employ their forelimbs during sudden braking maneuvers (e.g., at pool edges or when approaching conspecifics) by pitching and extending them to increase drag (Figure 2D; Video S1).

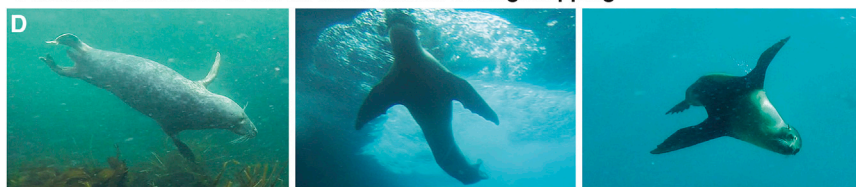
The basic structure of the phocid forelimb stroke resembles that of otariids (Video S1)^{2,16} but differs in terms of the propulsive surface: whereas the shape of otariid flippers is largely fixed, phocids spread their digits during the power stroke and then relax them during recovery to minimize drag.^{13,15} In phocines (e.g., gray seals), a stroke starts with the forelimbs resting against the trunk, with the paws relaxed and pointing backward. The arms are then abducted and raised until they extend almost at right angles from the body, and the paws remain closed and trail behind (Figures 2A and 2E). Once the arms are fully extended, the paws abruptly pivot forward and the fingers splay out, revealing the webbing between them. Finally, the forelimbs are forcefully moved downward and adducted toward the abdomen, with the splayed paws acting as paddles (Figure 2B). As the arms come to rest, the fingers relax in preparation for the next stroke (Figure 2C). Monachines follow the same pattern but generally have less digital flexibility and more streamlined flippers. As a result, their forelimb stroke is even closer to that of otariids, with the resemblance being particularly obvious in leopard seals.

Like propulsive forelimb strokes, hindlimb behavior also shows some common patterns across all seals. As is widely acknowledged,¹ phocids mostly use their feet for propulsion. During turns, however, they sometimes also employ them as a rudder, with both feet splayed out as seen in otariids (Figure 2E). Similarly, the hindlimbs of otariids are generally used for steering^{17,18} but, in some instances, complement

Forelimb propulsive stroke



Forelimbs extended to act as water brakes during stopping



Turn using feet as a rudder


Figure 2. Seals use the same repertoire of swimming behaviors, irrespective of their main method of propulsion

(A–C) Different stages of a propulsive forelimb stroke in a gray seal (left), leopard seal (center), and NZ fur seal (right). Note the almost identical structure of the stroke across the three species.

(D) Use of the extended and rotated forelimb as a water brake.

(E) Use of the splayed feet as a rudder during turns. Again, note the similar structure of this behavior across the species.

To view footage, please see [Video S1](#). Video timecodes are at 50 frames per second.

(Figures 3 and 4). Compared to gray seals, less of the total drag is caused by the shape of the flipper (65.6% at AoA_N), suggesting better streamlining. The main flow structures are the equivalent of wing-tip vortices, which arise from the pressure difference between the upper and lower flipper surfaces.

Monachines once again occupy an intermediate position, with their smaller claws and less-mobile fingers creating a more streamlined flipper surface and therefore less drag than in phocines (Figures 3 and 4). At the same time, the higher aspect ratio of their flipper produces a thinner wake and enables lift generation. Consistent with their more streamlined flipper anatomy, leopard seals outperform crabeater seals in terms of less overall drag and better streamlining (Figures 3 and 4).

Overall, the lift and drag profiles of all species show similar trends recalling engineered airfoils and cetacean flippers.¹⁹ The drag profiles of the clawed and clawless gray seals are symmetric and rather similar, although the latter performs slightly better at negative angles of attack. By contrast, drag associated with the streamlined forelimbs of crabeater, leopard, and New Zealand (NZ) fur seals increases disproportionately at $AoAs > 20^\circ$. This asymmetry likely reflects shape differences between the dorsal and ventral flipper surfaces and is absent in gray seals because of their separation-dominated wake. Increased drag at high $AoAs$ is likely a side product of the relatively large surface area of the flipper but may also promote the use of the forelimb for midwater braking (Figure 2D).

Lift coefficients (C_L) and hydrodynamic efficiency are again similar and largely symmetric in the two gray seals, with the clawless one being slightly more efficient (Figure 4A). By contrast, both measures are asymmetric in the remaining species and only fall to zero at slightly negative angles of attack (Table S1; Kulkarni and Leftwich, 2017, APS Div. Fluid Dyn., abstract). Maximum lift and efficiency are higher, and achieved at smaller $AoAs$, in crabeater ($C_{L,max} = 0.89$ at $AoA = 15^\circ$), leopard (0.72 at 10°), and NZ fur seals (0.74 at 15°) than in gray seals (0.49 at 40°). The lift profiles of these three species show higher

the forelimb propulsion via phocid-like propulsive strokes (Video S1).

Hydrodynamic performance

Computational fluid dynamics reveal a stark contrast between the paw-like forelimb of phocines and the wing-like flippers of monachines and otariids (Figure 3). Across all species, minimum drag generally is achieved at, or very close to, an angle of attack (AoA) of 0° , whereas neutral lift (AoA_N) occurs between -3.2° and 0.89° (Figure 4). At an AoA of 0° , the prominent claws of gray seals introduce strong vortices into the wake and limit hydrodynamic efficiency, as shown by drag being especially high along the center of the paw (Figure 4B). Additional support for this observation comes from a hypothetical clawless gray seal, which experiences notably less drag than its real-life counterpart (Figure 4B).

Despite their comparatively short span, gray seal paws induce a high rate of kinetic energy loss due to turbulence within the wake and experience high drag. The latter is parasitic and mostly related to the bluntness of the paw (87.13% at AoA_N), suggesting poor streamlining. By contrast, flow around the flipper of otariids is smooth, resulting in a thin wake and considerably less drag

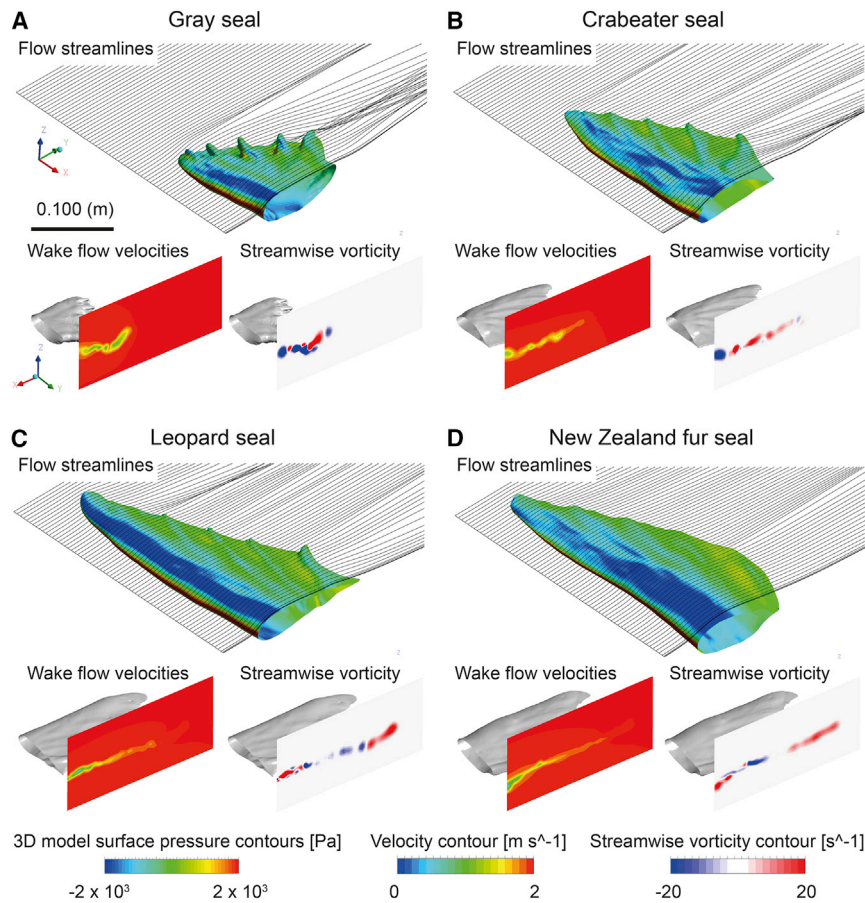


Figure 3. Flow fields visualize a functional transition series toward greater streamlining

Flow field surrounding the flippers of (A) a gray seal, (B) a crabeater seal, (C) a leopard seal, and (D) an NZ fur seal (all in anterodorsomedial view), with the streamlines released from a line in front of the flipper. Specimen numbers are as in Figure 1. Smaller figures show contours of velocity (left) and streamwise vorticity (right) in the wake of each flipper. The experimental setup is illustrated in Figure S3.

gradients near $AoA = 0^\circ$ (3.4, 3.5, and 2.9 rad^{-1}) than gray seals (1.9 rad^{-1}), suggesting a steeper change of efficiency at small $AoAs$. Hydrodynamic loading in these species is thus more sensitive to flipper orientation, which in turn facilitates maneuverability.^{20,21}

DISCUSSION

Our observations reveal that the swimming styles of true and eared seals are not as distinct as commonly thought and instead form an anatomical, behavioral, and functional continuum. Anatomically, phocids show a broad range of forelimb morphologies, some of which approximate the streamlined flippers of otariids. In terms of behavior, both groups share the same basic repertoire of swimming movements and chiefly differ in when, how frequently, and how effectively the latter are used. Finally, there is a clear functional transition series ranging from turbulent bluff body type flow in gray seals to increasingly more efficient lift-producing flow in crabeater, leopard, and NZ fur seals. Although not directly studied here, it seems likely that walruses—the sole representatives of the third major pinniped lineage, odobenids—also fall within this continuum, given their intermediate axial²² and flipper anatomy (e.g., reduced claws and cartilaginous prolongation of the digits),²³ as well as their tendency to use both fore- and hindlimbs for propulsion.²⁴

Overall, our findings suggest that pinniped swimming styles are variations on a theme and, as such, do not necessarily reflect

separate evolutionary origins. Like those of monachines, the streamlined foreflippers of otariids may have arisen from a rear-propelled bauplan and thus an aquatically adapted ancestor. This scenario adds a novel pathway to Fish's⁶ seminal “drag to lift” framework for the evolution of tetrapod swimming (Figure S2) that is consistent with both a single origin of aquatic pinnipeds and the fossil record. Thus, stem seals like *Enaliarctos*, *Potamotherium*, and *Puijila* probably swam either quadrupedally²⁵ or with their feet^{12,26} and—like living phocids—presumably used their paw-like forelimbs to help with maneuvering and propulsion. Early otariids and walruses may have inherited this behavioral repertoire and—like living monachines—improved its effectiveness by evolving more streamlined flippers. Eventually, the forelimbs eclipsed the feet as the main source of propulsion, giving rise to the modern otariid swimming style.

Beyond otariids and monachines, apparent trends toward forelimb propulsion have also been suggested for the extinct desmatophocid *Allodesmus kelloggi* and dusignathine walruses, based on their stout forelimbs and, in the case of *Allodesmus*, large supraspinous fossa of the scapula and flexible thoracic section of the vertebral column bearing tall neural spines.^{12,22,27} This recurrent pattern is striking and raises the question of potential drivers and/or constraints. Adaptation of the forelimb for swimming in phocines could plausibly have been constrained by the use of claws as hooks for increased traction during terrestrial locomotion. Yet otariids, despite their clawless flippers, are even more agile on land, thanks largely to their ability to walk on their fore- and hindlimbs.³ The same was presumably true of stem pinnipeds,^{25,26,28,29} suggesting that claws were not a prerequisite of terrestrial locomotion in early seals. Similarly, use of the claws for moving on ice is unlikely to have played a role, given that pinnipeds seemingly diversified in relatively warm waters of the Northern Hemisphere prior to the onset of large-scale glaciation.^{27,30}

Many carnivorans, including otters and phocines, use their forelimbs to secure food during prey processing.³¹ The same likely was true of stem pinnipeds like *Enaliarctos* and *Potamotherium*, judging from their well-developed claws and

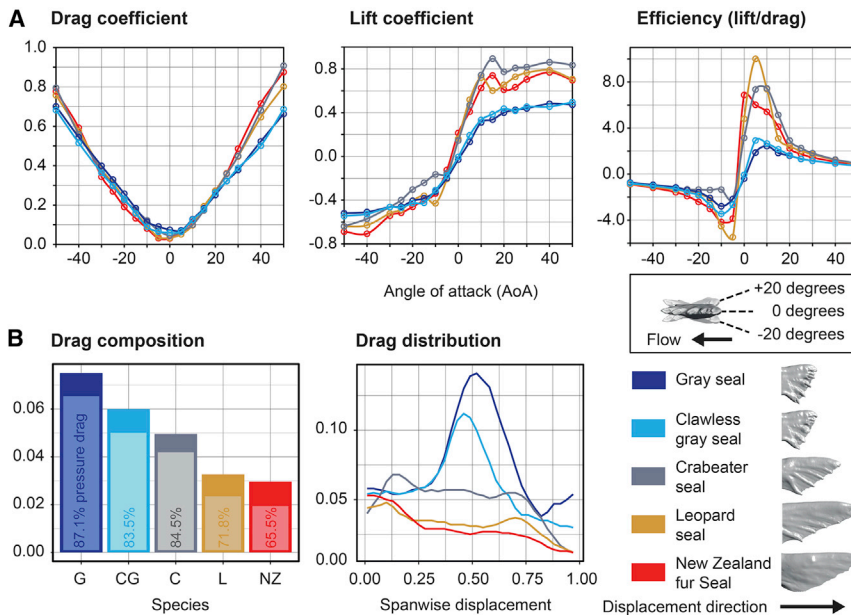


Figure 4. Hydrodynamic characteristics reveal a trend toward increased streamlining and lift generation

(A) Drag, lift, and hydrodynamic efficiency as a function of angle of attack. (B) Drag composition and spanwise distribution at the angle of neutral lift. Percentage values in bars show pressure drag percentage, i.e., drag due to the shape of the flipper itself, with the remainder reflecting skin friction. Data presented in Table S2. Validation of numerical setup is provided in Figure S4 and Table S3.

trochleated finger joints.^{26,29,31,32} Grasping and manipulating prey requires claws and/or manual dexterity, both of which detract from a hydrodynamically efficient flipper (Figure 4).³³ Building on previous hypotheses regarding the retention of a paw-like forelimb in otters,³⁴ we therefore propose that functional constraints imposed by prey processing may explain why seals initially adopted hindlimb propulsion when they took to the water.

As pinnipeds diversified, the conflicting requirements of prey processing and hydrodynamic efficiency created a functional trade-off (as seen in living phocines), with some adaptations to improve swimming performance (e.g., interdigital webbing) but still enough manual dexterity to grasp food using the claws. Changes in habitat, diet, prey size, or feeding ecology would likely have upset this balance, tilting the scales in favor of one function to the detriment of the other. Whereas selection for prey processing (or other functions, such as using claws to haul out on ice) would have comparatively little impact on an already paw-like forelimb, improved swimming performance appears to mandate the loss of anatomical features essential for dexterity (e.g., trochleated finger joints), resulting in a “one-way street” toward a flipper-like morphology.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.03.019>.

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AUTHOR CONTRIBUTIONS

Conceptualization, D.P.H., F.G.M., and A.R.E.; Formal Analysis, D.P.H., F.G.M., S.W., and D.B.; Investigation, D.P.H., F.G.M., S.W., D.B., M.T., T.P., B.B., H.L.R., R.S., J.R., R.P.M., E.M.G.F., D.J.S., and A.R.E.; Resources, A.R.E., D.B., M.T., E.M.G.F., and D.J.S.; Writing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

- Ray, C.E. (1963). Locomotion in pinnipeds. *Nat. Hist.* 72, 10–21.
- English, A.W. (1976). Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). *J. Zool.* 178, 341–364.
- Kuhn, C., and Frey, E. (2012). Walking like caterpillars, flying like bats—pinniped locomotion. *Palaeobiodivers. Palaeoenviron.* 92, 197–210.
- McLaren, I.A. (1960). Are the Pinnipedia biphyletic? *Syst. Biol.* 9, 18–28.
- Hafed, A.B., Koretsky, I.A., and Rahmat, S.J. (2020). Current status of pinnipeds phylogeny based on molecular and morphological data. *Hist. Biol.* Published online August 3, 2020. <https://doi.org/10.1080/08912963.2020.1795649>.
- Fish, F.E. (1996). Transitions from drag-based to lift-based propulsion in mammalian swimming. *Am. Zool.* 36, 628–641.
- Wolsan, M., and Sato, J.J. (2020). Parallel loss of sweet and umami taste receptor function from phocids and otarioids suggests multiple colonizations of the marine realm by pinnipeds. *J. Biogeogr.* 47, 235–249.
- Paterson, R.S., Rybczynski, N., Kohno, N., and Maddin, H.C. (2020). A total evidence phylogenetic analysis of pinniped phylogeny and the possibility of parallel evolution within a monophyletic framework. *Front. Ecol. Evol.* 7, 457.
- DeBlois, M.C., and Motani, R. (2019). Flipper bone distribution reveals flexible trailing edge in underwater flying marine tetrapods. *J. Morphol.* 280, 908–924.
- King, J.E. (1964). A note on the increasing specialization of the seal fore flipper. *Proc. Anat. Soc. Great Britain Northern Ireland* 98, 476–477.
- King, J.E. (1969). Some aspects of the anatomy of the Ross seal, *Ommatophoca rossi* (Pinnipedia: Phocidae). *Br. Antarct. Surv. Sci. Rep.* 63, 1–54.
- Bebej, R.M. (2009). Swimming mode inferred from skeletal proportions in the fossil pinnipeds *Enaliarctos* and *Allodesmus* (Mammalia, Carnivora). *J. Mamm. Evol.* 16, 77–97.
- Backhouse, K.M. (1961). Locomotion of seals with particular reference to the forelimb. *Symp. Zool. Soc. Lond.* 5, 59–75.
- Williams, T.M., and Kooyman, G.L. (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol. Zool.* 58, 576–589.
- Tarasoff, F.J., Bisaillon, A., Piérard, J., and Whitt, A.P. (1972). Locomotory patterns and external morphology of the river otter, sea otter, and harp seal (Mammalia). *Can. J. Zool.* 50, 915–929.
- Feldkamp, S.D. (1987). Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool. (Lond.)* 212, 43–57.
- Godfrey, S.J. (1985). Additional observations of subaqueous locomotion in the California Sea Lion (*Zalophus californianus*). *Aquat. Mamm.* 11, 53–57.
- Friedman, C., and Leftwich, M.C. (2014). The kinematics of the California sea lion foreflipper during forward swimming. *Bioinspir. Biomim.* 9, 046010.
- Weber, P.W., Howle, L.E., Murray, M.M., and Fish, F.E. (2009). Lift and drag performance of odontocete cetacean flippers. *J. Exp. Biol.* 212, 2149–2158.
- Fish, F.E., Hurlley, J., and Costa, D.P. (2003). Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design. *J. Exp. Biol.* 206, 667–674.
- Cheneval, O., Blake, R.W., Trites, A.W., and Chan, K.H.S. (2007). Turning maneuvers in Steller sea lions (*Eumetopias jubatus*). *Mar. Mamm. Sci.* 23, 94–109.
- Pierce, S.E., Clack, J.A., and Hutchinson, J.R. (2011). Comparative axial morphology in pinnipeds and its correlation with aquatic locomotory behaviour. *J. Anat.* 219, 502–514.
- Murie, J. (1871). Researches upon the Anatomy of the Pinnipedia. Part I: On the Walrus (*Trichechus rosmarus*, Linn.) (Transactions of the Zoological Society of London, Volume 7, Part 6, Article 11) (Zoological Society of London).
- Gordon, K.R. (1981). Locomotor behaviour of the walrus (*Odobenus*). *J. Zool.* 195, 349–367.
- Rybczynski, N., Dawson, M.R., and Tedford, R.H. (2009). A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* 458, 1021–1024.
- Savage, R.J.G. (1957). The anatomy of *Potamotherium*, an Oligocene Lutrinae. *Proc. Zool. Soc. Lond.* 129, 151–244.
- Berta, A., Churchill, M., and Boessenecker, R.W. (2018). The origin and evolutionary biology of pinnipeds: seals, sea lions, and walruses. *Annu. Rev. Earth Planet. Sci.* 46, 203–228.
- Berta, A., Ray, C.E., and Wyss, A.R. (1989). Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science* 244, 60–62.
- Berta, A., and Ray, C.E. (1990). Skeletal morphology and locomotor capabilities of the archaic pinniped *Enaliarctos mealsi*. *J. Vertebr. Paleontol.* 10, 141–157.
- Herbert, T.D., Lawrence, K.T., Tzanova, A., Peterson, L.C., Caballero-Gill, R., and Kelly, C.S. (2016). Late Miocene global cooling and the rise of modern ecosystems. *Nat. Geosci.* 9, 843–847.
- Hocking, D.P., Marx, F.G., Sattler, R., Harris, R.N., Pollock, T.I., Sorrell, K.J., Fitzgerald, E.M.G., McCurry, M.R., and Evans, A.R. (2018). Clawed forelimbs allow northern seals to eat like their ancient ancestors. *R. Soc. Open Sci.* 5, 172393.
- Mitchell, E., and Tedford, R.H. (1973). The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bull. Am. Mus. Nat. Hist.* 151, 203–284.
- Howell, A.B. (1930). Aquatic Mammals: Their Adaptations to Life in the Water (Charles C. Thomas).
- Estes, J.A. (1989). Adaptations for aquatic living by carnivores. In *Carnivore Behavior, Ecology, and Evolution*, J.L. Gittleman, ed. (Springer US), pp. 242–282.
- Hocking, D.P., Evans, A.R., and Fitzgerald, E.M.G. (2013). Leopard seals (*Hydrurga leptonyx*) use suction and filter feeding when hunting small prey underwater. *Polar Biol.* 36, 211–222.
- Hocking, D.P., Ladds, M.A., Slip, D.J., Fitzgerald, E.M.G., and Evans, A.R. (2017). Chew, shake, and tear: prey processing in Australian sea lions (*Neophoca cinerea*). *Mar. Mamm. Sci.* 33, 541–557.
- Hocking, D.P., Salverson, M., Fitzgerald, E.M.G., and Evans, A.R. (2014). Australian fur seals (*Arctocephalus pusillus doriferus*) use raptorial biting and suction feeding when targeting prey in different foraging scenarios. *PLoS ONE* 9, e112521.
- Gregory, N., and O'Reilly, C.L. (1970). Low-speed aerodynamic characteristics of NACA 0012 aerofoil section, including the effects of upper-surface roughness simulating hoar frost. Aeronautical Research Council Reports and Memoranda no. 3726. <http://citeseerx.ist.psu.edu/viewdoc/download?rep=rep1&type=pdf&doi=10.1.1.227.696>.
- von Doenhoff, A.E. (1940). Investigation of the boundary layer about a symmetrical airfoil in a wind tunnel of low turbulence. NACA Wartime Report no. L-507. <https://digital.library.unt.edu/ark:/67531/metadc61381/>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT OR RESOURCE	SOURCE	IDENTIFIER
Deposited data		
3D flipper models	Morphosource	https://www.morphosource.org/projects/0000C1070 ; Project title: The evolution of swimming in tetrapods.
Software and algorithms		
Ansys Fluent	Ansys	https://www.ansys.com/products/fluids/ansys-fluent
Geomagic Wrap	3D Systems	https://au.3dsystems.com/software/geomagic-wrap

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the Lead Contact, David Hocking (david@dphocking.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The published article and supplementary materials includes all datasets generated and analyzed during this study. The 3D models analyzed in this study are provided in the Morphosource project “The evolution of swimming in tetrapods” (<https://www.morphosource.org/projects/0000C1070>).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Our anatomical comparisons focused on the manus because it contributes most of the flipper surface area; is the main region of variation between our study species; and can be scanned and modeled consistently. Representatives of each major pinniped lineage were obtained as part of the marine mammal stranding programs at Museums Victoria (NMV, Melbourne, Australia) and the Natural History Museum (NHMUK, London, United Kingdom), and included an adult female gray seal (*Halichoerus grypus*, NHMUK ZD.2018.144); a sub-adult crabeater seal (*Lobodon carcinophaga*, NMV C38154); an adult male leopard seal (*Hydrurga leptonyx*, NMV C39957); and a sub-adult male New Zealand fur seal (*Arctocephalus forsteri*, NMV C40065).

METHOD DETAILS

Specimens and 3D Scanning

Specimens were scanned via medical computed tomography (CT) at either Monash Biomedical Imaging (Monash University, Melbourne, Australia) or the Royal National Orthopaedic Hospital (Stanmore, UK). 3D models were created by thresholding the CT data in Avizo v9 (Thermo Scientific, Waltham, USA). For the gray, crabeater and NZ fur seals, the left flipper was scanned with the fingers relaxed (resting position), and the right one with the fingers splayed out (swimming posture). For the leopard seal, only a left flipper was available and thus scanned in both positions.

For the swimming posture, the flippers were fixed to a flat board by threading string through the soft tissue near the first and last digits. Small holes and tissue bulges resulting from this procedure, as well as some minor folds reflecting a lack of skin tension (following detachment of the flippers from the body) were digitally removed and/or amended using the ‘fill holes’ function in Geomagic Wrap (3D Systems, South Carolina, USA), which follows the curvature of the surrounding mesh. The repaired models were then smoothed using the ‘relax surface’ and ‘remove spikes’ tools.

Phocines differ from other seals in having well-developed claws that are used for prey processing.³¹ To test whether the latter substantially affect streamlining, we created a hypothetical clawless version of the gray seal paw by digitally removing the claws using Geomagic Wrap and repairing the resulting holes using the ‘fill holes’ tool. This hypothetical model was then directly compared to its real-life counterpart via computational fluid dynamics (see below).

Behavioral Observations

Video footage of swimming behavior in captive leopard seals, Australian fur seals (*Arctocephalus pusillus doriferus*), Australian sea lions (*Neophoca cinerea*), California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*) was sourced from our previous research.^{31,35–37} In addition, we examined archival video footage of swimming in wild gray seals at Farne Islands (UK) filmed by Ben Burville. Archival footage of New Zealand fur seals and Australian sea lions at Olive Island, and Australian fur seals at Montague Island and Deen Maar Island (Australia), was provided by Robert Harcourt. Finally, archival footage of wild Hawaiian monk seals (*Neomonachus schauinslandi*) was provided by Jonathan Bird, while YouTube footage of captive Hawaiian monk seals filmed at The Marine Mammal Center (Sausalito, USA) was provided by Megan McGinnis (see: <https://youtu.be/DBjMcOZw3oE>, <https://youtu.be/ZeLsxSOP1w>).

QUANTIFICATION AND STATISTICAL ANALYSIS

Computational Fluid Dynamics

Computational fluid dynamics simulations were performed using Ansys Fluent (Ansys, Canonsburg, USA). Flippers were scaled to their mean width (chord length) to remove the effects of body size; attached to one side of a rectangular domain, with the remaining walls located far enough away to achieve a blockage ratio < 0.1%; aligned to the flow so that the angle of attack was approximately zero; and assumed to have surfaces with no-slip wall boundary conditions. All walls of the domain were modeled with zero-shear wall boundary conditions to simulate a free stream environment. A uniform velocity boundary condition (~2.0 ms⁻¹) corresponding to a Reynolds number (based on the chord length, 0.164 m) of 2.88×10^5 was applied to the inlet boundary, and a zero static pressure condition to the outlet boundary (Figure S3A).

We used a Cartesian cut-cell approach as our general meshing strategy, with multiple levels of mesh refinement zones around the flipper and in the wake to resolve the large velocity variation across the boundary layer (Figure S3B). The flipper surface had 12 inflation layers and the wall y_+ at the first cell was maintained below 5 with a typical value varying from 0.5 to 4. A mesh resolution study (based on the NZ fur seal flipper) using three sequentially refined meshes comprising 0.8, 4 and 11 million cells, respectively, showed that predictions of drag and lift agreed to within 1% between the medium and fine meshes. The medium mesh was thus adopted for the simulations.

Hydrodynamic characteristics were resolved via Reynolds-Averaged Navier-Stokes (RANS) equations, using the commercial CFD code FLUENT (part of the ANSYS 19.2 software suite) as the numerical solver. For all cases, flow fields were predicted with a second-order accuracy steady-state RANS simulation based on the Shear Stress Transport (SST) $k-\omega$ turbulence model. The latter was designed to predict separation in flows over surfaces subject to adverse pressure gradients, as can occur near the trailing edge of an airfoil (or flipper) oriented at an angle to the oncoming flow.

The SST $k-\omega$ model resolves the near-wall boundary layer with a $k-\omega$ model (which more accurately reflects near-wall flow), but predicts the higher-turbulence flow field away from the no-slip surface with a fully turbulent $k-\epsilon$ model. As mentioned, this approach performs well under unfavorable pressure gradients and predicts flow separation, and as such is well suited to modeling complex external flows. Furthermore, its capability has been validated through accurately predicting both the aerodynamic loading of a NACA0012 airfoil across different AoAs, and the contribution of skin friction to overall drag at AoA = 0°.

Lift (C_L) and drag (C_D) coefficients were calculated based on the planform area of the flippers and freestream velocity:

$$C_{D,L} = \frac{2F_{D,L}}{\rho U^2 A},$$

where $F_{D,L}$ is the predicted drag and lift force in newtons; and ρ , U and A are fluid density, free stream velocity and planform area of the flipper models, respectively. The fluid was modeled as seawater with a density of 1026 kg m⁻³ and a viscosity of 0.00117 kg m⁻¹s⁻¹. The free stream velocity was set to 2 m s⁻¹ for all simulations, and the planform areas of the flippers were 0.0186 m² for the clawed gray seal, 0.0185 m² for the clawless gray seal, 0.0275 m² for the crabeater seal, 0.0387 m² for the leopard seal, and 0.0412 m² for the New Zealand fur seal.

To validate our numerical approach, we simulated a NACA0012 airfoil using the same turbulence model and meshing strategy as for the flippers. We chose an airfoil aspect ratio of 4 and a Reynolds number of 3 million to match experimental wind tunnel data.³⁸ The simulated lift coefficients and pressure distributions on the upper surface of the airfoil closely match the wind tunnel measurements across different AoAs, especially prior to stall (Figure S4). Wind-tunnel testing and theoretical analysis of a NACA0012 airfoil at AoA = 0° over Reynolds numbers ranging from 2.675 to 7.560 million show that skin friction accounts for approximately 80% of profile drag,³⁹ which is consistent with our own numerical model prediction (81.4%).