



Optimization of swim depth across diverse taxa during horizontal travel

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Semiaquatic taxa, including humans, often swim at the air–water interface where they waste energy generating surface waves. For fully marine animals however, theory predicts the most cost-efficient depth-use pattern for migrating, air-breathing species that do not feed in transit is to travel at around 2 to 3 times the depth of their body diameter, to minimize the vertical distance traveled while avoiding wave drag close to the surface. This has rarely been examined, however, due to depth measurement resolution issues at the surface. Here, we present evidence for the use of this strategy in the wild to the nearest centimeter and document the switch to shallow swimming during naturally occurring long-distance migrations. Using high-resolution depth-accelerometry and video data for little penguins (*Eudyptula minor*) and loggerhead turtles (*Caretta caretta*), satellite-relayed data for green turtles (*Chelonia mydas*), and literature data for further sea turtle, penguin, and whale species, we show that near-surface swimming is likely used broadly across nonforaging diving animals to minimize the cost of transport.

behavioural allometry | dive behaviour | locomotion | movement ecology | optimal migration

Regardless of whether animals are walking, flying, or swimming, optimization of movement is important so that animals do not expend more energy than necessary (e.g., 1, 2). One important consideration for marine species when undertaking long-distance movements is their swim depth, which can impact energy expenditure (3, 4). Theoretical work has shown that travel through water at the surface is energetically costly owing to increased drag resistance, which arises due to the creation of waves and associated dissipative energy at the air–water boundary (Fig. 1A). Experiments have demonstrated that for a streamlined object, this wave drag is at its peak when the traveling object is just submerged and attenuates to minimal drag (comprising friction drag and form drag) once the object is at a depth of 2 to 3 times its maximal diameter (3; Fig. 1B). Subsequent experimental towing of frozen animal carcasses (e.g., 5, 6), model animals and mannequins (e.g., 7), and live humans and seals (8) has confirmed that travel at the surface incurs far greater drag forces than when submerged (Fig. 1B–C). Measurements of oxygen consumption rates of aquatic animals swimming inside experimental flumes further demonstrate that swimming at depth is far more efficient than swimming at the surface at the same speed (6, 9). It might be expected that migratory species that do not feed pelagically or are traveling between prey patches should optimize their swim depth by avoiding the zone of high wave drag just under the surface, as well as unnecessary further travel caused by diving significantly deeper than three times their maximal body diameter.

Despite these extensive considerations, there are few datasets from free-living animals to examine predictions of optimum swim depths during directed travel. Certainly, humans generally swim at the surface, which is very inefficient (7), and the same pattern of inefficient surface swimming is sometimes seen in semiaquatic animals such as American mink (*Mustela vison*) (5). Data for free-living marine animals traveling near the surface are harder to obtain. Satellite-relayed data lacks the resolution to precisely define near-surface swimming. Archival tracking devices can provide this resolution but must be retrieved in order to download data directly, a feat not usually possible for long-distance marine migrants dispersing to disparate end points. To examine near surface depth-use during open-water travel across taxa, diving animals with high re-encounter probability were tracked using high-resolution data loggers, allowing physical retrieval of data. Penguins and sea turtles were selected despite their divergent thermoregulatory strategies and consequent swim speeds, as they are both fore-flipper swimmers with an inflexible body and therefore hydrodynamically comparable to the inflexible streamlined object in Hertel's experiments (3) (the results of which should apply regardless of speed of travel). Little penguins traveling to offshore foraging sites were equipped with high-resolution depth-accelerometers or video cameras that could be recovered when they returned to land. Loggerhead turtles were experimentally displaced away from their nesting beaches so that they migrated across the open ocean in order to return, thus enabling

Significance

Three-dimensional tracking of animals has become an integral part of the study of their movement ecology, but the top few meters of depth data for diving animals are often routinely disregarded and so shallow diving is rarely recorded. We show that near-surface travel may be a conservative trait across diverse marine taxa and follows an allometric pattern with body size across various reptilian, avian, and mammalian species. We match theory with empirical data from animal tracking to present a common principle of energetic optimization during oceanic travel, with implications for the protection and conservation of migratory species.

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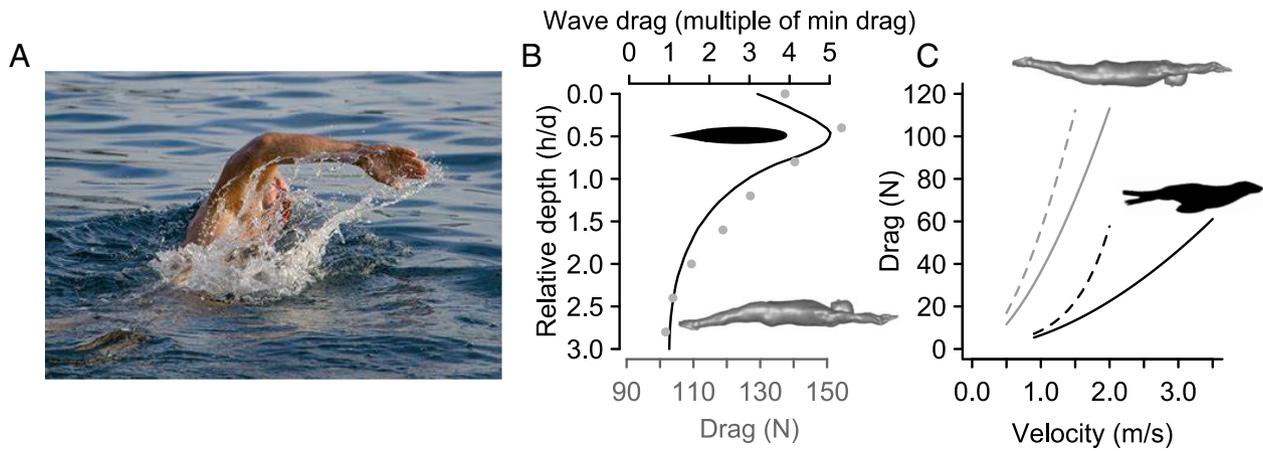


Fig. 1. Theoretical considerations. (A) A human swimmer. Even Olympic swimmers are swimming inefficiently because they generate wave drag. (B) Trials towing a spindle-shaped object and a mannequin at varying depths have shown that wave drag reaches a minimum value once the object is moving at a depth of around 2 to 3 times its body thickness (3, 7). (C) This has been confirmed by towing live seals and humans at different depths to show the increased drag when traveling at the surface (dashed lines vs. solid lines: submerged) (8). These theoretical considerations suggest that ocean swimmers including marine mammals, birds and reptiles should swim just below the surface, not at the surface or very deep, if their only goal is to travel horizontally as efficiently as possible rather than to achieve other goals such as looking for prey en route. Relative depth in experimental conditions refers to submersion depth to the central axis (h) divided by the maximal body diameter (d), while in animal tracking depth is often measured to the dorsal surface (field-measured relative depth being 0.5 body depths less than experimental relative depth).

recovery of high-resolution depth loggers and triaxial accelerometers when the turtles reentered. In both cases, archival logging allowed depth measurement at a very fine scale (resolution: 0.2 cm, sampling rate: 1 s, accuracy: 1.5 cm; accelerometry sampling rate: 25 Hz little penguins, 10 Hz loggerhead turtles). To test for this pattern in naturally migrating animals, green turtles were tracked using depth-enabled satellite tags, which compressed depth information

into proportion of time spent in surface waters (0 to 5 m) to enable remote transmission of data.

Archival Tracking: Little Penguins

Ten little penguins were tracked from Phillip Island, Australia, using high-resolution GPS-depth-accelerometers, each for the duration

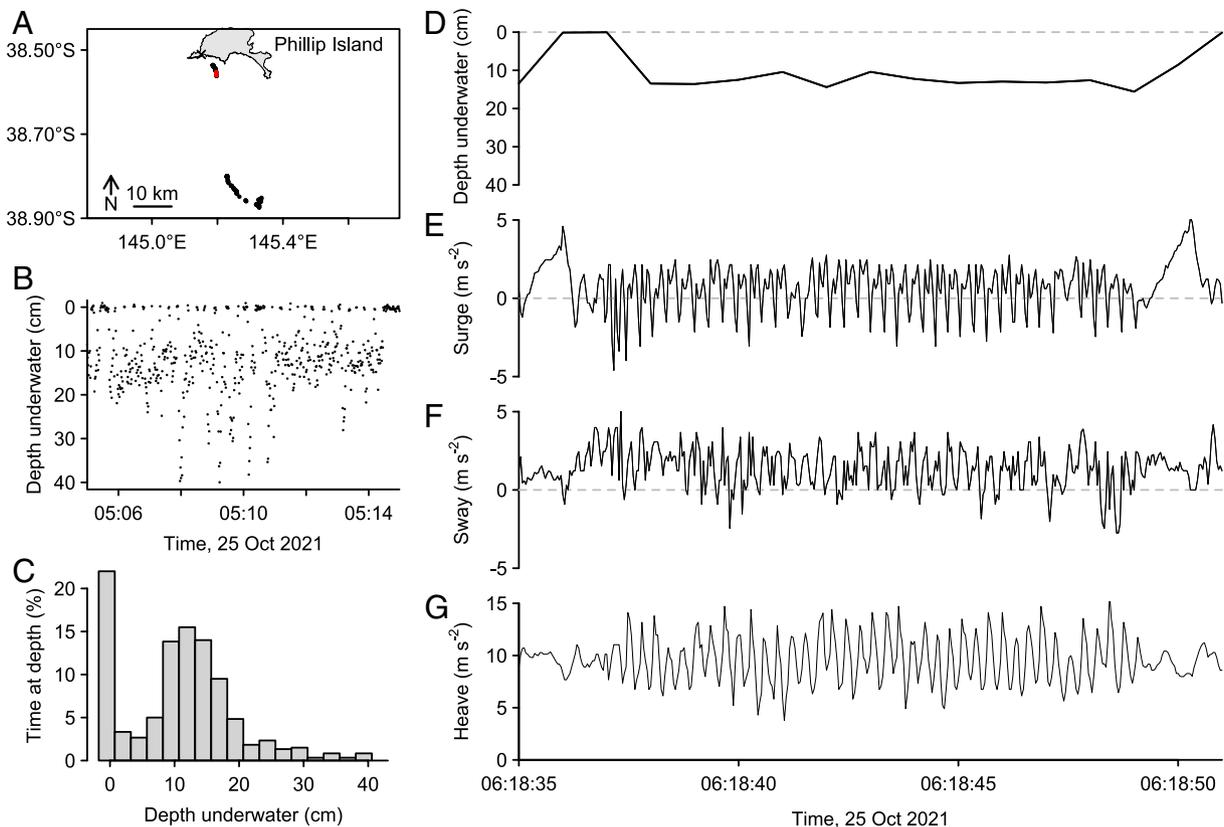


Fig. 2. 3D movements during a little penguin foraging trip in south-east Australia—a representative example. (A) GPS fixes obtained over the foraging trip, including parts of the commute (Upper locations, from nest box at "x") and foraging area (Lower locations). Panels (B) and (C) show the penguin's depth use for the 10-min commute period shown in red in panel (A), during which time average speed of horizontal travel was 1.37 m s^{-1} . Panels (D–G) show depth and accelerometry traces for a 16 s period within this timeframe. Active swimming is characterized by regular cycles in the surge and heave axes corresponding to flipper-beat frequency. Rising to the surface creates a peak in surge acceleration, followed by a drop on reaching the surface. See also *SI Appendix, Figs. S1–S3*.

of a single foraging trip, and later intercepted for data retrieval having returned to their nest box. All individuals with sufficient data quality ($n = 9$) had a clear commute period at the start of the journey consisting of shallow active travel dives (Figs. 2 and *SI Appendix*, Figs. S1–S3) varying from 9 to 90 min in duration, before commencing deep foraging dives for the majority of the trip. Mean bottom depth of dives during commute periods averaged 0.17 ± 0.05 m (range of means: 0.11 to 0.25 m), and average dive duration was 8 ± 3 s (range of means: 4 to 13 s). Average depths for each penguin were 1.1 to 2.5 times the estimated body diameter for little penguins (*SI Appendix*, Table S1), giving an estimated 75 to 100% reduction in wave drag (3; adjusted to account for depth measurement to dorsal surface). Accelerometry data recorded during these shallow commute dives show regular cycles in the surge and heave axes, indicating flipper strokes (Fig. 2, *SI Appendix*, Figs. S1–S2). Active swimming during shallow diving is further demonstrated via video footage taken using a head-mounted camera deployed at the same colony (*Movie S1*).

Archival Tracking: Loggerhead Turtles

Loggerhead turtles were experimentally displaced offshore from their nesting beach in Türkiye (10), tracked using Argos telemetry and high-resolution archival loggers on their journey back to the shore, and reintercepted on the nesting beach for data retrieval having returned to lay subsequent nests. Depth and accelerometry data from four individuals are analyzed here as examples of animals traveling to reach a target endpoint. Turtles traveled back toward the coastline during daylight hours using shallow, active travel dives, interspersed with fewer longer, deeper dives, typically considered midwater resting dives (e.g., 11) (Fig. 3, *SI Appendix*, Fig. S4). Accelerometry traces for the shallow dives demonstrate active swimming, with clear and regular surges in forward propulsion indicating flipper strokes (Fig. 3, *SI Appendix*, Fig. S5). Turtles made between 115 and 562 of these shallow “travel” dives during the 7 h period after reorientation and before dark (mean 337 ± 191 dives), to mean bottom depths averaging 1.00 ± 0.28 m (range of means: 0.71 to 1.38 m), of 69 ± 29 s average duration (range of means: 40 to 107 s). The average depths of these dives equated to between 2.5 and 4.6 times the estimated body diameter for each individual loggerhead (*SI Appendix*, Table S2). The turtles therefore largely avoided the wave drag zone while not wasting energy traveling further than necessary from the surface. Turtles traveled at average horizontal speeds of around 0.5 m s^{-1} over this time.

Satellite Tracking: Green Turtles

In order to observe this pattern in naturally migrating animals, we satellite-tracked six postnesting green turtles from the Chagos Archipelago in the Indian Ocean over a total distance of 18,185 km (range: 512 to 4,422 km). Five were tracked to foraging grounds spread across the Western Indian Ocean, in Kenya, Madagascar, Seychelles, and on the Pitt Bank within the Chagos Archipelago (Fig. 4A). Depth was recorded every 10 s (0.5 m resolution, ± 1.01 m accuracy at 1 m depth), incorporating 1,266 h of oceanic migration (defined as portions of track in water depths $> 1,000$ m), and compressed into depth and duration summaries per dive when dives were ≥ 5 m, or per shallow period when dives were < 5 m.

Depth-use during pelagic crossings was markedly different from that during coastal migration or pre- and postmigratory tracking (Fig. 4B). When crossing deep water, all tracked turtles switched from mainly deeper diving day and night to shallow dive depths during the day (time spent < 5 m: $73.5 \pm 5.7\%$) and deeper dive depths at night (time spent ≥ 5 m: $73.6 \pm 3.9\%$) (*SI Appendix*,

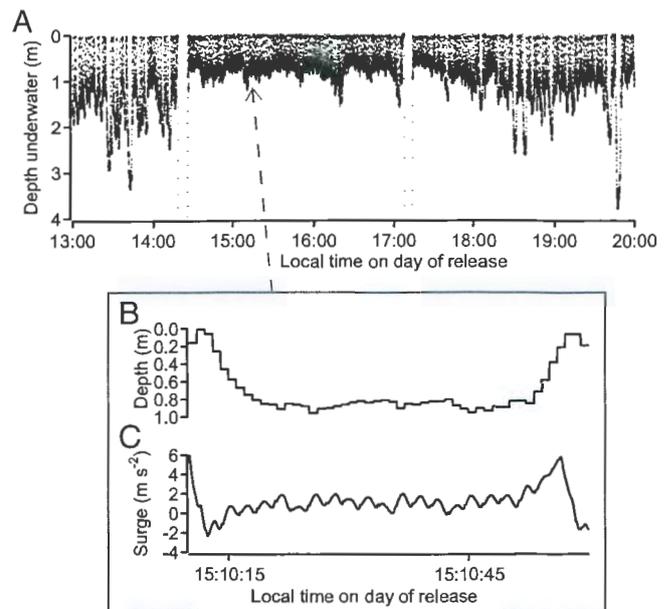


Fig. 3. Loggerhead turtles in the Mediterranean travel at around 1 m depth when not feeding. Diurnal depth use for experimentally displaced loggerhead turtles *en route* back to the coast in Türkiye—a representative example. Turtles performed shallow active travel dives ($n = 115$ to 562) interspersed with varying amounts of deeper, longer dives ($n = 2$ to 8). Depth taken every 1 s; darker areas in panel (A) show denser clusters of depth readings. Depth and accelerometry for a single dive are shown in panels (B) and (C). Rising to the surface to breathe causes a peak followed by a trough in surge acceleration. Flipper strokes are evident as regular forward thrusting in the surge axis, indicating active swimming during these dives. For all individuals, see *SI Appendix*, Figs. S4–S5.

Table S3). Collectively, the tracked turtles spent 80% of diurnal time < 5 m (Fig. 4C). Coastal migratory depth-use, in contrast, resembled pre- and postmigratory depth use, with the majority of time spent at depths ≥ 5 m both diurnally and nocturnally. This dichotomy in depth-use patterns indicates a clear preference for shallow travel when crossing open water as predicted.

Allometry of Swim Depth

To compare our results for sea turtles and penguins with other marine taxa, we searched for studies describing marine vertebrate depth use during traveling, nonforaging dives. Animals traveling in shallow water and data on juveniles were not included owing to the potential use of ground effects (12) and drafting (13), which could influence depth choice. Articles and theses were included where depth recorders had been set to record shallow as well as deep dives, and sensor resolution was adequate. Only a handful of studies could be found, owing to the routine disregard of depth data within the top few meters—a result of tag design prioritizing capture of deep dives over resolution close to the surface. Studies that adequately described dive depth in transiting, nonforaging animals either recovered archival pop-off tags using radio or GPS tracking (North Atlantic right whales *Eubalaena glacialis*, Bay of Fundy: (14); pygmy blue whale *Balaenoptera musculus breviceauda*, southwest coast of Australia: (15)) or recovered tags directly from animals they were able to predictably re-encounter (Magellanic penguins *Spheniscus magellanicus*, Argentina: (16); Adélie penguins *Pygoscelis adeliae*, Antarctica: (17); experimentally displaced green turtles returning to nest on Ascension Island: (11); a green turtle migrating within Hawaii: (18)). In all these examples, animals traveled at relative depths of around 3 body thicknesses when migrating or commuting and not foraging (Fig. 5). Smaller bodied animals

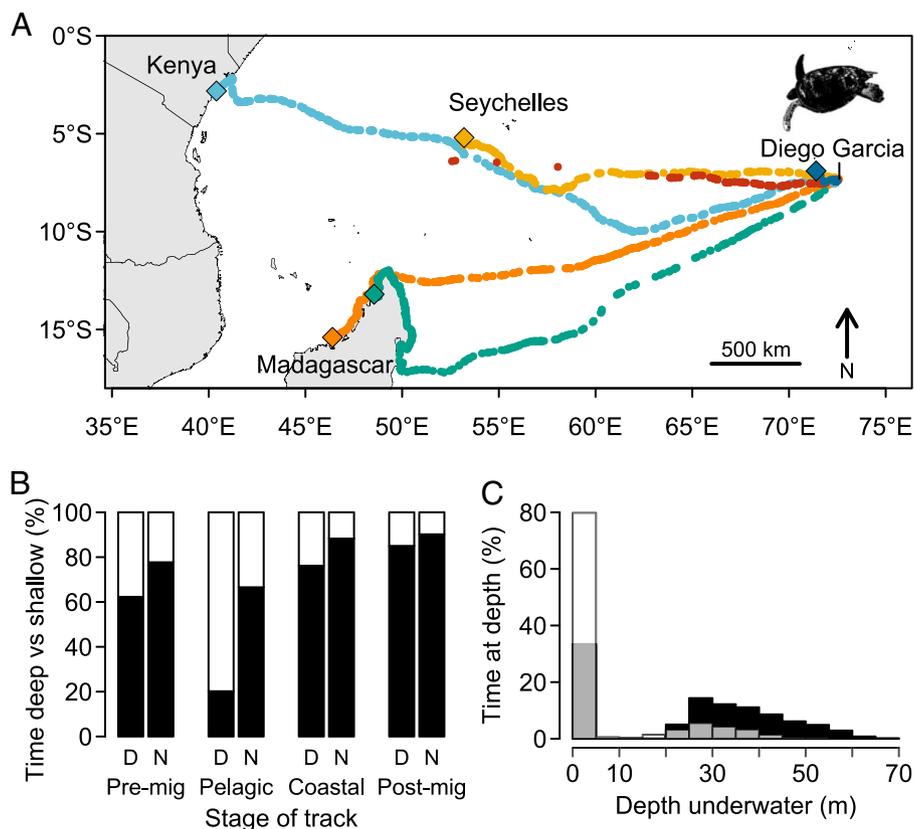


Fig. 4. Green turtles switch to shallow diving when crossing deep water. Diel depth use varied with stage of migration for six postnesting green turtles tracked from Diego Garcia, Chagos Archipelago, Indian Ocean (A). Colors distinguish individual turtles, and diamonds show where turtles reached their foraging ground. (B) Percent depth use of shallow water (0 to 5 m; white) vs. deeper water (≥ 5 m; black), split into premigratory, pelagic migratory, coastal migratory, and postmigratory stages, and by diel phase (D: diurnal, N: nocturnal), for all turtles. During the pelagic migratory stage, there is a consistent diel difference in depth use, with 80% of collective diurnal travel time in shallow water < 5 m and nocturnal travel typically at greater depths (67% ≥ 5 m) (see *SI Appendix, Table S3* for mean \pm SE per stage and diel phase). (C) Further breakdown of depth use during the pelagic migratory stage: diurnal travel occurs largely at subsurface depths (white), while at night there is increased use of greater depths (black). Gray sections indicate overlap between diurnal and nocturnal depth use.

traveled within the top 2 m, with little penguins at 0.1 to 0.25 m (current study), Magellanic penguins at 0.2 to 0.5 m (16), Adélie penguins at 0.6 to 0.9 m (17), and sea turtles between 0.7 and 1.9 m (current study, 11, 18) (*SI Appendix, Tables S1, S2, and S4*). Larger-bodied animals traveled further down the water column, with North Atlantic right whales traveling at around 8 m (14) and a pygmy blue whale traveling at 13 m when not feeding (15) (*SI Appendix, Table S4*). Linear regression of the current available data presents striking similarity with the predicted 2 to 3 \times body diameter allometric relationship with optimized swim depth (travel dive depth = $0.04 + 3.01 \times$ body diameter, $F_{(23, 24)} = 658$, $P < 0.0001$, $r^2 = 0.97$; Fig. 5 G–H). Furthermore, salmonids on their upstream migrations have been shown to swim far enough away from the riverbank to gain the depth required to avoid wave drag, with larger fish swimming more centrally where it is deeper despite having to swim against faster-flowing water (19). Optimization of swim depth may be a common principle underpinning vertical movement patterns of air-breathing marine vertebrates during travel-only dives, making wave drag avoidance a key driver (20) of vertical movement in diving animals. This pattern is expected to be particularly important during long-distance migrations.

Some variability in the relationship between swim depth and body size might be expected (21). For example, sea state should also be important in dictating near-surface swim depth, with animals swimming slightly deeper in choppy conditions, when waves passing overhead will mean animals must travel at greater relative depths in order to benefit from the same avoidance of wave drag.

Consistent with this prediction, the pygmy blue whale migrating through exposed waters west of Australia traveled slightly below its calculated optimal depth, while adult North Atlantic right whales in the sheltered Bay of Fundy traveled at 2.5 \times their estimated body diameter—the minimum depth for zero wave drag according to Hertel’s experiments (3) once differences between depth measurement to the central axis and to the dorsal surface are accounted for. Differences in sea state between coastal and pelagic environments might also impact the tendency for animals to swim at a depth of around three body thicknesses. Tracking animals across different sea states might help to answer this question.

Other factors might often drive the depth of swimming animals aside from minimization of energy expenditure, such as foraging or avoidance of predators. Seals forage opportunistically when traveling and so this kind of shallow “travel-only” dive behavior is not expected in this group. Elephant seals, for example, have a typical diving pattern of very deep V-shaped dives (22), and have been shown to consume prey *en route* during these dives (23). Leatherback turtles (*Dermochelys coriacea*) have a similar “deep V” diving pattern (24) as they search the water column for zooplankton prey as they travel. A modelling study using parameters taken from elephant seal tracking found that horizontal swimming beneath the surface would be more energetically efficient despite the energy savings made during gliding descent, concluding that other factors such as feeding and predator avoidance are more likely drivers of their deep migratory diving pattern (25). Indeed, elephant seals are a favorite prey species for white shark (*Carcharodon carcharias*) owing to their

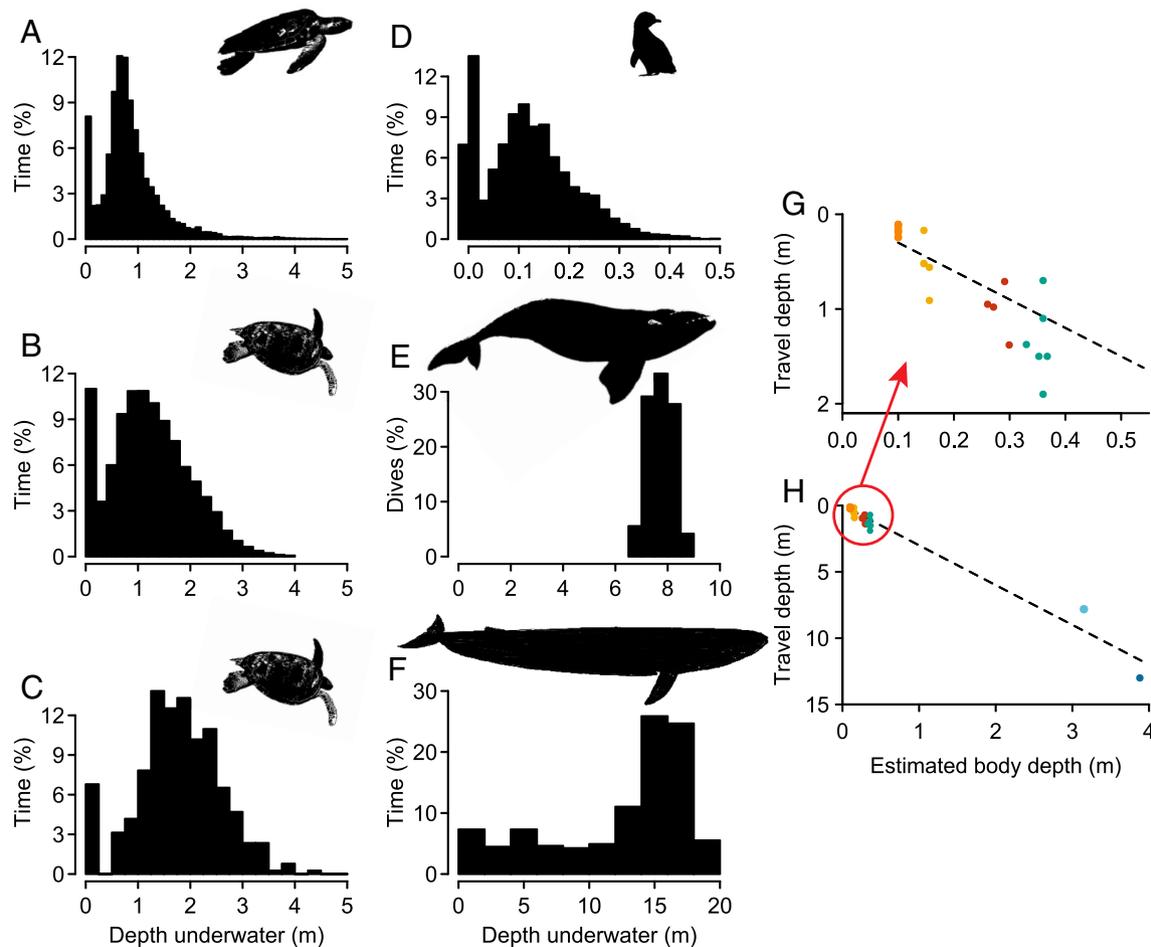


Fig. 5. Marine reptiles, birds, and mammals travel at optimized swim depths when not feeding *en route*. Loggerhead (A) and green turtles (B–C) travel at depths that minimize wave drag and vertical distance traveled during daylight hours, homing to the nesting beach in the Mediterranean Sea (A) or migrating in the Atlantic (B, 11) and Pacific Oceans (C, 18). Little penguins avoid the zone of highest wave drag when commuting to a prey patch (D). North Atlantic right whales in the Bay of Fundy travel at predicted optimal depths (E, 14). A pygmy blue whale consistently dived to depths just below $3 \times$ body diameter while migrating along the southwest coast of Australia (F, 15). (G–H) Travel dive depth depends on body size and is around three times estimated body diameter (dashed lines; see *SI Appendix, Tables S1, S2, and S4*). Panel G shows a close-up of the detail for the smaller-bodied animals, while panel H zooms out to all species to show that this scaling relationship persists across the full size range of these animals. *Left to Right*: little penguins (orange; $n = 9$), Magellanic penguins (yellow; $n = 2, 16$), Adélie penguins (yellow; $n = 2$ datapoints, 4 individuals, 17), loggerhead turtles (brown; $n = 4$), green turtles (green; Hawaii, $n = 1, 18$; Ascension Island, $n = 5, 11$), north Atlantic right whales (light blue; $n = 1$ datapoint, 9 individuals, 14), pygmy blue whale (dark blue; $n = 1, 15$).

abundant fat stores, and it has been suggested that their deep diving pattern even when crossing the continental shelf to reach the deep-water prey fields beyond serves to reduce the proportion of time spent visible to sharks scanning for prey against light from the surface (26, 27). Sharks are another notable exception as they have sometimes been observed traveling at the very surface, this kind of swimming pattern being their most energetically expensive (28). Drivers for this behavior could include thermoregulation (29), surface feeding behaviors [e.g., whale shark *Rhincodon typus*: (30), white shark: (31)], and even navigation (32). Nevertheless, our findings suggest that when the primary purpose of movement is for animals to travel horizontally to a distant target, swimming at subsurface depths to reduce energy expenditure seems to be a strategy that is widely used across diverse taxa. A similar strategy in humans would provide a major energetic advantage at the Olympics, but subsurface swimming at competitive events is highly regulated to protect athlete safety (33).

Like formation flight in birds (34), use of wind energy in soaring flight (35), and swim-and-glide strategies in deep diving animals (1, 36), our findings provide compelling evidence that swimming at optimal near-surface depths to reduce the energetic cost of forward motion is likely a conservative trait among diving marine vertebrates during long-distance migration, where animals are not foraging *en route*.

Data, Materials, and Software Availability. The data reported in this paper are available from the Dryad Digital Repository (37). All other data are included in the manuscript and/or [supporting information](#).

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1. T. M. Williams *et al.*, Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science* **288**, 133–136 (2000), 10.1126/science.288.5463.133.
2. C. M. Bishop *et al.*, The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science* **347**, 250–254 (2015), 10.1126/science.1258732.
3. H. Hertel, *Structure Form Movement* (Reinhold, 1966).

4. R. W. Blake, Biological implications of the hydrodynamics of swimming at or near the surface and in shallow water. *Bioinspir. Biomim.* **4**, 015004 (2009), 10.1088/1748-3182/4/1/015004.
5. T. M. Williams, Locomotion in the North American mink, a semi-aquatic mammal: I. Swimming energetics and body drag. *J. Exp. Biol.* **103**, 155–168 (1983), 10.1242/jeb.103.1.155.

6. T. M. Williams, Swimming by sea otters: Adaptations for low energetic cost locomotion. *J. Comp. Physiol. A* **164**, 815–824 (1989), 10.1007/BF00616753.
7. R. Vennell, D. Pease, B. Wilson, Wave drag on human swimmers. *J. Biomech.* **39**, 664–671 (2006), 10.1016/j.jbiomech.2005.01.023.
8. T. M. Williams, G. L. Kooyman, Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 576–589 (1985), 10.1086/physzool.58.5.30158584.
9. R. V. Baudinette, P. Gill, The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *J. Comp. Physiol. B* **155**, 373–380 (1985), 10.1007/BF00687481.
10. P. Luschi *et al.*, A biphasic navigational strategy in loggerhead sea turtles. *Sci. Rep.* **10**, 18139 (2020), 10.1038/s41598-020-75183-6.
11. G. C. Hays *et al.*, The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: Dive durations, dive profiles and depth distribution. *J. Exp. Biol.* **204**, 4093–4098 (2001), 10.1242/jeb.204.23.4093.
12. J. Finn, J. Carlsson, T. Kelly, J. Davenport, Avoidance of headwinds or exploitation of ground effect – why do birds fly low? *J. Field Ornithol.* **83**, 192–202 (2012), 10.1111/j.1557-9263.2012.00369.x.
13. D. Weihs, The hydrodynamics of dolphin drafting. *J. Biol.* **3**, 8 (2004), 10.1186/jbiol2.
14. A. E. Nousek-McGregor, *The Cost of Locomotion in North Atlantic Right Whales* (Duke University, 2010).
15. K. Owen, C. S. Jenner, M.-N.M. Jenner, R. D. Andrews, A week in the life of a pygmy blue whale: Migratory dive depth overlaps with large vessel drafts. *Anim. Biotelemetry* **4**, 17 (2016), 10.1186/s40317-016-0109-4.
16. D. G. Ainley, R. P. Wilson, *The Aquatic World of Penguins* (Springer, 2023).
17. K. Yoda *et al.*, Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* **202**, 3121–3126 (1999), 10.1242/jeb.202.22.3121.
18. M. R. Rice, G. H. Balazs, Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* **356**, 121–127 (2008), 10.1016/j.jembe.2007.12.010.
19. N. F. Hughes, The wave-drag hypothesis: An explanation for size-based lateral segregation during the upstream migration of salmonids. *Can. J. Fish. Aquat. Sci.* **61**, 103–109 (2004), 10.1139/f03-144.
20. A. M. M. Sequeira *et al.*, Convergence of marine megafauna movement patterns in coastal and open oceans. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3072–3077 (2018), 10.1073/PNAS.1716137115.
21. K. P. Dial, E. Greene, D. J. Irschick, Allometry of behavior. *Trends Ecol. Evol.* **23**, 394–401 (2008), 10.1016/j.tree.2008.03.005.
22. B. J. Le Boeuf, D. P. Costa, A. C. Huntley, S. D. Feldkamp, Continuous, deep diving in female northern elephant seals *Mirounga angustirostris*. *Can. J. Zool.* **66**, 446–458 (1988), 10.1139/z88-064.
23. C. E. Kuhn, D. E. Crocker, Y. Tremblay, D. P. Costa, Time to eat: Measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *J. Anim. Ecol.* **78**, 513–523 (2009), 10.1111/j.1365-2656.2008.01509.x.
24. S. Fossette *et al.*, Behaviour and buoyancy regulation in the deepest-diving reptile: The leatherback turtle. *J. Exp. Biol.* **213**, 4074–4083 (2010), 10.1242/jeb.048207.
25. R. W. Davis, D. Weihs, Locomotion in diving elephant seals: Physical and physiological constraints. *Phil. Trans. R. Soc. B* **362**, 2141–2150 (2007), 10.1098/rstb.2007.2107.
26. B. J. Le Boeuf, D. E. Crocker, "Diving behavior of elephant seals: Implications for predator avoidance" in *Great white sharks: The biology of Carcharodon carcharias*, A. P. Klimley, D. G. Ainley, Eds. (Academic Press, 1996), pp. 193–205.
27. J. M. Kendall-Bar *et al.*, Brain activity of diving seals reveals short sleep cycles at depth. *Science* **380**, 260–265 (2023), 10.1126/science.adf0566.
28. Y. Y. Watanabe, N. L. Payne, J. M. Semmens, A. Fox, C. Huveneers, Swimming strategies and energetics of endothermic white sharks during foraging. *J. Exp. Biol.* **222**, jeb185603, (2019), 10.1242/jeb.185603.
29. M. Thums, M. Meekan, J. Stevens, S. Wilson, J. Polovina, Evidence for behavioural thermoregulation by the world's largest fish. *J. R. Soc. Interface* **10**, 20120477 (2013), 10.1098/rsif.2012.0477.
30. P. J. Motta *et al.*, Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico. *Zoology* **113**, 199–212 (2010), 10.1016/j.zool.2009.12.001.
31. C. Huveneers *et al.*, White sharks exploit the sun during predatory approaches. *Am. Nat.* **185**, 562–570 (2015), 10.1086/680010.
32. R. Bonfil *et al.*, Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 100–103 (2005), 10.1126/science.1114898.
33. D.-P. Born, M. Schönfelder, O. Logan, B. H. Olstad, M. Romann, Performance development of European swimmers across the Olympic cycle. *Front. Sport Act. Living* **4**, 894066 (2022), 10.3389/fspor.2022.894066.
34. H. Weimerskirch, J. Martin, Y. Clerquin, P. Alexandre, S. Jiraskova, Energy saving in flight formation. *Nature* **413**, 697–698 (2001), 10.1038/35099670.
35. H. Weimerskirch, C. Bishop, T. Jeanniard-du-Doit, A. Prudor, G. Sachs, Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science* **353**, 74–78 (2016), 10.1126/science.aaf4374.
36. A. C. Gleiss *et al.*, Convergent evolution in locomotory patterns of flying and swimming animals. *Nat. Commun.* **2**, 352 (2011), 10.1038/ncomms1350.
37. K. L. Stokes *et al.*, Data from "Optimization of swim depth across diverse taxa during horizontal travel." Dryad. <https://doi.org/10.5061/dryad.rn8pk0pks>. Deposited 10 July 2024.