

Annual Review of Marine Science

The Functional and Ecological Significance of Deep Diving by Large Marine Predators

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Annu. Rev. Mar. Sci. 2022. 14:129–59

First published as a Review in Advance on
August 20, 2021

The *Annual Review of Marine Science* is online at
marine.annualreviews.org

<https://doi.org/10.1146/annurev-marine-032521-103517>

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Keywords

ocean twilight zone, telemetry, mesopelagic, bathypelagic, top predators

Abstract

Many large marine predators make excursions from surface waters to the deep ocean below 200 m. Moreover, the ability to access meso- and bathypelagic habitats has evolved independently across marine mammals, reptiles, birds, teleost fishes, and elasmobranchs. Theoretical and empirical evidence suggests a number of plausible functional hypotheses for deep-diving behavior. Developing ways to test among these hypotheses will, however, require new ways to quantify animal behavior and biophysical oceanographic processes at coherent spatiotemporal scales. Current knowledge gaps include quantifying ecological links between surface waters and mesopelagic habitats and the value of ecosystem services provided by biomass in the ocean twilight zone. Growing pressure for ocean twilight zone fisheries creates an urgent need to understand the importance of the deep pelagic ocean to large marine predators.

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Pelagic: the open ocean away from continental shelves

Epipelagic: the portion of the open ocean between 0- and 200-m depth

Deep scattering layer (DSL): a dense layer in the ocean where organisms living at depth (primarily myctophid fishes, squids, crustaceans, and jellyfishes) cause backscattering in echosounders

Mesopelagic: the portion of the open ocean between 200- and 1,000-m depth

Bathypelagic: the portion of the open ocean between 1,000- and 3,000-m depth

Dive: here, a convenience term referring to vertical excursions of LMPs, regardless of whether it is a true dive by a surface obligate (e.g., a marine mammal or turtle) or a vertical excursion by a non-air breather (e.g., a teleost fish)

1. INTRODUCTION

1.1. Vertical Zonation of the Pelagic Ocean: A Paradigm Shift

The pelagic ocean represents Earth's largest biosphere and provides ecosystem services worth trillions of dollars to the global economy annually. Historically, biologists believed that most of the life in the open ocean resided in the upper 200 m, or the epipelagic zone. In fact, some of the earliest hypotheses suggested the ocean was azoic below approximately 500 m and that life in the midwater was nearly or entirely absent. The discovery of deep scattering layers (DSLs) at midocean depths of the northwest Atlantic in the late 1940s challenged this perception and hinted at the presence of significant biomass below 200 m (Balls 1948). Gjøsæter & Kawaguchi (1980) later provided a first estimate of the global biomass of mesopelagic fishes, on the order of 1 Gt (1×10^9 t), based on net tows. More recent studies using active acoustics suggest that mesopelagic fish biomass may in fact be closer to 7–10 Gt (Irigoien et al. 2014). We still lack an estimate of the global biomass of bathypelagic (1,000–3,000 m) fishes, although Sutton (2013) found that this zone had higher biomass than the mesopelagic in waters above the Mid-Atlantic Ridge. Nonetheless, the sheer abundance of life in the deep pelagic ocean suggests that these communities are critical to both the functioning of open-ocean ecosystems and the services that they provide.

While the deep pelagic zone remains mysterious, there is growing evidence for the importance of ecological connections across classical depth zones in the global ocean. For example, sperm whales are hypothesized to consume a biomass of mesopelagic squid equivalent to the annual global marine fisheries landings (Whitehead 2003). Similarly, results from gut content analysis suggest that mesopelagic fishes, squids, and crustaceans provide a significant amount of the daily rations of commercially important pelagic fishes (e.g., tunas; Duffy et al. 2017). Regular dives of marine mammals across depth zones (and their excretion in the epipelagic) may also be a key upward offset to the biological carbon pump (Roman & McCarthy 2010), which moves carbon downward from surface waters to the deep ocean. This process is, in part, driven by the diel vertical migration (DVM) of many fish and invertebrate taxa that spend nighttime hours in surface waters before moving down to the meso- and bathypelagic during the day. Taken together, these findings highlight the importance of a full-water-column approach to support a more holistic understanding of ocean ecology (Sutton 2013).

1.2. Electronic Tagging: A Window into the Depths

Our ability to study the deep pelagic ocean has historically been limited largely to nets and sensors deployed from research vessels. Unfortunately, these ship-based methods have provided limited information on the ecological links between large marine predators (LMPs) normally observed in epipelagic habitats and the fauna that inhabit the deep pelagic ocean. More success has been met with the proliferation of simple in situ sensors integrated into electronic tags deployed on marine animals. Electronic tags have revealed remarkable long-distance migrations (e.g., Block et al. 2011) and precise open-ocean navigation (e.g., Braun et al. 2018). Many of these studies have also identified behavioral modes in which LMPs make excursions into the deep pelagic ocean. In particular, leveraging instrumented animals as evolutionarily informed oceanographers has yielded predator perspectives on mesopelagic prey distribution (McMahon et al. 2019) and composition (Yoshino et al. 2020). Tagging studies have also shed light on the biophysical drivers that might modulate connectivity between epi- and mesopelagic ecosystems (e.g., Braun et al. 2019b) and the

potential trophic interactions occurring at depth in the open ocean (Abrahms et al. 2018, Yoshino et al. 2020). Together, studies like these suggest that accessing the deep pelagic may be a common behavioral mode across diverse taxonomic groups and demonstrate that animal-borne sensors are a powerful tool for studying the structure and function of ocean ecosystems. Yet, despite significant effort, the last few decades of tagging of LMPs has resulted in surprisingly limited progress toward understanding the ecological significance of deep diving. Indeed, while most authors propose foraging as the likely adaptive behavior for the observed use of deep-ocean habitats by seemingly epipelagic LMPs, robust direct evidence to support this hypothesis is limited or absent in all but a few marine mammal taxa.

This review is an attempt to synthesize our understanding of the primary drivers, ecological significance, and function of deep diving by LMPs that researchers typically observe in the epipelagic. In Section 2, we explore the challenges and opportunities for LMPs accessing the deep pelagic ocean. In Section 3, we present the frequency and behavioral modes of deep diving exhibited by LMPs. In Section 4, we synthesize published observations of deep pelagic habitat use with ecological theory and oceanographic observations to explore plausible hypotheses for the functional role(s) and significance of deep diving across diverse LMP taxa. In Section 5, we detail two case studies that highlight particularly compelling examples of these behavioral modes. In Sections 6 and 7, we synthesize our collective progress toward understanding the potential functional roles and ecological significance of this behavior. Finally, we propose several priorities for future research.

2. CHALLENGES IN THE DEEP PELAGIC OCEAN

2.1. Oceanographic Processes

The vertical zonation and associated gradients (**Figure 1**) in oceanographic properties of the open ocean are modulated at various scales. Macroscale dynamics occur on the regional or basin scale and persist for months to years. These processes include boundary currents, midocean gyres, and regional upwelling systems that result in large-scale changes in biophysical properties, ranging from strong three-dimensional gradients in temperature to patchiness in communities of primary producers and diel vertical migrators (Behrenfeld et al. 2019). For example, regional oceanographic processes that alter water clarity and affect light attenuation may directly or indirectly influence daytime depths occupied by swordfish (Dewar et al. 2011), while upwelling of cold, hypoxic waters may lead to vertical habitat compression among pelagic fishes (Carlisle et al. 2017, Vedor et al. 2021).

(Sub)mesoscale features in the open ocean, including eddies, meanders, and fronts, impact water-column structure and biophysical dynamics (meso- and submesoscale reviewed in McGillicuddy 2016 and Mahadevan 2016, respectively). While it is well established that (sub)mesoscale processes generate hot spots in oceanic primary production, there is growing evidence that these features also modulate DSL communities, which may in turn influence the use of deep pelagic habitats by LMPs. For example, a survey of mesoscale eddies in the western North Atlantic revealed that, on average, the cores of anticyclones contain elevated acoustic backscatter, with magnitudes up to 40 times higher than that observed in cyclones (Della Penna & Gaube 2020). In regions characterized by large-amplitude mesoscale eddies, the enhanced foraging opportunities in anticyclones suggested by these acoustic surveys are also often associated with warm subsurface temperature anomalies (up to 6°C in the mesopelagic), which may also increase access for LMPs that would otherwise be inhibited from accessing mesopelagic prey due to thermal constraints (e.g., white and blue sharks; Gaube et al. 2018, Braun et al. 2019b). Further evidence from

Diel vertical migration (DVM): refers primarily to the migration made by DSL organisms between epipelagic depths (0–200 m) during the night and mesopelagic depths (typically 300–500 m) during the day, presumably to escape visual predators at the surface

Large marine predators (LMPs): large marine animals, such as whales, dolphins, seals, turtles, penguins, sharks, rays, and fishes, that primarily occupy the epipelagic realm and make movements into the meso- or bathypelagic during one or more life stages

Deep dive: a dive away from the epipelagic, i.e., to depths greater than 200 m

(Sub)mesoscale: variability in the physical dynamics of the ocean environment with spatial scales on the order of 1–100 km that persists for days to months

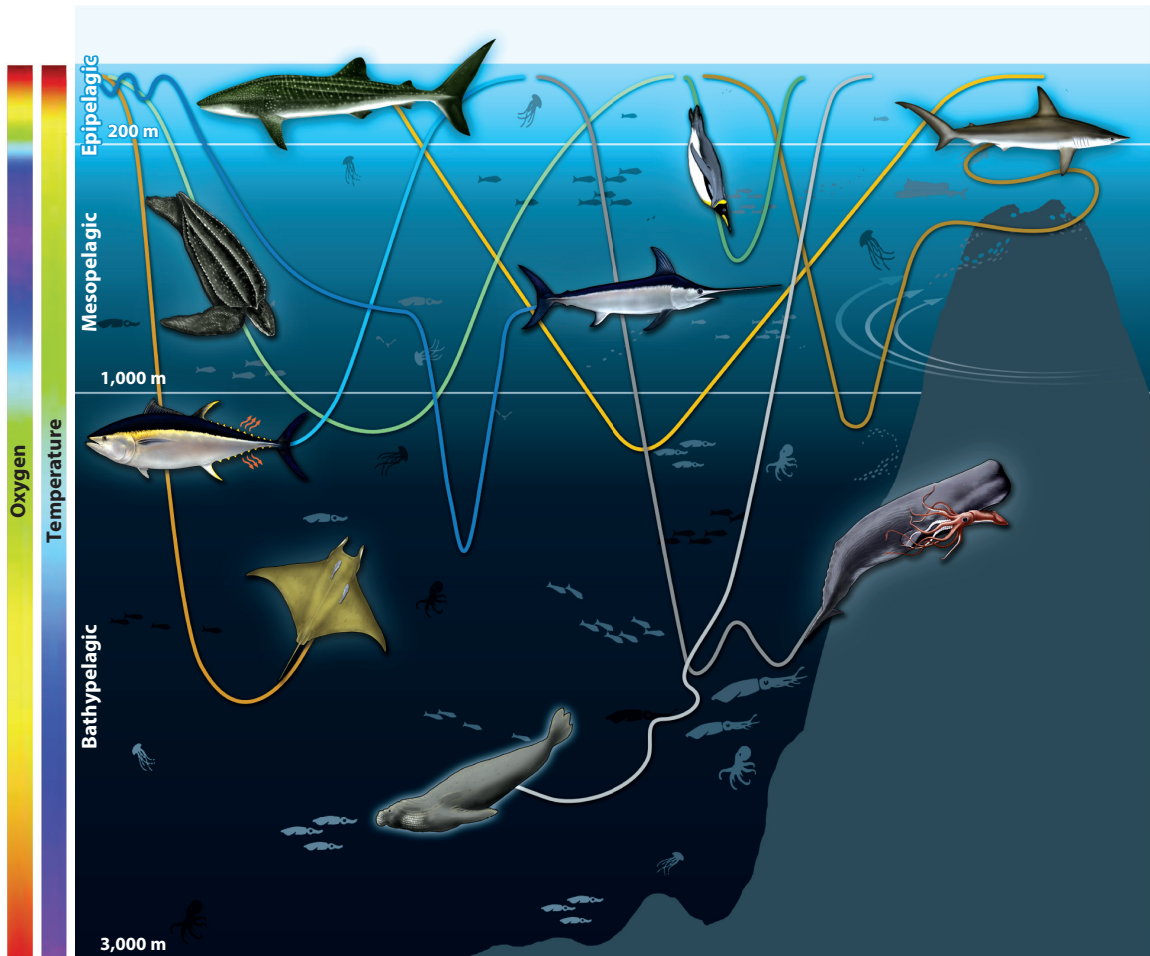


Figure 1

Typified example deep dives by representative large marine predator taxa, such as thermoregulatory dives by bluefin tuna, deep foraging dives by sperm whales and northern elephant seals, and navigational dives to sense geomagnetic cues around seamounts by scalloped hammerheads. Oxygen and temperature bars (*left*) indicate generalized vertical gradients. Illustration created by Les Gallagher (Fishpics, Institute of Marine Research, and Department of Oceanography and Fisheries, University of the Azores).

Convergent evolution: the process in which organisms that are not closely related independently evolve similar traits as a result of having to adapt to similar environments or ecological niches

the dynamic North Pacific Transition Zone and the Antarctic Circumpolar Current suggests that elephant seals experience significant increases in daily energy gain by foraging in regions of elevated (sub)mesoscale activity (Section 5.1). Together, these results suggest that biophysical interactions at the (sub)mesoscale may be particularly important determinants of deep pelagic habitat use by LMPs.

2.2. Physiological Modulation and Adaptations

The prevalence of deep-diving behavior across diverse LMP taxa suggests the convergent evolution of a suite of behavioral, physiological, and anatomical adaptations to the environmental challenges posed by movements into the meso- and bathypelagic (**Figure 1**). These challenges include cold temperatures and low oxygen concentrations, which can hinder proper functioning

of organs; low light levels, which can preclude visual targeting of prey, conspecifics, and other predators; and high pressure, which can potentially cause decompression sickness and influence enzyme performance.

Cold conditions at depth reduce metabolic rates, the effects of which many deep-diving species have overcome or attenuated with endothermy. This capacity is present in various degrees, including full endothermy in marine mammals and penguins, whole-body endothermy in opahs (Wegner et al. 2015), inertial endothermy in leatherback sea turtles (Paladino et al. 1990), and regional endothermy in three lineages of teleosts, three lineages of elasmobranchs (Legendre & Davesne 2020), and green sea turtles (Standora et al. 1982). Vascularized systems acting as countercurrent heat exchangers (retia), which conserve body heat by transferring it among neighboring blood vessels flowing in opposite directions, are perhaps the most notable anatomical adaptations facilitating endothermy in LMPs (Bernal et al. 2017). Fatty tissue or blubber (Liwanag et al. 2012a, Wegner et al. 2015) and air trapped in fur (Liwanag et al. 2012b) or feathers (Williams et al. 2015) also provide insulation to maintain internal temperatures. Blubber constitutes the primary insulation for most air-breathing LMPs, especially the most extreme divers within each taxonomic lineage (Favilla & Costa 2020). Some species also exhibit behavioral thermoregulation, returning repeatedly to shallower water to rewarm after deep dives, as well as physiological thermoregulation, in which they alter their blood circulatory routes to minimize heat loss while diving into cold water and maximize heat gain while ascending into warm water (e.g., common mola; Nakamura et al. 2015).

To permit meso- and bathypelagic forays, deep-diving species must either hold their breath for extended periods while submerged (e.g., air-breathing marine mammals) or maximize oxygen uptake from often hypoxic waters at depth (teleosts and elasmobranchs). Some species in both groups have heightened myoglobin concentrations in locomotory muscles that aid in the diffusion and storage of oxygen [e.g., pinnipeds and cetaceans (Mirceta et al. 2013) and thresher and mackerel sharks (Bernal et al. 2003)] or have blood with heightened oxygen affinities that increase available oxygen [e.g., bigeye tuna (Lowe et al. 2000) and emperor penguins (Meir & Ponganis 2009)]. In addition to increasing aerobic capacity, breath-holding species regularly rely on a transition to an anaerobic metabolism that enables extreme dives beyond aerobic limits, albeit at the cost of increased recovery time between dives (e.g., Blainville's and Cuvier's beaked whales; Joyce et al. 2017). Among some high-performance teleosts and elasmobranchs, increased gill surface area also enhances hypoxia tolerance by augmenting oxygen uptake (e.g., swordfish; Wegner et al. 2010).

Minimal sunlight penetrates the ocean below 200 m (Costello & Breyer 2017), imposing the need for adaptations to enhance vision or alternative senses to forage effectively in or below the mesopelagic zone. Bioluminescence is the predominant source of light in the deep ocean, and LMPs may detect it as point-source flashes or as shadows against the extended, dim background light it produces (Warrant & Locket 2004). Many deep-diving species have large eyes with increased sensitivity to both forms of light. There is, however, an anatomical trade-off in the detection of point-source versus extended light, and, therefore, some LMPs have specialized eyes to detect one type of light over the other (Kröger et al. 2009). Furthermore, some deep-diving LMPs have a specialized, reflective tissue in their eyes (the tapetum lucidum) that increases photosensitivity [e.g., bigeye tuna (Somiya et al. 2000), hooded seals (Hogg et al. 2015), and all sharks (Collin 2018)]. This ocular adaptation is present in cetaceans (Mass & Supin 2007), but these species are also able to circumvent light limitations to vision by using acoustic vocalizations to echolocate prey and communicate with conspecifics during deep dives (e.g., short-finned pilot whales; Pérez et al. 2017). Pinnipeds rapidly acclimate their eyes to dark conditions but also use their sensitive facial whiskers (vibrissae) for short-range detection of tactile and hydrodynamic stimuli (Schusterman et al. 2000).

Endothermy: an animal's capacity to regulate its internal temperature; a given species may have full, whole-body, inertial, or regional endothermy

Retia: a vascular network of blood vessels that can conserve body heat by transferring it among neighboring blood vessels flowing in opposite directions (i.e., a countercurrent heat exchanger)

The immense pressures experienced at depth, along with rapid changes in pressure during dives, pose a substantial challenge to LMPs. Decompression sickness may occur when tissues accumulate dissolved gases (e.g., nitrogen) at depth and then become supersaturated as the animal ascends and the ambient pressure drops, leading to the formation of gas bubbles in tissues and the bloodstream. Indeed, the bends, or gas emboli formation, is known to occur in deep-diving air breathers, including sperm and beaked whales (Hooker et al. 2012) and loggerhead sea turtles (García-Párraga et al. 2014), with potentially fatal consequences. Air-breathing divers face additional risks associated with shallow-water blackout. Decreased ambient pressure may cause a precipitous decline in O₂ partial pressure and subsequent hypoxia during ascent. Deep-diving LMPs may avoid the consequences of decompression by slowing their rate of ascent, especially at shallower depths, where the pressure change is the greatest [e.g., king and Adélie penguins (Sato et al. 2002) and oceanic whitetip sharks (Howey et al. 2016)], to reduce the gradient between tissue tensions and ambient pressure. Many marine mammals and sea turtles also have collapsible lungs that minimize diffusion of gases into body tissues at depth (Ponganis 2016). Alveoli collapse prevents the on-gassing of nitrogen in air into the blood, reducing the chance of decompression illness. This adaptation also helps prevent shallow-water blackouts, as oxygen kept in the upper airways during collapse acts as a reservoir that can reenter alveoli and be extracted by the blood upon lung expansion during ascent (e.g., California sea lions; McDonald & Ponganis 2012).

Many of the adaptations to the challenging environmental conditions experienced while deep diving develop and become more effective as animals grow [e.g., physiological thermoregulation in bigeye tuna (Hino et al. 2020), aerobic dive capacity in Steller sea lions (Richmond et al. 2006), and tracheal compression in leatherback sea turtles (Davenport et al. 2009)]. The capacity for deep diving therefore often increases with ontogeny, and expansion in vertical movements with increasing size has been recorded in many tagging studies of LMPs, including pinnipeds (e.g., Australian sea lions; Fowler et al. 2007), teleosts (e.g., swordfish; Braun et al. 2019a), and elasmobranchs (e.g., tiger sharks; Afonso & Hazin 2015).

3. FREQUENCY AND MODES OF DEEP DIVING

The frequency and magnitude of deep-diving behaviors vary widely across LMP taxa. In this review, we focus primarily on inter- and intraspecific comparisons of deep dives and synthesize existing efforts to understand the drivers of these behavioral modes. We found it helpful to distinguish between deep dives and more prolonged periods of residency in the deep ocean. We defined deep dives to include both true dives by marine mammals, seabirds, and reptiles and excursions from the epipelagic by teleost fishes and elasmobranchs; seasonal and full-time residency of deep pelagic habitats was therefore excluded from our review.

Nearly every oceanic taxa studied with electronic tags exhibits some form of deep diving or occupation of a deep pelagic habitat (**Figure 2**). Individuals exhibit several distinct patterns in their use of deep pelagic habitats within species and across phylogenetic lineages. For example, the frequency of deep diving varies widely, from multiple excursions per hour (elephant seals; Section 5.1) to consistent DVM (swordfish; Section 5.2) to only occasional, seemingly sporadic dives (e.g., leatherback turtles; Houghton et al. 2008). Comparisons of diving behavior are complicated by the existence of diverse strategies for deep pelagic habitat use both by individuals of the same species and by a given individual across time, which is at least partially a function of oceanographic regime (Section 2.1) and biology (e.g., ontogeny and physiology; Section 2.2). Multiple deep-diving modes are often used by the same individual even over the course of a relatively short

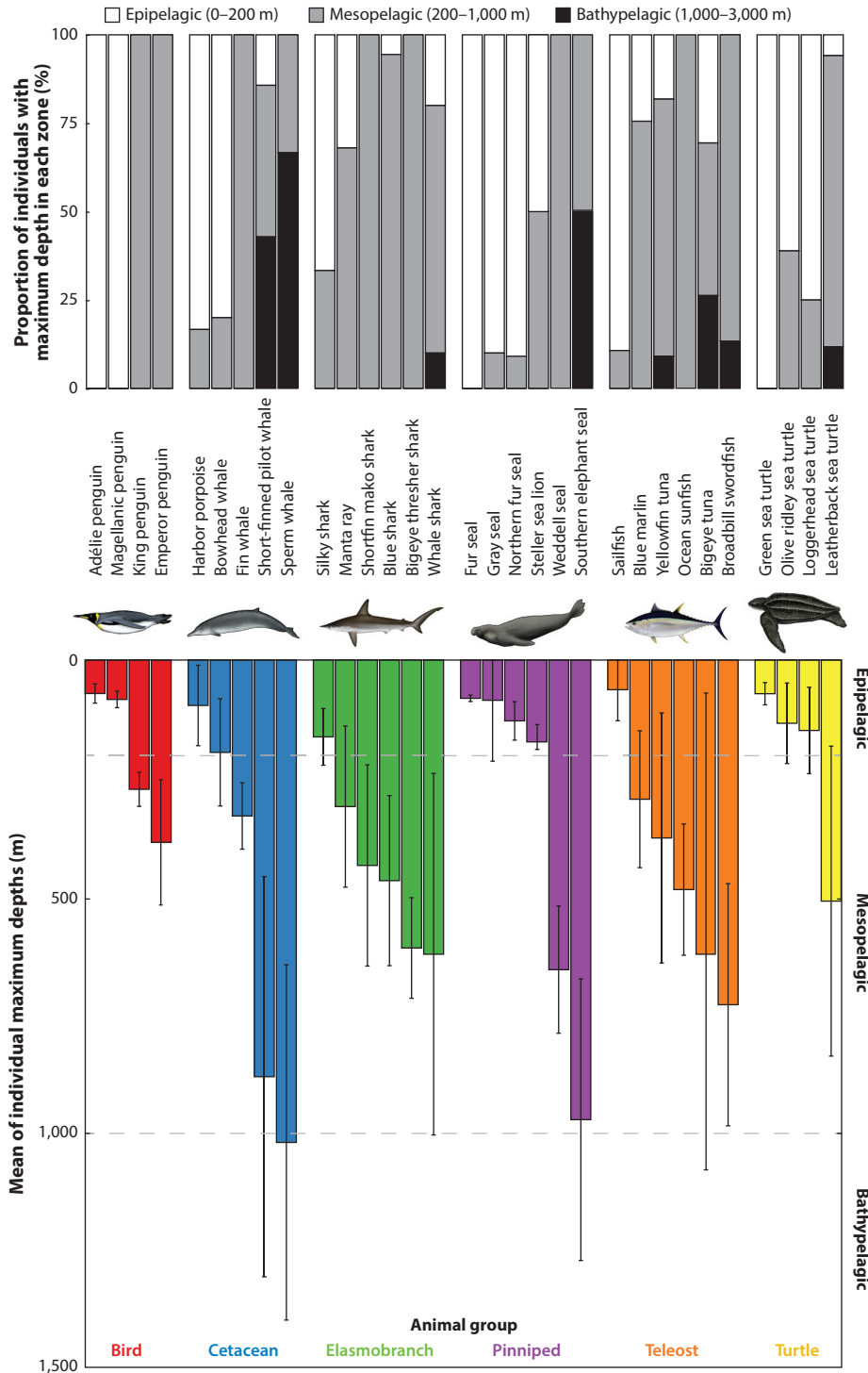


Figure 2

Deep diving is a variable but ubiquitous behavior mode across diverse LMP taxa. A review of maximum recorded depths from a representative set of taxa demonstrates that species within each predator group exhibit a gradient (*top panel, left to right within each group*) in depth range, from most individuals occupying the epipelagic (*white*) to increasingly more individuals' maximum depth occurring in the mesopelagic (*gray*) and bathypelagic (*black*). This within-group gradient in habitat use is also apparent in individual maximum dive depths (*bottom panel, mean \pm SD*) observed across a number of tagged individuals. Together, these metrics show that while some taxa appear better adapted to make excursions to the deep pelagic ocean (*top*), most LMPs studied with electronic tags conduct some form of deep diving (*bottom*). For the data used to create this figure, see the **Supplemental Data**. Abbreviation: LMP, large marine predator.

Supplemental Material >

Lévy flight foraging hypothesis:

a theory describing characteristics of random animal movement that are thought to optimize search efficiency

tag deployment, presumably indicating different functions and/or constraints. A consensus has emerged over the last three decades, based on electronic tagging studies, that these diverse behavioral modes must be related largely to foraging (Section 4.1). However, direct evidence supporting the foraging hypothesis remains sparse. Given the emerging diversity of observed diving behaviors and their patterned occurrence in space and time (e.g., Jorgensen et al. 2012), we propose that deep diving may serve a more complex and diverse set of functions for LMPs than previously recognized. Several authors have postulated other motivations for LMPs using the deep pelagic ocean, including escape from predators and harassment from conspecifics (Section 4.2), probing of the water column for navigational purposes (Section 4.3), reduction of energetic costs during migrations (Section 4.4), eviction of parasites (Section 4.5), thermoregulation (Section 4.6), and social interaction (Section 4.7). To our knowledge, none of these hypotheses have been tested or systematically analyzed in order to evaluate the functions of observed deep-diving behavior across a variety of LMP taxa.

4. DEEP-DIVING FUNCTIONS

4.1. Foraging in the Mesopelagic and Beyond

The patchiness of prey in the epipelagic realm, the putative abundance of deep-ocean biomass, and the highly migratory nature of most LMPs suggest that some diving modes have evolved to exploit food resources in the deep ocean (**Figure 3**). Many LMPs exhibit regular excursions to the mesopelagic at depths that correspond to the approximate position of the primary DSL (e.g., blue shark; Carey 1990, Braun et al. 2019a) and are coincident with the timing of DVM by the mesopelagic community (e.g., bigeye tuna; Josse et al. 1998) (**Figure 3e**). Foraging at depth has been confirmed in several studies on mammalian LMPs (e.g., elephant seals) (**Figure 3a–c**; see also Section 5.1). Furthermore, while some have argued that infrequent extreme deep dives are unlikely to be associated with foraging (Andrzejczek et al. 2019), significant prey resources are located well into the bathypelagic (Sutton 2013, Kaartvedt et al. 2020), and there is mounting evidence that air-breathing deep divers, in particular, are consistently feeding well below the primary DSL (e.g., southern elephant seals; McIntyre et al. 2012) (**Figure 3**) to as deep as nearly 3,000 m (Cuvier's beaked whales; Schorr et al. 2014).

Most deep diving by teleost and elasmobranch LMPs is also thought to be related to foraging. However, there is surprisingly little direct evidence to support foraging as the primary functional role for deep-diving behavior in these groups. In the absence of direct observations, several authors have sought to match observed LMP behaviors with theoretical expectations for foraging in the deep pelagic. Foraging behavior in the deep ocean is likely to vary depending on the predator's physiology and specific sensory abilities as well as the ambient environmental conditions encountered during a dive. It is therefore difficult to establish expectations for characteristics of deep dives that may be reasonably generalized beyond specific taxa. However, theoretical developments using models with a generic visual predator suggest that crepuscular interception of a mesopelagic community that undergoes normal DVM should be the most efficient foraging strategy (Thygesen & Patterson 2019). The temporal frequency of deep foraging dives should also approximate a Lévy distribution, as predators alternate between many small steps (dives) connected by longer relocations, with the frequency of deeper dives approximating an inverse power law that is repeated at all spatial scales (Humphries et al. 2010). The Lévy flight foraging hypothesis further predicts that Lévy flights are more efficient search strategies when prey are sparse, while Brownian motion is more efficient when resources are abundant (Humphries et al. 2010). Occasional very deep dives would also be consistent with a Lévy flight search strategy. The dive patterns of several pelagic

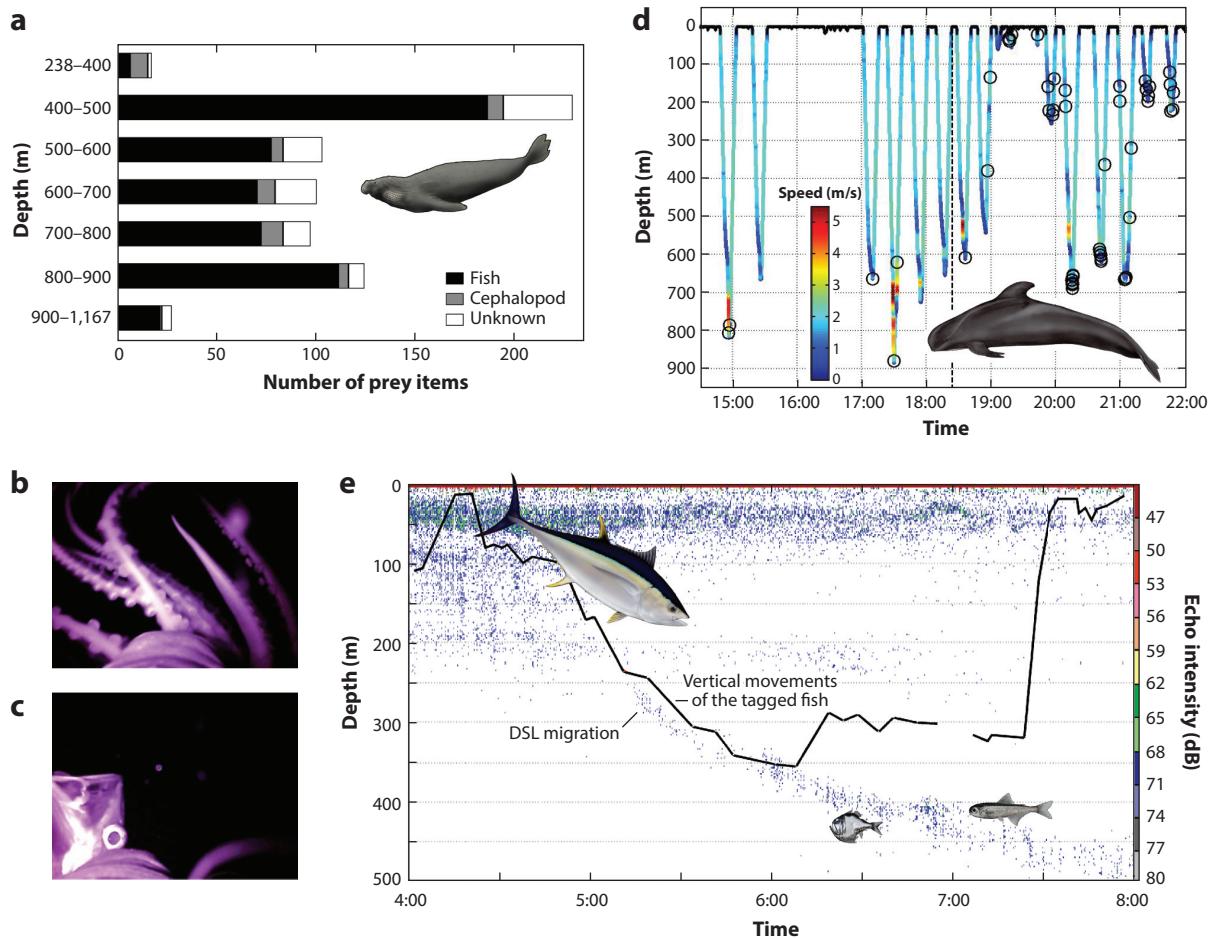


Figure 3

Robust evidence from electronic tags has been used to confirm (panels *a–c*) or support (panel *d*) foraging as a driver of deep diving for a handful of mammalian LMP taxa. For example, acceleration-triggered camera tags deployed on northern elephant seals provided one of the only unequivocal examples of LMPs foraging at depth, in this case on both squid (panel *b*, which shows a head-mounted camera image of a seal capturing a squid, *Belonella* sp.) and fishes (panel *c*, which shows an unidentified mesopelagic fish). These images facilitated the characterization of captured prey along a depth gradient (panel *a*). Short-finned pilot whales exhibit hypothesized foraging (panel *d*), indicated by rapid acceleration near the bottoms of dives (with bursts of up to 5 m/s) and associated echolocation buzzes (black circles), presumably to capture mesopelagic prey. Most other nonmammalian LMP taxa exhibit putative foraging behaviors at depth, such as bigeye tuna tracking the vertical migration of potential mesopelagic prey (panel *e*), but foraging has proven more difficult to confirm for these species. Abbreviations: DSL, deep scattering layer; LMP, large marine predator. Panels *a–c* adapted with permission from Yoshino et al. (2020); panel *d* adapted with permission from Aguilar Soto et al. (2008); panel *e* adapted with permission from Josse et al. (1998).

predators appear to match these predictions, as the frequencies of their dive depths approximate an inverse power law when the predators are in the open ocean but not when they are in coastal waters, where prey are presumably more abundant.

Theoretical predictions of search strategies have yet to be tested in a coordinated fashion using LMP behavioral data. Several authors have, however, tested a subset of the predictions to assess the likelihood of foraging at depth in a few taxa. For example, oceanic whitetip sharks are

regularly observed making excursions into the meso- and bathypelagic zone. Howey et al. (2016) analyzed more than 600 individual dives from 16 individuals and found evidence using individual dive characteristics (dive duration and shape) that supported foraging as the most viable reason for mesopelagic excursions. By contrast, other taxa, such as leatherback sea turtles, are only rarely observed diving into the deep ocean (e.g., 95 of >26,000 leatherback dives, or 0.4%; Houghton et al. 2008). Diel distribution of leatherback dives around midday, slow vertical descents, short dive durations, and occurrence predominantly during transit periods match expectations that the behavior is used to survey the water column. Other taxa that exhibit infrequent bathyal dives may also be conducting a similar probing behavior in search of deep prey resources [e.g., Chilean devil ray (Thorrold et al. 2014) and swordfish (Abecassis et al. 2012)], although it remains unclear whether these infrequent dives are primarily for foraging or serve other purposes (see Section 4.3).

Several telemetry studies on both teleost and elasmobranch species report potential overlap with DSL organisms that are suggestive of foraging. Concurrent, shared habitat use of predators and DSL prey at depth has been reported in tunas (Josse et al. 1998) (**Figure 3e**) and swordfish (Carey 1990). However, the majority of observed overlap between LMPs and mesopelagic prey has been based on depth records measured by tagged predators and are thus limited to highlighting general occupation of the mesopelagic realm and putative overlap with expected DSL depth. In some taxa, hypothesized foraging is based on a DVM signal in the tagged predator's use of the mesopelagic that may be interpreted as pursuing vertically migrating prey (e.g., swordfish; Braun et al. 2019a). Recent work by Arostegui et al. (2020) provided additional context for DSL-mediated deep diving by a tagged pelagic thresher shark, using concurrent measurements from an ocean glider and well-constrained empirical irradiance and attenuation functions to characterize the subsurface light environment. Together, these measurements demonstrated that, while the shark's vertical habitat use was apparently constrained by hypoxic conditions at depth, it exhibited crepuscular and daytime overlap with distinct scattering layers of small mesopelagic fishes.

The examples above highlight how tag-based approaches have generally been unable to definitively link deep-diving behavior and successful foraging, particularly for nonmammalian LMPs. Future studies should leverage innovation in tag technologies (see the sidebar titled Technology) alongside a transdisciplinary tool kit that includes, for example, food web studies

TECHNOLOGY

The emergence and rapid development of electronic tagging have dramatically expanded our knowledge of LMP ecology. We can now track movements; measure behavior, physiology, and the ambient environment over multiple temporal and spatial scales; and overlay that information with key environmental variables observed from space. Tags often consist of a combination of ambient pressure, temperature, and light sensors and a satellite transmitter but may also include a three-dimensional accelerometer and magnetometer, visceral or intramuscular thermistor, hydrophone, and video camera, enabling a diversity of concurrent measurements.

Yet there are still great technological (and methodological) challenges ahead before we can systematically and concurrently measure behavior, physiology, and the environmental context of deep divers. In terms of sensor development, innovation is needed to accurately measure additional environmental (O_2), biological (chlorophyll, prey field), behavioral (feeding, swim speed) and physiological (heart rate, blood chemistry) metrics. Tag miniaturization and streamlining are essential to reduce tag-induced drag and allow for the tagging of smaller LMPs (including juveniles) with minimal impact on the animals' behavior and well-being. Data recovery is also still a major limitation, as there is currently a mismatch between the capacity to remotely recover data via satellite and the large volume of data produced by fine-scale, multisensor platforms.

(e.g., using mercury isotopes; Le Croizier et al. 2020) and environmental sampling (e.g., using acoustics; Benoit-Bird et al. 2020). Intriguing evidence of food web connections between surface- and deep-ocean ecosystems comes from trophically transmitted parasites that must infect a series of intermediate host species progressively higher up the food chain (and are dependent on the next host eating the currently infected host) before arriving in the final, definitive host, where they reproduce (Rossiter & Sukhdeo 2011). Low- and mid-trophic-level fauna of the meso- and bathypelagic host intermediate life stages of parasites that end their life cycles in apex predators such as cetaceans or sharks (e.g., Klimpel et al. 2011). These linkages suggest that LMPs foraging at meso- and bathypelagic depths do so with enough consistency to support the evolution of parasite life cycles that rely on that requisite trophic interaction. However, as long as evidence for foraging in the deep pelagic remains limited to a few special cases or to specific taxa, additional direct evidence will be required to better understand the role that foraging plays in determining deep-diving behavior.

4.2. Escaping to the Dark

While commonly placed at the apex of oceanic food webs, most LMPs are both predators and prey for at least some period of their life history. Marine mammals (e.g., killer whales; Ford et al. 2011) and large sharks are the most notable predators of other LMPs in the open ocean. The selection of habitats characterized by low predator abundance is thought to commonly occur in LMPs and is generally associated with the most vulnerable life stages (e.g., high-latitude oceanic nurseries of juvenile blue sharks; Vandeperre et al. 2016).

Putative predation events are not uncommon in electronic tagging studies (e.g., Kerstetter et al. 2004), suggesting that LMPs may themselves encounter potential predators frequently. Lam et al. (2020) identified six cases of potential predator interaction among 17 successful tag deployments on yellowfin tuna near Hawai'i (range of deployment duration 3–59 days). One of these events was a confirmed mortality in which the tuna was ingested by a warm-bodied predator, such as a false killer or short-finned pilot whale, both of which are common predators in the region. Lam et al. (2020) interpreted another event as a likely escape from a predator when a tagged yellowfin tuna descended from 134 m to 1,501 m in less than 5 min and exhibited a vertical descent speed of more than 3 m/s. This isolated bathypelagic dive was followed by approximately 24 h of abnormal activity near the surface before the tuna resumed a behavioral mode that resembled previous ones. These observations align with the suggestion that the primary predation pressure on LMPs likely comes from other predators that spend the majority of their time in the epipelagic (e.g., white sharks and killer whales) and thus render predator avoidance a plausible functional role for at least some modes of deep diving by LMPs.

Theoretical predictions (Heithaus & Frid 2003) and empirical evidence (Frid et al. 2007) suggest that diving vertebrates—including large-bodied species—should, and sometimes do, modify their diving and surfacing patterns in response to the risk of predation. However, these studies have focused largely on shallow dives by air breathers. A remarkable exception is the recent finding that northern elephant seals engage in drifting rest periods in the darkness at or near mesopelagic depths, presumably to reduce predation risk. Seals performed deep daytime resting events in which positively buoyant individuals began their drifts more than 100 m deeper than those that were negatively buoyant to avoid floating into overly lit waters (Beltran et al. 2021). Thus, there are limited examples of LMPs deep diving to (a) actively escape a predation attempt initiated in the surface ocean or (b) position themselves in conditions that reduce the likelihood of encountering a predator, suggesting that these are important drivers but are unlikely to be primary motivations for consistent deep-diving behavior. Nonetheless, the potential for predation risk to drive extreme, rapid descents (as observed in the yellowfin tuna example) or otherwise infrequent

deep-diving behaviors that facilitate evading detection (as observed in the northern elephant seal example) requires additional study.

Neritic: relating to coastal waters overlying the continental shelf

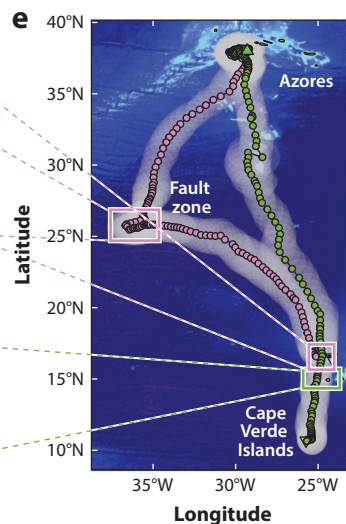
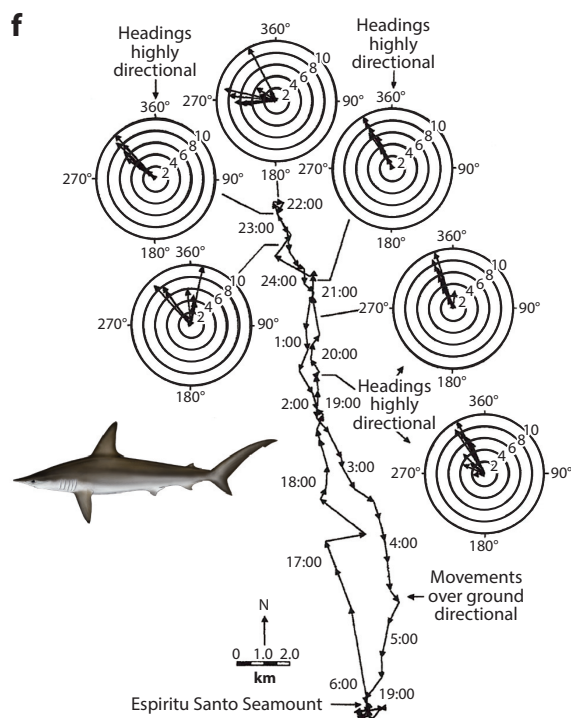
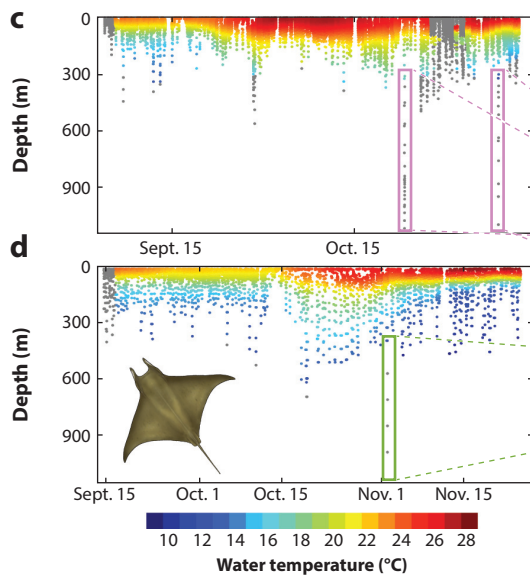
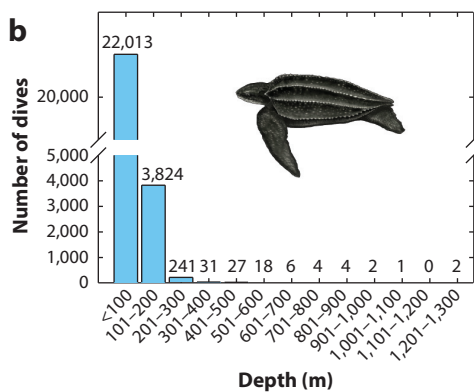
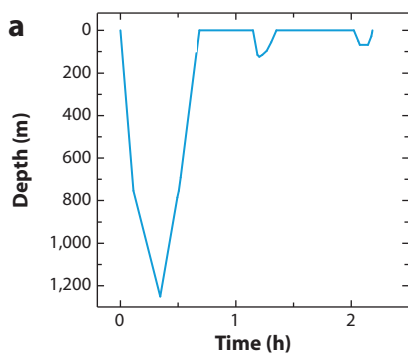
4.3. Diving as Nature's GPS

Nearly all LMPs conduct long-range movements during at least one life stage that can cover tens of thousands of kilometers per year (Block et al. 2011). Sea turtles, whales, seals, sharks, and teleost fishes clearly possess the necessary sensory capabilities to traverse what humans often perceive as a vast, homogeneous oceanscape (Chapman et al. 2015). While many features of a dynamic ocean, especially below the surface, are not readily detected by humans, pelagic migrants may use a diverse suite of environmental cues and gradients to navigate, perhaps in a multistage process (Mouritsen 2018). Accurate navigation requires the ability to identify direction of travel and, in more advanced forms, to determine geographic (map) position. Cues used to determine direction or map position may include gradients in geophysical factors (e.g., magnetic field intensity and/or inclination) or chemical concentrations (e.g., reef or river plumes) that exhibit predictable variations over a relevant spatial scale. Compass orientation requires reliable directionality that can be calibrated to a reference system such as Earth's magnetic field or solar cues (Mouritsen 2018). Ultimately, animals must be able to integrate these cues to prompt movements in a desired direction, but the nature of these cues and how they integrate with the sensory ecology of the animal remain largely unknown.

The independent evolution of deep diving across LMP taxa may have coincided with the necessity to precisely navigate over large scales in the open ocean. For example, the leatherback sea turtle conducts extensive oceanic migrations as an adult and has evolved the capacity for deep diving (**Figure 4a,b**). By contrast, other sea turtles that primarily occupy neritic habitats as adults have not developed comparable diving abilities (**Figure 2**). However, the environmental cues (such as light and magnetic or electrical fields) associated with or enhanced by deep diving are poorly characterized, and it remains unclear how they might enable precise, long-range navigation.

Light-based navigational cues are widely accepted as important for migratory terrestrial taxa (Mouritsen 2018). In the marine environment, there is some evidence for the necessary sensory systems to support a light-dependent compass related to navigation in vertically active fishes that favor crepuscular diving (southern bluefin tuna; Willis et al. 2009). This suggests that at least some examples of LMP navigation may be light mediated, whereby diving behavior exhibits diel periodicity. However, light-based cues alone are unlikely to explain the ubiquity of high-precision navigation among LMP taxa that regularly traverse thousands of kilometers of open ocean (e.g., Braun et al. 2018).

In contrast to the tenuous relationship between diving and celestial orientation cues, several studies provide evidence supporting deep diving as a navigation strategy using other cues. Earth's magnetic field is well known to exhibit global and regional gradients and is a key source of both compass and positional information across a range of taxa, including sea turtles, salmon, and birds (Lohmann et al. 2007). Sea turtles and a diversity of teleost and elasmobranch fishes are capable of using Earth's magnetic field for navigation, likely using specialized magnetoreceptor cells (Lohmann et al. 2008). In a pioneering field study, Klimley (1993) showed that magnetic sensitivity may play an important role in the remarkable ability of hammerhead sharks in the Gulf of California to precisely navigate back to seamounts during consistent daily migrations to and away from these features (**Figure 4f**). A three-dimensional map of geomagnetic intensity indicated that the hammerheads may be sensing the magnetic landscape and thus be able to follow peaks or valleys in the magnetic topography of the region, presumably by diving to below 200 m, where the magnetic gradient was three times stronger than it was near the surface. Several



(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Some LMPs exhibit infrequent, extreme deep dives that could serve a navigational role. Leatherback sea turtles make excursions to as deep as 1,200 m (panel *a*) that constitute an exceedingly small fraction of total dive behavior (panel *b*) and occur only during large-scale migratory movements. Similarly, Chilean devil rays appear to conduct extreme dives to depths greater than 1,000 m (panels *c* and *d*) around complex bathymetric features such as seamounts and island chains (panel *e*). Scalloped hammerheads demonstrate that these complex bathymetric features might serve a navigational role; this species demonstrates highly directional swimming in open water away from and back to specific seamounts (panel *f*), which may be driven by subsurface irradiance, temperature, bathymetry, and the geomagnetic field. Circle plots represent a sequential series of headings (with increasing heading line length) calculated along the shark's outbound track, indicating highly directional swimming away from the seamount. Compass headings were not recorded on the return movement to the seamount due to sensor malfunction, although shark movements suggest similar directional persistence as the outbound movement. Abbreviation: LMP, large marine predator. Panels *a* and *b* adapted with permission from Houghton et al. (2008); panels *c–e* based on data from Thorrold et al. (2014); panel *f* adapted with permission from Klimley (1993).

subsequent studies have demonstrated a similar sensory capability among other highly migratory sharks (Meyer et al. 2005), but concrete evidence showing that these taxa use magnetic gradients for navigation remains absent. While the sensory mechanisms and thresholds for most LMP taxa remain unclear (but see Kalmijn 1982), depth gradients in magnetic anomalies may be as much as 25 times stronger than horizontal gradients (Macdonald et al. 1980), suggesting that magnetic fields at depth may be particularly important for navigation.

In addition to magnetic cues, elasmobranchs are known to be sensitive to electrical fields (Kalmijn 1982) in the range of the extant gradients in conductivity (driven by temperature, salinity, and pressure) found in the top 2,000 m of the water column (Tyler et al. 2017). However, additional work is needed to understand these gradients and their potential impact on LMP navigation.

Based on the results of these studies, it seems plausible that deep diving may serve as a probing behavior that allows LMPs to detect the main gradients useful for navigating, such as the magnetic field at depths greater than 500 m, where current-induced noise is often negligible (Willis et al. 2009). Deep-diving behavior will also increase the probability of detecting geologic features (e.g., seamounts) and their associated magnetic anomalies, which may be useful for navigating (Klimley et al. 2017). Examples of infrequent, rapid, extremely deep dives by a diversity of LMP taxa during periods of relatively directed, long-distance migratory swimming are quite common, especially when prominent chemical or geophysical gradients are present (e.g., around bathymetric features) (**Figure 4c–e**). However, further experimental work is required to determine which navigational cues and thresholds may be useful based on available sensory systems and how these cues may be integrated to generate the precise navigation evident from telemetry studies. Additional observational work is needed to test these navigation-related hypotheses, including concurrent measurements of the three-dimensional movements of LMPs and the putative gradients that might facilitate navigation along with more rigorous statistical analyses of the interaction between magnetic fields and animal movements.

4.4. Saving Energy by Deep Diving

Diving has long been postulated as a strategy for energy conservation in negatively buoyant animals, enabling them to minimize the costs of horizontal travel by bounce or yo-yo dive behavior, in which they glide during descent and then perform powered swimming on the ascent (Gleiss et al. 2011). The use of acceleration sensors has revealed that many LMPs exert minimal effort while descending on dives and instead rely on their negative buoyancy to move deeper in the water column (Gleiss et al. 2011, Nakamura et al. 2011). Hence, it is possible that LMPs may perform deep dives to minimize their horizontal cost of transport. However, modeling efforts and empirical evidence suggest that (*a*) yo-yo diving is not the optimal strategy if the goal is to maximize energy surplus per unit distance traveled (Iosilevskii et al. 2012, Papastamatiou et al.

Cost of transport:
the energy required to
move a fixed distance

2018) and (b) natural selection should have favored neutral buoyancy in LMPs if minimizing horizontal cost of transport were the primary functional role of bounce diving (Sato et al. 2013). Data from tiger sharks and white sharks suggested that individuals were minimizing their transport costs by yo-yo diving in shallow water, although the energy expenditure was not directly measured (Watanabe et al. 2019, Andrzejczek et al. 2020). Hence, the available evidence suggests that yo-yo dives will maximize the animal's energy surplus while searching the water column, but conserving energy per se may not be the primary functional role of this behavioral mode.

If deep dives are primarily a tool for energy conservation, we might expect the behavior to be more common in individuals that are less well adapted for efficient swimming. For example, as sharks grow, they become more buoyant to maintain swimming efficiency, and therefore juvenile animals might be expected to perform more energy-saving dives than adults (Iosilevskii & Papastamatiou 2016). Specific morphological traits, such as body diameter and relative pectoral fin length, also influence swimming performance. Species with slender bodies and long pectoral fins, such as blue and oceanic whitetip sharks, are able to swim more efficiently at slower speeds compared with species without these adaptations (Iosilevskii & Papastamatiou 2016). However, many species with morphological adaptations for slow, efficient swimming frequently make deep dives into the mesopelagic, and the juvenile stages of the LMPs studied to date have typically been confined to shallower waters. Further testing of the energy conservation hypothesis will require high-resolution measurements of swim speeds, as the speed profiles during dives can reveal intricacies of the function of dives (e.g., are swim speeds constant during ascent versus descent, or do they vary throughout the profile?) (Iosilevskii et al. 2012).

4.5. Evicting the Freeloaders

Parasite infestation is ubiquitous among LMPs, from large whales (Hermosilla et al. 2015) to sharks (Caira & Healy 2004), and occurs in virtually every organ. Although very little is known about parasite effects on the health of their LMP hosts, the cost of parasitism is likely high, as it can directly cause or promote diseases by transmitting other invasive pathogens, impair the functioning of infected organs, and reduce metabolic performance. For example, infestation and injuries caused by ectoparasites on the gills of tuna are known to lead to blood loss and a weakening of their immune system (Balli et al. 2016), eye-parasitic copepods can lead to blindness in sharks (Benz et al. 2002), and the hydrodynamic drag caused by large ectoparasites (including otherwise commensal organisms) may represent a considerable waste of net energy for their host in the long term (Beckert et al. 2016). Therefore, it should be advantageous for LMPs to develop behaviors that reduce parasite infestation and concomitant symptoms. Indeed, the removal of ectoparasites has long been assumed to be the motivation for the surface-breaching behavior described among some cetaceans, such as spinner dolphins (Weihs et al. 2007). Several pelagic elasmobranch taxa (e.g., pelagic thresher sharks; Oliver et al. 2011) are also known to form daily aggregations at reefs, where they benefit from the active ectoparasite removal of cleaner fishes.

A functionally similar behavioral strategy may be employed by oceanic LMPs if diving through the inhospitable clime of the deep ocean helps to evict parasites and control infestation. For example, parasites requiring stable environmental conditions (e.g., temperature and pressure) or adapted to the epipelagic may be affected by the sudden and/or prolonged exposure to extreme conditions they might experience during the deep dives of LMPs. Despite these expectations, we found only one study that mentions this hypothesis as a possible explanation for deep diving in LMPs (in yellowfin tuna; Dagorn et al. 2006). At the broader biogeographic scale, marine parasite loads are smaller in hosts living in colder, high-latitude waters and hosts living in deeper habitats than they are in hosts living in warmer, shallower habitats (Rohde 2010). This is paralleled by the

Ectothermy: an animal's inability to regulate its internal temperature, which is instead determined by the temperature of the surrounding environment

rarity of evolutionary transitions from shallow- to deep-ocean habitats seen in some parasites (e.g., trematodes; Bray 2020). However, there is no direct evidence that the common conditions in the deep ocean are inhospitable to parasites, and there are no studies assessing the direct or indirect relationship between deep diving of LMPs (or any other animals) with parasite load.

Thus, while it is possible that LMPs may evict parasites by exposing them to extreme temperatures and pressures during deep diving, there is no evidence that this would be the case or that it constitutes a motivation to adopt this behavior. Additional work is needed to better address this potential mechanism, especially with regard to testing the direct effects of sudden, extreme changes in temperature and pressure on parasite survival; this would verify the putative reduction of parasite load by deep diving of LMPs.

4.6. Thermoregulation

Although many LMPs exhibit adaptations that enhance internal heat production or retention to prevent heat deficit while in cold water (such as during deep dives), deep-diving behavior may also serve to prevent or help LMPs recover from heat excess when they experience conditions warmer than their optimal thermal niches. In both ectotherms (Huey & Stevenson 1979) and endotherms (Speakman & Król 2010), physiological performance declines rapidly after optimal temperatures are exceeded. However, among animals of similar size and morphology, those with endothermic capacity or higher metabolic rates—which maintain higher internal temperatures—should exhibit a higher likelihood of thermoregulatory deep diving when occupying temperatures above their optimal thermal regimes.

Among high-performance teleosts, Atlantic bluefin tuna exhibit a particularly advanced form of regional endothermy that allows them to occupy cold-temperate climes for months at a time (Bernal et al. 2017). This species makes seasonal, long-range migrations to the warm (sub)tropical waters of the Gulf of Mexico, where they typically dive to below 200 m while spawning and below 500 m while entering and exiting this region, presumably to reduce their body temperature (Teo et al. 2007) (**Figure 5**). Evidence for thermoregulation as a driver of deep diving is lacking for other LMP taxa. For example, while the frequency of meso- and bathypelagic dives by oceanic whitetip sharks was found to be positively correlated with sea surface temperature, the average temperatures prior to those deep dives were anomalously cool, suggesting that these dives were unlikely to be related to thermoregulation (Howey et al. 2016). Initial hypotheses also suggested that retia found in the cephalic and pectoral fin regions of Chilean devil rays served as a heat exchanger for these animals to effectively eliminate excess heat acquired from solar heating at the surface by diving into cooler water (Alexander 1995). More recent telemetry data found that meso- and bathypelagic diving by the devil rays was preceded and followed by surface basking events, presumably for thermal recovery from dives to water temperatures as low as $<4^{\circ}\text{C}$ (Thorrold et al. 2014). Similarly, a telemetry study suggested that leatherback sea turtles may dive into cooler waters to prevent overheating while in the tropics (Wallace et al. 2005). However, theoretical model predictions suggested that the turtles could eliminate excess heat simply by resting and minimizing metabolic heat production (Bostrom & Jones 2007) and that maximal surface perfusion of blood would be sufficient to prevent overheating even while actively swimming (Bostrom et al. 2010).

We found no direct evidence of thermoregulatory deep diving in marine mammals, even though hyperthermia may be quite common in the group. For instance, bowhead whales depart from a region of Baffin Bay in advance of rising temperatures even as the foraging opportunity there reaches its peak, suggesting active evasion of warm conditions that could lead to hyperthermia (Chambault et al. 2018). Bowheads have a thermoregulatory organ that aids the dissipation

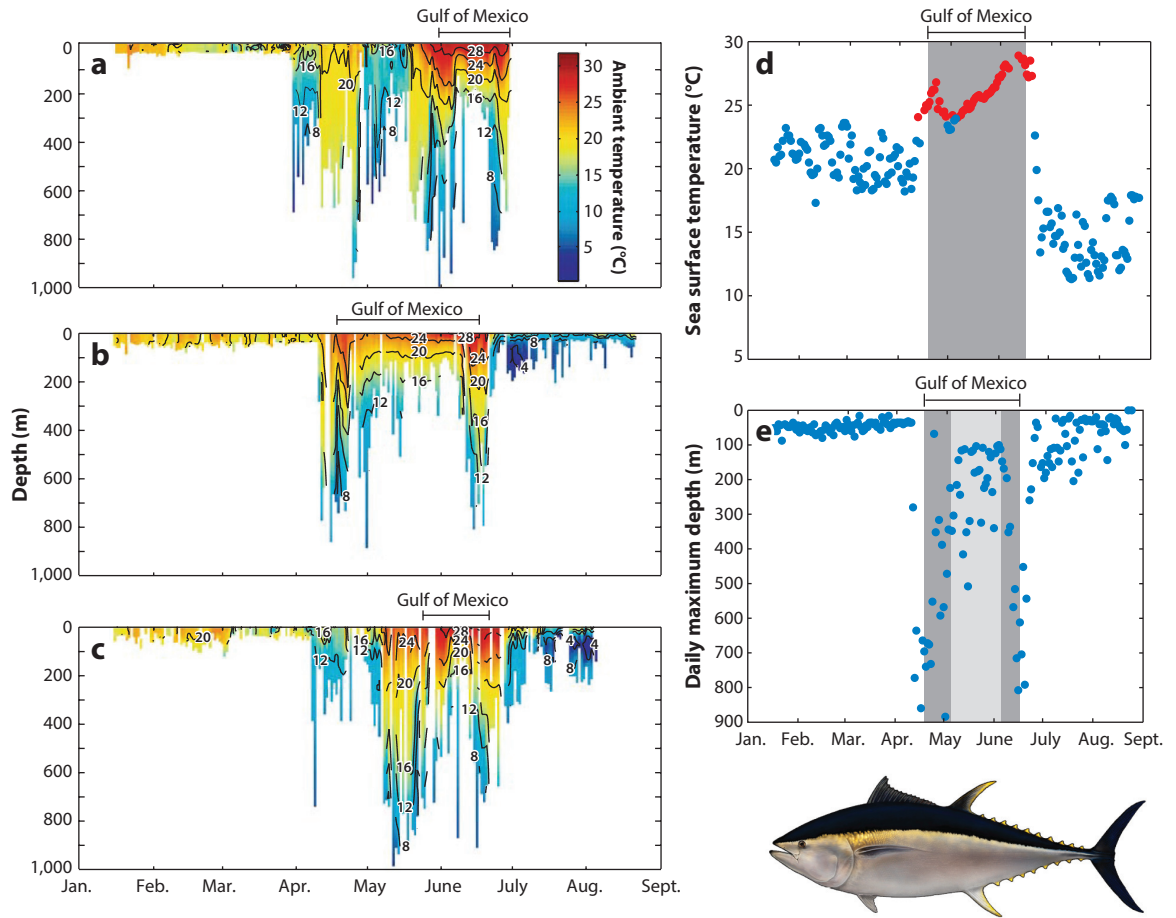


Figure 5

Atlantic bluefin tuna appear to exploit deep pelagic habitats to reduce excess heat during spawning migrations in the (sub)tropical Gulf of Mexico. Daily depth–temperature profiles of three individual tunas (panels *a–c*) indicate dives to as deep as ~1,000 m that occur primarily in the Gulf of Mexico. The sea surface temperatures (panel *d*) and daily maximum depths (panel *e*) experienced by one of these tuna (panel *b*) indicate that this individual initiated deep diving upon entering the Gulf of Mexico, where it experienced temperatures above 24°C, and abruptly ceased deep diving upon exiting the Gulf of Mexico and its associated warm surface temperatures. Figure adapted with permission from Teo et al. (2007).

of internal heat to the surrounding seawater and mitigates the risk of hyperthermia in the brain (Ford et al. 2013). Experimental heating of the brain stems of restrained harbor seals during forced dives resulted in sustained dilation of flipper blood vessels (Hammel et al. 1977) that facilitated heat loss. Similarly, bottlenose dolphins preempt the absorption of excess heat when in warm waters by redistributing heat from their cores to their peripheries, thereby delaying hyperthermia (Heath & Ridgway 1999). Future in situ studies will be needed to link the documented circulatory mechanisms for hyperthermia prevention in marine mammals with thermoregulatory deep-diving behavior. At least one theoretical model of marine mammal heat loss suggests that both dermal circulation and deep diving would be needed to maintain the heat balance of large whales sustaining maximum exertion in warmer waters (Hokkanen 1990).

Together, the diversity and variability in the thermal biology of deep-diving taxa suggest that thermoregulation to reduce body temperature is unlikely to be a primary function of deep diving for LMPs. Larger LMPs with greater thermal inertia exhibit reduced rates of heat exchange (Nakamura et al. 2020) and, therefore, would likely need to spend more time at depth to shed sufficient heat when experiencing hyperthermia. Instead, thermal limitations (i.e., cold waters) may be the most significant constraint to deep diving (Thums et al. 2013) due to strong vertical gradients in temperature. Many LMPs limit deep-dive duration, presumably to prevent internal temperatures from declining below a certain value, followed by warming in surface waters (e.g., Brill et al. 1998). Thus, temperature is likely a key modulator (rather than motivation) of diving behavior and provides a key lens with which we should interpret all other hypothesized functional roles of deep diving.

4.7. Social Interaction

Many LMPs interact with conspecifics to cooperate or compete, potentially relying on vision, olfaction, hearing, mechanosensation (e.g., the lateral line in fishes; Ritz et al. 2011), or electroreception (e.g., the ampullae of Lorenzini in elasmobranchs; Bodznick et al. 2003). While opportunistic direct observations have increased our knowledge of the social behavior of LMPs, this information has been restricted to shallow waters for logistical reasons. Furthermore, there remains considerable uncertainty in terms of specific social outcomes that may be achieved by particular methods of communication (e.g., sound generation by tunas; Allen & Demer 2003).

Cetaceans constitute the group of LMPs for which social interactions in the deep ocean have been most extensively studied, with particular focus on acoustic communication. In their normal shallow-water environments, substantial ambient noise, such as that generated by wind, limits the distance at which acoustic social communications by cetaceans can be effectively detected (Dunlop 2018). By contrast, the sound fixing and ranging (SOFAR) channel is a region of the water column from a few hundred to more than 1,000 m deep in the open ocean that reduces sound attenuation and increases propagation distance, creating ideal conditions for long-distance acoustic communication. For example, the acoustic communication range of blue and fin whales in the Southern Ocean during spring is estimated to be up to 1,700 km in the SOFAR channel (Shabangu et al. 2020). Although propagation distance is maximized if both the source (i.e., calling animal) and receiver (i.e., listening animal) are in the SOFAR channel, sound propagation is enhanced even if the source or receiver occupies shallower depths (Payne & Webb 1971). Thus, while deep diving represents a potential long-range communication mechanism for some LMPs, it remains unclear whether and (if so) how these animals use it, as some of the most commonly detected frequencies in the SOFAR channel appear to be generated when these species are in the epipelagic zone (e.g., fin whales; Stimpert et al. 2015).

Cetacean species produce a variety of vocalizations when occupying meso- or bathypelagic depths, but it can be difficult to confirm their purpose and isolate social interaction as the driver of a given deep dive. For example, solitary male sperm whales at foraging grounds off of northern Norway produce the usual clicks and buzzes that are highly directional and thought to be used in echolocating prey at the bottom phase of deep dives, but they also produce slow clicks during ascent and at the surface that are less directional and most plausibly used as aggressive, long-range signals to ward off potential competitors (Oliveira et al. 2013). Similarly, short-finned pilot whales, which travel in pods, produce echolocation clicks and buzzes during deep dives concurrent with an increase in acceleration indicating pursuit of prey, but they also produce communicative calls and rasps during ascent and at the surface, most likely to maintain cohesion with their social group (Pérez et al. 2017). By contrast, Blainville's beaked whales remain entirely silent during

ascents and at depths of less than 170 m (where they spend ~60% of their time) and instead produce vocalizations consistent with echolocation and communication only during the latter part of descents and during the deepest phase of dives up to 900 m (Aguilar de Soto et al. 2012). Social group members are almost perfectly synchronized in their movement throughout these deep dives and in their sound production during the deep vocal phase, which is thought to benefit predator avoidance because shallow vocalizations can be intercepted and their source more easily tracked by epipelagic predators (Aguilar de Soto et al. 2020).

Combined, these cetacean examples suggest that social interaction may not be an isolated driver of deep diving. Instead, acoustic communication at depth appears to be one of two or more concurrent drivers (e.g., deep dive to forage, avoid predators, and communicate safely). By contrast, the degree to which noncetacean LMPs exhibit social interaction in deeper ocean layers at all remains unknown. Thus, more research is needed to understand whether and (if so) how they communicate or interact in the deep ocean.

5. CASE STUDIES

5.1. Elephant Seals: Paving the Way for Exploring Epi- and Mesopelagic Coupling

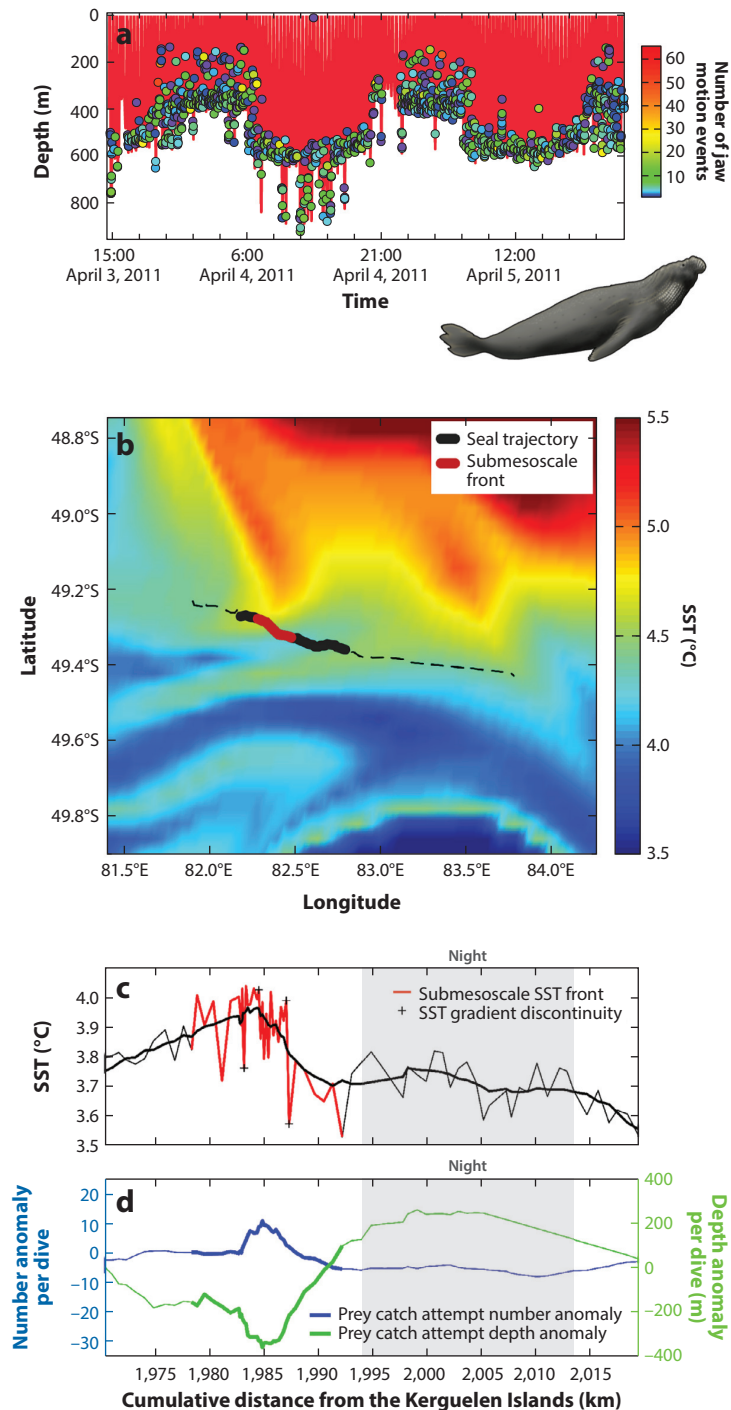
Elephant seals (*Mirounga* sp.) are among the best examples of a deep-diving mesopelagic forager (Figures 3a–c and 6). Individuals typically dive throughout the day and night, nearly continuously for two to three months during the postbreeding migration in the open ocean (e.g., northern elephant seals; Naito et al. 2013). In general, dive depths average approximately 500 m, fluctuating with the expected depth of the primary DSL in a given region. However, most tagged individuals have been recorded performing some bathypelagic dives during daytime as deep as 1,735 and 2,133 m in northern and southern elephant seals, respectively (McIntyre et al. 2012, Robinson et al. 2012). Many of the deepest observed dives are performed by larger adults and occur in proximity to oxygen minimum zones, where it is believed elephant seals are taking advantage of reduced prey mobility due to hypoxic conditions at depth (Naito et al. 2017).

Technological advances combined with the convenient, land-based life history of elephant seals have led to several groundbreaking studies on the functional role of deep diving in LMPs. For example, Naito et al. (2013) pioneered the jaw motion event recorder that uses jaw acceleration to infer prey capture attempts at depth. The event recorder was subsequently paired with a camera tag that was duty cycled based on jaw accelerations, providing the first reconstructions of predator foraging in the deep pelagic ocean across an ocean basin (Yoshino et al. 2020). The results highlighted not only where elephant seals were foraging but also specific prey taxa in the context of predator diving and oceanographic conditions.

These wide-ranging pelagic migrations and the deep-diving behavior of elephant seals have also led to a growing body of knowledge on how ocean dynamics modulate connectivity between surface waters and deep pelagic ecosystems in the open ocean. Using these rich data sets, several studies have demonstrated that (sub)mesoscale features such as eddies and fronts may act as focal points for predators that dive deep to forage in the open ocean (e.g., Bailleul et al. 2010), which in some cases has been linked to energy gain for the foraging seals (Abrahms et al. 2018). While these oceanographic relationships may be a product of enhanced prey accessibility in dynamic frontal regions (Rivière et al. 2019), the degree to which these surface dynamics are coupled to mesopelagic communities remains unknown. In particular, the lack of concurrent, fine-scale physical and biological measurements in the mesopelagic zone means that the impacts of readily measured surface dynamics on mesopelagic communities and associated trophic dynamics are unclear.

Figure 6

Elephant seals make extended oceanic migrations during which they perform numerous meso- and bathypelagic bounce dives per day that have been linked to foraging. For example, the seals exhibit jaw motion acceleration events (panel *a*, color-scaled circles), typically near the bottoms of dives, which are indicative of mesopelagic foraging (see also **Figure 3a–c**). During these migrations away from the rookery (in this case, the Kerguelen Islands), elephant seals also appear able to rapidly sample ambient oceanographic properties during their migration to take advantage of submesoscale ocean dynamics, such as fronts (indicated in SST in panels *b* and *c*). Submesoscale fronts in this region appear to yield increased foraging opportunities (measured by acceleration-based prey catch attempts) for elephant seals at depth (panel *d*). Abbreviation: SST, sea surface temperature. Panels *a* and *b–d* adapted from Naito et al. (2017) and Rivière et al. (2019), respectively, under CC BY 4.0 licenses (<https://creativecommons.org/licenses/by/4.0>).



5.2. Broadbill Swordfish: A Formidable Mesopelagic Predator

Early in situ observations of broadbill swordfish (*Xipbias gladius*) at depth (Church 1968) and subsequent pioneering tagging studies (Carey & Robison 1981) led to the swordfish's reputation as a formidable predator in the deep ocean. Swordfish are perhaps best known for their often textbook DVM, in which they occupy the mesopelagic during the day and migrate to the surface mixed layer at night (reviewed in Braun et al. 2015) (**Figure 7**). This DVM is assumed to be driven by the same diel pattern exhibited by many of the organisms that form DSLs. Combined, the observations of swordfish seemingly tracking vertically migrating prey and the presence of these

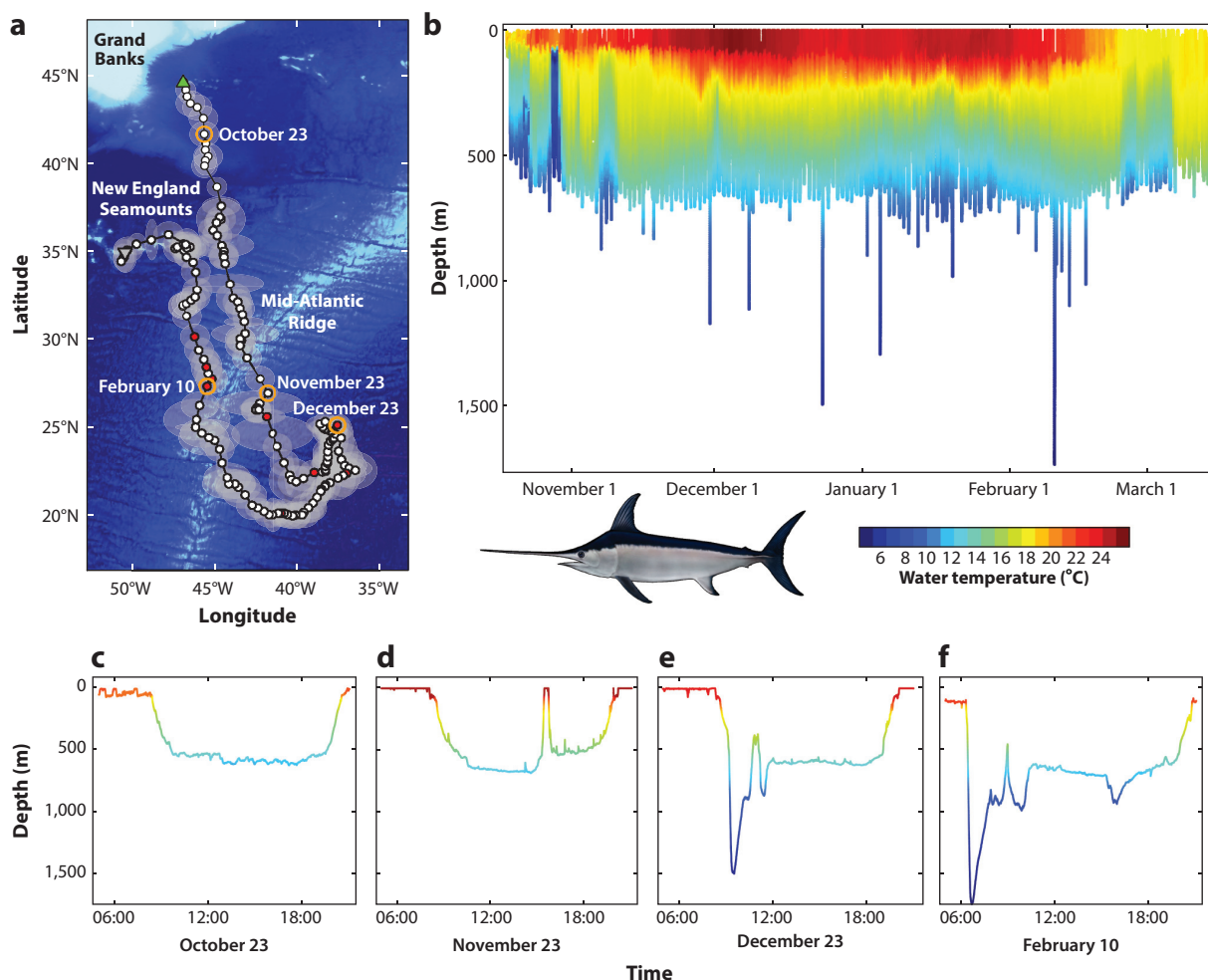


Figure 7

Swordfish make extensive open-ocean migrations (panel a), during which they make daily excursions into the mesopelagic and beyond (panel b). This species is well known to closely track the DVM of DSL organisms (panel c) and spends the daylight hours in the mesopelagic except during occasional surface basking events (panel d). However, extreme deep dives (>1,000 m, locations indicated by red points in panel a) are notable deviations from these common DVM-related behaviors (panels e and f). These dives typically occur around complex bathymetric features (such as the Mid-Atlantic Ridge), which may indicate that they serve a different functional role than tracking the DSL community, which is hypothesized to be the primary driver of the DVM commonly exhibited by swordfish. Abbreviations: DSL, deep scattering layer; DVM, diel vertical migration. Figure based on data from Braun et al. (2019a).

prey in swordfish gut content (e.g., Young et al. 2010) are strong evidence that swordfish make these daily excursions to the mesopelagic zone to forage. Swordfish are also unusual in that they remain at depth from sunrise to sunset, whereas most LMPs make dives of considerably shorter duration.

Swordfish have evolved a set of visual, locomotory, circulatory, and neural adaptations that give them a distinct advantage over many potential prey items in the cold, dark waters of the deep pelagic ocean (Carey 1982, Fritsches et al. 2005). However, there is strikingly little evidence to confirm that they are indeed reliant on mesopelagic prey resources. In fact, most authors still refer to a single pioneering study by Carey (1990) that actively tracked the movements of swordfish along the edge of the continental shelf with electronic tags while recording backscatter from potential prey in the DSL using a shipboard echosounder. They found that the movements of the tagged swordfish matched the DVM of the mesopelagic community at the same location. However, more evidence is needed to confirm that foraging is indeed the primary functional role of the vertical movements that are consistently observed by tagged swordfish across the global ocean.

While the ascent and descent times exhibited by swordfish undergoing normal DVM align with the same diel movements of mesopelagic organisms, swordfish also exhibit some striking variability in the depths they occupy during the daytime. The most notable deviation from this otherwise textbook DVM are occasional very rapid deep dives (~1,000–1,700 m) (**Figure 7**). Although this behavior appears to be infrequent, a few cases have been noted when high-resolution (~1 Hz) depth data have been recovered from archival tags. Rapid, extreme deep dives have been recorded around crepuscular periods (**Figure 7e,f**; but see figure 5 in Abecassis et al. 2012); in geographic proximity to bathymetric features, including seamounts; and during periods of navigational complexity prior to a significant change in direction (**Figure 7**). While deep crepuscular diving aligns with theoretical expectations for maximizing foraging opportunities during these times by intercepting migrating DSLs (Thygesen & Patterson 2019), some of these observed very deep dives (e.g., >1,500 m; Abecassis et al. 2012) are well beyond the depth of the primary DSL, which is typically found between approximately 400 and 650 m (Proud et al. 2017). Recent evidence points to significant biomass in the bathypelagic (Sutton 2013, Kaartvedt et al. 2020), which is deeper than the detection limits of most shipboard echosounders and thus remains largely unknown.

Many LMPs are highly migratory and therefore require well-developed abilities to navigate across large swaths of open ocean. Swordfish often conduct annual migrations from tropical spawning grounds to productive temperate feeding habitats (Braun et al. 2019a) and therefore presumably possess advanced navigational skills as well. Interestingly, the southern bluefin tuna is another long-distance migrant that also makes deep crepuscular dives with similar profiles to those conducted by swordfish (Willis et al. 2009). Tunas, istiophorid billfishes, and other closely related species possess a light-mediated pineal organ (Rivas 1953) that may act as a compass. Therefore, it seems plausible that the extreme dive behavior displayed by swordfish allows for deep profiling of the water column to enhance cues that are used for navigation (Section 4.3). Further study is clearly required to adequately document and understand this seemingly rare but potentially important variation in the consistent DVM exhibited by swordfish.

6. CONCLUSIONS

Many LMPs make regular excursions into the meso- and bathypelagic zones, and nearly all species exhibit at least occasional forays into the deep ocean. Deep-diving behavior appears to have arisen independently across diverse phylogenetic lineages, yet few studies have sought to explicitly test potential functional roles of these behaviors. Efforts to offer mechanistic explanations for deep diving are complicated by a dynamic oceanographic context that modulates the observed behaviors (Section 2.1) and by different physiological capabilities across taxa (Section 2.2). The patchiness

of prey in the epipelagic realm, the highly migratory nature of most LMPs, and recent estimates of abundant meso- and bathypelagic biomass all suggest that deep diving may have evolved to exploit prey resources in the open ocean (Section 4.1). Yet direct evidence for foraging as the primary function of deep diving by most LMPs remains surprisingly limited. Notable examples of confirmed foraging at depth by some pinnipeds and cetaceans show that new technology will be needed (see the sidebar titled Technology) to confirm foraging as at least one of the key motivations for deep diving in nonmammalian LMPs.

Nearly all LMPs conduct long-range movements during at least one life history stage and may cover tens of thousands of kilometers during seasonal migrations. Sea turtles, whales, seals, sharks, and teleost fishes all regularly exhibit the ability to accurately navigate during these movements (Section 4.3). Deep diving may serve as a probing behavior by which LMPs are better able to detect gradients in a diverse suite of environmental cues useful for navigation. While the evidence is currently limited, the interplay between LMP navigational abilities and deep diving seems a particularly valuable avenue for future research. We caution, however, that significant advances in our understanding of sensory biology and technological developments in animal-borne sensors will be necessary to explore the role that deep diving plays in LMP navigation.

Limited evidence exists to support most of the other hypothesized functional roles of deep diving, although these often appear to be relatively specific to particular taxa. Recent theoretical and empirical evidence demonstrates that LMPs modify their diving and surfacing patterns in response to predation risk (Section 4.2), but the frequency and ecological significance of this behavioral mode remain poorly understood. Social interaction, particularly communication, provides a compelling potential motivation for deep diving by cetaceans that may leverage the acoustic properties of the deep sound channel to communicate across large distances (Section 4.7). While it seems likely that communication interacts with other motivations for deep diving (e.g., foraging) in some marine mammals, additional work is needed to explore the potential social function of this behavior in nonmammalian LMPs. Finally, empirical and theoretical studies suggest it is unlikely that deep diving is a strategy to minimize an individual's cost of transport during migration. However, deep diving may allow LMPs to combine efficient prey searching or movement with energy-saving strategies (Section 4.4) for cost-effective foraging or travel, and new tag technologies are poised to better quantify the energetic implications of deep diving (see the sidebar titled Technology).

While we are unable to explicitly rule out the remaining drivers of deep diving, the taxonomic and physiological diversity among deep-diving LMPs suggests that thermoregulation to reduce body temperature is unlikely to be a primary function of deep diving for most species (Section 4.6). Instead, temperature is likely among the most significant constraints and thus is a modulator, rather than a motivation, of most diving behavior. Furthermore, our rudimentary understanding of the ecology of LMP parasites and the current lack of evidence supporting parasite eviction as a functional role of deep diving (Section 4.5) suggests that additional work is needed before this driver can be properly evaluated.

7. SIGNIFICANCE

Our review demonstrates that deep diving is far more frequent and ubiquitous across taxa than previously recognized and that this behavior is intricately tied to many key questions in ocean ecology. Several groups appear to have independently evolved behavioral and physiological adaptations to occupy the deep pelagic ocean, suggesting significant selection pressure in favor of deep diving. Based on our synthesis of the literature, we suggest that while many animals may dive deep to forage, it appears that more extreme diving behavior may also serve other functions. We propose several testable hypotheses and research priorities (see the Future Issues list below) that, together,

will help uncover the ecological significance of this behavior and improve our understanding of the function and ecological significance of deep diving in LMPs.

Regardless of the specific functional role(s) or ecological significance of deep diving, the frequency and extent of dives to meso- and bathypelagic realms by primarily epipelagic LMPs highlight both the ecological significance of deep-ocean ecosystems and the ubiquity of connectivity across vertical ocean domains. The frequency with which we observe deep-diving behavior suggests that active carbon transfer between the surface and deep ocean by LMPs may be a significant component of the marine carbon budget. The potential impacts of climate change, including expanding oxygen minimum zones, may have widespread effects across taxa and trophic levels in the marine environment. These results also highlight the potential contribution of deep-ocean resources to the convergent evolution of a suite of profound behavioral and physiological adaptations that enable, and perhaps explain, the emergence of deep diving across such diverse LMP taxa. Future advances will require significant technological development and more integrated, multidisciplinary approaches to develop a holistic understanding of the potential function and ecological significance of vertical connectivity between surface- and deep-ocean ecosystems. In particular, making observations of specific animal behaviors (e.g., via electronic tagging as well as new technologies) will remain critical for disentangling the potential ecosystem services and the ecological value of mesopelagic communities to a suite of commercially important LMPs and those of conservation concern. Understanding the role of deep diving and its ecological significance is fundamental to the conservation and management of LMPs in a changing world and supports a critical need for a three-dimensional approach to ocean management.

FUTURE ISSUES

1. Foraging remains a leading hypothesis for at least some deep-diving behavioral modes, but the general occurrence and abundance of potential prey in the deep ocean remain almost completely unknown. Concurrent measurements of the three-dimensional movements of predators and prey fields are needed at both broad and fine spatial and temporal scales.
2. Validation of specific large marine predator (LMP) behaviors at depth will be a key next step to understanding the potential significance of hypothesized drivers. For most drivers, this remains beyond the capability of current approaches, but new technologies are providing new opportunities to, for example, directly observe prey capture at depth.
3. As the ocean changes (e.g., increasing temperatures, acidification, and expanding oxygen minimum zones), it will become increasingly important to understand the function of deep diving and quantify the physiological limitations of LMPs when accessing the deep ocean. For example, what may be the impact of expanding oxygen minimum zones on the available vertical habitat for LMPs and their interactions with deep fauna and associated fisheries?
4. The navigational capabilities of LMPs have amazed scientists for decades, yet making direct measurements to understand how they navigate has proven extremely difficult. It seems plausible that deep diving may serve a navigational role for at least some LMP taxa, adding to the difficulty of studying this phenomenon. Experimental approaches coupled with field measurements may further illuminate the mechanisms and potential significance of deep diving for LMP navigation.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank the *Annual Review of Marine Science* Editorial Committee for their invitation to write this article, the editorial staff at Annual Reviews for their assistance with its completion, and Roxanne Beltran for helpful comments on an earlier version. We also thank Les Gallagher (Fishpics) for contributing illustrations for the figures and for creating **Figure 1**. C.D.B., M.C.A., and P.G. were supported by the NASA New Investigator Program (80NSSSC20K1132). S.R.T. was supported by funding as part of the Audacious Project, a collaborative endeavor housed at TED. Additional funding was provided by the Fundação para a Ciência e a Tecnologia (FCT) through the strategic project UIDB/05634/2020 granted to Okeanos at the University of the Azores. J.F. and P.A. were supported by Fundo Regional para a Ciência e Tecnologia grant M3.1.a/F/062/2016 and FCT grant IF/01640/2015, respectively. This work is a contribution to projects AtlantOS (EU/H2020/REP-633211-3), MEESO (EU H2020-LC-BG-03-2018-817669), and IslandShark (PTDC/BIABMA/32204/2017). This is contribution #261 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University.

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