

## ESSAY

**Whales and cephalopods in a deep-sea arms race**Henk-Jan Hoving , <sup>1</sup>\* Fleur Visser <sup>2,3\*</sup><sup>1</sup>GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany; <sup>2</sup>Department of Coastal Systems, Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands; <sup>3</sup>Kelp Marine Research, Hoorn, The Netherlands**Scientific Significance Statement**

Millions of predator–prey interactions between deep-diving toothed whales and cephalopods occur daily in the dark deep sea. While predatory whales developed traits to detect and hunt their prey, cephalopods had to expand their anti-predatory strategies specialized for visual predators, to counteract acoustic predators. Since toothed whale–cephalopod interactions have never been directly observed in the deep sea, it remains unknown what selective pressures and traits evolved from this arms race. Combining current knowledge, we formalize four hypotheses and associated research approaches that will guide future investigation on oceanic predator–prey systems. We identify whale echolocation as an unprecedented armament to hunt distant prey and propose that deep-sea squids avoid acoustic predators by (1) reducing their acoustic cross-section through body shape and posture, (2) deep-sea migration, and (3) not schooling. Toothed whale predation emerges as a potential driver of the cephalopod live-fast-die-young strategy—which may now leave cephalopods at competitive advantage under global change.

**Whale–cephalopod interactions in the deep sea**

The pelagic deep sea is an enormous three-dimensional space that poses unique selective pressures. In absence of sun light, the dominant forms of communication are bioluminescence and sound. Diverse, abundant taxa inhabit the pelagic deep sea (water column >200 m). These taxa range from microplankton to meganehton, which may aggregate and migrate, resulting in a dynamic system with patches of high biomass—and rich hunting grounds for oceanic predators.

Toothed whales are mammalian top predators that occur in all oceans. Many of these, including beaked and sperm whales, hunt for deep-sea cephalopods, in particular squids (Clarke 2006) (Fig. 1). They have evolved a range of morphological, physiological, and behavioral traits enabling prolonged breath-

hold dives to 100 or 1000s of meters (Kooyman 2009). Deep-diving toothed whales (i.e., odontocetes routinely foraging deeper than 200 m) are efficient, often generalist predators, daily capturing hundreds of prey (Visser et al. 2021). Most cephalopods are fast-growing, relatively short-lived predators with a single reproductive cycle followed by death (semelparity), a life history adaptation that is possibly driven by a massive increase in predation pressure subsequent to the evolutionary loss of the external shell (Amodio et al. 2019). Their size and high gonadal investment makes them nutritious prey (Boyle and Rodhouse 2005).

The evolution of cephalopod avoidance strategies is strongly rooted in their response to predominantly visual predators. Cephalopods have co-existed with their main predators, fishes, for 530 million years (Jaitly et al. 2022). The

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**Fig. 1.** Social mammals hunting for solitary deep-sea cephalopods. Left: Deep-sea squids of two different families observed in the deep sea by remotely operated vehicles. The vertical position, elongated shape, and solitary lifestyle may be traits to reduce the acoustic cross-section and detectability by whale echolocation. Right: Two species of social deep-diving toothed whales, with large sound production structures (bulbous forehead) for powerful echolocation. These predators perform synchronized, individual hunting on deep-sea squids, a foraging strategy that may have evolved in response to hunting for non schooling prey (Photo credits cephalopods: left *Stigmatoteuthis dofleini* © 2015 MBARI, right *Chiroteuthis calyx* © 2018 MBARI, cetaceans: top: *Grampus griseus* KMR, bottom: *Physeter macrocephalus* Jeroen Hoekendijk).

much more recent entry of mammals into the marine realm and ensuing evolution of predatory toothed whale echolocation (34 million years ago), created strongly different selective pressures on cephalopod adaptive strategies to avoid predation—this time by acoustic predators. The resulting evolutionary arms race in predator–prey adaptations has shaped the cephalopods and toothed whales into the organisms roaming our modern oceans. Their interactions, however, remain unobserved, and unknown. Have pelagic cephalopods succeeded in eluding large, warm-blooded predators geared for long-range detection of prey? Which traits drive the deep-sea arms race between toothed whales and cephalopods?

Here, we combine the current knowledge on deep-diving toothed whale predators and their cephalopod prey (focused on oegopsid squids) to reconstruct their sequence of predatory interactions, from search to selection and capture. In the light of current ecological concepts, we form four testable hypotheses supported by research approaches, advancing to a scientific framework that will help understand the selective pressures shaping deep-sea predator–prey systems.

### Cephalopod traits to avoid predation

Cephalopods can sense vibrations using a system analogous to the lateral line system of fishes, and rely on advanced visual capabilities to detect their predators (Jaitly et al. 2022). The

unusually large eyes of giant squid allow detection of the bioluminescent trail stimulated by approaching whales (Nilsson et al. 2012). Histioteuthids, a dominant prey for many toothed whales, have dimorphic eyes. Oriented obliquely in the water column, the large upward-looking eye is likely used to detect prey, and predator silhouettes. The smaller downward-oriented eye visualizes bioluminescent point sources (Thomas et al. 2017).

Marine species avoid predators via various strategies, including gigantism, speed, external defensive structures, crypsis, and schooling. Cephalopod gigantism, as found in giant squid *Architeuthis* sp. and colossal squid *Mesonychoteuthis hamiltoni*, is exceptional. Most oceanic squids have mantle lengths <500 mm (Jereb and Roper 2010). Although many squids are agile and powerful swimmers (e.g., Gonatidae, Ommastrephidae, Octopoteuthidae), certain taxa have limited escape responses (e.g., Histioteuthidae, Chiroteuthidae). Cephalopod oxygen-binding protein (hemocyanin) is less efficient than the myoglobin of their mammalian predators, leaving them at physiological disadvantage (Seibel 2016). The absence of an external shell limits the capacity for physical confrontation. Instead, cephalopod primary defense is to avoid detection, through physical and behavioral crypsis (Jaitly et al. 2022).

To hide in a featureless epipelagic and mesopelagic environment where some light still penetrates, some cephalopods use their mantle for cryptic cover (e.g., *Japetella heathi* and

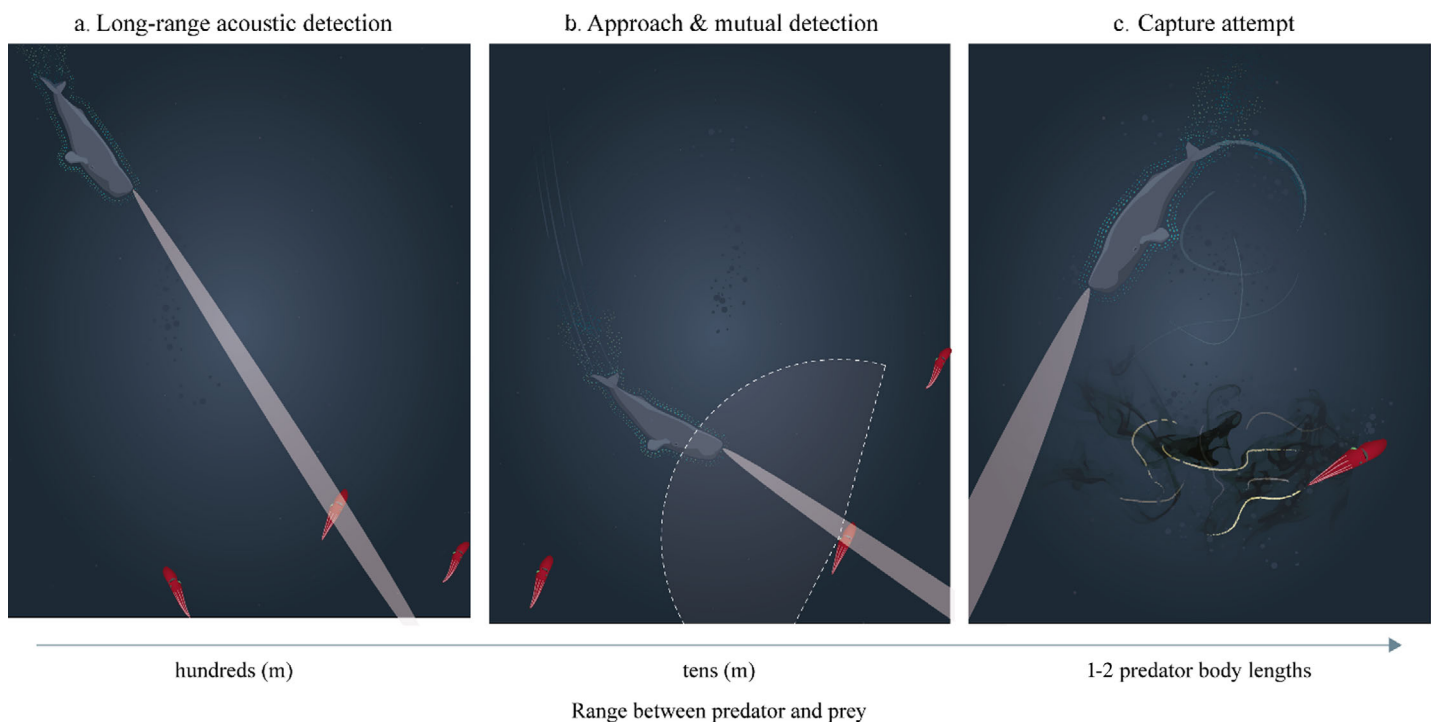
*Onychoteuthis banksi*) (Zylinski and Johnsen 2011). They can effectively switch between varying degrees of mantle pigmentation, counterillumination, shape and sometimes transparency, to optimize their camouflage to fluctuating light conditions (reviewed in Jaitly et al. 2022) and hide from visually attuned predators.

To avoid predation in the only, and critical reproductive phase, many deep-sea squids (e.g., Cranchiidae, Gonatidae, Histiotteuthidae) perform ontogenetic migration (Boyle and Rodhouse 2005), resulting in larger individuals occurring deeper, or close to the seafloor. This ontogenetic migration poses a constraint for the mammalian predators, as per their need for oxygen. Once detected, cephalopods may startle or confuse predators, through inking, bioluminescent flashes, retaliation with beaks and armature, or even autotomy (Jaitly et al. 2022).

### Toothed whale traits to detect and capture prey

In the absence of light, toothed whales detect prey using echolocation (e.g., Jensen et al. 2018). Irrespective of body

size, species have converged on a relatively narrow acoustic beam (the sensory field of view) and hyperallometric investment into sound production structures. Combined, this suggests a strong selective pressure for a sensory system optimized for long-range (i.e., high power), high-resolution detection of individual or patchily distributed prey (Jensen et al. 2018). It creates an especially powerful long-range sense, with an estimated detection distance of 100 s of meters for the larger toothed whales (Fais et al. 2015; Jensen et al. 2018) (Fig. 2). Hunting whales thereby, have a rapid, detailed, and unobstructed overview over large water volumes. In comparison, elephant seals (*Mirounga* sp.), large nonecholocating marine mammals targeting the deep scattering layer, have a prey detection range of 7–17 m and require foraging trips of more than 100 km to detect sufficient prey (Chevallay et al. 2023). Teuthophagous toothed whales use sonar frequencies that have strong energy in the 10–40 kHz band, which is also where some cephalopod species reflect sound most strongly (Benoit-Bird and Lawson 2016; Jensen et al. 2018). Conversely, provided they share the same general auditory anatomy as their shallow-water relatives, deep-sea



**Fig. 2.** The stages of whale-cephalopod predatory interactions. **(a)** Search: long-range acoustic detection. Whale acoustic power increases twice as steeply with body mass as expected (Jensen et al. 2018). The resulting acoustic detection range strongly outcompetes cephalopod visual detection range (max. 350 vs. 120 m, respectively; Nilsson et al. 2012; Tønnesen et al. 2020). Cephalopod's often-observed vertical posture, and elongated shape, will render a small acoustic cross-section, and they may refrain from schooling to reduce probability of detection and pursuit. **(b)** Selection: approach and mutual detection. Cephalopods have unique, complex, and large eyes. Whales stimulate bioluminescence that becomes visible to the cephalopod up to 120 m away (white dashed line: cephalopod's sensory field) (Nilsson et al. 2012), eliciting unknown avoidance responses that may include further dispersion. **(c)** Capture attempt. The whale rapidly modulates inspection range, resolution, and information flow. At close range, cephalopod defenses (e.g., jetting, release of ink) evolved to reduce predation by nonsonar species seem insufficient to counter the biosonar system. However, cephalopod cognitive abilities and confusion strategies may enable yet unknown, dynamic escape responses.

cephalopod prey are likely “deaf” toward the echolocation frequencies and remain unaware of remote, approaching whale predators (Wilson et al. 2007). The cephalopod will only sense its predator at close range (tens of meters; Fig. 2), visually, or due to particle displacement.

Deep-diving toothed whales are fast, agile swimmers, sized ~3–18 m, and therefore are larger than terrestrial top predators. A larger body volume enables higher relative oxygen stores and resilience to temperature gradients—larger animals can dive deeper, for longer (Kooyman 2009). In the cold deep sea, the homeothermic predators can maintain endurance and fast swimming, providing significant advantage over their poikilothermic prey. These physical and physiological advantages do come at high metabolic costs, demanding many, or large prey (Kooyman 2009). Most deep-diving toothed whale species lack functional teeth for feeding and likely ingest complete prey through suction. This puts an upper limit on prey size, exemplified by individuals dying following ingestion of large cephalopods (MacLeod et al. 2006; Fernández et al. 2017). With some exceptions, toothed whales feed on small prey, 1–5% of their own length, thus depending on the presence of numerous prey (MacLeod et al. 2006).

### Reconstructing the sequence of whale–cephalopod interactions

When a toothed whale searches for and approaches a squid, the interaction between predator and prey takes different shape as a function of distance and mutual capability of detection (Fig. 2). The primary anti-predatory behaviors evolved in cephalopods against visually hunting fish (Jaitly et al. 2022) do not suffice for pelagic deep-sea squids eluding echolocating toothed whales. The main sensory systems employed by toothed whales and squids for remote detection, respectively, biosonar and vision, provide a strong advantage for the predatory toothed whale. Their long-range acoustic detection of squids is up to an order of magnitude higher than the presumed maximum visual detection range (e.g., disturbances in the bioluminescent field) of giant squid, which have the largest eyes of all cephalopods (Nilsson et al. 2012). Hence, cephalopods are likely under strong selective pressure to avoid remote acoustic detection.

Hypothesis 1: Prey modulate body posture to reduce remote detection.

Cephalopods may be able to reduce the possibility of remote detection by minimizing their acoustic cross-section (reflective surface). Similar to fish, many deep-sea squids, have elongated body shapes (Boyle and Rodhouse 2005; Jereb and Roper 2010) (Fig. 1). While this shape reduces drag, it also results in a small visual silhouette when animals position themselves vertically in the water column, a cryptic position for visual predators that come from above or below (e.g., Miller et al. 2014). At the same time, it may be a yet

unrecognized defense mechanism in cephalopods against the probability for remote detection by a foraging whale descending from the surface. A vertical position also reduces the acoustic cross-section (detectability), and possibly leads predators to underestimate detected prey size.

The role of deep-sea squid body posture in reducing remote acoustic detection during the search phase could be tested using an acoustic model estimating squid detectability (i.e., reflecting signal strength) by whale echolocation under varying squid acoustic cross sections and geometry of predator or prey. Given the typically steep dive descents of the acoustic predators, we predict detectability to be significantly reduced in oblique vs. horizontally-oriented squids, when ensounded remotely from above.

Hypothesis 2: Prey downregulate density to reduce remote detection.

While some cephalopods occur in aggregations (e.g., ommastrephids, some species in the deep scattering layer; Benoit-Bird et al. 2017), or as mating pairs (Hoving and Vecchione 2012), surprisingly, the vast majority of deep-sea cephalopods are observed as single individuals (Hoving et al. 2012; Vecchione 2019). Biologging records of toothed whale hunting behavior also support non schooling prey. Prey is typically captured during a transitory movement, with capture attempts spaced apart in time and space while the predator moves through its prospect foraging zone. With few exceptions, there is no indication of circling or other movements indicative of backtracking the same area, to target a school (e.g., Fais et al. 2015; Aguilar de Soto et al. 2020).

Limited food availability may be an explanation for low prey densities in the deep sea. Single, non schooling individuals, however, are unexpected in a featureless environment, given the apparent evolutionary advantage of group-formation across terrestrial and marine prey taxa, in predator defense (e.g., flocks, schools and herds) (Krause and Ruxton 2002). However, schooling may only be an effective strategy against visual, but not acoustic marine predators. Toothed whale foraging decisions are likely strongly driven by prey density, and particularly so as the predators rely on numerous, relatively small prey (MacLeod et al. 2006). Schooling will result in enhanced local density and likely enhanced long-range detectability. The high plasticity of the echolocation system allows for high-resolution tracking of single targets (Jensen et al. 2018). Hence, schooling could prove detrimental for the pelagic cephalopods. Instead, dispersed individuals may remain below the density threshold and escape pursuit. In this light, it becomes apparent that mating in deep-sea cephalopods might be dangerous, possibly explaining brief, nonselective mating behavior in some (Hoving et al. 2012) and sperm storage in most deep-sea squids (Hoving et al. 2012; Hoving and Vecchione 2012; Vecchione 2019). Increased acoustic backscatter from the bentos, limiting the detection by acoustic predators, may have

selected for close occurrence and mating near the seafloor (e.g., *Pholidoteuthis adami*) (Hoving and Vecchione 2012). A disadvantage of occurring closer to the seafloor is that escape directions are reduced. We propose that the evolution of long-range acoustic predators shifted predator–prey trade-offs in the deep sea. Schooling posed increased risk to squids, resulting in common occurrence of single individuals.

Whether dispersal vs. schooling reduces acoustic detection can be assessed through modeling the acoustic detectability of remote dispersed vs. schooling individuals. Cephalopod schooling strategies, that is, whether schooling is modulated as a function of acoustic predator presence, can be tested in field experiments and observations that consider squid schooling behavior preceding known toothed whale predatory interactions. Echo sounders placed close to the prey field, can simultaneously record squids and their cetacean predators, and identify predatory interactions (e.g., Urmy and Benoit-Bird 2021). Combining echo sounders with hydrophones will allow the analysis of schooling behavior during predator presence and absence and also during predator search phases with and without ensuing approach and pursuit. Finally, this approach allows analysis of schooling behavior under high vs. low predation pressure. We predict that, if squid dispersal is driven by predation (opposed to environmental drivers), prior to being located, most deep-sea squids will be dispersed (non schooling), and respond to a first cue of an approaching predator presence by further dispersion. We also expect a positive relation between the local level of acoustic predation pressure and the degree of cephalopod dispersion.

**Hypothesis 3:** Predators synchronize and separate to enhance detection of dispersed prey.

If deep-sea cephalopods do not school, how do their mammalian predators maintain efficient foraging on small, remote, and dispersed prey? Deep-diving toothed whales are typically social (24 out of ~26 species), living in cohesive groups. Near-surface spatial proximity is broken, however, during foraging (e.g., Visser et al. 2014 for pilot whales, *Globicephala macrorhynchus*)—contrasting the adaptive coordinated hunting of social shallow-diving toothed whales (e.g., Pitman and Durban 2012 for killer whales, *Orcinus orca*). For the nine species of deep-diving toothed whales for which foraging strategy has been described, tightly spaced social groups at the surface will spread out over hundreds of meters and hunt synchronously, but individually, at depth. This becomes apparent from (1) the significant increase in inter-individual distance either at surface, or during the dive descent (e.g., Whitehead 1989; Aguilar de Soto et al. 2020) and (2) from the echolocation signals and movement patterns during foraging dives. These show individual searching and hunting patterns (while other foraging group members can be heard), and no evidence of, for example, joint corralling of prey (e.g., Fais et al. 2015 for sperm whale *Physeter macrocephalus*; Aguilar de Soto et al. 2020 for beaked whales).

Synchronization of the foraging effort between group members, recorded across the different deep-diving toothed whale genera, suggests that this is an adaptive strategy that may facilitate detection of prey. This may be achieved through information sharing (reviewed by Hansen et al. 2023), and possibly by cover reduction of disturbed cephalopods through behavioral response to another detected predator. Particulate feeding on small prey is a rare foraging strategy in vertebrate social foragers, which typically hunt on individual large, or small schooling prey (Hansen et al. 2023). The ratio of predator : prey size predicts the strategy of herding or condensing of prey for deep-diving toothed whales, as observed for, for example, herring-feeding killer whales (Hansen et al. 2023). Instead, we propose that a non schooling predator response in cephalopods leads social toothed whales to adopt synchronized, yet individual hunting.

We predict that coordinated searching and social information transfer between individual predators will increase the energetic efficiency of hunting non schooling deep-sea prey. This can be tested using high-resolution, multisensor tags, or moorings equipped with echo sounders and multihydrophone arrays, which track the positions, acoustic behavior, number of nearby conspecifics and foraging performance of multiple foraging group members (Aguilar de Soto et al. 2020; Jang et al. 2023), in relation to the prey field (Chevallay et al. 2023). We predict that foraging return is higher in individuals that forage in spatiotemporal synchrony than in individuals foraging alone. If foraging-decisions are not socially enhanced, but driven primarily by environmental factors, foraging return will be independent of group size, or reduced, due to competition.

**Hypothesis 4:** Prey have limited escape-potential when acoustic predator closes in for capture.

If the predators coordinate their search efforts to overcome cephalopod crypsis, how do cephalopods avoid predation? Given their investment in large, complex eyes, at moderate range (tens of meters) perhaps there is still an option for eluding detection or pursuit, for example, by sensing disturbed conspecifics, adapting orientation, or by exiting the acoustic beam (Fig. 2). However, this may render the individual cephalopod vulnerable for detection by other, nearby-hunting whales. In final pursuit, whales strongly accelerate their biosonar repetition rate and widen their echolocation beam, enabling tracking of rapidly moving nearby targets (Jensen et al. 2018). Overall high apparent capture rates (~90%), short sprints and onsets of final approach at only 1–2 predator body lengths (Fais et al. 2015; Tønnesen et al. 2020; Visser et al. 2022), suggest that, once pursued, prey has little chance of escape. Testing this hypothesis requires the documentation of the exact interaction between cephalopod and toothed whale just before capture. To date, these interactions remain unobserved. Escape responses can be studied using whale-mimicking robotics programmed to identify, approach, and

follow mesopelagic squids, as has been done for hydromedusae (Yoerger et al. 2018). The predatory interaction and potential for escape (or predator success rate), can be studied using high-resolution, multisensor tags which record predator foraging behavior and success, together with the prey field (Chevallay et al. 2023) and squid behavior while under attack (Aoki et al. 2015). We expect that escape responses include dynamic swimming, inking and bioluminescent displays and that these responses are generally not successful to avoid the acoustic predator.

### Shedding light on the arms race

The whale–cephalopod system involves interaction between two cognitively advanced animal groups, characterized by apparently strong sensory and physiological advantages for the mammalian predator. Under the unique conditions of the deep ocean environment, the selective pressures that have shaped their adaptive traits differentiate from those in other, well-studied habitats. Specifically, deep-sea cephalopods hunted by whales cannot rely on physical protection or agility and may not find safety in numbers, by schooling. Cephalopod principal “dis-armament” in the foraging interaction with acoustic predators can explain their “live fast die young” strategy (semelparity), highly abundant populations (r-selection), sometimes rapid, nonselective mating behavior, and propensity to seek refuge at large depths (ontogenetic migration). These traits may now allow cephalopods to become increasingly successful in changing oceans with overexploited finfish stocks and rapid warming (Doubleday et al. 2016). Whether in response to, or driving whale exceptional sensory capacity and uncommon social foraging strategies, it exemplifies that deep-sea predatory interactions differ from those in better known systems, such as shallow-water and terrestrial systems, and require direct observation to understand their dynamics. We take a critical step in our understanding of deep-sea ecosystem dynamics through identification of predation by whales as a key driver of the life history patterns and density distribution of the abundant and diverse deep-sea cephalopods and advocate a research strategy that considers the selective pressures of the habitat and the well-developed senses of the species.

### References

- Aguilar de Soto, N., F. Visser, P. L. Tyack, J. Alcazar, G. Ruxton, P. Arranz, P. T. Madsen, and M. Johnson. 2020. Fear of killer whales drives extreme synchrony in deep diving beaked whales. *Sci. Rep.* **10**: 13. doi:10.1038/s41598-019-55911-3
- Amodio, P., M. Boeckle, A. K. Schnell, L. Ostojíc, G. Fiorito, and N. S. Clayton. 2019. Grow smart and die young: Why did cephalopods evolve intelligence? *Trends Ecol. Evol.* **34**: 45–56. doi:10.1016/j.tree.2018.10.010
- Aoki, K., M. Amano, T. Kubodera, K. Mori, R. Okamoto, and K. Sato. 2015. Visual and behavioral evidence indicates active hunting by sperm whales. *Mar. Ecol. Prog. Ser.* **523**: 233–241. doi:10.3354/meps11141
- Benoit-Bird, K. J., and G. L. Lawson. 2016. Ecological insights from pelagic habitats acquired using active acoustic techniques. *Ann. Rev. Mar. Sci.* **8**: 463–490. doi:10.1146/annurev-marine-122414-034001
- Benoit-Bird, K. J., M. A. Moline, and B. L. Southall. 2017. Prey in oceanic sound scattering layers organize to get a little help from their friends. *Limnol. Oceanogr.* **62**: 2788–2798. doi:10.1002/LNO.10606
- Boyle, P., and P. Rodhouse. 2005. *Cephalopods: Ecology and fisheries*. Blackwell Publishing Ltd. doi:10.1002/9780470995310
- Chevallay, M., P. Goulet, P. T. Madsen, J. Campagna, C. Campagna, C. Guinet, and M. P. Johnson. 2023. Large sensory volumes enable southern elephant seals to exploit sparse deep-sea prey. *Proc. Natl. Acad. Sci. USA* **120**: e2307129120. doi:10.1073/pnas.2307129120
- Clarke, M. R. 2006. Cephalopods as prey. III. Cetaceans. *Philos. Trans. R. Soc. London. Ser. B Biol. Sci.* **351**: 1053–1065. doi:10.1098/rstb.1996.0093
- Doubleday, Z. A., and others. 2016. Global proliferation of cephalopods. *Curr. Biol.* **26**: R406–R407. doi:10.1016/j.cub.2016.04.002
- Fais, A., N. Aguilar Soto, M. Johnson, C. Pérez-González, P. J. O. Miller, and P. T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behav. Ecol. Sociobiol.* **69**: 663–674. doi:10.1007/s00265-015-1877-1
- Fernández, A., E. Sierra, J. Díaz-Delgado, S. Sacchini, Y. Sánchez-Paz, C. Suárez-Santana, M. Arregui, M. Arbelo, and Y. Bernaldo De Quirós. 2017. Deadly acute decompression sickness in Risso's dolphins. *Sci. Rep.* **7**: 1–9. doi:10.1038/s41598-017-14038-z
- Hansen, M. J., P. Domenici, P. Bartashevich, A. Burns, and J. Krause. 2023. Mechanisms of group-hunting in vertebrates. *Biol. Rev.* **98**: 1687–1711. doi:10.1111/BRV.12973
- Hoving, H. J. T., S. L. Bush, and B. H. Robison. 2012. A shot in the dark: Same-sex sexual behaviour in a deep-sea squid. *Biol. Lett.* **8**: 287–290. doi:10.1098/rsbl.2011.0680
- Hoving, H. J. T., and M. Vecchione. 2012. Mating behavior of a deep-sea squid revealed by in situ videography and the study of archived specimens. *Biol. Bull.* **223**: 263–267. doi:10.1086/BBLv223n3p263
- Jaitly, R., E. Ehrnsten, J. Hedlund, M. Cant, P. Lehmann, and A. Hayward. 2022. The evolution of predator avoidance in cephalopods: A case of brain over brawn? *Front. Mar. Sci.* **9**: 1840. doi:10.3389/fmars.2022.909192
- Jang, J., F. Meyer, E. R. Snyder, S. M. Wiggins, S. Baumann-Pickering, and J. A. Hildebrand. 2023. Bayesian detection and

- tracking of odontocetes in 3-D from their echolocation clicks. *J. Acoust. Soc. Am.* **153**: 2690. doi:[10.1121/10.0017888](https://doi.org/10.1121/10.0017888)
- Jensen, F. H., M. Johnson, M. Ladegaard, D. M. Wisniewska, and P. T. Madsen. 2018. Narrow acoustic field of view drives frequency scaling in toothed whale biosonar. *Curr. Biol.* **28**: 3878–3885.e3. doi:[10.1016/j.cub.2018.10.037](https://doi.org/10.1016/j.cub.2018.10.037)
- Jereb, P., and C. F. E. Roper. 2010. *Cephalopods of the world—An annotated and illustrated catalogue of cephalopod species known to date. Vol 2. Myopsid and oegopsid squids. FAO Fisheries Synopsis (FAO Species Catalogue. v3) No.125.* p. 1–2. Food & Agriculture Organization of the United Nations (FAO). <https://www.fao.org/fishery/en/publications/51518>
- Kooyman, G. L. 2009. Diving physiology, p. 327–332. In *Encyclopedia of marine mammals*. Elsevier Ltd. doi:[10.1016/B978-0-12-373553-9.00079-1](https://doi.org/10.1016/B978-0-12-373553-9.00079-1)
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford Univ. Press. doi:[10.1093/oso/9780198508175.001.0001](https://doi.org/10.1093/oso/9780198508175.001.0001)
- MacLeod, C. D., M. B. Santos, A. López, and G. J. Pierce. 2006. Relative prey size consumption in toothed whales: Implications for prey selection and level of specialisation. *Mar. Ecol. Prog. Ser.* **326**: 295–307. doi:[10.3354/meps326295](https://doi.org/10.3354/meps326295)
- Miller, M. J., S. Koyama, N. Mochioka, J. Aoyama, S. Watanabe, and K. Tsukamoto. 2014. Vertical body orientation by a snipe eel (Nemichthyidae, Anguilliformes) in the deep mesopelagic zone along the West Mariana Ridge. *Mar. Freshw. Behav. Physiol.* **47**: 265–272. doi:[10.1080/10236244.2014.926128](https://doi.org/10.1080/10236244.2014.926128)
- Nilsson, D. E., E. J. Warrant, S. Johnsen, R. Hanlon, and N. Shashar. 2012. A unique advantage for giant eyes in giant squid. *Curr. Biol.* **22**: 683–688. doi:[10.1016/j.cub.2012.02.031](https://doi.org/10.1016/j.cub.2012.02.031)
- Pitman, R. L., and J. W. Durban. 2012. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Mar. Mamm. Sci.* **28**: 16–36. doi:[10.1111/j.1748-7692.2010.00453.x](https://doi.org/10.1111/j.1748-7692.2010.00453.x)
- Seibel, B. A. 2016. Cephalopod susceptibility to asphyxiation via ocean incalcescence, deoxygenation, and acidification. *Phys. Ther.* **31**: 418–429. doi:[10.1152/physiol.00061.2015](https://doi.org/10.1152/physiol.00061.2015)
- Thomas, K. N., B. H. Robison, and S. Johnsen. 2017. Two eyes for two purposes: In situ evidence for asymmetric vision in the cockeyed squids *Histioteuthis heteropsis* and *Stigmatoteuthis dofleini*. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **372**: 20160069. doi:[10.1098/rstb.2016.0069](https://doi.org/10.1098/rstb.2016.0069)
- Tønnesen, P., C. Oliveira, M. Johnson, and P. T. Madsen. 2020. The long-range echo scene of the sperm whale biosonar. *Biol. Lett.* **16**: 20200134.
- Urmy, S. S., and K. J. Benoit-Bird. 2021. Fear dynamically structures the ocean's pelagic zone. *Curr. Biol.* **31**: 5086–5092.e3. doi:[10.1016/j.cub.2021.09.003](https://doi.org/10.1016/j.cub.2021.09.003)
- Vecchione, M. 2019. ROV observations on reproduction by deep-sea cephalopods in the central Pacific Ocean. *Front. Mar. Sci.* **6**: 403. doi:[10.3389/fmars.2019.00403](https://doi.org/10.3389/fmars.2019.00403)
- Visser, F., and others. 2014. The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). *Behaviour* **151**: 1453–1477. doi:[10.1163/1568539X-00003195](https://doi.org/10.1163/1568539X-00003195)
- Visser, F., V. J. Merten, T. Bayer, M. G. Oudejans, D. S. W. De Jonge, O. Puebla, T. B. H. Reusch, J. Fuss, and H. J. T. Hoving. 2021. Deep-sea predator niche segregation revealed by combined cetacean biologging and eDNA analysis of cephalopod prey. *Sci. Adv.* **7**: eabf5908. doi:[10.1126/sciadv.abf5908](https://doi.org/10.1126/sciadv.abf5908)
- Visser, F., M. G. Oudejans, O. A. Keller, P. T. Madsen, and M. Johnson. 2022. Sowerby's beaked whale biosonar and movement strategy indicate deep-sea foraging niche differentiation in mesoplodont whales. *J. Exp. Biol.* **255**. doi:[10.1242/jeb.243728](https://doi.org/10.1242/jeb.243728)
- Whitehead, H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galapagos Islands. *Can. J. Zool.* **67**: 2131–2139. doi:[10.1139/z89-303](https://doi.org/10.1139/z89-303)
- Wilson, M., R. T. Hanlon, P. L. Tyack, and P. T. Madsen. 2007. Intense ultrasonic clicks from echolocating toothed whales do not elicit antipredator responses or debilitate the squid *Loligo pealeii*. *Biol. Lett.* **3**: 225–227. doi:[10.1098/RSBL.2007.0005](https://doi.org/10.1098/RSBL.2007.0005)
- Yoerger, D. R., and others. 2018. Mesobot: An autonomous underwater vehicle for tracking and sampling midwater targets. In *Proceedings of the AUV 2018–2018 IEEE/OES Autonomous Underwater Vehicle Workshop*. Institute of Electrical and Electronics Engineers Inc. doi:[10.1109/AUV.2018.8729822](https://doi.org/10.1109/AUV.2018.8729822)
- Zylinski, S., and S. Johnsen. 2011. Mesopelagic cephalopods switch between transparency and pigmentation to optimize camouflage in the deep. *Curr. Biol.* **21**: 1937–1941. doi:[10.1016/j.cub.2011.10.014](https://doi.org/10.1016/j.cub.2011.10.014)

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### Conflict of Interest

None declared.

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