Chapter 23 Ethology and Behavioral Ecology of Odontocetes: Concluding Remarks



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The Huzza Porpoise. This is the common porpoise found almost all over the globe. The name is of my own bestowal; for there are more than one sort of porpoises, and something must be done to distinguish them. I call him thus, because he always swims in hilarious shoals, which upon the broad sea keep tossing themselves to heaven like caps in a Fourth-of-July crowd. Their appearance is generally hailed with delight by the mariner. Full of fine spirits, they invariably come from the breezy billows to windward. They are the lads that always live before the wind. They are accounted a lucky omen. If you yourself can withstand three cheers at beholding these vivacious fish, then heaven help ye; the spirit of godly gamesomeness is not in ye.

(Melville 1851)

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Abstract The odontocetes—especially the sperm whale (*Physeter macrocephalus*) and delphinids (family Delphinidae)—have been the subjects of much attention by ancient to modern cultures, exemplified well by Herman Melville's writings of the 1850s. Most odontocetes have multilayered sophisticated societies, probably relying much on living together for several decades, knowing each other well, and remembering the past to unknown degree. Odontocete schooling has similarities to moving terrestrial ungulate herds, and perhaps even more similarities to three-dimensional flocking of birds and schooling of fishes. As mammals, they have the disadvantage of needing to stop feeding and other activities to regularly come to the surface to breathe, and the advantages of echolocation and large brains. It is possible but unproven that dolphins can learn about each other to some degree by echolocating into each other. Large brains and long lives make cultural ways particularly possible,

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but culture can be or become maladaptive if, for example, a particular way of feeding is no longer efficient but is not abandoned. There is evidence especially from captivity that individuals of a species—just as in humans—have vastly different capabilities, but this aspect of individuality has not been explored in detail in nature. Odontocetes are being impacted by humans, often but not always in detrimental ways. We strive for a greater understanding of them, our impacts on them, and their relationships and impacts on us.

Keywords Societies · Schools · Aggregations · Intelligence · Large brains · Matriarchies · Echolocation · Conservation · Culture

One of the finest books about cetaceans in the English literature is that of Herman Melville's *Moby Dick* (1851 in original three-book form as *The Whale*), a fantasy but with plenty of truths, written over 150 years ago. In it, Melville describes the behavior of ocean-going dolphins (such as those in Chap. 9). I am imagining Melville's whaling and US Navy voyages through the eastern tropical Pacific in the 1840s, encountering ancestors of the same multi-species shoals described in more modern terms in the present book (Fig. 23.1).



Fig. 23.1 Short-beaked common dolphins, *Delphinus delphis delphis*, "running" off the Channel Islands, Southern California Bight. While this kind of hurried movement is probably what Melville was describing, when movement is this rapid, it tends to signal that the animals are not joyful but more likely fearful and in fleeing mode. This could be due to killer whales, *Orcinus orcas*, a shark attack, speedboats associated with tuna fishing, etc. In this photo, no obvious cause for alarm was seen. Photo by Sophie Webb

Another fine book about cetaceans is Karen Pryor's *Lads Before the Wind* (1975), taking Melville's quote as an inspiration for her own description of a scientific voyage with dolphins and other toothed whales in nature and as subjects of training. Both books have been inspirations to my life. While dolphins habitually approach ships and smaller vessels to ride the bow and stern waves "for fun" (Fig. 23.2), it is unlikely that the "lads" (and lasses and their offspring) do so more often from windward than any other direction. What Melville may have meant by his oft-quoted expression is that dolphins approaching the vessel are "making haste", are "in a hurry", as "before the wind" usage of that time may have meant. Never mind our post-analyses, poetry does not need to ascribe to strict science, and "dolphins before the wind" as they approach a ship's bow they will always be for me.

The present book opens with a poem from one of my former graduate students, but the rest sticks close to science (see also Chap. 3). I had asked the authors to speculate—if they wish to, even strongly—about the ethology and behavioral ecology of the animals and systems they are describing, perhaps as conclusion sections to their chapters. Speculation is accepted more easily in a compendium such as this book, unlike for most mainstream science journals. Wisely, none took my suggestion, and all stayed remarkably close to facts of science, with solid cautious interpretations based solely on the data. We chose good scientists.

While largely sticking to science as we know at present, I take this opportunity to also discuss digressions from science, as there has been much written especially on topics of supposed dolphin intelligence. I take issue with some (most?) of this



Fig. 23.2 Long-beaked common dolphins, *Delphinus delphis bairdii*, riding the bow pressure wave of the 44 m barquentine research vessel *Regina Maris*, off Panama. Bow-riding was a common sight for sailors in Melville's days. Photo by B. Würsig

discussion, in part because we do not know much about intelligence (not even in our own species, Gould 1981); in part because there are almost 40 species of dolphins and about 30 species of other odontocetes, with vastly different capabilities among them; and in part because discussion of purported intelligence almost perfectly ignores the individuality of animals, points to get back to later.

Shannon Gowans (Chap. 1) discusses the social structural plasticity of most delphinids, as well as the strong matriarchies of several odontocete species. While there appear to be general rules—such as flexibility in social grouping per behaviors in inshore societies with predictable food resources and low predation risk vs. enhanced capabilities of large (and "more stable"?) societies in open waters with dispersed prey and high danger of predation—there are exceptions. Thus, rough-toothed dolphins (*Steno bredanensis*) may occur in generally small gregarious societies with temporary aggregations of such small groups in near-island oceanic waters (Baird et al. 2008; Baird 2016), and nearshore societies of killer whales (*Orcinus orca*) may be virtually closed (Chap. 11).

Serengeti and other migrating herds of ungulates are aggregations that follow simple (seeming) rules of (1) avoiding crowding their nearest neighbors, (2) steering toward an average heading of neighbors, and (3) positioning themselves at some average distance, give or take, from their nearest neighbors. There is no central leadership, no central control (Delgado-Mata et al. 2007). Within that aggregation there is almost constant feeding (part of the reason for migrating) and constant vigilance for predators (another part of the reason for migrating), with the need of each individual to pay at least some attention to others nearby, by sight, sound, small intention movements, and perhaps taste, which has been termed a sensory integration system, SIS (Norris and Schilt 1988; Whitehead and Rendell 2015). Within that aggregation there is also much sociality going on: juvenile play as probably parts of learning to be a sexual adult, attempted mating, avoidance of such attempts, mothercalf interactions including giving birth in the moving herd (!), and nursing and other care-giving behaviors. At times, such individual activities result in sub-structuring of the herd, so that (for example) mating groups may form (probably largely because others avoid the rambunctious activities of mating); mothers and calves may have some tendency to stay together as well, possibly to combat boisterous activities by males while needing to be especially vigilant for predators of their calves (Boinski and Garber 2000 provide several excellent reviews).

Bird flocks and fish schools are similar to the above terrestrial mammal summary, but their herding goes on in three-dimensional space, so there is that extra complication of "depth" while staying close to but not too close to nearest neighbors. As well, they move much faster than herding terrestrial mammals. In three dimensions, the concept of a three-dimensional "chorus line," of sensing nearest neighbors but also those beyond them, is apparently of critical need to keep the ever-moving, evergyrating flock or school aggregation in synchrony (Potts 1984). Otherwise, overall movements, including avoidance of predators, could not be as rapid as they are, and animals would more often than they do (very rarely) crash into each other, or the school split apart. Just like herding creatures on land, flocking and schooling individuals can carry out personal functions—including breathing—without concern for the others. Dolphins in a school, especially a large one, are a (social) aggregation, with movement apparently without leadership, almost-synchronous turns and occasional bursts of speed, etc. (but see Markowitz 2004, for possible indications of "leader-ship" in determining directions of movement). Norris and Dohl (1980) pointed out that a resting group of spinner dolphins (*Stenella longirostris*) behaviorally appears similar to a fish school—when humans approach with a kayak, for example, the resting group may deviate left or right, or dive, or split apart only to reform behind the kayak's intrusion, almost in ameboid-shape fashion. A school of fish and a flock of birds confronted by an object do the same, but more rapidly.

However, for odontocetes, there are several major added aspects to those of threedimensional bird flocks and fish schools. (1) As mammals, odontocetes need to come to the surface to breathe. They need to stop most other activities to ascend from at times prodigious depths to gain that life-giving set of breaths. Dusky dolphins (Lagenorhynchus obscurus) can feed down to about 130 m depths, but that's it-they can take a few bites of aggregations of myctophids or squid and then need to ascend those 130 m, take several breaths, and go back down again to 130 m while the prey, accessibility time-limited as prey are only at these shallow depths for a few hours at night, is available. Whether dolphins do this as a cohesive subgroup of animals, perhaps for safety in sensory integration and for potential coordinated herding at depth, or alone, depends on the occasion and whims we do not yet fully understand (Benoit-Bird et al. 2004; Benoit-Bird and Au 2009). Sperm whale (*Physeter macrocephalus*) females with young occur in tight matriarchies. They need to dive deep and for long, and there is evidence that they do so synchronously when without small calves but asynchronously when newborns are present, presumably for alloparenting calves at and near the surface while mother is diving (Whitehead 1996). (2) All odontocetes have "that extra" sense of discerning each other, prey, predators, and the outside world in general, by echolocation. Only one other mammalian group, the bats, have this capability in similarly sophisticated fashion, and bats also feed and avoid predators in a three dimensional environment. (3) Dolphins are social mammals that have evolved large brains, larger than the terrestrial ungulates to whom they are related and rivaling the carnivores that they also resemble, for after all, they are carnivorous creatures that prey on fish and squid and-for several species such as killer whales, Orcinus orca-on other marine mammals as well.

The mention of echolocation above leads me to one aspect of "seeing" by sound that has received little attention by researchers, and probably merits more. The logic goes thusly: Dolphins can detect fish prey some distance below a sandy bottom, leading to "crater feeding" by Bahamian spotted dolphins (*Stenella frontalis*), apparently by echolocation alone (Rossbach and Herzing 1997). It has long been known that bottlenose dolphins and several other species of odontocetes can be trained to detect human explosive mines and other metal objects buried below the substrate, and details of this capability were recently published (Ridgway et al. 2018a). Human-made sonar within the frequency range of echolocation of many toothed whales can "see" the lungs of dolphins even many meters below the surface (Benoit-Bird et al. 2004). While Norris and Harvey (1974) demonstrated that

blubber and muscle tissue are not very good sound propagators, it is nevertheless possible that dolphins can "see" into each other by echolocation. At least, they may be able to see lungs, trachea, and other cavities with gasses and perhaps bones of fetuses and some particularly hard-bodied tumors, etc. I am surprised that apparently very little work has been carried out in this realm (confirmed by Sam Ridgway, pers. comm, 22 Dec 2018), as even partial positive answers would open up a wealth of new understanding of odontocete capabilities, including how much information (if any) they may have on aspects of physiological state of conspecifics.

Dolphins while resting/sleeping appear to operate at the level of a sensorally integrated fish school (Norris and Schilt 1988) but can quickly "wake up" and be representatives of a sophisticated social network of cognizant higher-level mammals, with complex patterns of communication (Chap. 2), divisions of synchronous feeding (Chap. 3), social/sexual strategies (Chap. 4), mother-calf interactions and long-term teaching and care (Chap. 5), most efficient movements for life support (Chap. 6), fearing and attempting to avoid predators (Chap. 7), and conducting mammalian-type interactions while constrained by the need to gain the surface every few minutes but empowered by the capabilities of echolocation and large brains (all other chapters of this book).

Large brains and sophisticated social groupings and behaviors take us to the oft-repeated idea that toothed whales and dolphins have reached a pinnacle of "intelligence" unrivalled on this Earth, save perhaps humans. The literature is replete with such assertions, as one of the earliest by Lilly (1962), and there has been much else written on the subject. One of the first to do so is the edited book of Mind in the Waters: A Book to Celebrate the Consciousness of Whales and Dolphins (McIntyre 1974), and others have lent considerable intellectual discussion. Donald R. Griffin's The Question of Animal Awareness (1976) asked us to open a window on the potential minds of all creatures; Rachel Smolker described her experiences with and thoughts about dolphins in To Touch a Wild Dolphin (2001); Toni Frohoff and Brenda Peterson edited a compendium Between Species: Celebrating the Dolphin-Human Bond (2003); Denise Herzing and Christine Johnson edited a book Dolphin Communication and Cognition: Past, Present, and Future (2015); Hal Whitehead and Luke Rendell wrote the finest book available on The Cultural Lives of Whales and Dolphins (2015); Janet Mann edited a book on Deep Thinkers: Inside the Minds of Whales, Dolphins, and Porpoises (2017), and Richard Connor wrote a compelling description of his life with dolphins in Dolphin Politics in Shark Bay: A Journey of Discovery (2018). I especially like the book edited by Philippa Brakes and Mark Peter Simmonds on Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions (2011) and Justin Gregg's summary Are Dolphins Really Smart? (2013). There are more, and please (you editors and authors) do not chastise me too strongly for not mentioning all. Such contributions represent a wealth of knowledge and speculation, with at times bold assertions about possible or believed capabilities of odontocete lives.

There are missteps, and they should not be minimized. John Cunningham Lilly was one of the earliest authors, but much of what he had to say about dolphin behavior and supposed intelligence turned out to be incorrect (Lilly 1962, 1967, 1975), as are

the writings of Joan Ocean, *Dolphin Connection: Interdimensional Ways of Living* (1989), who seems to have no concept of the real lives of dolphins—they with amazing capabilities, constraints, and dangers. There are more such "inspirational" writers, and while assertions from "feelings" or beliefs can be good, the inspiration so often presented could stick more to the realisms of what we know, do not know, and might imagine.

Some delphinids do indeed have, on average, very large brains as compared to carnivores and even great apes (Marino et al. 2004). It is likely that these brains make possible sophisticated processing abilities related to communicating and interacting in complex societies, and with detailed spatiotemporal memories of conspecifics and events, such as in humans, other great apes, some terrestrial carnivores (de Waal and Tyack 2003), and elephants (Douglas-Hamilton et al. 2006). While there have been numerous speculations on how such large brains evolved in the sea, Ridgway et al. (2018b) point out that carnivorous cetaceans (instead of their related vegetarian terrestrial ungulates) (1) have a high caloric intake per time spent feeding, providing much energy for the energy-expensive brain; (2) live in a buoyant environment, freeing a large brain from the constraints of gravity; and (3) gestate calves that already have well-developed hearing capabilities in utero in later stages of pregnancy, can likely hear external sounds including echolocation and whistle communication signals of conspecifics, and that this capability may have further driven large brain size from an early age. By the way, it stands to reason that if the fetus can hear echolocation clicks, that enough echoes bounce back for the outside emitter to (potentially) detect aspects of the fetus as well, as discussed for "seeing into bodies" above.

The largest odontocete on Earth, the largest toothed creature on Earth, the sperm whale, also has the largest brain on Earth. It has a matriarchal society and complicated interweaving sets of cultures (Whitehead 2003) but as a part of cultural beings (such as humans!) also engages in some apparently maladaptive behaviors, such as mass stranding to an entire groups' final detriment (Whitehead and Rendell 2015). Killer whales also have intricate tight matriarchies and sophisticated communication and cooperative behaviors but due to cultural ways of feeding on salmon, for example, may be so linked to that feeding style that as salmon are depleted, certain pods do not change behaviors and may not survive (Whitehead and Ford 2018). Rough-toothed dolphins have particularly large brain to body size ratios ("encephalization quotient," Jerison 1973), as well as amazingly quick and complicated learning abilities in captivity (Pryor et al. 1969), Fig. 23.3. They along with bottlenose dolphins and killer and sperm whales may possibly be the "brightest" creatures in the seas, with the understanding that we humans do not have present ways to rigorously define or compare "intelligences" (Würsig 2018).

There are small societies of dolphins living in particular near-shore (inshore) bays and bayous (Wells 2018 and Chap. 15, provide an excellent long-term study example), and we have huge "societies" of oceanic dolphins traveling over hundreds to thousands of kilometers, quite certainly with subgroupings of animals that know each other reasonably well. But, how much can one intelligent mammal really take in? How many animals can be accepted as a part of the closest associations, with a concept of a large complex social system that requires every member to keep track of



Fig. 23.3 Subgroup of rough-toothed dolphins, *Steno bredanensis*, off Kona, Hawai'i. They often seem unhurried and unbothered, as seen here. From a distance, "steno" could be confused with bottlenose dolphins (*Tursiops* sp.), but their forehead to upper jaw is not demarcated by a surface crease as in many other delphinids and a sidewise glance reminds of some dinosaur heads. They are often termed "lizard dolphin" in the earlier literature. They have very large brain to body size ratios and sophisticated rapid learning. Photo by Deron S. Verbeck

(i.e., to remember) a large number of individuals "personally," as well as interrelationships and histories (and how far back?), as well as spatiotemporal memory? Such complex societies with needs for long-term memory may also be drivers for large brain development, as in carnivores, elephants, and great apes including humans (Marino et al. 2004). In humans, there may well be a practical limit of what "we" can efficiently remember and how many colleagues with whom we can knowledgeably associate, within a framework of stable relationships. This limit has been termed Dunbar's Number (Hill and Dunbar 2003) and seems to be around 150 well-known individuals. It is possible that coastal bottlenose dolphin society sizes (e.g., Vermeulen and Bräger 2015) may not have developed simply by chance but what "our" (human and perhaps delphinid) societies are capable of handling. Such potential limits of the closest of social networks need to be explored further and will be with time.

An important conclusion that Gowans (Chap. 1) brings to the discussion is that it would be advantageous for us to progress to a more "agent based model" (Axelrod 1997; Sun 2006) of appreciating odontocete social organization, ethology, and aspects of behavioral ecology. I interpret this as meaning we should be concerned with the group, of course, but should also progress to the stage where we can obtain

data on-and discuss-the individual. To put this in human terms, we have a collective of university students in (say) math class. Some are math prodigies and understand and appreciate everything the professor writes on the board; some others do so after long thought while doing problems at night; some others do not, even after concerted study, understand the ways or the concepts. In a different class such as (say) history, the roles may be at least partially reversed—some of the brightest math students may have problems in keeping up with historical (and philosophical) discussions, while some of the worst math students may excel here. One is not more capable than the other, one is not more "intelligent," but their capabilities go in very different directions. Of course, we also have the students (and, by extension, the dolphins) who may be very good at everything and those who may not be good at much of anything. It is this flavor that we generally tend to omit in aspects of animal associations and behavior, in part due to our lack of depth of having or understanding the data, in part due to our present sophistication of thinking about animal capabilities. This has been put well for members of the great apes, where we know more about societies and individuals than for dolphins (Byrne 1995). Do dusky dolphins efficiently cooperating to herd fish into a tight ball have those members who are good at it and those who are not? The bridge to individuality of better understanding odontocete societies will not be easy.

Many of the "herding-type" cetaceans—*Stenella, Lagenorhynchus, Delphinus*, and *Cephalorhynchus*—are perhaps not as variably capable ("intelligent") as *Physeter, Orcinus, Tursiops*, and *Steno* (for the latter, Pryor et al. 1969). And, it is also possible (likely?) that among each of these species, among each of each species' populations, among each group, there are those individuals who are the run of the mill of them as capabilities of mind and action are concerned, those that are the "Einsteins" among them, and those that are merely biding time and not all that helpful to themselves or their society. The latter may be quirks, and they may be tolerated and perhaps even respected as quirks within society, as was the European medieval "village idiot" (or "village savant") of human society (Oliver 1989). It is up to a new set of data and paradigms (and science history) to ascertain whether my assertion here is "mere twaddle," perhaps similarly as history has judged the writings of John C. Lilly.

It would be wrong to write about odontocetes and not mention our human interactions with them and the amazing, often distressing, changes in habitats we have created and continue to create. These go from as little as a near-shore factory putting chemicals into the environment to the huge global conundrum of climate change and ocean acidification (Reeves 2018). Quite a few populations and several species of odontocetes—especially in human-degraded areas near shores—are in danger due to human activities. While "only" one species of odontocete cetacean, the Chinese baiji (*Lipotes vexillifer*; Turvey et al. 2007), has gone extinct in modern times, the Gulf of California harbor porpoise, vaquita (*Phocoena sinus*), is hanging on by a tenuous thread, and several others are also faring poorly (Chap. 22). Bearzi et al. (Chap. 10) explore the multifaceted ways that many odontocetes have adapted to live with humans and the ways that we humans have done so as well. Some adaptation, perhaps much of it, comes with costs such as disruption of human

fisheries, and Bearzi et al. enjoin us—as human individuals and societies—to more adequately adapt to, respect, and enjoy the odontocetes so ubiquitous in our humanaltered oceans, seas, and several mighty rivers (as, e.g., Bezamat et al. 2018). An important part of this appreciation is for us to pro-actively understand and appreciate the rich social lives of odontocetes, and to thereby aid local and international efforts to save cultural entities and diversity through conservation/management actions (Brakes et al. 2019). A giant biologist of our time, Edward O. Wilson, asks us to more actively and more fully engage in a love of all life and living systems (the concept of biophilia, Wilson 1984, 2010), even as we encroach evermore on the nature that is an intricate part of us.

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