Rugh, D., DeMaster, D., Rooney, A., Breiwick, J., Shelden, K., and Moore, S. (2003). A review of bowhead whale (*Balaena mysticetus*) stock identity. *J. Cetacean Res. Manage.* **5**, 267–279.
Shelden, K. E. W., and Rugh, D. J. (1995). The bowhead whale, *Balaena mysticetus*: Its historic and current status. *Mar. Fish. Rev.* **57**(3–4), 1–20.
Vladimirov, V. L. (1994). Recent distribution and abundance levels of whales in Russian far–eastern seas. *Russ. J. Mar. Biol.* **20**, 1–9.
Würsig, B. (1988). The behavior of baleen whales. *Sci. Am.* **258**, 102–107.
Würsig, B., and Clark, C. (1993). Behavior. *In* Burns, J. J., Mantage, J. J., and Cowles, C. J. (eds). "The Bowhead Whale." Spec. Pub. 2, *Soc. Mar. Mammal.*, Lawrence, KS.

Bow-Riding

BERND WÜRSIG

One of the most fascinating behaviors of dolphins is when they ride the bow pressure waves of boats. Dolphins probably have been bow-riding ever since swift vessels plied the seas, propelled by oar, sail, or very recently in the history of seafaring, motor. The Greeks wrote of bow-riding in the eastern Mediterranean and Aegean Seas by what were most likely bottlenose (*Tursiops truncatus*), common (*Delphinus delphis*), and striped dolphins (*Stenella coeruleoalba*).

Bow-riding consists of dolphins, porpoises, and other smaller toothed whales (and occasionally sea lions and fur seals) positioning themselves in such a manner as to be lifted up and pushed forward by the circulating water generated to form a bow pressure wave of an advancing vessel (Lang, 1966; Hertel, 1969). Dolphins are exquisitely good at bow-riding, able to fine-tune their body posture and position so as to be propelled along entirely by the pressure wave, often with no tail (or fluke) beats needed. Bow-riders at the periphery of the pressure wave do need to beat their flukes, and so do bow-riders of a slowly moving vessel or one with a very sharp cutting instead of pushing bow.

There is often quite a bit of jostling for position at the bow, as dominant animals of a group edge others to a less favorable position, or as one is displaced from the bow by another one approaching (Fig. 1). It is great fun for a person to lean over the bow of a vessel and watch these inter-animal antics, as well as the fine-tuning of positioning, effected by slight body turns and almost imperceptible movements of the flippers. Bow-riding dolphins also tend to emit what sounds to the human listener like a cacophony of underwater whistles and "screams," sounds implicated in high levels of social activity (Brownlee and Norris, 1994). Bow-riding is probably the dolphin behavior most noted, and most enjoyed, by seafaring people the world over.

Of course, riding the bow also makes these animals susceptible to being lanced or harpooned in areas where they are taken by humans. Where this occurs near shore and in apparent smaller populations, dolphins become shy of the bow (Norris, 1974), but on the high seas or in deeper water, probably in larger populations, dolphins often still ride the bow after tens to hundreds of years of (generally small scale) human hunting.

While many species of dolphins, porpoises, and small toothed whale ride the bow, some do not; and in some species, certain populations do not. Bottlenose dolphins are well-known bow-riders the world over, but even they do not ride in some areas (even where they are not hunted) or on some types of vessels. For example, off the shores of Texas in the Gulf of Mexico, they generally do not approach any vessel smaller than 15 m long to bow-ride, apparently finding the smaller bows not worth their while. Instead, they "hitch a ride" on the oil tankers and freighters, sometimes larger shrimping vessels while enroute to and from the shrimping grounds, at times bow-riding for 20 or more kilometers at a stretch. Dolphins ride underwater, and must leave their position to breathe, leaping forward and at an angle to the surface before falling back toward the advancing bow in a welter of foam (Fig. 2). Dolphins also ride the stern waves (or wakes) of boats, which present a different hydrodynamic challenge than bow-riding; and in some areas, dolphins that do not approach the bow will nevertheless ride in the influence of a large (or fast small) vessel's wake.

Figure 1 *Common dolphins* (Delphinus delphis) *on the bow of a sailing vessel off Panama. Photo by Bernd Würsig.*

Figure 2 *Two bottlenose dolphins* (Tursiops truncatus) *leap for a breath between rides on the bow of a shrimp vessel near shore in the Gulf of Mexico. Photo by Bernd Würsig.*

Most oceanic dolphins ride bow waves, with notable exceptions in areas of intensive hunting, such as by tuna vessels of the eastern Tropical Pacific, where vessels chase dolphins in order to net the tuna often affiliated with a dolphin school (Perrin, 1968). However, riding the bow is also "mood dependent"; dusky dolphins (*Lagenorhynchus obscurus*), for example, will not approach vessels when they have not fed for two or more days. These same dolphins will race toward a boat from several kilometers during and after social/sexual activities that take place immediately after bouts of feeding on schooling anchovy (Würsig and Würsig, 1980).

Why do dolphins bow-ride? It has been proposed that it is a mechanism to efficiently travel from one place to another. However, this is unlikely, for one often sees bow-riding dolphins after some time heading back to whence they picked up the vessel. Instead, it is more likely that riding the bow is done for enjoyment, for the sport of it; in other word, play. This is of great interest to behaviorists, for there are not too many non-domesticated adult mammals that habitually engage in activities just for the fun of them, although the list is growing with detailed observations in nature.

Bow-riding was certainly not "invented" by dolphins as a sport when human-made vessels first came on the scene. Instead, it appears to have been adapted from other wave-riding forms. Dolphins ride on the lee slopes of large oceanic waves and on the curling waves (or surf) that are formed as oceanic waves touch near-shore bottom (these two "rides" are hydrodynamically quite different; Hertel, 1969). Dolphins "body surf" much as do humans, but dolphins are generally much better surfers than humans. Dolphins also ride the bow waves of surging whales such as baleen whales and sperm whales (*Physeter macrocephalus*). Dolphins even "entice" whales to surge ahead by rapidly crossing back and forth a whale's eyes and snout. The whale surges forward in response (and apparent annoyance), often blowing forcefully during the surge. An abrupt bow wave is formed, and the previously heckling dolphins are all lined up in that wave, apparently enjoying its momentary pressure effect. This activity can go on with one whale for 20 min or more, until the whale tires, the bow wave becomes less distinct, and the dolphins abandon it to try with another whale or to go about other activities. They have had their fun, and we are left to wonder what is going on in that large brain during these bouts of quite obvious play.

See Also the Following Articles

Group Behavior ■ Playful Behavior ■ Aerial Behavior

References

Brownlee, S. M., and Norris, K. S. (1994). The acoustic domain. *In* "The Hawaiian Spinner Dolphin" (K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, eds), pp. 161–185. University of California Press, Berkeley.

Hertel, H. (1969). Hydrodynamics of swimming and wave-riding dolphins. *In* "The Biology of Marine Mammals" (H. T. Anderson, ed.), pp. 31–63. Academic Press, New York.

Lang, T. G. (1966). Hydrodynamic analysis of cetacean performance. *In* "Whales, Dolphins, and Porpoises" (K. S. Norris, ed.), pp. 410–434. University of California Press, Berkeley.

Norris, K. S. (1974). "The Porpoise Watcher." Norton Press, New York.

Perrin, W. F. (1968). The porpoise and the tuna. *Sea Front* **14**, 166–174.

Würsig, B., and Würsig, M. (1980). Behavior and ecology of the dusky dolphin *Lagenorhynchus obscurus*, in the south Atlantic. *Fish. Bull.* **77**, 871–890.

Brain

Helmut H.A. Oelschläger and
Jutta S. Oelschläger

Adaptation to aquatic environments is a multiconvergent phenomenon seen in a number of mammalian groups and species (Oelschläger and Oelschläger, 2002). In toothed whales (odontocetes), both the body shape and the morphology of the sensory organs and brain intimate the selective pressures, which may have led to exclusively aquatic life. There are some obstacles, however, in understanding brain evolution in these animals. First, we are only marginally familiar with the brain morphology of very few species, and here we are familiar with mainly the bottlenose dolphin (*Tursiops truncatus*; discussed later). Second, the brain itself does not fossilize; only the outer shape can be studied in natural endocasts, and these are biased covering blood vessels, meninges, and by geological artifacts. Thus, the tracing of brain evolution in fossils is difficult and should be supplemented by phylogenetic reconstruction on the basis of extant relatives. Third, although the comparative consideration of analogous developmental trends (primates) may be useful for the understanding of brain evolution in highly encephalized aquatic mammals, the paucity of data often leads to an overestimation of these analogies.

Among the most fascinating characteristics of toothed whales are the exceptionally large size of their brains, both in absolute and in relative terms, and the extremely dense folding of the neocortex. Whereas dolphins usually have a brain mass of about 200–2000 g, the maximal size is attained in killer whales (*Orcinus orca*) and (giant) sperm whales (*Physeter macrocephalus*) approximating 10,000 g. Basically, odontocete brains show the typical mammalian bauplan and are as complicated morphologically as those of other mammalian groups. To some extent, they parallel the simian and the human brains. In this respect, however, it has to be kept in mind that cetaceans have been subject to profound modifications in brain morphology and physiology during 50 million years of separate evolution in the aquatic environment. Moreover, it is still very difficult to correlate the results of behavioral and physiological research on dolphins with existing neuroanatomical data. Because invasive experimentation is not possible in cetaceans, the functional significance of such data can only be elucidated via comparison with other aquatic or terrestrial mammals.

Most studies during the last decades have focused on the morphology and the potential physiology of the adult toothed whale brain and its functional systems (Jelgersma, 1934; Jansen and Jansen, 1969; Glezer *et al*., 1988; Ridgway, 1990). Concerning the development of the odontocete brain, the very few recent papers were dedicated to the striped dolphin (*Stenella coeruleoalba*), harbor porpoise (*Phocoena phocoena*; Buhl and Oelschläger, 1986), spotted dolphin (*Stenella attenuata*), narwhal (*Monodon monoceros*), and sperm whale (Oelschläger and Kemp, 1998). Reviews of information on the mammalian brain, including that of marine mammals can be found in Nieuwenhuys *et al*. (1998).

I. Morphology of the Cetacean Brain

A. General Appearance

Whereas its development in the embryonal and early fetal period is similar to that of other mammals, the brain of adult whales and dolphins is rather spherical in comparison with that of generalized land mammals (Oelschläger and Oelschläger, 2002) and somehow reminiscent of a boxing glove (Fig. 1). In correlation with the so-called "telescoping" of the skull along the beak-fluke axis, both the cranial vault and the brain are short but wide and even more so in toothed whales (odontocetes) than in baleen whales (mysticetes). In the bottlenose dolphin (Fig. 1), the hemispheres are rounded and high, and the anterior profile is rather steep. In ventral aspect (Fig. 2), the contour of the odontocete forebrain is more trapezoidal, whereas in mysticetes it is more trilobate, with the area of the insula (Fig. 3) being visible externally as an indentation between the orbital and the temporal lobes only (Figs 1 and 2). In comparison with hoofed animals, the telencephalic hemisphere seems to be rotated rostralward and ventralward