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## TERRITORIAL BEHAVIOR

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### I. Territoriality in Marine Mammals

“Territoriality” refers to the exclusive use of fixed space, and “territorial behavior” refers loosely to behavior involved in obtaining, defending, or advertising occupancy of the space. All agonistic social interactions occur within a spatial framework, but by themselves do not constitute territorial behavior. As in other animals, territoriality in marine mammals can evolve if space is defensible, enabling monopolization of resources within that space. Territoriality is absent in most marine mammal species simply because no whales are territorial; the polar bear (*Ursus maritimus*) and most Sirenia also are not territorial. The best known examples of territoriality are breeding males in the sea otter (*Enhydra lutris*) and many pinnipeds (aquatic or terrestrial mating systems, or both) plus: One population of dugong (*Dugong dugon*; in Shark Bay, Western Australia); and female marine otters (*Lontra felina*).

All marine mammals that are territorial when breeding are polygynous; polygyny is most extreme in land-breeding pinnipeds, because density of breeding females can be very high (Fig. 1). Territories can be well defined in such circumstances (Fig. 2), and a small number of large mature males appear to dominate reproduction throughout their tenure, which covers the estrus of multiple females (Fig. 3). Recent research has refined this conventional view (Section II), but a basic link between sexual-size dimorphism (present by 27Ma) and polygyny appears to be firm, underscoring the importance of physical competition as a primary mechanism through which males gain access to females in systems such as territoriality (Trillmich and Trillmich, 1984; Cullen et al., 2014; Morris and Carrier, 2016).

Superficially, territoriality appears to characterize the land-breeding elephant seals (*Mirounga* spp.) and gray seal (*Halichoerus grypus*; some populations also breed on ice), because males are fairly sedentary when hauled out. However, neither of these species is territorial or exhibits territorial behavior as defined above. Territoriality is expressed differently even between closely related species, is not rigid or invariant in any species, and varies intraspecifically through short-term opportunistic behavior, throughout development, seasonally, and geographically (Section II). Territoriality away from the breeding site and outside the breeding period occurs but has been studied little. Key publications highlighting various aspects of territorial behavior include Peterson (1968), Bartholomew (1970), Stirling (1983), Boness (1991), Miller (1991), Boness et al. (2002), and Tyack and Miller (2002).

### II. Territoriality, Mating Strategies, and Mate Selection

Land-breeding pinnipeds were central to Bartholomew's (1970) model of pinniped polygyny. His model remains the core paradigm

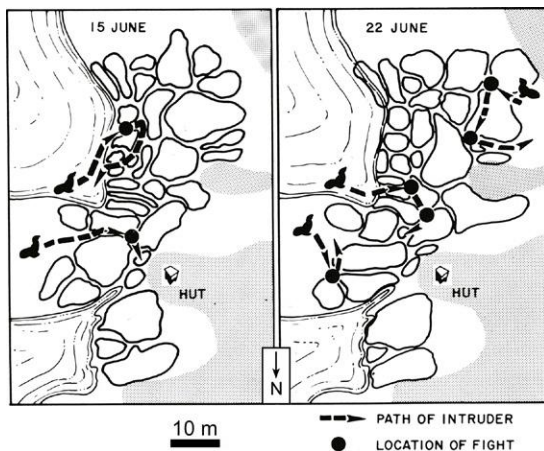
to explain otariid polygyny and territoriality, which assumes lengthy uninterrupted male territoriality, when males fast and expend much energy in territorial display and defense. Therefore, especially in otariids, male reproductive success has been viewed as closely tied to possession of a territory, with territorial males (1) accounting for most fertilizations and (2) fertilizing most females that pup on their territories. This scenario applies well to some species, perhaps especially in low-density colonies (e.g., Antarctic fur seal, *Arctocephalus gazella*), but many deviations occur. For example, scattered observations over many years have pointed to mating in varied situations: Young male northern fur seals mate with females late in the breeding season, after the main period of reproduction; some mating occurs before pupping in the Cape fur seal (*Arctocephalus p. pusillus*) and New Zealand fur seal (*Arctocephalus forsteri*); and males mature sexually (i.e., physiologically) years before they are large enough to compete for territories. Recent molecular evidence has confirmed that fertilizations occur regularly outside the territorial structure, and involve nonterritorial males; furthermore, female Antarctic fur seals actively seek and mate with territory holders that are heterozygous and unrelated to them. Thermoregulatory factors influence movements of males and females, and males may hold aquatic or semiaquatic territories (Juan Fernández fur seal *Arctocephalus p. philippii*, South American sea lion *Otaria byronia*, California sea lion *Zalophus californianus*, etc.); males may vacate their territories for periods ranging from hours to days, even in classically territorial species like the northern and Antarctic fur seals (Fig. 3); males may change from territoriality to female defense later in the season (South American sea lion); and so on. In parts of the range, thermoregulatory factors can influence the expression of territoriality even within single days (Fig. 4).

In the Steller sea lion (*Eumetopias jubatus*), males may be territorial for up to seven consecutive years, but about half of postpartum females mate with males other than those in whose territories they gave birth (Fig. 5). Multiple factors influence male reproductive success in the Galápagos sea lion (*Zalophus wollebaeki*). This species has a very long breeding season (5.5 months) and semiaquatic territoriality is present; therefore males cannot monopolize postpartum females. Nevertheless, in this species the overall amount of time spent by males in territoriality is important to reproductive success, even though males must break up this time over the breeding period.

Mixtures of territorial and nonterritorial mating strategies also occur in phocid seals. In a long-term (16 years) study of male bearded seals (*Erignathus barbatus*) in Alaska, site fidelity and breeding territoriality across years was the norm, but some males switched from territorial to roaming strategies (some individual territorial males were present in every year of the study). Likewise, inter-annual site fidelity and territoriality by males occur in the seasonally breeding ringed seal (*Pusa hispida*) and the Mediterranean monk seal (*Monachus monachus*), which breeds year-round (in one study, a male was present in 13 successive years). Variability in territorial and mating behavior may (1) reflect distinctly different



**Figure 1** Female fur seals and sea lions (*Otariidae*) return seasonally to particular terrestrial sites on islands free from predation, to give birth and raise offspring. These factors have enabled the evolution of male territoriality and polygyny; the tendency of females to aggregate when ashore increases polygyny levels further (see text). This photograph illustrates a breeding aggregation of northern fur seals (*Callorhinus ursinus*) at Tuleny Island, Sea of Okhotsk, Russia, in July 2005 (Photo from Wikimedia Commons).



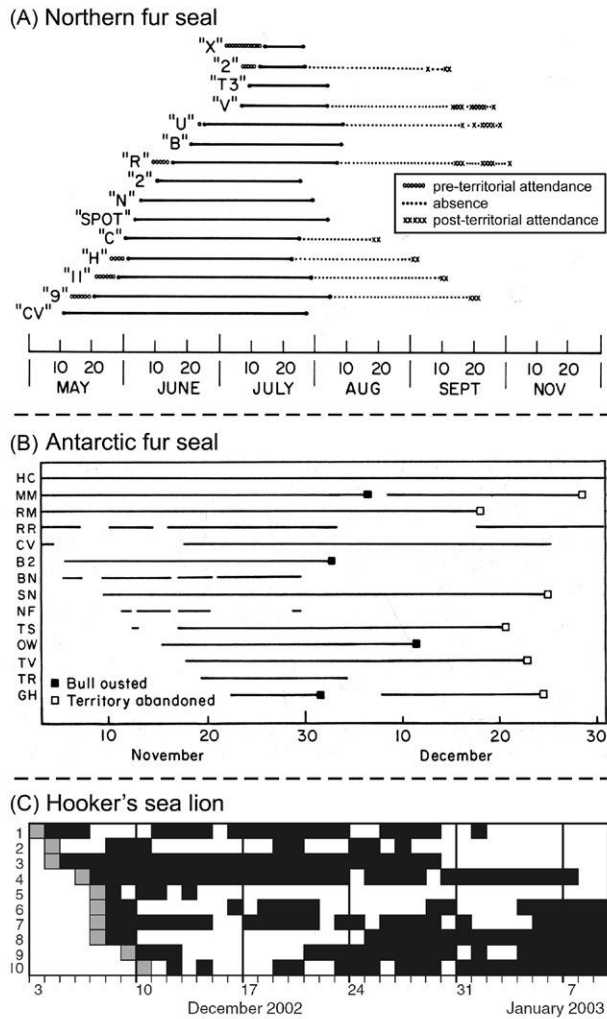
**Figure 2** Territories are small and fairly fixed in size, shape, and location in many species of fur seals and sea lions (*Otariidae*). This figure depicts territories (in outlines) and some territorial behavioral events of male northern fur seals (*Callorhinus ursinus*) at Kitovi rookery, Pribilof Islands, Alaska, in 1962. "HUT" is the point of observation. Adapted from Fig. 11 of Peterson, R.S. (1968). Social behavior in pinnipeds with particular reference to the northern fur seal. In "The Behavior and Physiology of Pinnipeds" (R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice, and R.J. Schusterman, Eds), pp. 3–53. Appleton-Century-Crofts, New York.

strategies or a continuum, (2) represent evolved adaptations or behavioral plasticity, or (3) is related to male age or other characteristics (e.g., phenotype; in the nonterritorial gray seal, males of different body sizes adopt different mating tactics).

### III. Obtaining, Defending, and Advertising Territories

Dramatic and potentially injurious fights between males occur in all territorial species, particularly when new males attempt to establish themselves. Severe injuries or even death can result, so fighting is uncommon, and most interactions between territorial males instead take the form of display.

Territorial male dugongs in Shark Bay repeatedly patrol the margins of their territories along fixed routes. Acoustic displays can travel long distances (especially under water) and are energetically cheap to produce, but long-distance sounds are lacking from the diverse vocal repertoire of this species. Patrolling males perform various distinctive behaviors, e.g., they may swim upside-down or rear high out of the water; fights also occur. Male sea otters likewise patrol their large territories, and announce their presence by exaggerated kicking, splashing, and grooming; males interacting near territorial boundaries may engage in mutual porpoising, and they sometimes fight. Like dugongs, sea otters have a rich vocal repertoire, but also lack sounds for long-distance communication. In contrast, walrus (*Odobenus rosmarus*) and aquatically territorial



**Figure 3** Attendance patterns of territorial male fur seals and sea lions (Otariidae) vary within and across species. Territorial attendance patterns are shown for: (A) 15 northern fur seals (*Callorhinus ursinus*) at Kitovi rookery, Pribilof Islands, Alaska, in 1962; (B) 14 Antarctic fur seals (*Arctocephalus gazella*) on Bird Island, South Georgia, in 1975–76; and (C) 10 Hooker's sea lions (*Phocarctos hookeri*) at Enderby Island, Auckland Islands, in 2002–03 (gray squares represent days when males were marked). (A) Adapted from Fig. 12 of Peterson, R.S. (1968). *Social behavior in pinnipeds with particular reference to the northern fur seal*. In "The Behavior and Physiology of Pinnipeds" (R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice, and R.J. Schusterman, Eds), pp. 3–53. Appleton-Century-Crofts, New York; (B) Adapted from Fig. 2 of McCann, T.S. (1980). *Territoriality and breeding behavior of adult male Antarctic fur seal, Arctocephalus gazella*. *J. Zool.* 192, 295–310 (McCann, 1980); C—Adapted from Fig. 3 of Robertson, B.C., Chilvers, B.L., Duignan, P.J., Wilkinson, I.S., and Gemmel, N.J. (2006). *Dispersal of breeding, adult male Phocarctos hookeri: implications for disease transmission, population management and species recovery*. *Biol. Conserv.* 127, 227–236 (Robertson et al., 2006), respectively.

phocids possess acoustic signals that travel under water for long distances.

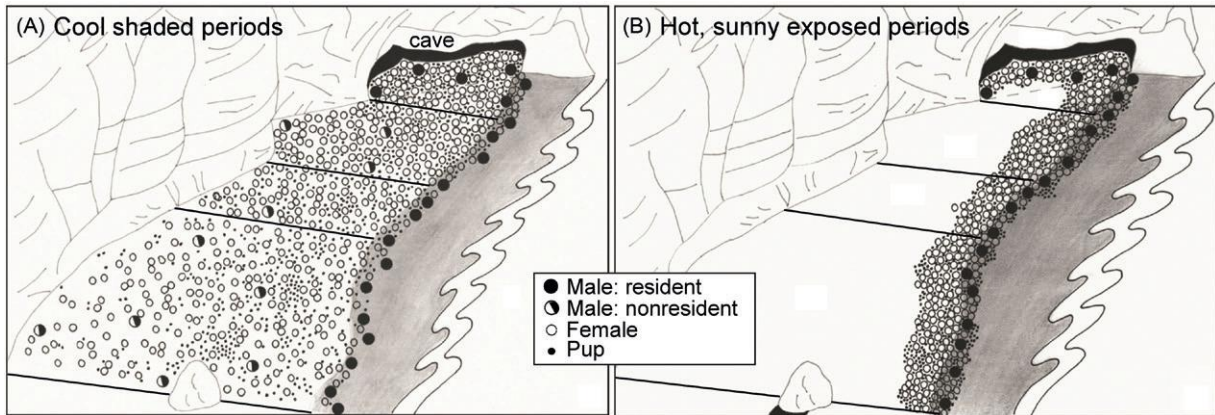
Long-distance underwater sounds of territorial pinnipeds tend to be stereotyped, and to convey little behavioral information; nevertheless,

they must be informative to several classes of receiver (e.g., nonterritorial males, females), not just other territory holders; in fact, male bearded seals in Alaska vocalize for much of the year, not just during the breeding period. Long-distance sounds are not universal in aquatically territorial species; for example, high vocal activity and long-distance sounds probably have been selected against in the ring seal, to minimize detection by polar bears. Otariids are highly vocal and have rich vocal repertoires. Vocalizations of territorial male otariids are transmitted over medium to short distances; the stereotyped "full-threat call" (Phillips and Stirling, 2001, p. 423) is the loudest, and carries the farthest. Many male calls have been interpreted simply as communication of "threat" but carry much richer behavioral information. Most call types of male otariids are variable, have complicated syntactical arrangements, and are used in multiple social contexts. Many morphological specializations for sound production occur in marine mammals but have evolved to serve general communicative functions, not solely for functions related to territoriality (discussed later).

Likewise, optical signaling is complex in territorial marine mammals and involves numerous morphological features. Some optical displays of otariids are relatively passive and undirected (e.g., the distinctive nose-up upright resting posture of otariids), but most optical displays are active and directed toward specific individuals. These signals involve motor patterns such as distinctive head-and-neck swinging in locomotion, or rapid and complex sequences of feints, oblique stares, sprawls, facial expressions, etc., in displays between neighbors across territorial boundaries. The distinctive appearance of adult male otariids is communicatively important in the context of territoriality. For example, in contrast to females or young males, adult male Hooker's (*Phocarctos hookeri*) and California sea lions are much darker than females or young males, and adult male South American sea lions have especially distinctive manes. Many other morphological adaptations for communication occur in marine mammals, including optical patterns of the pelage, sound-producing structures, and weapons. Some structures may have become enlarged, strengthened, or otherwise modified for use in fights (e.g., claws of bearded seal; lower canines of otariids), and tusks (upper incisors) have evolved as weapons and optical display structures in the walrus. However, no morphological features have evolved specifically to serve territorial functions, as such features (e.g., tusks) have evolved independently in marine mammals with diverse nonterritorial systems.

Chemical communication is probably important in all land-breeding territorial species of marine mammals but is virtually unstudied. Facial glands are unknown in sea otters, but the species has well developed anatomical (neural) characteristics for olfaction, and individuals often actively smell the air. Facial glands (many associated with vibrissae) occur in walruses, phocids, and otariids, and are known to vary seasonally in size and secretory activity in some species. Male fur seals emit distinctive odors during boundary displays between neighbors, apparently from the oral cavity, and also have distinctive body odors during the breeding season; they may be produced by apocrine sweat glands. Breeding male ringed seals hold underwater territories that are near or overlap with areas used by breeding females. During the breeding season, adult males of this species acquire a strong odor which is the origin of terms like "tiggak" ("stinker") among Inuit, and "gasoline seal" among trappers (Ryg et al., 1992). Territorial male ringed seals may actively deposit secretions from facial sebaceous glands on entrances to their breathing holes and subnivean ("below-snow") resting lairs, as well as within the latter.

The roles of taste or use of the vomeronasal organ (VNO) in marine mammal communication are unknown, although the VNO is absent



**Figure 4** Thermoregulatory factors can affect the expression of territoriality and movements of breeding adults, thereby altering mate-choice dynamics of females. In cool parts of the day at a Peruvian colony, male South American sea lions (*Otaria byronia*) are territorial on the upper parts of the beach, where females with pups also are mainly distributed (A). In hot parts of the day, all animals move to the shoreline, where it is more crowded and males are not territorial (B). Adapted from Fig. 2 of Soto K.H., and Trites, A.W. (2011) South American sea lions in Peru have a lek-like mating system. *Mar. Mamm. Sci.* 27, 306–333 (Soto and Trites, 2011).

in Sirenia but present and well developed in pinnipeds. Otariids commonly exhibit slow, repeated, tongue extrusion following agonistic displays (e.g., boundary displays or fights involving males; females, juveniles, and even pups also express the behavior), suggestive of behavior of other mammals that are known to use the VNO in chemical communication (at the very least, tongue extrusion is a conspicuous optical signal and likely has become ritualized as an optical display).

Tactile communication in marine mammals likewise is important but essentially unstudied. Breeding males of all species engage physically and contact one another extensively in biting, wrestling, or pushing. Male sea otters and Weddell seals (*Leptonychotes weddellii*) often try to bite the opponent's penis, and fractured bacula (penis bones) of mature male sea otters are relatively common (see "Baculum" article). In phocid species that fight aquatically, the rear flippers (necessary for aquatic locomotion) are frequently bitten and injured in fights; walruses use the tusks in fights at and below the water surface (all sex and age classes of the walrus use tusks in numerous other agonistic contexts, of course).

#### IV. Costs of Territoriality

Territoriality carries benefits and costs. In dispersed aquatically territorial species, most costs fall on territory holders, which must expend energy and time to establish, maintain, and advertise a territory, and must occasionally fight with other males. In fur seals and sea lions, some costs fall on pups and on breeding females as well.

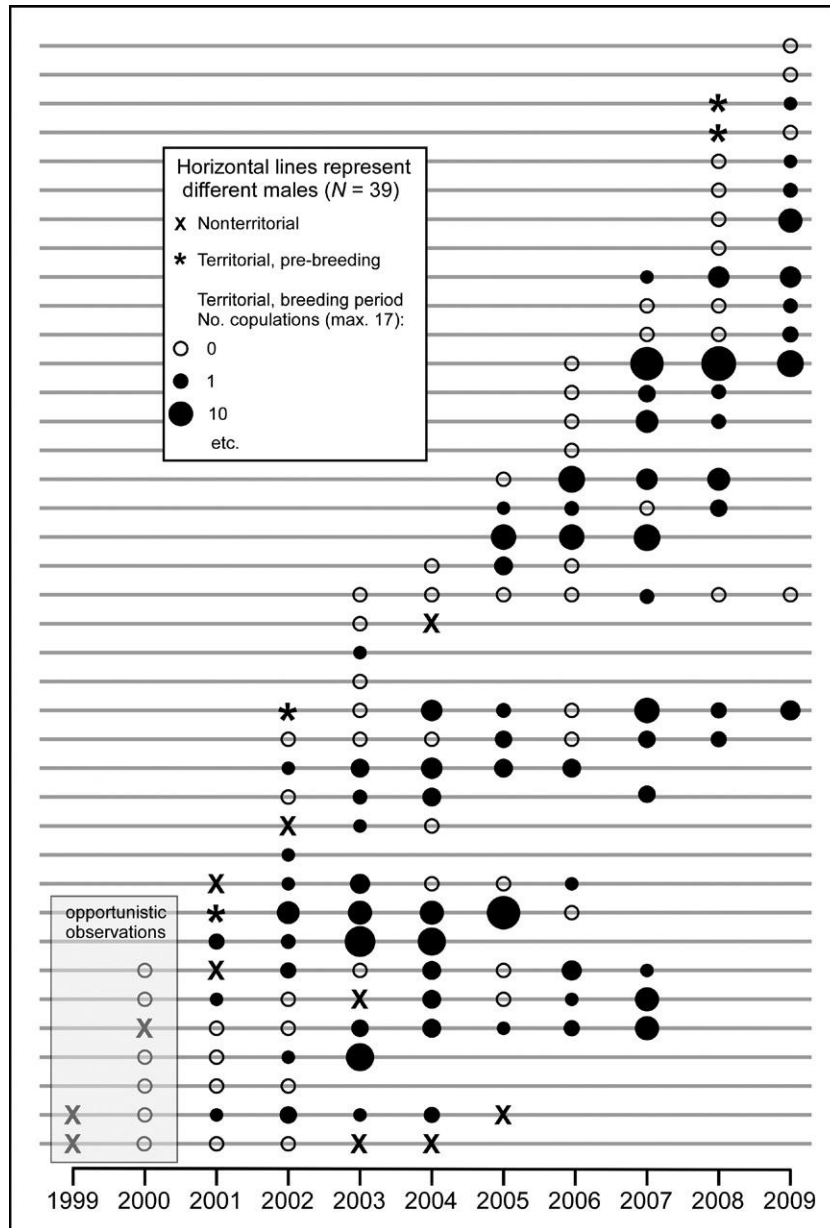
Territorial males must balance the need to be vigilant, advertise and defend territories, and signal about their own behavioral and physical attributes. Male sea otters hold large territories, and do not use long-distance advertisement, so must spend a lot of time patrolling: On average, territory holders spent 17% of their time in this activity in Prince William Sound, Alaska. In one long-term study, territorial male northern fur seals spent 1.5% of their time in overt interactions with neighbors; however, other types of activities also serve territorial functions, such as simply moving around the territory (1.7%), or resting in an upright position (21.1%). In the New Zealand fur seal, males spend about 14% of their time upright, compared with 5% for females.

The impact on males of time and energy spent in territorial activities is compounded by other factors: Effects of fasting or

reduced food intake; and time spent as a territory holder. On average, territorial male northern fur seals fast and do not drink for about a month (maximum 87 days), and decline in body mass by about one third over that time. This loss in body mass is equivalent to about 0.7% of initial body mass per day, similar to some other species: About 0.8% in the Antarctic fur seal and the aquatically territorial Weddell seal. Breeding male harbor seals (*Phoca vitulina*) do not fast completely, and body mass declines more slowly (about 0.4% per day), but overall costs can be high (one male lost 30% of his initial body mass over the breeding season). At least some territorial male Weddell seals feed, as do adult male Galápagos sea lions between periods of territoriality within the breeding season (as noted, this is >5 months in duration). Male Mediterranean monk seals are territorial throughout the year-long breeding cycle, and feed during that time.

Costs and risks of territoriality include the danger of suffering severe physical injury. Most (80%–90%) of Antarctic fur seals found dead in a study on South Georgia had died as a direct or secondary consequence of fighting injuries, especially to the foreflippers or dorsal surface of the forequarters. Fitness of adult female and pup otariids also is affected by male behavior. For otariids, it is believed that female aggregation on land has been selected for, to reduce harassment by males and to protect pups from males. The significance of harassment is evident in the incidence of injuries and deaths in adult female Hooker's sea lions: Greater than 80% of females have permanent scars inflicted by males, and annual mortality of adult females is about 0.5% due to male attacks; infanticide by males also occurs (e.g., Hooker's sea lion). Finally, abduction of pups from colonies by males occurs in many otariid species, and can be a substantial contributor to pup mortality, especially in small colonies (Section V).

Mortality rates of males are similar to those of females until social maturity is attained and males begin territorial activity. Male mortality increases at that time, and thereafter remains much higher than for adult females: 32% vs 15% in Galápagos fur seals (*Arctocephalus galapagoensis*); 30% vs 10%–15% in northern fur seal; 30% vs 12% in Cape fur seals; and 50% vs 8% in Antarctic fur seals. This pattern is presumed to be due largely to direct and indirect effects of male territoriality.



**Figure 5** Male territoriality can be expressed over multiple years in some otariids, and yet such males do not necessarily monopolize reproduction. Male Steller sea lions (*Eumetopias jubatus*) in Alaska can hold territories in up to seven consecutive breeding seasons, but only about half of the postpartum females on their territories mate with them, and territoriality is not the only kind of male mating strategy. Adapted from Fig. 5 of Parker, P., and Maniscalco, J.M. (2014). A long-term study reveals multiple reproductive behavior strategies among territorial adult male Steller sea lions (*Eumetopias jubatus*). *Can. J. Zool.* 92, 405–415 (Parker and Maniscalco, 2014).

## V. Development of Territorial Behavior

Territoriality involves complex behavioral patterns used repeatedly in interaction and communication, which emerge in play early in life. In one study, the complex underwater vocal displays of territorial male bearded seals appeared at 4–5 years of age in several captive males, but not in females. Vocalizations are stable for life in most males, but change if a male's mating strategy changes (e.g., from territorial to roaming). Sexual differences in behavioral development have been documented in most detail for fur seals and sea lions (Otariidae), in which pups segregate by sex, male pups are more aggressive than females, and male pups engage in more

play-fighting and territorial displays. Such social interactions occur even in the appropriate topographical context for breeding territoriality; e.g., Steller's sea lion pups locate themselves on opposite sides of any available ridge and use boundary display postures, open mouth lunges, and other behavior characteristic of boundary defense in adult males (Gentry, 1974). Young male otariids of all ages engage extensively in play-fighting throughout the year.

Many territorial male otariids appear to try to influence females to stay on their territories by herding. Such behavior appears early in life, and male pups preferentially direct this behavior toward female pups (e.g., New Zealand fur seal). Herding is expressed also

by nonterritorial or peripheral males during the breeding season; for example, when they encounter females outside breeding aggregations. Outside the breeding season, juvenile and subadult male otariids occasionally herd pups or young juveniles, at wintering haulouts or colony sites (e.g., New Zealand fur seal). In most or all otariid species, nonterritorial males (including subadults) may rush simultaneously into ("raid") breeding aggregations, and herd or interact with females in various ways before they are chased away by territorial males. An extreme form of behavior occurs in several otariid species, in which nonterritorial (generally subadult) males carry pups away following raids on breeding sites. In the South American sea lion, males may carry pups to the ocean, and then to nonbreeding areas where the males herd and mount them, sometimes over several days; in one study, ~6% of pups treated in this manner died as a result. In some species, males may cannibalize pups.

Breeding territoriality in otariids develops within the context of strong colony and natal-site fidelity, which become increasingly precise with age [e.g., for male northern fur seals (*Callorhinus ursinus*) aged 2–6 years]. Male northern fur seals start to haul out near the breeding site when they are 2 years old, and hold their first territories at about 7 years of age; first territories tend to be located peripherally, and are occupied late in the breeding season. Over successive breeding seasons, territories become stabilized in location and size, and are established progressively earlier.

## VI. Territorial Functions

Nonbreeding territoriality is poorly documented and understood. Male otariid territoriality occurs at some nonpupping sites during the breeding season. Many minor disputes over space take place throughout the year at both breeding colonies and nonbreeding haulouts, where individuals of various classes tend to use and interact agonistically repeatedly at the same sites. Nonbreeding (winter) territoriality in some individuals of some phocid species may provide exclusive (or priority) access to breathing holes in stable ice. The function of another form of territoriality also is not known: Mature male otariids may return to occupy their territorial sites for several days in the fall, weeks after abandoning them (Fig. 3A).

The best known, most dramatic, and most interpretable forms of territoriality in marine mammals are shown by breeding adult males, which establish territories seasonally where females enter estrus and copulate. The ultimate function of male territoriality in all cases is to gain access to estrous females; proximate functions that mediate male reproductive success are more difficult to identify and are both varied and variable. As noted above, male pinnipeds are not tied rigidly to territories and territorial behavior; they may change locations (e.g., in response to female movements), attend and defend isolated lone females, or even defend and copulate with female carcasses.

In many otariids, males hold territories where females give birth and remain on land until they enter estrus; in such cases, male territories hold resources that are needed by females (sites for pupping, reuniting with pups between foraging trips, and nursing). However, territoriality is fluid in many populations, because breeding animals must move regularly for thermoregulatory reasons or due to tide levels, or because the breeding substrate is homogeneous and hence territorial boundaries are ill defined (Section II). Resource-based territoriality is expressed clearly in sea otters. Adult male sea otters establish territories seasonally in or near areas of high female density. Male territories hold multiple resources used by females, including prey, resting areas, protection from wind and waves, and protection from harassment by other males.

The distinction between territories with and without resources needed by females blurs in many cases. In the Weddell seal, mature males set up and defend territories seasonally in traditional areas of stable ice where females congregate, give birth, and later enter estrus; females need access to water for foraging, so these access points can be considered as the key defensible resource on which male territoriality is based. Similarly, male ring seals hold underwater territories that are near or encompass the birth lairs of several females. Male harbor seals establish territories near female haulouts, or on access routes to and from those haulouts. At an extreme, male territories may hold no resources needed by females, and male reproductive success depends solely on female visitation for purposes of copulation (e.g., Shark Bay dugongs; walrus; bearded seal). In some situations (e.g., walrus), the presence of males near a small number of females can be construed as defense of females, rather than of space.

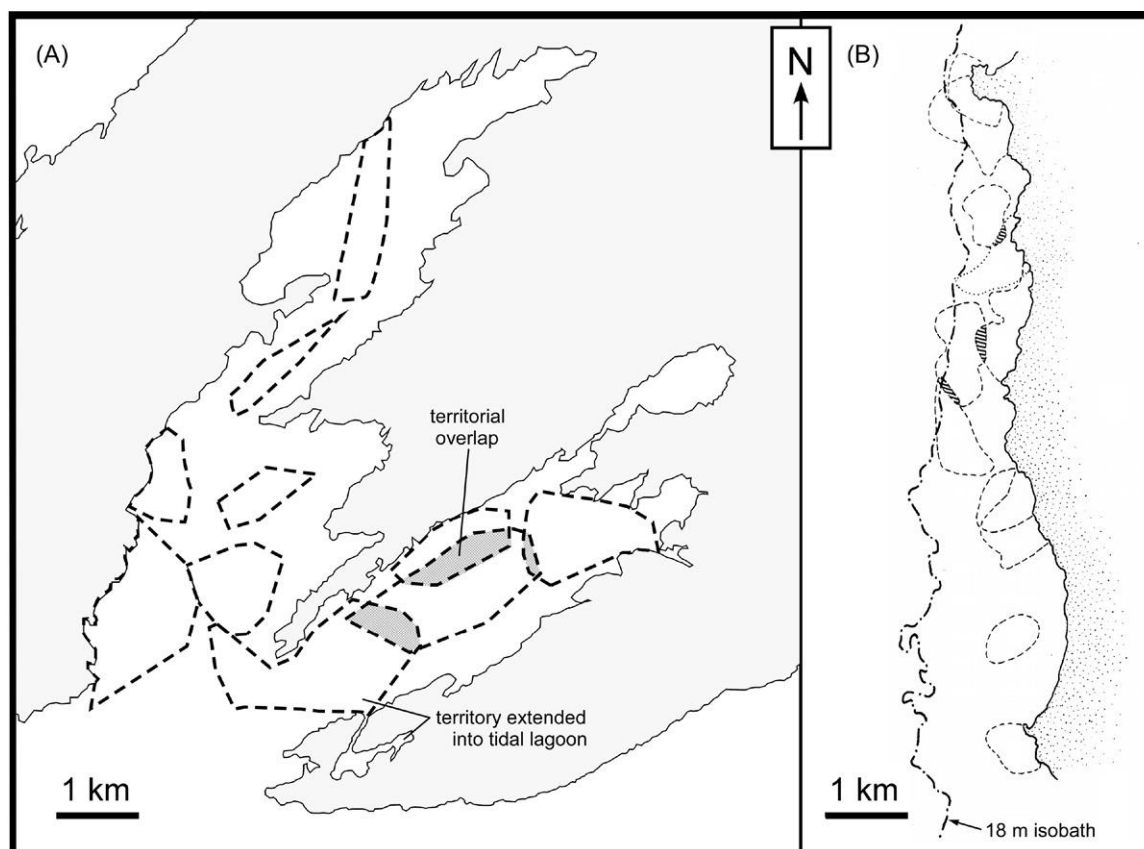
## VII. Spatial Aspects of Territoriality

Discrete, clearly defined territories are most apparent on small temporal scales, in situations of crowding, in species that have good locomotory abilities so can efficiently patrol or defend their territories, and where environmental features (e.g., topographical irregularities) occur that can be used by the animals to demarcate territories (Fig. 6). Such conditions are lacking in the lives of cetaceans, especially open-ocean species, so territoriality does not occur in that group. River dolphins, with their spatially restricted distributions, or species that feed on concentrated prey that are sedentary or spatially predictable, may prove to be territorial, but this is not known at present. In Scotland's Moray Firth, year-round resident common bottlenose dolphins (*Tursiops truncatus*) may be territorial and exclude seasonal (winter) conspecific visitors from deep waters, which are most favorable for feeding; group territoriality also has been suggested for this species in Ecuador.

Most species of otariids breed on crowded colony sites and hold small territories; territories of male Hooker's sea lions often are no more than 3 m in diameter, for example, and some northern fur seals hold territories that are little larger in diameter than a male's body length (Figs 1 and 2). Larger territories occur in related species (e.g., about 200 m<sup>2</sup> in male Steller's sea lions). Small aquatic territories are held by Juan Fernández fur seals adjacent to breeding aggregations on land, and by walruses adjacent to mixed herds on ice. In general however, aquatic territories are large: More than 100 m in length in some male Weddell seals, up to 1 km across in male sea otters, and up to 10 km across in some male harbor seals. Many aquatic territories are noncontiguous, but contiguous territories invariably overlap some extent, both in linear and in more complex spatial arrangements.

Phocids are specialized for aquatic locomotion, so their locomotion on land is slow and energetically costly. The poor locomotory abilities and large size of the two species of elephant seal usually preclude territoriality, although in small confined areas or rough terrain, defense of space and of females amounts to the same thing. In contrast, fur seals and sea lions can move quickly and efficiently on land, so offer many clear examples of terrestrial territoriality.

Precise delimitation of territories occurs at many breeding sites of otariids, because rocks, fracture lines, and other natural features are present; in these situations, territorial boundaries may be stable within and across years. On featureless terrain (e.g., sandy beaches), territories are less clearly defined. Territories of northern fur seals are smaller in exposed terrain, and larger in protected terrain. Aquatic territories also are influenced by physical environmental



**Figure 6** Size, shape, and configuration of marine mammal territories are influenced by the physical environment. Aquatic territories held by adult male sea otters (*Enhydra lutris*) hold multiple resources needed by females. They are large, overlap, and exhibit more complex spatial arrangements in enclosed waters (A—Prince William Sound, Alaska, 2003) than along coasts (B—central California, 1978–1982; overlapping territories held indifferent years are shown with areas of overlap not cross-hatched). Adapted from Fig. 1 of Pearson, H.C., Packard, J.M., and Davis, R.W. (2006). Territory quality of male sea otters in Prince William Sound, Alaska: Relation to body and territory maintenance behaviors. *Can. J. Zool.* 84, 939–946 (Pearson et al., 2006); B—Adapted from Fig. 2 of Jameson, R.J. (1989). Movements, home range, and territories of male sea otters off central California. *Mar. Mamm. Sci.* 5, 159–172 (Jameson, 1989).

structures. In species that breed in association with ice, underwater features of ice or fractures or leads in ice may be important in determining territorial density, size, and shape. In the walrus, male territories are established in the water adjacent to mixed herds on ice, which may be stable land-fast ice (e.g., in the Canadian Arctic) or unstable drifting pack ice (e.g., Bering Sea). Some territorial boundaries of male Mediterranean monk seals correspond to underwater geological features.

### VIII. Temporal Aspects of Territoriality

Territories of fur seals and sea lions are most clearly defined at the peak of breeding, when territorial density is highest and territorial size is smallest (Figs 1 and 5). Absence of females from their territories sometimes leads to territorial desertion by male otariids, but more commonly males attempt to acquire a new territory where females are present. In the Hooker's sea lion, males establish territories several times during the breeding season in response to movement of the female aggregation down the beach. Southern sea lion males defend territories early in the breeding season but gradually change to defense of females as the season progresses.

Male otariids may haul out at the site of their future territory before territorial behavior begins and, as noted, may also return to their territories after the breeding season has ended (Fig. 3). Territorial occupancy may be continuous for weeks or months,

or males may leave the territory for periods for thermoregulatory or other reasons, and then return; this pattern is extreme in the Galápagos sea lion due to the long breeding season, as noted. Territorial occupancy is highly variable in the Hooker's sea lion, and males move extensively within and between breeding sites (Fig. 3C); this is similar to behavior of breeding males in the nonterritorial gray seal on Sable Island, Nova Scotia.

Male otariids habituate to neighboring males and engage in fewer and less aggressive interactions with neighbors over time. A similar effect occurs even across years between returning territorial neighbors.

Long-term fidelity (philopatry) to territorial locations has two components. First, there is a tendency for males to return to breed near the site of their birth (natal philopatry). Second, males tend to return in successive years to where they first established a territory. Both forms of site fidelity are well documented in otariids; e.g., about 50% of returning male Antarctic fur seals occupy a territory that is within half a body length of the territorial site held in the previous year. Site fidelity by breeding males occurs also in species that breed in association with land-fast ice (e.g., ringed seal, Weddell seal), or near land (e.g., harbor seal, sea otter); in one study, male sea otters hold territories in the same location for up to seven successive years. Site fidelity even occurs in aquatically territorial

phocids that display away from land or land-fast ice, as noted above for bearded and ring seals. The extremely strong natal- and territorial-site fidelity shown by otariids, coupled with their high breeding densities, results in kin breeding in proximity to one another.

### See Also the Following Articles

Earless Seals ■ Eared Seals ■ Mating Systems ■ Reproductive Behavior

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## THERMOREGULATION

MICHAEL CASTELLINI

Marine mammals have evolved the ability to retain heat in cold seas through a suite of physiological, biochemical, anatomical, and behavioral methods. Yet, they must be able to lose excess heat when on land or extremely active in the water. If the problem was solely how to stay warm in a cold ocean, it would be easiest to use thick blubber and fur, or to stay very active. However, the difficulty of that solution is that the animal could potentially overheat, which would cause problems with metabolic regulation, reproductive chemistry and neural function. Consequently, thermoregulatory mechanisms have evolved in marine mammals to not only conserve heat, but to also dump it when necessary.

### I. Physics of Heat

The temperature of an object is defined by the level of heat energy contained in that object. Heat flows from where the energy is high (the object is “hot”) to an environment where the energy is low (“cold”). The unit of heat energy is the calorie, defined as the amount of heat necessary to raise 1 g of water by 1°C. The “calorie” commonly associated with food and dieting is the kilocalorie (kcal; 1000 calories). In scientific notation, a calorie is defined as 4.184 J.

As with any energy that flows, there is resistance that impedes the flow of heat. The resistance to heat energy transfer is insulation (the inverse of insulation is thermal conductance). Poor conductors are excellent insulators. Blubber, for example, makes an excellent insulator and conducts heat poorly, while materials such as silver are poor insulators and conduct heat well (Table 1). Heat flows from a warm to a cold body in relation to the magnitude of the temperature gradient, the thermal conductance of the material, the area exposed to the gradient, and inversely with the thickness of the material (Fick equation). This means that heat flows from the interior of a warm blooded mammal through the fat and skin to

**TABLE 1 Thermal Conductance of Various Materials. Units are cal s<sup>-1</sup> cm<sup>-1</sup> C<sup>o-1</sup>**

Silver	1.0181
Aluminum	0.50
Ice	0.005
Water	0.0013
Organic tissue	0.0011
Leather	0.0004
Asbestos	0.0004
Crude oil	0.00025
Blubber (as pelt)	0.0001
Wool felt	0.0001
Fur	0.00009
Air	0.00006
Eider down	0.00001

Data modified from Castellini, M.A., and Mellish, J.A.E. (2015). Thermoregulation. In “Marine Mammal Physiology: Requisites for Ocean Living” (M.A. Castellini and J.A.E. Mellish, Eds), pp. 193–216. CRC Press, Boca Raton, FL.



the cold outside air or water. Since water conducts heat 25× times more effectively than air, heat flows out of a warm object in cold water much more efficiently than it does when that same object is in air. This becomes important for how air trapped in fur helps keep some marine mammals warm. For example, as humans we can easily be outside in 70°F air, but would find being in 70°F water “cold.” Therefore, to stay warm, an animal needs an effective insulator, a small surface area (reduced appendage size, rolling up into a ball, etc.), a low temperature gradient (seek a warmer area) and a thick insulator.

## II. What Is “Thermoregulation”?

Most animals can be classified as either endotherms or ectotherms. An endotherm generates and controls its internal heat so that its body core temperature can be regulated at a level independent of the ambient temperature. Birds and mammals are common examples of endotherms. By contrast, an ectotherm allows its body temperature to mimic and follow ambient temperature. Most fish and invertebrates are ectotherms. All marine mammals are endotherms and regulate their body temperature at about 37°C. Animals that hold their body temperature constant are called homeotherms, while those that vary body temperature are called heterotherms. Most mammals are therefore homeothermic endotherms and have evolved to balance a myriad of metabolic biochemical reactions at 37°C. Much warmer or colder, the system comes out of equilibrium and there can be significant failures in metabolic regulation.

To maintain a constant body temperature in an endotherm, the produced metabolic heat must equal the heat lost to the environment. Too much insulation and the core temperature goes up. A whale or a seal may put on large amounts of blubber, but as a consequence could overheat when extremely active. A human can simply take off a jacket while exercising. A whale however, does not have the option of taking off its blubber layer; it must be able to dump heat and therefore to thermoregulate using other methods.

There are several ways in which heat transfers to the environment from a warm body. Evaporation is the process of applying heat to a liquid to turn it into a gas (e.g., sweating). Radiation is the movement of heat through the release of electromagnetic energy from the warm body to the cold environment without physical contact. Conduction refers to the transfer of heat energy by physical contact (putting your warm hand into cold water). Finally, convection is a specialized case of conduction where the heat that is transferred from the warm body is moved away from the area by a current of air or water (wind chill is the example in air).

In order to maintain a constant body temperature, the heat generated by an endothermic mammal must be balanced by the heat lost or gained through radiation, evaporation, conduction, and convection. This is the fundamental equation of thermoregulatory biology (Scholander et al., 1950).

## III. Thermoregulation in Marine Mammals

### A. Heat Conservation and Generation

Marine mammals have no unusual heat generating mechanisms or tissues. While some large warm-bodied fishes have specialized heat generating tissues, no such organs or tissues exist in marine mammals. Some data suggest that marine mammals may have an elevated metabolic rate for their mass, but this theory is not generally accepted with the possible exception of the sea otter. There appears to be nothing special about marine mammals that would

distinguish them from terrestrial mammals when it comes to heat generating mechanisms.

Given the particularly nondescript aspects of marine mammal heat generation, there must be something that is different because they can live in an extremely cold liquid environment that would be fatal to terrestrial mammals. Following the fundamental heat balance equation of thermoregulation, this suggests that they must have adapted significant ways to alter heat loss. They have done this through the use of blubber, fur, and vascular adaptations (Castellini and Mellish, 2015).

### B. Blubber

Blubber is not a simple, inert fat layer beneath the skin, but is a complex, active tissue consisting of a loose protein matrix of collagen fibers with the volume made of adipocytes (fat or lipid cells). The movement of lipid in and out of the matrix accounts for the change in blubber characteristics, as the collagen matrix remains the same. Blubber varies across species in the ratio of collagen to lipid, and can even vary within the same animal. Blubber depth can range from a few millimeters in newborn pinniped pups to 50 cm thick in large whales. By itself, blubber is a good insulator because it can be up to 93% lipid, has even less thermal conductance than asbestos, and about 1/10th that of water (Table 1). Because blubber is deposited below the skin, it acts as an internal insulator for marine mammal while the skin layer will be only marginally warmer than the surrounding water. In polar waters for example, the skin of a whale or a seal would be just a degree or two above freezing while the core temperature would remain about 37°C (Mellish et al., 2013).

Blubber quality or thickness can also vary across time in the same animal. This can be seen in the significant seasonal variation in blubber thickness in a seal as it moves between the breeding season (where it is fattest) and the leaner periods associated with molting and mating. Northern elephant seals (*Mirounga angustirostris*) can range between 50% to less than 20% body fat depending on the season. This seasonal change in blubber affects not only thermoregulation, but also buoyancy and energy reserves during periods of fasting or lactation. Consequently, the role of blubber and its relative thickness as an indicator of nutritional condition is followed quite closely to address the population health of marine mammals. If a marine mammal is nutritionally compromised, one would hypothesize that the blubber layer should be reduced due to consumption of the blubber as a fuel source.

Blubber is a very dynamic tissue with multiple stressors and pressures on its biology. Because it is a critical tissue for several different processes in marine mammals, it cannot be understood in a strictly thermal scenario. During a time of fasting, the animal will utilize blubber heavily, which would be incompatible to also being challenged with an increasing thermal demand. Therefore, for most marine mammals, fasting periods associated with breeding usually occur in warmer months or in warmer water.

### C. Fur

Fur functions by trapping dry air next to the skin and keeping cold water away from the skin surface. The temperature gradient is from the skin outwards, with a warm skin surface and cold outer layers of the fur (Hammel, 1955; Liwanag et al., 2012). The sea otter is faced with a major thermal challenge, because it is a small mammal (large surface area to volume ratio through which to lose

heat) and utilizes dense fur to keep its skin warm. However, the cost of this luxurious fur coat is a tremendous amount of maintenance with up to 20% of daily energy expenditure being spent on grooming the coat.

Many species of seals utilize blubber for thermal protection as adults, but most species use a specialized fur (lanugo) as newborns. Lanugo is a very effective insulator in the air as it is usually both long and very “fluffy.” It functions as protection against the cold air during the time pups are on land or ice for nursing. Lanugo does not stop water and allows the skin to “wet” to essentially water temperature when submerged. A pup must shed its lanugo and develop a significant blubber layer before it can enter the water and be an effective swimmer and diver. Not all species of seal or sea lion pups are born with lanugo, for example, harbor seals are usually born in the adult-like hair coat, but the insulator function of lanugo in air is well documented.

The high-quality fur in the sea otter and fur seals makes these mammals particularly vulnerable to oil spills. Oil permeates the fur and destroys the air pockets that provide thermal insulation. After the Exxon Valdez oil spill (EVOS) in Alaska, there was a massive clean-up operation for the hundreds of sea otters that were brought to rescue centers. The goal was to clean the fur to restore its thermal insulation properties. However, cleaning the fur of human-made oils also cleans the fur of the natural oils that help make the fur water resistant. Therefore, small amounts of lipid had to be groomed back into the fur of the otters after they were cleaned of the heavy oil.

#### D. Vascular Adaptations

Marine mammals have evolved several unusual adaptations that utilize vascular thermoregulation. The first is the *rete mirabile*, Latin for a “wonderful net.” This vascular net, which is a counter-current heat exchanger, involves an intertwined network of veins and arteries such that the cold venous blood returning from the extremities runs next to the warm arterial blood going out to extremities. Heat flows from the warm arteries to the cooler veins, consequently conserving the heat in the core and cooling the arterial blood going out to the colder regions of the body.

Marine mammals have exquisite control of blood flow for thermoregulation and also for diving. However, these two demands are themselves interrelated, and the control of one affects the other. For example, it would be detrimental for a diving seal to be closely controlling blood flow for oxygen conservation, but then to override that control to dump or gain heat. It has been demonstrated in diving seals and dolphins that they favor oxygen conservation over temperature regulation when these vascular adjustments conflict. Circulatory retes are found in several locations in marine including the flukes of whales, the flippers of pinnipeds, and even near the reproductive organs of some dolphins and seals to bring in cool blood from the extremities.

Another important vascular adjustment occurs in species that utilize thick blubber as an insulating material. Recall that thick blubber is a good mechanism for staying warm, but can cause serious problems for cooling. In fact, some whales have such a large thermal mass and a low surface area to volume ratio that they may have a much more serious problem dumping heat than conserving it (Hokkanen, 1990).

Blubber is vascularized with a series of anastomoses, or blood flow shunts, that regulate the amount of blood moving through the blubber and reaching the skin, thereby controlling the amount of heat lost to the environment (Fig. 1). If a seal needs to dump heat,



**Figure 1** Cross section through a bowhead whale (*Balaena mysticetus*) fluke showing blood vessels near the surface of the skin and blubber that can be used for thermoregulation. We thank the Barrow Whaling Captains' Association for allowing us to photograph their whales, and the Alaska North Slope Borough Department of Wildlife Management for logistical assistance (Photo by M. Castellini).

the anastomoses open and warm blood can reach the surface of the skin. When Antarctic Weddell seals (*Leptonychotes weddellii*) resting on the sea ice dump excess heat in this manner, clouds of steam come off the animal as the blood reaches the surface of their skin. In some cases, the seals get so warm that they partially melt their way into the ice and leave perfect “seal shadows.” Conversely, when these blubber circulatory shunts are closed, the same seals will be completely covered in snow with no signs of melting at any location except near the eyes and nose.

As mentioned earlier, the balance of blood flow throughout the body of marine mammals is complex and controlled by multiple demands including diving, exercise, and heat regulation. Diving requires limited blood circulation, simultaneous underwater exercise requires increased circulation, and thermoregulation can require both (Elsner, 2015). One of the central demands for diving is that oxygen must be conserved in order to extend the dive. This is done by a variety of means and one of those is to reduce the demand for oxygen by reducing metabolic rate. If a marine mammal reduces its body temperature while diving, it would decrease the demand for oxygen, thus extending dive time. There is some evidence from freely diving pinnipeds suggesting that the animals can drop their core temperatures during diving and would thus gain some diving time by reducing metabolic rate (Meir and Ponganis, 2010; Rosen et al., 2007).

#### E. Behavioral Thermoregulation

Most of the mechanisms discussed so far have been biochemical, anatomical, or physiological methods for regulating heat production or loss. But marine mammals can also alter their thermal balance with behavioral modifications. For example, sea otters will often float with all four paws out of the water. The paws are highly vascularized but not well insulated with fur and are a tremendous source of heat loss if in contact with the water. Weddell seals will move into the water if the actual or convective temperature drops below about  $-40^{\circ}\text{C}$ . Elephant seals will flip cool sand onto their backs to help keep their body temperature down on sunny days and Hawaiian monk seals (*Monachus schauinslandi*) will find shade under bushes or in small ravines out on hot, sandy atolls. These behavioral

mechanisms are not unique to marine mammals, except that these animals have the ability to use the sea to cool down as necessary (Beenijes, 2006).

## IV. Current Issues and New Research

### A. Climate Change

As concerns about climate change increase, there has been a considerable focus on what will happen with polar species of whales, seals, polar bears, penguins, etc. (Huntington and Moore, 2008). In terms of absolute thermoregulation, a several degree change in water temperature is of almost no impact to physiology or biochemistry. These animals are endothermic homeotherms and can easily regulate their body temperature to be constant over such a small environmental change. For example, a sea lion will haul out from cold water onto a hot beach, and a polar seal will come out from freezing sea water onto the relatively warm shore or sea ice. These are much larger temperature changes than those being induced by climate change.

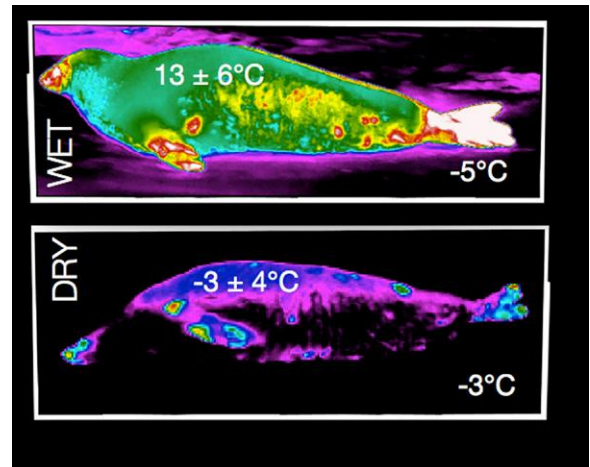
However, what does impact these species is how water and air temperature alter the sea ice platforms that they use to haul out, and how a changing climate can alter distribution of oceanic food sources. As the sea ice retreats, the animals that depend on the ice for pupping, calving, resting and hunting must retreat with it. If there is no ice for ringed seals to have their pups, then the survival of pups will decrease. If there is no ice for polar bears to hunt on, then they will need to swim great distances to find the remaining ice. Walrus are already hauling out on land because of the lack of Arctic sea ice, with subsequent increases in stampeding deaths, lack of food etc. As fish distributions change, the hunting areas for seals and whales will need to change. If the fish move to deeper water to stay in the colder ocean layers, then seals will need to dive deeper to find them, or may not be able to get to them at all if they do not have the aerobic ability to dive deep and long.

The impact of climate change is significant for marine mammals, but not because of the absolute temperature change: It is because of its impact to their ecosystem, hunting, pupping and resting demands.

### B. New Research Tools

The development of telemetric devices used to study marine mammals continues to advance at an incredible rate (see TELEMETRY). Modern instruments can measure a suite of physiological traits and also collect oceanographic data on water temperature, salinity, etc. Researchers can “see” the environment in which marine mammals are diving and swimming. Thermal balance equations can be more sophisticated as “tags” measure deep body, stomach, skin and blood temperatures along with water temperature and swimming speed. This allows calculations of heat loss (or gain), the effective “wind chill” of moving through cold water and the potential impact of changes in body temperature on diving metabolic rate. Recently developed long-lived implanted instruments can now measure the body temperature of seals over years, archive the data, and then float to the surface to transmit their data when the animal dies and decomposes (or is eaten!). This allows measurements of birth patterns, diving behavior and potential causes of death.

Improvements in whole body thermal imaging (infrared thermography), heat flow skin sensors and body morphometric modeling are being used to develop on-surface (ice, beaches, sand, etc.) models of heat exchange, evaporative heat loss and balance in the pinnipeds (Nienaber et al., 2010; Tattersall and Cadena, 2010). It is now possible to image a seal and describe regional blood flow, heat



**Figure 2** Weddell seals. Thermal whole body imaging of Weddell seals on the sea ice near McMurdo station, Antarctica. In the top figure, the animal is wet, and in the bottom figure, it is dry. The images show the greater loss of heat in the wet animal. Wet Weddell seals maintain standard internal thermal profiles, but cumulative heat loss is high due to a large temperature gradient to the environment. Surface temperatures of dry seals can even approach ambient temperatures below freezing, greatly reducing heat loss (Photo by J. Mellish. Marine Mammal Permit NMFS 15748 and Antarctic Conservation Act 2012-003).

loss areas, thermally active areas, and to estimate the metabolic costs of thermoregulation (Fig. 2).

Finally, heat flow sensors can be attached to animals that are underwater and direct measurements of heat loss can be obtained during resting, swimming and diving conditions. While related to the development of Time Depth Recorders (TDRs) and other such gear, these devices have been used by themselves in semi-controlled conditions (e.g., “swimming with dolphins”), to allow humans and animals to be together in the same region, and to develop highly specialized studies on heat flow (Noren et al., 1999).

## IV. Summary

What are the essential elements of thermoregulation in marine mammals? Like all endotherms, they must obey the physics of heat balance to hold body temperature constant. The methods for producing heat (resting metabolism and exercise) must balance the windows for heat loss. Because marine mammals do not appear to have any special adaptations for producing excess heat, most of their ability to thermoregulate comes with their ability to control heat loss. Control of heat loss mechanisms are via biochemical, anatomical, physiological, and behavioral means. However, as in all levels of adaptation to the environment, systems cannot be considered or modeled in isolation. For example, balancing blood flow for thermoregulation while also controlling blood flow for diving is an excellent example of multiple demands being put on this system.

It is easy to observe the behavioral means that marine mammals use to stay warm or to cool down: The movement up or down a beach with the tide, the use of shade, flipping of sand, swimming to warmer or colder water, exposing flippers, and so on. Behind all of these behavioral patterns are physiological or anatomical mechanisms that make the behavioral patterns effective. Counter-current heat exchangers, blood shunts through the blubber, and even the chemistry of the blubber and the microstructure of the fur are all part of the thermoregulatory system. Ultimately, we are left with

the paradox of heat balance in marine mammals: They live in a cold, thermally challenging environment that no terrestrial mammal could survive. However, the very means they have utilized to stay warm in cold seas come at a cost: For many species, they have also had to evolve the means to get rid of excess heat. The exquisite balance between all these competing demands and systems is what makes the study of thermoregulatory biology in these mammals such a rewarding experience.

### See Also the Following Articles

Blubber ■ Circulatory System ■ Energetics ■ Skin

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The structure and function of specific organs or organ systems are described in other articles of this encyclopedia. This article provides a “road map” that orients a prosector to the organs and organ systems of marine mammals. For comparative purposes, we focus on the California sea lion (*Zalophus californianus*), Florida manatee (*Trichechus manatus latirostris*), harbor seal (*Phoca vitulina*), and common bottlenose dolphin (*Tursiops truncatus*). Our descriptions are at the gross anatomical level.

Although there is no “typical” mammal, we shall use our own species and the domestic dog as the norms against which to make comparisons. To appreciate human and dog anatomy, we suggest Hollinshead and Rosse (1985) and Evans (1993), respectively. Anatomy of internal organs of domestic mammals is covered by Schummer et al. (1979). For discussions of the anatomy of various types of marine mammals, consult Fraser (1952), Green (1972), Herbert (1987), Howell (1930), King (1983), Murie (1872, 1874), Pabst et al. (1999), von Schulte (1916), Slijper (1962), and St. Pierre (1974). A useful review of thorax and abdomen anatomy is found in the section “Evolutionary biology, ecology, and behaviour,” Chapters 7 and 8, of an up-to-date textbook on marine mammals by Berta et al. (2015). Whenever possible, anatomical terms follow the Nomina Anatomica Veterinaria as illustrated by Schaller (1992).

## I. Mammalian Postcranial Landmarks

Marine mammals are generally dissected either ventrally or laterally, but some large, stranded animals must be examined in whatever position they are found. For consistency, we provide figures that describe anatomy in terms of a lateral view, and we discuss organs and organ systems in the order in which they are revealed during necropsy. Although this approach may take some getting used to if one is accustomed simply to the ventral approach, the lateral orientation approximates the living condition more closely.

### A. The Diaphragm

The diaphragm of most marine mammals is generally similar in orientation to that of the diaphragm in both the human and the dog. It lies in a transverse plane and provides a musculotendinous sheet to separate the heart and its major vessels, the lungs and their associated vessels and airways, the thyroid, thymus, and a variety of lymph nodes (all located cranial to the diaphragm) from the major organs of the digestive, excretory, and urogenital systems (all typically caudal to the diaphragm). The diaphragm is generally confluent with the transverse septum (a connective tissue separator between the heart and the liver) and, thus, attaches medially at its ventral extremity to the sternum.

Although the diaphragm separates the heart and lungs from the other organs of the body, the diaphragm is traversed by nerves and other structures such as the aorta (crossing in a dorsal and medial position), the caudal (inferior) vena cava (crossing more ventrally than the aorta, and often slightly right of the midline, although appearing to approximate the center of the liver), and the esophagus (crossing slightly right of the midline, at roughly a midhorizontal level). This approximately transverse orientation exists in most marine mammals, although the orientation of the diaphragm may be more or less diagonal, with the ventral portion being more caudal than the dorsal portion, especially so in cetaceans (Rommel and Reynolds, 2000). Contractions of the muscular diaphragm of marine mammals may help change adjacent pleural cavities, and affect buoyancy as well as roll and pitch (Rommel and Reynolds, 2000; Berta et al. 2015).

The West Indian manatee’s diaphragm differs from this general pattern of orientation and attachment. The diaphragm and the

## THORAX AND ABDOMEN, ANATOMY

JOHN E. REYNOLDS, III AND SENTIEL A. ROMMEL

The general organization of the postcranial soft tissues does not vary appreciably among mammals. Factors that may influence the relative proportions or positions of organs and organ systems include phylogeny and adaptations to a particular environment or trophic level.

transverse septum are separate, with the septum occupying approximately the “typical” position of the diaphragm and the diaphragm itself occupying a horizontal plane extending virtually the entire length of the body cavity (Fig. 1B). This apparently unique orientation contributes to buoyancy control (Domning, 2000; Rommel and Reynolds, 2000). Additionally, there are two separate hemidiaphragms in the manatee (Fig. 2B and C). The central tendons attach firmly to the ventral aspects of the thoracic vertebrae, producing two isolated pleural cavities. The position of the manatee diaphragm stands in contrast with the curved, oblique diaphragm (DIA, Fig. 3) of the sea lion, seal, and dolphin.

## B. Regions and Structures Cranial to the Diaphragm

The region cranial to the diaphragm is typically compartmentalized into three sections (1) the pericardium (containing the heart), (2) the pleural cavities (containing the lungs), and (3) the mediastinum (Figs 3 and 4).

The pericardium is a fluid-filled sac surrounding the heart (HAR, Fig. 3); in manatees, it often contains more fluid than is found in the pericardium of the typical mammal or in those of other marine mammals. The heart occupies a ventral position in the thorax (immediately dorsal to the sternum), making it easy to see when the overlying muscles, ribs, and sternum are separated. The heart lies immediately cranial to the central portion of the diaphragm (or just the transverse septum in the manatee). Some lungs may embrace the caudal aspect of the heart, separating the heart from the diaphragm. As do the hearts of all other mammals, marine mammal hearts have four chambers, separate routes for pulmonary and systemic circulation, and the usual arrangements of great vessels (vena cavae, aorta, coronary arteries, and pulmonary vessels). Cardiac fat is commonly found in manatees but is typically absent in pinnipeds and cetaceans.

The pleural cavities and lungs of mammals are generally found dorsally and laterally to the heart and are separated along the midline by the heart and mediastinum (discussed later). In the manatee, the lungs are unusual in that they extend virtually the length of the body cavity and remain dorsal to the heart (Rommel and Reynolds, 2000). Lungs of some marine mammals (cetaceans and sirenians) often lack lobes. The size of the lungs of marine mammals varies according to each species’ diving proficiency. Marine mammals that make deep and prolonged dives (e.g., elephant seals, *Mirounga* spp.) tend to have smaller lungs than expected (based on allometric relationships) whereas shallow divers (e.g., sea otters, *Enhydra lutris*) tend to have larger than expected lungs.

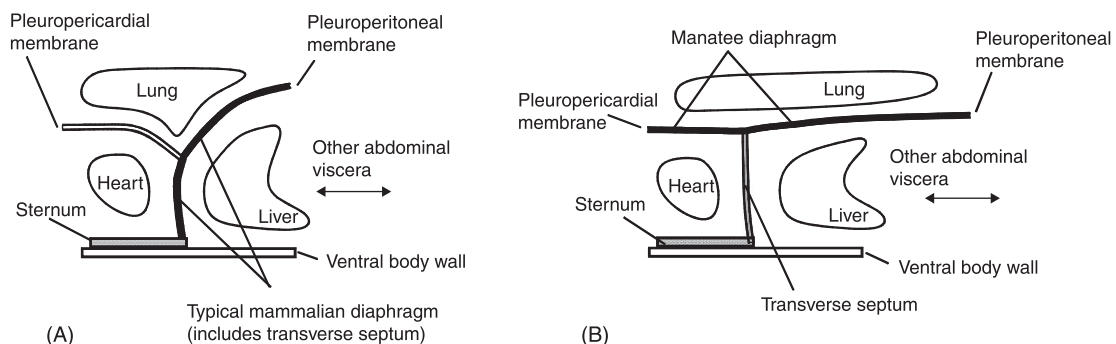
The mediastinum is typically considered to be the area between the lungs, excluding the heart and pericardium. The mediastinum contains the major vessels leading to and emanating from the heart, nerves (e.g., the phrenic nerve to the diaphragm), and lymph nodes. The thymus, which is larger in younger individuals, is found on the cranial aspect of the pericardium (sometimes extending caudally to embrace almost the entire heart) and may extend into the neck in some species. The thyroid gland is located in the cranial part of the mediastinum along either side of the distal part of the trachea, cranial to its bifurcation into the bronchi (in sea lions, but not in other marine mammals, the bifurcation is cranial to the thoracic inlet). In most marine mammals, the mediastinum is generally not remarkable; in the manatee, however, the unusual placement of the lungs and the unique diaphragm change how one must define the mediastinum (Rommel and Reynolds, 2000).

One additional structure, located on the cranial aspect of the diaphragm in seals, sea lions, and the walrus, is an atypical mammalian muscular feature associated with the heart. This is the caval sphincter (CAS, Fig. 3), which can regulate the flow of oxygenated blood in the large hepatic sinus to the heart during dives (Elsner, 1969). Cetaceans do not have a CAS.

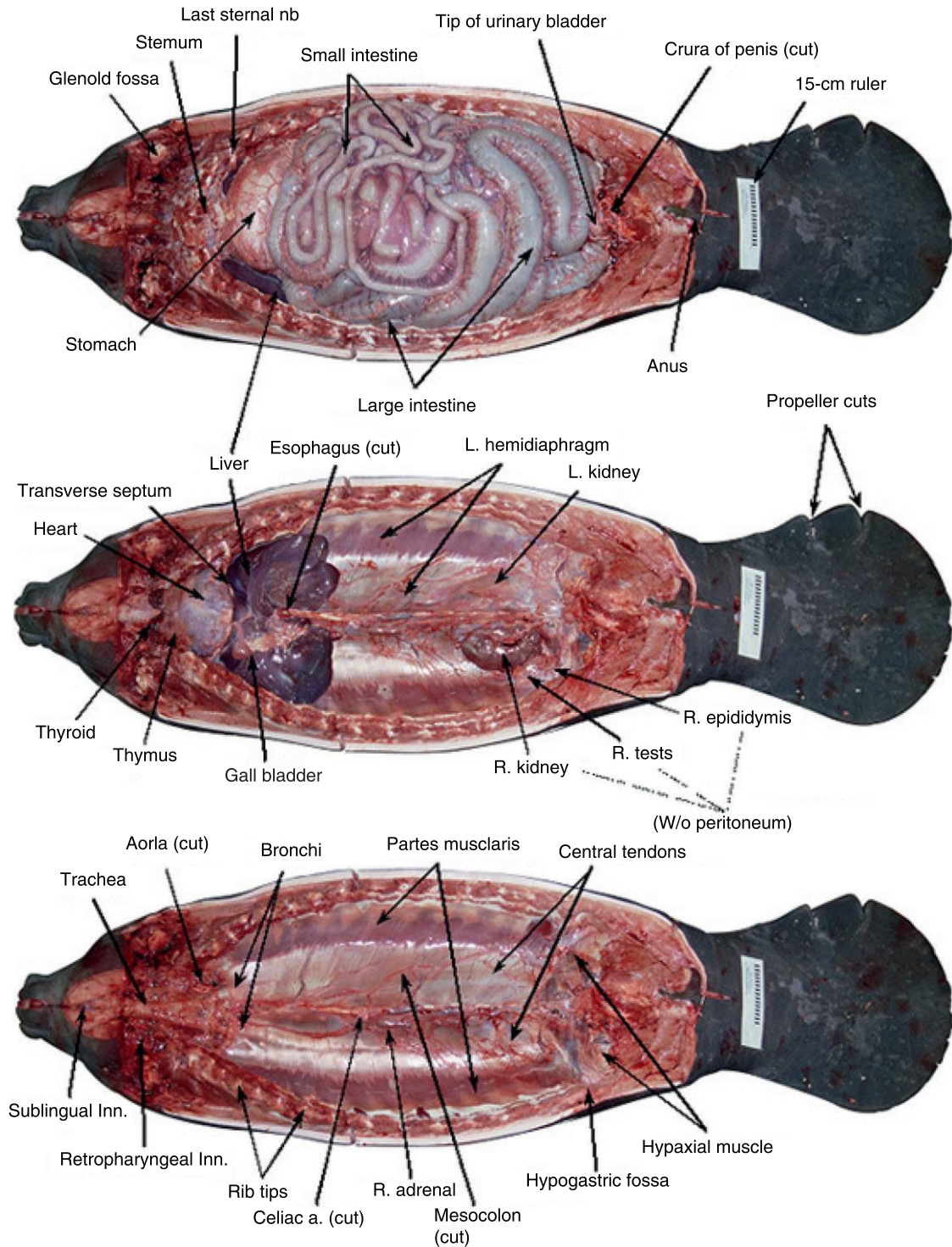
## C. Structures Caudal to the Diaphragm

Easy to find landmarks caudal to the diaphragm include a massive liver and the various components of the gastrointestinal (GI) tract. The urogenital organs are generally found only after removal of the GI tract (note that the exception is the uterus of the pregnant female).

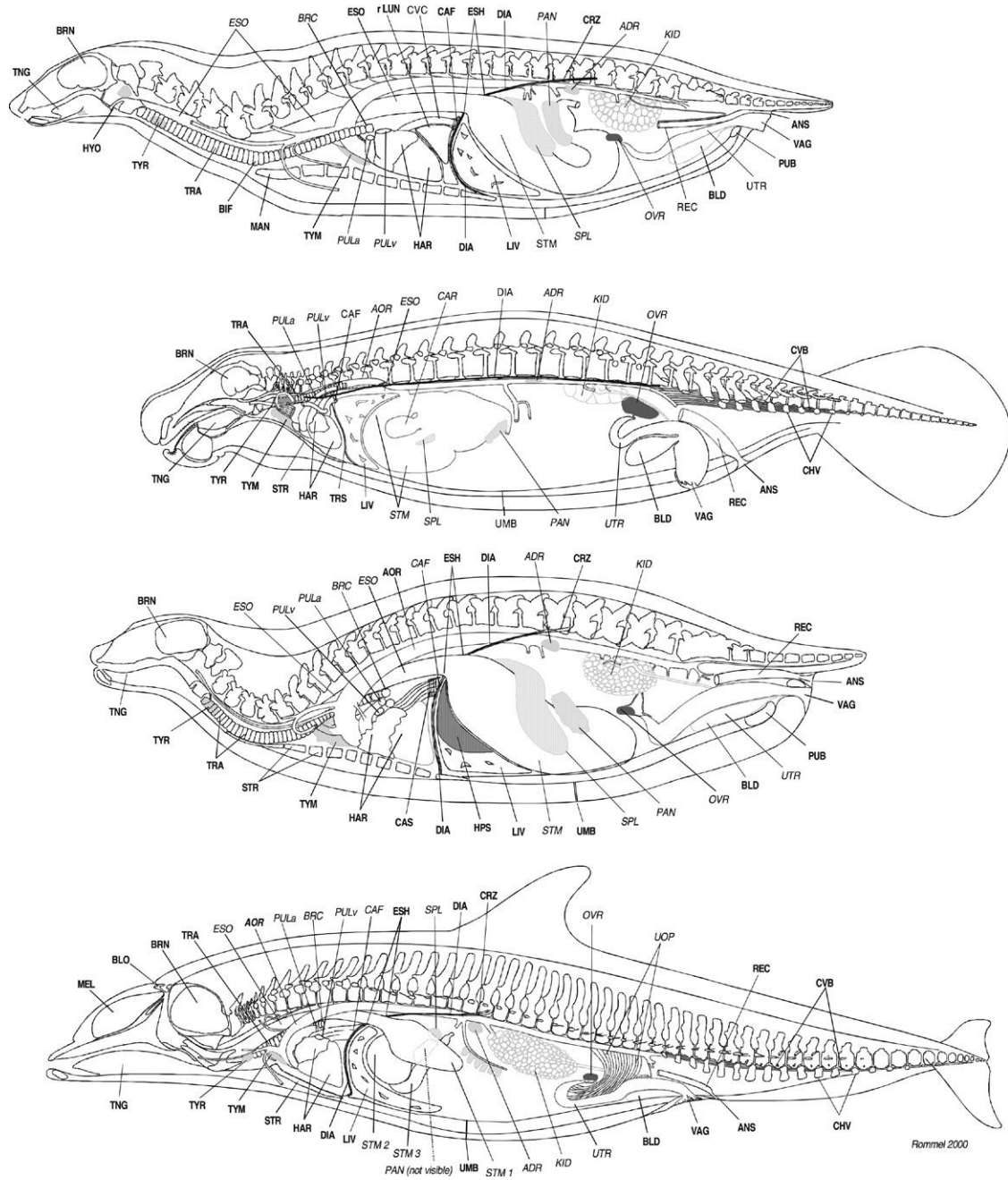
1. *The Liver.* Typically, the liver is located immediately caudal to the diaphragm. It is a large, brownish, multilobed organ positioned so that most of its volume/mass is to the right of the midline of the body. Although marine mammal livers are generally similar to the livers of other mammals, in manatees, the organ is displaced somewhat to the left and dorsal relative to its location in most other mammals. The size, color, and “sharpness” of the liver margins can be used to assess the nutritive state and health of individual animals. Bile is stored in a gallbladder (often greenish in color) in pinnipeds, located ventrally between the lobes of the liver, but cetaceans lack a gallbladder. Bile enters the duodenum to facilitate the chemical digestion of fats.
2. *The GI Tract.* Most of the volume of the cavity caudal to the diaphragm (the abdominal cavity) is occupied by the various



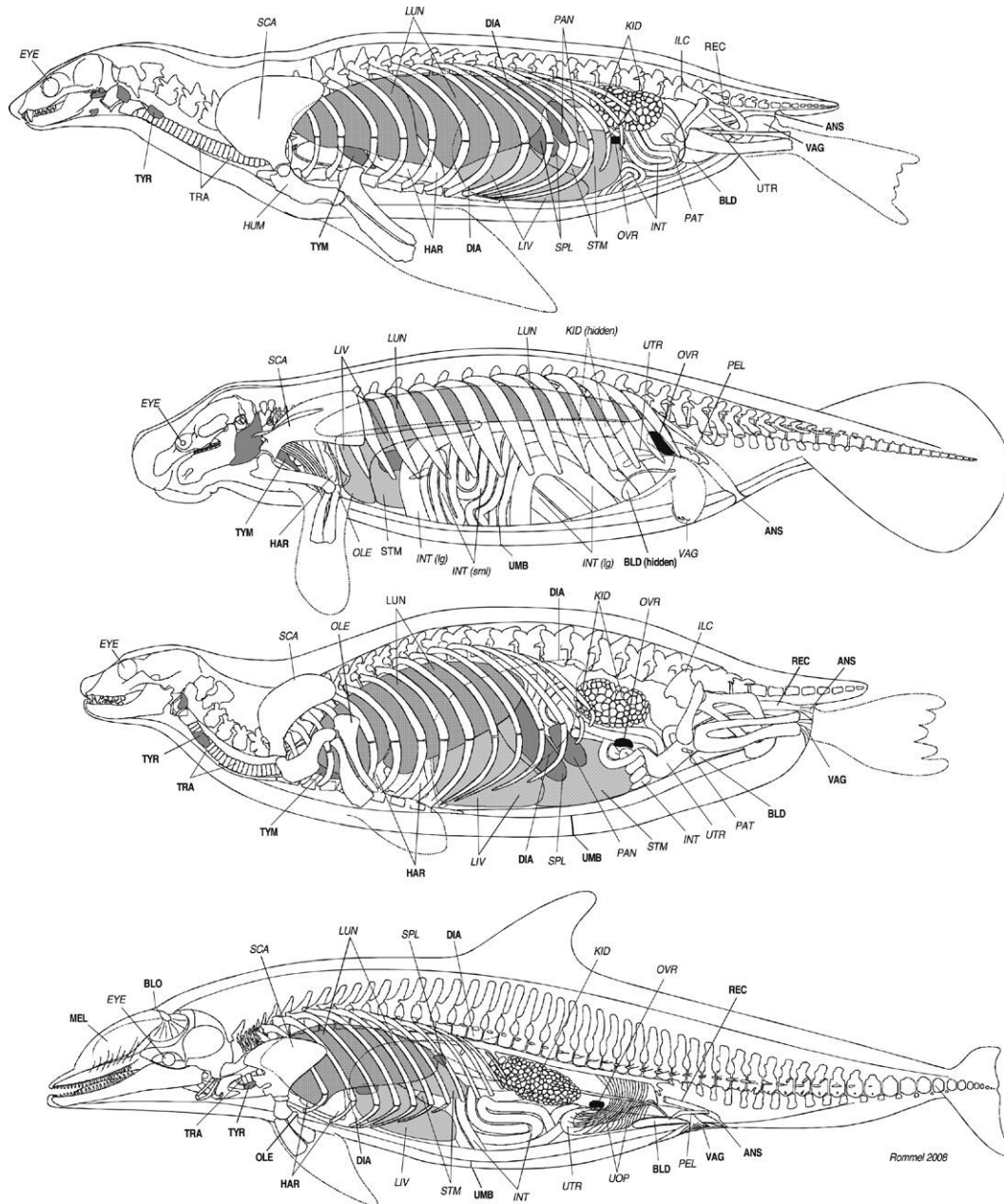
**Figure 1** Schematic arrangements of mammalian diaphragms (modified after Rommel and Reynolds, 2000). (A) The typical mammalian diaphragm extends ventrally from the dorsal midline to attach to the sternum. The typical diaphragm is a separator between the heart and lungs in the front and the liver and other abdominal organs in the back. (B) The manatee diaphragm extends dorsal to the heart and does not touch the sternum. There is a mechanical barrier between the heart and the liver and other abdominal organs but it is a relatively weak barrier called the transverse septum.



**Figure 2** Photographs of ventral views of the Florida manatee (modified after Rommel and Reynolds, 2000). The ruler is 15-cm long. (A) After removal of the ventral skin, fat, and musculature, the small and large intestines are exposed; the large intestine (with contents) may account for 10% of the total body weight and can measure 20-m long. Portions of the stomach and ventral margins of the liver are visible caudal to the sternum. (B) Removal of the sternum and GI tract reveals the heart, transverse septum, liver, hemidiaphragms, and right kidney (the left kidney was removed to expose that portion of the hemidiaphragm). (C) The two central tendons of the hemidiaphragms attach medially to the ventral aspects of the vertebral column. The diaphragm muscles attach laterally to the ribs. The lungs are flattened, elongate structures dorsal to the hemidiaphragms; when fully inflated, the lungs extend almost the entire length of the region dorsal to the hemidiaphragms. Note the junctions of the central tendon and the pars muscularis of each hemidiaphragm; this approximates the lateral margin of each lung.



**Figure 3** Left lateral illustrations of the superficial internal structures and “anatomical landmarks” of the California sea lion (*Zalophus californianus*), Florida manatee (*Trichechus manatus latirostris*), harbor seal (*Phoca vitulina*), and bottlenose dolphin (*Tursiops truncatus*) with the skeleton (minus the distal appendicular elements) superimposed for reference. Our view is a left lateral view, focused on relatively superficial internal structures (labeled in bold) visible from that perspective; the other important bony or soft “landmarks” are not necessarily visible from a left lateral view but they are useful for orientation and are labeled in *italics*. Skeletal elements are included for reference, but not all are labeled—for these details, consult the figures in the skeleton postcranial and skull chapters. Each drawing is scaled so that there are equivalent distances between the shoulder and the hip; thus, the thoracic and abdominal cavities are roughly equal in length. The shoulder joints are aligned. The left kidney (not visible from this view in the manatee) is illustrated. The relative sizes of the lungs represent partial inflation—full inflation would extend margins to distal tips of ribs (except in the manatee). The following abbreviations are used as labels (structures on the midline are in bold, those off-midline are in *italics*): ANS, anus; BLD, urinary bladder; BLO, blowhole of dolphin; DIA, diaphragm, midline extent (except manatee); EYE-eye (note small size in manatee); HAR, heart; ILC, iliac crest of the pelvis; INT, intestines; note the large diameter of the large intestines in the manatee; KID, left kidney (not visible from this vantage in the manatee); LIV, liver; LUN, lung (note that in this illustration, the lung extends under the scapula except in the seal); MEL, melon, dolphin only; OLE, olecranon of ulna; OVR, left ovary; PAN, pancreas (in this view visible only in seal and sea lion); PAT, patella; PEL, pelvic vestige; REC, rectum; SCA, scapula; SPL, spleen; STM, stomach; TRA, trachea (not visible in this view of the manatee); TYM, thymus gland; TYR, thyroid gland; UMB, umbilical scar; UOP, uterovarian plexus in dolphins; UTR, uterine horn; VAG, vagina. © S.A. Rommel.



**Figure 4** A view slightly to the left of the midsagittal plane illustrates the circulation, body cavities, and selected organs of the California sea lion (*Zalophus californianus*), Florida manatee (*Trichechus manatus latirostris*), harbor seal (*Phoca vitulina*), and bottlenose dolphin (*Tursiops truncatus*), with the skeleton for reference. The left lung is removed. Note that the diaphragm separates the heart and lungs from the liver and other abdominal organs. Each drawing is scaled so that there are equivalent distances between the shoulder and the hip; thus, the thoracic and abdominal cavities are roughly equal in length. The shoulder joints are aligned. Note that the manatee's diaphragm is unique and that the distribution of organs and the separation of thoracic structures from abdominal structures require special consideration in manatees. The following abbreviations are used as labels (structures on the midline are in bold, those off-midline are in *italics*): ADR, adrenal gland; ANS, anus; AOR, aorta; BLD, urinary bladder; BLO, blowhole; BRC, bronchus; BRN, brain; CAF, caval foramen; CAR, cardiac gland, in manatee only; CAS, caval sphincter, surrounding the vena cava in the seal and sea lion; CHV, chevron bones; CRZ, crus (plural crura) of the diaphragm; CVB, caudal vascular bundle, in manatee and dolphin; DIA, diaphragm, cut at midline, extends from crura dorsally to sternum ventrally (except in manatees); ESH, esophageal hiatus; ESO, esophagus (to the left of the midline cranially, on the midline caudally); HAR, heart; HPS, hepatic sinus within liver, in seals only; KID, right kidney; LIV, liver, cut at midline; LUN, lung, right lung between heart and diaphragm; MEL, melon, dolphin only; PAN, pancreas; PUB, pubic symphysis (seals and sea lions only); PULA, pulmonary artery, cut at hilus of lung; PULv, pulmonary vein, cut at hilus of lung; REC, rectum, straight part of terminal colon; SPL, spleen; STM1, fore stomach; STM2, main stomach (STM in noncetaceans); STM3, pyloric stomach; STR, sternum, sternabrae; TNG, tongue; TRA, trachea; TRS, transverse septum; TYM, thymus gland; TYR, thyroid. © S.A. Rommel.



components of the GI tract: The stomach, the small intestine (duodenum, jejunum, and ileum), and the large intestine (cecum, colon, and rectum). The proportions and functions of these components reflect the feeding habits and trophic levels of the different marine mammals. Therefore, the gastrointestinal tracts of marine mammals vary considerably.

Food and water travel from the mouth, through a muscular pharynx, and into the esophagus. As noted earlier, the latter pierces the diaphragm to join the stomach, which is typically a single, distensible sac. The distal end of the stomach (the pylorus) is marked by a strong sphincter before it connects with the small intestine (duodenal ampulla in cetaceans). The separation between jejunum and ileum of the small intestine is difficult to distinguish grossly, although the two sections are different microscopically. The junction of the small and large intestines is often (but not in cetaceans) marked by the presence of a cecum (homologous to the human appendix). In manatees, the midgut cecum has two blind pouches called cecal horns. In some marine mammals, the large intestine, as its name implies, has a larger diameter than the small intestine.

The gastrointestinal tracts of pinnipeds and other marine mammal carnivores follow the general patterns outlined earlier, although the intestines can be remarkably long in some species. Cetaceans, however, have some unique specializations (Gaskin, 1978). Cetaceans can have two or three stomachs (usually three) depending on the species being examined. The multiple stomachs of cetaceans function in much the same way as the single stomach found in most other mammals. The first stomach of cetaceans, called the forestomach (essentially an enlargement of the esophagus), is muscular and very distensible, and it acts much like a bird crop, i.e., as a receiving chamber. The second or glandular stomach is the primary site of chemical breakdown among the stomach compartments; it contains the same types of enzymes and hydrochloric acid that characterize a “typical” stomach. Finally, the “U-shaped” third or pyloric stomach ends in a strong sphincteric muscle that regulates the flow of digesta into the duodenum (the duodenal ampulla is sometimes mistakenly called a fourth stomach) of the small intestine. The cetacean duodenum is expanded into a sac-like ampulla. The only other remarkable feature at the gross level is the lack of a cecum, which makes it difficult to tell where the small intestine ends and the large intestine begins. The intestines of some cetaceans may be extremely long (especially in the sperm whale, *Physeter macrocephalus*; Slijper, 1962), but they are not especially long in many other marine mammal species.

Among marine mammals, sirenians have the most remarkably developed gastrointestinal tract. Sirenians are herbivores and hindgut digesters (similar to horses and elephants) so the large intestine (specifically the colon) is extremely enlarged, enabling it to act as a fermentation vat (see Marsh et al., 1977; Reynolds and Rommel, 1996). In horses, the cecum is the region of the large intestine that is enlarged, but in sirenians, the cecum is relatively small and has two “horns.” The sirenian stomach is single chambered and has a prominent accessory secretory gland (the cardiac gland) extending from the greater curvature. The duodenum is capacious and has two obvious diverticulae projecting from it. The GI tract and its contents can account for more than 20% of a manatee’s weight.

The length and mass of the gastrointestinal tract are impressive and create three-dimensional relationships that can be complex. Simplifying the organization is the fact that tough sheets of

connective tissue called mesenteries suspend the organs from the dorsal part of the abdominal cavity and shorter bands of connective tissue (ligaments) hold organs close to one another in predictable arrangements (e.g., the proximal spleen is always found along the greater curvature of the stomach and is connected to the stomach by the gastrosplenic, or gastrosplenic ligament). Also suspended in the mesenteries are numerous lymph nodes and fat.

Accessory organs of digestion include salivary glands (small in most marine mammals but very large in the manatee), pancreas, and liver (where bile is produced and then stored in the gall bladder). The pancreas is sometimes a little difficult to locate because it can be a rather diffuse organ and it decomposes rapidly postmortem; however, a clue to its location is its proximity to the initial part of the duodenum, into which pancreatic enzymes flow. Another organ that is structurally, but not functionally associated with the GI tract is the spleen, which is suspended by a ligament, generally from the greater curvature of the stomach (the first stomach in cetaceans) on the left side of the body. The spleen may be a single organ accompanied by accessory spleens in some species. The spleen is bluish in color and varies considerably in size among species; in manatees and cetaceans it is relatively small but is more massive in some deep-diving pinnipeds (Zapol et al., 1979) in which it acts as a storage region for red blood cells.

3. *Urogenital Anatomy.* The kidneys lie in a retroperitoneal position, typically against the musculature of the back (epaxial muscles) at or near the dorsal midline attachment of the diaphragm (crura). In the manatee, the unusual placement of the diaphragm means that the kidneys lie against the diaphragm, but not against the epaxial muscles. All mammals have metanephric kidneys (i.e., containing cortex, medulla, and calyces). In many marine mammals, the kidneys are specialized as reniculate (multilobed) kidneys, where each lobe (renule) has all the components of a complete metanephric kidney. Why marine mammals have reniculate kidneys is uncertain, but the fact that some large terrestrial mammals also have reniculate kidneys has led to speculation that they are an adaptation associated simply with large body size (Vardy and Bryden, 1981).

The renal arteries of cetaceans enter the cranial poles of the kidneys, whereas in other marine mammals, they enter the hilus (typical of most mammals). Additionally, in manatees, there are accessory arteries on the surface of the kidney. The kidneys are drained by separate ureters, which carry urine to a medially and relatively ventrally positioned urinary bladder. The urinary bladder lies on the floor of the caudal abdominal cavity and, when distended, may extend as far forward as the umbilicus in some species. The pelvic landmarks are less prominent in fully aquatic mammals. In the manatee, the bladder can be obscured by abdominal fat.

Pabst et al. (1999) noted that the reproductive organs tend to reflect phylogeny more than adaptations to a particular niche. If one were to examine the ventral side of cetaceans and sirenians before removing the skin and other layers, one would discover that positions of male and female genital openings are different, permitting rather easy determination of sex in some species without dissection. In all marine mammals, the female urogenital opening is more caudal than the opening for the penis in males. One way to approach dissection of the reproductive tracts is to follow structures into the abdomen from their external openings.

The position and general form of the female reproductive tract in marine mammals are generally similar to those of the female

reproductive tracts in terrestrial mammals. In at least many cetaceans, the vagina has one to several muscular folds of indeterminate utility, recently described in detail especially for common bottlenose dolphins (Orbach et al., 2016). The vagina opens cranial to the anus and leads to the uterus, which is bicornuate in marine mammal species. The body of the uterus is found on the midline and is located dorsally to the urinary bladder (the ventral aspect of the uterus rests against the bladder). Although the body of the uterus lies along the midline, it has bilaterally paired, relatively large diameter projections called uterine horns (cornua), which extend laterally. The relatively small-diameter oviducts conduct eggs from the ovaries to the uterine horns where implantation of the fertilized egg and subsequent placental development occur. The dimensions of the uterine horns vary with reproductive history and age. Often the fetus may expand the pregnant horn to the point that it fills a substantial portion of the abdominal cavity. The horns terminate abruptly, narrowing and extending as uterine tubes (fallopian tubes) to paired ovaries. The uterus and the uterine horns are held in place in the abdominal cavity by the broad ligaments. Uterine and ovarian scarring may provide information about the reproductive history of the individual.

The ovaries of mature females may have one or more white or yellow-brown scars, called corpora albicantia and corpora lutea, respectively. Although ovaries are usually solid organs, in sirenians they are relatively diffuse.

Mammary glands are ventral, medial, and relatively caudal in most marine mammals, but they are axillary in sirenians. Many marine mammals have a single pair of nipples; sea lions and polar bears, *Ursus maritimus*, (DeMaster and Stirling, 1981), have two pairs of nipples, and cetaceans have mammary slits (but some male cetaceans also have distinct mammary slits).

The male reproductive tracts of marine mammals have the same fundamental components as the tracts in “typical” mammals, but positional relationships are significantly different. This difference is due to the testicond (ascrotal) position of the testes in most marine mammal species. Sea otters are scrotal (J. Bodkin, personal communication); polar bears are seasonally scrotal (I. Stirling, personal communication); and sea lion testes become scrotal when temperatures are elevated. The testes of some marine mammals are intraabdominal, but in phocids, for example, they lie outside the abdomen, partially covered by the oblique muscles and blubber. The position of marine mammal testes creates certain thermal problems because spermatozoa do not survive well at body (core) temperatures; in some species, these problems are solved by the circulatory adaptations mentioned later.

The penis of marine mammals is retractable and it normally lies within the body wall. The general structure of the penis relates to phylogeny (Pabst et al., 2015). Overall, it is hardened by musculature in the cetaceans and sirenians, evolved from proto-ungulates, and by a combination of muscles and an os penis (bone) in marine carnivores.

4. **Adrenal Glands.** The term “suprarenal gland” is often used interchangeably with “adrenal gland.” Although the suprarenals often lie immediately atop or very close to the kidneys of terrestrial mammals, adrenals of marine mammals may lie several centimeters cranial to the kidneys, along either side of the median. Adrenal glands can be confused with lymph nodes, but if one slices the organ in half, an adrenal gland is easy to distinguish grossly by its distinct cortex and medulla.
5. **Circulatory Structures.** Blood vessels are often named for the regions they feed or drain. Thus, the fully aquatic marine

mammals (cetaceans and sirenians) lack femoral arteries that supply the pelvic appendage. However, most organs in marine mammals are similar to those of terrestrial mammals so their blood supply is also similar. Therefore, readers who want to learn details of typical circulatory anatomy should consult one of the anatomy references cited earlier. The thoracic aorta leaves the heart and lies ventral to the vertebral column, giving off segmental arteries to the vertebrae and epaxial muscles (and in the case of cetaceans and manatees to the thoracic retia). The aorta continues through the aortic hiatus of the diaphragm (between the crura) and into the abdomen as the abdominal aorta and lumbar aorta, which give off several paired (e.g., renal and gonadal) and unpaired (e.g., celiac and mesenteric) arteries. The caudal aorta follows the ventral aspect of the tail vertebrae. In the permanently aquatic marine mammals, there are robust ventral chevron bones that form a canal in which the caudal aorta, its branches, and some veins are protected.

Some of the diving mammals (e.g., seals, cetaceans, and sirenians) have few or no valves in the veins (Rommel et al., 1995); this adaptation simplifies blood collection. Other exceptions to the general pattern of mammalian circulation are associated with thermoregulation and diving. Countercurrent heat exchangers abound, and extensive arteriovenous anastomoses exist to permit two general objectives to be fulfilled (1) regulating loss of heat to the external environment, while keeping core temperatures high and (2) permitting cool blood to reach specific organs (e.g., testes, uteri, and spinal cord) that cannot sustain exposure to high body temperatures (see reviews by Rommel et al., 1998; Pabst et al., 1999).

In mammals, several paths for supplying blood to the brain exist: via the internal carotid, the external carotid, and the vertebral/basilar arteries. Some species use only one, others use two, and manatees use all three pathways. In cetaceans, the path for supplying blood to the brain is unique. The blood destined for the brain first enters the thoracic rete, a plexus of convoluted, small-diameter arteries in the dorsal thorax. Blood leaves the thoracic rete and enters the spinal rete where it surrounds the spinal cord and enters the base of the skull (McFarland et al., 1979). There are two working explanations for this convoluted path of blood to the brain: (1) the elasticity of the retial system allows mechanical damping of the blood pulse pressure wave (McFarland et al., 1979) and (2) the juxtaposition of the thoracic retia to the dorsal aspect of the lungs may provide thermal control of the blood entering the spinal retia. Combined with cooled blood in the epidural veins, the spinal retia may provide some temperature control of the central nervous system.

## II. Overview

Marine mammal postcranial soft tissue anatomy is, in many regards, similar to that of “typical” mammals. However, the relative proportions of and, to some extent, the positions of organs may be somewhat different from the norm.

We close with a reminder about orientation: Namely the orientation of the prosector relative to the orientation of the specimen and the orientation of the specimen to the orientation of that animal when it was alive. The position of animals during necropsy may be belly-up, obviously not the usual position of the living animals. Thus, gravitational forces make the positional relationships we may observe during necropsy somewhat artificial; we assess “dead anatomy” rather than “living anatomy.” We suggest that people examining marine mammal postcranial anatomy bear this fact in mind and try to constantly picture how the structures being observed during

necropsy might be arranged in a free-ranging animal. The more the latter perspective can be maintained, the easier it will be to envision dynamic relationships among organs and systems and to relate function (physiology) to structure (anatomy).

### See Also the Following Articles

Forelimb Anatomy ■ Gastrointestinal Tract ■ Hind Limb Anatomy ■ Musculature ■ Reproductive Anatomy ■ Skeleton ■ Skull

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## TOOL USE

JANET MANN AND ERIC PATTERSON

Tool use can be defined as “the *conditional* external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool” (Mann and Patterson, 2013). The use of the word “conditional” is critically important, especially in marine environments, because many marine animals perpetually wear or hold objects regardless of context and thus do not appear to use the object “purposively.” Once considered the defining feature of hominids, tool use is rare in wild animals and even more so in marine fauna (Mann and Patterson, 2013). Here we review the known cases of tool-use and tool-use like behavior in wild marine mammals, with particular focus on one of the best-studied cases, sponge tool use by wild Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia.

### I. Explaining the Rarity

It would be hard to argue that natural selection favored tool use in marine mammals. Neither their physiology (streamlined body, limited appendages), nor their environment (vast, open, and mostly devoid of objects) are conducive to tool use (Mann and Patterson, 2013). When marine mammals do use tools, most tools originate from the substrate (Table 1). In fact, terrestrial living, compared to arboreal living, may have driven primate tool use due to the larger number of substrates and objects, and opportunities for tool reuse, combining tools, and cumulative technology (Meulman and Sanz, 2012). Despite the rarity of tool use in the ocean, under specific ecological conditions, tool use might still be adaptive for marine mammals, but only a few species have physical adaptations that facilitate tool use. For example, sea otters (*Enhydra lutris*) have retractile claws on their forelimbs and object-carrying pouches.

## II. Examples of Marine Mammal Tool Use

*Sea otters.* Like terrestrial animals, marine mammals mostly use tools to forage (Table 1). Perhaps the most accomplished tool-users among marine mammals are sea otters. Most commonly, sea otters bring rocks, large shells or other objects (e.g., anthropogenic litter) to the surface to be used as hammers and/or anvils to smash open prey. Occasionally otters wrap crabs in kelp to immobilize them while consuming other captured prey, or use rocks or large shells to pry or hammer abalone from the substrate (Riedman and Estes, 1990; Fujii et al., 2015). Key features of sea otter tool use are its variation within and across populations, its vertical transmission, and that it involves learning. For example, across eight populations, the prevalence of tool use ranges from less than 1% of foraging dives in the Aleutian Islands to about 17% in Monterey Bay (Fujii et al., 2015). Similarly, while the majority of otters in Monterey use tools (65.8%–92.8%), only 10%–20.5% do so in the Aleutian Islands (Fujii et al., 2015). These differences can be largely attributed to prey type: Prey with thick, calcium carbonate shells are disproportionately associated with tool use (Fujii et al., 2015). Although ecological factors are clearly evident, social learning and vertical transmission of tool type and technique are also well documented (Estes et al., 2003).

*Killer whales and Irrawaddy dolphins.* Both killer whales (*Orcinus orca*) and Irrawaddy dolphins (*Orcaella brevirostris*) use water as a tool during hunting. Killer whales near Antarctica create pressure waves, singly or in groups, to wash seals off ice floes (Pitman and Durban, 2012). This behavior is clearly planned with whales spy hopping to locate preferred prey, sometimes recruiting additional whales when necessary, and using different techniques depending on floe size and prey species. Irrawaddy dolphins spit water jets at fish, presumably to assist in fish capture as the behavior is seen in foraging contexts (Stacey and Hvenegaard, 2002). This behavior is reminiscent of the better-known archer fish water-spitting, which has long been considered tool use (Mann and Patterson, 2013).

However, in some cases it is difficult to consider the water itself as a tool. For example, in killer whale wave-washing, the wave is difficult to distinguish from the greater water medium. In archer fish and Irrawaddy dolphins, the water jets often fully detach from the surrounding medium, but since both species also spit jets underwater, considering archer fish's and Irrawaddy dolphins' behavior tool use and killer whales' not, seems dubious.

*Humpback whales and common bottlenose dolphins.* Bubblenet feeding, characteristic of several populations of humpback whales (*Megaptera novaeangliae*), is another behavior that may be considered tool use. When bubblenet feeding, whales singly or collectively expel bubbles to create nets that encircle, contain, and concentrate schooling prey (Wiley et al., 2011). In what appears to be a somewhat convergent behavior, common bottlenose dolphins (*Tursiops truncatus*) in Florida also employ a netting technique to forage, but this time using mud. In the cooperative case, a single dolphin encircles prey with a mud-plume by beating its tail flukes on the substrate, causing fish to jump into the mouths of one or more waiting dolphins (Torres and Read, 2009). Singly, dolphins have been observed generating arched mud-plumes to aid in prey capture (Lewis and Schroeder, 2003).

*Unclear cases.* While the function of the above behaviors is fairly clear, there are several examples of purported tool use where the function is less obvious. For example, Amazon river dolphins (*Inia geoffrensis*) occasionally carry sticks, rocks, lumps of clay, and/or shells, perhaps as a form of socio-sexual display (Martin et al., 2008), and humpback dolphins (*Sousa* spp.) have been observed throwing shells during play (Saayman and Tayler, 1979) and carrying a sponge (Parra, 2007). Young Indian Ocean bottlenose dolphins in Shark Bay occasionally carry and/or play with seagrass, perhaps as a form of "practice foraging" (Mann and Patterson, 2013). Shark Bay dolphins have also been observed "shelling" (surfacing with trumpet (*Syrinx aruanus*) or bailer (*Melo amphora*) shells on their beaks, at least some of which contain fish prey), but

TABLE 1 Tool Use by Marine Mammals

Taxa	Common name	Behavior	Function
<i>Enhydra lutris</i>	Sea otter	Immobilize prey with kelp	Foraging
<i>Enhydra lutris</i>	Sea otter	Extract prey using objects as Hammers & Anvils	Foraging
<i>Enhydra lutris</i>	Sea otter	Pry and Hammer prey to detach them	Foraging
<i>Enhydra lutris</i>	Sea otter	Use kelp to maintain buoyancy and location	Other
<i>Inia geoffrensis</i>	Amazon river dolphin	Carry and hold objects	Unclear <sup>a</sup>
<i>Megaptera novaeangliae</i>	Humpback Whale	Encircle prey with bubble nets	Foraging
<i>Orcinus orca</i>	Killer Whale	Wash prey off ice floes with waves	Foraging
<i>Orcaella brevirostris</i>	Irrawaddy dolphin	Squirt water jets during foraging	Unclear <sup>a</sup>
<i>Sousa chinensis</i>	Indo-Pacific humpback dolphin	Throw sea shells during social play	Unclear <sup>a</sup>
<i>Sousa sahalensis</i> <sup>b</sup>	Indo-Pacific humpback dolphin	Carry marine sponge	Unclear <sup>a</sup>
<i>Tursiops aduncus</i>	Indo-Pacific bottlenose dolphin	Wear sponges for protection during foraging	Foraging
<i>Tursiops aduncus</i>	Indo-Pacific bottlenose dolphin	Play with seagrass, possibly as practice foraging	Unclear <sup>a</sup>
<i>Tursiops truncatus</i>	Common Bottlenose Dolphin	Encircle prey with mud plumes	Foraging

<sup>a</sup>Several of these examples may or may not constitute tool use, depending on one's definition. For example, those in which the function is unclear might not be considered tool use by some and in the case of killer whales, it is difficult to differentiate the wave "tool" from the environmental medium. Table adapted from Mann J. and Patterson E.M. 2013. Tool use by aquatic animals. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 368: 20120424.

<sup>b</sup>Taxonomy revised from Parra, G.J. 2007 Observations of an Indo-Pacific humpback dolphin carrying a sponge: object play or tool use? *Mammalia* 71, 147–149 based on Jefferson, T.A. and Rosenbaum, H.C. 2014. Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. *Mar. Mammal Sci.* 30, 1494–1541 (Jefferson and Rosenbaum, 2014).



**Figure 1** A dolphin with a basket sponge.

considerable ambiguity remains regarding this behavior (Patterson and Mann, 2015).

**Sponge tool use.** One of the best-studied cases of tool use among marine mammals is sponge tool use by Shark Bay bottlenose dolphins. In 1984, Rachel Smolker observed a dolphin named “Halfluke” with a marine sponge on her rostrum (Smolker et al., 1997). Within the year, four other adult females were seen carrying sponges (referred to as “spongers”), and did so until their deaths 13–34 years later (one female is still alive and sponging). The original sponge tools were identified as *Echinodictyum mesenterinum*, (Smolker et al., 1997), but since then, at least 4 other sponge tool species (*Ircinia* sp., *Pseudoceratina* sp., and 2 undetermined sponge species) have been documented (Patterson et al., 2015). During sponging, a dolphin removes a basket sponge from the seafloor, places it on its beak (Fig. 1), and uses it to scour the cluttered substrate in 7–13 m deep channels (Mann and Patterson, 2013). When a sponger locates prey (presumably disturbed from the seafloor), it drops the sponge, grabs the prey, swallows it, and retrieves the sponge to be reused, typically for about an hour. However, sponge use duration, as well as other aspects of tool-use efficiency, increases with age, peaking when females are most likely to have a dependent offspring, and thus would benefit from increased foraging efficiency (Patterson et al., 2015).

In 1989, Halfluke’s 2-year-old daughter Demi was observed carrying a sponge (Smolker et al., 1997), suggesting that the behavior was vertically transmitted, which was later confirmed through long-term behavioral observation and genetics (Mann and Patterson, 2013; Patterson and Mann, 2015). Since 1984, over 50 regular spongers have been documented in the eastern gulf of Shark Bay (~5% of the population), and 40 in the western gulf, and in both locations, vertical social transmission is evident (Mann and Patterson, 2013; Patterson and Mann, 2015). Individuals only develop the tactic if their mother was a sponger, but horizontal transmission has clearly occurred since more than one mitochondrial DNA haplotype is present among the three known populations of spongers (Patterson and Mann, 2015). In fact, occasionally individuals whose mothers were not spongers carry a sponge for a brief period of time, often in the company of other spongers. Such rare occurrences may eventually lead to horizontal transmission. Nevertheless, spongers tend to form their own social group and sponging has been characterized as a cultural trait based on preferential association and cliquishness among spongers (Mann et al., 2012).

A strong female bias, both in the prevalence of sponging, and its adoption, is also present in both gulfs. In the eastern gulf, where more extensive long-term data exist, over 90% of daughters, but

only 50% of sons, born to spongers become spongers. The reason for this bias is still unclear but it likely has to do with sex-specific reproductive interests. Female mammals require significant resources to support offspring, while male reproduction depends on gaining access to mates. Given that male reproduction in Shark Bay may be limited by ones’ ability to roam widely with his alliance partners to consort receptive females, sponging, which requires years to learn and a very specific habitat, is probably too restrictive for males (Patterson et al., 2015). Consistent with this, adult male spongers spend less time sponging than adult female spongers (Mann and Patterson, 2013). Furthermore, the sex bias in the adoption of maternal foraging tactics is not limited to sponging. Females exhibit a far wider range of foraging tactics than males, and daughters continue using their mothers’ foraging tactics well after weaning (Patterson and Mann, 2015).

Similar to sea otter tool use, ecological factors strongly correlate with sponge tool use, specifically the use of deep water channels with high conical sponge density (Patterson et al., 2015). In fact, several lines of evidence indicate that sponge tools afford access to a unique niche. Spongers can access prey inaudible to echolocation and they have a distinct fatty acid signature (Mann and Patterson, 2013; Patterson and Mann, 2015; Patterson et al., 2015). Furthermore, spongers appear to specialize in this untapped resource, spending ~94% of their foraging time using sponge tools, and foraging substantially more than non tool-users (Mann and Patterson, 2013).

### III. Conclusion

Marine mammal physiology and ecology do not lend themselves to tool use. Not surprisingly there are very few cases of tool use among these taxa, and in fact, tool use is rather rare in marine environments in general (Mann and Patterson, 2013). Like terrestrial mammals, most cases of marine mammal tool use involve foraging. The two best-known cases, sea otters and sponging dolphins, involve using tools for prey extraction, similar to most tool use in birds and terrestrial mammals. Both sea otter and bottlenose dolphin tool-users are able to exploit difficult-to-access resources, and data suggest that such behavior may be driven by high population densities and resource limitations (Mann and Patterson, 2013). Marine mammal tool use, although rare, does provide comparative insight into such processes as niche specialization, social learning, cultural evolution, and life history.

### See Also the Following Articles

Bottlenose Dolphins ■ Feeding Strategies and Tactics ■ Otters ■ Culture in Whales and Dolphins

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## TOOTHED WHALES (ODONTOCETI)

SASCHA K. HOOKER

The toothed whales comprise the suborder Odontoceti of the order Cetacea. This suborder includes 10 diverse extant families, 2 of which contain large numbers of species. There are at least 74 extant species in all, including the true dolphins, monodontids, river dolphins, porpoises, beaked whales, and sperm whales (Table 1). These species occur in three primary clades, the superfamilies Delphinoidea (true dolphins, monodontids, and porpoises), Ziphoidea (beaked whales), and Physeteroidea (sperm whales), whereas river dolphins probably do not form a monophyletic clade. With the exception of the sperm whale (males of which reach up to 18 m) and the larger beaked whale species (*Berardius* and *Hyperoodon* spp.), most odontocetes are small to medium-sized cetaceans, ranging in size from the vaquita (1.4 m) to the killer whale (8.5 m). These species show a range of distributions, with some such as river dolphins being found only in quite specific areas, whereas others such as sperm whales or killer whales show a global distribution.

TABLE 1 Modern Odontocete Families

Family	Common names	No. species
Kogiidae	Pygmy and dwarf sperm whales	2
Physeteridae	Sperm whale	1
Ziphiidae	Beaked whales	22
Delphinidae	True dolphins	37
Monodontidae	Narwhal and beluga	2
Phocoenidae	Porpoises	7
Iniidae	Amazon, Bolivian and Araguaian river dolphins	1
Pontoporiidae	Fransiscana	1
Lipotidae	Baiji (Yangtze river dolphin)—now extinct	(1)
Platanistidae	South Asian river dolphin	1
	TOTAL	74

### I. Diagnostic Characters and Taxonomy

Odontocetes and mysticetes differ fundamentally in three major ways: The way that the bones of the skull have become telescoped, the specialized echolocation system (and associated anatomy) of odontocetes, and the specialized filter-feeding mechanism of the baleen whales (Table 2). The name Odontoceti derives from the Greek *odous* or *odontos* for “tooth,” and *ketos* for “sea-monster,” hence “toothed sea-monster,” referring to the presence of teeth (Rice, 1998). In contrast, modern mysticetes do not possess teeth, but instead have baleen plates, which hang from the upper jaw and are used to filter small prey items from the water. However, although all odontocetes possess teeth, in some species (or sexes) these teeth are much reduced and may not erupt.

Other distinctive features include the possession of a single nares or blowhole, whereas mysticetes have two blowholes. Most odontocetes show some degree of dorsal asymmetry in their skull and facial soft tissue, whereas all mysticetes have a symmetrical skull and facial soft tissue. Odontocetes possess a large ovoid melon in the anterior part of the facial region. This fatty tissue is thought to be an important component of the echolocation system. Although mysticetes possess a fatty structure just anterior to the nasal passages, which may represent a vestigial melon, this is only a fraction of the size of that present in odontocetes.

Odontocetes (with the notable exception of the sperm whale) tend to be smaller in size than mysticetes, although there is some overlap. Odontocetes also show variation in sexual dimorphism. In some species, males are much larger than females (e.g., sperm whale and killer whale), whereas in others there may be reverse sexual dimorphism, in which females are larger than males (e.g., harbor porpoises and Baird’s beaked whale). Among mysticetes, adult females are always slightly larger than adult males.

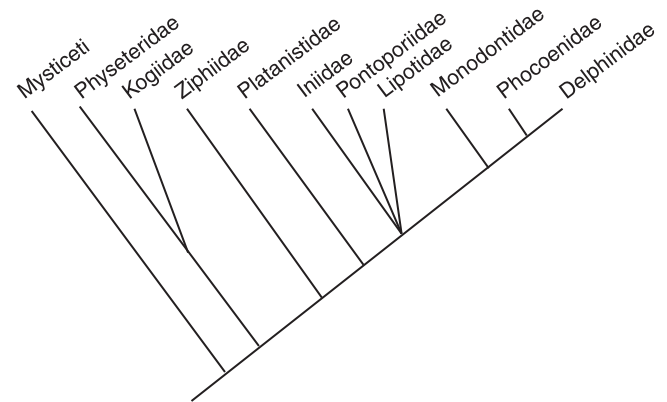
The skull and lower jawbone of odontocetes also contain a number of diagnostic characteristics. The odontocete mandible is symphyseal (the two jawbones lock together in a bony symphysis anteriorly) and each jawbone spreads into a fat-filled hollow pan at the posterior, non tooth-bearing section, whereas mysticete mandibles are nonsymphyseal and the bone is more solid. When viewed from above, the odontocete jawbone is relatively straight, whereas

**TABLE 2** Major Differences Between Modern Representatives of Odontocete and Mysticete Suborders of Cetaceans

Odontocetes	Mysticetes
Teeth (sometimes not protruding)	Baleen plates
Single blowhole	Two blowholes
Dorsally asymmetric skull and facial tissue	Symmetrical skull and facial tissue
Presence of a melon	No melon
Variable size	Always large
Variation in sexual dimorphism	Always reverse sexually dimorphic
Symphyseal mandible provides powerful bite	Elastic mandibular symphysis permits lower jawbones to be rotated independently in two planes (assists in dynamic expansion of oral cavity)
Hollow pan bone of lower jaw	Lower jawbones solid, no pan bone
Maxillae project outward over expanded supraorbital processes	Maxillae project under the eye orbit, and possess bony protuberance anterior to the eye orbit
Tympanic and periotic fused and equal sized	Tympanic bulla much larger than periotic and not fused.

the mysticete jawbone is convex on its lateral side. The maxilla of both odontocetes and mysticetes has “telescoped,” migrating posteriorly to form the long rostrum and dorsal nasal openings. In the odontocetes, the maxillae have extended outwards over the orbits to form an expanded bony supraorbital process of the frontal bone. This process forms an anchoring point for the facial musculature associated with sound production. In contrast, the maxillae of mysticetes project under the eye orbit and have developed a bony protuberance on the maxilla anterior to the eye orbit. Odontocetes lack this antorbital process of the maxilla. The bones of the ear of odontocetes are also quite different from those of mysticetes. In odontocetes, the tympanic bulla and periotic bone are fused together, equal size, and not fused to the skull. The odontocete tympanic is thin-walled on its lateral side and conical, tapering anteriorly. In mysticetes, the tympanic bulla is much larger (nearly twice the volume of the periotic bone) and is thick-walled and spherical. Bony flanges of the periotic wedge it against the skull, such that only the large bulla can be removed without breaking the bone.

The clear morphological differences between odontocetes and mysticetes suggest monophyly of the odontocetes. There has been some disagreement about this issue, based on some molecular sequence data that supported a closer relationship between the sperm whales and the baleen whales than between the sperm whales and the other toothed whales. However reanalysis of these data and more recent work on both morphologic and molecular data continue to support odontocete monophyly (see Cetacean, Evolution). Relationships among extant odontocetes are somewhat

**Figure 1** Generally accepted odontocete phylogeny.

controversial, but there is a consensus as to the order of branching of the phylogenetic tree, despite controversies over smaller scale relationships (Fig. 1; see River Dolphins, Evolution).

Odontocetes first appeared in the fossil record in the early Oligocene (Gatesy et al., 2013). Odontocete diversity increased during the warm temperatures of the early Miocene, during which time the earliest ziphiids and platanistids appeared in the eastern North Pacific. Middle Miocene diversity was also high and included diversification of these families, together with extensive radiation of the delphinoids, while the platanistoids progressively declined. Modern odontocete families are known from the late Miocene of the eastern North Pacific (monodontids and phocoenids) and western South Atlantic (pontoporiids). Evolutionary trends among odontocetes included the expansion and increase in size of the face, shortening of the intertemporal region, elevation of the cranial vertex posterior to the nasals, increased facial asymmetry and isolation of the ear-bones from the skull resulting in the diagnostic features described earlier. There has also been a trend toward either long, slender jaws with increased number of teeth, or short, robust jaws and reduced number of teeth.

## II. Distribution and Range

Different odontocete species can be found across a wide range of habitats in all oceans of the world. The cyclical changes in sea level over the Quaternary (Pleistocene to Recent) period are thought to be responsible for much of the recent speciation within odontocete families. Sea-level drops associated with cooling are suggested to have isolated populations which then speciated allopatrically. The distributions of modern odontocetes range from species found globally, such as sperm whales and killer whales, to those with more restricted coastal distributions, such as harbor porpoises. Some species are found only in polar regions, including the narwhal and beluga, others only in tropical waters, such as Fraser's dolphin (Jefferson et al., 2008). Segregation by warm tropical waters created antitropical distributions of some species pairs now found only in the Northern and Southern Hemispheres respectively (e.g., the northern and southern right whale dolphin, northern and southern bottlenose whale).

Few odontocetes show the kind of long distance seasonal migration that is found among mysticetes. The only odontocete species which is known to show a large (ocean-basin) scale of movement is the sperm whale. At approximately 10 years of age, male sperm

whales will leave their natal group in the tropics and subtropics and migrate to cold temperate and sub-polar waters where they feed. Once physically mature, they return to the tropics to breed. Other odontocetes may show much smaller migrations as they follow their prey movements (e.g., long-finned pilot whales in the North Atlantic will move from shelf edge up onto shallower banks in response to changes in squid distribution). Other species (e.g., killer whales) show negligible seasonal changes in distribution.

Many odontocete species show variation across their ranges, leading to the definition of several subspecies or races. With increasing scrutiny of both genetic and morphological differences, subspecies and population level differences are continually being identified. In some cases, this is leading to revision of the currently established species (Committee on Taxonomy 2016).

### III. External Appearance

In general, many odontocete species tend to have darker coloration on the dorsal surface (back and cape) and lighter pigmentation on the ventral surface (Fig. 2). Such countershading is relatively common in the marine environment and functions essentially as camouflage, such that when viewed from above the dark dorsal surface is seen against the darker depths, and when viewed from below the lighter ventral surface is seen against the brighter downwelling light from the surface (e.g., harbor porpoise). Exceptions to this include the beluga, which has a uniform color pattern, although this is thought to be related to the bright ice-covered habitat that it lives in. The general tendency toward countershading has become quite elaborate in some species, which also have striped and saddle patterns (e.g., striped dolphins, short-beaked common dolphins), and has become radically modified in others (e.g., killer whale, Dall's porpoise). It has also been suggested that these color patterns may function in signaling between individuals in a group (Norris et al., 1994), in addition to their function in concealment (from both predators and prey). Both dwarf and pygmy sperm whales have a white false gill behind the eye, which may (along with the ejection of up to 12 L of dark red 'ink' from a sac in the lower portion of their intestinal tract) confuse or discourage predators.

Odontocetes tend to show greater body flexibility than mysticetes (Castellini and Mellish, 2016). This is presumably due to differences in prey capture strategies between odontocetes, which chase fast, mobile, single prey, and mysticetes, which engulf less

mobile prey schools. This flexibility is quite pronounced in some odontocete species (e.g., belugas).

### IV. Diet and Feeding Strategies

Different odontocete species feed on fish, squid, large crustaceans, birds, and occasionally other marine mammals. They differ from mysticetes in that they generally chase, capture, and swallow single relatively large prey items, rather than filtering and swallowing large quantities of small prey items. This more generalized and more adaptable feeding method is thought to account for much of the diversity of odontocete species and their range of habitats. Many odontocetes also feed on much deeper prey than the surface water plankton diet of many species of mysticetes. Additionally, whereas the diet of baleen whales is highly seasonal due to the seasonal nature of zooplankton biomass and production, that of odontocetes is generally more constant year-round.

Unlike the heterodont condition of most terrestrial mammals, the teeth of odontocetes are uniformly shaped (homodont). There is a wide variation between (and some variation within) species in tooth number, size, and shape (see Dental Morphology). The teeth of most odontocete species tend to be peg-shaped with single, open roots. Exceptions to this include the porpoises, which have spade-shaped teeth, and the beaked whales, which show great variation in size, shape, and location of teeth in the jaw.

Narwhals have only two teeth, both in the upper jaw. In females, these teeth usually remain embedded in the upper jawbones, but in males the left tooth grows out through the front of the head into a tusk up to 3-m long. These tusks are thought to be involved in male–male competition. These are used primarily as a display, although males have been seen sparring with their tusks above the water. The teeth of beaked whales have similarly become adapted for use in male–male competition and generally erupt only in males. In some species, such as the Blainville's beaked whale, these teeth form large structures which protrude above the upper jaw. In another beaked whale, the strap-toothed whale, the teeth, which emerge from the middle of the lower jaw, curl backward and inward, extending over the upper jaw, often prevent it from opening more than a few centimeters.

The diet of a particular species is generally reflected in the morphology of the jaw, and the type and number of teeth. For example, species which feed primarily on fish tend to have more teeth (e.g., spotted dolphin), and use these teeth for grasping single prey. Species which feed primarily on squid tend to show reduced dentition (e.g., sperm whales, beaked whales, narwhals, and Risso's dolphin), and are thought to feed by suction. This suction is achieved by using the tongue as a piston in combination with a small gape. The suction feeding mechanism of beaked whales involves distension of the floor of the mouth by expanding the throat grooves together with retraction of the tongue by the styloglossus and hyoglossus muscles (Heyning and Mead, 1996). Additionally, it has been suggested that some species may debilitate prey by directing high-intensity sounds at them, prior to capturing them (Norris and Mohl, 1983). Such feeding methods are thought to explain the occasional observation of healthy animals with severe deformity of the jaws (as has been noted in sperm whales).

Notable specializations associated with odontocete feeding are shown by several bottlenose dolphin populations. In Shark Bay, Western Australia, a small number of Indian Ocean bottlenose dolphin females have been observed carrying sponges (Mann et al., 2000). These are thought to function as "tools" to protect the dolphin's rostrum as it roots in bottom coralline sediments in order to



**Figure 2** Short-beaked common dolphin pigmentation, shows countershading with dark pigmentation on dorsal surface and light pigmentation on the ventral surface, common to most odontocetes (Photo by Sascha K. Hooker).



flush bottom-dwelling fish out. Another bottlenose dolphin population, in North Carolina, USA, has been observed beaching themselves and the fish they were pursuing up onto the surrounding mudbanks, thus immobilizing their fish prey which they can easily catch, and then slide or wriggle back down into the water (Reynolds and Rommel, 1999). The same behavior has also been observed in killer whales in Patagonia and the Crozet Archipelago in their pursuit of seals up onto steeply shelving beaches.

Foraging specializations of killer whales in British Columbia, Canada, and Washington State, USA, waters have resulted in two separate forms, “transients” which feed on marine mammals, and “residents” which feed on fish. These two forms are thought to potentially represent a case of incipient speciation. The primary difference between these two forms is in their dietary specialization, which has resulted in their social separation and behavioral, morphological, and genetic differences.

Some odontocetes appear to feed throughout the day and the night (e.g., sperm whales and northern bottlenose whales), but many smaller delphinids show marked diurnal differences in feeding (e.g., spinner dolphin and pantropical spotted dolphin). Since many prey species rise to shallower depths during the darkness of night, it is energetically more efficient for some species to conduct the majority of foraging behavior at night.

As mentioned previously, odontocetes tend to feed at greater depths than mysticetes (Castellini and Mellish, 2016). The use of novel technologies such as the attachment of time-depth recorders to monitor dive profiles of these species have lagged behind work done on pinnipeds or mysticetes, primarily due to difficulties in deployment, attachment and recovery (Hooker and Baird, 2001). However, new developments in these technologies and attachment mechanisms are increasingly resulting in the initiation of new studies. Such work has highlighted the remarkable diving ability of beaked whales, which regularly reach depths of 1500 m. In fact, a Cuvier’s beaked whale was recorded attaining a depth of approximately 3000 m, although whether this was a normal foraging dive or a response to coincident military sonar was unknown.

Odontocete cetaceans show an unusual form of mammalian sleep, sleeping with only half of their brain at a time, termed “uni-hemispheric” sleep. Their body movement can be continuous and REM sleep is suppressed. Observationally some species show pronounced resting (often termed “logging”) behavior at the sea surface (e.g., sperm whales, northern bottlenose whales) while other species appear to be continuously active (e.g., harbor porpoise). Some dolphins have specific resting locations (e.g., Hawaiian spinner dolphins).

## V. Sound Production and Reception

Toothed whales have developed specialized sound production and reception mechanisms for the use of biosonar. All modern odontocetes are thought to use echolocation, in the same manner as bats, to gain an “image” of their environment. Although only a few species of odontocete are unequivocally known to echolocate, all odontocetes known to produce pulse-like sounds in the wild are assumed to be able to echolocate.

The sound production mechanism of odontocetes consists of a sound generator located in the “monkey lips”/dorsal bursae (MLDB complex) associated with the upper nasal passages. In most odontocetes, there are two bilaterally placed MLDB complexes, but sperm whales (physeteroids) have only a single complex. The central components of the MLDB complex are the fatty dorsal bursae, the monkey lips, the bursal cartilages, and the blowhole ligament

(Cranford et al., 1996). A series of air sacs (premaxillary, vestibular and accessory) support the pneumatic operation of the complex. Sounds are generated as air is forced between the monkey lips, setting the MLDB complex into vibration. Sound is propagated into the water by the melon, a low-density lipid filled structure which acts as an acoustic lens to focus a directional sound beam ahead of the animal (Au and Hastings, 2008; see Echolocation). The short-duration clicks produced as a result of this are used primarily for echolocation, although some species appear to use these clicks in a social context (e.g., Hector’s dolphin).

Most odontocete species produce broadband echolocation clicks in the ultrasonic sound range, well above the range of human hearing. The pulse duration, frequency, interclick interval, and source level are adjusted by the animal for optimal performance according to the prevailing conditions of ambient noise, reverberation, target distance, and target characteristics (Au and Hastings, 2008). With low ambient noise, bottlenose dolphins, belugas, and false killer whales often echolocate using frequencies from 20 to 60 kHz, although at higher noise levels, they emit stronger pulses at 100–130 kHz. Echolocation clicks of porpoises and many small dolphins are at frequencies greater than 100 kHz, while those of the sperm whale range from less than 100 Hz to 30 kHz, with most energy from 2–4 to 10–16 kHz.

In addition to echolocation clicks and loud impulse sounds, many toothed whales also produce other sounds, usually described as whistles, squeals, or less distinct pulsed sounds such as cries, grunts, or barks. These tend to be narrow band (sometimes pure tone), frequency modulated sounds, often with a harmonic structure. Most whistles tend to have most of their energy below 20 kHz. These whistles can show a variety of patterns of frequency and amplitude over the duration of the whistle. For many species, the frequency, duration, and level may vary. Observations of both captive and wild bottlenose dolphins have shown that individual animals can be identified from the contour of the whistle on a sonogram (a representation of the whistle as sound frequency plotted against time). The distinctive character of a whistle is thought to function in identifying the sound producer to other animals. These whistles are therefore known as signature whistles. There may be population or group-level distinctions between whistles of bottlenose dolphins. Recent work among captive dolphins has shown that individuals have long-term memory (spanning decades) for the signature whistles of their former companions.

Group-specific sounds have also been found among killer whales and sperm whales. Among killer whales, groups appear to have a repertoire of approximately 10 calls. Different groups may share some but not all of the calls within their repertoire, and relationships between groups can be established based on the similarities in their repertoires. In a similar fashion, the codas (rhythmic patterns of clicks) produced by sperm whales also appear to be characteristic of the social group.

The high-frequency hearing of odontocetes is reflected in the structures of the lower jaw and ear (Castellini and Mellish, 2016). The lower jaw of odontocetes is flared out in a thin hollow pan bone at the rear. This is filled with a fat body that directly connects with the bulla of the middle ear. These fat bodies act as low-density sound channels to conduct sounds to the ears. Within the ear, the tympanic bulla is separated from adjacent bones of the skull by peritympanic sinuses filled with an insulating emulsion of mucus, oil, and air. The bulla is suspended in this emulsion by connective tissue, so that the middle ear functions as a sound receiver isolated from the skull to better localize sound signals. The tympanic bulla

**TABLE 3** Social Strategies Employed by Odontocete Species Known from Long-Term Studies of Wild Animals

	Social groups	Mating system
Bottlenose dolphin	Male coalitions Female groups	“Capture” of females by a coalition of males
“Resident” killer whale	Matrilineal groups of females and descendents	Intergroup matings thought to occur when groups meet
Sperm whale	Matrilineal groups of females and juvenile males Solitary adult males	Males rove between groups in search of estrus females

membrane of odontocetes is also stiffened with bony ligaments, which appear to be associated with ultrasonic hearing (Reynolds and Rommel, 1999).

## VI. Social Organization and Culture

Toothed whales are particularly well known for their brain size and rich social lives (Mann et al., 2000). The absolute brain size of odontocetes ranges from 840 g in common dolphins to 7820 g in sperm whales (Berta et al., 2006). However, a more useful way to compare brain sizes is to use the ratio of brain size to body size, the encephalization quotient (EQ). The relative brain sizes of odontocetes (ranging from EQ 0.02% for the sperm whale to EQ 1% for the bottlenose dolphin) are much larger than most terrestrial mammals but are similar to those of anthropoid primates (EQ 0.3% in the gorilla). Captive studies of bottlenose dolphins have shown that they may have a “pecking order” similar to that of chimpanzees, in which both males and females have a social hierarchy, but that generally males are dominant to females.

The social systems of only a few odontocete species are known from long-term studies of wild animals, but these suggest some novel adaptations to standard mammalian patterns (Table 3; Connor et al., 1998). In Shark Bay, Western Australia, male Indian Ocean bottlenose dolphins form tight associations with one or two other males with whom they cooperate to form aggressively maintained consortships with individual females. These alliances further appear to form moderately strong associations with one or two other alliances and will defend each other in competition over females. A completely different strategy is found among the fish-eating “resident” killer whales living along the coast of British Columbia, Canada, and Washington State, USA. Here, neither males nor females disperse at maturity, but instead they remain with their mothers in stable matrilineal groups. Genetic data suggest that a similar pattern of natal philopatry may exist among long-finned pilot whales. Sperm whales appear to have a different social structure again. Groups of females and immature males are found in the tropical lower latitudes. Juvenile males remain in these natal groups until they reach puberty, at which stage they depart to lead more solitary lives in colder temperate and polar waters. They later return to the tropics when fully mature and search for estrus females with which to mate. Long-term studies of sperm whales have demonstrated strong cooperative bonds between individuals in groups of females and immature males (Fig. 3). These groups were thought to be composed of matrilineally related individuals,



**Figure 3** Group of female and immature sperm whales in the Galápagos Islands (Photo by Sascha K. Hooker).

however recent evidence suggests that they are not purely matrilineal in structure but are comprised mainly of clusters of related individuals but also of some animals with no close relations. Baird's beaked whales may have one of the most unusual social systems among odontocetes, although this is inferred only from studies of dead animals. It appears that males mature an average of 4 years earlier than females and may live up to 30 years longer (Kasuya et al., 1997). This has led to speculation that males may be providing significant parental care.

An interesting congruence between low levels of mitochondrial diversity and the presence of matrilineal social systems in four species of odontocete may suggest the cultural transmission of matrilineally inherited traits (Whitehead, 1998). Apparent culture in cetaceans includes the learning of particular feeding techniques from the mother or members of the matrilineal group. In fact, many attributes of cetaceans (and odontocetes in particular) favor the evolution of social learning and culture. These include their long lives (~60–90 years), advanced cognitive abilities, prolonged parental care, permanent and cohesive groups, and an environment that varies substantially over large spatial and temporal scales (such that individual learning would be costly) (Rendell and Whitehead, 2001). However, claims of animal culture are argued to be subject to weaknesses, in that behavioral differences thought to be cultural may in many cases result from a combination of genetic, ecological, and cultural variation (Laland and Janik, 2006).

A potential offshoot of the advanced sociality observed in some species of odontocetes is the presence of postreproductive care, i.e., “menopause.” Pilot whales, killer whales, and possibly sperm whales show similar attributes to human females, with reproduction ceasing at approximately 40 years of age although females live on for several more decades. Short-finned pilot whales show a decreasing pregnancy rate with increasing maternal age, and a parallel age-related decline in the ovulation rate. Up to 25% of adult females may be postreproductive, ceasing to ovulate after age 40 even though the maximum lifespan exceeds 60 years (Marsh and Kasuya, 1991). However, lactation may continue for up to 15 years after the birth of their last calf. It is unclear whether communal nursing exists. Postreproductively aged female resident killer whales have been found to benefit the survival of their offspring, a mechanism for which is suggested to be their acquired knowledge as it has also been found that they are more likely to lead collective movement, particularly in times of low food abundance.

Another apparent consequence of the strong social bonds found among odontocetes is the phenomenon of mass strandings (Sergeant, 1982; see Strandings). This tendency for animals to come ashore in groups to die is found only among the most highly social odontocete families. Several explanations for this behavior have been suggested. These include disorientation due to geomagnetic anomalies, panic flight responses from predators or underwater noise, morbillivirus infections, parasitic infections of the respiratory system, brain, or middle ear, or the strong social bonds of a group causing the entire group to follow one intentional strander. It has also been noted that many locations in which mass strandings occur share certain structural characteristics. These sites are often composed of a sandy peninsula or promontory, which extends perpendicular to the coastline and appears to form a “whale-trap,” potentially due to the loss of echolocation abilities in the shallow sandy environment.

## VII. Mating System, Reproduction, and Life History

Many odontocete species have promiscuous mating systems, in which several adult males may mate with a female. However, other species such as the bottlenose dolphins in Shark Bay, and Dall’s porpoises in the eastern Pacific appear to show a form of mate guarding. Among many beaked whale species males compete, suggesting that there may be a hierarchical nature to their social organization, probably for access to females. However, detailed comparative data on the mating systems of odontocete species will await genetic analyses to determine paternity from offspring within groups.

Gestation periods of odontocetes range between 7 and 17 months and almost all species have interbirth intervals of greater than 1 year (Reynolds and Rommel, 1999; Berta et al., 2006). Length of gestation and fetal growth rate are related to calf size at birth such that larger species tend to require longer periods of gestation. Odontocetes produce a single offspring, which is physically well developed (able to swim and surface to breathe), but socially undeveloped. As a result, odontocete species have characteristically long lactation periods, averaging between 32 and 100 weeks (Berta et al., 2006). Females continue to feed throughout this long lactation period.

Odontocetes tend to show extended maternal care, resulting in a strong mother–calf bond. For most species, calves will remain with their mothers for a few years, but for some they will remain in close family groups for their lives (e.g., some killer whale populations, possibly long-finned pilot whales). This high level of investment needed to successfully raise calves may have led to the need to practise mothering behavior. Association between infants and nonmothers, termed allomaternal behavior, has been described for a variety of odontocete cetaceans (Mann et al., 2000). Among bottlenose dolphins, such behavior appears to primarily benefit the nonmother, providing experience in parenting. Similar babysitting has also been documented in sperm whale groups, which stagger their deep-diving behavior such that calves are almost always accompanied by an adult at the surface. However, the function of this behavior in these circumstances appears to relate to increasing calf survival and defense against predation rather than to practise mothering (Mann et al., 2000).

Much of the life history data available for odontocetes has come from studies of dead animals (either from those taken in whaling operations, as bycatch to other fisheries, or from strandings). The age of an odontocete can be estimated from its teeth using much the same technique as counting the growth rings of a tree trunk. As an individual grows, incremental growth layers are deposited in the teeth and bones. In order to determine the age, the tooth is usually thinly sliced and polished and may often be etched or stained to better

resolve the growth layer groups. In most species, each growth layer group is thought to represent an annual increment, but this needs to be independently verified in order to use this method for each species. By establishing the ages of animals, researchers are able to investigate the age-structure of the population, to look at ages at which animals mature, reproduce, the lifespan, etc. Long-term studies of odontocete species in the wild (e.g., those listed in Table 3) are gradually allowing life history parameters to be recorded from living animals. In some cases, particularly in establishing lifespan, these are providing records of lifespan to a much greater age than were estimated from catch records.

The life histories recorded in this manner show large differences between different odontocete species. Harbor porpoises have a maximum longevity of 12 years (although some may live up to 17 years); they reproduce at age 3 and become pregnant every year thereafter. In contrast, killer whales have a maximum longevity of about 80 years and first give birth at approximately 15 years of age, with a 5-year interbirth interval. Many species also show sex-specific differences in life history parameters. For example, sperm whale females become sexually mature at approximately age 9–10, whereas sperm whale males do not appear to become sexually mature until approximately age 26–27.

## VIII. Human Interaction and Conservation Status

In the past, the majority of human interaction with odontocetes involved the capture of animals from the wild, either for consumption as part of the whaling industry, or more recently to obtain animals for captivity. Only a few odontocete species were hunted to the same scale as the fisheries for baleen whales in the last two centuries. The main odontocete species taken historically were the sperm whale, some beaked whale species (northern bottlenose whales and Baird’s beaked whales), and pilot whales. However, although the moratorium on large whale hunting essentially put an end to the hunting of mysticetes, the only odontocete species included in this moratorium was the sperm whale. Thus today, many odontocete species are still taken in aboriginal subsistence hunts. Unfortunately, many of these go unmonitored, and so the exact numbers taken are unknown, although they are suspected to be high (Bowen, 2000).

Several odontocete species are or have been maintained in captivity for display, research, or conservation purposes (Twiss and Reeves, 1999). Some species are maintained in captivity for research or public display (e.g., bottlenose dolphin, killer whale, and beluga) whereas others have only rarely been kept in captivity following live stranding (e.g., sperm whales and beaked whales). Some species are successfully bred in captivity, including bottlenose dolphins, Commerson’s dolphins, and killer whales. Captive animals have been vital to research efforts worldwide, and it is now somewhat debatable that these animals would have a “better” life in the wild, in habitats that are rapidly deteriorating. In fact, the attempt to return the killer whale, Keiko (star of the film “Free Willy”) to the wild was both costly and unsuccessful (Simon et al., 2009).

Humans are also increasingly attempting to interact with odontocetes in the wild. Whale-watching operations are popular worldwide, and bottlenose dolphins and killer whales are particularly heavily impacted. There are concerns about the impact of whale watching on the animals involved, with documentation of immediate adverse impacts such as erratic behavior with boat approach, and a reduction in resting behavior with increasing number of boats present. The long-term impact of these short-term behavioral responses to disturbance is more difficult to assess. However, some

work has shown a decline in abundance of dolphins as the number of tour operators increased, raising concerns in terms of the viability of the populations concerned. Swim-with-dolphin programs have also increased in frequency, potentially misinforming the public that association with wild animals is endorsed, when in reality this can be dangerous to both human and dolphin. In Florida, many people continue to solicit interactions with wild dolphins, and, despite legislation against it, often encourage this by provisioning.

Lone animals of several odontocete species have, at times, been recorded to solicit associations with humans. This behavior has been recorded a number of times all over the world. In all cases, animals have become resident in a small area, where they approach and interact with boats or people in the water. In many cases, the animals involved have been bottlenose dolphins, but this behavior has also been recorded from belugas and rough-toothed dolphins.

Today, conservation problems exist for nearly all odontocete species. In fact, since the International Whaling Commission moratorium on catching large whale species, many of the current conservation threats faced by cetaceans are likely greater for odontocete species than for mysticetes. These include climate change, habitat loss and degradation, competition with fisheries, incidental bycatch in fisheries, impacts of noise from oil exploration and military sonars, and the consequences of our growing human population in terms of contaminants, plastics and other waste (see Conservation).

In general, noise is thought to be less of a problem for many odontocete species than for mysticetes, since much oceanic anthropogenic noise is low frequency. However, higher frequency noise (such as that created by fishfinder units) is likely to coincide with the hearing range of many odontocetes (Twiss and Reeves, 1999). Additionally, some odontocete species (particularly beaked whales) appear to be highly susceptible to disturbance from mid-frequency sonar, although the mechanism by which this causes mass strandings and death remains unknown.

The squid diet of many odontocete species renders them prone to plastic ingestion and extremely large quantities of plastic have been found in the stomachs of many stranded animals. The higher trophic levels of odontocetes also magnify their pollutant load, such that some populations, such as the belugas of Canada's St. Lawrence River are even treated as toxic waste.

The habitat specificity shown by many odontocete species means that they have little recourse in the face of habitat destruction. The typically smaller size of many odontocetes means they are less likely to be able to free themselves when trapped in nets, leading to high incidence of bycatch. Intense pressure from fisheries has resulted in species such as the vaquita becoming reduced to only tens of individuals remaining. Similarly, uncontrolled and unselective fishing has resulted in the baiji (or Yangtze river dolphin) becoming extinct, representing the loss of an entire mammalian family.

### See Also the Following Articles

Cetacean Life History ■ Conservation ■ Echolocation ■ Mating Systems ■ River Dolphins, Evolution ■ Sperm and Beaked Whales, Evolution

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## TOURISM

ERICH HOYT

Marine tourism is defined as "recreational activities that involve travel away from one's place of residence and which have, as their host or focus, the marine environment" (Orams, 1999). Marine mammal tourism is a sister category to bird, shark, and other

wildlife watching by the shore or at sea. These activities, because of their focus on charismatic animals, can help to educate people and stimulate interest toward protecting marine wildlife and their habitats, while at the same time having the potential for disturbance and long-term detrimental effects to the very species that are being watched.

The wide variety of marine mammal watching activities, largely whale watching, includes tours lasting from 1 hr to 2 weeks, using platforms ranging from kayaks to large ships, from land points including cliffs and beaches, from sea planes and helicopters, as well as swimming and diving activities in which the tourist enters the water with marine mammals. See Hoyt (2009), for further details.

### I. The Birth of Whale Watching

In 1955, the first commercial whale watching operation charged USD \$1 to see gray whales (*Eschrichtius robustus*) on their near-shore winter migration off San Diego. By the 1970s, boat tours and land-based whale watching were spreading up the US west coast and south to Mexico, following the gray whale migration, and jumping to the St. Lawrence River in Canada where fin (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*) were seasonally resident. It was public response to the humpback whale (*Megaptera novaeangliae*), however, that turned commercial whale watching into an industry and led operators to invest in purpose-built boats. Humpback whales tend to be more active at the surface than other whales, frequently breaching clear of the water—ideal for whale watchers wanting photographs.

In New England and Hawai'i, tours to see humpbacks began in 1975. New England operators established their own brand of commercial whale watching with scientific and educational components—with naturalists on every trip who were often working researchers. Educational programs to introduce school-children to wild cetaceans, which were started in southern California by such groups as the American Cetacean Society, soon expanded to New England. New England was fortunate to have humpback, North Atlantic right (*Eubalaena glacialis*), fin, and minke whales available close to shore. The Stellwagen Bank feeding grounds, 5 km north of Cape Cod, were accessible to Boston and other New England ports.

### II. Science and Education as Part of Marine Mammal Tourism

The scientific and educational aspects of marine mammal tourism were greatly facilitated by the development of photographic identification (photo-ID) of whales in the early 1970s—humpback whales in the North Atlantic, gray and killer whales (*Orcinus orca*) in the North Pacific, and southern right whales (*E. australis*) and common bottlenose dolphins (*Tursiops truncatus*) off Argentina.

Marine mammal watching tourists and tour staff have adopted the tool of photo-ID and thereby contributed to research. Of course, commercial tourism is incompatible with much of marine mammal research which focuses on behavioral and acoustic studies, transect surveys, biopsy darting, and collecting skin and fecal samples. In some cases, however, a commercial enterprise has funded or facilitated research that operates from separate boats and with different personnel. In several areas, such as the Maldives, northern Gulf of St. Lawrence, Quebec, and southern Chile, whale watching operations have uncovered new populations of cetaceans, and helped make them accessible for study. In all, whale watching worldwide has led to many cetacean photo-ID programs supported in part or conducted aboard commercial whale watching boats. This has

contributed to public support for research through greater familiarity, as well as through the involvement in citizen science programs.

### III. Growth of Commercial Marine Mammal Tourism

Besides tourism directed toward cetaceans, there are educational wildlife day trips focusing on: Harp seals (*Pagophilus groenlandicus*) in the Gulf of St. Lawrence; gray seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) in England and Scotland; West Indian manatees (*Trichechus manatus*) in Florida; California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*) off California; giant otters (*Pteronura brasiliensis*) in Brazil, Peru, and Guyana; African manatees (*Trichechus senegalensis*) in Senegal; dugongs (*Dugong dugon*) in the Philippines and Australia, and many more.

Whale watching tours also started in Norway and Japan, two countries with whaling industries. In both countries, the number of whale watchers has increased steadily. In 2008, Norway had 35,360 whale watchers spending more than \$10 million USD, whereas Japanese operators escorted some 191,970 whale watchers who spent USD \$22.7 million in seven communities (Hoyt, 2001; O'Connor et al., 2009). Mainland Norway's whale watching industry offers sperm whales and various dolphins (May–September) and killer, humpback, sperm and fin whales during the low-light winter months; the whale watchers primarily come from other European countries. In High Arctic Norway, in the waters around Svalbard, white whales (*Delphinapterus leucas*) and a host of baleen whales are routinely seen by tourist ships during the summer. Japan's whale watching industry, is largely domestic, targeting: Bryde's whales (*Balaenoptera edeni*) and sperm whales at several warm-water locations from Shikoku Island and adjacent Honshu; humpback whales and tropical dolphins in the island archipelagos off southern Japan; minke whales and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) from Hokkaido in the north; and bottlenose and other dolphins at a variety of locations and narrow-ridged finless porpoises (*Neophocaena asiaorientalis*) off southern and eastern central Japan.

The compatibility of whaling and whale watching has been debated by whaling and non whaling countries within the International Whaling Commission (IWC). Since the 1980s, whale watching has started in most member countries; whales have been shown to be “worth” much more alive than dead (Cisneros-Montemayor et al., 2010). Whaling can reduce the number of whales available for watching, change whale behavior, and potentially affect the larger tourism industry (Hoyt and Hvenegaard, 1999). Yet, despite the persistence of whaling, Iceland has become one of the fastest growing whale watching destinations in the world, with five main communities hosting more than 272,000 whale watchers, as of 2015, with approximately one in every five visitors going whale watching.

Whale watching remains more popular in non whaling countries. According to the most recent worldwide figures (2008), six countries, led by the USA, were attracting more than 500,000 whale watchers per year with three surpassing 1 million. In order, they were USA (4,899,809), Australia (1,635,374), Canada (1,165,684), Canary Islands (Spain) (611,000), South Africa (567,367), and New Zealand (546,445) (O'Connor et al., 2009). The 2008 world totals revealed that nearly 13 million people went whale watching in 119 countries and overseas territories, spending more than USD \$2.1 billion (Hoyt, 2001; O'Connor et al., 2009) (Table 1).

The value and extent of dedicated non cetacean marine mammal tourism has been estimated in a number of areas. Harbor seal sites in the glacier fjords of Alaska have experienced a ten fold increase

**TABLE 1** Estimated Worldwide Growth of Whale Watching Tourism

Year	Number of whale watchers	Average annual growth rate (%)	Direct expenditure USD (million) <sup>a</sup>	Total expenditure USD (million) <sup>b</sup>
1981	400,000		\$4.1	\$14.0
1988	1,500,000	20.8	\$11.0–16.0	\$38.5–56.0
1991	4,046,957	39.2	\$77.0	\$317.9
1994	5,425,506	10.3	\$122.4	\$504.3
1998	9,020,196	13.6	\$299.5	\$1,049.0
2008	12,977,218	3.7	\$872.7	\$2,113.1

Hoyt, E. (2001). *Whale Watching 2001: Worldwide Tourism Numbers, Expenditures, and Expanding Socioeconomic Benefits*. International Fund for Animal Welfare, Yarmouth Port, MA; O'Connor, S., Campbell, R., Cortez, H., and Knowles, T. (2009). *Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare, Yarmouth MA, USA, prepared by Economists at Large*. 295 pp.

<sup>a</sup>Direct expenditure = Cost of whale watching tour (ticket price).

<sup>b</sup>Total expenditure = The amount spent by tourists going whale watching from point of decision, including transport, food, accommodation, and souvenirs, as well as ticket price, but not including international air fares.

in tour-ship visitation since the 1980s (Jansen et al., 2015). Around Monterey, California, sea otters (*Enhydra lutris*) have become mascots for the region, with a value to tourism in the millions of dollars. That value became clearer when a plan to allow sea otters to expand their range southward to Santa Barbara, was subjected to a cost-benefit analysis. Annual sea otter tourism benefits to the region were estimated at USD \$1.5–\$8.2 million in direct income, as well as a median non market (mainly existence) value of USD \$21 million against annual potential losses to commercial fishing amounting to USD \$610,000 (Loomis, 2006).

In some areas where marine mammals are hunted, comparisons have been made between the value of tourism vs hunting. In Namibia, more than 100,000 people watched Cape fur seals (*Arctocephalus pusillus*) in 2008, spending USD \$2 million, while the seal hunting industry that year had an estimated landed catch value of USD \$513,000 (Campbell et al., 2011). Seal hunting in Namibia has expanded nearly three fold since 1990 and is thought to be at or near capacity in terms of the number of pups that are taken, while the young tourism industry has a greater capacity for growth and spreading benefits throughout the community. In Canada, home to two-thirds of the world's polar bears (*Ursus maritimus*), a study of their total economic value, including passive and indirect-use values of scientific, educational and conservation benefits that come from an iconic species, as well as the value humans put on knowing that polar bears exist in the wild—produced estimates of USD \$5,750 million per year for all Canadians (ÉcoRessources Consultants, 2011). The value of polar bear tourism, calculated as the tourism spend in Churchill, Manitoba, was USD \$6.5 million per year. By comparison, sport hunting of polar bears in the Canadian Arctic earned USD \$1.2 million/year and subsistence hunting was worth USD \$545,000/year.

#### IV. Growing Pains and the Institution of Guidelines and Regulations

The explosive growth in whale watching and other marine mammal tourism has led to management problems. Typical

scenarios include: Too many boats on the water in a confined area due to the size or location of the marine mammals' critical habitat; too many close approaches; strain on the infrastructure of a community and the environment of marine mammals from too many visitors; disputes and a competitive atmosphere among tourism companies; ineffective guidelines, regulations and enforcement; and poor compliance to existing rules (Hoyt, 2005, 2012). South Africa and New Zealand have addressed many of these problems via the establishment of permit systems, offering a limited number of permits.

Guidelines and regulations for viewing marine mammals have been adopted in more than 50 countries with marine mammal tourism (Carlson, 2014). The minimum distance and approach rules have been put forward, largely without scientific foundation, as precautionary limits. Most guidelines and regulations are considered to be mainly for the animals' benefit but, if followed, they help address human safety issues as well. However, the sheer numbers of boats on the water with whales day after day in so many places has increased the risk of accidents.

Since 1983, more than a dozen marine mammal tourism-related fatalities, mainly due to breaching whales, and overturned boats, have occurred in at least six different places. The number of fatalities and injuries is small considering the millions of people who engage in marine mammal tourism every year. Most accidents have happened due to the operation or maintenance of the boats—issues that are not specific to marine mammal tourism but could happen as part of any type of marine tourism.

Safety is also a concern for the tours involving swimming or diving with marine mammals. Organized swimming tours have a good safety record with thousands of encounters in such places as New Zealand, the Bahamas, and Japan, although incidents of people swimming with lone, sociable dolphins have sometimes led to aggressive head butting. At Crystal River National Wildlife Refuge, in Florida, hundreds of thousands of people every year swim with the local manatees. Some researchers maintain that swimming with this endangered marine mammal should not be allowed—not just on human safety grounds but related to the risk of disturbing a threatened species.

#### V. Tourism Impacts on Marine Mammals and Marine Mammal Populations?

Many researchers have documented short-term behavioral responses of whales and dolphins to whale watching boats including animals: avoiding or approaching boats; suddenly changing speed or direction; staying down longer; reducing the time spent resting, socializing or foraging; altering vocalization patterns or other natural behavior (Higham et al., 2014; New et al., 2015). But, different species, populations and even, individuals may not consistently react to the same stimulus and certain individuals may not react at all (New et al., 2015). Behavioral responses also vary depending on whether individuals are breeding, feeding, resting, socializing or migrating, and can differ according to vessel type, number of vessels and closeness of the approach. Some behavioral responses are less visible, such as “masking” effects from vessel noise that may pose a problem for species dependent on sound for communication, navigation, foraging and breeding (Erbe, 2002; Foote et al., 2004; Sousa-Lima and Clark, 2008).

To what extent are short-term behavioral responses leading to long-term negative impacts? Some answers are evident with small, inshore populations of bottlenose dolphins living in restricted areas or close to shore at Doubtful Sound, New Zealand (Lusseau,

2003, 2006) and Shark Bay, Australia (Bejder et al., 2006a). In these populations, repeated exposure of individuals to whale watching has led to long-term impacts including habitat displacement, decline in populations and decline in reproductive success (Bejder et al., 2006b; Foote et al., 2004; Higham et al., 2014; Lundquist, 2014; Report of the Workshop on the Science for Sustainable Whalewatching, 2004; Williams et al., 2002, 2006, 2009). These and other studies have highlighted the sensitivity of, particularly, small dolphin populations chronically exposed to whale watching. Yet even large whales sometimes show behavioral changes because of whale watching which, for some populations, may become problematic for survival.

Both recreational boats and commercial whale watching boats have struck whales, with particular examples highlighted in Lammers et al. (2013) for humpback whales off Hawai'i and common bottlenose dolphins run over by speed boats off Panama (Sitar et al., 2016). In most areas of the world, commercial whale watching boats are vigilant about the presence of whales, but they spend more time in proximity to whales than other boats. To avoid collisions, all boats operating in whale areas should post watches, maneuver carefully, give cetaceans a wide berth, and cut their speed to 12 knots or less.

In the Arctic, the spread of nature tourism in general has put more people in polar bear habitat while in Florida mass tourism has contributed to an increase in pleasure boat traffic in manatee habitat—in both cases with results fatal to the animals. Polar bears that present danger to human life are shot, while manatee deaths are accidental, often due to careless boat driving in the inland waterways.

The impacts of mass tourism on marine mammals and their habitats present another concern. The mass tourism industry, for example, has played a role in the decline of Mediterranean monk seal (*Monachus monachus*) populations in the islands off Spain and Greece, as well as Turkey, Tunisia and Madeira, mainly due to habitat destruction from building hotels or persistent human presence (Johnson and Lavigne, 1999). Monk seals have been driven from breeding areas on beaches and along rugged coastlines where they may live in caves; they are being displaced by pleasure boating, diving, and speargun fishing. The situation is exacerbated as the high season for tourism corresponds to the May to November pupping season (Johnson and Lavigne, 1999).

## VI. Tourism and Conservation: Making Marine Mammal Tourism Sustainable

Well managed, sustainable marine mammal tourism begins with a government policy protective of marine mammals and their habitats. Ideally, such a policy would employ a competitive permit system, and a regulatory and enforcement regime to control the number of operators engaged in marine tourism, the number of boats on the water and the rules to limit the closeness of their approach as well as the amount of time they spend with particular marine mammal populations (IFAW et al., 1995; Higham et al., 2009, 2014; Hoyt, 2012). A practical, precautionary plan would keep one-third of every marine mammal tourism area and one-third of daylight hours free from any tourism activity (Hoyt, 2012; Tyne et al., 2014). Such restrictions on areas and times would also prove useful as controls for researchers doing comparative studies.

Management of this industry should also be actively engaged in education of marine mammal tourism operators, passengers, and recreational vessel operators who use the same waters as marine mammal tourism boats. Numerous operator associations have

sprung up for education on proper protocols. Central to education, especially on tour boats, is the role of naturalists, or nature guides, who are the public face of marine mammal tourism as well as marine protected areas (IFAW et al., 1997; Hoyt, 2012). Naturalists can act as a bridge between the largely urban wildlife tourists and the ocean. The tourists themselves, as well as government regulations (e.g., New Zealand), have called for a stronger educational component on tours (Lück, 2003, 2015, 2016). Considerable thinking, informed by surveys of tourists, has gone into devising effective interpretation programs to achieve greater tourist satisfaction (Orams, 1999). To maximize the educational and conservation benefits, much more must be done to mandate the use of naturalists on every tour, and to formalize and empower marine mammal nature guiding as a profession.

Still other strategies attempt to manage the development and practice of marine mammal tourism to minimize the risk from adverse impacts. In some areas of the world, watching whales from a large, comparatively quiet ship may reduce the pressure exerted by numerous small boats with outboard engines, while watching from a land-based lookout can eliminate negative effects on cetaceans, sirenians, as well as pinnipeds and otters when they are not on or close to land. Marine mammal tourism needs to adopt more of the principles of the best bird and land-based wildlife watching—unobtrusive watching stations, or blinds, the ethic of watching without disturbing natural behavior, the idea of leaving the lightest possible footprint (Hoyt, 2012).

Responsible sustainable marine mammal watching offers an economic alternative to whaling or sealing, by protecting marine mammal populations. The issue is not marine mammal watching vs hunting, but rather how to create a public more interested in conserving wildlife, the ocean, and the environment. To the extent that marine mammal tourism can serve these goals, it may be welcomed, or at least receive less criticism.

Wildlife managers and tourism authorities are increasingly called upon to balance human needs and impacts on wildlife and ecosystems. Higham et al. (2014) call for a multi-stakeholder approach to attain sustainability. Researchers have suggested the modeling of cumulative effects to investigate the population consequences of individual changes in cetacean behavior and physiology due to disturbance. One approach to achieve sustainability is to put marine mammal tourism in a cost-benefit scenario in which a concerted effort is made to increase the benefits associated with marine mammal tourism while reducing, as much as possible, the cost to marine mammals, coastal communities and the ocean ecosystem (Hoyt, 2012). With these sorts of approaches marine mammal tourism could become a sustainable industry, and an overall conservation success story for the marine mammals themselves.

### See Also the Following Articles

Conservation ■ Ethics ■ Marine Protected Areas ■ Popular Culture and Literature

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## TRAINING

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### I. Introduction

Marine mammal training gained formal recognition in the late 1940s. One of the first facilities to successfully manage a breeding population of bottlenose dolphins (*Tursiops* spp.), Marineland of Florida (St. Augustine), also became the first organization to institute a training program. Early methods of training were considered industry secrets and often included techniques that would not be used today, such as trial and error learning, fixed ratio schedules



of reinforcement, and aversive consequences that could produce unwanted behavior. However, as the field evolved, the practice of applied behavior analysis (ABA), which is the application of principles of learning to improve and modify behavior, became the gold standard. Today, animal training, research, and behavior medicine are utilized to foster animal health and welfare, shape and maintain prosocial behaviors, manage breeding groups, contribute to a growing body of scientific literature, and educate the public. These efforts also cultivate public interest in wildlife conservation and concern for the world's oceans.

Many of the recent developments in the field of training can be attributed to the use of applied operant conditioning, where singular behaviors are systematically approximated, shaped, and strengthened by the consequences that immediately follow. While operant conditioning is not the only mechanism used to train marine mammals, it is highly effective and central to sound animal management programs (see Pryor, 1995). In the broader context, successful behavior management is not confined to the training and learning of individual responses within controlled settings, but instead coordinates principles of behavior that serve to modify and improve the behavior of large groups, both captive and wild, with complex social structures. Behavior management encompasses a multitude of applied learning principles, including classical, operant, and observational learning. It also involves multiple disciplines, as these efforts shape and maintain behaviors that support optimal animal health and well-being and conservation research.

The field of marine mammal training and behavior management emphatically discourages the use of aversive techniques and as such, stands as a model for ethical animal training and animal welfare. This philosophy of applied reinforcement, in conjunction with eliminating aversive practices, has created a much safer and more harmonious environment for both trainers and animals by reducing stress and the rehearsal of escape, avoidance, and aggressive behaviors. Though some criticize captivity, the world zoo and aquarium community allocates significant funds to conservation research and animal rescue and rehabilitation efforts, in amounts upwards of \$350 million dollars (USD) annually (Gussett and Dick, 2011). Additionally, many marine mammals are flagship species, inspiring those who are able to view and interact with them to actively protect ocean ecosystems. Though gaining popularity worldwide, US legislation prohibits interactions with wild marine mammals due to the inherent safety risks and the potential to disrupt behaviors critical to animal survival (e.g., Baker et al., 1988; Corkeron, 1995; NOAA Fisheries, Office of Protected Resources, 2012; Salden, 1988; Scarpaci et al., 2000). As such, marine mammal facilities provide a comparatively safe, legal, and educational alternative, while also instilling in visitors a motivation for continued education and a sense of environmental stewardship.

## II. Animal Learning and Behavior

Animal learning is the modification of behavior in response to various stimuli and experiences. It is critical to survival, as it enables animals to adapt to ever-present social and environmental changes. The study of animal learning involves evaluations of not only specific responses and biological processes but also detailed aspects of psychology, such as memory, early development, classical and operant conditioning, and cognition (e.g., Spear and Riccio, 1994). Here, we include some of the most widely utilized psychology principles (see Domjan, 1993), with an emphasis on those with significant future impact on animal care and well-being.

### A. Observational Learning

Also known as *modeling*, this vicarious process is defined as learning by observing another (i.e., the model). During observational learning, the animal (observer) need not emit the behavior, experience direct consequences, or receive applied reinforcement for learning to occur. Mimicry is a by-product of observational learning. It is a primary learning mechanism for young animals reared in a complex social environment and theoretically contributes to socialization, vocal development, foraging success, and fitness.

Among newborn killer whales and dolphins, motor skill development occurs rapidly within a few weeks postparturition. During this time, observational learning becomes evident, and increased independence (i.e., time and distance away from the mother) begins to emerge as motor skill, buoyancy control, visual acuity, communication/echolocation, and auditory learning strengthen. In some cetaceans, when teeth begin to erupt, the mother initiates the weaning process through food sharing, involving partially digested/regurgitated or masticated food. This appears to coincide with accelerated learning and may signal the beginning of a *sensitive learning phase* or *critical period*, defined as a developmental stage during which rapid acquisition of behaviors occurs. For marine mammals born in zoological facilities, most formal training begins during this stage, and many of these behaviors are “captured,” meaning they are opportunistically reinforced, to accelerate the learning process. Although regression often occurs when the model is no longer present, observational learning clearly plays a critical role in the development of marine mammals.

### B. Classical Conditioning

Classical conditioning is characterized by the pairing of a conditioned stimulus (CS) with an unconditioned stimulus (US) and was first described by Pavlov in the early 1900s. Early interpretations of his work investigating anticipatory salivation in dogs led to a restricted view that classical conditioning only produced a conditioned response (CR) via reflex systems. In recent years, research in the field of experimental psychology has replaced this view with a more dynamic understanding of Pavlovian learning. Associations between conditioned and unconditioned stimuli have been linked to learning phenomena such as *sign tracking* (movement towards a stimulus that signals the availability of a positive reinforcer such as food), *conditioned emotional responses* (anxiety/fear), and *conditioned taste aversion* (food preference/avoidance) (Cole et al., 1996).

The accidental or deliberate pairing of events, which occurs regularly in both the wild and captivity, can create learning via classical conditioning and can profoundly influence the training of marine mammals. In the wild, the presence of fish in nets (US) and the sound of fishing boats (CS) can elicit boat following (CR) instead of avoidance. However, pairing a loud noise (CS) with a painful (US) medical procedure can exacerbate and increase the probability of a fear reaction (CR) to that same noise in the future. In this scenario, a minor avoidance response by the animal could intensify into a panic response, causing injury to the animal or the animal handlers. In another applied example, pairing food with an aversive medical procedure can cause an animal to avoid eating, leading to weight loss even after the illness is no longer present. As such, a conditioned food aversion (i.e., the Garcia Effect) can be an unintended by-product of seemingly unrelated events. Pavlovian or respondent learning can even be utilized to produce a condition food *preference* by pairing the US (novel food item) with a CS (familiar food item) to produce a CR (eating response).

### C. Operant Conditioning

Commonly defined as behavior that is modified by consequences, operant conditioning leads to instrumental learning and is the most widely employed training regimen for marine mammals (Ramirez, 1999). The three basic components of instrumental learning, however, must occur in precise order for learning to be achieved. This temporal and proximal relationship among components defines the Law of Contiguity. The entire learning cycle is represented by an *antecedent* (a stimulus or cue that precedes the behavior), followed by the *behavior* (the resultant response emitted by the animal), and finally, the *consequence* (a stimulus or applied reinforcement that immediately follows the response and acts to increase or decrease the preceding behavior) (see Honig and Staddon, 1977).

Consequences play a key role in operant conditioning, as they cause a behavior to become more or less frequent in the future (Baldwin and Baldwin, 1998). Reinforcers will strengthen a behavior and increase the likelihood of it occurring in the future, whereas punishers decrease the frequency of a behavior. The terms “positive” and “negative” are used as mathematical descriptions to indicate if a stimulus is being applied or removed and not whether something might be “good” or “bad.” Therefore, positive reinforcement would consist of applying a rewarding stimulus as a consequence of a behavior, whereas negative reinforcement would consist of removing or terminating an aversive stimulus. In both cases, the preceding behavior will be strengthened. Conversely, positive punishment is the application of an aversive stimulus as a consequence of a behavior, while negative punishment is the removal or subtraction of a rewarding stimulus. In both scenarios, the preceding behavior will decrease in frequency. Central to managing and modifying optimal animal behavior and care is a clear understanding of how all consequences, produced by the trainers (purposefully or accidentally), the environment, or the animals themselves, affect behavior.

During a typical marine mammal training session, a hand signal (antecedent) is usually presented to the animal, followed by the animal’s response (behavior). If correct, the behavior is reinforced (consequence) by the trainer with either primary reinforcement (i.e., food) or secondary reinforcement (e.g., touch, toys, play, and activities). Incorrect or undesired behaviors are usually ignored with minimal or no consequence applied. Punishment and negative reinforcement is avoided or eliminated.

Principles critical to a successful training session include but are not limited to: *Stimulus consistency, stimulus fading, behavioral criterion, behavioral development, delay of reinforcement, schedule of reinforcement, magnitude, and placement of reinforcement* (see Kazdin, 1994). Like other forms of learning, operant conditioning should not be characterized as a “technique” or “system” of training that can be switched on and off conveniently; instead, it is a dynamic and ever-present environmental learning phenomenon that influences the acquisition, maintenance, intensity, and extinction of specific behaviors. Behaviors are in the constant process of strengthening or diminishing as a result of the consequences, or lack of consequences, that follow.

As a whole, marine mammal training programs emphasize the following:

1. *Optimal Learning Conditions* Naïve animals, defined as those with limited to no prior training experience, are often cautious and wary of their surroundings. This apprehension can be reduced by establishing optimal learning conditions, specifically by minimizing or eliminating elements that can create anxiety

and avoidance, such as aversive procedures, an unstable environment, incompatible conspecifics, and/or unfamiliar sounds. The process of extinguishing avoidance behavior is aided by the cumulative positive effect of daily feedings and time spent with the animal, allowing both desensitization and familiarity to foster a more comfortable learning environment. Marine mammals will readily take food from a familiar caregiver and generally allow some calm contact during feeding times. This provides the foundation for positive reinforcement when food and tactile can be applied contingent upon an appropriate response. As a reinforcement history develops, unavoidable aversive events, such as routine medical treatments, have less impact and cause minimal regression. The opposite is also true, with repeated, aversive procedures and unstable environments present early in the process may cause profound anxiety and avoidance, thereby delaying the favorable response to the trainer.

2. *Conditioned Reinforcers* Unconditioned reinforcers, such as food and water, satisfy a biological need and therefore, are effective without having to be learned or conditioned. In contrast, conditioned reinforcers, such as toys or tactile contact from a trainer, are stimuli that were once neutral but gain reinforcing properties by repeated pairing with unconditioned reinforcers. The consistent delivery of an *unconditioned reinforcer* (such as food) as an immediate consequence to a desired behavior establishes the foundation for training a *conditioned reinforcer* (a stimulus that has acquired reinforcing properties through learning) (Chance, 1994). These conditioned reinforcers are an important tool for marine mammal behaviorists, as they provide a greater variety of positive consequences to motivate and shape behavior.

Arguably, one of the most important conditioned reinforcers is the audible whistle, called a “bridging” stimulus. This bridging stimulus acts as a cue that signals the imminent application of reinforcement. It is referred to as a “bridge,” because it acts to bridge the time delay between the precise behavior targeted for increase and delivery of a positive consequence. This minimizes the delay of reinforcement gradient, which is a decrease in learning efficacy as a function of increasing time between the response and the reinforcer.

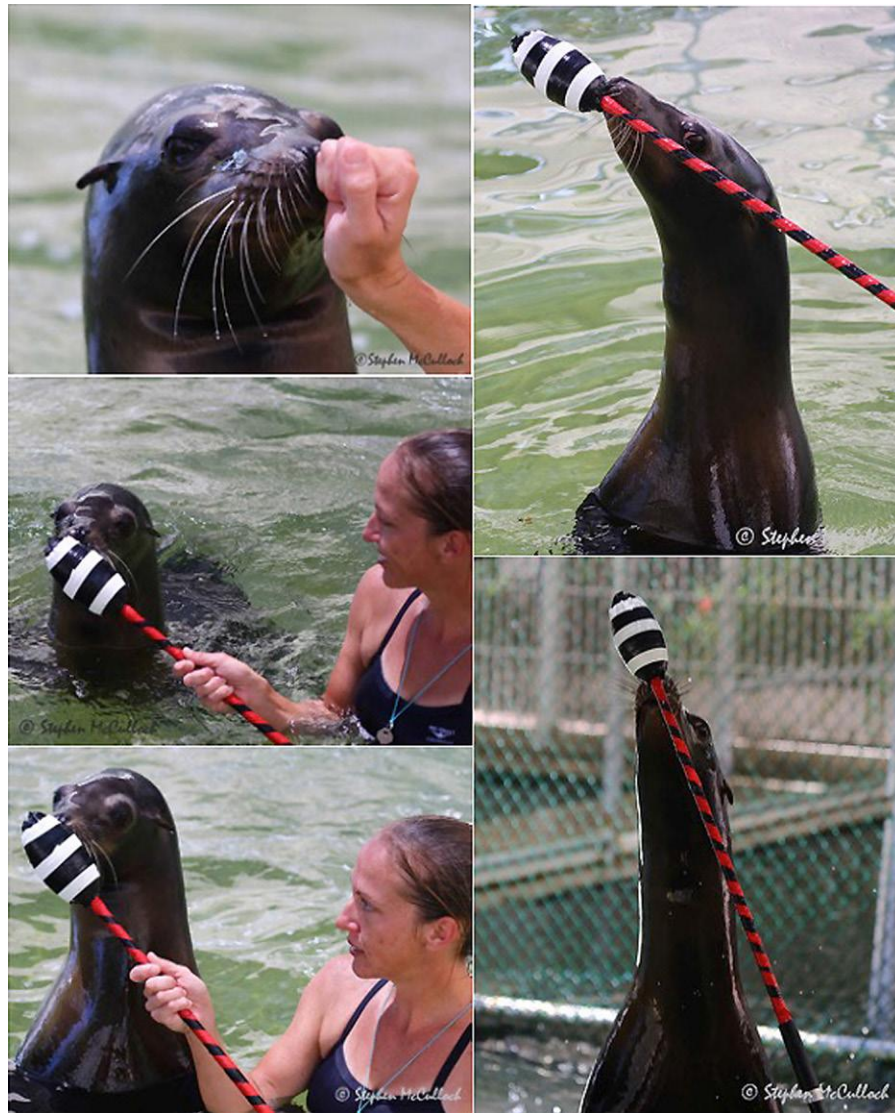
3. *Increasing the Attention Threshold* Maintaining an animal’s attention is critical to advancing learning and facilitating a safe and productive environment. As such, an early emphasis on *attention threshold*, defined as the duration a stimulus will control behavior, is necessary. This is achieved by systematically increasing the amount of time the animal will continue to engage with and orient towards the trainer, typically shaped using increments of a few seconds, prior to reinforcement delivery. Eventually, an attention span of several minutes can be conditioned if bridging and reinforcement is precise, while a lack of precision can interfere with or delay the acquisition of a lengthened attention threshold. This is particularly important in the training of species such as Commerson’s dolphins (*Cephalorhynchus commersonii*), young animals, or animals in high stimulus environments.
4. *Following a Target to Shape Behavior* If the pairing of the delivery of food by hand with the bridge stimulus has been well timed and consistent, the animal will readily move towards and touch a trainer’s hand prior to the bridge. The behavior of touching is then reinforced. For a naïve animal, this can be accomplished after the first few feedings. Eventually, the hand can be moved back and forth to shape and strengthen the hand-touch response, and in time, the animal will move to the

hand wherever it is placed. Target poles (i.e., a long pole with a small round float, or “target,” attached to the end) are often introduced at this stage to simulate an extended reach (Fig. 1). Touching and following the target can be reinforced, allowing trainers to safely shape a variety of high-energy behaviors, which are an important component of exercise and animal health.

5. *Achieving Stimulus Control* As animals begin to understand the relationship between their emitted response (behavior) and the delivery of reinforcement by the trainer (consequence), they also learn which behaviors are likely to produce reinforcement. Discrimination between learning events occurs when animals respond differently to distinctive antecedent cues, often presented as visual or audible signals (*discriminative stimulus* or an  $S^D$ ) preceding each behavior. The trainer offers reinforcement only for specific responses and thereby facilitates discrimination learning. This is referred to as *stimulus control*, in which behaviors are reinforced in the presence of a particular signal or stimulus but not for others. *Random sampling*, characterized by emitting several behaviors in an attempt to gain access to

reinforcement, is a common phenomenon early in the training process. However, trainers ignore all but the requested behavior, thereby facilitating the process of stimulus control and discrimination learning. Discriminative stimuli are introduced early in the shaping process and precede each behavioral response. New cues are acquired if they precede previously learned cues, which are eventually faded out as the animal learns to anticipate the correct response, resulting in the novel cue evoking the desired behavior (i.e., achieving stimulus control).

6. *Successive Approximations* The most effective trainers break each behavior down into simple and planned steps. Each small step, or *approximation*, is reinforced if completed successfully, until the animal consistently responds to the antecedent cue ( $S^D$ ). Each behavior will be shaped using individual approximations preceded by specific  $S^D$ s. The trainer will continue with the approximations in sequence, gradually adding new steps until the goal is achieved. For example, a high jump with a sea lion begins with the lifting of the head to touch a raised hand or target. If this small step is successfully completed, the sea lion



**Figure 1** Like dolphins, sea lions are also trained to follow targets, which helps shape behavior (Photos by Steve McCulloch, Theater of the Sea).

will receive reinforcement, and the trainer will raise the criterion slightly on the next approximation. In effect, each behavior can be visualized by the trainer as a systematic process of small approximations, each preceded by a cue ( $S^D$ ). All behaviors, including very complex behaviors, can be broken down in such a manner, facilitating animal learning and minimizing frustration.

7. *Schedules of Reinforcement* A schedule of reinforcement refers to the timing and frequency of reinforcement, and behavioral plans lacking precision in this regard can lead to learning problems. Various schedules of reinforcement have been empirically derived in learning laboratories and applied in marine mammal training programs. Initial training efforts involving positive reinforcement utilized a Fixed Ratio(1), or FR1, schedule in which every correct response was rewarded with a fish. While initially effective, the use of a strict FR1 reinforcement schedule produces the greatest frequency of aggression, known as Schedule-Induced Aggression, and rapid behavioral extinction when a response is not reinforced. It also relies on the animal being constantly hungry and therefore, does not promote optimal health and weight maintenance. Through practical application, many facilities are beginning to recognize the importance of *variable schedules of reinforcement* and reinforcement variety [i.e., primary reinforcement (food variety), secondary reinforcement (toys, objects, tactile variety) and Premack reinforcement (favored activities, environmental changes, socialization opportunities)]. This type of delivery provides reinforcement and enrichment intermittently and unpredictably and has been proven in experimental settings of both humans and nonhuman animals to produce the highest and most reliable rates of behavioral response.

Learning, whether observational, instrumental, or Pavlovian, is ever-present and is constantly shaping behavior independent of a formal training program. Law of Effect of Thorndike (1898) describes these phenomena and the plasticity of behavior that occurs as an ebb and flow in response to various environmental consequences. Even daily cleaning, feeding, and operational activities at a zoological facility can effectively act to shape and modify behaviors. For example, the arbitrary appearance of the staff veterinarian, a possible conditioned aversive stimulus, might inadvertently act to suppress courtship behavior depending on the timing of the appearance. In another example, trainers emerging with lunch may act as a reinforcer to an animal, thereby strengthening the preceding behavior—whether the behavior was appropriate or inappropriate. As such, behavior management objectives can be significantly impacted if behavior is not evaluated prior to the application of these environmental stimuli. The principles of learning and the effects of timing can even drive stereotypic patterns, such as anticipatory pacing prior to feeding time, creating an opportunity for *adventitious* or unintended reinforcement. This is why, in addition to strategic animal training objectives, comprehensive behavior management plans should be utilized at all zoological institutions to avoid unintended negative effects of accidental reinforcement on animal welfare and well-being.

### III. An Emphasis on Positive Reinforcement

Positive reinforcement-based training creates an environment that is nonthreatening and therefore, facilitates learning, while maintaining a strong desire to interact with trainers. Significantly, the most effective training programs develop a foundation of voluntary cooperation as opposed to forced compliance and are often

applied to elephants, horses, dogs, and even humans. With voluntary cooperation as a highest priority in training, behaviors once thought impossible have been achieved, and positive reinforcement has been the common element in many of the breakthroughs in marine mammal training. These programs emphatically discount the use of *negative reinforcement* and *punishment*, which often results in aggression. Establishing and maintaining behavioral consistency via the sole use of positive reinforcement may prove to be the marine mammal training industry's most profound contribution to animal welfare and the social sciences.

## IV. Training, In General

Many cetacean species have been successfully trained using operant conditioning, including but not limited to killer whales, pilot whales, belugas, rough-toothed dolphins, white-sided dolphins, Commerson's dolphins, and bottlenose dolphins, the latter representing the majority of cetaceans in formal training programs. While each species requires some adjustment in training to address unique natural history, energetics, diet, sociality, and size, the principles are the same for all. Regardless, there are some specific applications relevant to cetaceans:

- Most behaviors are trained in relatively deep water. The use of long target poles, PVC out-rigger poles fitted with a Styrofoam float, are commonly used to help guide the animal through the required approximations and away from shallow water hazards, especially when training high aerial behaviors.
- With average peak-hearing sensitivity in ranges upwards of 20kHz for most cetaceans, trainers often utilize a high-frequency dog whistle as a bridging stimulus. Although there is evidence that average human speech frequencies (0.085–0.250kHz) may be detectible by dolphins at their lowest hearing threshold, high-frequency dog whistles provide greater reliability, particularly when ambient noise is present during training programs.
- Frequent dietary adjustment, specific to each demographic, that maintains optimal body weight year-round produces more stable behavior while maintaining optimal health. As such, scale training, without the use of forced restraint, is essential. Without this, cetaceans often experience significant weight gain or loss, causing instability in behavioral response and social stress.
- Gate training (i.e., moving to and from various enclosures on cue) is critical to the care and safety of any cetacean population. Gating allows for individual training sessions, separation into medical pools for diagnosis and treatment, and the use of sanctuary zones for animals that are very young or old and cycling females.

### A. Training Pinnipeds

Various pinniped species have been successfully trained for a wide variety of applications, including shows, guest interactive programs, open ocean research, rescue and recovery operations, and military applications, though California sea lions (*Zalophus californianus*) represent the vast majority of trained pinnipeds housed in zoos and aquariums. Since most pinnipeds can locomote well in water and on land, there is versatility in training procedures, with a large proportion of training accomplished on dry land. Those applications specific to pinnipeds include:

- On land, training is easier but often risky, since pinnipeds can be aggressive if not handled properly. Sea lions live in large colonies and exhibit aggressive behavior and dominance displays

regularly in the wild, and these behaviors should be expected in managed care, particularly during breeding season or during periods of significant weight gain. If managed inappropriately with the use of aversive techniques, including threat displays, forced restraint, or other learned aversive stimuli referred to as stimulus-delta ( $S^{\Delta}$ ), aggression will escalate and can become a significant safety risk. While aversive stimuli may produce a temporarily desired effect through negative reinforcement (avoidance/removal of the  $S^{\Delta}$ ), it will eventually produce a very dangerous environment for trainers.

- Pups, particularly males, should be maintained in a calm environment early in the training process using differential reinforcement, because they mature into animals the size and strength of bears. Pups with a history of rough handling, such as a force-feeding regimen when stranded and malnourished, will often challenge handlers with aggressive threat displays at a very young age. While this behavior can be diminished over time with correct technique, stimulus control from a distance should be established initially (i.e., reinforcement for remaining at a safe distance from the trainer), followed by tactile desensitization utilizing protected contact (e.g., touch and reinforce through a fence or secure barrier) until the animal is nonreactive to tactile interactions. Once these important foundations are established, training can accelerate.
- Like cetaceans, pinnipeds benefit from the use of a bridging stimulus to assist in learning; however, their hearing thresholds (0.10–35 kHz) make them better suited to recognize and respond to the human voice. Therefore, a simple word, such as “good,” can be an appropriate and common substitute for a whistle and eliminates superfluous training tools. Though both visual and acoustic cues ( $S^D$ s) are equally effective in training pinnipeds, verbal cues are particularly useful among sea lions experiencing age related deterioration in vision.
- During spring breeding season, male California sea lions can gain weight rapidly, even on a restricted diet, triggering an increase in barking, dominance posturing, and fighting. The use of body weight maintenance and scale training for daily measurement should be considered essential to humane care. Frequent dietary adjustment combined with differential reinforcement training helps stabilize behavior and maintains sea lions within healthy weight ranges. This prevents rapid gains or losses, as well as resultant aggression, associated with seasonal/hormonal changes, such as breeding, molting, and changes in seasonal thermoregulatory metabolic demand (Turner and Stafford, 2000).

## B. Evolving Applications and Advanced Concepts

Marine mammal training and behavior management is becoming increasingly sophisticated due to its utility in mitigating complex behavior problems, such as stereotypies, self-injurious behavior, stress, hyperactivity, lethargy, social aggression, and schedule-induced frustration. Utilizing reduction techniques derived from applied behavior analysis, unwanted behaviors can be measurably reduced in frequency, intensity, and/or duration. In many cases, these behaviors can be eliminated altogether and even replaced with more appropriate behaviors. An understanding of information processing in marine mammals, pioneered by scientists like Ron Schusterman (1932–2010) and Lou Herman (1930–2016), improves our ability to manage the behavior of marine mammals to optimize their fitness, health, and welfare in multiple environmental settings. Investigations of memory retrieval, short and long-term memory

capacities, context specific learning (i.e., learning in one environment that does not transfer to another environment), and cognition may even contribute to the management of wild populations by better understanding environmental factors that influence the expression of different behaviors.

## C. Calf Survival and Reproduction

Epimeletic or care-giving behavior can be shaped by applied behavior management to increase the probability of calf survival. Classical conditioning has been successfully used to help elicit orienting response, suckling, and bottle-feeding among orphaned cetacean calves and pinniped pups. During the first few hours of life, the primary challenge for marine mammal newborns is maternal acceptance, as healthy neonates are sometimes rejected for reasons not fully understood. Though rare, this phenomenon has been observed in many marine and terrestrial species, both wild and captive, including humans. Training can be applied to this scenario to prompt nursing behavior (i.e., presentation of the mammary to the soliciting calf), which is particularly important for first-time mothers and/or those without observational models. Applied behavior analysis can also accelerate the expression of other epimeletic behaviors, such as parallel swimming, calf protection, and calf retrieval, while also encouraging calm behaviors and avoiding accidental or *adventitious* reinforcement of calf rejection.

Access to females and their offspring has provided unprecedented opportunities to better understand reproductive biology, parturition, and neonate development, with important implications for wild populations for which observations are difficult or sometimes impossible. For example, separation training combined with calf retrieval training led to the discovery that mothers utilize distinctive calls to reunite with their calves (Kuczaj et al., 2015a). Among stranded marine mammals, data collected in captivity can influence the course of treatment, the development of species-specific formulas, and other behavior management decisions necessary to improve the odds of survival. In 1997, SeaWorld San Diego assisted in the rescue and managed the recovery and release of an orphaned gray whale (*Eschrichtius robustus*) calf using operant conditioning to increase activity level and adjust eating patterns to more closely match the bottom feeding strategies of wild gray whales (SeaWorld, 2006).

## D. Reintroduction Programs

The translocation of wild animals and the release of marine mammals held for short periods, typically for research or rehabilitation purposes, can be successful with thorough behavior management plans and may support unique research opportunities. However, the release of animals born or housed long-term in zoological facilities should be approached carefully and should always include health screening and scientific monitoring of released animals to ensure their well-being and the success of the reintroduction. Some marine mammal releases have been over-simplified by extremist anti captivity groups. Although emotionalizing their concept of “freedom,” these groups generally discount the biological need of such experiments, particularly for nonendangered species, while often disregarding the very real and complex survival obstacles an animal must confront in the wild. Therefore, a thorough and unbiased scientific review must be completed before a required permit to release an animal can be granted in the United States. Past attempts at poorly executed and even illegal releases have resulted in the needless suffering and death of marine mammals, and

unfortunately, claims of success have been reported without proper conditioning, scientific verification, or follow-up.

However, a number of captive-born terrestrial mammal species have been released into historical home ranges with success. Endangered animals, such as red wolves (*Canis rufus*), golden lion tamarins (*Leontopithecus rosalia*), and black-footed ferrets (*Mustela nigripes*), are examples of well-managed and scientifically sound protocols that contribute to the recovery of wild populations. Due to their endangered status and the biological necessity to make their genetic material available in the wild, the risks and costs of such programs are deemed acceptable. These animals are carefully managed at reputable facilities, candidate animals are selected based upon stringent criteria, population and environmental dynamics carefully reviewed, behavioral repertoires (e.g., predator avoidance and foraging skills) are strengthened, tracking and follow-up protocols scrutinized, unbiased scientific review completed, and legal permits obtained before such an undertaking begins.

## V. Animal Acclimation

The Yerkes-Dodson law (see Malott and Shane, 2013) suggests that learning and performance are influenced both positively and negatively by stress and arousal. For example, the assumption that resident animals will behave towards an unfamiliar conspecific with acceptance, or at best indifference, is a dangerous one. Most species commonly express aggression during periods of high arousal (e.g., play) and as a mechanism to develop predatory behavior, acquire and maintain territory, defend resources, establish breeding rights, and express social dominance. During any introduction and acclimation of a new member into an established group, wild or captive, arousal levels are typically high, which intensifies the likelihood of aggression and risk of injury. Young calves and pups are particularly vulnerable, especially if animal management principles are not employed proactively in preparation for an introduction. Introduction order (from most subordinate to most dominant), the use of unfamiliar environments (eliminating territorial defense), and separation management (a previously trained response), combined with *differential reinforcement* when prosocial behaviors or calm behavior patterns are observed, helps achieve more rapid compatibility while maintaining stimulus control (Turner and Tompkins, 1989).

Differential reinforcement modifies the frequency, intensity, and/or duration of behavior using five main procedures: DRO (*Differential Reinforcement of Other behavior*), DRI (*Differential Reinforcement of Incompatible behavior*), DRA (*Differential Reinforcement of Alternate response*), DRH (*Differential Reinforcement of High rates of response*), and DRL (*Differential Reinforcement of Low rates of response*) (see Kazdin, 1994; Malott and Shane, 2013). Trainers observe social interactions and apply reinforcement immediately after appropriate behaviors are observed, which fosters long-term compatibility among captive animals and could contribute to improved survivability among wild-release candidates.

## VI. Enrichment and Variety

Just as we recognize the importance of play in the development of young animals, other physical and cognitive challenges are crucial to optimal animal health and welfare. An emphasis on enrichment programs that produce productive changes in behavior, health, and well-being, has gained wide acceptance at zoos and aquariums (e.g., Shepherdson et al., 1998). In the past, most believed that “natural” behaviors, such as instinctive, innate, or

fixed-action patterns, would be an automatic by-product of a well-designed, naturalistic exhibit. It was soon recognized that the expression of appropriate, species-specific behaviors required more encouragement and prompting than just high quality food, health care, and strategically modeled environments.

The goals of *environmental enrichment*, or the application of environmental complexity to stimulate beneficial activity, clearly fit within the animal training model (i.e., behaviors can be shaped, maintained, and modified using animal learning and training principles). In fact, experienced animal trainers and behaviorists coordinate environmental change, food placement, toys, games, and other behavioral prompts and reinforcers that target specific behaviors and patterns. Well-intentioned enrichment cannot be arbitrarily applied but instead must follow the laws and principles of learning (i.e., timing of applied reinforcement and the Law of Contiguity) to strengthen or regulate appropriate behavior, while avoiding accidental reinforcement of unwanted behavior (Kuczaj et al., 1998). Enrichment programs are advancing from the simple practice of placing items in enclosures to the paradigm of complex objects blended with cognitive challenges (e.g., problem solving and cooperation; Kuczaj et al., 2015b). Research is another form of enrichment, specifically scenarios in which animals are asked to solve problems and respond in unique ways to new stimuli (Fig. 2). Thus, the process of gathering data to address important conservation goals benefits both the scientific community and the study subjects.

## VII. Research in Managed Care

Maintaining marine mammals in managed care has evolved from recreational display facilities to reputable research and conservation organizations. Contribution to research-based investigations has become the benchmark, particularly since evaluations of wild marine mammals are often limited by access, time, and funding. Zoos and aquariums continue to expand the scale and breadth of research conducted to include advanced technologies and studies that focus on the development of innovative strategies to address marine mammal threats, management, and conservation issues, while holding the welfare of the study population as the highest priority. These data include novel findings related to marine mammal behavior, anatomy, physiology, disease, metabolism, cognition, reproduction, nutrition, communication, welfare, and acoustics. Scientific advances and discoveries generated by captive populations have been cited and published extensively in peer-reviewed journals and are considered significant contributions to the global marine mammal database.

Psychologists Herman, Kuczaj, and Schusterman developed cognitive studies, using training as a tool, that contributed to a foundation of understanding regarding the comprehension of basic principles of language (e.g., semantics and syntax, action to object instruction sequences, present/absent), imitation, working memory (match to sample) through time delay and rotation, as well as innovative behavior in marine mammals. Although deriving skill-level appropriate tasks to test cognitive abilities with high efficacy and practicality, while capturing and maintaining animal motivation, is challenging, these unprecedented discoveries were only possible through the use of trained subjects.

Behavioral audiogram studies are typically accomplished through extensive training, as subjects are taught to report the experience of hearing. Long Marine Laboratory and the US Navy's marine mammal program have conducted audiometric



**Figure 2** Bottlenose dolphins engaging with a feeding device developed to provide cognitive enrichment while simultaneously studying the potential for cooperation among cohorts. See *Eskelinen et al., 2016; Kuczaj et al., 2015a; Kuczaj, Winship, and Eskelinen, 2015b* (Photos by National Geographic, Brian Skerry).

investigations through psychophysical procedures, providing insight into hearing sensitivity and variation among pinnipeds and cetaceans. Captive studies have also contributed to a greater understanding of the physical characteristics of sound, the specifics of echolocation, detection and recognition, as well as sensitivities to sound, which has improved our understanding of the effects of anthropogenic noise on free ranging marine mammals.

Accomplished through intensive training, animals at most zoological facilities voluntarily participate in medical evaluations, which allow scientists to not only gain a deeper appreciation for marine mammal anatomy and physiology, but also to actively identify, diagnose, and treat various conditions and diseases. These applications then improve the response to and treatment of marine mammals in distress, expanding the value of these studies to wild populations. For example, voluntary blood samples from captive bottlenose dolphins provided comparative data and titer analyses that helped investigators at NOAA Fisheries identify *Morbillivirus* spp., a virulent pathogen that has devastated many wild populations.

Endocrine monitoring and ultrasonographic imaging have significantly advanced the understanding of marine mammal reproductive biology. Research on bottlenose dolphins, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), Indo-Pacific humpback dolphins (*Sousa chinensis*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), killer whales, false killer whales (*Pseudorca crassidens*), and belugas have revealed detailed male and female reproductive characteristics, such as sperm concentrations, cycle duration, follicular development, gestational characteristics, reproductive viability, and seasonality. This information is critical to wild stock assessments and predicting the recovery of depleted stocks. Additionally, success in conditioning voluntary semen collection in male cetaceans (dolphins and killer whales) and voluntary artificial insemination in females has led to increased genetic variability and fitness. This technology is likely to be critical to the preservation of endangered marine mammals, such as the Hector's dolphin (*Cephalorhynchus hectori*) and the Vaquita (*Phocoena sinus*), the latter of which is currently being considered for ex-situ breeding to prevent species extinction. As such, the scientific contributions of marine mammal facilities are likely to be

essential to future species conservation, and the utility of marine mammal training has a strong impact on the science generated in managed care.

### VIII. Behavior Medicine

Achievements in veterinary care, diagnosis, and treatment has been possible through the training of specific medical behaviors, many of which were once thought only obtainable through forced restraint, sedation, or anesthesia. Optimal animal health is achieved via voluntary routine examinations. In contrast, untrained animals typically express fear, apprehension, and a “fight or flight” response (*activation syndrome*) that can create safety risks for both animals and trainers. Commonly referred to as “husbandry training,” the effort to begin training medical procedures gained momentum in the early 1980s. Simple procedures, such as allowing a veterinarian to touch an animal without restraint, conduct up-close visual examinations, or inspect an open mouth, were the first behaviors trained for health purposes. Aware of the risks associated with forced restraint or anesthesia, coupled with the need to obtain ongoing biological sampling for health maintenance and research, the field of marine mammal training took a new direction. A well-known field in psychology, behavior medicine combines traditional medicine with behavior modification techniques to diagnose and successfully treat complex medical issues, such as chronic regurgitation, stereotypies, kidney dysfunction, eating disorders, and conditioned food aversions. Today, marine mammals have been successfully conditioned to voluntarily participate in blood, urine, milk sampling, radiographs, sonography, weights and morphometrics, endoscopy, intubation, EKG, CT scans, and even tooth drilling to mitigate infection, all without restraint, sedation, or anesthesia (Figs 3 and 4).

Engineering a behavioral training program that targets a specific behavioral goal can treat chronic medical conditions, such as kidney stones in older animals. Daily hydration therapy via gastric intubation training effectively delays and prevents the development or growth of kidney stones in bottlenose dolphins. Acute medical conditions such as wound treatment can be successfully conducted if prior desensitization training is completed. With success like these increasing in frequency, it is no coincidence that many marine



**Figure 3** Various, voluntary husbandry procedures, including from left to right: Ophthalmic examination, Doppler echocardiography, and dental radiography (Photos by Dolphins Plus).



**Figure 4** Computerized tomography (CT) scan of bottlenose dolphins, which provides detailed 3-D imaging of internal anatomy to diagnose, treat, and monitor injuries and pathology (Photo by Dolphins Plus).

mammals housed in quality aquariums live as long as or longer than their wild counterparts (e.g., Willis, 2007), and neonate mortality is lower in zoological facilities than in the wild. In fact, the oldest known bottlenose dolphin lived at Marineland in Florida where she was born in 1953 and lived until May of 2014. Many zoos are now emulating the success of marine mammal husbandry training, and good animal health programs utilize behavior medicine as an important standard of care.

### IX. Animal Welfare

Animal welfare is difficult to define but broadly encompasses physical health, mental well-being, and access to an enriching environment. The welfare of an animal can be likened to their “quality of life,” which is undeniably subjective and difficult to both quantify and evaluate. Regardless, and largely as a result of society’s ethical concerns about animals in managed care, welfare research and assessments have been widely applied to farm animals for decades. Early efforts focused on the reduction of suffering and have evolved in concert with human perception and empathy to include health and psychological well-being. Initial efforts to measure zoo animal welfare began in the early 2000s and have evolved to include non invasive measures of stress among captive elephants and the first comprehensive welfare assessment for bottlenose dolphins, adapted from the Five Freedoms model (FAWC, 1992) and the Welfare Quality® project (Clegg et al. 2015; Welfare Quality 2009a,b,c).

Though zoological facilities in the United States are held to high standards of animal care by the USDA, APHIS, and the AWA, most zoos and aquariums now strive to exceed those expectations, fueled by a dedicated network of international professionals committed to fostering optimal animal health and care.

In its most basic form, a welfare assessment is likely to encompass evaluations of diet and body condition, hydration, energy budgets, thermal comfort, access to enrichment, quality of habitat, health, and both the presence of normal behaviors (e.g., social behaviors) and the absence of abnormal behaviors (e.g., stereotypies). These measures, by design, include both resource-based (i.e., resources provided to the animals by humans) and animal-based (i.e., animal responses to various practices, their environment, and/or resources) measures, thereby directly linking animal learning and behavior management with welfare. For example, all measures of body condition (Fig. 5), hydration, and health ideally require the voluntary participation of the animals under human care, through the training and conditioning of behaviors that support physiological and psychological health. A forced restraint would decrease animal welfare by increasing the likelihood of fear, aggression, injury, and stress. Furthermore, when used in conjunction with established behavioral principles, environmental enrichment programs can enhance the well-being of individual animals and populations as a whole. Effective enrichment programs can also improve animal welfare but require a fundamental understanding of animal learning principles, the ability to vary task complexity and efficacy, as well as maintain a flexible approach to enrichment application.

### X. Conclusion

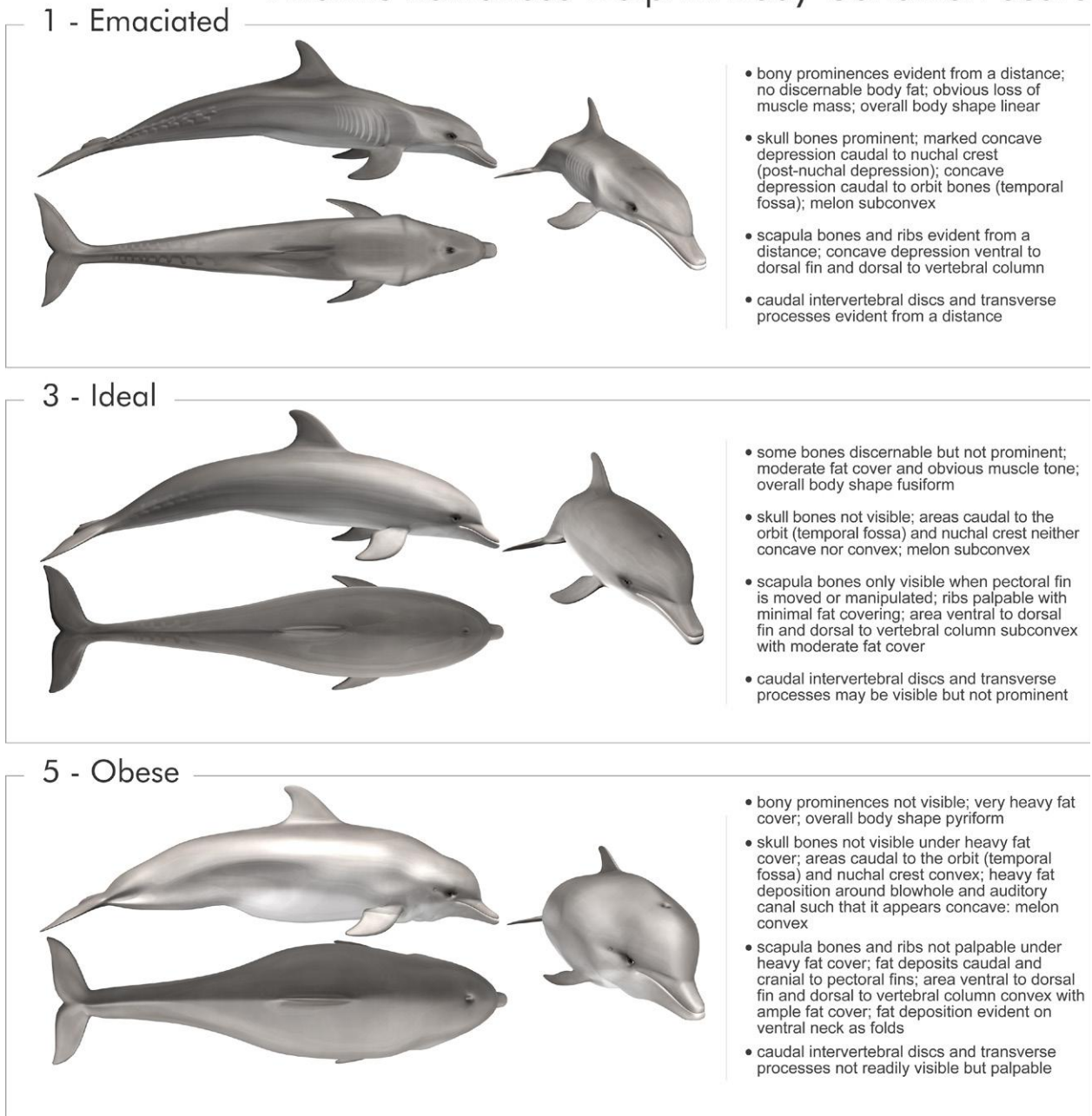
As formal behavior management continues to assimilate and apply the learning principles and laws that explain, predict, and modify animal behavior, these techniques can also be useful to wildlife managers, particularly as they relate to the conservation of highly endangered species, widespread changes in habitat quality, competition between marine mammals and fisheries, and population recovery. Solutions to many extant and emergent crises will require a specialized understanding of the learning and training processes applied in the field of marine mammal training.

#### *See Also the Following Articles*

Behavior, Overview ■ Captivity ■ Ethics ■ Marine Parks, Zoos, and Aquariums ■ Reproductive Physiology



## Atlantic Bottlenose Dolphin Body Condition Score



**Figure 5** Body condition scoring model for bottlenose dolphins (*Tursiops truncatus*), including numeric values relevant to general appearance and fat deposition associated with critical areas of the body, applied practically as a rapid, noninvasive tool to evaluate animal health and welfare.

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## TUCUXI AND GUIANA DOLPHINS

*Sotalia fluviatilis* and *S. guianensis*

PAULO A.C. FLORES, VERA M.F. DA SILVA AND DANIELA DE C. FETTUCCIA

### I. Characteristics and Taxonomy

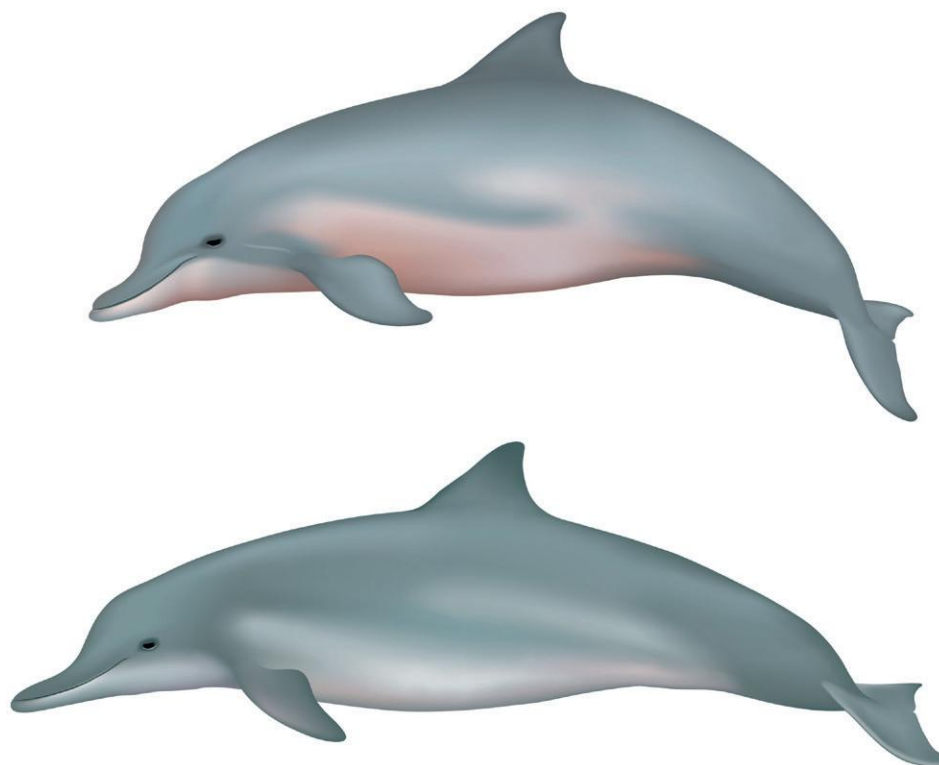
The genus *Sotalia* of the family Delphinidae was once considered to comprise five species, but in the 20th century, this was reduced to two, the riverine *Sotalia fluviatilis* and the marine *Sotalia guianensis*. Later these were further lumped into a single species (*S. fluviatilis*), with marine and riverine ecotypes. Recent morphological and genetic studies, however, concluded that marine and riverine *Sotalia* are different species (Monteiro-Filho et al., 2002; Cunha et al., 2005; Caballero et al., 2007; Fettuccia et al., 2009). Based on priority criteria, the name *Sotalia guianensis* was assigned to the marine animals, whereas riverine dolphins retained the oldest species name *Sotalia fluviatilis*. No fossil record is known.

The common name tucuxi comes from *tucuchi-una* after the Tupi language of Indians from the Amazon region of Brazil, where it is also called *boto-tucuxi*, *boto-cinza*, or simply *boto*. In the other Amazon countries it is usually called *delfin* or *bufeo gris del rio*, *bufeo gris*, *bufeo blanco*, or *bufeo negro* in Colombia and Peru; *tonina de rio*, *delfin blanco*, or *soplón* in the Venezuela Amazon, *tonina del lago* in Lake Maracaibo, and *bufeo negro*, *bufete*, or *soplón* in the Orinoco River basin in Venezuela. *S. guianensis* is also known simply as *boto* or *golfinho* and as *boto comum* and *golfinho cinza* along the Brazilian coast; *lam* in Nicaragua; *guyana dolphin* or *Guiana white dolphin* in Guyana; and *profuso* or *dolfijn* in Surinam. There is some controversy about a definitive international common name for *S. guianensis*. Various names have been used in the literature, most frequently marine tucuxi, gray dolphin, estuarine dolphin, and costero. We avoid the controversy here by using “Guiana dolphin,” based on the scientific name.

The two *Sotalia* species are very similar in coloration, differing mainly in body size and skull shape (in marine dolphins, the opening of the foramen magnum is located further posterior, whereas in Amazonian dolphins this opening is directed downwards), and somewhat resembling a small bottlenose dolphin, *Tursiops* (Fig. 1). They are light gray to bluish gray on the back and pinkish to light gray ventrally, with a distinct line from the mouth gape to the flipper’s leading edge. There is a lighter area on the flank between the flippers and the dorsal fin and another mid-body at the level of the anus. The marine species has another light gray rounded streak on both sides of the caudal peduncle. In both species, the eyes are large, and there is black countershading around the eyes, and 29–36 teeth in each mandibular ramus. The dorsal fin is triangular and sometimes slightly hooked on the tip. The tucuxi has a moderately slender beak, and a rounded melon. The Guiana dolphin is larger with a maximum total length of 220 cm and about 121 kg body mass vs a maximum length of around 152 cm and mass of 53 kg.

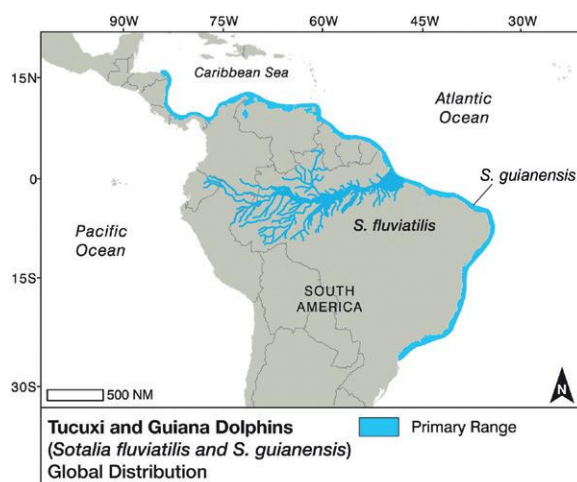
### II. Distribution and Abundance

The tucuxi occurs in the main tributaries of the Amazon/Solimões River basin in Brazil as far inland as southeastern Colombia, eastern Ecuador, and northeastern Peru, with records



**Figure 1** Tucuxi, *Sotalia fluviatilis* (top), and Guiana, *S. guianensis* (bottom), dolphins (Illustrations by Uko Gorter).

in all three types of river water that occurs in this region. Several rivers contain impassable falls, rapids, and shallow waters. On the tributaries of the right side of the Amazon Basin, the Teotônio and Santo Antônio Falls on the Madeira River, the Santa Isabel Falls on the R. Negro, Belo Monte on the R. Xingú, and S. Luis Falls on the Tapajós River are impassable barriers, whereas on the left side the falls on the Rio Negro and Raudal La Libertad on the Caquetá River (Colombia) are also important barriers. The tucuxi does not occur in the Beni/Mamoré River basin in Bolivia and is not known in the upper Rio Negro above the city of Barcelos. The presence of this species in the Orinoco River basin is unlikely, since a stretch of rapids and falls in the Negro River and the 354km of numerous rapids and outcrops of the Cassiquiare Channel block the species' movements (Fig. 2). Its distribution is influenced by seasonal river level fluctuations, with channels and lakes occupied during rising and high waters but avoided at low water. The tucuxi is abundant in most white water rivers as the Solimões, Japurá, and Purus Rivers as well as in large black water lakes such as Tefé Lake (Brazil) and the El Correo lakes system (Colombia). Tucuxis do not go into flooded forest as does the sympatric boto, *Inia geoffrensis*, but these species share a preference for areas with reduced current and waterway junctions. Mean density along the margins of main rivers in the central Amazon, Brazil within 150m survey strip of 1319.7km was 3.2 individuals per km<sup>2</sup>, where 54% of the individuals occurring within 50m of the edge (Martin et al., 2004). At the border of Colombia, Brazil, and Peru Vidal et al. (1997) found along about 120km of the Amazon River a density of 8.6/km<sup>2</sup> in lakes, 2.8 along main banks and 2.0 around islands. A more recent survey in Colombia, Peru and Venezuela revealed that the estimated population size was higher in the main river and confluences when compared to other habitat types, with a density of 3.35, 4.87, and



**Figure 2** Tucuxi and Guiana dolphin distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). In "Marine Mammals of the World: A Comprehensive Guide to Their Identification", 2<sup>nd</sup> ed. Elsevier, San Diego.

1.06 dolphins/km<sup>2</sup> and 28.14, 8.69, and 1.41, respectively (Gomez-Salazar et al., 2012).

The Guiana dolphin is found in the Western Atlantic coastal waters of South and Central America from southern Brazil (27°35'S, 48°35'W) to Nicaragua (14°35'N, 83°14'W), including Colombia, Costa Rica, French Guyana, Guyana, Panama, Suriname, Trinidad, Venezuela, and possibly Honduras (15°58'N, 79°54'W). In the Orinoco River, dolphins seen as far up as Ciudad Bolívar may

be of this species. The Guiana dolphin is found mostly in estuaries, bays, and other protected shallow coastal waters, although it has also been recorded at the Abrolhos Archipelago, around 70 km off the coast of Bahia State, Brazil (Rossi-Santos et al., 2006). The species' southernmost limit is influenced by the cold waters of the Malvinas current in South Brazil. It is notably recorded throughout the year in many coastal locations such as Baía Norte in Santa Catarina State, Cananéia Estuary and Baía de Guanabara (both in southeastern Brazil), Baía de Todos os Santos and around Fortaleza (northeastern Brazil), Bahía Cispatá and Golfo de Morrosquillo (Colombia), as well as on the Cayos Miskito Coast in Nicaragua (da Silva et al., 2010). Standard abundance estimates are scarce for the Guiana dolphin, but the species seems to be abundant in few locations along its distribution, mainly in South-Southern Brazil outside of Guanabara Bay where the population size decreased over 90% in the last three decades (Azevedo et al., 2017). Stocks or significant evolutionary units are evident from residency, site fidelity, genetic and acoustical data.

### III. Ecology

The Guiana dolphin feeds on neritic prey, mainly on fishes such as clupeids and sciaenids, and occasionally cephalopods, shrimps, crabs, and flounders. Usually young specimens of at least 70 species of teleost fishes are important diet items. Tucuxis feed mainly on schooling pelagic fish such as characiforms, freshwater clupeids, and sciaenids, no larger than 37 cm. Feeding may occur in pairs, usually mother and calf, and in larger groups or subgroups when different strategies and cooperation among individuals are employed. During feeding activities, Guiana dolphins often associate with birds such as the brown booby (*Sula leucogaster*), terns (*Sterna* spp.), frigate bird (*Fregata magnificens*), and kelp gull (*Larus dominicanus*). Mixed-species flocks of up to a hundred birds can be seen in such associations. In the Amazon, tucuxis may feed occasionally in association with terns (*Phaetusa simplex*).

Because of the huge regional differences in habitats from temperate waters in the south to the tropical waters, including estuaries such as the Amazon estuary, Guiana dolphins are found in a wide range of water depth, temperature, salinity, and turbidity.

There are no known predators for either species, although bites from sharks of unidentified species have been seen on Guiana dolphins. Individuals often wash ashore, sometimes due to incidental catch in fisheries in both marine and freshwater environments. In the Amazon estuary incidental catch is common; there is a record of one event with over 80 individuals in one net.

### IV. Behavior and Physiology

*Sotalia* dolphins show a variety of aerial behaviors such as full leaps, somersaults, fluke-ups, spy-hopping, surface rolling, and porpoising (Fig. 3). In coastal areas, feeding and traveling are by far the most common behaviors. Socializing involves various tactile contacts, and herding of females by males has been occasionally seen in southern Brazil. Bow-riding has not been recorded, but Guiana dolphins may surf in waves and wakes produced by passing boats.

Spontaneous swimming interactions with domestic dogs (*Canis familiaris*) and a lone wild Guiana dolphin sociable toward humans were recorded in southeastern Brazil. Epimeletic behavior and hand feeding were also recorded in the same area. Apparent mating behavior with bottlenose dolphins was recorded off Costa Rica. In Baía Norte, South Brazil, at the southernmost distributional limit, Guiana dolphins do not associate with bottlenose dolphins, and



Figure 3 Guiana dolphins socializing (Photo by P.A.C. Flores).

rare encounters even result in aggression by bottlenose dolphins or escape behavior by the Guiana dolphins. Epimeletic behavior toward an offspring was recorded at that locality.

Dives for Guiana dolphins last about 30–120 s with shorter dives of 5–10 s in between. Tucuxis are fast swimmers, spending less than a second at the surface, with an average dive time of about 2 min.

The *Sotalia* species are social dolphins, almost always in cohesive groups engaged in the same activities. Tucuxis are often found in groups of one to six individuals, although larger groups up to 20 individuals are also recorded. Groups of up to 50 or 60 Guiana dolphins are common, whereas the average group size is two to six. Large aggregations of up to 200 are reported at Baía de Sepetiba and around 400 individuals in Baía da Ilha Grande on the Rio de Janeiro coast, where these larger aggregations are usually engaged in cooperative feeding. Apparently, larger groups are more common in the south and southeastern Brazilian coast. Mixed groups of adults and calves are common. Individual associations are known only for the Cananéia Estuary population in Brazil; these are weak to moderate, except for a few pairs of individuals with apparently stronger associations, suggesting a relatively fluid society with individuals in fission–fusion.

Photo-identification studies have shown that Guiana dolphins may be resident within and between years for up to 10 consecutive years (Flores and Bazzalo, 2004). Home ranges are poorly known and apparently among the smallest for small cetaceans with a mean of about 15 km<sup>2</sup> in southern Brazil and up to 265 km<sup>2</sup> in another location. Movement patterns vary among warm and cold seasons in the temperate region, whereas no variation was found in warm waters. In any case, daily movements are small. Freeze-branded tucuxis in Central Amazon were recorded for several years in the same area, suggesting residency and seasonal use of areas.

Comparative analysis of the whistles of Guiana dolphins in different areas along the Brazilian coast revealed significant effects of geographical location. However, it is difficult to discriminate between adjacent populations. Guiana dolphins produce mainly upsweep whistles, shorter and less complex in shape than for other species of dolphins. The range of whistle fundamental frequencies recorded was 0.21–24 kHz and durations 38–1064 ms (Azevedo and Van Sluys, 2005). Whistles produced by the tucuxi vary geographically and the fundamental frequency is broad, emitted in a range of 15 to 20 kHz. The majority of the sounds are of short duration but considered complex with modulation, varying from 0.02 to 2.66 s (Bivaqua, 2015).

## V. Life History

Calving is year-round and gestation is estimated to be around 11–12 months for the Guiana dolphin, with calves ranging in size from 90 to 100 cm of total length. Calving interval is believed to be 22–24 months based on photo-identification data. Tucuxi calving occurs between September and November, during low water season, after a gestation time estimated at 11 months, with calves at birth measuring from 71 to 83 cm (da Silva and Best, 1994).

According to tooth growth layer groups (GLGs), life span can reach 30 and 43 years for the Guiana dolphin and tucuxi, respectively. Natural mortality rates are unknown for both species.

## VI. Interactions With Humans

Historically, these species have not been exploited commercially, although incidental mortality in local and commercial fisheries such as those using gillnets and seines are a direct threat. Bottom-set nets for lobsters also occasionally capture Guiana dolphins. On the coasts of Amapá, Maranhão, and Pará States, northern Brazil, Guiana dolphins are killed for shark bait, although they have some protection from myths and legends. This is especially true for the tucuxis in the Amazon. There, their genital organs and eyes have a local market as love charms, and teeth and bones are used for arts and crafts. Guiana dolphins in some parts of their distribution, mainly on the northern and northeastern coasts of Brazil, may also be used for human consumption. These dolphins are fully protected by federal laws in Brazil, forbidding the harassment, hunting, fishing, or capture of tucuxis and all cetaceans, pinnipeds, and sirenians in national waters, but law enforcement may not always be effective. In other countries such as Colombia, Ecuador, Peru, and Venezuela, tucuxis are also protected by laws.

Acoustic pingers attached to gillnets may successfully reduce or prevent by catch of Guiana dolphins as suggested by a single study conducted with free ranging dolphins in northeastern Brazil during 345 hr of experiment (Monteiro-Neto et al., 2004).

Dams and hydroelectric power facilities in the Amazon region interrupt fish migration, reducing fish abundance, and consequently prey availability for dolphins. Mercury from gold mining, water pollution, seismic activities, oil spills, and boat traffic are other potential threats to tucuxis in the Amazon, while the same factors, except gold mining, plus marine culture farms and destruction of habitats, mainly mangroves and salt marshes, strongly affect the Guiana dolphins. Hand feeding and the behavioral effects caused by boat activities also deserve concern, as these may affect at least populations off the coasts. Bioaccumulation of contaminants and growing pollution outfalls are also concerns (Lailson-Britto et al., 2010).

*Sotalia* dolphins are susceptible to capture stress, quickly become entangled and sometimes suffocate in nets, and are not robust to long periods of transportation or handling after capture. However, Guiana dolphins captured off the coast of Panamá in the late 1970s were kept in captivity in Europe for more than 20 years. Two Guiana dolphins were kept in Colombian facilities, although since 2005 it became illegal to maintain dolphins in captivity.

The two *Sotalia* species are listed as “insufficiently known” by the World Conservation Union (IUCN). Because of its coastal habits, aggregating in estuaries and bays, and in river channels and lakes, *Sotalia* dolphins are vulnerable to almost all human activities throughout their range. A large proportion of the distributional area of the two species is close to human habitation. Consequently,

these habitats are subject to intense fisheries, boat traffic, sewage, industrial waste, and high levels of contaminants. Examples are the Santos and Rio de Janeiro harbors in southeast Brazil, Recife and Rio Grande do Norte in the northeast Brazil, Maracaibo in Venezuela, Golfo de Morrosquillo in Colombia, and Belém, Santarém and Manaus in the Brazilian Amazon.

## See Also the Following Articles

Delphinids, Overview ■ River Dolphins ■ River Dolphins, Evolution

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## TUNA-DOLPHIN ISSUE

TIM GERRODETTE

### I. The Tuna-Dolphin Association

In the tropical waters of the Pacific Ocean west of Mexico and Central America, large yellowfin tuna (*Thunnus albacares*) swim together with several species of dolphins: Pantropical spotted (*Stenella attenuata*), spinner (*S. longirostris*) and, to a lesser extent, common (*Delphinus delphis*) dolphins. The association of tuna and dolphins appears to be related to reducing the risk of predation when the habitat of the tuna is restricted to warm surface waters by the oxygen minimum zone (Scott et al., 2012). Tuna-dolphin associations occur in other oceans but are most common in the eastern tropical Pacific (ETP), where the oxygen minimum zone is especially well-developed.

The regularity and strength of the tuna-dolphin association in the ETP has permitted the development of a purse-seine fishery based on it (National Research Council, 1992). The fishermen capture tuna and dolphins together, then release the dolphins from the net. In the early years of the fishery, bycatch of dolphins was very high, leading to significant reductions in the dolphin populations. The public outcry over the large dolphin bycatch was one of the factors behind the passage of the US Marine Mammal Protection Act. The number of dolphins killed since the fishery began is estimated to be over 6 million animals. For comparison, the total number of whales of all species killed during commercial whaling in the twentieth century was about 2.9 million. However, the dolphin bycatch has now been reduced to a small fraction of its former level.

### II. Purse-Seining for Tuna

Prior to the development of modern purse-seines, tropical tuna were caught one at a time using pole-and-line methods. The twin technological developments of synthetic netting that would not rot in tropical water and a hydraulically driven power-block to haul very large nets made it possible to deploy purse-seines around entire schools of tuna, and thus to catch many tons of fish at a time. Purse-seining for tuna in the ETP can be conducted in one of three

ways: The net may be set around schools of tuna associated with dolphins (“dolphin sets,” which catch large yellowfin tuna), around schools of tuna associated with logs or fish-aggregating devices (“log sets” or “floating-object sets,” which catch mainly skipjack but also bigeye and small yellowfin tuna), or around unassociated schools of tuna (“school sets” or “unassociated sets,” which catch small yellowfin and skipjack tuna). The proportions of the three set types have varied over the history of the fishery, but in recent years have been about equal.

Dolphins are killed almost exclusively in dolphin sets. In dolphin-set fishing, schools of tuna are located by first spotting the dolphins or the seabird flocks which are also associated with the fish. Speedboats are used to chase down the dolphins and herd them into a tight group; then the net is set around them (Fig. 1). The tuna-dolphin bond is so strong that the tuna stay with the dolphins during this process, and tuna and dolphins are captured together in the net. Dolphins are released from the net during the backdown procedure (Fig. 2). If all goes well, the dolphins are released alive, but the process requires skill by the captain and crew, proper operation of gear, and conducive wind and sea conditions. As with any complicated procedure at sea, things can go wrong, and when they do, dolphins may be trapped in the net and killed.

From the perspective of an ecosystem approach to fisheries management, the ETP purse-seine tuna fishery poses interesting challenges. The three methods of purse-seining for tuna in the ETP, log-, school- and dolphin-set fishing, catch different mixes of tuna species and sizes, and in addition have different amounts and composition of bycatch. The effect of the fishery on the ecosystem includes both the targeted catch (tuna) and bycatch. Most of the bycatch, even in dolphin sets, is fish. Log-set fishing has about twice the ecosystem effect of dolphin- or school-set fishing when measured by the time it takes to replace the biomass removed (Gerrodette et al., 2012).

### III. Actions to Reduce the Dolphin Bycatch

The magnitude of dolphin mortality in the ETP tuna fishery first came to widespread attention in the mid-1960s. The dolphin kill at that time is not known with precision, but without question was very high (Fig. 3). When the US Marine Mammal Protection



**Figure 1** Purse-seine being set on tuna and dolphins in the eastern tropical Pacific Ocean. The net is not yet closed, and four speedboats are driving in tight circles near the opening to keep the dolphins and tuna from escaping.



**Figure 2** Backdown procedure in progress. As the tuna vessel moves backwards, the net is drawn into a long channel. The corkline at the far end (to the right in this photo) is pulled under water slightly, and the dolphins escape at the surface while the tuna are retained. Speedboats are positioned along the corkline to keep the net open.

Act was passed in 1972, it included provisions for reducing the dolphin bycatch to “insignificant levels approaching zero” after a 2-year moratorium on regulation, during which time the US tuna industry was expected to solve the problem through development of improved fishing methods. Under this law, scientific studies were initiated, observers were placed on fishing boats, fishing gear was inspected, and boat captains with high dolphin mortality rates were reviewed. Modifications of fishing gear and procedures were developed to reduce dolphin kill. After much litigation, the first regulations to reduce the dolphin kill on US vessels were promulgated (Gosliner, 1999). By 1980 the kill had declined from about 500,000 to about 20,000 dolphins per year (Fig. 3).

As the size of the US tuna fleet decreased and the fleets of Mexico, Venezuela, Ecuador, and other Latin American countries increased, the dolphin kill began to grow again. Actions to monitor and reduce the dolphin bycatch became international. The Inter-American Tropical Tuna Commission began a dolphin conservation program in 1979 modeled on the US effort. By 1986, an international observer program with all countries participating showed that total dolphin mortality had increased to 133,000 per year (Fig. 3). Because US boats operated under restrictions that did not apply to boats of other countries, the United States began requiring that imported tuna be caught at dolphin mortality rates comparable to US boats. The concept of Dolphin-Safe tuna—tuna caught without setting on dolphins (i.e., in log and school sets)—became popular. The trade actions were important because the United States is a large market for the canned tuna product of the fishery.

The dolphin kill again declined between 1986 and 1993 due to these various management actions and economic pressures (Fig. 3). Starting in 1993, the ETP fishing countries decided to increase observer coverage, institute skipper review panels, and meet a schedule of decreasing dolphin quotas on an individual boat basis (the La Jolla Agreement). The Declaration of Panama of 1995 carried these ideas further, proposing observers on every boat over 400 tons and strict by-stock dolphin mortality limits. These features became part of the International Dolphin Conservation Program Agreement

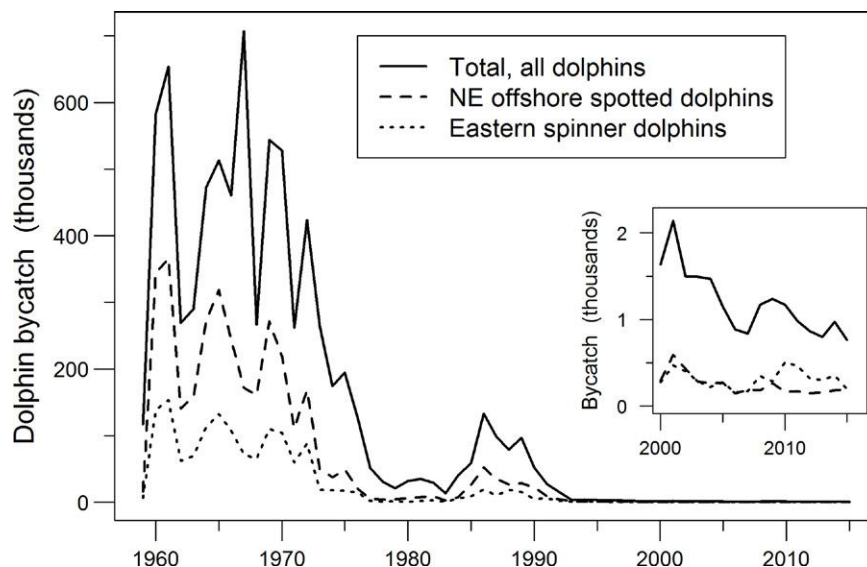
(Hedley, 2001), a binding document among the major fishing countries that went into force in 1999. By this time, total reported dolphin mortality had fallen to fewer than 3000 dolphins per year. In recent years, dolphin mortality has declined further to about 1000 animals per year, and for each dolphin stock, the annual bycatch is less than 0.1% of the estimated population size. The reduction of the dolphin bycatch by >99% is a conservation success story.

The applicable standard for use of the Dolphin-Safe label on canned tuna in the US market is a continuing issue. Mexico, whose fleet catches tuna primarily by setting on dolphins, argues that the labeling standards discriminate unfairly against Mexico and are inconsistent with US obligations under the World Trade Organization. The primary issue is whether US Dolphin-Safe standards are applied in a consistent and reasonable way to all tuna fisheries.

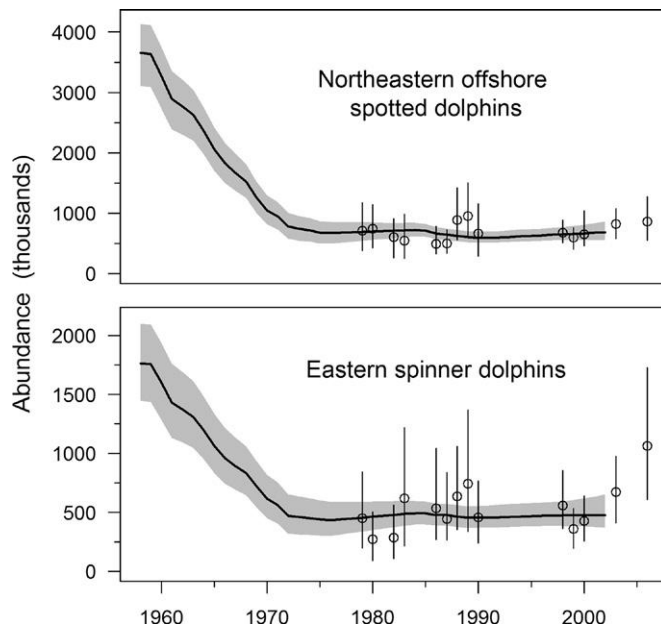
#### IV. Status of the Dolphin Populations

Determination of the status of ETP dolphin stocks (management units) is based primarily on two time-series of data: Estimates of the number of dolphins killed, based on data from observers on tuna vessels (Fig. 3), and estimates of abundance, based on line-transect data from research vessel surveys (Fig. 4). Combining these data in a population model has indicated that the stocks most affected by the tuna fishery are the northeastern stock of offshore pantropical spotted dolphins (*S. attenuata attenuata*) and the ETP-endemic stock of eastern spinner dolphins (*S. longirostris orientalis*).

Both populations declined between 1960 and 1970 during the period of high mortality on US boats, then stabilized as dolphin bycatch declined under the Marine Mammal Protection Act (Fig. 4). Since the early 1990s, under the international dolphin conservation agreements mentioned above, reported dolphin mortality has been low enough that the two dolphin populations, based on their reproductive rates and assuming that deaths in the fishery were the only factor impeding recovery, should have started to recover. By 2002, neither dolphin population appeared to be recovering at expected rates (population trajectory in Fig. 4, Wade et al., 2007), but population estimates in 2003 and 2006 suggested that the two populations



**Figure 3** Estimated annual number of dolphins killed in the eastern tropical Pacific purse-seine tuna fishery, total for all dolphins and separately for the two dolphin stocks with the highest number killed. The inset graph has an expanded vertical scale to show details from 2000 to 2015.



**Figure 4** Estimated population trajectories from 1959 to 2002 of the two dolphin stocks most affected by tuna purse-seine fishing in the eastern tropical Pacific. Estimates of abundance between 1979 and 2006 are shown as points with 95% confidence intervals. The populations declined due to high numbers of dolphins killed in the tuna fishery from 1960 to 1975, as shown in Fig. 3.

have begun to increase more rapidly. Besides the observed kill in the fishery, factors that might affect dolphin recovery include ecosystem changes (affecting reproductive and survival rates, movement across stock boundaries), cryptic effects of chase and encirclement

(stress, induced abortion, separation of mothers, and calves), unobserved or under-reported kill, and a lag in recovery due to interactions with other species. Studies have shown support for most of these hypotheses, but it is not clear how strongly each may affect dolphin population dynamics. Further, there have been no population estimates since 2006, so the present status of the dolphin populations is uncertain. At the time of this writing (2017), a new ETP dolphin survey and comprehensive assessment modeling are being discussed.

### See Also the Following Articles

Fishing Industry ■ Effects of Management

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