Cetaceans

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Cetaceans display numerous anatomic and physiologic adaptations to life in a dense, three-dimensional medium. Their bodies have changed radically from those of their terrestrial ancestors, yet their behaviors and types of social organization are broadly similar to those of animals on land. An exploration of cetacean ways helps in understanding how habitat influences habits. For example, it is now recognized that in some important ways, cetacean residents of the open ocean resemble some of their mammalian relatives on the savanna. As air breathers that are inseparably tied to the surface, cetaceans are highly trackable; they may thus help in the monitoring of habitat degradation and other long-term ecologic change.

THE TAXONOMIC ORDER CETACEA CONSISTS OF ABOUT 75 living species of mammals (*1*) that evolved from a carnivorous stock of ungulates over 50 million years ago. They lost external hindlimbs, gained a paddle-like tail for propulsion, and developed a streamlined body without insulating hair but with thick padding of a modified fatty tissue, the blubber (*2*). Blubber allows small cetaceans to survive in the heat-sapping environment of even polar regions and allows large cetaceans to store energy supplies that permit fasts of many months as the animals migrate and breed away from feeding grounds (*3*).

Two suborders comprise the order Cetacea, the mysticetes (baleen whales) and the odontocetes (toothed whales) that are probably descendants of a common ancestral group, the archaeocetes. The baleen whales lost their teeth and grew thin, long keratinous plates of ectodermal origin, like fingernails and hair, that hang from their upper jaws. These baleen plates strain out invertebrates and small fishes from water taken into the mouth (*4*). The larger filtering apparatus allowed more efficient capture and retention of aggregating prey. The baleen whales evolved disproportionately large mouths and large body size. Large size permitted huge fat reserves which made possible seasonal migrations to take advantage of food blooms and to fast for prolonged periods while reproducing in warmer but less productive waters.

The toothed whales evolved sophisticated echolocation, in which rapid sequences of high-frequency clicks are sent into the environment and the whale listens for the modified return of echoes to discriminate distances, sizes, shapes, and textures of objects (*5*). This allows feeding in the absence of light, and probably allows efficient predator detection. Echolocation may be the single most important new adaptation that has helped odontocetes to expand through all ocean basins and into several major rivers.

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Anatomy and Physiology

Much of cetacean success in adapting to life in the seas is due to straightforward adaptations of ancestral stock. For example, (i) the kidneys have increased capacity for handling ionic concentrations of solutes due to compartmentalization into many interconnecting renal units, which increases the total surface area over which ions can be transferred; (ii) blood has a high concentration of hemoglobin, and muscle is richly supplied with myoglobin for storage of large amounts of oxygen (*6*); and (iii) soft body and skeletal morphology has been adapted for propulsion in a dense, three-dimensional medium, sustained breath-holding, temperature regulation, and storage of energy.

Diving. Dolphins dive repeatedly to depths of at least 300 m (*7*) and sperm whales (*Physeter macrocephalus*) to over 1 km (*8*). The baleen whales are probably not deep divers, although humpback whales (*Megaptera novaeangliae*) dive to at least 148 m and fin whales (*Balaenoptera physalus*) to 355 m (*9*).

Dolphins and whales dive with full lungs. Considerable attention has centered on how they avoid the bends. Several physiologic adaptations seem responsible. First, alveolar collapse probably occurs below a depth of about 70 m and stops respiratory gas exchange in the lungs. As air volume decreases, blood-absorbing bundles of arterioles and venules fill in the spaces in the head, preventing tissue compression. The lungs can collapse because of a flexible rib cage and an oblique diaphragm that can cave in the chest cavity. Second, an extensive bundle of blood vessels (the thoracospinal "retia mirabilia") may trap gas bubbles that are generated, and release them between dives more slowly than in other swimming vertebrates. Blood chemistry differences may also be involved (*7, 10*).

Our incomplete knowledge of cetacean diving physiology stems from two major problems. First, it is logistically difficult and expensive to monitor cetaceans. The ability to measure physiologic parameters on a free-swimming animal and then either store the information on a recoverable device or telemeter it to a base station promises to expand our knowledge in the future (*11*). Second, the Marine Mammal Protection Act (*12*) makes it difficult for U.S. researchers to obtain permits to study cetaceans by even slightly invasive methods. Thus, studies of cetacean physiology have lagged behind those of other animals for which research is not similarly restrained.

Brain size. Large brain size may be linked to a life strategy of great longevity, slow maturation, single births after a long gestation, and late weaning (*13, 14*), rather than to metabolic rate per se (*15*) or to dive duration (*16*).

What do cetaceans accomplish with those large brains? A practical definition of intelligence (and its relationship to brain size) still eludes us (*17*), but numerous other behaviorally related reasons for large brain size have been proposed: the complexity of foraging strategies and the possible need for forming and remembering social relationships in complex societies that have to avoid predation and secure food in three-dimensional space may be likely candidates. Interspecific comparisons of EQ [encephalization quotient; a measure of brain size as the ratio of brain to body mass (*18*)], as made for several terrestrial groups (*19*), could help correlate brain size of the delphinidae with home range foraging strategies and social relationships. It has also been suggested that sophisticated click-based echolocation, which requires analysis of multiple echo parameters for fine-scale object discrimination, resulted in large brain size (*13, 20*). Most species of dolphins are capable of rapidly learning tricks in captivity and often cooperate in securing food in apparent sophisticated fashion (*21*). Bottlenose dolphins can also learn through observation, extrapolate information from basic symbols, and remember for long periods of time. This was shown in experiments on two captive dolphins in Hawaii over 10 years and may help in correlation of behavior with brain size and complexity (*22*).

Fig. 1. Hawaiian spinner dolphins rest near the bottom of a 20-m-deep bay on the island of Lanai. Rest and social activity occur nearshore in daytime; apparently the shallow nearshore habitat helps dolphins avoid deep water shark predation. Feeding occurs offshore at night, because only then are mesopelagic fishes and squid, which are several hundred meters deep during the day but rise towards the surface at night, available to dolphins. Daytime activity occurs over sandy bottom, not rocks or coral, probably so that predators can be more easily detected over an unbroken visual field.

Sound Production

Sound is an important production and sensory modality, although the senses of taste, touch, and sight are also well developed in dolphins and whales (*23*). The two suborders have different suites of sounds that are produced in a different manner.

Sounds are picked up by an underwater microphone, or hydrophone, and recorded onto audiotape. Analysis of the frequency, duration, and repetition rate with a sound spectrograph device provides a visual representation. Relative intensity can also be measured. To ascribe functions to cetacean sounds, sound-behavior correlations are studied. Sound descriptions and some sound function deductions have been carried out on numerous whales and dolphins in the past 10 years. Despite the general absence of playback studies, which are used to ascertain sound function in terrestrial animals, the behavioral importance of sound to cetaceans is becoming clear.

Mysticetes. The baleen whales generally produce sounds below 5000 Hz that differ greatly among the three families and, although well described, are of incompletely known function. An individual mysticete producing a given sound can now be pinpointed with sophisticated hydrophone arrays (*24*). The largest of whales, the blue (*Balaenoptera musculus*) and fin whales of the balaenopterid family, produce intense moans, from 1 second to many seconds long, in the 10- to 20-Hz range. These sounds probably serve to communicate to conspecifics over tens of kilometers, although hypothesized long-distance communication covering entire ocean basins is more questionable (*25*). Fin whale moans may serve a reproductive function (*26*). Higher frequency sounds, to several hundred hertz, are also produced by the balaenopterid whales.

The humpback whale has an extensive and varied sound repertoire, with both chirp and moan-like social sounds (*27*), and trains of repeating sounds termed song, reaching to 5000 Hz in frequency (*28*). Songs are produced primarily by adult males on the breeding grounds, and, like song in birds, crickets, and gibbon monkeys, probably communicate their species, sex, location, readiness to mate, and readiness to engage in agonistic behavior with other males (*29*), perhaps by length or complexity of song (*30*). More analysis of concurrent behavior and song are necessary before true function of song is explained. Especially valuable will be an analysis of song from individuals of known age or size, perhaps by combining photogrammetric size-measuring techniques (*31*) with recording sessions.

Gray whales (*Eschrichtius robustus*) produce relatively simple series of pulses and moans, with no known behavior correlate. The short duration pulses that are heard most frequently have the appropriate physical structure to serve as a rudimentary echolocation function (*32*). Gray whales may stay in contact with each other by sound, but appropriate research on sounds and behavior has not been done. Gray whales migrate close to the shores of the Pacific Northwest in large numbers twice yearly, and it is now apparent that fruitful sound studies can be carried out.

The Balaenidae, right (*Eubalaena* sp.) and bowhead (*Balaena mysticetus*) whales, produce complex sets of moans in the several hundred hertz frequency range, and they appear to be vocal at almost all times—on the mating grounds, on the feeding grounds, and during migration. Certain sound types correlate with certain social contexts in right and bowhead whales (*33*). Bowhead whales also have repeating notes of sound, or song, which may serve a similar mating-related function as in humpback whales (*34*). Baleen whales do not have vocal cords, and it is probable that sounds are made by air passing through the tracheal region.

Odontocetes. Toothed whale sounds are rich and varied and tend to have higher frequencies than sounds of the mysticetes. There are two basic sound types: pulsed clicks and click series, and unpulsed, frequency-modulated whistles. Both types are used for communication, and a subset of pulsed sounds is used for echolocation as well. Whistles have not been reported for certain odontocetes such as sperm whales, river dolphins, and harbor porpoises (*35*), although sperm whales produce some tonal sounds.

It is likely that both click and whistle sounds are generated near the nasal region, where a muscular plug and several sets of air sacs connected to the narial passages allow for shunting of air back and forth in the odontocete forehead and cause the vibration of tissue (*36*). The entire process probably evolved from the sibilant nasal sounds made by ungulates on land, transposed during evolution to an internal shunting of air due to the necessity of keeping the nares closed underwater. Some delphinids can produce clicks and whistles simultaneously, possibly by bilateral use of the paired air sac system (*37*).

Sperm whales produce intense clicks in series termed "codas." These may have some individuality (serving a signature function)

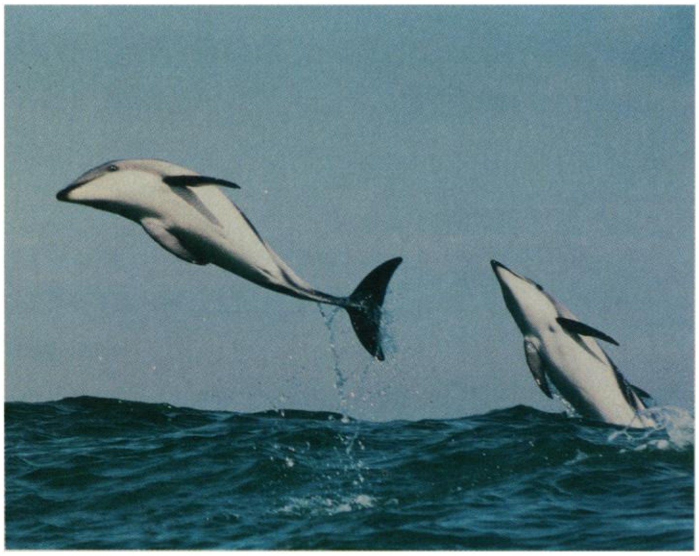

Fig. 2. Two dusky dolphins leap during social-sexual activity within a 12-member group in deep water off Kaikoura, New Zealand. Such dual leaps often end in brief copulations after the animals reenter the water. They may represent chases or may merely be a part of sexual play, but at all time they signify a large degree of social interactions in a dolphin group. Other acrobatic leaps such as somersaults and spins are performed by lone animals; they also indicate high excitement but are not necessarily sexual. Other surface activity may consist of tail slaps, flipper slaps, and low breaches with body side slaps. In dusky dolphin societies, these are often associated with various stages of cooperative surface herding of schooling fish prey.

and also are different between different populations, thus helping to identify individuals of a group. Since sperm whale clicks often occur between animals alternately, or in duetting fashion, they probably serve for communication. Whether clicks are also used for echolocation is not known. An untested hypothesis is that, because of the peculiar head of the sperm whale, different sized whales may produce differently spaced click trains that would communicate their size. Data are needed to correlate click trains from known individuals with their overall size, difficult information to obtain in nature (*38*).

Most odontocete sound studies are done on bottlenose dolphins in captivity, and it was in this species that echolocation was first noted (*39*). Echolocation frequencies can be over ten times our upper hearing of 20 kHz; dolphins can discriminate objects differing by a size ratio of about 1.1 (*40*). A single 13.5-cm fish can be detected at a distance of at least 9 m, and a school of fish may be detected at a range of 100 m or more (*35*). The similar skull morphology among the odontocete families suggests that echolocation was an early adaptation of evolving toothed whales and is probably shared by all present groups.

Some high-intensity click sounds (230 dB at 1 μPa at 1 m for bottlenose dolphins) by bottlenose dolphins, beaked whales, and sperm whales may serve to debilitate prey by overloading fish lateral lines, ears, or shattering bony ossicles and other tissue (*41*). No direct evidence exists for prey stunning, but it may explain the good health of whales and dolphins with badly deformed jaws, or those missing a lower jaw, although tests have not been conclusive (*42*).

Non-echolocatory sounds are also complex and varied, and the cacophony of whistling and squawking sounds heard from schools of dolphins gave rise to the notion that they possess a language. They do communicate with each other, and particular sound types correlate with rest, social-sexual behavior, travel, alarm, or feeding (*43*). However, there is no evidence of a language-like syntactical structure to sequences of sounds. A recently developed telemetry device that attaches to a dolphin's head and identifies which dolphin in a group is vocalizing makes possible an analysis of vocal interactions between individuals of a group (*44*). The device, called a "vocalight" because it lights up during sound production, promises to become a useful tool in sound-related studies.

Dolphins have individual "signature whistles" that may identify members of a social group (*45*). Whistles and pulsed calls are mimicked; mimicry may be useful in dialect formation, as in discrete pods of killer whales in Puget Sound (*46*). Dialects may be important to populations where ranges or possible territories overlap; but, as in humans and white-crowned sparrows, dialects may simply be the result of relatively isolated populations of animals that learn sound repertoires from each other (*47*).

Behavior and Societies

Cetaceans are gregarious mammals, almost always traveling as a pod or school, in which cumulative sensory awareness presumably enhances prey and predator detection, and where long-term social affiliations and interactions can be played out (*48*). Group size and structure are guided by an incompletely understood matrix of factors, including foraging type, need for predator detection and avoidance, social and sexual interactions, and the care and maintenance of developing young.

Foraging strategies help to determine the social life of animals. However, only when cetaceans feed at or near the surface can we directly describe prey taken and method of capture. Researchers rely on indirect cues of feeding, such as long-duration dives, scats at the surface, or a correlation of the potential prey distribution to the stomach samples of net-caught or beached animals. Data on depth of dives is particularly important. This can be obtained from gray whales when they feed at the bottom because they surface with mud streaming from their mouths, by fish-finding sonar traces of whales below the surface, or by electronic dive-telemetry packages attached to whales or dolphins (*49*). The latter technique is used for seals (*50*), and its use with cetaceans will give us much better information on when and at what depth individuals feed. This information, coupled with prey availability studies and behavioral observations of feeding groups, will enable us to describe foraging habits, capabilities, and constraints and make better comparisons between foraging strategies and social structure (*51*). Behavioral information can also be gleaned by noninvasive techniques such as photo-identification of individuals, theodolite tracking groups for information on movement patterns relative to prey distribution, and by high-resolution video for later analysis of behavior (*52, 53*).

Mysticetes. Each family of baleen whales exhibits a morphology and behavioral repertoire suited to its feeding type. The right and bowhead whales are passive sievers of small invertebrate prey such as calenoid copepods and euphausiid crustaceans (or "krill"). They have large mouths with long, finely fringed baleen that allow huge volumes of water to be filtered out of the sides of the mouth while the prey stay inside. While feeding, the balaenids move forward slowly, passing water continuously through the baleen plates. They have large heads and relatively chunky bodies, indicative of a mode of feeding not requiring bursts of speed. Although much feeding takes place individually, whales often travel staggered in a V-formation, like the echelon of flying geese, apparently so that adjacent bodies can serve as walls to cut off the escape of prey to the sides (*54*).

The gray whale is also a relatively passive feeder, but with a small mouth and short, coarse baleen. The gray whale sucks from the substrate inbenthic invertebrate fauna such as tube-dwelling ampeliscid amphipods. It then winnows the edible from inedible and pushes a muddy slurry out of the sides of the mouth, often while surfacing after a feeding dive. It leaves behind visible traces of disturbed benthos, and the impact of feeding on habitat can be most completely assessed for this species (*55*). Gray whales generally feed in loose aggregations; they do not appear to coordinate feeding activities. They graze on productive stands of benthos, and it is possible that individual feeding ranges (*56*), and even defense of pasture, may have evolved.

The rorqual whales consist of six streamlined species ranging in size from the 9-m minke whale (*Balaenoptera acutorostrata*) to the 25-m blue whale. They, too, are generally gregarious, although minke and Bryde's (*B. edeni*) whales may live alone in certain nearshore areas (*57*). The rorquals have short baleen in mouths that can open to greater than a 90° angle between the lower and upper jaw. Rorquals lunge into their prey, which may consist of clouds of krill or schools of small fishes. They gulp up to 70 tons of food and water into mouths that distend as accordion-like furrows or pleats in the throat expand and, by contraction of throat muscles, push water out of a partially closed mouth while prey is trapped against the slit of baleen (*58*). They may also push part of the head above water and thereby allow water to cascade out of the mouth by gravity. Feeding is a highly active, lunging affair requiring bursts of speed to trap especially maneuverable krill and fishes. Cooperative foraging occurs as up to a dozen or more whales lunge simultaneously side by side or in a tight cluster. Humpback whales use a variety of strategies to control and contain prey, such as blowing a bubble net around the prey, circling rapidly, or smacking and apparently stunning prey with the tail (*59*).

Baleen whale species are gregarious to various degrees; basic ecological rules discovered for terrestrial animals probably apply. There are correlations between increasing body size, greater degree of dietary specialization, larger home ranges, and increasing group size in antelope, deer, and to some degree in primates (*60*). When the smaller fish-feeding minke and Bryde's whales of the Gulf of California, Mexico, are compared to the larger plankton-feeding fin and blue whales, whales with increased body size tend to have larger ranges, feed on fewer types of prey, and occur in larger groups than the smaller whales (*61*). One major difference may be the constraint of obtaining enough energy to support a large body, perhaps done most efficiently by feeding low on the trophic level, and ranging widely in search of large concentrations of food (*62*). Antarctic minke whales, which feed largely on plankton instead of fish, occur in aggregations and travel widely, as do fin and blue whales of the Gulf of California (*63*). However, although the size-food-lifestyle relationship is a useful first approximation to explain general social patterns, it is by itself overly simplistic (*60*, *62*, *63*). Research on whales killed by the whaling industry provided information on calving seasonality, gestation time, size at first ovulation, and so forth (*64*). We know very little, however, about mating systems and strategies. The most detailed descriptions of sexual activity have been made from circling aircraft, and sex can be determined when whales roll ventrum up at the surface (*65*).

In right, bowhead, and gray whales, several males often jostle to get close to a female. Males may cooperate to allow one male to copulate (*53*), but it is more likely that each is attempting to get to the female first. The female may be practicing mate choice by rolling belly up at the surface, swimming rapidly away, and otherwise making it difficult for a male to insert his penis, for the largest or most aggressive male is often able to copulate with the female as the others fall behind. Females that have copulated may then copulate with other males, suggesting that the system is not purely polygynous, where one male inseminates several females.

Further evidence for nonpolygyny is that, in general, mammalian testes are larger relative to body size than would be predicted when the breeding system is a multimale-multifemale one tending toward promiscuity (*66*). Right, bowhead, and gray whales have extremely large testes, capable of producing large quantities of sperm, and it is suggested that they practice a form of sperm competition which allows males to attempt to displace or outnumber rival sperm in the vagina and uterus (*67*).

Very little is known about the mating behavior of most rorquals except that humpback, right, and bowhead whales have surface-active groups where animals butt, ram, and inflict bloody wounds on each other (*68*). This may represent aggression between males as they battle for access to a female. Direct competition may make sperm competition unnecessary, possibly because only one male gets to inseminate a female, and, indeed, the testes of humpbacks (and those of all other rorquals) are correspondingly small (*67*). Male humpback whales also sing on mating grounds, which may be an alternative mating strategy, either to mediate male-male competition or to attract the attention of females (*69*). There is no evidence that rorquals are monogamous; however, a lack of extreme secondary sexual characteristics and the relatively low levels of differential male-female mortality in utero suggest that these whales are not extremely polygynous (*70*).

Several techniques will allow the rapid advance of our knowledge of mysticete (and odontocete) social and mating structure. One, used extensively in the past 10 years, involves long-term reidentification of whales and dolphins from natural marks (*71*). This technique is used in conjunction with sex and relationship information obtained by small biopsy samples from whales in nature. Samples are collected by shooting (with crossbow or compound bow) a hollow dart connected to a fishing reel. Sex is determined from karyotypes and genetic relationships assessed from protein, chromosomes, and DNA polymorphisms (*72*). Correlation between behavior, sex, and relationship is still in its infancy, but is likely to grow rapidly in the next several years.

Odontocetes. The six families of toothed whales include the small harbor porpoise (*Phocoena*) to the mighty sperm whale (*Physeter macrocephalus*). Almost all species are gregarious and probably all echolocate. Most species feed on fish and squid; and most feeding, social activity, mating, and rearing of young take place in the group or school.

In general, animals travel in flocks and schools for enhancement of predator detection, confusion, and avoidance (*73*), as well as for foraging efficiency. Polarized schools (that is, with all members pointed the same direction) may have increased vigilance, where each individual is able to react to danger faster than if alone. But a nonpolarized school (or social aggregation) has more freedom of movement, perhaps essential to corralling food and to social-sexual activity. We see dolphins vacillate between these two school types as they rest in polarized fashion and as they interact socially (including feeding and sex) in nonpolarized fashion (*74*) (Fig. 1).

There is a relationship between habitat and group size in odontocetes, with nearshore species usually occurring in groups of a dozen or so individuals, while offshore species tend to have larger groups. This reaches its extreme form in the small pelagic delphinids, where groups of several thousand are not uncommon, perhaps like herds of African plains antelopes (*75*).

Nearshore odontocetes generally have an open group structure. That is, dolphins live in groups that number only one or a few dozen animals, but they often exchange members with groups that have adjacent or overlapping ranges. We therefore must consider a larger pool of animals as the population unit (*76*, *77*). In bottlenose dolphins and pilot whales (*Globicephala* sp.), mothers and female offspring form long-term bonds; males account for the fluidity of associations. Group sizes can change daily, which allows for the most efficient group size in the face of changing environments. For example, bottlenose dolphins in Argentina had larger group sizes when they fed on anchovy in an apparent coordinated manner and smaller group sizes when they fed on nonschooling, rock- and bottom-dwelling prey in a more individual manner (*78*).

Dolphins in the open ocean live entirely within the large school envelope. The extent of fluidity in associations between members of subgroups within the school is unknown. Although the physical scale is different, fluidity between subgroups is probably similar to that of the nearshore environment. Males cannot be assured of paternity for their young, especially in a nonmonogamous society; we therefore expect that males and their offspring have no special bonds.

Adult male dolphins in captivity are often aggressive toward younger members, to the point of killing youngsters (*79*). Bateson studied the dominance relationships of a mixed group of spinner and spotted (*Stenella* sp.) dolphins at Sea Life Park, Hawaii, and noted a pecking order that consisted of nonlinear relationships in a matrix of associations. One dolphin could bite a second, that could bite a third, and the reverse did not occur. But dolphin number three could have similar access as number one to food or a mate. A similar imperfect hierarchy exists in baboons (*76*, *80*). Dominance-subservience relationships in nature probably result in a structuring of the society: the young is relegated to a particular physical space, possibly for its own safety. However, infanticide is common in a number of species and could occur in dolphin species in nature (*81*).

Toothed whales appear to cooperate with each other during foraging; for example, killer whales (*Orcinus orca*) herding pinnipeds and fish, and bottlenose dolphins herding fish (*82*). Dusky dolphins (*Lagenorhynchus obscurus*) of coastal water in Argentina herd anchovy (*Engraulis* sp.) into tight balls against the surface. When the fish become lethargic, possibly due to oxygen deprivation in the tight cluster, dolphins take turns feeding on the fish. Thus, temporary restraint from feeding appears to be practiced by all for the common goal of debilitating the prey. We do not know whether differential age and sex roles are played during herding, nor whether a feeding hierarchy exists (*83*).

Fish and sea bird predators that cooperate can more effectively take schooling prey than when alone or in very small groups (*84*). This can lead to the alternative strategies of forming groups when taking prey larger than oneself or prey that needs to be herded, and operating singly when foraging for small or nongrouping prey (*85*). Dusky dolphins of Argentina look for prey schools in many spread-out, small groups of dolphins, aggregate when prey is found, cooperatively herd and socialize as an aggregated group, and then split again. They thus display a fission-fusion society directly related to the taking of schooling prey (*83*, *86*). However, dusky dolphins in deep water off New Zealand, where there are no appropriate schooling fishes, feed instead on mesopelagic, loosely or nonaggregated fishes and squid. The dolphins seldom split into small groups, but remain in the safety of the school of several hundred animals, feeding singly and apparently noncooperatively on nonschooling prey (*87*). In this case, the large school serves as the important stable social unit and probably has little direct relationship to foraging efficiency.

Dolphins copulate often and engage in much homosexual activity in the wild and in captivity. Copulation may be an important part of social bonding and of reinforcing hierarchical structure (*43*) (Fig. 2). Since we have difficulty discerning when a female dolphin is physiologically ready for conception, we cannot determine which copulations are for procreation and which are simply part of the social repertoire. We are, therefore, unsure of mating systems, but because of the fluidity of associations of males and the observation that females mate with more than one male, most delphinids are probably polygynous tending toward promiscuity. This is supported by long-term observations of a bottlenose dolphin population in Florida, where associations between animals of known sex and age have been monitored for about 18 years (*88*). The promiscuous mating hypothesis is being tested by measuring the relative reproductive success of different males; chromosome banding patterns of calves, mothers, and possible fathers are being correlated with mating. Further indirect evidence for promiscuity comes from the extremely large testes of delphinids which, like the baleen whales discussed above, may indicate sperm competition (*89*).

Movements and Migrations

Large whales undergo extensive annual migrations that place them in winter on low-latitude mating and calving grounds and in summer on productive high-latitude feeding grounds. The specifics of movements by particular populations are being elucidated by photographic recognition of whales at different times of the year (*90*). Migrations of the large baleen whales and of male sperm whales tend to be on the order of about 3,000 to 5,000 km one way, although the gray whale moves up to 10,000 km between Mexico and the Chukchi Sea (*91*). Since humpback males of the same population sing the same song in any one breeding season, one can determine which whales spend at least part of the year together. Humpbacks that breed near the Revillagigedo Islands of Mexico, the Hawaiian Islands, and Japan may feed together along the Aleutian chain and elsewhere in high latitudes (*92*). Alternatively, enough animals travel between these widely separated mating grounds in order to carry the song between areas.

Migrations of the baleen and sperm whales may occur to allow feeding in productive waters and calving in warmer waters. But there seems no a priori reason for calving to necessitate warm waters; bowhead whales breed and calve near the ice edge and a few of the smaller toothed whales, which should be physically more susceptible to cold than the large baleen whales, can live near ice as well. Migrations may be a holdover from when lower latitude waters near breeding grounds were more productive, and whales moved farther from those grounds as prey abundances shifted but kept their traditional mating grounds since those are important aggregation points (*93*). Although this is somewhat fanciful without substantial support in all but a few cases, it may have some merit along with the thermodynamic hypothesis. Predation should be considered as another possible force toward migration. Killer whales are less abundant in lower latitudes, and movement toward such areas may be a useful ploy for protecting the newly born young. A similar force for the extensive migrations of wildebeest and other terrestrial mammals has been proposed (*94*).

Not all whales migrate. Some individual gray, fin, Bryde's, minke, and blue whales may stay yearround in particular, usually protected, nearshore areas. However, except for the often sedentary minke whale, it is not known to what degree such pockets of animals constitute reproducing units, or whether they are mainly composed of juveniles, postreproductive, or nonmating resting members of more extensive populations.

Toothed whales smaller than sperm whales often show seasonal movements, although they are not necessarily in a north-south direction. Thus, in the north Pacific, northern right whale dolphins (*Lissodelphis borealis*) move northward and shoreward in spring, southward and offshore in autumn; Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) make onshore movements in autumn and offshore ones in spring; and harbor porpoises appear to be closer to shore in summer than in winter (*95*). Toothed whales follow seasonal shifts in food supplies since they do not have the fasting capability of the baleen whales. Movements have been related directly to prey concentrations (*96*) and to indirect indicators of prey, such as temperature variations (*97*), sea-surface chlorophyll concentrations (*98*), and such stationary features as depth and bottom type (*99*, *100*).

Dolphins nearshore tend to show diurnality in feeding and predator avoidance. Argentine dusky dolphins, Hawaiian spinner dolphins, and Bay of Fundy harbor porpoises show offshore nighttime and onshore daytime movements, albeit for different major prey with different behavior patterns (*101*). In contrast, Florida bottlenose dolphins are more sedentary, probably because of opportunistic feeding on several prey species, and the general presence of mullet [*Mugil cephalus* (*102*)]. The nearshore preference while resting or socializing of dolphins that feed farther from shore probably occurs to reduce predation by deepwater sharks and killer whales (*103*). In New Zealand and Argentina, I have on four separate occasions observed dusky dolphins retreat to very shallow water when killer whales approached, usually successfully hiding in the turbulent surf zone or behind shallow-water rocks. The situation appears generally similar to baboons that feed in open, exposed habitats but retreat to trees or cliffs to rest or when threatened by predators (*104*).

Short-distance movements to follow food supplies and avoid predation can be explained by direct experience and by learning favorable aspects of all parts of the range. As in terrestrial animals, dolphins and whales likely know their immediate milieu well. But longer distance movements and seasonal migrations, especially those away from shore, must pose substantial problems of orientation and navigation (which implies knowledge of a map). Our knowledge of how marine mammals obtain locational cues from their environment is incomplete. How, for example, do humpback whales that feed in southeast Alaska find the relatively small Revillagigedo or Hawaiian Islands in a huge expanse of sea? Sun orientation (*105*), cueing onto underwater topography by passive listening (*99*), echolocation of the bottom (*106*), detection of thermal structure (*107*), chemoreception by tasting of water masses and current systems (*108*), and magnetoreception (*109*) have all been proposed. Animals in general make use of a multiplicity of cues available to them, and it is possible that all cues above can come into play for various species and areas (*110*). Recent hypotheses on magnetic sensing, however, suggest that this sensory modality may be used by long-distance migrating cetaceans. It may help to explain the well-known incidence of mass live strandings by several migratory pelagic odontocete cetaceans, such as sperm whales, pilot whales, and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (*111*). But magnetic orientation or navigation, even if cetaceans use it, is probably not the final answer for marine mammal strandings, nor is it likely to be the only method used in navigation. Further insight into migratory cues may come from long-distance satellite-tracking studies, used only experimentally on cetaceans to date but with promise of becoming a major tool as electronic telemetry packages are reduced in size (*112*).

Concluding Remarks

The study of cetaceans is of intrinsic interest as an exploration of the morphological and behavioral adaptations of mammals to a totally aquatic environment. Cetacean adaptations such as diving, communication, and sociality may help us to better understand aspects of mammalian morphology and behavior. Research on cetaceans has reached the "mainstream" of science. Whereas 10 years ago we were continually apologizing for knowing so very little, we now are on a more confident footing. We are pursuing lines of research in sophisticated and innovative manners: radiotelemetry for physiologic and behavioral data, chromosome and protein analyses for relationship information, and new methods of digitizing and analyzing sounds to describe communication and echolocation abilities.

Early information on morphology, life history, and behavior of baleen and sperm whales came from observations of the whaling industry during hunts and after death. For the smaller toothed whales, most of our knowledge of social interactions, use of sound, and physiology came from dolphins in captivity. Few researchers went out into the field and spent months (and years) observing wild animals, as is now common. Much of the older data helped build a solid foundation for our present knowledge; some of it has been discarded in light of modern findings under more natural conditions. This is less true for morphologic and life history information and more true for data on foraging behavior, social-sexual behavior, and society structure. In the latter realm, several primate researchers are presently comparing the social behavior of coastal bottlenose dolphins and the society structure of terrestrial social mammals, and this cross-fertilization between land and sea mammal research cannot fail to provide new insight into both systems (*113*).

Large whales are no longer hunted commercially, except for small "local" fisheries and an ongoing small hunt for minke and fin whales, thinly disguised as "scientific whaling" (*114*). For the time, at least, no large whale is in danger of extinction, although right whales are still scarce in the Northern Hemisphere. However, various species of pelagic dolphins have been killed in great numbers in the eastern tropical Pacific in the past 25 years, in association with purse-seining for tuna, and the killing continues unabated. Exact amounts of population declines are not known, although estimates place spinner dolphins, spotted dolphins, and common dolphins at only a fraction of their preexploitation numbers (*115*). Local populations of nearshore dolphins and whales are also affected by human harvesting and by habitat degradation (*116*). The Gulf of California harbor porpoise (*Phocoena sinus*) and the river dolphins, most notably the Chinese river dolphin (*Lipotes vexillifer*), are in imminent danger of extinction. Their plight is due to habitat destruction, including overfishing, and due to incidental kills from fish hook and net operations (*117*).

Organochlorine pollutants such as polychlorinated biphenyls and DDE accumulate in long-lived cetaceans, and their levels in whales and dolphins have been used to trace movement patterns (*118*), indicate reproductive parameters (*119*), and provide an overall index to the chronology of organochlorine toxin input into the ecosystem (*120*). As such, marine mammals may be used as tracers of pollutants, especially if the traced animals have a well-known, perhaps relatively confined, range. These pollutants are harmful when bioaccumulation is great, and there is a direct link between lowered testosterone levels and raised DDE concentrations in Dall's porpoises (*121*). Similar results in other species are likely to follow as appropriate measurements are made.

Many nearshore areas, and some of the world's major river systems, have become so ecologically degraded as to drive several cetacean species to near extinction. We should be warned by these more visible marine mammals, which come to the surface to breathe and thereby may be seen and counted, and realize that due to human action on the seas as well as on shore, other more ecologically encompassing disasters are taking place beneath the surface.

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