Cetacean Life History

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A species' life-history strategy is defined by parameters that describe how individuals allocate resources to growth, reproduction, and survival. The allocation of resources presumably results from natural selection maximizing the reproductive fitness of individuals within a species. Biologists studying life-history strategies collect data to answer questions about how long individuals of a species live, the ages at which they become sexually mature and first reproduce, and where and when they travel to find sufficient food to survive (Fig. 1). In search of answers, these biologists may be found in a laboratory estimating an individual animal's age, at a computer modeling growth rates, or at sea observing animals in their natural habitat.

Among cetacean species, the life-history strategies are diverse and differ markedly between the two cetacean suborders: baleen whales (suborder Mysticeti) and toothed whales (suborder Odontoceti). This diversity demonstrates the range of successful strategies that have evolved and enable cetaceans to live in a completely aquatic environment as well as the influence of their phylogeny on adapting them to a particular niche. Reviewing the strategies of species within each suborder reveals that the baleen whales share more similar life-history characteristics. All species are large and long-lived, and all of the baleen whales, except the bowhead whale (*Balaena mysticetus*) and Bryde's whale (*Balaenoptera edeni*), make long-range annual migrations between breeding grounds in tropical waters and feeding grounds in temperate or polar waters. However, the life-history patterns observed among odontocetes are more varied. These species range in size from the small, relatively short-lived (<24 years) harbor porpoise (*Phocoena phocoena*) to the large, relatively long-lived (>70 years) sperm whale (*Physeter macrocephalus*) and occupy diverse habitats, ranging from pelagic and coastal ocean waters to estuarine and fresh waters.

The life-history strategies for relatively few cetacean species are known in detail. Most of the biological data available for baleen whales were collected during whaling operations, whereas odontocetes have been studied from animals incidentally taken during fishery operations, taken in directed fisheries, found stranded on the beach, or observed in the wild or in captivity. Among the most well-known cetacean life histories are those of the humpback whale (*Megaptera novaeangliae*), fin whale (*B. physalus*), common bottlenose dolphin (*Tursiops truncatus*), and killer whale (*Orcinus orca*). Three of these species—the humpback whale, common bottlenose dolphin, and killer whale—have each been the subject of long-term studies, which have provided unique data about the natural variability of a species' life-history strategy based on the observed demographics of individual animals. Our knowledge about the life-history strategies of cetacean species is still incomplete, particularly for rarely encountered species, but our knowledge is expanding rapidly as more specimens are collected and new techniques are developed.

I. Characteristics of Cetacean Life Histories

Although a diversity of life-history strategies is exhibited by cetacean species, there are a few common characteristics that are likely the necessary adaptations for life in a completely aquatic environment. All species give birth to single, large, and precocial young. The presence of multiple fetuses or multiple births has been documented only rarely, and there are no known cases of successfully reared multiple offspring. Gestation times are approximately a year. Among the baleen whales, the estimates for gestation range from 10 to 12 months, and among the odontocetes, estimates range from 10 months for the harbor porpoise (Gaskin *et al.*, 1984) to 14 or 15 months for the sperm whale (Best *et al.*, 1984) and 17 months for the killer whale (Olesiuk *et al.*, 1990; Baird, 2000). Most of the small delphinids (e.g., *Stenella* spp.) have gestation periods of 11 to 12 months (Perrin and Reilly, 1984). The length of the gestation period in part balances the cost of producing a large neonate. Additionally, all cetaceans are relatively long-lived. Among odontocetes, estimates of longevity range from approximately 2 decades for the harbor porpoise to up to 7 decades for the sperm whale, and for the baleen whales, estimates of longevity range from 6 decades for the common minke whale (*B. acutorostrata*) up to 9 or 10 decades for the fin whale. Additional generalizations about life-history strategies are presented in Section III.

- Mating Strategy
- Age at First Birth
- Birthing Interval
- Parental Care
- Senescence

REPRODUCTION · SURVIVAL

Life History

GROWTH

- Longevity
- Predation
- Movement Patterns
- Feeding Ecology

- Rates / Patterns of Growth
- Maximum Size or Length
- Size-at-Birth
- Morphology

Figure 1 *Studies of cetacean life history integrate data describing an individual animal's allocation of resources to growth, reproduction, and survival. Compiling data from many individuals allows the parameters listed next to each category to be estimated, which in turn describes the growth, reproduction, and survival strategies of a species. Life-history data may be collected by observing individual animals in directed photo identification, tagging, marking, or telemetry studies or by necropsying animals to collect teeth for aging, body length measurements for quantifying growth rates, gonads for determining reproductive condition, and skin for estimating individual relatedness or determining "local" adaptations using molecular genetic techniques.*

II. Methods of Studying Life Histories

Longitudinal and cross-sectional studies of cetacean species have provided data necessary for understanding their life-history strategies. Longitudinal studies are rare but valuable because they provide unique data on the variability of individual demographics. Three species—the humpback whale (Clapham, 1996), the common bottlenose dolphin (Wells and Scott, 1990), and the killer whale (Olesiuk *et al.*, 1990)—have been the subject of ongoing studies that originated during the 1970s. These studies are possible because individuals are relatively accessible and easily distinguishable in the field by natural markings. These studies have quantified individual variability in reproduction and survival through time and have provided unique insights into the species' life-history strategy by incorporating observations of the species' social behavior and ecology. However, most of our knowledge about cetacean life-history strategies is the result of cross-sectional studies. In these studies, data are collected from individual animals sampled primarily from directed or incidental takes. The primary advantage of these studies is that a complete suite of morphological and biological data can be collected, which allows explicit determination of reproductive and physical maturity as well as an estimate of age. Estimates of age are made from the layering patterns evident in the ear plugs or ear bones of baleen whales (Lockyer, 1984; Christensen, 1995) and in the teeth of odontocetes (Perrin and Myrick, 1980). Accurate determination of reproductive maturity in both sexes requires examination of the gonads. In females, the presence of one corpus or more in the ovaries indicates sexual maturity, and in males, the presence of spermatazoa and large seminiferous tubules in histologically prepared testes tissue indicates sexual maturity (Perrin and Reilly, 1984). Physical maturity is determined in both sexes by examining the vertebral column for evidence of fusion. That is, when the vertebral epiphyses are fused with the centrum, an animal is considered physically mature.

Life-history studies are designed to collect data on body size, age and reproductive and physical maturity from many individuals in order to estimate parameters that characterize a species' allocation of resources to growth, reproduction, and survival. Estimated parameters may include age-specific growth and pregnancy rates, the average age at attainment of sexual maturity, calving interval, and longevity. Age is the primary independent variable for all studies because age explicitly demonstrates the trade-off in resource allocation to growth and reproduction during an individual animal's life. The expected pattern of resource allocation from birth through attainment of sexual maturity is primarily for growth and then for reproduction once sexual maturity is attained. Also, the probability of an individual surviving to the next age class increases with increasing age after weaning until sexual maturity is attained and then remains high throughout the individual's reproductive years. Data on age-specific growth and reproductive rates, combined with estimates of age-specific survival rates, are essential to comparing and contrasting the life-history strategies of different species.

III. Cetacean Life-History Patterns

Neonates of all cetacean species are relatively large when compared to those of other mammal species. In fact, neonate size ranges from approximately 29% of the female's asymptotic total body length in most of the baleen whales to between 40 and 48% of the female's length in odontocetes. The large size of neonates, combined with their ability to swim and grow rapidly immediately after birth, increases their probability of survival. The lactation period for the baleen whales lasts only about 6 months, and the young grow rapidly during that period because the fat content of the milk is high. However, the calves of odontocetes grow more slowly, and the lactation period lasts approximately a year or more. The difference in calf growth rates between the two suborders of cetaceans is probably due to the transfer of energy to the young through the milk. Oftedal (1997) estimated that the energy output through milk ranges from 0.40 to 1.06 MJ/kg$^{0.75}$ for mysticetes and from 0.09 to 0.17 MJ/kg$^{0.75}$ for odontocetes. For species with a lactation period of more than a year, the additional investment likely further increases the calf's probability of survival by facilitating the learning of social behaviors [e.g., common bottlenose dolphin, short-finned pilot whale (*Globicephala macrorhynchus*)].

Patterns of growth differ between the sexes of many cetacean species, resulting in some degree of sexual dimorphism. Both males and females have high growth rates while suckling, but growth slows after weaning and again after reaching sexual maturity. However, the sex that grows largest tends to grow for a longer period of time and may have higher growth rates after weaning. Among baleen whales, females attain lengths that are generally 5% larger than males. Similarly, among odontocetes, females are slightly larger than males in the porpoises and river dolphins. However, for other odontocetes, males are larger than females. Sexual dimorphism is most marked in sperm whales, in which males are 60% larger than females. Among the smaller delphinids, such as the common bottlenose dolphin, pantropical spotted dolphin (*Stenella attenuata*), and common dolphins (*Delphinus* spp.), males are approximately 2 to 10% larger than females.

The breeding cycle for all cetacean species has three parts: a gestation period, a lactation period, and a resting, or anestrous, period. This cycle is 2 years or more for most cetacean species. Exceptions are the minke whale and harbor porpoise, which can breed annually. The breeding cycle of blue (*B. musculus*), Bryde's, humpback, sei (*B. borealis*), and gray (*Eschrichtius robustus*) whales includes an 11-month gestation period, a 6- to 7-month lactation period, and a 6- to 7-month resting, or anestrous, period for a minimum of a 2-year cycle, while the breeding cycle for the bowhead and right whales (*Eubalaena* spp.) is 3 to 4 years starting with a 10- to 12-month gestation period. Furthermore, the breeding season of baleen whales is synchronized with their migration cycle. These species travel long distances to breed in tropical waters. Exceptions are the Bryde's whale, and the pygmy Bryde's whale, which spend all year in tropical waters and do not breed synchronously (Lockyer, 1984). Several hypotheses have been proposed for the adaptive significance of the large-scale migrations of baleen whales. Although the phenomenon remains unexplained, hypotheses of increased survival rates for neonates in tropical waters by reducing thermoregulatory demands or the risk of predation by killer whales have been proposed (Corkeron and Connor, 1999).

Similar to other life-history characteristics, the breeding cycle for odontocetes is more variable than that of mysticetes. Porpoises have the shortest breeding cycle, which is approximately 1 year and includes a 10-month gestation. In fact, annual breeding among porpoises has been well documented for the harbor porpoise. The smaller delphinid species seem to have 2- to 3-year calving intervals, which include an 11- to 12-month gestation and a 1- to 2-year lactation period. However, larger odontocetes, such as the killer whale, short-finned and long-finned (*G. melas*) pilot whales, and sperm whale, have calving intervals of >3 years, which includes a 12- to 17-month gestation period and a 2- to 3-year, or longer, lactation period. Breeding synchrony also varies among odontocetes. Species inhabiting temperate waters, such as the harbor porpoise, have been found to have more synchronous breeding seasons than species inhabiting tropical waters. For example, studies of the pantropical spotted dolphin (Fig. 2) and the striped dolphin (*S. coeruleoalba*), which inhabit tropical waters in the Pacific Ocean, found that young are born throughout the year, although most births occur during the spring and fall (Perrin and Reilly, 1984).

Age at attainment of sexual maturity is delayed in all cetacean species as would be expected for large, long-lived mammals. However, the range of ages is quite broad and reflects the unique set of adaptations that characterize the life-history strategy of each species. The range in age of sexual maturity among baleen whales is from approximately 4 years for the bowhead and humpback whales to approximately 10 years for fin and sei whales (Lockyer, 1984). Among odontocetes, the range in age at attainment of sexual maturity is about the same as that observed for baleen whales and seems to be correlated to a degree with longevity and body size. The youngest age at attainment of sexual maturity is 3 years for the harbor porpoise, which is among the smallest odontocetes and is estimated to live approximately two decades (<24 years). However, many of the larger odontocetes reach sexual maturity at ages of 10 years or more and live for four or more decades (Perrin and Reilly, 1984).

Reproductive success varies throughout the life of female cetaceans. Initially, reproductive success is relatively low, peaks several years after the age at attainment of sexual maturity, and then declines as the female ages. This phenomenon is also characteristic of large terrestrial mammals and is probably due in part to a trade-off in costs between reproduction and growth that must occur because physical maturity is attained several years after sexual maturity and to learning to care for young. Evidence for low reproductive success among newly matured females has been documented in the common bottlenose dolphin and the fin whale. Lower reproductive rates for older females have also been documented in the common bottlenose dolphin as longer interbirth intervals for older females that include a 3- to 8-year lactation period. Postreproductive females with senescent ovaries have been identified in only a few odontocetes, including the short-finned pilot whale (Marsh and Kasuya, 1986) and the pantropical spotted dolphin (Myrick *et al.*, 1985), but senescence has not yet been identified in any of the baleen whales. The adaptive significance of senescence is not yet understood but likely contributes to increased reproductive success. For example, several species that exhibit senescence also have fairly complex social structures (e.g., sperm whale, short-finned pilot whale), and the role of postreproductive females in their societies may be associated with increased survival rates of the young by these females participating in the care of young that are not their own.

IV. Characteristics of Male Life Histories

The life-history characteristics of males are less well known than those of females, primarily because this knowledge is less critical to understanding a species' reproductive potential and population dynamics. In this sense, females are the limiting sex. However, knowledge about the life-history strategies of males provides a more complete picture of a species population dynamics and provides information about the species' breeding strategy and social structure.

One of the major differences between the life-history strategies of male and female cetaceans is the age at attainment of sexual maturity. In species with the greatest degree of sexual dimorphism, the difference in age at attainment of sexual maturity for males and females is greatest. This difference reflects the additional time required to grow to about 85% of their asymptotic length, which is the approximate size at which all mammals become sexually mature. For example, sperm whale males reach sexual maturity at a much later age than females. The estimated age at attainment of sexual maturity for the female sperm whale is from 7 to 13 years and for males is approximately 20 years (Rice, 1989; Best *et al.*, 1984). The difference is similar in the killer whale and the short- and long-finned pilot whales (Baird, 2000; Lockyer, 1993). However, the smaller delphinid species that show less sexual dimorphism
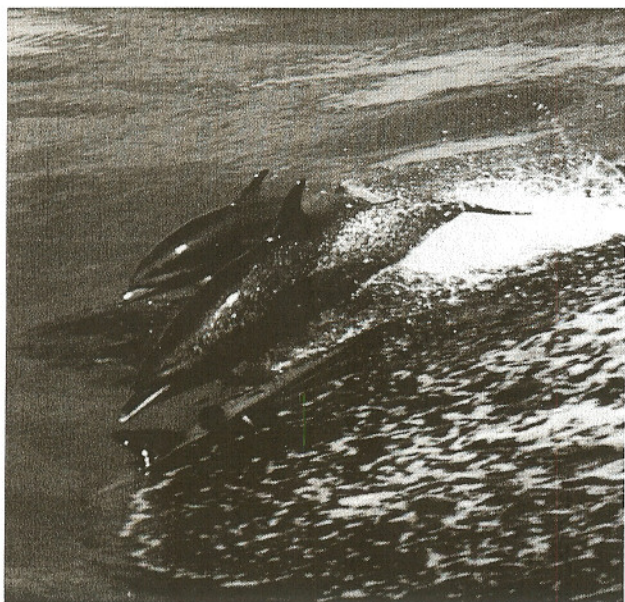

Figure 2 *Mother and calf pantropical spotted dolphin (Stenella attenuata) in the eastern tropical Pacific. Photograph by R. L. Pitman.*

reach sexual maturity at more similar ages. In fact, the difference in age between the sexes is about 3 years for the common bottlenose dolphin, pantropical spotted dolphin, and spinner dolphin (*S. longirostris*), with males reaching sexual maturity at the older age (Perrin and Reilly, 1984).

Sexual dimorphism has been used as a predictor of cetacean mating systems. For example among odontocetes, the degree of sexual dimorphism exhibited by the sperm whale, short-finned pilot whale and killer whale has been hypothesized to indicate male-male competition in a polygynous mating system. The presence of scars inflicted by other males provides evidence of male-male competition in sperm whales. However, fairly recent data that the short-finned pilot whale and killer whale have limited male dispersal from natal pods and likely breed promiscuously suggests that sexual dimorphism may have evolved for reasons other than mating. One interpretation of these data is that the presence of large males in their natal pod enhances their reproductive fitness by improving, for example, the foraging efficiency of the pod (Wells *et al.*, 1999).

V. Life-History Parameters and Demography

Knowledge of a species' life-history strategy provides the foundation for understanding the species' demography because their life-history characteristics reflect the species' adaptations to a particular niche, which is bounded by constraints of the environment as well as their morphology and physiology. Whereas life-history studies focus on individual variability in traits that express these adaptations, each study can usually only focus on a particular group of animals within the species. The comparison of studies made on different groups of animals within a species' range, however, reveals variability in life-history parameters. For example, pantropical spotted dolphins north and south of the equator have different breeding seasons, and the estimates of asymptotic length for animals in the western Pacific are 4 to 7 cm longer than those from the eastern Pacific (Perrin and Reilly, 1984). Similar examples exist for other cetacean species. There are also examples in the literature of cetacean populations responding to changes in the availability of resources through time. This is called density dependence. For example, changes in the age at attainment of sexual maturity for fin, sei, and minke whales through time have been reported and are presumed to be a response to increased per capita resource availability following reductions in population abundance that resulted from commercial whaling (Lockyer, 1984). Similarly for the striped dolphin and the spinner dolphin, changes in the age of sexual maturity and pregnancy rates have been reported and explained as responses consistent with increased resource availability that resulted from decreased population abundance (Perrin and Reilly, 1984). In addition to understanding a species' life-history strategy and its inherent variability, recognition of these types of population-level responses is important to consider when developing conservation and management plans.

Estimates of age-specific reproductive rates and survival rates are critical to quantifying a species' demography. However, for nearly all cetacean species, age-specific survival rates are unknown and are likely to remain so. Because demographic studies must include age-specific survival rates, unique solutions have been sought to allow the estimation of survival rates based on imperfect knowledge (Barlow and Boveng, 1991). Longitudinal studies like those of the common bottlenose dolphin and the humpback whale provide the only source of data to estimate survival rates, and these data are generally used as a guide for estimating survival rates for other species with similar, but less well-known, life histories.

VI. Life-History Studies and the Future

Several new technologies are being actively applied to studies of cetacean species and contribute to our knowledge about the adaptive significance of their life-history strategies. Specifically, the expansion of molecular genetic techniques and the development of satellite and VHF (Very High Frequency) tracking technology allow more detailed data collection on individual animals. For example, the application of molecular genetic markers as tags for individuals has been demonstrated successfully with the humpback whale data set (Palsbøll, 1999). Application of this technique to cetacean species whose individuals cannot be recognized readily by natural marks may facilitate life-history studies for those species. Additionally, the results of molecular genetic studies on several cetaceans, including the beluga whale (*Delphinapterus leucas*) and Dall's porpoise (*Phocoenoides dalli*), have confirmed hypotheses of male-biased dispersal (O'Corry-Crowe *et al.*, 1999; Escorza-Treviño and Dizon, 2000). Although this is not a surprising result because male-biased dispersal is common among large terrestrial mammals, molecular genetics provided the tool to examine large enough data sets to ask this question for cetacean species. In addition to the expansion of molecular genetic analy-

Figure 3 *A pantropical spotted dolphin* (Stenella attenuata) *wearing a radio tag and time-depth recorder to study diving behavior. Photograph by M. D. Scott.*

ses to studying cetaceans, the development of satellite and VHF tracking technology is continuing. There have been notable successes in the use of satellite tags to study beluga whales in the Arctic (Martin *et al.*, 1998) and blue whales in the North Pacific (Mate *et al.*, 1999). Broader application of this technology to study more individuals of more species has been limited in part by problems with tag attachment, but this technology, together with the expansion of molecular genetic techniques, will provide us opportunities for new insights into the life-history strategies of more cetacean species (Fig. 3).

See Also the Following Articles

Age Estimation ▪ Female Reproductive Systems ▪ Pinniped Life History ▪ Population Dynamics ▪ Sexual Dimorphism

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Cetacean Physiology, Overview

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> Though whales are the strangest of all mammals—the farthest out from the mainstream of mammalian life—they have no structures fundamentally new but only familiar ones reworked.
> —V. B. Scheffer, "The Year of the Whale," 1969.

Dolphins, porpoises, and whales occupy a special place in human interactions with the world of nature. Our fascination with them has its origins in a distant past. However, despite that long association, they remain the least accessible and least known of the mammals. Important pioneer investigations have been successfully applied to small captive cetaceans, but the obvious constraints of sheer magnitude have prevented all but the most rudimentary physiological studies of great whales.

The obligate cetacean aquatic lifestyle imposes environmental constraints with physiological consequences vastly different from those of terrestrial mammals in their atmospheric environments. However, most, if not all, of their adaptations are extensions of or variations on the general mammalian theme. The physical properties of water dominate these considerations: