TREE vol. 1, no. 6, December 1986

Population Biology, Social Behavior and Communication in Whales and Dolphins

Peter Tyack

The baleen whales differ from the toothed whales and dolphins in life history and in social organization. Even though they grow to a larger size, young baleen whales tend to develop more rapidly than dolphins and toothed whales. Except for the mother–calf bond, most groups of baleen whales are short-lived, lasting only for hours, and individual-specific associations appear to be exceptions to the norm. Most toothed whales live in more structured groups, in which young animals have a long period of dependency and social learning. The communication signals described for different cetacean species have functions suited to the interactions that predominate in their societies.

Whales, dolphins and porpoises all belong to the taxonomic order Cetacea. In common English usage, all cetaceans more than several meters in length are called 'whales'. But the toothed whales such as the sperm, killer and pilot whales are much more closely related to dolphins and porpoises than to the baleen whales. Dolphins, porpoises and toothed whales are all classified together as odontocetes. As the name indicates, all odontocetes have teeth. Baleen whales do not have teeth, but instead use baleen to filter small prey from seawater. Baleen whales also have two external blowholes while odontocetes have only one. Beyond these physical differences, recent studies indicate striking differences between the two groups in life history, social organization and communication.

Reproduction and feeding in baleen whales is strongly seasonal

Most baleen whales exploit schooling planktonic crustaceans or small fish which abound during the summer in polar waters. Each spring, most species of baleen whales in the southern hemisphere migrate from breeding grounds near the tropics to their summer feeding grounds in the Antarctic. During the summer feeding season, adult whales are usually caught with full stomachs, while during the winter breeding season their stomachs are often empty[1]. Essentially, baleen whales feast during the summer and fast for the rest of the year.

Birth in most baleen whale species is also highly seasonal; the calves are born in tropical waters during the winter. The gestation period of two typical baleen whales is nearly one year (Table 1); both mating and calving occur during the same season. Baleen whales probably grow faster than any other animal. While nursing, a calf blue whale *(Balaenoptera musculus)* grows approximately 80 kg/day and 3.5 cm/day[1]. The period of lactation is relatively short, the calf being weaned within six months to one year. As Table 1 shows, blue whales wean at seven months of age, when the calf is on average 12.8 meters long[2]. Their growth is so rapid that after the short period of lactation, a calf will be 50–70% of its length at sexual maturity. On the breeding grounds of humpback whales *(Megaptera novaeangliae)* one can occasionally identify yearlings, but animals older than one year can seldom be readily distinguished from adults.

The usual range of age at sexual maturity for baleen whales is 4–10 years, with blue and humpback whales maturing as early at 4–5 years[2]. Females of some species are capable of having one calf per year, but a two- or three-year breeding cycle is more common, perhaps allowing a female to build up her fat reserves during feeding seasons when she is not pregnant.

Young toothed whales are dependent for many years

Few odontocetes are known to have long yearly migrations between separate feeding and breeding grounds. Nor do they have the annual cycle of feast and famine typical of baleen whales. Both mating and calving are seasonal in odontocetes, but the peaks are often less defined than those of baleen whales. The mating and calving seasons of odontocetes may not overlap, for the gestation periods often exceed one year. Their mating seasons are not as synchronized with the annual cycle as those of baleen whales, and there may be several seasons per year within one odontocete population. The gestation periods of the odontocetes tend to increase with body size (Table 1), and the larger odontocetes gestate for about 15 months. By contrast, the annual cycle of the baleen whales appears to have constrained both the gestation period and period of lactation to under one year.

Most odontocetes also take longer to wean their young than baleen whales. Dolphins only 2–3 m in length (e.g. *Tursiops truncatus*) may suckle their calves for 18–20 months. The mean duration of suckling is 2 years for sperm whales *(Physeter catodon)*[3] and 4–5 years for the pilot whale species *Globicephala macrorhynchus*[4]. But some young of both these two species may suckle for much longer periods. Male sperm whales as old as 13 years and females up to 7.5 years have lactose in their stomachs, indicating the presence of milk[3]. The maximum duration of suckling has also been estimated for *G. macrorhynchus* in Japanese waters where entire schools are sometimes caught; comparisons of the number of lactating females with the ages of immature animals in these schools indicate that individuals as old as 15.5 years may still be suckling[4].

These extremely long times to weaning have been a puzzle for biologists. Both *P. catodon* and *G. macrorhynchus* start taking solid food by the end of their first year. The large difference between the mean and maximum ages for weaning in these species suggests that young do not require milk for as long as some of them suckle. It has been suggested[3,4] that lactation is nutritionally important only in the first few years of life for these species. This conclusion is supported by comparisons with *T. truncatus*; although these dolphins wean by 18–20 months, they stay with the

Peter Tyack is at the Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. This article is contribution No. 6302 of WHOI.

Table 1. Life history parameters for selected cetacean species[a]

Species	Gestation period (mo)	Inter-calf interval (yr)	Age at weaning	Length at weaning (m)	Sex	Age at sexual maturity (yr)	Max. longevity[b] (yr)	Length at sexual maturity (m)	Max. length[c] (m)
Baleen whales									
Blue whale[2]	11	2	7 mo	12.8	M	5		22.6	
Balaenoptera musculus					F	5		24	31
Humpback whale[2,35]	11	1–2	11 mo	8.8	M	4–5		11.5	
Megaptera novaeangliae					F	4–5		12	15
Odontocetes									
Sperm whale[3,10]	15–16	5.8	mean 2 yr	6–7	M	20–25	42	13	18
Physeter catodon			max 13 yr		F	9	61	8.5	12
Killer whale[36]	15	3–8	>12 mo	>3	M	16	35	5.8	9.8
Orcinus orca					F	10	34	4.7	8.5
Short finned pilot whale[4,36]	15	3.3	mean 4–5 yr	2.7	M	17	46	4.2	6.1
Globicephala macrorhynchus			max 13–15 yr		F	9	63	3.2	5.5
Bottlenosed dolphin[36]	12	2.3	18–20 mo	2	M	11	25	2.5	3.8
Tursiops truncatus					F	12	>30	2.3	3.7
Harbor porpoise[30]	11	1–3	6–8 mo	1.1	M	4–6	12–13	1.4	1.5
Phocoena phocoena					F	4–6	12–13	1.5	1.7
La Plata river dolphin[29]	10.5	2	8–9 mo	1	M	2.3	16	1.3	1.6
Pontoporia blainvillei					F	2.7	13	1.4	1.7

[a] The values for any given parameter in this table were not all derived using the same technique.
[b] Ageing techniques are not as reliable for baleen whales as for toothed whales, so longevity is not indicated for these species.
[c] Baleen whales are not strongly sexually dimorphic, although females tend to grow slightly larger than males; maximum length figures have only been indicated for female baleen whales.

mother for the next two years[5]. The prolonged lactation may be seen as a ritualized display reinforcing the mother–calf bond. However, the apparent tendency for males to suckle for longer in both species suggests another interpretation. Both of these species appear to be polygynous, and prolonged suckling of male offspring may enhance their growth and increase the likelihood of their becoming successful breeders. One must be cautious in interpreting this phenomenon, however, because in neither species is it known whether lactating females only suckle their own offspring.

Brodie[6] was one of the first to suggest that the prolonged period of lactation in odontocetes may be related to the importance of social learning. These animals do appear to require a long period to learn about feeding, predator avoidance and social behavior from their mother and other group members. Young captive dolphins learn many new behavior patterns through imitation of adults. For example, captive dolphins that were caught in the wild are skilled at preparing large fish for eating, while captive-born dolphins are clumsy in their attempts to imitate this behavior[7]. In keeping with the apparent importance of social learning, dolphins are highly skilled at vocal as well as postural or motor mimicry[8].

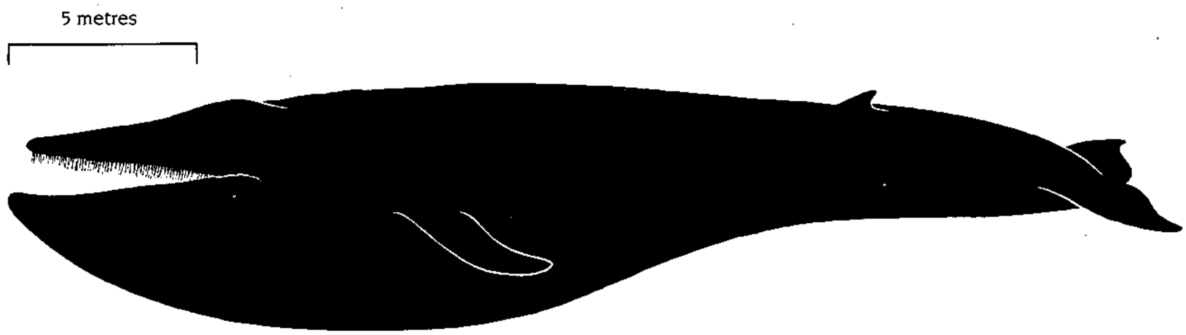
The importance of a long period of parental care is marked by a clear postreproductive phase in the life cycle of *G. macrorhynchus*[9]. Over 25% of the mature females caught in the Japanese fishery have senescent ovaries (histologically similar to those of postmenopausal women), and 25% of these postreproductive females are lactating. Female *G. macrorhynchus* cease to ovulate before the age of 40, but females live for up to 63 years. The postreproductive females have presumably switched their reproductive effort from producing new offspring to lactation and caring for existing offspring, although it is not known whether these postreproductive lactating females suckle offspring other than their own.

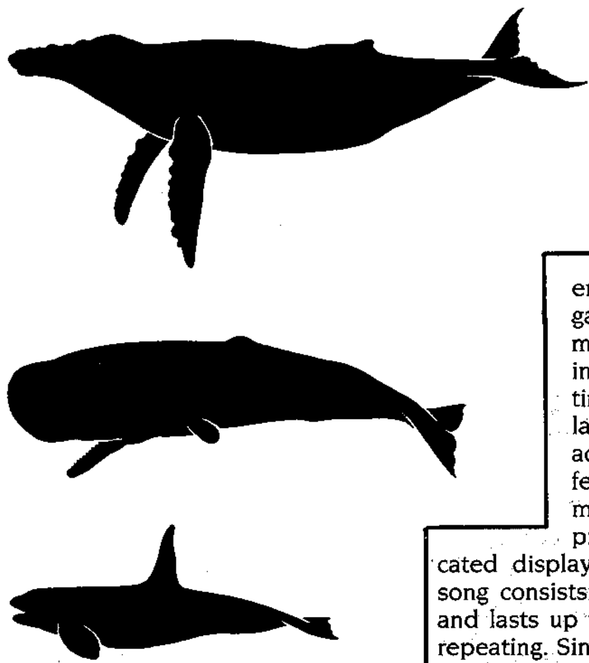
Many odontocete species take longer to reach sexual maturity than baleen whales, and there tends to be a larger gap between the sexes in age of onset of sexual maturity. The most extreme example is the highly polygynous sperm whale. This species is the most sexually dimorphic of all cetaceans; the length ratio of physically mature males to females is 1.44[10]. While male sperm whales may produce spermatozoa when as small as 10 m long, the large males over 14 m long (and more than 20–25 years old) are probably the successful breeders[3]. Female sperm whales reach sexual maturity at an average age of 9–10 years[3]. *G. macrorhynchus* shows a similar pattern; the females reach sexual maturity at about 9 years, males at about 17[4].

Social interactions among baleen whales are brief

In baleen whales, the most stable bond is between a female and her calf, and this lasts less than one year. In keeping with their exploitation of patches of prey that are highly variable in time and space, the groupings of most baleen whales during the feeding season are temporary.

Group structure has been most intensively studied in humpback whales. Humpback whales off Newfoundland feed in groups that are seldom stable for more than a few hours; the size of these feeding groups is often proportional to the size of the patches of prey[11], and individuals are not identified together in different groups more often than would be predicted by a





Top to bottom: blue whale, humpback whale, sperm whale, killer whale.

random model. There are a few reports from other areas of more stable groups of humpback whales, in which individuals appear to learn to coordinate feeding; the same whales may be sighted together in these groups in several different feeding seasons[12], but their patterns of association have not been subjected to statistical analysis.

The traditional view of whale biologists has been that baleen whales are monogamous[2], but there is very clear evidence that this is not always the case. In fact, all of the species whose breeding behavior has been studied are polygamous. These species, which include humpback, right and gray whales, favor coastal or shoal waters during the breeding season (which is why these species are the most extensively studied). Again, humpback whales can be used as an example.

In the fall, humpback whales migrate to winter breeding areas near islands in tropical waters. Males have several strategies for gaining access to females on the breeding grounds. Sometimes, males join in large groups to fight for access to one central female[13]; when alone, males may instead produce long complicated displays, called songs. The song consists of a series of notes and lasts up to 20 minutes before repeating. Since humpback song is sung by males primarily during the breeding season, it has often been interpreted as a reproductive advertisement display. Some behavioral observations of singing whales support this idea. Singing whales tend to approach other whales nearby, and when singers join with other whales, they stop singing[14]. If they join with another male, an aggressive interaction usually follows. On the few occasions when singers have been observed to join with females, behavior associated with sexual activity is observed. But the pairing is brief, and whether a male has joined with a female after singing or as a result of fighting in a larger group, he only escorts the female for a few hours[13,15]. When the same females are reidentified, they are seldom seen with the same male, even after intervals of only several days. The same is true of humpback groups in general. No groups which were resighted on the Hawaiian breeding ground on different days had the same composition[15].

Odontocetes have stable associations

Groups of odontocetes are more structured than those of baleen whales. The members of an odontocete group tend to surface with more synchrony than is typical of baleen whales and the spatial structure of odontocete groups also tends to be more distinct. Baleen whales are often spread out in diffuse herds, and it can be difficult for the observer to ascertain where one group begins and another ends. While individuals of some odontocete species such as the sperm whale may separate by many hundreds of meters when diving, members of a group usually regroup to surface at the same time within tens of meters of one another[16]. Groups of odontocetes are also much more stable over time than those of baleen whales.

The most stable of odontocete groups occur amongst the killer whales *(Orcinus orca)* which have been studied near Vancouver Island, British Columbia. Individuals of this species have been identified in about 30 groups for over 13 years. These groups seem to be made up of related individuals; with low birth and death rates, group composition often does not change for several years at a time. Even though different groups may travel together for a few weeks, no permanent exchange of any animal between groups has been observed[17].

No other odontocete groups are known to be as stable as those of the killer whales. There are generally fewer mature males than females in groups with young, and males do not tend to remain in the same group as long as females do.

In many odontocete species, adult males may associate with female groups for only a few days at a time. As young males mature, they tend to leave their natal group and form juvenile groups, which may also contain juvenile females in some species. The long mother–calf bond provides the stablest unit of group structure in odontocete species. Odontocete groups are typically formed of females with their young, sometimes spanning several generations. Mark–recapture studies of sperm whales have shown that mature females tagged within a group are likely to be caught from the same group even after intervals of 5–10 years[18]. This is not the case with mature males. Studies of bottlenosed dolphins inhabiting inshore waters show that group composition in this species changes frequently[19]. However, clusters of females that share preferred habitats tend to be sighted in the same groups. Males tend to range over a wider area and may even leave the well defined population boundaries for periods of several months[5].

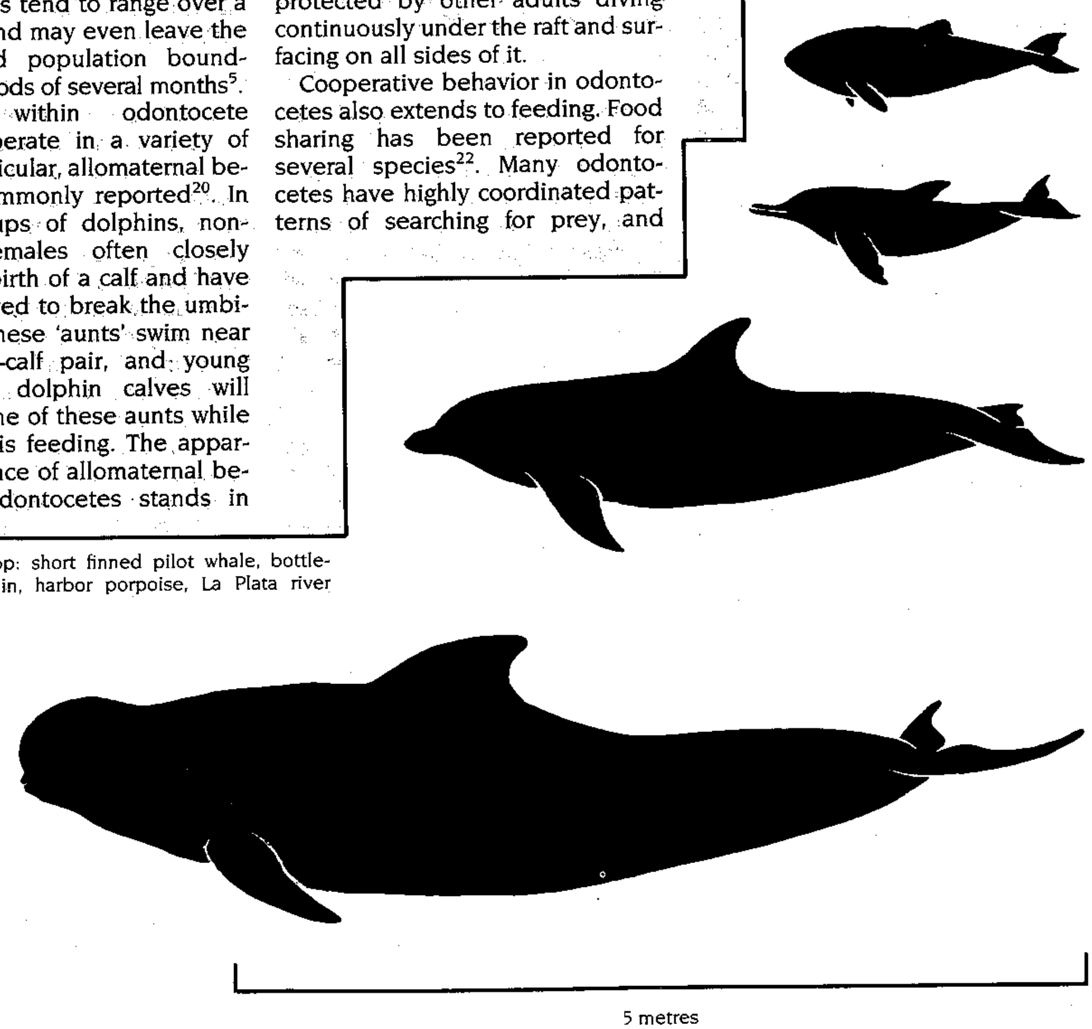
Animals within odontocete groups cooperate in a variety of ways; in particular, allomaternal behavior is commonly reported[20]. In captive groups of dolphins, non-pregnant females often closely attend the birth of a calf and have been observed to break the umbilical cord. These 'aunts' swim near the mother–calf pair, and young bottlenosed dolphin calves will swim with one of these aunts while the mother is feeding. The apparent importance of allomaternal behavior in odontocetes stands in strong contrast to the behavior of humpback whales; when female humpback whales have a young calf, they avoid other whales[20].

Care-giving behavior has been reported surprisingly often for odontocetes, even between members of different species. Wild and captive odontocetes will stand by, assist, or physically support distressed or injured individuals[21]. Typically, a pair of healthy animals will move to either side of a distressed one and lift it up to breathe in a highly coordinated fashion.

Social defense from predators is also considered to be a major function of odontocete schools, and to be a determinant of their size and structure. The responses to disturbance of spotted dolphins *(Stenella attenuata)* in the Pacific are among the best studied[7]. Upon disturbance, these dolphins form a tight school. Mothers with young raft in the center of the group and are protected by other adults diving continuously under the raft and surfacing on all sides of it.

Cooperative behavior in odontocetes also extends to feeding. Food sharing has been reported for several species[22]. Many odontocetes have highly coordinated patterns of searching for prey, and there is evidence that individuals may display to advertise the location of prey[23]. Many odontocete species herd fish in order to capture prey[7]; during this process, some individuals that are herding fish appear to forego feeding while other individuals feed[23]. The structure of odontocete groups and the manifold reports of cooperation in these animals have led to speculation that odontocetes maintain individual-specific social relationships through reciprocal altruism[22].

Large assemblages of odontocetes are typically made up of smaller subgroups that are often distinctly separated from one another and which remain together even after the larger assemblages break up. However, in some species, including the bottlenosed dolphin, interchange of animals between subgroups within a larger



Bottom to top: short finned pilot whale, bottlenosed dolphin, harbor porpoise, La Plata river dolphin.

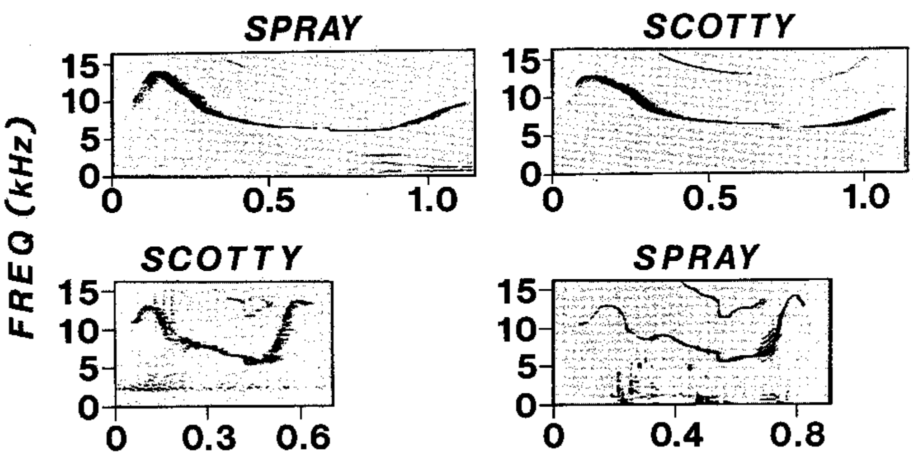


Fig. 1. Sound spectrograms of whistles recorded from two captive bottlenosed dolphins (*Tursiops truncatus*), a female named Spray and a male named Scotty. On the left of the top row is the signature whistle of Spray; on the top right is an imitation of this whistle produced by Scotty. On the bottom left is the signature whistle of Scotty; on the bottom right is an imitation produced by Spray. The horizontal axis shows time in seconds. *Reproduced, with permission, from* Ref. 26.

assemblage is common[19]. Nevertheless, individuals may show strong patterns of association with other individuals, even within otherwise fluid patterns of grouping. For example, some pairs of adult male bottlenosed dolphins are almost always sighted together, even in different groups, for many years[5]. As odontocetes develop, they may leave their natal group and join different groups for long periods. The combination of highly structured patterns of association

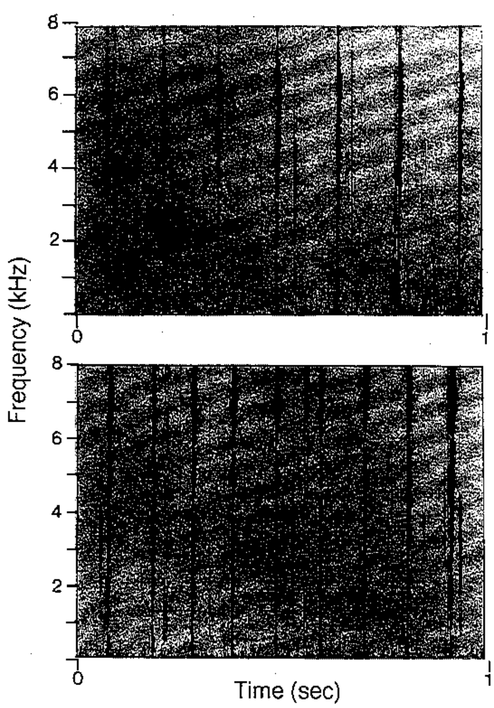


Fig. 2. Sound spectrograms of codas produced by two sperm whales (*Physeter catodon*) as they approached one another. Such codas typically differ in both rhythmic pattern and number of clicks (the coda above has seven clicks, that below has nine). *Reproduced, with permission, from* Ref. 28.

between individuals coupled with occasionally fluid patterns of social grouping argues that individual-specific social relationships are important elements of the social structure of many odontocete species. What we know about communication in dolphins and sperm whales reinforces this view.

Individually distinctive signals in dolphins and sperm whales

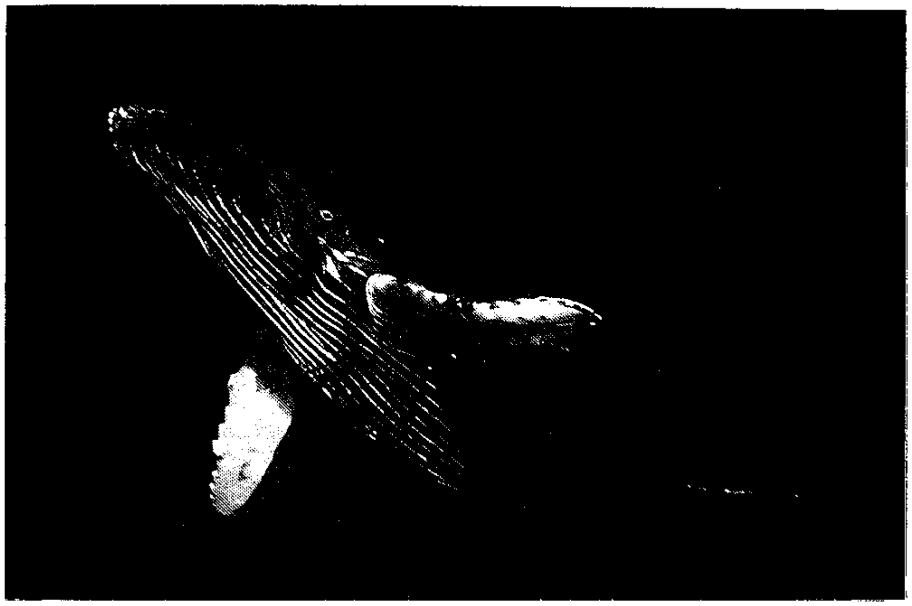
Dolphins of many species produce high-pitched pure tone whistle sounds which are modulated in frequency[24]. Recordings from over 100 captive dolphins have shown that each adult dolphin, when isolated, tends to produce one certain kind of whistle which is distinct from the whistles of other dolphins in its group[25]. These whistles have been called signature whistles; they apparently function to broadcast the individual identity of the whistler. Bottlenosed dolphin calves produce unstereotyped whistles on their first day of life; most develop a stereotyped whistle within their first year. While dolphins are interacting, they tend to produce their own signature whistle, but they do also mimic the signature whistles of others in their tank (Fig. 1)[26]. What might the function of this mimicry be? Carefully controlled experiments have shown that dolphins are skilled at mimicking man-made whistle-like sounds, and that dolphins can be trained to label arbitrary objects with these arbitrary whistles[27]. Perhaps such cognitive skills function in untrained dolphins to allow them to label other members of their social groups by mimicry of their signature whistles.

Sperm whales also produce a sound that appears to be individually distinctive, with an acoustic structure completely different from dolphin whistles; the sound takes the form of a short series of clicks, called codas, with highly stereotyped rhythmic patterns (Fig. 2)[28]. Several lines of evidence indicate that each whale within a group has a distinctive coda. When the locations of whales producing codas are calculated, similar codas appear to come from the same source, while different codas come from different sources. The sound level and timbre of the clicks that make up codas also tend to be similar for the same codas and different for other codas during recording periods of an hour or so. Like dolphins and their signature whistles, sperm whales can mimic the codas more typical of other individuals in well defined coda exchanges[28].

Communication in other cetacean species

Individually distinctive signals have not been definitely identified for any of the baleen whales nor for several groups of odontocetes. Not enough is known about social communication in any of these species for one to conclude categorically that they do not use vocalizations to communicate individual identity. More extensive studies may reveal such signals in the future. However, most of these species have social structures that differ from the whistling dolphins and the coda-producing sperm whales. The signals that have been described for these species have functions that appear more suited to the kinds of interaction that predominate in their societies.

Some dolphin species, including the platanistid river dolphins and phocoenid porpoises, have never been reported to whistle[20]. Interestingly, these animals are more similar to baleen whales than other dolphins in several respects[29,30]. As the last two rows of Table 1 show, their timespans for gestation, weaning and sexual maturation are similar to those of baleen whales. Little is known about the social structure of these dolphins, but many sightings are of lone animals; when not



Young humpback whale off Hawaii. *Photo by Graeme Ellis.*

alone, they tend to be in groups of only a few animals. They are clearly much less social than the dolphin species that do whistle[20].

There are no reports of individually distinctive signals for killer whales, but they do produce group-specific dialects for one sound – the 'S' call[31]. Each killer whale group has a different repertoire of S calls, and apparently every individual within the group produces each S call. As was mentioned above, even when different groups mingle, they always separate into the original groups. Whereas dolphins and sperm whales apparently use their individually distinctive signals to maintain associations between individuals within changing groups, the communication system described for killer whales appears to function to maintain the cohesiveness of their stable groups.

Little is known about the social function of sounds produced by baleen whales during the feeding season, but there are some hints that humpback wales and finback whales (*Balaenoptera physalus*) may produce individually distinctive sounds while feeding in groups. This may help to maintain the rare associations of individuals that feed together in a coordinated fashion.

During the breeding season, several species of baleen whales produce advertisement displays. The best studied of these are the songs of the humpback whale. Not only has humpback song not been shown to be individually distinctive, but it has an acoustic structure that renders individual identification extremely difficult. Humpback songs recorded within a few weeks of each other on the same breeding ground are very similar. But every aspect of the songs changes gradually throughout each singing season[32]. Sounds may change in pitch, duration and timbre; they may disappear from the song entirely, and new sounds may appear in some other part of the song. These changes are cumulative. Over a twenty-year period, entire songs are transformed; not one sound from the song's first version is left intact in the last[33]. As Fig. 3 indicates, whales singing at any one time within a population sing very similar sounds compared to the changes that occur within even one year[34]. This is very different from the signature whistles of dolphins, which are stable over periods of many years.

Future research

Future studies should reveal whether these associations between social organization and communication reflect fundamental differences in the social relations of different cetacean groups. Long-term studies of the social behavior and patterns of association between identified individuals are under way for many cetacean species. Current studies of social communication in cetaceans are also advancing rapidly. New techniques have been developed to locate sound sources underwater and to identify which animal produces which call. These will facilitate study of the social functions of cetacean signals and in particular, should help to determine whether other cetacean species produce individually specific signals.

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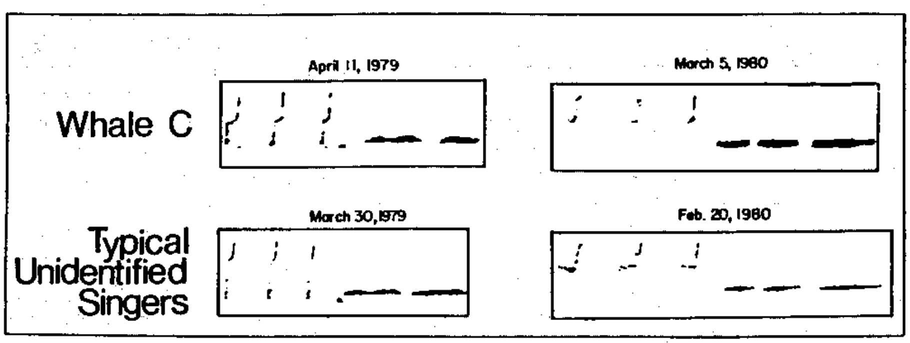

Fig. 3. Sound spectrograms of one phrase from the songs of humpback whales (*Megaptera novaeangliae*) recorded in Hawaiian waters. The phrases on the top row were sung by the same individual, labelled whale C, approximately one year apart. The phrases on the lower row were recorded from unidentified whales (very likely to be different individuals) within two weeks of the phrases directly above them on the top row. It is obvious that the phrases of different whales sung within the same two week interval (vertical comparisons) are much more similar than phrases of the same individual whale with a one year interval (top horizontal comparison). *Reproduced, with permission, from Ref.* 34.

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Regeneration of Canopy Trees in Tropical Wet Forests

Deborah A. Clark

The most diverse tree communities on earth, the tropical wet forests, to a large degree remain ecological enigmas. What accounts for the coexistence of 100 or more tree species per hectare, compared to the 15 or fewer found in most temperate forests? What are the lifespans of tropical forest trees? What factors control their populations through time and space? Do the different species have highly individual regeneration patterns, or are many in fact ecological equivalents? Although we are far from having satisfactory answers to these questions, recent studies of regeneration processes are leading toward new interpretations of these complex communities.

Until recently, surprisingly little detail was available about the process of regeneration of trees in tropical forests. Whereas the annual rings formed in the wood of temperate trees can reveal each individual's age and growth history, this fundamental tool of the tree population biologist cannot be used with most tropical species because they do not form clear annual growth rings[1]. A second major challenge for the study of tropical tree ecology is presented by the species diversity itself; in relatively few sites have all the tree species been identified. Furthermore, most tree species in tropical forests occur at densities of <1 adult/ha (Ref. 2). For all but the few most common species, any population study requires an area much larger than would be needed in most temperate forests. The extensive ecological observations and interpretations made over the years by foresters with long-term experience in tropical wet forest unfortunately remain poorly documented (see Ref. 3). Current research on the processes of regeneration in different tropical canopy tree species is now providing a basis for preliminary comparative analyses. This review focuses on these current approaches and the insights they are providing into the complexity of tree population dynamics, with particular emphasis on neotropical research.

Deborah Clark is at La Selva Biological Station, Organization for Tropical Studies, Apartado 676, 2050 San Pedro, Costa Rica.

The impact of natural enemies on early survival

Much recent research has derived from the idea, proposed 15 years ago by Janzen[4] and Connell[5], that a major factor affecting the pattern of regeneration in tropical tree species is the activity of seed predators, pathogens or herbivores. Janzen and Connell predicted that such agents would act in a density- or distance-dependent fashion, causing proportionately more mortality in seeds or seedlings present at higher densities close to parent trees. Seeds dispersed over greater distances would have a greater chance of escaping these natural enemies, and the maximum number of surviving seedlings should occur at some intermediate distance away from parent trees. Because such differential mortality in these youngest stages of a tropical tree species could have important repercussions on both the evolution of dispersal and the distribution of adults, Janzen's and Connell's proposals stimulated research in a variety of tropical forests. Even before much evidence had accumulated, the hypothesis became a textbook example of the importance of biological interactions in the maintenance of tropical species diversity.

The Janzen–Connell model was challenged by the results from a large-scale tree mapping project in a tropical dry forest[6], where most tree species were found to have clumped distributions. This interesting finding was taken as evidence that most species did not experience an increase in inter-individual spacing due to natural