GRAY WHALE MIGRATORY, SOCIAL AND BREEDING BEHAVIOR

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ABSTRACT

The recovery of the Chukchi-California stock of gray whales from depletion and the species unique coastal habits make it relatively accessible for study, and numerous studies of living whales have contributed new behavioral information from various portions of the gray whale's range. This paper reviews the findings of recent demographic and behavioral studies regarding gray whale migration, natural history, social behavior and mating system. Their annual polar-to-semi-tropical migration occurs along the eastern Pacific coast of North America and brings the whales in contact with a variety of prey species which is reflected in the diversity of the whale's diets. During the fall southward migration the whales travel 7,602 km between the Arctic and Baja California in approximately 66 days at a rate of 4.8 km/hr. Their migration rate between the Arctic and Monterey is approximately 7.1 km/h, while their rate between Monterey and the breeding lagoon of San Ignacio is approximately 2.2 km/h or 31% as fast as the first leg of the migration. An apparent overlap of southward and northward migrating whales may account for this slowing and suggests that only a proportion of the population occupies the coastal waters of Baja California at any time while the remainder are distributed throughout the Southern California Bight and elsewhere. The departure of whales from the southern range appears to be segregated according to age, sex and reproductive condition, and is bimodal. Whales without calves lead the spring northward migration and travel more rapidly than females with calves. The majority of females with calves depart later in the spring and their northward migration is more protracted; thus, female whales spend more time in the winter range in years in which they give birth to calves, and they would spend less time on the summer feeding grounds. Courting whales were most abundant in San Ignacio lagoon in January and February, and there was a rapid exchange of these animals with lengths of stay between 1 and 4 weeks. Females with calves remained up to 13 weeks in the lagoon and some circulated between different lagoons both within and between years. Female-calf pairs avoided courting whales in San Ignacio resulting in a spatial and temporal segregation between these two groups. Courting activities were primarily concentrated in the area nearest the inlet, while females and calves utilized the interior areas farthest from the sea as nurseries. With the departure of courting whales, female-calf pairs abandoned the lagoon interior and shifted their distribution to the inlet areas. The calving period ranged approximately 66 days with a mean birth date around 27 January. Calving periodicity for 30 females ranged from annual to two years between calves, and their mimimum birth rate weas 0.50 to 0.55 calves/females/yr. Given that most females reproduce biennially, they would alternate between a longer period on the summer range feeding when newly pregnant and a shorter period on the summer range when lactating. The logic and evidence for opportunistic feeding by late migrating whales to compensate for less time spent on the summer range is discussed. The segregation of gray whales into two groups, females with calves and other whales, is suggestive of their behavioral incompatibility and appears prominent during migration, on the winter grounds, and apparently on the Arctic summer grounds. The early development of calves in San Ignacio lagoon included imprinting on their mothers, mimicry of adult behaviors, and socialization with other calves and adults. Adult gray whales demonstrated epimeletic or care giving behavior toward unrelated calves. Mating groups were fluid and involved up to 32 individual animals. These groups were characterized by high speed chases interrupted by mating bouts that lasted up to four hours. Adult males and females mated with more than one partner during the same season, and males did not appear to compete for females. Sperm competition in gray whales may account for the lack of obvious male–male competition and sexual selection in this species.

INTRODUCTION

During the past four decades, the eastern Pacific or Chukchi-California stock of gray whales (*Eschrichtius robustus*) has demonstrated a remarkable recovery from severe depletion by modern whalers (Reilly, 1981) and has become the best studied group of baleen whales. This population makes an extensive migration each year between its major summer feeding grounds in the Bering, Chukchi and Beaufort Seas and its winter breeding grounds in the near-shore waters, bays and lagoons of Southern California, Baja California and to some extent the Gulf of California. Compared to more pelagic species, the gray whale's unique coastal habits throughout most of its range make it relatively accessible for study. Consequently, more is known about these whales than any other mysticete. Until relatively recently, however, information on gray whale distribution and behavior was based on observations of a depleted stock, and many important aspects of gray whale migratory, social and breeding behavior remained little known.

The first description of the migration and natural history of the gray whale was written by the American whaling captain Charles M. Scammon (1874) and based on his observations of the whales on their summer feeding grounds, along their migration routes and during their winter occupation of the breeding lagoons. Not until 1947 and with the slow recovery of the stock from depletion did scientists begin to show interest in this cetacean. A series of short-term aerial surveys to monitor the winter abundance of whales in Baja California was conducted by Gilmore (1960), Hubbs and Hubbs (1967) and Gard (1978). These studies clearly showed that the gray whale population was increasing, and prompted additional investigations.

Between 1959 and 1969 Rice and Wolman (1971) examined 316 gray whales taken by whalers along the central California coast. Their analysis of these specimens contributed to the study of gray whale reproductive physiology and migration timing. Within the past decade detailed non-consumptive studies of the winter abundance and behavior of gray whales have been conducted in Laguna San Ignacio (Swartz and Jones, 1979; 1980; 1981, 1983; Jones and Swartz, 1984a), Laguna Ojo de Liebre (White, 1975; Rice *et al.*, 1981; Fleischer and Carlson, 1981; Fleischer *et al.*, 1984), Laguna Guerrero Negro (Bryant, 1980 Bryant *et al.*, 1981, 1984), Bahia Magdalena (Norris *et al.*, 1977, 1983; Lawson, 1984; Fliescher *et al.*, 1984) and the Gulf of California (Findley and Vidal, 1982). Additional studies by Soviet scientists on the summer feeding grounds (e.g. Zimushko and Ivashin, 1980; Blokhin, 1984, 1986; Yablokov and Bogoslovskaya, 1984) and by Canadian and American investigators along the migration route (Jones *et al.*, 1984) have contributed new information that enables a preliminary synthesis of gray whale migration and behavior following the recovery of the stock.

In this paper I review the findings of recent demographic and behavioral studies of gray whales (*Eschrichtius robustus*) in the breeding lagoons of Baja California along with observations of gray whales throughout their range, and present a preliminary synthesis of their natural history, migration, social behavior and mating system in light of recent theories on the evolution of the social structure of mysticetes.

MIGRATION

The migrations of mysticete whales are thought to have arisen as an evolutionary response to the seasonal production of prey in the Antarctic and Arctic seas (Lipps

and Mitchell, 1976). The paleontological records indicate that the relatively mild temperatures of the world's seas changed radically with the breakup of the super-continent of Pangea and the resulting changes in the circulation patterns of the oceans. The creation of mountain ranges radically affected regional temperatures, wind patterns and rainfall on a world wide scale. When temperatures dropped and seasons became more pronounced in the late Miocene and early Pleistocene, marine organisms such as plankton, fish and squid must have changed both qualitatively and quantitatively. Predators on these organisms, for example the early cetaceans, were also affected. Presumably, early cetaceans were able to exploit local perennial sources of prey. However, coincident with these geologic changes, their prey species became seasonal and their distributions more specific. Thus, seasonal movements of certain marine mammals tracked those of their prey, and may have been the origins of today's migration routes (Scheffer, 1976).

Seasonally predictable sources of food shaped the life history of baleen whales into two periods: summers when animals feed in the higher latitudes when food is abundant and the weather reasonable for an aquatic mammal; and winters when whales migrate to the lower latitudes to escape inclement weather and to reproduce in warmer waters that are more conducive to the rearing of calves and mating. These lower latitudes, however, generally do not afford the high standing crop of prey found in the polar seas, and thus baleen whales also evolved an energy storage strategy whereby they fast during their reproductive period and survive on stored energy reserves in the form of body fats accumulated during summer feeding (Slijper, 1976; Matthews, 1978). Although the gray whale's migration is typical of baleen whales, its coastal habits have resulted in some modifications of the general mysticete life history pattern which appear unique to this species.

Gray whales participate in an annual polar-to-semi-tropical winter migration, but, unlike the more pelagic species that migrate across vast deep ocean basins which offer little food, they migrate along the coast of North America where upwellings of nutrient rich waters drive some of the world's most productive marine ecosystems. Thus, except perhaps in the southernmost portion of their range, the gray whale's migration brings them into contact with a wide variety of prey species. Analysis of stomach contents confirms that gray whales consume numerous kinds of prey (Nerini, 1984), and that they are capable of feeding off the bottom, in the water column and by surface skimming (Rice and Wolman, 1971, Swartz and Jones, 1981; Oliver et al., 1984; Wursig et al., 1984). The gray whales' association with the rich coastal ecosystems along the Pacific coast of North America that provide a variety of resources throughout virtually the entire year has no doubt contributed to their resiliency as a species and their remarkable recovery from depletion (e.g. see Reilly, 1984b).

The coastal migration of the gray whale in the eastern North Pacific has been described by numerous investigators including Scammon (1874), Gilmore (1960), Pike (1962) and Rice and Wolman (1971), and is one of the best known movements of all the large cetaceans. Recent studies throughout the range of this, the Chukchi-California, stock have provided detailed information on the timing of the fall (southerly) and spring (northerly) migrations at specific locations along the migration route (Jones et al., 1984). Shore based censuses provide daily counts of the number of whales passing each location, and from these the distribution and rate of movement of the population during migration may be inferred. The distribution of the gray whale population during migration may be visualized as a

bell-shaped curve that moves along the migration route at a particular rate. For the purposes of describing the timing of the migration, I have chosen to use the day with the greatest number of whales counted at a census station as an index of the average date that the population passes that location. In cases where more than one year of counts were available. I have used the mean day of the peak counts as the average date of passage.

Fall southward migration

Gray whales are commonly found in the Bering and Chukchi Sea feeding grounds between June and October (Rice and Wolman, 1971) with some remaining in feeding areas off the Soviet Coast of Chukotka as late as November (Blokhin, 1984; 1986). By mid-August gray whales seen near Barrow, Alaska are predominantly moving south (Braham, 1984; Moore and Ljungblad, 1984), and by late October southward migrating whales begin to arrive at Unimak Pass where they leave the Bering Sea (Fig. 1). The mean date of the peak counts of whales passing through Unimak Pass, Alaska, between 1977 and 1979 was 5 December (Rugh, 1984). From Alaska, southbound gray whale migrants pass Vancouver Island, British Columbia from November to late January with peak numbers passing during the last two weeks in December (Darling, 1984).

The first southward migrants past Newport, Oregon are observed in early December with maximum numbers passing during the first week in January. The average mean day of the southward migration between 1978 and 1981 was 6 January, after which counts declined until by early February few whales were seen until the onset of the northward migration (Herzing and Mate, 1984). During this first leg of their southerly migration the population travels approximately 4,815 km between Unimak Pass and Newport in 32 days (based on dates of peak counts)—an average rate of 6.3 km/h.

Southward migrating gray whales begin to pass Monterey, California as early as late-November, although these early arrivals may represent animals that spend the summer along the Pacific coast of Canada (Darling, 1984), Washington (Braham, 1984), Oregon (Herzing and Mate, 1984) and northern California (Dohl, 1979), and reach central California in addition to those that have travelled from the Bering Sea through Unimak Pass. Censuses conducted at Monterey by the National Marine Fisheries Service between 1967 and 1980 obtained peak numbers of passing whales during the second week in January (Reilly et al., 1983). The mean peak count date for the southward migration during these 13 consecutive censuses was 9 January, after which counts of southbound whales declined until the first northward migrants were observed during the first week in February (Reilly, 1981). Gray whales begin to arrive at the breeding lagoons in December, and reach maximum abundance there in early February. Peak counts of whales were obtained around 10 February in Laguna Guerrero Negro between 1980 and 1982 (Bryant et al., 1984), around 15 February in Laguna Ojo de Liebre between 1980 and 1981 (Rice et al., 1981; 1983), around 15 February in Laguna San Ignacio between 1978 and 1982 (Jones and Swartz, 1984a), and between 7 and 10 February in northern Magdalena Bay between 1982 and 1985 (Lawson, 1983; Fleischer et al., 1985). If 9 February is used as an index of the average date of maximum counts at the lagoons, it appears that the whales travel the 1,657 km between Monterey and Baja California in approximately 31 days at 2.2 km/h, or about 31% as fast as their migration rate between Unimak Pass and Monterey. The reason for this reduced

migration rate through southern and Baja California is not understood. The whale's overall southward migration rate between Alaska and the breeding grounds would be 4.8 km/h, or 7,602 km in approximately 66 days.
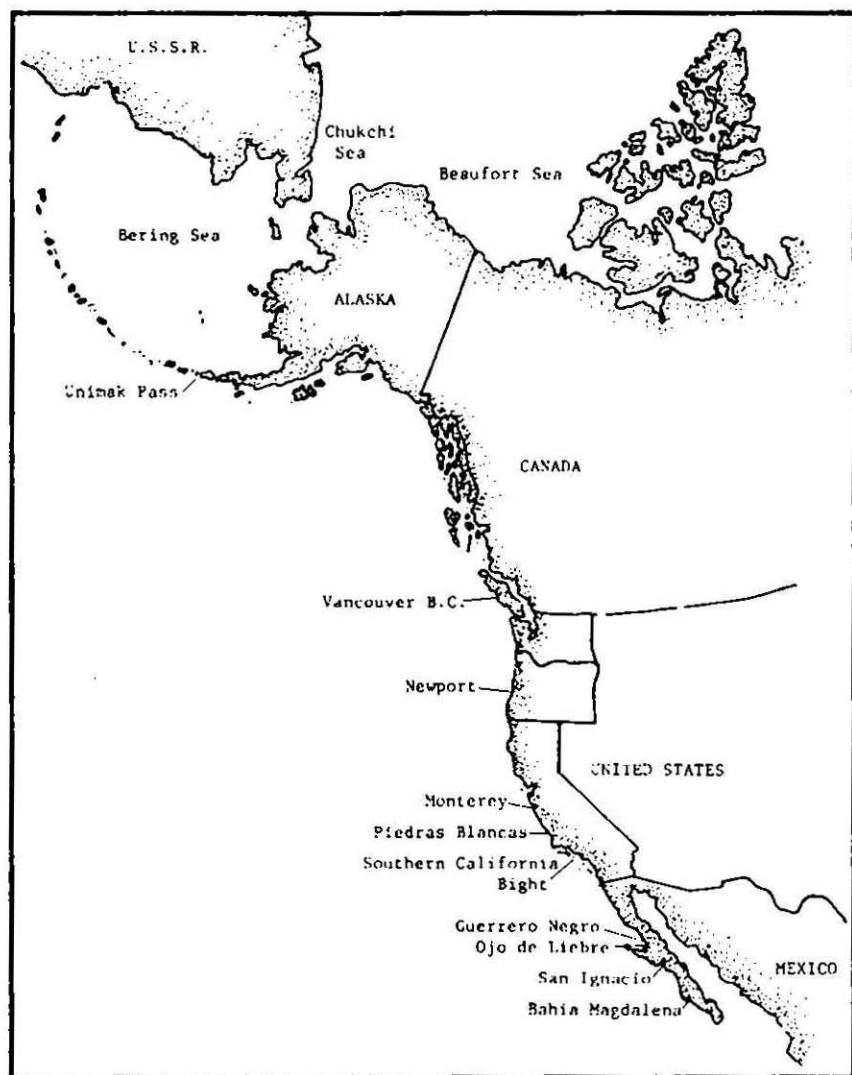

Fig. 1. Range and migration route of the Chukchi–California stock of gray whales along the eastern Pacific coast of North America.

The timing of the gray whale migration south of Point Conception raises some interesting points that have yet to be adequately studied. For example, between Alaska and Monterey the population is travelling at approximately 7 km/h and passes during a period of 4 to 6 weeks. Travelling at this rate, the population would be distributed over approximately 4,700 to 7,100 km of coastline, the majority of

the west coast of North America. As the whales move south they apparently slow down, and by the time the last of the southward migrants reach the central California coast in early February, they begin to overlap with the first of the northward migrants leaving the southern range (Reilly, 1981; Poole, 1984; Herzing and Mate, 1984). This overlap suggests that only a proportion of the migrating whales are in Mexican waters during the winter while the remainder are distributed throughout the Southern California Bight and to some extent the migratory corridor along the Central California coast.

Evidence in support of this mixing of southward and northward migrants in the Southern California Bight comes from several sources. As early as 1950 the late Carl L. Hubbs reported three female–calf pairs in the kelp off Isla Guadalupe in April (Gilmore, 1955). Rice (1965) discussed the offshore southward migration of gray whales off Southern California and noted that an undetermined proportion of the population migrated beyond sight of the Point Loma (San Diego) census station. Gilmore (1969) concluded that south of Point Conception, California, the migration divided with some whales taking the 'inter-island leg', and later returning to the coast below Ensenada, Mexico. The most convincing evidence that significant numbers of gray whales occur in the Southern California Bight during the winter comes from aerial surveys conducted by Leatherwood (1974) and Dohl (1979) who observed migrating gray whales 80 to 160 km from shore with the same relative frequency as within 80 km of shore. Finally, the discrepancy between the National Marine Fisheries Service population estimates from shore based counts in 1980 of approximately 16,000 whales (Reilly *et al.*, 1983) and estimates of 7,600 whales counted in the breeding lagoons and coastal waters of Baja California in mid-February of the same year (Rice *et al.*, 1981) could be the result of more migrating whales being distributed north of the Mexican border than had been previously assumed. The difference between these estimates, approximately 8,400 whales, is probably a reasonable estimate of the proportion of the population in the Southern California Bight in February.

The spring northward migration
The departure of gray whales from the southern range appears to be segregated according to age, sex and reproductive condition. Vessel censuses and aerial surveys of the breeding lagoons indicate that the departure of females with calves occurs after the departure of whales without calves, and is more protracted. For example, although maximum counts of female-calf pairs were obtained in mid-February in Laguna Guerrero Negro (Bryant *et al.*, 1984), Laguna Ojo de Liebre (Rice *et al.*, 1981; 1983), and in northern Bahia Magdalena (Lawson, 1983; Fleischer *et al.*, 1985), counts of female-calf pairs in Laguna San Ignacio increased steadily throughout the winter and reached peak numbers in late-March or early-April with a 5-year mean peak day of 19 March (Jones and Swartz, 1984a). Vessel counts in San Ignacio between 1978 and 1982 indicated that after mid-March the lagoon is occupied by female-calf pairs alone, and that some of these remain until late-April and early-May of some years. From these data, Jones and Swartz (1984a) estimated that female-calf pairs may remain in the lagoon 1 to 1.5 months longer than whales without calves.

Rice and Wolman (1971) also found that in both the southward and northward migration, mature females migrate earlier than males, and adults migrate earlier than sexually immature animals. Near-term pregnant females lead the southward migration, but following the birth of their calves, these females are the last group

of whales to leave the winter range. Newly pregnant females comprise the first northward migrants past central California in mid-February, and they are followed approximately two weeks later by adult males, anestrous females and immatures of both sexes (Rice and Wolman, 1971).

In 1980 and 1981 a shore based census was taken of northward migrating gray whales at Pt Piedras Blancas, California (Poole, 1983) which indicated the northward migration to be bimodal, consisting of two distinct pulses of whales temporally spaced and comprising two distinct groups: whales without calves and female-calf pairs. The first pulse, Phase A, occurring during February and March, comprised whales without calves passing 1 to 2 km offshore, and had a mean peak passage date of 1 March. This suggests that these whales travelled the 1,472 km in 20 days following their 9 February mean peak day in the lagoon at an average rate of 3.1 km/h.

The second pulse, Phase B, occurring from late March to mid-May, consisted primarily of females with calves of the year passing within 1 km of shore, and had a mean date of peak passage of 26 April. If maximum counts of female-calf pairs occur in the lagoons from mid-February to mid-March, their rate of migration to Piedras Blancas would range from 0.9 km/h (15 February departure) to 1.6 km/h (19 March departure). Compared to single whales, this slower rate of movement is undoubtedly due to the presence of the calf, its need to nurse, and probably opportunistic feeding by the female as she encounters food along the migratory route. There are a few scattered reports of female-calf pairs feeding during the northward migration (Mate and Harvey, 1984; Malme et al., 1984; Leatherwood, pers. comm.), but additional data will be required to verify the utilization of food resources by females with calves during their northward migration, and to determine to what extent lactating females rely on food resources in this portion of their range.

The first northward migrants to pass Newport, Oregon (between 1978-79 and 1980-81 winters) were seen during the last week in February, just a few days after the last of the southward migrants were counted (Herzing and Mate, 1984). The first group, or Phase A, was composed entirely of whales without calves and counts of these whales peaked around 15 March, declining to zero by the end of April. Phase A whales had thus travelled the 2,787 km from the lagoons in 34 days averaging 3.4 km/h. The second group of northward migrants was primarily females with calves of the year, Phase B, and were first seen passing in late March. Maximum counts of these whales were obtained by 10 May, declining to near zero by June, and thus suggesting that Phase B female-calf pairs travelled the distance from the lagoons to Oregon in 52-84 days at average rates of 1.4-2.2 km/h.

If the two groups of whales maintained their northward migration rates, the peaks of Phase A whales would reach Unimak Pass, Alaska on 13 May, approximately 59 days after they passed Newport, Oregon, and Phase B female-calf pairs around 9 August, approximately 91 days after passing Newport. These estimated rates are corroborated by the following field observations. First, a single whale without a calf radio-tagged in Laguna San Ignacio reached Unimak Pass, Alaska 95 days after its radio signal was last received in the lagoon (Mate and Harvey, 1984), and thus averaged 3.4 km/h for 3.2 months during its northward migration. In addition, the arrival of northbound spring migrants at Unimak Pass begins in late March and reaches its peak around 5 May. Hessing (1981) observed two phases to the northward migration of gray whales through Unimak Pass between 23 March and 17 June in 1981. Although all sizes of whales were

observed throughout her study, no females with calves were seen until May, and female–calf pair counts continued to increase until mid-June when her study was terminated. The duration of the female-calf pair spring migration thus remains unknown.

The segregation between Phase A and B northward migrating gray whales supports the concept that gray whales behave as two distinct groups, with females alternating between two migration timetables. Females with calves travel more slowly than females without calves (anestrous and newly pregnant) during the northward spring migration, and subsequently have less time to spend feeding on the summer grounds. Based on the migration rates estimated above, the interval between summers on the Arctic feeding grounds would be approximately 5.1 months for newly pregnant females (as well as males and juveniles) and 8.5 months for females with calves that remain in the lagoons longer and whose departure from the southern range is more protracted than that of the single whales. This yields a summer feeding period of 6.9 months for newly pregnant females and only 3.5 months for females that had given birth to a calf the previous winter.

OCCUPATION OF BREEDING LAGOONS

The overall seasonal abundance of gray whales within the breeding lagoons of Baja California, Mexico can be divided into two periods. The first is the period of maximum gray whale abundance in the lagoons and occurs during the first half of each winter. At this time the population is composed of courting whales without calves (males, mature females, and immatures) and females with newborn calves. The second period occurs during the latter half of the winter after the departure of whales without calves from the lagoon when the lagoon populations are composed entirely of female–calf pairs. In this section I will describe the timetable of occupation for Laguna San Ignacio as being representative of the occupation of other major breeding lagoons.

The abundance of courting whales (whales without calves) increases rapidly during a six week period from the last week in December through the second week in February. Maximum counts of these animals in the lagoon occur in mid-February, after which their numbers decline as they begin their spring northward migration. Courting whales are encountered in the lagoon for approximately three months, but there appears to be a substantial turnover rate. Evidence for a rapid exchange of courting whales through the lagoons during each season comes from a photographic identification study between 1977 and 1982 (Jones and Swartz, 1984a) (Fig. 2), and shore-based observations of the main entry channel of San Ignacio lagoon in 1982. The photographic identification results revealed that 81% of the courting whales photographed in Laguna San Ignacio remained there for one week or less (Jones, 1985). In addition, the fact that two of these whales photographed by D. Withrow (National Marine Mammal Laboratory, pers. comm.) in Laguna Ojo de Liebre were re-sighted approximately one week later in Laguna San Ignacio suggests the possibility of a relatively rapid circulation of courting whales between breeding areas (Jones and Swartz, 1984a). Finally, counts of whales moving through the inlet of San Ignacio demonstrated that substantial numbers of single whales enter and exit the lagoon every day. For example, at the time of the maximum counts in 1982, when 270 whales were counted within the lagoon, a minimum of 341 others entered and 185 left the lagoon during a seven hour daylight period. Because the majority of the adult
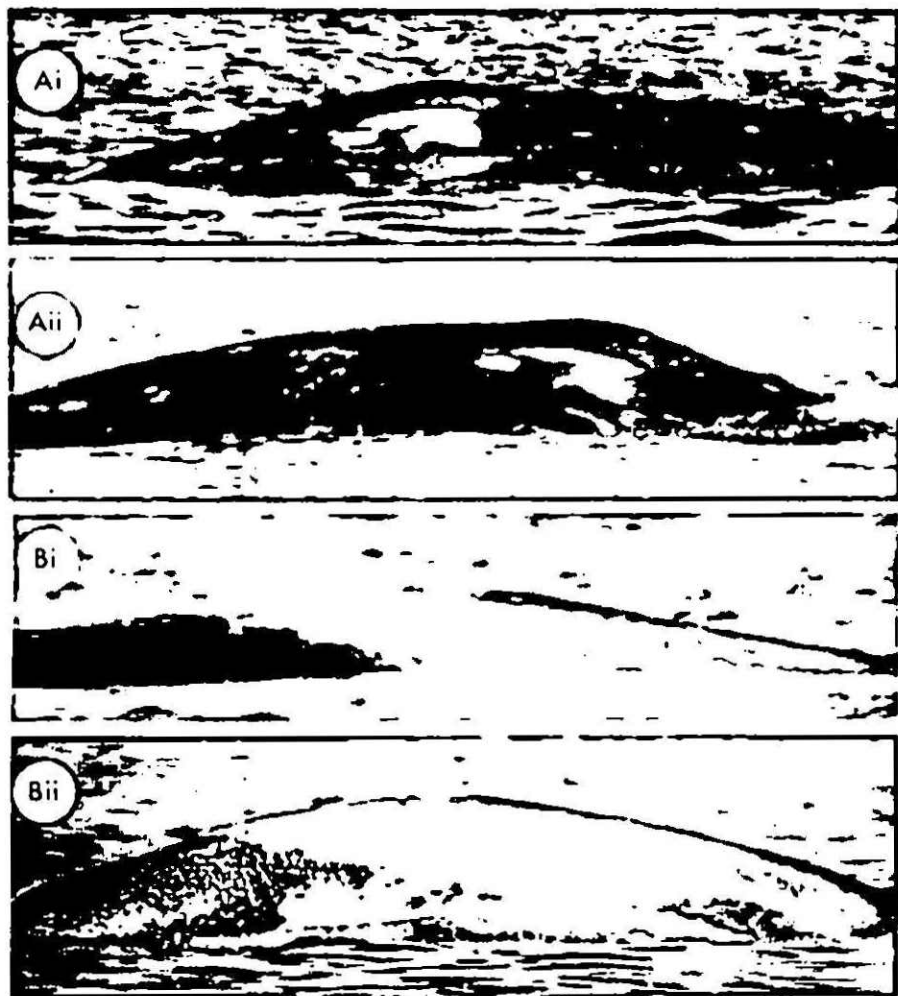
Fig. 2A. A female gray whale photographed during the 1976–77 winter in San Ignacio lagoon (i), and again during the 1978–79 winter (ii). This whale was re-photographed on 12 January 1986 during the southward migration off Monterey, California.

Fig. 2B. A female gray whale with extenhsive white areas on her tail. This whale was first photographed during the 1976–77 winter in San Ignacio Lagoon (i), and re-photographed each winter until 1981–82 (ii). During this six year period she produced three calves.

whales present in the inlet throughout the winter were actively transiting and their movement was independent of the tides, counts of these whales through the inlet were indicative of a real exchange of animals rather than being repeat counts of the same individuals passively moving into and out of the lagoon with the tide.

The pattern of female–calf pair abundance is more complex and they remain longer in the lagoon. The abundance of females with calves of the year increases continuously between early January and mid-February as whales arrive in the

lagoon and as calves are born. Following the end of the birth period, some females circulate with their calves between the breeding lagoons prior to departing from the winter range (Jones, 1985). Although arriving at about the same time as the courting whales in the lagoons, the departure of cow–calf pairs is more protracted than that of the courting whales, and continues all spring with some females and their calves remaining within the southern range until the end of April and early May of some years (Jones and Swartz, 1984a). Thus, the duration of the female–calf season in the lagoon can be as long as 4 to 4.5 months.

In San Ignacio, but apparently not in other lagoons, numerous females and calves congregate and reach peak abundance in March and April, indicating that this lagoon may serve as a staging area for female–calf pairs prior to their departure from the southern range. There are two sources of evidence supporting this idea. First is the observation that this late season influx is not due to continued births, for these late season females have calves that are approximately two to three months old (Swartz and Jones, 1981). Second, the results of the six year photographic identification study, in combination with a three year program in Laguna Guerrero Negro by Bryant and co-workers, a two year study by the National Marine Fisheries Service in Laguna Ojo de Liebre, and a one year project in Boca de Soledad by Lawson (1983), revealed that some female with older calves were immigrating to Laguna San Ignacio after leaving these breeding areas (Jones, 1985; pers. comm.).

Prior to the extension of photographic identification studies to other breeding areas, investigators had speculated that the late season influx of whales consisted of females with calves that were moving northward from areas south of San Ignacio, e.g. Bahia Magdalena (Swartz and Jones, 1979; Rice et al., 1981). This is only partly true. In addition to northbound immigrants, some females with calves photographed early in the season in more northerly lagoons (e.g. Laguna Guerrero Negro and Laguna Ojo de Liebre) vacated these areas and moved south to Laguna San Ignacio late in the season (Jones, 1985). Some females radio-tagged in Laguna San Ignacio (Harvey and Mate, 1984) and in Bahia Magdalena (Norris et al., 1977) also moved south after leaving the areas in which they were tagged.

DISTRIBUTION WITHIN THE BREEDING LAGOONS

Although the lagoons of Baja California are important areas for both courting whales and females with calves, these two groups utilize them quite differently. As whales enter Laguna San Ignacio, they become segregated spatially and temporally such that their distribution, gross movement and timetable of occupation differs. Courting whales are found at highest densities near the lagoon inlets and their density then decreases with increasing distance from the inlet. The courting whales' preference for the lower lagoons may be related to ease of access to (1) the relatively deep and wide channels that characterize these areas and remain unrestricted even at low tides or, (2) to the open ocean, or (3) both. While in these areas, these whales are predominantly engaged in social activities associated with courtship and mating. Most female–calf pairs are concentrated in the inner lagoon nurseries farthest from the open sea (Swartz and Jones, 1981; Jones and Swartz, 1984a). Mothers and calves in the inner lagoon are primarily engaged in the tranquil activities of resting, nursing and moving about with the changing tides. Moreover, the nursery furthest from the inlet provides an area of

relative solitude for the females following parturition and during early calf development.

This localization of courting whales in the inlet and outer lagoon region of San Ignacio and the preponderance of female–calf pairs within the lagoon is a feature found in other breeding areas. Scammon (1874) wrote '. . . the cows enter the lagoons on the lower (Baja) coast to bring forth their young, while males patrol outside along the sea shore'. Gilmore (1960) reported that lone adults, courting adults and juveniles predominate at the entrances to Laguna Ojo de Liebre and Bahia Magdalena, and suggested that courting and mating are the primary activities of the whales in these areas. In addition, Samaras (1974) stated that adult male and female gray whales use the inlet of Laguna Ojo de Liebre as a staging area for precopulatory behavior, while pregnant females occupy the inner lagoon calving area. Norris et al. (1983), who studied lagoon entrance aggregations of gray whales at La Entrada (the main entrance to Bahia Magdalena) and Canal Rehusa (the entrance of the southernmost calving lagoons at Bahia Almejas and Santa Maria), reported that they were composed entirely of males, nonparturient females and juveniles, whose primary behaviors appeared to be courtship, mating and possibly feeding. Although, Bryant et al. (1984) described Laguna Guerrero Negro as hosting very few courting whales with no apparent aggregations in the area nearest the inlet, they noted that this lagoon did not have any deep-water areas comparable to those in the larger breeding lagoons. They further remarked that a large number of courting whales were observed in the deep-water area just offshore. This finding, then, is similar to the distribution of courting whales seen in other breeding areas.

Following the period of combined maximum counts, and with the gradual departure of courting whales from the lagoons, females and calves gradually shift their distribution to the outer lagoons and inlets, essentially abandoning the nurseries. The trend for female–calf pairs to occupy the area nearest the sea following the end of the birth period and the departure of courting whales from the lagoons suggests that females prefer these areas when their calves are 2–3 months old. Scammon (1874) and Norris et al. (1977) interpreted this shift as being the first stage of the migration preparatory to leaving the lagoons.

FEMALE BREEDING STRATEGIES

Photographic records of 30 females and 15 whales of unconfirmed sex (but presumed to be males) collected between 1977 and 1982 provided data on reproductive behavior and vital rates of females in Laguna San Ignacio. In her analysis of these photographs, Jones (1985) found a range of birth dates from 26 December to 1 March, suggesting a 66-day minimum calving period with a mean birth date of 27 January (Rice and Wolman, 1971). Calving periodicity ranged from annual (one instance) to a two year resting period between calves. Overall, 30 females produced 55 to 58 calves over the six year study to yield a minimum realized birth rate of 0.50 to 0.55 calves per female per year. Thus, most females produce a calf every other year, which is comparable to estimates of the pregnancy rate of 0.46 per year (Rice and Wolman, 1971) and 0.467 (Reilly, 1984a) from studies of whales taken by the Soviet whale fishery.

Jones (1985) analysis of photographs from Laguna San Ignacio confirmed that adult female gray whales alternate between two behavioral strategies; longer stays

in the lagoon when nursing, and shorter visits as courting whales in non-calving years. The longest period between first and last sightings within one season of a known female without a calf was three weeks, and of a female-calf pair was 13 weeks. Her data suggested a minimum of three patterns of lagoon occupation for breeding females: 'residents' consisted of females which were photographed for long periods during calving years, and for short periods early in the season in non-calving years; 'transients' included females with older calves which emigrated to the lagoon from other areas late in the season for a short period, and were responsible for the late-season maximum female-calf pair counts in this lagoon; and the third pattern (a combination of resident and transient) was of females photographed with a calf during a long period throughout a season in calving years, for a short period early in the season in non-calving years, and with an older calf for a short period late in the season in calving years. Finally, re-sightings in other breeding lagoons of whales photographed in Laguna San Ignacio demonstrated that some females utilized different calving lagoons in different years, some females changed lagoon areas within the same year (as with late season immigrants) and that males visited more than one breeding lagoon within a winter.

If gray whales cease feeding when they leave the Arctic, courting females would not feed for approximately five months between the beginning of their southern migration in November and their return, as pregnant females, to the summer range in May. They would spend approximately seven months on the summer grounds feeding extensively to develop food reserves in the form of body fat. For newly pregnant females these 'stores' would nurture the developing fetus and provide energy reserves for lactation and body maintenance of the female following the birth of her calf. After giving birth, mothers would spend only four months feeding on the summer range, in contrast to newly pregnant females. Having left the summer grounds in November as near-term females, they would have given birth sometime during January and February, remained in the winter range until April or May when they would have migrated northward with their calves and reached the summer range in August, approximately nine months after their departure the previous fall (Fig. 3).

The duration of stay of gray whales in the lagoons has important implications in terms of their energetic requirements, particularly for lactating females. Because courting whales leave the breeding areas approximately one month earlier than the majority of the female-calf pairs, they presumably arrive on the summer feeding grounds earlier and spend more time there than females that give birth to calves during the same year (Rice and Wolman, 1971). Given that gray whale females normally reproduce biennially, this suggests that adult females would alternate between a longer period on the summer range feeding when newly pregnant and a shorter period on the summer range when lactating. Males, however, would be able to spend the same amount of time feeding on the summer range each year. For newly pregnant females, this extra summer feeding time is of obvious energetic significance related to their need to acquire more fat reserves for the gestation of a calf and a 6 to 8 month lactation period. Females with calves, on the other hand, would have to feed more extensively during a shorter period of time to meet both their own energetic maintenance cost and that of their calves.

It is possible that females that do not feed outside the summer range may be energetically stressed following their southern migration, parturition and lactation during the northward migration. Opportunistic feeding during the spring northward migration could serve to augment their reduced feeding period on the
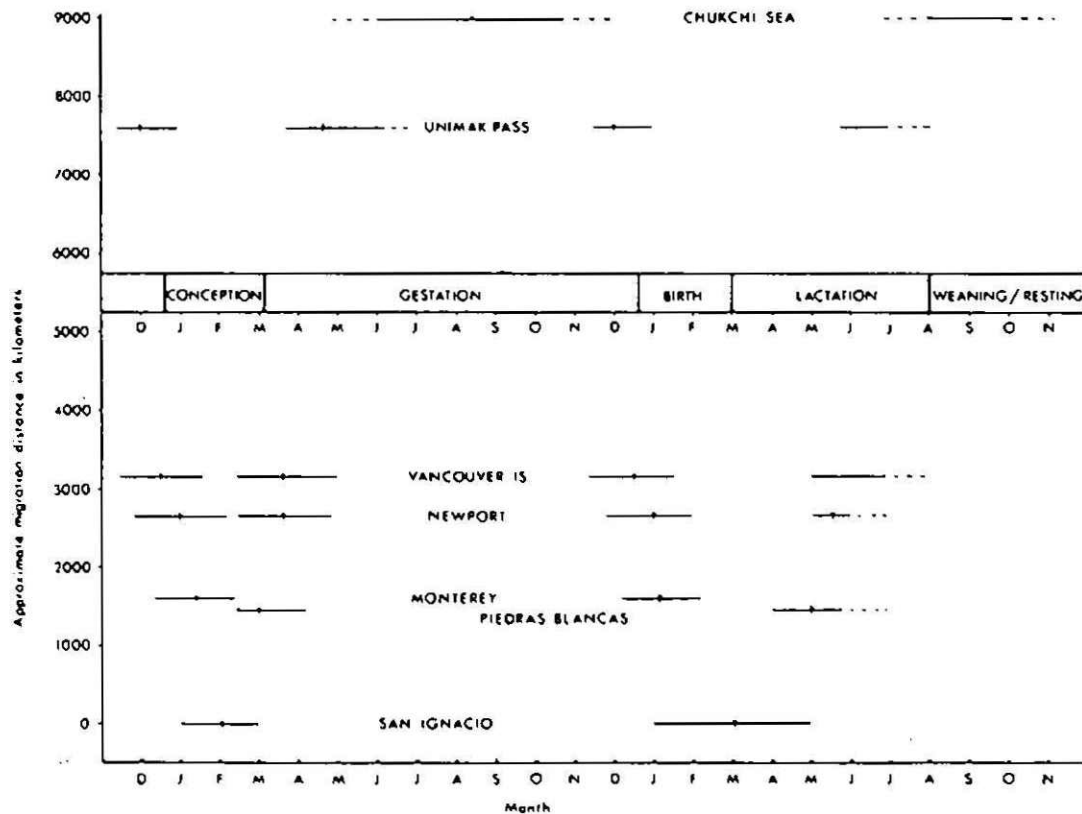
Fig. 3. The distribution of female gray whales of the Chukchi–California stock during their two year reproductive cycle. Horizontal lines represent the range of sighting dates during southward (fall) and northward (spring) migration for each location. Vertical bars indicate mean date of passage at a specific location. Broken lines indicate probable occurrence.

summer range in calving years and could help to explain the protracted departure
of these whales from the southern range, and their slow rate of movement through
the Southern California Bight. Evidence of opportunistic feeding by gray whales
has been obtained by Swartz and Jones (1981), Norris et al. (1983), Mate and
Harvey (1984) for Baja California; by Darling (1977, 1984), Murison et al. (1984)
and Oliver et al. (1984) for Vancouver, British Columbia; and by Braham et al.
(1984), Rough (1984) and Rugh and Braham (1979) for Southeast Alaska.
Additional field studies are required to determine the extent that females with
calves feed during their northward spring migration, and whether this feeding is
critical to the survival of their calves.

SEGREGATION BY AGE AND SEX

It is clear from the discussion so far that the most prominent feature of gray whale
behavior is the temporal and spatial segregation of the population into females
with calves and whales without calves (including mature females and males,
juveniles). This segregation exists during both the fall southward and the spring
northward migrations of the California-Chukchi population. Andrews (1914) and
Mizue (1949) also reported temporal segregation in the Okhotsk–Korean
population of gray whales as they migrated past Uslan, Korea. Their records of
whales taken in the Korean fishery indicated that the first southbound migrants
past Uslan were near-term pregnant females, and that following the birth of their
calves, these females migrated north apart from the herd.

This segregation according to age, sex and reproductive condition appears to
exist to the Arctic feeding grounds, although relatively few studies have been
conducted in this portion of the species range. Ljungblad et al. (1985) noted that
female–calf pairs were distributed in specific near-shore portions of the northern
Bering and eastern Chukchi Seas during the summer months while few calves were
seen in more offshore areas and on the feeding grounds around St Lawrence
Island. Krupnik's (1984) analysis of numerous archaeological sites along the
Chukotka Peninsula reveals that 1st Century AD native whalers concentrated on
young gray whales, particularly calves, as the bones of these animals were found in
large numbers in the ancient middens. Because aboriginal hunters did not have the
ability to travel far offshore, the predominance of gray whale calf bones in the
excavations suggest that these whales were taken near-shore.

In their review of the Soviet literature on gray whale distribution in the Bering
and Chukchi Seas, Yablokov and Bogoslovskaya (1984) described the age
differentiation of the stock, with young animals congregating around the Koryak
coastline from Glubokiv Bay to Cape Navarin, and groups of adults found in more
northern waters. Soviet whaling records further indicated that small animals
predominated in the catches from specific coastal areas (Bogoslovskaya et al.,
1982), and that females with young were mainly distributed in shallow coastal
waters while larger whales were found further offshore at depths of 50 to 60 m
(Votrogov and Bogoslovskaya, 1980). The segregation of gray whales by age and
reproductive condition, thus, appears to be a behavioral characteristic that prevails
throughout the species range.

The segregation of courting whales from females with calves is indicative of the
behavioral incompatibility of these two groups and appears to be the primary

mechanism behind their spatial distribution within the breeding lagoons. Harassment by courting whales is probably a major factor in the female–calf pair avoidance of courting whales inhabiting the outer lagoon areas. Females with calves avoid courting groups; despite this, they are occasionally pursued by groups of single whales that appear to harass and attempt to mate with them (Jones and Swartz, 1984a). Mating bouts appear to be very disruptive events and may involve groups of a dozen or more individual whales thrashing at the surface and throwing their flukes and flippers about as they jocky for mating position. It is certainly reasonable to think that a calf might be separated from its mother or could sustain injuries or even be killed in these circumstances. Norris *et al.* (1977) studied reproductive behavior in the Boca de Soledad area north of Bahia Magdalena, and remarked that 'courting-mating aggregations are almost certainly disruptive places for mother–calf pairs'. .

Additional evidence for this interaction comes from observations in Laguna San Ignacio of females and calves passing through areas in the outer lagoon where courting whales are concentrated. In January and February females with calves occupied the lagoon with courting whales, and although female–calf pairs routinely travel the entire length of the lagoon, only 23% of the female–calf pairs passing through areas with courting whales utilized the center of the lagoon channel while courting whales were concentrated there. The remaining 77% hugged the sides of the channel while travelling through areas occupied by courting whales. By early March and with the departure of courting whales from the lagoon this condition reversed. Now 75% of the female–calf pairs utilized the central channel, suggesting that central deeper portion of the lagoon channel was preferred by all whales, but as in other areas throughout the lagoon, females with calves avoided mixing with whales without calves (Swartz and Jones, 1981).

CALF DEVELOPMENT

Quantitative studies of gray whale calf behaviour and development have yet to be conducted; however, observations of female-calf pairs behavior in Laguna San Ignacio between 1978 and 1982 suggest that gray whale calves progress through various developmental stages during their first few months of life in the lagoon, and that these stages are similar to the activity stages of southern right whales (*Eubalaena australis*) described by Thomas and Taber (1983) and Thomas (1986).

Although concentrated in the inner lagoon nursery at peak season, gray whale mothers remain mostly alone with their calves while they rest, nurse and move with the tides during the first few weeks of the calf's life. For example, 90% of all female–calf pairs encountered during lagoon censuses were solitary pairs. Eighty percent of those in the inner lagoon nursery were not moving, while in the lower lagoon nearest the inlet 40% were actively swimming (Swartz and Jones, 1981), suggesting that females with calves behave differently in different portions of the lagoon, and that their least active periods occur while they are within the nursery.

Shortly after birth, the calf's coordination is erratic and it lacks endurance for prolonged swimming. During this period the calf remains close to its mother while she rests and often 'rides' just above or to the side of the female when she travels. As the season progresses, females abandon the nursery and occupy the outer lagoon and inlet with their calves, where the channels are deeper and currents stronger. Here, females position themselves into the ebbing tides, swimming just

enough to match the speed of the water and thereby remain stationary in the channel. Their calves swim rapidly in these situations as if on a treadmill, and no doubt develop strength and swimming endurance from the experience.

Calves and mothers do interact with other whales in female–calf social groups characterized by intense physical contact (Jones and Swartz, 1984a). Group members cavort, rolling and rubbing against each other, wheeling and diving at the surface and below as if chasing each other in play. Multiple bubble bursts often mark their location while submerged, and whale calls are frequent (Dahlheim, 1986). The size and duration of these groups vary, but can involve up to 20 mother–calf pairs at a time, and can last from a few minutes to over three hours. The groups are fluid, with pairs coalescing and exchanging continually. These activities may erve as a 'socializing' mechanism to expose the young whales to the behavior of their conspecifics, as compared to the imprinted behavioral attraction to their mothers which characterized their previous development period.

The calves, although still nursing, mimic adult foraging behavior and are frequently seen filtering bottom sediments through their baleen, gulping mouthfulls of sea water, and skimming eel grass pattys from the water surface. These activities appear to prepare the calf for its eventual life at sea, particularly the mimicry of foraging behavior that presumably will aid the calf in learning to locate prey after weaning. The development of social behavior through play and metacommunication in immature mammals has been widely discussed e.g. by Beckoff (1972) for canids and by Kummer (1971) and Poirier (1972) for primates. In his study of play in Steller sealions (*Eumetopias jubatus*), Gentry (1974) identified adult-like behavioral patterns in 2 week old animals, and concluded that play experience was a vehicle by which the frequency, intensity and combination of behavioral patterns present in the young are changed over time and ultimately manifest themselves in the adult as behavior with entirely new functions other than play.

CARE GIVING OR EPIMELETIC BEHAVIOR

Beyond the female–calf bond, courtship and mating and their migration, gray whales (and mysticetes in general) have been presumed to lack complex social behavior described for the social odontocetes (IWC, 1986). Reports of care giving or epimeletic behavior are, however, widespread throughout the Cetacea, and examples from studies of Odontoceti and Mysticeti have been reviewed by Scott (1958), Caldwell and Caldwell (1966) and Connor and Norris (1982). Examples include observations by Soviet biologists who describe 'supporting' and 'standing-by' behavior of gray whales toward injured companions (and see Bogoslovskaya, this volume). Bogoslovskaya *et al.* (1982) reported that on the Arctic feeding grounds it was common for a second whale to remain with a harpooned one. In one instance, a harpooned pregnant female was supported at the surface by a second pregnant female that put her head and tail under the animal.

On two occasions in different years interactions were observed that were suggestive of 'reciprocal altruism' between presumably non-related individuals (two adults) as described by Connor and Norris (1982). In both instances the scenario was similar and began with a calf swimming out of a channel and over the

shallow sand bar toward shore until it grounded itself. In no more than a meter of water, the calf began frantically rolling and thrashing. Within moments, an adult, probably the mother, surged out of the channel and lunged up onto the sand bar beaching itself next to the calf. A second adult followed behind the first and positioned itself on the opposite side of the calf. Sandwiching the young whale between them, both adults rocked their bodies in the shallow water, pivoted while lifting the calf, and slid back into the deep channel and disappeared. Each time, the rescue maneuver was performed within fifteen to twenty seconds, and appeared as deliberate and coordinated activity on the part of both adults. It seemed as though the whale helping the mother knew what was required and how best to offer assistance. For this it appears that gray whales have achieved a level of social organization and communication necessary to coordinate the assistance between conspecifics (Jones and Swartz, 1984b).

COURTSHIP AND MATING SYSTEM

The principal activities of whales without calves within the lagoon are courtship and mating. In contrast to the solitary nature of female–calf pairs, 50% or more of the courting whales without calves counted each year in Laguna San Ignacio were in groups of two or more animals. The proportion of these whales that were actively travelling and those involved in social interactions and courtship were about equal, 57% and 43% respectively (Swartz and Jones, 1981).

Courting whales engage in high speed chases where group members (presumably males) appear to pursue a lead animal (presumably a female). These groups lunge through the water creating spectacular bow-waves, and sometimes travel 3–4 km before beginning a mating bout.

The principal gray whale mating group has been described by Gilmore (1960) and Samaras (1974), amongst others, as a 'mating-trio', consisting of a mating pair and a third animal who has been implicated as a helper. Given the 1 : 1 sex ratio of gray whales at birth (Rice and Wolman, 1971; Swartz and Jones, 1983), equal mortality rates for mature males and females (Reilly, 1984a), and a female breeding cycle of two or more years, there necessarily would be a surplus of adult males within a breeding season. Reports of 'mating-trios' are likely oversimplifications, as observations in Laguna San Ignacio confirm that mating groups were not limited to trios, but ranged from pairs up to groups of 18 animals of mixed sexes and sizes (except calves). Courting bouts lasted for two or more hours with some group members departing while other passing whales joined in as if stimulated by the sexual activity of the core group. On one occasion a mating bout lasted over four hours and in the end involved at least thirty individuals. Females appear to control the duration of the mating bouts by either accepting the advances of males or rejecting them by lying ventral side up at the surface or fleeing. Females are promiscuous and repeatedly copulate with more than one male during the same mating bout.

While social odontocetes invest energy in calf rearing as a reproductive strategy (Caldwell and Caldwell, 1966; Wursig, 1978; Wells et al., 1980; Connor and Norris, 1982; Best et al., 1984), mysticetes apparently invest energy in calf bearing with little or no parental care beyond the mother–calf relationship. In this context, the mating system of gray whales appears polygynous with males breeding with more

than one female and females being predisposed for the care of the offspring (Wittenberger, 1981). In gray whales, however, important departures from classic mammalian polygyny are that males do not appear to be able to monopolize females, they lack the male–male aggressive displays that may determine which males mate (Krebs and Davies, 1981), and that females are also promiscuous.

In gray whales, female breeding is relatively synchronous. The effective mating period lasts at least as long as the birth period of approximately 66 days compared to 3 to 5 months in humpback whales (*Megaptera novaeangliae*) (Dawbin, 1966; Darling, 1983). During this time gray whales are dispersed along the Pacific coast of North America as they migrate south for the winter. Their compressed breeding season and dispersed geographical distribution limits, and may even preclude, the monopolization of available females by males. Thus, male defense of mates in 'harems' or other similar aggregations that give dominant males exclusive access to females, as seen in other polygynous mammals with compressed breeding seasons [e.g. ungulates like the red deer, *Cervus elaphus*, (Vlutton-Brock *et al.*, 1982), mountain sheep, *Ovis canadensis*, (Geist, 1971); or marine species such as the elephant seal, *Mirounga angustirostris*, (Le Boeuf, 1981); or as proposed for the sperm whale, *Physeter macrocephalus*, (Best, 1979)] may not exist in gray whales.

Given a two year breeding cycle (Rice and Wolman, 1971), the unavailability of half the mature females for breeding each season skews the operational sex ratio 2 : 1 toward males, and as a season progresses the number of females available for mating further declines as they are mated (Emlen and Oring, 1977). Thus, competition between gray whale males for mates would be expected. At this time, evidence for male–male competition for available mates, such as social displays, dominance hierarchies, the defense of territories or the aggressive behavior seen in humpback whales (Darling, 1983), has yet to be identified in gray whales. Females of some species presumably utilize criteria such as these to select the most 'fit' mate in terms of his genetic superiority (Partridge, 1980) or territory offering superior resources (Barash, 1982).

Emlen and Oring (1977) describe 'male dominance polygyny' as occurring in situations where mates are not economically monopolizable. Under these circumstances males aggregate during the breeding season and females 'select' their mates. There is little evidence that female mammals are able to detect genetic superiority in males (Bateson, 1983). In most cases of female choice, it appears that females are choosing males that are likely to be good fathers or males with territories that provide superior resources (Krebs and Davies, 1981). Because gray whale males do not assist with the rearing of offspring, or defend territories, it is unlikely that females select mates on these criteria. Rather, observations in San Ignacio lagoon suggest that females control mating bouts, but repeated copulation with different partners suggest that they, like males, are promiscuous.

Emlen and Oring predict that promiscuity will occur in what they term 'explosive breeding assemblages' where both sexes converge for a short-lived, highly synchronized mating period—as seen in gray whales. One apparent function of the gray whale migration is to bring sexually mature animals together when they are receptive for mating. Because sexual activity occurs during their migration and lagoon occupation (Gilmore, 1960; Pike, 1962; Fay, 1963; Rice and Wolman, 1971; Baldridge, 1974; Hatler and Darling, 1974; Jones and Swartz, 1984a) rather than in one specific portion of their range, the timing of reproduction may be more important than a specific breeding location. Although the lagoons are important core areas for females with calves, mating activities of breeding animals do not

appear restricted to particular locations. A 'core time' rather than area might be the important factor in assuring fertilization in gray whales, particularly if female breeding is highly synchronized. Terrestrial analogues for the occurrence of effective breeding during migration include the barren ground caribou (*Rangifer sp.*) and the blue wildebeest (*Connochaetes sp.*) (Wilson, 1975).

Finally, Emlen and Oring (1977) predict that communal displays will be frequent in any species in which the male is totally emancipated from parental care and where the environment provides little potential for resource (mate) control. In these situations, male–male dominance competition will drive the evolution of social displays, such as those seen in polygynous birds and mammals. For example, the songs of the humpback whale have been implicated as secondary sexual characteristics in the form of acoustic displays between breeding males (Darling, 1983).

The lack of direct evidence for male–male competition in gray whales, such as extreme sexual dimorphism, male territorial defense and communal displays, suggests that competition and sexual selection may occur at some level other than that of the individual. In species where females mate with more than one male, sperm competition may determine male paternity (Parker, 1984). Dewsbury (1981) found that in golden hamsters (*Mesocricetus auratus*) the order of mating, differential fertilizing capacity and sperm competition all affected individual male mating success in situations where females subsequently mate with different males. Landino (1985) and Payne and Bird (1985), reviewed the literature on sperm competition and sexual selection theory which indicated that relative testes-to-body weight ratio was indicative of breeding systems in primates. On the basis of testes-to-body weight ratios, they predicted that cetacean mating systems would be either unimale (monogamous or polygynous) or multimale (promiscuous or polyandrous). According to this idea, in multimale breeding systems, a male has to provide enough sperm to compete with the sperm of other males and should have large testes. In unimale polygynous systems, the male can presumably be secure in assuming paternity and must produce only enough sperm to service the females in his harem. The unimale systems, then, would not necessarily require large testes. The testes-to-body weight ratio in gray whales predicted a multimale breeding system, which is consistent with the breeding behavior seen in this species.

Brownell and Ralls (1986) reviewed the literature on baleen whale testes size, penis length and mating system. They reasoned that in species with sperm competition large testes that produce large amounts of sperm per ejaculation would serve to dilute and displace the sperm of rival males, and that longer penises would deliver the sperm closer to the ova. They reported that species without obvious male–male competitive behavior (right, gray and bowhead whales) possessed both large testes-to-body weights and penis-to-body lengths. Because gray whales had testes that were smaller than those of right and bowhead whales, they concluded that sperm competition may be less intense than in these species. The relatively smaller testes of the humpback whale, together with its shorter penis and the conspicuous interactions between breeding males suggest that this species has been selected to compete to a greater extent by preventing matings of rival males than by sperm competition.

If sperm competition exists in gray whales, either by displacement due to differential volume delivered to the female (Dewsbury, 1981) or by physiological deactivation (Whittenberger, 1981), it may account for the lack of obvious

male–male sexual displays. Future long-term studies, particularly individuals which can be repeatedly recognized in the field over periods of several seasons, should make significant contributions to our understanding of the evolution of gray whale social behavior and the life history of this unique mysticete.

ACKNOWLEDGEMENTS

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