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The Reproductive Cycle in Gray Whales Based on Photographic Resightings of Females on the Breeding Grounds from 1977–82

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ABSTRACT

Gray whales (*Eschrichtius robustus*) with distinctive natural markings were systematically photographed in San Ignacio Lagoon, Mexico from 1977 to 1982. In this paper, information is presented on breeding cycles for individually known females, including the range of values observed for length of calving interval and the relative frequencies of different length calving intervals (expressed in years). About 6,000 photographs were taken and 562 different gray whales were identified. Among these were 55 sexually mature females that were followed through 2 to 6 seasons on their winter breeding grounds; they produced a total of 115 calves over the 6-year period.

The length of time between the birth of consecutive calves was documented for 42 cows. Calving intervals ranged from 1–4 years, but were predominantly 2 years (1 calf every other year). The observed intervals were: 1 year (n=1), 2 years (n=48), 3 years (n=6) and 4 years (n=5). The mean length of the calving interval, or breeding cycle, for the population from 1977–82, was estimated as 2.11 (SD=0.403) years.

INTRODUCTION

Knowledge of the periodicity of calving, or the duration of the reproductive cycle, is useful information in fishery biology for predicting birth rate, population growth and recruitment, and hence production (Lockyer, 1984). For the eastern Pacific stock of gray whale (*Eschrichtius robustus*) life history data for the estimation of vital rates are available from two fisheries: a series of gray whales examined from the Soviet subsistence fishery in the waters of Chukotka Peninsula (reviewed in Tomilin, 1957; Zimushko, 1969; Yablokov and Bogoslovskaya, 1984; Blokhin, 1984; 1985; 1986; 1987) and a series collected off the California coast for US scientific research (Rice and Wolman, 1971). In both samples, estimates of reproductive rates come from examination of ovarian and other morphological data. Although these studies provide the best information available, sampling bias in terms of both selecting the animals taken in the fishery and selecting which of the animals taken are to be examined, makes it difficult to determine how representative the data are of the population as a whole.

Several questions remain unresolved from the examination of the catch data. One of these is the minimum biologically possible calving interval, important for the estimation of the maximum rate of increase of a population (Reilly, 1984). While it is generally agreed that the most common cycle is two years between calves (e.g. Rice and Wolman, 1971; Blokhin, 1984a and c) there is some disagreement over the extent to which a one-year cycle can occur. Zimushko (1969) reported examining seven simultaneously pregnant and lactating females but did not state how many females he had examined. Yablokov and Bogoslovskaya (1984) stated that between 1965–68 'about 20% of such females were encountered' but do not report 20% of what. Rice and Wolman (1971) however proposed that the potential for post-partum pregnancy was being or had been genetically eliminated from the stock. Recent reports on the Soviet harvest (e.g. Blokhin, 1984b; 1985; 1986; 1987) have not recorded simultaneously pregnant and lactating females. It should be noted, however, that in addition to the sampling bias referred to earlier, the representativeness of the catch is further confounded because cows accompanied by calves (essentially, lactating females) are protected under International Whaling Commission regulations. The catch data also provide little information on the range and frequency of calving intervals and whether this varies with time. Yablokov and Bogoslovskaya (1984) hypothesise that pregnancy rate decreases with age, while Blokhin (1984a) believes it does not.

The annual migration of the eastern Pacific stock of gray whales between its northern feeding grounds in the Bering and Chukchi Seas and its southern breeding grounds off California, the Baja Peninsula and mainland Mexico makes it especially well suited to study by means of photo-identification. Members of this population travel close to shore during their migrations and breed near shore and in coastal lagoons. In the breeding areas, the likelihood of observing a large number of whales from year to year is very good, which makes the task of assessing reproductive parameters, like calving interval, relatively easy, albeit time consuming.

One of the distinguishing features of gray whales is their mottled gray skin, due to both natural pigmentation and extensive scarring from dead barnacles. The darkness of the background and the extent of light blocking vary in each whale and can serve as a visual tag, of which no two are alike. Research by Hatler and Darling (1974) and Darling (1984), who were the first to study gray whales using individual photo-identification techniques, has shown that the longevity of markings is at least 11 years, and that the technique can be reliably used as a basis for long-term studies of this species.

This paper presents some of the findings of a six-year photo-identification study of live, free-ranging gray whales on their breeding grounds in San Ignacio Lagoon, Baja California, Mexico (Jones and Swartz, 1985). From 1977 through 1982, mature females were identified and their reproductive histories were documented in an effort to further clarify and verify the existent knowledge on breeding cycles and other aspects of their life history. Data on periodicity of calving were analyzed with three goals in mind: (1) to determine the range of values for length of the

breeding cycle; (2) to ascertain the relative frequencies of the different intervals; and (3) to discover whether the length of the breeding cycle for individual females was constant or variable over time.

METHODS

Study site

San Ignacio Lagoon, on the Pacific coast of Baja California, Mexico, is an estuary on the extremely arid and barren Desierto De Vizcaino (Fig. 1). Opening off the wide bight of Bahía de Ballenas at 26°45′N, the lagoon is about 32km long, and from 1.8 to 6.5km wide. The shoreline is composed of areas of sand beach, rock-shell conglomerate and mangrove marshes. The interior has a basin at its head and a system of channels (cut by the tidal currents) separated by shoals, many of which are exposed at low tide. Much of the lagoon is shallow. Extensive intertidal sand and mud flats along the shore restrict whales to more central locations. Although the lagoon's surface area is 152km², only about 87km² (57%) is deep enough (>2m) for whales.

San Ignacio Lagoon, which supports the second largest number of gray whales was selected as the study site because it is the least developed of all the major breeding lagoons, facilitating studies of 'normal' whale behavior.

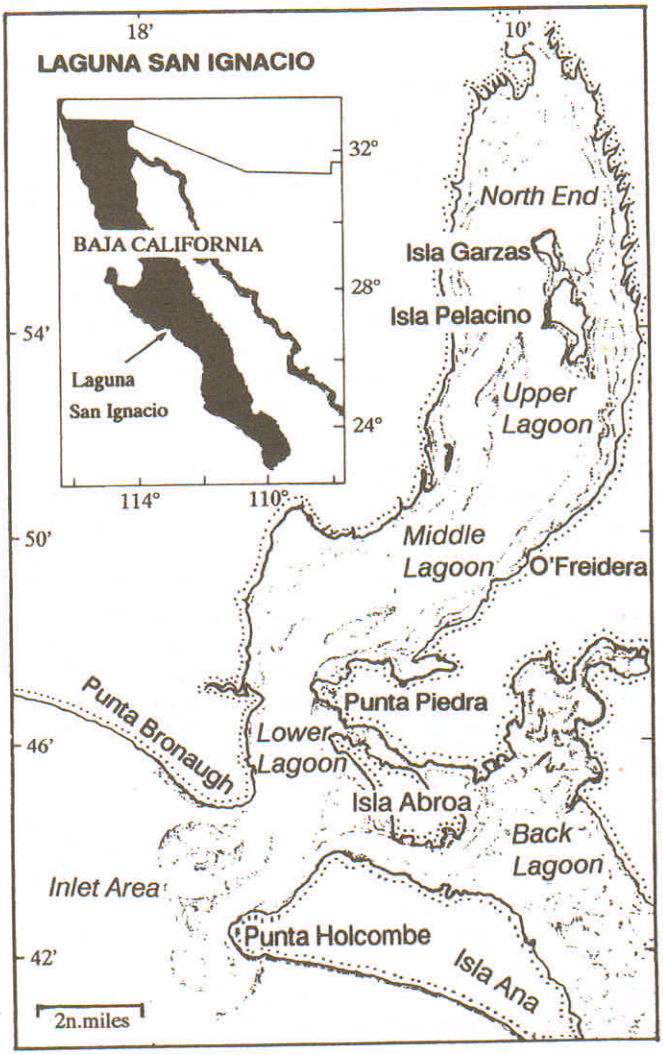

Fig. 1. San Ignacio Lagoon, Baja California Sur, Mexico.

Study design

It was not feasible to photograph every whale in every season because up to 500 or 600 whales occupied the lagoon at any one time during the peak of the season (Jones and Swartz, 1986). To reduce the number of photographs to be analysed, it was decided to photograph selectively only those whales bearing obvious marks which were visible to the naked-eye at moderate ranges for observers in small boats. It was assumed that all whales had an equal opportunity of being encountered, and that the animals with obvious marks were a representative sample of the population. Analysing the data using capture-recapture methods to estimate population size was not an objective of the study.

To identify gray whales, photographs were taken of the dorsal ridge, back (preferably close to the middle of the back) or anterior portion of the peduncle. The dorsal ridge was preferred since it was the most prominent and easily observed portion of a surfacing whale and was consistently visible each time the whale surfaced. If the left and right sides of the whale had distinctive marks, photographs of both sides were obtained (when possible) to prevent counting the animal as two whales. Individuals with unique features such as a broken back or peduncle, deformed or missing flukes and wounds were also photographed. Fluke patterns generally could not be used for identification because whales in San Ignacio Lagoon rarely raised their flukes above the water's surface when diving, as they do on the northern range and during migration.

Whales were photographed with *Ektachrome* 200 film, using 35mm single-lens reflex cameras with motor-drives and 70–210mm or 100–300mm zoom telephoto lenses. To minimize parallax and angular distortion, photographs were taken directly perpendicular to the longitudinal axis of the whale, with the sun behind the camera; where possible a sequence of photographs taken at slightly different angles (ahead and behind) were taken to allow a choice of the most useful angle for identification.

The general procedure for obtaining photographs was as follows. Prior to approaching a whale, its breathing pattern was timed and its behavior noted. A slow approach was made, preferably from behind and to the side of the whale. It was followed through several dive sequences until several identifying photographs were taken. If the whale showed evasive behavior, the approach was discontinued. Otherwise the approach continued to within 30m whenever possible.

Sighting data recorded included date, time of day, location, behavior and presence of a calf. An effort was made to determine the sex of animals, but the sex could be determined only for females with calves or in the rare case of matching a ventral view of a whale with a dorsal view of the same animal.

Photographs (slides) were classified chronologically according to type and size of the mark, the side or sides of the whale depicted and the location of the mark on the body (ordered from anterior to posterior). A catalog was then compiled which contained a clear picture and an information file on each whale.

Field work began in late December or early January and continued until early April of each year from 1977 through 1982. Whales were systematically photographed on two days per week (separated by a 4–5 day interval) from a 4.7m outboard-powered boat. Generally, weather permitting, a roundtrip traverse of the lagoon was made along a mid-lagoon transect from the breaker line near the

inlet, north to the head of the lagoon; diversions were made to photograph whales as they were encountered. This provided a minimum of four opportunities per week to identify additional individuals, and to resight whales encountered earlier in a given season or seasons. The photo-identification study was one task in a multi-task research program on gray whales, human activities and the ecosystem in San Ignacio Lagoon (Swartz and Jones, 1981; Jones and Swartz, 1986; Swartz, 1986). Additional photographs were taken opportunistically two days per week during vessel surveys (to census the number of whales) and two days per week during shore-based surveys from an observation tower (to record whale behavior). During the six-year study, a total of 1,710 hours of photographic field work was conducted; the annual level of photo–identification effort was approximately constant at about 285 hours (Table 1).

Table 1

Summary of six-year photo-identification effort at San Ignacio Lagoon.

	Year						
	1977	1978	1979	1980	1981	1982	Total
No. photos taken	1,100	500 [1]	1,044	1,080	1,150	1,200	6,074
No. gray whales identified	87	72	128	85	66	124	562
No. resighted in previous years	0	11	20	29	30	42	132
No. resighted in other years	17	26	31	34	29	42	179

[1] In 1978, 50% of the photographs were lost due to a processing malfunction.

RESULTS

Whale identifications and re-sightings

From 1977 to 1982, 562 gray whales were identified in San Ignacio Lagoon. Of these, 55 mature females were photographed among years: 13 were photographed in 2 years, 8 in 3 years, 8 in 4 years, 16 in 5 years and 10 in all 6 years.

The reproductive histories collected for the 55 females during the study revealed: 1 female gave birth to 4 calves in a 6-year period; 16 females each had 3 calves in a 5 or 6-year period; 25 females each had 2 calves in a 3 or 4-year period; and 13 females had 1 calf in a 2-year period. The sum of the number of years from the first to the last sighting of these known whales was 223 and the total number of calves observed was 115.

All of the births were of a single calf; no twins were observed. Although at least one set of twins has been found *in utero* in the gray whale (Blokhin, 1987), there is no evidence of mature delivery of these young.

None of the females observed in this study exhibited long lasting or overlapping maternal care for successive offspring. All calves were young-of-the-year. This corroborates other observations that gray whale calves are dependent upon lactating mothers only until weaning occurs. Bogoslovskaya (1986), in her review of the social behavior of gray whales on their northern feeding grounds off Chukotka and Koryaka between 1977 and 1983, stated that:

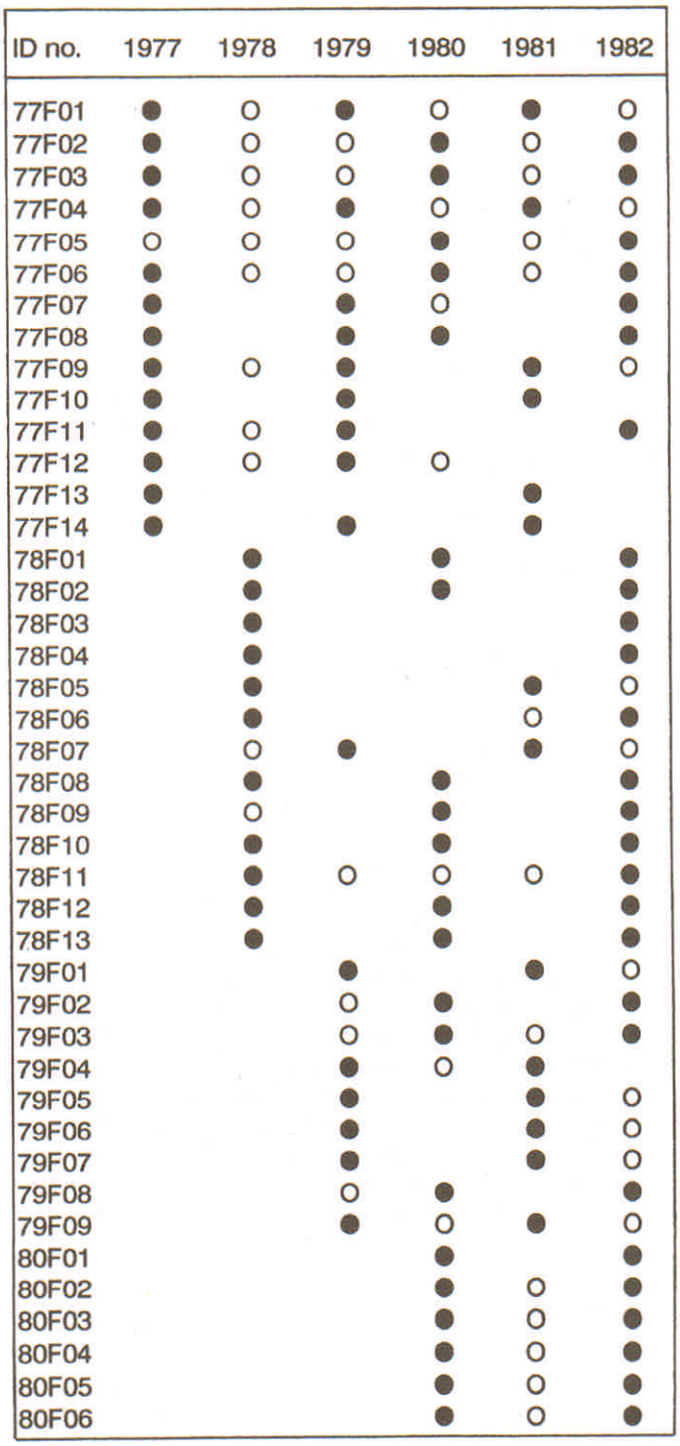

Fig. 2. Reproductive histories of the 42 female gray whales observed with two or more calves during the study period in San Ignacio Lagoon. Solid circles indicate years females were observed with a different calf, open circles represent years they were seen without a calf and blank spaces indicate years they were not seen at all.

'In July and August, the calves generally leave their mothers and assemble together in certain areas. Some mothers remain with their calves for much longer periods, usually if the calf is weak (either through ill health or if it was born late in the season).'

Calving interval

The calving interval, as defined here, is the period of time (given in years) between the birth of successive calves. Barlow (1990) discussed different ways of estimating calving interval. The time span between calvings was

recorded for 42 cows, which gave birth to a total of 102 calves during the study, providing information on a total of 60 calving intervals (Fig. 2). Periodicity of calving ranged from annual (1 case) to a 4-year period between calves (1 case), but was predominately biennial (80%) (Table 2). The observed intervals (and frequencies) were: 1 year (n=1), 2 years (n=48), 3 years (n=6) and 4 years (n=5).

The average length of the calving interval, or breeding cycle, for the female population during the six-year period was 2.25 ±SD 0.628 years. One bias inherent in this estimation, however, is that some of the longer calving intervals may represent animals that had an undetected calf in the interim. In particular, this estimate may be biased upward by the four females in the sample that had a calf in the first and fifth years of a 5-year period (apparent 4-year calving interval), but for which no data are available for the presence or absence of a calf in the third year because they were not seen in that year. Considering that 80% of all the calving intervals lasted two years, and because annual breeding appears to be rare (1 case in 223 female years), this suggests that the four cows did produce a calf during the third year resulting in two biennial cycles, rather than one 4-year cycle. Using this assumption as one way of correcting for the biased representation of longer intervals results in a revised mean calving interval of 2.11 ±SD 0.403 years (n=64, Table 2).

Of the 42 sexually mature females sampled on the winter grounds, 30 (71.4%) animals exhibited only a two-year breeding cycle, 1 (2.4%) was on a three-year cycle, 5 (11.9%) were on an apparent four-year cycle, 5 (11.9%) were on a variable two/three-year cycle and 1 (2.4%) female was on a variable one/two-year cycle. As explained previously, 4 of the 5 females on an apparent four-year cycle were possibly on a shorter breeding cycle, hence the value may be as low as 1 (2.4%) for this category (Table 3).

The one female that produced a calf in two successive years probably lost her first calf shortly after its birth. This cow was seen early in the season with her first calf, and was photographed without a calf later in the season. She was then seen again with a calf the next year. This suggests that the postpartum ovulation with conception possibly resulted because of the loss of the calf.

Table 2

Frequency distribution of the calving intervals documented for mature female gray whales photographed in San Ignacio Lagoon from 1977 through 1982.

Length of calving interval [1] (in years)	Frequency		Proportion	
	n = 60	(n = 64) [2]	n = 60	(n = 64)
1	1	(1)	0.017	(0.016)
2	48	(56)	0.800	(0.875)
3	6	(6)	0.100	(0.093)
4	5	(1)	0.083	(0.016)
Mean	2.25	(2.11)		
Standard Deviation	0.628	(0.403)		

[1] Calving interval is defined as the time between births of consecutive calves. Calving intervals longer than the study period will not be represented at all.

[2] Assumes that 4 of the 5 females that had a calf in the first and fifth years of a 5-year period (apparent 4-year calving interval) produced a calf during the third year that went undetected. In this case, two consecutive biennial cycles, rather than one 4-year cycle, would be indicated for each female, thus increasing the number of intervals from 60 to 64 (see text).

Table 3

Summary of the reproductive histories of 42 female gray whales showing length of the breeding cycle for individuals observed from 1977 through 1982.

Length of breeding cycle (in years)	No. females	Proportion
2	30 (34) [2]	0.714 (0.809)
3	1	0.024
4	5 (1)	0.119 (0.024)
1 & 2 [1]	1	0.024
2 & 3	5	0.119

[1] Variable cycle (some females had cycles of different lengths).

[2] Assumes that 4 of the 5 cows that had a calf in the first and fifth years of a 5-year period (apparent 4-year calving interval) produced a calf during the third year that went undetected. In this case, two consecutive biennial cycles, rather than one 4-year cycle, would be indicated for each cow, thus increasing the number of females with 2-year cycles from 30 to 34, and decreasing the number of females with 4-year cycles from 5 to 1 (see text).

DISCUSSION

The most common breeding pattern observed during our study period was a biennial cycle. This is consistent with previous reports. It is important to note, however, that there was considerable individual variation in calving interval. One female was found to breed annually (see below) while from 8 to 11 others reproduced after two or more resting years between calves. This agrees with Zimushko's (1969) finding that some females rest more than one year between calves. The apparent flexibility in reproductive cycle may be dependent upon a female's age, general health and nutritive condition. The occurrence of longer calving intervals (2, 3 and 4 years) could also be indicative of some cows having missed pregnancies or having failed to carry pregnancies to term. Missed pregnancies indicate either a failure to ovulate, or a failure to conceive following ovulation (Rice and Wolman, 1971).

Further data are needed to address the question of whether calving interval is a function of age. Sociobiological research on the pattern of age-specific fecundity for large wild mammals supports Blokhin's (1984) view that pregnancy rate does not increase with age; findings suggest that

> 'if experience improves reproductive performance, young individuals reproduce at a lower rate than fully mature individuals. If not, reproductive rate is relatively constant for all age groups until senescence set in' (Wittenberger, 1981).

To verify the existence and/or pattern of age-specific fecundity in gray whales, long-term behavioral studies of identified females of known age will be needed.

Our results indicate that annual pregnancy can occur but that postpartum ovulation in females which have not lost a calf is probably not a regular occurrence in this species. This contrasts with the Yablokov and Bogoslovskaya's (1984) report of 'about 20%' between 1965–8, but is in accord with recent reports from the harvest (Blokhin, 1984–7). However, the question of protection of whales accompanied by calves, and the possibility that the percentage of occurrence of annual breeders may decrease as a population approaches carrying capacity, makes resolution of the apparent inconsistency difficult. Due to

the limited sample size of this study additional research is needed to address this question adequately. As noted by Rice (1983):

> 'even with the gestation period longer than 365 days, a female could still bear a calf two years in succession, but in the second year the reproductive cycle would be somewhat delayed. Successive annual pregnancies could not be repeated very long, however, because the reproductive cycle would soon get out of phase with the annual cycle.'

Closing remarks

Although gray whales are perhaps the best studied of all baleen whales, much research is still needed to describe fully their life history, population dynamics and social structure. The photographic identification data collected during this six-year study provide a foundation for further studies.

The eastern Pacific stock is relatively easy to study in this regard. The confined breeding area, with consistent presence of a large number of whales during the winter and the clement weather conditions in the breeding lagoons readily permit photo-identification work; there is a very good chance of resighting many known gray whales from year to year. The importance of *continuous* long term photo-identification studies to obtain information on biological parameters has been recognised (IWC, 1990). It is important that such studies on this stock begin again before the value of the present study is lost. A program to obtain photographs of the Soviet catch of gray whales for comparison with animals individually identified elsewhere has been discussed (IWC, 1987, p.113). Comparison of the biological material from this catch with photographic histories obtained from individually known animals on the breeding grounds provides a unique opportunity to calibrate some of the reproductive parameters previously derived solely from the study of harvested whales.

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