



DOLPHIN SOCIETIES

Discoveries and Puzzles

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CHAPTER NINE

AN OVERVIEW OF THE CHANGES IN THE ROLE OF A FEMALE PILOT WHALE WITH AGE

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The short-finned pilot whale (*G. macrorhynchus*) has been hunted by traditional Japanese whaling teams since the early seventeenth century. To study the life history and reproductive biology of this species, data and specimens were collected during the flensing of 483 females and 234 males from twenty schools caught in a driving fishery between 1975 and 1984, inclusive. This fishery is unselective in that it captures entire schools of whales; however, there is evidence of some geographic segregation of schools in the hunting season. Schools with a high proportion of pregnant females apparently congregate in the whaling area, which occurs in coastal waters at the northern limit of the range (Kasuya and Marsh 1984).

In the absence of known-age material, age was estimated by counting dentinal and/or cemental growth layers as outlined in Kasuya and Matsui (1984), the growth layer deposition rate being deduced from the seasonal pattern of layer deposition. The reproductive organs were examined using standard macroscopic and histological procedures (Kasuya and Marsh 1984, Marsh and Kasuya 1984). The age determination and reproductive studies were done independently.

The apparent pregnancy rate (proportion of mature females pregnant) declined markedly with increasing maternal age. Even though the ages of the females examined ranged up to 63 years, none of the 92 females over 36 years old was pregnant. The two oldest pregnant whales were aged 34.5 years and 35.5 years, respectively. Using the fetal growth equation

developed by Kasuya and Marsh (1984), we calculated that these animals were scheduled to give birth before age 36. Another female subsequently estimated to have been 35.5 years old was observed to give birth the day before being killed. Using the life table data in Kasuya and Marsh (1984), we calculated that the mean life expectancy of a female pilot whale aged 36 years is fourteen years.

There was a parallel age-related decline in the ovulation rate. All females over 40 years old had apparently ceased to ovulate, as corpora lutea and young corpora albicantia were absent from their ovaries (Marsh and Kasuya 1984). Ovulation was less likely to be followed by pregnancy in older whales, the proportion of well-developed corpora lutea accompanied by a confirmed pregnancy being significantly lower in females older than 20 years than in younger whales. The infertility of the older females was associated with ovarian changes. Macroscopic (> 1 mm in diameter) follicles occurred in only six of the forty-nine females over 40 years old studied by Marsh and Kasuya (1984). When examined histologically, such follicles were invariably atretic and thus incapable of ovulation. Semiquantitative histological study of the ovarian cortex of thirty whales spanning the age range of 4 to 63 indicated that the oocyte stock of older females was severely depleted (ibid.). Old pilot whale ovaries also exhibited other features characteristic of postmenopausal human ovaries, including a general decrease in cortical volume, thickening and sclerosis of the arterial walls, in-growth of the surface epithelium, and increased pathology (Benirschke and Marsh 1984, Marsh and Kasuya 1984). We conclude that female pilot whales in this population become reproductively senescent by age 36 to 40 and that about 25 percent of the mature females sampled were probably postreproductive.

Investment in rearing as opposed to bearing young apparently increases with maternal age in *G. macrorhynchus*. Although pilot whales start taking solid food when less than one year old (Kasuya and Marsh 1984), the duration of lactation seems to be highly variable. The number of females that are lactating in relation to the number that are pregnant is significantly greater for whales older than 30 than for those in the age range of 15 to 30. Our estimates of the lactation period for pilot whales in various age groups (corrected for the geographic bias in the sample discussed above as detailed in Kasuya and Marsh 1984) indicate an increase from 2.8 years for the 15 to 20 age group to 6.4 years for both the age groups above 30. Older female pilot whales clearly have fewer calves but lactate longer.

The ages of the lactating *G. macrorhynchus* ranged up to 51, at least eleven years after ovulation had presumably ceased. Fostering and/or communal nursing have been documented in several terrestrial mammals

(Gubernick 1981). However, these phenomena have not been confirmed in any wild cetacean (although Whitehead [1984] recently observed two calves apparently suckling from one sperm whale). While not denying the possibility that postreproductive, lactating *G. macrorhynchus* may be exhibiting these behaviors, our analysis of the schools in which such females occur (see Kasuya and Marsh 1984) suggests that extended lactation by older females will, in most cases, be attributable to the prolonged nursing of their own calves. Indeed, a female's last calf may occasionally be suckled until puberty, that is, up to about 8 years (female calves) and up to about 13 years (males).

The majority (80/102) of the older (>age 35) female pilot whales in our sample were not lactating; their role within the pilot whale school is unknown. Recent examination of mucus from the uteri of pilot whales of a range of ages, however, indicates that mating is not restricted to estrous females in this species. Small quantities of spermatozoa were found in the uteri of lactating and resting females, including one postreproductive female, suggesting that mating has more than a purely reproductive function in this species.

Schools of *G. macrorhynchus* are frequently involved in mass-stranding incidents and are believed to be highly cohesive (Geraci and St. Aubin 1979). Our analysis with respect to age, sex, and reproductive status of thirteen schools sampled completely (Kasuya and Marsh 1984) provides insight into the social structure of this species. With an average membership of twenty-five whales, most schools are breeding units composed of adult male(s), adult females spanning the entire range of age and reproductive status, and immature animals of both sexes. The marked excess of reproductive females over mature males (which weigh twice as much as mature females) suggests polygyny (see Ralls 1977). These schools appear to be essentially matrilineal kinship groups like pods of killer whales (Bigg 1982).

The oldest male pilot whale sampled was aged 46, seventeen years younger than the oldest female. This sex difference in longevity (which is characteristic of polygynous species in which males are larger than females; Ralls et al. 1980) means that most of the older whales in a breeding school are female. However, postreproductive resting females and/or old (>35 years) lactating females do not occur in every school (see Kasuya and Marsh 1984).

Rather than focusing on the significance of the postreproductive phase in the life cycle of female *G. macrorhynchus*, it is more meaningful to consider it as a consequence of the trade-off between bearing and rearing in a species that has the following characteristics: (1) a low lifetime reproductive output; on average, female pilot whales produce only four or

five calves (Kasuya and Marsh 1984); (2) maternal care that is so lengthy that the care of successive offspring overlaps; (3) a female adult mortality rate that increases with increasing age (the usual mammalian pattern; see Caughley 1966, Ralls et al. 1980). The mortality rate of female pilot whales older than 45 is significantly higher than in younger adults (Kasuya and Marsh 1984).

In such a species, the death of an older mother could substantially reduce the survival chances of several dependent young and perhaps other close relatives as well. In these circumstances, selection would tend to favor females that phase out their investment in bearing young as the probability of living long enough to rear them declines. This would be particularly important if reproduction in old age substantially increases the risk of mortality. It is significant that the expected length of post-reproductive life in short-finned pilot whale females is close to the maximum time taken for the young to reach puberty.

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