Demographic features of killer whales in oceanaria in the United States and Canada, 1965–1987

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ABSTRACT

Fifty-six killer whales collected from North Pacific or North Atlantic waters have been maintained in U.S. and Canadian aquaria and marine zoological parks, beginning in 1965. Twenty-one of these whales and one calf conceived and born in captivity were in these facilities as of 31 October 1987. Age-at-capture for many of these 56 whales was estimated from their growth curves. In Pacific whales, growth is approximately linear, at a mean rate of 38 cm/yr up to 10–12 or 12–16 years of age, for females and males, respectively. Atlantic killer whales follow the same growth pattern but with mean growth rates of either 39 cm/yr or 21 cm/yr. Estimated age at primiparity for females was 11 for one Pacific and 12, 13 and 15 for three Atlantic killer whales. One Pacific male was estimated to be 16 years of age at sexual maturity. For the one captive female bearing more than one calf, birth intervals averaged 23 months. Annual mortality rate estimated from "animal years" in captivity is 8.9%. Annual survivorship is 0.91.

INTRODUCTION

The killer whale, *Orcinus orca,* is an odontocete species with a cosmopolitan distribution (Mitchell 1975; Leatherwood *et al.* 1982; Leatherwood and Reeves 1983). Data on the species' general biology have been obtained from studies of both wild and captive animals (e.g., see Jonsgård and Lyshoel 1970; Hui and Ridgway 1978; Ridgway 1979; Mikhalev *et al.* 1981; Cornell *et al.* 1982; Perrin 1982; Christensen 1984; Hoyt 1984; Lyrholm 1984; Greenwood and Taylor 1985; Hall and Cornell 1986; Leatherwood *et al.* 1986; Ellis *et al.* in press). To date, however, there are few demographic data on longevity, survivorship, mortality and reproductive rates (exceptions: Bigg and Wolman 1975; Hui and Ridgway 1978; Bigg 1982; DeMaster and Drevenak 1988). Such data are important to understanding killer whale population biology. Age estimations, important for accurately characterizing these demographic measures, have been limited to the use of growth layer groups (GLG's) in teeth to 1) age a single museum specimen from Australia (Mitchell and Baker 1980) and 2) calibrate dental layers by tetracycline marks in captive killer whales (Myrick *et al.* 1988 – this volume). Photographic studies are useful for determining ages of whales for which the birth year is known and the animal is monitored through long term observational and photographic study (Balcomb *et al.* 1982; Bigg and Wolman 1975; Ellis 1984; Leatherwood *et al.* 1986; Hall and Cornell 1985; Ellis *et al.* in press; Lyrholm *et al.* 1987; Sigurjónsson *et. al.* 1988 – this volume). So far, whales with known birth years represent only small proportions of photoidentified animals in a few well-known pods.

Given the difficulty of determining exact ages of killer whales, scientists studying them have tended to assign individuals to broad age

classes (e.g. as calf, juvenile or adult or as sexually immature or sexually mature) and to use these classes to describe killer whale demography and life history. For example, Bigg (1982) reported photoidentified killer whales in known pods in British Columbia as calves, juvenile males, adult females and mature bulls, noting the difficulty in distinguishing between some females and juvenile males. Assessments of age and reproductive status of individuals taken by whalers have been used to calculate reproductive rates for populations and estimate age at sexual maturity (as indicated by first pregnancy or occurrence of ovulation in females, or testes size, weight and sperm count in males) for individuals in broad age/length classes (Nishiwaki and Handa 1958; Jonsgård and Lyshoel 1970; Perrin 1982). Hui and Ridgway (1978) and Bigg and Wolman (1975) compared survivorship for immature and mature killer whales in captivity. DeMaster (1984) and Perrin and Reilly (1984) critically examined techniques for estimating sexual maturity and other reproductive parameters of marine mammal species, including the killer whale.

This paper reviews demographic data available through 31 October 1987 on killer whales taken for public display in U.S. and Canadian aquaria and marine zoological parks. It presents a census of the whales in these facilities, growth curves, estimates of age, survivorship and mortality and a summary of data on reproduction in captivity.

METHODS

This analysis included only those killer whales intentionally collected for public display in the United States and Canada. Three stranded animals handled by the parks, two whales held by the Navy for research and whales born in captivity were excluded, although calves conceived and born in facilities in the U.S. and Canada are discussed. The following data, collected from censuses of captive marine mammals in the United States and Canada (Cornell and Asper 1978; Cornell *et al.* 1982; Asper *et al.* in press), include: number of killer whales collected, dates acquired, collection sites and status as of 31 October 1987. Data were updated and confirmed by direct contact with each institution maintaining killer whales and were compared with information summarized by Bigg and Wolman (1975), Hui and Ridgway (1978) and Hoyt (1984).

Length measurements, usually taken during routine annual checkups, were plotted for each whale. The slope of the linear regression of at least four measurements in the linear portion of a whale's growth curve (usually the first 10+ years) approximated its annual growth rate. Slopes of these lines were tested for heterogeneity by analysis of covariance (Snedecor and Cochran 1980; Zar 1984). Age at collection was estimated for each whale by extrapolation of the linear portion of the growth curve to a mean birth intercept length of 235 cm, the average length at birth of four calves conceived and born alive in captivity to Pacific parents.

Annual mortality, M, was estimated as

$$M = D/A$$

where D is the total number of deaths and A is the sum of "whale years" for all individuals (after Bigg 1982). "Whale years" are defined as the total number of years (including fractions of years) the animals spent in captivity from the date of collection to the end of the study (31 October 1987) or to death. Day of month was set to 15, if the exact day of collection or death was not known. Annual survival rate, S, is given by

$$S = 1 - M$$

Annual mortality and survival rates were also calculated based on "animal days" (a = number of days from collection to final date summed for all individuals), as defined by DeMaster and Drevenak (1988), based on Trent and Rongstad (1974). For these calculations, daily survival rate (DSR) is

$$DSR = 1 - D/a$$

Annual survival (S) is

$$S = DSR^{365.25} = (1 - (D/a))^{365.25}$$

and annual mortality (M) is

$$M = 1 - (DSR)^{365.25}$$

In both of the above calculations, DSR is simply raised to the power 365.25, the mean number of days in a year, to approximate annual rates.

These methods assume that 1) the death of an individual animal does not affect probability of another individual's surviving and 2) the probability of surviving each day remains constant (DeMaster and Drevenak 1988).

TABLE 1

Killer whales collected from June 1965 to November 1984 for display in U.S. and Canadian aquaria and marine zoological parks.

Individual number	*Sex*	*Collection date*	*Collection site*	*Status*	*Status date*
PACIFIC: 1965–1975					
1	Male	Jun 65	Namu, B.C.	Died	Jul 66
2	Female	Oct 65	Carr Inlet, WA	Died	23 Aug 71
3	Female	Feb 67	Yukon Harbor, WA	Died	Oct 80
4	Male	Feb 67	Yukon Harbor, WA	Died	23 Sep 78
5	Male	Feb 67	Yukon Harbor, WA	Died	Jan 82
6	Female	Feb 67	Yukon Harbor, WA	Died	16 Jun 71
7	Female	Feb 67	Yukon Harbor, WA	Died	May 67
8	Male	Jul 67	Port Hardy, B.C.	Died	22 Jul 69
9	Female	Feb 68	Vaughn Bay, WA	Died	Sep 68
10	Male	Feb 68	Vaughn Bay, WA	Died	4 Mar 80
11	Female	Apr 68	Pender Harbour, B.C	Died	Dec 70
12	Male	Apr 68	Pender Harbour, B.C.	Alive	31 Oct 87
13	Female	Apr 68	Pender Harbour, B.C.	Died	Nov 68
14	Male	Apr 68	Pender Harbour, B.C.	Alive	31 Oct 87
15	Female	Apr 68	Pender Harbour, B.C.	Died	Jul 68
16	Male	Oct 68	Yukon Harbor, WA	Died	Oct 82
17	Male	Oct 68	Yukon Harbor, WA	Died	Jun 74
18	Female	12 Dec 69	Pender Harbour, B.C.	Alive	31 Oct 87
19	Female	12 Dec 69	Pender Harbour, B.C.	Died	Aug 71
20	Male	Dec 69	Pender Harbour, B.C.	Died	May 72
21	Male	Dec 69	Pender Harbour, B.C.	Died	10 Jul 80
22	Female	17 Dec 69	Pender Harbour, B.C.	Alive	31 Oct 87
23	Female	Mar 70	Pedder Bay, B.C.	Died	Nov 72
24	Female	Mar 70	Pedder Bay, B.C.	Died	May 70
25	Female	Mar 70	Pedder Bay, B.C.	Alive	31 Oct 87
26	Male	Aug 70	Penn Cove, WA	Died	Apr 86
27	Female	11 Aug 70	Penn Cove, WA	Alive	31 Oct 87
28	Male	Aug 70	Penn Cove, WA	Died	18 Mar 71
29	Male	Aug 71	Penn Cove, WA	Died	Oct 79
30	Female	Aug 71	Penn Cove, WA	Died	15 Jun 75
31	Female	Aug 71	Penn Cove, WA	Died	28 Sep 77
32	Male	Mar 72	Carr Inlet, WA	Died	30 Nov 74
33	Female	Aug 73	Pedder Bay, B.C.	Died	May 74
34	Female	Aug 73	Pedder Bay, B.C.	Died	Nov 73
35	Male	Aug 73	Pedder Bay, B.C.	Died	29 Jan 74
36	Female	Aug 75	Pedder Bay, B.C.	Died	May 76
37	Male	Aug 75	Pedder Bay, B.C.	Alive	31 Oct 87

TABLE 1 (continued).

Individual number	*Sex*	*Collection date*	*Collection site*	*Status*	*Status date*
ATLANTIC: 1976–1987					
38	Female	Oct 76	Iceland	Alive	31 Oct 87
39	Male	Oct 77	Iceland	Died	Aug 81
40	Female	Oct 77	Iceland	Died	15 Oct 87
41	Female	Oct 77	Iceland	Alive	31 Oct 87
42	Male	Oct 78	Iceland	Alive	31 Oct 87
43	Female	Oct 78	Iceland	Died	3 Sep 79
44	Female	Oct 78	Iceland	Alive	31 Oct 87
45	Female	Oct 78	Iceland	Alive	31 Oct 87
46	Female	Oct 78	Iceland	Alive	31 Oct 87
47	Female	Oct 79	Iceland	Alive	31 Oct 87
48	Male	Nov 79	Iceland	Died	Oct 83
49	Female	Nov 80	Iceland	Alive	31 Oct 87
50	Male	Nov 80	Iceland	Alive	31 Oct 87
51	Female	Nov 80	Iceland	Alive	31 Oct 87
52	Female	Nov 81	Iceland	Alive	31 Oct 87
53	Male	Oct 82	Iceland	Alive	31 Oct 87
54	Female	Oct 82	Iceland	Alive	31 Oct 87
55	Female	Oct 82	Iceland	Died	Jun 83
56	Male	Nov 84	Iceland	Alive	31 Oct 87

RESULTS

Census data

Fifty six whales (23 males, 33 females) were collected for display in U.S. and Canadian aquaria and marine zoological parks between June 1965 and November 1984 (Table 1). Thirty seven (17 males, 20 females) were collected from eight different sites in Washington and British Columbia between June 1965 and August 1975, nineteen (6 males, 13 females) from Icelandic coastal waters between October 1976 and November 1984. As of 31 October 1987, 21 (38%) of the 56 whales were alive and 35 (62%) had died (Fig. 1).

Growth rates

For the available sample of both Atlantic and Pacific killer whales, growth had an approximately linear phase followed by a slowing period (Fig. 2). The increase in body length was linear for the first 9–12 years in both Atlantic and Pacific females and for the first 12–16 years in Pacific males. The Atlantic males in captivity are still growing. The animals' ages were estimated from the regression and the growth curves were re-plotted as length versus estimated age (Figs. 3 and 4). The oldest animal in this data set, a reproductively active Pacific male estimated to have been 28 years old in 1987, has remained the same length for over 12 years. Estimated ages of the captive killer whales at time of capture and at death or the end of this study are given in Table 2 and Figures 5A and 5B. Maximum length of the Pacific whales ranged from 580 to 640 cm for females and 650 to 750 cm for males. The Atlantic whales whose growth has peaked are smaller than any of the Pacific whales (500–540 cm).

Annual growth rates were calculated for 16 whales (Table 2), as the slope of the linear portion of the growth curve. Mean annual growth rate for six Pacific whales was 38 cm/yr (range 26–52 cm/yr) and did not appear to differ consistently by sex or collection site. Mean annual growth rates among 11 Atlantic whales ranged from 17 to 48 cm/year. Heterogeneity

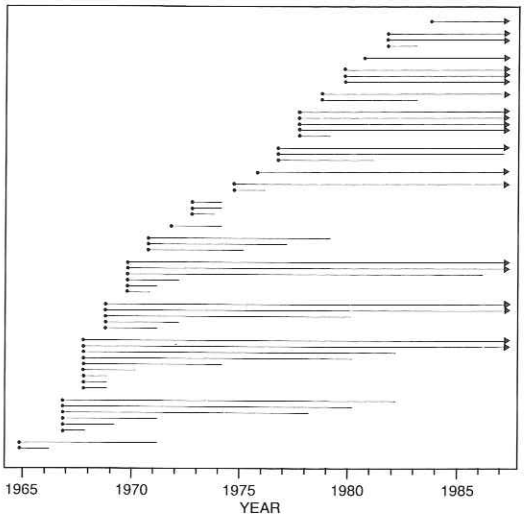

Fig. 1. Status of killer whales in U.S. and Canadian aquaria and marine zoological parks from June 1965 to 31 October 1987 showing capture year (●) and status of the individual at the end of the census on 31 October 1987 (⟶ indicates the whale was still alive).

analysis supported the separation of the Atlantic whales into two groups, based on different mean growth rates ($p < 0.001$): one of 21 cm per year (range : 17–25 cm/yr) and the other of 39 cm per year (range : 31–48 cm/yr), as in the Pacific group. Some of the slower growing female Atlantic whales have left the linear growth phase and are apparently near maximum length (Fig. 4). There was some indication of differences in growth rates by collection date among the Atlantic whales (Table 2: 1982, No. 53 and 54, vs. 1980, No. 50 and 51).

Reproduction

From 1977 to 1986, six calves were born to one breeding pair of Pacific killer whales that had been together since 1969. The calves were born on 28 February 1977 (live birth; 231 cm), 31 October 1978 (live birth; 236 cm), 1 April 1980 (stillbirth; 189 cm), 18 June 1982 (live birth; 241 cm), 22 July 1985 (live birth; 231 cm) and 6 July 1986 (stillbirth; 108 cm). Birth intervals were 20, 18, 26, 37 and 12 months, respectively (B. Andrews pers. comm.). None of these calves survived longer than 42 days. In addition calves were born to three Atlantic female killer whales, on 26 September 1985 (live birth; 206 cm), 5 January 1986 (live birth; 213 cm) and 31 January 1986 (stillbirth; 238 cm). A Pacific killer whale collected in 1970 sired all three calves (Cornell and Leatherwood 1986; Sea World unpublished data). The calf born in September 1985 was alive and well on 31 October 1987.

Primiparity for a breeding pair of Pacific whales (arrows, Fig. 3) occurred when the female was estimated to be 11 years old and

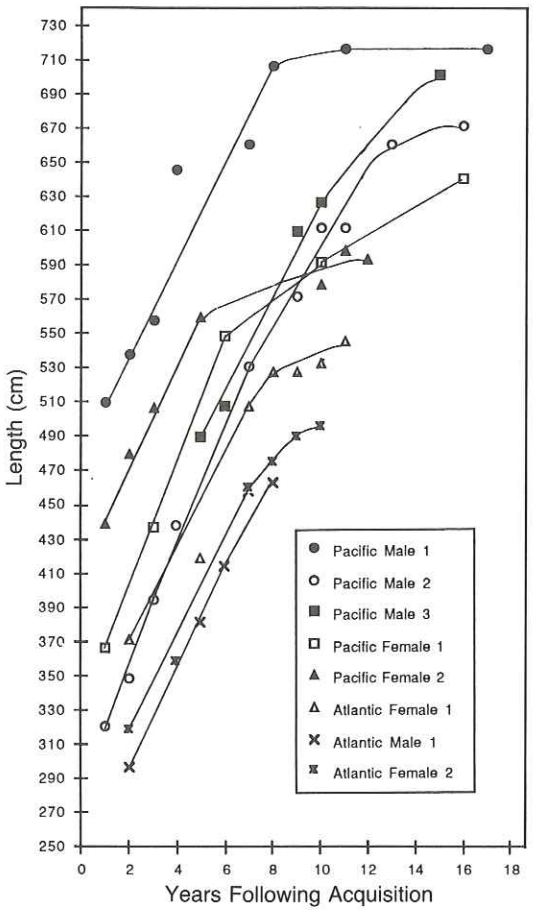

Fig. 2. Growth curves (standard length over time) for Pacific (n = 5) and Atlantic (n = 3) captive killer whales plotted from date of acquisition to date of last available measurement.

TABLE 2

Estimated ages for killer whales in U.S. and Canadian aquaria and marine zoological parks. Ages estimated from growth curves are given at the time of collection and date of death or final date (= whale still alive, 31 October 1987). For individuals with less than three length measurements, age was estimated (e) by matching lengths with growth curves in Figures 3 and 4. Annual growth rate is given for individuals with three or more length measurements during the linear growth phase.*

Individual number	Sex	Length: Start (cm)	Age: Start (years)	End (years)	Growth rate (cm per year)
PACIFIC: 1965–1975					
1	Male	655	11+e	12	
2	Female	410	4e	10	
3	Female	439	7	20	26
4	Male	290	1e	12	
5	Male	406	4e	19	
6	Female	312	2e	6	
7	Female	249	1e	1	
8	Male	419	5e	7	
9	Female	556	10+e	10	
10	Male	399	4	16	52
11	Female	401	4e	6	
12*	Male	510	9	28*	36
13	Female	579	11+e	11	
14*	Male	304	2	21*	38
15	Female	610	11+e	11	
16	Male	365	4e	18	34
17	Male	396	4e	10	
18*	Female	366	3	21*	43
19	Female	318	2e	4	
20	Male	411	4e	7	
21	Male	366	3e	14	
22*	Female	430	5e	24*	
23	Female	351	3e	5	
24	Female	579	11+e	11	
25*	Female	430	5e	22*	
26	Male	406	4e	20	
27*	Female	430	5e	22*	
28	Male	320	2e	3	
29	Male	396	4e	12	
30	Female	323	2e	6	
31	Female	434	5e	11	
32	Male	290	1e	3	
33	Female	579	11+e	12	
34	Female	540	9e	9	
35	Male	594	11+e	12	
36	Female	381	4e	5	
37*	Male	427	5e	17*	
ATLANTIC: 1976–1987					
38*	Female	300	2e	13*	
39	Male	335	4e	8	23
40	Female	351	4	14	25
41*	Female	370	6e	16*	
42*	Male	280	1	10*	31
43	Female	295	2e	3	
44*	Female	312	3	12*	25
45*	Female	292	2	11*	30
46*	Female	350	5e	14*	20
47*	Female	300	2e	10*	
48	Male	300	2e	6	
49*	Female	320	4e	11*	
50*	Male	394	8e	15*	19
51*	Female	404	9e	16*	17
52*	Female	300	2e	8*	
53*	Male	290	1	7*	48
54*	Female	380	3	8*	44
55	Female	310	2e	3	
56*	Male	351	3	6*	

the male 18 years old. Assuming a gestation period of approximately 17 months (based on serum and urine progesterone studies: B. Andrews pers. comm.; Walker 1986; Sea World unpublished data) pregnancy occurred when the female was nine years of age and the male was 16 years, shortly after he entered the slowing portion of his growth curve. Estimated ages of primiparity for the Atlantic females were 12, 13 and 15 years, respectively.

Mortality and survival

Annual mortality rate was 8.9% for all captive killer whales in this sample, 9.1% for females and 8.6% for males. Annual survivorship (and calculated 95% confidence intervals) was: 0.91 (0.88–0.94) overall, 0.91 (0.87–0.95) for females and 0.91 (0.87–0.96) for males. Calculations based on animal days and whale years produced identical results.

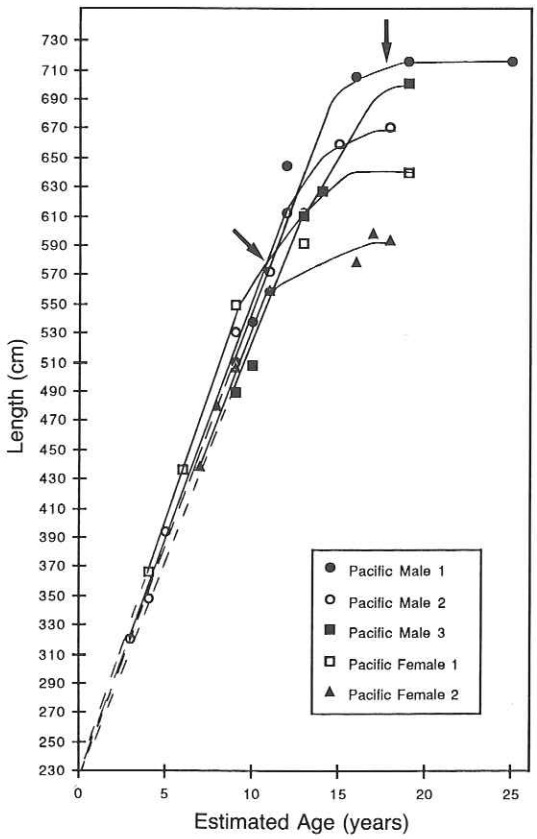

Fig. 3. Growth curves (standard length at estimated age) for five captive Pacific killer whales. Ages of primiparity for members of one breeding pair are indicated by arrows.

DISCUSSION

Growth curves for killer whales in captivity in U.S. and Canadian aquaria and marine zoological parks demonstrated that: 1) there is a relatively linear growth phase followed by a decrease in growth rate (coinciding with sexual maturity in one breeding pair); 2) individuals differ in growth rate, and females and males differ in the age at which their growth slows; 3) in Atlantic killer whales from Iceland, there are two distinct groups, one slow-growing and one fast-growing group; and 4) there is no secondary acceleration in growth rate following the onset of sexual maturity based on length.

Reproductive data from captive animals support previous estimates that age at sexual maturity, at least for North Pacific killer whales, is about 16 years for males (Perrin and Reilly 1984, based on Christensen 1982) and about 10 years in females (Jonsgård and Lyshoel 1970; Perrin and Reilly 1984, based on Christensen 1982). In captivity, a male Pacific killer whale estimated to be 16 years old impregnated a female Pacific killer whale estimated to be 9 years old. The two whales had been maintained together for 6 years. When the female first became pregnant, the male had just entered the slowing portion of his growth curve, suggesting that sexual

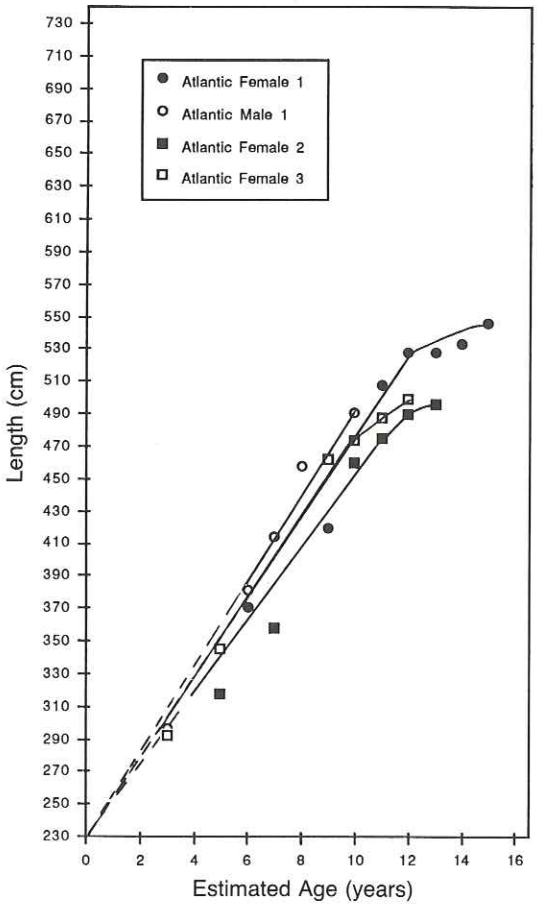

Fig. 4. Growth curves (standard length at estimated age) for four captive Atlantic killer whales.

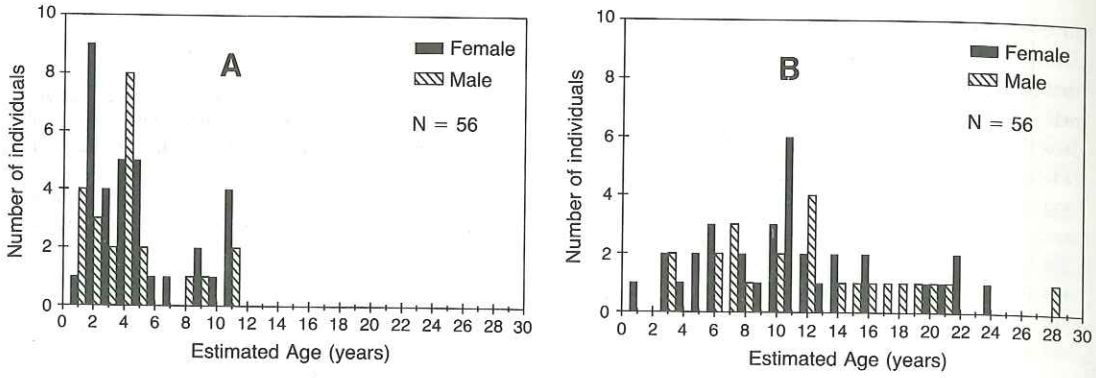

Fig. 5. Estimated ages of killer whales at collection (A) and final status (B), i.e. death or end of study, 31 October 1987.

maturity may be attained when growth rate slows. The female's growth began slowing two to three years before the male's. Hui (1979) showed that in the common dolphin, *Delphinus delphis,* body length, *per se,* is a poor indicator of sexual maturity. In killer whales, change in length growth rate rather than absolute length may be a good indicator of sexual maturity.

Christensen (1984) suggested that male Norwegian killer whales have a secondary acceleration of growth when they reach 550–610 cm in length (13–17 GLG's); no such acceleration was seen in the growth curves of the captive whales in this study. An alternate explanation to Christensen's interpretation of the Norwegian data is that the variation in length of whales between 13 and 17 GLG's reflects the presence of whales of different growth rate classes, with different maximum lengths. Substantial differences in length among killer whales have been reported, perhaps representing differences between populations or stocks. For example, maximum reported lengths of 900+ cm for males and 770+ cm for females (Jonsgård and Lyshoel 1970; Mikhalev *et al.* 1981). Maximum lengths for captive Pacific whales and those in Christensen's (1984) sample from the coast of Norway are smaller (males 750+ cm, females 640+ cm).

Previous estimates of mortality rates vary from 1–9.06% for free-ranging killer whales (Ohsumi 1979; Dahlheim 1981; Balcomb *et al.* 1982; Bigg 1982) and from 2.1–7.0% for captive killer whales (Asper and Cornell 1977; Hui and Ridgway 1978; DeMaster and Drevenak 1988). Demaster and Drevenak discuss problems with some of these methods.

Bigg and Wolman (1975) reported that the maximum time a killer whale had spent in captivity was 7 years; that figure can now be updated to 19.5 years, through 31 October 1987. We hesitate to examine closely certain measures of survivorship and longevity of captive killer whales because either critical assumption are violated or the analysis is not meaningful with the present sample. Specifically, we did not calculate the number of years these animals can be expected to live in captivity because the figure is too sensitive to relatively small differences in the annual survival rate, and mean time spent in captivity can be misleading because some animals from the first cohorts are still alive (DeMaster and Drevenak 1988). Furthermore, calculations of longevity of killer whales in captivity are not accurate because we cannot accurately represent age-specific survival, particularly later in life.

Pertinent to this last point, we note what is already known about the maximum age in killer whales. Maximum age in killer whales has been reported to be 35 years ("Old Tom", a reputedly long-lived killer whale in Australia, aged from sectioned teeth at approxi-

mately 35 GLG's: Mitchell and Baker 1980); 25 GLG's (Jonsgård and Øynes 1952 as quoted by Mitchell 1975); 48 years for males and a questionable 143 years for females (based on estimates of longevity from an "unrealistically low" mean annual mortality rate – Bigg 1982); and at least 35 years (based on tooth aging data from Norwegian catches – Christensen 1984). Theoretical maximum longevity for killer whales based on an earlier survey of captive killer whales was estimated to be 47.8 years (Hui and Ridgway 1978). In the frequency distribution of GLG's from wild Norwegian killer whales, there was an abrupt drop beyond 26 GLG's (to a maximum of 34 GLG's) (Christensen 1984). As the captive population continues to mature, the estimates of maximum ages of captive and free-ranging killer whales might be expected to converge.

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