MARINE MAMMAL SCIENCE, 4(4):297–311 (October 1988)

SURVIVORSHIP PATTERNS IN THREE SPECIES OF CAPTIVE CETACEANS

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ABSTRACT

Survival rates for three species of captive cetaceans are reported, based on records of dates of capture, birth, and death of individual animals. The annual survival rate was 0.93 for bottlenose dolphins and killer whales and 0.94 for white whales. Confidence limits of these estimates are discussed. Differences in survival rates between institutions were significant for bottlenose dolphins only. Calf survival for bottlenose dolphins was lower than non-calf survival. Survivorship of male killer whales was significantly less than survivorship of female killer whales; sex-specific survival rates were similar for the other two species. Estimates of average or maximum longevity alone were not useful in comparing rates of survival. Because survival in the first year of captivity may be lower than subsequent years, estimates of the expected lifespan, based on data from the first few years of captivity, may be biased.

Key words: survival, captivity, cetaceans, *Tursiops, Orcinus, Delphinapterus.*

Many species of marine mammals, especially cetaceans and pinnipeds, are maintained in captivity for purposes of public display and scientific research. In 1983 over 1,300 marine mammals, including more than 300 bottlenose dolphins (*Tursiops truncatus*), were held in oceanaria and zoological parks around the world (Duffield and Dimeo-Ediger 1984). The U.S. Marine Mammal Protection Act of 1972 (MMPA) and similar legislation in other countries recognize that marine mammals are resources of great aesthetic and recreational, as well as economic, significance. Over the last 15 yr, some individuals and groups have questioned the ethics of capturing and maintaining marine mammals in captivity for purposes of either public display or scientific research, particularly dolphins and larger cetaceans (*see* the Proceedings from the "Whales Alive" Conference, 1983; Journal of Mammalogy 65:740–741). One reason for this is the concern

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that the apparent longevity of captive animals is substantially less than that of their counterparts in the wild. Another reason is differences in the ability of different institutions to care for and maintain marine mammals, particularly cetaceans, in captivity.

The primary objectives of this study were to: (1) estimate the post-capture survival rates for three species of cetaceans (bottlenose dolphins; white whales, *Delphinapterus leucas*; and killer whales, *Orcinus orca*) commonly held in captivity for purposes of scientific research and public display, and (2) determine whether survival rates vary significantly by institution, age, or sex. Secondary objectives were to determine, if possible, whether survival in captivity differs significantly from survival in the wild, and to provide estimates of the expected longevity of each of the three species in captivity.

Methods

The data used in this analysis were obtained from the inventory of captive marine mammals maintained by the National Marine Fisheries Service (referred to as the Marine Mammal Inventory Report). These data are provided to the Service as part of the requirements for obtaining a permit to capture and maintain marine mammals for public display. The Marine Mammal Inventory Report, therefore, does not include all marine mammals held in captivity, but does represent a significant portion of marine mammals held in captivity in the U. S. and elsewhere. The following information for 864 bottlenose dolphins, 40 killer whales, and 48 white whales was transcribed into a data base: institution, animal identification number, number of days survived in captivity, whether or not the animal was alive at the end of the reporting period, sex, age (calf or non-calf), and date of acquisition. For a few animals the date of acquisition was not provided in the inventory; these animals were not included in the analysis. Finally, stillbirths were not included in the analysis. The number of days survived in captivity was calculated using a technique presented by Poole *et al.* (1981) and was based on the date of acquisition and either the date of the Inventory Report, the date of death, or the date the animal was transferred to a different institution.

The method for estimating rates of survival was taken from Trent and Rongstad (1974). This technique is similar to the estimator used by Mayfield (1975), except that information on an animal's survival is available on a daily basis. With this approach, animal-days are based on the number of days that an individual could have successfully survived. Obviously, once an animal has died, additional animal-days for that individual can not be accumulated. Recent work by Bart and Robson (1982) and Heisey and Fuller (1985) suggest that because the sampling interval is fixed at one day, the simple estimator suggested by Trent and Rongstad is a maximum likelihood estimate.

The following methodology was used to calculate annual survival rates:

$$\mathrm{DSR} = 1 - \sum_{i=1}^{K} (y_i) \Big/ \sum_{i=1}^{K} (x_i) \qquad (1)$$

where DSR is the daily survival rate, Y_i is one if the ith individual died during the reporting period and zero if the ith individual survived through the entire reporting period, x_i is the total number of days, including any days in which deaths may have occurred, in the reporting period for the ith individual, and K is the number of animals in the sample. The summation of y over all animals is the total number of deaths that occurred; the summation of x over all animals is the total number of animal-days observed. The daily survival rate was converted to an annual survival rate (ASR) by raising the DSR to the 365.25th power (*i.e.*, the average number of days in a year).

There are two assumptions that must be met in using this method (Trent and Rongstad 1974): (1) the death of one individual does not affect the probability of another individual surviving (*i.e.*, animal-days are independent sample periods), and (2) there is a constant probability of surviving each day. If these two assumptions are met and because each animal-day can have only one of two outcomes, survival or death, each individual animal-day is a binomial event. Therefore, the probability an animal survives x days is simply the daily survival rate raised to the power of x and the distribution of deaths over that period will be distributed binomially.

Both assumptions seem reasonable. With regard to the first, dates of death appear to be independent for animals at any institution for any of the three species. That is, there were no apparent concentrations of mortalities by date for any institution. With regard to the second assumption, it is conceivable that husbandry practices have improved significantly over the last 20 yr and are continuing to improve. Klinowska and Brown (unpublished manuscript prepared for the Department of the Environment, United Kingdom 1986) reported that husbandry practices in the United Kingdom, as indicated by an analysis of mortality rates for some cetacean species, have improved, at least since 1980. However, in the analysis of these data we found no difference between the mean survival rate for killer whales and white whales between 1975–1979 and 1980–1984. For bottlenose dolphins, however, where the sample size was considerably larger than for the other two species, the survival of animals in captivity between 1975 and 1979 was significantly less than the survival of animals between 1980 and 1984. However, because most of the available data are from animals held in captivity since 1980, there was no difference between the pooled survival rate for all years and the survival rate based on data from animals held in captivity between 1980 and 1984.

Another source of bias in estimating the average survival of animals held in captivity would occur if survival were not constant with age. It was not possible to test for age effects on survival of captive killer whales and white whales because of a lack of either known-age or captive born animals. For bottlenose dolphins, it was possible to compare the survival rates of young of the year and one year old animals. The survival of one year old bottlenose dolphins was not significantly different from the survival rate of non-calves (*see* Results). Because of the small number of known-age animals that were older than 10 yr of age, it was not possible to test for differences in the survival rate of animals as they approach the age of maximum longevity.

A 95% confidence interval for the DSR was calculated directly from a binomial distribution, where the binomial parameter was set equal to (1-DSR) and *n* was set equal to the total number of animal-days. The upper and lower limits (probabilities of 0.025 and 0.975, respectively) for the number of deaths were interpolated to the nearest 0.01 animal. These limits, after being divided by *n* and subtracted from 1.0, were raised to the 365.25 power to determine the confidence interval for the ASR.

For example, if six mortalities were observed over 10,000 animal-days, the DSR would be 0.9994 (1 − 0.0006) and the ASR would be 0.80 (0.9994 raised to the 365.25 power). Using the standard formula for the frequency distribution of a binomial distribution (Freund 1971), one can calculate that the probability of having one or zero deaths in a given year is 0.02; the probability of having two or fewer deaths in a given year is 0.06. Therefore, the lower limit (*i.e.*, $P = 0.025$) for the number of deaths was estimated to be 1.17 by linear interpolation. Likewise, the upper limit to the number of deaths was estimated to equal 10.77. The 95% confidence interval for the ASR is then calculated as:

$$\text{upper limit} = (1 - 1.17/10{,}000)^{365.25} = 0.96$$

$$\text{lower limit} = (1 - 10.77/10{,}000)^{365.25} = 0.67$$

For most of the calculations, the lower and upper limits for the expected number of deaths was calculated directly from the binomial distribution, given a certain number of deaths and animal-days. However because of machine limitations in handling large factorials, we used a normal approximation to estimate the upper limit for the number of deaths when the observed number of deaths was greater than five. In this approximation, we assumed that the mean number of deaths equals the observed number of deaths and that the standard deviation of the number of deaths for a particular institution equals the square root of the mean number of deaths. The upper limit for the mean number of deaths was estimated as the product of 1.96 and the standard deviation of the number of deaths plus the mean number of deaths. Differences between survival rates were tested using the variance test for homogeneity of the binomial distribution (Snedecor and Cochran 1967). A 95% confidence interval around the median survival rate was calculated in the usual fashion (Snedecor and Cochran 1967).

Results

Bottlenose Dolphins

The mean annual survival rate of 864 bottlenose dolphins was 0.93; the 95% confidence interval was 0.92–0.94 (Table 1). The median rate of survival for the 57 institutions listed in Table 1 was 0.94. The 95% confidence interval around the median was slightly greater than the 95% confidence interval around the mean. The distribution of survival rates by institution was skewed towards higher values with a modal value of 1.00.

Significant differences were found among survival rates for the 57 institutions listed in Table 1 ($P < 0.005$). Because the statistical test employed is based on the expected number of mortalities per animal-day per institution and because institutions with less than 20,000 animal-days would have fewer than five expected mortalities, we reanalyzed the data using data from only those institutions where the expected number of mortalities was greater than four. Again we found significant differences in the survival rate among institutions ($P < 0.025$). To identify those institutions that had a significantly different survival rate from the overall mean survival rate, we compared the survival rate of each institution with the pooled survival rate of all other institutions. Six institutions were found to have survival rates that were significantly below the average rate of survival for all 57 institutions; two institutions had survival rates that were significantly better than the average survival rate of all institutions (Table 1).

The minimum ASR for the 57 institutions listed in Table 1 was 0.01. The institution responsible for this extremely low survival rate (Table 1: #34) had accumulated only 168 dolphin-days. The minimum ASR for institutions that had at least 3,650 dolphin-days experience (*i.e.,* ten dolphin-years) was 0.75 (Table 1: #47). The median ASR for the 43 institutions with over 3,650 dolphin-days of experience was 0.94 (± 0.02). There was no difference between the survival rate of male and female bottlenose dolphins (Table 2).

The survival rate of calves that were born in captivity was found to be significantly less than the survival rate of non-calves (Table 2). The annual survival rate of newborn animals was 0.61. The ASR of these animals increased to 0.97 after the first year (Table 3). This was not significantly different than the ASR of animals removed from the wild and maintained in captivity, but suggests that captive born animals that survive their first year may be better adapted to captive maintenance than animals removed from the wild. Obviously, more information is needed before a definitive statement can be made. The survival rate of non-calves that survived the first year of captivity was 0.95; this is not significantly different from the overall mean rate of survival (Table 3).

To test whether the differences between the survival rate of dolphins at a particular institution and the overall mean rate of survival was influenced by the age distribution of animals, we reanalyzed the data excluding information from animals less than one year old. All of the institution-specific survival rates that were reported in Table 1 to be significantly less than the mean rate of survival were still significantly less than the overall mean. With information excluded from animals less than one year old, only one institution had an average survival rate that was greater than the mean survival rate for all institutions.

Recently captured animals are infrequently acclimated to captivity at the institution that will permanently maintain them. Acclimation is generally assumed to occur between 30 and 90 d. To test whether the differences reported in Table 1 were related to institutional differences in the acclimation process, we compared the survival rate of non-calves that were known to have survived the first 90 d of captivity with the overall mean survival rate of non-calves. Four of the six institutions that had lower survival rates than the average were still found to have significantly lower survival rates than the average. Only one institution had an average survival rate that was greater than the average survival

Table 1. Summary of survival data for captive bottlenose dolphins. Data are from the National Marine Fisheries Service's Marine Mammal Inventory Reports. Data are through 10-11-85.

#	# Animals	Live dolphin days	Deaths	Total	Average survival + (95% CI)
1	1	341	0	341	1.00 (–)
2	7	4,177	0	4,177	1.00 (–)
3	16	6,001	2	6,003	0.89 (0.75–1.00)
4	17	43,817	6	43,823	0.95 (0.91–0.99)
5	1	657	0	657	1.00 (–)
6	67	130,984	30	131,014	0.92 (0.89–0.95)
7	9	31,809	4	31,813	0.96 (0.91–1.00)
8	8	7,930	2	7,932	0.91 (0.79–1.00)
9	2	2,137	2	2,139	*0.71 (0.44–1.00)
10	4	17,525	1	17,526	0.98 (0.94–1.00)
11	10	18,341	4	18,345	0.92 (0.85–0.98)
12	5	17,173	3	17,176	0.94 (0.88–1.00)
13	3	1,645	0	1,645	1.00 (–)
14	5	15,211	3	15,214	0.93 (0.87–1.00)
15	3	5,376	1	5,377	0.93 (0.82–1.00)
16	5	11,780	1	11,781	0.97 (0.91–1.00)
17	5	11,508	4	11,512	0.88 (0.78–1.00)
18	33	55,928	20	55,948	*0.88 (0.83–0.93)
19	2	10,850	0	10,850	1.00 (–)
20	10	18,222	6	18,228	0.89 (0.81–0.98)
21	8	10,000	3	10,003	0.90 (0.79–1.00)
22	12	32,162	6	32,168	0.93 (0.88–0.99)
23	23	75,597	9	75,606	0.96 (0.93–0.99)
24	4	8,386	0	8,386	1.00 (–)
25	7	22,735	2	22,737	0.97 (0.92–1.00)
26	11	10,959	0	10,959	1.00 (–)
27	7	13,887	3	13,890	0.92 (0.85–1.00)
28	17	58,642	4	58,646	*0.98 (0.75–1.00)
29	8	15,204	0	15,204	1.00 (–)
30	2	6,118	0	6,118	1.00 (–)
31	6	11,527	1	11,528	0.97 (0.91–1.00)
32	3	3,428	0	3,428	1.00 (–)
33	2	2,470	1	2,471	0.86 (0.64–1.00)
34	2	166	2	168	*0.01 (0.00–1.00)
35	11	8,119	4	8,123	0.84 (0.70–1.00)
36	10	18,476	3	18,479	0.94 (0.87–1.00)
37	6	1,341	0	1,341	1.00 (–)
38	4	1,979	1	1,980	0.83 (0.57–1.00)
39	155	214,765	72	214,837	*0.88 (0.86–0.91)
40	16	17,025	2	17,027	0.96 (0.90–1.00)
41	2	590	1	591	*0.54 (0.06–1.00)
42	33	30,033	9	30,042	0.90 (0.83–0.96)
43	4	2,116	1	2,117	0.84 (0.60–1.00)
44	2	8,293	0	8,293	1.00 (–)
45	6	1,965	1	1,966	0.83 (0.58–1.00)
46	3	466	0	466	1.00 (–)
47	5	3,753	3	3,756	*0.75 (0.54–1.00)
48	43	118,025	25	118,050	0.93 (0.90–0.95)

Table 1. Continued.

#	# Animals	Live dolphin days	Deaths	Total	Average survival + (95% CI)
49	4	2,380	0	2,380	1.00 (–)
50	16	23,493	8	23,501	0.88 (0.80–0.97)
51	32	112,070	15	112,085	0.95 (0.93–0.98)
52	10	14,172	1	14,173	0.97 (0.93–1.00)
53	121	235,891	31	235,922	*0.95 (0.94–0.97)
54	17	33,101	7	33,108	0.93 (0.87–0.98)
55	22	46,783	10	46,793	0.92 (0.88–0.97)
56	7	30,332	2	30,334	0.98 (0.94–1.00)
57	10	10,721	3	10,724	0.90 (0.80–1.00)
Totals	864	1,618,582	319	1,618,901	0.93 (0.92–0.94)

* An asterisk denotes that the institution-specific survival rate is significantly different from the survival rate pooled over all institutions.

rate of all institutions. The annual survival rate of non-calves, based on data from the first 90 d of captivity, was 0.53; significantly different from the industry-average of 0.93. Therefore, while this factor is generally not adequate in discriminating among institutions with poor, average, or good rates of survival, it does explain some of the differences between institution-specific rates of survival.

The institutional differences in the survival rate of dolphins reported in Table 1 does not seem to be related to the age composition (although only calf and non-calf survival were compared) or sex composition of the captive population. Also, it is only partially related to mortalities that occurred during the acclimation period. It is clear that institutions that rear a large number of calves, everything else being equal, will have an overall mortality rate that is greater than institutions that do not breed their animals in captivity. This effect may be partially offset by the slightly increased survival of non-calves that were born in captivity relative to captive animals that were not born in captivity.

It is also clear that the power of the test statistic is related to the total number of dolphin-days in the sample. Because of this, we recommend that investigators that apply this test statistic to a particular data set also provide the power of a particular test when the test results are insignificant. In our analysis, we would have been able to detect a significant difference between the survival rates of an

Table 2. Summary of average survival rate for bottlenose dolphins by sex and age (calf vs. non-calf). Data are from NMFS Marine Mammal Inventory Report, 1985.

	Days alive	Deaths	Average survival
Sex: Male	657,197	120	0.94
Female	934,993	170	0.94
Age: Calf	23,586	32	0.61
Non-calf	1,495,340	276	0.93

Table 3. Summary of bottlenose dolphin survivorship, conditional on animal surviving the first year.

Treatment	Days alive	Deaths	Average survivorship
All animals	1,599,285	214	0.95
Non-calves	1,479,554	204	0.95
Born in captivity	119,731	10	0.97

institution and the pooled survival rate from all of the institutions reported in Table 1 if there would have been a difference of seven percentage points and a sample size of at least 20,000 dolphin-days from the institution that was being tested.

Killer Whales and White Whales

The annual survival rate of 40 captive killer whales was 0.93 (Table 4); the 95% confidence interval was 0.90–0.96. The range of ASRs for the 10 institutions listed in Table 4 was 0.73 to 1.00. There were no significant differences in the ASR among the different institutions. Given the sample size reported in Table 4, institutional specific survival rates would have to be less than 0.86 with a sample size of 10,000 animal-days to be significantly different from the overall mean. With a sample size of 1,000 animal-days, the observed survival rate would have to be less than 0.69 to be significantly different from the overall mean.

The annual survival rate of 48 white whales was 0.94 ± 0.03 (Table 5). The range of ASRs for 9 institutions was 0.80 to 1.00. There were no significant differences in survival rates among the institutions. The power of this test was

Table 4. Summary of survival data for captive killer whales. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

#	Number animals	Live dolphin days	Deaths	Total	Average survival	95% conf. int.
1	1	656	0	656	1.00	(–)
2	5	15,110	2	15,112	0.95	(0.89–1.00)
3	4	6,907	1	6,908	0.95	(0.85–1.00)
4	2	3,344	1	3,345	0.90	(0.72–1.00)
5	18	39,943	9	39,952	0.92	(0.87–0.97)
6	3	2,859	1	2,860	0.88	(0.68–1.00)
7	2	3,437	1	3,438	0.90	(0.73–1.00)
8	2	20,264	1	10,265	0.97	(0.90–1.00)
9	1	2,486	0	2,486	1.00	(–)
10	2	2,276	2	2,278	0.73	(0.45–1.00)
Totals	40	87,282	18	87,300	0.93	(0.90–0.96)

Table 5. Summary of survival data for captive white whales. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

#	Number animals	Live dolphin days	Deaths	Total	Average survival	95% conf. int.
1	8	6,665	4	6,669	0.80	(0.65–1.00)
2	10	23,781	4	23,785	0.94	(0.88–1.00)
3	2	6,047	0	6,047	1.00	(–)
4	3	15,148	1	15,149	0.98	(0.93–1.00)
5	2	224	0	224	1.00	(–)
6	3	1,481	0	1,481	1.00	(–)
7	11	21,443	5	21,448	0.92	(0.86–0.98)
8	3	9,118	1	9,119	0.96	(0.89–1.00)
9	6	13,384	2	13,386	0.95	(0.87–1.00)
Totals	48	97,291	17	97,308	0.94	(0.91–0.97)

similar to the power of the test statistic for killer whales. There was insufficient information to test the influence of age on survival for either of these two species. However, there was sufficient information to test for differences in survival between sexes. For killer whales there was a significant effect ($P < 0.025$) with female survival being significantly greater than male survival; for white whales the effect was not significant (Table 6).

Longevity of Bottlenose Dolphins, Killer Whales, and White Whales

For bottlenose dolphins, killer whales and white whales, the average number of days survived in captivity was 1,873.4 d (5.13 yr), 2,182.0 d (5.97 yr), and 2,026.9 d (5.54 yr), respectively. However, these statistics are of no real use in evaluating the husbandry record of the public display industry unless the entire cohort of animals that are used in estimating this statistic is dead. When this is not the case, this method of calculating longevity is very sensitive to the proportion of animals that have been recently acquired. In this study most of the animals included in the marine mammal inventory were not dead. Because

Table 6. Summary of average survival rate of killer whales and white whales by sex. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

	Days alive	Deaths	Average survival
Killer whales			
Male	34,863	12	0.88
Female	52,366	6	0.96
White whales			
Male	42,482	6	0.95
Female	54,809	11	0.93

some animals have survived in captivity for over 30 yr, it is not possible to do a meaningful analysis of the data at this time with this statistic because of the limited number of animals that could be used in the analysis.

The expected number of years that an animal will survive, given that survival is constant from year to year, is estimated as follows (Seber 1973):

$$E \text{ (years to live)} = -1/\ln(\text{ASR})$$

In addition, this relationship is based on the assumption that survival is constant over all ages. Based on the average ASR for all animals of all three species reported in this study and assuming that this rate was constant, the expected number of years that an animal would survive in captivity is 14 yr. Based on the average survival rate for each species (Tables 1, 4, 5), estimates of species-specific life expectancies are 14 yr for bottlenose dolphins, 13 yr for killer whales, and 16 yr for white whales. For bottlenose dolphins, a non-calf that had been born in captivity would be expected to live an additional 33 yr. A free-ranging bottlenose dolphin having survived its first year in captivity would be expected to live an additional 19 yr. These estimates of life expectancy are all based on survival rates that are statistically indistinguishable. Because relatively small differences in the ASRs can result in large differences in estimates of life expectancy and because it is commonly accepted that at some point survival does start declining with age, we think that the ASR and not average longevity should be used in comparing the survival rate of free-ranging and captive dolphins or in comparing the survival rate of dolphins held at different institutions.

Discussion

Unfortunately most of the published reports of dolphin mortality in captivity are not comparable to one another. Estimates of the average number of days or years survived (often referred to as longevity) are of little use in comparing husbandry practices, unless all of the animals in the analysis are dead or unless "longevity" is standardized against the maximum number of days that could have been survived. As an example, Greenwood and Taylor (1985) reported that the mean survival time of 9 killer whales that died in captivity was 2.21 yr, while the mean survival time of 15 animals still alive in captivity was 5.37 yr. The ASR based on the mean survival of the 9 dead animals is 0.64. The ASR based on the 15 animals still alive is 1.00, while the ASR for the entire sample of animals is 0.91. We encourage researchers to discontinue publishing the mean survival time of animals that have died in captivity, unless all of the animals acquired at a certain time have died and can be included in the analysis.

Furthermore, published estimates of dolphin mortality in captivity are often unweighted averages of annual survivorship, where sample sizes usually decrease over time (*see* Best and Ross 1984). This tends to weight the early years disproportionately. Because mortality in the first year of life or captivity may be higher than subsequent years (Bigg and Wolman 1975, Greenwood and Taylor 1985, results of this study), such an approach will produce negatively biased estimates of survival. For example, if a hypothetical sample of 12 animals were

Table 7. Hypothetical data set for comparing estimates of survival for captive dolphins.

Animal #	Date acquired	Date of death	Animal-days survived	Deaths
1	1-1-85	1-1-85	0	1
2	1-1-85	7-1-85	180	1
3	1-1-85	2-1-86	395	1
4	1-1-85	8-1-86	576	1
5	1-1-85	3-1-87	788	1
6	1-1-85	9-1-87	972	1
7	1-1-85	4-1-88	1,185	1
8	1-1-85	10-1-88	1,368	1
9	1-1-85	5-1-89	1,580	1
10	1-1-85	11-1-89	1,764	1
11	1-1-85	6-1-90	1,976	1
12	1-1-85	12-1-90	2,159	1
Totals			12,943	12
Annual Survival rate = 0.71				
Number of animal-years = 42				
Number of animal-years survived = 30				
Annual Survival rate = 0.71				

all captured on 1 January 1985 and survived as shown in Table 7, the actual survivorship based on the procedure recommended in this paper or an analysis of animal-years survived/total animal-years is 0.71. However, if the 6 yr of annual survival are averaged, the resulting estimate is only 0.41. In general, estimates of captive survival should be weighted by either animal-days or animal-years.

Also, estimates of survival from date of capture to the present are somewhat misleading (*see* Walker 1975) because they also incorporate survival data over years, during which survival rates may have changed. For example, Walker (1975) reported that 50% of bottlenose dolphins captured between 1966 and 1972 survived the initial two year period. The annual survival estimate for these data is 0.71 (data are from Walker 1975, table 4); the survival rate given an animal survived the first year is 0.79. We recommend that estimates of captive survival be based on annual estimates of survival and that factors such as acclimation period be considered in comparing husbandry practices.

Finally, various researchers have estimated survival in captivity based on what Bigg (1982) referred to as animal-years (*see* Hui and Ridgway 1978, Best and Ross 1984). As demonstrated in Table 7, estimates of survival based on animal-years and animal-days should be identical. However, it is necessary in using animal-years to prorate partial years, where an animal may have died mid-year or where the reporting period ended. We recommend authors specify how this proration was accomplished to facilitate the comparison of survival rates between studies.

Ohsumi (1979) reported that existing data were not suitable to estimate the natural rate of mortality for bottlenose dolphins and killer whales. He further reported that the annual mortality rate of free-ranging white whales was 0.06. However, this latter figure is actually the percent calves in the population 8 mo after the peak of calving (*see* Sergeant 1973, p. 1089), and is not a valid estimate of annual mortality. Sergeant (1973) suggested a mortality rate of 0.10 for newborn calves between months 1 and 6. Based on a regression analysis, Ohsumi predicted that the annual mortality rate of bottlenose dolphins, killer whales and white whales would be 0.13, 0.09 and 0.12, respectively. In this analysis of survival in captivity, mortality rates for these same three species were 0.07, 0.07 and 0.06, which indicates that survival in captivity may be better than or equal to survival in the wild. The only published report of mortality rates in the wild for any of these three species is for killer whales off Vancouver Island, British Columbia, Canada (Bigg 1982), where 11 deaths occurred over 637 animal-years for an annual rate of mortality of 0.02; the 95% confidence interval is 0.01–0.03 (calculated by DPD based on data from Bigg 1982). This rate includes data from juveniles (27% of animal-years), adult males (28%), and adult females (45%). These data indicate that, at least for killer whales, survival in captivity may be less than survival off Vancouver Island, British Columbia.

Until additional studies are completed, it will not be possible to compare the survivability of free-ranging animals for these three species with captive animals. One reviewer noted that the average age of captured animals is generally less than the average age of free-ranging animals. Therefore, in comparing survival of captive and free-ranging animals, the effect of age composition on average survival may be important.

Indirect comparison of the survival rate of captive animals to free-ranging animals is possible by computing the mortality rate needed to give a stable population, given estimates of reproductive rates. Reilly and Barlow (1986) cite an example for free-ranging bottlenose dolphins with a 12-yr age of attainment of sexual maturity and a 2 to 4 yr calving interval. Given these reproductive rates and assuming the population is stable, adult survival rates must be between 0.92 and 0.95 (Reilly and Barlow 1986, fig. 4). This range of survival rates is consistent with the rates estimated for captive animals.

Sergeant (1973) and Jones (1982) reported that the maximum reported longevity for bottlenose dolphins in captivity is 25 yr. The maximum reported longevity in the Marine Mammal Inventory was 28 yr. As previously mentioned, we do not feel this statistic is particularly informative for the purposes of comparing husbandry practices.

Best and Ross (1984) reported that bottlenose dolphins caught in South African waters and maintained in captivity survived at an average rate of 0.87, given they survived the first year. These data cover the years 1961 through 1982. They further noted that first year survival was low (0.58). The 0.87 survival rate does not include 9 animal-years for a single animal that survived 19 yr in captivity. If these data are included, the (unweighted) annual survival rate is 0.92, while the survival rate, weighted by animal-years, is 0.86. We feel the weighted estimate of survival is a better representation of the data.

Table 8. Recalculated previously published survival rates for killer whales.

	Years survived	Total years	Survival rate
Bigg and Wolman (1975)	118	139	0.85
Hui and Ridgway (1978)	134.47	151.47	0.89

Reynolds (1987) reported that the average survival rate of bottlenose dolphins maintained in captivity in the southeastern U.S. was 0.86 ± 0.04. He further noted that survival was independent of facility, but was affected by the area in which animals were originally captured. The survival rates reported in Best and Ross (1984) and Reynolds (1987), are significantly less than the rate of survival reported in this study. In addition, Klinowska and Brown (unpublished manuscript prepared for the Department of Environment, U.K. 1986) reported survival rates for captive bottlenose dolphins in the U.K. that were also significantly lower than those reported here. However, the range of survival rates for individual institutions is similar for all the above reports. The reason(s) for the observed difference in average survival is (are) not clear at this time.

For killer whales, reported rates of captive survival vary from 0.50 for adults and 0.89 for immatures (data are from Bigg and Wolman 1975) to 0.95 for adults and immatures combined (Hui and Ridgway 1978). Data from the former study are through April 1974 and for the latter study through May 1976. Hui and Ridgway (1978) did not account for the entire animal-year in those years in which deaths occurred and may have assumed that animals survived all of 1976, even though data are provided only through May. Given the data provided by Hui and Ridgway (1978) in their table 1, survival estimates were recalculated based on the methods presented in this paper. In addition, data on the survival of adults and immatures from Bigg and Wolman (1975) were pooled because of the relatively small number of adults in their sample. The results of this reanalysis are presented in Table 8.

These rates are not significantly different, although they are slightly lower than the average rate reported in this study. If the one stillborn animal included in the data reported by Hui and Ridgway is excluded from the analysis, the resulting survival rate is 0.91, which is not significantly different from our results. Furthermore, Hui and Ridgway (1978) reported that adult male survival was greater than the survival rate of adult females. The opposite was reported in this study. Klinowska and Brown (unpublished manuscript prepared for the Department of the Environment, U.K. 1986) reported an average annual survival rate of 0.89 for captive killer whales in the U.K. This rate of survival was not significantly different from our results.

At this time it is not possible to compare the survivability of animals in captivity with that of animals in the wild. It is clear that differences between institutions exist. Additional data from free-ranging animals are needed to determine if captive animals have similar life expectancies. From our review of the literature, we strongly recommend that data concerning captive survival of cetaceans be reported such that it includes the acquisition date, date of death, reporting date for animals still alive, the age-class of an animal, and its sex. In addition, because estimates of longevity are extremely sensitive to small differences in survival, we recommend that this parameter not be used in comparing the survival rates of captive or free-ranging cetaceans. Also, the data reported here indicate that the survival rate of the three species of captive cetaceans referred to in this study is generally between 0.90 and 0.95. Rates of survival above this range are indicative of superior husbandry practices; survival rates below this range indicate that there may be room for improvement. Additional information is needed on how the area of capture influences rates of survival. Finally, in comparing survivability, age composition must be considered. Additional work is needed to investigate the importance of how mortality patterns change with age.

Acknowledgments

Funding for this research was provided by the Marine Mammal Commission. We are grateful to the Office of Protected Species and Habitat, National Marine Fisheries Service, for providing us with the Marine Mammal Inventory Reports for these three species. The original manuscript and a series of drafts were greatly improved by comments from Jay P. Barlow, Robert L. Brownell, Jr., Robert J. Hofman and Aleta Hohn. In addition, comments by the Journal's reviewers improved the paper considerably. Finally, Tracy Richter and Mark Wimer's help in programming and database editing was appreciated.

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Received: July 13, 1987
Accepted: June 8, 1988