Marine Mammal Science

How long do dolphins live? Survival rates and life expectancies for bottlenose dolphins in zoological facilities *vs.* wild populations

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ABSTRACT

Survival rates and life expectancies are commonly agreed upon indicators of well-being for animals in zoological facilities, but even the most recent survival statistics for bottlenose dolphins (*Tursiops truncatus*) in marine mammal parks and aquariums use data that are now more than 25 yr old. The current study provides a comprehensive assessment of life expectancy and survival rates for bottlenose dolphins in U.S. zoological facilities from 1974 to 2012, utilizing three different analyses (annual survival rate, age-at-death, and Kaplan-Meier), examining historical trends, and comparing to comparable data from wild populations. Both survival rate and life expectancy for dolphins in zoological facilities increased significantly over the past few decades, with a modern ASR of 0.972, and mean and median life expectancies calculated *via* Kaplan-Meier of 28.2 and 29.2 yr, respectively. Survival rates and life expectancies for dolphins in U.S. zoological facilities today are at least as high as those for the wild dolphin populations for which there are comparable data.

Key words: bottlenose dolphins, cetaceans, annual survival rate, life expectancy, Kaplan-Meier.

Increasingly, the issue of how long bottlenose dolphins live in marine mammal parks and aquariums compared to how long they live in the wild has become an important part of the debate as to whether these animals should be kept in zoological care. To be sure, survival rates and life expectancies are commonly agreed upon indicators of overall health and well-being, both for human populations and for animals in zoological facilities (*e.g.*, Broom 1991, Walker *et al.* 2012, World Health Organization 2016, Central Intelligence Agency 2018). To properly inform this debate, then, it is crucial that these statistics are assessed accurately.

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Unfortunately, comparing survival rates and life expectancies for dolphins in the wild to those in zoological care is difficult, for several reasons. First, neither "the wild" nor "zoological care" are single populations. Rather, there are a number of distinct populations of wild dolphins worldwide, with different health challenges and subsequent life expectancies. Similarly, marine mammal facilities worldwide may operate under different animal welfare laws and regulations, and employ varying husbandry practices that might also affect life expectancies. Second, the mathematical calculations used in different methods of assessing survival rates and life expectancy have different underlying assumptions—for example, whether the probability of dying must be constant at all ages—and may give different results. Valid comparisons between populations are thus difficult when the relevant studies do not use comparable methods. Third, survival rates and life expectancies of dolphins in zoological facilities have improved over time (DeMaster and Drevenak 1988, Small and DeMaster 1995). While this is obviously positive for the dolphins, it complicates the task at hand because the most prevalent method that has been used for calculating survival rates for marine mammals under zoological care (DeMaster and Drevenak 1988, Small and DeMaster 1995) assumes that the survival rate of the population is constant over the time period being investigated. Moreover, although the data from decades ago may be of some historical interest, if these data are not representative of the current population, then they are of little use for assessing the survival rate and life expectancy of dolphins in zoological facilities today.

DeMaster and Drevenak (1988) introduced the method of calculating annual survival rate (ASR) for marine mammals in zoological care, using a method developed by Trent and Rongstad (1974). They found that bottlenose dolphins in the United States had an overall ASR of 0.93, and that the survival rate from 1980 to 1984 was higher than from 1975 to 1979. Performing a similar analysis several years later, Small and DeMaster (1995) found that this increase in survival rate had continued, with dolphins' ASR for 1988–1992 calculated at 0.95, which was significantly higher than pre-1988 rates.

Today, even the most recent data in the survival rate studies for the U.S. population are more than 25 yr old. Given that these studies found survival rate increases even within the span of several years, it is reasonable to suspect that further increases may have occurred in the years since. These increases could be driven by several factors, including: (1) demographic changes in the population, which has moved from one in which all of the animals were collected from the wild to one in which, since 1989, animals are added to the population almost exclusively from births in facilities, with the occasional addition of a stranded dolphin that the U.S. government has deemed unreleasable due to its young age or permanent disability (Marine Mammal Inventory Report [MMIR]); (2) improvements in training and husbandry practices (Brando 2010, Ramirez 2012); and (3) increased knowledge of dolphin biology and subsequent improvement in medical care (Dierauf and Gulland 2001).

Methods of Assessing Survival Rate and Life Expectancy

Annual survival rate (ASR)—The primary method for assessing survival rate and life expectancy of dolphins in zoological facilities has been to calculate annual survival rate (ASR) (*e.g.*, DeMaster and Drevenak 1988, Small and DeMaster 1995). This method has also been used to assess survival in the wild (Wells and Scott 1990). For a particular population over a given time period, ASR is calculated based on two numbers: the observed number of deaths (d) and the total number of animal-days lived (n). "Animal-days" is defined as the total number of days each animal in the population was alive during the targeted period. For each animal, this begins either on the first day of the time period or on the day the animal first appeared in the population, and ends either on the day of the animal's death, the day it leaves the studied population, or on the last day of the time period. Using these two numbers, the daily survival rate (DSR) is first calculated as $DSR = 1 - \frac{d}{n}$. This daily rate is then converted into the annual rate by raising the DSR to the 365.25th power (*i.e.*, the average number of days in a year): $ASR = DSR^{365.25}$.

As a measure of life expectancy, the ASR has a number of convenient features: it incorporates data from both living animals as well as those that died within the time period of the study; it does not require knowledge of the ages of the animals; and it is relatively easily calculated. However, calculation of ASR in this manner is only valid when the following two assumptions in the data set are met (Trent and Rongstad 1974, DeMaster and Drevenak 1988, Tsai *et al.* 1999): (1) The death of one animal must not affect the probability of death of another animal, that is, deaths are independent events. (2) The probability of survival is a constant for all animals at all times in the calculation. That is, there are no age-related changes in mortality, and no historical changes in mortality, for animals during the period under study.

Once calculated, ASR can be directly and easily converted into both average (mean) and median life expectancies. There are no additional assumptions required. If an animal has a constant x% probability of living from one year to the next, that means it has an ($x*x$)% probability of living for the next 2 yr, an ($x*x*x$)% probability of living for the next 3 yr, and so on. For example, with an ASR of 0.90, an animal has a 90% chance of living 1 yr (by definition), an 81% chance (0.90*0.90) of living 2 yr, and a 72.9% chance (0.90*0.90*0.90) of living 3 yr. The median life expectancy occurs when that probability reaches 0.50, which can be directly calculated as ln(0.50)/ln(ASR). Similarly, the average life expectancy can be directly calculated as $-1/\ln(ASR)$ (Seber 1973).

Even though the conversion between ASR and the more intuitive concept of life expectancy is direct, the relationship between these parameters is highly nonlinear. Thus, even small differences in estimated ASR values can lead to large differences in estimated life expectancies. Because of this perceived asymmetry, and because the conversion relies on the assumption of a constant survival rate for all ages, DeMaster and Drevenak (1988) recommended that researchers use ASR rather than life expectancy for comparing survival across different groups. However, it is important to note that in that original study, DeMaster and Drevenak compared ASR between individual facilities, which necessarily meant

utilizing much smaller sample sizes, leading to much larger variability and large estimation errors. For example, approximately 44% of the facilities in that study either had an ASR of 1.0 (which would convert to an immortal life expectancy) or an ASR with a 95% CI at least as wide as 0.75–1.0 (which would convert to a median life expectancy between 2.4 yr and immortal). For data sets with that level of variability, the recommendation against converting to life expectancy seems prudent. However, by examining a data set such as the MMIR for bottlenose dolphins as a whole, rather than individual facilities, the sample sizes are greatly increased, leading to far less error in estimates. In addition, the assumption of a constant survival rate for all ages is not specific to the conversion between ASR and life expectancy, but is an assumption already necessary for calculating ASR in the first place. Therefore, since ASR-to-life expectancy is a direct conversion, there is no reason to avoid this conversion when relevant for comparison and interpretation.

Analysis of age at death data—An approach used to calculate demographic parameters such as average life spans in wild populations is to create life tables using age-at-death information gathered from stranded dolphin carcasses. In this method, the age of stranded dolphins is estimated by counting the number of growth layer groups (GLGs) in stained cross-sections of extracted teeth (Hohn 1980, Hohn and Fernandez 1999). Each layer represents one year of growth (Hohn *et al.* 1989). A table is constructed using the number of stranded dolphins at each age as input, then calculating the annual probabilities of death, and combining this information to give the percent of animals that live from birth to each subsequent age. From this, one can theoretically estimate the overall mortality rate and life expectancy of the population.

One advantage of the life table method is that it does not require the assumption of equal probability of survival at different ages. However, one must exercise caution when comparing life expectancies based on age-at-death information with life expectancies derived from ASR, because one is based only on dead animals while the other incorporates information from both dead and still-living animals. For this comparison to be valid, the deceased animals must be representative of the population as a whole, which may not be the case if, for example, the population is increasing or decreasing in number, or the survival rate has been increasing or decreasing over historical time.

Kaplan-Meier survival analysis—Finally, a number of studies have used the Kaplan-Meier survival analysis to assess life expectancy in a variety of animal species (*e.g.*, Ostermann *et al.* 2001, White *et al.* 2005, Nuss and Warneke 2010, Jett and Ventre 2015, Mendyk 2015, Robeck *et al.* 2015). This analysis is similar to a life table, with the notable exception that the time intervals analyzed are much smaller (*i.e.*, a day rather than a year). It also incorporates data from still-living animals as right-truncated data, which adjusts the risk calculation for each interval (Cleves *et al.* 2010).

Unlike ASR analyses, the Kaplan-Meier does not require any assumptions about the shape of the mortality rate function over the lifespan (Kaplan and Meier 1958), and thus can accommodate increasing or decreasing mortality rates, or even more complicated cases in which

there are multiple life stages with differing mortality rates. Like the other analyses discussed, however, it does assume that mortality rate is constant over historical time.

The goal of this article is to provide a rigorous assessment of survival rate and life expectancy of bottlenose dolphins in zoological care, considered within the context of survival rate and life expectancy in wild dolphin populations. To do this, we (1) calculate updated ASRs for bottlenose dolphins in U.S. zoological facilities, examining historical trends; (2) compare current survival and life expectancy data for this population with comparable data for wild populations for which these have been calculated, using both ASR and age-at-death analyses; (3) analyze the strengths and weaknesses of each methodology for use with bottlenose dolphins in zoological care; and (4) analyze life expectancy data for dolphins in zoological care with the Kaplan-Meier survival analysis, which better conforms to the real-world characteristics of bottlenose dolphin survival.

STUDY 1: ASR

Materials and Methods

Study population—The data set most often used to calculate how long dolphins live in zoological facilities is the Marine Mammal Inventory Report (MMIR), maintained by the U.S. National Marine Fisheries Service (NMFS). This report was established as a part of the U.S. Marine Mammal Protection Act of 1972, which requires all U.S. facilities that maintain marine mammals to report, for each animal in its care: name or other identification, sex, estimated or actual date of birth, date and source from which the animal was acquired, date and facility or person to whom the animal was transferred (if applicable), and the date and cause of death when determined. From 1973 through 1994, facilities were required to make this report on a yearly basis. In 1994 the MMPA was amended such that starting in 1995, facilities were required to report all MMIR events (*i.e.*, births, transfers, and deaths) within 30 d of their occurrence.

An independent comparison of MMIR birth data with records obtained directly from facilities that house marine mammals concluded that the MMIR is "an excellent source of highly accurate, unbiased and complete data" (Temte 1993). When differences between the two data sources did appear, they were almost invariably either: (1) births that had occurred after the facility's last annual report to the MMIR, or (2) animals that had died very young (including miscarriages and stillbirths), which presumably had therefore not been alive on the day of reporting.

At the time of its inception in 1973, data were submitted for the MMIR on paper forms, then collated by the staff at NMFS and entered into a computer database. In 1996 a new database software program, the Permit Program Information Management System (PPIMS), was adopted. Under this system, data were stored in four underlying files that listed: (1) the names and codes of species; (2) the names and codes of facilities; (3) the complete inventory of the animals; and (4) all animal events (*i.e.*, information on births, captures, strandings, transfers, releases, and

deaths). When information from the MMIR was requested, it was usually exported in a PDF report that combined information from all four files regarding animal origin, current or last facility, and disposition (*i.e.*, death or release) for each animal, but excluded information on transfers. However, one could also request and receive the four underlying files. The use of this software was discontinued in 2013, and the software that replaced it does not export data.[2] Instead, information from the MMIR[3] can now only be obtained in the PDF format.

Unfortunately, condensing all animal events into a single line in the PDF format obscures transfers into or out of the U.S. population and introduces other inconsistencies. For example, the custody date listed in the PDF format sometimes reflects initial custody in the U.S. population, other times reflects initial custody in a foreign facility (with a later unnoted transfer into the U.S. population), and yet other times reflects a later transfer date to another facility either within or out of the U.S. population. Because MMIR reporting is mandatory only for U.S. permit holders, this distinction between U.S. and non-U. S. facilities is critical for accurate data. For example, once an animal is transferred to a foreign holder/facility, that holder/facility might or might not report a subsequent death. In the absence of that subsequent report, that animal will be considered alive in the data set in perpetuity. In the current study, therefore, we utilized the data from the original underlying PPIMS data files to include only animals in the U.S. population, and only during the time they were in the U.S. population. Thus, our analyses include MMIR data between 1 January 1974 and 27 September 2012. The beginning date was chosen because the MMPA became effective at the end of December 1972. Therefore, since facilities were required to report once per year, we can assume that facilities made their first mandatory report by the end of December 1973. The end date was chosen because the PPIMS files were only available until early 2013, and 27 September 2012 was the date that the files we received from NMFS were last updated.[4]

From the list of bottlenose dolphins that were in the MMIR database during that time period, we excluded all animals listed as foreign or of unknown origins, and those that had never been owned by a U.S. holder or housed in a U.S. facility. We also excluded animals that were missing crucial information (*i.e.*, birthdates, original custody dates, and/or death dates for those animals who were listed as having died), or whose crucial information was contradictory (*i.e.*, animals that had a transfer date listed

after a recorded death date). This left 1,323 animals remaining in the data set.[5]

Analyses—We conducted ASR analyses separately for two age classes: calves in their first year and dolphins over one year of age. This was done for three reasons. First, as with many animals, the survival rate of dolphin calves under one year of age is typically different from the survival rate of older animals, both in zoological care and in the wild (*e.g.*, DeMaster and Drevenak 1988, Wells and Scott 1990, Small and DeMaster 1995, Mann *et al.* 2000). This is problematic for assessing survival rates because the ASR calculation assumes a constant probability of survival (*e.g.*, DeMaster and Drevenak 1988, Small and DeMaster 1995). Second, since MMIR information was only reported on a yearly basis prior to 1995, animals that were born and died in a single year would not necessarily have been reported unless they were alive on the reporting date (typically December 31). Thus, MMIR information on calves younger than 1 yr is inconsistent, and we wanted to minimize that inconsistency for the primary analyses. Third, the only study that has conducted a comparable ASR calculation for a wild population also analyzed adult data separately from that of calves <1 yr of age (Wells and Scott 1990). For purposes of comparison, it is crucial that the age classes represented for the populations in the wild and in zoological care are similar.

For both age classes, we calculated ASR separately for each of four approximately equal time periods, using the method discussed in the Introduction. Specifically, the number of deaths (*d*) was simply the number of animals who died during that period. For each dolphin, the number of days in that period was calculated beginning from the latest date among the first day of the time period, the animal's first custody date in the U.S. population, or the animal's first birthday (for older animals), and ending with the earliest date among the date of the animal's death, release, or transfer out of the U.S. population, their first birthday (for calves), or the last day of the time period. In other words, the calculated days for each dolphin included the number of days that dolphin was alive in that age class in the U.S. population during that time period. The days for each animal were then summed to get the total number of animal-days (*n*) in the period, and ASR was calculated as $ASR = \left(1 - \frac{d}{n}\right)^{365.25}$. We also calculated 95% confidence intervals (CIs) for each *ASR* by estimating the upper and lower limits for the number of deaths based on the binomial distribution, using the methods outlined in DeMaster and Drevenak (1988). Finally, we used the variance test for homogeneity of the binomial distribution (Snedecor and Cochran 1967) to test for differences between survival rates across time periods, and between modern-day dolphins in zoological facilities (*i.e.*, those in the

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[5]Our final data set in presented in Appendix S1. Because it is possible that excluding animals with missing information could theoretically introduce bias if, for example, poor data management at some facilities reflected a poor quality of care for the animals, we also ran a second set of analyses including animals with missing birthdays and those for which we could substitute captivity dates for missing custody dates. The pattern of results was identical in both cases. This additional data set and resulting analyses are presented in Appendix S2.

most recent time period) *vs.* those in the wild Sarasota population (using the data from table 2B of Wells and Scott 1990).

Results and Discussion

Historical analysis—Figure 1 shows the survival rate for dolphins in marine mammal facilities older than one year of age in each of the four time periods. As shown in the figure, ASR has significantly increased over historical time. Specifically, ASR in the first time period (1974–1982) was significantly lower than in all later time periods ($P < 0.001$), and *ASR* in the most recent time period (2003–2012) was significantly higher than in all earlier time periods ($P < 0.001$). This most recent ASR (0.972) corresponds to a median life expectancy of 24.0 yr (CI 20.3–29.7) and a mean life expectancy of 34.6 yr (CI 29.3–42.8).

As shown in Figure 2, the survival rate for calves has also significantly increased over historical time. Specifically, calf ASR was significantly higher in the two latest time periods (1993-2002, 2003-2012) than it was in the two earliest time periods (1974–1983, 1984–1992), $P < 0.001$. Because the deaths of young calves may have been underreported in the MMIR prior to 1995, calf ASR for the first two time periods is best considered a maximum estimate, and this increase in calf survival between the first two and last two time periods should therefore be considered a minimum estimated increase.

Zoological care vs. wild populations—To date, only one study has applied DeMaster and Drevenak's ASR calculations to wild dolphins. Wells and Scott (1990) calculated an ASR of 0.961 for dolphins over 1 yr of age in the well-studied population in Sarasota, Florida, which corresponds to a median life expectancy of 17.4 yr (CI 12.4–29.1) and a mean life expectancy
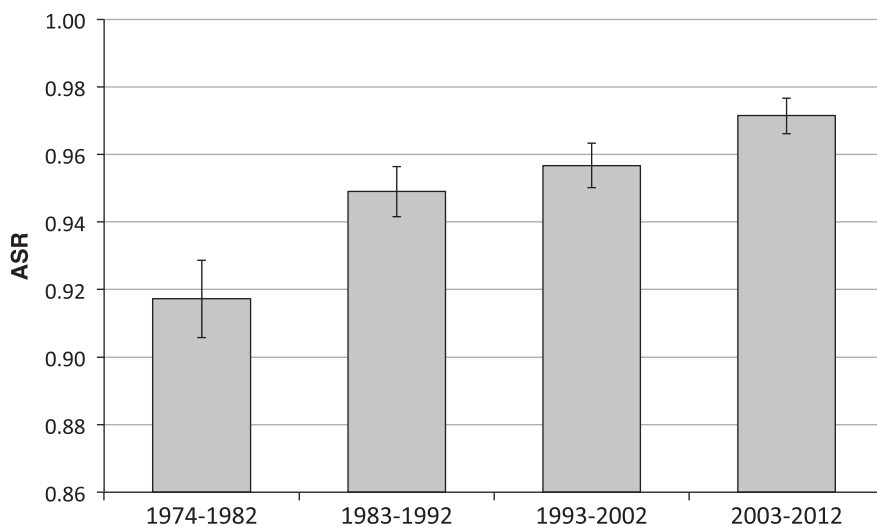

Figure 1. ASR (±95% confidence intervals) of bottlenose dolphins >1 yr old in zoological care across historical time periods.
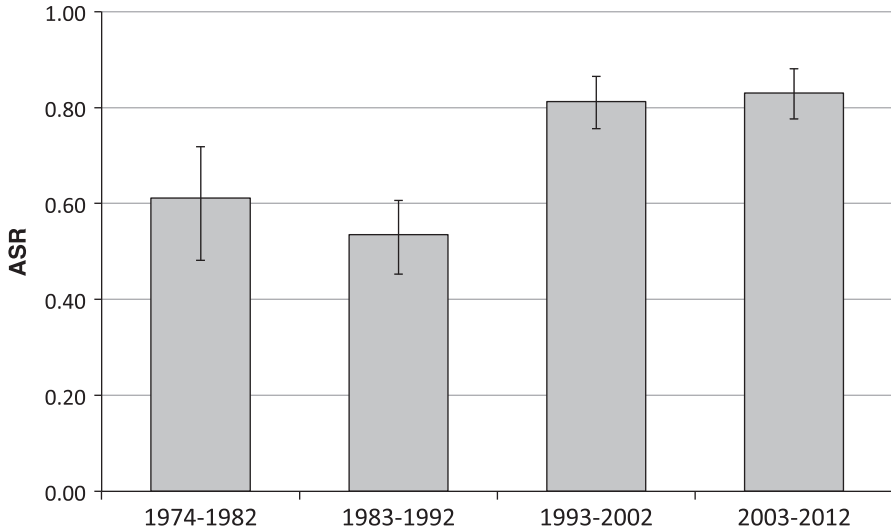
Figure 2. ASR (±95% confidence intervals) of bottlenose dolphin calves <1 yr old in zoological care across historical time periods.

of 25.1 yr (CI 17.8–42.0). Note that because this is a wild population, for those cases in which an animal was not resighted but no carcass was recovered, it is not possible to be certain whether the animal's disappearance was due to death or to permanent emigration out of the study area. However, since emigration from this population is very rare (Wells and Scott 1990), this ASR is likely close to the true survival rate in this population.

At the time the Wells and Scott (1990) study was published, the survival rate they calculated for dolphins older than 1 yr in Sarasota (0.961) was higher than the survival rate reported for dolphins in zoological care (0.93; DeMaster and Drevenak 1988). In contrast, the updated survival rates for modern-day dolphins in zoological care are higher than the survival rates for the Sarasota dolphins, both for dolphins older than one year (0.972 *vs.* 0.961) and for young calves (0.830 *vs.* 0.803), although significant differences were not found ($P > 0.19$ and $P > 0.69$, respectively). It may be worth noting that the number of deaths of very young calves was likely underestimated in the Sarasota population, because "on occasion calves may have been born and died before [Wells and Scott 1990] had a chance to record them" (Wells and Scott 1990, p. 411), whereas neonatal deaths and even stillbirths were included in the MMIR data. Thus, the comparison of calf ASR between these two populations should be considered conservative.

Analysis of assumptions—As noted in the introduction, ASR calculations assume a constant mortality rate for all animals in the calculation, which is violated by both historical and age-related changes in mortality. This problem can be minimized for historical changes by analyzing smaller time periods as we did here, but age-dependent mortality is still an issue. It is unclear to what extent this violation affects the results and therefore whether they may still provide a reasonable enough approximation for practical purposes.

In this study, we compared age-at-death of modern-day dolphins in zoological facilities with age-at-death from the two published studies that have analyzed this information for wild dolphin populations.

Materials and Methods

Study populations—Age at death of modern-day dolphins in zoological facilities was calculated from animals in the MMIR that died during the most recent time period defined in Study 1 (2003–2012). Age at death for the wild populations was taken from table 1 of Stolen and Barlow (2003) and from figure 5 of Mattson *et al.* (2006). These studies extracted teeth from stranded dolphin carcasses in the Indian River Lagoon System in Florida (Stolen and Barlow 2003) and in the Mississippi Sound Region of the north-central Gulf of Mexico (Mattson *et al.* 2006), and then calculated ages based on growth layer groups in stained cross-sections of those extracted teeth.

Analyses—We constructed life tables for each population using the traditional method as described in Krebs (1989). In this method, the number of deceased dolphins at each age is used to calculate age-specific mortality rates, which are then used to calculate the proportion of the population that is still alive at the start of each age interval. The median life expectancy can then be read or extrapolated directly from the table or graph of results as the point where this proportion crosses 0.50. We used the Wilcoxon-Gehan test to assess differences in survivorship between the zoological care population and each wild population. For consistency with Study 1, these analyses were first conducted on dolphins older than 1 yr of age, and then repeated including young calves.

Results and Discussion

Zoological care vs. wild populations—Figure 3 shows the survival curve for dolphins older than 1 yr in all three populations. Median life expectancies were 8.3 yr (CI 5.6–13.0) and 9.0 yr (CI 6.2–11.7) for the wild populations, and 21.0 yr (CI 15.1–25.5) for modern-day dolphins in zoological care. Survivorship for the dolphins in zoological care was significantly higher than for both wild populations (Wilcoxon-Gehan = 31.52 and 29.31 for comparisons with Stolen and Barlow and Mattson *et al.* populations, respectively; $P < 0.001$).

Because neonates are not excluded in studies of wild strandings, and because there is no assumption of an age-independent survival rate in life table analyses, one might argue that calves under 1 yr of age should be included in these calculations as well. Including those animals does not change the pattern of results. Although the median age of death decreases in all populations (now 5.0 yr (CI 3.9–7.5) and 6.4 yr (CI 5.1–9.4) for the wild populations, and 12.0 yr (CI 6.6–15.9) for modern-day dolphins in zoological care), the survivorship for dolphins in zoological care is still significantly higher than for both wild populations (Wilcoxon-Gehan = 8.92 and 7.68 for comparisons with Stolen and Barlow and Mattson *et al.* populations respectively, $P = 0.003$ and 0.006).
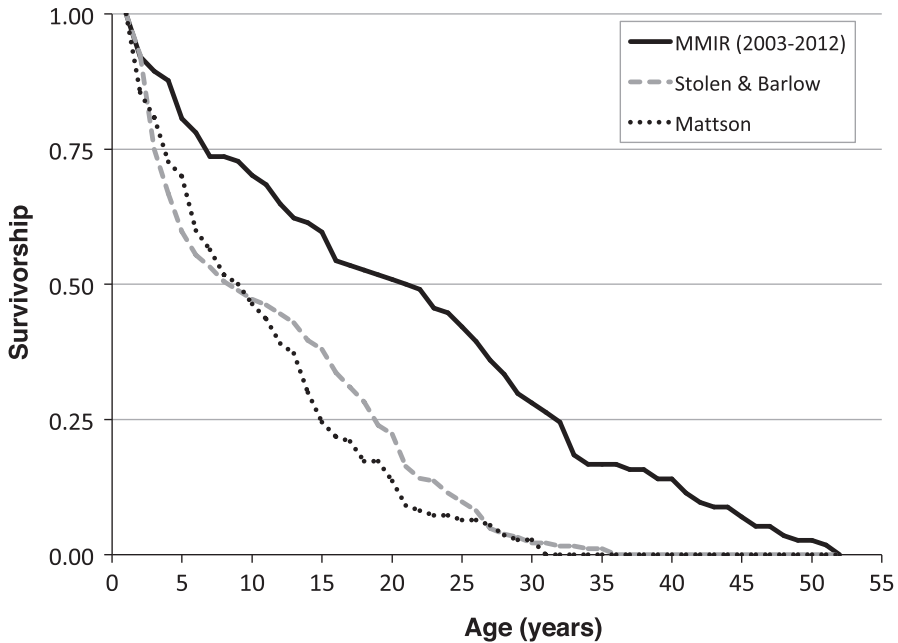
Figure 3. Survivorship to each age as calculated for age-at-death data for modern-day dolphins in zoological care and two wild populations.

Factors affecting survival rate of wild populations—As noted in the introduction, "the wild" does not consist of a single homogeneous population, but rather of multiple populations with different environmental challenges. In this respect, it is important to note that one of the two wild populations compared here (Stolen and Barlow 2003) has previously been characterized as immune compromised with a number of pervasive health challenges (*e.g.*, Bossart *et al*. 2003, Reif *et al*. 2008, Schaefer *et al*. 2011, Fair *et al*. 2017). As a result, this group likely has a lower survival rate than many other wild populations. Also notable is that dolphins from neighboring coastal populations travel into and out of that study area (Scott 1990, Durden *et al*. 2011) and may therefore account for some of the strandings. If these neighboring populations do not share the same health challenges, this could artificially increase the calculated life expectancy. Both of these factors should be taken into account in order to interpret and contextualize the data from that population. No such pervasive health challenges have been suggested for the other wild population (Mattson *et al*. 2006) during the time period discussed here (although several years after these data the Deepwater Horizon oil spill undoubtedly impacted the survival of wild dolphins in that area; Mullin *et al*. 2017).

Analysis of assumptions—The use of only dead animals to calculate life expectancy can lead to systematic biases. In the case of stranded animals, this method assumes that recovered animals are representative of all animals who have died. If younger animals are more or less likely to be recovered than older animals, this would introduce a systematic bias that would
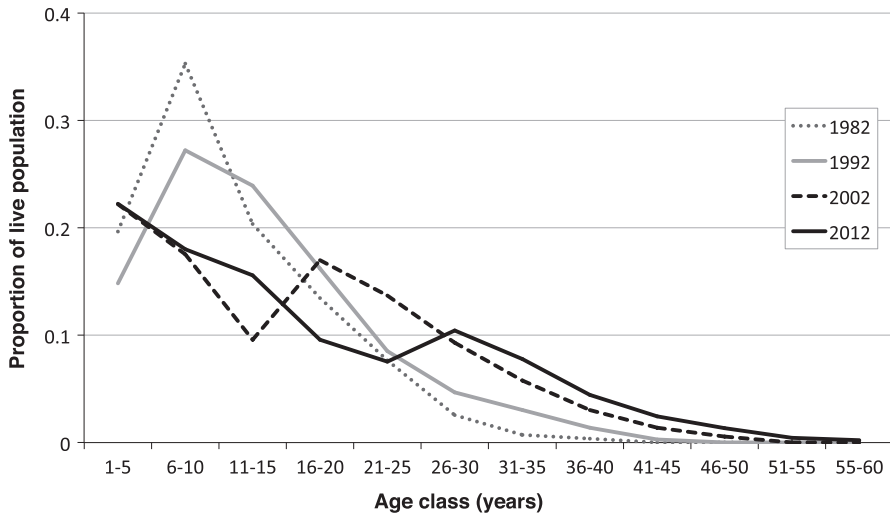
Figure 4. The population age structure for bottlenose dolphins in zoological care on the last day of each time period.

underestimate or overestimate life expectancy, respectively. This should not be an issue for the animals in the MMIR, with the exception of neonatal deaths prior to 1995 when reporting regulations changed, but these data were not part of the current analysis (2003–2102).

Bias can also be expected if there is an unstable age structure in the population, as might be the case with an increasing or decreasing birth rate. For example, if there are proportionally more younger dolphins than there would be in a stable population, then this necessarily means that there are more animals at risk of potentially dying in these younger age classes. Therefore, including only dead animals in the calculation will systematically underestimate the true life expectancy of that population (Stolen and Barlow 2003). As shown in Figure 4, this describes the situation for the dolphins in zoological care. This figure depicts the proportion of living dolphins falling into each 5 yr age class on the last day of each of the four time periods (*i.e.*, four snapshots of the age structure of the population). This shows that the original population captured from the wild several decades ago was comprised of primarily younger dolphins, and that the age structure has progressively flattened since then as enough time has elapsed for these dolphins to reach progressively older age classes. Because this age structure has not yet stabilized (see Fig. 4), the persisting (albeit shrinking) overabundance of young dolphins in the population means that the median life expectancy calculated in this study should be considered an underestimate of this population's current life expectancy.

STUDY 3: KAPLAN-MEIER

In the final study, we analyze life expectancy data for dolphins in zoological care with a survival analysis (Kaplan-Meier) that better conforms to the real-

world characteristics of bottlenose dolphin survival than the previous two methods did. As noted in the introduction, this analysis incorporates information from both dead and still-living animals, and does not require any assumptions about the shape of the mortality rate function over the lifespan (Kaplan and Meier 1958). It should therefore be expected to provide a more representative estimate of survival than the analyses utilized in the first two studies.

Materials and Methods

Study population—This study utilized the same MMIR population as in Study 1. For consistency with Study 1, and with past and future studies of wild populations, we again restricted our analyses to dolphins above 1 yr of age.

Analyses—For each of the time periods defined in Study 1, we performed separate Kaplan-Meier survival analyses using Stata/MP 15 statistical software, which has the ability to handle left truncated data (realized in the current study as individuals who entered the population analysis window at different ages). Note that Stata originally excluded the three animals in the earliest time period who died on the same day that they entered the U.S. population (*i.e.*, time = 0). To make sure these animals were included, we recoded their starting date as 0.5 d prior. We then used the Wilcoxon-Gehan test to assess differences in survivorship between time periods, and calculated 95% confidence intervals in both mean and median life expectancies.

Results and Discussion

Historical analysis—Figure 5 shows the Kaplan-Meier survival curves for dolphins in marine mammal facilities older than 1 yr of age during each time period, with corresponding mean and median life expectancies presented in Table 1. Wilcoxon-Gehan comparisons revealed significant differences in survivorship between time periods (χ^2 = 96.08, P < 0.0001). Specifically, survivorship in marine mammal facilities has significantly increased over historical time, with pairwise comparisons between consecutive time periods showing significant differences between the first (1974–1982) and second (1983–1992) time periods (χ^2 = 19.95, P < 0.0001), and also between the third (1993–2002) and fourth (2003–2012) time periods (χ^2 = 15.65, P = 0.0001).

Zoological care vs. wild populations—Unfortunately, no study has yet applied the Kaplan-Meier analysis to evaluate survival in any wild dolphin population.

Analysis of assumptions—As noted earlier, the Kaplan-Meier analysis does not require assumptions about mortality rates across ages. However, it does assume that mortality rates are constant across the time period of the analysis. While this issue cannot be entirely eliminated until the mortality rate and life expectancy for this population stops increasing, the effect of this issue can be minimized by analyzing smaller time periods as we did here.
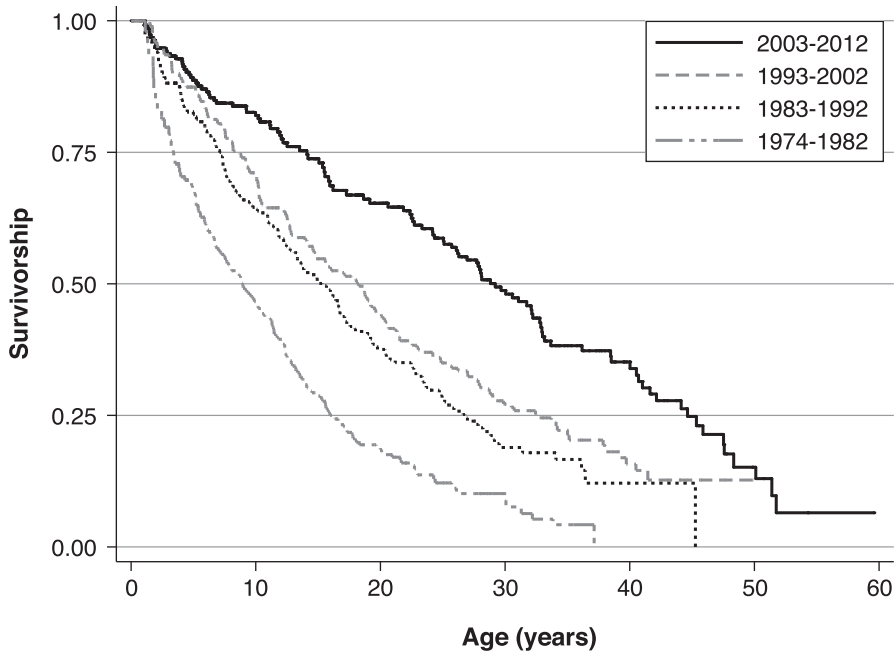
Figure 5. Kaplan-Meier survival curves depicting the proportion of bottlenose dolphins in zoological care surviving to each age (calculated in days, then transformed to years) during four time periods.

Table 1. Mean and median life expectancies (in years, with 95% confidence intervals) for bottlenose dolphins in zoological care as calculated by Kaplan-Meier analyses.

Time period	Median LE (CI)	Mean LE (CI)
1974–1982	9.0 (5.9–11.4)	10.6 (8.8–12.5)
1983–1992	15.3 (12.5–17.1)	17.3 (15.2–19.4)
1993–2002	18.2 (14.1–20.3)	20.3 (18.0–22.5)
2003–2012	29.2 (25.0–32.9)	28.2 (25.3–31.0)

GENERAL DISCUSSION

This study analyzed life expectancy and survival rates for bottlenose dolphins in U.S. zoological facilities, examining historical trends and comparing to wild populations. Two essential patterns emerged. First, since the last published studies examining this issue (DeMaster and Drevenak 1988, Small and DeMaster 1995), dolphin survival rates and associated life expectancies in zoological care have continued to increase. Second, survival rates and life expectancies of dolphins in U.S. zoological facilities today are at least as high as their counterparts in the wild for which we have comparable data.

Given the fact that each of the methods utilized in this study (ASR, age-at-death analyses, and Kaplan-Meier) resulted in different estimates of dolphin life expectancy, one obvious question is which method provides the most accurate estimate. As each has been used to assess survival and life expectancy in previous studies, an argument could be made for any of them. We would note, however, that the requirements of the Kaplan-Meier analysis conform best to the real-world characteristics of bottlenose dolphin populations. Unlike ASR, it does not require the incorrect assumption of equal probability of survival across all ages, and unlike age-at-death analyses, it does not exclude relevant data from living animals in the population. Therefore, we suggest that the Kaplan-Meier is likely the most accurate. Regardless of which analysis is used, however, it is crucial to stress that the different analyses are not statistically comparable. Because each has different underlying mathematical assumptions, and violations of different assumptions affect the calculations in different ways, calculated life expectancies of two populations should be considered directly comparable only when those life expectancies are calculated using the same analysis.

A second question concerns which specific descriptive number should be used to best characterize the typical lifespan of animals in a population (*e.g.*, to answer the question "How long do dolphins live?"). One possibility might be to cite the maximum known age to which any member of that population has survived. By definition, however, this number is an outlier; not typical. Two other commonly used measures are the average (*i.e.*, arithmetic mean) and the median, which is the age at which half of the animals are expected to die before and half are expected to die after. Mathematically speaking, for situations in which the data conform to a normal (*i.e.*, "bell-shaped") distribution, the arithmetic mean provides a good characterization of the data. However, dolphin survival data do not fit this pattern. For data that are not normally distributed, the median is generally considered a better representation. This is because whereas outliers have a large, disproportionate effect on the mean, the median is affected similarly by every individual in the population.

Regardless of which numerical description (maximum, mean, or median) is used, however, it is again crucial to note that these measures are not interchangeable. Although this may seem obvious, it is worth stressing because unfortunately, this faulty argument has been used repeatedly in discussions of cetaceans in zoological care, with claims that wild orcas/belugas/dolphins may live as long as x yr (*i.e.*, relevant to maximum), but their counterparts in zoological care routinely die before some much younger age (*i.e.*, relevant to median or mean) (*e.g.*, Marino 2018, Parsons and Rose 2018). This is a nonsensical comparison, akin to noting that people in Jamaica may live as long as 117 yr,[6] but people in the U.S. routinely die before the age of 79[7]

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[6]Gerontology Research Group. 2018. GRG World Supercentenarian Rankings List. Retrieved 1 September 2018 from http://supercentenarian-research-foundation.org/TableE.aspx.

[7]World Bank. 2018. Life expectancy at birth, total (years). Retrieved 1 September 2018 from https://data.worldbank.org/indicator/sp.dyn.le00.in.

(whereas in point of fact, the average life expectancy in Jamaica is lower than the average life expectancy in the U.S.[8]).

Ideally, a comprehensive comparison of survival rates and life expectancies between populations would include more than the three wild studies examined here (Wells and Scott 1990, Stolen and Barlow 2003, Mattson *et al.* 2006). Due to the nature of field studies, however, any comparisons of survival statistics between wild populations and those in zoological care will always be fraught with logistical hurdles. Dolphins in zoological facilities are observed consistently for their entire lives, providing researchers with accurate and complete data regarding births, deaths, and transfers into and out of the population. The same cannot be said of wild populations, where researchers typically follow the animals for much shorter time periods, *via* sporadic sightings, and must infer whether an animal who is no longer sighted has died, emigrated, or was only passing through in the first place. Because of the nature of these data, studies of wild dolphins in recent years have begun to calculate something called an "apparent survival rate," using complicated statistical models constructed on the basis of how often individual animals are resighted over independent sequential samples (*e.g.*, Corkrey *et al.* 2008, Speakman *et al.* 2010, Fruet *et al.* 2015). Such techniques have served as invaluable tools for tracking mortality trends in specific populations, providing insight into the effects of environmental challenges such as the Deepwater Horizon oil spill (*e.g.*, Mullin *et al.* 2017) and freshwater input from a hydroelectric power station tunnel (*e.g.*, Currey *et al.* 2009). However, there is wide variability in the specifics of how these techniques have been applied to studies of different populations with respect to factors such as definitions to determine which animals are calves to exclude, the mathematical models utilized, and ways of determining and weighting which model(s) with which set of assumptions to use, which has resulted in apparent survival rates in wild populations ranging from 0.86 per week (Brusa *et al.* 2016) (which, if equated to ASR, would convert to a life expectancy of less than a year) to 1.0 (Reisinger and Karczmarski 2010, Methion and López 2018) (which would equate to immortality). Due to this extensive variability, it is simply not possible at this time to use such studies for any sort of consistent comparison with animals in zoological care.

In conclusion, the current study shows that survival rates have increased significantly for bottlenose dolphins in U.S. zoological facilities. Median life expectancy has more than tripled over the last few decades (Table 1), and both mean and median life expectancy today are at least as high as in the wild populations for which we have comparable data. As a next step, we would encourage further research to examine the causes of this increase, and survival analyses like the Kaplan-Meier to be conducted on a variety of dolphin populations around the world, both in the wild and in zoological care. To be sure, this analysis requires more comprehensive data (*i.e.*, known ages), necessitating a much longer time commitment, than either ASR calculations or apparent survival rate models, and is therefore unrealistic for short term field studies. However, it might be

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[8]See note 7 above.

possible for long-running field studies such as the Sarasota Dolphin Research Program (*e.g.*, Wells 2014) or the Dolphin Alliance Project (*e.g.*, Connor and Krützen 2015). Ideally, this would eventually create a database of well-documented life expectancies for dolphin populations around the world, both in zoological facilities and the wild, that are assessed with the same metric to allow the most meaningful comparisons and better inform ongoing conservation and management issues.

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Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12601/suppinfo.

Appendix S1. Final data set, including dates of birth, U.S. custody, and disposition (death, transfer, or release) for bottlenose dolphins in the Marine Mammal Inventory report between 1 January 1974 and 27 September 2012. See main text for inclusion/exclusion criteria. Any pre-1974 custody dates were set to 1 January 1974. If a release or death date was recorded after an animal transferred out of the U.S., it is coded as "post nonUS."

Appendix S2. Additional data set listing dolphins older than 1 yr of age who were previously excluded due to (1) missing birthdates or (2) missing custody dates for which it was possible to substitute missing captivity dates (marked with *). Any pre-1974 custody dates were set to 1 January 1974. If a release or death date was recorded after an animal transferred out of the U.S., it is coded as "post nonUS."