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Intrinsic growth ($r_{\max}$) and generation time (T) estimates for the cetacean genera *Sousa*, *Orcaella*, and *Neophocaena*, in support of IUCN Red List assessments

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Analysis objective

A workshop was held May 20 – 21, 2015, in San Diego, California, USA, titled: "Workshop to Assess/Re-Assess IUCN Red Listings for Indo-Pacific Species of Coastal Marine Small Cetaceans." Species included were *Orcaella brevirostris*, *O. heinsohni*, *Neophocaena asiaeorientalis,* and two of the three Indo-Pacific *Sousa* species: *S. chinensis* and *S. plumbea*. *Sousa sahulensis* and *Neophocaena phocaenoides* were not assessed, largely for lack of information about these species. Red List assessments require estimates of generation time for a pristine population, i.e., one with stable age structure and abundance at carrying capacity such that the annual per-capita population growth rate is $\lambda = \exp(r) = 1$. Let this generation time be denoted T_0. Estimating T_0 for the above species is the primary goal of this analysis. Additionally, this analysis provides point estimates of the anthropogenic mortality rate required to reduce a population by 30%, 50%, or 80% over three generations ($3T_0$). These reductions warrant Vulnerable, Endangered, or Critically Endangered status, respectively, under the Red List criterion A; IUCN 2012).

Model framework for estimating $r_{\max}$ and associated generation time

Life history theory predicts the following allometric relationship:

$$r_{\max} * T_{\text{opt}} = a_{\text{rT}}, \qquad (1)$$

where $r_{\max}$ is the intrinsic growth rate, T_{opt} is the associated generation time ("opt" implies "optimal" environmental conditions that allow for the population to grow at a rate of $r_{\max}$), and a_{rT} is an allometric constant, also referred to as a demographic invariant (e.g., Niel and Lebreton 2005). The mean value (across species) for a_{rT} has been empirically estimated to be ≈ 1 for several vertebrate taxa, including mammals (Dillingham et al., in press; Fig. 1). More specifically, Dillingham et al. (in press) conducted a meta-analysis that included data from 41 mammalian species (including 5 pinniped and 6 cetacean species) that found the variance in a_{rT} estimates across species was 0.09. It is assumed for the current analysis that half of this variance is due to sampling error in the a_{rT} estimates, while the other half is "real" (i.e., process variance); thus a value of 0.045 is used as a first-order approximation of the true variance in a_{rT} across mammalian species. This implies a 95% confidence interval for a_{rT} ranging from 0.58 to 1.42 across mammals. True variation in a_{rT} across species within a taxon is due to real life-history variation (i.e., not all species exactly conform to the archetypal expectation from life-history theory), but the apparent similarity in a_{rT} across species in nature reflects well-known life history trade-offs (e.g., species with long lives also tend to mature late and have low reproductive rates), so that as $r_{\max}$ goes up, the associated T_{opt} goes down and vice versa (Fig. 1). Let the a_{rT} estimates from the meta-analysis of Dillingham et al. (in press) be referred to as $a_{\text{rT.A}}$.

Knowing that a_{rT} for a species should be approximately 1 is useful because it reduces the mathematically plausible set of vital rate combinations to those that are also evolutionarily realistic and allows some missing life-table rates to be estimated. For example, the product of $r_{\max}$ and T_{opt} for a species that under the best resource circumstances matures late (age 10), breeds infrequently (single calf every 3 years), but has only moderately high natural annual adult survival (e.g., 0.94), would have corresponding $r_{\max} \approx 0.01$ and $T_{\mathrm{opt}} \approx 23$ and thus $a_{\mathrm{rT}} \approx 0.23$. This would be an extreme value relative to the distribution of a_{rT} observed for mammals in the meta-analysis by Dillingham et al. (in press) and would thus seem to be an improbable life history. This insight can help improve the estimation of $r_{\max}$ and T_{opt}. The analysis process works conceptually as follows: (1) Given an empirical distribution for best-case vital rate parameters (e.g., survival, reproduction), standard Euler equations or Leslie-Lefkovitch methods are used to calculate resulting distributions for $r_{\max}$ and T_{opt}, from which the distribution for a_{rT} can also be computed (call this $a_{\mathrm{rT.MM}}$, with the subscript 'MM' denoting that the estimates are from matrix-model methods). (2) The plausibility of the empirical vital rate combinations can then be evaluated by comparing the distribution for $a_{\mathrm{rT.MM}}$ to that of $a_{\mathrm{rT.A}}$. (3) Combinations of vital rates that result in $\mathrm{a}_{\mathrm{rT.MM}}$ being much different from 1 are considered implausible and discarded, thus resulting in a revised set of vital rate combinations and distributions for $r_{\max}$ and T_{opt}. The formal approach for implementing this is described below.

Modeling steps

1. Calculating $r_{\max}$ and T_{opt}

Initial Monte Carlo distributions for $\lambda_{\max}$ were constructed given input distributions for various vital rate parameters for the case study species. This was done by drawing K samples from the vital rate distributions and for each sample k solving for $\lambda_{\max}$ using the following derivation of the Euler-Lotka equation (Skalski et al. 2008), which assumes constant annual survival, s, and fecundity, f (females per female), for all ages following (and including) the age of first reproduction, α:

$$0 = \lambda^{\alpha-1}(s - \lambda) + l_a f, \qquad (1)$$

where survivorship to age α is $l_a = s_0 * s^{\alpha-1}$ with s_0 being the first-year (calf) survival rate. T_{opt} for sample k is then calculated as (Niel and Lebreton 2005):

$$\overline{T_{\mathrm{opt}}} = \alpha + \frac{s}{\lambda - s}\,. \qquad (2)$$

Then, $a_{\mathrm{rT.MM},k} = \log(\lambda_{\max,k}) T_{\mathrm{opt},k}$. The Monte Carlo distribution for $\mathrm{a}_{\mathrm{rT.MM}}$ was then refined by generating K samples from $a_{\mathrm{rT.A}} \sim \mathrm{Normal}(1, \sigma^2 = 0.045)$, pairing each $\mathrm{a}_{\mathrm{rT.MM},k}$ randomly with a sample $a_{\mathrm{rT.A},k}$, and retaining the combination of vital rates for sample k only if $|\mathrm{a}_{\mathrm{rT.MM},k} - \mathrm{a}_{\mathrm{rT.A},k}| \leq \delta$, where δ is a numerical tolerance criterion. A tolerance of $\delta = 0.05$ was used here; the choice of this value is not consequential provided it is small relative to a_{rT} (smaller values will trivially improve the precision of the retained vital rate distributions but require a larger Monte Carlo sample to draw from). This process generates a restricted distribution for the vital rates (and associated estimates of $r_{\max}$ and T_{opt}) that are consistent with both the data for the population and ecological theory.

2. Estimating generation time for a stable population (r = 0)

For a population with stable age structure growing at any rate, generation time is defined generally as:

$$\bar{T} = \sum_{i=1}^{w} i l_i f_i \lambda^{-i}, \qquad (3)$$

where i is age in years, and w is the maximum potential age. Equation 2 is equal to equation 3 for a population with age-constant adult survival, age-constant fecundity, and $w = \infty$. Simulations and exploratory analyses indicate that *for a growing population*, estimates of $\bar{T} = T_{\text{opt}}$ for cetaceans are generally insensitive to w; that is, equations 2 and 3 produce nearly the same estimates of T_{opt} (generally within 1 or 2 years of each other). However, for a stable population ($r = 0$), and if it is assumed that the density-dependent reduction in r from $r = r_{\max}$ to $r = 0$ is the result of reduced calf survival or reproductive rates (rather than adult survival), then the generation time estimate is highly sensitive to w, so that equation 2 is a poor estimator of T_0. Equation 3 was therefore used to estimate T_0, by setting $\lambda = 1$, specifying a distribution for w in addition to those for s, s_0, and α as constrained by the above-described method for finding $r_{\max}$ and T_{opt}, and solving for new f to satisfy the general Euler-Lotka equation:

$$1 = \sum_{i=1}^{w} \lambda^{-i} l_i f. \qquad (4)$$

Data Inputs

Tables 1 and 2 summarize the input distributions for vital rates. These were based on a combination of information from the scientific literature, predictive modeling, and input from species experts participating in the workshop. Many of these rates are based on sparse data; ultimately the life history parameters for these species are fairly poorly known.

Adult survival, s

Adult survival, and maximum potential adult survival in particular, has not been well-estimated for any species considered here. The inputs used (Table 1) are fitted estimates from a simple beta regression model of adult survival as a function of body size and taxonomic variables (see Fig. 2 for details).

Calf survival (s_0)

Maximum calf survival is unknown. The prior distribution for calf survival was constructed by multiplying the distribution for s, by a scaling factor: c0 ~ Uniform(0.75, 0.90), allowing for calf survival rates on the order of 0.65 to 0.90 (but always lower than the adult survival rate). More work is needed to better inform this prior, but the results of this analysis are fairly insensitive to this parameter.

Maximum age (w)

The oldest age recorded in mortality datasets tends to underestimate maximum natural lifespan for several reasons. Only a small percentage of the population reaches the maximum age, so the oldest individuals are unlikely to be observed in sample data. For populations subjected to human-caused mortality, there are even fewer old animals available to the sample because fewer reach their natural potential age. Moreover, mortality data may be biased; for example, younger animals may be more likely than older animals to get caught in fishing nets, and old animals dying from natural causes may be less likely to strand on a beach (if they were depredated, died offshore, or were emaciated and sank) than healthy animals discarded by a fishermen near shore. Additionally, age estimation (typically done by examining teeth) is difficult for older animals (higher measurement error, biased toward underestimation), especially for species with small teeth. Therefore, uniform distributions were used for oldest age, with the minimum value given by the oldest recorded age from mortality data, and maximum value set to 5x the median age-of-first-reproduction value (from Table 2). The 5x longevity:AFR ratio is close to the upper ratio known for various odontocete species according to estimates provided by Taylor et al. (2007) (e.g., ≈ 4.5x – 7x for harbor porpoise, beluga whale, Pacific white-sided dolphin, dusky dolphin, striped dolphin, common bottlenose dolphin, narwhal, short-beaked common dolphin, franciscana, Dall's porpoise).

Age at first reproduction (AFR)

Prior distributions used for AFR are given in Table 2, along with some description and references on which these were based. Note, AFR = age at sexual maturity + 1.

Inter-birth or calving interval (IBI)

Input distributions for IBI are given in Table 2, along with some description and references on which these were based. Fecundity is calculated as 1/IBI, and then multiplied by 0.5 to express it in terms of females per female (assuming 50:50 sex ratio at birth).

Estimating threshold rates of anthropogenic mortality

Assume a simple model for exponential growth:

$$N_t = N_0 \exp(rt),$$

where N_t is abundance at time t, N_0 is the initial abundance, r is the population growth rate. A more realistic model would include density dependence and other realisms (population age structure, environmental stochasticity, etc.), but a simple deterministic exponential model is used here for computational simplicity, since the goal of this exercise is mainly to provide *qualitative* inference about the approximate level of anthropogenic mortality required to drive populations to different Red List categories after three generations. By assuming this model, the actual mortality rate thresholds from this analysis are likely biased high. True anthropogenic mortality rates should be kept lower than these values if populations are to avoid the various threatened-status categories.

Let $N_0 = 1$ (arbitrarily) and let $r = r_{\max} – m$, where m is the annual mortality rate (number animals killed per 100) from anthropogenic causes. Also set $t = 3*T_0$. Then after three generations, the fractional population size would be:

$$N_t = \exp[\ (r_{\max} - m)*3T_0\ ]. \qquad (5)$$

Setting N_t to 0.7 (30% decline), 0.5 (50% decline) or 0.2 (80% decline), the corresponding anthropogenic mortality rate required to achieve these population levels after three generations is:

$$m = r_{\max} - \log(N_t)/3T_0.$$

For this simple and largely qualitative analysis, I simply use point estimates for $r_{\max}$ and T_0 from the life history analysis to obtain point estimates of m for the various relative N_t levels.

Results and Discussion

Estimates of intrinsic population growth and generation time are in Table 3, along with refined estimates of adult survival (as influenced by the allometric model). The estimates for s are slightly higher than the input distributions. This suggests that, given inputs for the other vital rate parameters (namely AFR and IBI), higher estimates for s are generally required for the estimated life history schedule to be consistent with ecological theory. This is not surprising, given that empirical estimates of adult survival for odontocetes rarely reflect maximal-growth conditions but rather incorporate some level of anthropogenic mortality or density dependence. The refined distributions for other parameters were similar to the prior distributions, suggesting the method did not affect these parameters. The final survival estimates are generally consistent with those of Taylor et al. (2007), who used a fixed value of 0.95 for all the species considered here.

The means of retained a_{rT} estimates were all around 0.80 – 0.85, toward the lower end of the distribution for mammals in general. This implies that odontocete generation length is slightly shorter for a given $r_{\max}$, or that $r_{\max}$ is slightly less for a given T_{opt}, than would be expected for an archetypal mammal species. Alternatively, it could suggest bias in the input parameters (e.g., perhaps a population if not resource-limited would have younger AFR than those used here).

For comparison, some r and T estimates from Taylor et al. (2007) are in Table 4. The new estimate of T_0 for *S. chinensis* is greater (by 5 years) than that used by Taylor et al. (2007), since the current analysis allowed for a slightly older AFR, less frequent calving interval and older maximum age. The new estimate of T_0 for *N. phocaenoides* is slightly younger than that of Taylor et al (2007), as a younger AFR was specified here.

Table 5 summarizes the direct human-caused mortality rate estimates that would lead to 30%, 50%, or 80% declines in population abundance after three generations (given by $3{*}T_0$ in Table 3). These decline thresholds correspond to Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) Red List status, respectively. An important qualitative result is that the difference between annual human-caused mortality rates that would lead to a 30% vs. 80% decline after three generations is quite small. This is most notable for *Sousa*, for which only 3.7% annual mortality (e.g., from fishing nets) would qualify the species for VU (expected 30% decline after 75 years) and just a slightly higher mortality rate of 5.3% per year would qualify it for being CR (80% decline after 75 years). For a small subpopulation of, say, 100 individuals, this is the difference of 1 or 2 extra animals per year killed in a fishing net.

Importantly, the threshold mortality rates in Table 5 are based on a very simple model of exponential (density-independent) population growth with no age-structure or stochasticity. The populations of concern for this report may already be substantially depleted, so it may not be unreasonable to assume that they could grow at a near-maximum rate if direct kills were eliminated. However, if these populations were experiencing density-dependent resource limitation at their current abundances, lower rates of *m* than those in Table 5 would be sufficient to drive initial population declines. Other factors could also result in current *m* estimates being optimistic (in the sense that the true critical *m* is actually lower than these): for example if bycatch mortality disproportionately affects younger animals; if we factor in the loss of calves whose mothers succumb; or if impacts on the ecosystem (e.g., pollution, disturbance, habitat degradation) indirectly compromise vital rates so that the maximum potential growth rates in the absence of direct kills are lower than the current $r_{\max}$ estimates.

As a specific example, even if we assumed a *Sousa* population to be at carrying capacity (*K*) in the recent past and we applied a theta-logistic population model with $\theta = 2$ (weak density dependence until the population size gets fairly close to *K*), a value for *m* of 0.046 (rather than 0.053 as in Table 5) would reduce the population by 80% (CR) within 75 years from when it was at *K*. And if the population can now only grow at a maximum rate of 2.5% per year instead of 3.2% (hypothetically because habitat degradation and pollution have resulted in low pregnancy rates, sensu the discussion by Jefferson et al. 2012), then the associated *m* would reduce to about 0.04.

Considering this information, and that direct mortality estimates for these populations are generally unavailable, it may be worth using a structured expert decision-making process to evaluate (based on local expert knowledge) the relative plausibility of cumulative mortality from human causes exceeding the different threshold levels of *m* (Table 5). Precautionary inference should be applied given that the true values for *m* are probably lower than those estimated from the current analysis.

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Table 1. Prior distributions for survival and longevity parameters. Distributions for *s* are predictions from generalized linear models based on body size and taxon (see text and Fig. 2). Range for *w* is from the oldest known individual (from Taylor et al. 2007) to 5 times the median AFR (from Table 2).

Species	Adult survival, *s**	Oldest age, *w*	Notes for *w*
O. brevirostris	μ = 0.93, σ = 0.02	Unif(28, 45)	No data: assume same as for *O. heinsohni*
O. heinsohni	μ = 0.93, σ = 0.02	Unif(28, 45)	Marsh et al. 1989 (max age of 28 was reported for *O. brevirostris*, but the study population was actually *O. heinsohni*, which had not yet been taxonomically delineated)
N. asiaeorientalis	μ = 0.92, σ = 0.02	33	No data for this species, but 33 is oldest known age for *N. phocaenoides* (Jefferson et al. 2002) and exceeds 5x AFR
S. chinensis	μ = 0.94, σ = 0.02	Unif(43, 53)	38 from Jefferson et al. 2012; 43 from Huang et al. 2012
S. plumbea	μ = 0.94, σ = 0.02	Unif(46, 50)	46 from Cockcroft 2002, Plön et al., in press.

* Adult survival modeled as beta distribution with mean (μ) and σ listed in the table

Table 2. Prior distributions for reproductive parameters. AFR = age of first reproduction; IBI = inter-birth interval

Species	AFR	IBI	Basis and sources
O. brevirostris	Unif(7, 11)	Unif(2, 5)	No data. Assume same as *O. heinsohni* but with broader uncertainty for AFR
O. heinsohni	Unif(8, 10)	Unif(2, 5)	AFR: Marsh et al. 1989 IBI: No data. U(2,5) represents total uncertainty range for delphinids
N. asiaeorientalis	Unif(5, 7)	Unif(1, 2)	AFR: reviewed by Jefferson et al. 2002; Gao and Zhou 1993 identified two lactating 5-yr olds in Yellow Sea region. Kasuya (2011) noted a captive *N. phocaenoides* that gave first birth at age 3 but considered this non-representative of animals in the wild IBI: range speculated by Kasuya 2011, based on data from Shirakihara et al. 1993. For *N. phocaenoides*, Mei et al (2012), citing others, reported 1.4, but expert working group believed this to be too optimistic and based on fairly weak data; they speculated 2 as being more likely, which is max interval for other porpoises
S. chinensis	Unif(10, 11)	Unif(3, 4)	AFR: Jefferson 2000, refs in Huang et al. 2012 IBI: based on range of values summarized by Huang et al. 2012 and Jefferson et al. 2012, but excluding uppermost values (>4) because younger values would be expected in optimal conditions, and truncating range below 3 based on advice of the working group
S. plumbea	Unif(9, 11)	Unif(3, 5)	AFR: reported age-at-maturity = 8 (Plön et al., in press) and 10 (Cockcroft 2002) IBI: reported estimates range from 3 (Cockcroft 2002) to 5 (Plön and Bernard 2007, Plön et al., in press)

Table 3. Parameter estimates: mean, sd (in parentheses), and 95% range of distribution

Species	s_{max}	r_{max}	T_{opt}	T_0
O. brevirostris	0.96 (0.01)	0.038 (0.01); 0.02 – 0.06	21 (2.7); 17 – 27	20 (1.9); 16 – 23
O. heinsohni	0.96 (0.01)	0.037 (0.01); 0.02 – 0.06	21 (2.7); 18 - 26	20 (1.7); 17 – 23
N. asiaeorientalis	0.93 (0.01)	0.071 (0.02); 0.04 – 0.11	13 (1.2); 11 – 15	15 (0.9); 13 – 17
S. chinensis	0.97 (0.01)	0.032 (0.01); 0.02 – 0.05	26 (1.1); 24 – 28	25 (1.2); 23 - 28
S. plumbea	0.97 (0.01)	0.031 (0.01); 0.02 – 0.05	26 (1.8); 23 – 29	25 (1.0); 23 – 27

Note: If using the same estimator for both T_{opt} and T_0, and if density-dependence is assumed to act only on reproductive or juvenile survival parameters, then $T_0 > T_{opt}$. In this table, $T_0 < T_{opt}$ for *Orcaella* and *Sousa*. This is an artifact of using equation 2 to calculate T_{opt} and equation 3 to calculate T_0, as the former equation tends to estimate slightly higher generation time estimates, more so as the adult survival estimate increases.

Table 4. Parameter estimates from Taylor et al. (2007). Note, *r* and *T* correspond to vital rates obtained from literature; they are not necessarily r_{max} or T_{opt}.

Species		r	T	T_0
O. brevirostris		--	--	--
O. heinsohni		--	--	--
N. phocaenoides		0.04	14.4	16.5
N. asiaeorientalis		--	--	--
S. chinensis		0.01	19.8	20.4
S. plumbea		--	--	--

Table 5. Human-caused mortality rates that would lead to 30% (VU), 50% (EN) and 80% (CR) declines in population abundance after 3 generations ($3*T_0$ from Table 3), based on the simple model given by equation 5 in main text. Red List categories: VU = vulnerable; EN = endangered; CR = critically endangered. *Orcaella and Sousa* species are collapsed into genera in this table given the similarity of within-genus estimates for r_{max} and generation time.

Species	VU	EN	CR
Orcaella spp.	0.044	0.050	0.065
N. asiaeorientalis	0.079	0.086	0.107
Sousa spp.	0.037	0.041	0.053

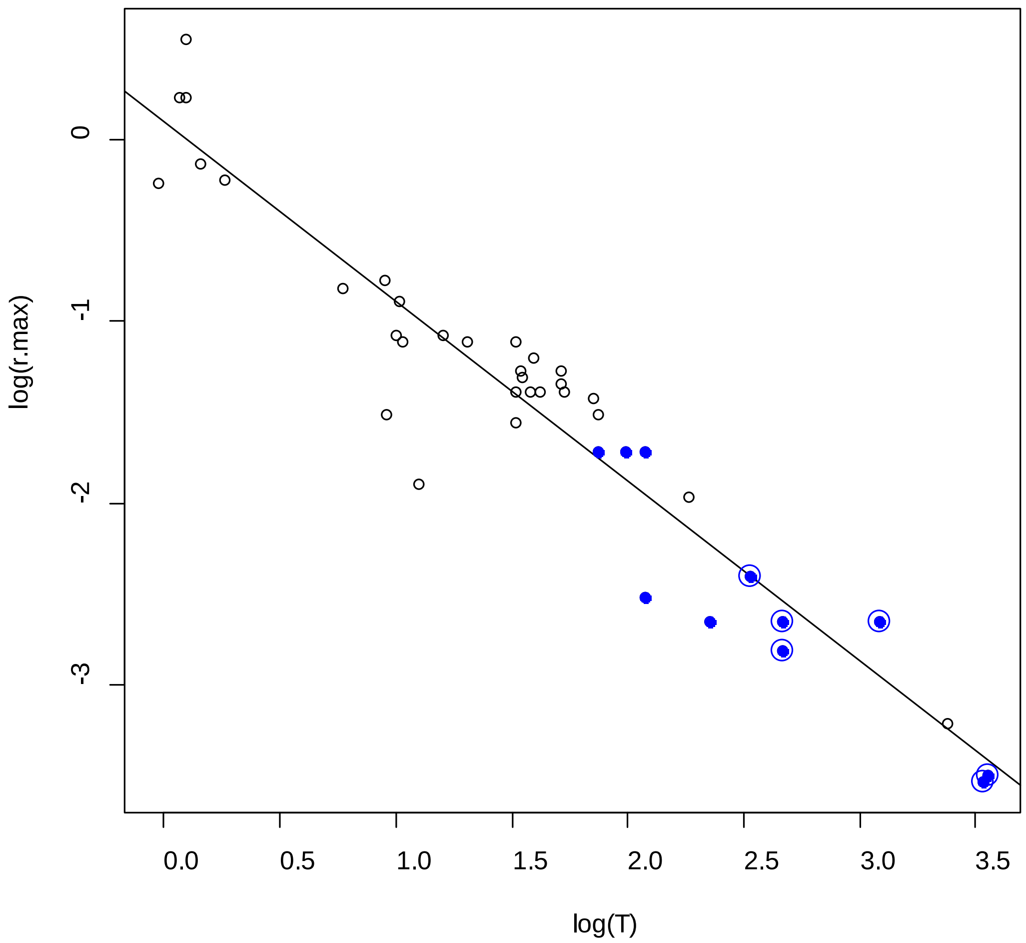

Fig. 1. Relationship between log (T_{opt}) and log (r_{max}) for mammals, based on meta-analysis conducted by Dillingham et al. (in press). The slope of this line is -1 and the intercept is close to 0, consistent with allometric theory (Niel and Lebreton 2005). Blue points are marine mammals. Those with open circles around them are cetaceans (all mysticetes except for one odontocete, *Orcinus orca*); the others are pinnipeds.

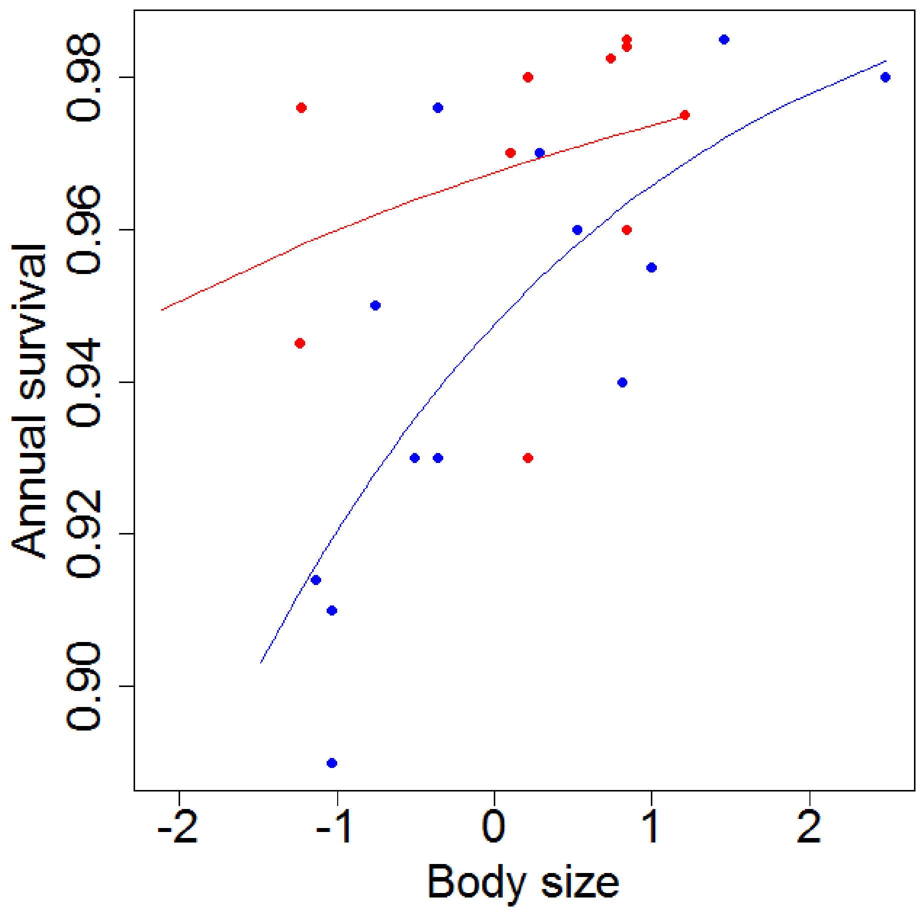

Fig. 2. Relationship between body size and survival for mysticetes (red) and odontocetes (blue). Point estimates of adult survival were available in the literature for 13 odontocete and 10 mysticete species (data not shown). Female body size inputs (max mass in kg for mysticetes; max length in meters for odontocetes) are mostly from Jefferson et al. (2008); these were standardized within each of the two taxa to z-scores (mean = 0, SD = 1). Survival was modeled as a function of the standardized body size score and a categorical fixed effect variable for suborder (odontocete vs. mysticete) using beta regression (function betareg in software R). Fitted adult survival (S) estimates (solid lines) were given the by the regression equation: logit(S) = 3.394 + 0.218*log(body size) – 0.500(if odontocete) + 0.228*log(body size)(if odontocete).