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INTRINSIC GROWTH (r_{\max}) AND GENERATION TIME (T) ESTIMATES FOR *INIA GEOFFRENSIS*, IN SUPPORT OF AN IUCN RED LIST RE-ASSESSMENT

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Background and Analysis objective

The Amazon River dolphin, *Inia geoffrensis*, is currently listed as Data Deficient on the International Union for Conservation of Nature (IUCN) Red List, on the basis of an assessment completed in 2008 and the current documentation for that listing notes that “much of the information summarized in this assessment is dated and may no longer be valid” (Reeves et al. 2011). Also, the IUCN Species Survival Commission (SSC) Cetacean Specialist Group has a responsibility to reconsider and appropriately revise assessments of species and populations whose status is known to have deteriorated, which is the case for *Inia geoffrensis*. Relevant new data on both abundance trends and life history are now available for the species in one large part of its extensive range, and frequent reports of apparent declines and targeted hunting demonstrate the urgent need for a formal re-assessment of the conservation status of this dolphin (Gómez-Salazar et al. 2012, Mintzer *et al.* 2013, Williams et al. 2016, da Silva and Martin 2017, da Silva et al in press). A new Red List assessment is therefore under way.

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 $\lambda = \exp(r) = 1$. Estimating this value for the Amazon River dolphin *Inia geoffrensis* is the primary goal of this analysis. Let this generation time be denoted T_0 . Additionally, this analysis provides distribution estimates for the intrinsic population growth and 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). This report closely follows – in purpose, methodology and format – one written in support of updating IUCN Red List assessments for several Indo-Pacific cetacean species (Moore 2015).

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

Life history theory predicts the following allometric relationship:

$$r_{\max} * T_{\max} = a_{rT}, \quad (1)$$

where r_{\max} is the intrinsic growth rate, T_{\max} is the associated generation time (Moore 2015 referred to this as T_{opt}), 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, birds and elasmobranchs (Dillingham et al. 2016; Fig. 1). Dillingham et al. (2016) estimated the variance in a_{rT} estimates for 41 mammal species, including 5 pinnipeds and 6 cetaceans, to be 0.09. It is assumed for the current analysis (as in the previous analysis by Moore 2015) that half of this variance in the a_{rT} estimates was sampling variance, while the other half was “real” (i.e., process variance); thus a value of 0.045 is used here 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, which means, for example, that a species with an intrinsic growth rate of $r_{\max} = 0.05$ would likely have a generation time between 12 and 28 years with an expected value of 20. 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 general similarity in a_{rT} across vertebrates in nature reflects well-known life history trade-offs and correlation life history parameters. Species that live a long time also tend to mature late and have low reproductive rates, so that as r_{\max} goes up, the associated T_{\max} goes down and vice versa (Fig. 1). These correlations are often ignored by risk assessment analysts who draw random values from parameter distributions independently from each other to generate distributions for r_{\max} , which as a result can have unrealistic characteristics (such as much of the distribution being negative). We denote the a_{rT} estimates from the meta-analysis of Dillingham et al. (2016) as $a_{rT,A}$ (the subscript ‘A’ implies that the distribution for a_{rT} is consistent with allometric theory).

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. Consider a hypothetical example in which the following life-history parameter field estimates are obtained for a species believed to be increasing at a maximum potential rate: age at first reproduction = 10 years; inter-birth interval = 3 years; natural annual adult survival = 0.94. Depending on the calculation method and some other life history values (e.g., calf survival rate), this population would have a corresponding $r_{\max} \approx 0.01$ and $T_{\max} \approx 23$ and thus $a_{rT} \approx 0.23$. This would be an extremely low a_{rT} value relative to the distribution of $a_{rT,A}$ observed for mammals in the meta-analysis by Dillingham et al. (2016) and would thus seem to be an improbable life history. We would expect a species that matures this late and breeds this infrequently to have a higher adult survival rate (or, a species with such a low adult survival rate should breed earlier and more often) and thus either a higher r_{\max} or T_{\max} . We might therefore conclude that the field estimates were inaccurate or that the population is not growing at its intrinsic rate (perhaps the population is suffering human-caused or density-dependent impacts). Formalizing this insight can help improve the estimation of r_{\max} and T_{\max} .

The analysis process thus works conceptually as follows: (1) Given empirical distributions (field estimates) for vital rate parameters that the researcher assumes would be realized under density-independent conditions, a Monte Carlo approach is used to calculate an empirical distribution for a_{rT} (denoted $a_{rT,MM}$, where the subscript ‘MM’ implies that the estimates are from matrix-model methods). That is, for randomly drawn combinations of vital rate parameters, standard Euler

equations or Leslie-Lefkovich methods are used to calculate r_{\max} and T_{\max} , and hence $a_{rT.MM}$, for each draw. (2) The plausibility of each empirical vital rate combination can then be evaluated by comparing the associated $a_{rT.MM}$ to randomly drawn values of $a_{rT.A}$ (the latter are drawn from a normal distribution with mean = 1 and process variance = 0.045 (see above)). (3) Vital rate combinations are retained or discarded according to their plausibility, resulting in a revised set of vital rate combinations and distributions for r_{\max} and T_{\max} . The formal approach for implementing this is described below.

Modeling steps

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

Initial Monte Carlo distributions for $\lambda_{\max} = \exp(r_{\max})$ were constructed given input distributions for the vital rate parameters for *Inia*. This was done by drawing K samples from the vital rate distributions and for each sample k solving for λ_{\max} using an Euler-Lotka equation.

Moore (2015) used a simplifying derivation of the Euler-Lotka equation (Skalski et al. 2008), for which annual survival, s , and fecundity, f (females per female) are assumed to be constant for all ages following (and including) the age of first reproduction, α :

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

where survivorship to age α is $l_{\alpha} = s_0 * s^{\alpha-1}$ with s_0 being the first-year (calf) survival rate. For this derivation, T_{\max} for sample k can simply be calculated as (Niel and Lebreton 2005):

$$\bar{T} = \alpha + \frac{s}{\lambda - s}, \quad (2)$$

where λ and \bar{T} are taken to be λ_{\max} and T_{\max} , respectively. This simplification of the more general Euler-Lotka is convenient because it does not require estimates of longevity (maximum lifespan) and ultimately produces good estimates of r_{\max} , and also of T_{\max} if annual survival is not very close to 1 (e.g., < 0.95). However, Moore (2015) found this estimator generally problematic (biased) for calculating T_0 , and it also increasingly over-estimates T_{\max} as adult survival becomes very high (e.g., > 0.95). Therefore, rather than equation 1, we used a more general Euler-Lotka equation to find λ for *Inia*. For a population with stable age structure growing at any rate,

$$1 = \sum_{i=1}^w \lambda^{-i} l_i f, \quad (3)$$

where i denotes age and w is the maximum potential age. We still used a constant s for all i following the calf year and constant f for all $i \geq \alpha$. The important difference between equations 1 and 3 is the specification here of w . Generation time is then calculated:

$$\bar{T} = \sum_{i=1}^w i l_i f_i \lambda^{-i}. \quad (4)$$

It then follows that $a_{rT.MM,k} = \log(\lambda_{\max,k})T_{\max,k}$. The Monte Carlo distribution for $a_{rT.MM}$ was then refined by generating K samples from $a_{rT.A} \sim \text{Normal}(1, \sigma^2 = 0.045)$, pairing each $a_{rT.MM,k}$ randomly with a sample $a_{rT.A,k}$, and retaining the combination of vital rates for sample k only if $|a_{rT.MM,k} - a_{rT.A,k}| \leq \delta$, 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_{\max}) that are consistent with both the population data and ecological theory.

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

We assume that a density-dependent reduction in r , from $r = r_{\max}$ to $r = 0$, would manifest through reduced calf survival or reproductive rates (rather than adult survival). Therefore, for each sample k , we set $\lambda = 1$ and used equation 3 to re-solve for f and then based on these values used equation 4 to estimate T_0 .

Data Inputs

Table 1 and the following sections summarize the input distributions for vital rates for *Inia*. Derivation of these rates is based on capture-recapture analyses of data from a long-term field study based in the Mamirauá Sustainable Development Reserve, Amazonas State, Brazil (2° 16' S, 65° 41' W) (Martin and da Silva, in press).

Adult survival, s

Female adult survival was estimated by Mintzer et al. (2013) for two periods: 1994 – 2000, and 2001 to 2011. During the latter period, survival has been reduced by fishery-caused mortality. The estimated survival rate for the former period (0.973, SE=0.011) is assumed for this analysis to represent the maximum potential survival rate under natural conditions. Survival rates were drawn from a beta distribution for the Monte Carlo analysis.

Calf survival (s_0)

In the study by Martin and da Silva (in press), 180 of 226 animals that were first documented at less than one year of age, including many first recognized at less than one month of age, survived to age 1. The corresponding survival rate estimate is 0.796 with binomial SE = 0.052. A beta distribution was used to generate random values for the analysis. This field estimate may give a biased view of true calf survival rates under a max-growth scenario because the influence of density dependence and human-caused mortality on these data are unknown (these factors, if important, would bias the estimates low), and because some calves would have died before ever being observed (this would bias the estimate high). This latter form of bias is offset, however, by a countering bias in the estimate of fertility. That is, in the life table model, we are only concerned with how many animals survive to reproductive age. Undetected calves will inflate the calf-survival estimate but also reduce the calving-rate estimate; the recruitment rate estimate will be the same. Moreover, for long-lived species such as *Inia*, estimates of r_{\max} and T_{\max} are fairly insensitive to the accuracy of calf survival rate estimates, especially when applying the allometric model used in this analysis.

Maximum age (w)

The oldest age recorded in mortality datasets tends to underestimate true maximum potential lifespan for several reasons. Only a small percentage of populations achieve very old age, so the oldest individuals are unlikely to be observed in sample data. For populations subjected to substantial human-caused mortality, there are even fewer old animals available to sample because fewer reach their natural potential age. And mortality data may be biased; for example, young animals that disproportionately die in fishing nets may be more likely to be observed in nets or on beaches than older animals that are likely to have died from natural causes (e.g., if they were depredated or were emaciated and sank). 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. In summary, this parameter is typically poorly known. And this particular study, the study duration is shorter than lifespan of the oldest animals; thus animals known from birth have not yet had a chance to be observed to a very old age. Therefore, we used a broad uniform distribution to describe w , with the minimum value given by the oldest recorded age from mortality data (age 32.3), and maximum value set to 5x the median age-of-first-reproduction value, which is 9.7 (see below). 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., $\approx 4.5x - 7x$ 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, α)

Based on a sample of 22 individuals (Martin and da Silva, in press), mean age of first reproduction is estimated to be 9.7 with SE = 0.34. Note, AFR = age at sexual maturity + 1. We assumed a normal distribution to generate random values for the analysis.

Inter-birth or calving interval (IBI)

From a sample of 71 individuals (Martin and da Silva, in press), mean IBI was estimated to be 4.56 years, with a SE of 0.24. Fecundity, f , 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:

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

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 (0.032) and generation time (22 years) are described fully in Table 2, along with refined estimates of adult survival and oldest age (as influenced by the allometric model), which 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 mean of retained a_{rT} estimates was 0.70, toward the lower end of the distribution for mammals in general. This implies that the generation length for *Inia* is shorter for a given r_{\max} , or that r_{\max} is slightly less for a given T_{\max} , than would be expected for an archetypal mammal species. Alternatively, it could suggest bias in the input parameters (e.g., perhaps a less stressed population would have younger AFR than those used here).

We estimated T_0 to be 24.8 years. For comparison, Taylor et al. (2007) estimated $T_0 = 10.2$ years for *Inia*. This difference is explained by substantially different vital rate estimates used by Taylor et al. (2007), who used much faster reproductive schedule (IBI = 1.6 yrs and AFR = 6 yrs) and shorter lifespan (18 years) than in the current analysis, which reflects more up-to-date knowledge about life history parameters for this species.

Inia are subjected to direct mortality as bycatch in fisheries and direct hunting. Animals are hunted for fishing bait and as an act in response to perceived conflicts (competition) with fisheries (Loch et al. 2009, Alves et al. 2012, Iriarte and Marmontel 2013, Brum et al. 2015). Table 3 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.

Importantly, the threshold mortality rates in Table 3 are based on a very simple model of exponential (density-independent) population growth with no age-structure or stochasticity. The

Inia study population of this report may already be substantially depleted, so it may be reasonable to assume that they could grow at a near-maximum rate if direct kills were eliminated. However, if the population has been experiencing density-dependent resource limitation, lower rates of m than those in Table 3 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 human-caused 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, dam construction) 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.

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Table 1. Prior distributions for survival and reproductive parameters for *Inia geoffrensis*, and derived prior distributions for r_{\max} , generation time T_{\max} , and their product

Parameter	Specified distribution	Mean (SE)
Adult survival, s	Beta (210.28, 5.84)	0.973 (0.011)
Calf survival, s_0	Beta (47.01, 12.05)	0.796 (0.052)
Oldest age, w	Unif (32, 49)	32 – 49
Age of first reproduction (AFR, α)	Normal (9.7, 0.3)	9.7 (0.3)
Inter-birth interval (IBI)	Normal (4.56, 0.24)	4.56 (0.24)
r_{\max}	NA	0.017 (0.012) 95% CRI: -0.012 – 0.037
T_{\max}	NA	21 (1.2)
$a_{rT.MM}$	NA	0.35 (0.27)

Table 2. Results from joint allometric Euler-Lotka model. Distribution summaries for r_{\max} , T_{\max} , T_0 , and life history parameters for which the model-refined distribution differed from the input distribution (in Table 1).

Parameter	Mean (SE)
r_{\max}	0.032 (0.006) 95% CRI: 0.020 – 0.042
T_{\max}	21.8 (1.0)
T_0	24.8 (1.7)
$a_{rT.MM}$	0.70 (0.13)
Adult survival, s	0.984 (0.005)
Oldest age, w	44 (4)

Table 3. Human-caused mortality rates that would lead to 30% (VU), 50% (EN) and 80% (CR) declines in *Inia* population abundance after 3 generations ($3 * T_0$ from Table 2), based on the simple model given by equation 5 in main text. Red List categories: VU = vulnerable; EN = endangered; CR = critically endangered.

VU	EN	CR
0.037	0.041	0.054

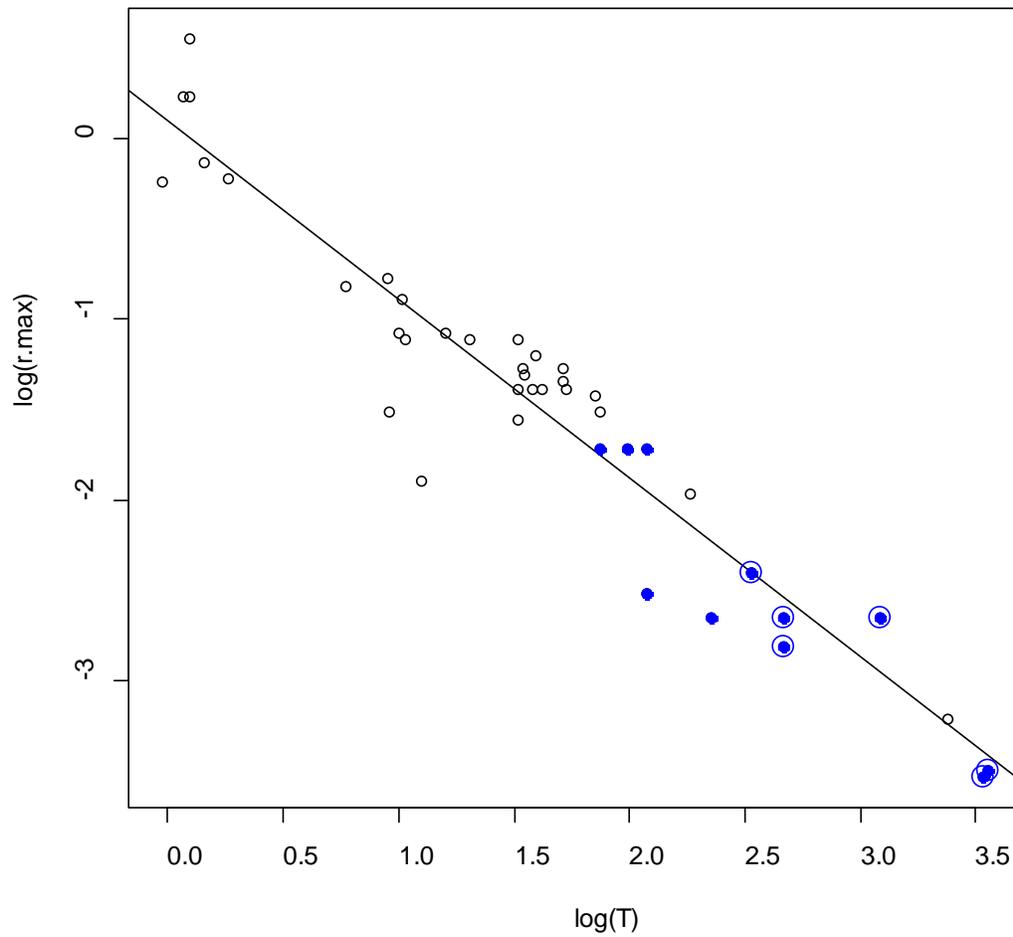


Fig. 1. Relationship between $\log(T_{\text{opt}})$ and $\log(r_{\text{max}})$ for mammals, based on meta-analysis conducted by Dillingham et al. (2016). The slope of this line is -1 and the intercept is close to 0, consistent with allometric theory (Niel and Lebreton 2005). Blue points are marine mammals. Those with open circles around them are cetaceans (all mysticetes except for one odontocete, *Orcinus orca*); the others are pinnipeds.