Conflicting rates of increase in the sperm whale population of the eastern Caribbean: positive observed rates do not reflect a healthy population

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Supplement.

Likelihood model for the mortality and recruitment of calves

We consider each interval between the observation of a known individual calf and the subsequent observation of the unweaned calf, the now weaned individual, or the mother without the calf. Suppose this interval lasts t years, then there are three possibilities:

The probability that the calf is observed and still a calf at this second observation is:

$$P(C,C,t) = (1-\delta_C)^t (1-g)^t \ . \ \text{(S1)}$$

The probability that the calf is not with the mother at the second observation is (assume it died in year x, after possibly weaning, and so recruiting to adulthood, in year y):

$$P(C,0,t) = \delta_C \sum_{x=1}^{t} (1-\delta_C)^{x-1} (1-g)^{x-1} + g\delta_A \sum_{x=2}^{t}\sum_{y=1}^{x-1} (1-\delta_C)^y (1-g)^{y-1} (1-\delta_A)^{x-y-1}$$

$$= \delta_C \frac{1-(1-\delta_C)^t (1-g)^t}{1-(1-\delta_C)(1-g)} + g(1-\delta_C)\delta_A \sum_{x=2}^{t} (1-\delta_A)^{x-2} \frac{\left(1-((1-\delta_C)(1-g)/(1-\delta_A))^{x-1}\right)}{(1-(1-\delta_C)(1-g)/(1-\delta_A))}$$

$$= \delta_C \frac{1-(1-\delta_C)^t (1-g)^t}{\delta_C + g - \delta_C r} + g(1-\delta_C)\delta_A \sum_{x=2}^{t} \frac{(1-\delta_A)^{x-1} - ((1-\delta_C)(1-g))^{x-1}}{\delta_C + g - \delta_C g - \delta_A} \ . \ \text{(S2)}$$

The probability that the calf has been weaned by the second observation (at year y) is:

$$P(C,A,t) = g\sum_{y=1}^{t}(1-\delta_C)^y(1-g)^{y-1}(1-\delta_A)^{t-y}$$

$$=g(1-\delta_C)(1-\delta_A)^{t-1}\frac{1-(1-\delta_C)^t(1-g)^t/(1-\delta_A)^t}{1-(1-\delta_C)(1-g)/(1-\delta_A)}$$

$$=g(1-\delta_C)\frac{(1-\delta_A)^t-(1-\delta_C)^t(1-g)^t}{\delta_C+g-\delta_Cg-\delta_A} \ . \qquad \text{(S.3)}$$

The log-likelihood of the observations, given δ_C, δ_A and g is then (using equations S1-3)

$$L = \sum_t n(C,C,t)\mathrm{n}\, Log\big(P(C,C,t)\big)+n(C,0,t)\mathrm{n}\, Log\big(P(C,0,t)\big)+n(C,A,t)\mathrm{n}\, Log\big(P(C,A,t)\big). \text{(S.4)}$$

Where $n(C,C,t)$ is the number of intervals between identifications t years apart in which the animal was still a calf at the second observation, etc.

Estimates of population parameters of eastern Caribbean sperm whales

The parameters that we estimate for the matrix population model are not all standard. However, when possible we have attempted to translate them into measures used in the literature, so that we can assess their consistency.

Calf mortality: There is no other good estimate of the mortality rate of sperm whale calves. But ours of 0.168 yr^{-1} is substantially higher than the International Whaling Commission's 0.093 yr^{-1}, obtained from a "balance equation" which adjusted calf mortality to give a set of life history parameters resulting in a population at equilibrium (International Whaling Commission 1980). Given the dubious nature of this estimate, and high calf mortalities calculated for somewhat socio-ecologically similar species like killer whales where the estimate is 37% mortality during the first six months of life (Olesiuk et al. 1990), we believe our estimate of calf mortality to be nearer the reality both for sperm whales in the eastern Caribbean, and more widely. Calf mortality almost certainly decreases with age from birth to weaning. This is indicated by the higher value estimated for first-year mortality (0.294 yr^{-1}). As we never observed births, our estimate excludes perinatal mortality; perinatal mortality is included in our model as a negative element of fecundity. Perinatal mortality is generally substantial in cetaceans (Browning et al. 2010, Olesiuk et al. 1990), and given fairly frequent reports of dead new-born sperm whales (e.g. Best et al. 1984) is it expected to be so in this species as well.

Recruitment, weaning: A major discrepancy between our estimates of sperm whale life history parameters and those permeating the literature is in our low recruitment rate and high weaning age. Both Chiquet et al. (2013) and Whitehead (2003) cite Best et al. (1984) as estimating a mean weaning age of two years old. However, while Best et al. (1984) usually found solid food in the stomachs of young sperm whales more than two years old, they also found signs of lactose in most females less than 7.5 years old, and in the stomachs of some older males. Thus a weaning age of five is fairly consistent with Best et al.'s (1984)

data. The sperm whales gradually shift from suckling to solid food between about two and seven years old.

Adult mortality: Our estimate of adult mortality (excluding male dispersal) of 0.033 yr^{-1} is not very far from the International Whaling Commission's (1980) 0.055 yr^{-1} for adult females, or 0.022 yr^{-1} calculated by Chiquet et al. (2013) using data from Australian strandings (the original paper (Evans & Hindell 2004) calculates a mean adult female survival of 0.095 yr^{-1} using life tables), and a very preliminary estimate of 0.021 yr^{-1} from movement analyses of photoidentifications in the South Pacific (Whitehead 2001). However all these previous estimates are very imprecise and may be biased.

Fecundity: Of sperm whale population parameters, the best estimates are for fecundity, and the most reliable of these data are from scientific catches by South African whalers provided by Best et al. (1984). Using their age-specific "early" pregnancy rates, an age of first birth of nine years, and a mortality of adult females of 0.0331 yr^{-1}, gave a fecundity of 0.133 pregnancies per mature female per year. The use of "early" pregnancies, i.e. small foetuses, avoids animals being counted as pregnant with the same calf in successive years, as the gestation period is about 15 months (Best et al. 1984). This estimate is quite little affected by the input mortality (going from 0.121 with a mortality of 0.02 yr^{-1} to 0.147 for a mortality of 0.05 yr^{-1}), or age of first birth (going from 0.137 with an age of first birth of seven years to 0.124 for an age at first birth of 12 years). It also includes foetuses that miscarried after early pregnancy, as well as calves that died at or just after birth, and so is an upper limit for adult female fecundity as used by us. Thus we think that the adult female fecundity of 0.0883 yr^{-1} calculated by us for the eastern Caribbean and the South African pregnancy data are in reasonable agreement, as a 50% rate of miscarriage plus perinatal mortality is probably reasonable (e.g., Browning et al. 2010).

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