A Bayesian uncertainty analysis of cetacean demography and by-catch mortality using age-at-death data

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Abstract
We are challenged to make the most of sparse information for understanding demography of many species, especially those that are long-lived and difficult to observe. For many odontocete populations, only fertility and age-at-death data are feasibly obtainable. We describe a Bayesian approach for using fertilities and two types of age-at-death data (age structure of deaths from all mortality sources, and age structure of anthropogenic mortalities) to estimate rate of increase, mortality rates, and impacts of anthropogenic mortality on those rates for a population assumed to be in a stable age structure. We used strandings data from 1977-1993 (n = 96) and observer bycatch data from 1989-1993 (n = 233) for the Gulf of Maine/Bay of Fundy harbor porpoise (*Phocoena phocoena*) population as a case study. Our method combines mortality risk functions from Siler (1979) and Heligman and Pollard (1980) to estimate parameters describing age-specific natural and bycatch mortality rates. Separate functions are simultaneously fit to bycatch and strandings data, the latter of which are described as a mixture of natural and bycatch mortalities. Euler equations and an estimate of longevity are used to constrain parameter estimates. We fit models under multiple scenarios intended to correct for possible data bias due to unequal probabilities of natural deaths and bycatch deaths occurring in a strandings sample, and due to indirect bycatch of calves (i.e.., death following bycatch mortality of mothers) being underrepresented in the bycatch sample. Results from the most plausible scenarios were "model averaged" by sampling from all MCMC chains with uniform probability. The median estimate for potential population growth (r_{nat}) was 0.043 (90% CI = 0.003 – 0.113). The median for actual growth (r) was -0.015 (90% CI = -0.141 – 0.072). The probability of population decline due to added fisheries mortality, prior to management to reduce bycatch, was 0.616. Our approach takes into account multiple sources of uncertainty in data and process, and provides posterior distributions for a rich set of demographic rate parameters that are unknown for most cetaceans. This method should be easily adaptable to other taxa for which fertility and age-at-death data are available.

Keywords: age distribution, Atlantic Ocean, conservation, fisheries, gillnets, growth, incidental catches, modeling, mortality rate, North America, survivorship

INTRODUCTION

Demographic statistics – such as population abundance, age-specific mortality and fertility rates, and population growth rates – are central to the study of species' life histories and are important for management of protected species. However, demographic rate estimates are lacking for many protected taxa (Heppell et al. 2000, Morris et al. 2002), especially those that are long-lived, wide-ranging, and difficult to observe, such as many large marine vertebrates (Musick 1999). Managers of marine populations are thus charged with making decisions based on information that may be highly uncertain and incomplete (Taylor et al. 2000, Thompson et al. 2000, Harwood 2000, Hilborn 2003, Botsford and Parma 2004). In the face of this challenge, new approaches are continually emerging to make inference about animal population dynamics and to guide management based on limited information and full characterizations of uncertainty (e.g., Taylor et al. 2000, Holmes 2001, Harwood and Stokes 2003, Ellner and Fieberg 2003, Tinker et al. 2006, Nicholson and Possingham 2007).

For example, management of incidental take (bycatch) of marine mammals in US fisheries, under 1994 amendments of the Marine Mammal Protection Act (MMPA), is based on

estimating a quantity called the Potential Biological Removal (PBR). This is the maximum allowable take from a population that still allows it to equilibrate at a level above which maximum net productivity occurs, and its calculation depends in part on an estimate of the intrinsic population growth rate, r_{max} (Wade 1998). The equation for PBR explicitly aims to minimize risk that could result from the large degrees of uncertainty inherent to most demographic estimates (Wade 1998, Taylor et al. 2000, 2007). However, there are few empirical estimates of r_{max} with which to calculate PBR, so a default value is typically used. For cetaceans the default is 0.04, and it is assumed that this value is conservative yet appropriate for most cetaceans for which no data are available (Wade 1998, Taylor et al. 2000). Yet potential growth rate estimates considerably lower (e.g., 2-3%: Brault and Caswell 1993, Wade 1998, Fujiwara and Caswell 2001; Alvarez-Flores and Heide-Jørgensen 2004) and higher than 4% (e.g., 6.5% - 14%: Best 1993; Barlow and Clapham 1997, Mizroch et al. 2004) exist, with reported rates appearing higher on average for mysticetes than odontocetes. Thus, the default value of 0.04 is unlikely to accurately represent true population growth rates in some cases, necessitating information about individual species demographic rates where possible.

More generally, knowledge of r_{max} is important for understanding species ecology and conservation under any policy framework, and it is central to population risk assessments (e.g., Caswell et al. 1998, Slooten et al. 2000, Burkhart and Slooten 2003, Dans et al. 2003). In the absence of survival rates or abundance trends to enable estimation of population growth, modeling efforts have been undertaken to determine plausible values of r_{max} for several odontocete species. Reilly and Barlow (1986), followed by Woodley and Read (1991) and Slooten and Lad (1991), used a Leslie matrix approach to estimate r_{max} for dolphins and porpoises under hypothetical vital rate values assumed to span the reasonable limits for these taxa. Other efforts have relied heavily on the use of "model life tables", whereby r_{max} is calculated from reproductive information for the case study species in conjunction with survivorship schedules of other species considered to have reasonably similar life histories to odontocetes (Woodley and Read 1991, Barlow and Boveng 1991, Slooten and Lad 1991, Caswell et al. 1998, Dans et al. 2003). The first approach is useful for identifying plausible upper limits for growth rates of odontocete populations but provides no means to assess which parameter combinations (and hence which value for r_{max}) are most likely. The second approach explicitly addresses uncertainty when conducted using Monte Carlo methods (Caswell et al. 1998, Dans et al. 2003), but inferences from these models are entirely dependent on the suitability of model species used and the appropriateness of age rescaling that is often performed (e.g., by longevity or age at first reproduction), both of which are unknown. Neither of these approaches provides insight about the actual survivorship schedule or related demographic rates (e.g., generation time, reproductive values, etc.) for the species of interest.

Data to directly estimate odontocete survival rates may be difficult or impossible to obtain, but for many species other types of information are often available – namely age structured data from carcasses and observations of reproductive schedules. We describe a flexible Bayesian approach for using age data from animals killed in fisheries and stranded on beaches, combined with reproductive data, to make inference about cetacean demographic rates and impacts of bycatch on population parameters. Our model is best viewed as an uncertainty analysis in that many combinations of demographic processes can predict the observed data equally well (Nelson et al. 2004). Our framework comprehensively explores the set of processes that may have generated the observed data and then inference is probabilistically based. The merits of using Bayesian methods to make use of limited and disparate datasets and characterize

uncertainty have been reviewed elsewhere (Wade 2000, Harwood and Stokes 2003, Clark 2005), and Bayesian approaches have been applied to study odontocete demography and risk assessment due to overharvest or bycatch (Kinas 2002, Alvarez-Flores and Heide-Jørgensen 2004). Our goal is to provide an analytical framework that is useful for gaining new insight about odontocete life histories, for which empirical information is rare.

We present a case study for the Gulf of Maine/Bay of Fundy (GOF/BOF) population of harbor porpoise (*Phocoena phocoena*), a small odontocete with a long history of fisheries bycatch (Read and Gaskin 1988, Read et al. 1993, Trippel et al. 1999). Concern about high take levels prior to the mid 1990s stimulated efforts to understand the impacts of bycatch on this population (Woodley and Read 1991, Caswell et al. 1998) and it was proposed for listing under the US Endangered Species Act in 1993 (Federal Register 58:3108-3120). Subsequent management to reduce harbor porpoise bycatch has been effective and the GOF/BOF population was removed from the candidate species list in 2001 (Federal Register 66:53195-53197). However, recent take has been increasing (Waring et al. 2007) and most harbor porpoise demographic rates are still unknown. Our analysis yields the first direct empirical estimates of many demographic parameters for this population, and provides quantitative evidence of historical impacts of bycatch on these parameters. Through providing new insight to harbor porpoise life history, our results may help with its future management, and our methods should be applicable to this or other taxa for which adequately large samples of these data types are available or could be collected.

METHODS

Harbor porpoise data

Strandings data (n = 96; Fig. 1) used in this analysis are taken from Wenzel (2000), who examined stranded porpoises from the coast of Massachusetts from 1977 to 1993. Bycatch data (n = 233; Fig. 1) come from carcasses retrieved by observers working aboard commercial gill net vessels in US waters of the Gulf of Maine from 1989 to 1993 (n = 92) and from Canadian waters of the Bay of Fundy from 1989 to 1993 (n = 141), obtained through a co-operative program with commercial gill net fishermen (Read and Hohn 1995). Reproductive parameters used in this analysis were age-specific estimates (from Read and Hohn 1995) of fertility (number of female calves per female), calculated for each age t as the product of sexual maturity rate and pregnancy rate (given maturity) at age $t - 1$, multiplied by 0.476, which is the expected proportion of calves that are females assuming a conservative 1.1:1 male-biased sex ratio (Lockyer 2003). Standard errors of maturity and pregnancy rates were weighted to arrive at the final fertility estimates: 0.284 ± 0.060 for age-4 individuals and 0.442 ± 0.033 for age 5+. We did not distinguish between sexes in the model because of limited observations in the strandings dataset and a similarity of age structure between sexes in the bycatch dataset (Read and Hohn 2005).

Basic model framework

We begin with the competing risk model of Siler, which has been used to describe survivorship curves from life table data for many mammal species (Siler 1979, Barlow and Boveng 1991, Bloch and Lockyer 1993, Gage 1998, Stolen and Barlow 2003). Age-specific mortality is a function of three hazards that separately describe mortality risk for juveniles, mature adults, and senescing animals. These three risks decrease, remain constant, and increase with age t, respectively, and are expressed as

$$\mu_{j,t} = a_1 \exp(-b_1 t), \quad (1)$$
$$\mu_{m,t} = a_2,$$
$$\mu_{s,t} = a_3 \exp(b_3 t),$$

where the a's and b's are parameters (non-negative) to be estimated from the data. Total mortality risk through time is the sum of these three hazards, i.e.,

$$\mu_t = \mu_{j,t} + \mu_{m,t} + \mu_{s,t}\ , \quad (2)$$

and the age specific mortality rate (i.e., the probability of dying between years t and t+1, given survival to age t) is

$$q(t) = \mu_t /(1+ \mu_t). \quad (3)$$

For a population in stable age distribution and growing at exponential rate r, the number of animals dying in each age class is proportional to the number of individuals alive in each age class multiplied by the mortality rate for each age class (Caughley 1977). Thus, if the age distribution of beach-stranded animals is representative of animals dying in the population, the expected proportion of stranded animals in each age class is

$$p(t) = \frac{e^{-rt} l(t) q(t)}{\sum_{t=0}^{T} e^{-rt} l(t) q(t)}, \quad (4)$$

where $l(t)$, is the probability of surviving from birth to age t, with $l(0) = 1$ and $l(t) = l(t-1)\cdot[1 - q(t-1)]$ for all other age classes. The goal is to estimate the population growth rate and the parameters describing the shape of the age-specific mortality or survivorship [$l(t)$] curve. In the absence of growth rate or recruitment estimates, mortality has traditionally been estimated based on assumed values for r (Caughley 1977, Stolen and Barlow 2003). However, we had no basis for choosing possible values of r in our system, and obtaining inference about this parameter from the model was an important motivation of our study.

A mixture model

For a population impacted by bycatch mortality, beach-stranded animals are a mixture of animals that die from natural causes and in fishing nets. Secchi and Fletcher (2004) proposed the following extension of the Siler model for using age-structured strandings and gillnet-mortality data to investigate demography of franciscana dolphins (*Pontoporia blainvillei*):

$$p'(t) = \alpha \cdot p(t) + (1 - \alpha) \cdot Q(t), \quad (5)$$

where α is a mixture parameter describing the relative contribution of natural deaths [$p(t)$; eqn. 4] and bycatch mortality [$Q(t)$, approximated as the age-structured bycatch data y_t] to the age structure of stranded animals [$p'(t)$]. The strategy of this model is to isolate natural population dynamics from the dynamics affected by bycatch mortality. Estimation occurs on the former. Thus, given an estimate of r (describing potential growth in the absence of bycatch), the natural-

survivorship parameters (a_1, a_2, a_3, b_1, b_3) and α are estimated by maximizing the multinomial likelihood

$$L(\mathbf{n}) = \prod_{t=0}^{T} \left[p'(t)\right]^{n_t} . \qquad (6)$$

This model was an important conceptual advance for using strandings data to study cetacean demography in systems significantly impacted by fisheries mortality. However, as in the non-mixture case, r must be known to estimate the survivorship parameters. Also, this model does not allow one to evaluate the impacts of bycatch mortality on population dynamics; estimation is restricted to parameters that describe natural survivorship and is conditional on a value for r that describes growth in a system with no bycatch mortality. Finally, this model implicitly assumes that population dynamics underpinning $p(t)$ and $Q(t)$ are independent of each other, which is unlikely to be the case.

We desire a model that allows us to: (1) make inference about both the survivorship parameters and r, rather than having to assume or independently estimate a value for r, and (2) evaluate demographic rates not just for the population in the hypothetical absence of fisheries impacts, but to assess the impacts of bycatch on demographic rates as well.

Extending the mixture model

We extended the model of Siler to include a description of mortality due to fisheries bycatch. For this we draw on work by Heligman and Pollard (1980), who modeled human mortality as the sum of four risk components, including one for which risk is maximized at some point in the middle of life (e.g., mortality of men during war, or of women due to complications with childbirth). Based on their model, we express "bycatch risk" as

$$\mu_{b,t} = D \exp\{-E[\ln(t)-\ln(F)]^2\}, \qquad (7)$$

where D, E and F are parameters (non-negative) to be estimated from the data. Parameter D increases with bycatch risk. Parameter F is a location parameter, corresponding to the age at which bycatch risk is highest. Parameter E increases as risk becomes more concentrated around age F. Note that $\mu_{b,t}$ is undefined at $t = 0$, which we handled by estimating t itself as a value between 0 and 1 for animals in their first year of life and using the corresponding estimate of $\mu_{b,t}$ for $\mu_{b,0}$. The added mortality rate due to bycatch (e.g., the probability of being killed in a gillnet between year t and t+1, given survival to t is

$$q_{byc}(t) = \mu_{b,t} /(1+ \mu_{b,t}). \qquad (8)$$

We will view equation 2 as the risk function for animals that die of natural causes, so that $q(t)$ from equation 3 is renamed $q_{nat}(t)$, and total mortality rate is

$$q_{tot}(t) = q_{nat}(t) + q_{byc}(t). \qquad (9)$$

Our mixture model is as in equation 5, but we redefine the terms from that equation:

$$p(t) = \frac{e^{-rt} l_{tot}(t) q_{nat}(t)}{\sum_{t=0}^{T} e^{-rt} l_{tot}(t) q_{nat}(t)}, \tag{10}$$

$$Q(t) = \frac{e^{-rt} l_{tot}(t) q_{byc}(t)}{\sum_{t=0}^{T} e^{-rt} l_{tot}(t) q_{byc}(t)}. \tag{11}$$

Here, r is for the actual population and thus reflects all sources of mortality, so it can be negative if bycatch has a strong impact. Equation 10 says that for animals which die a natural death, the proportion of deaths in each age class is proportional to the relative frequency of individuals that are alive in each class [$\propto e^{-rt} l_{tot}(t)$] multiplied by the mortality rate due to natural causes for each age class. Equation 11 is similar for animals that die in gillnets; the proportion of deaths is each age class is proportional to the age-structure of animals that survive all sources of mortality to age t [hence the $l_{tot}(t)$ term in these equations] multiplied by the mortality rate due to bycatch for each age class. Dead animals are a mixture of these two mortality types. The proportion of deaths due to natural mortality is α, which is not estimated independently but rather is calculated directly from the other estimated parameters:

$$\alpha = \sum_{t=0}^{T} \left[\frac{e^{-rt} l_{tot}(t) q_{nat}(t)}{\sum_{t=0}^{T} e^{-rt} l_{tot}(t) q_{nat}(t) + \sum_{t=0}^{T} e^{-rt} l_{tot}(t) q_{byc}(t)} \right]. \tag{12}$$

The expression within brackets is just the numerator from equation 10 divided by the sum of denominators from equations 10 and 11. If strandings are an unbiased sample of deaths in the population, then α is also the proportion of strandings due to natural deaths (see below for dealing with biased strandings samples).

This model explicitly describes survivorship in both the real population and in the population under a scenario of no bycatch. The former [$l_{tot}(t)$] is calculated directly from all survivorship parameters (a_1, a_2, a_3, b_1, b_3, D, E and F), whereas the latter [denoted $l_{nat}(t)$] is calculated from the a's and b's only. Given estimates for $l_{nat}(t)$ and independent estimates of age-specific fertility rates [m(t)], we can additionally use the Euler equation to estimate population growth rate (r_{nat}) under a scenario of no bycatch (once stationarity is reached):

$$1 = \sum_{t=0}^{T} e^{-r_{nat} t} l_{nat}(t) m(t). \tag{13}$$

Parameter estimation

For a vector of age-structured strandings data **n** and bycatch mortality data **y**, the likelihood function is

$$\mathrm{L}(\mathbf{n}, \mathbf{y} \mid \theta) = \prod_{t=0}^{T} M(n_t \mid \theta) \cdot M(y_t \mid \theta), \tag{14}$$

where M denotes the multinomial distribution and θ is the parameter set (a_1, a_2, a_3, b_1, b_3, D, E, F, r). The first component of the likelihood can be calculated as in equation 6, where the components of $p'(t)$ in equation 5 have been replaced by equations 10 – 12, and the age-structured bycatch data, y_t, are substituted for $Q(t)$. The second likelihood component is

$$\mathrm{L}(\mathbf{y}) = \prod_{t=0}^{T} [Q(t)]^{y_t} , \qquad (15)$$

where $Q(t)$ is from equation 11.

We estimated parameters using WinBUGS 1.4.1 (Spiegelhalter et al. 2004), freely available software for performing Bayesian analysis via Markov Chain Monte Carlo (MCMC) methods. For each model, we kept samples from two MCMC chains of length 400 000 iterations, following a burn-in of ~ 15 000 to 50 000. We kept every 80th sample to reduce autocorrelation; thus we calculated posterior distributions for parameters from 10 000 samples.

Bayesian priors

We used uniform (flat) priors for all parameters in equation 14 (Table 1). Intervals were limited at one end of the distributions to the bounds of possible parameter values (e.g.: a's, b's, D, E, F, $r_{nat} \geq 0$). Interval bounds at the other end were specified to exceed what we considered plausible limits to parameter values. Thus, priors were uninformative with the following exception. Siler parameters (a's and b's) can take on any positive value, but we restricted their values to relatively small intervals in order to improve the stability of their estimates. A variety of combinations of Siler parameters can describe the same survivorship curve and we found a full range of survivorship curves can be described well by Siler parameters with values between the intervals specified by the prior distributions we used.

Constraints

Since r_{nat}, r, and the parameters for natural and bycatch mortality rates were not identifiable, some external information or assumptions to constrain parameter estimates for useful inference. First, we linked the model of equation 14 to two Euler equations: one describing natural (potential) dynamics (eqn. 13) and the other describing actual dynamics [like eqn 13, but using r and $l_{tot}(t)$ instead of r_{nat} and $l_{nat}(t)$]. At each MCMC sample, values of $l_{nat}(t)$ and $l_{tot}(t)$ (calculated from the survivorship parameters), age-specific fertilities [$m(4)$ and $m(5+)$], and r and r_{nat} had to satisfy Euler unity constraints. Informative beta prior distributions were specified for fertilities (Table 1). Second, we asserted that survivorship to the known maximum age for harbor porpoise (24 years old, North Sea; Lockyer 2003) had to be < 0.01. Additional constraints are possible with additional information about the system. For example, one might constrain natural calf mortality, mortality of a particular age, or overall non-calf mortality based on information from a mark-resight study. If independent abundance estimates were available, informative priors could be specified for r, and so on. Incorporating such information would increase precision of all estimated parameters in the model.

Sources of bias

One probable source of bias in strandings samples is that animals which die naturally may be less likely than carcasses discarded by fishers to show up on the beach (e.g., if the former are killed by predators or if they sink due to lack of buoyancy following death by starvation).

Thus bycatch may be overrepresented in strandings data and the proportion of strandings from natural deaths will be less than α. We addressed this source of bias by adding a correction term γ that represents the relative probability of washing up on shore for an animal which died of natural causes compared to an animal that died from interaction with fisheries:

$$p'(t) = \frac{\alpha\gamma}{\alpha\gamma + (1-\alpha)} p(t) + \frac{1-\alpha}{\alpha\gamma + (1-\alpha)} Q(t) . \qquad (16)$$

Here, we have multiplied the first α in equation 5 by γ and then rescaled both mixture terms [$\alpha\gamma$ and $(1 - \alpha)$] so they sum to 1. Unfortunately, γ and α are not identifiable and so cannot be estimated simultaneously without additional information. Thus we performed modeling using γ = 1, 0.5, and 0.15. These represent scenarios in which an animal that died in a gillnet is equally likely, twice as likely, or nearly seven times as likely, respectively, to occur in a strandings sample compared to an animal that died naturally. The third value is based on recent strandings, fisheries mortality, and abundance data from the 2005 stock assessment report (SAR) for harbor porpoise (Waring et al. 2005), and was approximated as follows. From 1993-1999 an average of 5.8 out of 417 (0.013) harbor porpoises killed in observed US fisheries were stranded along US coasts. Using hypothetical sets of plausible Siler parameters consistent with 4% annual growth and an abundance point estimate for 1999 of 89 700 animals, the expected number of natural deaths in the population is roughly 15 000 (about 17%). Of these, 36.4/year (0.0021) stranded from 1999-2003. The ratio of natural-death stranding rate to fisheries-death stranding rate is roughly 0.15. Calculating crude γ in a similar fashion based on the 2007 harbor porpoise SAR (Waring et al. 2007) yields a point estimate of ~ 0.41, while doing so based on data from Cox et al. (1998) yields $\gamma \sim 0.07$. This range of values highlights the considerable uncertainty in γ, and these values did not even address uncertainty in constituent values, but all suggest that γ is probably much less than 1.

We also expect calf mortality caused by fisheries to be underrepresented in observer samples. This is because calves whose mothers die in gillnets are subsequently likely to die of starvation (Woodley and Read 1991). This probable data bias should lead to underestimating the impact of fisheries on calf mortality and will in turn lead to high-biased estimates of natural calf mortality in order to explain the numbers of stranded calves. We addressed this by running two sets of models: one on the original data (we call these models A, B, C, each model corresponding to the three γ values above in descending order) and one on a dataset in which we artificially added 34 calf mortalities to the 32 calves recorded in observer samples (we denote these D, E, F). This added calf mortality represents a worst-case in which all sexually mature individuals in the bycatch sample had 0.28 (for 4-yr olds) or 0.44 (for age 5+) calves that were not included in the bycatch sample but that subsequently died.

We summarize results from individual models and then provide detailed results based on averaging results from models B, C, E, and F. We felt these models ($\gamma \leq 0.5$) were the most plausible for reasons mentioned above. Results were averaged by drawing a total of 10 000 samples from MCMC chains of the four individual models with uniform probability.

RESULTS

Inference from individual models

Median estimates of r and r_{nat} across the six model scenarios ranged from -0.038 to 0.000 and from 0.032 to 0.052, respectively (Table 2). Ninety-five percent upper limits (one-tailed) for r_{nat} varied from 0.098 to 0.121. Uncertainty in estimates of r was high, but the probability of population decline as a result of unsustainable bycatch mortality (i.e., proportion of posterior distribution for $r < 0$) varied from 0.50 to 0.73. All models suggested natural mortality of harbor porpoise calves is substantial, with median estimates ranging from 0.33 to 0.46 (Table 2). These are higher than published estimates for any other odontocete (Olesiuk et al. 1990, Wells and Scott 1990, Bloch and Lockyer 1993, Herzing 1997, Haase and Schneider 2001, Stolen and Barlow 2003, Kogi et al. 2004). High calf mortality rates were required to explain the disproportionately large number of calf carcasses in beach-strandings data relative to in the bycatch samples, even after we artificially inflated the latter. Calf mortality estimates were highest in scenarios when $\gamma = 0.17$ (models C and F) to account for the large numbers of beach-stranded calf carcasses when the natural-death component of the strandings sample was assumed to be comparatively small (Table 2). Annual natural mortality rates declined to a minimum between ages 5 and 6 [$q_{nat}(5)$] in all models except F, in which minimum mortality occurred between ages 4 and 5 (Fig 2). Median estimates for q_{nat}(min) across models ranged from 0.059 to 0.087. Median natural non-calf mortality (weighted by proportion of individuals alive in age class) varied from 0.110 to 0.133.

The extent to which bycatch risk increased mortality rate varied considerably across models (Fig. 2). However, in all cases, mortality risk was highest for two-year olds and in general was highest in early life. Across models, median estimates for the proportion of the population removed by bycatch annually ranged from 0.023 to 0.059 (Table 2). Median estimates of other derived demographic parameters, including generation times, net reproductive rates (expected number of female calves a female will have in her lifetime), and the proportion of deaths occurring in the population due to natural causes (α) are in Table 2. The proportional contribution of natural deaths to stranding samples (η) varied from 0.316 to 0.821 across models. Values from models with $\gamma \leq 0.5$ ($\eta = 0.316$ to 0.659) are more similar to values reported by Cox et al. (1998; 0.37) and provide additional justification for excluding models with $\gamma = 1$ for model averaging purposes.

Inference from model averaging

Posterior distributions for mortality parameters (Fig.3) did not appear unduly constrained by the priors we specified, with one exception. The upper bound of 5 used in the prior for parameter b1 appeared to constrain its posterior distribution slightly. However, this constraint was necessary for two reasons. First, larger values of b1 result in natural mortality curves in which one-year olds have the lowest mortality. This is biologically unrealistic, but estimates greater than 5 occur without the constraint because concomitant increases in parameter D enable high numbers of age-1 strandings to be explained by unrealistically high bycatch mortality of one-year olds. Second, for these data, the rate of decrease in juvenile risk increases asymptotically as b1 approaches ~ 7. Higher values of b1 therefore have no additional effect on the juvenile risk curve, so estimates of b1 become unstable, with values between about 7 and infinity occurring with equal probability. The posterior distribution for t_0 was constrained by its prior, but values > 1 are not possible under our assumption that the value of t for a 0-yr old must be less than t of a 1-year old (which is obviously 1). Posterior means for fertilities were slightly larger than priors (m[4]: mean = 0.30, SD = 0.06; m[5+]: mean = 0.46, SD = 0.016), indicating better model fit with fertilities higher than those reported by Read and Hohn (1995).

Because of skewness and correlation between parameters, using means or medians for all parameters is not appropriate for obtaining mortality or survivorship curves. We calculated curves for each MCMC sample of the mortality parameters and then age-specific mortalities and survivorships (and other related parameters) were subsequently summarized. As expected given the available information, there was considerable uncertainty in age-specific estimates of mortality and the survivorship schedule (Fig. 4). However, there was clear evidence of high natural mortality rates of calves (90% CI: 0.25 – 0.57; median = 0.40), with mortality declining to a minimum around the age of first reproduction [90% CI for $q_{nat}(5)$: 0.020 – 0.125; median = 0.067] and accelerating senescent mortality occurring before age 15. Natural mortality estimates for calves appeared approximately normally distributed (Fig. 5), whereas mortality estimates for young adults displayed much weaker central tendency, hence the wide credible intervals for $q_{nat}(5)$. Mortality estimates beyond about age 12 became increasingly uncertain due to lack of data for older age classes.

Mean natural non-calf mortality, $q_{nat}(t>0)$, had a median estimate of 0.113, with 90% CI = 0.058 – 0.156 (Fig. 6). Median r_{nat} was 0.043 (90% CI = 0.003 – 0.113) with a highly skewed-right posterior distribution that lacked any central tendency (Fig. 6). This is a result of the prior constraint for r_{nat} to be greater than zero. Estimates of r_{nat} were strongly correlated to non-calf mortality (Fig. 7). Conditional on low values of non-calf mortality (e.g., the lower 10th percentile), estimates of r_{nat} had a mean near 0.10 and median near 0.12 (Fig. 6, b1). Conditional on the center 10th (45th to 55th) percentile values of non-calf mortality, estimates of r_{nat} had a mean near 0.05, close to the median marginal estimate of r_{nat}. However, for larger estimates of non-calf mortality, conditional posterior distributions for r_{nat} begin stacking up against zero. This results in the highly skewed marginal posterior distribution for r_{nat}.

Based on median estimates, bycatch morbidity increased annual mortality rates by nearly 0.08 during the third year of life and about 0.05 until after the sixth year (Fig. 4). These estimates were highly uncertain, with 90% CI ranging from 0.01 to 0.23 for 2-yr olds (Fig. 4). However, models provided clear indication that peak risk to bycatch occurred between age 2 and 3. Total incidental take was as estimated at 4.2%, but with a wide credible interval (90% CI = 0.8 – 12.5%; Fig. 5). Importantly, because bycatch risk was higher for younger animals of higher reproductive value (Fig. 8), a given amount of take corresponded to a disproportionately large effect on r. This is clear from the relationships describing r and ($r_{nat} - r$) as a function of '% incidental take' (Fig. 7). Population decline was expected for take > 0.036 of the population even though the median estimate of r_{nat} was 0.042. This is because a 4% removal from the population corresponded to a 5% reduction in r under this model.

Mediate estimates of net reproductive rates (R_0) and generation times were 1.47 female calves/female (90% CI = 1.03 – 2.80) and 9.4 years (CI = 8.2 – 10.5), respectively, in the absence of fisheries mortality. These were reduced to 0.87 female calves/female (CI = 0.30 – 1.92) and 8.9 years (CI = 7.4 – 10.1), respectively, as a result of fisheries mortality under this model. Age-specific net reproductive rates peaked at age 5 (Fig. 8), coinciding with age of first reproduction for most females. Median estimates of life expectancy in a population not subject to fisheries mortality was 5.3 years for a newborn and peaked at 8.5 for an individual that reached its second birthday. In a population affected by bycatch, newborn life expectancy was 3.8 years and did not peak until an individual reached its fourth birthday, at which point life expectancy was 6.5 years.

Model goodness of fit

In general, models fit the data well (Fig. 9). We conducted χ^2 tests of frequencies in each age class, in which the median χ^2 value from MCMC samples was evaluated against χ^2 values from 100 000 random datasets generated from a multinomial distribution with expected frequencies equal to that of the fitted median age distribution. P-values across all 6 model scenarios varied from 0.34 – 0.60 for the strandings datasets (0.43 for the model averaged results), and from 0.66 – 0.80 for the bycatch datasets. However, the frequency of age-1 individuals in the strandings dataset was considerably higher than could be explained by the model (Fig. 9). This suggests that either strandings data were a biased sample of the population with respect to the number of age-1 individuals (e.g., if dead one-year olds are more likely to wash up than dead individuals of other age classes) or that the Siler model does not accurately characterize mortality of harbor porpoises in early years of life. Under the Siler model, juvenile risk decreases exponentially from birth. However, if age-1 mortality is similar to calf mortality and then drops sharply thereafter, the mortality function will be convex before becoming concave, and will not be described well by the Siler function during those years.

DISCUSSION

We have described an analytical framework for combining different sources of information that is either available or could be collected for many coastal odontocete populations to obtain detailed inference about their demography and the impacts of bycatch on their vital rates. Prior constraints on parameter estimation were specified with uncertainty (e.g., fertility rates) or were addressed through use of scenarios (e.g., for γ and age-0 bycatch data bias), and uncertainty in output parameters were fully described. Our framework is flexible in that it allows many types of additional information to be incorporated to inform parameter estimation. We only used reproductive information, the Euler equation, and a plausible longevity specification to help guide model fitting, although other information could have been incorporated if available. For example, current strandings data from the Marine Mammal Strandings Network in the US include information about the proportion of stranded carcasses that are due to interactions with fisheries (Waring et al. 2007). This information could be used to constrain estimates of the mixture parameter in equation 16, which should allow direct estimation of γ. Repeated abundance data and estimates of fisheries take could be used to place informative priors on r or on derived estimates of percentage take. Our framework should also be applicable for populations that do not interact substantially with fisheries but for which strandings data are available. In such cases, the basic Siler model could be used in conjunction with age-specific fertility data and use of the Euler equation.

The primary assumption of our model is that age structure is stable. Some methods have been developed to circumvent this assumption (e.g., Udevitz and Ballachy 1998, Doak and Morris 1999), but all rely on data typically not available in studies of odontocetes. For now, assuming stationarity is a limiting but unavoidable caveat of most demographic analyses of long-lived and data deficient species. However, demographic estimates for species with “slow” life histories (e.g., high survival rates and long generation times) may be reasonably robust to stochastic fluctuation in stationarity (Stolen and Barlow 2003) and our use of strandings data from over a 17-year time period may help buffer against temporary effects on age-specific survival or strandings structure. Fitting smooth functions to the data may similarly buffer against transient processes or data biases. For example, the large numbers of age-1 individuals in the strandings data suggest either higher natural mortality for 1-year olds than can be described by

an exponentially declining juvenile risk function, or that carcasses of 1-year olds are more likely to be recovered from beaches (e.g., if there is age variation in distribution due to differential habitat use). In the latter case, the model estimates would be correcting for this bias, since they predict fewer 1-year old carcasses in strandings samples than were observed. Permanent shifts in age structure due to chronic age-biased mortality would not be a problem if a new stable distribution had been achieved, since we were modeling this explicitly. More problematic would be if age structure was in the process of transition due to bycatch being a recent phenomenon relative to harbor porpoise life spans or due to shifts in bycatch regimes. Thus some caution should be exercised in the interpretation of our results.

The second main limitation in our model was the need to speculate on the upper probability of survivorship to maximum age. This was the only component of our estimation that was not entirely data driven. Maximum observed age in strandings data may significantly underestimate the maximum possible age (Barlow and Boveng 1991), especially for a population subject to additive human-caused mortality. Maximum-age records from many harbor porpoise populations suggest that longevity > 20 yrs is likely (Lockyer 2003) and as strandings datasets become larger, we will be better able to make informed guesses about maximum lifespan. However, what proportion of individuals lives to maximum age? We suggested a reasonable upper limit of 0.01. Subject to this constraint, the modal estimate for survivorship to age 24 was very close to zero (Fig. 3). Therefore, we are comfortable that an upper constraint of 0.01 did not unduly restrict or bias estimates. Still, it may also be difficult to place sensible constraints on longevity for systems that are more data limited. In systems where survival estimates can be incorporated to constrain the model (e.g., if non-calf survival estimates are available from photographically based "capture-recapture" studies), this would probably allow the longevity constraint to be removed.

Finally, we modeled both sexes of harbor porpoise together because of the relatively small strandings dataset. However, sex differences in survivorship have been observed in other mammal species including odontocetes, with females generally expected to have higher survival and longevities (Caughley 1966, Bloch and Lockyer 1993, Allman et al. 1998, Stolen and Barlow 2003, Toïgo and Gaillard 2003, Tinker et al. 2006). If this is the case for harbor porpoises, then estimated rates of survivorship and population growth are expected to be higher than what we present from this analysis. On the other hand, male-biased sex ratios have consistently been reported in harbor porpoises samples in the eastern Atlantic (Lockyer 2003) but whether this reflects a male-biased population (higher male survival) or male-biased gillnet mortality (lower male survival) is unknown (Lockyer and Kinze 2003). Moreover, species sex ratios have been observed to vary between populations and through time (Bloch and Lockyer 1993). In our data, bycatch samples were 1.2:1 male-biased and strandings data were 1.3:1 male-biased (44/77). More data should enable us to estimate sex-specific survivorship of harbor porpoise in future efforts.

Subject to the limitations we have mentioned, our study provides the first empirical estimates of several demographic parameters for harbor porpoise, and to our knowledge, we have provided the first entirely data-driven estimates for any odontocete of the impacts of bycatch on a species' mortality schedule and other age-related demographic parameters. Empirical estimates of mortality schedules only exist for a handful of odontocete species, so our results provide important rare insight to cetacean life histories in general. Previous efforts to investigate population growth or impacts of bycatch on harbor porpoise have relied on estimated survivorship schedules of other species, with highly variable outcomes. Barlow and Boveng

(1991) used a human survivorship curve rescaled to longevity near 10 years, in combination with harbor porpoise reproductive information, to obtain what they considered an upper bound estimate of $r_{max} = 0.09$. Woodley and Read (1991), assuming longevity of 12 or 15 years, estimated potential r_{max} to vary with input parameters from zero up to 0.10 and 0.05 under two different models, the first based on methods of Reilly and Barlow (1986), and the second based on an estimated survivorship schedule for Himalayan thar (*Hemitragus jemlahicus*). Finally, Caswell et al. (1998) used a Monte Carlo approach and rescaled survivorship curves from 9 other mammal species to estimate a median r_{max} for harbor porpoise of 0.09 with 95% upper limits between 0.14 and 0.18. Obviously, the results from these studies depended on the model survivorship schedules that were used and there is no way to evaluate which estimates were valid. No one has been able to estimate harbor porpoise mortality rates, let alone how these rates are affected by fisheries.

Our analysis suggests that during the late 1970s through early 1990s, the Gulf of Maine/Bay of Fundy population of harbor porpoise was likely declining as a result of unsustainable levels of bycatch, which was mostly likely around 4 – 5 % of the population per year, and possibly > 12%. Our posterior distribution for percentage take is similar to the confidence interval provided by Caswell et al. (1998), who used a bootstrap analysis of population size and incidental take data provided by Bravington and Bisack (1996). This provides some validation to our model. Precision of our estimates was low, as our method merely characterizes the set of possible parameter combinations that describe the data. However, it does so by accounting fully for uncertainty in all parameters and data inputs. Inclusion of additional information and constraints will narrow the set of possibilities and increase precision of estimates in future analyses.

Although we cannot determine whether our estimates of r_{nat} represent r_{max}, since we do not know if the harbor porpoise population was small enough for resources to allow maximum possible growth, our analysis provide important empirical validation for using a value of 0.04 as a growth rate estimate in PBR calculations for harbor porpoise. Our best point estimate suggests that harbor porpoise natural growth rates are near this level; however, given the disproportionate impact of bycatch on young individuals, it may be prudent to use a slightly smaller value for r_{max} in the PBR calculation. For example, assume for simplicity that $r_{max} = 0.04$ and a recovery factor = 1 (see Wade 1998, for an explanation of the recovery factor and the PBR equation). Then, allowable take under current PBR management would be $0.02 * N_{min}$. This rate ($r_{max}/2$) is the expected per capita growth when the population is at the minimum level to allow maximum net productivity (one half carrying capacity). However, if the population was at a level where $r = 0.02$, a 2% removal from the population would reduce r to -0.005 rather than to zero, based on the relationship shown in Fig. 7c. Although our estimates of r_{nat} contain considerable uncertainty, they nevertheless yield a lower plausible limit than that provided by Caswell et al. (1998), and they are more valid in general than previous studies by virtue of being anchored entirely to harbor porpoise data rather than to survivorship schedules from other species.

Our upper credible limits for r_{nat} exceed that typically considered plausible for odontocetes. In part, this probably just reflects a lack of additional information that could be used to constrain mortality estimates to a narrower range than that which fits the data. For example, the expected value of r_{nat} was 0.10 when non-calf mortality was 0.06 (lower 90% CI), based on the relationship shown in Fig. 7a. This mortality rate is probably unrealistically low, but it fits the data and we have no basis for setting a lower limit. Obtaining additional information to constrain any of the estimated parameters, whether calf survival or non-calf

survival (with or without impacts of bycatch), estimated take percentage, or independent estimates of *r* based on abundance trend data, would help increase the precision of other parameter estimates. Additionally, however, the relatively large values for r_{nat} may to some extent reflect a genuinely higher growth rate potential of harbor porpoises relative to other odontocetes. Harbor porpoises are unusual among odontocetes in their reproductive schedule; few other species have an earlier age of first reproduction or reproduce as frequently (Read and Hohn 1995). Considering that harbor porpoises seem to have similar life spans to some other small odontocetes that calve less frequently (e.g., franciscana [Kinas et al. 2002], Hector's dolphin [Slooten et al. 2000]), we would expect harbor porpoises to have higher population growth rate potential than these species unless harbor porpoises have substantially more severe mortality schedules. We did estimate harbor porpoise calves to have higher natural mortality rates than has been reported for any other odontocete, but information on mortality rates for calves or any other age class is very rare for odontocetes in general and does not exist for other species with short life spans.

In summary, we have demonstrated a new Bayesian application for obtaining inference and characterizing uncertainty about cetacean demography based on the types of information mostly likely to be available for many populations. Our model is flexible, can incorporate additional information beyond what we built into our models, and could be extended to other systems with age-at-death data, including terrestrial systems and possibly other marine taxa with abundant strandings data such as sea turtles (Epperly et al. 1996) or sea otters (Tinker et al. 2006). We used this application to obtain novel insight to harbor porpoise demography, and the historical impacts of bycatch on vital rates. As additional abundance estimates are obtained and as more recent age-at-death data based on strandings and observer programs become available, this framework could be applied to evaluate more current demographic trends with greater precision. We hope this framework will find utility in other systems to advance our understanding of demography for other odontocetes and that it will inform the process of setting incidental take limits for marine mammals.

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Table 1. Prior distributions and constraints

Parameter	Prior distribution	Interpretation
a_1	Uniform(0, 3)	Increases with age-0 mortality risk
a_2	Uniform(0, 1)	Parameter for constant mortality risk
a_3	Uniform(0, 1)	Parameter for senescent mortality risk
b_1	Uniform(0, 5)	Rate of decrease in juvenile mortality risk
b_3	Uniform(0, 1)	Rate of increase in senescent mortality risk
D	Uniform(0, 1)	Parameter related to severity of bycatch risk
E	Uniform(0, 5)	Shape parameter for bycatch risk
F	Uniform(0, 10)	Parameter related to age of peak bycatch risk
r_{nat}	Uniform(0, 0.5)	Population growth in absence of bycatch
ρ	Uniform(-0.5, 0)	Difference between r and r_{nat} ($r = r_{nat} - \rho$)
t_0	Uniform(0, 1)	Value for t in estimating $\mu_{b,0}$
$m(4)$[a]	Beta(8.2, 5.5) * 0.476	Fertility of 4-yr olds ($\mu = 0.284$, $\sigma = 0.06$)[b]
$m(5+)$[a]	Beta(12.0, 0.9) * 0.476	Fertility of 5+ yr olds ($\mu = 0.442$, $\sigma = 0.03$)[b]
$l_{nat}(24)$[c]	Uniform(0, 0.01)	Survivorship to age 24

a Fertilities estimates were used in Euler equation to constrain other parameters.

b Female calves per female, calculated based on data from Read and Hohn (1995) and an assumed 1.1:1 male-biased fetal sex ratio (Lockyer 2003).

c Estimates of $l_{nat}(24)$ derived from a and b parameters had to satisfy constraint of being between 0 and 0.01

Table 2. Demographic estimates (median and 90% Bayesian credible intervals) from 6 models fit to harbor porpoise beach-strandings and bycatch data. Models A – C were fit to original data. Models D – F were fit to data in which age-0 bycatch numbers were artificially increased to correct for probable bias in original data. See text for explanation of γ.

Model	A	B	C	D	E	F
γ	1	0.5	0.17	1	0.5	0.17
r_{nat} (%)	4.1 (0.3, 10.6)	4.9 (0.4, 11.9)	3.2 (0.3, 9.8)	3.9 (0.3, 12.1)	5.1 (0.5, 12.0)	4.1 (0.4, 10.7)
r (%)	-1.1 (-12.6, 6.6)	-1.1 (-10.4, 7.5)	0.0 (-6.6, 7.9)	-0.5 (-9.9, 6.3)	-2.2 (-14.8, 6.8)	-3.8 (-21.5, 6.3)
P($r < 0$)	0.596	0.583	0.499	0.559	0.645	0.729
Take (%)[a]	4.0 (0.5, 12.1)	4.5 (0.8, 10.1)	2.3 (0.6, 5.6)	3.8 (0.4, 11.4)	5.9 (1.1, 13.4)	5.9 (1.5, 15.6)
α (%)[b]	81.4 (57.2, 97.4)	79.4 (61.2, 95.8)	89.2 (78.7, 96.9)	82.1 (53.4, 97.7)	73.9 (53.0, 94.0)	75.5 (53.8, 92.3)
η (%)[c]	81.4 (57.2, 97.4)	65.9 (44.1, 91.9)	55.4 (35.7, 82.6)	82.1 (53.4, 97.7)	58.6 (36.1, 88.6)	31.6 (14.8, 64.2)
$q_{nat}(0)$	0.35 (0.24, 0.44)	0.38 (0.26, 0.51)	0.46 (0.30, 0.62)	0.33 (0.22, 0.42)	0.34 (0.22, 0.45)	0.42 (0.26, 0.58)
q_{nat}(min)	0.08 (0.03, 0.13)	0.06 (0.02, 0.12)	0.06 (0.02, 0.11)	0.09 (0.03, 0.13)	0.08 (0.03, 0.13)	0.07 (0.02, 0.12)
$q_{nat}(t>0)$	0.13 (0.07, 0.16)	0.11 (0.05, 0.16)	0.11 (0.06, 0.15)	0.13 (0.06, 0.16)	0.12 (0.06, 0.16)	0.11 (0.06, 0.15)
$T_{G.nat}$[d]	9.3 (8.3, 10.3)	9.5 (8.5, 10.6)	9.6 (8.6, 10.6)	9.3 (8.3, 10.3)	9.2 (8.1, 10.3)	9.1 (7.9, 10.3)
T_G[d]	8.9 (7.5, 9.9)	9.0 (7.8, 10.1)	9.3 (8.3, 10.4)	8.9 (7.7, 9.9)	8.7 (7.2, 10.0)	8.6 (7.0, 10.3)
$R_{0.nat}$[e]	1.44 (1.03, 2.61)	1.57 (1.04, 3.00)	1.34 (1.02, 2.50)	1.41 (1.03, 2.98)	1.56 (1.04, 2.95)	1.43 (1.03, 2.64)
R_0[e]	0.90 (0.34, 1.81)	0.91 (0.39, 1.97)	1.00 (0.53, 2.07)	0.95 (0.42, 1.77)	0.82 (0.29, 1.85)	0.71 (0.17, 1.77)

a = percentage of population removed by bycatch. b = percentage of deaths in population due to natural causes. c = percentage of beach stranded animals that died by natural causes. d = generation time for a population not affected by bycatch ($T_{G.nat}$) and one affected by bycatch (T_G). e = Net reproductive rate (females/female) for a population not affected by bycatch ($R_{0.nat}$) and one affected by bycatch (R_0). See text for descriptions of other statistics.

Figure Captions

FIG. 1. Age frequency data for the Gulf of Maine/Bay of Fundy population of harbor porpoise. Strandings data are from Massachusetts (1977-1993; Wenzel 2000). Bycatch data are from the Gulf of Maine, US, and Bay of Fundy, Canada (1989-1993; Read and Hohn 1995).

FIG. 2. Median survivorship and mortality curves from six models fit to harbor porpoise bycatch and beach-strandings data. (a) Survivorship schedule in the absence of fisheries mortality. (b) Survivorship including natural and bycatch mortality. (c) Annual mortality rates in the absence of fisheries mortality. (d) Annual mortality rate due to bycatch. Mortality in panels (c) and (d) sum to total mortality, which yield survivorship in (b). Models A – C (solid lines and symbols) were fit to original data. Models D – F (broken lines and open symbols) were fit to data in which age-0 bycatch numbers were artificially increased to correct for probable bias in original data.

FIG. 3. Model-averaged Bayesian posterior densities (with medians and 90% credible limits) for natural mortality parameters (a's and b's), bycatch mortality parameters (D, E, F), natural survivorship to maximum known age ($l_{nat}[24]$, constrained to be < 0.01), fertilities (m[4] and m[5+]), and t_0 (the value of t used to calculate $\mu_{b,0}$; see eqn. 7 in text).

FIG. 4. Median estimates (large symbols), 70% (medium symbols), and 90% (small symbols) Bayesian credible limits for (a) natural survivorship (no bycatch mortality), (b) actual survivorship (including effects of bycatch), (c) natural age-specific mortality, and (d) added bycatch mortality of harbor porpoises based on model averaged estimates. Fine gray lines depict 50 random curves selected from MCMC chains.

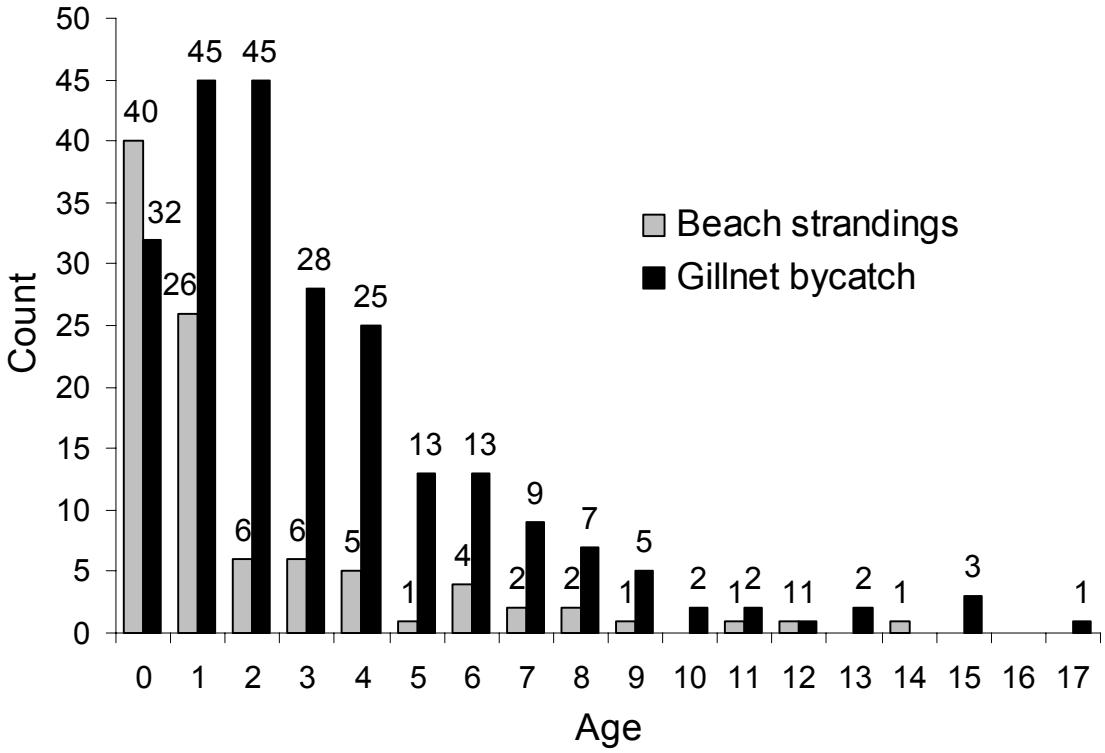
FIG. 5. Posterior distributions for (a) natural calf mortality, (b) natural mortality from age 5 to 6, (c) proportion of the population killed by interactions with fisheries, and (d) population growth rate, averaged from models B, C, E and F, fit to harbor porpoise strandings and bycatch data. Dashed line = median; Dash-dotted line = 70% Bayesian credible interval; Dotted line = 90% Bayesian credible interval.

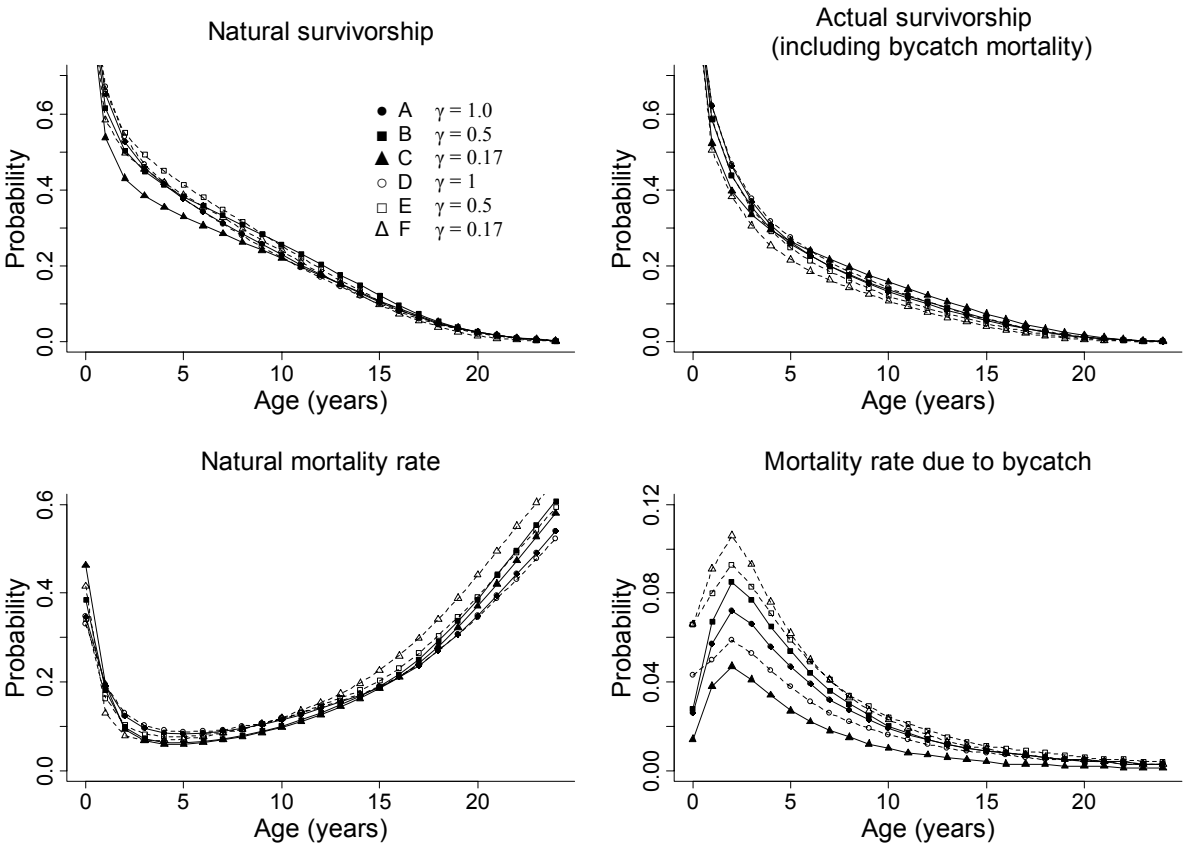
FIG. 6. Posterior distributions for (a) natural non-calf mortality and (c) r_{nat}, averaged from models B, C, E and F, fit to harbor porpoise strandings and bycatch data. Dashed line = median; Dash-dotted line = 70% Bayesian credible limits; Dotted line = 90% Bayesian credible limits. Arrows (b's) point to conditional posterior distributions of r_{nat} for 10-percentile ranges (b1 = 0-10%; b2= 10-20%; b3 = 45-55%; b4 = 80-90%; b5 = 90-100%) of non-calf mortality centered on median and CI non-calf mortality values (0.06, 0.08, 0.11, 0.14, and 0.16).

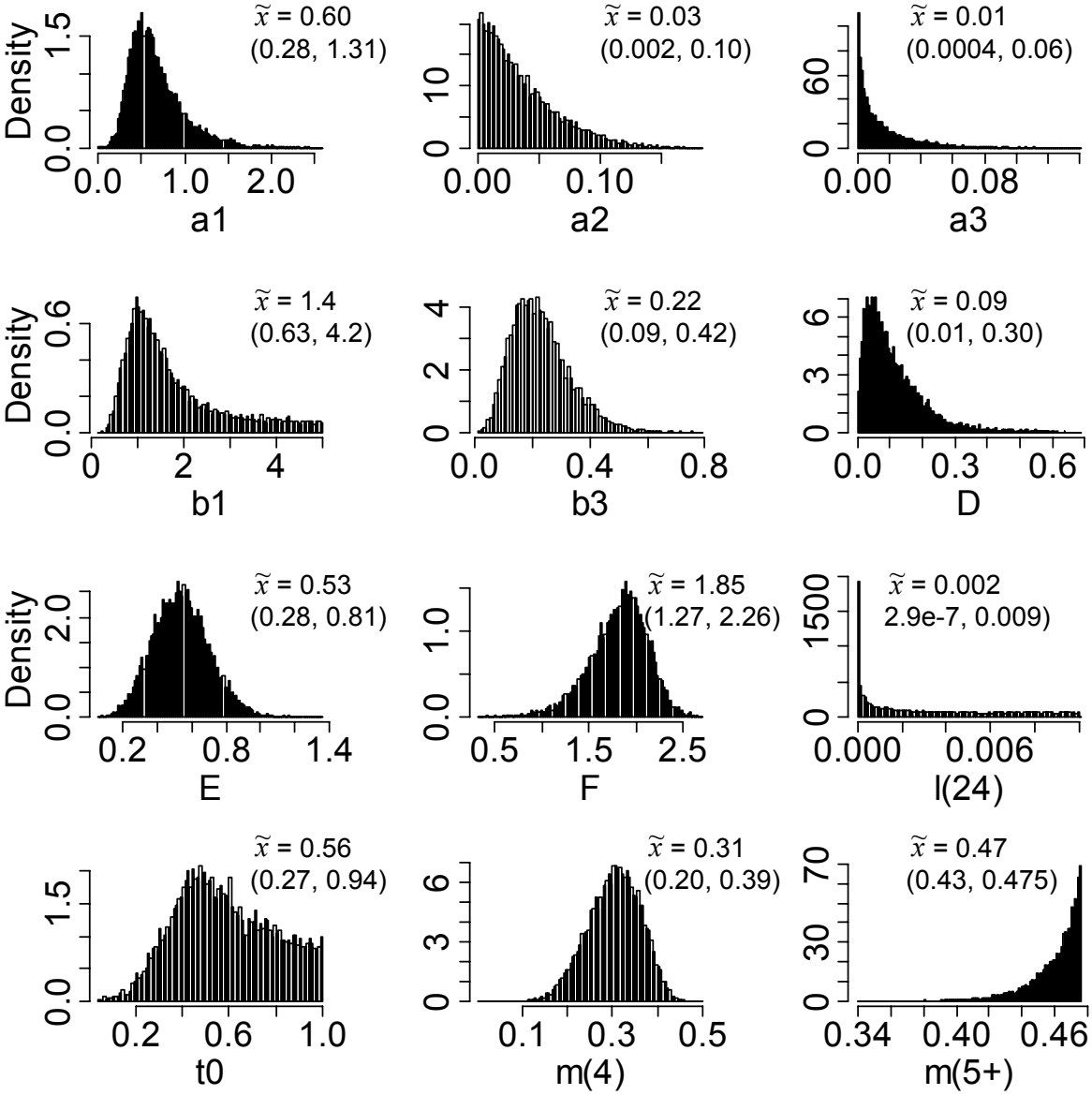
FIG. 7. Scatter plots showing relationships between model averaged estimates of harbor porpoise demographic parameters. Values from 1000 randomly selected MCMC samples are plotted. (a) Average non-calf survival [$1 - q_{nat}(t>0)$] vs. r_{nat}; vertical dashed line shows median survival estimate. (b) Incidental take vs. r; vertical arrow shows the incidental take value (~0.036) at which expected r is less than zero. (c) Incidental take vs. decline in per capita growth. Vertical arrow corresponds to the take level at which population decline is expected (see b). This corresponds to an expected decline in growth of ~ 0.045.

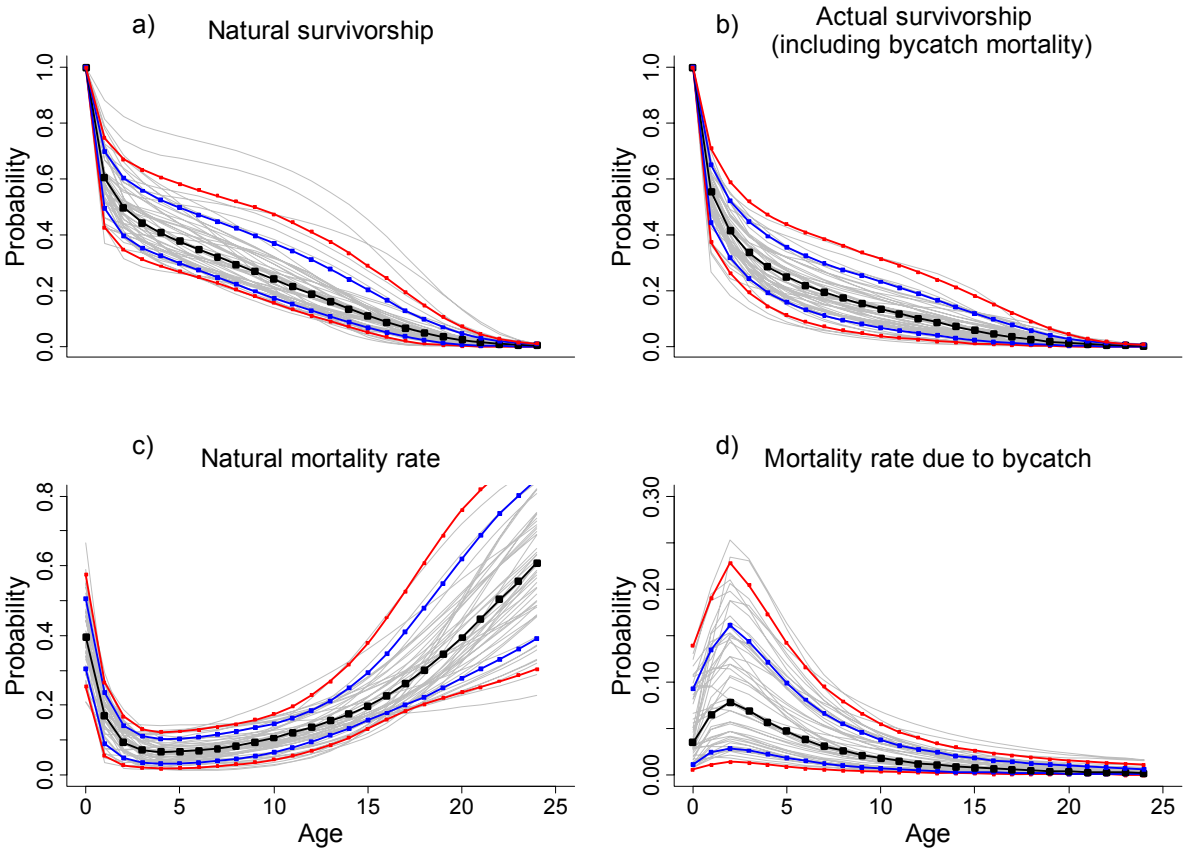
FIG. 8. Median (a) age-specific net reproductive rates (expected number of female calves a female will have in the rest of her live, given she has survived to age *t*) and (b) life expectancy of harbor porpoise, averaged from models B, C, E and F, fit to harbor porpoise strandings and bycatch data. Symbols denote median estimates for a population that is (□) or is not (▲) subjected to fisheries mortality. Broken and solid lines without symbols denote 95% Bayesian credible intervals for (□) and (▲), respectively.

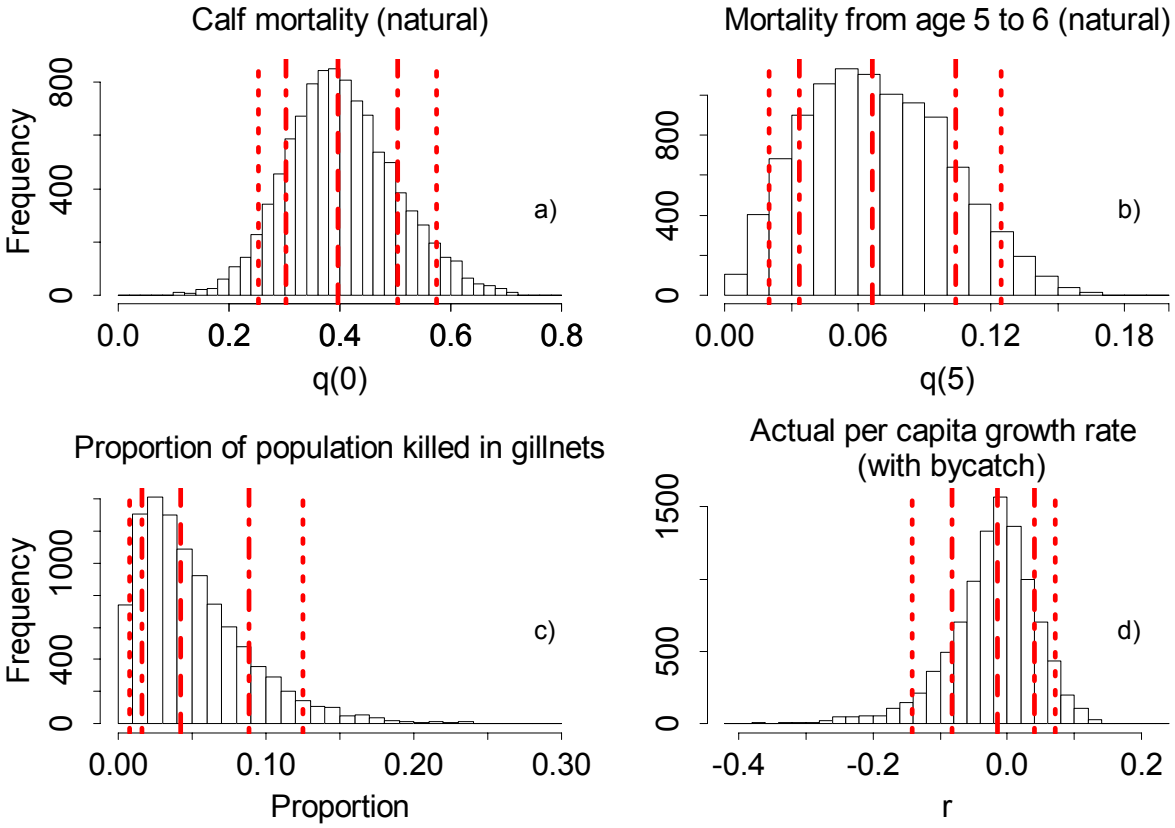
FIG 9. Expected and observed (bars) frequencies of harbor porpoise carcasses (a and c) stranded on beaches in Massachusetts, and (b and d) retrieved by US and Canadian fisheries observers. Top two panels are from model B ($\gamma = 0.5$, fit to original data). Bottom panels are from model E ($\gamma = 0.5$, fit to data with inflated age-0). Dashed line is the expected proportion of animals in each age class on a continuous scale. Solid points (●) are the median frequencies from 100 000 random datasets generated from a multinomial distribution described by the dashed line. Open points (○) depict the 2.5th and 97.5th percentile frequencies from the 100 000 random datasets.

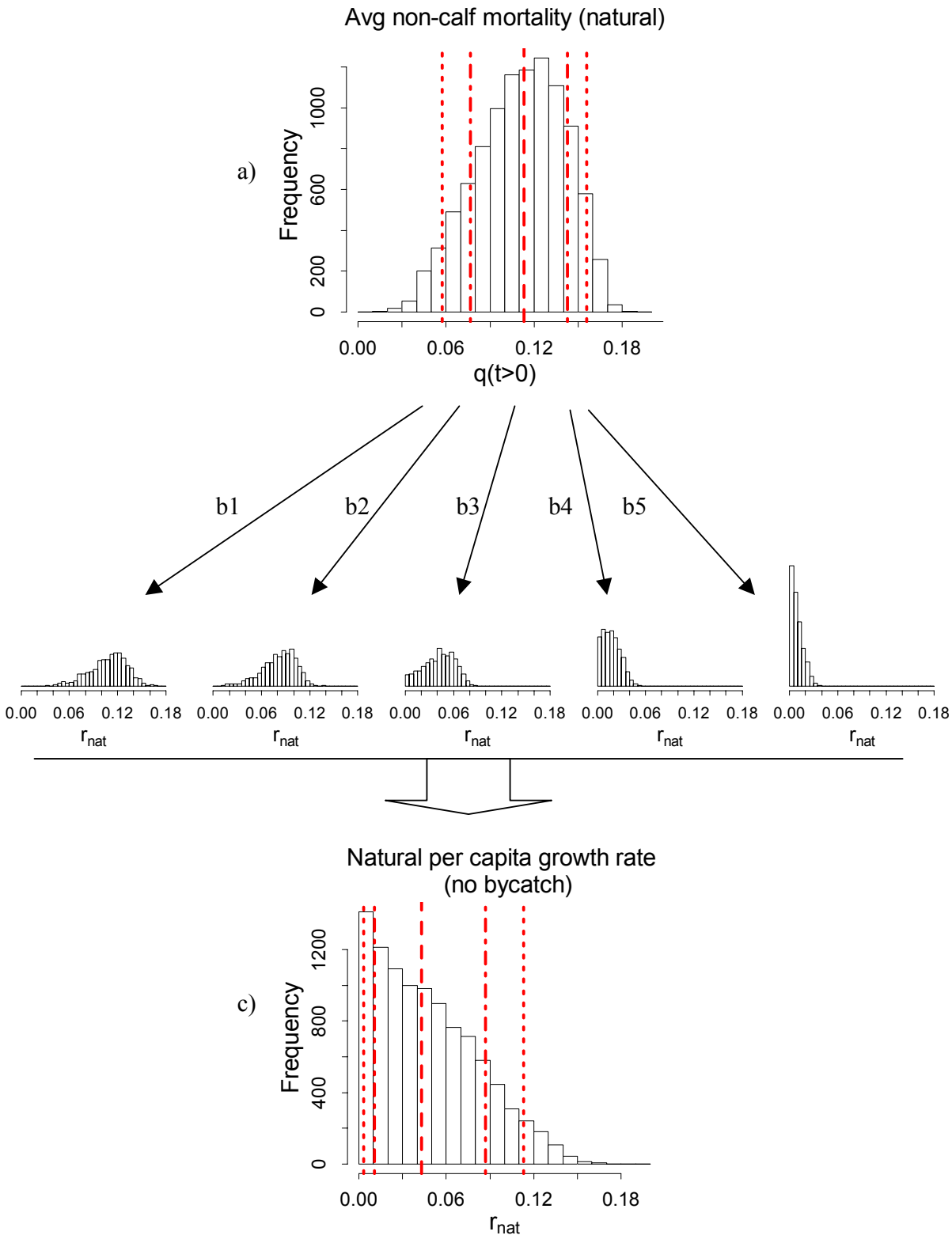

Count
Age
Beach strandings
Gillnet bycatch
0
5
10
15
20
25
30
35
40
45
50
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
40 32 26 45 6 45 6 28 5 25 1 13 4 13 2 9 2 7 1 5 2 1 2 11 2 1 3 1

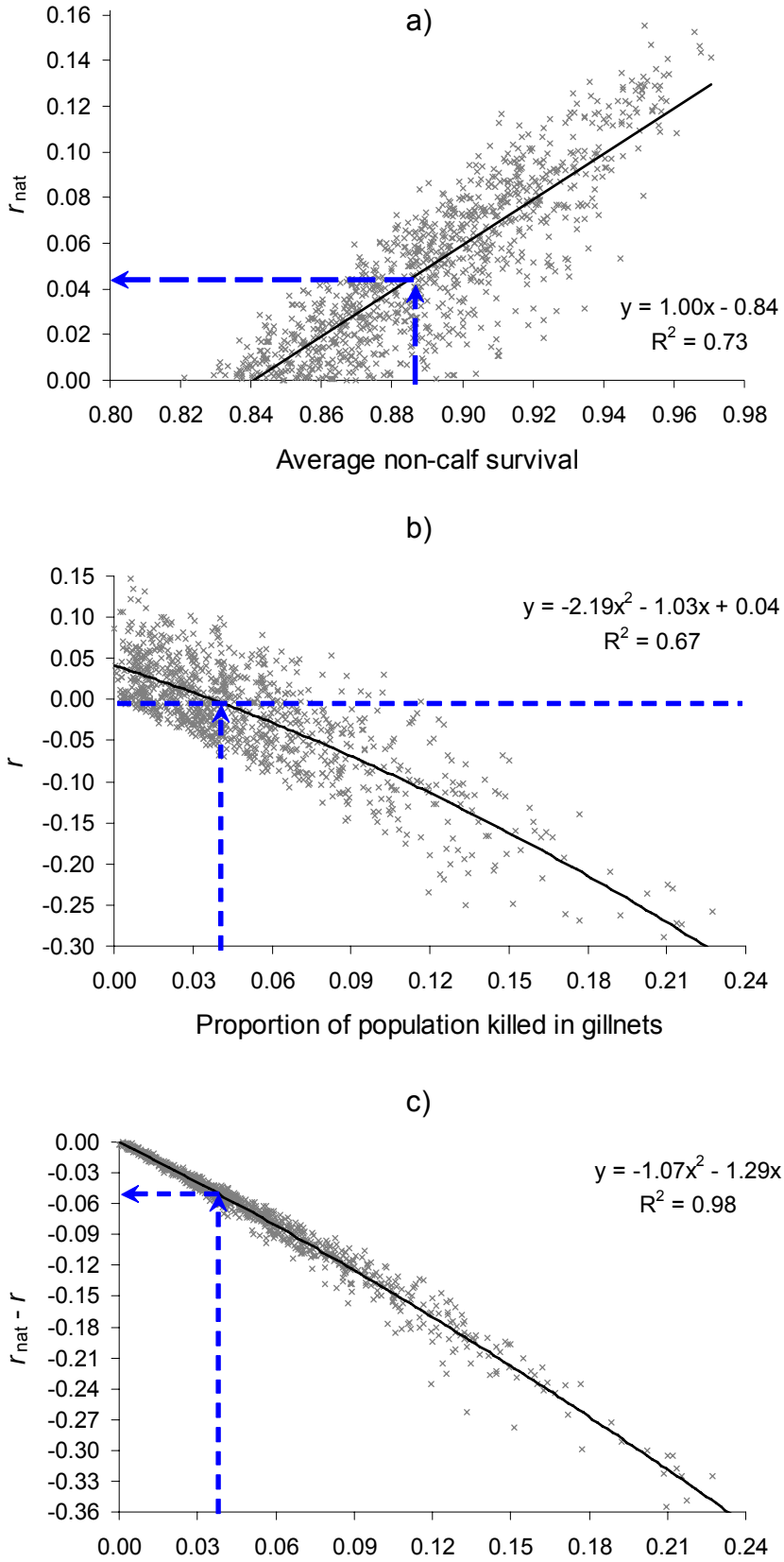

Natural survivorship
Actual survivorship
(including bycatch mortality)
Natural mortality rate
Mortality rate due to bycatch
Probability
Age (years)
A γ = 1.0
B γ = 0.5
C γ = 0.17
D γ = 1
E γ = 0.5
F γ = 0.17

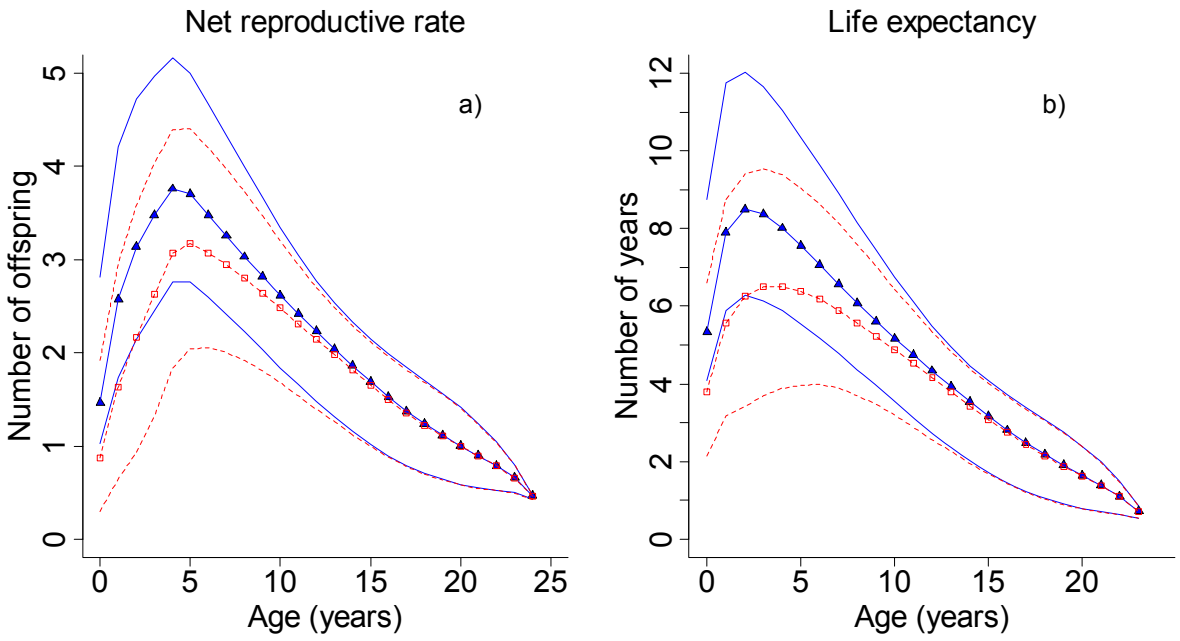

Density
$\tilde{x}$ = 0.60
(0.28, 1.31)
a1
$\tilde{x}$ = 0.03
(0.002, 0.10)
a2
$\tilde{x}$ = 0.01
(0.0004, 0.06)
a3
$\tilde{x}$ = 1.4
(0.63, 4.2)
b1
$\tilde{x}$ = 0.22
(0.09, 0.42)
b3
$\tilde{x}$ = 0.09
(0.01, 0.30)
D
$\tilde{x}$ = 0.53
(0.28, 0.81)
E
$\tilde{x}$ = 1.85
(1.27, 2.26)
F
$\tilde{x}$ = 0.002
2.9e-7, 0.009)
l(24)
$\tilde{x}$ = 0.56
(0.27, 0.94)
t0
$\tilde{x}$ = 0.31
(0.20, 0.39)
m(4)
$\tilde{x}$ = 0.47
(0.43, 0.475)
m(5+)

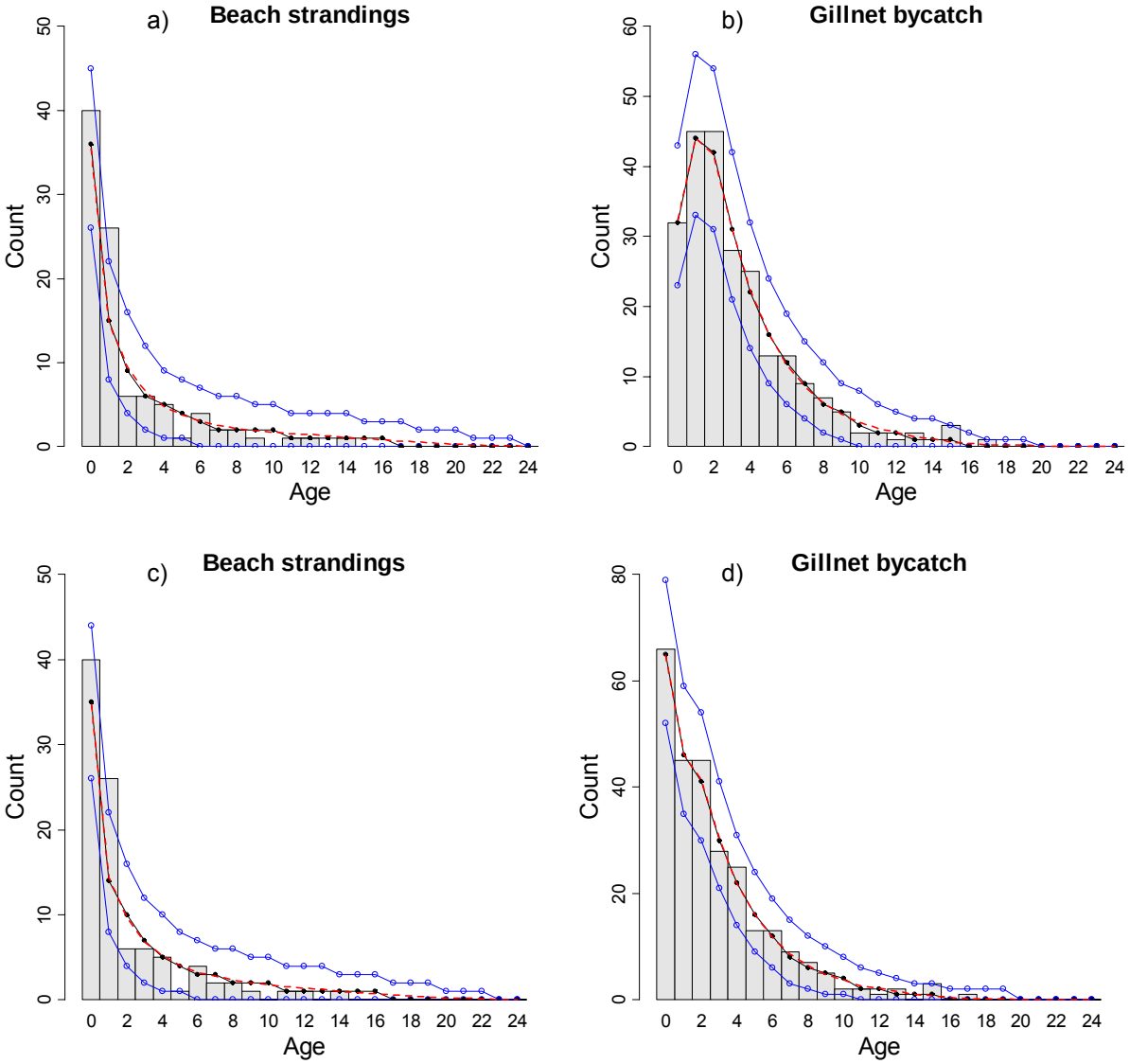

a)
Natural survivorship
Probability
0.0
0.2
0.4
0.6
0.8
1.0
b)
Actual survivorship
(including bycatch mortality)
Probability
0.0
0.2
0.4
0.6
0.8
1.0
c)
Natural mortality rate
Probability
0.0
0.2
0.4
0.6
0.8
0
5
10
15
20
25
Age
d)
Mortality rate due to bycatch
Probability
0.00
0.10
0.20
0.30
0
5
10
15
20
25
Age


Calf mortality (natural)
Frequency
0
400
800
0.0
0.2
0.4
0.6
0.8
q(0)
a)
Mortality from age 5 to 6 (natural)
0
400
800
0.00
0.06
0.12
0.18
q(5)
b)
Proportion of population killed in gillnets
Frequency
0
400
1000
0.00
0.10
0.20
0.30
Proportion
c)
Actual per capita growth rate
(with bycatch)
0
500
1500
-0.4
-0.2
0.0
0.2
r
d)


Avg non-calf mortality (natural)
a)
Frequency
0
200
600
1000
0.00
0.06
0.12
0.18
q(t>0)
b1
b2
b3
b4
b5
0.00 0.06 0.12 0.18
r_nat
Natural per capita growth rate
(no bycatch)
c)
Frequency
0
400
800
1200
0.00
0.06
0.12
0.18
r_nat


a)
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
r_{nat}
y = 1.00x - 0.84
R^2 = 0.73
0.80 0.82 0.84 0.86 0.88 0.90 0.92 0.94 0.96 0.98
Average non-calf survival
b)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
r
y = -2.19x^2 - 1.03x + 0.04
R^2 = 0.67
0.00 0.03 0.06 0.09 0.12 0.15 0.18 0.21 0.24
Proportion of population killed in gillnets
c)
0.00
-0.03
-0.06
-0.09
-0.12
-0.15
-0.18
-0.21
-0.24
-0.27
-0.30
-0.33
-0.36
r_{nat} - r
y = -1.07x^2 - 1.29x
R^2 = 0.98
0.00 0.03 0.06 0.09 0.12 0.15 0.18 0.21 0.24


Net reproductive rate
a)
Number of offspring
0
1
2
3
4
5
0
5
10
15
20
25
Age (years)
Life expectancy
b)
Number of years
0
2
4
6
8
10
12
0
5
10
15
20
Age (years)


a)
Beach strandings
b)
Gillnet bycatch
c)
Beach strandings
d)
Gillnet bycatch
Count
Age