

Appendix V

Management framework to assess the impact of bycatch and recommend safe bycatch limits for common dolphin and other small cetaceans

Arliss Winship & Philip S. Hammond

Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews
St Andrews, Fife KY16 8LB, UK

Objectives

The objectives of this work were to develop analytical techniques for assessing the impact of bycatch on populations of common dolphin (*Delphinus delphis*) and other small cetaceans and to develop a robust management procedure that uses available information to generate safe bycatch limits.

Background

The incidental catch, or bycatch, of small cetaceans in fisheries is a global conservation issue (Read et al. 2006). Common dolphins are bycaught in a range of fisheries operating in the Northeast Atlantic representing several countries (Tregenza et al. 1997, Tregenza and Collet 1998, Northridge 2006, Northridge et al. 2006, Northridge et al. 2007, Rogan and Mackey 2007). From a conservation standpoint, the major challenge is to ensure that this bycatch is not impairing the ability of these populations to maintain themselves over time. To meet this challenge requires an understanding of the impact of this bycatch on the size and dynamics of these populations (Lewison et al. 2004). Furthermore, there is a need for a robust procedure that can be used by managers to calculate limits to bycatch that will ensure that conservation objectives are achieved in the future.

As part of the EU SCANS-II project, assessment methods and management procedures were developed for harbour porpoise in the European Atlantic and North Sea (SCANS-II 2008, Winship 2009). As part of the CODA project, we developed these methods and procedures further and applied them to common dolphins in the Northeast Atlantic.

Assessing the impact of bycatch

An understanding of the state and dynamics of a population is a prerequisite for assessing the impact of bycatch on its conservation status. Four quantities of particular interest are: 1) the bycatch removed from the population, 2) the size of the population, 3) the rate at which the population can grow in the absence of bycatch, and 4) the population size that could be achieved in the absence of bycatch. While knowledge of these quantities is essential for management and conservation, estimates of these quantities are often lacking or highly uncertain, as is the case for common dolphins in the Northeast Atlantic.

An elegant approach to assessing the state and dynamics of a population is to fit a model of that population to all relevant data simultaneously—an integrated population dynamics model (e.g., Schaub et al. 2007). A population model ensures mathematical consistency among inferences about different aspects of population dynamics, and a population model can be fitted to a diverse range of data on population size, life history and bycatch. Embedding a population model in statistical inference allows appropriate representation of uncertainty in

estimates of population dynamics (Hilborn and Mangel 1997, Buckland et al. 2007). Bayesian statistics are particularly useful for characterising uncertainty in population dynamics models (Wade 2000, Harwood and Stokes 2003) and allow for seamless incorporation of estimation uncertainty into prediction for risk assessment, population viability analysis and management strategy evaluation (Harwood 2000, Maunder et al. 2000, Wade 2002).

We developed an integrated population dynamics model for assessing the state and dynamics of a small cetacean population subject to bycatch. The full specifications of the model are described below. In brief, the population model is an age-structured model of the female component of a small cetacean population. The model can be fitted to a range of data on the population (e.g., abundance), life history (e.g., pregnancy rate, sexual maturity at age, age structure of natural mortality) and bycatch (e.g., age structure of bycatch mortality). The numbers of animals bycaught can be treated as known input to the model or bycatch can be estimated by fitting the model to data on bycatch rate per unit fishing effort with total fishing effort as input. The model is flexible and allows for a range of scenarios with respect to population dynamics (e.g., density-independent or density-dependent dynamics) and population structure (e.g., multiple subpopulations with dispersal among them). The model is fitted in a Bayesian statistical framework using a Markov chain Monte Carlo method.

Integrated population dynamics model

The population model was an age-structured simulation of the female component of one or more subpopulations occupying non-overlapping geographic ranges with a time step of one calendar year. All births were assumed to occur simultaneously at the middle of each year (end of June).

First, natural mortality was applied prior to births:

$$[1] \quad N_{a+1,i,t+0.5} = N_{a,i,t} e^{-\left(\frac{M_a}{2}\right)}$$

where $N_{a,i,t}$ is the number of animals of age a (years) in subpopulation i at the beginning of year t and M_a is the instantaneous natural mortality rate from age a to $a+1$. Eq. 1 assumes constant instantaneous natural mortality rates throughout the year.

Instantaneous natural mortality rates were calculated from estimated age-specific survival rates (s_a):

$$[2] \quad M_a = -\log(s_a)$$

Age-specific survival rates were modelled in two ways. The first approach was to estimate separate annual survival rates for five age groups: age 0; age 1; $2 \leq \text{age} < a^{m50}$; $a^{m50} \leq \text{age} < 20$; $20 \leq \text{age} \leq \omega$, where a^{m50} is the age at which 50% of females are sexually mature (estimated) and ω is the maximum age. Observed maximum ages in samples of common dolphins range from 25 to over 30 (Ferrero and Walker 1995, Westgate 2005, Danil and Chivers 2007, Murphy et al. in revision). We fixed maximum age at 30. We assumed that all animals that survived to age $\omega+1$ died (naturally) at that age. The second approach to modelling age-specific survival was to use Siler's competing-risk model to describe survivorship (Siler 1979):

$$[3] \quad l_a = e^{\frac{-\alpha_1(1-e^{-\beta_1 a}) - \alpha_2 a + \alpha_3}{\beta_3} (1-e^{-\beta_3 a})}$$

where α_1 , α_2 , α_3 , β_1 , and β_3 are estimated parameters, $l_0=1$ and $s_a = \frac{l_{a+1}}{l_a}$.

Births were assumed to occur at the middle of each year so that:

$$[4] \quad N_{0,i,t+0.5} = b_{i,t} \sum_{a=1}^{\omega} N_{a,i,t+0.5} m_{a-1}$$

where $b_{i,t}$ is birth rate in subpopulation i during year t (number of female calves born per sexually mature female per year) and m_a is the proportion of females that are sexually mature at age a . The sexual maturity ogive was:

$$[5] \quad m_a = \left(1 + e^{-\frac{a-a^{m50}}{\sigma^m}} \right)^{-1}$$

where σ^m is an estimated parameter specifying the width of the ogive. Eq. 4 assumes that birth rate does not vary with age and that females must be sexually mature for at least one year before giving birth. There is some evidence of reproductive senescence in common dolphins, but old animals have been observed to be pregnant (Danil and Chivers 2007, Westgate and Read 2007, Murphy et al. in revision). For simplicity we assumed no reproductive senescence.

Birth rate was assumed to be either density-independent or density-dependent. When birth rate was assumed to be density-independent, the birth rate did not vary over time. When birth rate was assumed to be density-dependent, the birth rate was calculated as:

$$[6] \quad b_{i,t} = \max \left[b^K + (b^{\max} - b^K) \left(1 - \left[\frac{\sum_{a=1}^{\omega} N_{a,i,t}}{N_i^{1+K}} \right]^z \right), 0 \right]$$

where b^K is birth rate at carrying capacity, b^{\max} is maximum birth rate (estimated), N_i^{1+K} is the number of female non-calves at the beginning of the year at carrying capacity in subpopulation i (estimated), and z is a density-dependence shape parameter. Eq. 6 assumes that birth rate is a function of the number of non-calves alive at the beginning of the year. Birth rate at carrying capacity was calculated as:

$$[7] \quad b^K = \left[\sum_{A=1}^{\omega} \left(m_{A-1} \prod_{a=1}^A s_a \right) \right]^{-1}$$

We fixed z at 1 (i.e., a linear response in birth rate to population size).

After reproduction, natural mortality was applied for the remainder of the year followed by bycatch:

$$[8] \quad N_{a,i,t+1} = N_{a,i,t+0.5} e^{-\left(\frac{M_a}{2}\right)} - D_{a,i,t}^{\text{Byc}}$$

where $D_{a,i,t}^{\text{Byc}}$ is the number of females of age a in subpopulation i dying of bycatch mortality in year t calculated as:

$$[9] \quad D_{a,i,t}^{\text{Byc}} = d_{a,i,t}^{\text{Byc}} 0.5 B_t$$

where B_t is the bycatch estimate for year t (input) and $d_{a,i,t}^{\text{Byc}}$ is the proportion of female bycatch mortality composed of females of a given age from a given subpopulation in a given year calculated as:

$$[10] \quad d_{a,i,t}^{\text{Byc}} = \frac{N_{a,i,t+0.5}}{\sum_{a=0}^{\omega} N_{a,i,t+0.5}}$$

Eq. 9 assumes that the sex ratio of bycatch is 1:1. There is evidence that male common dolphins are bycaught more frequently than females in our study area, at least in some fisheries (Silva and Sequeira 2003, Northridge et al. 2004). If this is generally the case then Eq. 9 would overestimate the number of females bycaught. The time-series of bycatch (B_t) that we used for common dolphins was incomplete and was very likely an underestimate and this probably resulted in a much greater bias in estimates of female bycatch than the assumption of a 1:1 sex ratio in bycatch. Eq. 10 assumes that all animals are equally vulnerable to bycatch irrespective of age. Our integrated population dynamics model allows for the estimation of age-specific vulnerability to bycatch, however, because there were few age data for common dolphins that died naturally it was not possible to estimate age-specific vulnerability to bycatch.

Dispersal among subpopulations was assumed to occur at the end/beginning of the year:

$$[11] \quad N_{a,i,t} = N_{a,i,t} - \delta_i N_{a,i,t} + \sum_j^{j \neq i} N_{a,j,t} \frac{\delta_j}{I-1}$$

where δ_i is the rate of dispersal from subpopulation i (estimated or fixed) and I is the total number of subpopulations. Eq. 11 assumes that animals of all ages disperse at the same rate and that dispersing animals enter other subpopulations with equal probability.

The density-independent population model was initialised by estimating the total number of females alive at the beginning of the first year, $\sum_{a=0}^{\omega} N_{a,i,0}$, and assuming the stable age distribution at the beginning of a year specified by Eqs. 1-5 and 8 with zero bycatch (dominant eigenvector of the transition matrix adjusted for mortality in the latter half of a year of life).

The density-dependent population model was initialised in one of two ways. The first approach was to estimate the total number of female non-calves alive at the beginning of the first year, $\sum_{a=1}^{\omega} N_{a,i,0}$, and assume the stable age distribution at the beginning of a year under density-independent growth with the initial birth rate. The second approach was to assume that the population was at carrying capacity at the beginning of the study period.

Parameter estimation

Parameters of the population model were estimated using a Bayesian statistical framework (Table 1 lists the estimated parameters). Six likelihood functions related the data to the model. Errors in estimates of abundance were assumed to be log-normally distributed:

$$[12] \quad L^N = \prod_{i=1}^I \prod_t \frac{1}{x_{i,t}^N \sigma_{i,t} \sqrt{2\pi}} e^{-\frac{\left[\log(x_{i,t}^N) - \log\left(2 \sum_{a=0}^{\omega} N_{a,i,t+0.5}\right) \right]^2}{2\sigma_{i,t}^2}}$$

where L^N is the likelihood of the abundance data, $x_{i,t}^N$ is the mean abundance estimate for subpopulation i in year t and $\sigma_{i,t}$ is the standard deviation of the errors on a log-scale which was calculated from the coefficients of variation according to:

$$[13] \quad \sigma_{i,t} = \sqrt{\log(1 + CV_{i,t}^2)}$$

Eq. 12 assumes a 1:1 sex ratio and that surveys were conducted at mid-year immediately after births. It is possible that the population sex ratio is not 1:1 for common dolphins in our study

area (Silva and Sequeira 2003). For example, Murphy (2004) found more immature males than immature females in a sample of stranded common dolphins from Ireland, which could indicate a male-biased sex ratio or higher mortality for immature males (and thus possibly a female-biased sex ratio). Without specific data on population sex ratio we assumed a default ratio of 1 male to 1 female.

The proportion of females that were sexually mature at a given age was assumed to be binomially distributed:

$$[14] \quad L^M = \prod_{a=0}^{\omega} \binom{n_a^M}{x_a^M} (m_{a+0.5})^{x_a^M} (1 - m_{a+0.5})^{n_a^M - x_a^M}$$

where L^M is the likelihood of the sexual maturity data, n_a^M is the total number of females of age a (all subpopulations) that were sampled and examined for sexual maturity and x_a^M is the number of those females that was sexually mature. Eq. 14 assumes that the overall proportion of females of a given age that is mature is equal to the probability of being mature at the mid-point of that year of life. The sexual maturity ogive was assumed to be identical among subpopulations.

We assumed that the birth rate ($b_{i,t}$) was equal to half the proportion of mature females that was pregnant (1:1 sex ratio at birth) which was assumed to be binomially distributed:

$$[15] \quad L^P = \prod_{i=1}^I \prod_t \binom{n_{i,t}^P}{x_{i,t}^P} (2b_{i,t})^{x_{i,t}^P} (1 - 2b_{i,t})^{n_{i,t}^P - x_{i,t}^P}$$

where L^P is the likelihood of the pregnancy data, $n_{i,t}^P$ is the total number of sexually mature females in subpopulation i sampled in the last half of year $t-1$ and the first half of year t that were examined for pregnancy and $x_{i,t}^P$ is the number of those females that was pregnant. Eq. 15 assumes no prepartum mortality of foetuses; the occurrence of prepartum resorptions or abortions of foetuses would cause birth rate to be positively biased. We did not consider data on pregnancy from the months of June-August because of a potentially lower probability of detection of early-term foetuses.

The proportions of total natural mortality composed of females of each age were assumed to be multinomially distributed:

$$[16] \quad L^{DNat} = \prod_{a=0}^{\omega} \prod_{i=1}^I \prod_t (d_{a,i,t}^{Nat})^{x_{a,i,t}^{DNat}}$$

where L^{DNat} is the likelihood kernel for the natural mortality data (does not include the likelihood coefficient, which is not affected by parameter values), $d_{a,i,t}^{Nat}$ is the proportion of total natural mortality in subpopulation i in year t composed of females of age a and $x_{a,i,t}^{DNat}$ is the number of females of age a in subpopulation i sampled in year t whose probable cause of death was natural. The proportion of total natural mortality composed of females of a given age in a given subpopulation in a given year was calculated according to the following two equations:

$$[17] \quad d_{a,i,t}^{Nat} = \frac{D_{a,i,t}^{Nat}}{\sum_{a=0}^{\omega} D_{a,i,t}^{Nat}}$$

and

$$[18] \quad D_{a,i,t}^{\text{Nat}} = \left(N_{a,i,t} + N_{a,i,t+0.5} \right) \left[1 - e^{-\left(\frac{M_a}{2} \right)} \right]$$

where $D_{a,i,t}^{\text{Nat}}$ is the number of females of age a in subpopulation i dying of natural mortality in year t .

The likelihood of the bycatch mortality age-structure data was calculated in the same way as for natural mortality:

$$[19] \quad L^{\text{DByc}} = \prod_{a=0}^{\omega} \prod_{i=1}^I \prod_t \left(d_{a,i,t}^{\text{Byc}} \right)^{x_{a,i,t}^{\text{DByc}}}$$

Eqs 16 and 19 assumed that sampling errors in mortality age structure were independent among subpopulations and years. Unmodelled heterogeneity in age structure of mortality among subpopulations or years or non-random sampling of animals (e.g., bycatch of groups of females with different age structures) could have resulted in non-independence and overdispersion of the data relative to a multinomial likelihood function (and underestimation of credible intervals). For example, the age and sex composition of previous mass strandings and bycaught groups of common dolphins in our study area suggest segregation of animals by sex and age (Silva and Sequeira 2003, Murphy 2004). The integrated population dynamics model that we developed allows for modelling such overdispersion through the use of a Dirichlet-multinomial likelihood, however, for this analysis we used the multinomial likelihood.

The five likelihoods/likelihood kernels (Eqs 12, 14, 15, 16 and 19) were assumed to be independent (i.e., independent random sampling errors) so that the total likelihood kernel was the product of the individual likelihoods/likelihood kernels.

Posterior probability distributions for the parameters of the population model were estimated using a Markov chain Monte Carlo (MCMC) algorithm with a Metropolis acceptance/rejection rule (Gelman et al. 2004). Prior probability distributions were assumed to be uniform (Table 1) so that the acceptance rule operated only on the joint likelihood kernel. In practice, we used log-likelihoods instead of likelihoods for computational ease. Proposal values were drawn from the proposal distributions for each parameter individually followed by acceptance/rejection after each individual parameter draw. A proposed parameter value was accepted if the difference between the new total log-likelihood kernel and the previous kernel was greater than the log of a random uniform number between 0 and 1. Uniform proposal distributions were used with initial widths of 20% of the starting parameter values. These widths were adjusted during the burn-in period with a target acceptance rate of 40% (Gelman et al. 2004). Widths were increased when the acceptance rate was higher and decreased when the acceptance rate was lower. Draws outside the ranges of the prior probability distributions were assigned zero likelihood. With the density-dependent model further constraints were

placed on parameter draws so that $b^K < b^{\max}$ and $\sum_{a=1}^{\omega} N_{a,i,0} \leq N_i^{1+K}$; parameter draws that did not satisfy these constraints were assigned zero likelihood. These constraints on parameter space altered the uniform priors for some parameters so we present realized priors in our results, which we obtained by running the MCMC algorithm without consideration of the data. We assessed the convergence of the sample of the joint posterior using the Bayesian Output Analysis package for R for Windows (Smith 2001) including Raftery and Lewis, Geweke and Heidelberger and Welch diagnostics. The MCMC chain was run for 1,500,000 iterations

keeping every 100th iteration not including a burn-in of 500,000 iterations (posterior sample size = 10,000). When full posterior probability distributions are not presented, medians and 95% intervals of posterior probability are presented as summary statistics.

The population model and McMC algorithm were coded using the C computer language compiled with the free MinGW port (<http://www.mingw.org>) of the GNU GCC compiler (<http://www.gnu.org>) and the free software package R (R Development Core Team 2007).

We applied our integrated population dynamics model to data on common dolphins in the Northeast Atlantic to try to assess the historical and current conservation status and dynamics of the population and the impact of previous bycatch (see ‘Application to common dolphins’ section below).

It is important to understand the maximum level of bycatch that small cetacean populations can sustain while still maintaining desirable conservation status. Management actions can then focus on ensuring that bycatch is kept below this level. The results of an assessment can be used to calculate appropriate bycatch limits, but this approach is subject to failures arising from incorrect assessments (e.g., incorrect model specification and biased or misleading data). Furthermore, there is no guarantee that using a current assessment to calculate bycatch limits will achieve conservation objectives in the long-term. A preferable approach to managing bycatch from a population is to develop a robust, fully-tested management procedure that can be used to calculate bycatch limits. A management procedure takes information about a population as input and calculates a bycatch limit that will achieve the desired conservation objectives. Computer simulation can be used to explicitly evaluate the long-term performance of the management procedure, a technique known as management strategy evaluation.

Table 1. Estimated parameters of the population model. Prior probability distributions were uniform (described by a lower limit and an upper limit).

Symbol	Description	# of parameters	Prior probability distribution
$\sum_{a=0}^{\omega} N_{a,i,0}$	initial number of females (density-independent)	$1 \times I$	0, 500000
$\sum_{a=1}^{\omega} N_{a,i,0}$	initial number of female non-calves (density-dependent)	$1 \times I$	0, 500000
$N_i^{1+,K}$	number of female non-calves at carrying capacity (density-dependent)	$1 \times I$	0, 500000
a^{m50}	age when 50% of females are mature	1	3, 13
σ^m	width of maturity ogive	1	0, 2
b_i	birth rate (density-independent)	$1 (\times I)$	0, 0.5
b^{\max}	maximum birth rate (density-dependent)	1	0, 0.5
s_a	natural age-specific survival	5	0, 1
α, β	survivorship function parameters	5	0, 10

Calculating bycatch limits

We developed management procedures for calculating bycatch limits for small cetacean populations. We considered two existing management procedures, the Potential Biological Removal procedure of the US Government (PBR; Wade 1998) and the Catch Limit Algorithm procedure of the International Whaling Commission (CLA; Cooke 1999), as candidates for our purpose. Full specifications of the procedures are described below. In brief, both procedures take information about a small cetacean population as input and then they output a bycatch limit. The PBR procedure takes a single, current estimate of population size as input. The CLA procedure takes time-series of estimates of population size and estimates of previous bycatch as input. Both procedures explicitly incorporate uncertainty in the estimates of population size. Thus, the procedures also require estimates of the precision of the estimates of population size as input. Under the PBR procedure, the calculation of the bycatch limit proceeds using a single, relatively simple equation. Under the CLA procedure, the calculation of the bycatch limit is slightly more demanding computationally. The CLA procedure involves statistically fitting a simple population model to the input data series and then calculating the bycatch limit as a function of several quantities estimated through the model fitting.

A key element of both management procedures is the ability to ‘tune’ the procedure, or adjust the bycatch limits, so that specific conservation objectives are achieved. Another important element of both procedures is the ability to update the bycatch limit as new data on the population become available. However, only the CLA procedure makes use of historical data on the population. This feature of the CLA procedure allows it to learn about the population over time and allows for a more sophisticated rule for setting the bycatch limit whereby a threshold population size (relative to carrying capacity) can be specified below which the bycatch limit is set to zero. Under the PBR procedure, the bycatch limit is approximately a constant proportion of the estimated population size.

The management procedures are applied at the spatial resolution of defined management areas. A given procedure is applied separately to each management area resulting in a separate bycatch limit for each area.

We developed a computer-based simulation model, or operating model, for testing and comparing the performance of the two management procedures and for tuning the procedures so that one would expect to meet specific conservation objectives in practice. Full specifications of the operating model are described below. In brief, the operating model simulates a small cetacean population over time while periodically simulating surveys of the size of this population. Bycatch is removed from this population annually according to bycatch limits set by the management procedures. Importantly, the management procedures do not have knowledge of the true size of the population; they only have the simulated survey data and bycatch limits as input. This is the key aspect of the simulation model that mimics how the management procedures would operate in reality and thus how one would expect populations to fare under the management procedures in practice. The model of the cetacean population incorporates age structure, density dependence (in birth rate), multiple subpopulations (with dispersal among them), and environmental variation (represented by systematic changes in carrying capacity, periodic catastrophic mortality events, and random fluctuations in birth rate). Survey estimates are generated with random error and potentially directional bias. Similarly, bycatch is modelled as a random (and potentially biased) realization of the set bycatch limit. The operating model allows for multiple management areas that do not necessarily correspond to the spatial ranges of subpopulations. Thus, the

model allows for flexible spatial scenarios regarding management and subpopulation structure (e.g., seasonal mixing).

The operating model can be conditioned on the results of an assessment to examine the performance of the management procedures conditional on the estimated state and dynamics of the population. The density-dependent version of the integrated population dynamics model that we developed for assessment is very similar to the operating model used to test the management procedures. The output from the integrated model includes distributions of parameter estimates and distributions of previous bycatch that can be used as input to the operating model to condition performance-testing simulations of the management procedures on the results of the assessment. Winship (2009) describes the results of conditioned performance-testing simulations of the management procedures for harbour porpoise in the North Sea.

We used our operating model to tune the management procedures and calculate bycatch limits for common dolphins in the Northeast Atlantic (see ‘Application to common dolphins’ section below).

Management procedures

PBR

Under the PBR management procedure the bycatch limit for a management area is calculated using a relatively simple equation and a current estimate of absolute abundance (Wade 1998):

$$[20] \quad CL_{j,t} = N_{j,t}^{\min} \frac{1}{2} R^{\max} F$$

where $CL_{j,t}$ is the bycatch limit for area j in the year following time t , $N_{j,t}^{\min}$ is the ‘minimum’ estimated number of animals in area j at time t , R^{\max} is maximum population growth rate (i.e., population growth rate at low density), and F is a recovery factor—a parameter that can be tuned so that the PBR procedure achieves specific management objectives. Errors in estimates of abundance from surveys are assumed to be log-normally distributed so that $N_{j,t}^{\min}$ is calculated as:

$$[21] \quad N_{j,t}^{\min} = O_{j,t} e^{Z \sqrt{\log(1+CV_{j,t}^O)^2}}$$

where $O_{j,t}$ is a survey estimate of absolute abundance in area j at time t , $CV_{j,t}^O$ is the coefficient of variation of this estimate, and Z is a standard normal deviate corresponding to a specified percentile (fixed at -0.842 for the 20th percentile following Wade 1998). Eq. 21 assumes that $O_{j,t}$ is the median of the log-normal error distribution.

The PBR management procedure was implemented in the operating model by calculating $CL_{j,t}$ immediately after a survey for absolute abundance and using this annual bycatch limit until the next survey.

CLA

Under the CLA procedure the bycatch limit is calculated as a function of population parameter estimates that are derived by fitting a relatively simple, deterministic population model to time-series of estimates of absolute abundance (Cooke 1999). A time-series of bycatch estimates is input to the population model.

The population model of the CLA is:

$$[22] \quad N_{j,t} = N_{j,t-1} \left[1 + R_j^{\max} \left(1 - \left[\frac{N_{j,t-1}}{N_j^K} \right]^z \right) \right] - CL_{j,t-1}$$

where $N_{j,t}$ is total population size in area j at time t (years), R_j^{\max} is maximum population growth rate, N_j^K is population size at carrying capacity, and z determines the shape of the density-dependence relationship (fixed at 2). The population model is initialised by assuming that the population is at carrying capacity at $t=0$, the beginning of the bycatch time-series. It is important to note that the population might not have been at carrying capacity at the beginning of the bycatch time-series, for example if the time-series is incomplete.

Nevertheless, the CLA assumes that the population starts at carrying capacity.

The population model is fitted to estimates of absolute abundance using a quasi-Bayesian statistical framework (Cooke 1999, International Whaling Commission 1999).

If errors in estimates of absolute abundance are assumed to be independent over time and log-normally distributed with known $CV(s)$ then a likelihood kernel for non-zero estimates ($L_j^{O \neq 0}$) is:

$$[23] \quad L_j^{O \neq 0} = \prod_t^{t \in \mathbf{t}_j^{O \neq 0}} e^{-\frac{\left[\log \left(\frac{O_{j,t}}{B_j^O N_{j,t}} \right) \right]^2}{2 \log(1 + CV_{j,t}^{O \neq 0})^2}}$$

where $\mathbf{t}_j^{O \neq 0}$ is the set of years in which surveys for absolute abundance were conducted in area j resulting in non-zero estimates of abundance and B_j^O is a bias parameter specifying the expected absolute abundance estimated by a survey as a proportion of true abundance. The CLA procedure also allows for zero estimates of abundance. The likelihood of these estimates is based on the Poisson distribution:

$$[24] \quad L_j^{O=0} = \prod_t^{t \in \mathbf{t}_j^{O=0}} e^{-\frac{N_{j,t}}{\infty}}$$

where $\mathbf{t}_j^{O=0}$ is the set of years in which surveys for absolute abundance in area j resulted in zero estimates and ∞ is the reciprocal of the expected number of animals counted on a survey as a proportion of the number of animals in the population. The value of ∞ depends on various aspects of the surveys (e.g., effort, area covered), but we assumed a theoretical value of 1000. Zero estimates of abundance would have occurred extremely infrequently, if at all, in the simulations. Assuming independence between the zero and non-zero abundance estimates the joint likelihood is the product of Eqs 23 and 24.

The estimated parameters of the CLA procedure's population model are R_j^{\max} , B_j^O and $D_{j,T}$ (the current number of animals as a proportion of the number of animals at carrying capacity). Uniform prior probability distributions are assumed for all three parameters:

$R_j^{\max} \sim U(0, 0.07092)$, $B_j^O \sim U\left(0, \frac{5}{3}\right)$, and $D_{j,T} \sim U(0, 1)$. These prior probability distributions are assumed to be independent.

After each survey for absolute abundance, a posterior distribution of nominal bycatch limits is calculated from the posterior distribution of population model parameters and the

corresponding posterior distribution of predicted current population size using a numerical integration algorithm summarized by the following pseudocode:

- I. Start with the minimum R_j^{\max} , maximum N_j^K , and maximum $D_{j,T}$.
- II. If R_j^{\max} is less than the maximum R_j^{\max} then continue to step III, otherwise stop.
- III. Simulate the population from $t=0$ to T using Eq. 22 where T is the current year.
- IV. Calculate the new $D_{j,T}$ and the difference between the new $D_{j,T}$ and the previous $D_{j,T}$.
- V. If the new $D_{j,T}$ is ≤ 0 then increment R_j^{\max} and return to step II, otherwise calculate a nominal bycatch limit according to the catch control rule:

$$[25] \quad CL_{j,T} = \rho R_j^{\max} N_{j,T} \max \left\{ \min \left(\frac{N_{j,T}}{N_j^K}, 1 \right) - \gamma, 0 \right\}$$

where ρ is a tuning parameter that can be used to adjust the CLA procedure to achieve specific conservation objectives, and γ is a threshold population size relative to carrying capacity at which bycatch is set to zero (the internal protection level).

- VI. Integrate $(L_j^{O \neq 0} \times L_j^{O=0})^w$ over the prior for B_j^O and multiply by the difference between the new $D_{j,T}$ and the previous $D_{j,T}$ to get a weighted likelihood kernel corresponding to the nominal bycatch limit from step V. The parameter w weights the contribution of the likelihood to the posterior (fixed at 1/16). This weighting means that this is not a strict Bayesian analysis. The down-weighting is implemented to reduce variability in bycatch limits (Cooke 1999).
- VII. Decrement N_j^K and return to step III.

Finally, the set of nominal bycatch limits is sorted and the implemented bycatch limit is chosen to correspond to a specific quantile, Q , of the corresponding cumulative (normalized) weighted likelihoods. The CLA procedure was implemented in the operating model by calculating $CL_{j,t}$ immediately after a survey for absolute abundance and using this annual bycatch limit until the next survey. Time-series of previous bycatch limits were input to the CLA procedure.

There were several key differences between our version of the CLA procedure and the version used by the IWC. First, in the IWC version of the catch control rule (Eq. 25) R_j^{\max} is replaced by a productivity parameter that is equal to $R_j^{\max} / 1.4184$. Thus, ρ in our version of the catch control rule is not equivalent to the corresponding tuning parameter in the IWC version. Second, in the IWC version of the CLA procedure surveys are assumed to have occurred at the start of the last year of catch (or at the start of the last year within an inter-limit period). In our version surveys are assumed to have occurred at the end of the last year of catch (i.e., after the last catch not before). Third, covariance among estimates of abundance was not considered although covariance is straightforward to incorporate (Cooke 1999).

Operating model

The model of the known population was an age-structured, birth-pulse simulation of one or more subpopulations with a time-step of one year of life. Each subpopulation was modelled individually and during each time-step was subject to four processes in the following order: natural mortality, dispersal, bycatch and reproduction.

First, natural mortality was applied to each subpopulation according to:

$$[26] \quad N_{a,i,t} = \text{Binom}(N_{a,i,t}; s_a)$$

where $N_{a,i,t}$ is the number of animals of age a in subpopulation i at time t , s_a is the natural annual survival rate from age a to $a+1$, and $\text{Binom}(n, p)$ is a random binomial variable with sample size n and probability p (see Table 2 for a complete list of the parameters of the operating model). For common dolphins, natural survival rates were fixed at 0.8, 0.86, 0.92, 0.97, 0.92, 0.87, 0.82, 0.77 and 0.72 for ages $a=0, 1, 2, 2 < a < 26, 26, 27, 28, 29$ and 30, respectively. Survival rates for common dolphins are not well understood. We developed this survival schedule so that the chosen baseline maximum birth rate would result in the chosen baseline maximum population growth rate. Further constraints that we applied in developing the survival schedule were a calf survival of 0.8 (Taylor et al. 2007), high adult survival (Reilly and Barlow 1986), linearly increasing survival over the first few years, linearly decreasing survival in the last few years, and a survivorship of the oldest age class < 0.2 . After natural mortality, the model allowed for a catastrophic natural mortality event. These events were implemented as 50% mortality across all ages (subject to demographic stochasticity) after the usual natural mortality. These events occurred with a specified probability each year ($P^{\text{catastrophe}}$).

Second, the survivors of natural mortality dispersed amongst the subpopulations according to:

$$[27] \quad N_{a,i,t} = N_{a,i,t} - \text{Binom}(N_{a,i,t}; \delta_i) + \sum_k^{k \neq i} \text{Binom}\left(N_{a,k,t}; \frac{\delta_k}{I-1}\right)$$

where δ_i is the rate of dispersal from subpopulation i . Eq. 27 implies that dispersing animals entered other subpopulations with equal probability. δ_i was assumed to be the same for all ages. Note that because natural mortality rates did not vary by density or subpopulation, the order of natural mortality and dispersal did not affect dynamics.

Third, bycatch was removed from the population. Total bycatch from the population in management area j during the year following time t ($TC_{j,t}$) was modelled as a potentially biased, random deviation from the set bycatch limit for year t ($CL_{j,t}$):

$$[28] \quad TC_{j,t} = B^{\text{byc}} N\left(CL_{j,t}, [CL_{j,t} CV^{\text{byc}}]^2\right)$$

where B^{byc} is the directional bias in actual bycatch relative to the bycatch limit (expected $TC_{j,t}$ as a proportion of $CL_{j,t}$), CV^{byc} is the coefficient of random variation in bycatch and $N(\mu, \sigma^2)$ is a random normal variable with expectation μ and variance σ^2 . Random deviations from the bycatch limit were assumed to be independent between years. The expected proportion of the bycatch composed of animals of age a from subpopulation i in management area j during the year following time t ($v_{a,i,j,t}$) was calculated according to:

$$[29] \quad v_{a,i,j,t} = \frac{\eta_a \beta_{j,i}^{\text{byc}} N_{a,i,t}}{\sum_{a=0}^{\omega} \sum_{i=1}^I \eta_a \beta_{j,i}^{\text{byc}} N_{a,i,t}}$$

where η_a is the vulnerability of an animal of age a to bycatch relative to other ages, $\beta_{j,i}^{\text{byc}}$ is the proportion of subpopulation i residing in management area j during bycatch, ω is maximum age, and I is the total number of subpopulations. The calculation of vulnerabilities (Eq. 29) assumed that all animals within a management area mixed freely irrespective of age and subpopulation. The total bycatch in area j was then distributed stochastically among the subpopulations and ages within subpopulations according to:

$$[30] \quad C_{j,t} = \text{Multin}(TC_{j,t}; V_{j,t})$$

where $C_{j,t} = [c_{a,i}]_{j,t}$ is the matrix of bycatch c of age a from subpopulation i in management area j during the year following time t , $V_{j,t} = [v_{a,i}]_{j,t}$ is the matrix of proportions of bycatch, and

Multin($n; \mathbf{p}$) represents a random multinomial distribution with sample size n and probabilities \mathbf{p} . Note that $\sum_{a=0}^{\omega} \sum_{i=1}^I v_{a,i,j,t} = 1$. The age- and subpopulation-specific bycatch was then removed while incrementing ages by one year according to:

$$[31] \quad N_{a+1,i,t+1} = \max\left(N_{a,i,t} - \sum_{j=1}^J c_{a,i,j,t}, 0\right) \quad \text{for } a < \omega$$

where J is the total number of management areas. Note that removing bycatch after natural mortality maximized the overall mortality rate for a given absolute bycatch because all bycaught animals were survivors of natural mortality.

The only calf mortality resulting from bycatch (Eqs 28-31) was calves bycaught according to their age-specific vulnerability. However, if lactating females with dependent calves are bycaught then their abandoned calves will die, but potentially not be a part of the bycatch. The maximum additional calf mortality from subpopulation i in year t that could result from abandonment might be:

$$[32] \quad \left(1 - \frac{\sum_{j=1}^J c_{0,i,j,t}}{N_{0,i,t}}\right) b_{i,t} \sum_{j=1}^J \sum_{a=1}^{\omega} c_{a,i,j,t} m_{a-1}$$

which assumes that calves are entirely dependent on their mothers for their first year of life (i.e., the calf of a bycaught mother will die) and that the probability of a calf being bycaught is independent of the probability of the mother being bycaught. Similar assumptions were made by Woodley (1993) in a modelling study of dolphin bycatch. The latter assumption seems unlikely because mothers and calves would be together and thus experience similar risks of bycatch. Nevertheless, the effect of calf abandonment can be incorporated in the operating model according to Eq. 32.

Fourth, reproduction was applied:

$$[33] \quad N_{0,i,t} = \text{Binom}\left[\sum_{a=1}^{\omega} (N_{a,i,t} m_{a-1}); b_{i,t}\right]$$

where m_a is the proportion of animals that are sexually mature at age a and b is annual birth rate (number of calves per mature animal). The sexual maturity ogive was:

$$[34] \quad m_a = \left(1 + e^{-\frac{a-a^{m50}}{\sigma^m}}\right)^{-1}$$

where a^{m50} is the age at which 50% of animals are sexually mature and σ^m is a parameter determining the width of the maturity ogive. For common dolphins, we fixed the sexual maturity parameters, a^{m50} and σ^m , at 8.23 and 1.02, respectively, based on an analysis of this species' life history in the Northeast Atlantic by Murphy et al. (in revision). This age at sexual maturity is similar to that described for other common dolphin populations (Ferrero and Walker 1995, Westgate 2005, Danil and Chivers 2007). Note that maturity was not treated stochastically in order to simplify computation; in Eq. 33 the term $N_{a,i,t} m_{a-1}$ was rounded to the nearest integer. The main assumptions regarding natural mortality and reproduction were: 1) females could potentially give birth for the first time one year after they matured; 2) b did not vary with age; and 3) all animals died before $t=\omega+1$ (knife-edge survival senescence).

Birth rate was assumed to be density-dependent and a function of the number of non-calves

$(\sum_{a=1}^{\omega} N_{a,i,t})$:

$$[35] \quad b_{i,t} = \min \left\{ \max \left\{ b^K + (b^{\max} - b^K) \left[1 - \left(\frac{\sum_{a=1}^{\omega} N_{a,i,t}}{\sum_{a=1}^{\omega} N_{a,i,t}^K} \right)^z \right], 0 \right\} e^{\varepsilon_t}, 0.5 \right\}$$

where b^{\max} is maximum birth rate, b^K is birth rate at carrying capacity, $\sum_{a=1}^{\omega} N_{a,i,t}^K$ is the number of non-calves in subpopulation i at carrying capacity at the beginning of year t , z is a density-dependence shape parameter, and ε_t is a random deviation in birth rate in year t as a result of environmental variability. It was ensured that the expected birth rate was greater than zero and that realized birth rate was less than 0.5. Birth rate at carrying capacity was calculated as:

$$[36] \quad b^K = \left(\sum_{a=1}^{\omega} l_a m_{a-1} \right)^{-1}$$

where l_a is survivorship to age a . Survivorship was calculated as:

$$[37] \quad l_a = \begin{cases} 1 & \text{for } a = 0 \\ \prod_{x=0}^{a-1} s_x & \text{for } a > 0 \end{cases}$$

For common dolphins, we chose maximum birth rates (b^{\max}) of 0.179 and 0.250 to represent maximum population growth rates of 2% and 4% per year, respectively. These maximum birth rates correspond to inter-birth intervals of 2.0 and 2.8 years, respectively, assuming a 1:1 sex ratio. Two years is near the lowest estimated inter-birth interval for common dolphins (Danil and Chivers 2007). Lower annual pregnancy rates have been observed for several populations of common dolphins (e.g., 0.25-0.3; $b=0.125-0.15$; Westgate 2005, Westgate and Read 2007, Murphy et al. in revision), but these pregnancy rates might not correspond to populations growing at their maximum rate.

The number of non-calves at carrying capacity was not treated as a parameter, it was calculated from a parameter specifying the total number of animals at carrying capacity

$(\sum_{a=0}^{\omega} N_{a,i,t}^K)$ using the following relationship:

$$[38] \quad \sum_{a=1}^{\omega} N_{a,i,t}^K = \sum_{a=0}^{\omega} N_{a,i,t}^K \left[1 - \left(\sum_{a=0}^{\omega} l_a \right)^{-1} \right]$$

The model also allowed for linear changes in the number of animals at carrying capacity over time.

In addition to density dependence in birth rate, the operating model allowed for stochastic annual variation in birth rate over time representing environmental variability. Annual multipliers of birth rate were assumed to be log-normally distributed and potentially correlated over time (first-order autoregressive model) with mean 1 and coefficient of variation CV^{env} so that:

$$[39] \quad \varepsilon_t = -0.5 \log(1 + CV^{\text{env}^2}) (1 - \varphi) + \varphi \varepsilon_{t-1} + N[0; \log(1 + CV^{\text{env}^2}) (1 - \varphi^2)]$$

where $|\varphi| < 1$ is a parameter controlling the strength of the correlation in deviations over time ($\varphi = 0$ specifies no correlation). The first deviation was initialised to the mean value:

$$[40] \quad \varepsilon_0 = -0.5 \log(1 + CV^{\text{env}^2})$$

Immediately after births, survey estimates of absolute abundance ($O_{j,t}$) were simulated for each management area every f years for input to the management procedure. First, animals were distributed stochastically among management areas according to:

$$[41] \quad \mathbf{X}_{i,t} = \text{Multin} \left(\sum_{a=0}^{\omega} N_{a,i,t}; \boldsymbol{\beta}_i^{\text{srvy}} \right)$$

where $\mathbf{X}_{i,t} = [x_j]_{i,t}$ is the vector of numbers of animals in management areas j belonging to subpopulation i at time t , and $\boldsymbol{\beta}_i^{\text{srvy}} = [\beta_j^{\text{srvy}}]_i$ is the vector of expected proportions of animals belonging to subpopulation i in management areas j at the time of surveys. Survey estimates were then simulated for each management area assuming that the errors in the estimates were independent between years and surveys and log-normally distributed so that:

$$[42] \quad O_{j,t} = e^{\text{N} \left[\log \left(B^0 \sum_{i=1}^t x_{j,i,t} \right), \log \left(1 + \left(B^{\text{CV}^0} CV^0 \right)^2 \right) \right]}$$

where B^0 is a directional bias parameter specifying the expected absolute abundance estimated by a survey as a proportion of true abundance, and B^{CV^0} is a directional bias parameter specifying the true coefficient of variation in survey estimates of absolute abundance as a proportion of the estimated coefficients of variation of the estimates of absolute abundance. Eq. 42 assumes that the true population size is the median of the log-normal error distribution which is identical to the assumed error distribution for abundance estimates in the PBR and CLA procedures (Eqs 21 and 23, respectively).

Simulations were initialized by first setting the number of non-calves in subpopulation i to a proportion of the number of non-calves in that subpopulation at carrying capacity ($D_{i,0}$):

$$[43] \quad \sum_{a=1}^{\omega} N_{a,i,0} = D_{i,0} \sum_{a=1}^{\omega} N_{a,i,0}^{\text{K}}$$

Then $b_{i,0}$ was calculated according to Eq. 35. Next, the age distribution at $t=0$ for each subpopulation was set to the stable age distribution (dominant eigenvector of the transition matrix) specified by deterministic versions of Eqs 26 and 33 with $b_{i,0}$. Finally, the number of

animals of each age at $t=0$ were calculated from this age distribution and $\sum_{a=1}^{\omega} N_{a,i,0}$. Such a

stable age distribution would of course not be realized in a population governed by density-dependent dynamics. Nevertheless, this age distribution was used to represent more realistic age distributions for subpopulations that were initially at fractions of their carrying capacity. Note that while the population model of the CLA procedure assumes that the population is at carrying capacity at the beginning of the bycatch time-series, this does not have to be the case in the operating model.

The management procedures and operating model were coded using the free software package R (R Development Core Team 2007) and the C computer language compiled with the free MinGW port (<http://www.mingw.org>) of the GNU GCC compiler (<http://www.gnu.org>). The CLA routine was coded in C based on a FORTRAN CLA routine developed and provided by the IWC (International Whaling Commission 1994). Many random checks were performed to

confirm that the CLA routine gave the same limits as the IWC CLA routine after accounting for the differences described above.

Table 2. Parameters of the operating model and values used in generic performance-testing simulation trials. Baseline values are indicated by ‘*’ and ‘worst-case’ values used for the third tuning are indicated by ‘†’. Fixed parameters were held constant in all trials. In each trial the value of one bottom-level parameter was altered while keeping all others at their baseline values, and then simulations were run over all combinations of values of the top-level parameters.

Parameter(s)	Symbol	Values
<i>Fixed</i>		
Age at which 50% of animals are sexually mature	a^{m50}	8.23*
Width of maturity ogive	σ^m	1.02*
Maximum age	ω	30*
Age-specific vulnerability to bycatch	η_a	1* (for all a)
Age-specific natural annual survival rate	s_a	* 0.8 for $a=0$, 0.86 for $a=1$, 0.92 for $a=2$, 0.97 for $2 < a < 26$, 0.92 for $a=26$, 0.87 for $a=27$, 0.82 for $a=28$, 0.77 for $a=29$, 0.72 for $a=30$
Total number of animals at carrying capacity in each subpopulation	$\sum_{a=0}^{\omega} N_{a,i,t}^K$	100000*
<i>Top-level</i>		
Initial population status (number of non-calves in each subpopulation as proportion of the number at carrying capacity)	$D_{i,0}$	Two sets of trials (only the first set was done with the PBR procedure): 1)* 15 years of constant bycatch ($CL_{j,t}$) prior to the simulation period resulting in $\frac{\sum_{a=0}^{\omega} N_{a,i,t=0}}{\sum_{a=0}^{\omega} N_{a,i,t}^K} = 0.05$, 0.1, 0.3, 0.6, 0.8 and 0.99 2) $\frac{\sum_{a=0}^{\omega} N_{a,i,t=0}}{\sum_{a=0}^{\omega} N_{a,i,t}^K} = 0.05, 0.1, 0.3, 0.6, 0.8, \text{ and } 1$ and a historical bycatch of 1 animal for one year
Maximum birth rate	b^{\max}	0.1788998, 0.2497297* (result in maximum annual population growth rates of 2% and 4%, respectively)
<i>Bottom-level</i>		
Shape of density dependence	z	0.1, 1*, 13.5 (result in maximum net productivity levels of about 40%, 50% and 85% of carrying capacity, respectively)
Survey bias (expected estimated absolute abundance as proportion of true absolute abundance)	B^0	0.5, 1*, 1.5†
Survey precision (CV of estimates of absolute abundance)	CV^0	0.1, 0.2*, 0.6 (for $B^{CV^0} = 1$ and 2)
Survey CV bias (true CV of estimates of absolute abundance as proportion of estimated CV of these estimates)	B^{CV^0}	0.5, 1, 2*

Bycatch bias (realized bycatch as proportion of bycatch limit)	B^{byc}	0.5, 1*, 2 [†]
Bycatch precision (CV of realized bycatch)	CV^{byc}	0.1, 0.3*, 1.0
Survey frequency	f	5, 10*, 15
Change in carrying capacity	$\sum_{a=0}^{\omega} N_a^K$	no change*, 50% linear increase or decrease over simulation period
Catastrophes (annual probability of catastrophic natural mortality)	$P^{\text{catastrophe}}$	0*, 0.02
Environmental stochasticity (CV of birth rate deviations)	CV^{env}	0*, 0.2
Environmental stochasticity (autocorrelation in birth rate deviations)	φ	0*, 0.5 (when $CV^{\text{env}}=0.2$)
<i>Population structure</i>		
Number of subpopulations	I	1*
Number of management areas	J	1*
Proportion of subpopulation in management area (surveys)	$\beta_{j,i}^{\text{srvy}}$	1*
Proportion of subpopulation in management area (bycatch)	$\beta_{j,i}^{\text{byc}}$	1*
Dispersal rate	δ_i	NA

Application to common dolphins

Assessment

Data

We fitted our integrated population dynamics model to several datasets on common dolphins in the Northeast Atlantic. The SCANS-II and CODA surveys provided absolute abundance estimates for common dolphins in Northeast Atlantic shelf waters in July 2005 and offshore waters in July 2007, respectively. The SCANS-II design-based abundance estimate was 63,366 (CV=0.46). Density surface modelling improved the precision of the CODA design-based estimate and the model-based abundance estimate was 116,709 (CV=0.337). Life history data were available for stranded and bycaught females from the UK and Ireland including sexual maturity status of known-aged animals, pregnancy status of mature animals, and age-at-death of animals dying as a result of natural causes and bycatch (Tables 3 and 4). The life history data were provided by Rob Deaville and Paul Jepson (Institute of Zoology, London, UK), Sinéad Murphy (University of St Andrews, St Andrews, UK), and Emer Rogan (University College Cork, Cork, Ireland). Finally, estimates of previous bycatch of common dolphins in several fisheries in the Northeast Atlantic were available from the literature (Table 5). These bycatch estimates were treated as known input to the model. It is important to recognise that the bycatch estimates are extrapolations that are subject to substantial uncertainty. Furthermore, the bycatch estimates do not compose complete time-series for any of the fisheries, and bycatch occurs in other fisheries for which estimates were not available. Thus, these bycatch estimates are probably best considered as minimum estimates of previous bycatch, although bycatch estimates for individual fisheries in individual years could be overestimates.

Table 3. Data on sexual maturity and age structure of natural and bycatch mortality. Data are summarized for all years, but the model was fitted to mortality data from each year.

Age	Sexual maturity		Natural mortality	Bycatch mortality
	No	Yes		
0	18	0	1	11
1	6	0	1	6
2	8	0	0	4
3	5	0	0	2
4	6	0	1	4
5	3	0	0	3
6	8	0	0	5
7	2	1	0	2
8	2	2	0	3
9	0	4	0	0
10	2	2	0	3
11	1	3	0	4
12	0	3	0	2
13	0	5	2	3
14	0	4	0	4
15	0	5	0	2
16	0	8	0	5
17	0	4	0	1
18	0	7	0	6
19	0	5	0	2
20	0	2	0	1
21	0	2	0	0
22	0	1	0	0
23	0	0	0	0
24	0	0	0	0
25	0	7	1	1
26	0	3	1	1
27	0	0	0	0
28	0	0	0	0
29	0	0	0	0

Table 4. Data on pregnancy for sexually mature females. Years represent 1 September-31 May.

Year	No	Yes
1989/1990	0	0
1990/1991	2	1
1991/1992	8	3
1992/1993	6	1
1993/1994	10	4
1994/1995	4	2
1995/1996	5	2
1996/1997	8	1
1997/1998	0	0
1998/1999	4	3
1999/2000	4	2
2000/2001	7	5
2001/2002	10	3
2002/2003	3	3
2003/2004	10	0
2004/2005	10	0
2005/2006	5	2
2006/2007	1	0

Table 5. Estimates of common dolphin bycatch. Estimates are for years of life (1 July – 30 June) beginning in the year indicated.

Year	Fishery										Total
	Driftnet	Gillnet		Tanglenet	Pelagic trawl						
	Tuna (France, Ireland, UK) ¹	UK	Ireland	UK	Bass pair (UK)	Bass Area VII (European not including UK bass pair)	Bass Area VIII (European not including UK bass pair)	Hake (France)	Horse mackerel (Netherlands)	Tuna (European)	
1990	243										243
1991	390										390
1992	608										608
1993	1347	55 ²	179 ²								1581
1994	1580					25 ³		203 ³	101 ³	95 ³	2004
1995	666										666
1996	546										546
1997	947										947
1998	1706										1706
1999	2101										2101
2000	1589				190 ⁴						1779
2001					38 ⁴						38
2002					115 ⁴						115
2003					503 ⁴	60 ⁵	410 ⁵			128 ⁵	1101
2004		41 ⁶		86 ⁶	139 ⁴	60 ⁵	410 ⁵			128 ⁵	864
2005		98 ⁶		306 ⁶	84 ⁴						488
2006		57 ⁶		221 ⁶	20 ⁶						298

¹ Rogan and Mackey (2007)

² Tregenza et al. (1997); not clear whether these are annual values; bass and tuna estimates are for French fleet only; bass estimate is for all areas

³ Tregenza and Collet (1998); not clear whether these are annual values

⁴ Northridge (2006)

⁵ Northridge et al. (2006)

⁶ Northridge et al. (2007); estimates for calendar years were divided in half and allocated to the corresponding years of life

Design

The assessment was conducted for the time period 1990-2007. The population was treated as a single, panmictic population inhabiting the Northeast Atlantic. Murphy et al. (2008) reviewed information on common dolphins in the Northeast Atlantic and concluded that these animals can be considered a single population ranging from waters off Scotland to Portugal. We combined the SCANS-II and CODA abundance estimates into a single abundance estimate for this population, 180,075 (CV=0.272). The CV for the combined estimate was derived by assuming that the errors were independent between the two surveys and summing the variances of the estimates from the two surveys. We assigned the combined abundance estimate to the year between the two surveys, July 2006. If common dolphins were distributed differently between the SCANS-II and CODA survey areas in 2005 and 2007, then the combined estimate would be inaccurate. Ideally, the error arising from annual variability in spatial distribution should be incorporated in the CV of the combined abundance estimate (Skaug et al. 2004), but this was not possible as we only had two estimates from mutually exclusive areas and years. Common dolphins are also found outside of the combined SCANS-II/CODA area and if these animals are part of the same population then the combined abundance estimate that we used would be a minimum estimate.

Four model scenarios were considered with respect to model parameterisation and population dynamics. The first three scenarios modelled density-dependent population dynamics. In Scenarios 1 and 2 the population was assumed to be at carrying capacity at the beginning of the study period (i.e., 1990). Scenarios 1 and 2 differed in the parameterisation of age-specific natural survival rates: Scenario 1 modelled age-specific survival with the Siler competing-risk model while Scenario 2 modelled survival with five discrete age-class-specific survival rates. In Scenario 3 the population was allowed to be below carrying capacity in 1990 (e.g., due to bycatch prior to 1990) so that initial population size was an extra estimated parameter. Scenario 4 modelled density-independent population dynamics. Scenarios 3 and 4 both modelled survival using discrete age-class-specific rates.

Results

The main result of the assessment was that the combination of data and model used were not informative about the main population parameters of interest: population growth rate, maximum population growth rate and carrying capacity. Figures 1-4 show the posterior probability distributions for the model parameters. In the density-dependent Scenarios 1-3 the posterior probability distributions for maximum birth rate were wide and uninformative and the posterior for carrying capacity was similarly wide and uninformative unless it was assumed that the population was at carrying capacity in 1990 (Scenarios 1 and 2). The posterior probability distribution for initial population size in the density-independent model was also wide and uninformative. The model fit the single estimate of abundance reasonably well, but there were large uncertainties in estimated population size during the study period (Fig. 5). As a result of these uninformative posterior distributions the posterior distributions for maximum population growth rate (Scenarios 1-3) and population growth rate (Scenario 4) were also uninformative (Fig. 6).

The model fit the data on pregnancy rate and age at sexual maturity reasonably well (Figs 7 and 8), but the estimation of natural survival rates was problematic. It was difficult to obtain convergent estimates for some of the survival parameters with both the Siler survivorship model and discrete survival rate parameters. The posterior samples for several of the parameters of the Siler model (Scenario 1) exhibited substantial autocorrelation probably due to correlation in the estimates of these parameters and slow mixing in the MCMC algorithm.

Estimates of age-class-specific survival rates appeared to converge better with the density-dependent model (Scenarios 2 and 3), but the density-independent model revealed a bimodal posterior distribution for the annual survival rate of animals ≥ 20 years of age (Figs 4 and 9). A preliminary run of a density-dependent scenario with age-class-specific survival rate parameters also exhibited a multi-modal posterior but this only occurred near the end of the MCMC chain suggesting that convergence was problematic. Despite the convergence issues, all model scenarios suggested a senescent decrease in survival for the oldest ages in the model (Figs 10 and 11). The model underestimated the proportion of very young animals in the sample of bycaught animals in all scenarios (Fig. 11). The Siler model provided continuous predicted age distributions of mortality that were more visually appealing and likely more realistic than the irregular distributions that resulted from age-class-specific survival rates.

The assessment could be most improved in the future by including one or more historical estimates of abundance and more data on the age structure of natural mortality. Historical estimates of abundance should improve the estimation of population growth rate during the study period, although it is unlikely that there would be sufficient data to estimate maximum population growth rate or carrying capacity. More data on the age structure of natural mortality should improve the estimation of natural survival rates and may allow the estimation of age-specific vulnerabilities to bycatch. A different model for age-specific natural survival may also help improve parameter estimation.

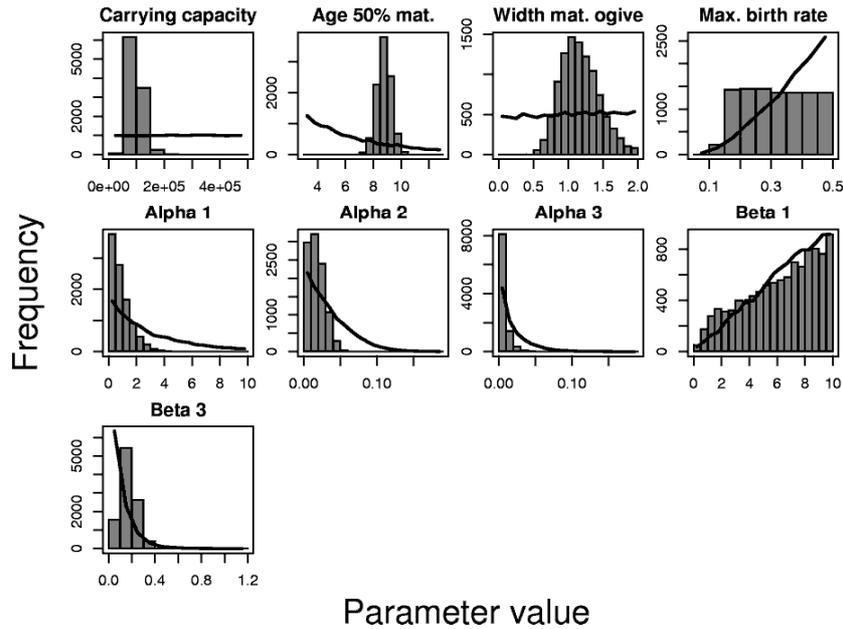


Figure 1. Marginal prior and posterior probability distributions of the estimated parameters (Table 1) of the density-dependent model assuming that the population was at carrying capacity in 1990 and with the Siler competing-risk model for survivorship (Scenario 1). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively.

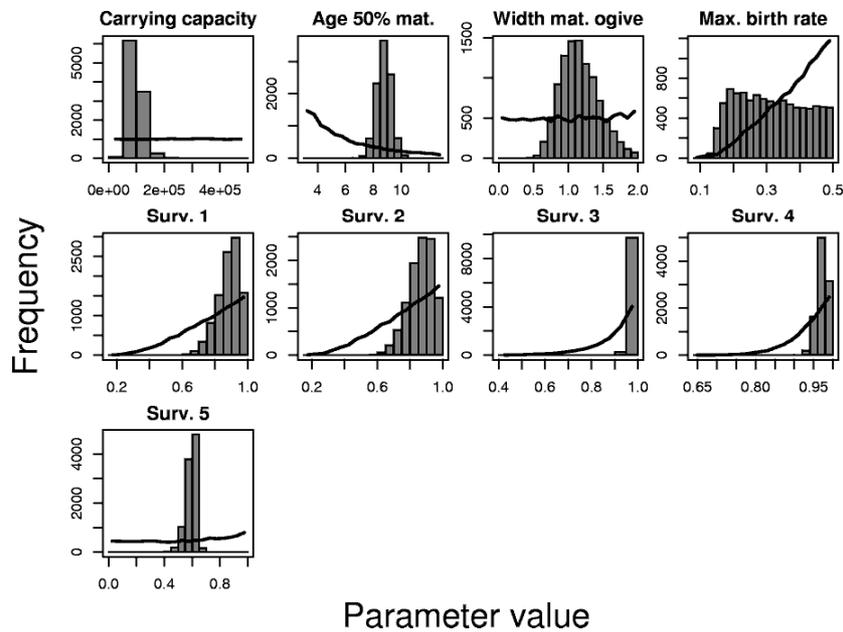


Figure 2. Marginal prior and posterior probability distributions of the estimated parameters (Table 1) of the density-dependent model assuming that the population was at carrying capacity in 1990 and with age-class-specific survival parameters (Scenario 2). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively.

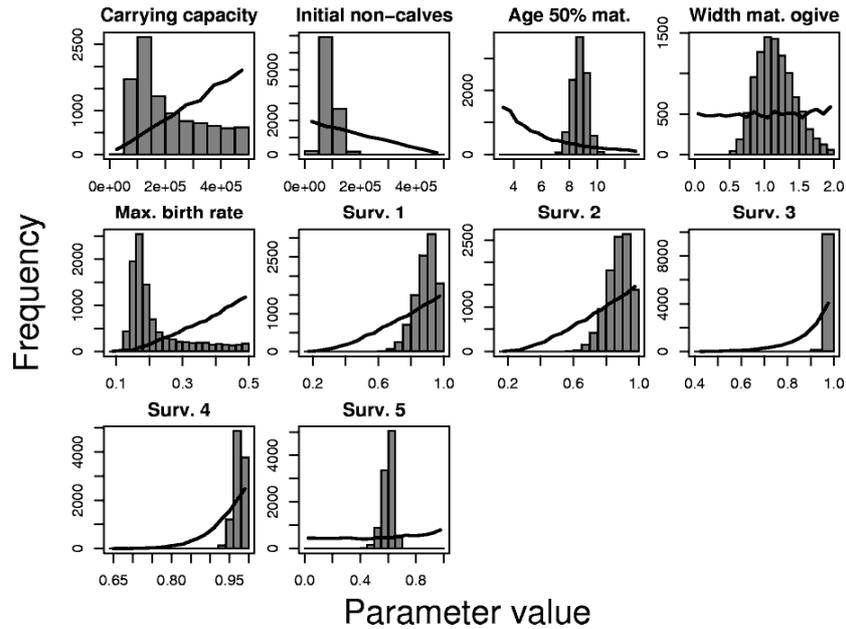


Figure 3. Marginal prior and posterior probability distributions of the estimated parameters (Table 1) of the density-dependent model with age-class-specific survival parameters and not assuming that the population was at carrying capacity in 1990 (Scenario 3). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively.

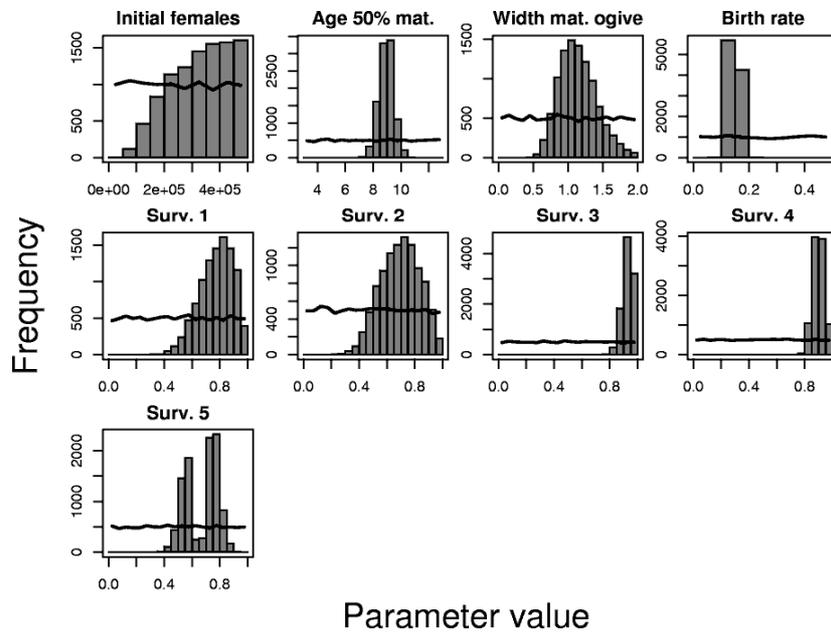


Figure 4. Marginal prior and posterior probability distributions of the estimated parameters (Table 1) of the density-independent model with age-class-specific survival parameters (Scenario 4). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively.

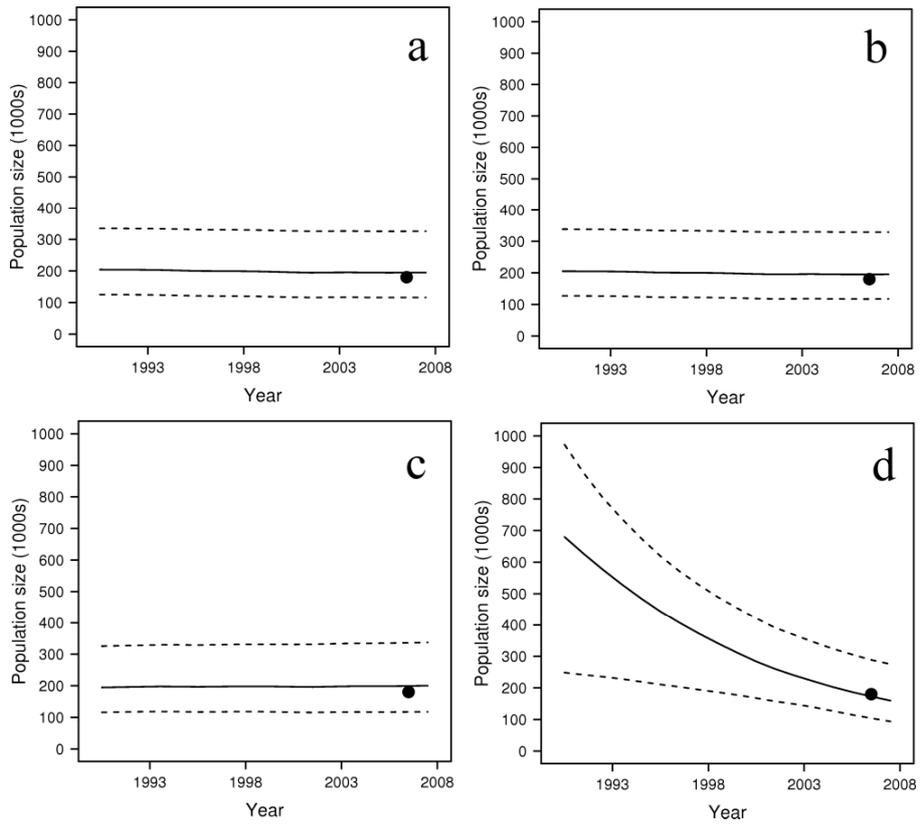


Figure 5. Observed (points) and predicted (lines) total number of males and females during the study period for all model scenarios (panels a-d represent Scenarios 1-4, respectively). The solid line represents median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample.

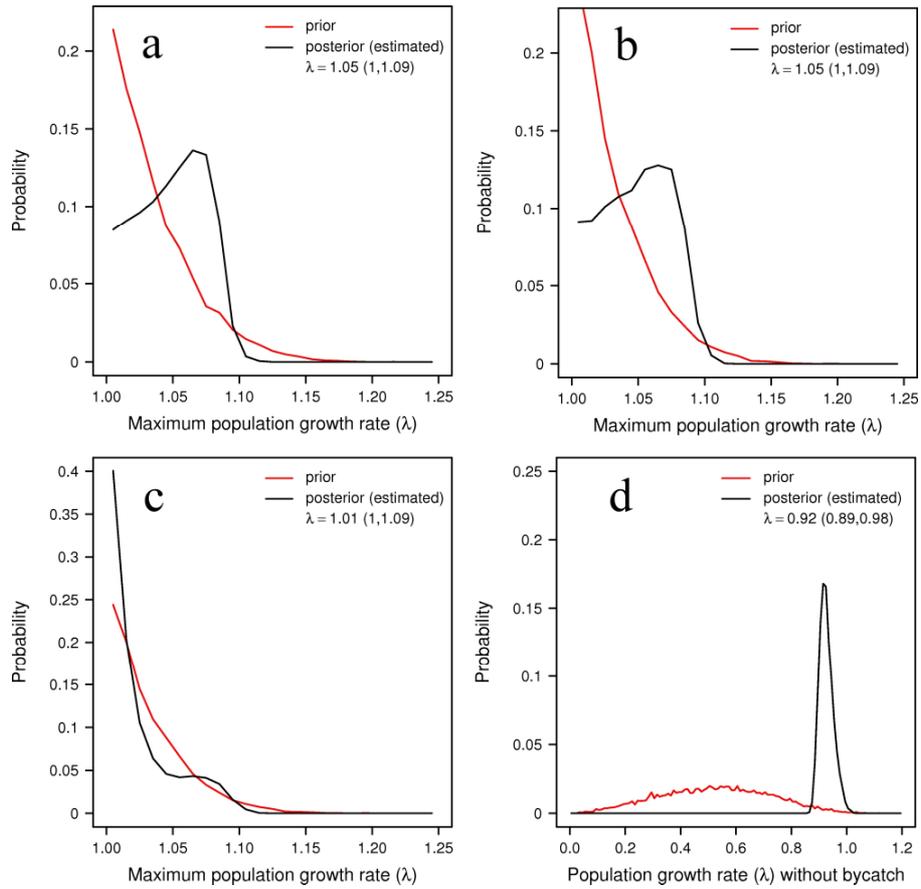


Figure 6. Prior and posterior probability distributions for (maximum) population growth rate in the absence of bycatch for all model scenarios (panels a-d represent Scenarios 1-4, respectively). The distributions for population growth rate were derived from the samples of maturity, birth and natural survival rates from the joint prior and joint posterior. The median estimates and 95% posterior probability intervals are indicated on the plots.

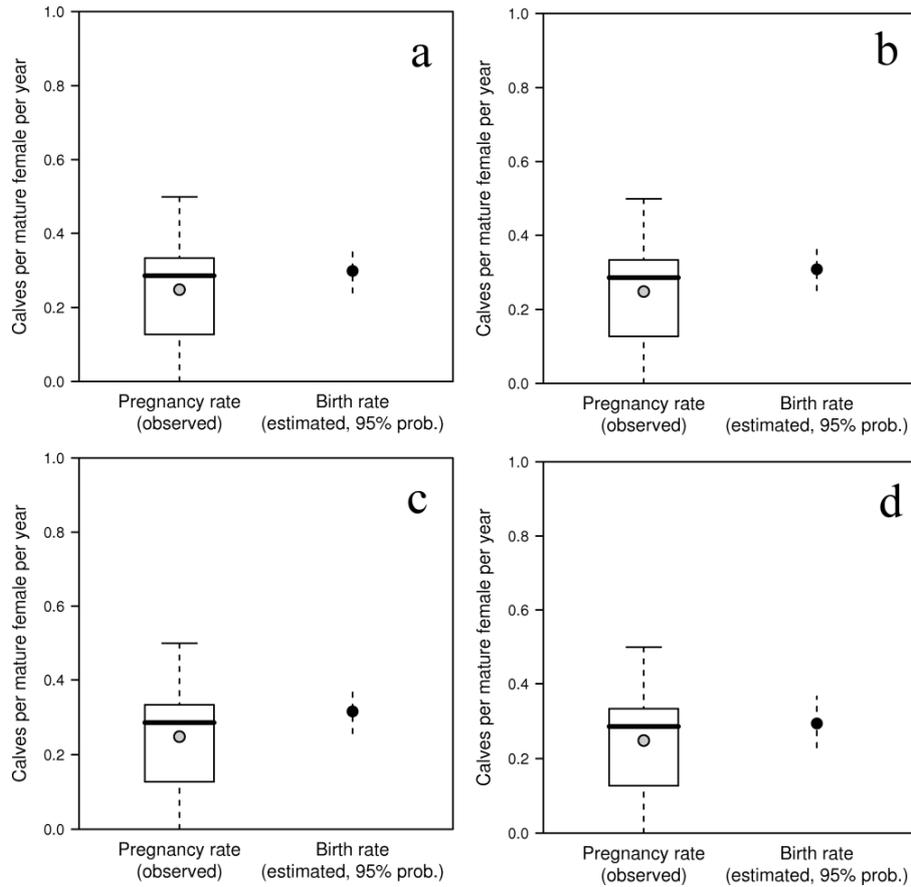


Figure 7. Observed pregnancy rate and predicted birth rate for the four model scenarios (panels a-d represent Scenarios 1-4, respectively). The boxplot on the left represents the distribution of observed pregnancy rates across years during the study period (point represents the overall pooled pregnancy rate). The data point and dashed line on the right represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively.

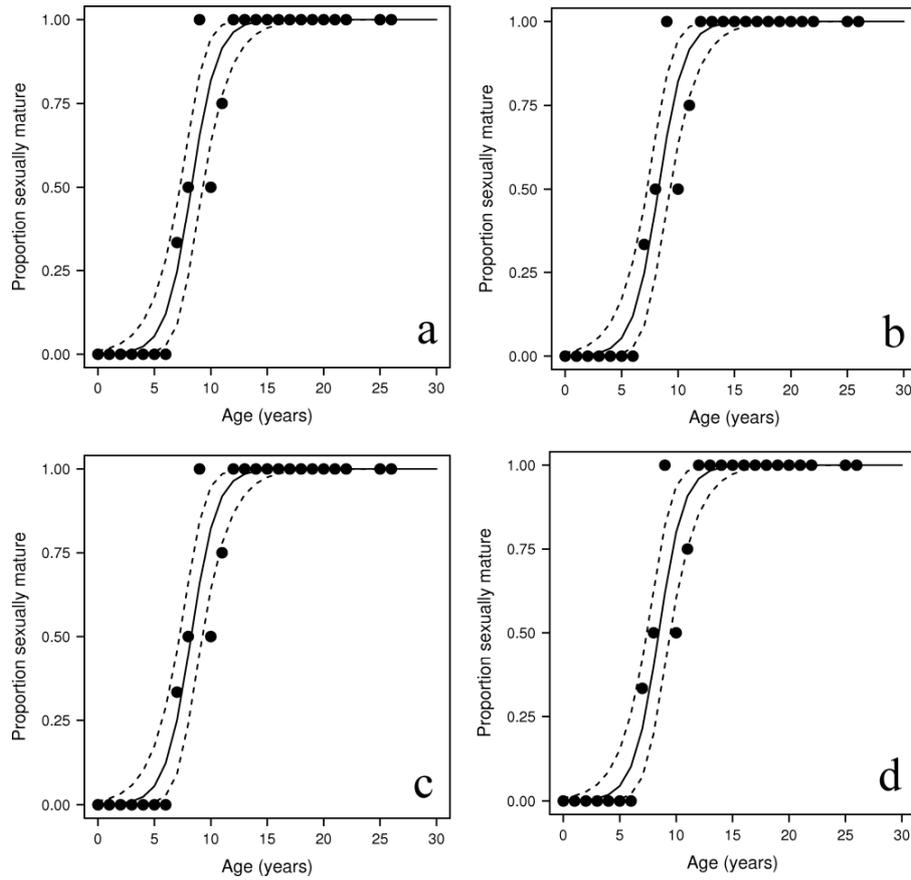


Figure 8. Observed (points) and predicted (lines) sexual maturity ogive for the four model scenarios (panels a-d represent Scenarios 1-4, respectively). Solid line indicates median values from the posterior sample and dashed lines represent the 95% interval of values from the posterior sample. The x-axis represents the mid-points of the indicated ages.

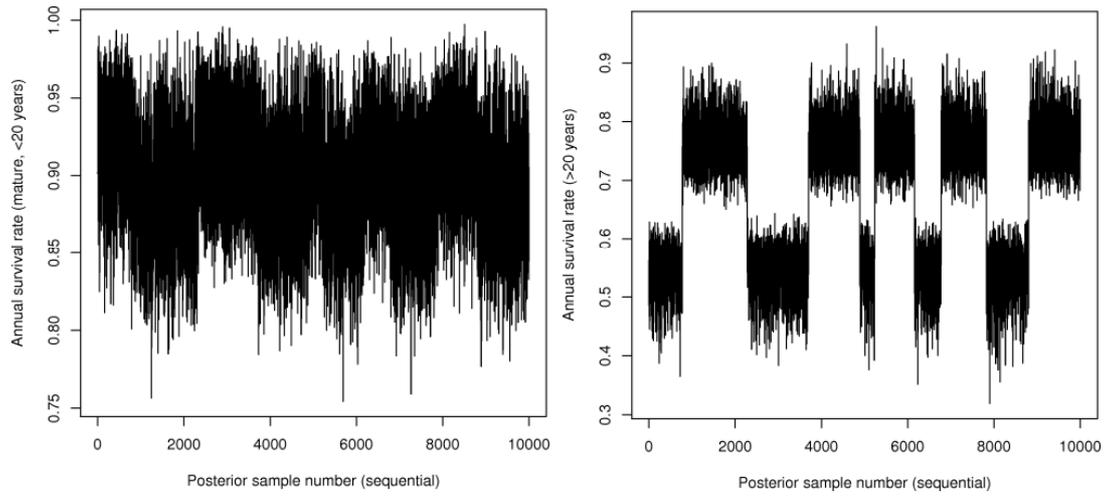


Figure 9. Trace plots of the posterior samples for the 4th and 5th age-class-specific survival rates in the density-independent model (Scenario 4).

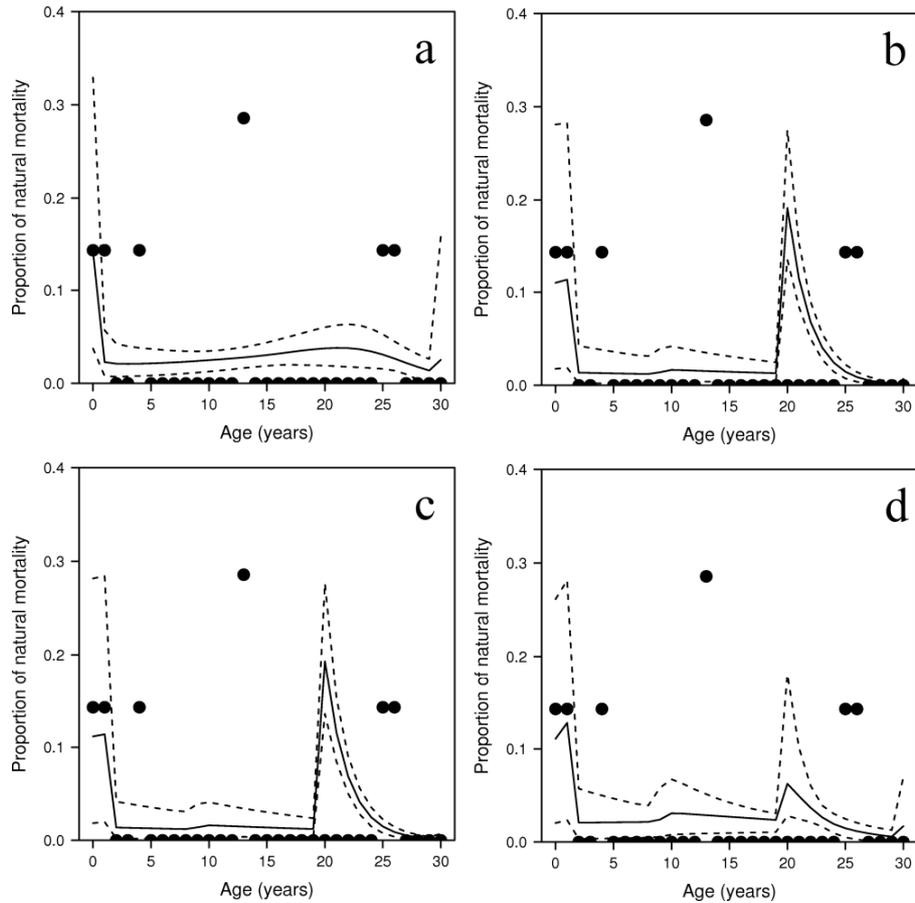


Figure 10. Observed (points) and predicted (lines) age structure of natural mortality for the four model scenarios (panels a-d represent Scenarios 1-4, respectively). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately, not the pooled data presented in this figure.

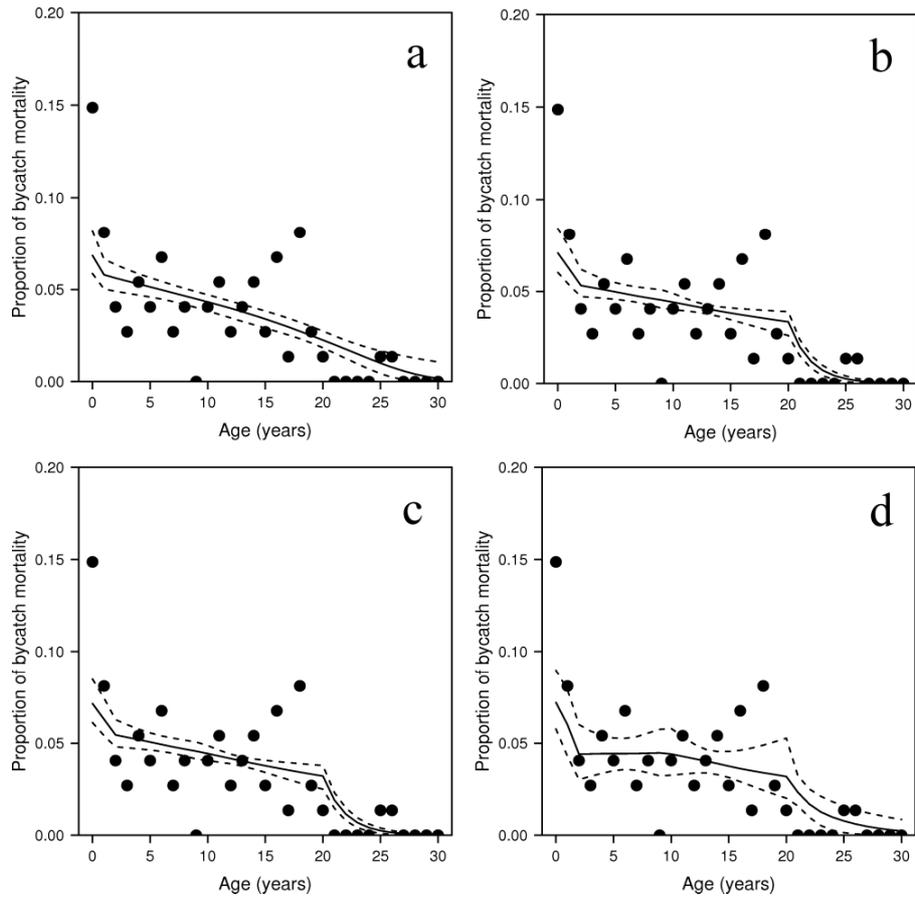


Figure 11. Observed (points) and predicted (lines) age structure of bycatch mortality for the four model scenarios (panels a-d represent Scenarios 1-4, respectively). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately, not the pooled data presented in this figure.

Management procedures and bycatch limits

Conservation objective(s)

The first step in generating safe bycatch limits for common dolphin and other small cetacean populations is the establishment of a conservation objective(s) in quantitative terms. This is a management decision. European policymakers have not established specific conservation objectives for small cetaceans in the CODA study region, or indeed anywhere. Therefore, for the purposes of this work we followed the approach taken in the SCANS-II project and adopted the interim conservation objective agreed by ASCOBANS: To allow populations to recover to and/or maintain 80% of carrying capacity in the long term.

Carrying capacity is defined as the population size that would theoretically be reached by a population in the absence of bycatch. Note that we do not need to know what this carrying capacity actually is to develop management procedures to set safe bycatch limits.

The ASCOBANS interim conservation objective is partially quantitative but two factors are not fully defined.

First, “long term” is not specified. We adopted a period of 200 years for the development of the management framework. This long period was chosen to allow sufficient time for heavily depleted populations to recover even in the absence of bycatch if natural rates of increase were low. However, because the status of populations in the shorter term is also of interest for conservation, it is also important to consider any delay in recovery of depleted populations due to continuing bycatch. Because of this, the performance of the management procedures with respect to recovery delay is presented in our results below.

Second, the most obvious quantitative interpretation of “recovering to and/or maintaining 80% of carrying capacity” is that this is an expected target that should be reached on average. This is important because, as described below, the management procedures developed must be “tuned” to achieve the conservation objective. Our first tuning therefore ensures that the procedures reach or exceed the conservation objective target on average (i.e., 50% of the time).

Alternatively, one could interpret the ASCOBANS interim conservation objective as meaning that the population should recover to and/or be maintained at or above 80% of carrying capacity. This could be implemented as a requirement to reach the target level a higher than average percentage of the time, although this percentage is not specified. To capture this alternative interpretation, we also developed management procedures that were tuned to achieve the conservation objective 95% of the time. This is a stricter target and this tuning produces a more conservative procedure.

In addition, although the approach used to develop the management procedures explicitly takes account of uncertainty in our knowledge, the limits to this uncertainty cannot be explicitly defined by the conservation objective and must be determined by expert judgement of the plausibility of the extent of our uncertainty. As described below, we developed management procedures that were tuned to meet the conservation objective assuming a certain level of uncertainty (values for maximum population growth rate and population level resulting in maximum productivity that were believed to be conservative) and then tested the robustness of the procedures to additional sources of uncertainty, following the approach used in the original development of the CLA and PBR procedures.

An extreme alternative is to tune the procedures to meet the conservation objective in the face of a “worst case” scenario. By definition, this scenario has lower plausibility than the scenarios for the other tunings specified above but, for comparison, we also present results for this much more conservative approach.

It is critically important to note that although the management procedures developed here are generic, the specific results presented below are entirely dependent on the conservation objective adopted. If it is determined that alternative and/or additional conservation/management objectives are appropriate, the management procedures developed can easily be tuned to the new objective(s) when a final policy/management decision is taken.

Tuning of the management procedures

The operating model was used to tune the management procedures so that one would expect to achieve the conservation objective in practice. As described above, three different tunings were developed. All three tunings were based on a single subpopulation inhabiting a single management area. The operating model was used to simulate this subpopulation subject to bycatch as limited by the management procedures for a period of 200 years. Population status at the end of the 200-year simulation period was examined to determine whether the conservation objective was achieved. If the objective was not achieved then the values of the tuning parameters of the management procedures were adjusted and the simulation was run again. This process was iterated until the conservation objective was achieved. In its original development by the IWC, the CLA procedure was tuned by fixing the values of the tuning parameters ρ and γ and adjusting the value of Q . Aldrin et al. (2006, 2008) advocated fixing Q at 0.5 and adjusting ρ to tune the CLA. They pointed out that it was impossible to tune the CLA to achieve final depletions <0.7 over a 300-year timeframe when ρ and γ were fixed at their default tuned values. This was because with infinite data the posterior distribution of nominal bycatch limits is degenerate to a single value and is therefore not affected by Q . We chose to use ρ to tune the CLA following Aldrin et al. (2008). However, Q was fixed at 0.4 to maintain the conservative feature that greater variance in the posterior distribution of nominal bycatch limits (for example because of greater uncertainty in abundance estimates) resulted in a lower bycatch limit. The internal protection threshold, γ , was set to 0.5, the assumed maximum net productivity level in the baseline version of the operating model ($z=1$).

The first tuning was developed in a manner similar to the tuning of the CLA procedure by the IWC. All parameters of the operating model were set at their baseline values (Table 2). Initial population status (population size as a proportion of carrying capacity) was set to 0.99. For the CLA procedure a 15-year historical time-series of bycatch was assumed that reduced the population to 99% of carrying capacity at the beginning of the simulation period. Maximum population growth rate was assumed to be 4% per year with a density-dependence relationship that resulted in maximum net productivity at 50% of carrying capacity. A maximum population growth rate of 4% per year was the default value used for cetaceans in the original development of the PBR procedure and this value was considered conservative for harbour porpoise by a joint IWC/ASCOBANS working group (International Whaling Commission 2000). The maximum rate at which common dolphin populations can grow is not well understood. Reilly and Barlow (1986) suggested that the maximum growth rate of dolphin populations was probably $<9\%$ per year based on general Leslie matrix models. In another Leslie matrix modelling study Woodley (1993) suggested that the maximum population growth rate for common dolphins was probably $\leq 4\%$. Gerrodette et al. (2008) reported trends in dolphin abundance in the eastern tropical Pacific as high as 11% per year with an estimate of almost 5% for common dolphins between 1986 and 2006. Given the

results of these studies we chose 4% per year as a conservative maximum population growth rate for common dolphins. A maximum net productivity level of 50% of carrying capacity is conservative in that it results in a lower absolute maximum sustainable removal than a higher maximum net productivity level would. The management procedures were then tuned under this scenario so that the median population status after 200 years was 80%. This tuning is therefore appropriate for a conservation objective of maintaining the population *at* 80% of carrying capacity in the long term.

The second tuning was developed in exactly the same way except that the management procedures were tuned so that there was a 95% probability that population status was $\geq 80\%$ after 200 years. This is similar to the way in which the PBR procedure was tuned in its original development except that in the PBR development case it was tuned to be $\geq 50\%$ of carrying capacity, the lower limit in the range 50-70%, and not a single target level. Our second tuning is therefore appropriate for a conservation objective of maintaining the population *at or above* 80% of carrying capacity in the long term.

The third tuning was developed considering a “worst-case” scenario. Population parameter values were identical to those used in the first two tunings and all parameters of the operating model were set at their baseline values except two. Exploratory simulations indicated that the two parameters with the largest effects on performance (other than maximum population growth rate and maximum net productivity level) were bias in survey estimates of population size and bias in estimates of bycatch. Worst-case values for the above parameters were chosen as follows. A 50% overestimate was chosen as the worst-case bias in absolute estimates of population size. It was assumed that future surveys would be conducted using a methodology similar to the SCANS-II and CODA surveys; these were robust, design-unbiased methodologies that were highly unlikely to systematically overestimate population size by more than 50%. A 50% underestimate was chosen as the worst-case bias in estimates of future bycatch (i.e., actual bycatch would be twice the estimated bycatch). The estimation of bycatch is fraught with uncertainty, but this tuning of the procedures assumed that estimates of bycatch in the future would by design not underestimate bycatch by more than 50%. Initial population statuses ranging from 0.05-1.00 were considered for this tuning. The management procedures were then tuned so that there was a 95% probability that population status was ≥ 0.80 after 200 years (under this worst-case scenario). This tuning is therefore appropriate for a conservation objective of maintaining the population *at or above* 80% of carrying capacity in the long term *under a worst-case scenario*.

The values of the tuning parameter (F) for the three tunings of the PBR procedure were 0.53, 0.38 and 0.12, respectively. The values of the tuning parameter (ρ) for the three tunings of the CLA procedure were 3.40, 1.89 and 0.50, respectively.

It is important to note that the performance of the management procedures beyond 200 years was not examined.

Figs 12 and 13 highlight the difference in the three tunings of the procedures in terms of the conservation objective. In the first tuning, PBR1 and CLA1, the population is maintained at 80% of carrying capacity, as defined by the objective. In the second tuning, PBR2 and CLA2, the population is maintained at a higher percentage of carrying capacity (~85-90%) because of the requirement to achieve the conservation objective 95% of the time. In the third tuning, PBR3 and CLA3, the population is maintained at an even higher percentage of carrying capacity (~95%) because of the additional requirement to achieve the conservation objective

under a “worst-case” scenario. As expected, long-term population status was highest and delay in recovery was shortest under the third tuning of the procedures (Fig. 12).

The delay in recovery of depleted populations to 80% of carrying capacity under the CLA procedure tended to be shorter than under the PBR procedure for a given tuning and initial population status (Fig. 12). This was due to the faster short-term recovery of highly depleted populations under the CLA procedure because of its internal protection mechanism (Fig. 13).

It is important to note that the specific values of the tuning parameters for the tunings presented here are different than those for the harbour porpoise tunings developed during the SCANS-II project and more recent harbour porpoise tunings presented by Winship (2009). These differences in the values of the tuning parameters arose because of technical differences in the implementation of the management procedures (e.g., PBR equation) and differences in the operating model (e.g., assumed observation error distribution, life history of common dolphins). Differences between the assumed life history of common dolphins and the assumed life history of harbour porpoise—lower birth rate, higher survival and older age at sexual maturity for common dolphins, but identical overall population growth rate—resulted in slightly higher bycatch limits for common dolphin populations. The higher bycatch limits arose because of the way that bycatch is removed from the population in the operating model. Bycatch is removed after natural mortality. Thus, when natural survival rates are higher (as in the common dolphin model) a given absolute bycatch will result in a lesser bycatch mortality rate for the survivors of natural mortality. As a result, it is assumed that the population can sustain slightly more bycatch in absolute terms. Nevertheless, the removal of bycatch after natural mortality is still a conservative approach: it assumes that none of the animals that are bycaught in a given year would have died naturally that year anyway.

The tunings of the management procedures presented here have relatively low precision compared to tunings of the CLA procedure developed by the IWC (e.g., International Whaling Commission 2002). However, the precision does not affect the relevance of our results. Higher precision tunings could be performed when a management procedure is finalised.

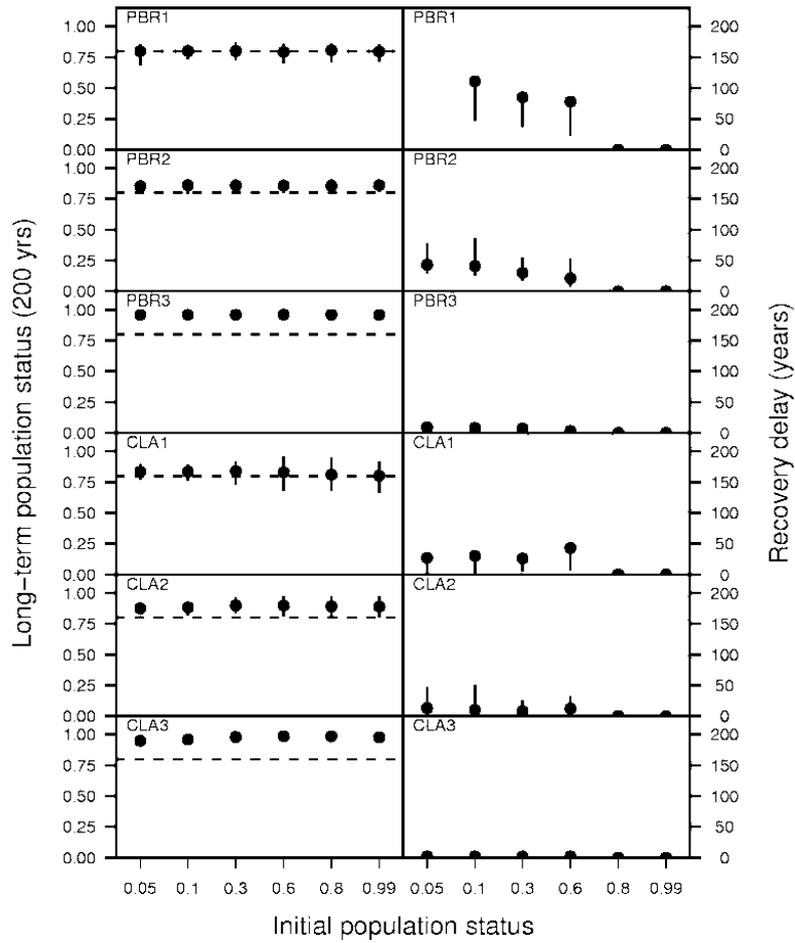


Figure 12. Performance of three tunings of the PBR and CLA management procedures under the baseline scenario with respect to the conservation objective (long-term population status) and recovery delay. Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. Population status is defined as population size as a proportion of carrying capacity. The horizontal dashed lines indicate the conservation objective: population status = 80%. Recovery delay is defined as the delay in recovery of a population to 80% of carrying capacity relative to a scenario without bycatch.

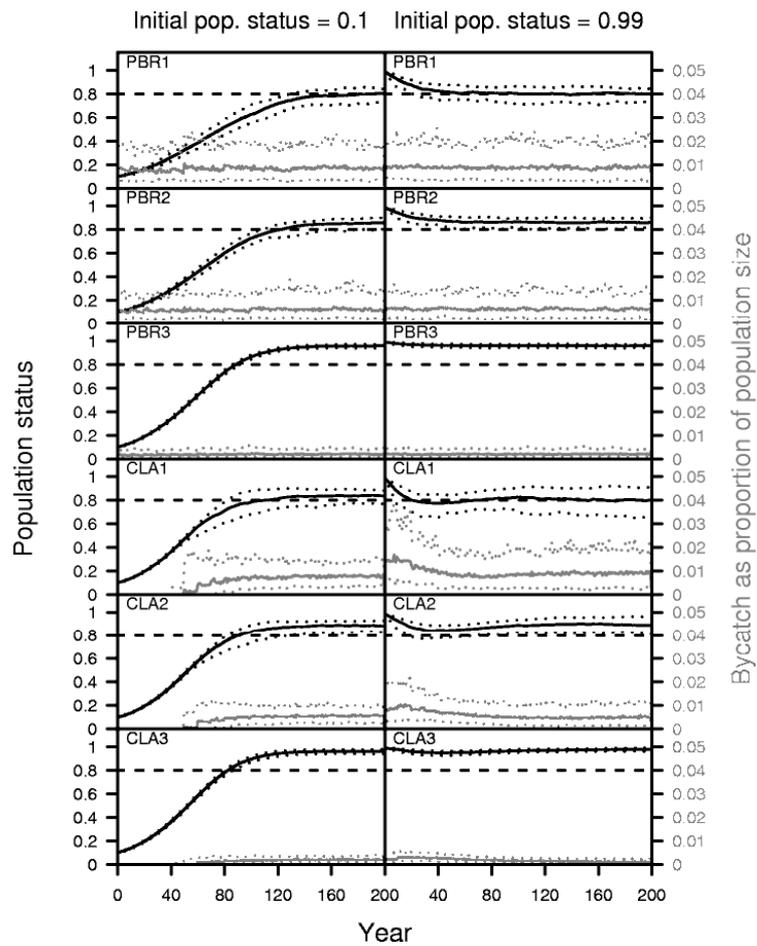


Figure 13. Trajectories of population status and bycatch (as proportion of population size) for three tunings of the PBR and CLA management procedures under the baseline scenario. Population status is defined as population size as a proportion of carrying capacity. Results are shown for two initial population statuses: 0.1 (left column) and 0.99. Solid lines represent median results from 100 simulations and dotted lines represent the 90% interval of simulation outcomes. The horizontal dashed lines indicate the conservation objective (population status = 80%).

Generic performance-testing simulations

Baseline and worst-case performance-testing simulation trials were conducted for all tunings and procedures, but the full set of generic trials was only conducted for the first tuning of the PBR procedure. Winship (2009) presented the detailed results of the full series of generic performance-testing simulation trials of all three tunings of the PBR and CLA procedures for harbour porpoise. The tunings and operating model used by Winship (2009) were identical to those presented here for common dolphins other than the aforementioned difference in life history and the resulting difference in the specific values of the tuning parameters. Thus, the general results of those simulation trials are applicable to the tunings presented here for common dolphins. The results of all trials conducted in this study were very similar to the results of the corresponding trials of the harbour porpoise tunings confirming that the results of the harbour porpoise trials are generally applicable to the tunings for common dolphins.

Bycatch limits

Before implementing a tuned management procedure in practice it should be subjected to species-specific simulation trials to test its performance in light of all of the information that is available for individual species.

One of the most important biological aspects of species-specific simulation trials is population structure. With respect to population structure, a conservative management approach is to create management areas no larger than the size of area within which animals are believed to mix and interbreed freely (Hammond and Donovan In press). Based on the available information about common dolphin population structure in the Northeast Atlantic, the combined CODA and SCANS-II survey area is potentially an appropriate management area (Murphy et al. 2008).

We calculated example bycatch limits for common dolphins in this area using the tuned PBR and CLA management procedures and the combined SCANS-II/CODA abundance estimate, 180,075 (CV=0.272). We treated this combined abundance estimate as applying to the summer of 2006—halfway between the SCANS-II and CODA surveys. The CLA management procedure can also make use of estimates of previous bycatch so we calculated a second set of bycatch limits using the tuned CLA procedure, the abundance estimate and the time-series of bycatch estimates presented in Table 5. Table 6 presents these example bycatch limits.

It is important to recognise that these bycatch limits are entirely dependent on the stated conservation objective, on the tunings that were used to achieve it under different interpretations, and on the data that were used to initiate the procedure. For example, bycatch limits under the CLA procedure were lower when historical bycatch was incorporated. As discussed above the historical bycatch time-series is likely an underestimate. Incomplete historical bycatch time-series can result in unsatisfactory performance of the first and second tunings of the CLA management procedure (Winship 2009). These bycatch limits are therefore indicative and should not be used for management purposes. Before that can happen a series of steps must be taken (as described below), initiated by agreeing conservation objective(s) at the policy level. The management procedures that were developed can easily be tuned to new conservation objectives when a final policy decision is taken.

Table 6. Example bycatch limits for common dolphins in the combined SCANS-II/CODA survey area. Bycatch limits were calculated using three tunings each of the PBR and CLA management procedures. The PBR procedure operated solely on the abundance estimate, while two sets of limits are presented for the CLA procedure: one based solely on the abundance estimate and one based on the abundance estimate and the time-series of historical bycatch up to mid-2006 (Table 5).

Historical bycatch time-series	PBR tuning			CLA tuning		
	1	2	3	1	2	3
no	1524	1092	345	1909	1061	280
yes	-	-	-	1547	860	227

Conclusions and recommendations

PBR or CLA management procedure?

The tuned PBR and CLA management procedures developed here are similar but there are some key differences. The only input to the PBR procedure is a single estimate of abundance, whereas the CLA procedure makes use of information on bycatch and on multiple estimates of abundance, if available, to give a more informed assessment of population status. As documented above, there are estimates of previous common dolphin bycatch available for several fisheries the Northeast Atlantic (Table 5). Potentially, there are also estimates of the historical abundance of common dolphins in the Northeast Atlantic. For example, Cañadas et al. (in press) present an absolute abundance estimate for common dolphins in 1995 in the W Block of the North Atlantic Sighting Survey (NASS), 273,159 (CV=0.26). This survey block was offshore and extended further west than the CODA survey. In general, areas that have been surveyed previously for common dolphins differ from the SCANS-II/CODA survey area (Murphy et al. 2008, Cañadas et al. in press) and these differences will have to be taken into account when combining abundance estimates in an assessment or management procedure framework. Nevertheless, the availability of historical data on bycatch and abundance means that there is an advantage to using the CLA procedure.

Another feature of the CLA procedure is its internal protection mechanism, which enhances the recovery of depleted populations by setting bycatch to zero if the population is estimated to be, in our version, <50% of carrying capacity. The PBR procedure cannot implement such an internal protection mechanism because it relies on a single estimate of population size and cannot, therefore, estimate the level of the population relative to carrying capacity.

An advantage of the PBR procedure is its simplicity but this simplicity does not give any advantage in the context of its use within the management framework presented here.

We conclude that the features of the CLA procedure and the advantages that these confer are sufficient for it to be considered as the best management procedure for common dolphins in the Northeast Atlantic.

Which tuning?

The three tunings developed allow for three interpretations of the conservation objective adopted from ASCOBANS (to allow populations to recover to and/or maintain 80% of carrying capacity in the long term). The first tuning of the management procedures is a robust mechanism for setting limits to bycatch to achieve the conservation objective of allowing a population to recover to and be maintained *at* 80% of carrying capacity. The second tuning achieves the conservation objective of maintaining a population *at or above* 80% of carrying

capacity. Satisfactory performance of the first and second tunings depends on the availability of data series of historical and current estimates of abundance and bycatch that are essentially unbiased. The third tuning is a highly conservative approach to maintaining a population *at or above* 80% of carrying capacity *in a worst case situation* where time series of estimates of abundance and bycatch are considerably biased upwards and downwards, respectively. If input data are judged to be of sufficient accuracy then either the first or the second tuning is appropriate. If consistent bias of the magnitude tested in either abundance or bycatch were considered plausible, then the third tuning would be more appropriate. We recommend that for application/implementation for any species in a particular region, the judgement of which tuning to use be based on an assessment of the available information. This may include conducting more simulation testing in cases where it is not clear whether or not a procedure is robust to plausible uncertainties. If the third tuning were adopted because of such uncertainty, more information on, in particular, bycatch, would allow a re-evaluation in the future.

Next steps

Before a management procedure can be implemented for a particular species in a particular region, the following steps need to be taken:

1. Agreement by policy makers on the exact conservation/management objective(s);
2. Agreement by policy makers to implement the procedure for one or more species in one or more regions;
3. Consideration by scientists of whether or not the available information for each species indicates that there is a need to conduct further simulation testing to examine uncertainties that may not have been fully explored;
4. In particular, if there is evidence for sub-population structure, consideration by scientists of any further simulation testing required and/or identification of any sub-areas that may be considered to contain sub-populations;
5. In addition, if there is evidence of historical bycatch but no data, consideration by scientists of any further simulation testing required including the generation of appropriate data series based on the best available information;
6. Final determination by scientists, based on the results of Steps 3 - 5, of how to implement the procedure for each species/region;
7. Agreement by policy makers to implement the procedure;
8. Generation by scientists of bycatch limits for a specified period (e.g., 5 years);
9. Establishment of a mechanism for feedback of information from bycatch monitoring programmes to inform the next implementation of the procedure when the period for which bycatch limits have been set expires.

In addition, the following step will need to be considered in the future:

- Planning for an absolute abundance survey in (approximately) 2015.

Step 1 should clearly be made at the European level. Similarly, Step 2 should ideally be made collectively although most species do not occur in all parts of the European Atlantic. Steps 3 – 6 can be done by the team of scientists that have developed the procedure or by others under their supervision/instruction. The amount of work involved depends on the species. The work accomplished in the SCANS-II and CODA projects for the harbour porpoise and common dolphin means that for these species these steps could be completed fairly rapidly; other species will take longer. Step 7 is another that should ideally be made at the European level; Step 8 can then be taken immediately. Step 9 is very important because removals from a population need to be incorporated when the procedure is re-implemented and this new

information (or lack of it) may determine which tuning of the procedure is implemented in the future.

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