

A Bayesian integrated population dynamics model to analyze data for protected species

S. D. Hoyle & M. N. Maunder

Hoyle, S. D. & Maunder, M. N., 2004. A Bayesian integrated population dynamics model to analyze data for protected species. *Animal Biodiversity and Conservation*, 27.1: 247–266.

Abstract

A Bayesian integrated population dynamics model to analyze data for protected species.— Managing wildlife–human interactions demands reliable information about the likely consequences of management actions. This requirement is a general one, whatever the taxonomic group. We describe a method for estimating population dynamics and decision analysis that is generally applicable, extremely flexible, uses data efficiently, and gives answers in a useful format. Our case study involves bycatch of a protected species, the Northeastern Offshore Spotted Dolphin (*Stenella attenuata*), in the tuna fishery of the eastern Pacific Ocean. Informed decision–making requires quantitative analyses taking all relevant information into account, assessing how bycatch affects these species and how regulations affect the fisheries, and describing the uncertainty in analyses. Bayesian analysis is an ideal framework for delivering information on uncertainty to the decision–making process. It also allows information from other populations or species or expert judgment to be included in the analysis, if appropriate. Integrated analysis attempts to include all relevant data for a population into one analysis by combining analyses, sharing parameters, and simultaneously estimating all parameters, using a combined objective function. It ensures that model assumptions and parameter estimates are consistent throughout the analysis, that uncertainty is propagated through the analysis, and that the correlations among parameters are preserved. Perhaps the most important aspect of integrated analysis is the way it both enables and forces consideration of the system as a whole, so that inconsistencies can be observed and resolved.

Key words: Bayesian analysis, Dolphin, *Stenella attenuata*, Model, Population dynamics, Yellowfin tuna.

Resumen

Modelo bayesiano integrado de dinámica de poblaciones para el análisis de datos de especies protegidas.— La gestión de las interacciones que se producen entre la flora y fauna y los seres humanos requiere disponer de información fiable acerca de las consecuencias probables que generarán las acciones de gestión. Este requisito es de carácter general, con independencia del grupo taxonómico. En el presente artículo describimos un método para estimar parámetros de dinámica de poblaciones y de toma de decisiones, de aplicación general, extremadamente flexible, que utiliza datos de un modo eficiente y proporciona respuestas en un formato útil. Nuestro ejemplo está relacionado con la captura accidental de una especie protegida, el delfín moteado (*Stenella attenuata*), en las pesquerías de atún de la costa este del océano Pacífico. Una toma de decisiones bien fundamentada requiere disponer de análisis cuantitativos que tomen en consideración toda la información relevante, permitiendo evaluar cómo afecta la captura accidental a estas especies y cómo afecta la normativa a las pesquerías, además de describir la incertidumbre en los análisis. El análisis bayesiano constituye un marco idóneo para proporcionar información sobre la incertidumbre que acompaña al proceso de toma de decisiones. Además de ser adecuado, permite incluir información acerca de otras poblaciones o especies en los análisis, así como un criterio experto. El análisis integrado pretende incluir en un único proceso todos los datos relevantes de una población, combinando análisis, compartiendo parámetros y estimando el conjunto de dichos parámetros de forma simultánea mediante el empleo de una función objetiva combinada. También garantiza que las presuposiciones del modelo y las estimaciones de parámetros sean coherentes a lo largo de todo el

análisis, que la incertidumbre se transmita a través del mismo, y que se mantengan las correlaciones entre los distintos parámetros. Quizá el aspecto más relevante del análisis integrado sea el modo en que permite y obliga a considerar el sistema como un todo, de forma que es posible observar y resolver las posibles contradicciones.

Palabras clave: Análisis bayesiano, Delfín, *Stenella attenuata*, Modelo, Dinámica de poblaciones, Rabil.

Simon D. Hoyle & Mark N. Maunder, Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, California 92037-1508, U.S.A.

Introduction

Managing wildlife–human interactions is increasingly important as human influence on natural habitats grows. Effective management requires defined objectives and reliable information about the likely consequences of management actions, or lack of such actions. These requirements are general across all taxonomic groups and management issues. We describe a method for estimating population dynamics and decision analysis that is generally applicable, extremely flexible, uses data efficiently, and gives answers in a format that can be directly measured against management objectives. Our case study involves bycatch of dolphins in the fishery for tunas in the eastern Pacific Ocean (EPO).

Impact on non–target species is a major concern in many fisheries worldwide (Hall et al., 2000), and is also a concern in areas such as harvest of waterfowl (Barbosa, 2001; Caswell et al., 2003), forestry (Noon & McKelvey, 1996), and pest control (Davidson & Armstrong, 2002). Many of these species are protected by governments. Unfortunately, it is often difficult or impossible to capture the target species without also affecting these protected species. This can result in restrictions on the harvest, leading to social, economic, and political problems. Such restrictions are often precautionary, based on inadequate information about both the target and the protected species. To make appropriate decisions, management must be able to predict the outcomes and estimate the associated uncertainty for alternative management actions. This will allow management to make informed decisions that consider the effects on both the protected and target species, while taking into consideration the uncertainty in the estimates.

Bayesian analysis has become one of the most common methods for describing uncertainty in fisheries stock assessment (McAllister et al., 1994; Punt & Hilborn, 1997; McAllister & Kirkwood, 1998; Maunder & Starr, 2001) and marine mammal management (Raftery et al., 1995; Punt & Butterworth, 1999; Maunder et al., 2000; Wade, 2002; Breen et al., 2003). It is also becoming popular in wildlife management (Taylor et al., 1996; Link et al., 2002; Brooks et al., 2002). In addition to describing uncertainty, Bayesian analysis facilitates the inclusion of additional information in the form of prior distributions. The prior distributions can be developed from previous studies on the same population, studies on different populations of the same species, studies of similar species, meta–analyses (Hilborn & Liermann, 1998), or expert judgment.

Bayesian analysis is a convenient way to include additional information into the analysis. However, development of priors from previous analyses has several disadvantages: it may be difficult to represent the distributional form of the prior, particularly if there is more than one parameter and the correlation among the parameters is important; also there may be information in the data about param-

eters in the current model that were not included in the previous analysis. For example, a constant survival rate estimate from a mark–recapture analysis could be used as a prior (replacing data) in a subsequent analysis with different animals from the same population. However, the prior gives no information about annual survival variation that may be in the data, since annual survival parameters were not included in the previous analysis; the combined information in both data sets may support annual survival variation, rather than constant survival.

These problems are resolved by integrating the analysis used to generate the prior with the current analysis (Maunder, 2003). This directly involves the data used to generate the prior in the current analysis. The integration of multiple sources of data in fisheries stock assessment models has been common for several decades (e.g. Fournier & Archibald, 1982), and is becoming popular in wildlife management (e.g. White & Lubow, 2002; Besbeas et al., 2002). However, even if an integrated approach is used, there is still a need to represent the uncertainty. Using an integrated model in a Bayesian framework allows for the most efficient use of information in the data and description of uncertainty (Maunder, in press), and is the most rigorous method for forward projection that incorporates both parameter and future demographic uncertainty.

Integrated analysis involves fitting a single model to data from multiple sources. This integration is achieved by measuring relative model fit to each data set in a common currency, the likelihood, and then combining the likelihoods by addition after transformation to a negative log likelihood. Likelihood is not an absolute measure of fit, but can be used to compare one model with another. Information integration can be extended beyond data alone, with integration of parameter distributions from similar species, results from other analyses, prior knowledge, and expert opinion. These are incorporated by expressing them in terms of likelihood with respect to the model, and are termed penalties (likelihoodist) or priors (Bayesian).

This paper switches back and forth between likelihoodist (Tanner, 1993) (rather than frequentist) and Bayesian philosophies, which involve making different kinds of inferential statements (see Wade, 1999). The likelihoodist philosophy is useful since it considers only the relative probability of alternative models, hypotheses, or parameter values, so does not require prior distributions on all parameters (Edwards, 1972). Choice of prior distributions can affect results (e.g. "non–informative" priors differ on a log or linear scale), and it can be convenient to avoid this problem when comparing models, for example (Wade, 1999; Maunder, 2003). Likelihoodist inference also has practical advantages when Bayesian Markov chain Monte Carlo (MCMC) will not converge without fixing parameters. However, some objectives, such as inference about a derived parameter independent of

the value of model parameters (*i.e.* integrating over parameter space to remove nuisance parameters and estimate marginal probability distributions), and forward-projection under uncertainty, are best carried out in a Bayesian context (although MCMC convergence sometimes requires fixing parameters). This is especially true in data-poor situations, or when considering process error in a non-linear model—both common circumstances in natural resource modeling. Bayesian posterior distributions permit probability statements about parameter values. However, these posteriors are still effectively conditional probabilities, since: (1) they are conditional on the priors, which must be selected for all model components, and (2) one cannot consider all possible model structures—unconsidered structures are effectively given a prior probability of zero. Thus probability statements are valid only relative to scenarios that have been modeled.

For the purposes of estimation, the combined likelihood behaves in the same way as an individual likelihood. A numerical search can be used to find the parameter values that maximize the combined likelihood. Model structures can be compared using information-theoretic approaches (Burnham & Anderson, 1998). Alternatively, Bayesian methods such as Markov chain Monte Carlo (MCMC) or sampling-importance-resampling (SIR) can be used to integrate across parameter values and model structures and estimate posterior distributions.

Description of uncertainty about the current status of a population is important for management advice. However, management is also concerned with the consequences of different management actions. Therefore, it is important to extend the Bayesian analysis to estimate the outcomes and associated uncertainty for different management actions. It is possible that some actions may be more robust to uncertainty than others; therefore both expected outcome and uncertainty can be used to choose the appropriate management strategy. Analyses should also estimate the effect of the management actions on both the protected species and the fishery (Maunder et al., 2000).

One high-profile example of interactions between a protected species and a commercial fishery is the tuna-dolphin interaction in the EPO (Joseph, 1994). The tuna purse-seine fishery in the EPO is of great economic importance, producing between 100 and 400 thousand metric tons of yellowfin tuna per year. The schools of yellowfin caught by purse seiners can be grouped into three categories: (1) those associated with floating objects; (2) those associated with dolphins; and (3) free-swimming schools. The majority of the catch comes from dolphin-associated schools, and only a small proportion comes from yellowfin associated with floating objects. Historically, large numbers of dolphins were killed in the sets on yellowfin associated with dolphins, which significantly reduced dolphin populations (Hall, 1997) such that

two are recognized as depleted by the U.S. government under the Marine Mammal Protection Act of 1972. There was substantial pressure to reduce the dolphin mortality, a challenge met by improved gear and dolphin-release procedures, international dolphin stock mortality limits, and individual vessel limits that together resulted in dramatic declines in mortality. With the later focus on "dolphin-safe" labeling and embargos by the United States on tuna caught in association with dolphins, pressure was exerted to reduce the fishing effort on tunas associated with dolphins, though these contentious policies have had little or no long-term effect on effort directed at yellowfin tuna associated with dolphins. These decisions were taken in a context of uncertainty about such important aspects of dolphin ecology as population sizes, reproductive rates, and natural mortality rates. Better information about these factors would facilitate decisions that take into account costs, benefits, and risks of alternative actions.

The aim of this research was to demonstrate the Bayesian and integrated approaches by applying them to data for a protected species. The objectives of the particular application were to examine the effect of incidental mortality on the population dynamics of Northeastern Offshore Spotted Dolphin (*Stenella attenuata*), estimate population parameters, and look at likely future population trajectories. First, an age- and stage-structured population dynamics model was developed for the Spotted Dolphin population of the northeastern Pacific Ocean. Then models were developed to predict the observed data from the population dynamics model. Statistical assumptions were developed to create likelihood functions to provide fitting criteria. Priors were developed for the relevant parameters of the model. An MCMC algorithm was used to estimate the Bayesian posterior distribution. Finally, samples from the posterior distribution were used to examine different management scenarios.

This analysis differed from previous analyses by Wade (1994) and Wade et al. (2002) in a number of structural assumptions (*e.g.* the use of recruitment deviates, modeling of stage structure, and different prior distributions), and in the integration of age and color phase data into the analysis.

Methods

Data

Three main sources of data were used to fit the model. Absolute estimates of abundance were based on surveys carried out in the EPO in 12 years between 1979 and 2000 (Gerrodette & Forcada, 2002). These estimates, which were based on modified line-transect methods, update earlier estimates (Wade & Gerrodette, 1992, 1993; Gerrodette, 1999, 2000). An additional source of line-transect abundance estimates from observers on tuna vessels

was not used to fit the model due to doubts about its reliability (Lennert-Cody et al., 2001), particularly concerning biases that vary through time.

Proportional incidental-mortality-at-age and color-phase data for 1973 to 1978 were provided by the U.S. National Marine Fisheries Service (NMFS) (Susan Chivers, NMFS, pers. comm.). These data were collected by NMFS observers aboard tuna purse seiners in the EPO. Sample sizes over the six years were 224, 322, 46, 98, 181, and 58 individuals sampled from the dead dolphins brought aboard tuna vessels. Ageing was carried out using growth-layer groups observed in sectioned teeth (Myrick et al., 1983; Barlow & Hohn, 1984). Because Spotted Dolphins undergo changes in color pattern as they mature, five color phases (Neonate, Two-tone, Speckled, Mottled, and Fused) have been identified (Perrin, 1969) and used as stages in the model.

Annual data on proportional incidental-mortality-at-color-phase from 1971 to 1990, and from 1996 to 2000 came from a summary of observer data (Archer & Chivers, 2002). Observers from the NMFS (1971 to 1990) and Inter-American Tropical Tuna Commission (IATTC) (1979 to 2000) recorded the sex and color phase of all dolphins killed during purse-seine operations. Sample sizes ranged from a high of 6,866 in 1975 to a low of 198 in 2000, and averaged 1,760 per annum over the period. Incidental-mortality-at-color-phase data were used only for years for which ageing data were not available.

Information on incidental mortality (henceforth also termed "catch") due to the fishery had three sources: total catch estimates for 1959 to 1972 from Wade (1995); for 1973 to 1978 from the IATTC (1994); and for 1979 to 2000 from the IATTC (2002). The estimates for 1959 to 1972 have "little or no statistical value" (National Research Council, 1992) because few vessels were monitored by observers before 1973, but are nevertheless used without error. The implications are considered in the discussion

Model structure

The Northeastern Spotted Dolphin population was modeled using a color-phase and age-structured projection model with an annual time step. Model structure was dictated by the available data and the modeling objectives. The population was structured by age and color phase (also referred to by the modeling term "stage"), which permitted use of two important data sources: long-term annual incidental mortality observed at color-phase, and a shorter time series of annual incidental mortality observed by color-phase and age, which gave better information about growth and color-phase transition rates. The model was implemented using a discrete formulation that assumed all incidental mortality occurred at the start of the year. As usual in marine mammal models, density-dependence was included, both to represent a

likely feature of population dynamics (Taylor & DeMaster, 1993; Taylor et al., 2000) and to permit an equilibrium-based MSY-like approach to be taken (see also Breiwick et al., 1984; Wade, 1993; Wade, 2002). This approach is similar to those needed to address the requirements of the Marine Mammal Protection Act. The population was assumed to be closed to migration.

Our notation represents time, stages, and ages, using the subscripts *t*, *s*, and *a*, with *T*, *S*, and *A* representing the maximum possible value in each category. The model is represented diagrammatically in figure 1.

Dynamics

The model had an annual time step, representing annual transitions through the year classes. Transitions through the two dimensions of the population (age and stage) were modeled differently, since every year each individual moves to the next year class, but may not move to the next stage. These transitions were combined with the mortality processes in two phases: the within-year process (equation 1) involving mortality, and the between-year process (equations 2 and 3) involving transitions between ages and stages.

Equation 1 gives the abundance in stage *s* and age class *a* at year end, as affected by incidental mortality and natural mortality, which are described later. Stage and age transitions occurred to start the following year (equations 2 and 3); these transition rates are also described later.

$$N'_{t,s,a} = N_{t,s,a} (1 - u_t v_{s,a}) (1 - M_{s,a}) \tag{1}$$

$$N_{t+1,1,a+1} = N'_{t,1,a} (1 - \psi_{1,a}) \tag{2}$$

$$N_{t+1,s,a+1} = N'_{t,s,a} (1 - \psi_{s,a}) + N'_{t,s-1,a} \psi_{s-1,a} \quad \text{for } s > 1 \tag{3}$$

Unlike other year classes, from which all individuals moved up a class each year, the final year class *A* was modeled using a self-loop (Caswell, 2001) or "plus group" (equation 4), which individuals leave only by dying. This method avoided assuming 100% mortality of individuals after reaching age *A*.

$$N_{t+1,S,A} = N'_{t,S,A-1} + N'_{t,S-1,A-1} + N'_{t,S,A} + N'_{t,S-1,A} \tag{4}$$

Incidental mortality was modeled using the product of a temporally-varying harvest rate parameter *u_t* and a stage and age class-dependent vulnerability parameter *v_{s,a}*. This assumed that the vulnerability of different stage and age classes did not vary through time. Harvest rate at time *t* (equation 5) was a function of the incidental catch *C_t* and the vulnerable population *V_t*, which was a product of *N_{t,s,a}* and *v_{s,a}* (equation 6).

$$u_t = \frac{C_t}{V_t} \tag{5}$$

$$V_t = \sum_{s,a} N_{t,s,a} v_{s,a} \tag{6}$$

Natural mortality $M_{s,a}$ was constant for all ages and stages.

Recruitment was modeled as a density-dependent process involving the number of sexually-mature individuals S_t (equation 7), population size as a proportion of estimated carrying capacity (Ndd_t/Ndd_{eq}), and an annual random variation term. The individual fecundity parameters (equation 8) were f_{eq} , the average recruitment rate in an unexploited population, which was calculated as described later in the section on initial conditions; and f_{max} , the maximum rate of recruitment at low population size, which was an estimated parameter. The shape parameter z adjusted the shape of the density-dependence relationship, with a value of one suggesting a linear relationship between population size and recruitment. Values greater than one, which are expected in cetacean populations (Taylor & DeMaster, 1993) imply that density-dependent reductions in fecundity rates occur more at high population sizes. Since recruitment is to age 0 the important density is in the year of conception, though given high dolphin survival rates density will not change much from one year to the next. This is a common functional form for density-dependence in marine mammal populations (e.g. Breiwick et al., 1984; Wade, 1994). The annual recruitment deviate ϵ_t was applied on a lognormal scale as per the usual practice, due to the multiplicative nature of mortality (Hilborn & Walters, 1992) and to avoid negative recruitment. Lognormal bias correction ($-0.5\sigma^2_R$) was applied to recruitment deviates to ensure that the average stochastic recruitment was equal to its deterministic equivalent. Proportion mature at stage and age was $m_{s,a}$, set to 0 for animals below the age of sexual maturity, and 1 above.

$$S_t = \sum_{s,a} N_{t,s,a} m_{s,a} \quad (7)$$

$$R_{t+1} = S_t \left[f_{eq} + (f_{max} - f_{eq}) \left(1 - \left(\frac{Ndd_t}{Ndd_{eq}} \right)^z \right) \right] e^{\epsilon_{t+1} - 0.5\sigma_R^2} \quad R_{t+1} \geq 0 \quad (8)$$

The size of the population as a proportion of carrying capacity, Ndd_t/Ndd_{eq} , was modeled using a flexible formulation whereby individuals of different ages and stages can make different contributions to density dependence. Thus population size and carrying capacity were expressed in terms of density-dependent individual equivalents, or Ndd_t and Ndd_{eq} . Ndd_t was calculated using equation 9. This approach was motivated by the contrast between a biomass-based model, where an individual's contribution to density-dependence would increase as it grew, and an individual-based model. The term $dd_{s,a}$ allows the contribution of each stage and age class to be adjusted.

$$Ndd_t = \sum_{s,a} N_{t,s,a} dd_{s,a} \quad (9)$$

Recruitment was always to age 0, but not always to the Neonate color phase: a proportion of 0 age

class dolphins had the Two-tone color pattern, presumably because the color phase change can occur during the first year of life. This phenomenon was accommodated with the parameter tr , representing the proportion of recruitment to the Two-tone color phase.

$$N_{t,1,0} = R_t (1 - tr)$$

$$N_{t,2,0} = R_t (tr)$$

Vulnerability and stage transition parameters

Vulnerability at age and stage represents the relative vulnerability of different groups within the population. It was modeled using a separate age-specific vulnerability curve for each stage. Vulnerability was assumed to be invariant through time and asymptotic with increasing age, and was modeled using the logistic with maximum vulnerability asy_s^v (equation 10). The most vulnerable group had asymptotic vulnerability of 1. The parameterization was designed to be informative, with $L50_s^v$ the age of 50% of maximum vulnerability for stage s , and sr_s^v the slope of the vulnerability curve.

$$v_{s,a} = \frac{asy_s^v c_{s,a}^v}{1 + c_{s,a}^v} \quad (10)$$

where $c_{s,a}^v = e^{\alpha_s^v + a\beta_s^v}$, $\beta_s^v = 2\ln(3)/sr_s^v$, $\alpha_s^v = -\beta_s^v L50_s^v$. Parameters asy_s^v , $L50_s^v$ and sr_s^v were estimated within the model.

An alternative parameterization was also used, with $V_{s,a} = V_s$: reducing the vulnerability model to four parameters.

The stage transition parameters $\psi^{tr}_{s,a}$ were modeled in the same way (equation 11).

$$\psi_{s,a} = \frac{asy_s^{tr} c_{s,a}^{tr}}{1 + c_{s,a}^{tr}} \quad (11)$$

where $c_{s,a}^{tr} = e^{\alpha_s^{tr} + a\beta_s^{tr}}$, $\beta_s^{tr} = 2\ln(3)/sr_s^{tr}$, $\alpha_s^{tr} = -\beta_s^{tr} L50_s^{tr}$. Parameters asy_s^{tr} , $L50_s^{tr}$ and sr_s^{tr} were estimated within the model.

Initial conditions

The unexploited equilibrium condition of the model was estimated at carrying capacity, with number of recruits to the 0 age class (the only location of recruitment in the model) balancing natural mortality. The following section describes the method used to estimate this state, and subsequently the initial population state. Calculations were on a "per-recruit" basis, which means that recruitment to age 0 was set to 1, and the numbers in all subsequent life history stages set relative to this single annual recruit. The pre-recruit calculations represent a generalized unexploited equilibrium state, so the time subscript is omitted.

Individuals per recruit at the start of the year were represented by $n_{s,a}$, and the number at the

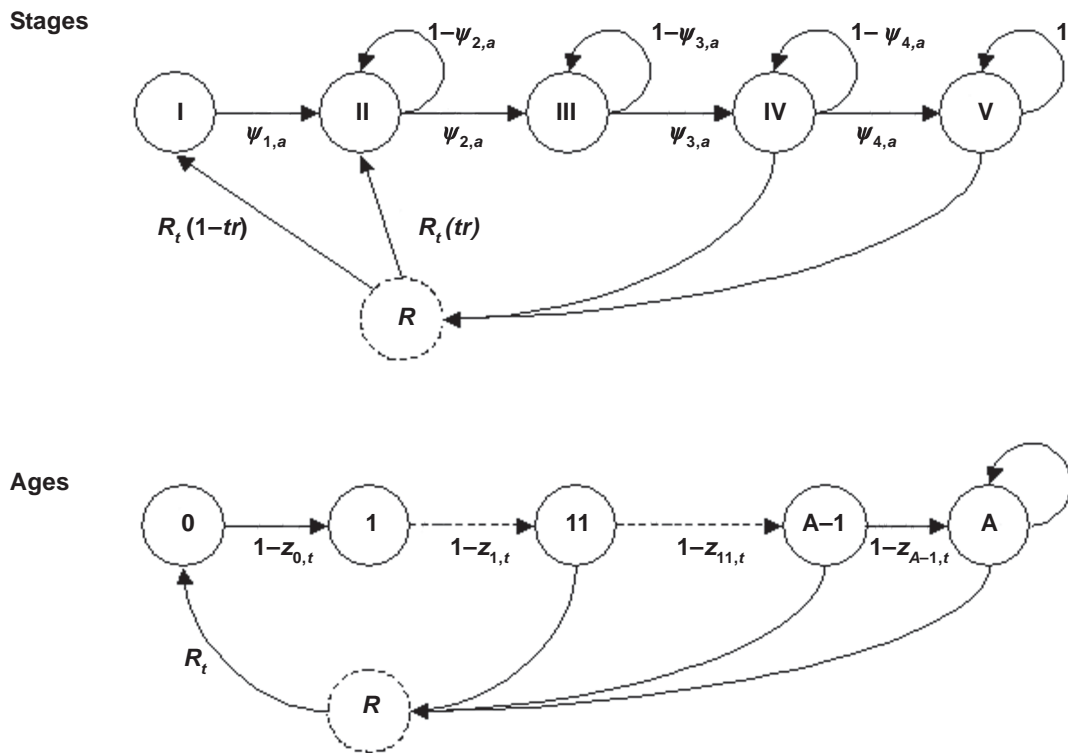


Fig. 1. Diagrammatic representation of the two dimensions on which individuals flow through the model: through color phases (I. Neonate, II. Two-tone, III. Speckled, IV. Mottled, and V. Fused) and through age classes (0 to A, with sexual maturity at age 11). R_t is recruitment at time t , $z_{t,a}$ is total mortality [$1 - z = (1 - M)(1 - u)$], $\psi_{s,a}$ is stage transition probability, and tr is the proportion of recruitment to the Two-tone stage.

Fig. 1. Representación diagramática de las dos dimensiones en las que los individuos fluyen a través del modelo: a través de fases de colores (I. Neonato, II. Dos tonos, III. Moteado, IV. Manchado, y V. Fusionado) y a través de clases de edades (de 0 a A, con madurez sexual a los 11 años). R_t es el reclutamiento en el tiempo t , $z_{t,a}$ es la mortalidad total [$1 - z = (1 - M)(1 - u)$], $\psi_{s,a}$ es la probabilidad de transición de fase, y tr es la proporción de reclutamiento en la fase dos tonos.

end of the year by $n'_{s,a}$. The key parameter to estimate in this section was f_{eq} , the fecundity rate per mature individual at equilibrium.

All relationships and parameter values were as in the dynamics section above, replacing $N_{s,a}$ with $n_{s,a}$ and $N'_{s,a}$ with $n'_{s,a}$, but with two main differences. Firstly, and obviously, the stochastic $e^{r_{i+1}-0.5\sigma_R^2}$ term in the recruitment equation 8 was omitted. Secondly, the self-loop or plus-group was modeled with $n'_{S,A}$ at the end of the year, rather than $n_{S,A}$ at the start.

$$n'_{S,A} = n_{S,A} \frac{(1 - M_{S,A})}{(1 - (1 - M_{S,A}))} \quad (12)$$

Fecundity rate per individual at equilibrium, f_{eq} , was calculated as the inverse of the number of breeders per recruit at carrying capacity, since together they produce one recruit (equation 13).

$$f_{eq} = \frac{1}{\left(\sum_{s=1}^{S-1} \sum_{a=1}^{A-1} n_{s,a} m_{s,a} \right) + n'_{A,S} m_{S,A}} \quad (13)$$

Recruitment at carrying capacity was estimated in two stages. First, the population size produced from a single annual recruit, or number per recruit (*NPR*) was calculated (equation 14). *NPR* was not strictly population size, but population size adjusted for the flexible contribution of individuals at different life stages to density-dependence. It was then straightforward to divide carrying capacity by *NPR* to obtain recruitment at carrying capacity, R_{eq} (equation 15).

$$NPR = \sum_{s,a} (n_{s,a} dd_{s,a}) + n'_{S,A} dd_{S,A} \quad (14)$$

$$R_{eq} = \frac{Ndd_{eq}}{NPR} \quad (15)$$

The starting year of the model was 1935, 20 years before significant fishing on dolphin-associated tuna began, to allow the 1955 population age distribution to differ from that for pre-exploitation equilibrium to the extent that the data suggested.

Initial conditions in the starting year of $N_{1935,s,a}$ and $N'_{1935,s,a}$ for all s and a were then calculated by multiplying $n_{s,a}$ and $n'_{s,a}$ by R_{eq} . R_{1935} was set to R_{eq} .

Parameter estimation

Parameters were estimated initially in a penalized likelihood context by estimating the mode of the joint posterior. The likelihood components included data from three sources: observed mortality at age and stage; observed mortality at stage; and line-transect estimates of absolute abundance. The objective function was the sum of the negative logarithms of the likelihood function components and the penalties. Adding the negative log likelihoods relies on the components being independent of one another. The data component's influence can be removed by removing its likelihood from the objective function.

The abundance estimate likelihoods (equation 16) were assumed to be lognormally distributed (Gerrodette & Forcada, 2002). The model was made more flexible by using scalars δ to scale the coefficient of variation (cv) (approximately the standard deviation of the log abundance indices) and q to scale abundance (see Maunder & Starr, 2003). For the base case both q and δ were set to 1.

$$-\ln[L(I_t|\theta)] = \ln(cv_t\delta) + \frac{\left[\ln(I_t) - \ln\left(q \sum_s N_{t,s} v_s^{survey}\right) \right]^2}{2(cv_t\delta)^2} \quad (16)$$

Observed mortality-at-stage data collected by observers were modeled using a multinomial likelihood (equation 17). Effective sample size values were used to scale the influence of data for different years, because each dolphin aged and/or staged was not an independent sample from the population. In most years a number dolphins had been sampled from each school or sub-region, and there is a certain amount of homogeneity in age and stage within schools and regions (Kasuya et al., 1974; Hohn & Scott, 1983). Lack of independence reduces effective sample size, as do processes, not modeled, that cause the age distributions to change over time (e.g. temporal variation in M). In addition, reported sample sizes were slightly inflated, since the data were preprocessed and adjusted for dolphins without a color phase recorded. The square root of the actual sample size for the year was used as the effective sample size, which is arguably superior to the alternatives of using the reported sample size (problems as above), or the common fisheries approach (e.g. Butterworth et al., 2003) of using a fixed arbitrary sample size for each year. The latter approach has the drawback of giving equal weight to years with large and small sample sizes.

$$-\ln[L(obs_{t,s}|\theta)] = -\frac{\left(\sum_s obs_{t,s}\right)^{0.5}}{\left(\sum_s obs_{t,s}\right)} obs_{t,s} \ln\left(\frac{\sum_a N_{t,s,a}}{\sum_{s,a} N_{t,s,a}}\right)$$

Observed mortality-at-stage-and-age data were modeled similarly, replacing equation 17's $obs_{t,s}$ with $obs_{t,s,a}$, the number of animals observed at time t in stage s at age a , and $\sum_a N_{t,s,a}$ with $N_{t,s,a}$. Effective sample size was equal to the square root of the true sample size.

Automatic differentiation software was used to estimate the many parameters in this model. Automatic differentiation provides very efficient fitting of statistical models (Greiwanck & Corliss, 1991). The model implementation language AD Model Builder (ADMB, Otter Research, <http://otter-rsch.com/admodel.htm>) gave access to the automatic differentiation routines, and estimated the variance-covariance matrix for all parameters of interest. For key parameters the software was also used to provide likelihood profiles, and Bayesian posterior probability distributions using MCMC methods with the Metropolis-Hastings algorithm (Hastings, 1970). ADMB combines the Hessian associated with the maximum likelihood estimate with any bounds on parameters to produce a bounded multivariate normal distribution, and uses this in the proposal function. A run of 10,000,000 iterations was analyzed using the Bayesian Output Analysis Program (Smith, 2001) to assess convergence using the Heidelberger & Welch (1983) stationarity and half-width tests, Geweke (1992) convergence diagnostic, and the Raftery & Lewis (1992) convergence diagnostic. The burn-in recommended by the Raftery & Lewis (1992) diagnostic was discarded, and the remaining values were used to generate the posterior.

Prior distributions

Prior distributions were specified for all the parameters estimated in the model, as required for Bayesian analysis. Normal priors were implemented as penalties on the negative log likelihood, equal to $(\hat{p} - \mu_p)^2 / 2\sigma_p^2$, where \hat{p} is the parameter estimate, and μ_p and σ_p^2 are the mean and variance of the prior. Priors without penalties were uniform (on a nominal or log scale), and bounded to make them proper. Prior distributions are given in table 1.

Natural mortality M was given a vague prior with mean 0.04 and standard deviation of 0.2. To improve convergence it was bounded at 0.1, which was well outside the 95% profile likelihood interval.

The prior for the recruitment shape parameter z implied maximum net productivity level between 0.5 and 0.85 of equilibrium population size (Taylor & DeMaster, 1993), and was bounded at 0.2 and 15.

A uniform prior was given to f_{max} . A normal prior could have been imposed, based on observed pregnancy rates of 0.167 females per female and inferred calving intervals (Myrick et al., 1986). However, natural mortality was parameterized as the

Table 1. Descriptions and prior distributions for model parameters. Justifications for priors are given in the text.

Tabla 1. Descripciones y distribuciones a priori para los parámetros del modelo. En el texto se detallan las justificaciones de tales distribuciones.

Parameter	Description	Distribution	Mean (SD)	Bounds
M	Natural mortality	Normal	0.04 (0.2)	0, 0.1
z	Shape parameter	Normal	2 (1)	0.2, 15
Ndd_{eq}	Equilibrium population size–density–dependent equivalent	Uniform		0, 10^8
f_{max}	Maximum fecundity	Uniform		0, 0.5
ϵ_t	Recruitment deviates	Normal	0 (σ_R)	n/a, n/a
tr	Two–tone recruitment	Uniform		0, 1
sr_s^{tr}	Stage transition slope	Uniform		0.001, 10
$L50_s^{tr}$	Age at 50% of max stage transition	Uniform		–1, 30
asy_s^{tr}	Asymptotic stage transition rate	Uniform		0, 1
sr_s^v	Vulnerability slope	Uniform		0.1, 10
$L50_s^v$	Age at 50% of max vulnerability	Uniform		–5, 35
asy_s^v	Asymptotic vulnerability	Uniform		0, 1
σ_R	Standard deviation of recruitment variation	Fixed	0.15	
Asm	Age at sexual maturity	Fixed	11	
A	Maximum age	Fixed	40	

same for all ages, which, given the higher mortality expected for Neonates, would bias f_{max} downward. Also, realized calving rates are likely to be lower than observed pregnancy rates, which would also bias the appropriate f_{max} downward. A uniform uninformative prior bounded at 0 and 0.5 was used, with the constraint that f_{max} must be greater than f_{eq} .

Vulnerability and stage transition parameters were bounded to increase the stability of the model. For the 15–parameter vulnerability model, asymptotic vulnerability of the final stage asy_5^v was fixed at 1. For the five– and two–parameter models all the $L50^v$ parameters were fixed at –3 and the sr^v parameters at 0.1, to give constant vulnerability within a color phase. In the five–parameter model asy_5^v was fixed at 1 and asy_1^v , asy_2^v , asy_3^v , and asy_4^v were estimated, while in the two–parameter model $asy_{2,5}^v$ was fixed at 1 and $asy_{1,3,4}^v$ was estimated.

To constrain recruitment deviates, a penalty term was added to the negative log–likelihood function

$$\sum_t \frac{\epsilon_t^2}{2\sigma^2}$$

This was equivalent to a lognormal prior on each individual annual recruitment deviate with a mean of 0 and standard deviation of σ . Each deviate was therefore estimated to be zero in the maximum

likelihood analysis, unless there was evidence to the contrary.

The standard deviation on the prior for individual recruitment deviates, σ_R , was fixed at the relatively low level of 0.15. This was justified biologically by the relatively low potential for recruitment to vary annually, given dolphins’ life history strategy.

Age at sexual maturity was fixed at 11 years. Myrick et al. (1986) report two estimates of age at sexual maturity (10.7 and 12.2), based on the ages estimated by two different readers.

The maximum age class implemented in the model affected dynamics only when a plus group was not used. The imposition of a maximum age class without a plus group implies senescence, about which there is little information for Northeastern Spotted Dolphins. This assumption is particularly influential if age at senescence is set too low in populations with low mortality rates. This element of the structure was investigated in the sensitivity analysis.

Forward projection

The population was projected forward 5 years from the final year estimated, using samples from the joint posterior of the Bayesian MCMC. Recruitment

deviates were assumed to be zero, as recruitment variability is substantially less than parameter uncertainty. The bias adjustment factor was therefore not applied.

As part of the forward projections, the effect of changes to the level of setting on dolphins was investigated by altering the mortality rate (observed mortalities/total population) due to setting on dolphins to 0, 0.5, 1, and 2 times the average level prevailing over the three years to 2000. Outcomes recorded were the relative change in total number of dolphins after 5 years.

Sensitivity analysis and hypothesis tests

The sensitivity of parameter estimates and management conclusions to different components of the data (line transect, stage data, and age and stage structure data) was tested by multiplying the standard deviation of the line transect data by 4 to reduce its influence, and by removing from the objective function the likelihood component associated with each of the other data components, one at a time.

The sensitivity of the model to several alternative structures (hypotheses about the state of nature) was examined. Models of long-lived species are sensitive to the maximum age in the model. This sensitivity was investigated by running the model with the last age in the model with and without a self-loop (plus-group). Using a plus-group is equivalent to assuming that senescence does not occur early enough to affect population dynamics. Sensitivity to variation in vulnerability between color phases was also examined. Vulnerability was modeled using three different approaches: the 15-parameter method described earlier with three parameters per stage; a five-parameter method with constant vulnerability within a stage; and a two-parameter model with Two-tone and adult stages fully selected, and common vulnerability for the Neonate, Speckled, and Mottled stages.

The support for alternative structures was investigated by comparing the likelihoods using the Akaike Information Criterion (AIC) ($-2 \log L + 2v$); and the posterior probabilities using the Bayes factor $B = (e^{\log L_2 - \log L_1})^{2(v_1 - v_2)/2}$, where L , L_1 , and L_2 are negative log likelihoods, and v , v_1 , and v_2 represent the number of parameters.

Results

Parameter estimates are presented in table 2 for the base case model, with standard deviations, profile likelihood confidence intervals, and MCMC intervals. To allow the MCMC chain to converge, z was fixed at the posterior mode. The fit of the model to the color-phase and age-structure data is presented in figure 2 and figure 3. The estimated population trajectory, with the line transect population size estimates for comparison, is presented in figure 4, with the recruitment deviates in fig. 5.

The modal estimate of f_{max} —fecundity rate at low population size—of 0.125, although less than the pregnancy rate given by Myrick et al. (1986), the difference is not statistically significant. The value suggested by recent re-analyses of pregnancy completion rates was lower than our estimate, significantly according to likelihood profile, but not MCMC intervals. Our estimate was significantly less than Wade's (2002) estimate according to the MCMC, but not the profile likelihood intervals. Natural mortality at 0.039 was little different from the prior mode of 0.04, but the standard deviation was far smaller. The posterior mode of the shape parameter z , at 1.69, was less than the prior mode of 2. Two-tone recruitment was estimated to be about 20%. Credibility intervals generated using MCMC were mostly narrower than the profile intervals, mainly due to fixing z to make the MCMC runs converge. When z was not fixed the chain was occasionally trapped for a period at very low values of z , near the lower boundary set at 0.2.

Sensitivity analysis and hypothesis tests

Fitting the model to the data with increased coefficient of variation on the abundance estimates and without each of the other two data components demonstrated the relative influence of each on parameter estimates and variance (table 3). Reducing the influence of abundance data affected primarily the variance on estimates of natural mortality and Ndd_{eq} . Removing the age by color phase by year data made the model unstable, with excessively high Ndd_{eq} and zero natural mortality, illustrating the strong influence of these data. Removing the color phase by year data resulted in slightly increased variance and slightly changed modal estimates of natural mortality, Ndd_{eq} , f_{max} . Two-tone recruitment, and vulnerability parameters, suggesting that it had only a small influence on results.

The investigation of the plus-group could be seen as exploring the alternative hypotheses that (1) senescence (the right side of the U-shaped mammalian mortality curve) occurs sufficiently late that it affects too few animals to matter, or (2) senescence generally occurs around the age of 40, and so it is important for population dynamics. The latter hypothesis carried more weight with a Bayes factor of 48, suggesting strong evidence (Kass & Raftery, 1995) for senescence (or ageing error causing the appearance of senescence).

Variation in vulnerability among color phases was apparent when all 15 vulnerability parameters were estimated separately. However, this model was over-parameterized, and had AIC of 1892.69. A five-parameter model with uniform vulnerability within each color phase had a lower AIC of 1872.95. A single parameter model where all animals had the same vulnerability had less support with AIC of 1879.97. Following the suggestion of Barlow & Hohn (1984) that age classes 5 to 15 and Neonates are under-represented, a parameter was added to differentiate the under-represented color phases (Neonates, Speckled, and Mottled) from the other

Table 2. Parameter estimates with standard deviations from the Hessian matrix, 95% likelihood profile intervals, and Bayesian posterior distributions from MCMC.

Tabla 2. Estimaciones de parámetros con desviaciones estándar de la matriz hessiana, intervalos de confianza de verosimilitud del 95%, y distribuciones bayesianas a posteriori a partir de las cadenas de Markov Monte Carlo (MCMC).

Parameter	Estimation	SD	95% Likelihood profile intervals		MCMC	MCMC
			Lower	Upper	2.5%	97.5%
M	0.039	0.011	0.017	0.060	0.020	0.057
Ndd_{eq}	3,406	206	3,068	3,857	3,086	3,791
f_{max}	0.125	0.018	0.090	0.166	0.093	0.162
Z	1.69	1.04	0.220	3.532	NA	NA
sr_{2}^{tr}	5.25	3.13				
sr_{3}^{tr}	5.73	0.61				
sr_{4}^{tr}	4.54	0.44				
$L50_{1}^{tr}$	-0.05	0.21				
$L50_{2}^{tr}$	2.31	0.94				
$L50_{3}^{tr}$	9.99	0.65				
$L50_{4}^{tr}$	16.00	0.76				
$asy_{1,3,4}^{tr}$	0.49	0.08				
$asy_{2,5}^{tr}$	1.00	0.00				
tr	0.196	0.080	0.043	0.373	0.068	0.379

two color phases (Two-tone and Fused). This two-parameter model was most strongly supported with AIC of 1867.68.

Depletion and implications for recovery

The model estimated a mean recovery from 1995 to 2000 of 7.4%, with 95% confidence interval from 0.00% to 17.3%. Current depletion level (number of individuals as a proportion of equilibrium) was estimated as 19% (15% to 24%).

Forward projections were carried out using MCMC with four scenarios of setting on dolphins. With the levels of mortality from setting on dolphins prevailing between 1998 and 2000, average recovery over the 5 years to 2005 was 4.1% (-2.1% to 12.7%). With no mortality from setting on dolphins, average recovery was 6.9% (0.5% to 15.9%). With 0.5 and 2 times the 1998–2000 mortality rates, recoveries were 5.5% (-0.8% to 14.2%) and 1.3% (-4.7 and 9.7%) respectively.

Discussion

The integrated approach used in this analysis is a very general methodology that can provide useful answers to some of the questions most relevant to

managers. Bayesian forward projections, such as those given above, can be used as statements of belief about the probability of future events, or relative probability given models that have not been considered. Measuring such forward projections against management objectives gives a direct way to compare the utility of management options.

Decision analysis based on projecting the population forward in time under different management strategies is a major component of many Bayesian analyses (e.g. Maunder et al., 2000; Breen et al., 2003). Several components of uncertainty, such as: (1) parameter uncertainty, (2) model structure uncertainty, and (3) demographic uncertainty can be included in forward projections. Parameter uncertainty is inherent in statistical estimation of model parameters. Many different values of the model parameters may adequately represent the data, and they must all be considered as possible true states of nature. Similarly, alternative model structures may represent different possible states of nature. Demographic uncertainty describes how model parameters change over time. In general, scientific knowledge reduces parameter uncertainty and model structure uncertainty, while demographic uncertainty in the future cannot be reduced. In many situations both model structure uncertainty

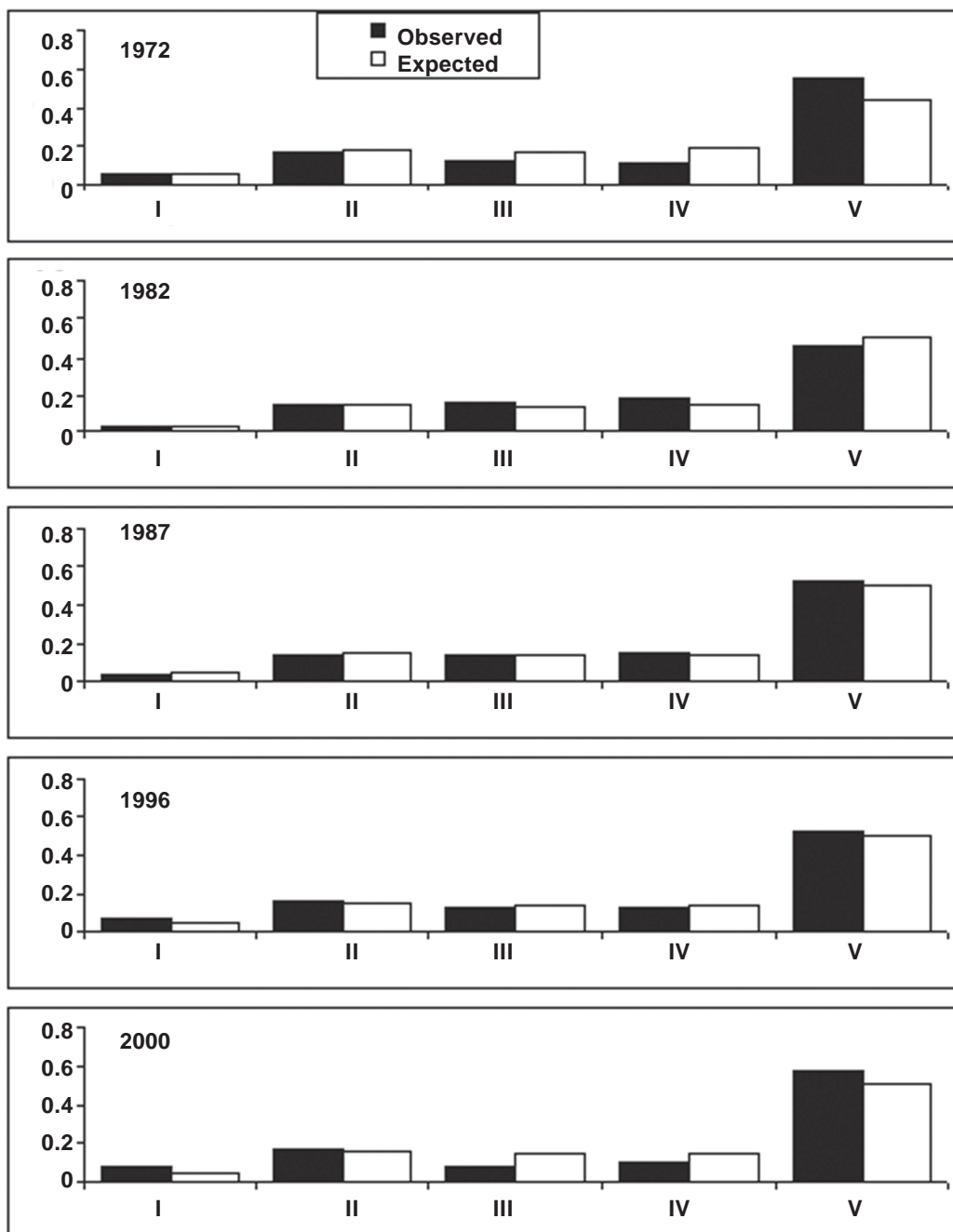


Fig. 2. Observed and estimated proportions of dolphins captured by color phase (Neonate–I, Two–Tone–II, Speckled–III, Mottled–IV, and Fused–V) for five of the years for which data were available. Sample sizes for each year are given in the text.

Fig. 2. Proporciones observadas y estimadas de delfines capturados por fase de color (Neonato–I, Dos tonos–II, Moteado–III, Manchado–IV, y Fusionado–V) para cinco de los años en que se disponía de datos. Los tamaños de las muestras para cada año se facilitan en el texto.

and parameter uncertainty are more important than demographic uncertainty in the future. This is particularly true for long-lived species such as dolphins, which have very low productivity

rates. For these populations, catastrophes can be a more important component of uncertainty than annual variation in model parameters (Breen et al., 2003).

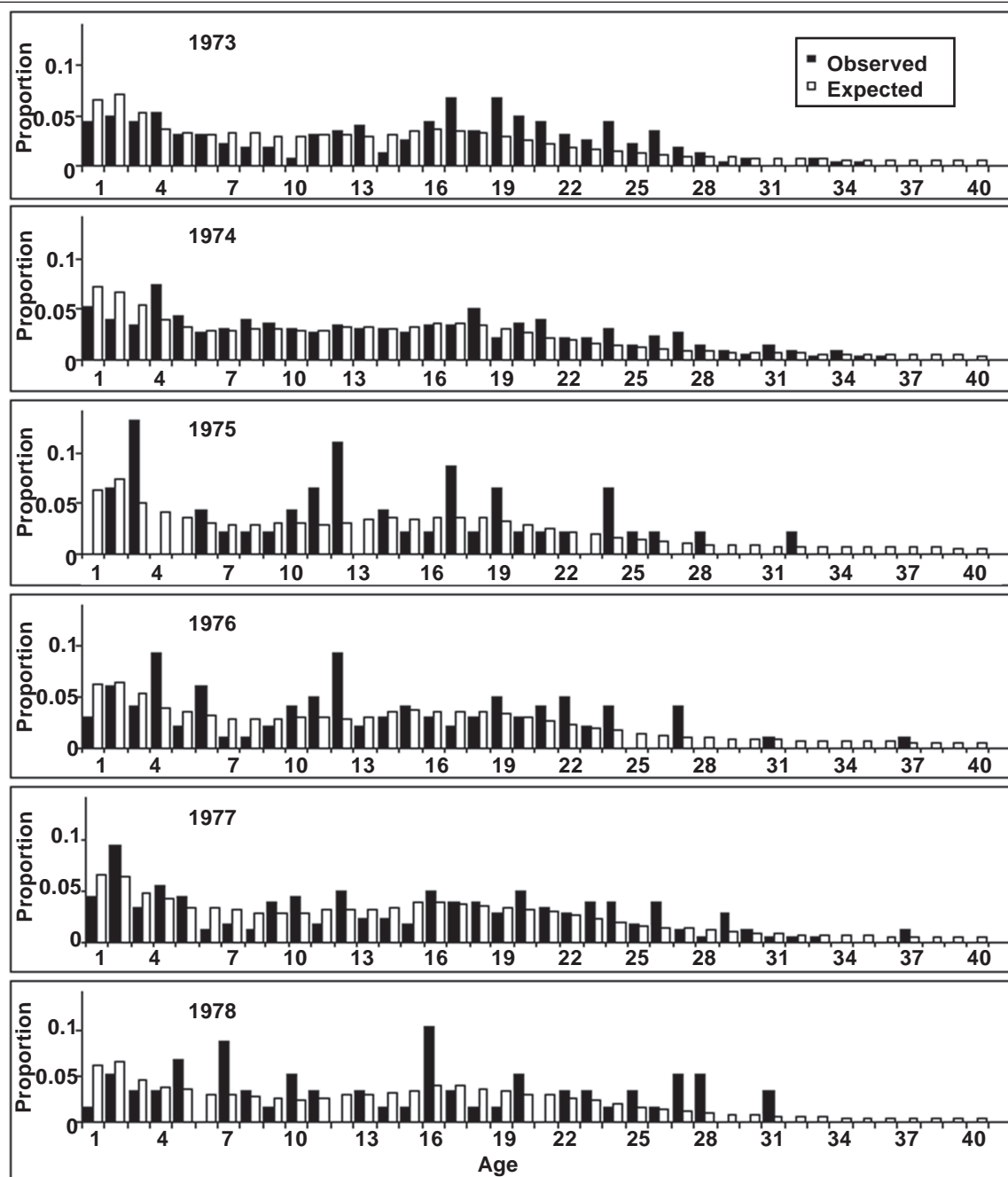


Fig. 3. Observed and estimated proportions of dolphins captured at age from 1973 to 1978. Data are pooled across color phase. Sample sizes are given in the text.

Fig. 3. Proporciones observadas y estimadas de delfines capturados según edad desde 1973 hasta 1978. Los datos se agrupan según la fase de color. Los tamaños de las muestras se facilitan en el texto.

Integrating several data sources requires more complexity in the model. For example, a model based on numbers alone can be used to estimate population trajectories based on removals and abundance estimates. Adding age structure data gave information about variability in recruitment and about

total mortality rates, but required that age structure be modeled and required assumptions about ageing error. Adding the longer time series of size structure data gave more information about total mortality and recruitment, but required that stage structure be modeled.

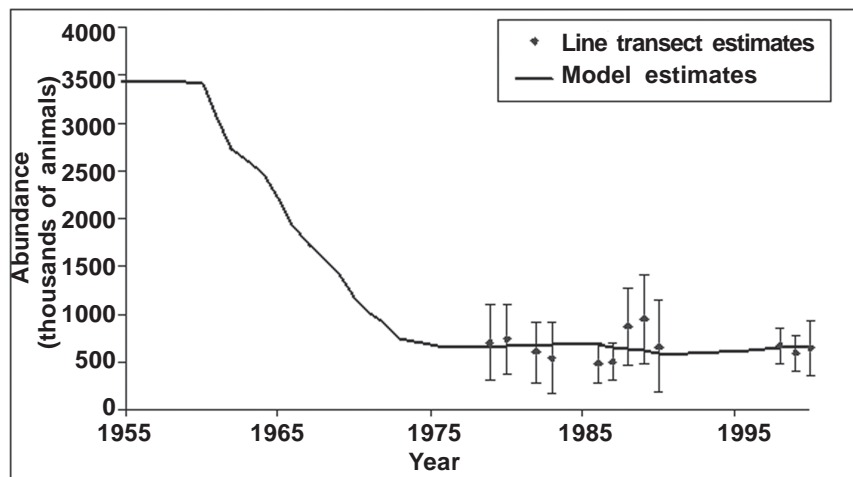


Fig. 4. Research line transect estimates of abundance, with 95% confidence intervals, compared with estimated population trajectory from the model.

Fig. 4. Estimaciones de abundancia a lo largo de los transectos investigados, con intervalos de confianza del 95%, en comparación con una trayectoria poblacional estimada a partir del modelo.

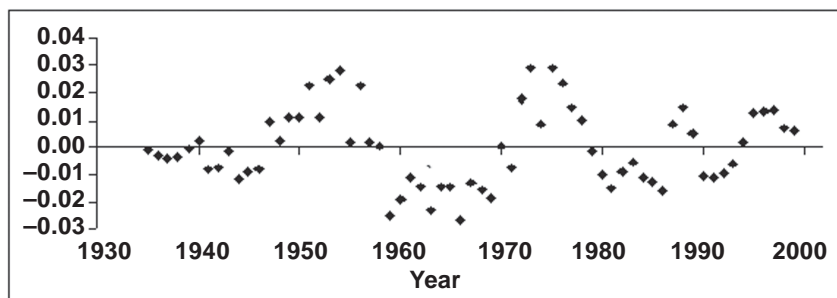


Fig. 5. Estimated recruitment deviates for all years.

Fig. 5. Desviaciones del reclutamiento estimado para todos los años de estudio.

In many applications of fitting population dynamics models to data, results are more sensitive to model structure than to parameter uncertainty within a single model structure, and even small structural changes can have significant effects. For example, in the dolphin model a simple model of senescence significantly affected estimates of depletion level and recovery rate. More complex models of age-specific survival, with the Gompertz (Wilson, 1993) and Siler functions (Siler, 1979; Barlow & Boveng, 1991), may further improve the fit of the model and alter parameter estimates. Different model structures represent different hypotheses about population dynamics. It is often possible to formulate the

model so that one or more parameters can be changed to represent the different model structures. In this case, the model structural uncertainty can be included in the analysis by estimating these parameters. In other situations, it is not possible to represent different model structures by model parameters, so other techniques such as Bayesian model averaging (Hoeting et al., 1999) must be used. For example, McAllister & Kirchner (2002) included uncertainty about the structure of the stock-recruitment relationship for a Bayesian stock assessment of Namibian orange roughy. Because only a few of the possible model structures can be considered, models tend to underestimate uncertainty.

Table 3. Parameter estimates for the model fitted without a plus group, and without each of the three fitted data components in turn.

Tabla 3. Estimaciones de parámetros para el modelo ajustado sin un grupo adicional, y sin cada uno de los tres componentes de datos ajustados sucesivamente.

	Without plus group		Abundance cv x 4		Without age		Without stage	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
M	0.056	0.008	0.044	0.022	0.000	0.000	0.037	0.014
Ndd_{eq}	3,535	229	3,549	552	79,821	1,679	3,377	222
f_{max}	0.147	0.019	0.125	0.020	0.466	0.011	0.117	0.028
z	1.73	1.04	1.82	1.11	4.90	0.64	2.09	0.98
sr_{2}^{tr}	5.91	2.43	5.25	3.13	0.02	70.10	5.64	2.52
sr_{3}^{tr}	5.77	0.60	5.74	0.61	6.69	0.52	5.51	0.62
sr_{4}^{tr}	4.48	0.43	4.54	0.44	3.10	0.40	4.54	0.44
$L50_{1}^{tr}$	-0.01	0.19	-0.05	0.21	2.93	0.15	-0.26	0.39
$L50_{2}^{tr}$	1.17	1.14	2.29	0.99	-0.22	729.65	2.05	1.26
$L50_{3}^{tr}$	9.92	0.65	9.96	0.65	9.54	0.49	10.66	0.91
$L50_{4}^{tr}$	16.40	0.83	15.97	0.78	9.83	0.28	16.19	0.92
$asy_{1,3,4}^{v}$	0.40	0.07	0.49	0.09	0.16	0.01	0.35	0.08
$asy_{2,5}^{v}$	1.00	0.01	1.00	0.00	1.00	0.01	1.00	0.01
tr	0.189	0.079	0.196	0.080	0.881	0.016	0.217	0.086

The form of integrated analysis presented in this study is simple, and more advanced methods could be applied. The model uses estimates of abundance from the surveys with the associated confidence intervals. More advanced forms of integrated analyses combine two analyses that are usually carried out independently. For example, Maunder (2001a) combined a generalized linear model standardization of catch-per-unit-of-effort data with a population dynamics model. In this analysis it would be possible to combine the analysis of the sighting surveys with the population dynamics model. This would ensure that model assumptions and parameter estimates were consistent throughout the analysis, that uncertainty was propagated through the analysis, and that the correlations among parameters (between population size estimates for example) were preserved. Integrating the sighting survey analysis with the population dynamics model would also allow some parameters of the survey analyses to be shared among years. Other data such as mark-recapture data could also be integrated into the population dynamics model (Hampton & Fournier, 2001; Maunder, 2001b, Besbeas et al., 2002).

It is common for analyses that use multiple data sets to have conflicting information in the data, and such conflicts must be resolved. How-

ever, the data are usually correct, if seen in the right context (barring falsification or transcription errors), and the conflict comes from inadequacy of either the population model itself, or the model used to pre-process the raw data and provide summary statistics for the analysis. Our analysis did not use the estimates of abundance based on data collected by observers on tuna vessels, as they are thought to be unreliable (Lennert-Cody et al., 2001) and contradict the other data. One reason the estimates of abundance collected by observers are thought to be unreliable is that more searching was carried out by helicopters in the later part of the time series. Including information about the methods of searching may help eliminate the contradiction between the observer data and the other data used in the model. Schnute & Hilborn (1993) describe a method that can be used to represent the uncertainty in the conflicting data sets when it is not known which data set is prone to model misspecification.

Data quality must always be considered as a source of uncertainty. It is common for historic data to be of doubtful quality, and the uncertainty this implies can be included in the analysis. For example, incidental dolphin mortality before 1973 is very uncertain, with some correlation in the uncertainty between years, but was treated as

accurate in this analysis. Preliminary investigation suggests bias in early incidental mortality, with implications for depletion and recovery estimates. Further analyses could investigate this uncertainty both by further investigation of the data themselves, and by estimating the value of a bias parameter, since there is unused information about early catches in the age structure and stage structure data. This method assumes that the uncertainty in historic catch–mortality is perfectly correlated among years. Alternatively, constant mortality rate (proportion of the population killed per year) could be assumed from 1959 to 1972; or the analysis could be started in 1973 at an exploited population size (e.g. Maunder & Starr, 2001). Other approaches that could be used to include this uncertainty include: (1) the method of Fournier et al. (1998) that fits to the catch data conditioned on effort rather than assuming it is known; or (2) sample the catch from the appropriate distribution each time the objective function is evaluated in the Bayesian analysis (e.g. Wade et al., 2002). The correlation in errors among years, due to methods used to estimate the catch, should be taken into consideration as much as possible, since correlation will increase bias. There may also be data quality issues with the age structure and color phase data, due to, for example: (1) changes through time in sampling methods, and (2) biases associated with higher probability of setting on larger groups of dolphins. Further analyses in these areas are planned.

Prior distributions are always informative in some sense, which may be important if there are few data about the parameter. This fact is illustrated by differences between this analysis and previous analyses (Wade, 1994; Wade et al., 2002). The prior implemented for adult natural mortality differed from Wade et al.'s (2002) 0.009 ± 0.02 (SE) bounded at 0.002, which implied (at the mode) that 76% of dolphins reaching adult mortality rates would survive to age 40 and die through senescence. Wade et al. (2002) sought a uniform prior on r_{max} (a derived parameter), implied by the combined priors on their estimated parameters. For the current model such low natural mortality and high senescence in a wild population were not considered the prior "belief" about parameter distribution, particularly given the influence of a fairly tight distribution on results. Adult natural mortality is often the parameter with most influence on population growth rate for long-lived animals (Heppell et al., 2000). The posterior mode of the natural mortality estimate from the current analysis was 0.039, and the 95% credibility intervals did not include 0.009.

The prior for maximum fecundity at low population sizes also differed from Wade et al.'s (2002) uniform prior with observed fecundity (Myrick et al., 1986) of 0.167 as a lower bound and 0.333 as an upper bound. Density-dependence occurs at high population sizes in cetacean populations (Taylor & DeMaster, 1993), the population was

depleted when pregnancy rates were observed, and pregnancy rate must be higher than fecundity rate, so 0.167 may well be close to or higher than f_{max} . Recent analyses that consider pregnancy completion rate suggest that realized fecundity rate during this observation period was considerably less (Susan Chivers, NMFS, pers. comm.). The posterior estimate from the current analysis was significantly below 0.167, but was lowered by some Neonate natural mortality and parameterization of survival constant at age. Truncation of f_{max} at 0.167 would be informative, since it permits no values below 0.167 in the posterior. This issue, and the related issues of (1) the causes of pregnancy failure, and (2) age, spatial, and school size effects on fecundity, could be investigated further by integrating the pregnancy observation data into an expanded analysis.

Catastrophes and environmental transition shifts (Fiedler & Reilly, 1994; Reilly & Fiedler, 1994) were not modeled, either for parameter estimation or for forward projection. Such discontinuities magnify the number of possible fits to the data and make parameters difficult to estimate, and it is not easy to determine the risk of catastrophic events affecting the population in the future (but see Gerber & Hilborn, 2001). For the primary objective of this model—examining how the tuna fishery affects dolphins—these considerations are not directly relevant, as they might be for a population viability analysis.

Models with vulnerability varying among color phases had more support than those without variation, and the best model included lower vulnerabilities for stages 1, 3, and 4 (color phases Neonate, Speckled, and Mottled). This difference in vulnerability explained the observed pattern of relatively fewer dolphins sampled at age 0 and between the ages of 5 and 15. Such a dip in catchability could result from a difference in behavior between immature and mature individuals, such as the formation of immature schools that for some reason (perhaps school size, Perkins & Edwards, 1999) are less likely to be targeted by purse seiners; immatures swimming on the edge of the school, where they are less likely to be encircled by nets; or immatures being more likely to split off from the school during the chase (Barlow & Hohn, 1984). There is some evidence for segregation into juvenile schools among Spotted Dolphins (Kasuya et al., 1974; Hohn & Scott, 1983), and for other species in the genus *Stenella* (Myazaki & Nishiwaki, 1978; Chivers & Hohn, 1985; Perryman & Lynn, 1994). Alternative explanations for a difference in vulnerability are also possible (Barlow & Hohn, 1984), but have not been included in the model. For example, this life stage may tend to lay down additional non-annual growth layer groups. This would result in fewer individuals being captured with each number of growth rings, and would also imply overestimation of age for older dolphins.

Further possible changes to model structure include modeling the sexes separately, since the age structure data also include sex information and there may be differences in vital rates. It may be useful to consider bias and uncertainty in ageing, which are likely to be significant, given the quality of the growth layer groups used to age Spotted Dolphins. The age of the oldest age classes may have been underestimated (Susan Chivers, NMFS, pers. comm.). Assuming that ages were underestimated would result in lower estimates of natural mortality, and perhaps lower productivity.

In summary, the methods presented here are very flexible and generally applicable to wide variety of taxa and problems, and easily extended to comparing management options and predicting future consequences. Uncertainty is an integral part of the analysis, and prior knowledge and model assumptions are handled consistently throughout. Perhaps the most important aspect of integrated analysis is the way it both enables and forces consideration of the system as a whole, so that inconsistencies can be observed and resolved.

Acknowledgements

This project was funded by Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Ocean and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subdivisions. The U.S. National Marine Fisheries Service provided data. Jay Barlow, Susan Chivers, Tim Gerrodette, and Steve Reilly of the NMFS helped with data and advice. Thanks to Cleridy Lennert-Cody and Michael Scott for help with the data, and Robin Allen, Bill Bayliff, Rick Deriso, Shelton Harley, Cleridy Lennert-Cody, Michael Scott, and three anonymous reviewers for reviewing the manuscript.

References

- Archer, F. & Chivers, S. J., 2002. Age structure of the northeastern spotted dolphin incidental kill by year for 1971 to 1990 and 1996 to 2000. *Administrative Report No. LJ-02-12*, NOAA Fisheries, Southwest Fisheries Science Center, La Jolla.
- Barbosa, A., 2001. Hunting impact on waders in Spain: effects of species protection measures. *Biodiversity and Conservation*, 10: 1703–1709.
- Barlow, J. & Boveng, P., 1991. Modeling age-specific mortality for marine mammal populations. *Marine Mammal Science*, 7: 50–65.
- Barlow, J. & Hohn, A. A., 1984. Interpreting spotted dolphin age distributions. *NOAA Technical Memorandum*, NMFS-SWFC-48.
- Besbeas, P., Freeman, S. N., Morgan, B. J. T. & Catchpole, E. A., 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, 58: 540–547.
- Breen, P. A., Hilborn, R., Maunder, M. N. & Kim, S. W., 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 527–541.
- Breiwick, J. M., Eberhardt, L. L. & Braham, H. W., 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 484–496.
- Brooks, S. P., Catchpole, E. A., Morgan, B. J. T. & Harris, M. P., 2002. Bayesian methods for analyzing ringing data. *Journal of Applied Statistics*, 29: 187–206.
- Burnham, K. P. & Anderson, D. R., 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Butterworth, D. S., Ianelli, J. N. & Hilborn, R., 2003. A statistical model for stock assessment of southern bluefin tuna with temporal changes in selectivity. *African Journal of Marine Science*, 25: 331–361.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Inc.
- Caswell, J. H., Afton, A. D. & Caswell, F. D., 2003. Vulnerability of nontarget goose species to hunting with electronic snow goose calls. *Wildlife Society Bulletin*, 31: 1117–1125.
- Chivers, S. J. & Hohn, A. A., 1985. Segregation based on maturity state and sex in schools of spinner dolphins in the eastern Pacific. Abstract, *Sixth Biennial Conference on the Biology of Marine Mammals, Vancouver*.
- Davidson, R. S. & Armstrong, D. P., 2002. Estimating impacts of poison operations on non-target species using mark-recapture analysis and simulation modelling: an example with saddlebacks. *Biological Conservation*, 105: 375–381.
- Edwards, A., 1972. *Likelihood*, Cambridge Univ. Press, Cambridge.
- Fiedler, P. C. & Reilly, S. B., 1994. Interannual Variability of Dolphin Habitats in the Eastern Tropical Pacific .2. Effects on Abundances Estimated from Tuna Vessel Sightings, 1975–1990. *Fishery Bulletin*, 92: 451–463.
- Fournier, D. & Archibald, C. P., 1982. A General-Theory for Analyzing Catch at Age Data. *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 1195–1207.
- Fournier, D. A., Hampton, J. & Sibert, J. R., 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Science*, 55: 2105–2116.
- Gerber, L. R. & Hilborn, R., 2001. Estimating the frequency of catastrophic events and recovery from low densities: examples from populations

- of otariids. *Mammal Review*, 31: 131–150.
- Gerrodette, T., 1999. Preliminary estimates of 1998 abundance of four dolphin stocks in the eastern tropical Pacific. *Southwest Fisheries Science Center Administrative Report*, LJ-99-04.
- 2000. Preliminary estimates of 1999 abundance of four dolphin stocks in the eastern tropical Pacific. *Southwest Fisheries Science Center Administrative Report*, LJ-00-12.
- Gerrodette, T. & Forcada, J., 2002. Estimates of abundance of northeastern offshore spotted, coastal spotted, and eastern spinner dolphins in the eastern tropical Pacific Ocean. *Administrative Report No. LJ-02-06*. NOAA Fisheries, Southwest Fisheries Science Center, La Jolla.
- Geweke, J., 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In *Bayesian Statistics 4*: 169–193 (J. M. Bernardo, J. O. Berger, A. P. Dawid and A. F. M. Smith, Eds.). Oxford Univ. Press, Oxford.
- Greiwank, A. & Corliss, G., Eds., 1991. *Automatic Differentiation of Algorithms: Theory, Implementation and Application*. SIAM, Philadelphia.
- Hall, M. A., 1997. Dolphin and other bycatch in the eastern Pacific Ocean tuna purse seine fishery. In: *Fisheries Bycatch: Consequences and Management*: 35–38. Alaska Sea Grant College Program Report No. AK-SG-97-02, Univ. of Alaska, Fairbanks.
- 1998. An ecological view of the tuna–dolphin problem: impacts and trade-off. *Reviews in Fish Biology and Fisheries*, 8: 1–34.
- Hall, M. A., Alverson, D. L. & Metuzals, K. I., 2000. By-catch: problems and solutions. *Marine Pollution Bulletin*, 41: 204–219.
- Hampton, J. & Fournier, D. A., 2001. A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. *Marine and Freshwater Research*, 52: 937–963.
- Hastings, W. K., 1970. Monte Carlo sampling methods using Markov chains and their applications. *Biometrika*, 57: 97–109.
- Heidelberger, P. & Welch, P., 1983. Simulation run length control in the presence of an initial transient. *Operations Research*, 31: 1109–1144.
- Heppell, S. S., Caswell, H. & Crowder, L. B., 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology*, 81: 654–665.
- Hilborn, R. & Liermann, M., 1998. Standing on the shoulders of giants: learning from experience in fisheries. *Reviews in Fish Biology and Fisheries*, 8: 273–283.
- Hilborn, R. & Walters, C. J., 1992. *Quantitative Fisheries Stock Assessment: Choice Dynamics and Uncertainty*. Chapman and Hall, New York.
- Hoeting, J. A., Madigan, D., Raftery, A. E. & Volinsky, C. T., 1999. Bayesian model averaging. *Statistical Science*, 14: 382–417.
- Hohn, A. A. & Scott, M. D., 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Abstract, *Fifth Biennial Conference on the Biology of Marine Mammals*, Boston.
- Inter-American Tropical Tuna Commission, 1994. Letter to Dr. Michael Tillman, Southwest Fisheries Science Center Director, September 6, 1994.
- 2002. Annual Report of the Inter-American Tropical Tuna Commission: 2001. La Jolla, California.
- Joseph, J., 1994. The tuna–dolphin controversy in the eastern Pacific Ocean: biological, economic, and political impacts. *Ocean Development and International Law*, 25: 1–30.
- Kass, R. E. & Raftery, A. E., 1995. Bayes Factors. *Journal of the American Statistical Association*, 90: 773–795.
- Kasuya, T., Miyazaki, N. & Dawbin, W. H., 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. *The Scientific Reports of the Whales Research Institute*, 26: 157–226.
- Lennert-Cody, C. E., Buckland, S. T. & Marques, F. F. C., 2001. Trends in dolphin abundance estimated from fisheries data: a cautionary note. *Journal of Cetacean Research and Management*, 3: 305–319.
- Link, W. A., Cam, E., Nichols, J. D. & Cooch, E. G., 2002. Of BUGS and birds: Markov Chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management*, 66: 277–291.
- Maunder M. N., 2001a. A general framework for integrating the standardization of catch-per-unit-of-effort into stock assessment models. *Canadian Journal of Fisheries and Aquatic Science*, 58: 795–803.
- 2001b. Integrated Tagging and Catch-at-Age ANalysis (ITCAAN). In: *Spatial Processes and Management of Fish Populations*: 123–146 (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith & D. Witherell, Eds.). Alaska Sea Grant College Program Report No. AK-SG-01-02, Univ. of Alaska, Fairbanks.
- 2003. Paradigm shifts in fisheries stock assessment: from integrated analysis to Bayesian analysis and back again. *Natural Resource Modeling*, 16: 465–475.
- 2004. Population Viability Analysis, Based on Combining, Integrated, Bayesian, and Hierarchical Analyses. *Acta Oecologica*, 26: 85–94.
- Maunder, M. N. & Starr, P. J., 2001. Bayesian assessment of the SNA1 snapper (*Pagrus auratus*) stock on the north-east coast of New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 35: 87–110.
- 2003. Fitting fisheries models to standardised CPUE abundance indices. *Fisheries Research*, 63: 43–50.
- Maunder, M. N., Starr, P. J. & Hilborn, R., 2000. A Bayesian analysis to estimate loss in squid catch due to the implementation of a sea lion population management plan. *Marine Mammal Science*, 16: 413–426.
- McAllister, M. & Kirchner, C., 2002. Accounting for

- structural uncertainty to facilitate precautionary fishery management: illustration with Namibian orange roughy. *Bulletin of Marine Science*, 70: 499–540.
- McAllister, M. K. & Kirkwood, G. P., 1998. Bayesian stock assessment and policy evaluation: a review and example application using the logistic model. *ICES Journal of Marine Science*, 55: 1031–1060.
- McAllister, M. K., Pikitch, E. K., Punt, A. E. & Hilborn, R., 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2673–2687.
- Myazaki, N. & Nishiwaki, M., 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Scientific Report of the Whale Research Institute*, 30: 65–115.
- Myrick, A. C., Hohn, A. A., Barlow, J. & Sloan, P. A., 1986. Reproductive–Biology of Female Spotted Dolphins, *Stenella–Attenuata*, from the Eastern Tropical Pacific. *Fishery Bulletin*, 84: 247–259.
- Myrick, A. C. Jr., Hohn, A. A., Sloan, P. A., Kimura, M. & Stanley, D. D., 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. *NOAA–Technical Memorandum–NMFS–SWFC–30*.
- National Research Council, 1992. *Dolphins and the Tuna Industry*. Committee on Reducing Porpoise Mortality from Tuna Fishing. National Academy Press, Washington, DC.
- Noon, B. R. & McKelvey, K. S., 1996. Management of the spotted owl: A case history in conservation biology. *Annual Review of Ecology and Systematics*, 27: 135–162.
- Perkins, P. C. & Edwards, E. F., 1999. Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean. *Fishery Bulletin*, 97: 542–554.
- Perrin, W. F., 1969. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani Lonnberg* (Cetacea, Delphinidae). *Zoological Journal, New York Zoological Society*, 54: 135–149.
- Perryman, W. L. & Lynn, M. S., 1994. Examination of stock and school structure of striped dolphins (*Stenella coeruleoalba*) in the eastern Pacific from aerial photogrammetry. *Fishery Bulletin*, 92: 122–131.
- Punt, A. E. & Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries*, 7: 35–63.
- Punt, A. E. & Butterworth, D. S., 1999. On assessment of the Bering–Chukchi–Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) using a Bayesian approach. *Journal of Cetacean Research and Management*, 1: 53–71.
- Raftery, A. E., Givens, G. H. & Zeh, J. H., 1995. Inference from a deterministic population dynamics model for bowhead whales. *Journal of the American Statistical Association*, 90: 402–416.
- Raftery, A. L. & Lewis, S., 1992. How many iterations in the Gibbs sampler? In: *Bayesian Statistics 4*: 763–773 (J. M. Bernardo, J. O. Berger, A. P. Dawid and A. F. M. Smith, Eds.). Oxford Univ. Press, Oxford.
- Reilly, S. B. & Fiedler, P. C., 1994. Interannual Variability of Dolphin Habitats in the Eastern Tropical Pacific .1. Research Vessel Surveys, 1986–1990. *Fishery Bulletin*, 92: 434–450.
- Schnute, J. T. & Hilborn, R., 1993. Analysis of contradictory data sources in fish stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1916–1923.
- Siler, W., 1979. A competing–risk model for animal mortality. *Ecology*, 60: 750–757.
- Smith, B. J., 2001. *Baysian Output Analysis Program (BOA)*. Version 1.0.1 for Windows R. URL: http://www.public-health.uiowa.edu/boa/boa_prog.html
- Tanner, M. A., 1993. *Tools for statistical inference: methods for the exploration of posterior distributions and likelihood functions*. Springer–Verlag, New York.
- Taylor, B. L. & DeMaster, D. P., 1993. Implications of Nonlinear Density–Dependence. *Marine Mammal Science*, 9: 360–371.
- Taylor, B. L., Wade, P. R., DeMaster, D. P. & Barlow, J., 2000. Incorporating uncertainty into management models for marine mammals. *Conservation Biology*, 14: 1243–1252.
- Taylor, B., Wade, P. R., Stehn, R. & Cochrane, J., 1996. A Bayesian approach to classification criteria for spectacled eiders. *Ecological Applications*, 6: 1077–1089.
- Wade, P. R., 1993. Estimation of Historical Population–Size of the Eastern Spinner Dolphin (*Stenella–Longirostris–Orientalis*). *Fishery Bulletin*, 91: 775–787.
- 1994. Abundance and Population Dynamics of Two Eastern Pacific Dolphins, *Stenella attenuata* and *Stenella longirostris orientalis*. Ph. D. Thesis, Univ. of California, San Diego.
- 1995. Revised estimates of dolphin kill in the eastern tropical Pacific, 1959–1972. *Fishery Bulletin*, 93: 345–354.
- 1999. A comparison of statistical methods for fitting population models to data. In: *Marine mammal survey and assessment methods*: 249–270 (A. A. Balkema, Ed.). Proceedings of the symposium on marine mammal survey and assessment methods, Seattle, Washington, U.S.A.
- 2002. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967–1996. *Journal of cetacean research and management*, 4: 85–98.
- Wade, P. R. & Gerrodette, T., 1992. Estimates of dolphin abundance in the eastern tropical Pacific: Preliminary analysis of five years of data (IWC SC/43/SM–13). *Report of the International Whaling Commission*, 42: 533–539.
- 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Report of the International Whaling Commission*, 43: 477–493.

-
- Wade, P. R., Reilly, S. B. & Gerrodette, T., 2002. Assessment of the population dynamics of the northeastern offshore spotted and the eastern spinner dolphin populations through 2002. *Administrative Report No. LJ-02-13*, NOAA Fisheries, Southwest Fisheries Science Center, La Jolla.
- White, G. C. & Lubow, B. C., 2002. Fitting population models to multiple sources of observed data. *Journal of Wildlife Management*, 66: 300–309.
- Wilson, D. L., 1993. A comparison of methods for estimating mortality parameters from survival data. *Mechanisms of Ageing and Development*, 66: 269–281.
-