



FEATURE ARTICLE

Depletion of spotted and spinner dolphins in the eastern tropical Pacific: modeling hypotheses for their lack of recovery

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ABSTRACT: We assess the status of 2 dolphin stocks affected by purse-seine fishing in the eastern tropical Pacific and evaluate hypotheses for their lack of recovery. We use Bayesian methods and fit generalized models of logistic population growth to abundance estimates for northeastern offshore spotted dolphins *Stenella attenuata attenuata* and eastern spinner dolphins *Stenella longirostris orientalis*. In 2002, using the definition of depletion stipulated in the USA Marine Mammal Protection Act, northeastern offshore spotted dolphins were almost certainly 'depleted'. There is, however, uncertainty in the degree to which the stock was depleted. Eastern spinner dolphins were most likely depleted in 2002, but there is a small probability that this was not the case. Uncertainty in the degree to which both stocks were depleted stems from uncertainties in maximum net productivity levels and carrying capacities. Based on abundance data from 1979 to 2000, both stocks were estimated to have had maximum growth rates of $<3\% \text{ yr}^{-1}$ with $>77\%$ probability, lower than the accepted minimum default value for dolphin populations with reproductive parameters (e.g. calving intervals) like those considered here (Reilly & Barlow 1986, Fish Bull 84:527–533; Wade 1998, Mar Mamm Sci 14:1–37). We fit models that are intended to be indicative of hypotheses that explain why neither dolphin stock has recovered. Our data and prior information provide equal posterior support to hypotheses which attribute the lack of recovery to the fishery and changes in the ecosystem. We conclude that (1) the purse-seine fishery can impact dolphin stocks beyond the impacts of observed fishery mortality, (2) there is uncertainty about the degrees to which such cryptic impacts have population-level consequences, and (3) the existing dolphin-safe labeling standard is, from a conservation perspective, robust to this uncertainty.



Populations of northeastern offshore spotted (top) and eastern spinner (bottom) dolphins in the eastern tropical Pacific have not recovered as expected.

Photos: Robert Pitman (NOAA)

KEY WORDS: Tuna–dolphin issue · Dolphin-safe labeling · *Stenella attenuata* · *S. longirostris* · Status assessment · Fishery · Ecosystem effects · Bycatch

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INTRODUCTION

Dolphins of several species are incidentally killed during tuna purse-seine fishing in the eastern tropical Pacific Ocean (ETP). Fishermen use the dolphins to locate schools of tuna, and often purposely chase and encircle the dolphins in their nets to maximize their catch of tuna (Perrin 1969, Joseph & Greenough 1979). The main species killed are spotted dolphins *Stenella attenuata*, spinner dolphins *S. longirostris*, and com-

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mon dolphins *Delphinus delphis*. Over the period 1960 to 1972, more than 4 million dolphins were killed by purse-seine vessels fishing for yellowfin tuna *Thunnus albacares* in the ETP (Wade 1995). At least 3 dolphin stocks—northeastern offshore spotted dolphins *S. attenuata attenuata*, coastal spotted dolphins *S. attenuata graffmani*, and eastern spinner dolphins *S. longirostris orientalis*—declined because of the mortality incurred during the 1960s and early 1970s, and were consequently designated 'depleted' under the USA Marine Mammal Protection Act (MMPA) (Smith 1983, Wade 1993, 1994). Gerrodette & Forcada (2005) provide a recent assessment of the trends of dolphin stocks in the ETP and conclude that, despite reductions in fishing mortality which span 2 orders of magnitude, neither the stock of northeastern offshore spotted dolphins nor that of eastern spinner dolphins had increased in abundance by the year 2000. Thus, neither stock was considered to be recovering.

The results presented by Gerrodette & Forcada (2005) set the stage for further retrospective study in 2 ways. First, Gerrodette & Forcada (2005) provide 12 estimates of abundance, covering the period 1979 to 2000, for both northeastern offshore spotted and eastern spinner dolphins. These abundance estimates can be used in combination with a population-dynamics model and data on observed kills to (1) re-assess whether the 2 stocks were depleted in 2002 relative to historical levels of abundance and (2) estimate each stock's maximum rate of population growth. Second, Gerrodette & Forcada (2005) initiate a discussion about hypotheses that can explain the apparent lack of recovery by dolphin stocks in the ETP. These hypotheses fall into 3 general categories: fishery effects, ecosystem effects, and effects from complex population dynamics. Evaluating the competition among these alternatives in a common model-based framework may be useful because some effects (e.g. fishery effects) have an obvious bearing on conservation and management issues while others (e.g. ecosystem effects) may not. In particular, one conservation issue that has received recent attention is whether fishing for tuna by chasing and encircling dolphin schools is harmless for the dolphin populations if no dolphin deaths are observed during such activities. Other lines of research have shown that there could be considerable 'cryptic' (unseen) deaths from chase and encirclement (e.g. Archer et al. 2001, 2004), which suggests that the apparent lack of recovery noted by Gerrodette & Forcada (2005) is from this source.

We have 2 objectives in this paper. First, we assess the status of the northeastern offshore spotted and eastern spinner dolphin stocks as of 2002. Second, we consider whether the lack of recovery by these stocks can be attributed to fishery effects or ecosystems effects, using a Bayesian model comparison method.

MATERIALS AND METHODS

Data. Estimates of bycatch and abundance, covering the period 1959 to 2002 (Table 1), provide the empirical bases for our work. We obtained stock-specific estimates of the numbers of dolphins killed by the purse-seine fishery from 3 sources. We used bycatch kill estimates from (1) Wade (1995) for the period 1959 to 1972, (2) J. Joseph (unpubl. data: letter from J. Joseph to M. Tillman dated 6 September 1994) for the period 1973 to 1984, and (3) IATTC (2002a,b, 2004) for the period 1985 to 2002. We obtained stock-specific estimates of abundance from Gerrodette & Forcada (2005). These abundance estimates were developed from covariate line-transect models (Marques & Buckland 2003, Forcada et al. 2004, Gerrodette & Forcada 2005) that were fitted to sighting data collected during research surveys in the ETP.

Models. We used generalized models of logistic population growth (Pella & Tomlinson 1969) to characterize the dynamics of both northeastern offshore spotted and eastern spinner dolphins. In discrete time, the abundance of dolphins from a single stock (we modeled each stock separately) in year t (N_t) is determined from the abundance in the previous year, the density-dependent net recruitment of new individuals to the stock (from births and natural mortality), and the number of deaths caused by fishing (C_t):

$$N_{t+1} = N_t + r_i N_t \left[1 - \left(\frac{N_t}{K_i} \right)^Z \right] - C_t \quad (1)$$

where K_i is the carrying capacity during period i , and r_i is the period-specific maximum rate of annual population growth at low levels of abundance. Periods indexed by i span multiple years indexed by t , and we used this structure to model temporal shifts in K and r (see below). Z is a shape parameter that determines both the rate at which population growth is slowed with increasing abundance and the abundance at which production is maximized. Larger values of Z cause the population growth rate to fall faster and production to be maximized at higher levels of abundance. The USA MMPA defines a depleted stock of marine mammals as a stock whose abundance is less than that which maximizes its production¹. This may be the maximum net productivity level (MNPL) and, as a proportion of K , it can be approximated from a function of Z (Smith 1983):

$$\text{MNPL} = (Z + 1)^{-1/Z} \quad (2)$$

Eq. (2) cannot be rearranged to provide an analytical solution for Z in terms of MNPL.

¹Public Law 92-522, 21 October 1972 and amendments, 16 U.S.C. § 1362

Table 1. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Bycatch kill and abundance estimates (ind. $\times 10^3$) used to assess the status of dolphin stocks in the eastern tropical Pacific Ocean as of 2002. Values are expectations and those inside parentheses are coefficients of variation

Year	Northeastern offshore spotted		Eastern spinner	
	Bycatch	Abundance	Bycatch	Abundance
1959	15.9 (0.53)		6.5 (0.47)	
1960	344.0 (0.52)		138.4 (0.47)	
1961	366.0 (0.48)		153.5 (0.43)	
1962	141.0 (0.42)		62.2 (0.40)	
1963	158.2 (0.36)		69.4 (0.37)	
1964	272.3 (0.28)		112.7 (0.34)	
1965	318.5 (0.29)		132.5 (0.34)	
1966	244.1 (0.22)		107.8 (0.33)	
1967	171.8 (0.23)		72.2 (0.33)	
1968	161.2 (0.22)		65.7 (0.33)	
1969	271.5 (0.22)		110.4 (0.35)	
1970	218.7 (0.22)		104.5 (0.33)	
1971	111.3 (0.22)		60.1 (0.32)	
1972	168.1 (0.17)		88.5 (0.32)	
1973	49.9 (0.18)		18.4 (0.16)	
1974	37.4 (0.11)		17.8 (0.11)	
1975	49.4 (0.18)		17.1 (0.11)	
1976	20.4 (0.23)		14.7 (0.12)	
1977	5.9 (0.12)		1.8 (0.12)	
1978	4.2 (0.20)		1.1 (0.11)	
1979	4.8 (0.17)	708 (0.28)	1.5 (0.24)	449 (0.35)
1980	6.5 (0.15)	740 (0.25)	1.1 (0.20)	271 (0.38)
1981	8.1 (0.19)		2.3 (0.28)	
1982	9.3 (0.17)	605 (0.29)	2.6 (0.33)	285 (0.39)
1983	2.4 (0.27)	548 (0.34)	0.7 (0.38)	619 (0.40)
1984	7.8 (0.19)		6.0 (0.52)	
1985	26.0 (0.12)		8.9 (0.16)	
1986	52.0 (0.16)	494 (0.22)	19.5 (0.19)	536 (0.35)
1987	35.4 (0.12)	501 (0.19)	10.4 (0.11)	443 (0.30)
1988	26.6 (0.10)	868 (0.24)	18.8 (0.09)	636 (0.28)
1989	28.9 (0.11)	954 (0.23)	15.2 (0.11)	734 (0.41)
1990	22.6 (0.11)	666 (0.35)	5.4 (0.18)	459 (0.30)
1991	9.0 (0.11)		5.9 (0.13)	
1992	4.7 (0.07)		2.8 (0.06)	
1993	1.1 (0.08)		0.8 (0.08)	
1994	0.9 (0.07)		0.7 (0.11)	
1995	1.0 (0.00)		0.7 (0.00)	
1996	0.8 (0.00)		0.5 (0.00)	
1997	0.7 (0.00)		0.4 (0.00)	
1998	0.3 (0.00)	676 (0.14)	0.4 (0.00)	557 (0.22)
1999	0.4 (0.00)	600 (0.16)	0.4 (0.00)	361 (0.25)
2000	0.3 (0.00)	647 (0.21)	0.3 (0.00)	428 (0.22)
2001	0.6 (0.00)		0.5 (0.00)	
2002	0.6 (0.00)		0.5 (0.00)	

We used Eq. (1) to build a set of 6 models. Our 'reference model' is the simplest, and for this model we assumed that the dynamics of an individual stock were governed by one K and one r (i.e. these parameters did not change during the period 1959 to 2002). We also assumed that the expected kills reported in Table 1 are unbiased estimates of the true kills. Next, we built

a model with 2 carrying capacities (K_1 and K_2 ; 2- K model) and another model with 2 maximum rates of population growth (r_1 and r_2 ; 2- r model); these represent change-point models. For each of these models, we introduced an additional parameter (δ) that identifies the year which separates Period 1 (1959 to δ) from Period 2 ($\delta+1$ to 2002). For the 2- K and 2- r models, we assumed that the expected kills reported in Table 1 are unbiased estimates of the true kills. Finally, we constructed 3 models (each with one K and one r) under the assumption that the expected kills reported in Table 1 underestimate the true kills. For these models, we respectively assumed that (1) in all years the true kills are estimated by values equal to 1.5 times those reported in Table 1, (2) in all years the true kills are estimated by values equal to 2.0 times those reported in Table 1, and (3) during 1992 to 2002 the true kills are estimated by values equal to 2.0 times those reported in Table 1 (in this case, we assumed that the expectations reported for 1959 to 1991 are unbiased). We used the coefficients of variation for estimated kills of dolphins reported in Table 1 to specify levels of prior uncertainty for all 6 of our models; this allows us to fully incorporate uncertainty in the level of dolphin kill from sampling error into the analysis. We parameterized all models by assuming that both dolphin stocks were at their carrying capacities in 1958 (K_1 in the 2- K model and K in all other models).

Parameter estimation and model comparison. We used Bayesian methods to fit our models and make comparisons among them. We used information from a variety of sources to specify prior distributions that were intended to bracket biologically reasonable parameter spaces but be uninformative within those spaces (Table 2). Our prior distributions for K were established by inspecting the results of previous modeling efforts (e.g. Wade 1994), and were selected to be uniform distributions across the plausible range of the posterior distribution for all the models. Any prior dis-

Table 2. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Prior distributions for parameters in our generalized logistic models. Numbers for carrying capacity (K) are reported as ind. $\times 10^3$. MNPL: maximum net productivity level; r : maximum rate of annual population growth; δ : year which separates K_1 from K_2 or r_1 from r_2 ; U: uniform distribution; DU: discrete uniform distribution

Model	Northeastern offshore spotted	Eastern spinner
K or K_1	U(2000, 7500)	U(1000, 3500)
K_2	U(0, 7500)	U(0, 5500)
r	U(0.00, 0.08)	U(0.00, 0.08)
r_2	U(-0.08, 0.08)	U(-0.08, 0.08)
MNPL	U(0.5, 0.8)	U(0.5, 0.8)
δ	DU(1981, 1999)	DU(1981, 1999)

tribution that is approximately uniform at least across the region where the likelihood function is not negligible for a quantity of interest will be non-informative with respect to that quantity (Savage 1962); this was true of our prior distributions for K for each model. We used results from Reilly & Barlow (1986) to derive our prior distributions for r , but we also included the possibility of negative growth rates in the 2- r models. We used results from Taylor & DeMaster (1993) to specify prior distributions for MNPL rather than Z , where MNPL is expressed as a fraction of K . This necessitated numerical solutions for Z after sampling from the MNPL priors; for this we used Brent's method (e.g. Press et al. 1986). Our prior distributions for MNPL implied a prior distribution for Z ranging from 1.0 to 11.2. We treated the bycatch kill estimates as prior information; therefore, the expected kills and coefficients of variation reported in Table 1 were used to specify log-normal prior distributions (1 distribution for each year) for the kills. For the models with higher kills, we scaled the entire prior distribution for the bycatch kill up by a factor of 1.5 or 2.0, as appropriate. The prior distribution for δ was chosen to be uniform across the range of years for which there was abundance data available. We specified a likelihood function by assuming that the abundance estimates from the research surveys were samples from log-normal distributions (again 1 distribution for each year, with expectations and variances determined by the values reported in Table 1). We simulated posterior distributions with the sampling-importance resampling algorithm (Rubin 1988), with >200 000 000 samples drawn from the prior distribution, and 10 000 values in the second sample. Diagnostic criteria used to confirm convergence were (1) >9900 unique values in the second sample and (2) no particular initial sample could occur in the second sample more than 5 times.

The 6 models we developed from Eq. (1) provide a framework in which to compare hypotheses for the lack of recovery (Gerrodette & Forcada 2005) by northeastern offshore spotted and eastern spinner dolphins. Our reference model is generic and does not represent a specific hypothesis. The 'extra mortality' models represent hypotheses in which fishery effects may prevent recovery, and the 2- K model represents a hypothesis in which ecosystem effects may prevent recovery. The 2- r model represents fishery effects, ecosystem effects, or effects from complex population dynamics. All such effects (acting independently or in combination) could conceivably cause r to shift. We used Bayes factors (Kass & Raftery 1995) to compare 5 alternative models (the 2- K , 2- r , and extra mortality models) with our reference model. We assign equal prior probability to each model; in this case, the Bayes factor also represents the posterior odds ratio (the

probability of one model divided by the probability of a second model). These comparisons, therefore, quantify the degrees to which the prior information about bycatch and the abundance estimates reported in Table 1 support each model and give a posterior probability of each model versus another. Note that there are many mechanisms which might plausibly lead to fishery and ecosystem effects, but our models are simple and do not provide explicit, mathematical descriptions of such mechanisms. Thus, our Bayes factors are only indicative of the types of effects that may prevent recovery of the 2 dolphin stocks. We used the probabilities provided by the Bayes factors to summarize the results across all models by creating model-averaged posterior distributions for the parameters of interest, with the results from each model weighted by its posterior probability.

RESULTS

Abundance and status of northeastern offshore spotted dolphins

The data provided in Table 1 was informative for estimating the carrying capacity and maximum rate of population growth for northeastern offshore spotted dolphins. The posterior distributions of both K (including K_1 and K_2 in the 2- K model) and r (including r_1 and r_2 in the 2- r model) were generally different from their respective prior distributions (Table 3). The model-averaged population trajectory, with 90% credible intervals for abundance in each year, indicates that the current population is approximately one-fifth of its initial abundance (Fig. 1). The details of each model's fit to the abundance data are shown in Fig. 2. K was a relatively well-estimated parameter; the posterior distributions of K were much narrower than their priors, and shrinkage usually occurred in both tails. The posterior distributions of r were also narrower than their priors, but here shrinkage usually occurred in the right-hand tails (although note that most of the priors for r did not allow for negative growth rates) (Fig. 3). Thus, the posterior medians of r were usually much less than their prior medians.

All 6 models provided similar fits to the abundance estimates in Table 1. However, the 2 models with extra mortality prior to 1992 had higher abundance than the other models in the 1970s and 1980s, and lower abundance in the 1990s (Fig. 2); they also estimated larger K and r values. The 2 change-point models suggested greater uncertainty in the parameters that changed. The reference model estimated initial abundance of northeastern offshore spotted dolphins to have a 95% credible interval from 3.0 to 3.9 million dolphins. How-

Table 3. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Summary of the posterior distributions for northeastern offshore spotted and eastern spinner dolphins. Value in the top row for each parameter is the posterior median, and the parenthetical pair below it represents the 95% credible interval (there is a 0.95 probability that the true value lies within the interval). The space has been left blank for parameters that are not applicable to that model. Vertical arrows: departures of the posterior distribution from the prior distribution for all the explicit parameters of the models (first 6 rows). For the posterior medians, the arrows identify estimates that have moved greater than 10% of the entire prior range from the prior mean. For the intervals, the arrows represent posterior interval bounds that are within the 80% credible interval of the prior distribution. Posterior probabilities were also calculated for additional output parameters (last 5 rows) from the joint posterior distribution for the model parameters. Carrying capacity (K) and abundance (N) are reported in ind. $\times 10^3$. Note that, for N_{2002}/MNPL , MNPL (maximum net productivity level) is expressed here not as a fraction of K , but as numbers of individuals. MNPL_2 represents the MNPL associated with K_2 . r : maximum rate of annual population growth. C : vector of the annual number of deaths caused by fishing for the years specified that is multiplied by the value of 1.5 or 2.0. See Table 2 for other parameter definitions

Parameter	Reference	2- K	2- r	$1.5 \cdot \bar{C}_{1959-2002}$	$2.0 \cdot \bar{C}_{1959-2002}$	$2.0 \cdot \bar{C}_{1992-2002}$	Model averaged
Northeastern offshore spotted							
K or K_1	3500 [↓] (3049 [↑] , 3914 [↓])	3476 [↓] (2921 [↑] , 4259 [↓])	3299 [↓] (2582, 3864 [↓])	4794 [↓] (4198 [↑] , 5406 [↓])	6000	3477 [↓] (3027 [↑] , 3909 [↓])	3653 [↓] (2842 [↑] , 5740 [↓])
K_2		3682 (553 [↑] , 7308)					
r or r_1	0.016 [↓] (0.002, 0.036 [↓])	0.017 [↓] (0.002, 0.048 [↓])	0.026 [↓] (0.002, 0.069 [↓])	0.025 [↓] (0.006, 0.045 [↓])	0.033 [↓] (0.013 [↑] , 0.053 [↓])	0.017 [↓] (0.002, 0.037 [↓])	0.021 [↓] (0.002, 0.054 [↓])
r_2			0.000 (-0.073 [↑] , 0.063 [↓])				
δ		1990 (1981, 1999)	1993 (1981, 1999)				
MNPL	0.641 (0.506, 0.791)	0.632 (0.505, 0.791)	0.632 (0.505, 0.791)	0.634 (0.506, 0.792)	0.638 (0.505, 0.792)	0.637 (0.505, 0.791)	0.641 (0.505, 0.791)
N_{2002}	690 (568, 856)	683 (560, 849)	643 (471, 868)	710 (575, 886)	733 (588, 911)	689 (562, 853)	689 (530, 870)
N_{2002}/K	0.197 (0.150, 0.273)	0.197 (0.149, 0.273)	0.197 (0.138, 0.277)	0.149 (0.109, 0.205)	0.122 (0.089, 0.168)	0.198 (0.149, 0.273)	0.194 (0.118, 0.274)
N_{2002}/K_2		0.189 (0.089, 1.090)					
N_{2002}/MNPL	0.312 (0.213, 0.456)	0.313 (0.214, 0.462)	0.312 (0.203, 0.463)	0.236 (0.157, 0.339)	0.193 (0.132, 0.277)	0.313 (0.212, 0.463)	0.308 (0.176, 0.460)
N_{2002}/MNPL_2		0.299 (0.129, 1.908)					
Eastern spinner							
K or K_1	1673 [↓] (1374 [↑] , 1901 [↓])	1645 [↓] (1244 [↑] , 1899 [↓])	1457 [↓] (1099, 1864 [↓])	2292 [↓] (1918 [↑] , 2604 [↓])	2875	1668 [↓] (1370 [↑] , 1903 [↓])	1795 [↓] (1190, 3010 [↓])
K_2		2294 (305, 5344)					
r or r_1	0.014 [↓] (0.001, 0.041 [↓])	0.016 [↓] (0.001, 0.067 [↓])	0.037 [↓] (0.002, 0.077)	0.017 [↓] (0.001, 0.043 [↓])	0.021 [↓] (0.002, 0.047 [↓])	0.014 [↓] (0.001, 0.042 [↓])	0.022 [↓] (0.001, 0.070 [↓])
r_2			-0.014 (-0.076, 0.042 [↓])				
δ		1990 (1981, 1999)	1991 (1981, 1999)				
MNPL	0.631 (0.505, 0.792)	0.629 (0.505, 0.790)	0.625 (0.506, 0.790)	0.636 (0.506, 0.792)	0.636 (0.505, 0.791)	0.631 (0.505, 0.790)	0.637 (0.505, 0.791)
N_{2002}	503 (399, 660)	493 (376, 649)	438 (310, 622)	501 (391, 667)	505 (387, 676)	500 (396, 660)	470 (371, 660)
N_{2002}/K	0.300 (0.224, 0.460)	0.300 (0.220, 0.466)	0.302 (0.196, 0.467)	0.218 (0.158, 0.335)	0.175 (0.123, 0.269)	0.297 (0.222, 0.463)	0.288 (0.155, 0.455)
N_{2002}/K_2		0.350 (0.088, 1.090)					
N_{2002}/MNPL	0.478 (0.315, 0.781)	0.482 (0.316, 1.315)	0.484 (0.287, 0.769)	0.348 (0.226, 0.339)	0.279 (0.177, 0.446)	0.477 (0.315, 0.789)	0.461 (0.230, 0.760)
N_{2002}/MNPL_2		0.299 (0.128, 2.321)					

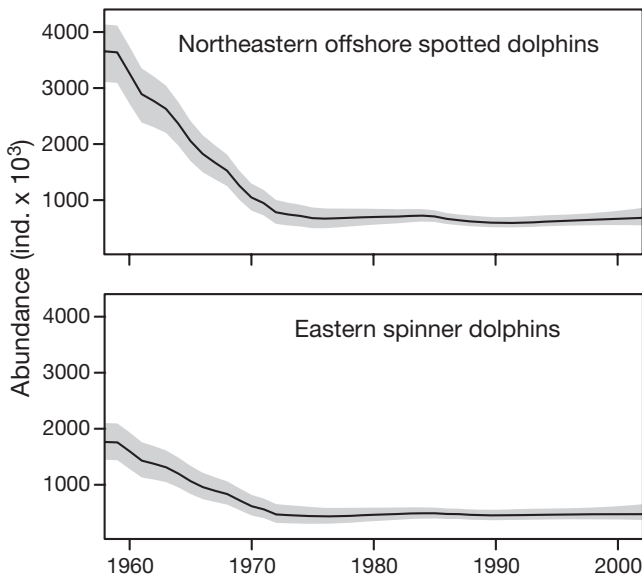


Fig. 1. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Model-averaged estimated population trajectories from 1958 to 2002. Line represents the median posterior population size in each year. Gray region represents the 90% credible interval for population size in each year (there is a 0.90 probability that the true value lies within the interval)

ever, pooling results from all the models expanded this range considerably at the higher end due to the models with extra mortality. The model-averaged posterior distribution for the initial abundance had a 95% credible interval that ranged from 2.8 to 5.7 million dolphins. The model-averaged posterior distribution for the maximum population growth rate (using r_1 from the 2- r model in the model average) estimated a 0.83 probability that the maximum growth rate was less than 3% yr^{-1} , and a 0.93 probability that it was less than 4% yr^{-1} .

Despite these general conclusions noted above, the posterior distributions of both K and r varied among models, and the information content of the abundance estimates was dependent on model choice (Table 3). Uncertainty in K and r was greatest for the 2 change-point models. These models also showed substantial uncertainty in the estimated times at which K and r may have changed. In general, the posterior distributions for bycatch recapitulated the prior distributions, and those results have not been presented.

All 6 models supported the conclusion that in 2002 the northeastern stock of offshore spotted dolphins was depleted relative to its initial abundance (Fig. 4, Table 3). Uncertainty in the degree of depletion (again, relative to the initial abundance) arose from uncertainty in MNPL. The posterior distributions of MNPL were not very different from their prior distributions and were nearly uniform over the range 0.5 to 0.8,

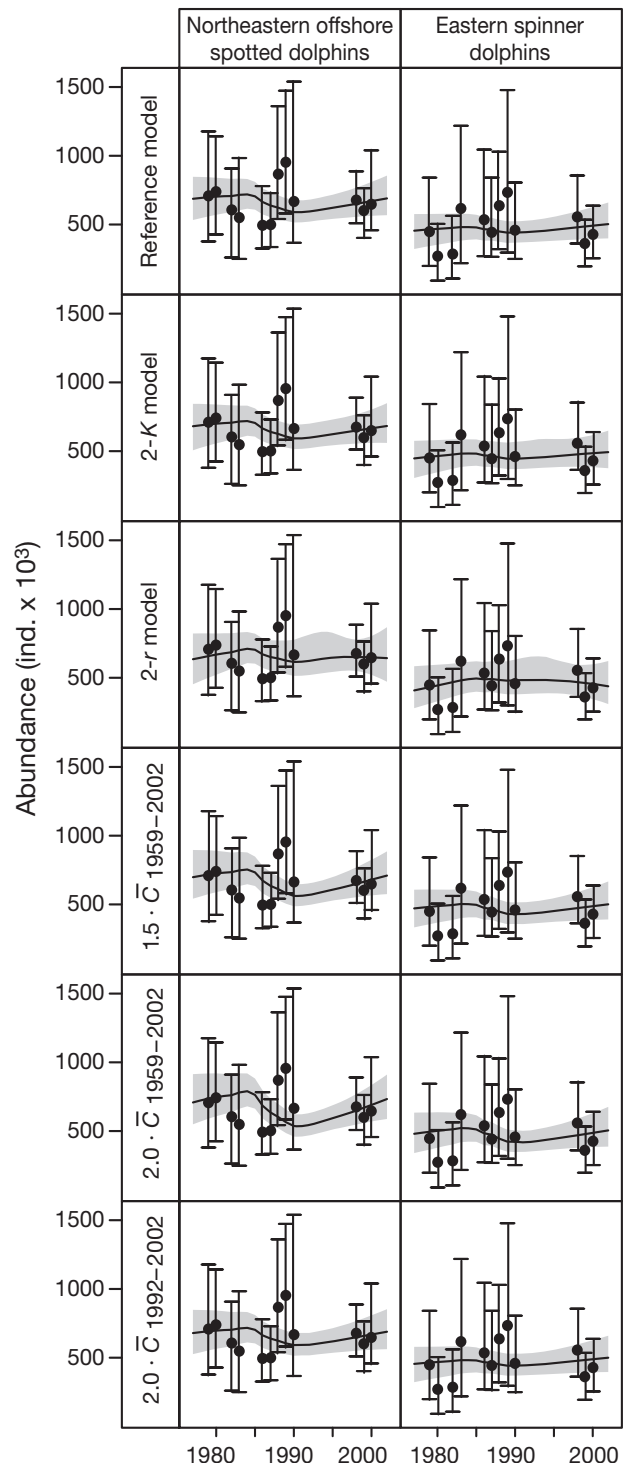


Fig. 2. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Fits of the models to the abundance estimates (●) provided in Table 1. Solid lines connect median abundance estimates; grey region represents the 90% credible intervals for population size in each year. Error bars are 95% confidence limits. K : carrying capacity; r : maximum rate of annual population growth; \bar{C} : vector of the annual number of deaths caused by fishing for the years specified that is multiplied by the value of 1.5 or 2.0

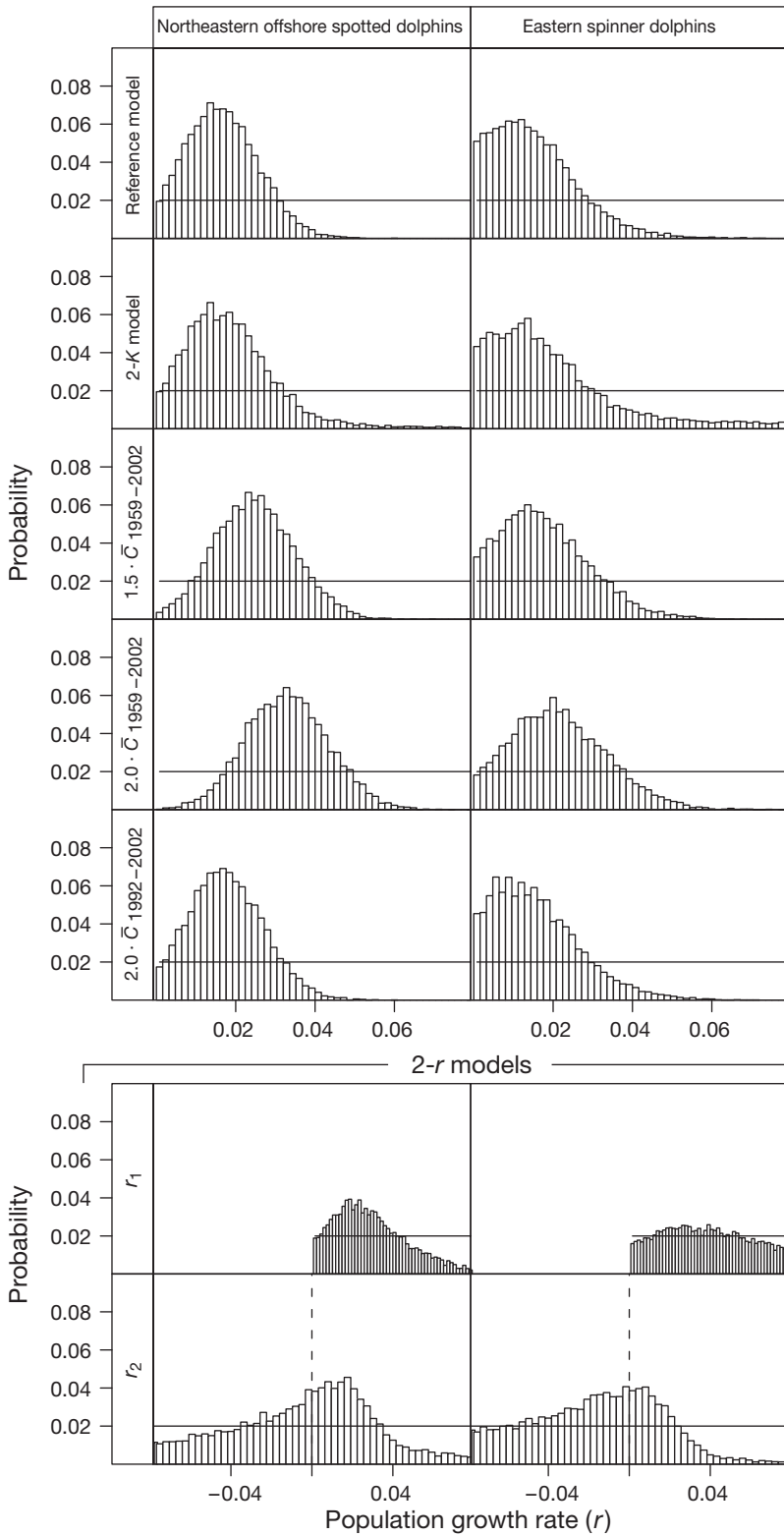


Fig. 3. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Posterior and prior distributions for r , the maximum population growth rate parameter. The prior distribution is plotted as a line and the posterior distribution is plotted as a histogram. Note that the distributions for the 2- r models are plotted on a different scale. See Fig. 2 for definitions

with a higher probability of lower values than of higher values (Table 3). Within any given model, depletion was least severe when MNPL = 0.5 defined the reference point and most severe when MNPL = 0.8 defined the reference point. Variations in K within and between models were further sources of uncertainty in the degree of depletion. Within models, depletion was less severe for values of K below the posterior median and more severe for values of K above the median. Between models, uncertainty in the degree of depletion derived from model-specific differences in the posteriors of K . The 2 models with extra mortality prior to 1992, not surprisingly, suggested greater degrees of depletion than the other models (Fig. 4). Nevertheless, to reiterate the general result, all of the models estimated that in 2002 the abundance of northeastern offshore spotted dolphins was less than 30% of the initial abundance of this stock (Fig. 1, Table 3) and was between about 500 000 and 900 000 individuals (Table 3). The model-averaged posterior distribution estimated a probability of 1.0 that the population was below MNPL (referenced to initial abundance), with a 95% credible interval for the depletion level (N_{2002}/K) of 0.12 to 0.27 (Fig. 5).

The 2- K model facilitated consideration of whether the northeastern stock of offshore spotted dolphins was depleted relative to a carrying capacity that was determined some time after the development of the purse-seine fishery. When MNPL was treated as a proportion of K_2 , there was a small probability (0.15) that in 2002 the stock was not depleted relative to K_2 (Fig. 4).

Abundance and status of eastern spinner dolphins

Our results for eastern spinner dolphins were generally similar to those for northeastern offshore spotted dolphins, e.g. the posterior distributions for K and r were similarly different from their respective priors, and the 2 change-point models suggested greater uncertainty in the parameters that changed. However,

there were some specific differences. In contrast to the case for northeastern offshore spotted dolphins, the Bayes factor indicated differences among models were not as great, perhaps due to the less precise abundance estimates available for eastern spinner dolphins (Table 4). However, similar to the spotted dolphin case, the models with extra mortality for the entire time period did fit the data least well. The reference model for eastern spinner dolphins suggested uncertainties in K and r that were similar in magnitude to those suggested by the 2- K model (Table 3). The one trajectory that shows a somewhat different dynamic from the other models is that of the 2- r model, where the population was showing recovery from the mid-1970s through the 1980s, but then began to slightly decline in the early 1990s (Fig. 2). This model also had the highest posterior probability, though the advantage was small and not great enough to consider this a clear 'best' model (Table 4). The reference model estimated a 95% credible interval for the initial abundance of eastern spinner dolphins of 1.4 to 1.9 million individuals. Summarizing results from all 6 models, the model-averaged posterior distribution for the initial abundance of eastern spinner dolphins had a 95% credible interval that ranged from 1.2 to 3.0 million individuals. The model-averaged posterior distribution for the maximum population growth rate (using r_1 from the 2- r model in the model average) estimated a 0.77 probability that it was less than 3% yr⁻¹, and a 0.86 probability that it was less than 4% yr⁻¹ (Fig. 5).

All 6 models supported the conclusion that in 2002 the stock of eastern spinner dolphins was depleted relative to its initial abundance. The reference model and the model-averaged posterior distribution estimated a probability of 0.998 and 0.999, respectively, that the population was depleted (Fig. 5). The estimates of N_{2002}/K indicate that the population was less than half of its initial abundance, with a 95% credible interval for the model-averaged posterior of 0.16 to 0.46.

All 3 factors that contributed to uncertainty in the degree to which the northeastern stock of offshore

spotted dolphins was depleted also contributed to the same uncertainty for eastern spinner dolphins (and the nature of these contributions were similar) (Fig. 4). The posterior distributions of MNPL were not very different from their prior distributions and were nearly uniform over the range 0.5 to 0.8, with a higher probability of lower values than of higher values (Table 3). Although there was little uncertainty about whether eastern spinner dolphins were depleted relative to their initial abundance, under the 2- K model there was a small probability (0.24) that the population was not depleted relative to MNPL associated with current carrying capacity (K_2), due to great uncertainty in the estimate of K_2 (the posterior distribution for this parameter was not different from the prior distribution). Viewed together, the results from all 6 models suggested that in 2002 the abundance of eastern spinner dolphins was between about 371 000 and 651 000 individuals (Table 3).

Comparison of alternative models

Our model comparisons were equivocal. This conclusion is based on categorizing Bayes factors as evidence in favor of one hypothesis over another that between 1 and 3 is evidence barely worth mentioning, between 3 and 20 is positive evidence, between 20 and 150 is strong evidence, and greater than 150 is very strong evidence (Kass & Raftery 1995). In Table 4, we present Bayes factors relative to the model with the lowest posterior probability, which was for both species the model assumed to have mortality during 1959 to 2002 at twice the levels reported in Table 1. For northeastern offshore spotted dolphins, the reference model, the 2- K model, the 2- r model, and the 1992 to 2002 extra mortality model were all 5.5 to 7.2 times more likely than this model, but about equally as likely among themselves (Table 4). Thus, for this stock there was a 'loser' but no clear 'winner' among the hypotheses. For eastern spinner dolphins, all of the alternative models had Bayes factors within the range 1–3, and so no hypothesis can be considered to have positive evidence for it compared to another hypothesis (Table 4).

Table 4. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Model comparisons based on Bayes factors. All comparisons are made to the model with the lowest posterior probability, which thus has a Bayes factor of 1.0. See Table 3 for parameter definitions

Model	Northeastern offshore spotted	Eastern spinner
Reference	7.0	2.0
2- K	7.0	2.3
2- r	5.5	2.6
1.5 · $\bar{C}_{1959-2002}$	2.8	1.5
2.0 · $\bar{C}_{1959-2002}$	1.0	1.0
2.0 · $\bar{C}_{1992-2002}$	7.2	2.2

DISCUSSION

Status and trends of dolphin stocks as of 2002

It is unlikely that, as of 2002, northeastern offshore spotted dolphins and eastern spinner dolphins had recovered to levels of abundance greater than thresholds marked by standard reference points for management. The MMPA stipulates that a marine mammal population is depleted if its abundance is less than that

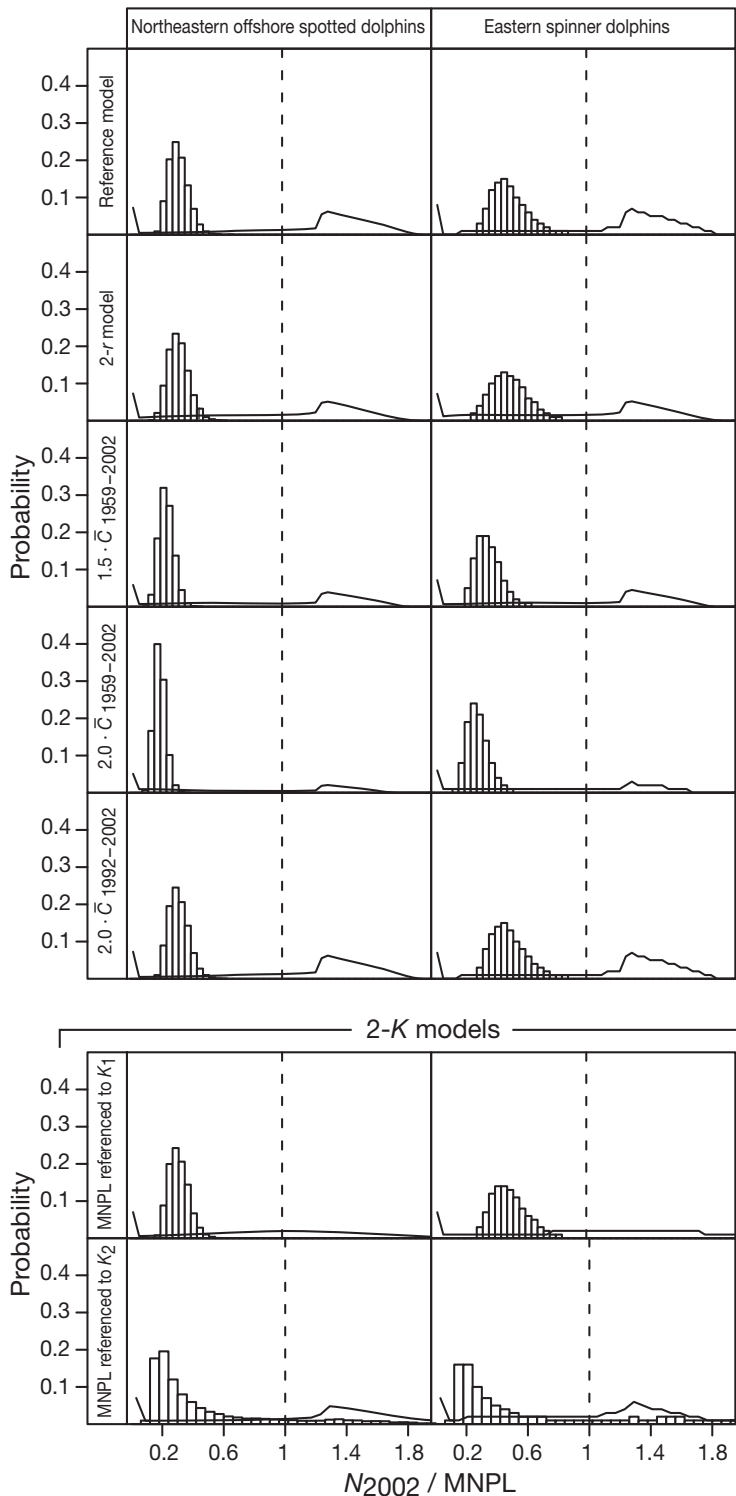


Fig. 4. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Posterior (histogram) and prior (line) distributions for $N_{2002}/MNPL$, the estimated depletion level relative to MNPL. Values <1.0 represent a population level considered depleted under the USA MMPA. The quantity $N_{2002}/MNPL$ is not an explicit parameter of the model; therefore we calculated the implicit prior distribution for this quantity from the joint prior distribution for the model parameters. Note the prior is relatively uninformative for this quantity, as desired. See Fig. 2 for definitions

which maximizes its production (here taken as MNPL). The International Whaling Commission has established a similar reference point (Cooke 1995). While MNPL is clear in concept and well established in the fisheries literature, it is difficult to estimate for marine mammal populations because the data are usually insufficient (Gerrodette & DeMaster 1990, Taylor & DeMaster 1993). The dolphin stocks considered here are relatively well-studied marine mammal populations with 12 abundance estimates over a period of 21 yr, yet the posterior distributions of MNPL were similar to their priors. Long-lived, slowly reproducing animals such as cetaceans are expected to have MNPLs, expressed as fractions of K , above 0.5 (Eberhardt & Siniff 1977, Fowler 1981, 1984). Although MNPL cannot be determined precisely for these populations, our analysis allowed us to integrate across considerable uncertainty in this parameter, and both populations were estimated to be depleted regardless of the value of MNPL. Our analyses show that there is little uncertainty in whether either population was depleted in 2002 relative to their initial abundance. In general, our results show that the abundance of northeastern offshore spotted dolphins was reduced to about one-fifth, and eastern spinner dolphins to about one-third, of their pre-fishery levels (Fig. 1, Table 3). Our results are consistent with those of previous workers who used various other population-dynamics models and showed that both stocks were reduced to similar fractions of their historical abundances (Wade 1993, 1994, 1999, Alvarez-Flores 2002, Hoyle & Maunder 2004).

There is an important caveat associated with assessing the status of these stocks. Reference points like those defined in the MMPA provide no guidance on which carrying capacity should be used to assess whether a stock is depleted, and in the analyses presented here we acknowledge the possibility that K may have changed. In fact, the 2- K models for both northeastern offshore spotted and eastern spinner dolphins were as well supported as their respective reference models. Thus, we temper our general conclusions by admitting that there is a small probability that, relative to their respective estimates of K_2 , neither stock was depleted in 2002. Nevertheless, even if these alternative reference points are adopted, there is substantially greater probability that neither stock had recovered.

Next, we consider whether the 2 dolphin stocks could have been recovering in 2002. Accepting that both populations were well below their estimated carrying capacities and that the number of dolphins killed in the fishery is small relative to the abundance of each stock ($< 0.1\%$ for both), we expect both stocks to be recovering at or near their maximum population growth rates, r . We estimated $r > 0$ with all of the models that had a single maximum growth rate. While this is hardly surprising, given our prior distributions for r , our posterior distributions indicated that there was high probability that both stocks were recovering at rates less than $4\% \text{ yr}^{-1}$, an accepted minimum default for dolphin populations with reproductive parameters (e.g. calving intervals) like those considered here (Reilly & Barlow 1986, Wade 1998). Additionally, there was considerable probability that both stocks were recovering at rates less than $3\% \text{ yr}^{-1}$. We estimated median recovery rates of 1.7 and $1.4\% \text{ yr}^{-1}$ for northeastern offshore spotted and eastern spinner dolphins, respectively; we also estimated the probability that each recovery rate was $< 3\% \text{ yr}^{-1}$ as 0.83 and 0.77 , respectively. We do not know whether such low intrinsic growth rates are natural for these species or whether the low rates are due to other factors impeding the recovery of these stocks. The alternative models considered here were intended to shed light on this central question.

Results from the 2- r models indicate uncertainty in the degree to which each stock was recovering. These

models acknowledge the possibility that the contemporary (as of 2002) dynamics of northeastern offshore spotted and eastern spinner dolphins are different than their historical dynamics. For the eastern spinner stock, contemporary growth rates (r_2) seem likely to be less than historical growth rates (r_1) and 'overall' growth rates (i.e. the rates estimated by models with a single r). With the 2- r models, we estimated approximately 50-50 odds (equal chances) that northeastern offshore spotted dolphins were recently growing or declining and 70-30 odds that eastern spinner dolphins were recently declining. We cannot discount these results, because the Bayes factors indicate that both of the 2- r models received about as much support as their respective reference models. Thus, we conclude that there is substantial uncertainty about whether either population was recovering in 2002. Our conclusion is consistent with those of Lennert-Cody et al. (2001) and Gerrodette & Forcada (2005), who respectively analyzed abundance estimates derived from fishing- and research-vessel data and concluded that neither stock was recovering at expected rates.

Causative factors for lack of recovery

Our results were equivocal with respect to attributing the apparent lack of recovery of northeastern off-

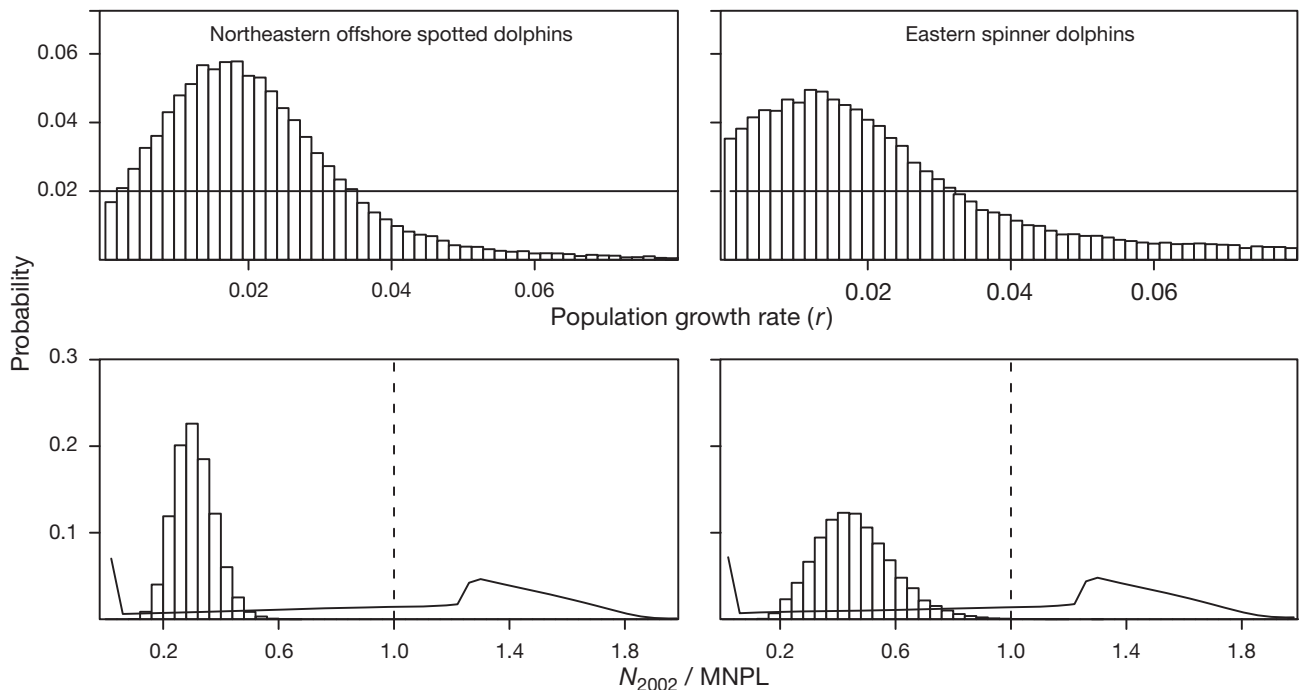


Fig. 5. *Stenella attenuata attenuata* and *S. longirostris orientalis*. Model-averaged posterior distributions for r (the maximum population growth rate parameter) and for N_{2002}/MNPL (maximum net productivity level), the estimated depletion level relative to MNPL. Model-averages were calculated using r_1 and MNPL referenced to K_1 (carrying capacity), respectively. Prior distribution is plotted as a line and the posterior distribution is plotted as a histogram

shore spotted and eastern spinner dolphins to one or more causative factors. The Bayes factors indicated that hypothetical effects from the fishery and the ecosystem are equally supported. Our exploration of alternative hypotheses for the lack of recovery has not, however, been comprehensive, and other workers have identified potential and definitive fishery effects, while ecosystem effects have been elusive. We summarize this literature here and briefly discuss the strengths and weaknesses of our analytical approach.

A summary of recent research (Reilly et al. 2005) clearly illustrates that the purse-seine fishery has the capacity to affect dolphins beyond the direct mortality observed as bycatches. Chase and encirclement by purse-seine vessels and their speedboats may (1) cause changes in tissue chemistry that are associated with stress (Dizon et al. 2002, Southern et al. 2002, St. Aubin 2002), (2) elevate body temperatures and physically damage organ systems (Cowan & Curry 2002, Pabst et al. 2002, St. Aubin 2002), (3) increase bioenergetic demands (Weihs 2004, Edwards 2006), and (4) influence swimming and schooling dynamics and behavior (Chivers & Scott 2002, Mesnick et al. 2002, Santurtún & Galindo 2002). While these physiological and behavioral changes may affect some individuals, they have not been shown to be common enough to have population-level consequences.

On the other hand, observations of mother–calf separation (Archer et al. 2001), declines in the numbers of calves (K. Cramer, W. Perryman, T. Gerrodette unpubl. data), and high fetal mortality (Perrin 1968) are population-level effects that directly address the lack of recovery. The calf deficits estimated from cows that were killed without their calves indicate minimum levels of additional mortality (about 14% yr⁻¹) not included in Table 1 (Archer et al. 2004). Reduced swimming ability and stamina of dolphin calves make mother-calf separation during fishing activity more likely, particularly during the first 6 mo of life (Edwards 2006, Noren & Edwards 2007); the implication is that the cryptic loss of calves could be much larger. The proportion of calves declined between 1993 and 2003 for both northeastern offshore spotted and eastern spinner dolphins (K. Cramer, W. Perryman, T. Gerrodette unpubl. data). In the case of spotted dolphins, the number of dolphin sets negatively affected both the proportion of calves in the population and the length of time calves remained with their mothers. Fetal mortality in these dolphin populations is higher than in other mammals (Perrin 1968), but whether this is natural or due to effects of chase and encirclement is not yet known. Ultimately, although the studies identified here demonstrate both potential and definitive fishery effects, we do not know the degree to which these effects are having cumulative impacts on either

dolphin stock. It is also clear that, over the past 5 or 6 decades during which the purse-seine fishery has operated, there have been changes in the structure of the pelagic ecosystem in the ETP, but these changes have not been linked to the lack of recovery by either dolphin stock. Changes in the physical and ecological environment of the ETP have been documented in (1) oceanography and climate (Fiedler 2002, McPhaden & Zhang 2002, 2004), (2) plankton community structure and dynamics (Bidigare & Ondrusek 1996, Landry et al. 1996), and (3) the abundances of other animals at middle and upper trophic levels (Ballance et al. 2002, Pitman et al. 2002, Watters et al. 2003, Hinke et al. 2004). Fiedler (2002) summarizes the findings of many other workers who have documented changes in the ETP. In general these changes have not been linked to the dynamics of northeastern offshore spotted and eastern spinner dolphins, because temporal variations in these ecosystem variables largely occur at El Niño scales, and to some degree at decadal scales, while this is not the case for temporal variations in dolphin abundance. Variations in dolphin abundance have, since the 1960s, primarily been driven by variations in the direct mortality caused by the purse-seine fishery. Nevertheless, the basic principles of ecology tell us that the physical and ecological environment ultimately determines how many dolphins can be supported by the pelagic ecosystem. For example, Watters et al. (2003) predict that a long-term, declining trend in the biomass of large phytoplankton (e.g. diatoms) in the ETP will cause the biomass of dolphins to decline regardless of potential fishery effects. Despite an inability to identify ecosystem effects on the recovery of either dolphin stock, this possibility cannot be dismissed.

We used an analytical approach that provides a logical framework for evaluating the competing hypotheses that attempt to explain the apparent lack of recovery by dolphin stocks in the ETP; this framework has at least 2 strengths. First, we used the same set of data to evaluate competing hypotheses (fishery versus ecosystem effects); this is not always feasible when a study is focused on considering a specific mechanism that might lead to an effect. Relying on a common data set leads to a more balanced competition between the hypotheses. A balanced treatment of alternative hypotheses in this case will not necessarily attribute delayed recovery to candidate causative factors with increased certainty, but such treatment may help temper inferences made from the competition of alternative hypotheses. For example, it would seem inappropriate to infer that fishery effects are solely responsible for a lack of recovery if 5 specific fishery effects have been in competition with only one ecosystem effect; equal weight would not have been given to the competing hypotheses. A second strength of our approach

is that we are able to directly consider fishery and ecosystem effects at the population level (rather than, say, identify effects on individuals and forecast how these might accumulate to have population-level consequences). This is important because management decisions are often based on population-level responses, and making inferential leaps from individual-level effects to population-level responses can conceivably introduce additional error into the management process.

Our approach has at least 2 weaknesses. First, mortality and abundance estimates may simply not contain sufficient information to resolve the competition between hypotheses representing potential fishery and ecosystem effects, especially if there is insufficient contrast between the effects. This appears to be the case here; the Bayes factors provided roughly equal support to both categories of hypothesis. This weakness suggests that it might be useful to move towards 'integrated models' (e.g. Hoyle & Maunder 2004) that synthesize information from other data sources. We are, however, uncertain whether such models, which are generally more complex than those used here, are better able to attribute a lack of recovery to causative factors because this ability will depend critically on the information content of the newly synthesized data. We have already mentioned the second weakness of our approach. Our generalized logistic models suggest feasible categories of effects, but these models do not explicitly describe the mechanisms that may make such effects operative. Identifying and understanding mechanisms is important because actions taken to mitigate broad categories of effects may be overly restrictive.

Definition of dolphin-safe tuna and its implications for ecosystem-based management of the fishery

The dolphin-safe label is a tuna-product labeling standard that was initially developed by environmental groups and tuna canners in the USA as a response to public concern over dolphin mortality in this fishery. It is intended to inform consumers that tuna products have been produced in an environmentally friendly and ecologically responsible way. Eco-labels are successfully used to market a diverse spectrum of other consumer goods, including such things as lumber, household cleaning products, cosmetics, packaging materials, and fuel. In 1990, the USA Dolphin Protection Consumer Information Act² legally defined dolphin-safe products to be those made from tunas cap-

tured in the ETP during fishing trips on which no sets were made on dolphin schools. In 1997, however, passage of the USA International Dolphin Conservation Program Act (IDCPA)³ raised the question of whether a less stringent definition of the labeling standard would be appropriate, where tuna caught by chasing and encircling dolphins could be called dolphin-safe as long as no dolphins were observed to be killed or seriously injured during an individual set. Given that directly observed mortality has been reduced to a low level relative to dolphin population size, the central issue in redefining dolphin-safe is whether the process of chasing, encircling, holding, and then releasing dolphins is harmful to the population. There is no question that chasing and encircling dolphins affects some individual dolphins negatively. The question posed in the IDCPA, however, was whether the effects on survival and reproduction are sufficiently strong to affect the population as a whole.

On December 31, 2002, the USA Secretary of Commerce determined that catching yellowfin tuna by chasing and encircling dolphins does not have a 'significant adverse impact' on the dolphin stocks considered here. The decision was challenged and overturned; the court found that the decision was based on political considerations more than science. In the USA, therefore, the original definition of dolphin-safe has been retained: tuna caught by methods that do not involve the chase and encirclement of dolphins. From the viewpoint of dolphin conservation, retaining this more conservative definition is clearly the most precautionary approach consistent with available data.

Dolphins are, however, only part of the larger ETP ecosystem. Other methods of fishing for tuna in the ETP result in bycatches of bony fishes, sharks, and turtles, but rarely dolphins (Hall 1998). In the developing paradigm of ecosystem-based fisheries management, framing conservation issues in the context of a 'significant adverse impact' on a single species (or 2 in this case) will not be sufficient. Revising the dolphin-safe definition in light of the ecosystem approach to management will likely require consideration of issues beyond the topic of dolphin recovery to more expansive, system-wide views of the potential ecological, social, and economic effects of regulatory and consumer marketing actions. Actions that change the allocation of fishing effort among the 3 types of purse-seine sets (sets on dolphins, floating objects, or unassociated schools of tuna) or that change the allocation of fishing effort among the purse-seine and long-line fleets will involve complex tradeoffs (Hinke et al. 2004).

²Public Law 101-627, 28 November 1990, 16 U.S.C. § 1385

³Public Law 105-42, 15 August 1997, 16 U.S.C. § 1361

Acknowledgements. We thank D. Goodman, W. Perrin, M. Haddon, and M. McAllister for providing critical reviews of our analytical approach and provoking thoughtful discussion of our conclusions. We also thank W. Perrin for a helpful review of this manuscript, as well as helpful reviews from anonymous reviewers.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: July 4, 2006; Accepted: May 30, 2007
Proofs received from author(s): June 26, 2007*