



Fisheries New Zealand

Tini a Tangaroa

**Population dynamic modelling of the Māui dolphin
based on genotype capture-recapture with
projections involving bycatch and disease risk**

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Executive Summary

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The Māui dolphin (*Cephalorhynchus hectori maui*) is endemic to the west coast of the North Island of New Zealand and is listed by IUCN as Critically Endangered. In this project an individual-based population model was fitted to genetic identification data collected during the period 2001 to 2016 from both living and beachcast or entangled animals (Baker et al. 2016). Data on cause of death from the Department of Conservation website and for three individuals necropsied by Roe et al. (2013) were also used. The model fits were used to provide estimates of recent population size and trend, and to project the population into the future under a range of mitigation scenarios.

In the absence of assumptions regarding the natural growth rate or anthropogenic threats, the best-fitting model involved no individual heterogeneity and no sex difference in survival or sampling probability and indicates a population declining at the rate of 3–4% per year over the period 2001–16. The estimated population trajectory was insensitive to the assumed age at first reproduction. The results imply that approximately 10% of Māui dolphin deaths occurring in this period were recovered.

Additional model runs were performed combining four sets of assumptions estimating the effects of commercial fisheries bycatch and/or other anthropogenic sources of death. Estimates of annual commercial fisheries death (hereafter ‘bycatch’¹) rates were generated externally, based on outputs of the spatially explicit multi-threat risk assessment described in Roberts et al. (2019). That assessment applied a spatially explicit Bayesian model fitted simultaneously to all commercial fisheries effort and fisheries observer data across the full geographic range of Hector’s dolphins (of which Māui dolphins are a subspecies); that external model estimated approximately 0.12 commercial fisheries deaths per year for Māui dolphins in the last five years. For runs including non-fisheries threats, non-fishery deaths were estimated directly in the current model, fitting to necropsy data and mark-recapture data for Māui dolphins only.

The first set of model runs (Group A) assumed that the time series of bycatch risk estimated in Roberts et al. (2019) is accurate, and that commercial fisheries are the only anthropogenic threat to the dolphins. These runs imply that if the population is not already near carrying capacity, then the population should be increasing, but the fit to the data is poor. Use of a lower value for the natural growth rate r_0 , instead of an externally derived prior from Edwards et al. (2018), improves the fit only slightly.

A second set of model runs (Group B) again assumes that commercial fisheries are the only anthropogenic threat affecting the dolphins, but this time treats the annual time series of fisheries risk by Roberts et al. (2019) as a relative index only -- i.e. the inter-annual pattern is considered accurate

¹ In this paper the term ‘bycatch’ is used in the broad sense referring to all dolphin deaths arising from direct interaction between dolphins and commercial fishing gear, including deaths in which carcasses drop out of nets or are otherwise lost in ways that make them undetectable by fisheries observers (termed ‘cryptic mortality’). In contrast, the risk assessment from which these estimates arise distinguishes between observable fisheries ‘captures’ (alive or dead) and ‘fisheries related deaths’ which excludes live released animals that survive but includes cryptic deaths. That is, ‘bycatch’ in this paper is equivalent to ‘fisheries related death’ in the SEFRA risk assessments referenced herein.

but the absolute magnitude of fisheries risk is unconstrained. Under these runs the absolute fisheries risk is estimated to be 15–20 times higher than was estimated by Roberts et al. (2019), (with a mean of 1.5–2.4 commercial fisheries deaths per year in the last five years, down from 3–6 per year in the early 2000s). Model fits are substantially improved. However, the plausibility of such a high fisheries risk is doubtful, in the absence of *a priori* reasons to expect that the catchability per encounter with fishing effort would be higher for Māui dolphins than for Hector's. These runs project that the population has declined due to historical bycatch and will continue to decline if commercial fisheries deaths continue at this level. A reduction in fisheries risk of 50% relative to the 2016 level would be just enough to stop the decline, unless the lower r_0 is assumed. A reduction of 75% would be sufficient in all the cases considered.

A third set of model runs (Group C) assumes that the time series of fisheries risk estimated in Roberts et al. (2019) is accurate and that the death rate from other (unspecified) anthropogenic threats has been constant over time. These runs estimate that approximately 2.8 – 4.1 annual deaths from non-fisheries anthropogenic threats are required in order to fit the historical population trajectory; model fits are better than under the first set of runs but worse than under the second set.

A fourth set of runs (Group D) were fitted to limited data on deaths attributable to the parasite *Toxoplasma gondii* (which was the diagnosed cause of death for two out of three Māui dolphin carcasses examined for this disease); outputs suggest that toxoplasmosis may account for all of the unexplained anthropogenic mortality (i.e. 2.8 – 4.1 deaths per year, comparable to Group C runs above). Under these runs, if toxoplasmosis (or other non-fisheries) risk remains at the estimated level, the population is predicted to decline towards extinction. A reduction of anthropogenic risk by 50% per decade beginning in 2030 would reduce the probability of extinction, while a reduction of the anthropogenic risk at the rate of 50% per 5 years beginning in 2025 would virtually eliminate the likelihood of extinction.

1. INTRODUCTION

The Māui dolphin (*Cephalorhynchus hectori maui*) (Baker et al. 2002) is endemic to the west coast of the North Island of New Zealand and is listed by IUCN as Critically Endangered (Reeves et al. 2013). It has been subject to incidental catches in fishing operations (Davies et al. 2008). Since 2001, the population size of Māui dolphin has been estimated using genotype capture-recapture (Baker et al. 2013, Hamner et al. 2014, Cooke et al. 2018). These analyses yield estimates of population size that are more precise but broadly consistent with estimates obtained from transect surveys (MPI and DoC, 2015).

A previous risk assessment (Currey et al. 2012) estimated that Māui dolphins were very likely to continue to decline (more than 95% probability), based on the judgment of an expert panel who, using a Delphi approach, estimated mortalities from a range of anthropogenic threats totalling approximately 5 individuals per year. The expert panel cited in Currey et al. considered that fishing-related impacts accounted for about 95% of the total anthropogenic impact on Māui dolphins. However, subsequent empirical estimation of annual deaths from commercial fisheries, combining spatial dolphin density estimates with fishing effort data and observed capture rates in a spatially explicit fisheries risk assessment (SEFRA) model fitted at the species level (Roberts et al. 2019; method framework as described in Sharp 2018) suggests that commercial fisheries bycatch rates are much lower. Furthermore, the diagnosis of haemorrhagic lesions caused by *Toxoplasma gondii* as the cause of death for two of three Māui carcasses examined (Roe et al. 2013) provides a potential alternative explanation for population decline.

This analysis uses the genotype capture-recapture records reported in Baker et al. (2013), augmented by more recent surveys extending the records to 2016 (Baker et al. 2016), to estimate population trajectories under various scenarios and to thereby to obtain estimates of the reduction in anthropogenic mortality that would be required to avoid extinction and allow recovery of the population.

Individual-based models have previously been used to investigate the expected effects of differing levels of fishing effort restrictions on the likelihood of survival and recovery of the Māui dolphin population (Slooten 2015). Individual-based models are the preferred approach to interpreting data and making population projections for populations which are so small that individual birth and mortality events can affect the chances of population survival. They are also well suited to fitting individual encounter histories such as those derived from genetic identification data, and to estimating the effects of threats for which threat intensities may vary on an annual basis. In this analysis, the likelihood function of the individual identification data is used in a Bayesian framework such that all probability estimates regarding the past, current and future status of the population are conditional on the observed individual data.

Externally derived priors were available for this analysis for the intrinsic growth rate r_0 (Edwards et al. 2018) and for the estimated annual time series of bycatch death rates (from Roberts et al. 2019), the sensitivity to which was examined.

2. Methods

2.1 DATA

2.1.1 Genotype capture-recapture data

Annual genotype capture-recapture records, with sex identification, were reported for the years 2001 to 2016 by Baker et al. (2016). The data consist of 239 samples collected from 115 individuals (65 females and 50 males) identified genetically as *Cephalorhynchus hectori maui* after removing those samples identified as *C.h. hectori* using the criteria specified by Hamner et al. (2014). Of this total, 225 samples

were from live biopsies collected during small-vessel surveys in 2001–04, 2006, 2010–11, and 2015–16. The remaining 14 samples were from entangled and beachcast specimens reported to the Department of Conservation. The live biopsy procedure avoided sampling calves of the year. Details of the molecular methods for DNA profiling are found in Hamner et al. (2014) and details of the small-vessel surveys are found in Oremus et al. (2012) and Baker et al. (2016).

Most of the samples were collected in summer (Jan–Mar) plus a few at other times of year. For the purpose of allocating samples to years, austral split years were used: e.g. 2004 refers to samples collected between July 1 2003 and June 30 2004. There were a total of 185 annual samples from 115 individuals, after eliminating within-season duplicates. The sample sizes by year are listed in Table 1.

Table 1: Summary of biopsied animals and carcasses.

Year	Live biopsy	Carcasses	Among carcasses				of which	
			Neonates	Found in net	other bycatch	Other/unknown	Examined for toxo	Toxo death
2001	21	2			1	1		
2002	3	4		2	1	1		
2003	19	1				1		
2004	8							
2006	5							
2007		4	2			2	1	1
2008		1				1	1	
2010	24	(1)				(1)		
2011	26	1				1	1	1
2012		(1)		(1)				
2014		1				1		
2015	38							
2016	27							
Total	171	14(+2)	2	2+(1)	2	8+(1)	3	2

(No genotype was available for the 2010 and 2012 carcasses)

Note. An individual sampled multiple times within the same season is counted only once.

2.1.2 Cause of death

The cause of death for the carcasses sampled during 2001–16 was obtained from www.doc.govt.nz/our-work/hectors-and-Māui-dolphin-incident-database (DoC 2019) supplemented by necropsy results for three individuals examined by Roe et al. (2013). The resulting cause of death assessments for those animals are listed in Table 1. Genotypes were unavailable for two carcasses that were observed not secured (and which would, therefore, not necessarily have been identified genetically as *C. h. maui*). Five animals were judged to have died from entanglement but only three of these were actually found in a net, of which two were in recreational setnets and one was reported by a commercial setnet fisher (not a fisheries observer)².

² Because fisher non-reporting rates are unknown, only captures observed by fisheries observers are used to inform estimates of commercial fisheries risk in the empirical SEFRA method applied by Roberts *et al.* (2019).

2.2 MODELS

2.2.1 Demographic model

Stage structure

The demographic model is an age-structured state-space model as shown in Figure 1. The state of the population in each year is defined by the number of animals in each of the states.

The time step for the model is 1 year. Population numbers refer nominally to the start of the summer season, i.e. the aged 1+ population in 2016 refers to animals alive on Jan 1, 2016 that were born in spring/summer 2014/15 or earlier.

The adult female population is divided each year into those which produce a calf in the current year (calving), and those which do not (pregnant or resting females). Following Slooten & Lad (1991) a minimum interval of two years is assumed between calvings by the same reproductive female. Following each calving, the individual transitions back to the pregnant/resting stage. The next transition to the calving stage occurs with a probability determined by the parameters of the model.

In order to avoid having to consider calf mortality rates, the calving state includes only successful calvings (in which the calf survives at least to the following year), so that calves that die in their first year are not included in the model. Unsuccessful calvings are subsumed into the pregnant/resting state. This implies that the data on the two sampled dead neonates were not used. The transition probability from the pregnant/resting state to the calving state represents the probability of a successful calving. There is no explicit maximum age in the model: the average longevity is determined by the survival rate.

There are a total of 15 living states in the base model: calves of the year (male or female); subadults in age classes 1–5 (male or female); adult males (aged 6+); adult females in a resting or unsuccessful calving year; and adult females in a successful calving year. All the living states are subject to mortality, except for the calves, for which the mortality rate is subsumed into the calf production rate. In addition, there are up to 6 carcass states, 3 for each sex: bycatch deaths; deaths by toxoplasmosis (when this is included in the model); and “natural” deaths. Each individual in a carcass state transitions the following year to a permanent “gone” state where it is no longer observable.

The minimum age at first calving allowed in the base model is 7 years, because a female must pass through age classes 1 through 5, and the pregnant/resting state, before entering the calving state. As a sensitivity test, trajectories were also computed with ages at first calving (i.e. age at first reproduction, AFR) set at 5 years (by dropping age classes 4 and 5) or 9 years (by adding age classes 6 and 7).

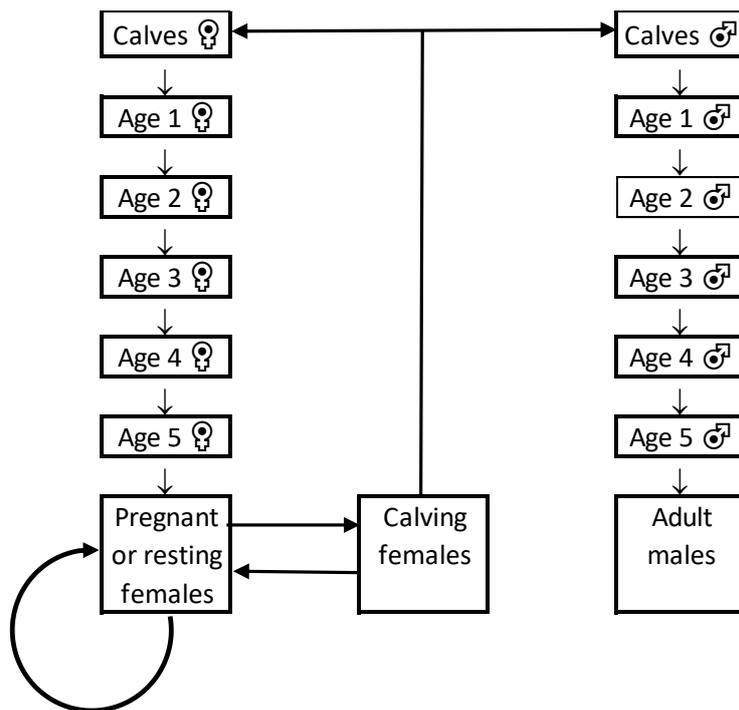


Figure 1: Stage-structured population model.

Parameters of the base model

The basic model has three parameters: a survival rate, a calving rate and a population size in a reference year. The calving rate parameter is the transition probability from the pregnant/resting state to the calving state, conditional on survival.

For the purpose of generating Bayesian posteriors of population trajectories, uninformative (Jeffreys) priors were used for the survival rate and calving rate. The prior distribution for the population size was scale-invariant (uniform on the log-scale) so that the posterior distribution of the population size in any year is independent of the choice of reference year.

A variant of the model included a sex-specific survival rate: this was implemented by adding a normally distributed random sex effect to the log odds ratio of the survival rate. The model parameters and their priors are listed in Table 2.

Maximum growth rate (r_0)

In the base case, the value of r_0 – the maximum (current) population growth rate in the absence of (additional) anthropogenic impacts and density-dependent effects – was in effect a free parameter, being determined by the other parameters of the model for which maximum likelihood estimates or uninformative priors were used. In some of the fits, an external prior was specified for r_0 in which r_0 is analogous to r_{\max} , i.e. where anthropogenic and density-dependent effects are assumed to be zero. In these cases, the prior for the survival rate was not used: the survival rate was instead that function of r_0 and the remaining parameters that yields an expected population growth rate of r_0 at low population size in the absence of anthropogenic effects.

Most of the fits used a prior for r_0 corresponding to the r_{\max} prior estimated by Edwards et al. (2018), i.e. normally distributed as $N(0.0449, 0.0107)$. This was based primarily on applying an inter-specific life history relationship between growth rate and age at first reproduction (as in Dillingham et al. 2016) and adjusting for small-population allee effects (described in Roberts et al. 2019).

However, there are reasons to doubt whether a high r_0 is likely for Māui's dolphin. The value of r_0 is a function not only of the species but also of its habitat. In principle, the edge of the natural range of a species is defined by the $r_0 = 0$ contour (Caughley et al. 1988). Thus, populations near the edge of the range tend to have a lower r_0 , and lower population density at K (carrying capacity) than populations within the core range. The actual picture can be more complex, because of environmental variability and the movement of animals, but the basic principle applies. Māui dolphins are the northernmost extant population of *C. hectori*, in a location where the abundance of suitable fish prey is estimated to be up to an order of magnitude lower than occurs in the core range for Hector's dolphins (Roberts et al. 2019). If this represents the extreme of the natural range of the species, then r_0 for Māui is likely to be below the average for populations of this species. Consequently, as a sensitivity test, runs were also conducted with r_0 set to 0.02. This particular value is arbitrary, but is close to the value of 0.018 estimated by Slooten & Lad (1991).

It is important to distinguish between r_0 , (which reflects species biology and habitat), and r_{max} which is an inherent species property irrespective of habitat effects. A situation in which r_0 is suppressed due to suboptimal habitat is not analogous to a situation where r_{max} is unchanged but K is reduced such that density dependence can be expected to reduce reproductive performance at a much lower population size. The point is illustrated schematically in Figure 2. In an optimal habitat, $r_0 = r_{max}$, in a suboptimal habitat, $r_0 < r_{max}$ and generally the population density at K would be lower than for an optimal habitat of similar size. The combination of high r_0 and low K could theoretically occur in a habitat that is of optimal quality, but small. Otherwise, the combination of a high r_0 and low K would imply that the presence of a small number of animals can cause strong density-dependent effects: this would seem unlikely in an odontocete which probably has a flexible diet.

Sensitivity runs with $K=250$ and $K=500$ animals were included in the analysis, both of which are sufficiently higher than current N to allow rapid initial population growth. The actual carrying capacity of the Māui dolphin habitat is unknown.

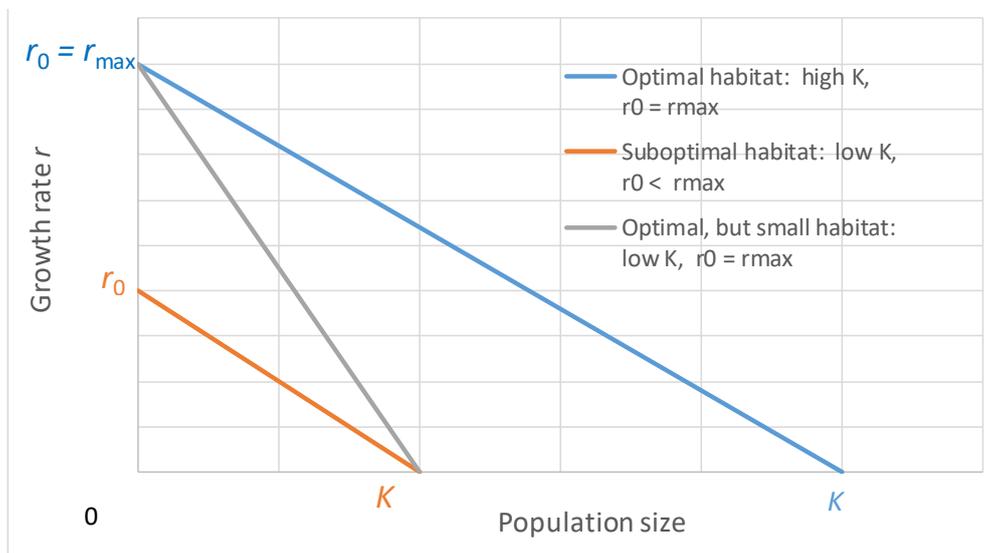


Figure 2: Growth rate vs population size for different habitats (schematic).

Density dependence

In runs that incorporate density-dependent effects, the successful calving rate was modelled as a logistic function of population size:

$$\rho = \frac{\exp(\zeta)}{1 + \exp(\zeta)}$$

where $\zeta = \zeta_0 - \alpha P/K$. P is the aged 1+ population size. The parameters ζ_0 and α are chosen so that the expected population growth rate r is equal to r_0 when $P = 0$ and to zero when $P = K$.

Values for K of 250 and 500 animals were considered. In view of the lack of quantitative information on the level of fishing and other anthropogenic mortality prior to 1992, no attempt was made to determine when in the past the population may have been near K . In fits without density dependence, the population was assumed to be at a low fraction of K such that $r = r_0$. The parameter K of this model represents the population size at which the net rate of increase, in the absence of anthropogenic factors, is zero. It will not be exactly equal to the mean equilibrium population size in the absence of anthropogenic effects.

2.2.2 Anthropogenic effects

Up to three types of anthropogenic effect were considered: (i) commercial fisheries bycatch; (ii) an unknown source of additional mortality; (iii) mortality due to toxoplasmosis.

Commercial fisheries bycatch

A time series of bycatch risk for Māui dolphins in commercial fisheries was estimated by Roberts et al. (2019) and supplied as a posterior distribution of time-varying annual fisheries exploitation rates for 1992–2016 (Figure 3). The bycatch risk represents the expected annual exploitation rate, i.e. the annual probability that any given individual will be killed by commercial fisheries (estimated separately for commercial setnets and for inshore trawls and subsequently combined). Recreational fisheries are not included, but may have involved significant bycatch, in particular before setnet closures were imposed in 2003.

The spatially explicit fisheries risk assessment method estimates the encounter rate between dolphins and fishing effort as a function of their spatial overlap, and estimates vulnerability (probability of capture or death per encounter) from fisheries observer data. Vulnerability is an inherent property of the species and fishing method, estimated across the full spatial domain of the assessment (including Hector’s dolphins, of which the Maui dolphin population is a subspecies), for each distinct gear type or fishing method (i.e. in this instance once for setnets and once for inshore trawl fisheries). The combined risk level for Māui dolphins is estimated to have declined by about 50% over the period 1992–2016 due to changes in the intensity and spatial distribution of fishing effort. The distribution of the absolute rates about the annual mean was close to lognormal with a CV of 0.42. The CV of the relative annual rates was negligible by comparison. Therefore, the time series was approximated by a deterministic relative index multiplied by a lognormal scaling factor with a CV of 0.42.

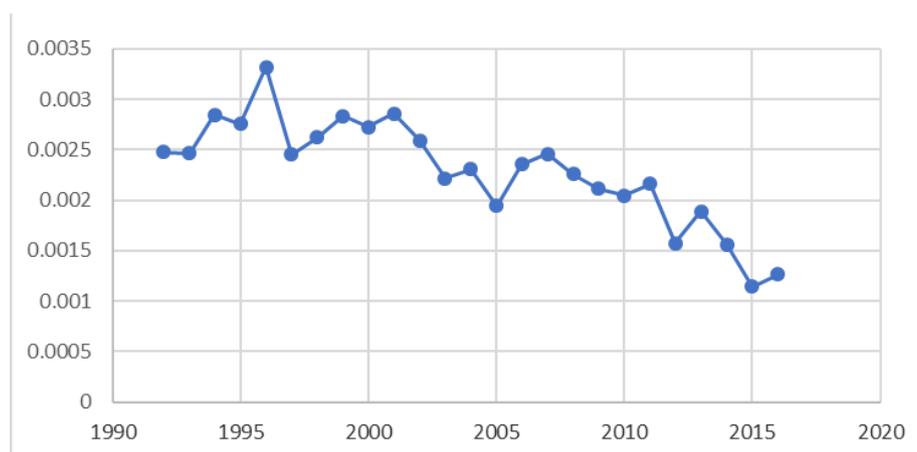


Figure 3: Maui dolphin bycatch mortality rate in commercial fisheries in 1992–2015.

The bycatch mortality time series was used in two ways in different sets of model runs: (i) as an estimate of the absolute bycatch mortality rate; and (ii) as an estimate of a relative rate, multiplied by an unknown proportionality constant. In the latter case the lognormally distributed scaling factor with a CV of 0.42 was replaced by a free parameter. The implication of the latter assumption is that annual time series of overlap (hence encounter rate) between dolphins and fishing effort is estimated accurately as a consequence of changing fishing effort patterns over time, but that the absolute catchability of Maui dolphins per encounter

may differ from the estimated value. A difference between the inherent catchabilities of Māui and Hector's dolphins would be one possible cause for the catchability to deviate from the estimated value, but there are no obvious *a priori* grounds to expect a substantial difference between the subspecies.

In model projections the commercial fisheries risk was assumed to remain at the 2016 rate during the period 2017 to 2019. For the period 2020 onwards, projections were made on the alternative assumptions: (a) fisheries risk continues at the 2016 rate; (b) all fisheries deaths stop from 2020. For those cases where commercial fisheries had an appreciable impact on the population dynamics, two intermediate scenarios were also run: (c) fisheries risk reduced by 50% from 2020; (d) fisheries risk reduced by 75% from 2020.

Additional anthropogenic mortality

In a third set of model runs, the fisheries time series was imposed and a constant rate of additional non-natural mortality of unknown cause was estimated. The additional mortality was assumed to be non-natural in the sense that the values of r_0 and K refer to a population unaffected by this impact. No mitigation scenarios were considered for this set of model runs.

Toxoplasmosis

In a fourth set of model runs, toxoplasmosis was included as a non-natural factor, in addition to the estimated fisheries risk. Toxoplasmosis mortality was modelled as a constant rate up to a given time in the future. Treatment of toxoplasmosis mortality as non-natural means that the parameters K and r_0 refer to a population free of toxoplasmosis.

In order that the data likelihood remained strictly comparable for AIC purposes between fits with and without a toxoplasmosis effect, the data on toxoplasmosis deaths were included in the likelihood in all fits, but in the fits without a toxoplasmosis effect they were considered equivalent to natural mortality. In the latter case, a parameter for the probability that a natural mortality was diagnosed as toxoplasmosis took the place of the toxoplasmosis mortality parameter. In either case an uninformative (Jeffreys) prior was used for the mortality or diagnosis parameter.

For the forward projections, four alternative mitigation scenarios were considered: (i) toxoplasmosis mortality continues at the current level; (ii) toxoplasmosis mortality is reduced beginning in 2030 by 50% per decade; (iii) toxoplasmosis mortality is reduced beginning in 2025 by 50% per 5 years; (iv) toxoplasmosis mortality is eliminated from 2020 onward.

Scenario (iv) is not realistic but was included to provide a disease-free reference trajectory relative to which progress towards management targets can be defined. Scenarios (ii) and (iii) may or may not be realistic if some means can be found to reduce the dolphins' exposure to toxoplasmosis; these runs provide an indication of how quickly the toxoplasmosis threat would need to be reduced in order to prevent extinction of the population.

2.2.3 Sampling model

In the genetic mark-recapture surveys there was a conscious effort, especially in later years, to avoid sampling the same animal multiple times within a season. Therefore, within-season recaptures were not used for this analysis; that is, multiple biopsy samples of a live individual within a year were merged and treated as a single sample without replacement. The biopsy samples were collected in certain years only, and the sample sizes were determined largely by collection effort, which was not quantified. Therefore, inference was conditional on the realized sample sizes, to eliminate the need to specify a prior for the annual sampling probabilities. The conditioning was achieved by fitting dummy parameters for the sampling intensities associated with each annual sample.

It is assumed that calves of the year were not biopsied. In the base case sampling model, each live animal aged 1 and above in the year of a biopsy sample was assumed to have an equal probability of being included in that sample at least once.

After eliminating within-season recaptures, there were 171 live biopsy samples, 2 net entanglements and 12 beachcast animals. A live biopsy followed by a dead recovery of the same individual in a season was treated as theoretically possible but in practice it did not occur. A constant detection probability over the period 2001–16 was assumed for beachcast animals. The net sample of two animals in 2002 was treated as if it were a deliberate sample. The selection of animals for necropsy by Roe et al. 2013 was assumed to be uncorrelated with the cause of death: the necropsy results were conditioned on the number of carcasses (3) selected for necropsy.

Alternative sampling models with a sex-biased sampling probability or with individual variation in the sampling probability were also considered. For sex-biased sampling a normally distributed random sex effect was added to the log-odds ratio of the sampling probability. Individual heterogeneity was modelled by treating each individual as belonging to one of three equally numerous availability classes, with a class-specific random effect added to the log-odds ratio of the sampling probability.

2.2.4 Likelihood and model fitting

The models were fitted in the first instance by maximum likelihood, and the goodness of fit evaluated using the AIC criterion. Maximum likelihood estimates and normal-theory standard deviations were obtained for each parameter, along with the maximum-likelihood population trajectories (for 2000–2020), for the aged 1+ population and for the mature female population.

The models were also fitted in a Bayesian framework, with the priors listed in Table 2. The posterior distributions of each parameter and of the population trajectories were estimated by importance sampling using 10 000 replicates for each fit. Selected percentiles of the posterior distribution were computed for each parameter and for the population size in each year. In addition, a random sample of 50 population trajectories was extracted and plotted (for the period 2000–2060) for each fit.

The WAIC (Widely Applicable Information Criterion, Watanabe 2009) was computed along with the AIC. The WAIC is a function of the full posterior distribution rather than just the point estimate. It is arguably more relevant than the AIC for evaluating model fit in a Bayesian context. However, it is less familiar to researchers than is the AIC, and its computation is subject to sampling error.

Because importance sampling results in a sample from the posterior with unequal weights, the effective sample size is lower than the nominal sample size. The realized effective sample size (i.e. the equivalent equal-weight sample size) was calculated for each fit. When this is low (e.g. less than 100), the estimated posterior distribution and the WAIC are unreliable.

The formal description of the individual-based model and the definition and method of computation of the likelihood are given by Cooke (2018).

Table 2: List of model parameters and priors.

Parameter	# of parameters	Range	Prior
Population dynamics model			
<i>Base case</i>			
Initial population size	1	>0	$\propto 1/N$
Natural survival rate	1	(0,1)	$[p(1-p)]^{-\frac{1}{2}}$ (Jeffreys prior)
Calving probability	1	(0,1)	N(0,1) on log-odds
<i>Optional parameters</i>			
<i>Sex-specific survival</i>			
factor	1	(0,1)	N(0,1) on log-odds
Toxoplasmosis mortality rate	1	(0,1)	$[p(1-p)]^{-\frac{1}{2}}$
Unknown factor mortality rate	1	(0,1)	$[p(1-p)]^{-\frac{1}{2}}$
logarithm of bycatch multiplier	1		a. N(0,0.42) b. uniform $(-\infty, \infty)$
r_0 : rate of natural increase at low population size	1	>0	a. N(0.0449,0.0106) b. = 0.02
K : environmental carrying capacity (aged 1+ population)	1	>0	a. 250 b. 500
Sampling model			
<i>Base case</i>			
Annual biopsy prob.	9	(0,1)	dummy (conditioned)
Carcass recovery prob.	1	(0,1)	$[p(1-p)]^{-\frac{1}{2}}$
<i>Optional parameters</i>			
Sex-specific sampling factor	1	(0,1)	N(0,1) on log-odds
Factor for heterogeneity strata	3	(0,1)	N(0,1) on log-odds

2.2.5 Management metrics

PBR

The Potential Biological Removal (PBR) is set for cetaceans to 2% of the lower 20%-ile of the estimated population size, times a recovery factor (Wade 1998). The recommended value for the recovery factor is 0.1 for endangered populations, and 0.5 for other populations below the OSP level (Taylor et al. 2003). Given the small size of the Māui dolphin population and the Critically Endangered status, the recovery factor of 0.1 is used here. The PBR was calculated for the austral year 2020 (i.e. the period 1.7.2019 to 30.6.2020).

PST / Relative Recovery

In the context of managing bycatch, the population sustainability threshold (PST) has been defined as that level of fisheries mortality that results in an equilibrium population size at or above a pre-defined proportion of the un-impacted population, to be achieved with a pre-defined level of certainty (Sharp 2018). The choice of population objective is a policy decision; adjusting the PST formulation to achieve the population

objective is achieved with the tuning factor ϕ . In multi-species implementations of the SEFRA method, a default ϕ value of 0.5 is often used (comparable to $F = 0.5$ in the PBR formulation). The Hector's-Māui risk assessment described in Roberts et al. (2019) uses a default ϕ of 0.2, corresponding to a median population recovery outcome to levels at or above 90% of un-impacted status. Note however, that in designing the Hector's-Māui Threat Management Plan, decision-makers may also choose different values of ϕ for different dolphin subpopulations including for Māui dolphins, reflecting different levels of precaution or urgency.

Since the formulation of the PST will depend on policy decisions not yet made, for use with the models and projections of this paper, a related metric "Relative Recovery" was used instead. In each impact scenario the population was projected 100 years into the future, and the lower 5%-ile of the population size recorded. The ratio of this to the lower 5%-ile of the population in a relevant reference scenario is defined as the Relative Recovery (RR).

An RR score of 0.5 or greater would correspond to satisfying the PST if it could be measured relative to a notional long-term equilibrium rather than an arbitrary 100 year time horizon.

If there are additional anthropogenic factors impacting the population, such as diseases of terrestrial origin, the reference scenario for the Relative Recovery can be the no-bycatch scenario in the presence of these other factors, or the scenario with both the bycatch and the other impacts eliminated. The choice may depend on whether the particular management issue relates only to managing bycatch or to the management of cumulative anthropogenic effects. Results are given here for both alternatives.

The choice to use a ratio of percentiles rather than a percentile of ratios to define the RR is based on the consideration that the relevant conservation metric should depend only on the distributions of population size in the impact and reference scenarios, and not depend on "pairing" of replicates between scenarios.

2.2.6 Candidate models and scenarios

Each run involves a model fit and, optionally, a projection scenario. The model fits are listed in Table 3 with a list of the projections run for each model fit.

- The first set of model fits (fits 1–4) involve variants of the basic model (without density-dependence and without an externally specified r_0 or r_0 prior) with a view to selecting the best-fitting variant for the subsequent runs: with and without sex-specific differences in survival rate and sampling probability, with and without individual heterogeneity in sampling probability.
- Fits 5–6 are a sensitivity test of the base model to the assumed age at first reproduction (AFR). The values tested are 7 year (base model) and 5 year and 9 year as alternative values.
- Model fits 8–9 and 11–12 examine the implications of using the external prior for r_0 (fits 8, 11) or $r_0 = 0.02$ (fits 9, 12), while treating the input bycatch risk index as either an absolute measure (fits 8–9) or relative measure (fits 11–12).
- Model fit 10 examines the effect of treating the index bycatch risk index as a relative measure (in contrast to model fit 7).
- Models fits 13–16 A-B examine the effect of incorporating density-dependence into the models used for fits 8–9 and 11–12, assuming $K = 250$ (fits 13A–16A) or $K = 500$ (fits 13B–16B).
- Fits 17–18 A-B include an additional un-identified non-natural threat (or threats) resulting in a constant rate of mortality, which is estimated as a parameter.

- Fits 19–20 A-B include toxoplasmosis mortality, estimated as a constant source of non-natural mortality.

For the models incorporating density-dependence, forward projections for 100 years were generated under differing assumptions regarding mitigation of anthropogenic threats. Long-term projections were not made for models without density dependence because this can result in unrealistic trajectories over longer time scales.

For each projected case, projections were generated for the scenarios: (a) bycatch risk continues at 2016 level; and (b) bycatch mortality is eliminated from 2020. For those cases where the level of bycatch led to an appreciable difference between scenarios (a) and (b), projections were also made for: (c) bycatch risk reduced by 50% from 2020 onward; (d) bycatch risk reduced by 75% from 2020 onward.

As noted in Section 3.2.3, four projection scenarios for toxoplasmosis were considered involving different levels of abatement of toxoplasmosis mortality over different time scales, from no abatement to complete elimination of toxoplasmosis risk by 2020.

Table 3. Fitted models and projection scenarios				
Fit no.	Fitted model	K	Bycatch scenarios	Toxoplasmosis scenarios
1	Base model (r free, no density-dependence, absolute bycatch, AFR = 6yr)			
2	base model + sex-biased sampling			
3	base model + sex-biased mortality			
4	base model + individual heterogeneity			
5	base model but AFR = 5yr			
6	base model but AFR = 9yr			
7	Base model		a. bycatch; b. no bycatch	
8	Absolute bycatch, $r = r_0$, prior for $r \sim N(0.045, 0.01)$			
9	Absolute bycatch, $r = r_0 = 0.02$			
10	Relative bycatch, r free			
11	Relative bycatch, $r = r_0$, $r \sim N(0.045, 0.01)$			
12	Relative bycatch, $r = r_0 = 0.02$			
13A	Absolute bycatch, density dependence $r_0 \sim N(0.045, 0.01)$	250	a. bycatch; b. no bycatch	
14A	Absolute bycatch, density dependence $r_0 = 0.02$	250		
15A	Relative bycatch, density dependence $r_0 \sim N(0.045, 0.01)$	250	a. bycatch; b. 50% reduction;	
16A	Relative bycatch, density dependence, $r_0 = 0.02$	250	c. 75% reduction; d. no bycatch	
17A	Absolute bycatch + additional mortality, density dep. $r_0 \sim N(0.045, 0.01)$	250	a. bycatch; b. no bycatch	
18A	Absolute bycatch + additional mortality, density dep., $r_0 = 0.02$	250		
19A	Absolute bycatch + toxoplasmosis mortality, density dep., $r_0 \sim N(0.045, 0.01)$	250	a. bycatch; b. no bycatch	Toxo mortality continues
20A	Absolute bycatch + toxoplasmosis mortality, density dep., $r_0 = 0.02$	250	c. bycatch; d. no bycatch	Toxo mortality reduced from 2030 (50%/10yr)
			e. bycatch; f. no bycatch	Toxo mortality reduced from 2025 (50%/5yr)
			g. no bycatch	Toxo mortality stopped from 2020
13B	Absolute bycatch, density dependence $r_0 \sim N(0.045, 0.01)$	500	a. bycatch; b. no bycatch	
14B	Absolute bycatch, density dependence $r_0 = 0.02$	500		
15B	Relative bycatch, density dependence $r_0 \sim N(0.045, 0.01)$	500	a. bycatch; b. 50% reduction;	
16B	Relative bycatch, density dependence, $r_0 = 0.02$	500	c. 75% reduction; d. no bycatch	
17B	Absolute bycatch + additional mortality, density dep. $r_0 \sim N(0.045, 0.01)$	500	a. bycatch; b. no bycatch	
18B	Absolute bycatch + additional mortality, density dep., $r_0 = 0.02$	500		
19B	Absolute bycatch + toxoplasmosis mortality, density dep., $r_0 \sim N(0.045, 0.01)$	500	a. bycatch; b. no bycatch	Toxo mortality continues
20B	Absolute bycatch + toxoplasmosis mortality, density dep., $r_0 = 0.02$	500	c. bycatch; d. no bycatch	Toxo mortality reduced from 2030 (50%/10yr)
			e. bycatch; f. no bycatch	Toxo mortality reduced from 2025 (50%/5yr)
			g. no bycatch	Toxo mortality stopped from 2020

3. RESULTS

3.1 Model fits

The results of each model fit, including the AIC, WAIC and values for key parameters, are listed in Table 4. Maximum likelihood trajectories of the aged 1+ population and the mature female population over the period 2000–2020, and samples of trajectories from the posterior distribution, are shown in Figs 3a–v. The mean annual number of bycatch deaths, and mean total deaths are also shown.

The runs of the basic model (without density-dependence and without an externally specified r_0 or r_0 prior) showed that there was no improvement in fit from including sex-specific differences in survival rate or capture probability, nor from including individual heterogeneity in capture probability (Table 4, model fits 1–4). The model without these factors was therefore selected as the basis for further fits. The trajectories from this model fit show a declining trend over the period 2001–2016, despite the low bycatch (Figure 4a). The estimate of r is negative.

Setting the age at first reproduction to 5 years or 9 years (fits 5–6) instead of the base case value of 7 years does not appreciably affect the fit nor the population estimates or trend.

Incorporating the external prior for r_0 , but without density dependence (i.e. assuming $r = r_0$), while applying the estimate of absolute bycatch exploitation rate from the Roberts et al. (2019) risk assessment (0.1–0.2 deaths per year), resulted in an increasing trend (Figure 4b) but a substantially worse fit (fit 8, $\Delta\text{AIC} = +7.8$). Replacing the r_0 prior with $r_0 = 0.02$ only slightly improved the fit (fit 9, $\Delta\text{AIC} = -1.7$, Figure 4c). Treating the bycatch time series as a relative index substantially improved the fit, regardless of the assumptions about r_0 (e.g. $\Delta\text{AIC} = -14.0$ for the external r_0 prior), but this fit implies that the vulnerability of Maui dolphins to fisheries bycatch is 14–20 times higher than the estimate obtained by Roberts et al. (resulting in 1.5–2.4 Maui deaths per year). The trajectories for these fits (fits 10–12, Figures 4d–f) suggest a declining population during the period 2001–2015, but possibly levelling off or beginning to recover after that.

Introducing density-dependence with $K = 250$ (fits 13A–16A) or $K = 500$ (fits 13B–16B) did not materially affect the AIC criterion or the fitted or sampled population trajectories over the period 2000–2016 (Figures 4g–n) compared with the corresponding density-independent cases (fits 8–9, 11–12, Figures 4b–c, e–f). This was because the population remained well below either assumed K value during this period. Indeed, for a given assumption about r , the AIC was virtually unaffected by the choice of $K = 250$, $K = 500$, or $K = \infty$ (the density-independent case). This means that the data have no power to discriminate between the different values of K . In each case, the fit using the relative bycatch assumption was much better than the fits using the absolute bycatch assumption (ΔAIC about -14).

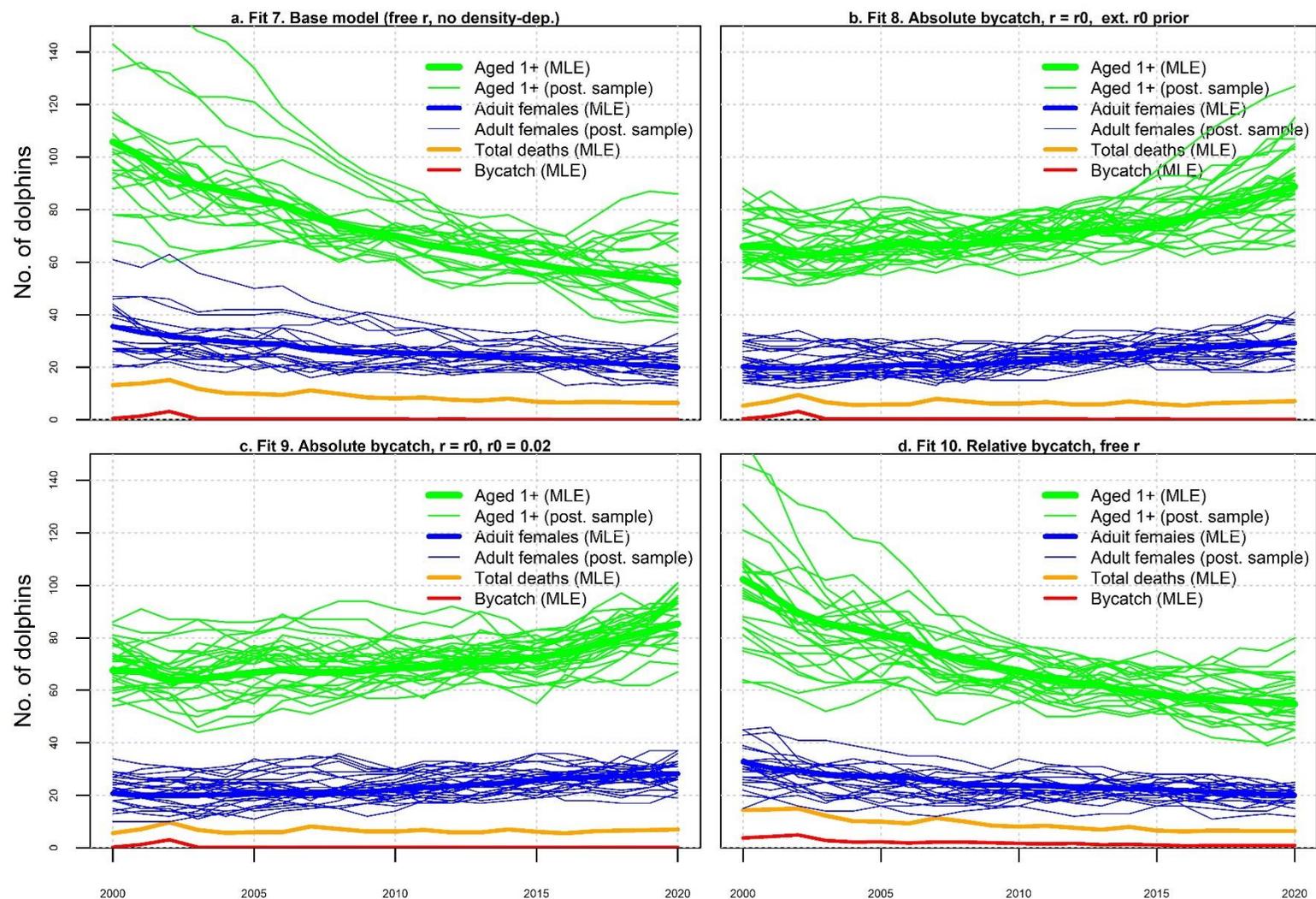
The fits of models which allow an additional level of non-natural mortality of unknown source (fits 17–18 A–B) imply that there were 2.8–4.3 additional anthropogenic deaths per year, resulting in declining trajectories similar to those for a free r or for the relative bycatch index assumption (Figures 4 o–r). Similarly, estimating mortality due to toxoplasmosis (fits 19–20 A–B) results in essentially the same number of additional deaths, and similar trajectories (Figures 4s–v) as for the fits with an unknown source of additional mortality, but a slightly better fit according to the AIC criterion (ΔAIC about -4), mainly because the latter favours explained over unexplained trends; however, the fits remain slightly worse than the fits with the relative bycatch assumption ($\Delta\text{AIC} = 2.0$ – 3.5).

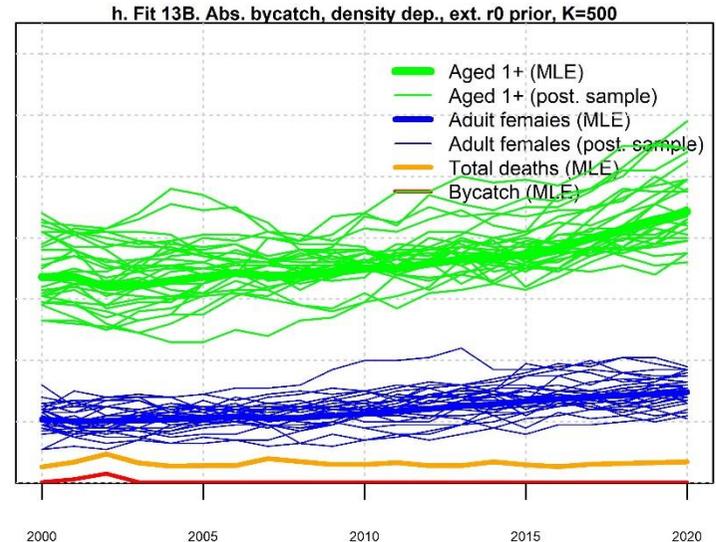
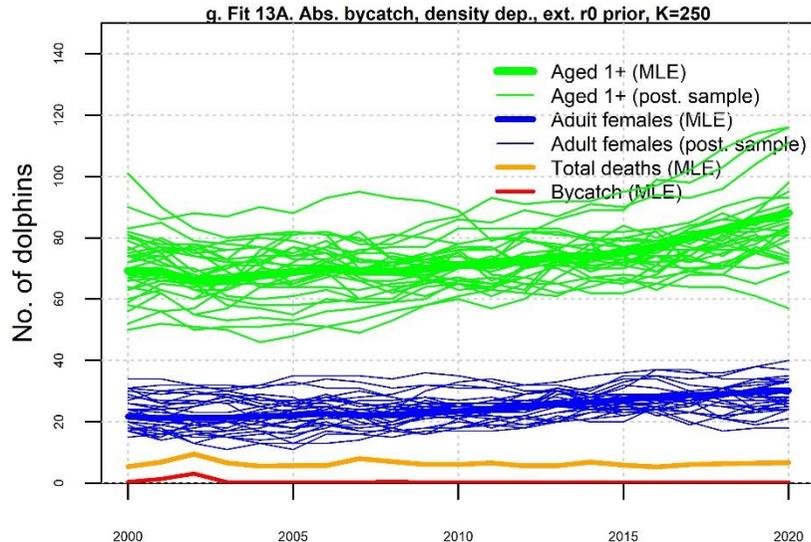
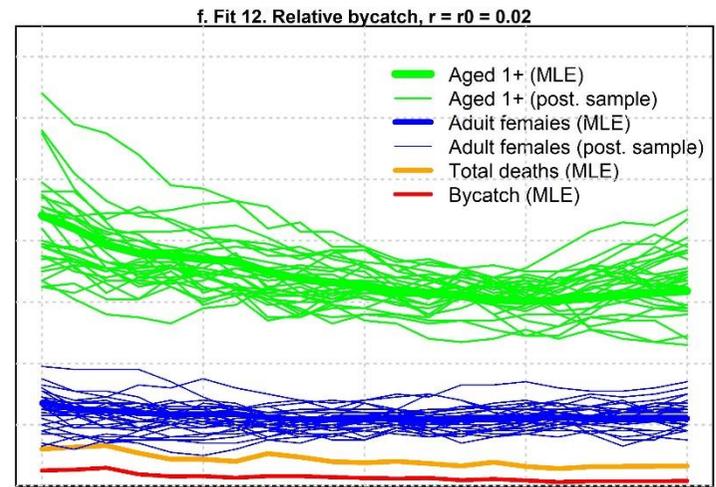
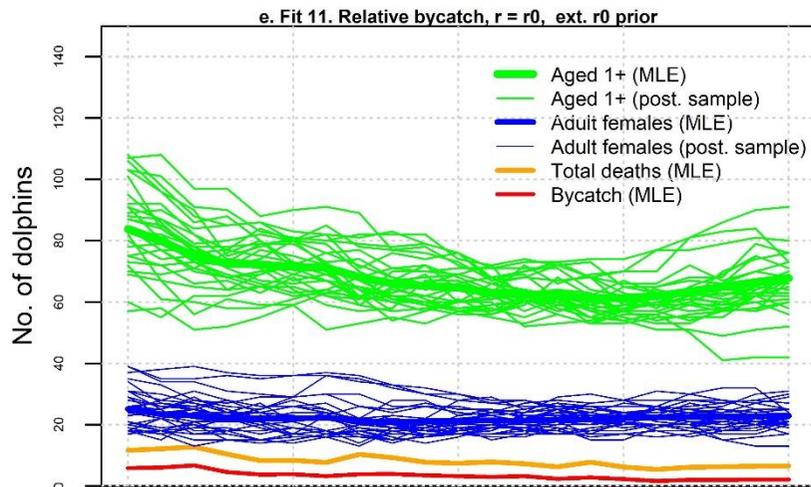
The fits that incorporate a higher level of bycatch risk or an additional source of non-natural mortality result in higher estimates of the natural survival rate, because the estimates of total mortality rate are largely data-driven.

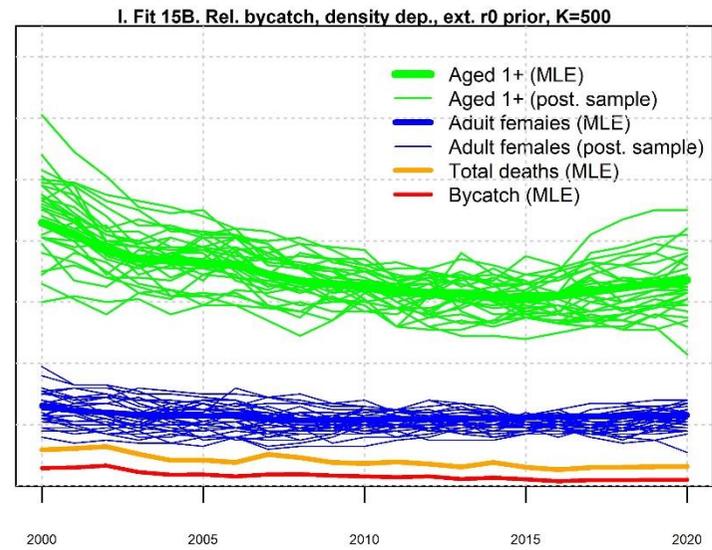
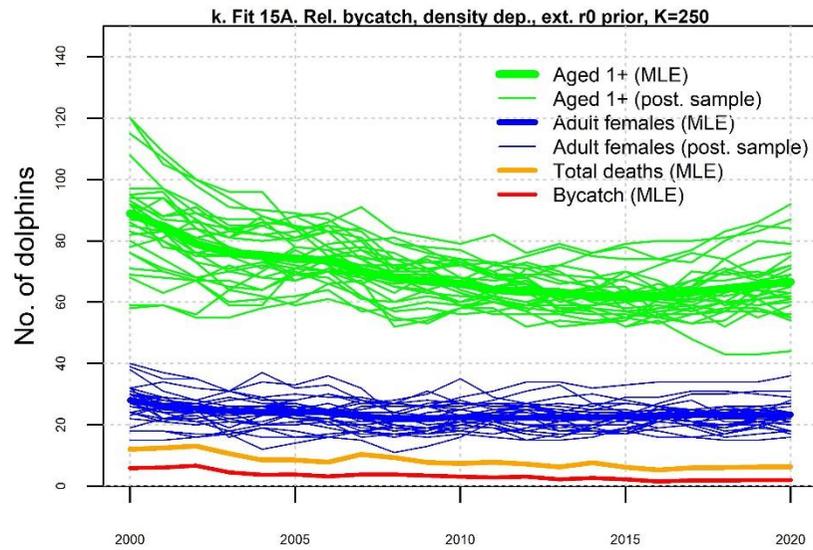
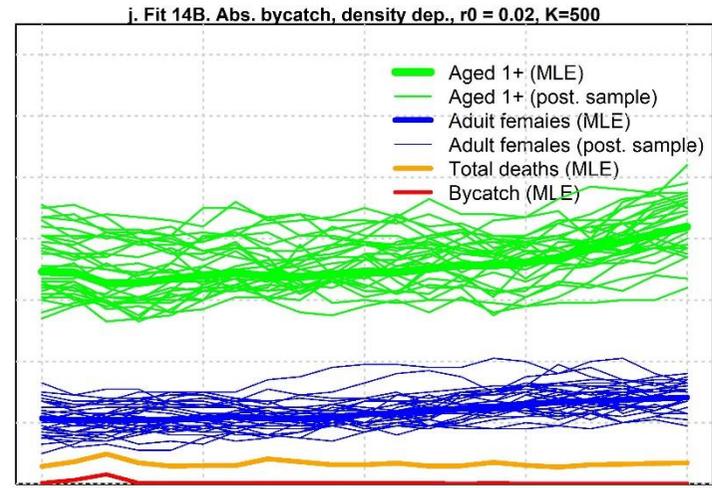
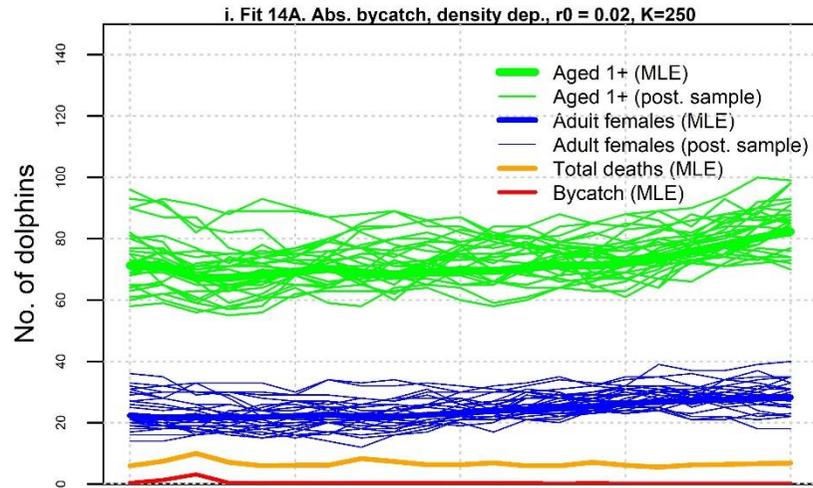
The realized equivalent sample sizes from the Bayesian posterior distribution exceeded 600 in all cases, hence the posteriors were reasonably well sampled. Overall, the AIC and WAIC values indicate essentially the same ranking of the fits.

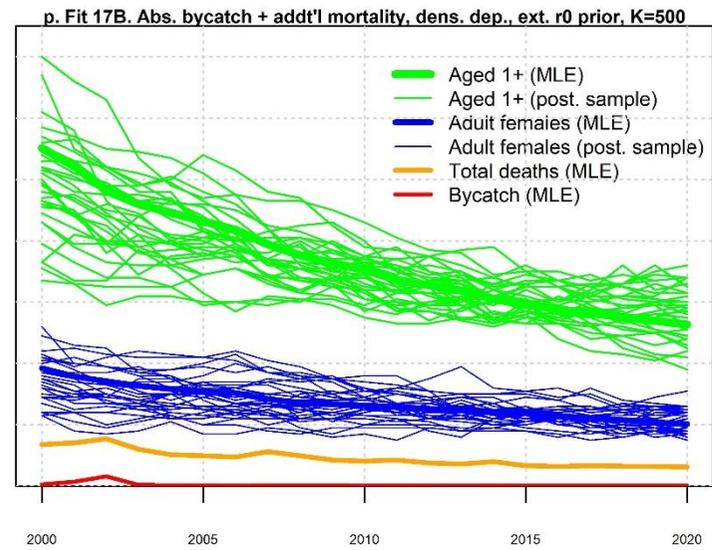
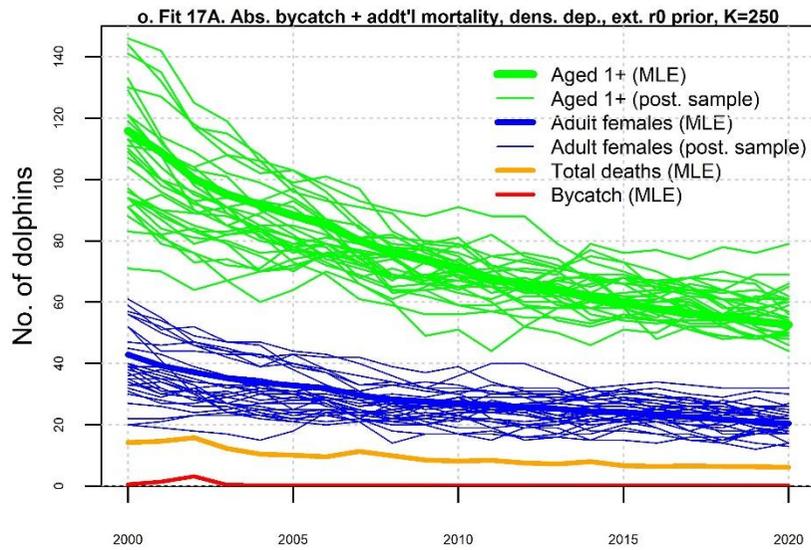
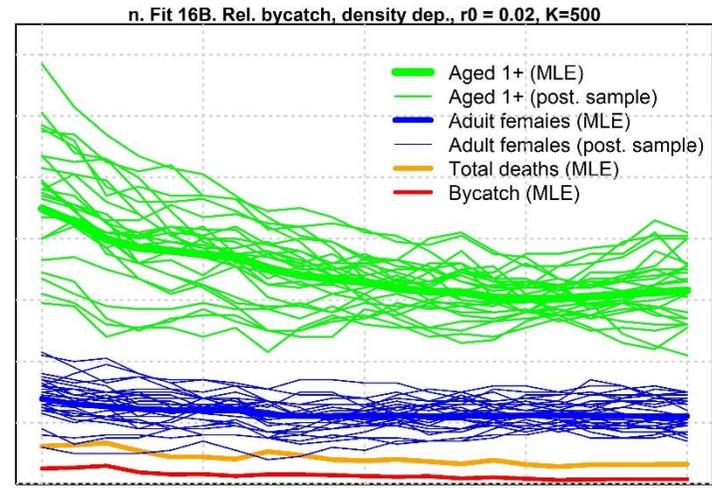
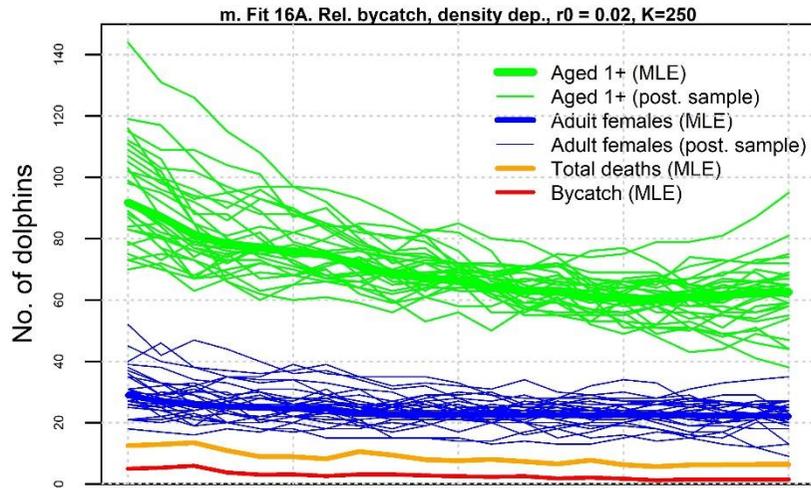
Table 4. Results of fitting alternative models																Average annual deaths 2012–16 (excluding animals aged < 1 yr)				PBR 2020	
Fit	log-likelihood	DF	AIC	Eff. post. sample	WAIC	$N_{2000}(1+)$		$N_{2016}(1+)$		Natural survival rate		r or r_0		K	Bycatch multiplier		By- catch	Toxo	Addit- ional	Total	PBR 2020
						MLE	SE	MLE	SE	MLE	SE	MLE	SE		MLE	CV					
1	-99.4	14.6	228.0			106	24	57	6	0.884	0.019	-0.035	0.020		1.8	1.23					
2	-98.7	15.5	228.4			104	23	60	7	0.887	0.019	-0.029	0.021		1.8	1.23					
3	-98.6	15.6	228.3			104	24	57	6	0.881	0.020	-0.031	0.020		1.8	1.23					
4	-99.5	15.8	230.5			107	26	58	7	0.884	0.019	-0.035	0.020		1.8	1.23					
5	-99.5	14.7	228.4			104	25	57	6	0.883	0.020	-0.034	0.020		1.8	1.23					
6	-99.4	14.4	227.6			109	24	57	6	0.886	0.018	-0.036	0.019		1.8	1.22					
7	-99.4	14.6	228.0	1 206	215.4	106	24	57	6	0.884	0.019	-0.035	0.020		1.8	1.23	0.11			7.96	0.09
8	-104.1	13.8	235.9	1 681	227.1	66	7	76	9	0.920	0.013	0.024	0.009		2.1	1.33	0.24			6.17	0.16
9	-103.6	13.5	234.1	1 595	221.1	68	7	74	8	0.917	0.011	0.020	0.000		2.1	1.32	0.24			6.27	0.15
10	-94.6	15.4	220.0	744	204.8	102	22	57	6	0.901	0.021	-0.010	0.023		14.7	0.59	1.53			6.77	0.10
11	-96.1	14.7	221.7	1 577	208.7	84	14	62	7	0.933	0.013	0.035	0.010		28.1	0.35	2.36			6.64	0.12
12	-95.2	14.5	219.5	1 331	213.2	88	15	60	6	0.922	0.013	0.020	0.000		22.7	0.37	1.90			6.81	0.11
13A	-103.9	13.8	235.4	1 323	226.3	69	8	77	9	0.924	0.013	0.027	0.009	250	2.1	1.32	0.26			6.03	0.16
14A	-102.9	13.6	233.0	1 616	220.5	71	8	73	7	0.918	0.011	0.020	0.000	250	2.0	1.31	0.24			6.24	0.15
15A	-95.8	14.7	221.1	2 104	207.5	89	16	62	7	0.934	0.013	0.037	0.010	250	26.2	0.36	2.26			6.55	0.12
16A	-95.1	14.5	219.2	637	208.1	92	16	60	6	0.921	0.012	0.020	0.000	250	21.5	0.38	1.82			6.77	0.11
17A	-99.3	14.6	227.8	1 293	219.7	116	30	58	6	0.957	0.019	0.045	0.011	250	1.8	1.22	0.17		4.09	7.16	0.09
18A	-99.4	14.6	227.8	956	215.9	110	26	58	6	0.934	0.018	0.020	0.000	250	1.8	1.23	0.18		2.84	7.25	0.09
19A	-98.3	13.7	223.9	1 766	217.3	111	27	58	6	0.952	0.017	0.044	0.010	250	1.8	1.23	0.19	3.96		7.21	0.09
20A	-98.0	13.6	223.2	1 154	215.6	108	25	57	6	0.933	0.017	0.020	0.000	250	1.8	1.23	0.18	2.75		7.22	0.09
13B	-104.0	13.8	235.7	1 848	226.7	67	8	77	9	0.922	0.013	0.025	0.009	500	2.1	1.33	0.25			6.13	0.15
14B	-103.2	13.5	233.6	2 026	220.0	69	7	74	8	0.918	0.011	0.020	0.000	500	2.0	1.31	0.23			6.27	0.15
15B	-96.0	14.7	221.4	1 522	208.2	86	15	62	7	0.933	0.013	0.036	0.010	500	27.2	0.35	2.31			6.57	0.12
16B	-95.1	14.5	219.4	1 266	205.0	90	15	60	6	0.922	0.013	0.020	0.000	500	22.1	0.38	1.79			6.74	0.11
17B	-99.3	14.6	227.8	1 610	219.1	110	27	58	6	0.959	0.020	0.045	0.011	500	1.8	1.23	0.18		4.32	7.23	0.09
18B	-99.4	14.6	227.9	1 350	216.1	108	25	58	6	0.936	0.018	0.020	0.000	500	1.8	1.23	0.17		2.92	7.24	0.09
19B	-98.4	13.7	224.2	1 481	216.9	106	24	58	6	0.954	0.018	0.044	0.010	500	1.8	1.23	0.18	4.11		7.38	0.09
20B	-98.1	13.6	223.3	1 252	216.0	106	24	57	6	0.934	0.017	0.020	0.000	500	1.8	1.23	0.17	2.85		7.28	0.09

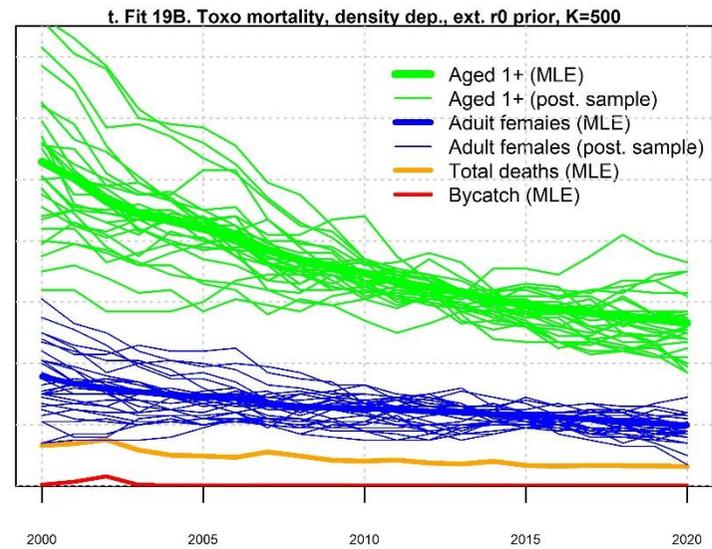
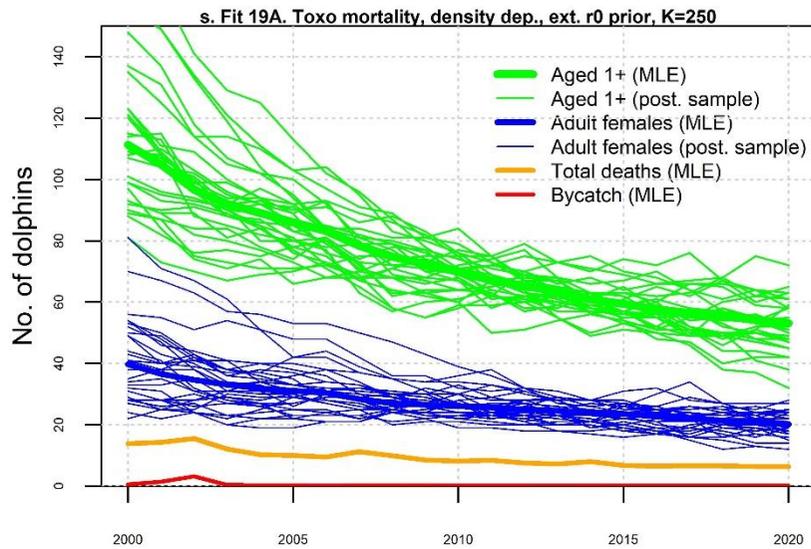
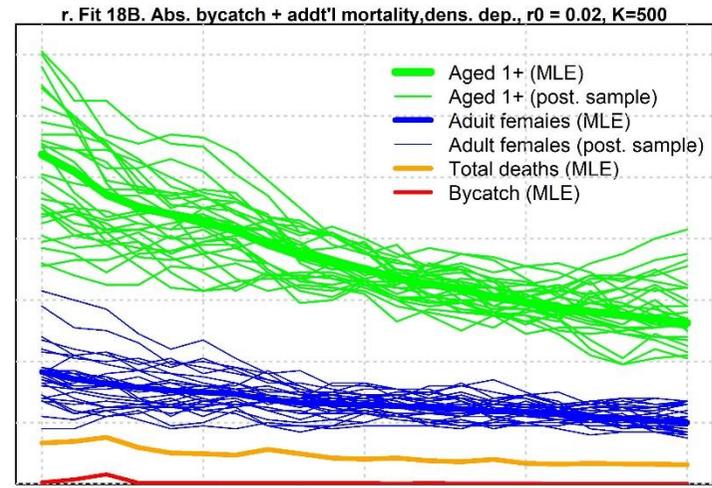
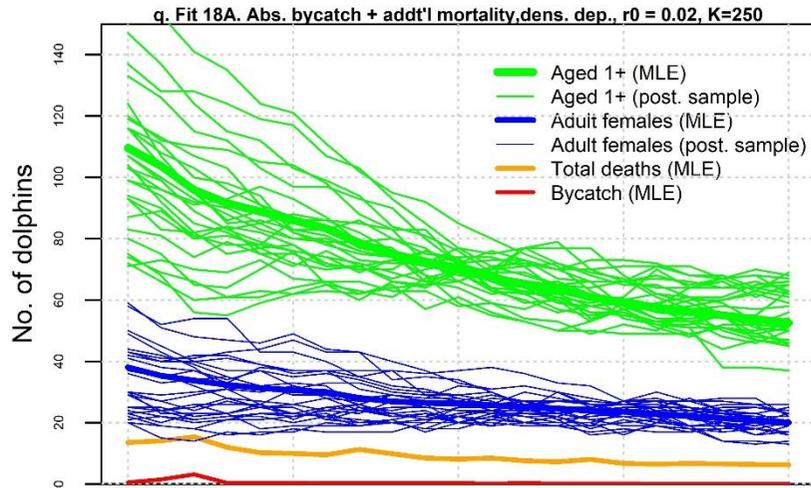
Figures 4a–v: Population trajectories 2000–2020 for each model fit. Maximum likelihood trajectories + samples of posteriors.

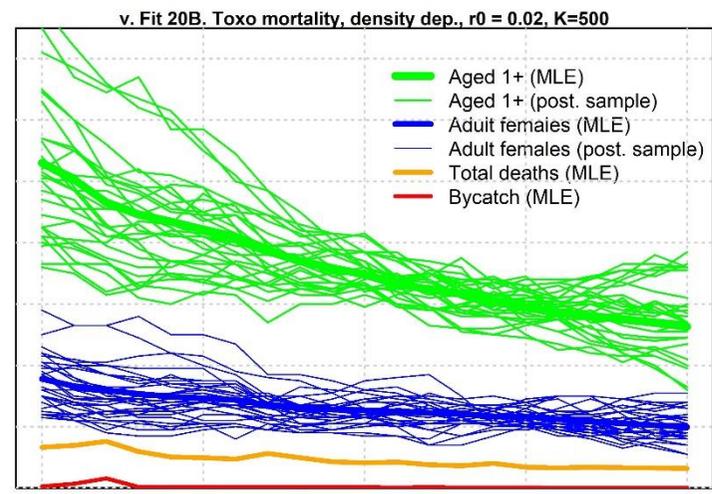
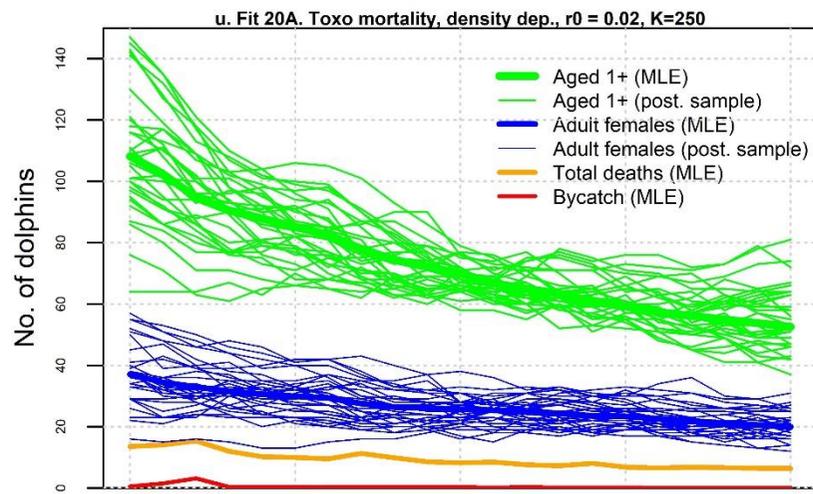












3.2 Mortality estimates

The mean annual number of deaths from different sources during the period 2016–2020 is shown in Table 4, as is the scaling factor for the bycatch. When the prior distribution of the scaling factor is used (lognormal with a CV of 0.42), the maximum likelihood estimates of the scaling factor range from 1.8 to 2.1, which means that the estimated posterior estimate of bycatch mortality is about twice the prior estimate (fits 1–9, 13–14 A–B, 17–20 A–B). This represents about 1.5 standard deviations above the mean. When the scaling factor is estimated as a free parameter, the maximum likelihood estimates of this factor range from 14 to 28 (fits 10–12, 15–16 A–B), which means that the bycatch mortality is estimated to be many times greater than its prior estimate. However these results should be interpreted with caution, because the bycatch scaling parameter may unwittingly be serving as a proxy for some other source of anthropogenic mortality that has also changed over time, noting that the latter fits require that non-fisheries threats are constant over time.

For those fits which allow additional mortality of unknown cause (fits 17–18 A–B), the estimated mortality levels are about the same as those for the corresponding fits including mortality due to toxoplasmosis (fits 19–20 A–B). This suggests that the mortality estimates are driven primarily by the model's desire to fit the population trend rather than by the limited data on toxoplasmosis deaths. In either case, the estimates of toxoplasmosis mortality or other additional mortality range from about one-third to two-thirds of total deaths, i.e. 2.8 – 4.3 deaths per year, out of 6–7 total deaths per year (excluding animals aged under one year old).

The estimated mean annual bycatch mortality during the period 2016–2020 ranges from 0.1 to 0.25 animals per year when the estimated annual time series of bycatch risk taken from Roberts et al. (2019) is treated as an absolute measure (i.e. the prior for the scaling factor is used), and from 1.8 to 2.4 animals per year when the bycatch risk time series is treated as a relative index (i.e. the scaling factor is a free parameter).

The PBR is somewhat exceeded by the bycatch in those fits that treat the estimated time series of bycatch risk as an absolute measure, and greatly exceeded in those fits where the bycatch risk time series is treated as a relative index.

When additional non-natural mortality or toxoplasmosis mortality is estimated, the mean estimates during the period 2016–2020 range from 2.8 to 4.3 anthropogenic deaths per year, in addition to bycatch mortality of about 0.2 animals per year.

3.3 Projections and management metrics

Key statistics from each of the forward projections are listed in Table 5. The projections are shown in Figures 5a–p in terms of the median and lower 5%-ile of the population by year, for the aged 1+ population and for adult females. Samples of individual trajectories are shown in Figs 5a–p.

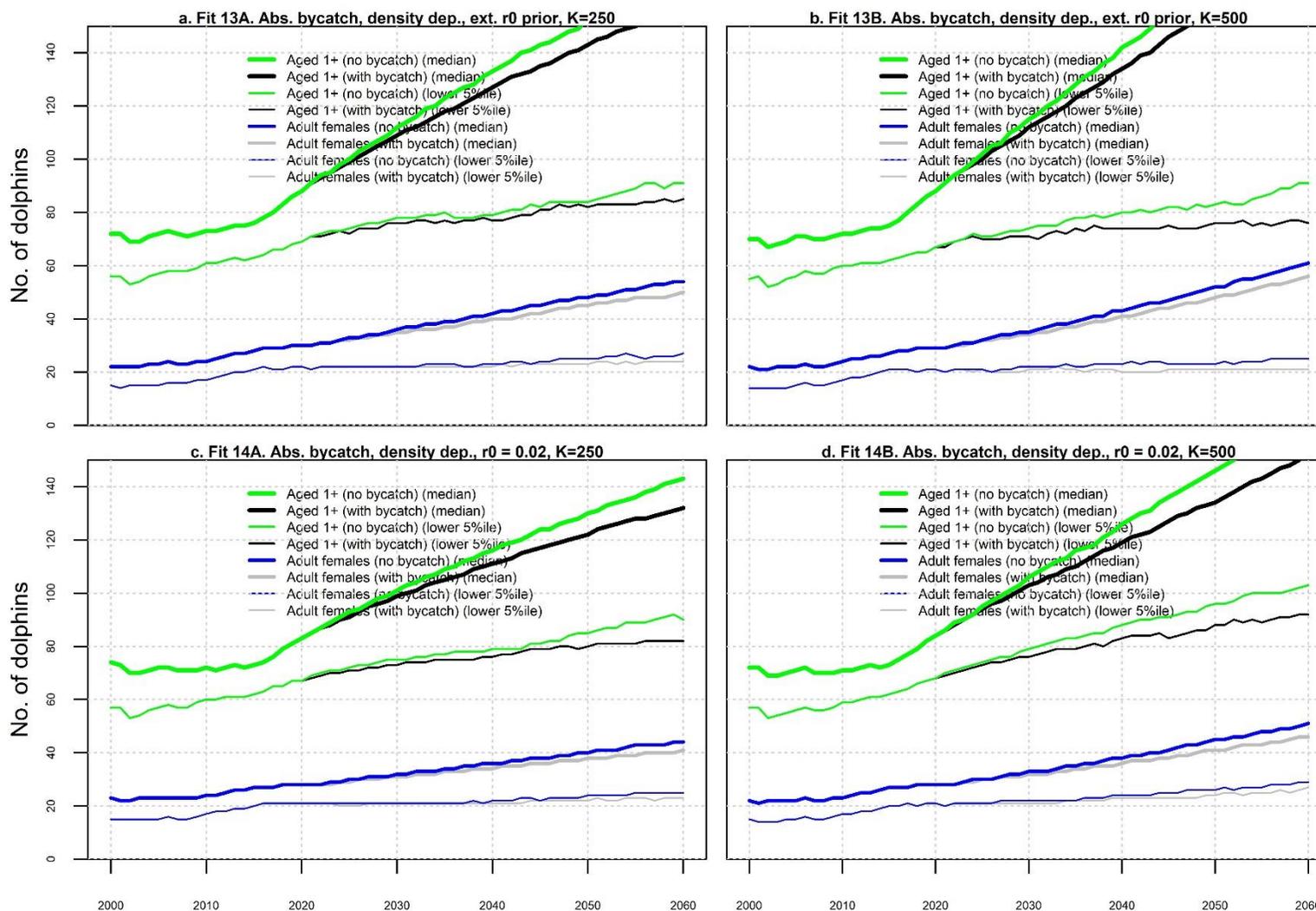
The projected population growth rate shown in Table 4 for the period 2020–2050 is defined as $\log(N_{2050}/N_{2020})/30$. Note that the median refers to the median of the population growth rates, not to the growth of the median population. It is possible for the median population growth rate to be slightly negative even when the median population increases over the same period, although the difference would be unlikely to be substantial.

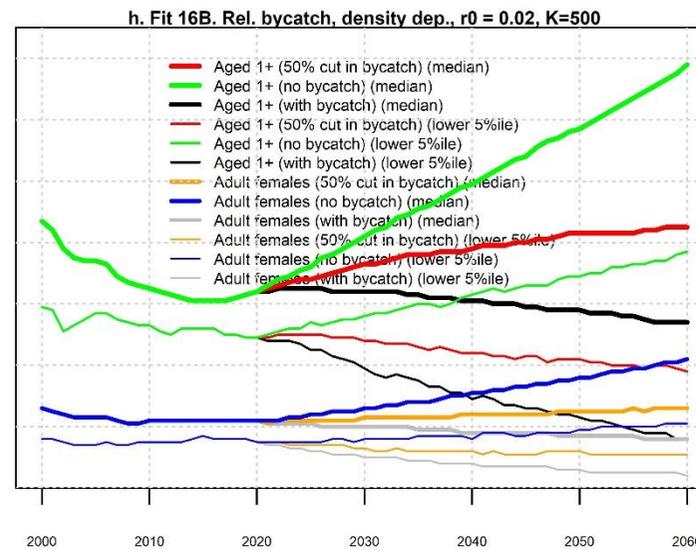
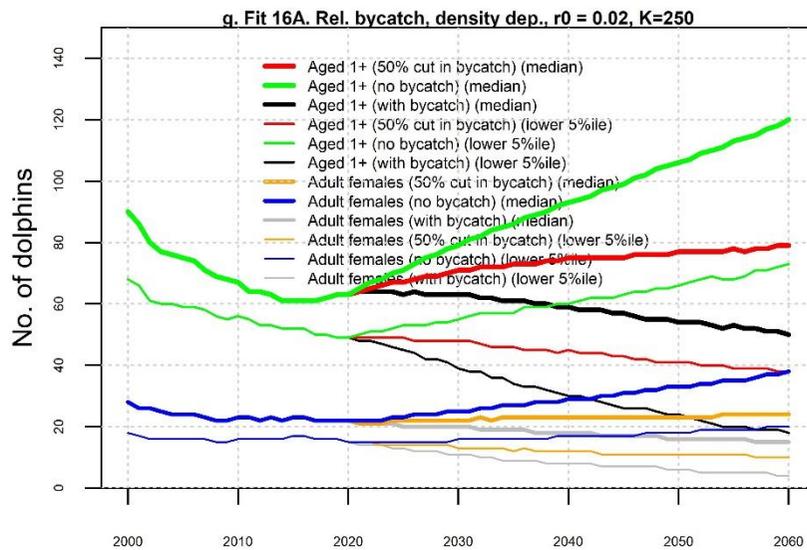
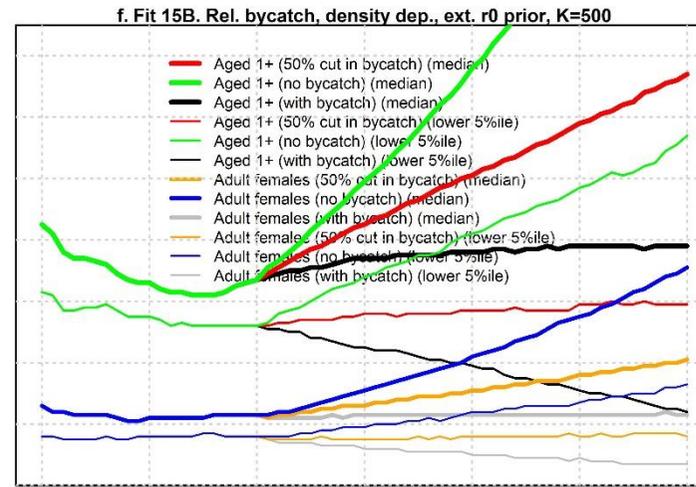
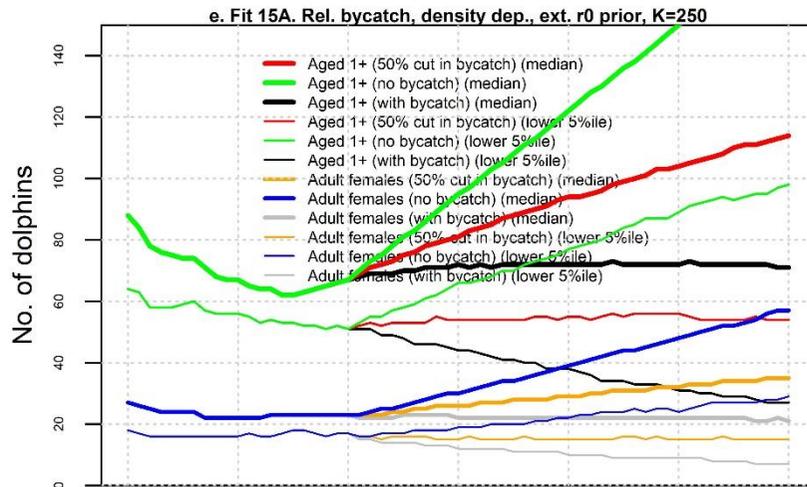
When the bycatch risk index is treated as an absolute measure, the forward projections with and without bycatch show that the level of bycatch does not have a major impact on the distribution of projected trajectories in terms either of the median or the lower 5%-ile of the trajectories (Figs 4a–d, i–p), although there can be an appreciable effect on individual trajectories (Figs 5a–d, i–p). The differences in the projected population growth/decline rates with and without bycatch do not exceed 0.4% p.a. (Tables 5a–b; fits 13–14 A–B, 17–20 A–B).

Table 5a. Summary of results of forward population projections (assuming $K = 250$)										Proj. annual growth		2120 pop relative to:	
Fit		Bycatch risk scenario	Toxo risk scenario	Population in 2020		Population in 2050		Population in 2120		rate 2020-50		no bycatch	no impact
				5%ile	median	5%ile	median	5%ile	median	5%ile	median	5%ile	5%ile
13A	a	no change		68	87	82	143	97	209	0.001	0.013	0.72	
13A	b	eliminate		68	87	90	152	135	233	0.002	0.014		
14A	a	no change		66	81	78	119	103	177	0.000	0.010	0.77	
14A	b	eliminate		66	81	83	128	133	206	0.001	0.011		
15A	a	no change		52	67	33	76	7	72	-0.013	0.004	0.04	
15A	b	50% cut		52	67	57	108	61	156	-0.001	0.012	0.34	
15A	c	75% cut		52	67	74	128	110	202	0.004	0.016	0.60	
15A	d	eliminate		52	67	92	152	182	245	0.009	0.020		
16A	a	no change		48	63	25	59	1	39	-0.018	-0.001	0.01	
16A	b	50% cut		48	63	40	80	26	99	-0.008	0.006	0.21	
16A	c	75% cut		48	63	52	93	62	140	-0.003	0.010	0.51	
16A	d	eliminate		48	63	65	110	121	203	0.002	0.014		
17A	a	no change		40	55	6	26	0	3	-0.043	-0.016		
17A	b	eliminate		40	55	7	27	0	4	-0.042	-0.015		
18A	a	no change		39	55	6	26	0	2	-0.041	-0.015		
18A	b	eliminate		39	55	7	29	0	3	-0.040	-0.014		
19A	a	no change	no change	40	54	6	26	0	3	-0.045	-0.016		0.00
19A	b	eliminate	no change	40	54	6	28	0	4	-0.042	-0.014		0.00
19A	c	no change	slow reduce	40	54	13	43	40	177	-0.036	-0.011	0.80	0.22
19A	d	eliminate	slow reduce	40	54	14	47	50	194	-0.035	-0.009		0.28
19A	e	no change	fast reduce	40	54	29	73	101	207	-0.020	0.001	0.80	0.56
19A	f	eliminate	fast reduce	40	54	33	77	126	222	-0.018	0.002		0.70
19A	g	eliminate	eliminate	40	54	83	140	181	234	0.011	0.023		
20A	a	no change	no change	40	55	6	25	0	2	-0.045	-0.016		0.00
20A	b	eliminate	no change	40	55	7	27	0	4	-0.042	-0.014		0.00
20A	c	no change	slow reduce	40	55	12	37	5	74	-0.040	-0.012	0.63	0.05
20A	d	eliminate	slow reduce	40	55	13	39	8	92	-0.038	-0.011		0.09
20A	e	no change	fast reduce	40	55	21	53	28	110	-0.025	-0.004	0.74	0.30
20A	f	eliminate	fast reduce	40	55	22	56	38	130	-0.024	-0.003		0.41
20A	g	eliminate	eliminate	40	55	54	92	92	172	0.001	0.013		

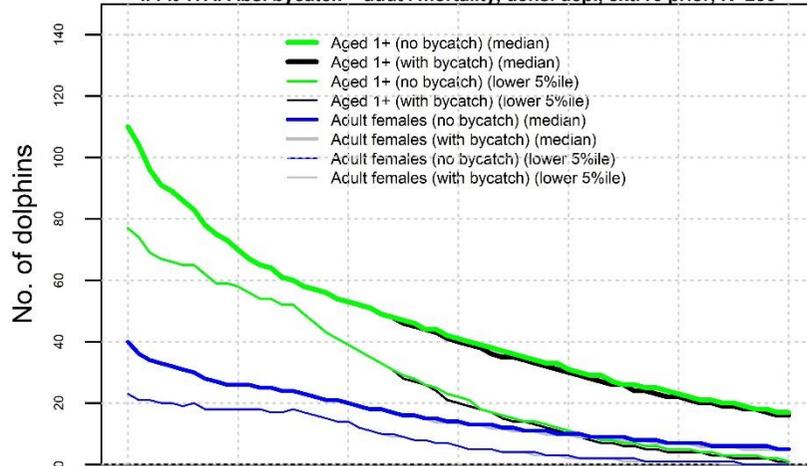
Table 5b. Summary of results of forward population projections (assuming $K = 500$)										Proj. annual growth rate 2020-40		2120 pop relative to:	
Fit		Bycatch risk scenario	Toxo risk scenario	Population in 2020		Population in 2050		Population in 2120		5%ile	median	no bycatch	no impact
				5%ile	median	5%ile	median	5%ile	median				
13B	a	no change		67	88	76	157	100	332	0.000	0.019	0.75	
13B	b	eliminate		67	88	83	169	133	387	0.005	0.022		
14B	a	no change		68	84	88	134	149	268	0.003	0.016	0.78	
14B	b	eliminate		68	84	96	146	192	325	0.006	0.019		
15B	a	no change		52	67	31	78	5	78	-0.021	0.005	0.02	
15B	b	50% cut		52	67	59	118	69	231	-0.001	0.019	0.26	
15B	c	75% cut		52	67	77	145	139	343	0.008	0.025	0.53	
15B	d	eliminate		52	67	97	177	263	461	0.016	0.033		
16B	a	no change		49	64	23	58	0	33	-0.029	-0.003	0.00	
16B	b	50% cut		49	64	42	83	27	110	-0.010	0.009	0.17	
16B	c	75% cut		49	64	56	99	76	185	-0.001	0.015	0.48	
16B	d	eliminate		49	64	69	117	159	294	0.006	0.021		
17B	a	no change		38	54	4	20	0	0	-0.080	-0.032		
17B	b	eliminate		38	54	4	22	0	1	-0.078	-0.029		
18B	a	no change		39	54	4	22	0	0	-0.080	-0.030		
18B	b	eliminate		39	54	4	23	0	1	-0.077	-0.028		
19B	a	no change	no change	38	54	4	21	0	0	-0.081	-0.031		0.00
19B	b	eliminate	no change	38	54	4	22	0	1	-0.077	-0.029		0.00
19B	c	no change	slow reduce	38	54	11	39	36	235	-0.047	-0.011	0.90	0.13
19B	d	eliminate	slow reduce	38	54	11	41	40	276	-0.047	-0.008		0.14
19B	e	no change	fast reduce	38	54	26	69	116	339	-0.018	0.008	0.87	0.41
19B	f	eliminate	fast reduce	38	54	25	74	134	378	-0.018	0.011		0.47
19B	g	eliminate	eliminate	38	54	86	163	284	439	0.019	0.037		
20B	a	no change	no change	39	54	5	22	0	0	-0.077	-0.030		0.00
20B	b	eliminate	no change	39	54	5	23	0	1	-0.073	-0.027		0.00
20B	c	no change	slow reduce	39	54	9	34	2	72	-0.052	-0.016	0.29	0.02
20B	d	eliminate	slow reduce	39	54	10	36	7	93	-0.049	-0.014		0.06
20B	e	no change	fast reduce	39	54	19	50	28	120	-0.028	-0.003	0.70	0.25
20B	f	eliminate	fast reduce	39	54	21	54	40	153	-0.026	0.000		0.36
20B	g	eliminate	eliminate	39	54	55	96	111	239	0.003	0.020		

Figures 5 a–p. Forward projections to 2060 (medians and lower 5%iles), for model fits with density dependence, with/without bycatch.

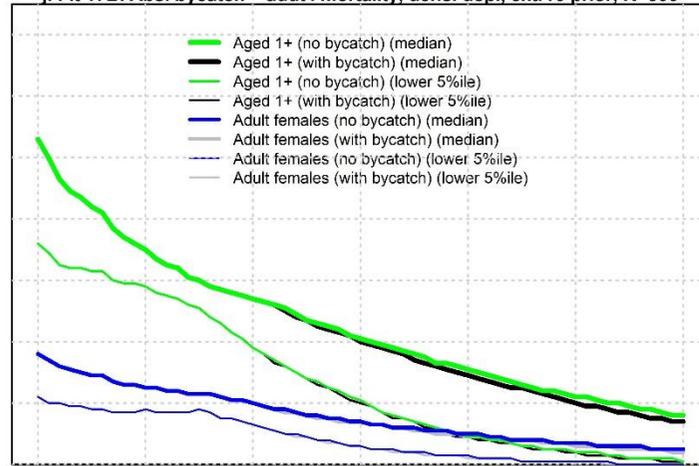




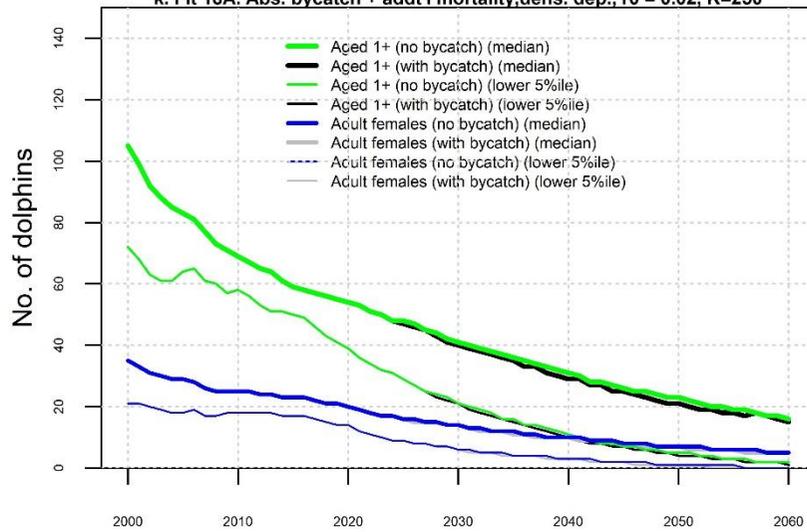
i. Fit 17A. Abs. bycatch + add'l mortality, dens. dep., ext. r0 prior, K=250



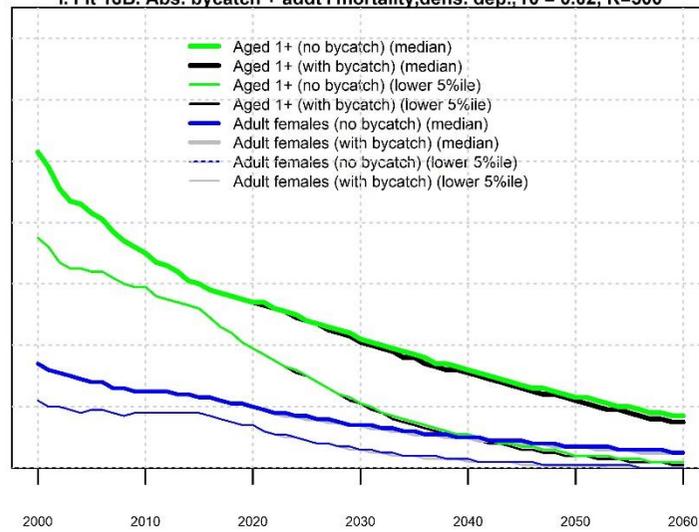
j. Fit 17B. Abs. bycatch + add'l mortality, dens. dep., ext. r0 prior, K=500

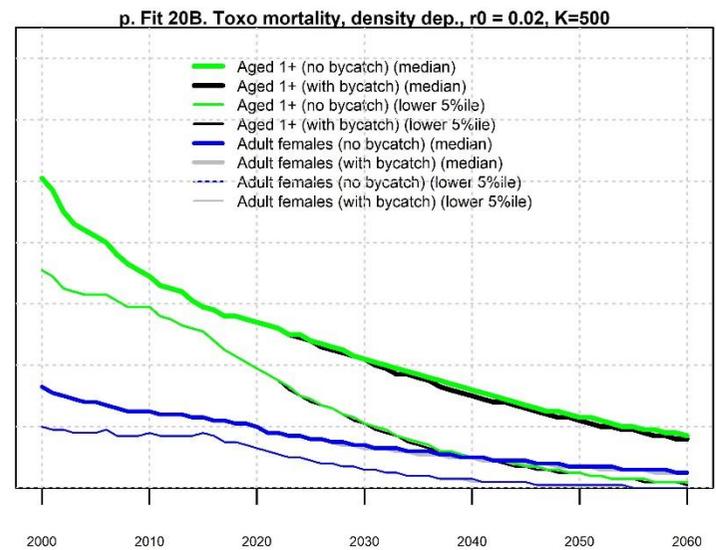
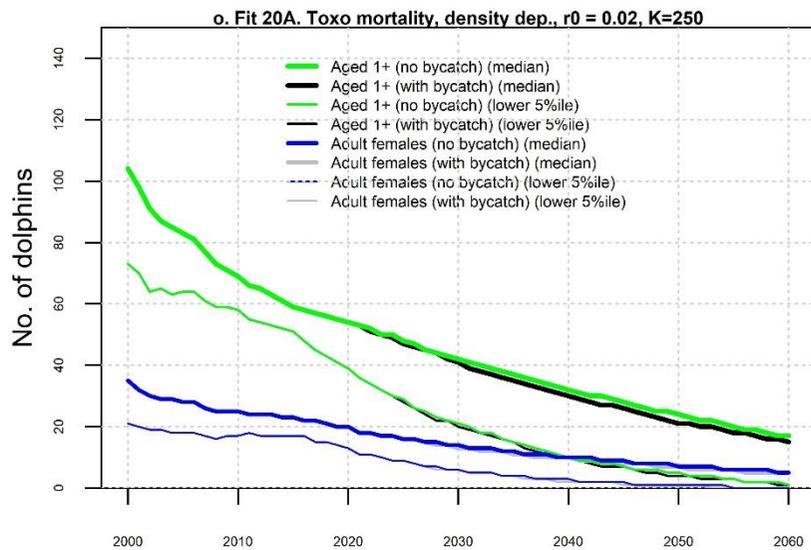
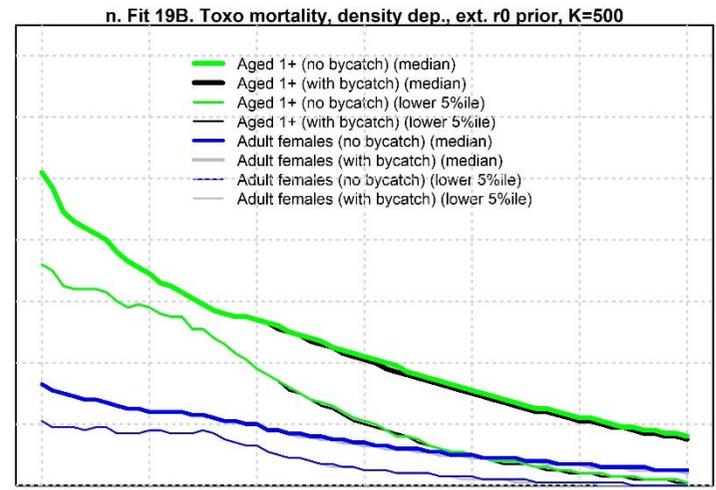
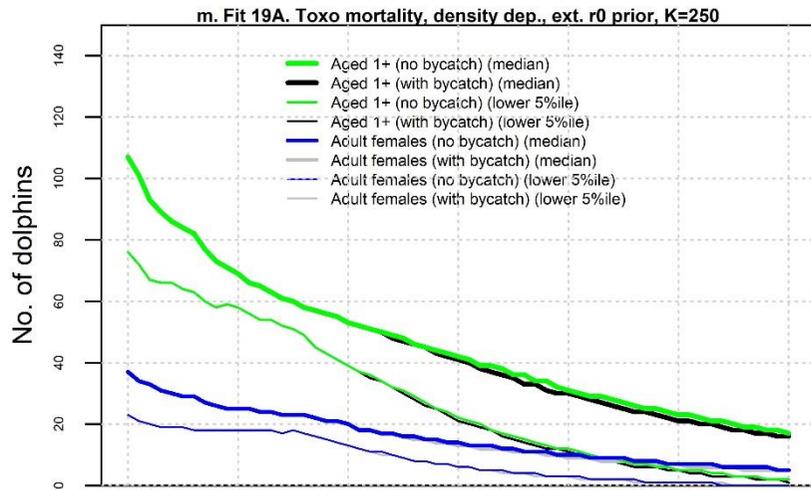


k. Fit 18A. Abs. bycatch + add'l mortality, dens. dep., r0 = 0.02, K=250

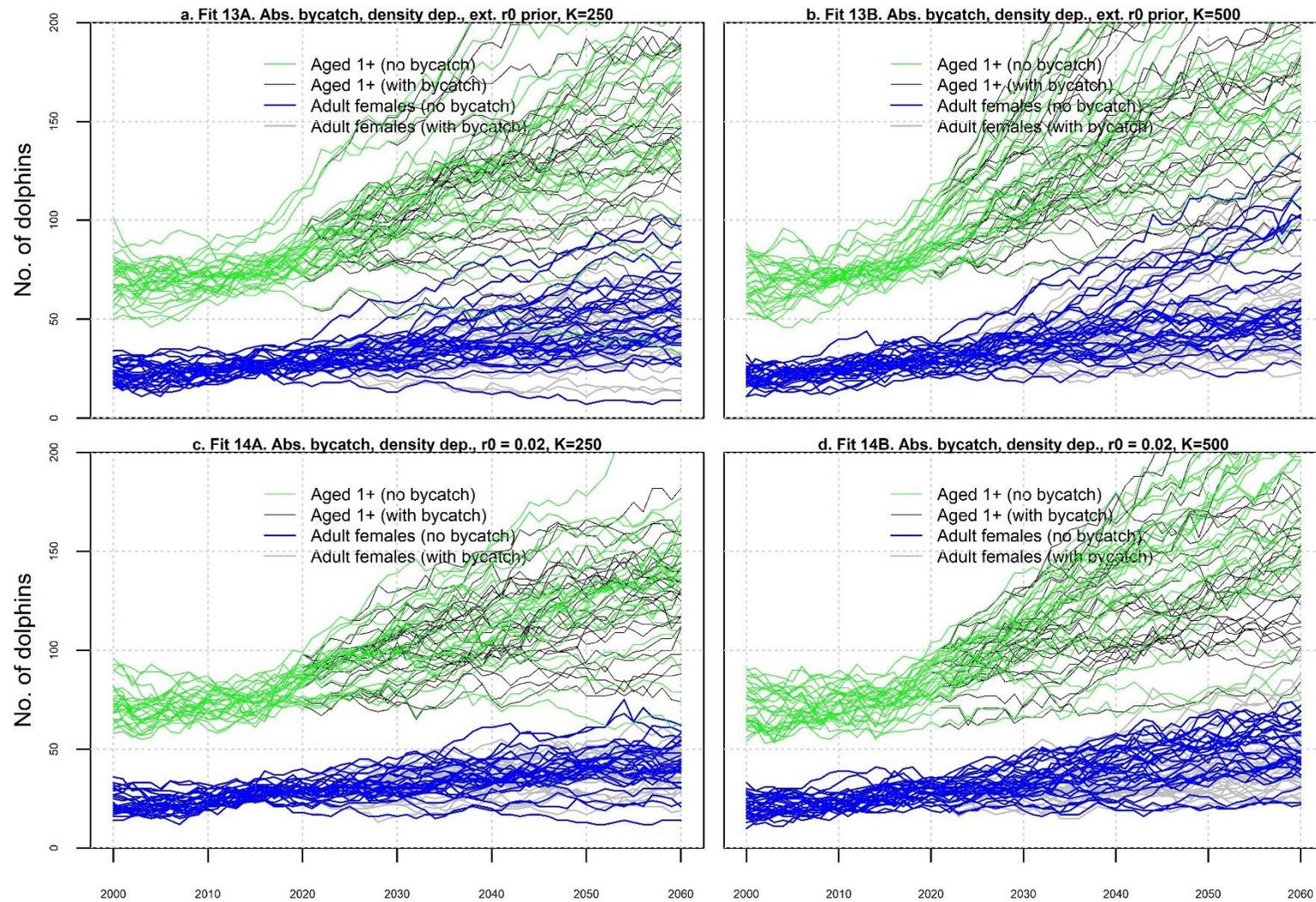


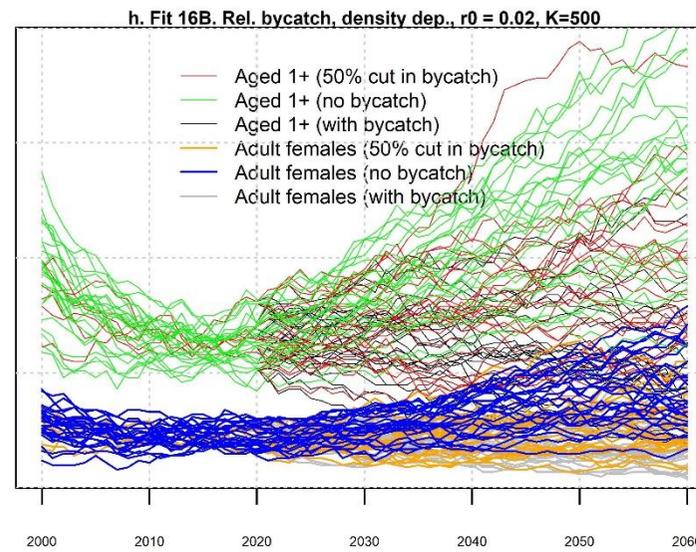
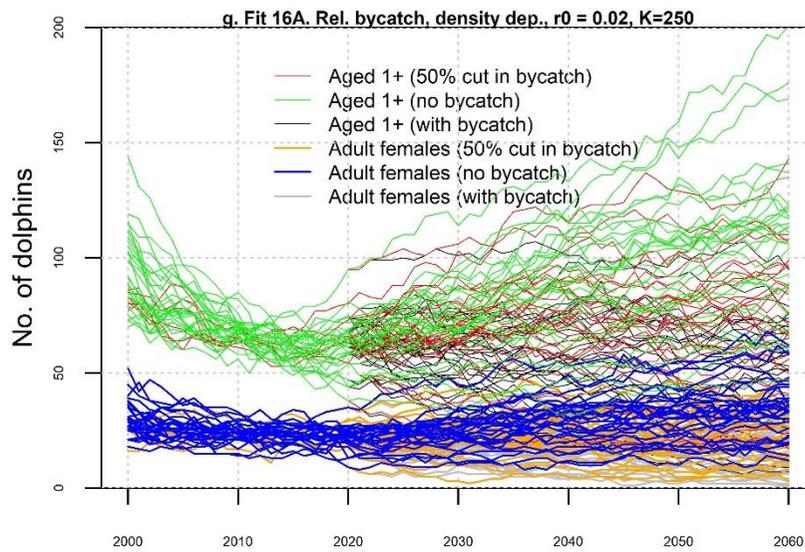
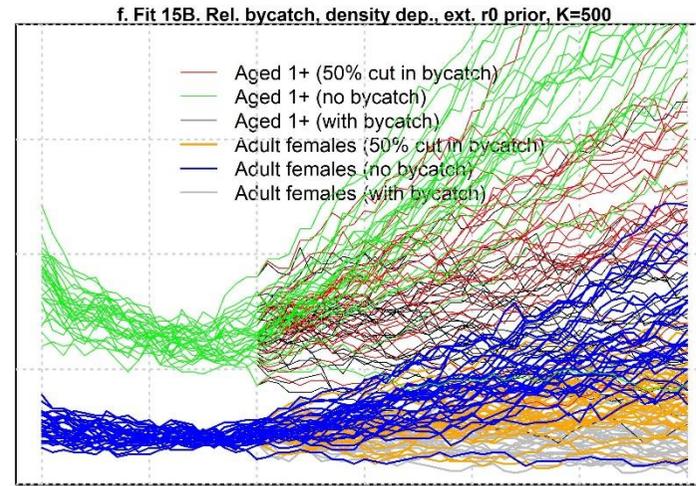
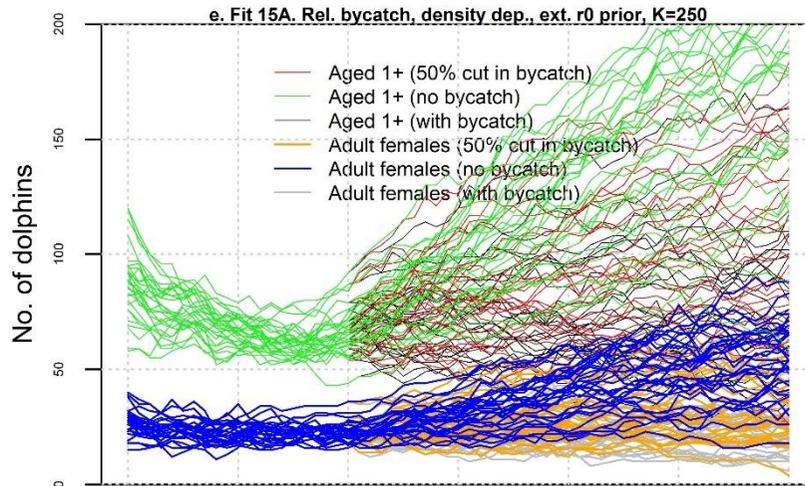
l. Fit 18B. Abs. bycatch + add'l mortality, dens. dep., r0 = 0.02, K=500

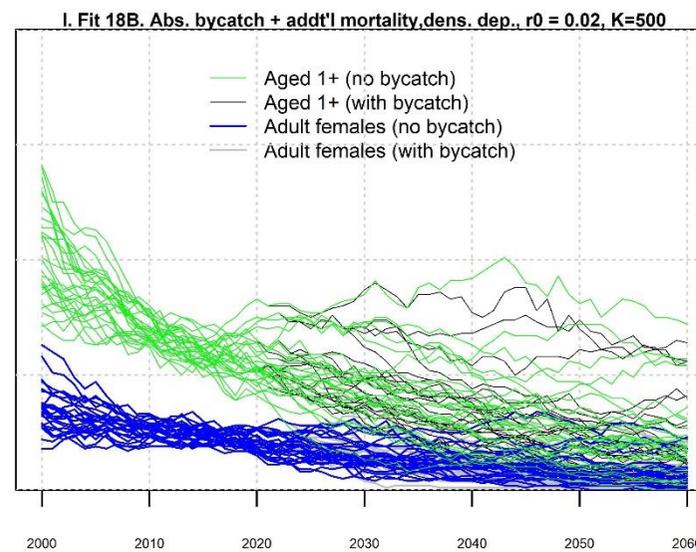
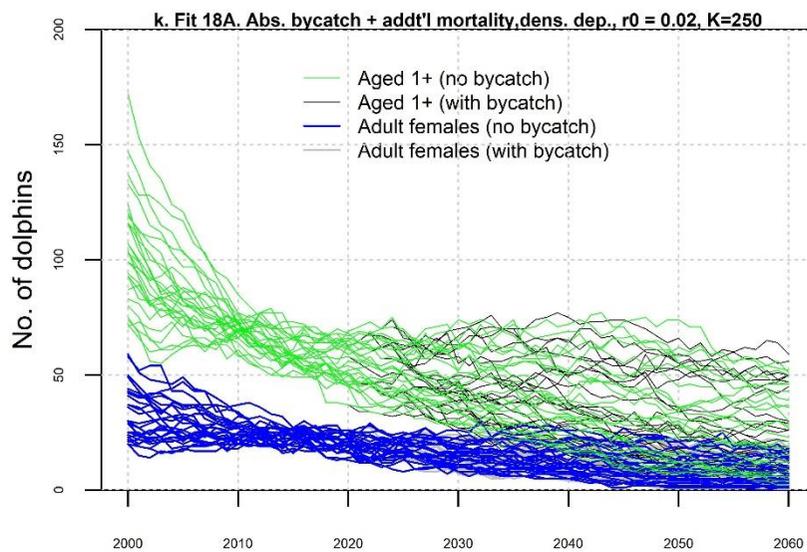
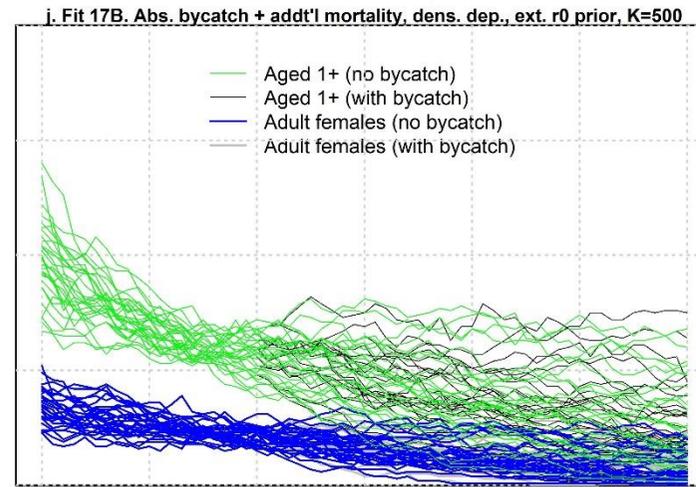
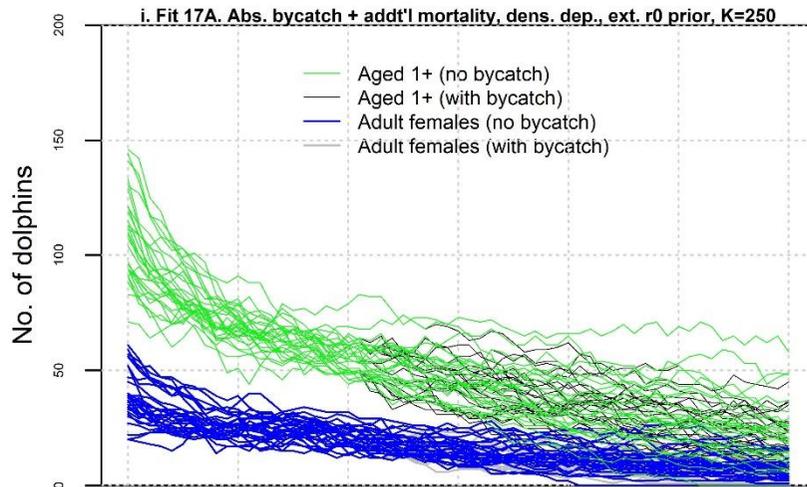


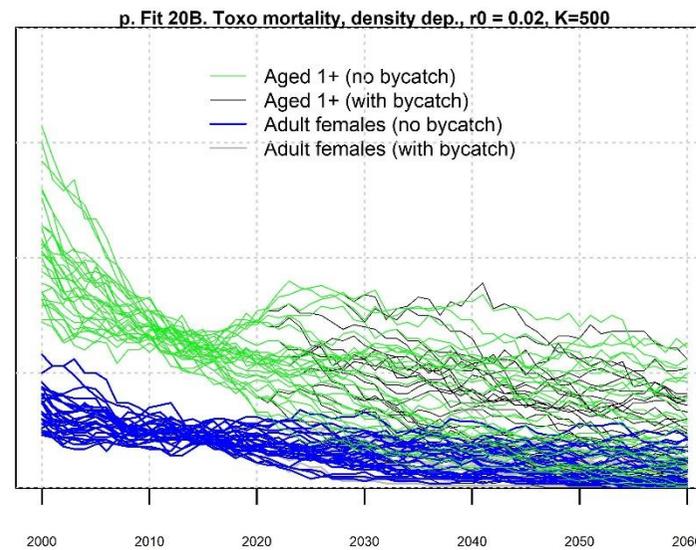
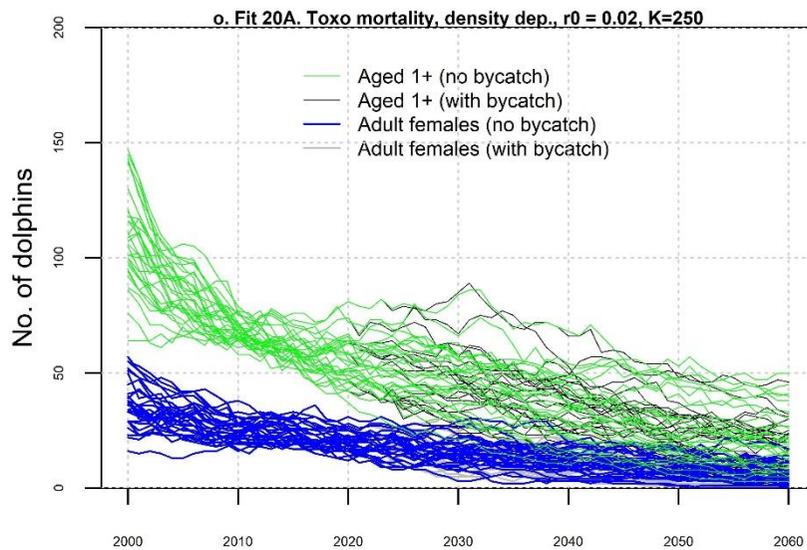
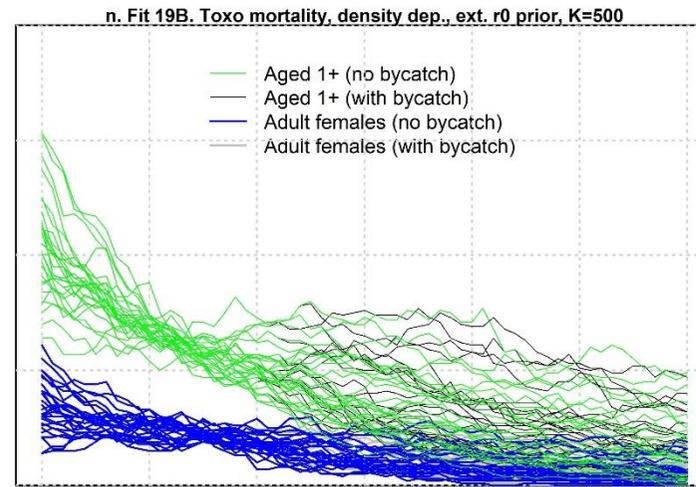
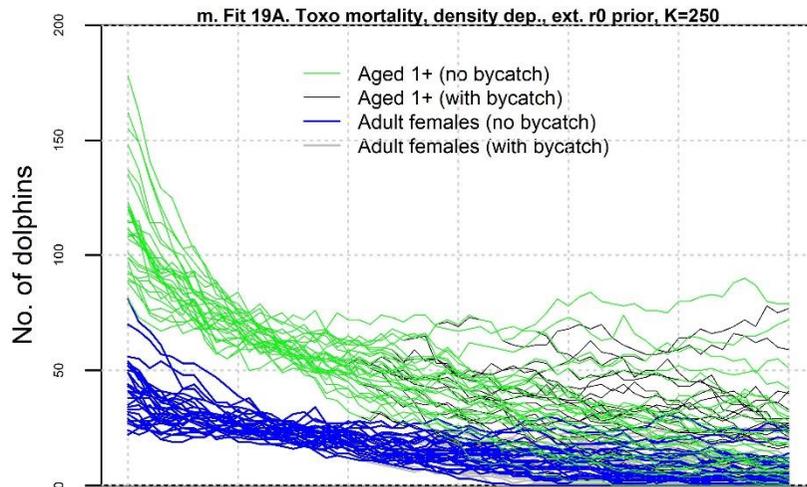


Figures 6 a–p: Forward projections to 2060 (samples of posterior distributions) for models with density dependence, with/without bycatch.









When the bycatch risk index is treated as a relative measure, the absolute bycatch level is estimated to be much larger, and the effect of bycatch is more substantial (Figures 5e–h, 5e–h; Tables 5a–b, fits 15–16 A–B). The population in that case is predicted to continue to decline at current bycatch rates. Reduction of the bycatch risk by 50% is just sufficient to stop the decline with the prior for r_0 but not in the $r_0 = 0.02$ case (Tables 5a–b, scenario b for each of the fits 15–16 A–B). Reduction of the bycatch risk by 75% stops the decline in the lower 5%-ile of the population size in all cases (Tables 5a–b, scenario c for fits 15–16 A–B).

If the estimated level of toxoplasmosis mortality continues unabated, or likewise an unknown alternative source of non-natural mortality continues at a constant rate, the population is predicted to decline towards extinction (Tables 5a–b, scenarios a–b in fits 17–20 A–B; Figures 5–6 i–p). Figs 6–7 a–d show the effects on population projections of abating toxoplasmosis mortality rates over different timescales.

A reduction of toxoplasmosis mortality beginning in 2030 and reduced at the rate of 50% per decade is just enough to avert population extinction at the lower 5% level with the prior distribution for r_0 (Tables 5 a–b, scenarios c–d with fits 19 A–B; Figures 7 a–b), but not quite enough to avert extinction for the case $r_0 = 0.02$ (Tables 5 a–b, scenarios c–d with fits 20 A–B; Figures 7 c–d). A reduction of toxoplasmosis mortality beginning in 2025 and reduced at the rate of 50% per five years would avert population extinction (Tables 5 a–b, scenarios e–f with fits 19–20 A–B; Figures 7 a–d).

3.4 Synopsis of results

In summary, the model fits and projection scenarios fall into four groups:

Group A (fits 8–9, 13–14 A–B): The commercial fisheries risk time series shown in Figure 3 is assumed to be accurate in absolute terms and there are no other anthropogenic threats. Under these assumptions, the population is projected to be increasing but the fit to the data is so poor that this group of fits and scenarios can be ruled out.

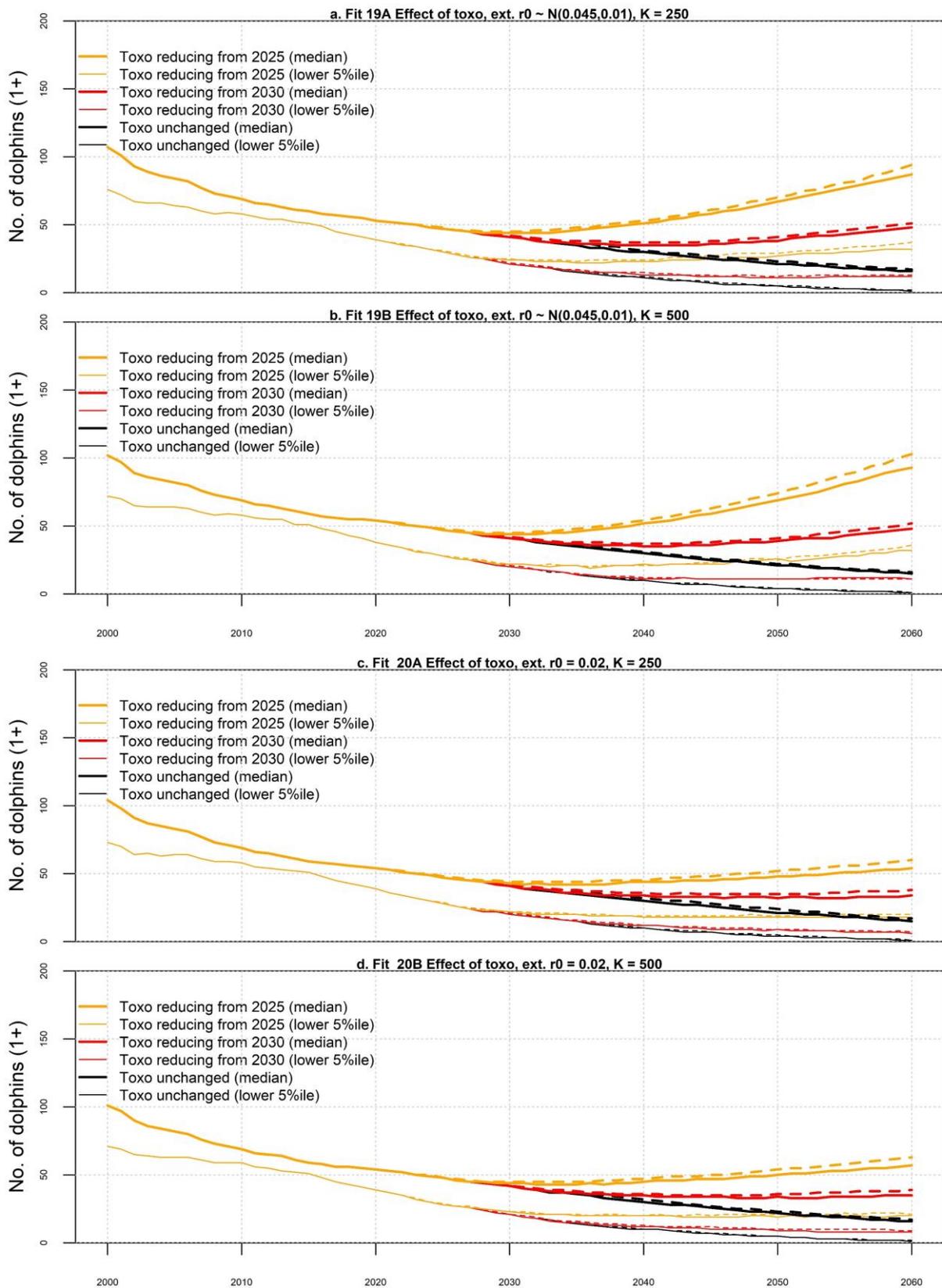
Group B (fits 11–12, 15–16 A–B): The commercial fisheries risk time series is assumed to be accurate as a relative index of bycatch risk and there are no other anthropogenic threats. These assumptions yield the best fit to the data and imply that the population will decline towards extinction if the bycatch risk is not further reduced, but the fit implies that Māui dolphins are 14–20 times more vulnerable to fisheries capture than has been estimated by Roberts et al. (2019) for all Māui-Hector’s dolphins. If this is not plausible, then the high estimated bycatch risk may be serving as a proxy for some other time-varying threat (or combination of threats). For example recreational fishing risk is known to have changed during the period of this time series, and it is possible that the effects of toxoplasmosis are also not constant over time. In any event, under this scenario a reduction in risk of 50% would be borderline sufficient to arrest the decline depending on assumptions about r_0 , whereas a reduction of 75% would be sufficient to arrest the decline and allow for some recovery.

Group C (fits 17–18 A–B): The commercial fisheries risk time series shown in Figure 3 is assumed to be accurate in absolute terms and there is an unidentified constant source of anthropogenic mortality. The goodness of fit to the data is intermediate between groups A and B. The population is predicted to decline towards extinction. The incremental effect of bycatch relative to that of the unidentified threat is minimal.

Group D (fits 19–20 A–B): The commercial fisheries risk time series shown in Figure 3 is assumed to be accurate in absolute terms and the mortality rate due to toxoplasmosis is estimated using the very limited data on toxoplasmosis deaths. The level of non-fisheries death and the fitted population trajectories are essentially the same as those in group C. Projections under different abatement scenarios show that a reduction in toxoplasmosis mortality of 50% per decade from 2030 would not quite be enough to eliminate the extinction risk, but a reduction of 50% per 5 years from 2025 would be sufficient to avert extinction. The incremental effect of bycatch on the forward projections is modest.

Fits 1–7 and 10 do not, in effect, distinguish between natural and anthropogenic mortality, because r is free in those fits; consequently, they are not assigned to any of the above groups.

Figures 7 a–d: Forward projections with toxoplasmosis (median and lower 5 percentile), various scenarios. Solid trajectories: bycatch continues. Dashed trajectories: bycatch eliminated.



4. DISCUSSION

With regard to the conservation of Māui dolphins the most important questions to be answered are:

(1) Is the estimate of commercial fisheries bycatch risk estimated by Roberts et al. (2019) for Hector's-Māui dolphins accurate for Māui dolphins? If it is, then the recent level of commercial bycatch is too low to have a major effect on the Māui dolphin population. Further reductions in bycatch risk would yield only a small conservation benefit, and an alternative explanation for the population decline is required.

Alternately if the estimate is valid as a relative index (accurately reflecting changing patterns of overlap with fisheries over time), but the catchability of Māui dolphins in fisheries is many times higher than estimated by Roberts et al. (2019) (such that commercial fisheries risk is the only anthropogenic threat), then the model suggests that the decline of the Māui dolphin population has slowed, but is still predicted to continue unless the bycatch risk is further reduced.

(2) Are levels of toxoplasmosis mortality really as high as are suggested by the limited available necropsy data? If so, then the results suggest that the population is declining towards extinction primarily as a consequence of toxoplasmosis, and that it will require a substantial reduction in toxoplasmosis risk, starting fairly soon, in order to save Māui dolphins from extinction.

It is worth noting that the averaged estimated number of deaths due to all causes, excluding calves of the year, during the period 2001–2016 is 7–10 annually or 110–160 in total, depending on the fit. During this period, only 12–14 non-calf carcasses were recovered (Table 1). Thus only about 10% of the estimated deaths are recovered. Efforts to recover a higher proportion of Māui dolphin carcasses may increase the precision of these estimates and improve our understanding of actual causes of death. Furthermore, the use of necropsy data to estimate deaths from different threats is subject to assumptions about the relative detectability of carcasses as affected by cause of death, resulting in potential biases.

With regard to the estimation of deaths from toxoplasmosis, the sample size of Māui dolphins examined for toxoplasmosis (three carcasses, of which two were diagnosed as having died from toxoplasmosis) is too small for reliable conclusions. However, the resulting estimates of mean toxoplasmosis mortality (in those fits where it is included) range from about a third to over half of total annual deaths including natural mortality (excluding neonates), sufficient to drive ongoing population decline. At the larger species scale, Roe et al. (2013) diagnosed toxoplasmosis as the main cause of death in 7 out of 22 carcasses of Hector's and Māui dolphins (excluding neonates), with no obvious geographical concentration. The spatial risk assessment of Roberts et al. (2019) estimated toxoplasmosis exposure at a subpopulation scale (including four subpopulations of Hector's dolphins, plus Māui dolphins) and estimated that Māui dolphins are the subpopulation at highest risk, with a mean toxoplasmosis exposure roughly four times higher than for ECSI Hector's dolphins (the only other subpopulation for which data exist in some locations to reliably estimate population demographic rates) and 3 and 10 times higher than the SCSi and NCSi subpopulations, respectively.

5. MANAGEMENT IMPLICATIONS

Clearly it is important to initiate a programme soon that includes both toxoplasmosis abatement efforts and further research to determine whether toxoplasmosis is having the impact it appears to have, and to inform the design and geographic focus of ongoing abatement strategies. At the same time the urgency remains to further quantify and reduce bycatch risk, and to collect improved information to identify other potential threats.

6. ACKNOWLEDGMENTS

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