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Calculating reference points for anthropogenic mortality of marine turtles

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ABSTRACT

1. Human-caused mortality threatens many marine turtle populations worldwide, with fisheries interactions being a primary cause for population declines. National and international management of fisheries interactions with marine turtles are rarely tied to turtle population biology. Quantitative tools tied to population-based objectives can provide insight into the effectiveness and urgency of bycatch mitigation.

2. A management approach is proposed based on a bycatch control rule called Reproductive Value Loss Limit (RVLL), generalized from the Potential Biological Removal management model for marine mammal populations. For RVLL, population size is scaled by reproductive value to account for strongly age-structured population dynamics and age-dependent fisheries mortality rates in marine turtle populations.

3. RVLL is an estimate of maximum sustainable mortality for a population, calculated from estimates of maximum population growth rate, total reproductive value in the population, and an uncertainty factor. RVLL estimates correspond to specified management goals and risk tolerances. For demonstration, simultaneous goals of maintaining populations above the maximum net productivity level (analogous to the population size that produces maximum sustainable yield) and preventing a decrease in adults are assumed, both with 95% probability. A management-strategy-evaluation-like process was used to explore parameterization of the RVLL equation for robust performance over a range of plausible life history characteristics and uncertainties in abundance and bycatch mortality estimates for marine turtle populations.

4. The RVLL-based management approach presented here proved robust to several important sources of uncertainty and to violation of several key underlying assumptions, and can be adapted to account for important sources of bias. The architecture presented, including tailored management strategy evaluation, provides a useful basis for further development of reference-point-based management of human-added mortality in populations that experience large changes with age in reproductive value and human-caused mortality rates, as is the case for marine turtles.
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INTRODUCTION

Incidental capture (bycatch) in fishing gear is one of the most severe global anthropogenic threats to non-target, long-lived marine vertebrate taxa, such as sea turtles, seabirds, and marine mammals (NRC, 1990; Stevens *et al.*, 2000; Tasker *et al.*, 2000; Tuck *et al.*, 2001; Lewison *et al.*, 2004;

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Read, 2008; Bolten *et al.*, 2011; Wallace *et al.*, 2011). The FAO Code of Conduct for Responsible Fisheries calls for minimization of fisheries impacts on non-target species. However, mitigation measures can be costly to fisheries (Bisack and Sutinen, 2006; Huang and Leung, 2007; Gallaway *et al.*, 2008), can displace ecological impacts to other areas or species (Rausser *et al.*, 2009; Watson *et al.*, 2009), and may be difficult or resource-intensive to implement or enforce (Rodríguez-Quiroz *et al.*, 2010; Gilman, 2011). Moreover, their effectiveness at protecting populations may be inadequate or unknown without proper assessment (Cox *et al.*, 2007; Gilman *et al.*, 2010). Mitigation measures must therefore be applied intelligently, associated costs justified, and management actions objectively prioritized and their effectiveness evaluated.

Estimating bycatch limit reference points that correspond to specific management goals can help address some of these issues and may be considered a basic form of implementing ecosystem-based fisheries management (Hall and Mainprize, 2004). Under reference-point-based bycatch management, fishing might proceed relatively unrestricted (within the scope of regulations) unless a bycatch limit is exceeded, which would trigger measures to reduce bycatch levels accordingly. Limit-based bycatch management may still result in lost fishery profits, requires resources for monitoring and enforcement (Diamond, 2005; Bisack, 2008), and should ultimately strive to minimize bycatch impacts on non-target species in an absolute sense. But using bycatch limits may increase flexibility in bycatch reduction strategies, allowing use of alternatives that meet other management objectives, such as minimization of opportunity cost (Bisack, 2008), or of more effective alternatives, based on transient perturbation analysis, when possible strategies benefit ages or stages differentially (Ezard *et al.*, 2010). They also provide the means to evaluate whether bycatch reduction efforts sufficiently protect populations, since bycatch per unit effort can be an unreliable indicator (Tuck, 2011), and to identify management priorities for allocating limited resources. Using management models that estimate how much bycatch is too much can allow for transparent and consistent bycatch impact assessments and better-informed decision-making by fishery managers and regulators (Taylor *et al.*, 2000; Hobday *et al.*, 2011).

The FAO (FAO, 2010) has recommended that nations and regional fisheries management organizations and arrangements (RFMO/As) consider use of limits for bycatch management in fisheries where bycatch is 'unavoidable,' but the practice to date is uncommon except as it relates to managing finfish species with economic value. As far as we know, no domestic or international fisheries management framework currently evaluates the cumulative fisheries-related mortality (or human-caused mortality in general) of marine turtles in relation to biologically-based limit reference points. For example, for jeopardy determinations under the US Endangered Species Act and for Marine Stewardship Council certification of fisheries, population impacts have been assessed separately for each fishery or fleet, without accounting for cumulative effects. Management of human impacts on marine turtle populations would benefit from a tool for assessing cumulative anthropogenic mortality rates on different life stages and setting appropriate limits on deaths over which managers have control (TEWG, 2000). Such a tool should address the uncertainties that plague assessment of marine turtles (Heppell, 2005; NRC, 2010). The need to manage proactively rather than in response to observed trends in population sizes is exacerbated due to late maturation in marine turtles, possibly exceeding 40 years in some populations (Scott *et al.*, 2011).

Perhaps the best known example of using limit reference points to guide management of human-caused mortality of charismatic species is the Potential Biological Removal (PBR) framework developed under the US Marine Mammal Protection Act (MMPA). PBR is an estimate of the maximum human-added mortality that, despite our uncertainty about population parameters, would allow a marine mammal population to recover to or remain at or above its 'maximum net productivity level' (*MNPL*), which is analogous to the population size that produces maximum sustainable yield in fisheries stock assessment parlance when take is non-selective to age. PBR is estimated by a straightforward equation based on an assumption of simple logistic population growth, with relatively modest data requirements that can be met in practice for most US marine mammal populations. It has undergone extensive simulation testing to ensure that it is highly likely to meet management goals under plausible data precision and accuracy conditions, irrespective of its biological realism (Wade, 1998; Taylor *et al.*, 2000). These properties make the PBR model attractive for assessing the

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sustainability of various sources of human-caused mortality for other data-deficient wildlife populations, and it has since been applied to non-US marine mammal populations (Marsh *et al.*, 2004) and adapted to seabirds and terrestrial species (Milner-Gulland and Akçakaya, 2001; Dillingham and Fletcher, 2008, 2011; Parry *et al.*, 2009; Runge *et al.*, 2009; Žydelis *et al.*, 2009; Warden, 2010).

In this paper, an age-structured extension of PBR for application to marine turtles is proposed. As is true for marine mammal populations, we can often estimate direct, human-caused mortality and abundance for marine turtle populations (the latter generally only for one component of the population, i.e. adult females). PBR also requires an estimate of potential population growth, which is generally unknown for both marine mammal and turtle populations, but can be approximated by reasonable values for management purposes. In contrast with marine mammals, however, ontogenetic stages for marine turtles change radically from hatchling to adult in their relative expected contribution to future population size (Crouse *et al.*, 1987; NRC, 1990) and are differentially vulnerable to the diverse sources of anthropogenic mortality that they encounter (NRC, 1990; Wallace *et al.*, 2010b). Specific fisheries may take predominantly adults, late juveniles, early juveniles, or a range of stages, depending on gear and area fished (Wallace *et al.*, 2010b). As a result, defining mortality limits in terms of individuals would be useless for sea turtle management, because the population consequences of killing a given number of adults are much greater than those of killing the same number of hatchlings (Crouse *et al.*, 1987; Heppell, 2005).

An individual's reproductive value quantifies its contribution to future population growth relative to individuals of other ages or life stages (Fisher, 1930). Multiplying age- or stage-specific numbers (e.g. mortality) by their corresponding reproductive values allows direct comparison of how a change in the number of individuals in one stage affects population growth relative to the same change in a different stage (Goodman, 1982; Heppell, 2005). Recent studies have demonstrated that reproductive value may be more relevant than traditional metrics, such as biomass or simple abundance, for evaluating population viability and the sustainability of exploitation for strongly age-structured populations (Gallucci *et al.*, 2006; Holmes *et al.*, 2007; Sæther *et al.*, 2010; Xu *et al.*, in press), including in the context of bycatch impacts on marine turtles (Heppell, 2005; Wallace *et al.*, 2008).

An equation for estimating anthropogenic mortality limits for marine turtles is proposed that is analogous in form to that for PBR under the MMPA, but with abundance and human-added mortality expressed in terms of reproductive value instead of individuals. The modified equation may be applicable to other taxa that face similar issues of large ranges in reproductive values over their life histories and age-dependent anthropogenic mortality. A process similar to management strategy evaluation (MSE; reviewed in Butterworth and Punt, 1999; Sainsbury *et al.*, 2000; Punt, 2006) was used, echoing that used by Wade (1998) for PBR under the MMPA, to explore parameterization and evaluation of the equation as a bycatch control rule over a range of life history characteristics and abundance and mortality estimation uncertainties plausible for marine turtle populations. The sensitivity of the resulting management approach's performance to several plausible biases and violations of assumptions was tested, with encouraging results. Finally, further work required to ensure the robustness of the approach for marine turtles and other practical matters associated with applying it to real systems are discussed.

METHODS

Equation for mortality limit in terms of reproductive value

PBR is estimated by

$$PBR = 0.5\ \mathrm{R_{max}N_{min}}f_r, \tag{1}$$

where $R_{\max}$ is the maximum annual net population growth rate, 0.5 is the fraction of $R_{\max}$ that corresponds to the *MNPL* under logistic growth (Figure 1), $N_{\min}$ is the minimum abundance estimate of the population, and f_r is a 'recovery' factor selected to address particular management considerations, such as potential biases in other parameters or minimizing impact on recovery time for a depleted population.

Following from PBR, the cumulative allowable human-caused mortality for an age-structured population, expressed in terms of reproductive value, which we call the 'reproductive value loss limit,' may be estimated as

$$RVLL = b\left(\hat{\lambda}_m - 1\right)\hat{N}'_{\min} f_u, \tag{2}$$

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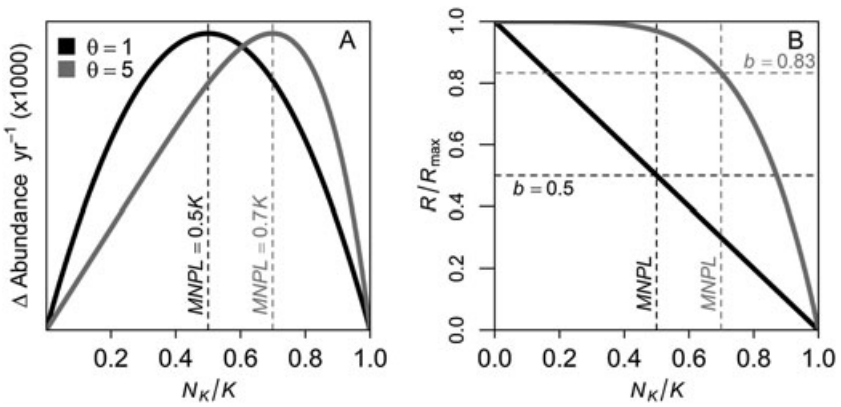

Figure 1. (A) Net population growth in terms of individuals with increasing N_K/K for a generalized, simple, discrete-time, logistic population model, and (B) corresponding net population growth rate (R) with increasing N_K/K standardized by net population growth rate at maximum productivity ($R_{\max}$). Vertical lines indicate $MNPL$, the point of maximum population change. Horizontal line in panel B is solution for b in the PBR management equation, equal to standardized net population growth rate at $MNPL$.

where $\hat{\lambda}_m - 1$ is the estimated maximum annual net population growth rate (the hat notation denotes an estimate); b is the fraction of $\hat{\lambda}_m - 1$ that corresponds to the $MNPL'$, where productivity is measured in terms of reproductive value (the superscript $'$ will be used to distinguish parameters defined in terms of reproductive value); $\hat{N}'_{\min}$ is the minimum abundance estimate of the population rescaled by reproductive value; and f_u is an uncertainty factor selected to address particular management considerations or potential biases in the other parameters. Each of these terms is discussed in detail below, referring to the PBR framework of the MMPA as a guiding model. A glossary of variables, constants, and parameters is provided in Table 1.

The PBR equation uses $b = 0.5$, based on an assumption of simple, discrete-time logistic growth, i.e. that for a population with abundance N_t,

$$N_{t+1} = N_t + \left(1 - \left(\frac{N_t}{K}\right)^{\theta}\right) R_{\max} N_t \qquad (3)$$

where K is carrying capacity and θ, which controls the density-dependent response, is 1, a conservative value for marine mammal populations, which most likely have convex population growth rate responses (i.e. $\theta > 1$; Fowler, 1981; Jeffries *et al.*, 2003). Under simple logistic growth, $0.5R_{\max}$ corresponds to the maximum net growth rate of a population, at $N = 0.5K = MNPL$ (Figure 1). A numerical exploration of plausible forms of density dependence in marine turtles, varying relative strength in different life history stages and acting on different vital rates (Fowler, 1981; Bjorndal *et al.*, 2000; Girondot *et al.*, 2002; Chaloupka and Balazs, 2007; Honarvar *et al.*, 2008), suggested that 0.5 is probably a precautionary value for b in a management model for marine turtles too (unpublished data).

The annual growth rate of a population (in its particular environment) with a stable age distribution when resources are not limiting is λ_m, following the notation of Caughley (1977) for intrinsic per capita population growth rate, $r_m = \ln(\lambda_m)$. Population growth rate in terms of reproductive value is not influenced by unstable age structure (Fisher, 1930; Charlesworth, 1980; Caswell, 2001). Empirically estimating λ_m is difficult, but for practical purposes it may be approximated based on abundance time series or vital rate estimates for small populations recovering from exploitation (TEWG, 2000; Balazs and Chaloupka, 2004; Zerbini *et al.*, 2010). In the absence of data to estimate λ_m directly, the parameter may be defined, for purposes of precautionary management, based on expert opinion, estimates for similar or model species, allometric analysis (Niel and Lebreton, 2005), or otherwise informative prior knowledge. Under the MMPA, for example, a default value is used in the absence of better information (Wade, 1998). Here, the performance of $RVLL$ was evaluated for a range of values of λ_m plausible for marine turtles.

Under the MMPA, $N_{\min}$ of the PBR equation is the 20th percentile of the sampling distribution of the abundance estimate based on real survey data. The 20th percentile was identified through simulation analysis as the maximum percentile that would suffice or nearly suffice to meet two criteria (with ≥ 0.95 probability) if annual removals were managed to PBR: (1) ensure that a population starting at 30% of carrying capacity would achieve

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Table 1. Glossary of variables, constants, and parameters

Symbol	Definition
$\mathbf{A}_d$	Density-dependent transition matrix
$\mathbf{A}_K$	Transition matrix at carrying capacity
$\mathbf{A}_m$	Transition matrix for population at maximum growth rate
$\hat{\mathrm{A}}_m$	Estimated transition matrix for population at maximum growth rate
b	Fraction of maximum productivity rate at which maximum net productivity occurs
$\mathbf{c}_t$	Age-classified female bycatch mortality at time t
$\hat{\mathrm{c}}_t$	Estimated age-classified female bycatch mortality at time t
C_t	Total individual female bycatch mortality
$\hat{\mathrm{C}}_t$	Total female bycatch mortality in terms of reproductive value
CV_C	Coefficient of variation for estimation of bycatch mortality
CV_N	Coefficient of variation for population estimation
F_m	Maximum theoretical fertility
F_K	Fertility at carrying capacity
f_u	Uncertainty factor in *RVLL* equation
f_r	Recovery factor in Potential Biological Removal equation
K	Carrying capacity
RVLL	Reproductive value loss limit
MNPL	Maximum net productivity level (as a fraction of carrying capacity) of a population in terms of individual females
MNPL′	Maximum net productivity level (as a fraction of carrying capacity) of a population in terms of total reproductive value of females produced per time step
N_K	Total abundance in stages contributing to carrying capacity
$N_{\min}$	Specified quantile of estimation distribution around population size (used in PBR)
$\hat{N}'_{\min}$	Specified quantile of estimated estimation distribution around estimated population size in terms of reproductive value
$\mathbf{n}_t$	Age-classified female population size at time t
$\mathbf{n}'_t$	Age-classified female population size at time t, in terms of reproductive value
$\hat{\mathbf{n}}_t$	Estimated age-classified female population size at time t
N_t	Total female population size in terms of individuals
N'_t	Total female population size in terms of reproductive value
$\hat{N}'_t$	Estimated total female population size in terms of reproductive value
$P_{1,m}$	Maximum theoretical survival probability for first juvenile stage
$P_{2,m}$	Maximum theoretical survival probability for second juvenile stage
$P_{\mathrm{adult},m}$	Maximum theoretical survival probability for adult stage
r_m	Intrinsic per capita population growth rate when no resources are limiting
$R_{\max}$	Maximum annual net population growth rate (used in PBR)
$\mathbf{u}_r$	Relative age-specific bycatch mortality rates
$\mathbf{U}$	Transition matrix with absolute age-specific bycatch mortality rates
$\hat{\mathbf{v}}_m$	Reproductive values for estimated transition matrix at maximum productivity
$\hat{\mathbf{w}}_m$	Stable age distribution for estimated transition matrix at maximum productivity
λ_d	Density-dependent population growth rate
λ_m	Maximum theoretical population growth rate and dominant eigenvalue of transition matrix at maximum productivity
$\hat{\lambda}_m$	Estimated maximum population growth rate
θ	Exponent determining density dependent response

MNPL within 100 years; and (2) ensure that populations starting at *MNPL* remained at or above *MNPL* after 20 years (Wade, 1998). In the *RVLL* calculation, $\hat{N}'_{\min}$ is derived from an adult female abundance estimate (e.g. from nest counts) and stable age distribution and reproductive values from an estimated population transition matrix corresponding to maximum growth rate, $\hat{\mathrm{A}}_m$, with dominant eigenvalue $\hat{\lambda}_m$. Taking this approach is precautionary because it is insensitive to a relative decrease in juvenile reproductive value that may occur as population growth rate is diminished by anthropogenic impacts, which could otherwise lead to take limits increasing as the population declines (Heppell, 2005). The vital rates in $\hat{\mathrm{A}}_m$ would probably be estimated from a combination of field and modelling studies (Heppell *et al.*, 2005) or inferred from better-characterized populations (Crowder *et al.*, 1994). An appropriate percentile for $\hat{N}'_{\min}$ in a given management context should be based on a specific operational management goal and on characteristic life history and uncertainties in reproductive value and abundance estimation for all ages. For the purposes of demonstrating the extension of PBR to an age-structured context, we echoed Wade's (1998) approach and identified a suitable percentile value for $\hat{N}'_{\min}$ that, over the course of 20-year simulations, would (1) achieve a management goal of *MNPL′* with 95% probability, (2) allow the number of adults to increase in 95% of populations, and (3) maintain extinction probability below 1%, based on a range of life history characteristics and adult abundance estimation errors that typify marine turtle populations.

The uncertainty factor, f_u, may be considered a tuning parameter to provide additional assurance of meeting species conservation goals in the face of case-specific concerns about parameter bias or other sources of uncertainty, or to meet other management goals, such as limiting the effect of anthropogenic impacts on the rate of population recovery for small populations to a defined management goal. Under the MMPA, the analogous recovery factor can vary from 0.1, for depleted populations, to 1, for well-characterized populations greater than *MNPL*, with a default of 0.5, based on bias trials conducted by Wade (1998). Adjustment of f_u was similarly explored to maintain population recovery rate to the specified management goal and to compensate for the effect of some key data limitations and violated model assumptions.

Evaluation

An MSE-like process was used to evaluate the application of *RVLL* as a bycatch control rule for age-structured marine turtle populations. Three interacting components were modelled: a biological or operating model, an observation

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model, and a management procedure. The biological model simulated the 'true' dynamics of populations responding to anthropogenic impacts and management. The observation model simulated data collection from the outputs of the biological model, including observation precision and bias. The management procedure comprised (1) estimation of variables (e.g. age-specific abundances) and parameters for the application of the bycatch control rule based on observed data, and (2) implementation of the *RVLL* equation to limit population removals, along with associated implementation error. The objective was to largely follow the example of Wade (1998) in exploring parameterization and evaluation of the effectiveness of the *RVLL* equation as a bycatch control rule in terms of its ability to achieve management goals over a range of life history characteristics and abundance and mortality estimation uncertainties plausible for marine turtle populations. This was achieved by simulating these interacting processes many times across a range of *RVLL* parameter values for a plausible range of marine turtle life histories, uncertainties in abundance and mortality estimation, biases, and violated model assumptions. The following sections describe the biological and observation models and the management procedure, and the approach used to parameterize and evaluate *RVLL*, which consisted of (1) 'base trials' to identify a percentile for $\hat{N}'_{\min}$ that accounts for typical estimation uncertainty in adult abundance and mortality and a value for f_u for recovering populations, and (2) 'sensitivity trials' to explore management procedure performance when confronted with several key forms of bias and violations of model assumptions and to inform necessary adjustments of f_u to improve robustness. All simulations and analyses were executed in R (R Development Core Team, 2010) with Tinn-R (Faria, 2010), using the popbio and MASS packages (Venables and Ripley, 2002; Stubben and Milligan, 2007).

Biological model

Marine turtle population growth was simulated by specifying age-structured, density-dependent population dynamics and age-structured bycatch mortality. The population model was based on a female-only, pre-birth-pulse census, age-classified transition matrix (Caswell, 2001) with a single parameter each for adult survival and fertility, so all adult age classes collapsed to a single adult stage (Heppell, 1998). This modified Leslie-Lefkovitch matrix model was chosen to simulate more realistic time lags in a population's response to changes in vital rates (due to management changes, density dependence, or stochasticity) than would a purely stage-based matrix model (Crowder *et al.*, 1994; Chaloupka, 2003). Juvenile survival rates were simplified to remain constant across age classes within two stages (Figure 2), corresponding to different size classes and potentially different habitats (e.g. oceanic and neritic; Carr, 1986; Limpus and Chaloupka, 1997; Bolten, 2003; NRC, 2010). Fixed stage durations allowed separate evaluation of model performance in the face of additional uncertainty introduced by unstable age structure due to age-structured population dynamics, without yet introducing uncertainty due to reproductive value estimation (discussed later). Two life histories spanning much of the published range of variation in marine turtles, with transition matrices $\mathbf{A}_m$ corresponding to vital rates at very low population density, were simulated in all trials (vital rates given in Table 2, details on sources in Appendix 1). Adult survival rates in $\mathbf{A}_m$ were set such that λ_m had plausible bounding values of 1.04 for the 'slow' life history (e.g. Hawaiian green turtles, *Chelonia mydas*, Chaloupka and

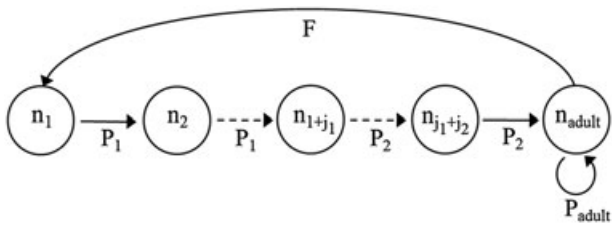

Figure 2. Life cycle diagram for simplified, age-classified (Leslie-Lefkovitch) matrix model of marine turtle population growth. F represents annual fertility rate (includes first-year survival rate), P_k represents annual survival probability for age classes in stage k, j_k is the number of age classes in the kth juvenile stage, and n_i is the abundance in age class i (just prior to the ith birthday). Dashed lines represent multiple annual steps and corresponding age classes.

Table 2. Life history parameters for base trials. Age at first reproduction is abbreviated as AFR. Length (years) of juvenile stages are j_1 and j_2. $P_{i,m}$ are stage-specific maximum survival rates. F_m is maximum fertility. λ_m is the maximum growth rate. See Appendix 1 for derivation and sources

Life history	Parameter values							
	AFR	j_1	j_2	$P_{\text{adult},m}$	$P_{1,m}$	$P_{2,m}$	F_m	λ_m
Fast	12	5	6	0.90	0.75	0.88	20	1.20
Slow	34	10	23	0.96	0.80	0.90	30	1.04

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Balazs, 2007) and 1.20 for the 'fast' life history (e.g. Kemp's ridley, *Lepidochelys kempii*, TEWG, 2000).

Density dependence was modelled as a matrix model generalization of the generalized, discrete-time, logistic growth equation for a scalar population model (see Appendix 2 for further technical details). Population growth followed $\mathbf{n}_{t+1} = \mathbf{A}_d\,\mathbf{n}_t$, with $\mathbf{A}_d$, the density-dependent transition matrix, determined by

$$\mathbf{A}_d = \mathbf{A}_m - \left(\frac{N_K}{K}\right)^{\theta} (\mathbf{A}_m - \mathbf{A}_K) \qquad (4)$$

where $\mathbf{A}_K$ governs a population at K and N_K is the population size being compared with K (potentially a subset of age classes). $\mathbf{A}_K$ was solved for numerically based on the proportional strength of density dependence on each vital rate relative to the others (see Appendix 2). K was set to 500 000 females.

For base trials, population growth was modelled with $\theta = 1$, individuals from all ages contributing equally to carrying capacity, and all vital rates density-dependent and changing by equal proportions as N_K increases. The resulting matrix population model produces simple logistic population growth if starting from a stable age distribution (i.e. as in Figure 1), and is characterized by constant vectors for stable age distribution and reproductive value over all population densities, so $MNPL = MNPL' = K/2$.

Relative bycatch mortality rates were modelled as zero for age classes in the first juvenile stage and increasing linearly with age from the first age class in the second juvenile stage through age at first reproduction (with one rate for adults). The resulting pattern of relative bycatch mortality with age was dome-shaped with a spike in the distribution for the adult stage, since it includes multiple age classes (Figure 3). This distribution mimics the cumulative, empirical size distribution of US strandings and bycatch across gear types for Atlantic loggerhead turtles (Wallace *et al.*, 2008).

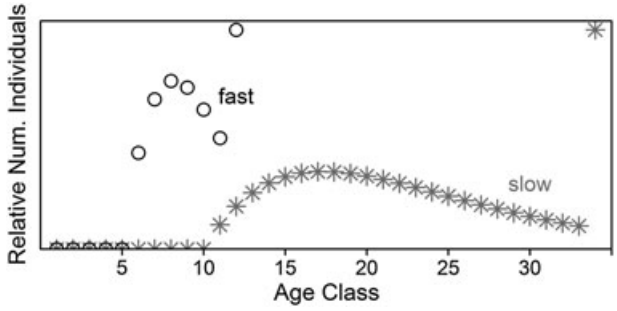

Figure 3. Expected relative bycatch mortality by age, for two life histories, given relative bycatch mortality rates that are zero for age classes in the first juvenile stage and increase linearly with age from the first age class in the second juvenile stage through age at first reproduction (with one rate for adults). The expected distribution is based on an assumption of stable age distribution for a bycatch-impacted population at $MNPL'$. The abscissa is scaled to years, so each point represents a year class, except the highest point on the right, which includes all adult age classes.

Observation model

To simulate collection of data on population size (for calculating $\hat{N}'_{\min}$), mean estimated adult female population abundance ($\hat{n}_{t,\text{adult}}$) was drawn at random each year from a log-normal distribution with mean equal to the true adult female population size ($n_{t,\text{adult}}$) and specified coefficient of variation (CV_N). The levels of CV_N explored here (0.25 and 0.5) only accounted for uncertainty in the adult female abundance estimate. The observation model also supplied $\hat{\mathbf{A}}_m$.

Management procedure

To estimate abundance and mortality in terms of individual females and reproductive value of females, the assessment process assumed that the population had a stable age distribution ($\hat{\mathbf{w}}_m$) and relative reproductive values ($\hat{\mathbf{v}}_m$) corresponding to the right and left eigenvectors of $\hat{\mathbf{A}}_m$. Thus, $\hat{N}'_{\boldsymbol{min}}$ was calculated as the specified percentile of a log-normal probability distribution with mean equal to $\Sigma_i\,(\hat{n}_{t,\text{adult}}\ \hat{v}_{m,i}\ \ \hat{w}_{m,i}/\hat{w}_{m,\text{adult}})$ and CV equal to management's estimate of CV_N. The values in $\hat{\mathbf{v}}_m$ were scaled to the reproductive value of adults, so $\hat{v}_{m,\text{adult}} = 1$ (*sensu* Heppell, 2005), the same scale used by the recovery team for the Northwest Atlantic loggerhead turtles (*Caretta caretta*) to scale individuals of different stages to 'relative reproductive equivalents' (NMFS and USFWS, 2008). In reality (i.e. in the biological operating model), simulated populations had unstable age distributions and varying relative reproductive values due to bycatch mortality. Therefore, simulations implicitly evaluated the robustness of the management strategy to transient population dynamics that violated the assumptions of stable age distribution and constant relative reproductive values.

Management of bycatch mortality was based on the use of *RVLL* as a bycatch control rule, where estimated annual population removals equalled *RVLL*. Age-specific (or size-specific) bycatch mortality can be estimated for many populations (e.g. from scientific observer programmes). Age-specific estimated mortality each year was calculated

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from reproductive-value-weighted $RVLL$ as $\hat{\mathbf{c}}_t = RVLL\,\mathbf{u}_r\mathbf{n}_t/\sum(\mathbf{u}_r\mathbf{n}_t\hat{\mathbf{v}}_m)$, where $\mathbf{u}_r$ is a vector of relative age-specific bycatch mortality rates. True annual bycatch mortality in terms of total females (C_t) was sampled from a log-normal distribution with mean $\hat{C}_t = \sum_i \hat{c}_{t,i}$ and $CV_C = 0.5$ (i.e. true annual mortality varied from that estimated by management due to observation error). We assumed that true $\mathbf{u}_r$ was known, so true age-specific bycatch mortality was $\boldsymbol{c}_t = C_t\hat{\mathbf{c}}_t/\sum_i \hat{c}_{t,i}$, feeding back into the biological model. The level of CV_C explored here did not account for uncertainty in the population structure of animals killed as bycatch or the uncertainty in relative age-specific bycatch mortality rates.

Base trials

The base trials assumed that true vital rates and CV_N were known; therefore λ_m was known too. Two base trials were run – the first to identify an appropriate percentile for $\hat{N}'_{\min}$ given specified management goals and levels of uncertainty in abundance and mortality estimation, and the second to identify a value of f_u that would allow managed populations to recover to a management target from a small population size with minimal change in recovery time relative to equivalent populations without bycatch (both *sensu* Wade, 1998). Each base trial included four cases, corresponding to two life histories and two levels of CV_N (0.25 and 0.5). Two thousand simulations were run for each case.

For the first trial, simulations for Wade's (1998) 20 year criterion were emulated, representing the upper end of management-relevant time frames (results were similar for simulations run for one generation time, equalling 17 and 51 years for fast and slow life histories, respectively). Percentiles for $\hat{N}'_{\min}$ from 2.5% to 50% were evaluated at $f_u = 1$. The true initial population size in the biological model (N_0) was set to $MNPL' = K/2$, with age-distributed abundance ($\mathbf{n}_0$) according to the stable age distribution for $\mathbf{A}_d - \mathbf{U}$, where $\mathbf{U}$ contains absolute, age-specific bycatch rates on the subdiagonal and bottom right elements. Relative magnitudes in $\mathbf{U}$ equalled $\mathbf{u}_r$, and absolute values were solved for numerically such that the eigenvalue of $\mathbf{A}_d - \mathbf{U}$ was one, so $\mathbf{n}_0$ approximated the stable age distribution for a bycatch-impacted population in steady state at $MNPL'$. The highest percentile for $\hat{N}'_{\min}$ permitting populations with a given life history to meet all three performance criteria, i.e. (1) to remain above $MNPL'$ after 20 years, and (2) to maintain or increase in number of adults, both with 95% probability (i.e. in 95% of 2000 simulations), as well as (3) to remain below 1% extinction probability (with extinction defined as falling below 25 adult females at any point during the simulation), was chosen for use in further simulations.

For the second trial, management outcomes for f_u values varying from 0.05 to 1 were evaluated, with $\hat{N}'_{\min}$ calculated at the percentile determined in the first base trial. Starting population size in the biological model was $0.05\,K$, and age distribution was set as described above, i.e. approximating the stable age distribution for a bycatch-impacted population in steady state at $0.05\,K$. Simulations ran for 100 years for the fast life history and 200 years for the slow life history to allow time for bycatch-impacted populations to recover to $MNPL'$. The highest value of f_u permitting 95% of simulated populations to recover to $MNPL'$ in ≤10% more time than required for a population without bycatch was identified as appropriate to limit impact on recovery from small population size. Extinction probability was also tracked.

Sensitivity trials

Sensitivity trials were used to assess the sensitivity of $RVLL$ management to several key estimation biases and violations of model assumptions supporting the calculation of $RVLL$. Taking a precautionary approach, biases were generally explored that would result in overestimating the bycatch limit relative to the level that would achieve management goals. The percentile for $\hat{N}'_{\min}$ was determined from the first base trial, and starting population size was $MNPL'$. Each sensitivity trial included the same four cases included in the base trials (two life histories, two levels for CV_N), simulated with f_u values of 1 and 0.5 (*sensu* Wade, 1998) to achieve a qualitative sense of the adjustment to f_u required to compensate for a given bias or model error. Starting age distribution in the biological model for each case in each trial was set as described for the base trials, i.e. approximating the stable age distribution for a bycatch-impacted population in steady state at $MNPL'$ (therefore potentially different in trials with different population dynamics or $\mathbf{u}_r$).

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The sensitivity trials, detailed in Table 3, can be organized into three groups: a broad survey of potential sources of bias and model error (Trials 1–10), an exploration of sensitivity to bias in stage-specific vital rates (Trials 11–14), and an exploration of sensitivity to different relative bycatch mortality rates with age (Trials 15–18). The sensitivity trials included biases that would lead to $\hat{N}'_{\min}$ being systematically overestimated (Trials 2 and 4), bycatch mortality being underestimated (Trials 3 and 5), and population productivity being overestimated (Trials 1, 11–14); stochastic population growth (Trial 6); increased periodicity of surveys to estimate adult abundance (Trial 7); mischaracterization of density dependence (Trials 8 and 9); and a pessimistic unstable starting age distribution (Trial 10, details below). For Trial 9, the alternative density-dependence scenario in the biological model resulted in stable age distributions and relative reproductive values corresponding to $\mathbf{A}_d$ that changed with population density, thus further evaluating the robustness of population estimation based on assumption of stable age distribution and relative reproductive values derived from $\hat{\mathbf{A}}_m$. To make results in Trials 11–14 comparable with Trial 1, where all vital rates were proportionally equally overestimated, the magnitude of overestimation of overall population productivity was the same.

Table 3. Specifications for sensitivity trials (see Appendix 1 for details and sources)

Trial	Description
(1)	$\lambda_m - 1$ overestimated by factor of two due to proportionally equal overestimation of all component vital rates
(2)	$n_{t,\text{adult}}$ overestimated by factor of two
(3)	C_t underestimated by factor of two
(4)	CV_N underestimated by factor of two
(5)	CV_C underestimated by factor of two
(6)	Stochastic population growth with CV of 0.02 for $P_{i,m}$, 0.35 for F_m (with range 0 to 110 for fast and 160 for slow), and no correlation among vital rates
(7)	Adult abundance survey periodicity of 5 years
(8)	Age classes in first juvenile stage not density-dependent nor contributing to carrying capacity
(9)	$\theta = 5$
(10)	Pessimistic scenario for unstable initial age distribution (see text for details)
(11)	$\lambda_m - 1$ overestimated by factor of two due to overestimation of $P_{1,m}$
(12)	$\lambda_m - 1$ overestimated by factor of two due to overestimation of $P_{2,m}$
(13)	$\lambda_m - 1$ overestimated by factor of two due to overestimation of $P_{\text{adult},m}$
(14)	$\lambda_m - 1$ overestimated by factor of two due to overestimation of P_m
(15)	Relative bycatch mortality rates with age were zero for age classes in first juvenile stage and constant for age classes in second juvenile stage and adults
(16)	Relative bycatch mortality rates with age were constant for age classes in first juvenile stage and zero for all other age classes
(17)	Relative bycatch mortality rates with age were increasing for age classes in second juvenile stage and zero for all other age classes
(18)	Bycatch mortality of adults only

Stochastic population growth was modelled by sampling survival probabilities in each year of the simulation from beta distributions and sampling fertility from a stretched beta distribution (Morris and Doak, 2002), with means given in $\mathbf{A}_d$ (as calculated for deterministic growth). The range for the stretched beta distribution was determined based on plausible ranges of component factors in fertility (more details in Appendix 1). The coefficients of variation for the beta distributions (Table 3) were based on published models of loggerhead population dynamics, which have relatively low variability compared to green turtles (Chaloupka, 2002; Chaloupka and Limpus, 2002).

To test explicitly the effect of unstable age distributions on management outcomes, unstable starting age distributions were set with a pessimistically high proportion of adults, so $\hat{N}'_{\min}$ and thus $RVLL$ would be overestimated. To generate possible starting age distributions, pre-simulations were conducted in which populations with fast or slow life histories were simulated for 20 or 60 years, respectively, in four scenarios of anthropogenic mortality: (1) reduction of survival in the first juvenile stage ($P_{1,m}$) to 0.85 its original value; (2) reduction of fertility (F_m) to 0.7 its original value; (3) reduction of both $P_{1,m}$ and F_m; and (4) reduction of F_m to zero for three consecutive years (note: reduction of $P_{2,m}$ alone shifted age structure to a lower proportion of adults than in the original population). Scenario 3 produced the highest ratios of adults to N'_t at any given time point (0.035 and 0.015 for fast and slow life histories, respectively, compared to 0.015 and 0.0068 in the first base trial), so the corresponding age distributions were used to initialize simulations for this sensitivity trial.

As for the first base trial, performance metrics included the percentage of simulated populations starting at $MNPL'$ to (1) remain above $MNPL'$ after 20 years, (2) maintain or increase in number of adults, and (3) go extinct. Results from sensitivity trials using $f_u = 1$ and 0.5 were compared with those from corresponding cases from the first base trial. For trials with alternative density-dependence scenarios, where $MNPL'$ varied from $0.5K$ (Trials 9 and 10), management outcomes were assessed

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using the $MNPL'$ solved numerically for that scenario and life history.

RESULTS

Base trials

For the first base trial, the greatest percentile for $\hat{N}'_{\min}$ at which more than 95% of the populations remained at or above $MNPL'$ after 20 years was the 20th percentile for the fast life history for both levels of CV_N, and, for the slow life history, the 25th percentile for the low CV_N and the 30th percentile for the high CV_N (Figure 4). For comparison, the proportion of populations whose adult abundance exceeded that of a population with stable age distribution and no bycatch at $MNPL'$ was much less in all cases (Figure 4), which can be expected since the relative proportion of adults at $MNPL'$ would be higher without age-dependent bycatch mortality. The highest percentile for $\hat{N}'_{\min}$ for which fewer than 5% of populations showed a decrease in adults from the starting abundance was the 15th percentile for the fast life history for both levels of CV_N, and, for the slow life history, the 30th percentile for the low CV_N and the 35th percentile for the high CV_N (Figure 5). Only populations with the fast life history go extinct within the 20-year simulation time frame. For populations with low CV_N, extinction likelihood was $< 1\%$. For

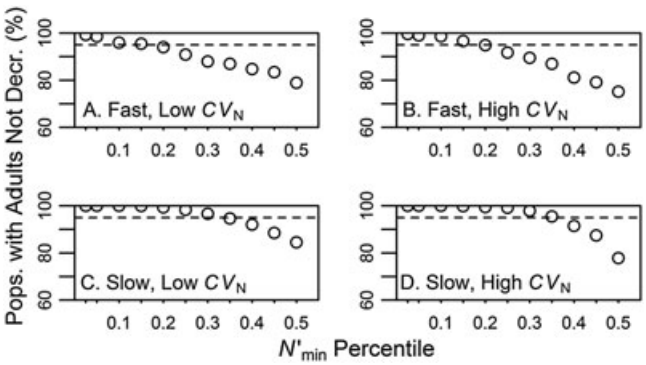

Figure 5. Results from first base trial, for population growth under $RVLL$-based management for 20 years, starting at $MNPL'$ and using a range of percentiles for $\hat{N}'_{\min}$, with $b = 0.5$ and $f_u = 1$: percentage of simulated populations with numbers of adults equal to or greater than original adult abundance. Panels show outcomes for (A) fast life history with low CV_N, (B) fast life history with high CV_N, (C) slow life history with low CV_N, and (D) slow life history with high CV_N. Black, dashed lines mark 95%.

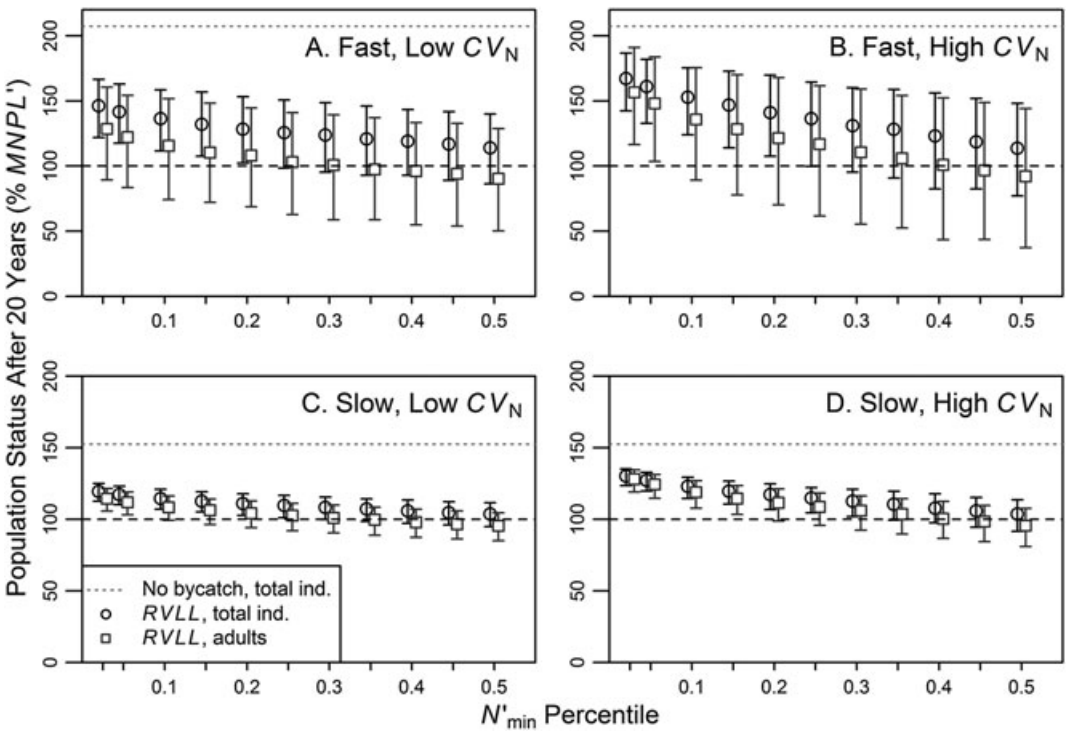

Figure 4. Results (medians and 90% confidence intervals) from first base trial, for population growth under $RVLL$-based management for 20 years, starting at $MNPL'$ and using a range of percentiles for $\hat{N}'_{\min}$, with $b = 0.5$ and $f_u = 1$. Population status, expressed as percentage, describes population size relative to $MNPL'$ (black), and adult abundance relative to that at $MNPL'$ (for a stable age distribution without bycatch, grey). Panels show outcomes for (A) fast life history with low CV_N, (B) fast life history with high CV_N, (C) slow life history with low CV_N, and (D) slow life history with high CV_N. Grey, dotted lines indicate percentage $MNPL'$ attained by an equivalent population without bycatch. Black, dashed lines represent $MNPL'$.

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populations with high CV_N, extinction likelihood exceeded 1% when using the 25th percentile for $\hat{N}'_{\min}$, increasing to 3.5% when using the 50th percentile. To satisfy all three performance criteria, percentiles for $\hat{N}'_{\min}$ used in further simulations were the 15th percentile for the fast life history type and the 30th percentile for the slow life history.

Relative performance of slow versus fast life histories and low versus high CV_N followed expectation and echoed the results seen in Wade (1998). Abundance estimation error led to variable population growth rates under the modelled bycatch management regime. Since average growth rate over time is the geometric mean of annual growth rates, a given proportional level of variance in growth rate is expected to lead to a greater decrease in average population growth rate at higher population growth rates.

For the second base trial, we sought the highest value of f_u sufficient for 95% of simulated populations to recover to $MNPL'$ within a time period no greater than 10% (or, in one case, 10.1%) longer than would be required by an unimpacted population. The value of f_u that achieved this criterion was 0.1 for the fast life history at low CV_N and 0.15 at high CV_N, and 0.1 for the slow life history at low and high CV_N (Figure 6). Thus $f_u = 0.1$ would achieve this goal across all four scenarios; this is the same value recommended for recovering populations by Wade (1998). As with the first base trial, population outcomes measured in terms of final adult abundance (relative to that of a population with stable age distribution and no bycatch at $MNPL'$) were generally worse than performance measured in terms of total population size (Figure 6). As in the first base trial, only populations with fast life histories go extinct, reaching 1% probability at $f_u = 1$, for populations with a low CV_N and at $f_u = 0.75$ for populations with a high CV_N.

Sensitivity trials

Results for the first group of sensitivity trials (Trials 1–10) are shown for fast and slow life histories at low

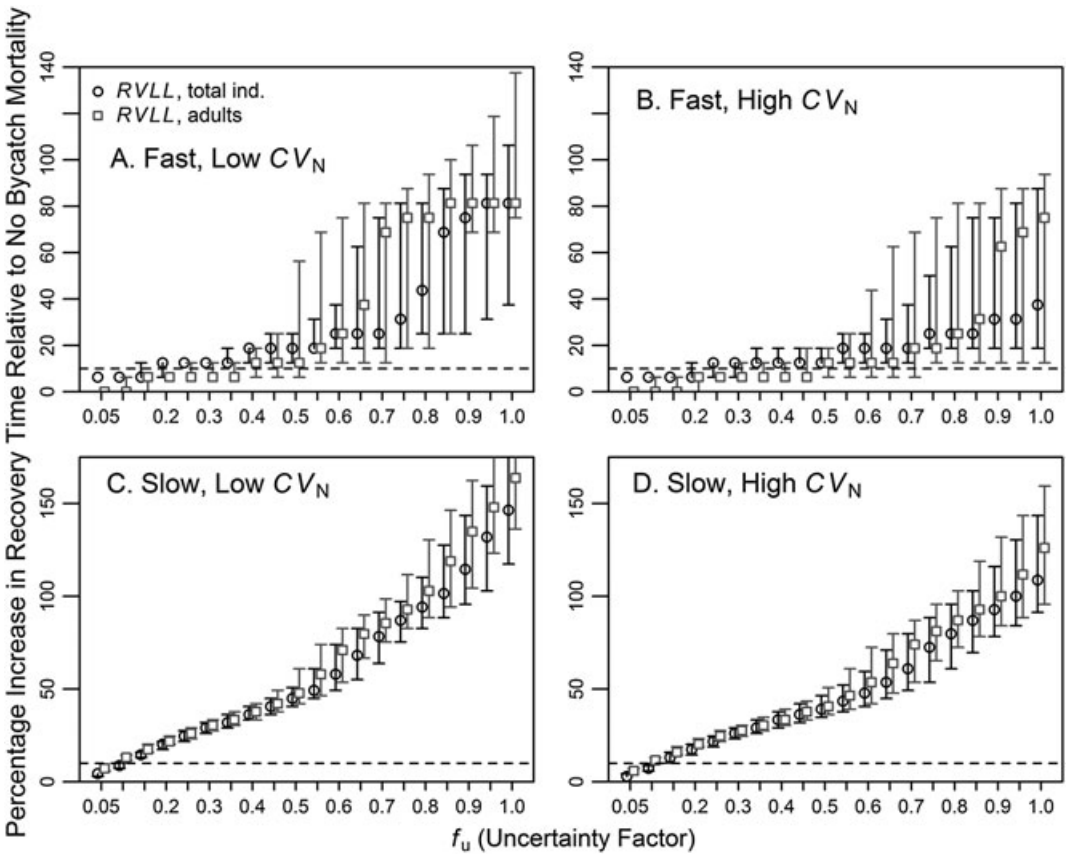

Figure 6. Results from second base trial, for population growth under *RVLL*-based management, starting at 0.05 *K* and using 15th and 30th percentiles for $\hat{N}'_{\min}$ for fast and slow life histories, respectively, over a range of values for f_u: percentage difference in recovery time, compared with population without bycatch, to $N_K = MNPL'$ (black) and adult abundance at $MNPL'$ (for stable age distribution without bycatch, grey). Panels show outcomes for (A) fast life history with low CV_N, (B) fast life history with high CV_N, (C) slow life history with low CV_N, and (D) slow life history with high CV_N. Black, dashed line marks 10%.

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CV_N only (Figure 7), since the patterns are similar to those at high CV_N. Adjusting f_u from 1 to 0.5 mitigated most tested biases and violations of assumptions sufficiently to meet all three performance criteria. Management outcomes were most sensitive to overestimation of λ_m (Trial 1), overestimation of adult female abundance (Trial 2), underestimation of total bycatch mortality (Trial 3), and a pessimistic unstable starting age distribution (Trial 10). Other biases in estimated population parameters also negatively affected performance relative to the base trial, but to a lesser degree. Underestimation of CV_N and CV_C, plausible stochastic population growth, and increased survey periodicity (Trials 4–7) all increased the spread of population outcomes relative to $MNPL'$ for both life histories and led to worse outcomes for populations in the lower end of the distribution relative to the first base trial. Only for populations with the fast life history did extinction probability increase compared with the first base trial at $f_u = 1$. This occurred in all of the above trials except overestimation of λ_m (Trial 1), a pessimistic unstable starting age distribution (Trial 10), and stochastic population growth (Trial 6). Since extinction was defined as a population falling below 25 adult females at any point during the simulation, non-adult components of the population might remain substantial – indeed, in all cases of 'extinction,' large numbers of juveniles recruited to reproductive age within a few years (data not shown, but note confidence intervals for population status in Figure 7). Trial 10 (pessimistic unstable starting age distribution) was exceptional in being the only trial for which $f_u = 0.5$ was insufficient to meet or nearly meet the second performance criterion concerning the number of adults in the population (Figure 7). This outcome can be expected given that the starting number of adults in the population in this trial was greater than it would be at stable age distribution at $MNPL'$ even without

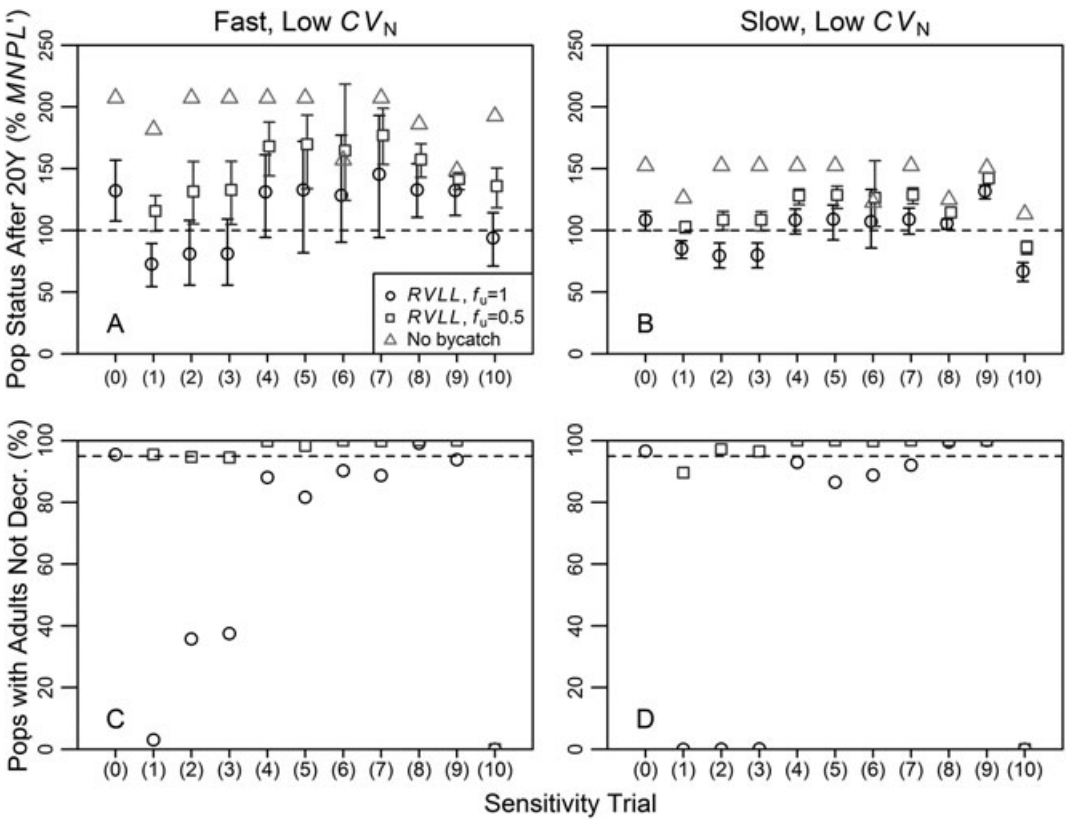

Figure 7. Results for sensitivity trials of population growth under *RVLL*-based management for 20 years, starting from $K/2$, using 15th and 30th percentiles for $\hat{N}'_{\min}$ for fast and slow life histories, respectively, with f_u equal to 1 or 0.5. Results of corresponding case from first base trial with $f_u = 1$ (0) are plotted for comparison. Bias trials represent a broad survey of potential sources of bias and model error: (1) overestimated λ_m, (2) overestimated adult abundance, (3) underestimated bycatch mortality, (4) underestimated CV_N, (5) underestimated CV_C, (6) stochastic population growth, (7) increased survey periodicity, (8) misparameterization of density dependence in terms of type (age classes in first juvenile stage not density dependent nor contributing to density) and (9) response (θ =5), and (10) pessimistic unstable starting age distribution. (A, B) Resulting population status as percentage $MNPL'$, shown as medians with 90% confidence intervals. Triangles are outcomes for equivalent populations without bycatch. Black, dashed line indicates $MNPL'$. (C, D) Percentage of populations with final number of adults equal to or greater than original adult abundance. Black, dashed line marks 95%. Panels show outcomes for fast life history with low CV_N (A and C) and slow life history with low CV_N (B and D).

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bycatch. Thus, this result probably reflects the population settling into a new age-structure consisting of proportionally fewer adults. Finally, violating the assumption of age-structured logistic density dependent growth by changing either stages involved in density dependence (Trial 8) or density dependent response (θ; Trial 9) resulted in similar population outcomes at $f_u = 1$; indeed, they improved for true θ =5 in the slow life history cases (Figure 7).

For the sensitivity trials to assess effects of bias in stage-specific vital rates (Trials 11–14) and different relative bycatch mortality rates with age (Trials 15–18), results are shown for the fast life history at low CV_N only, as these are representative of the patterns seen in other cases. Overestimation of population productivity due to overestimation of only survival in the first juvenile stage (Trial 11) or of only fertility (Trial 14) resulted in worse outcomes than other variations, including overestimation of all vital rates (Trial 1, Figure 8). In contrast, outcomes when only adult survival rates were overestimated (Trial 13) were only marginally worse than for the base trial (Figure 8). The relative reproductive values for the true transition matrices in Trials 13 and 14 were almost identical (Table 4), indicating that bias in estimation of relative reproductive values did not cause the disparity in performance. Rather, the sensitivity of outcomes to bias in different vital rates seems to reflect different effects on population estimation and different time lags before the bias in *RVLL* estimation becomes evident in the monitored adult abundance. Overestimating fertility (Trial 14) or early-juvenile survival (Trial 11) results in routine overestimation of relative abundances in young age classes (due to population assessment based on assuming a stable age distribution drawn from a biased transition matrix), as well as overestimation of population productivity. The resulting overestimation of *RVLL* continues for many years before the affected cohorts recruit to the monitored, adult portion of the population.

The sensitivity of management outcomes to the functional form of relative bycatch mortality rates with age (Trials 15–18) is generally low (Figure 9), except in the case where all bycatch occurs on the first juvenile stage (Trial 16). Performance in this trial is governed by similar mechanisms as for Trials 11 and 14: exclusive take from the first juvenile stage would result in a large change in effective survival rates for that stage, not captured by the population assessment based on a stable age distribution for an unaffected population. The consequent routine overestimation of allowable take, focused on early juveniles, would not be reflected in the surveyed number of nesting females for many years, resulting in a considerable decline in population status before takes are adjusted downward.

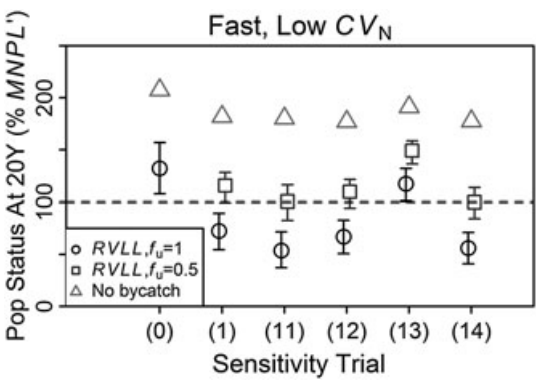

Figure 8. Resulting population status as percentage *MNPL′*, shown as medians with 90% confidence intervals, for exploration of sensitivity to bias in stage-specific vital rates in sensitivity trials of population growth for fast life history with low CV_N under *RVLL*-based management for 20 years, starting from $K/2$, using the 15th percentiles for $\hat{N}'_{min}$, with f_u equal to 1 or 0.5. Triangles are outcomes for equivalent populations without bycatch. Results of corresponding case from first base trial with $f_u = 1$ (0) are plotted for comparison. Bias trials shown all have the same estimated and true λ_m: (1) overestimated λ_m due to proportionally equal overestimation of all component vital rates, (11) overestimated λ_m due to overestimation of $P_{1,m}$, (12) overestimated λ_m due to overestimation of $P_{2,m}$, (13) overestimated λ_m due to overestimation of $P_{\text{adult},m}$, and (14) overestimated λ_m due to overestimation of F_m. Black, dashed line indicates *MNPL′*.

DISCUSSION

Robustness of *RVLL* as a management tool

A general architecture has been provided for how PBR-based management can be extended, in the form of the *RVLL* management tool and an MSE-like approach, to address bycatch of populations with strongly age-structured population dynamics and age-dependent bycatch mortality. In these situations, management based on individuals (i.e. PBR) fails (Appendix 3). It was specifically shown how management based on *RVLL* could maintain populations with life histories and uncertainties typical for marine turtles at some desired minimum level relative to carrying capacity and limit the impact of fisheries (and potentially other anthropogenic sources of harm) on the time required to recover populations from low levels to management targets. Results from sensitivity trials suggest that the *RVLL* management approach presented here can be robust (given precautionary

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Table 4. Relative reproductive values (scaled to reproductive value of adults) for $\mathbf{A}_m$ for fast life history used in sensitivity trials addressing bias in vital rates. Bias in estimation of population productivity is due to specified vital rates.

Trial	Age class											
	1	2	3	4	5	6	7	8	9	10	11	adult
base	0.015	0.024	0.038	0.061	0.097	0.156	0.212	0.289	0.394	0.538	0.733	1
(1) all	0.015	0.024	0.038	0.061	0.097	0.156	0.212	0.289	0.394	0.538	0.733	1
(11) $P_{1,m}$	0.010	0.019	0.037	0.070	0.136	0.262	0.328	0.410	0.512	0.640	0.800	1
(12) $P_{2,m}$	0.010	0.014	0.021	0.031	0.045	0.067	0.104	0.165	0.258	0.406	0.637	1
(13) $P_{\text{adult},m}$	0.039	0.057	0.083	0.122	0.179	0.262	0.328	0.410	0.512	0.640	0.800	1
(14) F_m	0.039	0.057	0.083	0.122	0.179	0.262	0.328	0.410	0.512	0.640	0.800	1

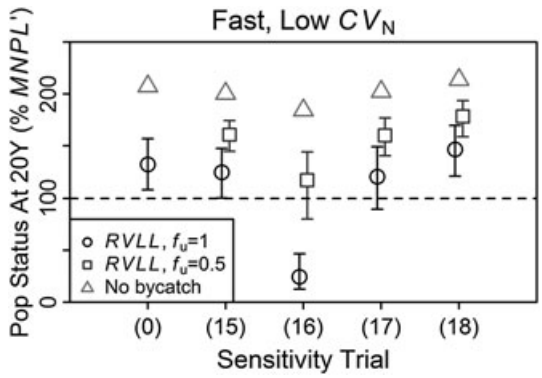

Figure 9. Resulting population status as percent $MNPL'$, shown as medians with 90% confidence intervals, for exploration of sensitivity to different relative bycatch mortality rates with age in sensitivity trials of population growth for fast life history with low CV_N under $RVLL$-based management for 20 years, starting from $K/2$, using the 15th percentiles for $\hat{N}'_{\min}$, with f_u equal to 1 or 0.5. Triangles are outcomes for equivalent populations without bycatch. Results of corresponding case from first base trial with $f_u = 1$ (0) are plotted for comparison. Bias trials shown are: (15) constant bycatch mortality with age starting from the first age class in the second juvenile stage (zero for the first juvenile stage), (16) relative bycatch mortality rates with age constant for age classes in first juvenile stage and zero for all other age classes, (17) relative bycatch mortality rates with age were increasing for age classes in second juvenile stage and zero for all other age classes, and (18) bycatch mortality of adults only. Black, dashed line indicates $MNPL'$.

specification of the percentile for $\hat{N}'_{\min}$ and the value for f_u as determined through simulation) to many important sources of uncertainty in assessing marine turtle populations and fisheries impacts (NRC, 2010). These uncertainties include biased estimates of potential population growth and of stage-specific vital rates, interannual variation in the number of clutches per female and remigration interval (evaluated via simulation of environmental stochasticity), imprecision and bias in bycatch mortality and female abundance estimates, unknown and biased abundances in non-adult age classes due to biased vital rate estimates and unstable age structure (the latter was evaluated implicitly in all simulations, and simulated explicitly in the sensitivity trial of a pessimistic unstable starting age structure), probable misspecification of the density-dependence form and response, and stochastic population growth.

We find it encouraging that the proposed $RVLL$ management approach appears robust to several likely violations of model assumptions and to some key uncertainties that are likely to remain poorly characterized for marine turtle populations. For example, misspecification of density-dependent dynamics seems highly probable, but a precautionary value for b was specified, and sensitivity trials 8 and 9 revealed that departures in the operating model from population growth assumptions for management (i.e. simple logistic growth, with all individuals in the population competing equally and $\theta = 1$) did not prevent management goals from being met at $f_u = 1$ (Figure 7). Therefore, we caution against basing b on a more complex form of density dependence unless there is strong evidence that certain stages do not exhibit density-dependent vital rates, or another form of density corresponds to a more conservative value for b at the desired management target relative to K. However, further exploration of the effect of structural error in the biological model on management outcomes is warranted (Hill *et al.*, 2007). Bias in relative reproductive values, while not explored in depth, also appears to have little effect on management outcomes (Table 4 and Figure 8). Finally, the stable-age-distribution assumption used for population assessment is likely to be violated in most real-world situations, yet the actual age structure for marine turtle populations will probably remain unknown, at least in the near term. These results suggest that even with a pessimistically high starting ratio of adults to other stages in the population or systematically severely biased estimates of the age distribution, effects on management outcomes can be mitigated by accounting for the uncertainty in parameterizing the equation for $RVLL$ (Figures 7–9).

The method was most sensitive to factors that both led to $RVLL$ being a severe, systematic overestimate and produced delayed or gradual feedback to the monitored adult abundance. Such factors included

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overestimation of potential population productivity (λ_m) due to overestimation of fertility or juvenile survival rates, systematic overestimation of adult abundance, systematic underestimation of true bycatch mortality, a pessimistic unstable starting age distribution, and bycatch mortality acting on early juveniles only (the latter could be dealt with easily by choosing an appropriate percentile for $\hat{N}'_{\min}$ for that selectivity). Thus, particularly careful consideration should be given to specification of fertility, juvenile survival rates, and $\hat{\lambda}_m$, using conservative estimates that are unlikely to be biased high and that take into account the effect of environmental stochasticity. Equal care should be taken in designing simulations to evaluate the tool's performance and to select appropriate values for the percentile of the abundance estimate for $\hat{N}'_{\min}$ and for f_u in the *RVLL* equation for a particular population. We suggest using precautionary parameter estimates and carefully specifying plausible scenarios and ranges of precision and bias for simulation. The long generation time of marine turtles makes precaution in parameterization and evaluation of such a management model all the more important, since negative management outcomes may not be evident for many years; however, it also allows time to correct for mistakes or adapt to new knowledge. These sensitivity results also highlight the importance of focusing research to improve estimation of bycatch mortality (via increasing scientific observer programme coverage), abundance, and vital rates.

Next steps in developing *RVLL*

The evaluation presented here was an extensive, but not comprehensive, exploration of uncertainty that partly paralleled that conducted by Wade (1998) for PBR and, further, explored some uncertainties and assumptions introduced by the extension of the model to a matrix population context. Simulated bycatch CV and bias levels did not consider error in age attribution of size-classified bycatch data, or in attributing mortality to the correct population or management unit where multiple units interact with the same fishery; these are considered major sources of uncertainty in assessing population impacts of bycatch mortality (NRC, 2010; Wallace *et al.*, 2010b). Simulated levels of abundance estimation uncertainty and bias did not account for uncertainty and temporal variability in stage duration or age at first reproduction. A parallel effort, which did include variation in stage duration, concluded that estimation error in reproductive value would be an important source of uncertainty in determining appropriate mortality limits in terms of reproductive value for marine turtles (Heppell, 2011). These sources of error need to be explored further and accounted for in setting the percentile for $\hat{N}'_{\min}$ and the value for f_u as part of any implementation of the *RVLL* model in a real-world management context. In general, any factors contributing to uncertainty in $\hat{N}'_{\min}$, including not only adult abundance estimation but also uncertainty in relative reproductive values and age distribution of the population of interest, might logically be addressed by including them in determination of the appropriate percentile for $\hat{N}'_{\min}$.

As implied in the above discussion, variation in simulated management outcomes across a representative range of life history types, CV_N levels, and other uncertainties (Figures 4–9) suggests that implementation of *RVLL*-based management in reality should be based on MSEs specific to individual marine turtle populations (or at least species) to appropriately parameterize the *RVLL* equation. These analyses should address case-specific issues with data availability, potential biases and other forms of uncertainty, and management goals (e.g. acceptable level of risk). Exploring these issues for individual marine turtle populations should be feasible given the relatively small number of species and suggested regional management units for marine turtles, even at the global level (Wallace *et al.*, 2010a).

Additional considerations for population-specific analyses include robustness of the method to combinations of multiple biases, serial correlation in stochasticity of vital rates in time or among stages (e.g. due to varying carrying capacity), higher levels of stochasticity in population growth rates, unresolved population structure among nesting beaches, and potential for depensation at very low population sizes (Chaloupka and Balazs, 2007). Some bycatch may be completely unobservable (Warden and Murray, 2011), leading to additional bias in bycatch estimates that will be problematic for any form of impact assessment or management approach. Consideration should also be given to the effects of historic and ongoing anthropogenic mortality on population variability, life history, and productivity in marine turtles (Ernande *et al.*, 2004; Gallucci *et al.*, 2006; Anderson *et al.*, 2008). In some cases, it may be appropriate to compare the performance of *RVLL*

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with that of other potential management models (e.g. adult or stage-based PBR; Gerrodette, 1996). Finally, the analysis presented here focused on conservation objectives only, but given information on mitigation options and associated economic costs, case-specific MSEs could also examine tradeoffs between conservation and economic or other objectives of interest (Maunder *et al.*, 2000).

Operationalizing *RVLL*

Using *RVLL* as a management tool is fairly straightforward in theory. To calculate *RVLL*, one must estimate the Leslie-Lefkovitch matrix ($\mathbf{A}_m$) and adult female population abundance, from which the *RVLL* parameters ($\hat{\lambda}_m$ and $\hat{N}'_{\min}$) can be derived. Evaluating whether anthropogenic mortality exceeds *RVLL* requires recording size distribution data for killed animals, converting these to age (or stage), and using the estimated reproductive value vector $\hat{\mathbf{v}}_m$ (from $\hat{\mathbf{A}}_m$) to convert the mortality estimate to units of reproductive value. If this value exceeds *RVLL*, mitigation measures to reduce bycatch to levels below this limit should be triggered.

In practice, estimating these parameters may be a key challenge, although this is no different from any fisheries stock assessment problem. With respect to estimating $\mathbf{A}_m$, empirical estimates of life history parameters exist for several sea turtle populations, and the life-history of long-lived late-maturing species constrains vital rates to relatively narrow plausible ranges. Estimates derived from life-history theory or surrogate species are viable alternatives. The objective is to approximate reality well enough and conservatively enough to accomplish management goals. This is the principle behind default precautionary estimates of $R_{\max}$ used in PBR management of marine mammals and indeed in vital rate parameters used in many target fish stock assessments. Cases will most likely arise for which the *RVLL* tool is not applicable, for example due to a lack of basis for estimating abundance for adult females, bycatch mortality, or population productivity. There are also issues with estimating adult abundance from turtle nest counts (Richards *et al.*, 2011), systematically underestimating bycatch (Warden and Murray, 2011), attributing animals of particular size to a particular life stage (Goshe *et al.*, 2010), and so on. But in most cases, given reasonable and conservative approximations to key parameters, it is the role of MSE-like analyses to ensure that the *RVLL* equation, when initially parameterized for a given population, will be robust to plausible uncertainties in terms of its ability to achieve management objectives. Once parameterized and tested for populations of interest, the *RVLL* tool would be straight-forward to calculate annually, and would provide a consistent, transparent basis for decision-making (e.g. across species and fisheries).

There will be other factors to address in practice that are beyond the scope of this initial framework development. For example, there will be unavoidable time lags between data collection, assessment, and management response. Comparing running averages (rather than annual estimates) of human-caused mortality and *RVLL* may be prudent to reduce management volatility that otherwise stem from random process and sampling variance. Such issues are common to fisheries management and will need to be explored more fully and considered in developing a real world management framework based on *RVLL*.

Using *RVLL* to assess cumulative and indirect impacts

We have discussed the *RVLL* management tool in a modelling context where bycatch mortality is the sole source of anthropogenic mortality on the population and all bycatch mortality (across all fisheries) is evaluated cumulatively. Impacts from all forms of direct mortality (egg poaching, hunting, boat strikes, etc.), including delayed mortality, could likewise be incorporated into an evaluation of takes against *RVLL* to inform management, provided they can be quantified in the same manner as bycatch. Less clear-cut is how one might quantify sublethal effects on population growth or deal with indirect mortality (such as by introduced predators), habitat degradation, declining ecosystem productivity, and decreasing carrying capacity, which are recognized weaknesses of the original PBR management framework for marine mammals (Goodman, 2005; Moore, in press). For marine turtles, the use of nest counts rather than direct counts of adults for abundance estimation might help account for declining population productivity. In any case, management decisions, which will generally address impacts from a single mortality source out of many (e.g. bycatch mortality from one of multiple national fishing fleets affecting a population), will probably present a considerable challenge, though a biologically meaningful approach to that problem has been proposed (T. Eguchi, NOAA Southwest Fisheries Science Center, pers. comm.). Ultimately,

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addressing direct anthropogenic mortality as informed by *RVLL* should only be one of a suite of management tools, including conservation of critical habitat and ecosystem function.

CONCLUSIONS

The National Research Council (NRC, 2010) concluded that we first need better data, then better assessments for marine turtles. In the meantime, a precautionary management approach, as prescribed by the FAO Code of Conduct for Responsible Fisheries, requires that we find ways to manage our impacts on marine biodiversity based on the best available scientific information, rather than postponing management decisions. This requires developing management tools that are robust to current uncertainties, rather than waiting for data or assessments that may not be feasible to obtain or complete (Taylor *et al*., 2000). The *RVLL* tool proposed, combined with MSE, provides the general architecture for managing age-structured, data-limited populations based on data types currently available or obtainable for many (though probably not all) marine turtle populations, while explicitly accounting for uncertainty and evaluating robustness. The tool has proven robust to several key uncertainties and can be further evaluated and tuned through MSE to deal with unaddressed uncertainties inherent to the matrix population model context and to adapt it to specific situations and mortality sources.

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