

INCORPORATING KNOWN SOURCES OF UNCERTAINTY TO DETERMINE PRECAUTIONARY HARVESTS OF SALTWATER CROCODILES

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Abstract. It has been demonstrated repeatedly that the degree to which regulation operates and the magnitude of environmental variation in an exploited population will together dictate the type of sustainable harvest achievable. Yet typically, harvest models fail to incorporate uncertainty in the underlying dynamics of the target population by assuming a particular (unknown) form of endogenous control. We use a novel approach to estimate the sustainable yield of saltwater crocodile (*Crocodylus porosus*) populations from major river systems in the Northern Territory, Australia, as an example of a system with high uncertainty. We used multimodel inference to incorporate three levels of uncertainty in yield estimation: (1) uncertainty in the choice of the underlying model(s) used to describe population dynamics, (2) the error associated with the precision and bias of model parameter estimation, and (3) environmental fluctuation (process error). We demonstrate varying strength of evidence for density regulation (1.3–96.7%) for crocodiles among 19 river systems by applying a continuum of five dynamical models (density-independent with and without drift and three alternative density-dependent models) to time series of density estimates. Evidence for density dependence increased with the number of yearly transitions over which each river system was monitored. Deterministic proportional maximum sustainable yield (PMSY) models varied widely among river systems (0.042–0.611), and there was strong evidence for an increasing PMSY as support for density dependence rose. However, there was also a large discrepancy between PMSY values and those produced by the full stochastic simulation projection incorporating all forms of uncertainty, which can be explained by the contribution of process error to estimates of sustainable harvest. We also determined that a fixed-quota harvest strategy (up to $0.2K$, where K is the carrying capacity) reduces population size much more rapidly than proportional harvest (the latter strategy requiring temporal monitoring of population size to adjust harvest quotas) and greatly inflates the risk of resource depletion. Using an iconic species recovering from recent extreme overexploitation to examine the potential for renewed sustainable harvest, we have demonstrated that incorporating major forms of uncertainty into a single quantitative framework provides a robust approach to modeling the dynamics of exploited populations.

Key words: Australia; *Crocodylus porosus*; density dependence; harvest; maximum sustainable yield; Northern Territory; process error; recovery; regulation; saltwater crocodile; time series; uncertainty.

INTRODUCTION

The theory of sustainable harvest of renewable animal and plant resources and our understanding of the mechanisms influencing variation in population size have advanced greatly in recent years (Lande et al. 1997). This is particularly apparent in fisheries science as a result of increasing computing power and more complex statistical modeling approaches (Beddington and Kirkwood 2005). However, despite this increasing sophistication, there is no unifying and generalized

methodology yet available to prescribe effective harvesting protocols, especially given that most biological systems are characterized by high uncertainty. Generalized approaches are particularly important for the large number of marine and terrestrial species facing direct exploitation by humans yet lacking robust data (Groombridge 1992, Fryxell et al. 2005) and for assessing the manner in which the frequency and magnitude of exploitation will increase as the global human population expands (Jackson et al. 2001, Pauly et al. 2002).

We do know that the choice of a particular harvesting policy can greatly influence variation in stock density over time. Traditionally, fixed-quota harvesting (removing a constant number of individuals) was, and in many cases still is, the mainstay of many resource management policies, especially in commercial fisheries (Rosenberg et al. 1993). However, notwithstanding the appeal of its relative simplicity of application, this policy tends to

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increase the probability of population collapse (Beddington and May 1977, Walters 1986, Lande et al. 1995, Fryxell et al. 2005) because it does not provide a compensatory mechanism to accommodate environmental variation (Fryxell et al. 2005). Thus, other harvesting policies have found favor in recent years (Ludwig et al. 1993, Pascual and Hilborn 1995), including fixed-proportion (removing a constant proportion of the population) and fixed-threshold (removing individuals only when the population exceeds a certain density) harvesting (Lande et al. 1995, 1997). The cost of employing the latter policies is that they require a regular assessment of population status and a constant adaptive readjustment of harvest limits, a requirement that may be expensive to implement and difficult to manage efficiently (Fryxell et al. 2005).

Assessment of environmental variability (process error) experienced by an exploited population is central to the determination of maximum sustainable yield using any applied harvest policy (Jensen 2005). Indeed, it has been shown that increasing environmental variability can reduce a population's capacity to sustain harvest (Beddington and May 1977, Bayliss 1989, Ludwig et al. 1993, Milner-Gulland et al. 2001), which is one reason why fixed-quota harvests tend to result in overexploitation in highly variable systems (Fryxell et al. 2005). Another consideration is the degree to which uncertainty in harvest model parameters propagates to estimates of supportable offtake rates (Ludwig 1999), especially if observation error spuriously inflates estimates of parameter variance (De Valpine and Hastings 2002). Approaches have been developed to account for parameter uncertainty in population models (Taylor 1995) and decision-making theory (Berger 1985), with simulation techniques providing particularly powerful results (Bolker 2003, Lehodey et al. 2003, Little et al. 2005).

Another fundamental consideration for models estimating the sustainability of harvest is the degree to which regulation operates in an exploited population because this has direct implications for a population's capacity to compensate for offtake (Boot and Gullison 1995, Freckleton et al. 2003). Classically, a single dynamical model has been assumed (e.g., Beverton and Holt 1957, Fox 1970). Yet this approach implicitly assumes complete knowledge of the underlying dynamical processes and the degree to which regulation operates on the exploited population. Although species-specific estimates of the strength of density dependence exist for some exploited taxa (e.g., Myers et al. 1999), some argue a precautionary approach should assume only weak density dependence unless there is strong evidence to the contrary (Beddington and Kirkwood 2005). A recent study assessed the relative support for particular models within a harvesting framework based on experimental data (Fryxell et al. 2005), although their selection of a single "best" model using parsimony trade-offs still ignores the relative contribu-

tion of extrinsic and intrinsic control in population dynamics (Brook and Bradshaw 2006). A more overarching method of addressing this uncertainty is to use multimodel inference based on information theory to incorporate the full range of density-independent to fully density-dependent population dynamical models in a unified inferential framework to describe population trends (Brook and Bradshaw 2006). However, uncertainty in the choice of models used to understand the dynamics of exploited populations, uncertainty in the parameter estimates derived from those models (Ludwig 1999), and uncertainty in the environmental conditions driving population change over time (Ludwig et al. 1993, Brook and Whitehead 2005) have rarely been incorporated simultaneously into analyses that attempt to provide direction in the management of exploited populations. Indeed, full model uncertainty should be combined with estimates of parameter error through model averaging (Burnham and Anderson 2002) coupled with simulation approaches that incorporate process (environmental) error.

Species recovering from past exploitation offer the opportunity to examine the combined effects of uncertainty in past and future harvest policies. One large species that was heavily exploited in recent times is the saltwater (estuarine) crocodile (*Crocodylus porosus*) of northern Australia. Intensive commercial hunting for the skin trade began in Australia in 1945 and resulted in the depletion of crocodile numbers across northern Australia (Messel and Vorlicek 1986, Stirrat et al. 2001, Read et al. 2004). The largely uncontrolled exploitation continued until the early 1970s before an export ban was imposed and full legal protection was established in 1972 (Messel and Vorlicek 1986). Although there are no definitive data on the population size immediately after protection, it is estimated that the total harvest during the period was 330 000 animals (Webb et al. 1984, 1987, Webb and Manolis 1993a, b). In 1975, *C. porosus* was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Webb and Manolis 1993b), and in 1979, all Australian populations of *C. porosus* were transferred to Appendix I, which includes species considered to be threatened with imminent extinction (Jenkins 1987).

Extensive abundance surveys were initiated across northern Australia during the 1970s (Messel et al. 1979–1986, Bayliss et al. 1986), and they have continued to varying degrees since that time (Stirrat et al. 2001, Read et al. 2004). These monitoring programs have consistently shown that the rate of population increase following legal protection has varied between river systems. Recent surveys in the Northern Territory suggest that some river systems are approaching carrying capacity due to notable reductions in the rate of population increase (Fukuda 2004). The apparent recovery has led to a recent proposal by the Northern Territory government to initiate a form of exploitation of crocodile populations through regulated recreational

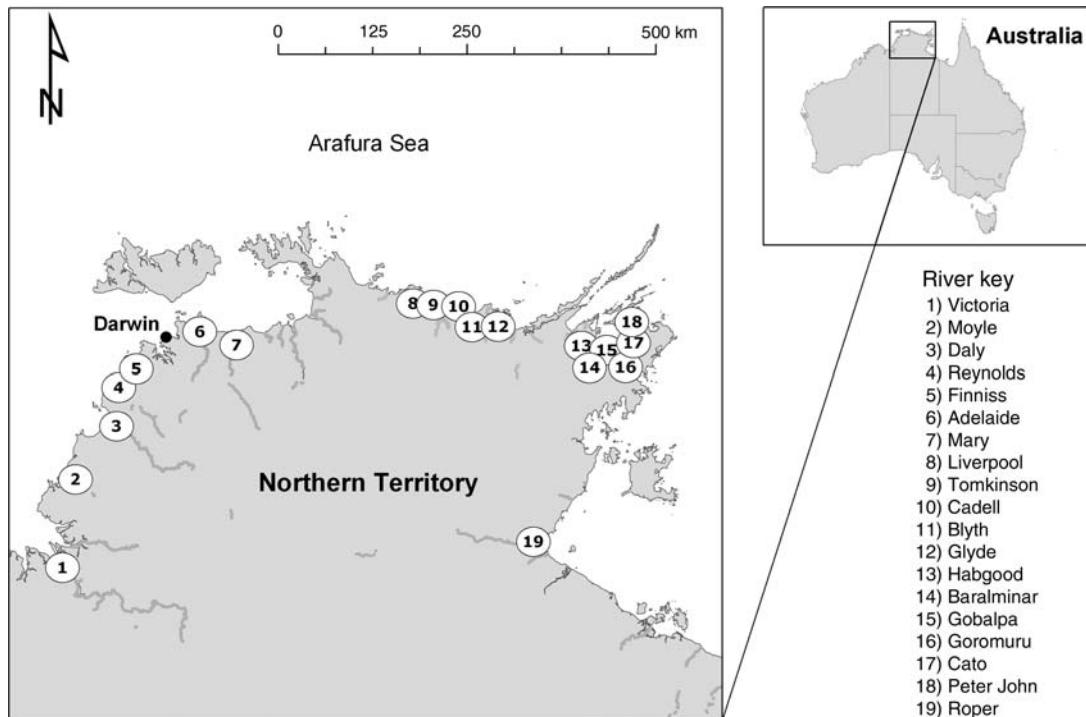


FIG. 1. Map of northern Northern Territory, Australia, showing the approximate positions of the 19 river systems examined.

hunting, stirring considerable community debate on the ethics and sustainability of harvest (ABC 2004, Bowman 2005, Letnic 2005). Resolution of this issue and the population's acknowledged vulnerability to overexploitation demands a quantitative appraisal of its capacity to withstand harvesting. Moreover, given the variable rates of population change, a river-specific harvest management plan may prove to be a useful tool for managing these populations.

The fortunate circumstance of having access to detailed crocodile monitoring data for many major river systems in the Northern Territory provides an excellent test case to develop a sustainable harvest framework incorporating known sources of uncertainty and to assess exploitation potential for this species. Therefore, in this paper we examine the time series data available for the saltwater crocodile populations in 19 river systems in the Northern Territory of Australia to provide: (1) evidence for density-regulated variation in the population rate of change using a novel multimodel inference approach (Brook and Bradshaw 2006); (2) robust estimates of sustainable proportional harvest levels (and the resultant yield) for each river system based on multimodel inference, parameter uncertainty, and environmental variability; and (3) a quantitative comparison of the stochastic approach incorporating these sources of uncertainty with more classic estimates of maximum sustainable yield. The methodology we develop to weave a number of strands of uncertainty into a single modeling framework provides a robust

approach to modeling the dynamics of exploited populations for which time series monitoring data are available.

METHODS

Time series data

Crocodile density data were collected during extensive surveys in the major Northern Territory river systems conducted by a number of organizations since legal protection. The data sets were provided by Parks and Wildlife Service of the Northern Territory and Wildlife Management International (Darwin). When combined, these data sets cover most of the species' distribution in the Northern Territory, although the continuity and length of the data sets differ among river systems. The river systems examined were the Adelaide, Mary, Victoria, Moyle, Daly, Reynolds, Finnis, Liverpool, Tomkinson, Blyth, Cadell, Glyde, Habgood, Baralminar, Gopalpa, Goromuru, Cato, Peter John, and Roper Rivers (Fig. 1). Surveys occurred in certain sections of river systems comprised of mainstream and side creeks (tributaries). We assume that each river system represents a unique population that is modeled in isolation. This assumption appears valid (especially over the duration of a typical management plan) given that there is evidence for genetic structuring of populations across different river systems, although some longer-term gene flow is likely (FitzSimmons et al. 2004).

Data were collected during either spotlight (Adelaide, Mary, Victoria, Moyle, Daly, Reynolds, Finnis, Liver-

TABLE 1. Nineteen river systems for which time series abundance data are available for saltwater crocodiles in the Northern Territory, Australia.

River system	Survey coverage (years)	Survey type	q	r_{MA}	AIC _c model weight					%wtDD	Carrying capacity (K)	
					RW	EX	RL	GL	TL		K_{DD}	K_{MA}
Victoria	1989–1999	helicopter	8	0.616	0.654	0.101	0.140	0.102	0.002	24.4	0.491	0.649
Moyle	1978–2002	spotlight	5
Daly	1978–2002	spotlight	16	0.298	0.055	0.123	0.391	0.368	0.064	82.2	4.546	4.681
Reynolds	1983–1998	spotlight	13	0.114	0.647	0.171	0.084	0.088	0.010	18.3	5.225	6.667
Finniss	1983–1998	spotlight	14	0.889	0.224	0.057	0.228	0.434	0.057	71.9	0.846	1.037
Adelaide	1977–2002	spotlight	21	0.131	0.575	0.196	0.115	0.071	0.043	22.9	3.953	4.654
Mary	1979–2002	spotlight	10	0.195	0.219	0.257	0.246	0.208	0.069	52.3	8.041	8.081
Liverpool	1976–2003	spotlight	20	0.187	0.397	0.134	0.182	0.238	0.049	46.9	2.611	3.398
Tomkinson	1976–2002	spotlight	25	0.611	0.026	0.008	0.131	0.692	0.144	96.7	3.236	3.328
Cadell	1975–2000	spotlight	25	0.663	0.063	0.020	0.375	0.438	0.104	91.7	3.872	4.068
Blyth	1975–2003	spotlight	21	0.202	0.364	0.111	0.236	0.238	0.051	52.5	4.992	6.585
Glyde	1972–2003	spotlight	3
Habgood	1989–1999	helicopter	8	0.289	0.759	0.118	0.063	0.060	0.001	12.3	1.358	2.184
Baralminar	1989–1998	spotlight	6	-0.527	0.786	0.202	0.006	0.006	0.000	1.3	5.438	0.462
Gobalpa	1989–1998	helicopter	5
Goromuru	1989–1999	helicopter	10	1.121	0.235	0.047	0.106	0.586	0.025	71.7	0.756	1.023
Cato	1989–1998	helicopter	9	0.778	0.448	0.090	0.175	0.279	0.007	46.1	1.099	1.369
Peter John	1989–1999	helicopter	8	1.509	0.134	0.022	0.598	0.24	0.007	84.5	0.906	1.103
Roper	1979–2001	spotlight	2

Notes: Shown are the number of years of survey coverage, the type of survey (spotlight or helicopter), the number of yearly transitions (q), the model-averaged maximum rate of population change (r_{MA}) incorporating density-independent (exponential) and density-dependent (Ricker logistic) models, and relative strengths of evidence for five a priori population dynamics models (corrected Akaike’s Information Criterion [AIC_c] weight) encapsulating density-independent (RW, random walk; EX, exponential) and density-dependent (RL, Ricker logistic; GL, Gompertz logistic; TL, θ logistic) growth. The sum of AIC_c weights for the density-dependent models represents the combined percentage weight for density dependence (%wtDD). The AIC_c model weights in boldface type indicate the highest support for that model per river system. The values in boldface type in the %wtDD column indicate there is >50% support for density dependence. Also shown are the density-dependent and model-averaged estimates of carrying capacity in units of number of crocodiles per kilometer of river (K_{DD} and K_{MA} , respectively), calculated as the weighted mean K over all models using AIC_c weights (with K equivalent to the maximum density recorded for the RW and EX models).

pool, Tomkinson, Blyth, Cadell, Glyde, Baralminar, Roper Rivers) or helicopter (Cato, Gobalpa, Goromuru, Habgood, Peter John, Victoria) surveys depending on the river and year of survey (Table 1). Generally, helicopter surveys recognized only non-hatchlings (>60 cm), whereas spotlight surveys included both hatchlings and non-hatchlings (Bayliss et al. 1986). There were also some cases in which data for individual sizes of crocodiles were not available. In spotlight surveys, crocodiles were located by their distinctive red eye shine and then approached to allow for species identification and an estimation of the individual’s total length. If a crocodile was obscured by vegetation or submerged before it could be approached closely enough for a size estimate to be made, it was recorded as “eyes-only.” Some river systems had both helicopter and spotlight surveys, so when this occurred we used the survey data from the method with the longest time series. There were also some cases in which two spotlight surveys had been done in one year. In those cases, the second survey’s data were used.

We included all eyes-only data and converted total numbers of crocodiles seen into densities (individuals seen divided by the number of kilometers of river surveyed) to standardize counts. In some river systems not all tributaries were surveyed each year, and survey

methods differed; therefore, after converting the abundance data to linear densities, we estimated the realized population growth rate (r_t) for each time interval and for each river system as

$$r_t = \log\left(\frac{D_{t+1}}{D_t}\right)$$

where D_t = linear density at time t (in years). To avoid the problems associated with varying survey methods and numbers of tributaries monitored between years, we calculated r_t only when D_t and D_{t+1} were based on identical survey methods. When more than one tributary was monitored in a particular river system, D_t was estimated as the weighted mean (\bar{D}_t) of the D_t for each tributary:

$$\bar{D}_t = \frac{\sum_{i=1}^k D_i}{\sum_{i=1}^k d_i}$$

where k = the number of tributaries (including the main channel) and d = the total number of kilometers surveyed for the i th tributary at time t .

To address the possibility of inflating the variance in r by the inclusion of the potentially more variable

hatchling size class, we examined the coefficients of variation (cv) of D_t , r , and $\lambda (= e^r)$ for the time series with and without the hatchling class included. In all rivers, the cv for all three measures was similar between the time series or was slightly larger for those that excluded hatchlings. Therefore, the inclusion of hatchlings does not inflate the variance in time series data, and so these data were included to provide a more realistic estimate of carrying capacity (K ; see *Contribution of exogenous vs. endogenous dynamics*) for each river. We also assume that the variance in r is due to process (environmental) and not observation error because there are no estimates of the latter; if violated, this assumption may cause our estimates of sustainable harvest to be over-precautionary (see *Discussion*).

Contribution of exogenous vs. endogenous dynamics

Previous methods used to examine the evidence for density dependence from time series data have generally ignored model selection uncertainty, even though there is no single population dynamical framework that can be applied to all taxa (Turchin 2003). Therefore, we adopted a multiple-working-hypotheses approach based on information-theoretic model selection and multi-model inference (Burnham and Anderson 2002). There are many potential mathematical simplifications of complex population dynamics; however, for simplicity and generality we used an a priori model-building strategy to arrive at a set of five population dynamics models used to describe phenomenological time series data that represent components of previous frequentist tests (Saether et al. 2002, Turchin 2003, Fryxell et al. 2005, Brook and Bradshaw 2006).

The model set was based on variants of the generalized θ -logistic population growth model:

$$\log\left(\frac{N_{t+1}}{N_t}\right) = r = r_m \left[1 - \left(\frac{N_t}{K}\right)^\theta \right] + \varepsilon_t$$

where N_t = population size at time t (D_t in the present study), r = realized population growth rate, r_m = maximal intrinsic population growth rate, K = carrying capacity, and θ permits a nonlinear relationship between rate of increase and abundance. The term ε_t has a mean of zero and a variance (σ^2) that reflects environmental variability in r . All models below were fitted assuming process error, and hence initial population size did not need to be estimated as a separate parameter. Density-independent model variants used were (1) nondirectional population fluctuations with a normally distributed error term (random walk; Foley 1994) where $r_m = 0$ with a single parameter estimated, σ ; and (2) the standard geometric Malthusian growth model (May 1975) with a normally distributed error term (exponential; $\theta = -\infty$, r_m , and σ estimated). Density-dependent model variants used were (3) a stochastic form of the Ricker logistic model (Dennis and Taper 1994) with r_m , K , $\theta = 1$, and σ ; (4) the stochastic Gompertz logistic

model where density dependence is proportional to the log of abundance (Reddingius 1971, Pollard et al. 1987), with r_m , $\log_e[K]$, $\log_e[N_t]$, $\theta = 1$, and σ ; and (5) the generalized θ logistic growth model (Gilpin and Ayala 1973) with r_m , K , θ , and σ all estimated. For each river system, we used maximum-likelihood estimation to fit model parameters (via linear regression for the random walk, exponential, Ricker logistic and Gompertz logistic models and nonlinear regression under Nelder-Mead optimization for the θ logistic model) and Kullback-Leibler information to assign relative strengths of evidence (corrected Akaike Information Criteria [AIC_c] weights) to each model (Burnham and Anderson 2002). An example time series and the associated model fits are shown for the Daly River in Fig. 2.

It could be argued that there was a biased loading of models in our a priori set toward a particular prediction (i.e., density dependence) given the predominance of density-dependent models (three of five models). However, Brook and Bradshaw (2006) explicitly addressed this issue by demonstrating that using the same five-model set did not introduce bias toward a particular conclusion. They used two pairwise comparisons (random walk vs. Gompertz logistic and exponential vs. Ricker logistic) on 1198 time series and showed that the support for density dependence was similar to the five-model evaluation. Furthermore, the Ricker and Gompertz logistic models capture different dynamical processes (linear and nonlinear, respectively) and as such do not describe identical patterns. Indeed, although the Ricker and Gompertz logistic AIC_c weights were similar for some rivers, other rivers, such as the Finnis, Tomkinson, and Goromuru, had substantially different support for the two models (see *Results*, Table 1).

Model-averaged estimates of K (K_{MA}) for each river system were assessed by multiplying each model's AIC_c weight by the model-specific estimate of K ; however, there is no meaningful K for the two density-independent models. For these we used the maximum density recorded for the time series as the density-independent " K " (assumed to represent maximum system productivity rather than any equilibrium density). A second measure of K was also calculated based only on the density-dependent models and their AIC_c weights (K_{DD}). Single-model comparisons were made using the information-theoretic evidence ratio (ER = AIC_c weight of the full model divided by the AIC_c weight of the intercept model) as a measure of the strength of evidence and the least-squares R^2 value to quantify structural goodness-of-fit.

Harvest models

We estimated the deterministic maximum sustainable yield as a fixed proportion of the density (annual yield proportional to D) in each river system. Here, we calculated the deterministic maximum number of additions to the population (equivalent to the balance

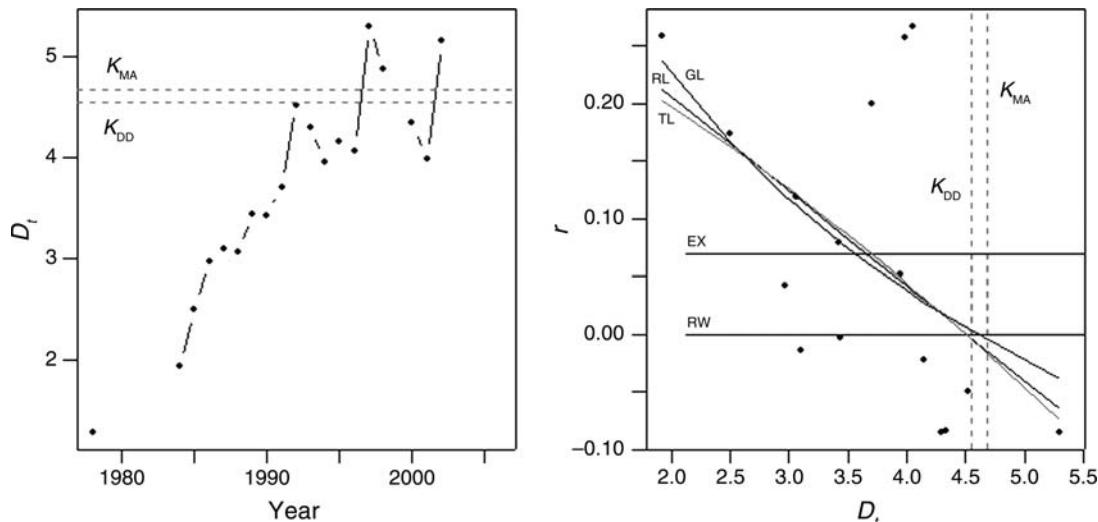


FIG. 2. Intrinsic rate of population change ($r = \log[D_{t+1}/D_t]$) vs. D_t (density of crocodiles per linear kilometer at time t) for the abundance time series data set from the Daly River, Northern Territory, Australia. Data were collected from 1978 to 2002 and gave $q = 16$ yearly transitions. Five population dynamics models (RW, random walk; EX, exponential growth; RL, Ricker logistic growth; GL, Gompertz logistic growth; and TL, θ logistic growth) were fitted to the relationship of r vs. D_t . Corrected Akaike's Information Criterion (AIC_c) weights for each model considered were 0.055 (RW), 0.123 (EX), 0.391 (RL), 0.368 (GL), and 0.064 (TL), indicating an overall weight of density dependence of 82.2% (Table 1). Also shown are the model-averaged and density-dependent estimates of carrying capacity in units of crocodiles per kilometer of river (K_{MA} and K_{DD} , respectively) calculated as the weighted mean K over all models using AIC_c weights (with K equivalent to the maximum density recorded for the RW and EX models).

of new recruits and individuals lost in a stage-structured model) by maximizing the expression

$$D \times \exp \left\{ r_m \left[1 - \left(\frac{D}{K} \right)^\theta \right] \right\} - D$$

for D using the parameters r_m , K , and θ estimated for each dynamical model. The proportional maximum sustainable yield (PMSY) is then calculated as the maximum number of additions divided by the sum of the additions and the population density D where this is realized. In the standard logistic model of population growth, the biomass level at which maximum sustainable yield is obtained occurs at $0.5M \times B_0$, where M is the instantaneous annual natural mortality rate and B_0 is the unexploited population biomass (Gulland 1971); however, using the full a priori model set, we calculated the model-averaged PMSY by combining the results of each model multiplied by their AIC_c weights. Here, the random walk model provides no maximum number of additions under the fully density-independent scenario (so the estimate is always zero), and the exponential model has a PMSY equivalent to $e^{r_m} - 1$ (i.e., $\lambda - 1$).

The estimates of parameter error using the relationship of r vs. D are not valid due to the autoregressive structure of the density-dependent models (McCallum 2000); therefore, estimating the variance in PMSY requires a different approach. For this we used a parametric bootstrap procedure (Buckland and Garthwaite 1990, Dennis and Taper 1994) in which we simulated 50 000 time series of the same length of the

observed data for each river system (starting with the same value of D_1 and randomly removing the same number of missing data as in each original data set). Here, r_t was calculated as a random normal deviate with a mean given by the maximum likelihood parameter estimates for a given model and its estimated process error (σ) after "plugging-in" the density from the previous simulated year. For each new time series we fitted the same five a priori population dynamical models described above (see *Contribution of exogenous vs. endogenous dynamics*) and recalculated the new parameter estimates and the 95% confidence intervals for each using the percentiles of the 50 000 simulated time series. To calculate confidence intervals for the PMSY values for each river system, we optimized the five models for each of the 50 000 parameter estimates derived from the parametric bootstrap procedure. The resulting additions and maximal D were weighted using the AIC_c weights to produce a model-averaged upper and lower 95% confidence limit of PMSY.

The confidence intervals for PMSY produced in this way only take the precision of the parameter estimates themselves into account and ignore the contribution of process (environmental) error. We therefore created 100 000 "generating-model" sets by sampling (with replacement) from the 50 000 model sets created during the parametric bootstrap step, and then used these models as a basis for stochastic projections. Using the value of D_n as the initial population size, we projected each population forward 30 years by calculating r_t as a random normal deviate based on the generating model

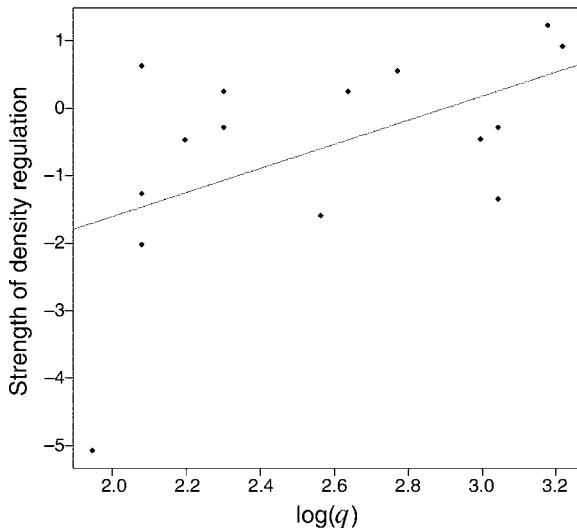


FIG. 3. Empirical relationship between the strength of density regulation (complementary log–log transformation of summed corrected Akaike Information Criterion [AIC_c] weights for the three density-dependent models) for crocodile densities and log(time series length, q) for 15 river systems in the Northern Territory, Australia. The evidence ratio (ER) for the relationship was 2.17, with an adjusted $R^2 = 21\%$.

and σ whilst applying one of two forms of harvest (same form of harvest during each and every time step). Harvest was expressed either as a proportional offtake up to and including the upper confidence limit for MSY for each river system calculated in the parametric bootstrap analysis or, alternatively, as a fixed proportion, in this case between 0 and 0.2 (i.e., harvest could take any value uniformly across this range for any given simulation) of the model-averaged K for each river system. Two output metrics were stored for each of the 100 000 time series projections: (1) the minimum model-averaged population size (expressed as a proportion of K to make it comparable across river systems) observed during the 30-year projection and (2) the total offtake achieved (expressed as proportional units of density rescaled to K). Each output metric was plotted against its corresponding harvest level, with the 50%, 75%, and 95% confidence limits calculated for each level of harvest.

RESULTS

The overall support for density dependence (standardized median over all river systems) was 49.0%, but this value ranged widely, from 1.3% (Baralminar) to 96.7% (Tomkinson) (Table 1). Not all model parameters were estimable in the Moyle, Glyde, Gobalpa, and Roper rivers due to an insufficient number of yearly transitions (Table 1), so these rivers were excluded from further analysis. Of the 15 rivers for which the evidence of density dependence was estimable, approximately half (eight) demonstrated >50% support for a density-dependent form being the best approximating model.

Model-averaged carrying capacities (K) expressed as crocodile density per linear kilometer ranged from 0.462 (Baralminar) to 8.081 (Mary) (Table 1). There was support for increasing evidence for density dependence as the number of yearly transitions over which the river system was monitored (q) increased (ER = 2.1, $R^2 = 21\%$; Fig. 3).

The deterministic proportional maximum sustainable yield (PMSY) models ranged widely among river systems, from 0.042 (Reynolds) to 0.611 (Peter John) (Table 2). As expected, there was strong evidence for an increasing PMSY with an increasing strength of density dependence among rivers (ER = 433, $R^2 = 64\%$, Fig. 4). Model-averaged confidence intervals for PMSY based on parameter precision were not symmetrical about the median and relatively wide in some rivers (Table 2).

The stochastic analysis examining various harvest rates on minimum population size and total offtake revealed a rather different outcome compared to the PMSY estimates. The results from three large example rivers near to the main urban center in the Northern Territory, Darwin, are shown in Figs. 5 and 6 (Adelaide, Mary, and Daly). The upper panels indicate the minimum proportional population size during the 30-year projection relative to harvest rates, with the 95th (dotted), 75th (dashed), and 50th (solid) percentiles shown. Also indicated is the range of proportional (Fig. 5) and fixed (Fig. 6) harvests (median and 95% ci) that achieve a minimum population size of 25% relative to starting values as an example output. Proportional harvest values for all rivers are presented in Table 3. For each river system we also calculated the proportion of simulations in which the crocodile population density fell below a fixed quasi-extinction threshold (sensu Ginzburg et al. 1982) of 0.10 individuals/linear kilometer under two different rates of harvest, (a) 0.05 and (b) 0.20. Results are shown for both fixed-proportional and fixed-quota harvest policies in Table 4.

The magnitude of process error (σ) explains the large overall discrepancy in sustainable harvest estimates between the PMSY values (Table 2) and those indicated for the 25% minimum population size target based on the stochastic projections (Table 3). The fixed-quota harvest strategy (fixed proportion up to $0.2K$) reduces population size much more quickly than a proportional harvest (cf. Figs. 5 and 6, Table 4). For example, to achieve 25% minimum population size for the Adelaide River requires a harvest rate ranging from 0.0133 and 0.1253 using proportional harvest, but this range is much lower for fixed harvest (0.0042–0.0396; see also Table 3).

DISCUSSION

The simulation approach developed in this study has provided a robust means of estimating sustainable harvest targets in a long-lived and large-bodied reptile. Generally some form of demographic parameter estimation (e.g., age-structured mortality rates, life span,

TABLE 2. Deterministic estimate of proportional maximum sustainable yield (PMSY) derived for crocodile populations in 15 different river systems in the Northern Territory, Australia, for which time series data of adequate length for modeling were available.

River system	PMSY (lower 95% CL limit)	PMSY	PMSY (upper 95% CL limit)	%wtDD
Peter John	0.412	0.611	0.713	84.5
Goromuru	0.321	0.678	0.736	71.7
Tomkinson	0.227	0.629	0.892	96.7
Finniss	0.218	0.518	0.651	71.9
Cadell	0.208	0.472	0.726	91.7
Cato	0.171	0.369	0.417	46.1
Daly	0.101	0.188	0.398	82.2
Victoria	0.080	0.167	0.214	24.4
Mary	0.059	0.103	0.201	52.3
Liverpool	0.053	0.119	0.314	46.9
Blyth	0.046	0.120	0.323	52.5
Adelaide	0.016	0.038	0.130	22.9
Habgood	0.015	0.067	0.133	12.3
Reynolds	0.013	0.042	0.124	18.3
Baralminar	0.002	...	0.194	1.3

Notes: For the right-most column, %wtDD is the combined percentage of corrected Akaike Information Criteria (AIC_c) weight of the density-dependent models. Also shown are PMSY and the 95% confidence intervals for PMSY calculated using parametric bootstrapping for each river. Rivers are ranked in descending order by the lower 95% confidence limit of PMSY.

growth rates) is used to provide information for sustainable yield models (Beddington and Kirkwood 2005); however, we have demonstrated that a lack of detailed age-structured data does not necessarily preclude assessment of a population’s exploitation potential provided sufficient spans of time series abundance data are available. This is particularly important where management agencies are constrained by the resources available to implement detailed monitoring programs

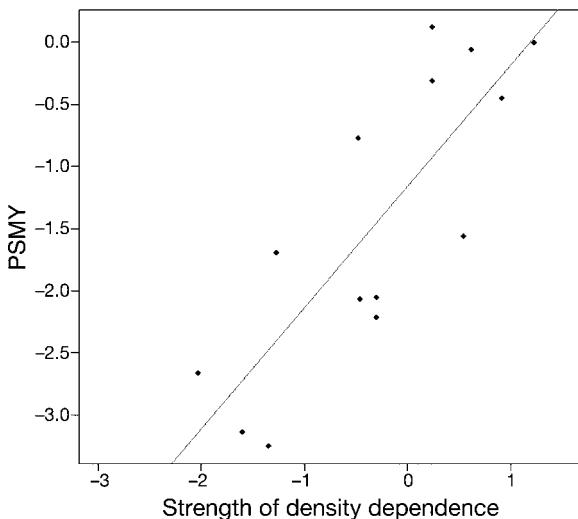


FIG. 4. Empirical relationship between optimized proportional maximum sustainable yield (PMSY, complementary log-log transformation) and the strength of density regulation (complementary log-log transformation of summed corrected Akaike Information Criterion [AIC_c] weights for the three density-dependent models) for crocodile populations in 15 river systems in the Northern Territory, Australia. The evidence ratio (ER) for the relationship was 433, with an adjusted R² = 64%.

measuring often difficult-to-obtain demographic parameters such as stage-specific survival, recruitment, and growth rates (Beddington and Kirkwood 2005).

The novel use of multimodel inference and parametric bootstrapping to incorporate three sources of uncertainty in yield estimation provides a robust means of quantifying sustainable levels of resource exploitation. Using multimodel inference and model averaging in place of assuming a single, known model is especially important for the estimation of key parameters in sustainable yield models such as *K* (Beddington and Kirkwood 2005) that can be strongly influenced by model structure and associated uncertainties. Further, the incorrect application of a particular dynamical model may heavily bias yield estimates. Indeed, we found that increasing evidence for regulation results in higher estimates of sustainable harvest (Fig. 3), indicating that conclusions about harvest will also depend heavily on the effort applied to monitoring populations over time. The precautionary management of crocodile harvest should therefore apply higher confidence to estimates of sustainable yield for river systems characterized by longer time series of abundance. It should be noted too that the multimodel inference approach using AIC_c weights does not measure the strength of density dependence per se; rather, it measures the strength of the Kullback-Leibler support for a given model or set of models. The strength of density dependence is reflected instead in the size of the model coefficients. Thus, the assessment of the support for density dependence combined with the observation that proportional harvests are more sustainable than fixed-quota harvests (Lande et al. 1995, 1997, Brook and Whitehead 2005, Fryxell et al. 2005) indicate that regular temporal assessments of population size should be done for

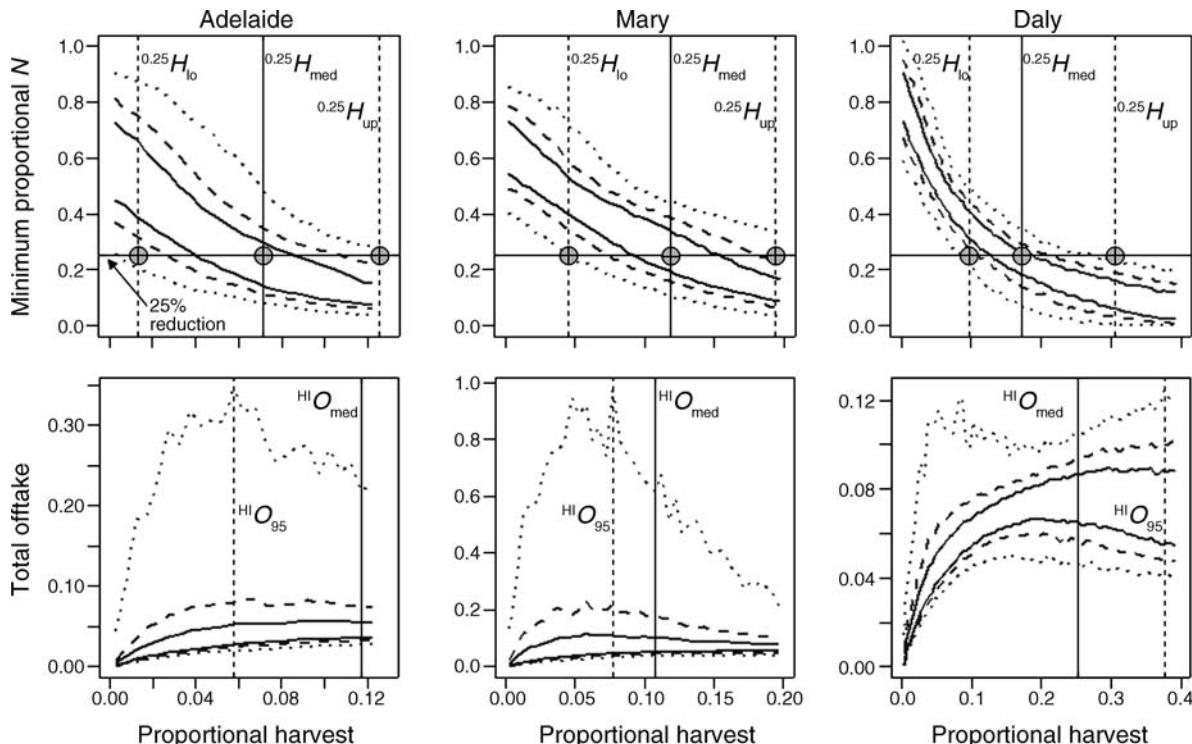


FIG. 5. Minimum proportional population size (N) over a 30-year projection (upper panels) and total expected offtake (lower panels) relative to proportional harvest rates for three example rivers in the Northern Territory, Australia. Shown are the 50th (solid lines), 75th (dashed lines), and 95th (dotted lines) percentiles for each relationship. The vertical lines in the upper panels represent the median (solid line, $0.25 H_{med}$) and 95% confidence intervals (dashed lines, $0.25 H_{lo}$ and $0.25 H_{up}$) of the harvest rate expected to result in a 25% reduction in initial population size over the 30-year projection. “Bull’s eyes” mark the intersection of the risk/harvest boundaries. The vertical lines in the lower panels represent the harvest rates resulting in the highest median (solid line, $HI O_{med}$) and 95th percentile (dashed line, $HI O_{95}$) offtake expected over the 30-year projection.

appropriate model parameterization and estimates of sustainable yield nested in the iterative feedback cycle of adaptive management (Walters 1986). Managers must therefore decide for their systems of interest whether the regular collection of abundance data is more tractable than measuring demographic rates used to parameterize stage-based models.

Importantly, we have demonstrated that ignoring process error in the estimation of sustainable yield for crocodiles may have grave consequences for effective population management because environmental fluctuation will constantly modify the realized population dynamics in unpredictable directions. This is illustrated in Figs. 5 and 6, in which the total offtake achievable for various levels of harvest were shown to vary widely. Because exploited populations should generally be harvested at a precautionary rather than the maximum sustainable level (Caddy and Mahon 1995), especially in a fluctuating environment (Jensen 2005), a conservative management strategy should avoid attempting to maximize offtake targets and instead choose some minimum population size considered acceptable under exploitation (a point, for instance, where offtake would cease; Lande et al. 1995, Fryxell et al. 2005). This is because fixed-quota harvesting tends to increase temporal

variability in population size and leads to a higher probability of population extinction (Fryxell et al. 2005). Similarly, our deterministic PMSY estimates were universally much larger than those derived using the stochastic approach because the former did not incorporate process error in their variance estimates, reinforcing the notion (e.g., Ludwig et al. 1993) that multiple sources of uncertainty need to be considered for precautionary resource management.

Our conclusions depend to some degree on the assumption that the observed variance in r was due mostly to process and not observational (sampling) error. Large relative observation errors can inflate the spurious detection of density dependence (Shenk et al. 1998), although the large meta-analysis of Brook and Bradshaw (2006) showed that this bias was minimal when using multimodel inference. Further, even under the extreme assumption that a large fraction of the observed variability was due to observation error, this would simply cause our estimates of sustainable yield to be over-precautionary. In the case of saltwater crocodile population dynamics, it is unlikely that most of the observed variance is due to sampling error given that this species appears to be highly sensitive to environ-

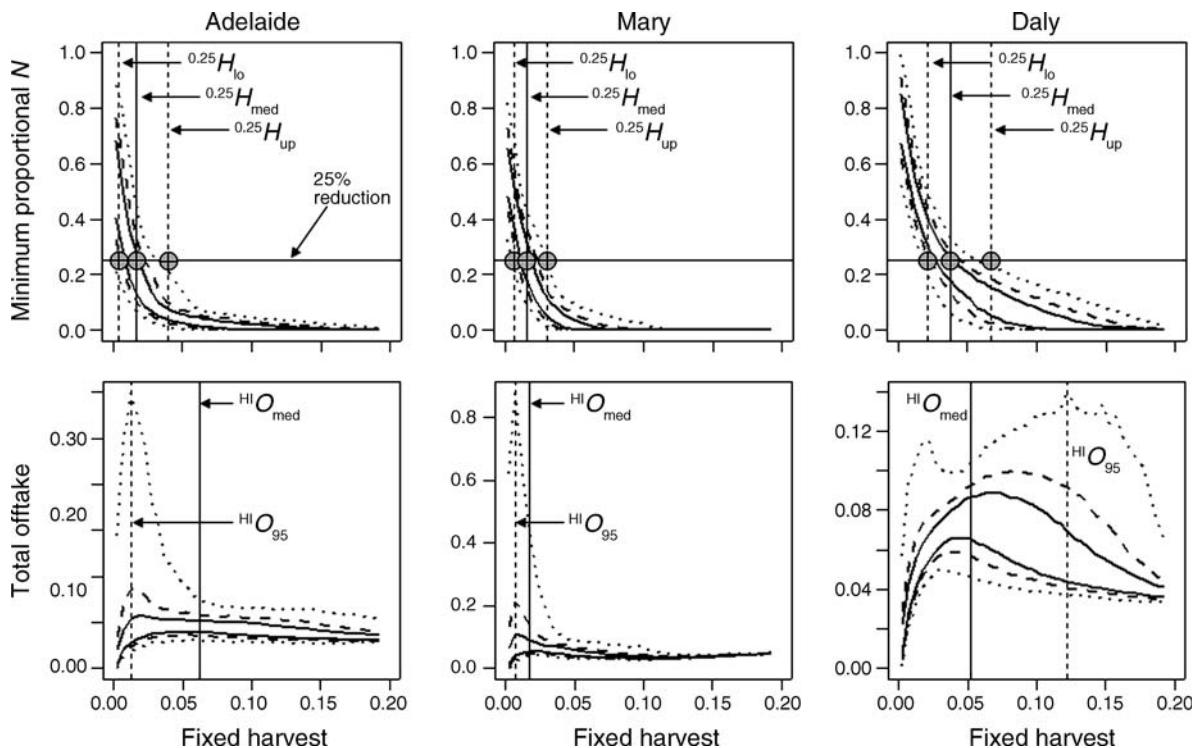


FIG. 6. Minimum proportional population size over a 30-year projection (upper panels) and total expected offtake (lower panels) relative to a fixed-quota harvest rate (up to $0.2K$, where K is the carrying capacity) for three example rivers in the Northern Territory, Australia. Shown are the 50th (solid lines), 75th (dashed lines), and 95th (dotted lines) percentiles for each relationship. The vertical lines in the upper panels represent the median (solid line, $^{0.25}H_{med}$) and 95% confidence intervals (dashed lines, $^{0.25}H_{lo}$ and $^{0.25}H_{up}$) of the harvest rate expected to result in a 25% reduction in initial population size over the 30-year projection. “Bull’s eyes” mark the intersection of the risk/harvest boundaries. The vertical lines in the lower panels represent the harvest rates resulting in the highest median (solid line, $^{HI}O_{med}$) and 95th percentile (dashed line, $^{HI}O_{95}$) offtake expected over the 30-year projection.

mental fluctuations (Magnusson 1982, Webb et al. 1983).

The recent proposal to initiate safari-type harvest of 25 crocodiles from the totality of Northern Territory

rivers (Letnic 2005) appears to be sustainable unequivocally even under the most-conservative estimates of yield potential indicated by our models. For example, if we consider that the model-averaged K for the Daly

TABLE 3. Stochastic estimate of proportional harvest levels (number of crocodiles per linear kilometer of river; median and 95% CL) for a target minimum population size of 25% of initial values over a 30-year projection for crocodile populations in 14 rivers in the Northern Territory, Australia.

River system	Harvest, $^{0.25}H$ (crocodiles/km)			Maximum offtake (crocodiles/km)	
	Lower 95% CL	Median	Upper 95% CL	Median	Upper 95% CL
Daly	0.0971	0.1722	0.3040	0.2525	0.3775
Cadell	0.0673	0.1812	0.3436	0.4125	0.0725
Mary	0.0449	0.1185	0.1941	0.1075	0.0775
Liverpool	0.0296	0.0848	0.1965	0.2975	0.0525
Blyth	0.0229	0.0647	0.1173	0.2875	0.3175
Adelaide	0.0133	0.0715	0.1253	0.1175	0.0575
Reynolds	0.0051	0.0425	0.0935	0.1125	0.0525
Tomkinson	0.0048	0.0652	0.1384	0.5525	0.0275
Finniss	0.0044	0.0462	0.1809	0.1175	0.0325
Peter John	0.0039	0.1028	0.4104	0.3475	0.0275
Victoria	0.0023	0.0386	0.1302	0.2075	0.0425
Goromuru	0.0017	0.0463	0.1946	0.0625	0.0275
Cato	0.0017	0.0387	0.1948	0.4075	0.0825
Habgood	0.0011	0.0384	0.1230	0.0925	0.0575

Notes: Also shown are the maximum proportional offtakes (in units of crocodiles per kilometer of river) using the median and upper 95% confidence limits of the proportional harvest rates (see Fig. 5). Rivers are ranked in descending order by the lower 95% confidence limit of harvest providing a minimum population size of 25% of initial values.

TABLE 4. Probability of the population density falling below a quasi-extinction threshold of 0.10 crocodiles per linear kilometer at two different harvesting (H) rates (0.05 and 0.20) based on fixed-proportional and fixed-quota harvesting policies for 14 rivers in the Northern Territory, Australia.

River system	$H = 0.05$ (fixed proportion)	$H = 0.05K$ (fixed quota)	$H = 0.20$ (fixed proportion)	$H = 0.20K$ (fixed quota)
Daly	<0.001	0.511	0.009	0.991
Cadell	<0.001	0.335	0.020	0.953
Mary	0.008	0.997	0.156	1.000
Liverpool	0.003	0.545	0.539	1.000
Blyth	0.007	0.922	0.651	1.000
Adelaide	0.198	0.961	0.787	1.000
Reynolds	0.354	1.000	0.936	1.000
Tomkinson	0.001	0.138	0.515	0.998
Finniss	0.148	0.723	0.313	0.788
Peter John	0.123	0.434	0.347	0.529
Victoria	0.209	0.219	0.865	0.755
Goromuru	0.293	0.473	0.771	0.813
Cato	0.132	0.349	0.808	0.941
Habgood	0.774	0.902	0.893	0.978

River is 4.681 crocodiles per linear kilometer (Table 1) and the tidal section of this river is ~ 115 km long, then this single river with an estimated population of 538 individuals could sustain a minimum mean proportional offtake of 9.7% (Table 3) per year over 30 years, or 52 crocodiles per year. This rate of harvest would be expected to reduce the population to 25% of its initial value as a worst-case scenario. Thus, the maximum proposed target of 25 individual crocodiles is clearly a relatively small offtake that should not affect populations negatively, especially if the target is spread among several major river systems within a given year (which is highly likely). It is also probable that proposed safari-type harvests would target only larger individuals; therefore, our non-age-structured predictions of sustainable offtake would have to be scaled appropriately to take into consideration the size and age structure of the harvested population. The harvests of large adult males could also result in the short-term increase in overall densities due to the reduction in density-dependent mortality of the smaller size classes.

The two survey types (spotlight vs. helicopter) may detect different components of the population; for example, helicopter surveys can miss many of the smaller individuals and therefore underestimate population density (Stirrat et al. 2001). It is therefore likely that in those rivers where helicopter surveys were employed (Cato, Gopalpa, Goromuru, Habgood, Peter John, and Victoria), our estimates of K are downwardly biased (Table 1). Additionally, the variance in r for helicopter-surveyed rivers may have been overestimated given the wider confidence intervals produced for these rivers (Table 3). This inflation of the variance would result in more-conservative recommendations for sustainable harvest levels. However, these estimates still provide good estimates of the temporal variation in r and as such represent an effective means of determining the relative contribution of endogenous processes to the

population trajectory over time and the potential for these rivers to sustain harvest. Another possible bias in the estimates of K includes the unknown number of crocodiles that inhabit the unsurveyed floodplain areas adjacent to the major river tributaries on which our data were based. Although estimates vary, between 20% and 40% of the total crocodile population is thought to reside in the floodplains adjacent to major rivers in the Northern Territory (Webb et al. 1984, Messel and Vorlicek 1986), implying that we have (conservatively) underestimated overall K .

Despite the apparent robustness of this species to exploitation, the reduction of genetic variation through harvest may lead to inbreeding depression that could cause reduction in survival and reproductive output and thus increase the probability of extinction at low population sizes (Frankham et al. 2002). Sex-biased harvest regimes (for example, targeting large males only) can also result in an overall reduction in genetic diversity (FitzSimmons et al. 1995). Perhaps a more serious short-term concern is the reduction in size of highly heritable traits such as body mass with sustained harvest of large males (Coltman et al. 2003, Birkeland and Dayton 2005), so avoiding the eradication of these individuals is advisable. Although our overall estimated harvest rates may indicate a high propensity for resilience to over-exploitation at least in some rivers, possibly more conservative harvest rates than those proposed are advisable to avoid the potential negative impacts on genetic diversity. Failing to incorporate dispersal among river systems may also alter predictions of sustainable harvest (Brook and Whitehead 2005) because heavily harvested populations can act as "sinks" that attract individuals from adjacent, lightly harvested populations (Watkinson and Sutherland 1995, Dias 1996). Heavily harvested populations can be buffered in this way from declines via immigration, and unharvested populations can be impacted indirectly due to losses from emigration

to sinks with lower population density (Brook and Whitehead 2005). Gene flow among river systems has been demonstrated for crocodiles using mitochondrial and microsatellite DNA markers (FitzSimmons et al. 2004), but there is still sufficient genetic structure to conclude that in situ production is the dominant force in stocking river systems.

In conclusion, our method demonstrates the simultaneous incorporation of dynamical model uncertainty, parameter precision, and process error to provide a robust and precautionary framework for the management of exploited populations for which demographic parameters (growth, survival, recruitment, etc.) are difficult to measure or unknown. In the case of saltwater crocodiles in northern Australia, our approach provides targets for sustainable harvest in each river system examined because of the differing dynamical nature and the variation in productivity within each. Therefore, detailed management plans should attempt to ascertain the carrying capacity of each river destined for harvesting through regular monitoring of population density (see also Brook and Whitehead 2005). In rivers with relatively low crocodile densities, alternative strategies such as optimal fixed-threshold (also known as “escapement”) harvesting (Lande et al. 1997, Fryxell et al. 2005) may also be considered.

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LITERATURE CITED

- ABC. 2004. Federal Government decide on whether or not to kill crocodiles. ABC Stateline Northern Territory, Darwin, Australia. 28 May. (<http://www.abc.net.au/stateline/nt/content/2003/s1118574.htm>)
- Bayliss, P., G. J. W. Webb, P. J. Whitehead, K. Dempsey, and A. Smith. 1986. Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider, in tidal wetlands of the Northern Territory: a mark-recapture experiment to correct spotlight counts to absolute numbers and the calibration of helicopter and spotlight counts. *Australian Wildlife Research* **13**:309–320.
- Bayliss, P. G. 1989. Population dynamics of magpie geese in relation to rainfall and density: implications for harvest models in a fluctuating environment. *Journal of Applied Ecology* **26**:913–924.
- Beddington, J. R., and G. P. Kirkwood. 2005. The estimation of potential yield and stock status using life-history parameters. *Philosophical Transactions of the Royal Society B* **360**:163–170.
- Beddington, J. R., and R. M. May. 1977. Harvesting populations in a randomly fluctuating environment. *Science* **197**:463–465.
- Berger, J. O. 1985. *Statistical decision theory and Bayesian analysis*. Springer, New York, New York, USA.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food, Fisheries Investigations Series 2 **19**:1–533.
- Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution* **20**:356–358.
- Bolker, B. M. 2003. Combining endogenous and exogenous spatial variability in analytical population models. *Theoretical Population Biology* **64**:255–270.
- Boot, R. G. A., and R. E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. *Ecological Applications* **5**:896–903.
- Bowman, L. 2005. That crocodiles should be hunted for money: no. *Australian Geographic* **78**:35.
- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**, in press.
- Brook, B. W., and P. J. Whitehead. 2005. Sustainable harvest regimes for magpie geese (*Anseranas semipalmata*) under spatial and temporal heterogeneity. *Wildlife Research* **32**:459–464.
- Buckland, S. T., and P. H. Garthwaite. 1990. Algorithm AS 259: estimating confidence intervals by the Robbins-Monro search process. *Applied Statistics* **39**:413–424.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodal inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- Caddy, J. F., and R. Mahon. 1995. Reference points for fisheries management. Technical Paper 347. Food and Agricultural Organization of the United Nations, Fisheries, Rome, Italy.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**:655–658.
- Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* **64**:205–224.
- De Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* **72**:57–76.
- Dias, P. C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* **11**:326–330.
- FitzSimmons, N. N., J. Buchan, M. A. Read, J. D. Miller, W. Kay, C. Mortiz, C. J. Limpus, D. Blair, and G. C. Grigg. 2004. Population genetics of Australia's crocodiles: a comparison between *Crocodylus johnstoni* and *C. porosus*. Page 65 in *Crocodiles*. Proceedings of the 17th Working Meeting of the Crocodile Specialist Group. International Union for the Conservation of Nature and Natural Resources and The World Conservation Union, Gland, Switzerland and Cambridge, UK.
- FitzSimmons, N. N., S. W. Buskirk, and M. H. Smith. 1995. Population history, genetic variability, and horn growth in bighorn sheep. *Conservation Biology* **9**:314–323.
- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying-capacity. *Conservation Biology* **8**:124–137.
- Fox, W. W. 1970. An exponential yield model for optimizing exploited fish populations. *Transactions of the American Fisheries Society* **99**:80–88.
- Frankham, R., D. A. Briscoe, and J. D. Ballou. 2002. *Introduction to conservation genetics*. Cambridge University Press, Cambridge, UK.
- Freckleton, R. P., D. M. S. Matos, M. L. A. Bovi, and A. R. Watkinson. 2003. Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology* **40**:846–858.

- Fryxell, J. M., I. M. Smith, and D. H. Lynn. 2005. Evaluation of alternate harvesting strategies using experimental microcosms. *Oikos* **111**:143–149.
- Fukuda, Y. 2004. Broad-scale influences on contemporary abundance of saltwater crocodiles (*Crocodylus porosus*) in northern Australia. Honours thesis. Charles Darwin University, Darwin, Northern Territory, Australia.
- Gilpin, M. E., and F. J. Ayala. 1973. Global models of growth and competition. *Proceedings of the National Academy of Sciences (USA)* **70**:3590–3593.
- Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* **2**:171–182.
- Groombridge, B. 1992. *Global biodiversity: status of the earth's living resources*. Chapman and Hall, London, UK.
- Gulland, J. A. 1971. *The fish resources of the ocean*. Fishing News Books, West Byfleet, UK.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.
- Jenkins, R. W. G. 1987. *The World Conservation Strategy and CITES: principles for the management of crocodylians*. Pages 27–31 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, editors. *Wildlife management: crocodiles and alligators*. Surrey Beatty and Sons and the Conservation Commission of the Northern Territory, Sydney, Australia.
- Jensen, A. L. 2005. Harvest in a fluctuating environment and conservative harvest for the Fox surplus production model. *Ecological Modelling* **182**:1–9.
- Lande, R., S. Engen, and B. E. Saether. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. *American Naturalist* **145**:728–745.
- Lande, R., B. E. Saether, and S. Engen. 1997. Threshold harvesting for sustainability of fluctuating resources. *Ecology* **78**:1341–1350.
- Lehodey, P., F. Chai, and J. Hampton. 2003. Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. *Fisheries Oceanography* **12**:483–494.
- Letnic, M. 2005. That crocodiles should be hunted for money: yes. *Australian Geographic* **78**:34.
- Little, L. R., A. D. M. Smith, A. D. McDonald, A. E. Punt, B. D. Mapstone, F. Pantus, and C. R. Davies. 2005. Effects of size and fragmentation of marine reserves and fisher infringement on the catch and biomass of coral trout, *Plectropomus leopardus*, on the Great Barrier Reef, Australia. *Fisheries Management and Ecology* **12**:177–188.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* **80**:298–310.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* **260**:17–19.
- Magnusson, W. E. 1982. Mortality of eggs of the crocodile *Crocodylus porosus* in northern Australia. *Journal of Herpetology* **16**:121–130.
- May, R. M. 1975. Biological populations obeying difference equations: stable points, stable cycles and chaos. *Journal of Theoretical Biology* **49**:511–524.
- McCallum, H. 2000. *Population parameters: estimation for ecological models*. Blackwell Science, Oxford, UK.
- Messel, H., and G. C. Vorlicek. 1986. Population dynamics and status of *Crocodylus porosus* in the tidal waterways of northern Australia. *Australian Wildlife Research* **13**:71–111.
- Messel, H., et al. 1979–1986. *Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations*. Pergamon Press, Rushcutter's Bay, New South Wales, Australia.
- Milner-Gulland, E. J., K. Shea, H. Possingham, T. Coulson, and C. Wilcox. 2001. Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation* **4**:157–167.
- Myers, R., K. Bowen, and N. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:2404–2419.
- Pascual, M. A., and R. Hilborn. 1995. Conservation of harvested populations in fluctuating environments—the case of the Serengeti wildebeest. *Journal of Applied Ecology* **32**:468–480.
- Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* **418**:689–695.
- Pollard, E., K. H. Lakhani, and P. Rothery. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* **68**:2046–2055.
- Read, M. A., J. D. Miller, I. P. Bell, and A. Felton. 2004. The distribution and abundance of the estuarine crocodile, *Crocodylus porosus*, in Queensland. *Wildlife Research* **31**:527–534.
- Reddingius, J. 1971. Gambling for existence. *Acta Biotheoretica* **20(Supplement 1)**:1–208.
- Rosenberg, A. A., M. J. Fogarty, M. P. Sissenwine, J. R. Beddington, and J. G. Shepherd. 1993. Achieving sustainable use of renewable resources. *Science* **262**:828–829.
- Saether, B. E., S. Engen, and E. Matthysen. 2002. Demographic characteristics and population dynamical patterns of solitary birds. *Science* **295**:2070–2073.
- Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs* **68**:445–463.
- Stirrat, S. C., D. Lawson, W. J. Freeland, and R. Morton. 2001. Monitoring *Crocodylus porosus* populations in the Northern Territory of Australia: a retrospective power analysis. *Wildlife Research* **28**:547–554.
- Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* **9**:551–558.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, New Jersey, USA.
- Walters, C. J. 1986. *Adaptive management of natural resources*. McGraw-Hill, New York, New York, USA.
- Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. *Journal of Animal Ecology* **64**:126–130.
- Webb, G., S. Manolis, P. Whitehead, and G. Letts. 1984. A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of C.I.T.E.S. Technical report 21. Conservation Commission of the Northern Territory, Darwin, Northern Territory, Australia.
- Webb, G. J. W., and S. C. Manolis. 1993a. *Australian crocodiles: a natural history*. Reed, Sydney, New South Wales, Australia.
- Webb, G. J. W., and S. C. Manolis. 1993b. *Conserving Australia's crocodiles through commercial incentives*. *Australian Zoologist, Herpetology in Australia*, pp. 250–256.
- Webb, G. J. W., G. C. Sack, R. Buckworth, and S. C. Manolis. 1983. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Australian Wildlife Research* **10**:571–605.
- Webb, G. J. W., P. J. Whitehead, and S. C. Manolis. 1987. *Crocodile management in the Northern Territory of Australia*. Pages 107–124 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, editors. *Wildlife management: crocodiles and alligators*. Surrey Beatty and Sons, Chipping Norton, Australia.