

Modelling population dynamics of estuarine crocodiles on Queensland's northern populated east coast

**Report to the
Queensland Department of Environment and Science**

**Dr Laurence Taplin
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Executive Summary

- i. This population modelling exercise results from Recommendation 6 of a 2021 review commissioned by the Queensland Department of Environment and Science into a major technical report on the population status of estuarine crocodiles in Queensland.
- ii. The Recommendation said (in part) *“In consultation with stakeholders, [DES] considers annual removal of a modest number of crocodiles 2.4 metres or more in length on the populated east coast for several years, in addition to the average number of problem crocodiles removed under current Management Plan arrangements, with appropriate frequency of monitoring. The number taken each year should be based on population modelling.”*
- iii. The initial ‘terms of reference’ for the exercise were to create and evaluate population model/s for some or all of Queensland, including by:
 - a. Detailed evaluation of the NT population model of Fukuda et al (2020);
 - b. Creating a population model for Queensland, derived from the NT model but catering for Queensland’s particular circumstances;
 - c. Evaluating assumptions in the NT model and their relevance/appropriateness for Queensland;
 - d. Evaluation of the population dynamics data available or derivable for Queensland from existing data and it’s suitability for incorporation into a Queensland model; and
 - e. If the modelling permits, evaluation of the potential effects of static or increased removals of crocodiles on the long-term population density in the northern reaches of the populated east coast.
- iv. Early examination showed that constructing a population model for the whole of Queensland or for several bioregions was not practicable. The project scope was limited to the high priority crocodile management area between Cooktown and Ingham on the populated east coast (PEC) - termed here the Northern Populated East Coast (NPEC).
- v. To provide context for departmental officers unfamiliar with population modelling, the report gives a brief overview of population modelling approaches and appends a summary of past models used for crocodilians.
- vi. The structure of the NT model and the underlying data used to inform their modelling are reviewed and the applicability of model elements to the NPEC population is examined.
- vii. Because Queensland’s crocodile habitat and climate are very different from the NT study area and there is virtually no Queensland-specific data on vital rates and density dependency functions, data is also drawn from studies of other crocodilians.
- viii. The NT model was modified in a few ways to accommodate NPEC-specific issues.
 - a. The proportion of females breeding in any year was changed from a density-dependent function to a fixed proportion.
 - b. Transition rates in the stage-based matrix model were calculated differently to better align estimates of rate of increase using a stage-based matrix and its corresponding age-based matrix.
 - c. Environmental stochasticity associated with the duration of the dry season was excluded because the NPEC has very different physiography and climate, there is no

data to inform an NPEC-specific model, and the stochastic effects in the NT model are small.

- ix. The reconstructed NT model was tested against the published NT data and reproduced it well. The NPEC model was then tested against the known trajectory of the NPEC population using NT values for population parameters. It was a poor fit.
- x. It was evident the modelling exercise would be affected by limited data on changes in the population size and size class structure of the NPEC population and the almost complete absence of data on Queensland-specific population parameters. Analysis was therefore focused on:
 - a. exploring the biologically likely parameter space that might be influencing the NPEC population;
 - b. identifying how different combinations of population parameters influenced population trajectories; and
 - c. exploring the subset of matrices which projected biologically plausible trajectories.
- xi. The approach adopted was a global sensitivity analysis based on sampling the entire parameter space very extensively (10^6 samples), constructing a projection matrix for each sample of vital rates and density dependencies and projecting the population from 1974 (the date of protection) to 2074.
- xii. The relatively small number of population parameters made it unnecessary to use multiple regression, generalised additive models or regression trees to dissect the results. They were explored but are not reported here.
- xiii. The equilibrium size of the non-hatchling population and the proportions of adults and juveniles at equilibrium were used to explore the influence of population parameters. The population rate of increase was calculated but not explored in detail as it tends always to converge on zero in density dependent models.
- xiv. The first iteration of modelling showed that:
 - a. Many different combinations of vital rates and density dependencies led to plausible population trajectories.
 - b. Some combinations of vital rates did reproduce the NPEC trajectory very well.
 - c. A very large proportion of samples (70-80%) projected population declines or trajectories that stabilised at very low non-hatchling numbers. These bore no relationship to the known NPEC trajectory.
- xv. In a second iteration, the modelled parameter space was reduced by fixing fertility and duration of the juvenile stage at their NT values. The range of 'plausible' trajectories for the NPEC population was limited to equilibrium non-hatchling numbers in the range 3,750-22,500, but with a more likely range of 3,750 – 7,500.
- xvi. Reducing the parameter space made little difference to the spread of parameter combinations that could lead to plausible population trajectories. However, many trajectories fell outside the 95% confidence limits (CLs) for survey estimates of non-hatchling numbers.
- xvii. Further exploration was confined to projected trajectories falling within the 95% CLs. This model set was used to analyse the possible impacts of the historical management program and the potential effects of future changes. A brief examination was made of the

very small subset of these trajectories that tracked within +/- 5% of the mean population estimates.

- xviii. The analysis reinforced the strong influence on projected population size of density dependency in the hatchling stage and the secondary influence of density dependency in adults. Low values for their Ricker function coefficients were responsible for most of the estimates of equilibrium non-hatchling numbers over 7,500.
- xix. Despite variability in the model outputs, the final outcomes proved quite consistent.
 - a. The overall effect of 1985-2022 management removals on the equilibrium numbers of non-hatchling crocodiles in the NPEC population appears to have been small.
 - b. In relation to varying levels of future removals (ranging from 0-50 adults and 0-50 juveniles – against the average removal of 20 juveniles and 20 adults from 2013-2022):
 - i. Removing adults had much larger effects on the projected non-hatchling population size than removing juveniles.
 - ii. Increasing the annual removals of adults from 20 to 50 greatly increased the number of trajectories that tracked to extinction before 2074.
- xx. The analysis suggests considerable caution is needed in managing the removal program for adult animals, including the large adults that pose the biggest risks to humans. Small numerical increases in the numbers removed have the potential for big impacts.
- xxi. Population management through controlled removals of juveniles appears likely to have less impact on the population and carry lower risk. This may be useful in managing the continuing influx of juveniles and subadults into the few management areas where all crocodiles are removed.
- xxii. The bigger the risk of severe impacts, the more requirement there will be for more detailed monitoring to ensure that small differences between an increasing and a decreasing population when it is close to equilibrium can be detected in a timely manner.
- xxiii. The results suggest there is quite limited scope for reducing the non-hatchling population by much more than 10-20% without increasing the risk of extinction. Only a small proportion of 'plausible' projections result in a population reduced by much more than 20% but less than 100%. It is possible the real population could remain stable, well above any extinction threshold and well below the level of an unmanaged population in the face of more adult removals. However, such an outcome appears unlikely.
- xxiv. It appears very likely that the NPEC population will stabilise with a ratio of adults to juveniles of about 20:80, quite different from the 43:57 expected for the NT population. The proportion of very large animals in that adult stage is expected to remain small.
- xxv. Improvements to the model made in light of reviewer comments resulted in no material change to the principal findings of the main report. That new work is set out in an Addendum.

Introduction

The origins of the population modelling exercise

1. This project had its origins in a review commissioned by the Queensland Department of Environment and Science in 2021 conducted by an expert panel chaired by Professor Hugh Possingham FAA, the Queensland Chief Scientist. Its final report and the Department's response were released publicly (OQCS, 2021; DES, 2021).
2. Among its numerous recommendations was the following:

“6. (Priority B) In consultation with stakeholders, [DES] considers annual removal of a modest number of crocodiles 2.4 metres or more in length on the populated east coast for several years, in addition to the average number of problem crocodiles removed under current Management Plan arrangements, with appropriate frequency of monitoring. The number taken each year should be based on population modelling. This trial, to constrain population growth and reduce overall numbers locally, is a form of adaptive management that could deliver improved crocodile management outcomes and new knowledge.”
3. The recommendation was built, in part, on a suite of quite simple propositions arising from a very detailed report on the population status of estuarine crocodiles in Queensland (Taplin et al, 2020):
 - 3.1. The estuarine crocodile population in Queensland has increased substantially since the early 1970s across its entire range, including the area from Cooktown to Ingham that carries relatively high densities of crocodiles and people (Figure 1).¹
 - 3.2. The crocodile management program in place since the mid-1980s has seen some hundreds of mostly subadult and adult crocodiles removed from the NPEC population (Figure 2) but the population has continued to increase.
 - 3.3. There are indications that the Queensland crocodile population is approaching an equilibrium with its environment in parts of its range, as indicated by State-wide declines in the rate of increase with time.
 - 3.4. The rate of increase in the NPEC population has declined over time. It is not yet possible to say what the equilibrium density will be in this region – but it may well be higher than it is today.
 - 3.5. In the long-term, an optimal management program would balance removal of crocodiles under the management program with the natural rate of increase in the population. It would aim to achieve a stable population that is biologically sustainable but minimizes conflict, including injuries and deaths to humans.
 - 3.6. Our best current estimate of the rate of increase in non-hatchling crocodiles in the NPEC population is some 67 animals per year across 3500km of waterways (Taplin et al, 2021). The management program has seen some 23 non-hatchlings removed per year on average since 1985, and 40 animals per year over the last 13 years. Those observations suggest a modest increase in the number of animals removed per year could reduce the rate of increase and either stabilize the population or tip it into a

¹ .. The crocodile population in the Cooktown-Ingham subregion of the northern Populated East Coast is referred to as the “NPEC population” throughout this report.

modest decline. Knowing where that tipping point lies² would be valuable if the government is to move from reactive to adaptive management of the population.

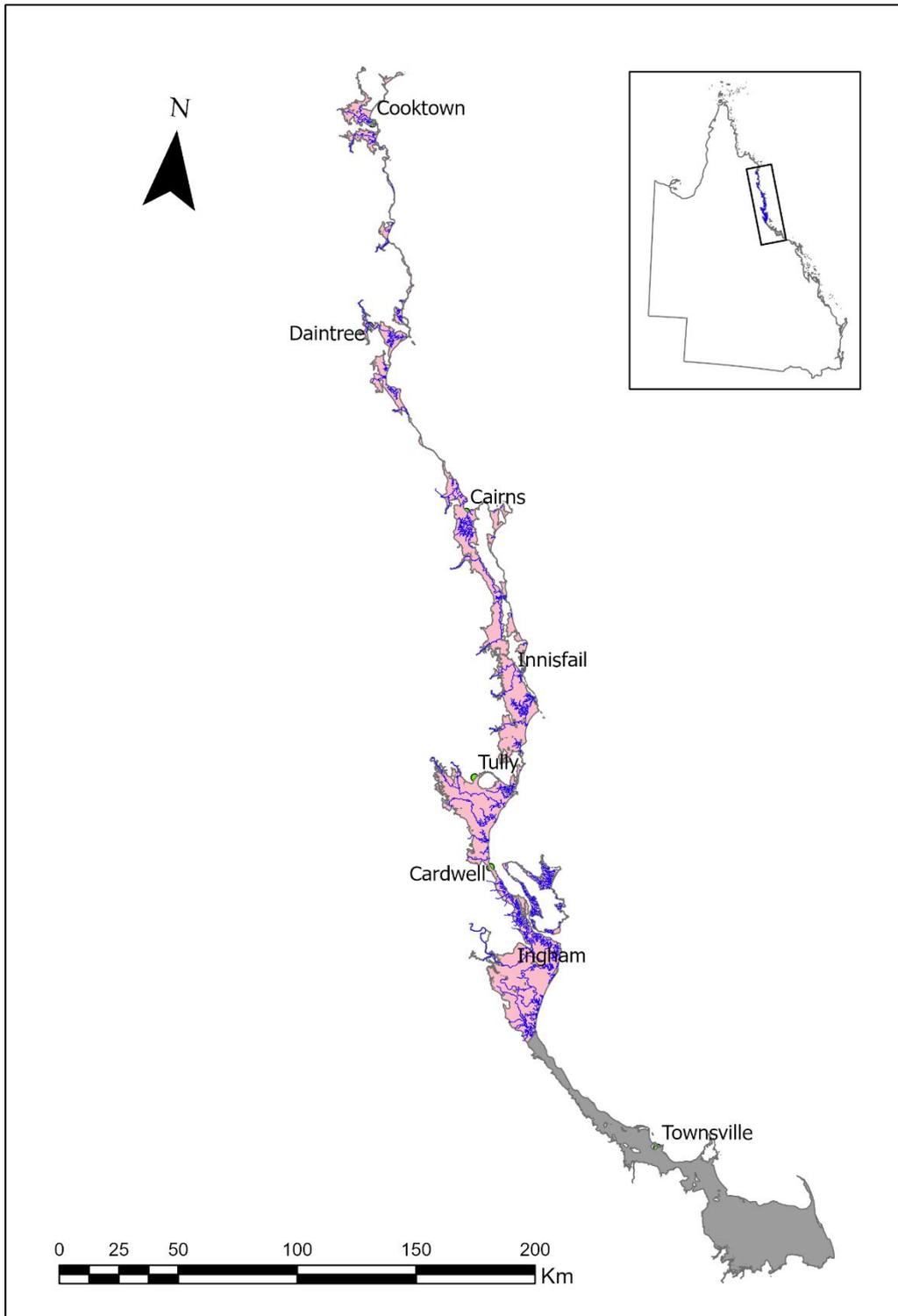
- 3.7. To date Queensland's crocodile population has been allowed to recover naturally throughout its range with only modest interventions in highly populated areas along the east coast. The numbers and size-classes of crocodiles removed have not been pre-determined but result from a broad policy approach to reduce the number of larger crocodiles (>2m) around urban areas. However, many actions involve decisions about individual animals.
 - 3.8. Decisions on individual animals would remain if an adaptive management framework was adopted, but would be informed by a better and more nuanced understanding of their likely biological consequences.
 4. Doing that work now makes sense because the NPEC crocodile population is healthy and increasing and still has considerable areas of remnant habitat available, including in protected reserves and national parks.
 - 4.1. The species is very resilient if it is protected and has habitat in which to live and breed. Its recovery since the 1970s is testament to that, especially in Queensland where it has increased consistently across a wide range of habitats and climates. The extent of nesting habitat available is estimated to have declined by less than 10% across the whole of the populated east coast from Cooktown – Rockhampton, notwithstanding intensive human activity and development (author's unpublished research).
 - 4.2. Changes in the population will be measured across decades, not years, given it takes about 10 years for females to reach maturity and adults likely live over 60 years. There is plenty of time to monitor and respond to change. Nonetheless, short-term interventions will need careful calibration as some of their effects will become apparent only in the longer term.
 - 4.3. Even if the population was driven to a modest decline in the short-term, it would be readily reversed with an adaptive reduction in removals.
 - 4.4. Doing the work now makes sense, as the human population of north Queensland will increase in coming years putting greater pressure on the crocodile population. Knowing how best to manage that pressure will prove important.
5. This is the backdrop to this current exercise in population modelling, which aims to inform decisions about whether changes in the management regime should be undertaken.

Why model the population?

6. Population modelling is an uncertain science. Among other things, the discipline attempts to describe the potential future trajectories of a population based on what we know historically and currently about its size, structure and dynamics and the way those dynamics respond to a changeable environment. That exercise is inherently uncertain because we cannot know many of the factor affecting population dynamics, even for the most tractable of populations. For intractable animals like crocodiles – large, hazardous to work with and very long-lived – the challenges are exacerbated.

² Notwithstanding that environmental changes will likely shift that tipping point over time and management will have to adapt.

Figure 1: The focal area for this report is the region of far-north Queensland between Cooktown and Ingham lying below 20m above sea level and is shown in pink outline in this map – the NPEC region. Blue lines are the associated perennial waterways that may be occupied by the NPEC crocodile population. This area is the northern part of crocodile Bioregion 5b as defined by Taplin (1987). The area south of Ingham (colored grey) has been excised because more recent studies have shown it to have much lower densities of crocodiles, different habitat and rather different climate (Taplin et al, 2021). It will be better incorporated into a revised mapping of Bioregion 5c which currently extends from the southern boundary of the grey area to Rockhampton, some 500km south.



7. That said, population modelling is one of few ways we can look into the future and gain insights into how a population might respond if left undisturbed or managed actively. The challenge is to construct a model that incorporates the essential features we believe are likely to affect the population's trajectory, but without going beyond the data available to inform it.
8. For the estuarine crocodile in Queensland that is an important task. Research over the past 40 years has documented the recovery of the Queensland population from very low levels in the early 1970s (when the species was commercially extinct but far from biologically extinct) to almost complete recovery throughout its historical range today (Taplin et al, 2020, 2021). But the crocodile must coexist with people over much of its range, especially in the densely populated parts of Queensland's east coast south of Cooktown. Coexistence brings conflict and some injury and death to both crocodiles and people (Brien et al, 2017).
9. The species must be managed actively if conservation efforts are to succeed, not least to ensure public confidence in the effectiveness of the government's program is built and sustained. Active management inevitably requires the removal of some animals from areas of high human habitation while allowing them to persist elsewhere. In an ideal world, decisions about how many animals should be removed, of what size, and from what locations would be based on detailed assessment of impacts on the population. But the world of crocodile biology is far from ideal and even the best-resourced and longest-running crocodile research programs manage only limited understanding of population dynamics and their variation across time and space.
10. Management cannot stop simply because we want or need more information. Arguments that action is premature because more information is needed can continue forever. There will never come a point with estuarine crocodiles in Australia where we can claim sufficient knowledge to predict its future with absolute confidence. Decisions about individual animals and segments of the population must be made based on what we know now and what we can reasonably infer or anticipate.
 - 10.1. McCallum (2000) put it well – *“All management decisions in ecology are based on models, even if those models are verbal or even less distinct ‘gut feeling’. If it is decided not to use a mathematical model because the parameters cannot properly be estimated, the management decision will proceed regardless. We often are not able to postpone decisions until the appropriate experiments can be done.”*
11. Population modelling has a role to play because it does allow us to look, with a circumspect eye, to possible or likely futures and the effects that today's decisions may have on the population's trajectory.

Lessons from egg-harvesting

12. Biological guidance is important but not sufficient when it comes to policy decisions in wildlife management. The dynamics of egg-harvesting in estuarine crocodiles is a useful example. Egg-harvesting began in the Northern Territory in the mid-1980s amid considerable controversy. Biological knowledge suggested strongly that a substantial harvest was possible without undue impact on the population because:
 - 12.1. natural mortality of eggs was very high;
 - 12.2. the available nesting habitat was so widespread that an excessive harvest was unlikely; and

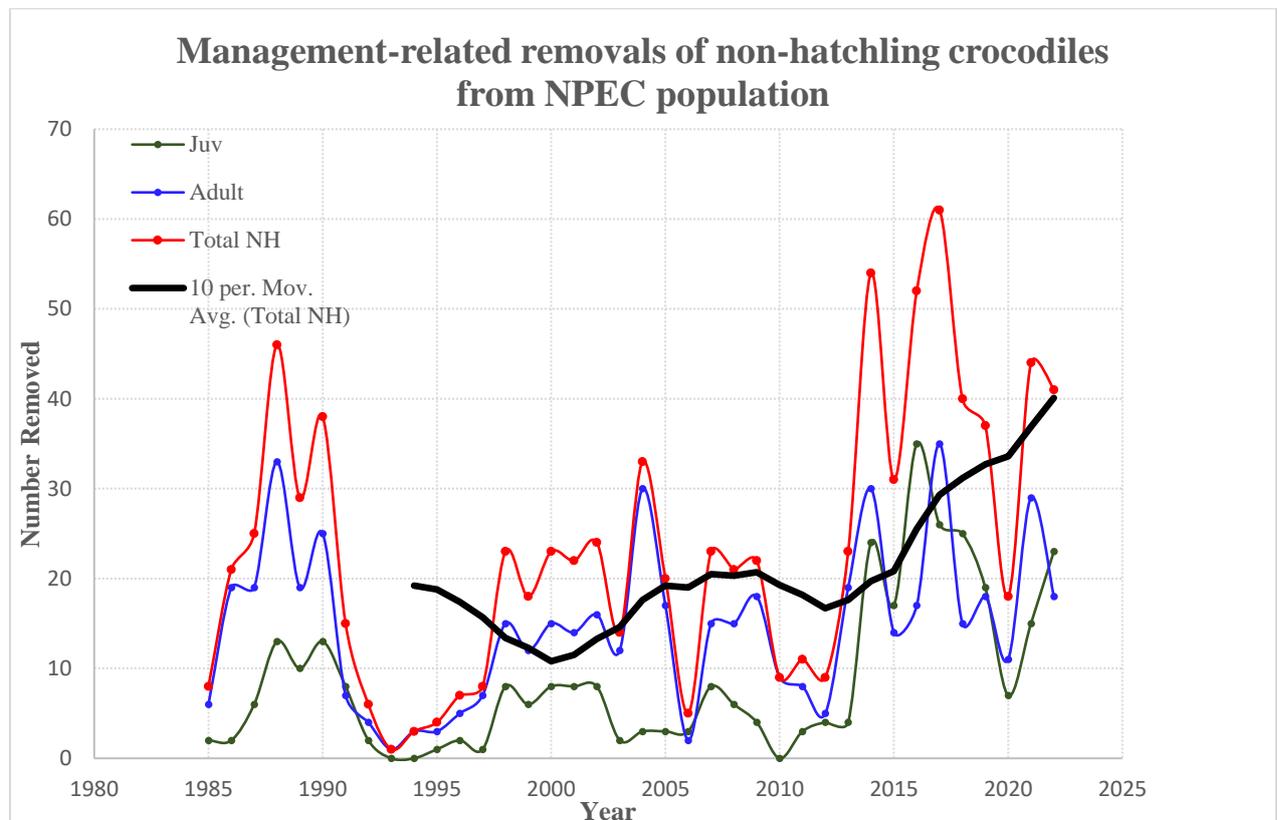
- 12.3. it seemed likely there would be some compensatory adjustments in the population dynamics.
13. In the event, the results confirmed the biological assessment. A large harvest of some hundreds of thousands of eggs has been sustained over 30 years and the crocodile population has continued to increase in harvested and unharvested systems (Fukuda et al, 2011; Saalfeld et al, 2014, 2016). Population modelling played a part in making the argument that a sustainable harvest was possible (Appendix 5 in Webb et al, 1984).
 14. In Queensland, egg harvesting was not permitted at all until 2017 despite calls for it to be allowed to help control an ‘exponentially increasing’ crocodile population and/or help the crocodile farming industry develop. One reason for the prohibition was a near absence of information on the extent of nesting activity in Queensland and the factors affecting nesting success. Some work on nesting and nest habitat during the 1980s suggested that egg harvesting was unlikely to be economically viable in remote northern Queensland because of the limited extent, wide dispersal and limited accessibility of nesting habitat (Taplin, 1987).
 15. However, egg harvesting policy in Queensland changed following review by the author (Taplin, 2017) of a successful research effort in the Pormpuraaw region of western Cape York Peninsula (CYP) that showed high levels of egg mortality comparable to the NT and modest numbers of nests in marginal habitat (Britton, 2007, 2009, 2017). The 2017 review found no biological reasons for opposing an egg harvest around Pormpuraaw. It again questioned, after better quantifying the extent of nesting habitat, whether egg harvest would be commercially viable across much or all of northern Queensland.
 16. Five years on, only the Pormpuraaw collection has proceeded. It appears to operate at commercially unviable levels well below those anticipated in the 2017 report (DES internal records). Only three other permits to collect eggs in Queensland have been sought and only one, in northern Cape York Peninsula was approved (in 2022). The others lacked supporting science. There has certainly been no rush to exploit the policy change and it looks likely that commercial realities will continue to restrain collection efforts. Thus far, there has been no discernible biological impact from the policy decision, which was informed by both biological and economic judgements.
 17. The egg-harvesting debate illustrates well how factors entirely external to population dynamics can and do have important impacts that influence policy decisions. Not least among these are differing community views on permissible commercial uses of wildlife. These are essentially philosophical positions that use both good and bad ‘scientific evidence’ to reinforce their positions. Population modelling can inform decision-making but is insufficient to provide prescriptions.

Crocodile removals

18. Removals of crocodiles from populated parts of Queensland’s east coast attract similar controversy. At the extremes, some would argue for complete protection of crocodiles from any removals for conservation management or commerce. Others argue for an extensive cull to reduce crocodile numbers to levels of the 1970s, when they weren’t seen to interfere with peoples’ rights to swim, surf, canoe and generally recreate in coastal waterways and beaches. These are philosophical positions that don’t need any science to inform them – but often draw on anecdote and idle speculation to support them.
19. The essential elements of the Queensland crocodile management program can be summed up as follows:

- 19.1. The government has a responsibility to balance protection of an important and iconic Queensland species with public safety.
 - 19.2. That responsibility cannot be fulfilled without active management of the population, especially around heavily populated areas.
 - 19.3. Active management requires carefully targeted removal of large, potentially dangerous, animals from selected areas and removal of all detectable crocodiles from a few populated areas like Cairns.
 - 19.4. Removed animals can be used by zoos or crocodile farms for commercial and educational purposes.
20. Relocation to zoos and farms is simply another form of mortality from a conservation standpoint. Outside animal welfare considerations, how they should be used in zoos and farms is principally a philosophical position, except to the extent that the use impinges positively or negatively on their future conservation. Opinions on acceptable uses and their conservation consequences vary.

Figure 2: Management-related removals of non-hatchling crocodiles (Juv[eniles] 0.6-2.2m and Adults >2.1m) from the study area between Cooktown and Ingham over time. A few animals were removed in 1985-86, before commencement of the first formal East Coast Crocodile Management Program in 1987. Removals before 2013 fluctuated over time in response to differing views of management requirements rather than estimates of underlying changes in the population (Brien et al, 2017). The 10-year moving average shows a steady upward trend of about +1 NH/year since 2000.



What type of population model?

21. There are many different types of population models. Those relevant to this exercise might be classed as deterministic, stochastic or density-dependent.
22. A deterministic model has no element of randomness in its vital rates³, in the factors affecting vital rates or in the model outputs, such as the rate of population increase or population size at some future time. Its future trajectory is determined by its current state. Such models are limiting, in the sense that they don't take account of the many external factors (particularly environmental influences) that can affect vital rates, the random demographic effects that can occur in very small populations by chance alone, or potential interactions between population size and vital rates.
23. Deterministic models can, however, be useful in exploring how fundamental features of a species' biology are likely to flow through to population trajectories and how sensitive the population trajectory might prove to changes in vital rates (Caswell, 2018). They are also generally more amenable to analytical solutions that can simplify the analysis of their behaviour as vital rates change.
24. A stochastic model seeks to incorporate random influences on vital rates into the estimation of population trajectories.
 - 24.1. Demographic stochasticity arises because populations consist of whole animals and, at low numbers, there are finite probabilities in any time interval that no animal will survive and/or reproduce. Demographic stochasticity is of limited interest for this exercise because it will have little or no impact given our population of interest amounts to several thousand animals.
 - 24.2. Environmental stochasticity is randomness driven by such things as varying climate and weather conditions e.g. (temperature and rainfall at the right times of year) and variation in the natural productivity of the river systems. Environmental stochasticity is relevant to our modelling and has been incorporated in the most recent NT model (Fukuda et al, 2020) as a modest influence of dry season rainfall on egg production.
25. Density-dependent models, which can be overlaid on an underlying deterministic or stochastic framework, allow some of the vital rates in a population to be influenced by the density of animals as a whole or the densities of particular age-classes or stage-classes⁴ (singly or in combination).
 - 25.1. These models attempt to cater for situations where survival, reproduction or growth in individuals is affected (usually but not always negatively) by actions of other individuals. Actions might be direct (cannibalism) or indirect (competition for resources like food, suitable habitat for residency or nesting sites).
 - 25.2. Density dependence is relevant to estuarine crocodile population models because there are indications that it operates, or is highly likely to operate, in important ways in NT populations and likely more widely (para 52).

³ Vital rates are the rates of survival, fecundity and growth that underly the essential growth trajectory of a population under a particular set of conditions. They are distinguished here from the parameters used in some models to define the strength of density-dependent influences on population increase.

⁴ Age-classes separate individuals by fixed time-steps, often yearly increments for large vertebrates. Stage classes identify important stages in individual development (for insects these might be eggs, larvae, pupae and adults) that influence vital rates. For animals like crocodiles that retain a single body-form through life, stages are commonly defined by size-classes - informed by such things as age at first reproduction or age at senescence.

- 25.3. However, identifying density dependence in any animal population and establishing its functional relationship to one or more vital rates is fraught with difficulties, some statistical and some practical. McCallum (2000) has a useful discussion of the challenges.

Age- and stage-structured models

26. Population models can also be classified according to how they deal with structure inherent in the population.
- 26.1. A population may be considered as simply a body of individuals, not distinguished as to age, size, stage of maturity etc. In this case an unstructured model would be generated that might simply seek to predict future numbers in a population based on applying a constant or variable rate of increase to some initial population number. These are sometimes termed ‘time-series models’ (Burgman et al, 1993; Schaub & Kery, 2022).
- 26.2. Alternatively, animals might be classified by age and their vital rates (fecundity and survival) varied according to age class. Such an age-structured model allows greater nuance in the characterisation of population trajectories but depends ultimately on the biologist’s ability to separate animals into age-classes.
- 26.2.1. For crocodilians that is especially difficult, because they are very long-lived, growth rates vary considerably between individuals, and the bones and osteoderms that show evidence of annual growth phases can be subject to extensive remodelling as the animal grows, ages and goes through reproductive phases that mobilise calcium reserves (Hutton, 1987a; Tucker, 1997a,b).
- 26.2.2. In addition, their longevity and size and the difficulties of working with them have made longitudinal studies, where the fates of individuals are followed over long periods, largely impractical.
- 26.2.3. Age-structured models are not, for the most part, a practical proposition for crocodilians, were not used for the latest NT model (Fukuda et al, 2020), and are not used here.
- 26.3. More appropriate for our purposes are stage-structured models where the vital rates that influence the population trajectory can be correlated with stages in the life-cycle of the species and/or when an age structure for the population is difficult or impossible to construct, as is the case for most crocodilians.
- 26.4. Both age- and stage-structured models use matrices of vital rates to model population trajectories – a Leslie matrix in the first instance and a Lefkovitz matrix in the second (Caswell, 2018). These matrices are populated with estimates of vital rates such as fecundity, survival and, for stage-structured models, time spent in each life-stage.
- 26.4.1. Estimating those vital rates and their uncertainties is itself challenging and has proven difficult for crocodiles.
- 26.4.2. Vital rates are commonly estimated from what can be termed individual-level approaches. For example, fecundity by age or stage is estimated by aggregating data on offspring produced by individuals. Survival is often estimated by mark-recapture experiments that aggregate data on the fates of individuals over time.
- 26.5. Modelling has also to try and account for the variation within and covariation between vital rates. This is challenging for matrix model approaches.

Integral projection and integrated population models

27. Two further classes of models - integral projection models and integrated population models - might also be employed.
28. Integral projection models relate vital rates to some trait of the individuals in the population, such as size. The functional relationships between vital rates and trait/s commonly derive from long-term monitoring of individuals (Ellner et al, 2016). Environmental variability can be modelled through its effects on vital rates. Unlike integrated population models, they make no use of population-level data such as counts of abundance.
29. Integrated population models are somewhat different beasts, despite their similar name. They use both data collected at the population level (e.g. counts of abundance) and data collected at the individual level (e.g. mark-recapture results and reproductive data). They can simultaneously estimate demographic rates and trajectories of population size (Schaub & Kery, 2022). This joint analysis improves the precision of estimates of demographic parameters and can allow estimation of parameters for which no data has been explicitly collected.
30. Plard et al (2019) developed a revised version of the integral projection model that incorporated elements of both integral projection and integrated population models, using data at both individual and population levels. The data are analysed jointly as a state-space model. They found it performed better than integrated population or traditional integral projection models, particularly in estimating demographic responses to changing environments.
31. All three of these classes of models rely on longitudinal data of a type that is very difficult to collect from crocodiles. Such data are rare for crocodylians in general and non-existent for *C. porosus*⁵. They are not pursued further here.

Previous crocodylian population models

32. A short overview of population models developed for various crocodylians is set out in Appendix 2 to provide a backdrop for consideration of the Fukuda model that this report builds on. For most of them, estimates of all-important survival rates are a core weakness because these rates are very hard and costly to estimate in such long-lived animals with generally low mortality rates. There are only two models informed by very long-term mark-recapture studies that have given good estimates of survivorship across a range of sizes/ages - one of *C. acutus* in Florida (Briggs-Gonzalez et al, 2017) and one of *C. johnstoni* in Queensland (Tucker, 1997a).

Choice of a modelling approach

33. Queensland has almost no data on vital rates in *C. porosus* that can inform a population model. Nor have there been sufficiently frequent surveys from any river system to provide a time series of population estimates to inform a simple model of total numbers over time. Details of what is available are set out later in this report.
34. The paucity of data constrains the modelling approach regardless of the terms of reference for this study, which require an evaluation of the relevance to Queensland of the most recent stage-structured matrix model for the NT population. Integral projection models and

⁵ Longitudinal data is available for the smaller and more tractable freshwater crocodile, *C. johnstoni*, but its applicability to *C. porosus* is very limited.

integrated population models are precluded by their demanding information requirements. Models dependent on size-age relationships are excluded because:

- 34.1. we have no short- or long-term mark-recapture studies from which to estimate size by age;
 - 34.2. there are no reliable methods for estimating an age-structure from a sample of the static size structure in estuarine crocodiles across their size range; and
 - 34.3. while there is good reason to expect growth curves to vary considerably across different climates, we do not know what influence the warm and much wetter climate of the northern tropical coast has on growth rates and age at maturity.
35. Nor is there data to populate a single projection matrix with reliable estimates of vital rates or density dependencies, as was done for the NT. Thus, the best available option for modelling the NPEC population is to explore the behaviour of the stage-based matrix model developed by Fukuda et al (2020) under a set of biologically reasonable assumptions about the likely range of variation in essential vital rates.

Essentials of the NT model

36. The model produced by Fukuda et al (2020) is a size-based, stage-structured model incorporating four life stages – eggs, hatchlings, juveniles and adults. Stage durations are fixed at 1 year for eggs and hatchlings, which either die or transition into the next stage. The juvenile stage includes animals from 0.6-2.1m and its duration is set at 8.3 years. This number is the mean of estimated ages on reaching maturity for males and females minus the one year spent in earlier stages and with 0.3 years added to account for the time between the nominal hatching date and the typical date of surveys. Animals in the model have a maximum longevity of 70 years and transition out of the adult stage only by dying.
37. The model incorporates some environmental stochasticity based on whether the preceding dry season was longer or shorter than the long-term mean. Longer dry seasons lead to lower egg production and shorter dry seasons to higher egg production. The model also incorporates several density-dependency functions that influence hatchling and adult survivorship and the proportion of females nesting each year.
38. Juvenile density dependency is not incorporated in the NT model as the regression analysis used to estimate the strength of the functional relationship had a coefficient not significantly different from zero. That is of some note as earlier analyses by Webb et al (1984) and Webb and Manolis (1992) suggested there might be strong density dependency influencing the survivorship of small juveniles in 2-, 3- and 4-year old age classes (mostly animals ranging in size from 0.9 – 1.5m) but not in larger juveniles. It appears possible that density dependent influences in the juvenile stage may have been smoothed out by their opposing influences on the smaller and larger size/age classes in the combined stage. A different picture of density dependencies might have emerged from splitting the juvenile stage into smaller (0.6-1.5m) and larger (1.5-2.1m) stages. That said, it seems likely the authors explored this option and found that either significant density dependencies did not show up with two juvenile stages or that the data available could not support the more complex model.

Survivorship

Egg survival

39. The estimate of survival rates of eggs (0.25) in the model is taken directly from Webb et al (1984), deriving from work in the 1970s and 1980s. This estimate benefits from detailed

and geographically broad studies of nesting biology in the NT during that period, across a range of riverine and swampland habitats. They encompassed nesting behaviour, causes of mortality (flooding, predation, developmental disorders) and variability of nesting success across space and time (Webb et al, 1977; Magnusson et al, 1978, 1980; Messel et al, 1981; Magnusson, 1982; Webb et al, 1983).

40. In those and later studies, losses unrelated to flooding accounted for about 30% of all eggs laid and were attributed to infertility, crushing and developmental failures due in part to low and high temperatures, genetic defects, bad orientation of eggs in the nest and waterlogging. Direct losses to floods accounted for a larger and more variable proportion depending on weather and nest site characteristics. Nests in freshwater swamps generally showed lower loss rates from flooding than river bank nests (Webb et al, 1984).

Hatchling survival

41. The survival rate for hatchlings (0.54) is estimated from:

- 41.1. A study of 58 hatchlings from three nests on the upstream Liverpool River in the 1973-74 nesting season. Forty-nine of those hatchlings were recaptured between 54 and 70 days after hatching, giving an estimated minimum survival rate of ~85% over 2 months. That is equivalent to ~37% survival over 12 months, assuming no change in mortality rate over the year (Webb et al, 1977a).

- 41.2. After one year, 23 of the 58 were again recaptured and another 10 of the same size-class were seen in the same area but not caught (Webb, 1977). Those numbers were combined to estimate an annual survival rate of 57% (Webb et al, 1984).

- 41.3. Messel et al (1981) separately estimated annual survival among hatchlings in the Blyth-Cadell River survey area over 12 months (356 days) in 1978-79 using mark-recapture. They estimated 115 of 226 hatchlings survived over the year, for a survival rate of 51%. This estimate is a little uncertain, as 24 of the 115 'survivors' after 1-year were sighted but not recaptured in 1979, so could not be confirmed as recaptures of animals marked in 1978. If this indeterminate group is excluded from calculations, the survival rate decreases to 39%. The authors considered a realistic estimate to lie somewhere between 39 and 51%.

42. Thus the survival rate estimates in the NT model available derive from the progeny of a very small number of nests in just two NT river systems in the mid-late 1970s. It is not likely that survival rates of hatchling crocodiles are invariant across geography and time, so we need to be cautious about applying these rates to Queensland populations living in areas that are very different physiographically and climatically (Taplin, 1987; Taplin et al, 2021).

Juvenile survival

43. The annual survival rate for juvenile crocodiles in the NT model (0.72) arises from the analysis of intensive spotlight surveys in the Blyth-Cadell River system from 1974-79, supplemented by less detailed but extensive surveys of other NT systems in the same era (Messel et al 1980, 1981, 1984; Webb et al, 1984).
44. This estimate of survival rate is confounded with unknown rates of emigration from the surveyed systems. That said, losses of a substantial proportion of the juvenile size classes were found across a very broad swathe of surrounding crocodile habitat (Messel et al, 1981, 1984), suggesting mortality might be a better explanation of the losses than emigration. However, Bayliss and Messel (1988) noted the difficulties inherent in interpreting loss rates of juvenile and subadult/adult crocodiles from the Blyth-Cadell and

Liverpool-Tomkinson systems. Mortality could not be distinguished reliably from emigration and some analyses suggested emigration might better explain some of the losses.

Adult survival

45. The annual survival rate for adult estuarine crocodiles is entirely unknown. Webb et al (1984) surmised it would be very high, based on studies of *Alligator mississippiensis* (Nichols et al, 1976) and *C. johnstoni* (Webb and Smith, 1984) and set it at 0.99 for animals 12-60 years old and 0.95 for those 60-70 years old. The NT model uses the unweighted mean of these estimates (0.97). Very low adult mortality (survival rates of 85%) have been found in two long-term recapture studies of other crocodylians (Tucker 1997a; Briggs-Gonzalez, 2017).

Summary

46. This quick survey of source data for survival rates shows how thin is the dataset available to underpin the NT model and inform a population model for Queensland. This is an observation, not a criticism. The paucity of data is consequence of the cost and difficulty of any research requiring mark/recapture and pragmatic decisions about research priorities for the NT and Queensland.
47. The difficulties are illustrated by another important factor that has a strong influence on interpretation of survey results but has proved very difficult to estimate – the relationship between counts of crocodiles sighted in surveys and the number actually present. Sightability (the probability of detecting a crocodile) is influenced by many variables but size is a key variable, as is the height of the tide in tidal waterways (Messel et al, 1981). Despite its importance, and the high likelihood sightability has changed over time in at least the larger size classes, only one mark-recapture experiment to estimate sighting probabilities has been conducted in some 50 years of research (Bayliss et al, 1986, 1987). In that exercise, no sightability estimates were possible for animals over 3m in length because too few large animals were resighted after marking.
48. That major exercise has never been repeated. Techniques devised more recently that are experimentally simpler do not help much either. State-space models for estimating abundance from repetitive counts of unidentified animals can be used to estimate real abundance (King et al. 2010; Kery and Schaub 2012; Kery and Royle, 2016). Extensive simulations of survey/sampling options were conducted by the author for rivers in the accessible Cooktown-Ingham region and in Rinyirru-Lakefield National Park on CYP, where there are higher densities of crocodiles but logistics are more difficult. Those simulations identified that no series of surveys able to provide good estimates of sightability across size classes could be conducted at reasonable cost and within a practical timeframe of 1-2 years (Taplin, unpubl obs). Major impediments were the limited tidal ranges, limited favourable tides within any one survey window and season, and relatively low densities of crocodiles.

Fecundity

49. Fecundity in estuarine crocodiles, measured as the number of eggs laid in a breeding season by mature females, has been quite extensively researched because of its relevance to commercial harvesting and sustainable-use conservation. Data are available across a considerable range of habitats and differences between the NT and Queensland appear small (see below).

Probability of transitioning to next stage

50. In the NT model, the likelihoods of transitioning from egg to hatchling and from hatchling to juvenile are set at 1 because all surviving eggs become hatchlings and all hatchlings become first-year juveniles at the end of their first year of life. The likelihood of transitioning in any year from the juvenile to the adult stage (termed γ_3 in the NT model) is more difficult to estimate.
51. Technical details of the estimation problem are set out in Appendix 1. It is sufficient here to note that the estimation method used for the NT model is problematical. For the NPEC model, a different approach referred to by Kendall et al (2019) as an ‘asymptotic age-within-stage structure model’ has been adopted. This approach ensures, among other things, that projections from the stage-structured matrix models align properly with their underlying age-structured equivalents.

Density dependencies

52. Density dependency in survivorship and fecundity have long been thought to be likely components of crocodilian population dynamics, not least because of evidence that larger crocodiles kill and eat smaller ones (Webb et al, 1984; Webb and Manolis, 1992). However, demonstrating density dependence is very difficult in practice and many of the approaches used for estimating the strength of density dependence remain controversial, especially those relying on regressions of successive population counts (Burgman et al, 1993; McCallum, 2000; Brook and Bradshaw, 2006; Knape and de Valpine, 2012; LeBreton and Gimenez, 2013).
53. One important outcome of incorporating density dependencies into a population model is that they will tend to impose a limit on population size, which would increase *ad infinitum* or decrease to zero in a deterministic model. That can be useful in models aimed at estimating equilibrium population numbers and the potential effects of harvesting strategies, but is not essential for estimating possible impacts of harvesting (e.g. Smith & Webb, 1985; Craig et al, 1992).

Density dependence in survival rates

54. Three population parameters in the NT model are treated as density-dependent. Hatchling, juvenile and adult survival rates were modelled using Ricker functions in which the annual survival rate of a life stage is the product of its maximum survival rate at low density and a negative exponential function of the density of some or all stages in the population (Morris and Doak, 2002; Caswell, 2018). Fukuda et al (2020) describe density dependency as ‘intra-stage’, if the density of animals in a stage in any one year affects the survival rate for the stage, or as ‘inter-stage’ if the density of one stage or stages influences the survival rate of another stage
55. To incorporate Ricker-modelled density dependency into the matrix model, a scaling coefficient β has to be estimated, which is a measure of the strength of the density dependency. Fukuda et al (2020) used a relationship suggested by Morris and Doak (2002) to estimate β values, which involves regressing the log of stage-specific survival rates against abundance. The slope of the regression line estimates β and the intercept estimates the log of the maximum survival rate at low density. This approach avoids some of the problems of serial autocorrelation that confound density dependency estimates derived by comparing successive population or stage counts (McCallum, 2000), but poses a different problem.

56. The difficulty is that direct estimates of age- and stage-specific survival rates for estuarine crocodiles are extremely limited (see above) and are certainly not known over long periods or at varying densities. Webb et al (1984) encountered this difficulty in their early modelling of the Blyth-Cadell system, for which mark-recapture estimates of survivorship were available only for hatchlings from the Liverpool River in 1974/75 and the Blyth-Cadell system in 1979/80. They had to rely on ‘retention rates’ to estimate annual survival probabilities.

Retention rates

57. To estimate retention rates, annual spotlight survey data for the Blyth-Cadell system were converted to estimates of absolute numbers by size class using estimates of sightability from Bayliss et al (1986, 1987). These counts were then converted into estimates of absolute numbers by age-class (0.3-1.3yr, 1.3-2.3yr ...4.3-5.3yr).⁶ Animals over 5.3-yr old were bundled into a single stage for want of information about growth rates in large animals.
58. Retention rates were then calculated as the ratio between the absolute number of animals in age class (x+1) in year (t+1) and the number of animals in age class x in preceding year (t). In a closed population at its stable age/stage equilibrium, these would estimate survival probabilities directly, but the Blyth-Cadell survey area was open to immigration and emigration, rates of which could not be estimated (Messel et al, 1981, 1984; Webb et al, 1984; Bayliss & Messel, 1988).
59. Webb et al (1984) noted this inescapable confounding of survivorship and migration and identified that, in addition to migration, uncertainty in the estimates of survival rates would also arise from (a) simple statistical variance in the spotlight counts over time (observation error) and (b) instances where nests hatched late in a season after spotlight surveys were completed, thus contributing to the following season’s yearling numbers without having shown up in hatchling numbers. Confounding showed up in instances where retention rates for some age classes in some years were greater than one (Webb et al, 1984). Messel et al (1984) highlighted a striking instance of apparent immigration and emigration to/from this system, in which the number of large crocodiles (> 7ft) sighted rose from 3-6 in earlier years to 26 in 1979 before falling back to 4-9 over the next two years.
60. Webb et al (1984) took the mean of 10 successive estimates of retention rate as the best estimates possible of survival rates, thus averaging out some of this inherent variability. They noted that dispersal is typically very low for the 0.3-1.3yr (hatchling) and 1.3-2.3yr (yearling) size classes (Webb and Messel, 1978b) and that the product of estimated survival rates from hatchling to 0.3 yr (70%) and retention rate from 0.3-1.3 yrs (81% averaged over 10 years) was 57%. This was close to the mean survival rate from hatching to 1 year (54%) measured in two mark-recapture studies (see above). The extent to which retention rates in older animals might be affected by migration or other confounding factors could not be estimated.
61. Fukuda et al (2020) used a related approach, noting “*With no time-series survival data for C. porosus available in the literature, and conducting mark–recapture surveys across the study area being impractical, we substituted ‘retention’ rates for survival as was done by Webb and Manolis (1992). Retention rate is the abundance of animals sighted in one year divided by abundance in the previous year. We assumed that the transition (G_i) and*

⁶ The 0.3yr element was required to allow for the gap in timings between hatching and spotlight surveys. Some hatchling mortality would occur in that interval and was estimated from related data for the Blyth-Cadell system in 1979/80 (Webb et al, 1984; Messel et al, 1981, 1984).

persistence (P_i) of each class was as shown in Table 1 and estimated the retention rates of N_2 , N_3 and N_4 from their relative densities derived from the time-series data (1975–2011) of spotlight surveys in 12 tidal rivers across the study area (Fig. 1; Fukuda et al. 2011; Fukuda and Saalfeld 2014).⁷”

62. Estimating survival rates, and hence density dependency coefficients, using retention rates can be problematical when they are uncorrected for sightability differences between size classes and employed in a population converging only slowly on its stable age/stage distribution (Appendix 3).
63. No attempt is made here to assess whether density dependencies incorporated in the NT model are good representations of underlying biological processes. Queensland does not have data that would allow an independent assessment. The NT estimates of density dependency coefficients and intra-/inter-stage relationships are used here as they are the best available.

How best to apply the NT model to Queensland

64. The NT model provides the best available starting point for a modelling exercise for Queensland but needs to be modified to exclude some of its density dependencies and environmental stochasticity (see below). This analysis is focused particularly on the possible size of the population under the current and possible future management regimes, assuming vital rates and density dependent functions remain constant over time. It is less focused on changes to the population's rate of increase. Thus a model that incorporates some density dependence is useful, as long as it is biologically realistic.
65. The resulting model is underpinned by very uncertain estimates of survival rates and better estimates of fecundity rates. The uncertainties are considerable for the NT population and doubly so for the NPEC population. Nor is it clear that the values for density dependency coefficients derived for the NT population are good fits for the NPEC population.
66. Faced with this, the best option available is to test the behaviour of the model while varying the matrix elements or their underlying vital rates within their likely biological limits. Fortunately, even in the absence of data for estuarine crocodiles, we can get some estimates of credible ranges from studies of other crocodylians, while noting that the alligatorids studied to date differ significantly from crocodylians in some aspects of their life history (Tucker, 2001).

Estimates of vital rates for the NPEC population

Survivorship

Eggs

67. Estimates of survivorship of estuarine crocodile eggs are well grounded in extensive research and depend greatly on the physiography and climate of the region. Nests in exposed riverside locations can suffer very high losses from flooding while those in swamplands can be more protected depending on local topography (Webb et al, 1977; Magnusson et al, 1978, 1980; Magnusson, 1982; WMI, 2007).
68. Queensland's crocodiles extend across such a wide range of climate and physiography that we should expect climate-linked mortality to vary considerably. The only data bearing on egg mortality for Queensland comes from a 10-year study of nesting on the central-west coast of Cape York Peninsula, reviewed in detail by Taplin (2017). Losses of viable nests from all causes amounted to 81%. Flooding accounted for 67% and predation (possibly

⁷ Stages in the NT model were termed N1 (eggs), N2 (hatchlings), N3 (juveniles) and N4 (adults).

after flooding in many cases) accounted for most of the balance. The losses are comparable to those in tidal river bank nests in the NT (Webb et al, 1984). That is unsurprising given similarities in climate, physiography and nesting habitat between the coastal plains of mid-western Cape York and parts of the northern coastline of NT (Magnusson et al, 1979, 1980).

69. One other tiny insight comes from an incidental survey of 19 active nests in north-western CYP, 17 in dense swamps and sedgelands and all at different stages of development (Taplin, unpubl obs). This snapshot indicated 5% of the eggs laid had failed to develop (presumed infertile) and none were crushed. These numbers are not markedly different from the 9% and 1% recorded by Webb et al (1983).
70. Given the extremely low numbers of hatchlings found in most rivers in the NPEC region over many years (Appendix 3 in Taplin et al, 2020 and 2021), it seems unlikely that egg survivorship will be higher than the NT. However, it may be considerably lower given the very high rainfall in the region and extensive clearing that is likely to have increased the impact of flood events. For modelling purposes egg survivorship will be allowed to vary from 5% to 25%.

Hatchlings

71. Estimates of hatchling survivorship from mark-recapture are very sparse and very dated for the NT (para 41ff). There are no data available for Queensland apart from one observation from the Daintree River by a tour operator who has operated near-daily there for over 20 years. He recorded a reduction in one creche from 37 to between 5 and 9 after 8 months (uncertain because about half the hatchlings later sighted were some 100-200m from the nest site and may have come from another nest). That equates to an annual survival rate of 5-12%, though Webb et al (1984) noted that some data suggest survivorship may increase after the first few months.
72. None of the data from repeated survey counts in Queensland has proven useful for estimating retention rates as even a rough approximation of survivorship year-on-year. Considering the very small numbers of hatchlings and yearlings counted over many years in NPEC systems, there is little to suggest hatchling survivorship in the Queensland study area is higher than in the NT.
73. We can get some sense of the variability in survivorship among hatchling crocodilians from the literature (Table 2). This summary suggests the estimated survivorship of hatchling *C. porosus* is on the high side compared to other crocodilians and other *Crocodylus* spp in particular. Comparably high annual survival has been reported in *C. acutus* by Moler (1991) but only at the high end of highly variable rates across years. Considering these data, hatchling survival rates in Queensland will be allowed to vary from 0.05 – 0.55.

Juveniles

74. Reported juvenile survival rates in crocodilians are all intermediate between those of hatchlings and adults and mostly exceed 50% (Table 2). Estimates are quite variable and confounded a little because the size/age classes included in the juvenile stage differ between species. Nonetheless, the NT estimate of 72% for combined juvenile/subadult survivorship in *C. porosus* lies in the mid-range of estimates and allowing it to vary from 50-90% in the NPEC population will cover their range.

Adults

75. Adult survivorship has only rarely been measured in crocodylians because of the practical difficulties, but published estimates lie between 0.88 and 1.00 (Table 2). The high survivorship is generally attributed to the lack of natural predators on large crocodylians.
76. There are no estimates of natural mortality for estuarine crocodiles in Queensland, but there is evidence of mortality linked to human interference in localised areas of Cape York Peninsula and the Gulf Plains and on the populated east coast, where large crocodiles have been killed quite frequently since at least the 1980s. Some have been through accidents such as drowning in fishing nets or crab pots, others through illegal killings. A review of DES reports from April 2020 to April 2022 identified 10 deaths of large (>3m total length) animals and 16 deaths of subadults or small adult females (2-3m) in the NPEC population. That equates to mortality rates of ~ 2% p.a. for adults and ~0.2% for the more numerous juvenile stage.
77. It is difficult to know what proportion of incidental deaths get reported to DES. It is likely quite high given (a) the high human population density in the region; (b) the quite intense focus in local media on crocodile numbers and sightings; (c) the high numbers of residents, visitors and boating enthusiasts using generally small coastal waterways; and (d) the online accessibility and frequent publicity given to the sighting report system. A reasonable guesstimate is that the real number of incidental deaths is likely not more than double the reported numbers.⁸ Equally, some of the dead animals reported may well be the result of natural mortality – i.e. mortality not imposed by human activity. Thus, an estimate of ca 2-4% incidental mortality in adults is likely in the right ball-park, making it comparable in size to the management offtake.
78. Allowing adult survivorship to vary between 0.85 and 0.99 for the NPEC population covers the range of estimates in other species and is broad enough to encompass the accidental and illegal mortality identified.

Fertility

79. The average number of eggs laid by a female does not vary greatly between the NT and Queensland. The average clutch size of 53.1 eggs used by Fukuda et al (2020) is taken from Webb & Manolis (1989). The estimate is very similar to the mean of 51.1 eggs from 713 nests in Melacca Swamp NT over a 28-year period (WMI, 2007). The distribution of egg counts in that sample approximates a normal distribution with a range of 15-82.
80. A late-1980s sample of 19 wild nests from north-western Cape York Peninsula had an average of 47.4 eggs (range 24-66) (Taplin, unpubl obs). A completely different sample of 323 nests laid down by captive crocodiles in Rockhampton, at the southern extremity of the natural range in Qld, between 2010/11 and 2016/17 gave a mean of 43.4 eggs (range 7-88) (data from J Lever, Koorana Crocodile Farm).. The mean egg count is about 20% lower than the wild estimate for NT nests but the range is similar. Data from captive crocodiles is not easily interpretable given the farm environment and the mixed origins of the breeding stock, though many are from north Queensland wild stocks. Nonetheless, the data do suggest animals living in a rather harsh and cold climate can produce eggs in numbers comparable to wild crocodiles in favourable conditions.⁹

⁸ Some animals are killed clandestinely and the killings concealed, However, even some of these come to the notice of the department.

⁹ The sample does differ in the high proportion of infertile eggs encountered – 34% vs 9% in wild NT nests.

Stage duration

81. Another important influence on population dynamics is the average time it takes for individuals to mature. Maturity occurs at about 2.1m in females at an age of about 10.3 years in the NT (Fukuda et al, 2020). No comparable data for Queensland is available, but females at Koorana Crocodile Farm near Rockhampton start nesting and laying eggs at 2.1m while laying more eggs, and more of them fertile, as they approach 2.4 – 2.5m (J Lever, pers comm). Quite a high proportion of the females at Koorana have been wild captures from the NPEC population, so it appears likely that at least size at maturity might be quite consistent between NT and Queensland.
82. There is no data to estimate age at maturity reliably for Queensland crocodiles – just two observations of female crocodiles observed over 20 years on the Daintree River which nested for the first time at ages of 14 years and 22 +/- 1 year (D White of Solar Whisperer, pers comm).
83. Considerable differences in mean stage duration have been found for juvenile and subadult alligators living in relatively warm climates in Florida and Louisiana and the considerably colder climate at the northern extreme of their range in North Carolina (Lance 2003, Dunham et al, 2014). Lance (2003) estimated age at maturity at about 10 years in Louisiana, about 12-14 years at similar latitudes in Florida and about 18 years in North Carolina. Dunham et al defined juveniles to be non-hatchling animals 0.3 – 1.21m (1-4ft) and subadults to be animals 1.22-1.82m (4-6ft). Their mean stage durations were 3 and 4 years respectively in Florida/Louisiana against 7 and 7 years in North Carolina. So the colder climate seemingly results in much slower growth and a doubling of the time taken to mature, as both populations mature at much the same size.
84. Male and female freshwater crocodiles in the Lynd River in Queensland matured at similar ages, between 14 and 23 years old (Tucker et al, 2006). Despite the study area lying close to the south-eastern extreme of the freshwater crocodile's natural distribution in Australia, ages at maturation were not markedly different from the McKinlay River population in the NT, which were 11-14 years in females and 16-17 years in adults (Webb et al, 1987). However, Tucker estimated stage durations in the Lynd River population to be 10 years for juveniles (3-11 years) and 10 years for young adults (12-22 years) against much shorter durations in the McKinlay River population – juveniles 7 years and young adults 2 years. Thus, the NT animals spent considerably more of their lifespan in a fully mature state.
85. Nile crocodiles have been estimated to mature at 22 years of age, spending 2 and 19 years in juvenile and subadult stages after a year as hatchlings (Wallace et al, 2013). The subadult stage in their analysis included young females breeding for the first time at a length of ~2.3m and aged 15 years. Growth to maturity appears to vary considerably with climate. Crocodiles in the generally cold climate of Lake Ngezi took 10 years longer to mature than those from more favourable habitat in Zimbabwe (Hutton, 1984, 1987b). Craig et al (1992) used an age at maturity of 16 years with upper and lower limits of 12 – 20 years) for their modelling.
86. The NPEC region is a long way from the southern extremity of the estuarine crocodile's range in Queensland. It experiences a favourable warm, wet climate in summer and a cooler (but not cold) wet winter (BOM, 2023). It is therefore reasonable to set the age at maturity at the mean of 10.3 years found for the NT with a range of 6.3 – 14.3 years, sufficient to accommodate likely variation.

Table 2. Reported rates of annual survival (p) in various life stages of crocodylians. Life stages for juveniles, subadults and adults are defined somewhat differently in the various studies but this is not important for our purpose of finding likely ranges for survival rates in Queensland *C. porosus*.

Species	p(Hatchling)	p(Juvenile)	p(Subadult)	p(Adult)	Source
<i>Crocodylus porosus</i>	0.54	0.72		0.97	Fukuda et al (2020); Webb et al (1984)
<i>Crocodylus johnstoni</i>	0.18 (0.13-0.24)	0.90 (0.80 – 1.00)		1.00	Craig et al (1992) derived from Smith & Webb (1985)
<i>Crocodylus niloticus</i>	0.11 (0.06-0.16)	0.92 (0.90-0.96)		1.00	Craig et al (1992) derived from Graham (1968)
<i>Crocodylus niloticus</i>	0.04 (0.03-0.06)	0.88 (0.81-0.93)		1.00	Craig et al (1992) from Hutton (1984)
<i>Crocodylus niloticus</i>	~0.20	~0.62	~0.98	~1.00	Bourquin & Leslie (2012)
<i>Crocodylus niloticus</i>	0.12	0.47	0.98	0.95	Wallace et al (2013)
<i>Crocodylus acutus</i>	0.20 (Range 0.07-0.43)	0.70	0.85	0.99	Moler 1991 cit Green et al (2010)
<i>Crocodylus acutus</i>	0.12	0.6-0.8		0.88	Briggs-Gonzalez et al (2017)
<i>Alligator mississippiensis</i>	0.35	0.89		0.99	Craig et al (1992) derived from Nichols et al (1976)
<i>Alligator mississippiensis</i>	0.38	0.78	0.73	0.88	Dunham et al (2014)

Is density dependency likely to be operating in the NPEC population?

87. The NPEC population generally has very low densities of hatchling and non-hatchling crocodiles. Non-hatchling relative density¹⁰ has ranged from 0.25 per km in the late 1980s, to 0.41 per km a decade later and 0.81 per km in 2016-19 (Taplin et al, 2020,2021). That is markedly lower than averaged densities in the NT reference rivers used for modelling, which have increased from ~1.5 per km in 1975 to over 5 per km in 2010 (Figure 6 in Fukuda et al, 2011). Thus density dependencies may not operate as strongly in the NPEC population, though they may come into play in a very few localized areas. For example, the upstream reaches of the Murray River have a dense population of subadult and adult

¹⁰ Relative density refers to density indices derived from spotlight or helicopter counts and is referred to here as ‘density’. Absolute density estimates are relative density estimates corrected for sightability.

crocodiles - 1.27 per km in 2017 along 26 km of a narrow waterway, equivalent to 51 per km² (Figure 13 in Taplin et al, 2020).

88. The total area of waterways in the NPEC below 20m in elevation (where over 95% of crocodiles are found) is estimated to be 217 km². The non-hatchling population there is estimated from 2016-19 surveys to be 2,848 of which 376 (13.2%) were adults (Table 24 and Figure 42 in Taplin et al, 2020, 2021). That gives a relative density of adults of 1.73 per km² equivalent to an absolute density of perhaps 4.5 per km², allowing for an adult sighting fraction of 0.383 (refer Footnote 13 para 142). That compares with an estimate for 2017 derived from Table 4 in Fukuda et al (2020) of 44,065 adults in 18,843 km² of NT waterways, for an absolute density of 2.34 per km². The high areal density in the NPEC region almost certainly reflects the many very narrow and mostly short waterways that characterize that area, compared with the very long and wide waterways of the NT study area.
89. Given the high areal density of the NPEC population, it is sensible to incorporate density dependent effects in the NPEC models.

Density dependency in survival rates

90. The estimated effect of adult density on adult survival rate in the NT is not great (Ricker function $\beta = 0.044$). The 2017 density for the NT would decrease adult survival from 0.97 at very low density to 0.88. The 2017 density in the NPEC population would reduce it still further. That is enough to be material.
91. The counts of hatchlings in most NPEC systems have been extremely low over the years, measured in zeros or single digits in most waterways and reaching maxima of 20-25 animals in the Daintree River in 2017, the Hull River in 2000 and 2007 and the Murray River in 2018.
92. The Murray and Hull River survey areas are comparable in size at 1.6 and 1.4 km² respectively, giving each a maximum hatchling density of 15 per km². In the Daintree River, the maximum hatchling density encountered was 12 in 6.7 km², or 1.8 per km². Thus the maximum density encountered in NPEC rivers was about half that seen in the Blyth-Cadell system in the NT between 1974/75 and 1989/90, where annual density ranged from 4.7 – 36 per km² (derived from Messel et al, 1981; Webb et al., 1984 and author's measurement of the area of the Blyth-Cadell survey region). These localised high densities are sufficient to give rise to density dependent effects if the processes modelled for the NT operate similarly in Queensland. It appears sensible, therefore, to include their potential influence on population dynamics across the whole region.
93. For the NPEC model, the density dependency coefficients for β_2 and β_4 will be allowed to vary from 0 to 0.2 and 0.05 respectively. The maximum values are slightly higher than in the NT model. The shapes of these two density dependent functions are shown in Figure 3 against selected values in the range modelled. The β_3 value for juvenile survivorship the NPEC model is set to zero, consistent with Fukuda et al (2020).

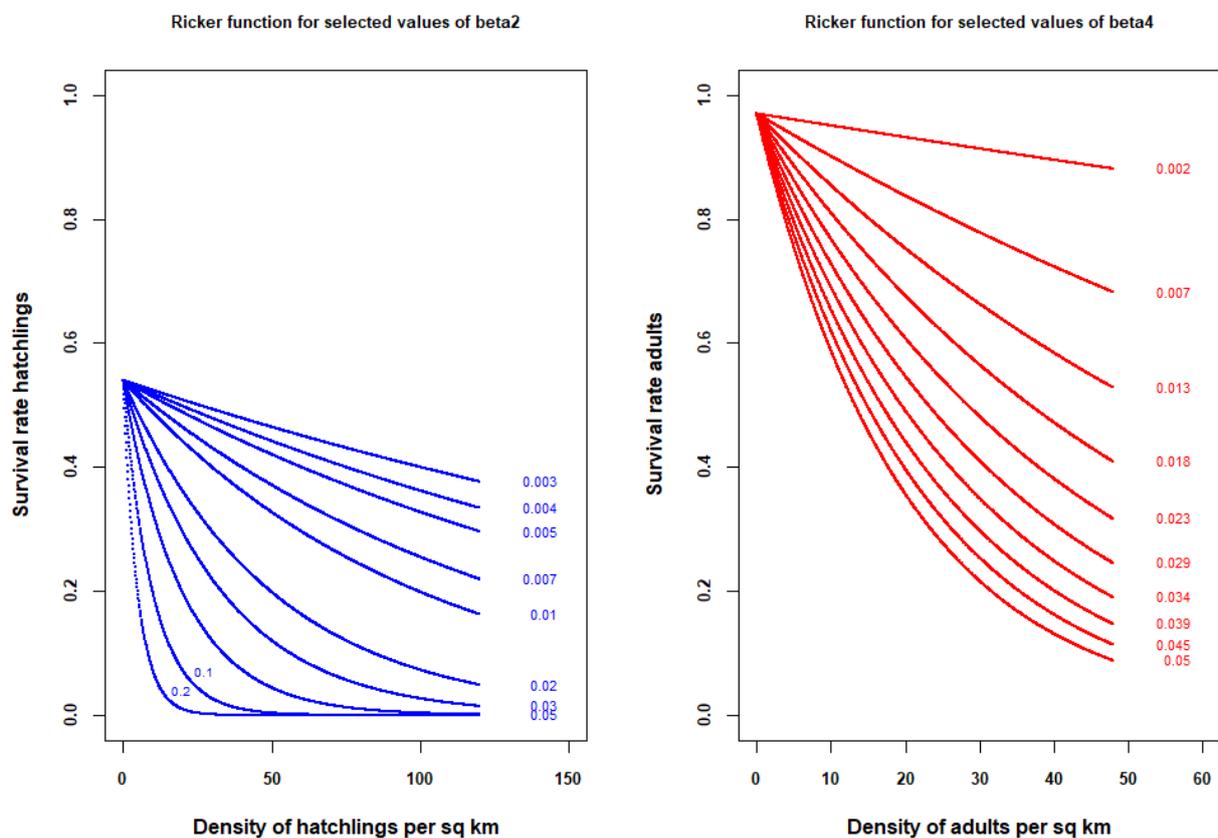
Density dependency in fecundity

94. The proportion of female crocodilians that breed in any year is generally less than 100%. Craig et al (1992) estimated 60 - 80% of female Nile crocodiles nested annually, with a central measure of 70%. Nichols et al (1976) cited estimates of 68% and 67% among alligators from Louisiana.
95. Fecundity in the NT model was modelled as a function of the proportion of adult females nesting in any year and of adult survivorship (itself density dependent). The proportion of

females nesting was modelled as a Beverton-Holt function decreasing sigmoidally from 100% to 50% as the density of females increased (Fukuda et al, 2020).

96. However, the evidence for density dependence is not strong (Woodward et al, 1984; Hines and Abercrombie, 1987; WMI, 2007) and we have no information about whether or how density might affect nesting activity in Queensland. We do know that the NPEC region generally has low densities of crocodiles (Taplin et al, 2020) and a large amount of nesting habitat – some 250 km², of which 130 km² is of medium or high quality (derived from data summarised in Taplin (2017)). Density dependence has therefore been excluded from the NPEC model and, instead, a fixed proportion of 75% of females nesting in any year included.

Figure 3: Shapes of the Ricker function relating annual survival rates of hatchling and adult crocodiles to the density of hatchlings or adults in the 217 km² of habitat available to the NPEC population. The value of β_2 or β_4 corresponding to each curve is shown. The parameters β_2 and β_4 influence the extent to which survival rate is reduced as hatchling or adult density increases. NT-derived values for β_2 and β_4 are 0.153 and 0.044 respectively.



Summary of population parameters included in the model

97. The vital rates and density dependency coefficients included in the initial NPEC matrix models are summarised in Table 3.

Environmental stochasticity

98. The NT model incorporates an element of environmental stochasticity through a relatively modest (+/-15%) effect of preceding dry season duration on the following year's egg production, based on analyses in Webb (1991), WMI(2007) and Fukuda &

Saalfeld (2014) . This introduces climate-dependent temporal variation into the population trajectory but the effect on the long-term population trajectory is small.

99. We have very little information on the effects of climatic variability on the amount of nesting activity and the recruitment of hatchlings in Queensland. It seems likely that some Queensland populations occupying habitats and climatic zones like those in the NT may be similarly influenced by prolonged dry seasons, but there is no data to verify or quantify the effect. And the NPEC region differs greatly in climate from anywhere in the NT, having very high winter rainfall and by far the highest summer rainfall in Australia (BOM, 2023).

Table 3: Ranges of values adopted for modelling of the NPEC population based on estimates of vital rates in *C. porosus* and other crocodilians.

Variable	Name	NT estimate	Queensland model minimum	Queensland model maximum
Annual survival rate (N1 – Eggs)	S1	0.25	0.05	0.25
Annual survival rate (N2 – Hatchlings)	S2	0.54	0.05	0.54
Annual survival rate (N3 – Juveniles)	S3	0.72	0.50	0.90
Annual survival rate (N4 – Adults)	S4	0.97	0.85	0.99
Annual production of female eggs per breeding female	m4	26.55	20	30
Proportion of females breeding	f0	1.0-0.5 Density dependent	0.75	0.75
Duration of juvenile stage (years)	T3	8.3	6.3	14.3
Strength of density dependent effect of hatchling numbers on hatchling survival	beta2	0.153	0	0.200
Strength of density dependent effect of adult density on adult survival	beta4	0.044	0	0.05

100. Given its limited impact on the long-term population trajectory in the NT model and the lack of evidence that such effects occur in Queensland, it is sensible to exclude environmental stochasticity from the modelling.

Can the NPEC population be considered closed?

101. It is reasonable to consider the NPEC population to be a closed population as it is bounded to the north by an inhospitable region in the Cape Flattery dunefields and to the south by an extended zone of very low crocodile density south of Ingham ((Hawkins et al, 1987; Taplin, 1987; Taplin et al, 2020, 2021). A recent study of the genetic makeup of populations throughout Queensland indicates strongly that there is very limited natural genetic interchange between the study area and the higher density populations in

Rinyirru/Lakefield NP to the north and the Proserpine River to the south (Lloyd-Jones et al, submitted).

Modelling the North Queensland population

102. For the initial investigation of the broad applicability of the NT model to the NPEC population, two principal questions are of interest:
 - 102.1. Is the model capable of projecting population change over time that maps onto estimated changes in the population based on survey results?
 - 102.2. How sensitive is the model to variation in the vital rates (survivorship, growth rates, fertility) and density dependency coefficients that inform it?

Estimates of the NPEC population trajectory over time

103. It is useful initially to examine how well the NT model with its NT-derived estimates of vital rates and density dependencies¹¹ fits the survey data available for the NPEC population. Because of the paucity of survey data over time for Queensland, we have only a handful of data points against which to test the population model. These come from estimates by Taplin et al (2021) of population size and size/stage distribution in Region 5b in three survey ‘Eras’ – 1984-89, 1994-99 and 2016-19 (Table 4). Hatchlings were very sparse in 1984-89 and increased substantially in numbers and proportions in later decades as did the proportion of adults in population. The proportion of adults may have been higher in 2016-19 were it not for the removal of significant numbers in the crocodile management program (Taplin et al, 2020).
104. We have good data from DES archives on the number of crocodiles removed for management purposes since the first East Coast Management Program was introduced in 1986/87 (Table 5). Between 1985 and 2022 some 920 crocodiles were removed, principally juveniles and adults. A few hatchlings were removed when a nest or some individual animals were found in places where they could not be left undisturbed.
105. These numbers can be converted to rough estimates of the proportion of adults and juveniles removed from the NPEC population by (a) interpolating and extrapolating estimates of total non-hatchling numbers for the survey Eras based on the population growth rate and (b) doing likewise for the point estimates of stage proportions over time (Figure 4).

¹¹ The density-dependent influence on fecundity of the proportion of females nesting has been set to zero for these and all other projections.

Table 4: Changes in estimated non-hatchling (NH) numbers and size/stage distributions over three major survey Eras. The middle three rows include hatchlings to illustrate the very low numbers/proportions of hatchlings encountered in the 1980s, which suggests unregulated hunting had a very big impact on numbers of breeding females. Confidence limits around stage proportions have been estimated by assuming the counts on which they are based would follow a Poisson distribution. Confidence limits around the 1984-89 adult counts are extremely wide because only one adult was sighted. These estimates of confidence limits do not account for geographic differences in sampling between Eras.

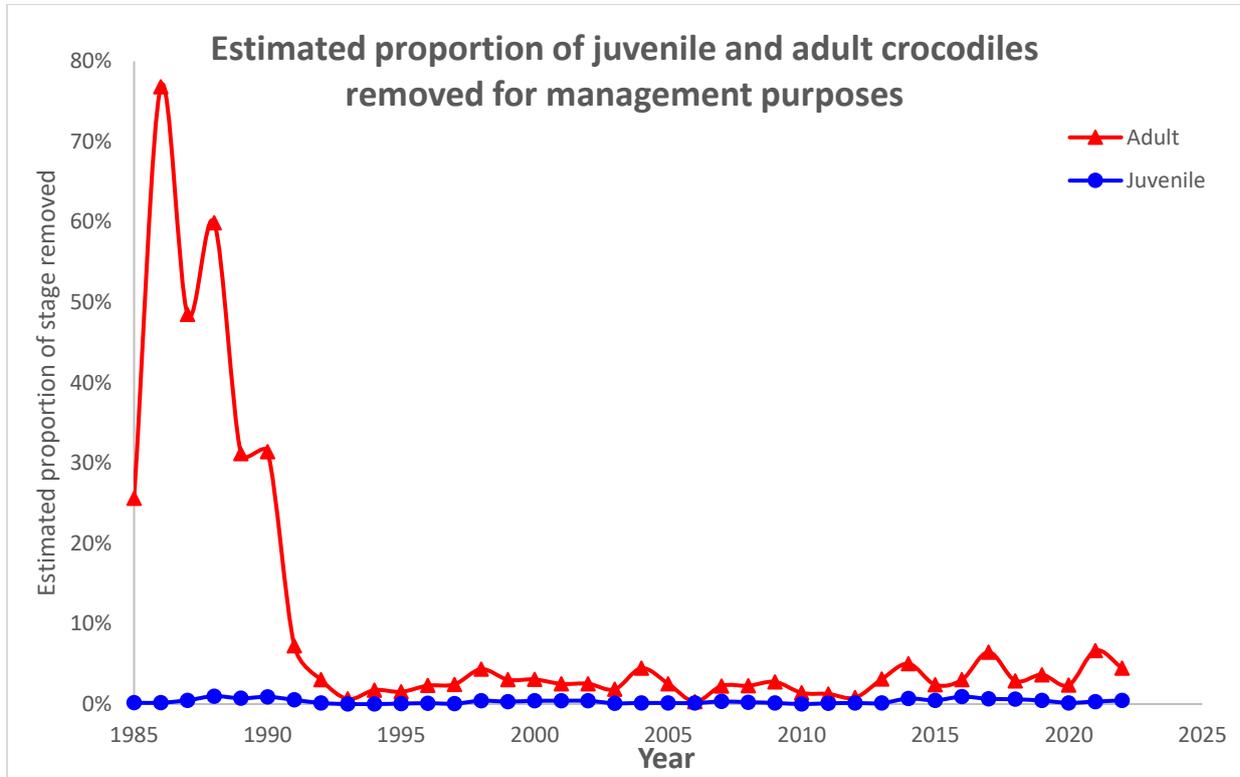
	1984-89	1994-99	2016-19
Estimated total non-hatchling numbers (sightability corrected)	1206 (477-1933)	2192 (1112-3272)	4521 (2589-6453)
Size class proportions including hatchlings	Stage %	Stage %	Stage %
Hatchlings (N2)	4.9	22.2	31.3
Juveniles (N3)	92.7	67.6	55.9
Adults (N4)	2.4	10.2	12.6
Size class proportions excluding hatchlings	NH Stage % Mean (95% CLs)	NH Stage % Mean (95% CLs)	NH Stage % Mean (95% CLs)
Juveniles (N3)	97.4% (91.3-100.0)	86.9% (79.3 – 93.7)	81.6% (77.7 – 85.3)
Adults (N4)	2.6% (0.0 – 88.6)	13.1% (6.3 – 20.7)	18.4% (14.7 – 22.3)

Table 5: Number of crocodiles removed for management purposes by year since protection in 1974. No documentary records exist for the period before 1984 when the estuarine crocodile research program commenced but few if any crocodiles are believed to have been removed.

Year	Hatchlings (<0.6m)	Juveniles (0.6-2.1m)	Adults (>2.1m)	Year	Hatchlings (<0.6m)	Juveniles (0.6-2.1m)	Adults (>2.1m)
1974	0	0	0	1999	0	6	12
1975	0	0	0	2000	0	8	15
1976	0	0	0	2001	0	8	14
1977	0	0	0	2002	0	8	16
1978	0	0	0	2003	0	2	12
1979	0	0	0	2004	0	3	30
1980	0	0	0	2005	0	3	17
1981	0	0	0	2006	0	3	2
1982	0	0	0	2007	0	8	15
1983	0	0	0	2008	0	6	15
1984	0	0	0	2009	0	4	18
1985	0	2	6	2010	1	0	9
1986	0	2	19	2011	0	3	8
1987	1	6	19	2012	1	4	5
1988	0	13	33	2013	1	4	19
1989	0	10	19	2014	3	24	30
1990	0	13	25	2015	3	17	14
1991	0	8	7	2016	17	35	17
1992	0	2	4	2017	3	26	35
1993	0	0	1	2018	2	25	15
1994	0	0	3	2019	0	19	18
1995	0	1	3	2020	0	7	11
1996	0	2	5	2021	1	15	29
1997	0	1	7	2022	0	23	18
1998	1	8	15	Total	34	329	560

106. The very high proportionate harvests in the early 1980s are almost certainly overestimates because of the very few adults sighted in surveys at that time, which make for extremely wide confidence limits (Table 4). Management offtake stabilised after the early 1990s while the crocodile population increased, removals averaging 2.8% per year for adults and 0.3% for the far more numerous juvenile stage. The rate of management removals was increased after 2013 and has averaged 4.1% (range 2.4 – 6.7%) for adults and 0.5% (range 0.2 – 0.9%) for juveniles. Those removals are large enough in the adult stage to be material given their estimated low natural mortality rate, but have not prevented the population increasing over time.

Figure 4: Estimated proportions of juvenile and adult crocodiles removed for management purposes between 1985 and 2022. These are rough estimates only as they derive from interpolation and extrapolation of the three-era estimates of non-hatchling numbers and stage proportions, The estimates for adult harvest proportions in the early 1980s are very likely considerable overestimates (see text).



107. These management removals and the incidental deaths discussed earlier (para 77) are built into the survey results used to estimate non-hatchling numbers in the 1984-89, 1994-99 and 2016-19 survey Eras. Those estimates might have been higher if those sources of mortality were removed – assuming the population dynamics do not result in complete compensation.

The NPEC population size and structure at protection in 1974

108. We can project the population over time from any starting point and it will eventually converge on a stable age distribution and, if density dependency is sufficient, an equilibrium population size. However, because we would like to test whether any particular configuration of vital rates and density dependency factors will lead to a population trajectory aligned with known survey results, it would be helpful to start it from a size/stage distribution approximating the situation when hunting ceased in 1974.

109. Fukuda et al (2020) derived an initial stage distribution for the NT from two sources. Firstly, an estimate that there were 4000 non-hatchling crocodiles in the NT in 1971. This estimate was combined with a calculation of the stable age distribution of the population in 1971 from the basic Lefkovich population matrix to estimate that the initial population included just 3044 juveniles and 956 adults.¹²

110. For the NPEC population, we have no estimates of surviving numbers in 1974. All we can really glean from the few reports on the crocodile industry in Queensland leading up

¹² Webb et al (App 2, p.42) estimated that in 1971 there were unlikely to be more than 2000 adult crocodiles over 26 years old (i.e. survivors from the pre-hunting period) in the NT population.

to protection in 1974 is that the number of hunters declined quite dramatically from 40 professionals in 1959-64 to around 5 in 1969. The annual take of estuarine crocodile skins declined over the same period from perhaps 4000 to a few hundred, by which stage hunting was becoming uneconomical (Roff, 1966; Blackman, 1968, 1970, Weaver, 1973; Webb et al, 1984 App. 2). By 1972-73 the number of professional shooters was estimated at 8 and casuals 10-12. The decline in hunter numbers was exacerbated by a big fall in skin prices from ca 1970, and by 1972-73 no professional hunters were targeting estuarine crocodiles in Queensland and most skins were from animals netted incidentally by fishermen (Weaver, 1973).

111. The Queensland data are badly confounded by difficulties in determining the origin of skins traded, some of which were exports (legal and illegal) from NT and WA, and a lack of information about the number of hunters targeting estuarine rather than freshwater crocodiles. Nonetheless, the few data are consistent with the general picture of estuarine crocodile hunting in Australia where an unregulated industry drove the species to economic extinction. By targeting both small and large size classes (small animals for the tourist 'stuffer' trade and large animals for skins) hunting would have reduced the accessible population to extremely low levels across all size ranges.
112. About 95% of Queensland's crocodile population is found in relatively navigable and accessible rivers and creeks less than 20m above sea level (Taplin et al, 2020, 2021). The population would have been more vulnerable to hunting than the NT population, which was protected by very extensive and much less accessible swamplands (Webb et al, 1984). The NPEC population in particular occupied a quite densely occupied area, with 224,000 people in the Townsville and Cairns Local Government Areas (LGA) in 1971 compared with 36,000 in the Darwin LGA at that time (O'Neill, 1971a,b). There would have been abundant opportunities for landowners and casual or professional hunters to target crocodiles and market them locally at relatively low cost. We should expect the population to have been driven to extremely low levels by 1971 with, most likely, a modest number of animals remaining in the very few large deltaic plains (e.g. the Herbert River and Murray River plains) that had lagoons and small areas of swampland that remained difficult to access.
113. Some of these animals were encountered by the author in the mid-1980s when research in this region first started. As land clearing progressed there were quite regular reports to the Queensland National Parks and Wildlife Service of animals over 4m in length that must have survived hunting. Some were shot when the protective lowland rainforest around their habitat was cleared for agriculture (Figure 5). Others were protected by landowners and some were removed as part of the East Coast [Crocodile] Management Program (Taplin, pers obs and DES records). For example, 86 adult crocodiles were removed to farms and zoos from the NPEC population from 1985-89 of which 19 were males over 4m in length. Fifteen of those 19 (79%) came from the Herbert River and Murray River plains, consistent with a small remnant population in those relatively protected areas.¹³

¹³ Another three came from the Daintree River where they had been somewhat protected by tourism operators offering crocodile spotting tours.

Figure 5: A large crocodile killed at Davidson’s Lagoon in the Tully/Murray River catchment of the NPEC region in 1985 and location map. Clearing of the surrounding area for agriculture exposed parts of the lagoon previously protected by dense vegetation. This was very likely one of a small number of large adults that survived hunting before 1974 in relatively protected waterholes. Similar waterholes on nearby Boar Creek hold numbers of large adults today.



114. The remnant adult population should have led to an early flush of hatchlings and juveniles into the river systems, where we would expect enhanced survivorship once the stuffer trade stopped. That some such response did occur is suggested by the limited

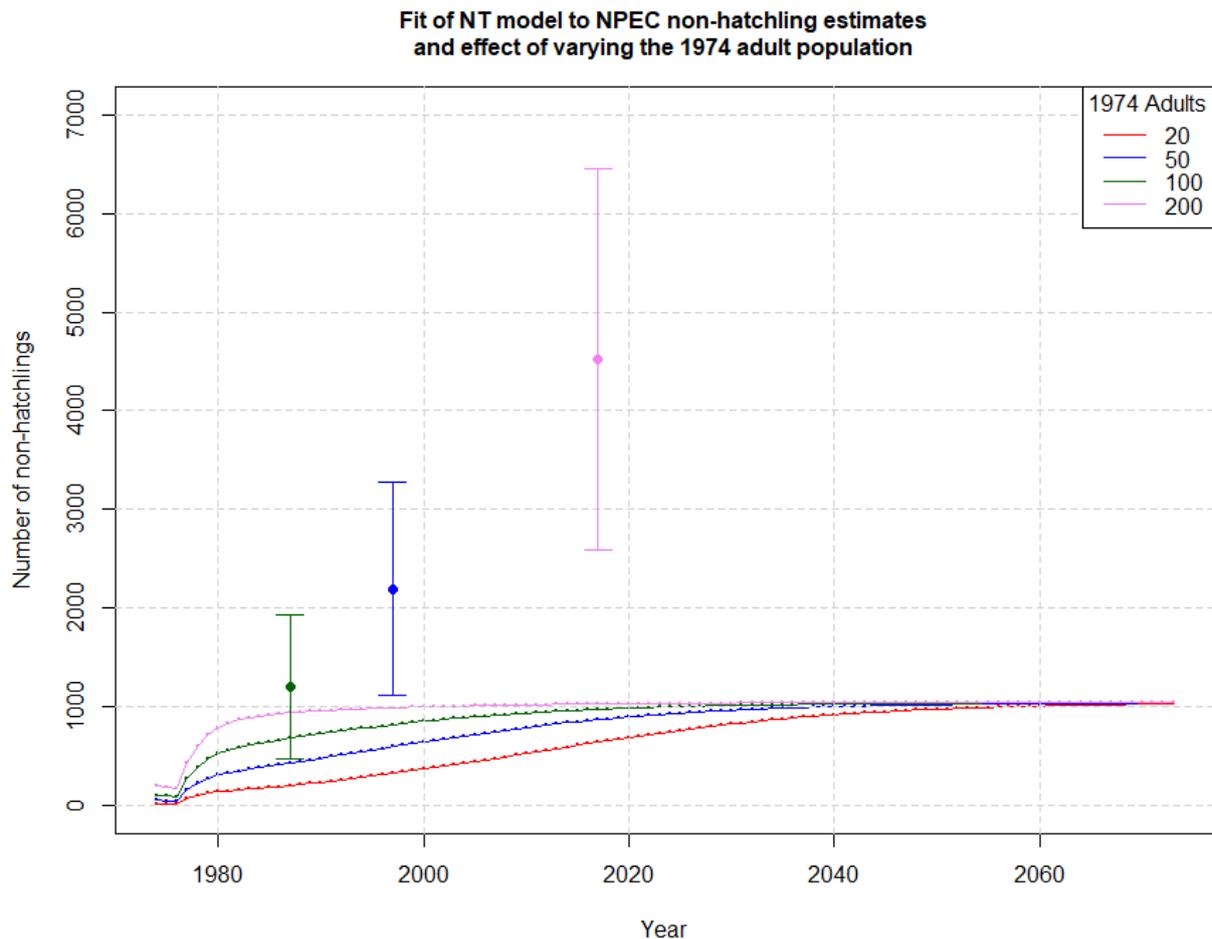
surveys of NPEC rivers in the 1980s, which revealed very small numbers of hatchlings and a population heavily weighted towards juveniles and small subadults up to about 2.1m (Taplin et al, 2020, 2021). The very small numbers of hatchlings found a decade after protection does suggest that successful breeding in these systems was heavily impacted by hunting, with long-lasting effects.

115. Particularly heavy mortality in the breeding female population may account for some of it, as it would then require a decade or more for the first new females to reach maturity and start nesting. It may also, however, simply mean that residual nesting and recruitment occurred mainly in the remnant swamps and billabongs and that the population grew initially in those unnavigable habitats.
116. It is not possible to generate a reliable estimate of the remaining numbers and size distribution of the NPEC population in 1974. There are some 2360 linear km of perennial waterways in the area occupied by the NPEC population. A reasonable starting point is a range of 20 adults on the low side (an absolute density of about ~1 animal per 100km) to 200 adults (~1 animal per 10 km) on the high side. These upper and lower bounds were used for projections to explore the transient responses of the model outputs to this initial estimate. The initial numbers of eggs, hatchlings and juveniles were set to an arbitrary value of 1, recognising that this would introduce some initial delay in the projected population's approach to a stable equilibrium. This was not considered likely to be material given the wide confidence limits around the estimate of non-hatchling numbers in the three survey Eras (Table 4) and the uncertainties in population parameter estimates.

How well do the NT estimates of vital rates and density dependencies fit the NPEC trajectory?

117. Using NT values for survivorships, duration of the juvenile stage, fecundity and density dependencies of the hatchling and adult survival rates, projection of the matrix model fits the Queensland population poorly regardless of the number of remaining adults assumed for 1974 (Figure 6). The question then becomes whether a different but biologically reasonable array of vital rates can generate projections that are a better fit.

Figure 6: Growth trajectory of the NPEC population using NT-derived values for the vital rates and density dependency coefficients to generate the projection matrix and four values for the initial population of adults in 1974. The model fits the observed data (shown as mean and 95% CLs for the three survey Eras) poorly.



Sensitivity analysis of the population model

118. The essence of sensitivity analysis is to try and determine the extent to which outputs from a model, such as the population's rate of increase or equilibrium numbers, are influenced by variation in either the matrix elements (a_{ij}) of the projection matrix or the vital rates and density dependencies that feed into those matrix elements. Such analyses can help:
 - 118.1. Illuminate the underlying population dynamics of the species.
 - 118.2. Inform decisions about management interventions that will most effectively help a vulnerable population to recover or an over-abundant population to be reduced.
 - 118.3. Inform decisions about the potential impacts of structured or unstructured harvests.
 - 118.4. Shed light on which aspects of the life cycle are most likely to contribute to population growth or decline.
119. An interesting and relevant example of the last item is a study of loggerhead turtle population dynamics by Crouse et al (1987), which showed that common management interventions aimed at egg and hatchling survivorship on nesting beaches were unlikely, based on sensitivity analyses, to result in significant changes in population growth rate.

They suggested that turtle excluder devices fitted to fishing nets and directed at increasing survivorship in juveniles were more likely to lead to population growth.

120. Sensitivity analysis is a complex topic (Morris & Doak, 2002; Cariboni et al, 2007; Caswell, 2018). In the absence of widespread and powerful computing capability, many early approaches relied on analytical approximations, often accompanied by quite strict assumptions. Many also relied on so-called one-at-a-time (OAT) analyses, where the effect of a single parameter is evaluated while holding others at fixed values. Quite a lot of effort was put into devising schemes for sampling effectively across often very-large parameter spaces (Swartzman & Kaluzny, 1987; McCallum, 2000) to reduce the computational workload.
121. Many of those methods remain useful today, depending on the context of the modelling, but increased computing power has allowed more use of global sensitivity analyses (GSA) which aim to explore model outputs across the entire range of parameter values and to better tease out interactions between factors (Cariboni et al, 2007; Harper et al, 2011; Iooss & LeMaitre, 2015; Renardy et al, 2019). The global sensitivity analysis used here is ‘model-free’, as it does not depend on assumptions of linearity, additivity or monotonicity in the relationships between model inputs and outputs (Saltelli, 2004). This approach is well-suited because only very approximate ranges for the vital rates likely to influence the growth and size at equilibrium of the NPEC are available and little or nothing is known of their interactions.
122. Another reason to adopt the GSA approach is our interest in the behaviour of the density-dependent model. Commonly-used analyses of the sensitivity of population growth rate (λ) to matrix elements and vital rates are not appropriate to models with density dependencies - not least because λ will usually tend towards zero over time as the population reaches some equilibrium level. Thus, a density dependent model has no single growth rate on which to focus a sensitivity analysis (Morris & Doak, 2002).
123. The outputs of global sensitivity analyses are often complex and require further analysis to make the relationships between inputs and outputs more understandable. Many different methods have been employed (Saltelli et al, 1999; Cariboni et al, 2007). Many are quite restrictive in their assumptions or limited in their capacity to deal with non-linear relationships and complex interactions between input parameters. In recent times classification methods and regression trees and generalised additive models (GAM) have found some favour because they can deal with many parameters, do not necessarily require massive sampling of the parameter space and can handle non-linearity and quite complex interactions (Harper et al, 2011; Prowse et al, 2016, Aiello-Lammens et al, 2017).
124. Consideration was given to applying a GAM or regression tree approach to the NPEC modelling exercise and some exploratory analysis was conducted. It was not adopted because the suite of population parameters used for analysis was small, the sample sizes needed to cover the parameter space proved computationally manageable, and the relationships between model inputs and outputs were sufficiently understandable in the raw output data without further abstraction.

Methods used for NPEC sensitivity analysis

125. Global sensitivity analysis incorporating multiple factors is challenged by the geometrically increasing number of possible parameter combinations as the number of factors increases arithmetically. In this particular case, the number of factors to consider was not huge (Table 3). Good randomised coverage of the parameter space was achieved

using Latin hypercube sampling (implemented in R package FME) and drawing each parameter from a uniform distribution between the ranges set out in Table 3. Latin hypercube sampling can provide better coverage of the parameter space than uniform random sampling (Aiello-Lammens et al, 2017). Uniform distributions were chosen as we have no information about the likely distribution of values around the NT-derived values, except in the case of egg numbers where there is good evidence for a near-normal distribution (WMI, 2007; author's analysis of Koorana Crocodile Farm data). Nonetheless, applying a uniform distribution in the case of egg numbers ensured the parameter was thoroughly sampled throughout its range.

126. For each simulation run, 10^6 random combinations of parameter values were generated and deterministic projection matrices were generated. Iterative estimation was used to calculate the transition probabilities for each initial projection matrix (Caswell, 2018). The transition probabilities were then held constant for subsequent iterations of the projection matrices. The initial deterministic matrix for each set of randomised parameter values was converted to its corresponding matrix incorporating density dependencies based on the randomly selected values of β_2 and β_4 and the initial number of adults in the population.
127. The density-dependent projection matrices were then iterated over a 100-year period covering 1974-2074, which was sufficient with most parameter combinations for the population to stabilise at an equilibrium number, whether through extinction or growth.
128. Density dependency coefficients (β_2 and β_4) for hatchling and adult survivorship were allowed in the sampling to fall to zero (i.e. removing their influence altogether). The large sample size chosen (10^6 replicates) ensured this small component of the parameter space was well sampled.
129. The principal model outputs tested for sensitivity were the equilibrium number of non-hatchlings in the population and the projected stage proportions. For the subset of population trajectories that resulted in positive growth and reached equilibrium within 100 years, several other output variables were recorded.
 - 129.1. The first year of equilibrium – defined as the first year in which the number of non-hatchlings fell within +/- 0.5% of its final value.
 - 129.2. Where trajectories showed a transitory peak and then declined to an equilibrium (refer Figure 15), the year in which the trajectory initially peaked was recorded. However, the equilibrium non-hatchling number and the year equilibrium was reached were calculated after the transitory peak had passed.
 - 129.3. The year at which the trajectory reached 50% of its equilibrium value and the number of non-hatchlings at that point.

Does any combination of population parameters result in projections that align with known data?

130. To compare population projections with survey data, this and later sections focus on growth in the non-hatchling element of the population, stages N3 and N4 which show a modest but progressive decline in the proportion of juveniles and a corresponding increase in adults (Table 4). The same trends have been seen in the NT (Fukuda et al, 2011). These estimates are used to test whether any combination of vital rates comes close to projecting results that align with the Era-specific population numbers and stage proportions.

131. The short answer to whether any combination of vital rates and density dependencies can reflect observed numbers over time and changes in size class proportions is ‘yes’. The ‘best-fit’ model from the parameter space explored is shown in Figure 7. It simply confirms that the model can provide a reasonable fit. It tells us little or nothing about whether the model is a reliable reflection of population processes that led to the actual trajectory. Many different combinations of parameters can generate similar trajectories (see below) not least because of the wide confidence limits around the three-Era population estimates and size class proportions.
132. The differences between vital rates in the NT model and the best-fit model in Figure 7 are set out in Table 6. The differences from the NT estimates are small for survivorship of eggs (S_1), hatchlings (S_2), adults (S_4), egg production (m_4) and duration of the juvenile stage (T_3). The principal differences are in a slightly higher value for juvenile survivorship (S_3) and very low values of β_2 and β_4 , which reduce markedly the effects of hatchling density on hatchling survivorship and adult density on adult survivorship.

Figure 7: Fit of the best-fitting model to estimates of absolute numbers of non-hatchlings and size class proportions of juveniles (green) and adults (violet). Confidence limits in size class proportions for the 84-89 Era are dotted as they are extremely wide for adults (see text).

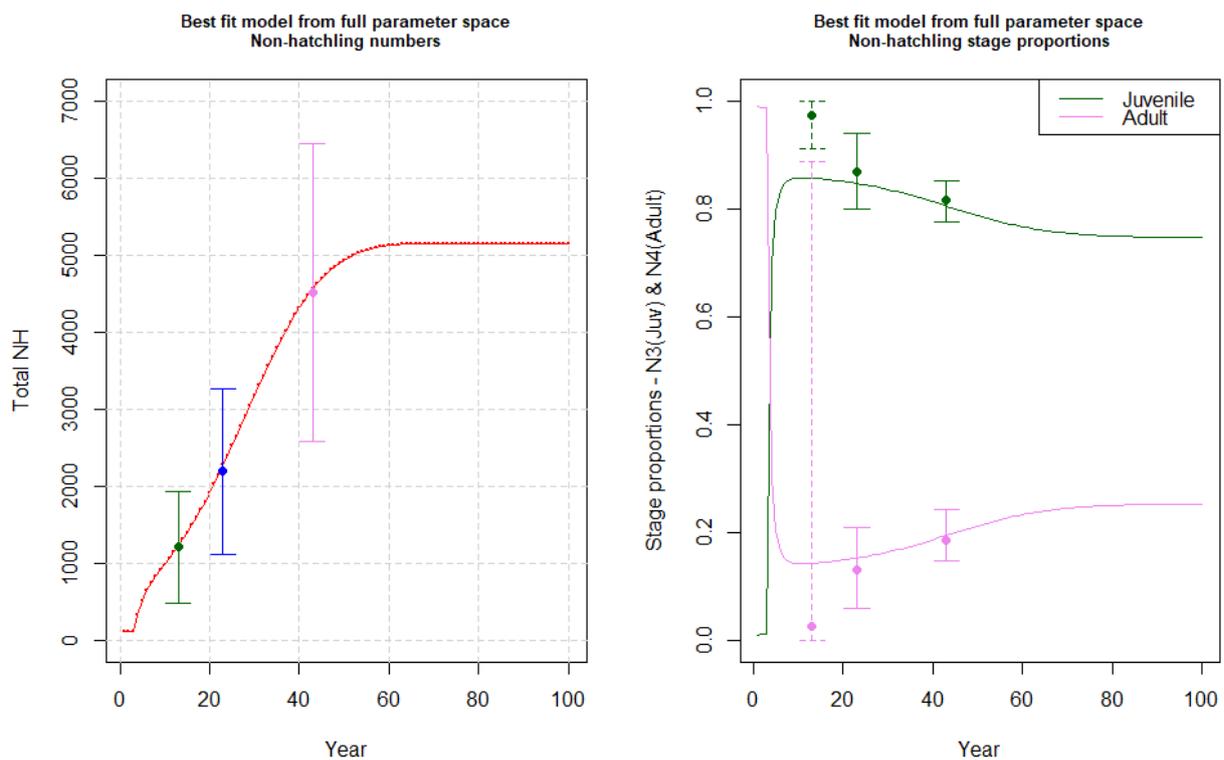


Table 6: Differences between vital rates and density dependency coefficients between the NT model and the ‘best fit’ Queensland model from initial exploration of the parameter space.

Variable	Name	NT parameter estimate	‘Best fit’ Queensland model
Annual survival rate (N1 – Eggs)	S1	0.25	0.24
Annual survival rate (N2 – Hatchlings)	S2	0.54	0.53
Annual survival rate (N3 – Juveniles)	S3	0.72	0.80
Annual survival rate (N4 – Adults)	S4	0.97	0.98
Annual production of female eggs per breeding female	m4	26.55	24.82
Duration of juvenile stage (years)	N3dur	8.3	9.3
Strength of density dependent effect of hatchling numbers on hatchling survival	beta2	0.153	0.049
Strength of density dependent effect of adult density on adult survival	beta4	0.044	0.005

133. Having established that the model is capable of approximating estimated numbers and size class distributions over time, this is a useful juncture at which to examine the responses of model outputs and the sensitivity of those outputs to all the underlying vital rates.

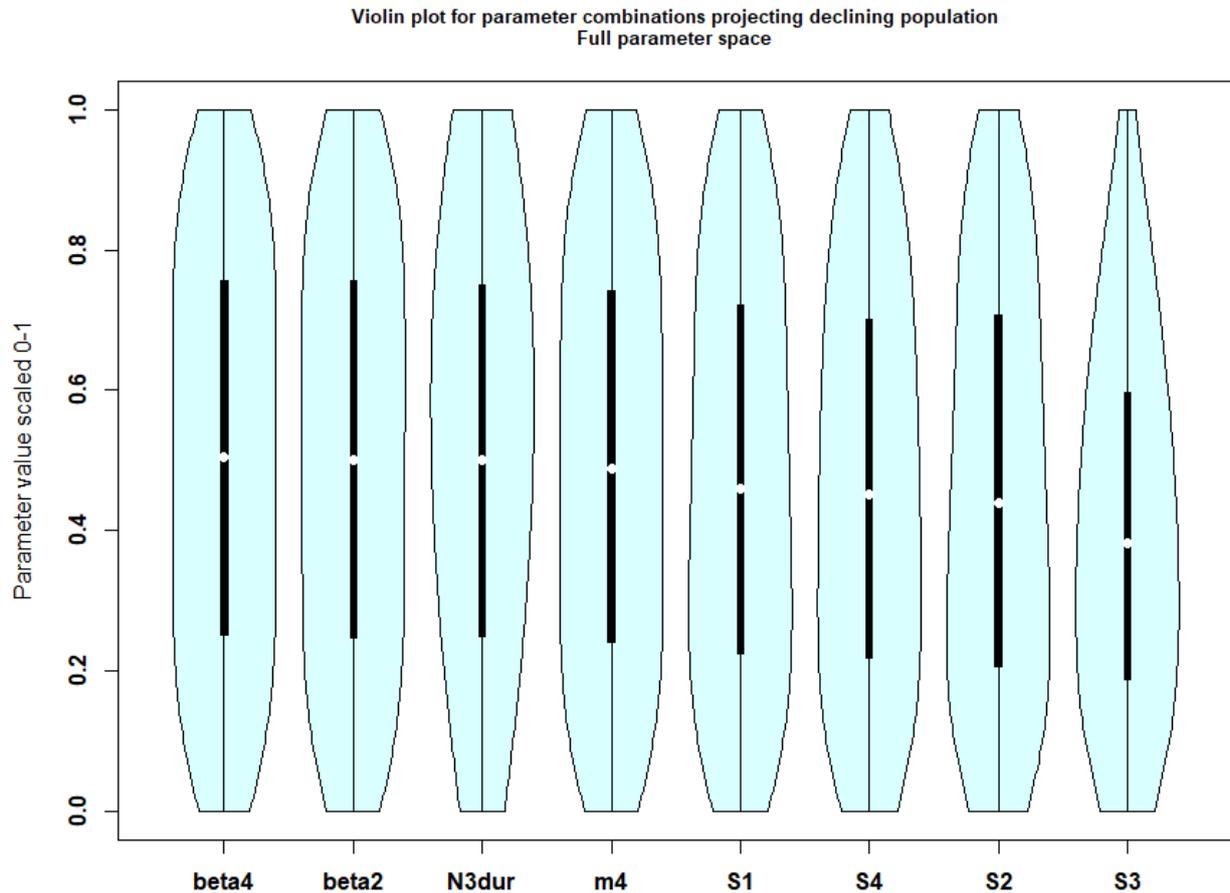
Model sensitivity across the entire parameter space

134. Of the 10^6 parameter combinations tested across the full parameter space, some 795,000 projected a population that either (a) declined from the outset; (b) declined after increasing increasingly initially for up to a decade; or (c) increased continuously after some initial fluctuation. None reached equilibrium in 100 iterations, unless it tracked to extinction. Only a very small fraction of the parameter space led to positive growth trajectories lying remotely close to survey estimates of non-hatchling numbers.

Drivers of projected population declines

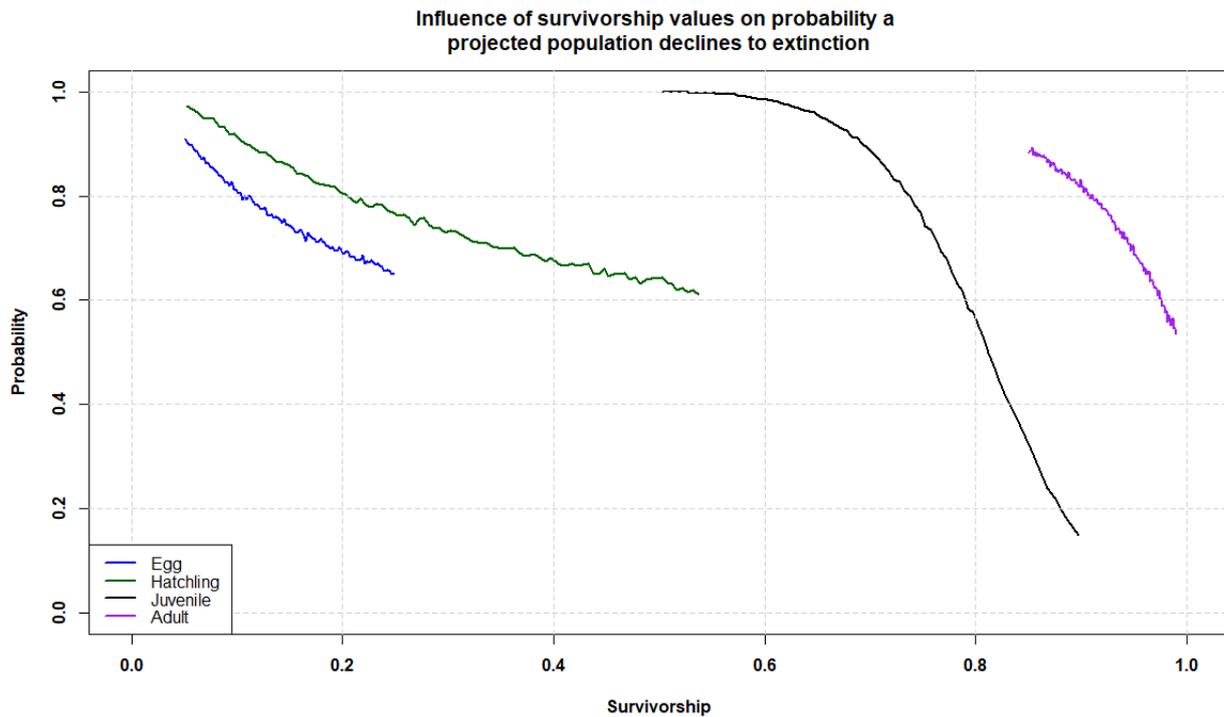
135. Declines to extinction in projected populations were driven principally by low values of juvenile survivorship (Figure 8), with only small effects attributable to survivorship of other stages. The density dependency coefficients (β_2 and β_4), the duration of the juvenile stage (N3dur) and fertility (m4) had essentially no effect.

Figure 8: Violin plot showing the kernel density distribution of population parameters in projected matrix models leading to population decline and extinction. The y-axis shows the value of the population parameter scaled between its minima and maxima for each parameter in the dataset (~755,000 parameter combinations). The kernel density is shown by the width of the blue band. The median and first and third quartile range are shown by a white point and a black bar respectively. Population declines and extinction were driven principally by low values of juvenile survivorship (S3).



136. Across all combinations of parameter values, a high proportion of the projected populations track to extinction (Figure 9). As might be expected, the likelihood of tracking to extinction increases with declining survivorship in all stages, but the likelihood of tracking to extinction is low only for high values of juvenile survivorship, above the NT model's value of 0.72. The likelihood of a projection matrix projecting positive growth and, therefore, equilibrium non-hatchling numbers consistent with survey estimates is high only at high values of S3. That is explored further below as it is this small subset of projection matrices that is of primary interest.

Figure 9: Influence of survivorship rates on the likelihood of population projections tracking to extinction.



Projection matrices that project positive population growth

137. Initial examination of model outputs for positive growth trajectories (Figure 10) showed that the equilibrium number of non-hatchlings was:
 - 137.1. quite strongly influenced by survivorship of, in decreasing order, juveniles, hatchlings, eggs and then adults;
 - 137.2. barely influenced at all by the duration of the juvenile stage ($N3dur$) and female fertility ($m4$);
 - 137.3. strongly influenced by the strength (β_2) of the density dependent effect of hatchling density on hatchling survivorship; and
 - 137.4. weakly influenced by the strength (β_4) of the density dependent effect of adult density on adult survivorship.
138. The strong influence of juvenile survivorship is consistent with the extinction probability curves in Figure 9 for matrices with $\lambda < 1$.
139. When β_2 was lower than about 0.05 the equilibrium number of non-hatchlings rose very rapidly, sometimes to unrealistic levels (as high as 600,000 in the most extreme case) as the model became more deterministic and growth essentially exponential.

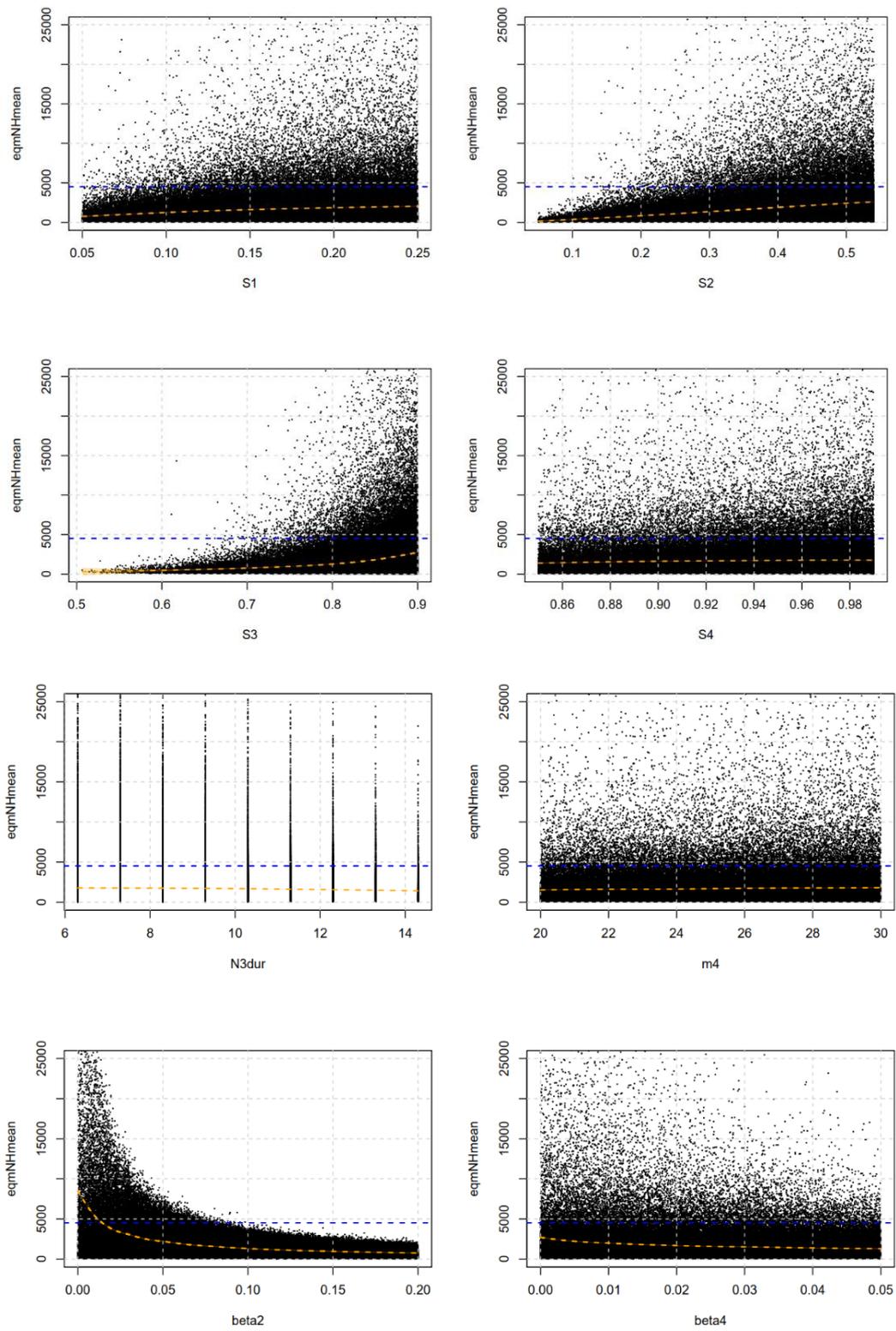
Constraining population trajectories to realistic estimates of the non-hatchling population

140. Preliminary exploration of the full parameter space (refer Table 3) showed that the resulting matrices can project unrealistically low or high estimates of the equilibrium population. It is useful therefore to set some reasonable bounds on likely non-hatchling densities and numbers.

141. Based on survey results across Queensland, the maximum density of non-hatchlings measured by spotlight counts appears unlikely to exceed 5 non-hatchlings (NH) per km (the uniquely high density in the Proserpine River) and will more likely peak at a considerably lower density from 1-2 NH/km (Taplin et al, 2020). No survey in any of these NPEC systems has found a density higher than 1.0 NH/km and the Hull River shows clear signs of having stabilised since the mid-1990s at a density below 0.8 NH/km.
142. The total extent of perennial riverine habitat with potential to be occupied by the NPEC population is some 2,360 linear km, so we can set some likely limits on the total number of non-hatchlings at equilibrium. Assuming that the stage/size class distribution seen in the 2016-19 surveys holds steady in future, the estimated correction factor from spotlight counts to absolute counts for the NPEC population is 1.59 – i.e. there are 159 crocodiles actually present for every 100 sighted in spotlight surveys¹⁴. Thus, at the lower and more likely extreme the spotlighted total is ~ 2,360, for an absolute number of 3,750, and at the upper end the expected spotlight total is 4,720 for an absolute number of 7,500.
143. Working against the upper estimate of 7,500 is the impact of intensive development on many NPEC catchments (see Figure 5 for an example). Development makes some waterways uninhabitable through clearing and subsequent siltation. For example, much of Davidson Creek in the once-favourable Murray River catchment has been so shallowed by siltation that it provides habitat only for very small animals despite high densities of adults a short distance downstream (Taplin, 2020 & Taplin and Brien, pers obs). Agricultural and pastoral development along many NPEC waterways has seen fringing vegetation cleared right down to the river bank, leaving crocodiles highly exposed and greatly reducing the extent of favourable habitat. Crocodiles persist in these habitats, but breeding size animals in highly developed areas are commonly restricted to deeper scours on river bends and near rock bars (Taplin & Brien, DES helicopter surveys 2016-19). There are good reasons to consider the lower limit of 3,750 non-hatchlings more realistic than the high-end estimate.
144. If, however, the NPEC population was to emulate more closely the mean population trajectory of twelve extensively monitored rivers in the NT (Figures 3 and 6 in Fukuda et al, 2011) then a mean equilibrium density of ~6 NH/km is possible. Allowing for sightability, that translates to a population of some 22,500 in the NPEC subregion.

¹⁴ For this calculation the estimates of detection probability of Bayliss et al (1987) were averaged these across the juvenile (N₃) and adult (N₄) stages, for values of 0.737 and 0.383 respectively. These give correction factors for N₃ of 1.36 and for N₄ of 2.61, giving a weighted average (by numbers in each stage) of 1.59.

Figure 10: Response of the equilibrium number of non-hatchlings (on the y-axis) to variation within biologically reasonable bounds of vital rates and density dependency coefficients as set out in Table 4 (sample size is 166,364). The estimated mean count for 2016-19 is shown in blue and a smoothing spline (orange) is fitted to the data points to show the general trend. Unrealistically high values of non-hatchling numbers have been excluded for clarity.



145. There are many reasons to think this estimate unrealistically high, not least of them the much smaller scale of NPEC habitat (217 vs 19,000 km²), the degraded quality of much of the habitat, and the inevitably greater human disturbance of crocodiles. Nonetheless, examination of historical records of estuarine crocodiles in eastern coastal Queensland sheds no useful light on pre-hunting densities (Taplin, unpubl obs). And it would be unwise to dismiss this high estimate as unrealistic given the Proserpine River had 5.2 NH/km in a 2017 survey and the trajectory of NH counts suggests it has not yet peaked (Appendices 1 and 3 in Taplin et al, 2020).
146. It seems sensible to confine attention mainly to the best estimates of reasonable bounds for the population (3,750-7,500) but also to explore the implications if the upper bound of 22,500 was to hold.

Reducing the parameter space

147. As well as excluding parameter combinations that lead to unrealistically low or high equilibrium numbers, it is reasonable to ask whether some of the population parameters in Table 3 might be fixed so as to reduce the complexity of the models.
148. Applying the limits of 3,750 - 22,500 animals for the equilibrium non-hatchling numbers reduced the output sample to 13,622 parameter combinations. It did not, however, reduce the number of parameters or their ranges, as the reduced sample still encompassed the full range of values for all of the vital rates and density dependency β s, including β_2 and β_4 values close to zero.
149. Combined parallel coordinates plots (Figure 11a, following Iooss and LeMaitre (2015)) and violin plots (Figure 11b) are useful in teasing out those combinations of vital rate values that lead to these constrained projections. Figure 11(a) is a random sample of 2,000 of the full set of 13,622 parameter combinations, revealing detail that would be overwritten if the full sample was plotted. This figure shows, unsurprisingly, that there is no highly constrained set of vital rates and density dependencies that leads to reasonable estimates of the equilibrium population. However, it is clear that some parameters (e.g. juvenile survivorship) have to lie within a much narrower range than others.
150. The parallel coordinates plot is more easily interpreted in conjunction with the violin plot (Figure 11b) which summarises the full set of 13,622 parameter combinations. This summarises quite neatly the response of the projected equilibrium non-hatchling number to each vital rate and density dependency. It also shows where the weight of each parameter distribution lies relative to the value used in the NT model (shown in blue). The plot illustrates that:
 - 150.1. Equilibrium non-hatchling numbers falling within the 3,750 - 22,500 limits can arise from a very diverse range of vital rates.
 - 150.2. “Reasonable” model outputs are more likely at high values of S_3 and (in decreasing order) S_4 , S_2 and S_1 .
 - 150.3. “Reasonable” model outputs are more likely at low values of β_2 .
 - 150.4. NT values for survivorship of eggs ($S_1 = 0.25$ p.a.) and hatchlings ($S_2 = 0.54$ p.a.) appear high for the NPEC population.
 - 150.5. The NT value for juvenile survivorship ($S_3 = 0.72$ p.a.) appears too low, fitting very few trajectories.
 - 150.6. The high estimated survivorship for adults in the NT ($S_4 = 0.97$ p.a.) lies reasonably close to the centre of trajectories in this plot.

- 150.7. The model output is quite insensitive to the values of female fertility (m_4).
- 150.8. It is also, as we would expect, quite insensitive to the number of adults in the 1974 population (chosen randomly from a uniform distribution between 20 and 200), as this number influences only the early convergence towards the stable equilibrium.
151. Figure 11a also shows that outputs falling within the 3,750 – 22,500 limits are somewhat more likely when the juvenile growth period is around 7.3-9.3 years. The median of the kernel density distribution matches the NT value of 8.3 years, though the model output can be consistent with longer and shorter maturation times.
152. Figure 11b also illustrates that the model output is highly sensitive to the value of β_2 . The NT value for this coefficient appears too high for NPEC models, as very few trajectories capture a value as high as 0.153. The median estimate across the parameter space for β_2 in the Queensland models is, after converting back to the original scale, about 0.04. Similarly, the NT density-dependency coefficient β_4 appears high relative to the distribution of values from the Queensland models, though its value has much less influence overall on the model output.
153. These low values for β_2 and β_4 are very likely driven principally by the differences in non-hatchling density between the NT and NPEC rivers when calculated per km² (areal density) rather than per km. The projected numbers of hatchlings and adults in the NT model give areal densities in 2017 of 36.2 and 2.34 animals per respectively. In contrast, a subset of NPEC models generated densities of 145.7 and 47.9 per km² at the highest end of equilibrium non-hatchling numbers. This is a simple consequence of the contrast between the predominant very short and extremely narrow rivers of the NPEC subregion and the very long, wide rivers used for the NT modelling. While high, the NPEC values are not entirely unrealistic – one section of the Murray River has a low linear density (1.27 NH/km) but an areal density of 51 NH/km² (para 87).
154. These high densities will, of course, drive much higher density dependency effects on population trajectories (Figure 3) so trajectories fitting the known survey data and modest population growth rates will lean towards lower density dependency coefficients. Thus, this particular difference between the NPEC and NT models may be driven more by the measure of density used than by the underlying biology. Fukuda et al (2020) used areal density to estimate density dependencies as they considered it better reflected habitat availability. It may be that linear densities, which are more similar in scale, would be a more useful metric for cross-regional comparisons. Ricker coefficients on a linear scale are not available, so areal density is used here. But the observation is important for interpretation of model outputs.
155. The data in Figures 10 and 11 were used to identify population parameters that could reasonably be fixed, simplifying the model. Female fertility (m_4) was fixed at 26.55 female eggs per mature female p.a. given the median lay very close to the NT value in Fig 11b and the value has little influence on non-hatchling numbers at equilibrium. Duration of the juvenile stage (N_{3dur}) was fixed at 8.3 years, corresponding to value in Fukuda et al (2020), given the median in Figure 11b matches the NT value and its value also has little influence (Figure 10).
156. Density dependency parameters β_2 and β_4 were allowed to decrease to zero in the reduced model, as trajectories fitting the 3,750 – 22,500 limits were encountered at extremely low values of β_2 and/or β_4 .

Figure 11: (a) Parallel coordinates and (b) violin plots for representative subsample of 2,000 combinations of vital rates and density dependency coefficients sampled from the full parameter space. Each orange line traversing graph (a) represents one combination of parameters that give rise to an equilibrium NH population between 3,750 and 22,500. The NT model's value for the parameter is in blue and the upper and lower bounds of parameters actually included in the sample are in black. The violin plot (b) presents full set of 13,622 parameter combinations, scaled for comparison between 0 and 1. The width of the light blue envelope represents the kernel density curve for each scaled parameter, with the median as a white point and the 1st and 3rd quartiles of the data as a black bar. See text for additional explanation.

Figure 11(a)

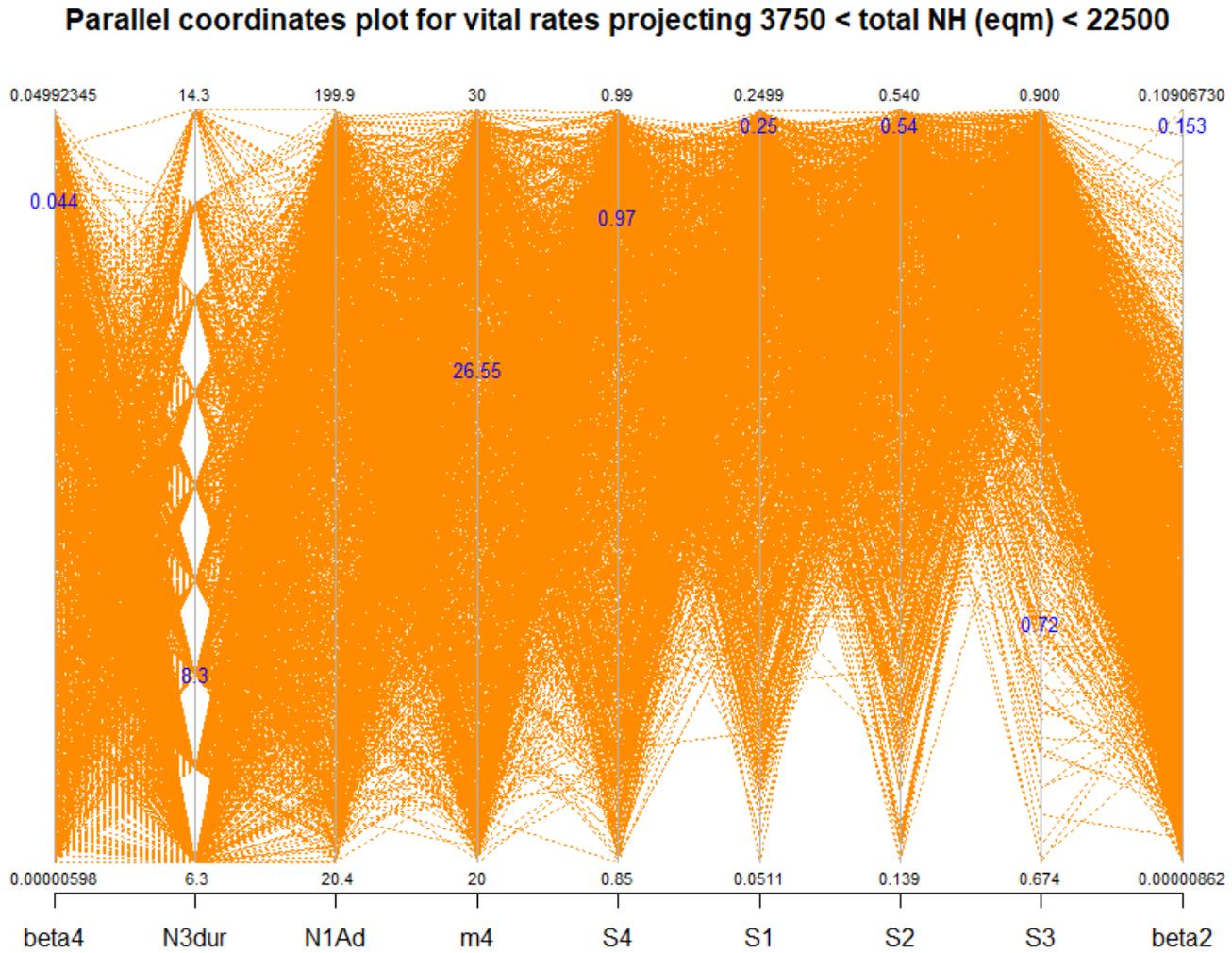
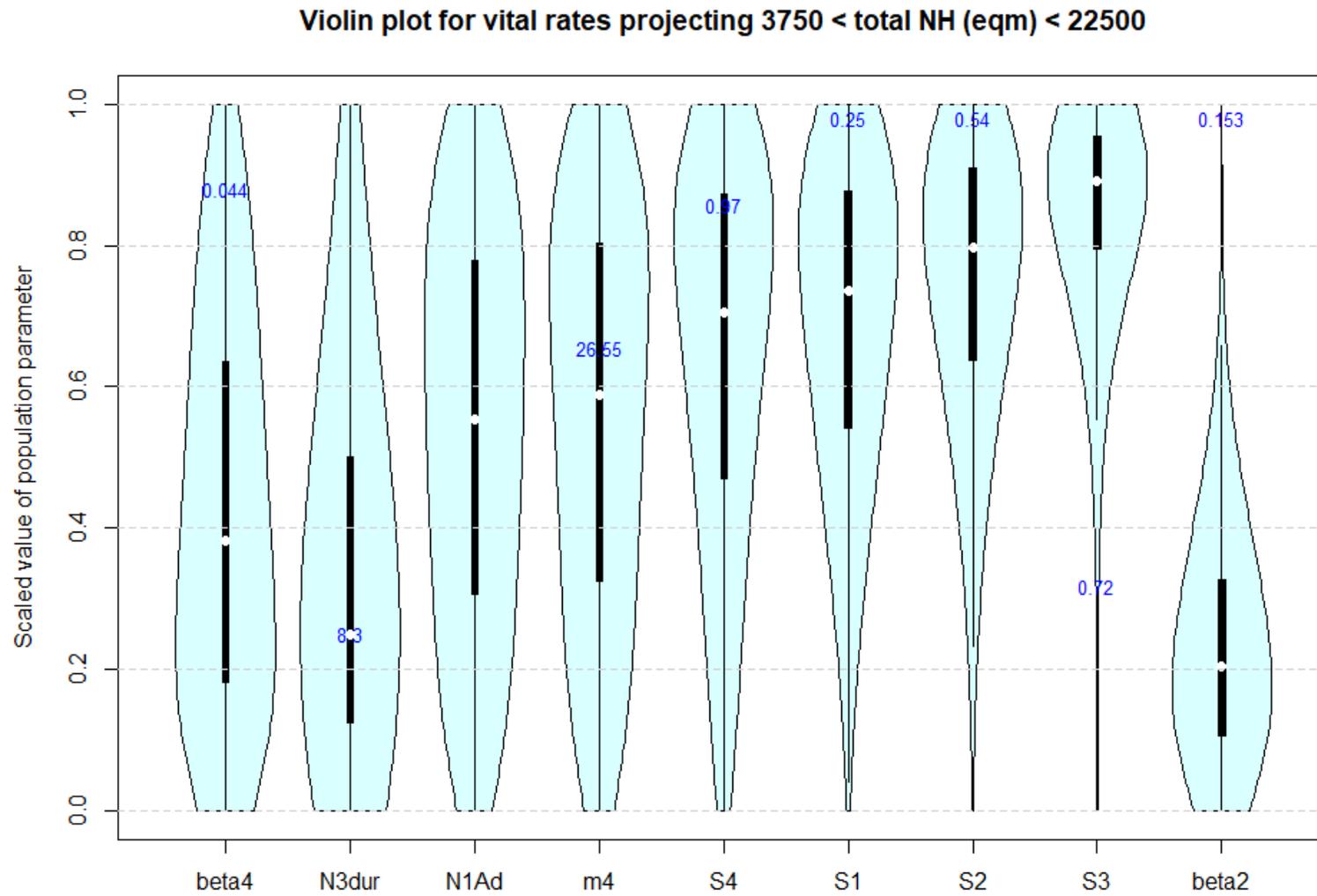


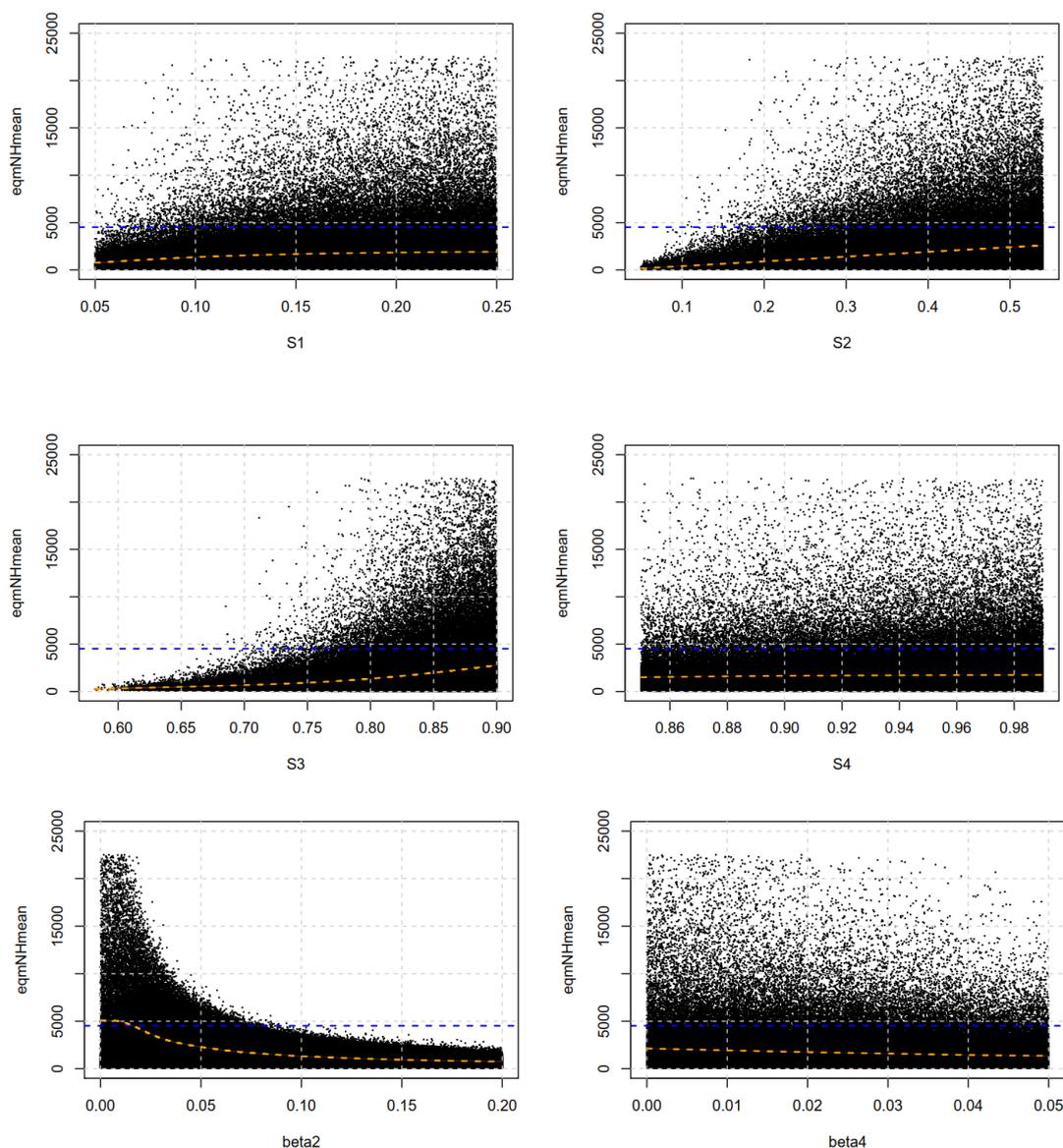
Figure 11(b)



Effects of simplifying the model

157. The model projections were repeated using fixed values for fertility and juvenile stage duration. In this reduced parameter space, about 72% of the 10^6 parameter combinations projected declining populations or failed to reach equilibrium over the 100 years of projection. As for the full parameter set, low values of β_2 led to exponentially increasing numbers that quickly exceeded (often by tens of thousands) the maximum 22,500 non-hatchling estimate.
158. The simplifications and constraints introduced did not, by and large, change the way in which equilibrium non-hatchling numbers responded to changes in vital rates apart from reducing the influence of density dependency at low values of β_2 (Figure 12).

Figure 12: Distribution of modelled non-hatchling numbers at equilibrium in the NPEC population across a reduced parameter space where m_4 and N_{3dur} were held constant at NT levels and population size was capped at 22,500 (sample size is 238,165). The blue line is the best estimate of absolute non-hatchling numbers based on 2016-19 surveys. The orange line is a smoothing spline fitted to the point cloud. Note that the lower limit on population size of 3,750 has not been imposed in these graphs to allow easier comparison with Figure 10.



159. Several of the smoothing splines show distinctly nonlinear relationships between changes in population parameters and resultant non-hatchling population size. Importantly, this preliminary examination doesn't account for possible interaction effects.

Constraining the reduced model within upper and lower limits

160. When the lower limit of 3,750 non-hatchlings was imposed as well, the subset of models projecting reasonable estimates between 3,750 and 22,500 NH included 21,870 samples. The parallel coordinates plot at Figure 13a shows the combinations of vital rates contributing to this subset as orange lines. Once again, a very wide array of combinations can give rise to equilibrium populations between 3,750 and 22,500. The violin plot for the reduced number of parameters (Figure 13b) is little changed from the full parameter set (Figure 11b).
161. The result is not surprising. It simply confirms that the paucity of data in Queensland and the weak underlying estimates of population parameters for the species in general result in a wide range of biologically feasible model matrices. Importantly, we don't have data to judge which, if any, of these model matrices is a good approximation to the processes operating in the population.

Figure 13: Parallel coordinates plot (a) and violin plot (b) for trajectories defined in the reduced parameter space where juvenile stage duration and fertility were fixed (see text). The first plot shows a random sample of 2000 from the 21,870 trajectories that project positive population growth since 1974 and an equilibrium non-hatchling population between 3,750 and 22,500. The second (violin) plot includes the full set of trajectories.

Figure 13(a)

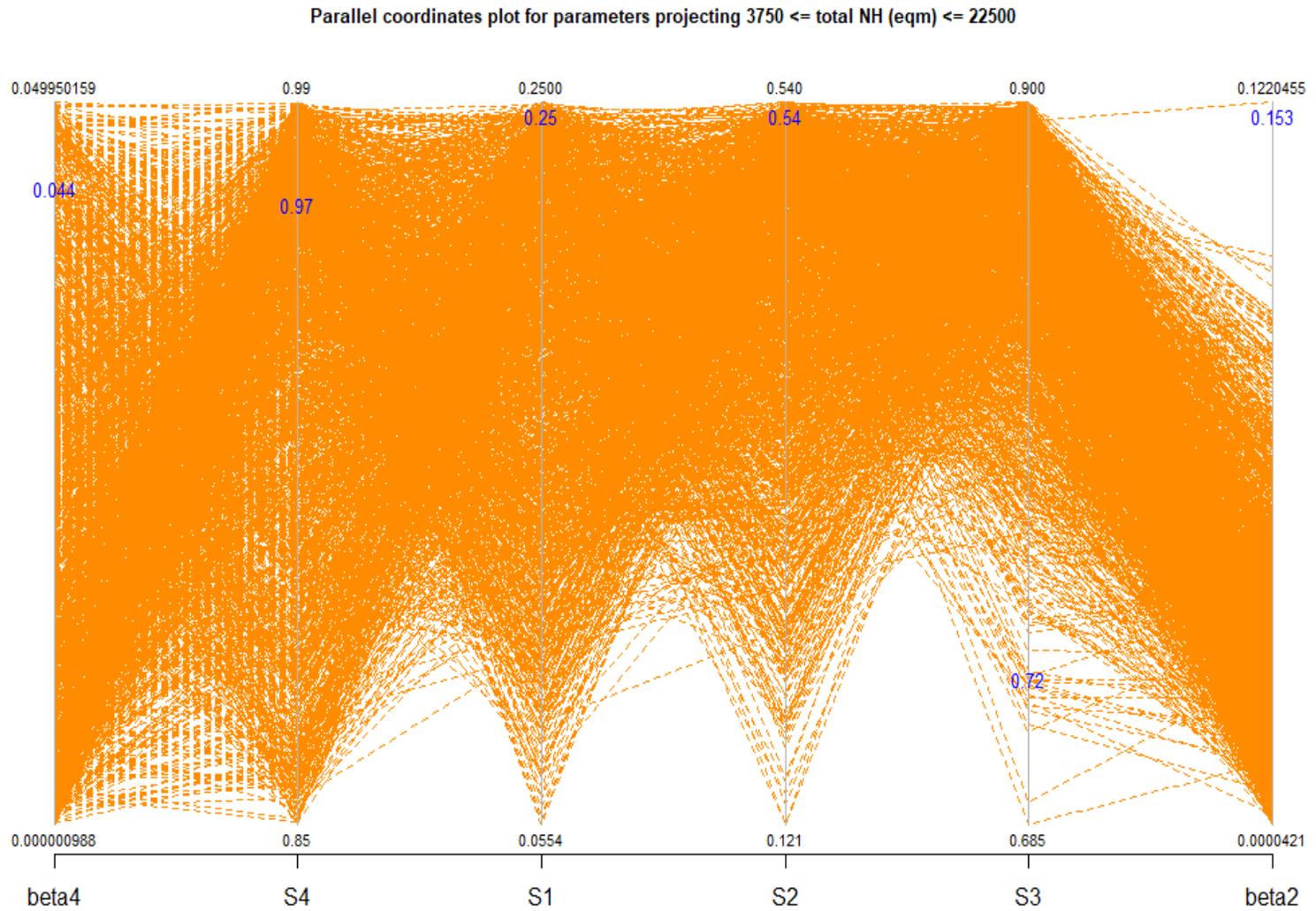
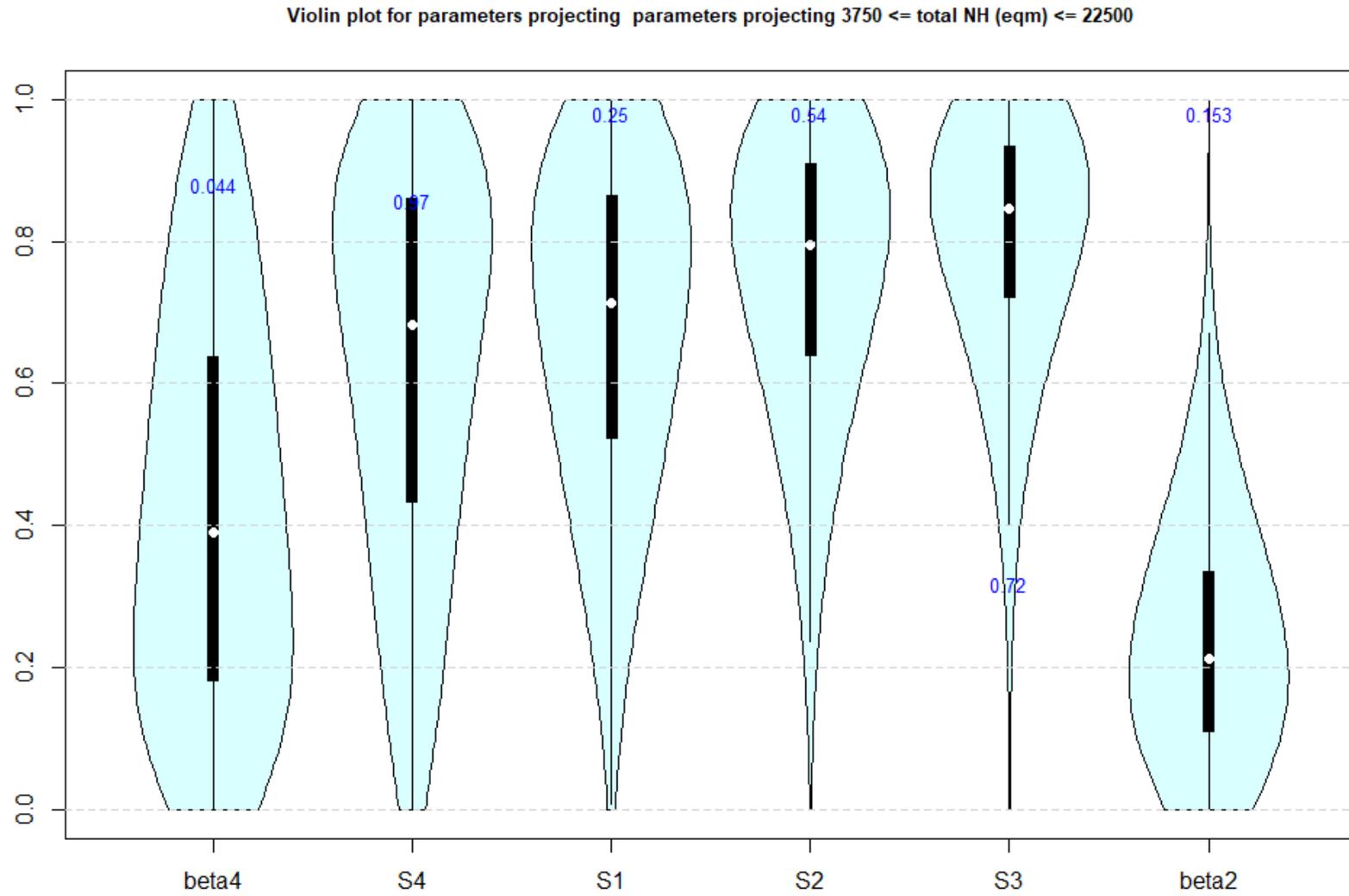


Figure 13(b)



Constraining trajectories within the 95% confidence limits from survey estimates

162. The parameter set that leads to ‘reasonable’ population trajectories can be further refined on the presumption that any viable model should have a trajectory that fits within the 95% confidence limits for the number of non-hatchlings in the three survey Eras. Its parallel coordinates plot is not shown – it mirrors Figure 13a but with about half the sample size. Table 7 shows how the parameter values captured in the ‘reasonable’ trajectories (11,706 samples) encompass much of the modelled parameter space.

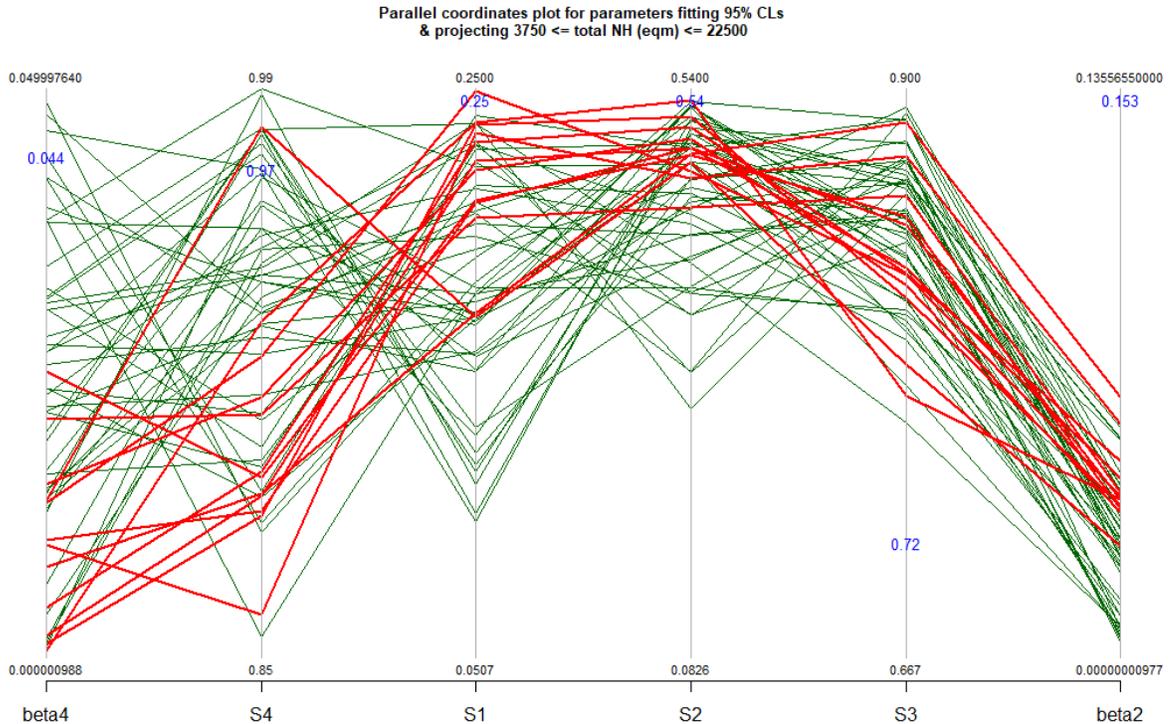
Table 7: Comparison of the parameter values modelled and the ranges that projected trajectories falling within 95% CLs for the estimated non-hatchling population (sample size is 11,706). Differences between modelled and result ranges are shown in red.

Parameter	Range modelled	Range in results
S1	0.05 – 0.25	0.05 – 0.25
S2	0.05 – 0.54	0.12 – 0.54
S3	0.50 – 0.90	0.67 – 0.90
S4	0.85 – 0.99	0.85 – 0.99
beta2	0.00 – 0.20	0.00 – 0.11
beta4	0.00 – 0.05	0.00 – 0.05

163. The trajectories can be even further refined by selecting those that track within 5% of the mean estimates of non-hatchling numbers in the three survey Eras (1984-89, 1994-99 and 2016-19) – i.e. tight fits to the estimated population trajectory. This ‘best-fit’ group is shown in Figure 14. Both green and red lines fit the criteria for non-hatchling numbers. The red lines are even closer fits because they also fall within the 95% CLs for stage proportions in the 1994-99 and 2016-19 Eras¹⁵ and show declining proportion of juveniles over time – mirroring the trend in Table 4. Figure 7 is an example of such a fit.
164. Even for these most tightly-constrained trajectories, a quite wide array of parameter combinations can fit the survey estimates (Figure 14), particularly for β_4 , adult survivorship (S4) and egg survivorship (S1). Values for hatchling and juvenile survivorship (S2 & S3) and for hatchling density dependency (β_2) are more constrained, but still wide. This result is not an artifact of selective sampling of the parameter space – the large number of combinations tested and the Latin hypercube sampling ensured sample combinations were spread quite uniformly.

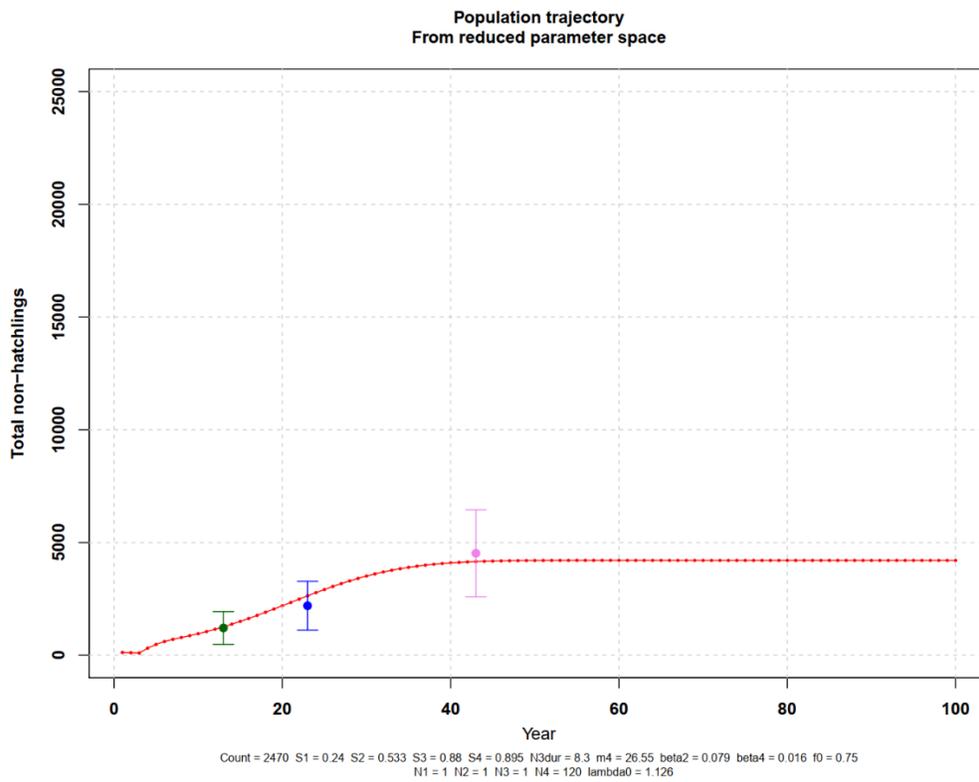
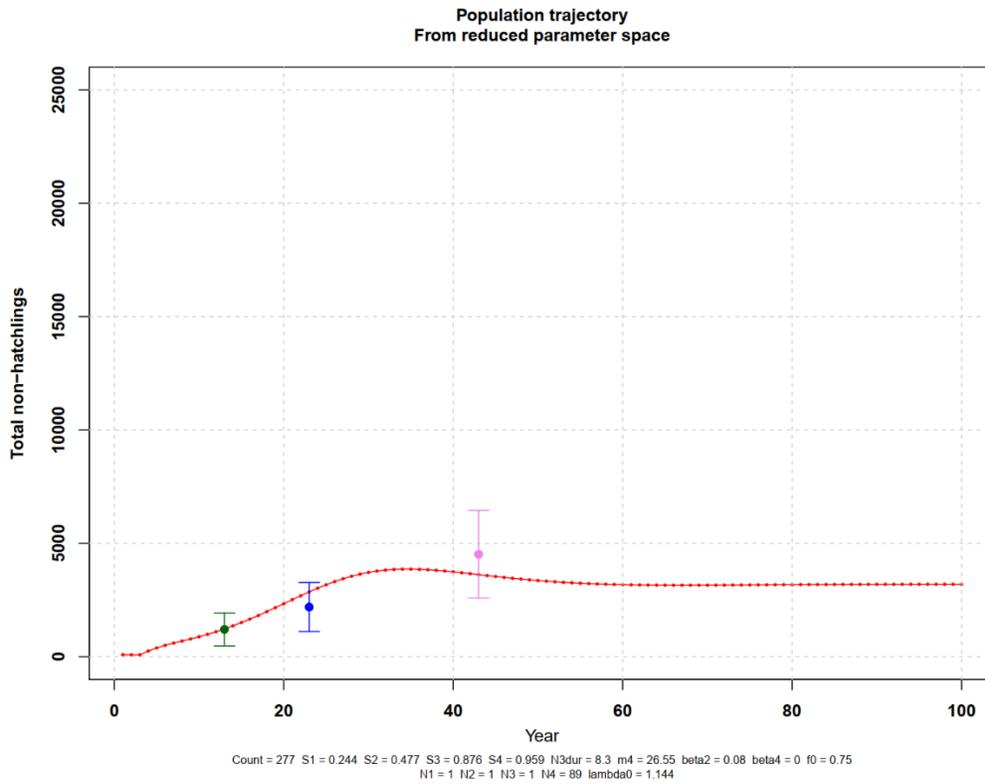
¹⁵ The 1984-89 Era stage proportions are excluded because of the extremely wide 95% CLs around the proportion of adults.

Figure 14: Parallel coordinates plot showing the 55 parameter combinations projecting trajectories that track within +/- 5% of the mean survey estimates of non-hatchling numbers across three Eras. See para 163 for explanation of the green and red lines.

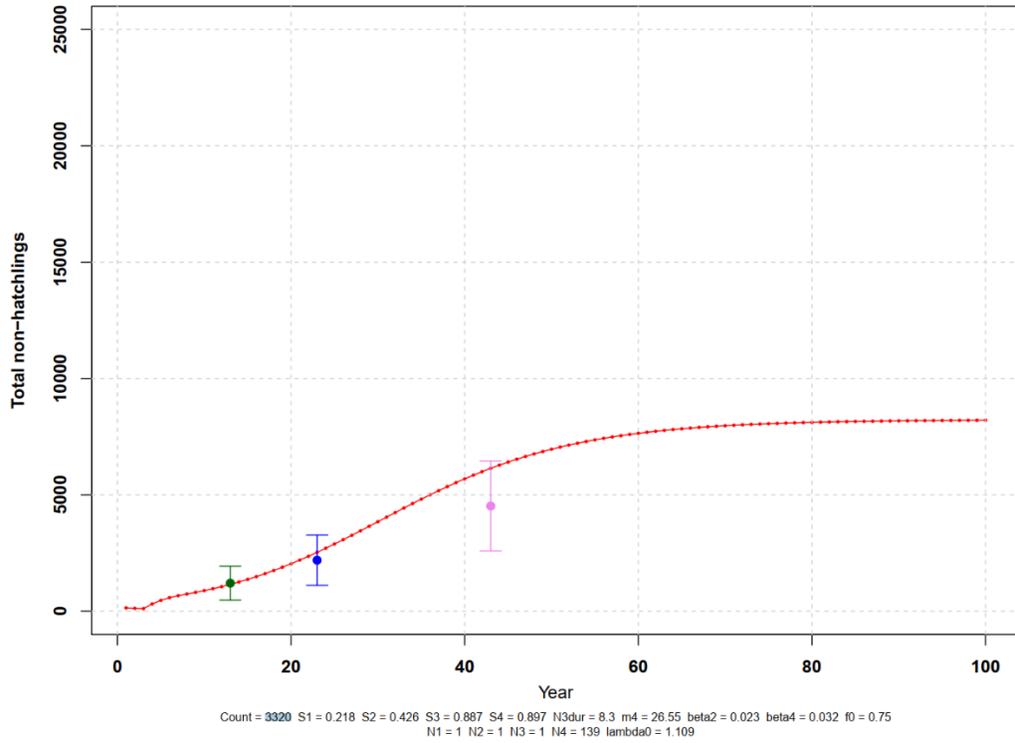


165. While this most refined subset of parameter combinations is of interest in relation to the behaviour of the NPEC model, it cannot be regarded as representing a ‘good’ model set for subsequent analysis. The survey data are too few and too uncertain to constrain the model outputs so tightly. Further analysis will therefore focus on the larger subset of 11,706 projections that fall within the 95% CLs for non-hatchling numbers and within the 3,750 – 22,500 limits previously imposed.
166. Four representative trajectories that fit within the 95% CLs for survey estimates of non-hatchling numbers illustrate different paths to equilibrium and different levels reached at equilibrium (Figure 15). Some peak before declining, some stabilise at levels close to the lower CL for 2016-19, and others continue to climb slowly beyond the 2016-19 Era upper CL.

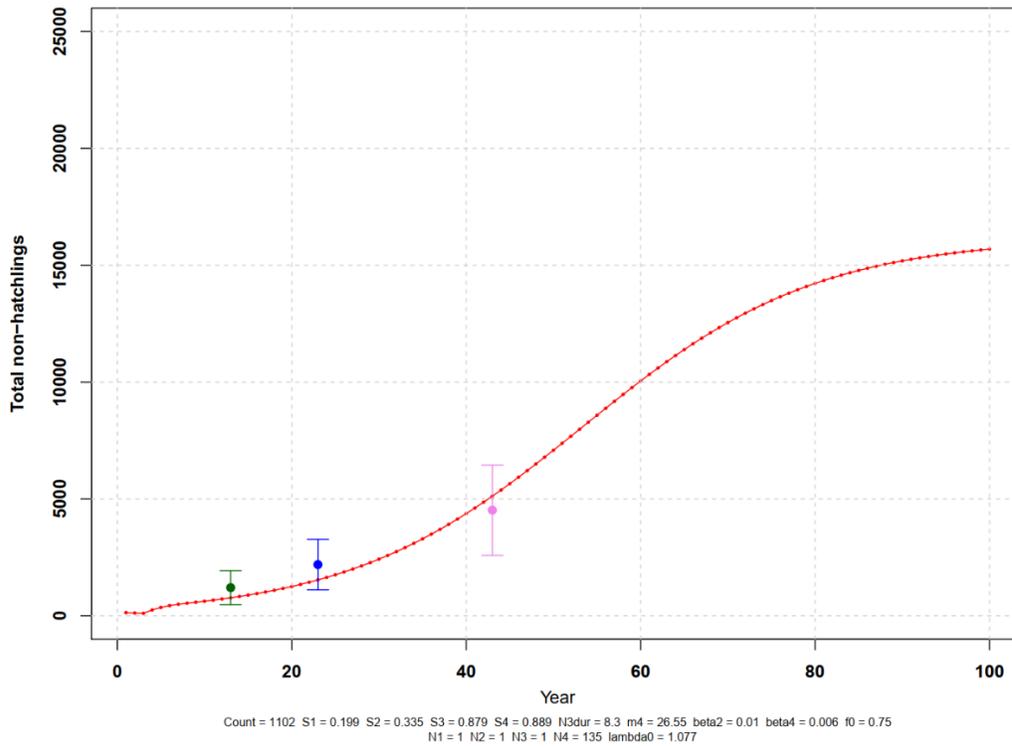
Figure 15: Representative population trajectories that fall within the 95% CLs for non-hatchling numbers in three survey eras (1984-89, 1994-99 and 2016-19) and reach end-state non-hatchling numbers between 3,750 and 22,500.



Population trajectory
From reduced parameter space



Population trajectory
From reduced parameter space



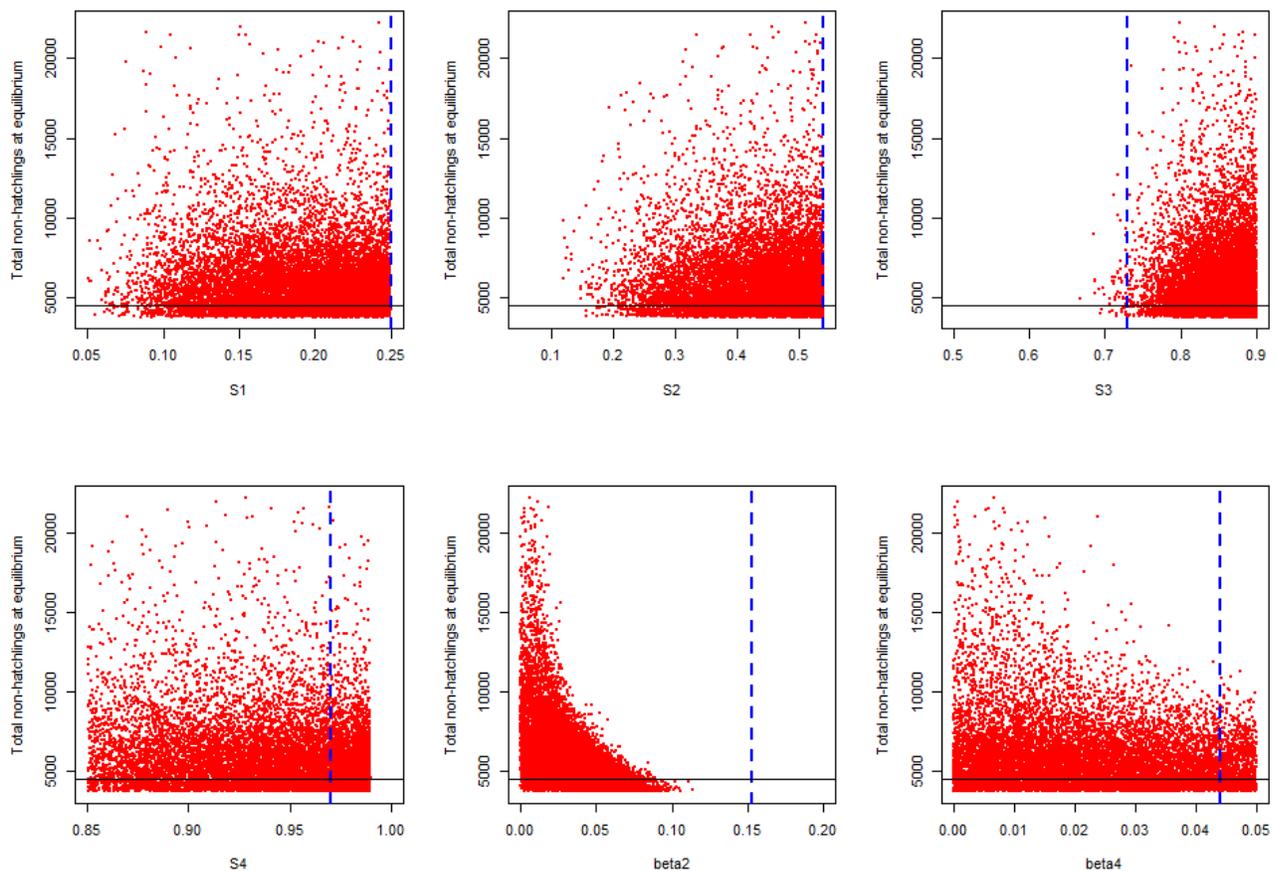
167. The overall behaviour of these models is reflected in the distributions of projected non-hatchling totals at equilibrium in relation to the six populations parameters (Figure 16). Of particular note are:

167.1. The weak influences on equilibrium non-hatchling numbers of the survival rate in adults (S_4).

167.2. The dominating influence of the strength of β_2 . Values of β_2 above ~ 0.9 cap projected equilibrium numbers below the mean survey estimate of NH numbers in 2016-19. And high values of non-hatchling numbers are heavily dependent on weak to very weak density dependency ($\beta_2 < \sim 0.025$).

167.3. The very high concentration of model matrices with values of juvenile survivorship (S_3) above the estimate of 0.72 in the NT model.

Figure 16: Distribution of projected non-hatchling totals for the NPEC population at equilibrium in relation to the six parameters in the reduced model set (sample size is 11,706). Each point represents a single randomised combination of parameter values. Blue vertical lines are the values used in the NT model. The black horizontal line is the mean non-hatchling estimate for the most recent 2016-19 surveys.

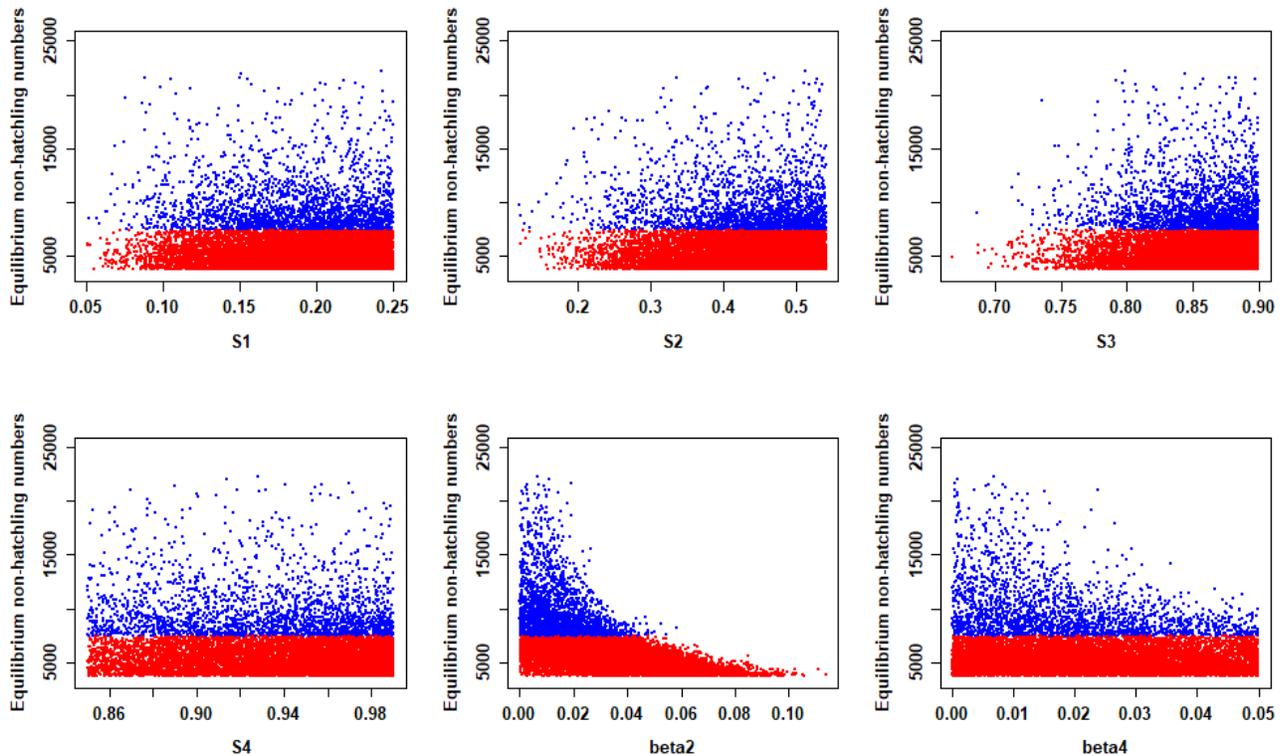


168. The overall heavy concentration of trajectories in the lower portion of most of these graphs, indicates that, among this diverse set of possible models, the vast majority project equilibrium non-hatchling numbers not far from the 2016-19 survey mean.

High equilibrium non-hatchling numbers are driven principally by density dependencies

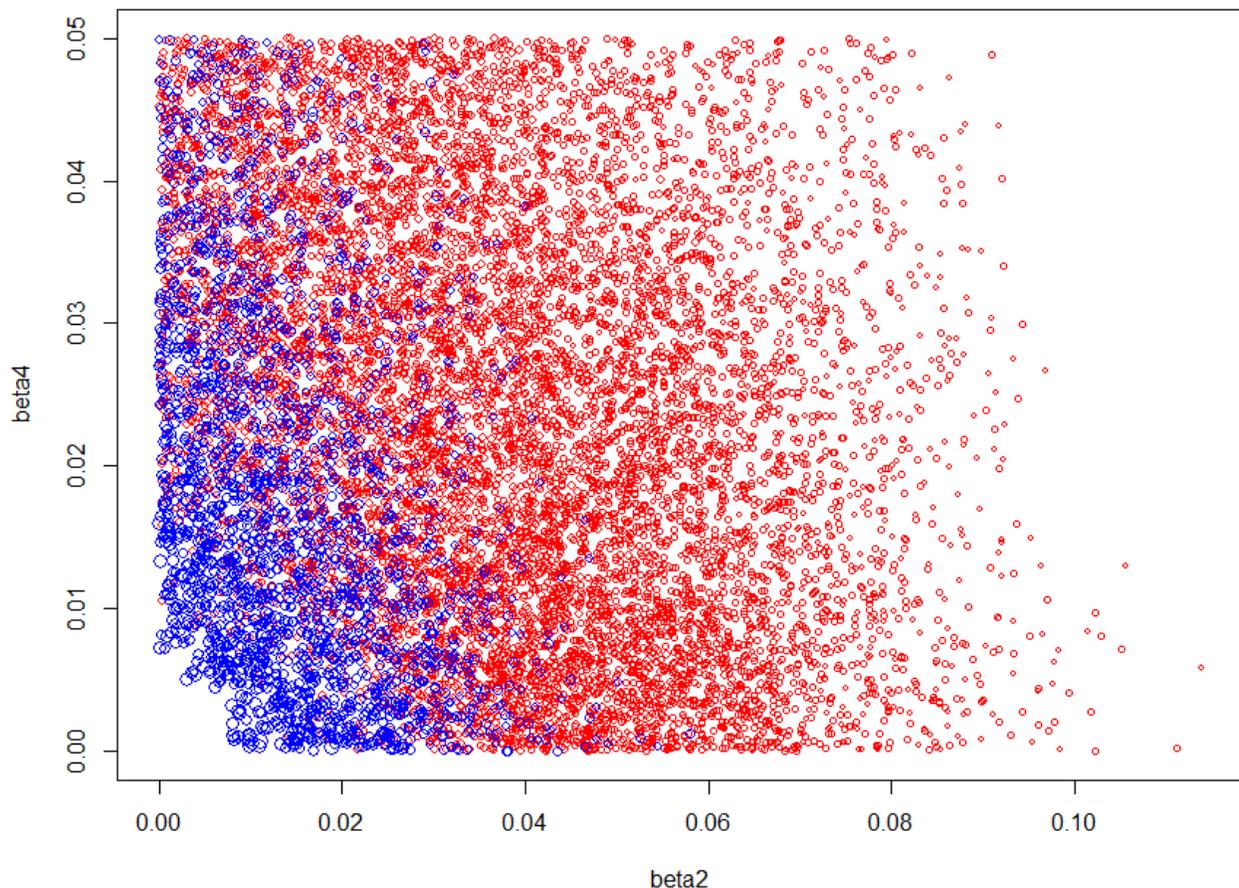
169. It is instructive to examine in a little more detail the parameter combinations that project non-hatchling numbers above the best estimate of 7,500 and towards the extreme estimate of 22,500 (refer para 141). In the 11,706 samples fitting the 95 CLs, ~9,700 combinations projected equilibrium non-hatchling numbers from 3,750-7,500 and ~2,000 from 7,500-22,500. Non-hatchling numbers over 7,500 resulted principally from low values of β_2 and to a lesser extent low values of β_4 (Figure 17).

Figure 17: Influence of parameter values on asymptoting population trajectories that fall within the 95% CLs for non-hatchling numbers in the three survey Eras and result in equilibrium numbers between 3,750 and 7,500 (red) or between 7,500 and 22,500 (blue). The actual maximum number of non-hatchlings for the NPEC population is estimated to lie most likely between 3,750 and 7,500 but could conceivably be as high as 22,500.



170. The relationship of equilibrium non-hatchling numbers to values of β_2 and β_4 reinforces that numbers over 7,500 are driven principally by low values of β_2 and to a lesser extent by low values of β_4 , while low values for both coefficients generate the highest NH numbers (Figure 18).

Figure 18: Influence of β_2 and β_4 on projected equilibrium non-hatchling numbers for the dataset in Figure 17. Trajectories resulting in numbers from 3,750-7,500 are shown in red and those for numbers 7,500-22,500 in blue. The size of the points is proportionate to the square root of the scaled equilibrium NH numbers and shows how the highest numbers are generated by projection matrices with very low values for β_2 and β_4 . The lower LH corner of the graph is unpopulated because extremely low values of beta2 and beta4 result in near-exponential growth and NH numbers exceeding the upper threshold.



Summary

171. These analyses have been focused principally on the behaviour of the model and its global sensitivity to changes in parameter values. They do not tell us what the Queensland population will or will not do in future but simply project a set of initial conditions into the future and show what would happen to the hypothetical population if those conditions held constant. There is no reason to think that any set of conditions would hold constant over such a long period. Long-term fluctuations or trends in climatic and environmental circumstances, for example, will influence the actual trajectory.

172. Nonetheless, the behaviour of this wide array of models is informative if it is accepted that:
- 172.1. the essential features of the NT model with its various density dependencies are as good a picture as we have of the dynamics of estuarine crocodiles in Australia;
 - 172.2. the estimates of upper and lower bounds on vital rates and density dependency coefficients are biologically realistic for the NPEC population;
 - 172.3. fixing female fecundity and the duration of the juvenile stage is reasonable;
 - 172.4. the application of a global sensitivity analysis to the exploration of model outputs against inputs is appropriate; and
 - 172.5. it is reasonable to constrain our exploration to the subset of parameter combinations that generates outputs consistent with the known history of the NPEC population and likely upper and lower limits on non-hatchling numbers;
173. There is no way of knowing whether the matrix models tested include any that are good reflections of the underlying population biology or, if they do, which particular ones they are.

Should the model be further simplified?

174. There are sound reasons to think that the model as analysed would benefit from further simplification. Craig et al (1992) commented on the merits of simple versus complex models in data-sparse situations. They noted in relation to the early alligator model of Nichols et al (1976) that incorporated density dependencies:

“There is little, if any, evidence of what causes ... ecological saturation in crocodilian populations. Neither is there much evidence of what would be the direct causes of self-regulation in such populations. ... Given doubts about the saturation densities and mechanisms of regulation any density dependence built into a model can only be an artifice to make the simulated population appear to behave in a sensible manner. Because it is an artifice, however, it really tells us nothing useful, either, about the saturation density ... or the results of harvesting near the saturation density. The latter will depend very much upon the precise mechanism of regulation about which relatively little is known. ...we prefer to not include density dependence in a model at all. We assume that crocodiles will always be harvested at population levels below saturation, where density dependent effects can be safely ignored ...”

175. This view was expressed in the context of their analyses of heavily exploited Nile crocodile populations for which estimates of equilibrium densities were essentially unavailable and where many estimates of the population parameters, especially survivorship by age/stage, were poorly defined. It is not so readily applicable to this exercise with a population:
- 175.1. that shows clear signs of declining rates of increase and a likely approach to some sort of equilibrium in both Queensland (Taplin et al, 2020, 2021) and the NT (Fukuda et al, 2011), after nearly 50 years of recovery from hunting;
 - 175.2. for which reasonable estimates of upper and lower limits on equilibrium numbers are available; and
 - 175.3. where the potential response of the population to changes in the management regime when the population is close to its equilibrium is of primary interest.

176. In this case, there is considerable evidence to suggest some form of density dependent regulation is occurring in crocodiles (Messel et al, 1981b, 1984; Bayliss & Messel, 1987; Webb et al, 1984; Webb and Manolis, 1992), but only anecdotal/observational data to give insights into how those density dependencies might operate biologically. The existence and importance of density dependency in animal populations has been debated for decades but it is now more widely accepted (Brook and Bradshaw, 2006; Hixon & Johnson, 2009). For our purposes, it is reasonable to accept that some form/s of density dependency operate in estuarine crocodile populations and that the NT modelling of those is the best available. It is extremely unlikely that the nature of those density dependencies will be teased out any time soon given the extraordinary difficulty and cost of monitoring, never mind actually manipulating populations over the time frames required.
177. It is beyond the scope of this project to devise a completely new model for the Queensland population, whether deterministic, stochastic or including density dependencies. Even if it was in scope, our virtually complete dependency on NT data for estimates of survival rates, age/size at maturity and fecundity pose formidable obstacles to constructing a realistic model for Queensland *de novo*. For these reasons, the model developed above has not been further simplified.

What can we learn from this suite of possible models?

178. At first blush, the very large array of matrix models that can be fitted reasonably well to the NPEC data appears too broad to offer much insight into the effects of past or future management regimes. However, if there are shared patterns of output responses across all of the models in response to changes in inputs, then useful insights might be gained.
179. There are two particularly useful questions we can ask. Firstly, is it possible to estimate in broad terms the impact of the crocodile management program since the 1980s? Secondly, is it possible to estimate what might be the likely impact if changes to the management program were contemplated? The second question is not seeking to predict the future of the population. That will only become apparent as time progresses and the population is monitored. Instead it asks what would happen to our hypothetical population if the vital rates and density dependencies inherent in the projections prevailed into the future but the offtake of adults or juveniles for management purposes was increased?

The effect of past and current removal levels.

180. We have good data from DES archives on the number of crocodiles removed for management purposes since the first East Coast Management Program was formally introduced in 1986/87 (Table 5). Those removals are already built into the survey results used to estimate non-hatchling numbers in the 1984-89, 1994-99 and 2016-19 survey Eras. To test their effect we need to ask what might have been the population trajectory if those animals had not been removed – i.e. add them back into the population year-by-year and project the population forward.
181. There is an issue with this approach that is unavoidable. The estimates of mean NH numbers for the three survey Eras and their 95% CLs incorporate the unknown effect of the management removals. Had there been no removals, we might expect the means to have been higher by some amount. So the ‘best-fit’ combinations of population parameters and the resulting projection matrices that would fit these unknowable means and CLs would be

somewhat different from the ones selected. Adding the known removals back into the matrix models is thus different from subtracting them from the unknowable set of ‘unmanaged’ matrix models. Nonetheless, given the many uncertainties in the modelling effort and the detailed sampling of the parameter space it should, cautiously interpreted, give us better insights than we would otherwise have into the impact of the program.

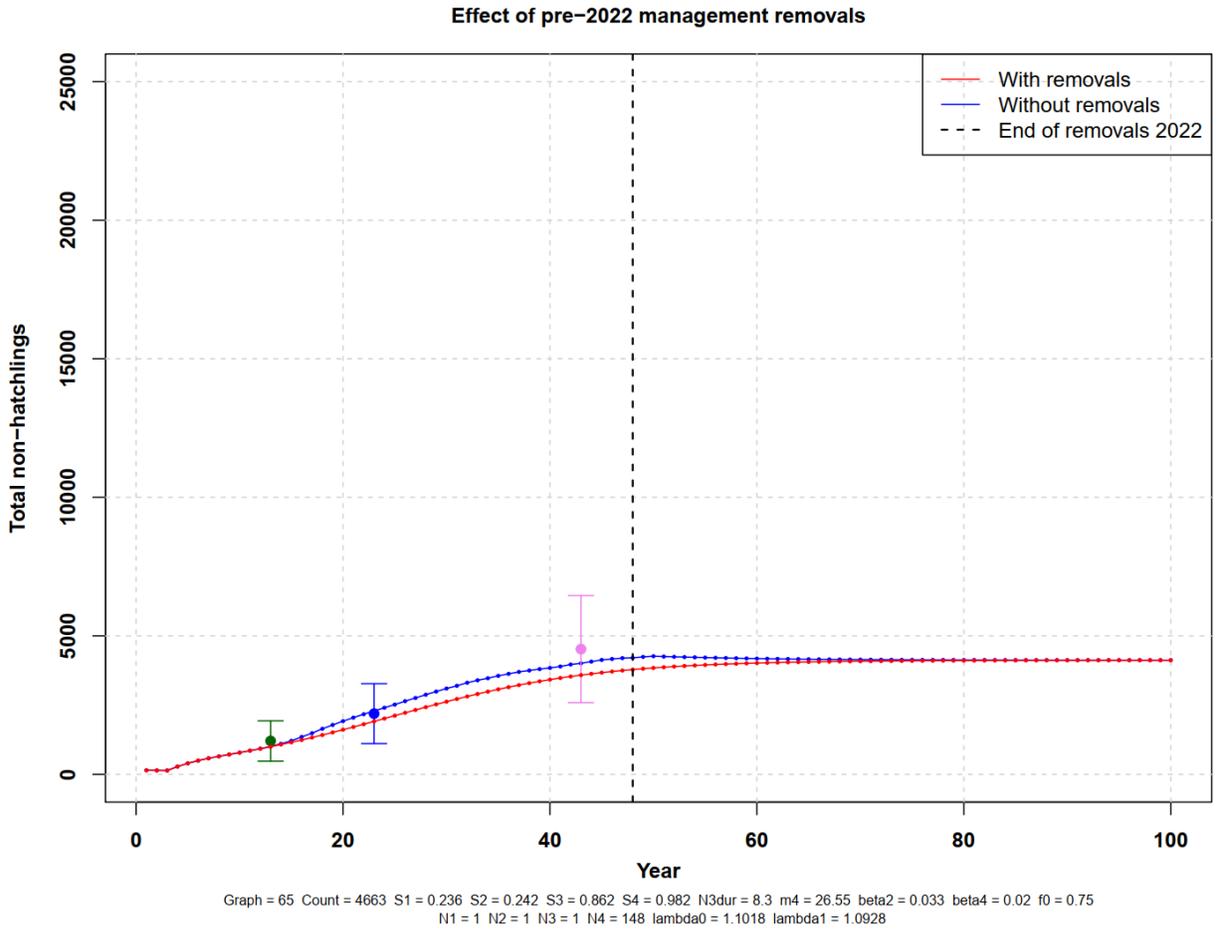
Methods used for models with removals

182. Projections for models incorporating removals were constructed by multiplying the no-removals survival rate in the matrix models by the factor $(1 - R_i / N_i)$, where R_i is the number of individuals removed in stage i and N_i is the number in that stage before removals. The same approach was used by Fukuda et al (2020). The projection matrices were otherwise constructed in the same way as earlier matrices, incorporating density dependencies.
183. To test the effects of past removals, adult and juvenile removals by year from 1974-2022 (following Table 5) were made negative, so that the modelled survival rates increased for juveniles and adults in affected years. Removals of both stages after 2022 were set to zero to model cessation of the management program.
184. When modelling post-2022 removal options, removals from 1974-2022 were set to zero because the projected trajectories already model the effects of the past removals. Future removals were modelled using constant annual rates of removal from 2023-2074. The annual rates for juvenile and adults were varied in steps of 10 from 0 to 50 and all combinations of the two rates were tested. If the programmed removal of juveniles or adults in any particular year exceeded the number of juveniles or adults in the projected population, survivorship of that stage in that year was set to zero.
 - 184.1. For this set of projections, the population trajectories follow the red curves illustrated in Figure 19 (which incorporate past removals) until 2022. They then diverge as future removals are imposed.

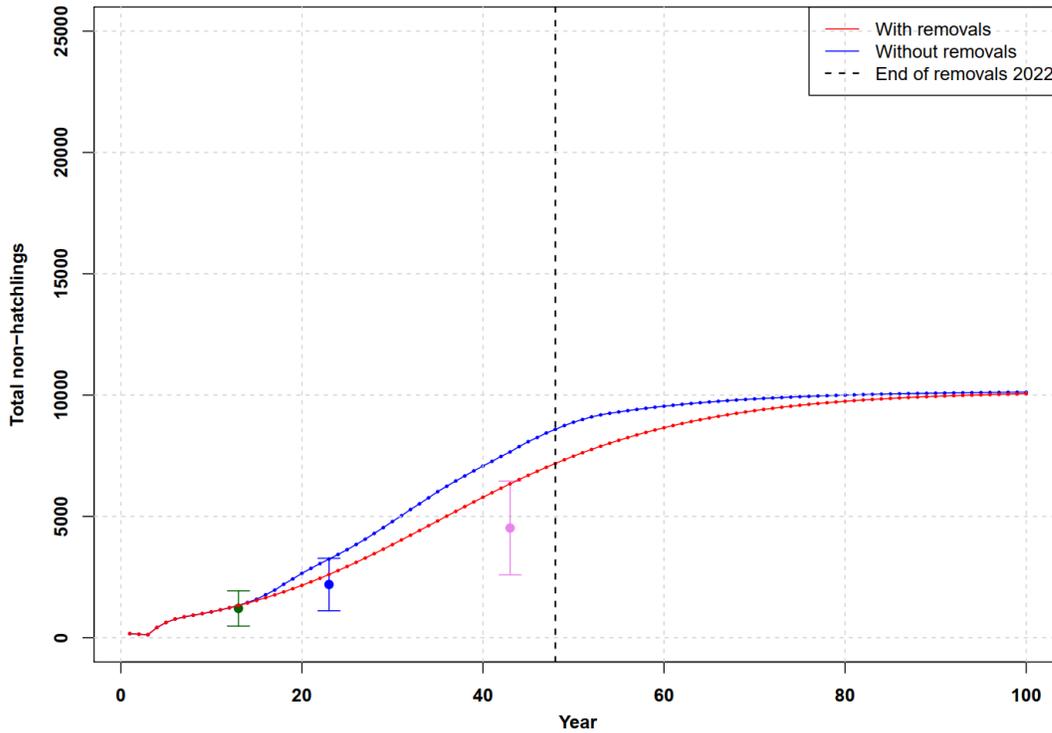
Results for models incorporating 1974-2022 removals

185. When this exercise is done for the 11,706 models detailed above, we find the trajectories for the managed (red) and the ‘unmanaged’ population (blue) diverge after the late 1980s as the effects of removals flow through to the non-hatchling population. Three example trajectories are shown in Figure 19, illustrating how projected trajectories include some with steep trajectories in the 1990s and 2000s and others shallower. All trajectories begin to converge after 2022 because the post-2022 offtake in these projections is zero.
186. Note that in the first example in Figure 19 the modelled management effect is very small and the divergence between managed and unmanaged trajectories reaches a maximum before 2022. In the third example, the values of β_2 and β_4 (shown in the subtitle) are very low, accounting for the steep trajectories and later divergence.

Figure 19: Three examples of the estimated effect of the 1985-2022 management removals on the population trajectory of non-hatchlings. The gap between blue and red lines reflects the number of non-hatchlings that would have been in the NPEC population if the removals had not occurred, assuming the vital rates and density dependency coefficients remained constant for each projection matrix. Each red (managed) trajectory falls within the 95% CLs for the three survey Eras.

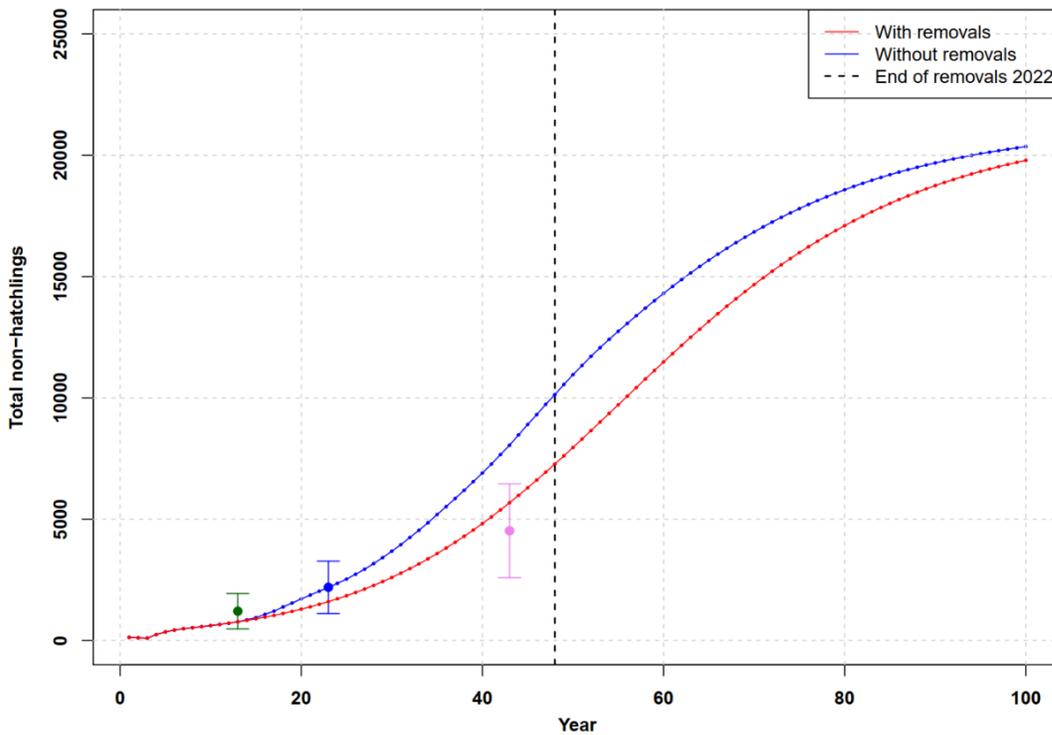


Effect of pre-2022 management removals



Graph = 51 Count = 3637 S1 = 0.232 S2 = 0.486 S3 = 0.851 S4 = 0.878 N3dur = 8.3 m4 = 26.55 beta2 = 0.008 beta4 = 0.035 f0 = 0.75
N1 = 1 N2 = 1 N3 = 1 N4 = 167 lambda0 = 1.0904 lambda1 = 1.0773

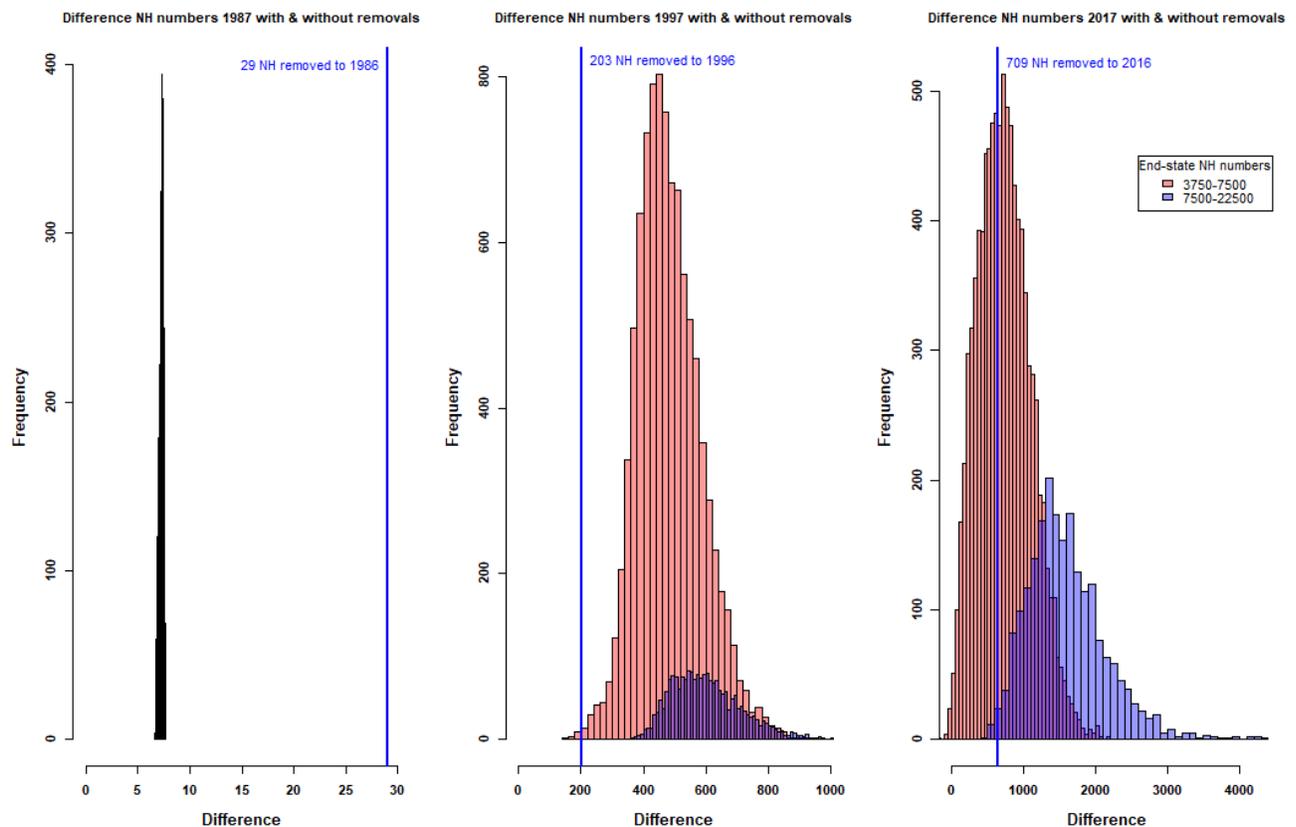
Effect of pre-2022 management removals



Graph = 59 Count = 3982 S1 = 0.23 S2 = 0.313 S3 = 0.886 S4 = 0.879 N3dur = 8.3 m4 = 26.55 beta2 = 0 beta4 = 0.016 f0 = 0.75
N1 = 1 N2 = 1 N3 = 1 N4 = 126 lambda0 = 1.0825 lambda1 = 1.078

187. The trajectories followed and the distances between managed and unmanaged trajectories are highly variable because of the wide range of parameter combinations captured by the 95% CLs around non-hatchling numbers. The patterns across these combinations are summarised in Figure 20, which shows frequency distributions across all 11,706 models for the maximum difference between harvested and unharvested trajectories. Projections with end-state non-hatchling numbers in the most likely range (3,750-7,500) are distinguished from those in the less likely range 7,500-22,500.
188. The effect by 1987 of the 29 removals up to 1986 is unsurprisingly small – it estimates an unmanaged population would have had only seven more animals than the managed population. By 1997, the cumulative effect of the removals shows through strongly and, across all projections, the managed population would have included from 150-1,000 more animals, with a median of 490. Thus, the projected reduction in equilibrium non-hatchling numbers is generally much greater than the number of animals removed.

Figure 20: Estimated effect of the 1985-2022 management removals on the NPEC estuarine crocodile population across all 11,706 projection matrices that generate trajectories falling within the 95% CLs for the three survey Eras (refer Figure 19). The histograms reflect the maximum projected reduction in the population over the 100 years of simulation for each combination of population parameters. The red and blue histograms represent trajectories projecting end-state numbers in the low and high ranges respectively.



189. However, by 2017 and despite the cumulative removal of some 709 non-hatchlings, the projections indicate that the unmanaged population would have been anywhere from the same size as the managed population (i.e. a maximum difference of zero) or, at the extremes, as much as 4,000 non-hatchlings bigger. The bigger differences arise, unsurprisingly, from matrices projecting end-state NH numbers over 7500, which are considered less likely than the lower range.
190. The median reduction attributable to the removals is 811 against actual removals of 709 animals to 2016, though the upper tail of the low-range (red) distribution suggests the population could have been reduced by up to 2000 while the lower tail extends to zero – i.e. no net effect on numbers.
191. Given the 2017 estimate of non-hatchlings is 4520, a difference of 2000 would represent a 31% reduction of the unmanaged population while the median difference of 811 represents a 15% reduction. Thus, the main weight of the results suggests the management program has achieved a modest reduction in non-hatchling numbers, while the survey data show clearly the population has continued to increase (Taplin et al, 2020, 2021).
192. It is useful also to examine the year in which the maximum difference between managed and unmanaged populations emerges from the projections (Figure 21). The graph shows this has a distinctly bimodal distribution, with 45% of trajectories showing a maximum impact between 1994 and 2012 and 55% suggesting the maximum impact would occur in the early 2020s. Late maxima dominate the high-NH (violet) distribution. The trajectories in Figure 19 illustrate the different patterns.
193. The bimodal distribution is driven principally by the value of β_2 and, to a lesser extent, β_4 . The relationships with β_2 are shown in Figure 22. Those with β_4 are similar but more diffuse. High density dependency in the hatchling stage (β_2) leads to early and relatively small differences between managed and unmanaged trajectories (Figure 22a). As density dependency decreases (β_2 is smaller and the plotted point colour shifts red to blue) the maximum difference between managed and unmanaged trajectories is greater and comes later in time. Figure 22b shows that the maximum difference also increases with the equilibrium population size.

Figure 21: Frequency distribution of the year in which the maximum difference between managed and unmanaged non-hatchling numbers occurs across 11,706 combinations of population parameters.

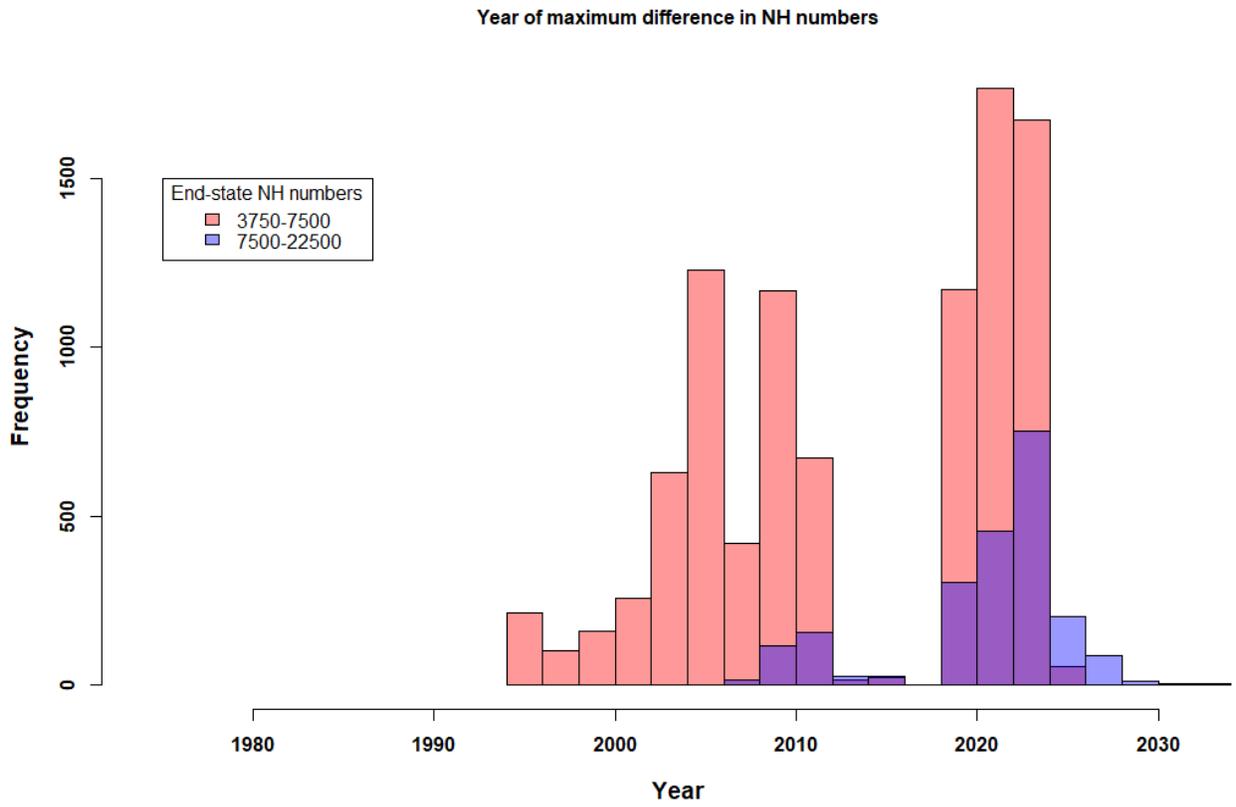
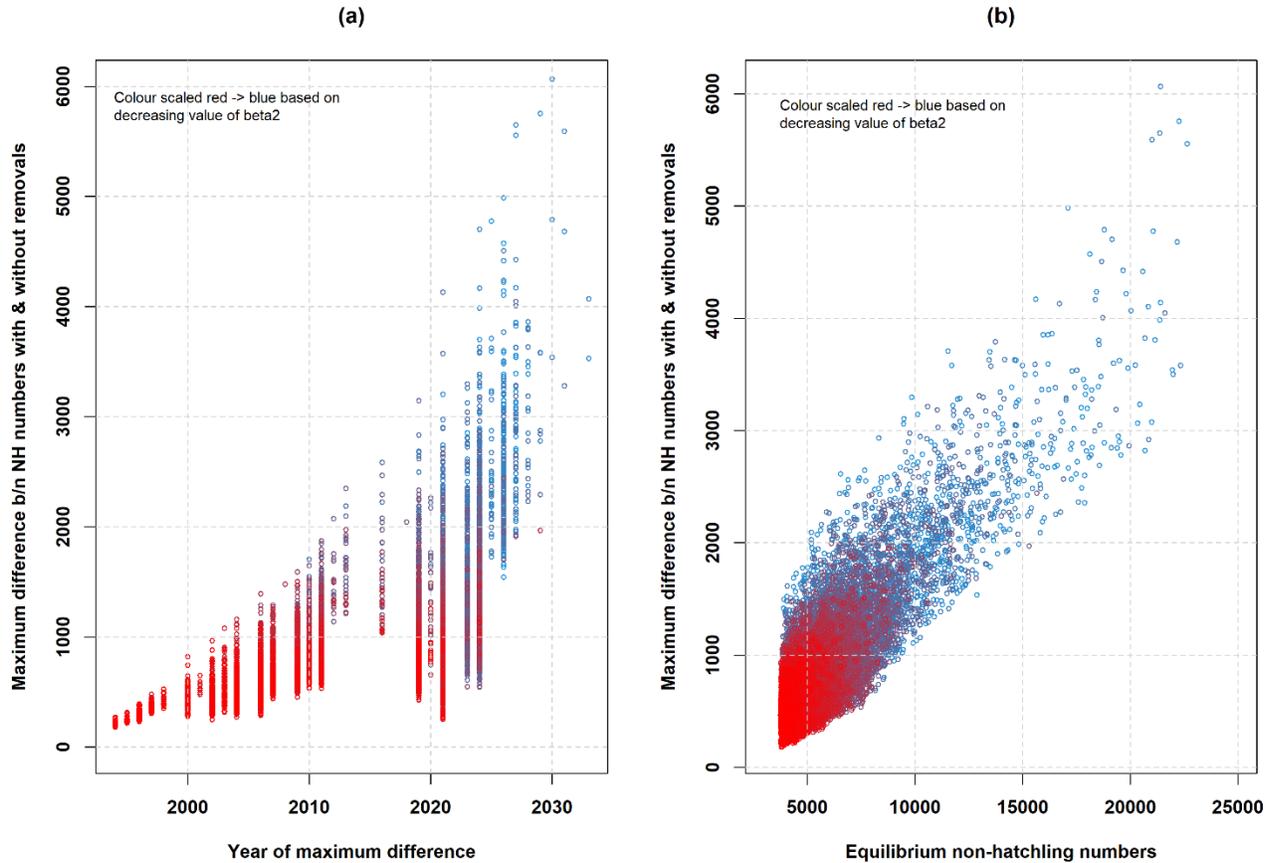
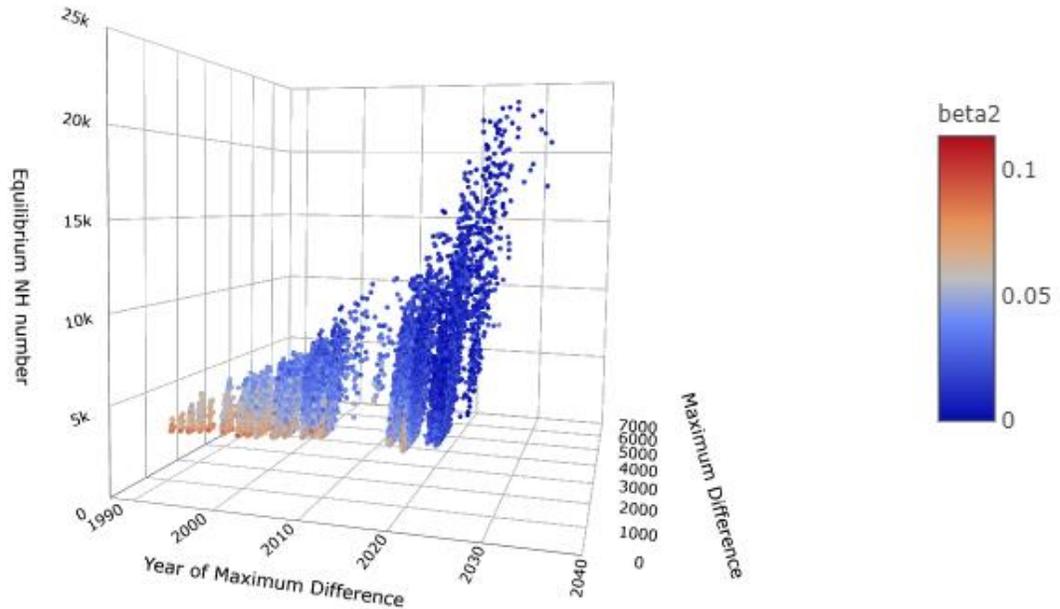


Figure 22: The timing and size of the management program’s modelled effect on non-hatchling population numbers is driven largely by the value of the density dependency coefficient β_2 . Greater differences between managed and unmanaged non-hatchling populations are correlated with later occurrence of those maximum differences and lower values of β_2 .



194. The relationships are perhaps better visualised in three dimensions (Figure 23) which shows the quite distinct bimodal separation between trajectories for which the impact of removal is maximal before 2010 or later than 2015, and the influence of low values of β_2 on that separation.
195. There appear to be two broad scenarios for the response of the NPEC population to the management removals since 1985. If density dependency is high in the hatchling or adult stages or both (albeit not as high as in the NT model) then the models project a population that has likely peaked in numbers already and will likely stabilise fairly close to its current numbers. On the other hand, if density dependency is low then the population might be expected to increase over the next decade or so before stabilising at a level some way above its current level. Only if density dependency is extremely low would the population stabilise at the very high end of the range of densities thought possible for the NPEC region and at a later time. The bulk of the projection matrices suggest a population at the low end of estimates is more likely, but a higher population cannot be ruled out given we have no information on possible density dependencies in Queensland.

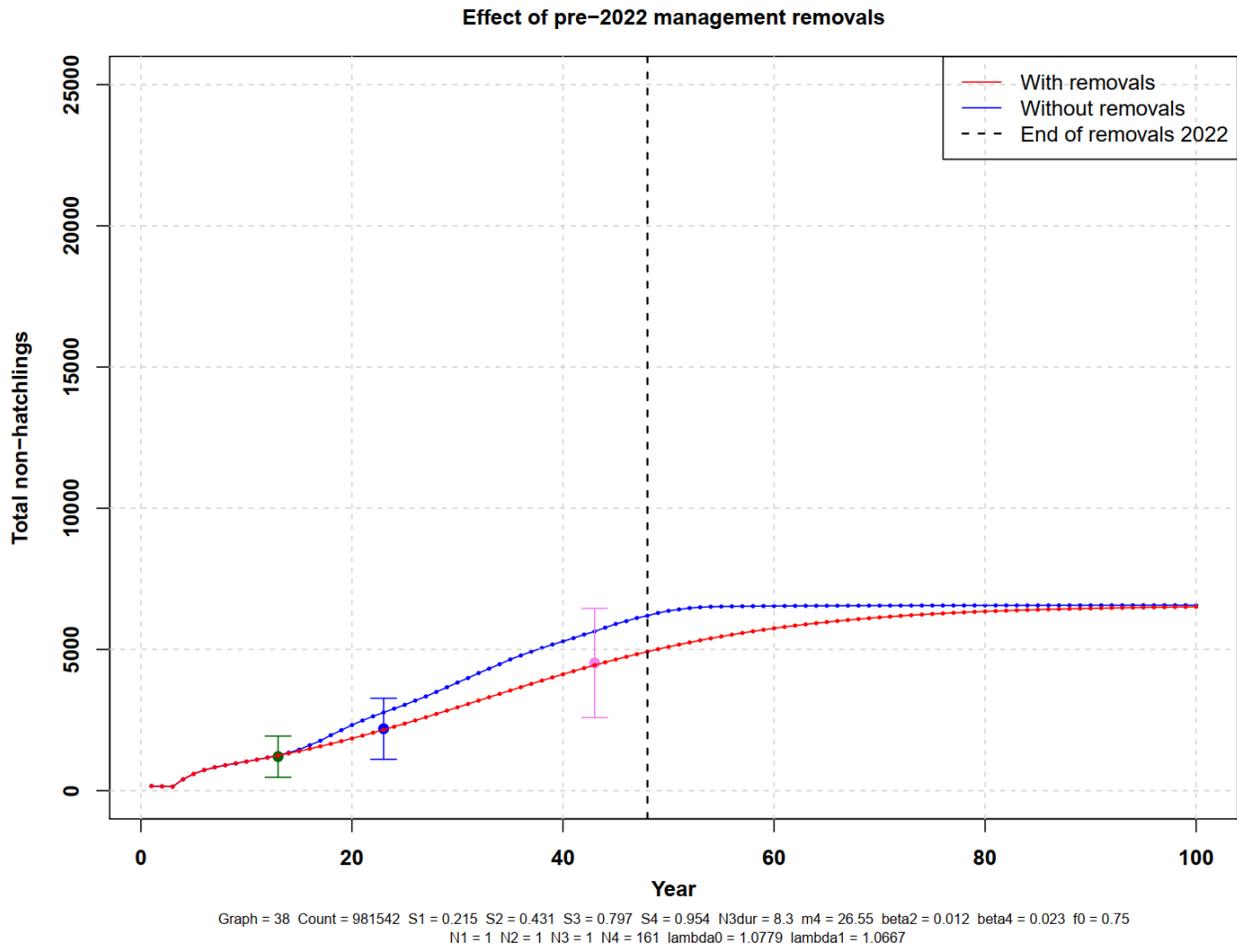
Figure 23: Three-dimensional view of the relationships in Figure 22.



Responses of the ‘best-fit’ models to past management removals

196. It is also useful to go back to the very small subset of 55 models with projected trajectories falling within 5% of the mean non-hatchling counts for the three survey Eras (para 162 ff). While too tightly constrained to be considered ‘good’ models, they do align the rates of increase projected by the models with the actual rates of increase reported by Taplin et al (2020, 2021) for the decade from 1984-89 to 1994-99 and the two decades from 1994-99 to 2016-19.
197. All of these models follow very similar trajectories – a typical one is shown in Figure 24 with, as previously, the trajectory in red modelling the population with the 1985-2022 management removals included and that in blue estimating the trajectory if there had been no removals. All of the 55 trajectories projected a population from ~4,500 – 7,000.

Figure 24: A representative trajectory from the 55 ‘best-fit’ models for which the 1985-2022 trajectory for the managed population (red) falls within 5% of the mean estimates for the three survey Eras (shown as means and 95% CLs). All 55 trajectories follow a similar pattern.



Results for models incorporating options for post-2022 removals

198. Figure 25 (set over two pages) shows the percentage reduction in the final non-hatchling population size after 100 years of projection under various removal scenarios. The dataset includes 11,706 sets of parameter combinations whose trajectories fit within the 95% CLs for the three survey Era estimates.
199. Removal of adults has a more significant impact than removal of the same numbers of juveniles, consistent with findings in Fukuda et al (2020). The number of trajectories showing a decline to extinction after 2022 (i.e. a 100% reduction in non-hatchlings in Figure 25) increases markedly as adult removals are increased. The marked effects of small numerical increases in the number of adults removed is notable and suggests that careful management of this number will be needed into the future.
200. It is useful to examine the effects of removal rates on non-hatchling numbers and the proportion of adults in the population after 100 years (Figure 26). Increasing the post-2022

removals of juveniles has limited impact on the proportion of adults regardless of the number of adults removed. Increasing the number of adults removed has little impact overall on end-state size class proportions but does drive non-hatchling numbers to lower levels for more combinations of parameters. More trajectories track towards extinction.

Figure 25: Effects of implementing various levels of post-2022 adult (A) and juvenile (J) removals on the 11,706 models for which the 1974-2022 trajectory falls within the 95% CLs for the estimated NPEC population. The blue histogram shows the results for a harvest that effectively continues the average removal rate of adults and juveniles from 2013-2022. The x-axis shows the proportion by which the unmanaged population would be reduced by the removals specified in the title. The vertical black line highlights the no-effect (0% change) line. Removal of adults has much bigger effects than removing juveniles and the proportion of trajectories that track to zero (i.e. extinction) within 100 years increases markedly with increased removals of adults.

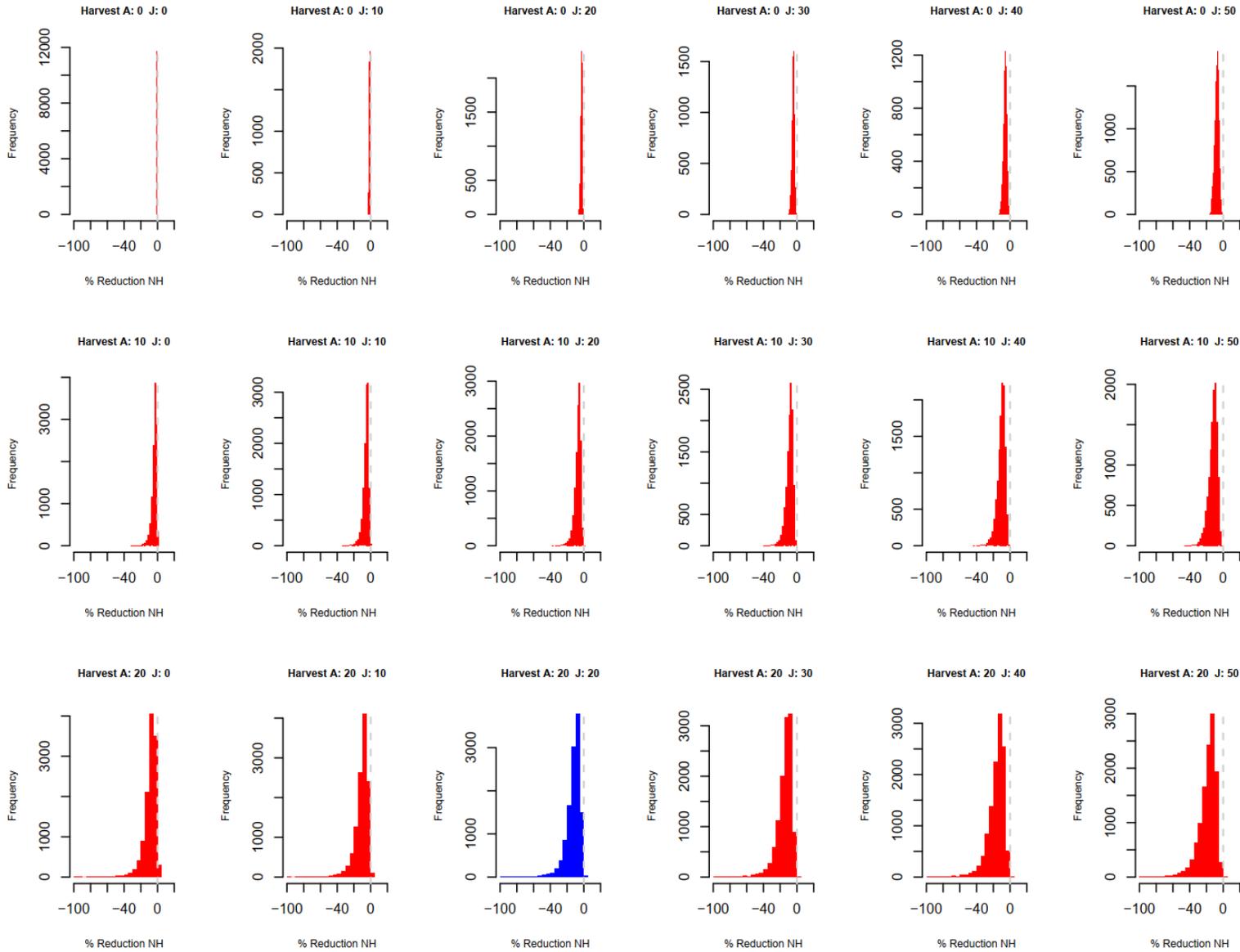


Figure 25 (cont).

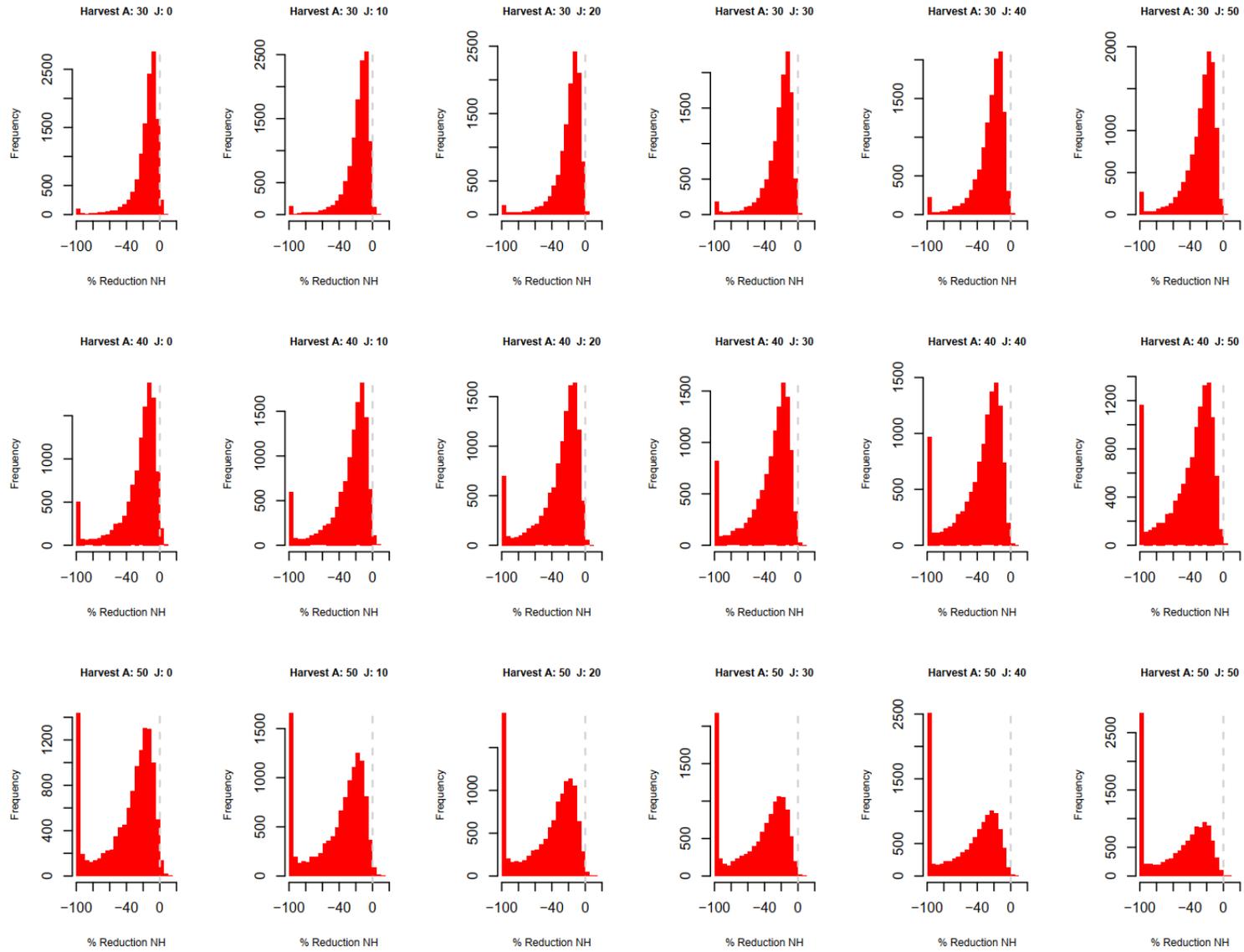
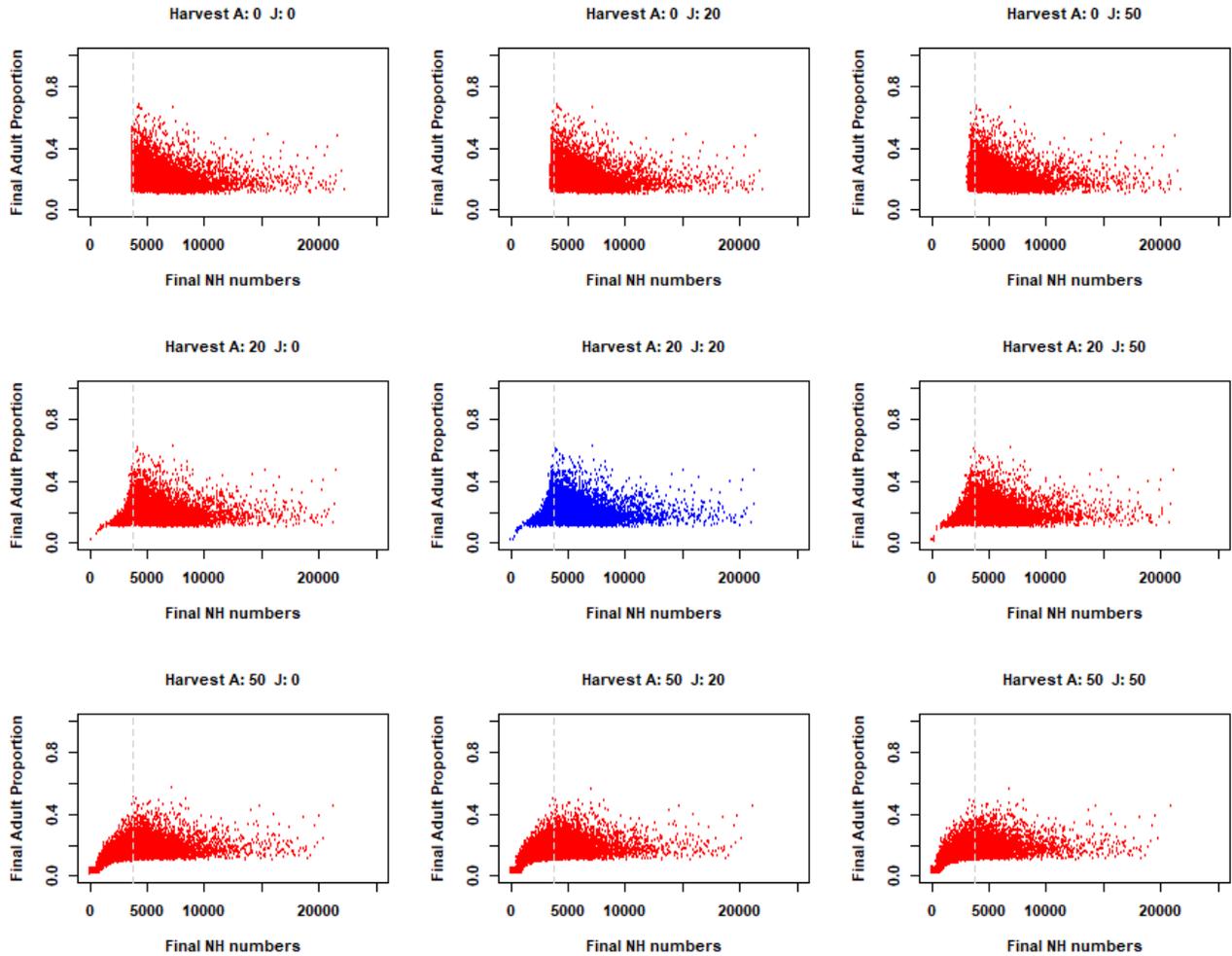


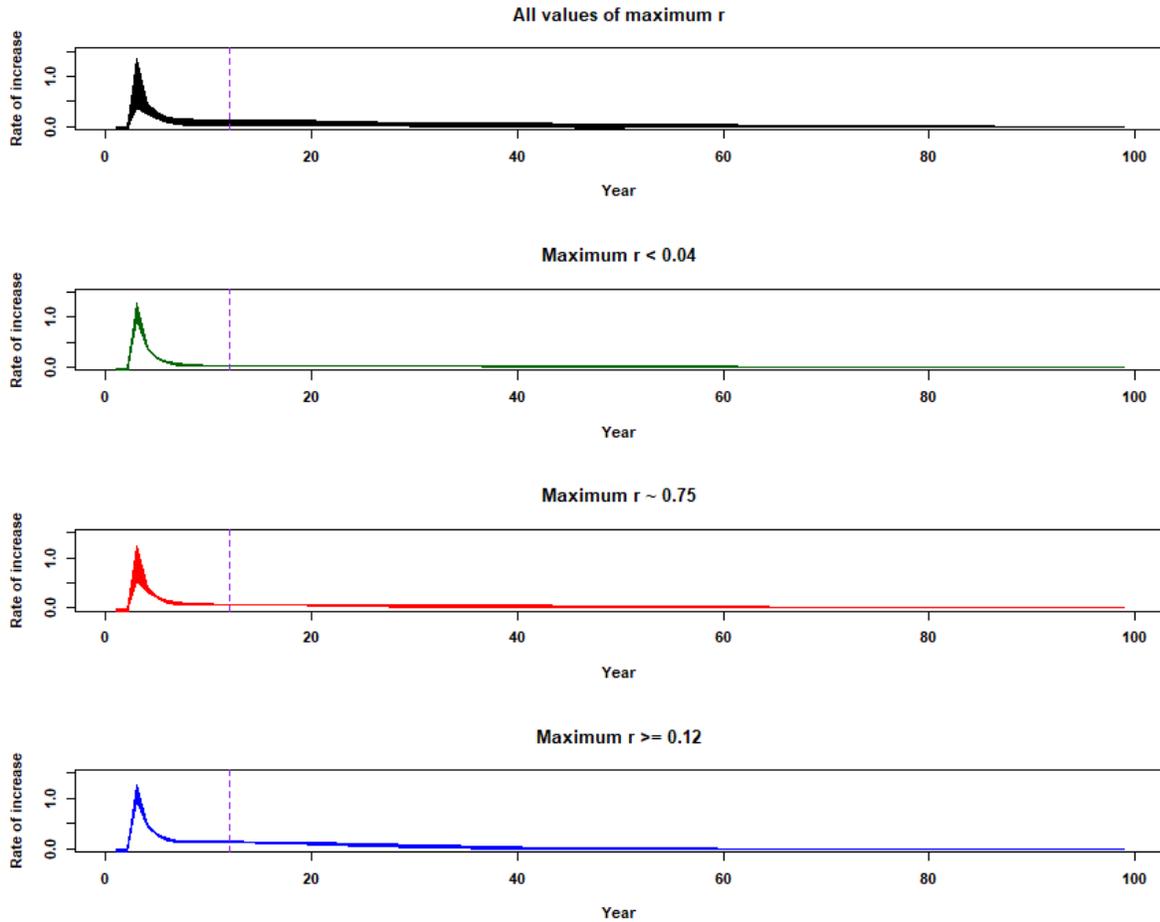
Figure 26: Effect of selected removal levels on the final (year 100) non-hatchling numbers and stage proportions in populations unmanaged after 2022 or subjected to different levels of adult and juvenile removals. The blue graph models continuation of the 2013-2022 removal program into the future, for 11706 combinations of population parameters. The vertical gray line marks the lower limit of estimated non-hatchling numbers for the NPEC population. The upper-left graph shows results for a ‘reference’ population left unmanaged after 2022.



Estimation of the maximum rate of increase

201. Rate of increase has not been a strong focus of this modelling exercise because of density dependencies in the projection matrices. However, it is useful to examine briefly the range of r_{\max} values generated by the projections to ensure they are biologically realistic. Because the projections were not initiated with the initial population at its stable stage equilibrium, it takes some years for the initial perturbations to flow through. Examination of projection trajectories indicated that the rate of increase in year 12 would provide a reasonable estimate of the maximum rate of increase (Figure 27) for this exercise.

Figure 27: The exponential rate of increase (r) in 11,706 projections of the NPEC population over 100 years of projection. The early population trajectory is perturbed because the initial populations were not at their stable stage distributions. The value of r at year-12 was taken to be a reasonable estimate of r_{\max} for all trajectories, including those at the extremes and close to the mean.¹⁶ The dotted vertical line shows the year-12 location.

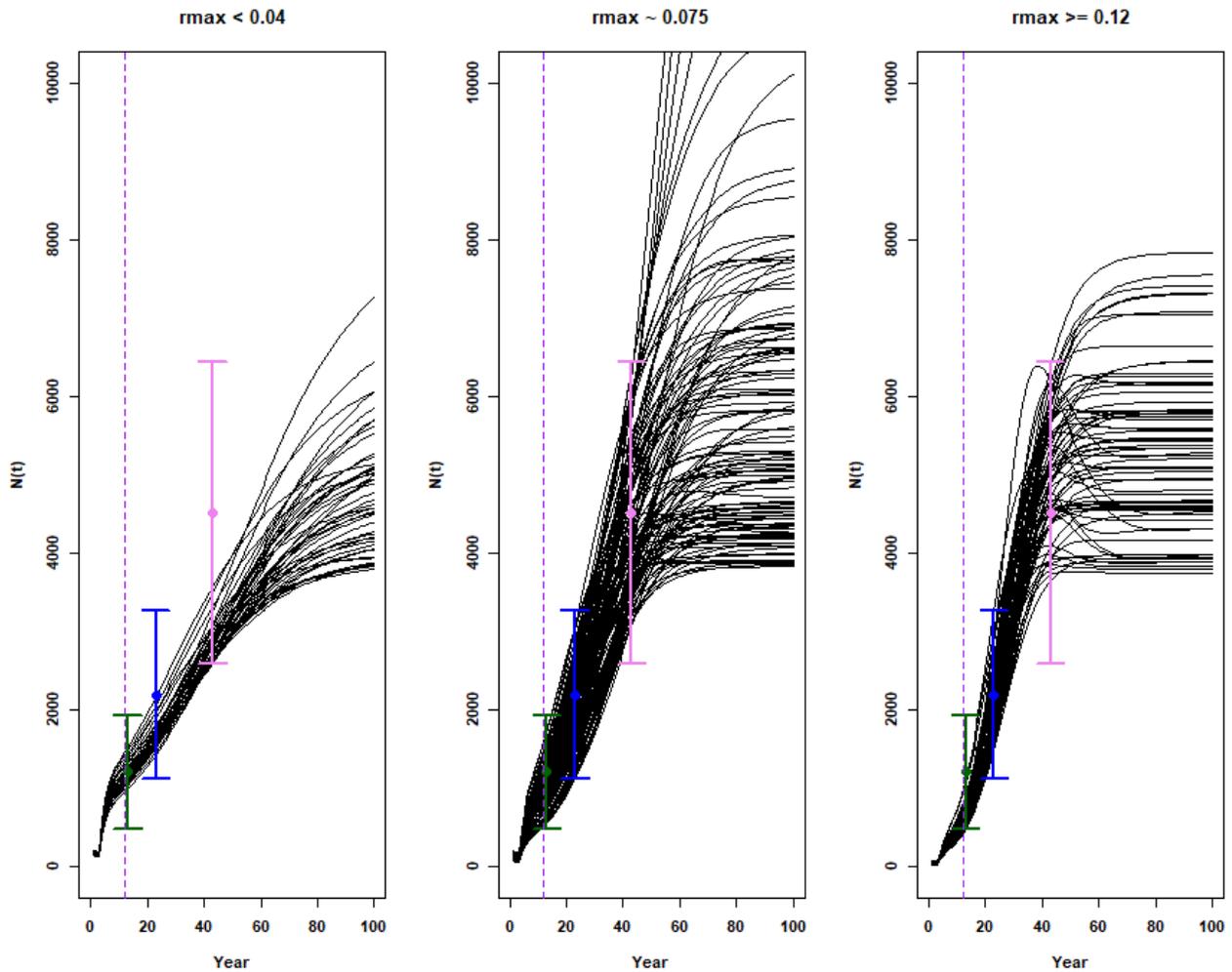


202. Values of r_{\max} at year-12 ranged from 0.029 – 0.142 with a mean of 0.0752, equivalent to $\lambda = 1.078$. The range of values is biologically reasonable. Fukuda et al (2011) estimated r_{\max} in the NT to be 0.11. Craig et al (1992) gave an estimate of 0.076 for Nile crocodiles and modelled the population with values ranging from 0.03 – 0.12. That the NPEC modelling gives reasonable estimates of r_{\max} is not altogether surprising, given the subset of projection matrices was selected for their fit to actual population estimates. It is useful, however, in showing that very high estimates (7,500 – 22,500) of the end-state NPEC population do not depend on biologically unrealistic values of r_{\max} .

¹⁶ Trajectories around the mean are plotted for the range $0.0750 < r_{\max} < 0.0754$.

203. It is useful in passing to note the relationship between r_{\max} and the end-state equilibrium numbers. Figure 28 shows trajectories at the upper and lower extremes of r_{\max} and in a narrow range around the mean. Trajectories with very low and very high r_{\max} values lead to low population estimates. Values close to the mean can lead to very low and very high non-hatchling numbers. These relationships are not explored further.

Figure 28: Trajectories for the results of the projections shown in Figures 24 and 25, characterised by values of r_{\max} at the lowest and highest end of their range and at the mean.



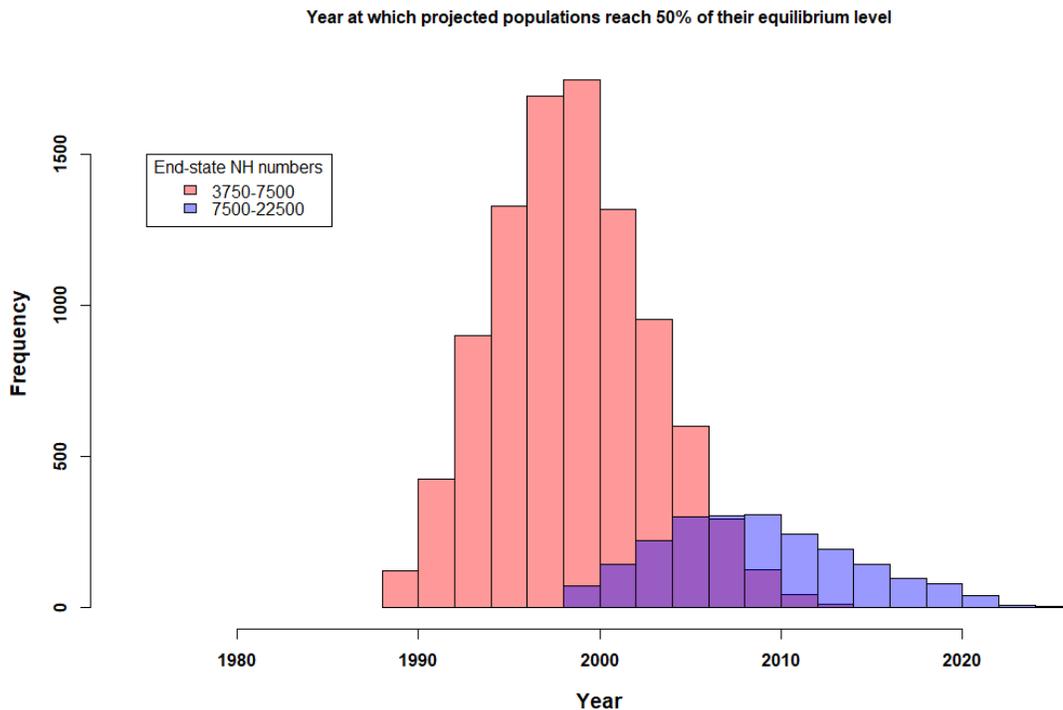
Discussion

204. Despite great uncertainty about the vital rates and density dependencies operating in the NPEC estuarine crocodile population, this analysis provides useful insights into the sensitivity of the matrix model outputs to the input parameters. More could be done in this space but the possible effects of historical and potential future management regimes are more relevant for this report.

Effects of past harvests

205. The analysis of historical removals suggests that, regardless of which parts of the biologically reasonable parameter space are tested, the management program's influence on the population has likely been relatively small – reducing non-hatchling numbers by perhaps 15% from where they would have been if left unharvested. Around that median estimate, it is about equiprobable that the removals have had either no net effect or may have reduced the population by about 30%, based on the most likely final numbers (3,750 – 7,500). That is an important finding given the management program has been controversial since its inception
206. The modelling also suggests that the removals had their highest impact in the 1990s but did not keep pace with population growth and their impact declined over the years (Figure 20). That conclusion does not, however, support increasing the number of removals. In simple terms, we might expect the absolute number of animals added to the population to be maximal under logistic growth when the population is at about half its equilibrium level, the point of maximum sustainable yield (Caughley, 1977). The model projections, while not strictly logistic, suggest the point of maximum increase in numbers has likely passed already (Figure 29) and for the low-NH group (3,750-7,500 NH at equilibrium) occurred 10-30 years ago.
207. It so happens that from about 1990 to 2010 the number of management removals was at a low ebb (Figure 2), so the changed impact of the management regime between 1997 and 2017 (Figure 20) might be attributable in part to that conjunction of peak growth and reduced control efforts.

Figure 29: Distribution of the year in which projected population trajectories reach 50% of their equilibrium level for the subset of 11,706 model matrices.



208. Given the peak of absolute population increase likely passed some time ago, there seems little reason to increase the rate of removals unless the desired management outcome is to reduce the population to a lower equilibrium.

Modelled effects of changing removal rates

209. Examination of the potential effects of post-2022 removal options in this report give useful insights into the possible consequences of changing the management regime. These are not, of course, predictions but simply illustrations of what would happen in future if the conditions and assumptions in the population projection matrices held steady over time and some additional ‘mortality’ was imposed. Examination of these effects is kept relatively simple given the wide range of parameter values in the underlying projections.
210. The population projections show some consistent patterns across the wide parameter space explored and suggest quite strongly that the NPEC population is likely to be particularly sensitive to removals of adults (Figure 25 and 26) and much less sensitive to removals of juveniles. It appears that maintaining the current offtake of 20 adults would hold the population at about its current level while increasing the offtake to 50 adults would increase the risk of a trajectory tracking to extinction. Taken together, Figures 25 and 26 suggest the parameter space explored ‘favours’ a population that is either reduced by only 15-20% from its unmanaged level or alternatively declines to extinction. Some middle-ground does exist but it arises from only a small proportion of the parameter combinations tested. It would be fortuitous if the actual population dynamics aligned with one of these few matrix models.
211. Figure 26 also shows that increasing the removals of adults can reduce the population considerably from its unmanaged level without generating a long-term decrease in the proportion of adults in the population. Thus, increasing adult removals increases the risk that the population could track to extinction while making little difference to relative proportions of juveniles and adults unless the population is reduced to very low levels. It appears very likely the NPEC population will stabilise with a ratio of adults to juveniles of about 20:80%, quite different from the 43:57% expected for the NT population (Fukuda et al, 2020).
212. Nonetheless, the proportion of very large animals in estuarine crocodile populations that pose real risks of fatal attacks (Brien et al, 2017; Fukuda et al, 2015) has always been small. Fukuda et al (2020) estimate the likely proportion of animals over 4.2m in the NT population at <2%. Taplin et al (2020) report the proportion of animals over 13ft (4.0m) in the Bioregion 5b population (largely comprised by of the NPEC population) at 6% in 2016-19, reducing from 8% in 1984-89. They also noted that the size class distribution has seen a decrease in the proportion of adults since the 2000-06 survey era, perhaps linked to the targeted management program. Thus, projections of relatively stable adult proportions in the population do not necessarily translate into higher risks to people.
213. In terms of the management implications of this study, continuing the current rate of removal beyond 2022 is likely a safe strategy from a species conservation standpoint and an effective strategy from a management standpoint. Only 2 of the 11,706 parameter combinations tested led to extinction of the NPEC population in the 100-year period (Figure 26 – centre graph). The analysis suggests that continuing the existing management regime has a high likelihood of leading to a population that is within the most likely bounds of 3,750-7,500 and a very small likelihood of seeing it reduced.

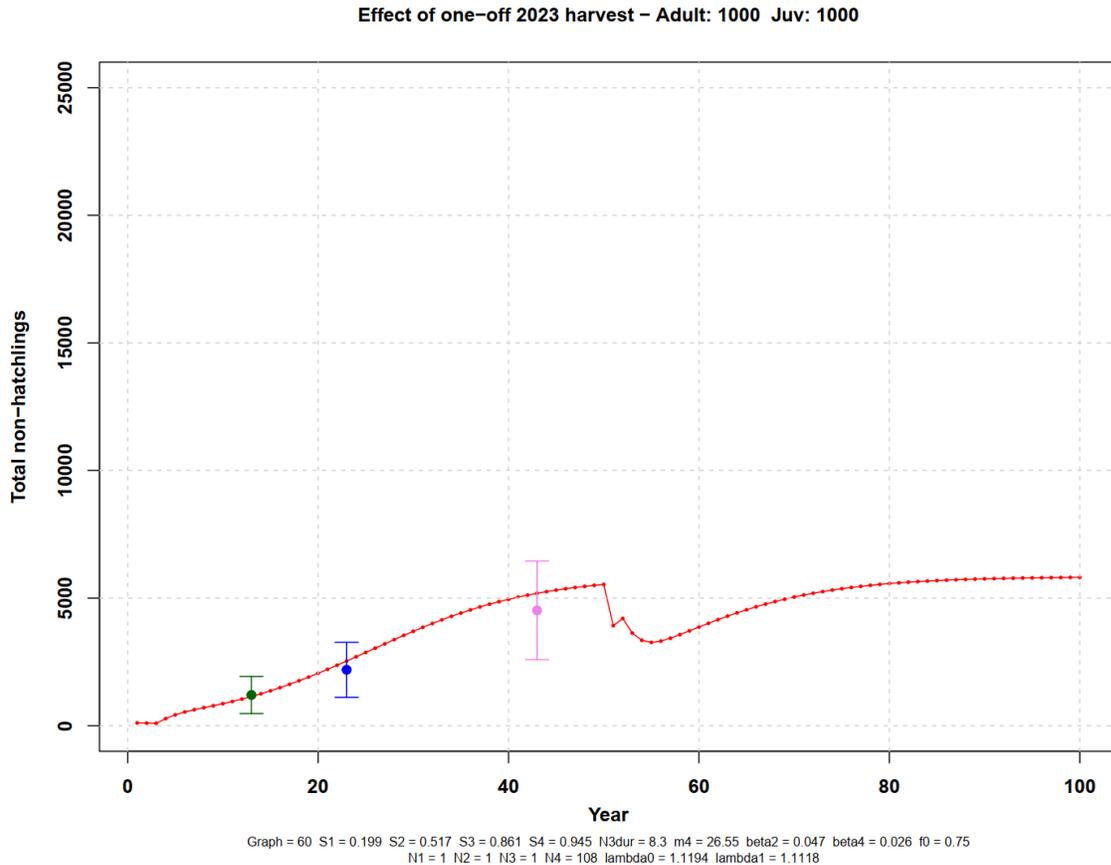
214. It appears that if the level of removals reached biologically unsustainable levels it would result in declines in the number of non-hatchlings and the proportion of adults in the population. Both of those quantities can be monitored relatively easily through an appropriately designed survey program and, given they will take many years to manifest, can be responded to if they begin to track in undesirable directions.
215. The design of a monitoring program that takes account of these findings and covers the ground in sufficient breadth and at sufficient frequency to detect change is not a trivial exercise. It would be important to complete if a policy decision to increase removals was contemplated.

Potential effects of large reductions in the population

216. If the population was driven to much lower levels, we might expect to see much the same population response as in the 1980s and 90s. There would likely be an increase in the population growth rate and a slow but steady return to a new equilibrium over a prolonged period.
217. This response shows up as expected when a one-off large-scale removal of 1000 adults and 1000 juveniles is applied in 2023. A substantial fall in non-hatchling numbers is followed by steady recovery over several decades - one example of the projected trajectories is shown in Figure 30. The projected population returns to equilibrium level it would have reached earlier if left undisturbed. The fall in non-hatchling numbers is smaller than the number of removals because a cohort of hatchlings remains available to repopulate the juvenile component of the non-hatchling population in 2024. Renewed growth has to await graduation of juveniles to the adult stage.
218. Modelling a range of one-off removals suggests the NPEC population at its 2022 level could be capable of recovering in the long term from very high levels of removals as long as a pool of hatchlings remains and survives into eventual adulthood. However, this finding takes no account of environmental stochasticity, where a sequence of bad years could impact survival and growth severely. Nor does it account for demographic stochasticity at the very low levels of non-hatchling numbers it would generate. Random chance alone could lead the local population to extinction when numbers are very low.
219. This aspect of the modelling, while not explored in any depth, lends weight to the proposition that the population is resilient and capable of recovering from shocks (see para 0 and particularly 4.1). However, the actual population response to such a large-scale one-off removal would be different from the 1970s-80s recovery because of the loss of much of the residual dense swamplands and lagoons/billabongs that previously protected a proportion of adults from hunting (para 110).
220. The present population of adults must inevitably be more concentrated in riverine habitats where they are generally much more vulnerable to human interference. That said, the NPEC population does successfully occupy considerable stretches of waterway that are hard to access and rarely visited – the distant upstream reaches of the Daintree River and Herbert River are examples. In addition, National Parks and other conservation reserves contain around 30% of the crocodile habitat in the NPEC subregion (Taplin, unpubl obs). Thus, refuge areas should persist from where gradual reoccupation of depleted and less protected coastal areas would occur. Recovery from a large population reduction would likely be

slower than in the 1970s-90s but should be expected, barring severe impacts from random environmental or demographic events.

Figure 30: An example of the response of one modelled population to a one-off removal of 1000 adults and 1000 juveniles in 2023. All matrix projections across the parameter space show similar short-term perturbation and long-term recovery.



Management implications

221. The results of modelling one-off removals illustrate the importance of monitoring surveys and adaptive management regimes. They reinforce that the risk of population decline that shows up in Figure 25 and 26 is linked to the annual repetition of fixed numbers of removals. If the ‘pressure’ of removals is released, then the population can be expected to bounce back more or less quickly depending on the residual stage structure and the availability of suitable habitat. A regime of continuing fixed numbers of removals carries different risks if they are not calibrated carefully. Bradshaw et al (2006) showed, in a commercial harvesting context, that fixed harvests of estuarine crocodiles reduced modelled population size much more rapidly than proportional harvests and carried greater risks of quasi-extinction¹⁷.

¹⁷ A proportional harvest in their modelling is one where the number of animals taken is a fixed proportion of the estimated population size at any particular time. Quasi-extinction occurred if the modelled population fell below a density of 0.1 crocodiles per km.

222. It is neither necessary nor practical to adopt complex regimes such as proportional removal quotas for management of the NPEC population. The analysis here suggests that continuation of the conservative management regime currently employed, combined with active monitoring of total adult removals and ongoing long-term monitoring is a sound prescription. Two small adjustments would, however, appear prudent:
 - 222.1. Because large mature crocodiles are rarely seen in spotlight surveys, more helicopter (or drone) monitoring will be important to ensure the subadult and adult population remains viable.
 - 222.2. Judgements about the fate of individual adult crocodiles should not be taken in isolation from the information about the overall number of removals from the population and the size classes and sex of animals removed. This is not intended to impose inappropriate criteria onto judgements about public safety, but to ensure early attention is drawn to possible unsustainable levels of removal.
223. If a ‘middle-ground’ target of much lower non-hatchling numbers was to be favoured, it would likely impose considerable costs. More monitoring would be needed to ensure the population was not tipped towards localised extinction. Long-lived, late maturing species can persist for long intervals as ‘ghost populations’ that may appear viable but are nonetheless tracking towards eventual extinction. A real-life example of a ghost population might be the small population in the Fitzroy River at the extreme limit of the breeding range in Australia. This population has grown a little since the 1980s but the rate of increase has been very low compared with favourable habitats further north (Taplin et al, 2020, 2021). Almost no hatchlings have been discovered despite known nesting and large numbers of surveys over many years.
224. To avoid the NPEC population becoming a ghost population in the event of increased adult harvest, it would be desirable, in addition to increased monitoring, to:
 - 224.1. improve the mapping of habitat, so as to better identify what proportion of the coastal waterway system is actually inhabitable by crocodiles and distinguishing between habitat suitable for hatchlings and juveniles and for adults;
 - 224.2. try to better estimate the relationship between the numbers of crocodiles seen in spotlight and helicopter surveys and the numbers actually present.
225. The bigger the risk of severe impacts, the more requirement there will be for more detailed monitoring – not least to narrow the currently wide confidence limits surrounding population estimates. These are too large at present to be confident that small differences between an increasing and a declining population would be detectable in a timely manner when it is close to equilibrium. This has not been an issue to date because the NPEC population has increased demonstrably over time. It will become more important as the population stabilises because observation errors in counts are larger in a bigger population (a consequence of following a Poisson or perhaps negative binomial distribution) while impacts from the human population in the NPEC will likely increase.
226. These steps, focused on improving the precision and accuracy of population estimates over time, would keep the research focused on monitoring the population’s response to changing circumstances. They would deliberately steer clear of resource-intensive and potentially unsustainable long-term studies aimed at improving estimates of the vital rates and density

dependency relationships that have informed this study. While a laudable aim, it is highly questionable whether the benefits of small improvements in our understanding of the parameter space influencing crocodile population dynamics would be worth the cost and the diversion of resources from research more directly and immediately applicable to management.

227. That said, there would be value in some further exploration of the population modelling done here to identify whether any particular aspects of the population dynamics might be informative in future for interpreting the trajectory of the population while being easily measured through changes to the monitoring program.
228. Separately from decisions about the appropriate level of adult removals, the analysis suggests that changes to the management program directed at juveniles will be much less impactful and carry lower risk than any involving adults. That might be useful in the context of managing the few areas where all crocodiles are removed as a matter of course, such as the Barron River catchment in Cairns. These waterways gain immigrants regularly after resident animals are removed (DES internal records) and recent genetic analysis suggests that across Queensland, the majority of animals remain within 50km of where they were born (Lloyd-Jones et al, submitted). Those immigrant animals are typically small juveniles and subadults – the juvenile stage in the NPEC population models. Thus, the Department might be able to effect better control at low risk in selected waterways through careful targeting of juveniles in adjacent areas, noting that about 50% of animals removed from 2013-2022 were juveniles.
229. As anticipated, this extensive analysis does not provide any prescriptions for management of the NPEC population but does give considerable insights into what might be influencing the population dynamics, the range of responses that might be expected from the population, and the sensitivity of the population's response to changes in the management harvest. Those insights can help guide policy decisions but are too uncertain to fully inform decisions. The policy response will require an informed assessment of the risks and a broader canvassing of the merits of various management options, taking account of the importance of retaining public confidence in the scientific underpinnings and the practical outcomes of the management program.

Some final observations

230. This analysis has touched lightly on the issue of localised extinctions. A deliberate decision was made to not pursue an extensive population viability analysis (PVA). The uncertainties inherent in the population parameters appeared too great to make this a worthwhile exercise and there seemed some prospect it could produce misleading results. Nor did it appear necessary when the GSA approach used generated sufficient guidance to inform policy decisions. The NPEC crocodile population is in no danger of extinction in the foreseeable future unless there is a radical change in management. A PVA may be useful for exploratory purposes in future but is not needed here.
231. Similarly, it would be possible to compare the results of this exercise with those from a purely deterministic model where the focus would be on rates of increase rather than numbers of non-hatchlings. It was not pursued because it appeared likely to add much additional complexity to the analysis and conclusions without necessarily shedding more light. Like a PVA, it may prove a useful exercise in the future.

References

- Aiello-Lammens M E and Akçakaya HR (2017). Using global sensitivity analysis of demographic models for ecological impact assessment. *Conservation Biology* 31(1): 116-125.
- Bayliss P, Webb GJW, Whitehead PJ, Dempsey K and Smith A (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. *Aust. Wild. Res.* 13: 309-20.
- Bayliss P (1987). Survey methods and monitoring within crocodile management programmes. In: Webb GJW, SC Manolis and PJ Whitehead (eds). *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty & Sons. pp. 157-175.
- Bayliss P and Messel H (1988). The population dynamics of estuarine crocodiles. I. An assessment of long-term census data. Proc. 9th Working Meeting IUCN Crocodile Specialists Group, Lae, PNG.
- Blackman JG (1968). Report of the crocodile survey, 1965-1968. Internal memorandum, Queensland Department of Primary Industries, Fauna Conservation Branch.
- Blackman JG (1970). Survey of the crocodile industry in Queensland, 1969. Internal memorandum, Queensland Department of Primary Industries, Fauna Conservation Branch.
- Blomberg GED, St Pierre BC, Smith KD, Caddell SM and Pett SR (1982). Simulated population dynamics of crocodiles in the Okavango River, Botswana. Proc 5th Working Meeting CSG pp:341-373. IUCN, Gland.
- BOM (2023). Average annual, seasonal and monthly rainfall maps. Bureau of Meteorology, Australia. <http://www.bom.gov.au/climate/maps/averages/>.
- Bourquin, S.L. (2007) The Population Ecology of the Nile Crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana. PhD Thesis, University of Stellenbosch, Stellenbosch.
- Bourquin SL and Leslie AJ (2012). Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana. *Afr.J.Ecol.* 50(1):1-8.
- Bradshaw CJA, Fukuda Y, Letnic M and Brook BW (2006). Incorporating known sources of uncertainty to determine precautionary harvests of saltwater crocodiles. *Ecological Applications* 16(4): 1436-1448.
- Brien ML, Gienger CM, Browne, CA, Read MA, Joyce MJ1 and Sullivan S (2017). Patterns of human-crocodile conflict in Queensland: A review of historical estuarine crocodile (*Crocodylus porosus*) management. *Wildlife Research* 44(4): 281-290.
- Briggs-Gonzalez V, Bonenfant C, Basille M, Cherkiss M, Beauchamp J and Mazzotti F (2017). Life histories and conservation of long-lived reptiles, an illustration with the American crocodile (*Crocodylus acutus*). *J. Anim. Ecol.* 86(5): 1102-1113.
- Britton A (2008). A survey of the estuarine crocodile (*Crocodylus porosus*) populations in Cape York Peninsula to support an experimental harvest of eggs. Final Report 2008: 2007/08 Nesting Season. Big Gecko P/L & Queensland Department of Primary Industries and Fisheries.

- Britton A (2009). A survey of the estuarine crocodile (*Crocodylus porosus*) populations in Cape York Peninsula to support an experimental harvest of eggs. Final Report 2009: 2008/09 Nesting Season. Big Gecko P/L & Queensland Department of Primary Industries and Fisheries.
- Britton A (2017). Results of an experimental harvest of estuarine crocodiles (*Crocodylus porosus*) eggs from wild nests around Pormpuraaw, Cape York Peninsula. Summary Report [draft version 26 June 2017]: 2011/2 – 2014/5 Nesting Seasons. Big Gecko P/L, Darwin, NT.
- Brook BW and Bradshaw CJA (2006). Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, 87, 1445–1451.
- Burgman MA, Ferson S and Akçakaya HR (1993). Risk Assessment in Conservation Biology. Chapman and Hall, London.
- Cariboni J, Gatellia D, Liskaa R, and Saltelli A (2007). The role of sensitivity analysis in ecological modelling. *Ecol. Modelling* 203: 167-182.
- Caswell H (1989). Matrix Population Models. Sinauer Press, Sutherland, Mass.
- Caswell H (2018). Matrix Population Models: Construction, analysis and interpretation. 2nd Edition. Sinauer Associates, Massachusetts.
- Caughley G (1977). Analysis of Vertebrate Populations. Wiley, New York.
- Chabreck RH (1966). Methods of determining the size and composition of alligator populations in Louisiana. Proc Southeastern Assoc Game and Fish Commissioners Conf 20:105-112.
- Chaloupka M (2002). Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling*, 148: 79-109.
- Chaloupka M (2003). Stochastic simulation modelling of loggerhead population dynamics given exposure to competing mortality risks in the western South Pacific. Chapter 17 in Bolten AB and Witherington BE. Loggerhead Sea Turtles, Smithsonian Books, Washington.
- Clark F, Brook BW, Delean S, Akçakaya HR, and Bradshaw CJA (2010). The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution* 2010(1): 253–262.
- Craig GC, Gibson DStC, and Hutton JM (1992). A population model for the Nile Crocodile and simulation of different harvesting strategies. In Hutton JM and Games I (Ed). The CITES Nile Crocodile Project. IUCN, Geneva.
- Crouse DT, Crowder LB, Caswell H (1987). A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* 68(5): 1412-1423.
- DES (2017). Monitoring Plan: Crocodile Monitoring. Queensland Department of Environment and Science.
- DES (2021). Department of Environment and Science’s Response to the Independent Evaluation of the Queensland Estuarine Crocodile Management Program. Queensland Department of Environment and Science.
- Dunham K, Dinkelacker S and Miller J (2014). A Stage-Based Population Model for American Alligators in Northern Latitudes. *J Wildlife Management* 78(3):440–447.
- Ellner SP, Childs DZ and Rees M (2016). Data-driven modelling of structured populations: A practical guide to the Integral Projection Model. Springer Int’l. Publ., Switzerland.

- Ennerson JJ and Litzgus JD (2008). Using long-term data and stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). *Biol. Conservation* 141(6): 1560-1568.
- Fordham DA, Georges A, and Brook BW (2007). Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. *Journal of Animal Ecology* (2007): 1231-1243.
- Fukuda Y, Webb GJW, Manolis C, Delaney R, Letnic M, Lindner G and Whitehead P (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *The Journal of Wildlife Management* 75: 1253-66.
- Fukuda Y and Saalfeld K (2014). Abundance of saltwater crocodile hatchlings is related to rainfall in the preceding wet season in northern Australia. *Herpetologica* 70(4): 439-448.
- Fukuda Y, Manolis C, Saalfeld K and Zuur A (2015). Dead or Alive? Factors affecting the survival of victims during attacks by saltwater crocodiles (*Crocodylus porosus*) in Australia. *PLoS ONE* 10(5):e0126778. doi:10.1371/journal.pone.0126778
- Fukuda Y., Webb G., Edwards G., Saalfeld K. and Whitehead P. 2020. Harvesting predators: simulation of population recovery and controlled harvest of saltwater crocodiles, *Crocodylus porosus*. *Wildlife Res.* <https://doi/10.1071/WR20033>.
- Ginzburg LR, Ferson S and Akçakaya HR (1990). Reconstructibility of Density Dependence and the Conservative Assessment of Extinction Risk. *Cons.Biol.* 4(1): 63-70.
- Harper, EB, Stella, JC and Fremier, AK (2011). Global sensitivity analysis for complex ecological models: a case study of riparian cottonwood population dynamics. *Ecol. Appl.* 21(4): 1225-1240.
- Hawkins P, Taplin LE, Duivenvoorden LJ and Scott F (1988) Limnology of oligotrophic dune lakes at Cape Flattery, North Queensland. *Aust J Mar Freshw Res* 39:535-553.
- Hines, TC and Abercrombie CI (1987). The management of alligators in Florida, USA. In Webb GJW, Manolis SC and Whitehead PJ (eds) *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons, Chipping Norton. pp 43-47.
- Hixon, MA, and Johnson, DW (2009) Density Dependence and Independence. *Encyclopaedia of Life Sciences*, pp1-6, John Wiley and Sons Ltd., Chichester.
- Hutton JM (1984). The population ecology of the Nile Crocodile *Crocodylus niloticus* Laurenti, 1768, at Lake Ngezi, Zimbabwe. D.Phil thesis, University of Zimbabwe.
- Hutton JM (1987a) Techniques for aging wild crocodilians. In: Webb GJW, SC Manolis and PJ Whitehead (eds). *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty & Sons. pp. 157-175.
- Hutton JM (1987b). Growth and feeding ecology of the Nile Crocodile, *Crocodylus niloticus*, at Ngezi, Zimbabwe. *Journal of Animal Ecology* (1987) 56: 25-38.
- Iooss B & LeMaitre, P (2015) A review on global sensitivity analysis methods. In Dellino G and Meloni C (eds) *Uncertainty management in simulation-optimization of complex systems*. pp. 101-122
- Janssen P, Barkmeijer J, Aldenberg T, Visser H, van Eijkeren J, Beusen A, and Mylius S (eds.) (2012) *Methods for Sensitivity and Uncertainty Analysis of Computer Intensive Simulation*

- Models. Report NMDC project Model and Data Quality working package. Nationaal Modellen - en Data Centrum (NMDC, <http://nmdc.eu>).
- Kendall BE, Fujiwara M, Diaz-Lopez J, Schneider S, Voigt J and Wiesner S (2019). Persistent problems in the construction of matrix population models. *Ecological Modelling* 406: 33–43.
- Kery M and Schaub M (2012). *Bayesian Population Analysis Using WinBUGS: a Hierarchical Perspective*. Academic Press.
- Kery M and Royle JA (2016). *Applied Hierarchical Modelling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS*. Volume 1. Elsevier, London.
- King R, Morgan BJT, Gimenez O and Brooks S (2010). *Bayesian Analysis for Population Ecology*. CRC Press, Boca Raton, Florida.
- Knappe J and de Valpine P (2012) Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance? *Ecology Letters*, (2012) 15: 17–23.
- Lance VA (2003). Alligator physiology and life history: the importance of temperature. *Experimental Gerontology* 38:801-805.
- LeBreton J-D and Gimenez O (2013). Detecting and Estimating Density Dependence in Wildlife Populations. *J Wildl Management* 77(1): 12-23.
- Lloyd-Jones LR, Brien ML, Feutry P, Lawrence E, Beri P, Booth S, Coulsen S, Baylis SM, Taplin LE, Villiers K, and Westcott DA. (submitted). Past and present genetic connectivity of saltwater crocodiles (*Crocodylus porosus*) in Queensland.
- Magnusson WE, Grigg GC & Taylor JA (1978) An aerial survey of potential nesting areas of the saltwater crocodile, *Crocodylus porosus*, on the north coast of Arnhem Land, northern Australia. *Aust Wildl Res* 5:401-15.
- Magnusson WE, Grigg GC & Taylor JA (1980) An aerial survey of potential nesting areas of *Crocodylus porosus*, on the west coast of Cape York Peninsula. *Aust Wildl Res* 7: 465-78.
- Magnusson WE (1982) Mortality of eggs of the crocodile, *Crocodylus porosus* in northern Australia, *J Herpetol* 16:121-30.
- Magnusson WE & Sanaiotti TM (1994) Growth of Caiman crocodilus in Central Amazonia, Brazil. *Copeia* 1995(2): 498 – 501.
- McCallum H (2000). *Population parameters: Estimation for ecological models*. Blackwell, Oxford.
- Messel H, Vorlicek GC, Wells AG & Green WJ (1980). *Surveys of the Tidal Rivers Systems in the Northern Territory of Australia and their Crocodile Populations*. Monograph 11. Tidal Waters of Arnhem Bay. Pergamon Press, Sydney.
- Messel H, Vorlicek GC, Wells AG & Green WJ (1981). *Surveys of the Tidal Rivers Systems in the Northern Territory of Australia and their Crocodile Populations*. Monograph 1. The Blyth-Cadell River Systems Study and the Status of *Crocodylus porosus* in Tidal Waterways of Northern Australia. Pergamon Press, Sydney.

- Messel H, Vorlicek GC, Green WJ & Onley IC (1984). Surveys of the Tidal Rivers Systems in the Northern Territory of Australia and their Crocodile Populations. Monograph 18. Population Dynamics of *Crocodylus porosus* and Status, Management and Recovery. Update 1979-1983. Pergamon Press, Sydney.
- Moler PE (1991). American crocodile population dynamics. Final report to study No. 7532, Florida Game and Fresh Water Fish Commission, Bureau of Wildlife Research: Tallahassee, FL, USA.
- Morris, WF and Doak DF (2002) Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, Massachusetts.
- Nichols JD, Viehman L, Chabreck RH and Fenderson B (1976). Simulation of a commercially harvested alligator population in Louisiana. Louisiana Agricultural Experiment Station Bulletin #691.
- O'Neill JP (1971a) Population and dwellings in local government areas and urban centres, Northern Territory and Australian Capital Territory in Census of population and housing, 30 June 1971. Bulletin 6. Commonwealth of Australia.
- O'Neill JP (1971b) Population and dwellings in local government areas and urban centres, Queensland in Census of population and housing, 30 June 1971. Bulletin 6. Part 3. Commonwealth of Australia.
- OQCS (2021). Findings from an Independent Evaluation of the Queensland Estuarine Crocodile Management Program. Office of the Queensland Chief Scientist, State of Queensland.
- Plard F, Turek D, Gruebler M and Schaub M (2019). IPM²: toward better understanding and forecasting of population dynamics. Ecological Monographs 89(3): e01364.10.1002/ecm.1364
- Prowse TAA, Bradshaw CJA, Delean S, Cassey P, Lacy RC, Wells K, Aiello-Lammens ME, Akçakaya HR, and Brook BW (2016). An efficient protocol for the global sensitivity analysis of stochastic ecological models. Ecosphere 7(3): 1-17.
- Puy A, Piano SL, Saltelli A, and Levin SA (2021) Sensobol: an R package to compute variance-based sensitivity indices. *arXiv preprint arXiv:2101.10103* (2021).
- Puy A, Piano SL, Saltelli A and Levin SA (2022). sensobol: Computation of Variance-Based Sensitivity Indices. Journal of Statistical Software 102(5), 1-37. doi:10.18637/jss.v102.i05.
- Renardy M, Hulsta C, Evans S, Linderman JJ and Kirschner DE (2019) Global sensitivity analysis of biological multi-scale models. Curr. Opin. Biomed. Eng. 11: 109–116.
- Richardson KC, Webb GJW, and Manolis SC (2002). Crocodiles: Inside Out. A Guide to the Crocodylians and their Functional Morphology. Surrey Beatty & Sons: Sydney, NSW, Australia.
- Roff C (1966). Crocodiles in Queensland. Department of Primary Industry Advisory Leaflet Number 883. Queensland. Agric. J. 92(9): 526-33.
- Saalfeld WK, Delaney R, Fukuda Y and Fisher AJ (2014). Management Program for the Saltwater Crocodile in the Northern Territory of Australia, 2014 - 2015. Northern Territory Department of Land Resource Management, Darwin.
- Saalfeld K, Fukuda Y, Duldig T and Fisher A (2016). Management Program for the Saltwater Crocodile (*Crocodylus porosus*) in the Northern Territory of Australia, 2016-2020. Northern Territory Department of Environment and Natural Resources, Darwin.

Saltelli A, Tarantola S and Chan KP-S (1999) A Quantitative Model-Independent Method for Global Sensitivity Analysis of Model Output. *Technometrics* 41(1): 39-56.

Saltelli, A (2004) Global sensitivity analysis: an introduction. In Hanson, K.M. and Hemez, F.M. (eds). *Sensitivity Analysis of Model Output*. Los Alamos National Laboratory, 2005.

Schaub M & Kery M (2022). *Integrated Population Models: Theory and Ecological Applications with R and JAGS*. Academic Press, London.

Smith and Webb (1985). *Crocodylus johnstoni* in the McKinlay River Area, NT VII. A population simulation model. *Aust Wildl Res*, 12: 541-554.

Staton MA & Dixon JR (1977) Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos. US Dept of Interior, Fish and Wildlife Service Report 5.

Swartzman GL and Kaluzny SP (1987) *Ecological Simulation Primer*. MacMillan, NY.

Taplin LE (1987) The management of crocodiles in Queensland, Australia. In Webb GJW, Manolis SC and Whitehead PJ (eds) *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons, Chipping Norton. pp 129-140.

Taplin LE (2017) Review of a Trial Harvest of Estuarine Crocodile Eggs in the Pompuuraaw Deed of Grant in Trust Lands and Recommendations as to an Experimental Commercial Harvest. Report to Department of Environment and Science, Queensland.

Taplin LE, Brien M, Beri P, Booth M, Mastro Monaco S, Browne C & Joyce M. (2020) Estuarine Crocodile Population Monitoring in Queensland (1979-2019). Technical Report to Queensland Department of Environment and Science.

Taplin LE, Brien M, Beri P, Booth M, Mastro Monaco S, Browne C & Joyce M. (2021) Estuarine Crocodile Population Monitoring in Queensland (1979-2019). Updated Technical Report to Queensland Department of Environment and Science.

Tucker AD (1995). Are sustainable harvest models relevant to Johnstone's crocodile? The role of population simulations in adaptive management. In 'Conservation through Sustainable Use of Wildlife' (G. Grigg, P. Hale, and D. Lunney, eds.) pp. 151 - 160. (University of Queensland Press, Brisbane).

Tucker AD (1997a). Ecology and demography of freshwater crocodiles (*Crocodylus johnstoni*) in the Lynd River of north Queensland. PhD Thesis, University of Queensland.

Tucker AD (1997b). Skeletochronology of post-occipital osteoderms for age validation of Australian freshwater crocodiles (*Crocodylus johnstoni*). *Marine and Freshwater Research* 48, 343–351. doi:10.1071/MF96113.

Tucker AD (2001). Sensitivity analysis of stage-structured demographic models for freshwater crocodiles. *Crocodylian Biology and Evolution*. (eds G.C. Grigg, F Seebacher & CE Franklin), pp 349-363. Surrey Beatty & Sons, Sydney.

Tucker AD and Limpus CJ (1997). Assessment of reproductive status in Australian freshwater crocodiles (*Crocodylus johnstoni*) by ultrasound imaging. *Copeia* 1997, 85:1-857.

Tucker AD, McCallum HI, Limpus CJ and McDonald KR (1994). *Crocodylus johnstoni* in the Lynd River, Queensland: continuation of a long term field study. In *Proceedings of the 2nd*

Regional Meeting of the IUCN Crocodile Specialists Group. pp. 469-473. IUCN, Gland, Switzerland.

Tucker AD, Limpus CJ, McCallum HI and McDonald KR (1996). Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia* 1996: 978-988.

Tucker AD, McCallum HI and Limpus CJ (1997a). Habitat use by *Crocodylus johnstoni* in the Lynd River, Queensland. *J Herpetol* 31: 114-121.

Tucker AD, Limpus CJ, McCallum HI and McDonald KR (1997b). Movements and home range of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildlife Research* 24: 379-396.

Tucker AD, McCallum HI, Limpus CJ and McDonald KR (1998). Sex biased dispersal in a long-lived polygynous reptile (*Crocodylus johnstoni*) *Behavioral Ecology and Sociobiology* 44: 85-90.

Tucker AD, Limpus CJ & McDonald KR (2006). Growth dynamics of freshwater crocodiles (*Crocodylus johnstoni*) in the Lynd River, Queensland. *Aust J Zool* 54: 409-415.

Wallace K, Leslie A and Coulson T (2013). Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology* 82: 155–165.

Weaver M (1973). Survey of the crocodile industry in Queensland, 1972. Internal memorandum, Queensland Department of Primary Industries, Fauna Conservation Branch.

Webb GJW (1977) Habitat and Nesting. Ch 14 pp 238-284 in Messel H and Butler ST (eds) *Australian Animals and their Environment*. Shakespeare Head Press, Sydney.

Webb GJW (1991). The influence of season on Australian crocodiles. In Ridpath MG, Haynes CD, and Williams MJD (eds) *Monsoonal Australia: Landscape, Ecology and Man in the Northern Lowlands*. pp. 125–131. AA Balkema: Rotterdam, The Netherlands.

Webb GJW, Messel H & Magnusson W (1977) The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia, *Copeia* 1977/2: 238-249.

Webb GJW & Messel H (1978a) Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, northern Australia. *Aust J Zool* 26: 1-27.

Webb GJW and Messel H (1978b) Movement and Dispersal Patterns of *Crocodylus porosus* in some Rivers of Arnhem Land, Northern Australia. *Aust Wildl Res* (1978) 5: 263-83.

Webb GJW, Messel H, Crawford J & Yerbury NJ (1978) Growth rates of *Crocodylus porosus* (Reptilia: Crocodylia) from Arnhem Land, northern Australia. *Wildl Res* 5: 385-89.

Webb GJW, Sack GC, Buckworth R & Manolis SC (1983) An examination of *C. porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality, *Aust Wildl Res* 10: 571-605.

Webb GJW, Manolis SC, Whitehead P and Letts G (1984). A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801) from Appendix I to Appendix II of CITES. Technical Report. Conservation Commission of the Northern Territory, Darwin, NT.

Webb GJW and Smith AMA (1984). Sex ratio and survivorship in the Australian freshwater crocodile, *Crocodylus johnstoni*. *Symp Zool Soc London* 52: 319-355.

Webb GJW and Manolis SC (1992). Monitoring saltwater crocodiles (*Crocodylus porosus*) in the Northern Territory of Australia. In McCullough R and Barrett HD (eds) *Wildlife 2001: Populations*. pp. 404-418. Elsevier Applied Science: New York, NY, USA.

Webb GJW, Whitehead P & Manolis SC (1987) Crocodile Management in the Northern Territory of Australia. Chap 11 in Webb GJW, Manolis SC & Whitehead P (eds) *Wildlife Management: Crocodiles and Alligators*, Surrey Beatty & Sons, Chipping Norton.

Webb GJW, Britton ARC, Manolis SC, Ottley B and Stirrat S. (2000) The recovery of *Crocodylus porosus* in the Northern Territory of Australia: 1971-1998. Pp. 196-235 in *Crocodiles. Proceedings of the 15th Working Meeting of the IUCN-SSC Crocodile Specialist Group*. IUCN: Gland, Switzerland.

WMI (2007) Monitoring saltwater crocodile (*Crocodylus porosus*) Nests in the Northern Territory: Trends in Melacca Swamp over 28 years (1980-2007). Wildlife Management International P/L, Darwin.

Woodward A, Hines T, Abercrombie C and Hope C (1984) Spacing Patterns in Alligator Nests. *J Herpetol*, 18(1): 8-12

Appendix 1: Estimating the probability of transitioning between stages

1. An important component of stage-base matrix models is the probability that animals in any particular stage will survive and transition into the next stage in the course of a single iteration of the projection model. Iteration intervals of one year are commonly used for crocodylian models. The term γ_i is used to designate the probability that an individual in stage (i) grows and enters stage (i+1) in any year. It is particularly relevant to the juvenile age class in the NT model, in which animals remain for some 8.3 years before transitioning into the adult stage. The term γ_i is used to partition survivorship for the stage into a probability of surviving and persisting in the same stage ($P_i = \sigma_i \cdot (1 - \gamma_i)$) and a probability of surviving and transitioning to the next stage ($G_i = \sigma_i \cdot \gamma_i$), where σ_i is the stage's survival rate.
2. Calculating γ_i is not a simple matter. Caswell (2018) sets out several different approaches including two that have been used in crocodylian population modelling. Which to use depends on whether we assume (a) each animal has a constant probability of graduating from one stage to the next in any particular year; or (b) each animal spends a fixed time in the stage before graduating.
3. For the NT population model, γ values for stages 1 (eggs) and 2 (hatchlings) are both 1, as individuals in these stages are presumed to either die or move the next stage. For the juvenile stage, Fukuda et al (2020) estimated $\gamma_3 = 0.12$ using assumption (a) in which $\gamma_3 = 1/T_3$, where T_3 is the time spent in stage 3 (8.31 years). Kendall et al (2019) describe this model for calculating γ as the 'flat age-within-stage structure' and noted that it is only a reliable measure of γ under quite restrictive conditions, where survivorship within the stage is equal to the rate of increase of the population (λ).
4. Herein lies a difficulty. The stages used in the NT model are based on age classes, with the juvenile stage lasting 8.3 years and adults living to a maximum of 70 years. If the parameters of a deterministic stage-structured model are estimated reliably, the corresponding age-structured matrix should project much the same rate of population increase (λ) at equilibrium as its stage-structured equivalent. In fact, the estimates for λ prove very different – 1.259 for the stage-based model and 1.080 for the equivalent age-based model. Those different estimates result in to very different projected population trajectories for the same population.
5. In contrast, Tucker (1997a) developed age- and stage-based models for two Australian freshwater crocodile populations, one in Queensland and one the NT. The Queensland model was based extensively on results of a mark-recapture study over 19 years in the Lynd River, Queensland (refer Appendix 2). The NT model was based on a much shorter study in the McKinlay River supplemented with information from other studies in the NT (Smith and Webb, 1985). For his stage-based model, Tucker (1997a) estimated transition rates between five stages using a formula for fixed stage durations from Caswell (1989) that assumes the population is not increasing ($\lambda = 1$). He found essentially identical values of λ for the age- and stage-structured models for Queensland and NT populations, as might be expected.
6. Caswell (2018) proposed an iterative approach to estimating transition rates because the value of γ is dependent on λ , which is in turn an eigenvalue of the projection matrix being estimated. Kendall et al (2019) considered that for models using fixed stage durations and directed at estimating asymptotic growth rates, iterative estimation of γ (which they term the 'asymptotic age-within-stage structure model') is the only approach that will generate the same results from age- and stage-structured matrices.

7. Applying this method to estimation of γ in the NT model, generates an estimate for γ_3 of 0.018, very different from the published estimate of 0.12 (Fukuda et al, 2020), and a lambda value of 1.078. This lambda value is a close match to the 1.080 found for the corresponding age-based model. The calculations were tested by applying them to Tucker's models for *C. johnstoni* in Queensland. They generated closely aligned lambda values of 1.031 for both age- and stage-structured models – slightly lower than Tucker's estimates of 1.037 based on non-iterated estimates of γ (Tucker, 1997a).
8. It is not necessary to consider here any implications of the changed estimate of γ for the NT model. But for the NPEC modelling it seems prudent to adopt fixed stage durations and iterative estimation of γ which together align the projections of age- and stage-structured models for *C. porosus*.

Appendix 2: Selected crocodylian population models examined

1. There have been numerous efforts over the years to develop population models for crocodylians. Their aims have included:
 - 1.1. Assisting and informing possible or actual commercial harvests.
 - 1.2. Providing insights into aspects of crocodylian biology that may have significant influences on aspects of their conservation or influence the way in which harvests are designed.
 - 1.3. Enabling comparisons of the life history of crocodylians with other reptiles and vertebrates.
2. A short review is useful in identifying the merits and challenges posed by different approaches to population modelling and identifying features of other crocodylians' biology that can inform a model for Queensland.

The 1976 American alligator model

3. This early model (Nichols et al, 1976) was constructed soon after the resumption of alligator harvesting when it was found to have recovered substantially from excessive hunting between the 1880s and 1960s. It aimed, *inter alia*, to simulate the effects of a commercial harvest in coastal marshes of Louisiana and was informed by intensive alligator research from the 1960s and 70s and some from much earlier.
4. The model was structured on age-classes and incorporated some environmental impacts such as (a) the effects of water level on the proportion of females breeding and on flood losses of nests; (b) nest predation; (c) effects of drought (low water levels) on mortality of hatchlings, juveniles and subadults; (d) a density-dependent function relating cannibalism to the overall population density and water levels (cannibalism increases during droughts); and (e) functions to relate non-cannibalism predation rates to water level (predation increases at low water levels) and to mortality from freezing at sub-zero temperatures.
5. Estimating overall mortality/survivorship proved challenging and could not be derived from survey data on the size-structure of the population. Instead, the survival rate of 7- and 8-year old male alligators (occupying single size classes) was calculated from experimental harvesting data for 1972 and 1973. That estimate was then assumed to apply for all age classes of males from 3-21 years, based on other research into predation rates. Female survival was assumed to be twice that of males given they did not venture as far afield as males. Mortality rates for adults (aged 8-21 years) were adjusted based on the known sex ratio. Survival rates for 1- and 2-year old animals were derived from other field observations.
6. The sex-specific age structure of the population was estimated from a 1966 size-structure derived from spotlight counts and nest counts (Chabreck, 1966) by calculating an age distribution assuming a stable age distribution within each size class and applying estimates of size-specific sex ratios. Alligators were presumed to die at an age of 21 years.
7. The model was constructed by applying the estimated functional relationships and vital rates to initial male and female population vectors over monthly intervals and updating the age-class structure annually. The model's core was deterministic but some environmental stochasticity was introduced by randomly generating water levels and freezing temperatures.
8. An initial simulation over 20 years identified that the initial estimate of hatchling numbers in the population vector was too low, so simulation results were used to correct it.

9. The model was used to examine the effects of different commercial harvest strategies including different offtake levels both for animals aged 4-21 years and for egg harvests with and without return of reared juveniles to the wild. Testing of model outputs against real-world estimates was only possible for nest numbers and showed reasonable correspondence.
10. The modelling identified that more information was needed on (a) growth rates and the effects of temperature and food availability on those rates; (b) the effect of water levels on the proportion of females nesting, flood losses, predation losses, cannibalism and losses from desiccation; and (c) interactions between predator density, water levels and juvenile mortality.
11. Craig et al (1992) characterized this early and detailed modelling effort as arguably more complex than necessary to measure key aspects of the population dynamics. They highlighted that the complex simulation appeared to result in a predicted rate of increase of 3% per annum, which was markedly lower than the 11% estimated from repeated field censuses – i.e. there was a serious mismatch between the modelled population trajectory and field data. They also argued that modelling should be kept as simple as possible to ensure we don't just add weakly estimated complexity and that claim that much the same answers could have been derived from a very much simpler Euler equation model based on a life table of survivorship and fecundity.

The Dunham model

12. Dunham et al (2014) created a stage-based model for American alligators in North and South Carolina using five stages – eggs, hatchlings, juveniles, subadults and adults and compared it to the same-structured model for a warmer climate Florida population. Estimates for survivorship, fecundity and stage duration were drawn from a range of sources but many vital rates had to be estimated from disparate studies because no longitudinal studies adequate to populate a Lefkovich matrix were available. Survival and fecundity data for the Carolinas population had to be drawn from southern populations in Florida and Louisiana.
13. The model did not incorporate any density dependencies or environmental stochasticity but did explore potential effects of climate perturbations by applying fixed levels of change to vital rates thought likely to be affected by changes in temperature and precipitation. Details of the methods used for sensitivity analysis were not reported, but they appear to have been calculated analytically using partial derivatives.

Nile crocodile models

The Blomberg model

14. Blomberg et al (1982) applied a similar model to that of Nichols et al (1976) to simulate Nile crocodile population numbers in the Okavango River. They modelled functions relating nest losses and cannibalism rates on young crocodiles to water levels and relating predation by monitors to the number of nests available to be predated. They estimated survival rates in the first four age classes from a 'derived population structure' and hypothesized the shape of the survivorship curve beyond that. Length-age relations were derived from the growth curve for a single wild individual observed over 22 years.
15. This was a complex model underpinned by very limited data on various of the important vital rates, especially survivorship. It incorporated several functional relationships with very little underpinning in field observations. Craig et al (1992) noted that the model implied an underlying population rate of increase of 2% p.a. ($\lambda = 1.02$) that appeared inconsistent with observed increases (not however measured by census) on the Zambezi River. Their

assessment was blunt “*It is clear that some of the results of modelling crocodile populations appear to be inconsistent with what we know, or suspect, to be true about the real populations. ... If the basic data necessary to solve [the Euler equation] is not available then there is no point in proceeding further*”. That basic data includes the survivorship schedule for the population.

The Craig model

16. Craig et al (1992) re-examined Nile crocodile population dynamics by focusing particularly on the Euler equation and its parameters. They examined the effects of harvest by modifying survivorship (l_x) or fecundity (m_x) schedules to simulate harvest of various sized animals or eggs and assumed any harvest that led to a finite rate of increase (λ) above 1 would be sustainable.
17. They incorporated no density-dependent influences on vital rates in the model, noting that:
 - 17.1. density-dependency in the Nichols et al (1976) alligator model didn't lead to any asymptotic behaviour in population estimates over their 20-year time-frames; and
 - 17.2. while the Blomberg model did result in asymptotic growth, the evidence that this resulted from density-dependencies was almost entirely lacking. They commented that death or dispersal of subadult crocodiles [presumably unrelated to density] may be a more plausible regulating mechanism for populations of large crocodiles.
18. Craig et al considered density dependency in models, in the absence of real evidence, as an artifice designed to make the population grow asymptotically rather than exponentially, thus appearing to behave more ‘realistically’. They argued for the use of simpler deterministic models whose results don't depend on ill-founded density-dependency functions. They also argued that density-dependent effects could be ignored safely because crocodile populations either (a) exist at low densities because of past hunting or (b) will tend to be managed at levels below ecological ‘saturation’ because people are intolerant of high densities and (c) because, given the focus on achieving a sustainable harvest, yields will tend to be higher at lower density.¹⁸
19. The authors used a Leslie matrix to simulate an age-classified population, noting that it is simpler to solve than the Euler equation, provides information on population structure and growth even when the age structure is not stable, and allows λ to be calculated readily.
20. The authors gave the following reasons for not using a range of alternative models, including:
 - 20.1. A size-class structured model, despite it perhaps relating more nicely to size-related differences in vital rates, because *inter alia* construction of a Lefkowitz matrix would be more difficult given the limited information on population parameters available.
 - 20.2. An individual-based stochastic model as used by Hutton (1984) for Nile crocodiles. Such a model tracks the fate of cohorts of individuals affected by random life history events drawn from specified distributions. The trajectory of the population arises from the sum of individual fates over time. They noted these models can be well approximated by a deterministic Leslie model and they assume independence among the

¹⁸ None of these three factors holds true for management of the NPEC estuarine crocodile population..

stochastic events, which is likely not biologically realistic. They are also arguably more complex than necessary and can hinder understanding.

- 20.3. Stochastic-deterministic models of the type used by Nichols et al (1976) and Blomberg et al (1982) which add stochastic elements to an otherwise deterministic Leslie matrix of vital rates. They argued such models arguably add unnecessary complexity that may be poorly based in empirical observations. Furthermore, the stochastic element may add little understanding beyond the deterministic estimates in long-lived animals that can ‘ride-out’ environmental stochasticity.
21. The authors noted that the Euler equation they used assumes that the population has an age structure aligned with its value of λ – but that assumption will not hold for a population where the harvest is directed against specific size/age-classes. In this case, the new stable age-structure may take years to emerge. They calculated some results by solving the Euler equation directly but used the Leslie matrix approach where the population deviated from its stable equilibrium.
22. One shortcoming of their approach, which the authors identified, was the modelling of females only in the population, which can affect predictions about harvesting effects when more males than females are taken at particular ages. The model therefore will tend to overestimate the impact of harvest on fecundity and underestimate the yield of skins. This approach was driven by the lack of any size-age curve for male crocodiles.
23. The size-age curve for Nile crocodiles was problematical to develop given the lack of any long-term mark-recapture information. It was achieved by modelling relationships between total length and femur diameter and estimating growth increments from just two growth rings, because rings are remodeled over time and the total number of rings cannot be estimated. This method has great uncertainties and resulted in estimates of age at maturity ranging from 12-20 years. Their data consisted of (a) known growth for one captive individual over ~50 years; (b) a good sample of individuals from a marginal wild environment whose ages were estimated by skeletochronology of osteoderms (Hutton 1984); and (c) another good sample of femur cross-sections from a more typical environment for Nile crocodiles.

The Wallace matrix model

24. Wallace et al (2011) developed a stage-structured matrix model to examine two successive spotlight surveys in 2006 and 2009 of the Nile crocodile population in a section of the Zambezi River. Demographic parameters to populate the projection matrix were derived from published estimates including survivorship from a 4-year mark-recapture study by Bourquin (2007) and growth data from earlier studies. The model was deterministic, incorporating no density dependencies or environmental stochasticity.
25. The authors used the projection matrix to examine the expected and observed size class distribution of crocodiles in the two survey years. The model predicted a higher proportion of subadults and a lower proportion of juveniles than was observed. The projected and observed size class distributions could be brought into conformity only by reducing estimates of subadult survivorship to levels judged biologically unrealistic. The large disparities between model projections and survey results were thought attributable to one or more of:
 - 25.1. an inadequate model;
 - 25.2. the population being a long way from its equilibrium state; or

- 25.3. bias introduced by eyes-only sightings that couldn't be assigned to a stage.
26. The authors also examined the sensitivity of the population growth rate (λ) to perturbations of the matrix elements. They found that harvesting of subadults and mature adults was likely to have the biggest effect on population growth while harvesting of eggs or hatchlings should have only small impacts.

The Wallace integral projection model

27. Wallace et al (2013) subsequently generated an integral projection model (IPM) for Nile crocodiles drawing on much the same body of field data as their earlier matrix model. They used the data to generate continuous functions describing survival, growth, and fertility as a function of size and an inheritance function relating the size of offspring to the size of adult females. Their model did not incorporate density dependencies or environmental stochasticity.
28. They found that this model generated different insights from earlier matrix models of Nile crocodiles. In particular, earlier models had suggested sensitivity to survivorship is (a) highest for animals at or above breeding size or that have reached maximum size and (b) lower for egg and hatchling stages (p. 161).¹⁹
29. The authors compared model estimates of key population parameters with known values to evaluate its performance but found few empirical estimates from field studies to compare with output variables.
- 29.1. The IPM predicted a finite rate of increase of 1.02, which was credible insofar as it was well below the maximum rate a crocodile population can increase, and in line with population growth rates observed in the wild (Smith & Webb 1985; Craig et al, 1992).
- 29.2. It projected a mean lifetime reproductive success of 2.32 offspring per female over its lifetime, a mean annual survival rate across all individuals of 0.25 and a mean recruitment rate of 0.77. No empirical estimates of these outputs were available from free-living populations.
- 29.3. They did find the projection broadly consistent with results obtained from traditional stage-structured crocodylian models (Smith and Webb, 1985; Craig et al, 1992).
30. Sensitivity in the IPM was estimated using brute-force simulation with:
- 30.1. one-at-a-time perturbations of +10% applied to each projection matrix element to examine their effects on survivorship and the fertility selection differential.
- 30.2. one-at-a-time perturbations of each model parameter by +10% to examine the effect on matrix elements and the combined effects on survivorship and fertility selection
31. The most important and management-relevant finding from this sensitivity testing was that bundling of size classes into stages for a stage-based matrix model, rather than treating size as a continuous variable, could lead to quite different conclusions about the

¹⁹ Similar findings are reflected in the NT stage-based model for estuarine crocodiles (Fukuda et al, 2020).

results of management interventions. For example, with respect to targeting of smaller size classes the authors concluded:

“When individuals are grouped into broad categories, we group sizes that are common with those that are rare, averaging the sensitivity across a range of sizes. Our analyses reveal that such averaging can lead to conclusions that are inconsistent with those found from continuous-size models.

Our results suggest caution in removing large numbers of smaller crocodiles from populations, as their selective targeting could depress population growth to a greater extent than previously assumed.”

32. They also found that perturbing different parameters can have contrasting effects on different pairs of population parameters. The details of these contrasting effects are not important here, but the potential existence of important interactions between projection matrix elements and their associated vital rates is important to note.

American crocodile models

The Florida Bay spatial model

33. Green et al (2010) constructed a spatially explicit stage-structured model for *C. acutus* in Florida Bay, at the north-eastern extremity of its natural range (Thorbjarnasson, 2010). Their model was much focused on the effects of salinity on survival and growth of small size classes and the population trajectories that flowed from them.
34. The model was a stage-structured matrix model based on 15 age/size classes, including five each for adult males and females – allowing for lower fecundity in small adult females. The likelihood of growth out of a stage was allowed to vary with estimated growth rate. The model was made spatially explicit by modelling daily numbers of animals in each stage at spatial locations defined with a 0.5 x 0.5km cell size. All individuals within a stage were assumed to share the same mortality, fecundity and growth rates.
35. The model incorporated density-dependence, assuming hatchling and juvenile survival rates were a sigmoid function of adult density, falling from 100% to 10% as the numbers of adult and subadult crocodiles in spatial cell rose from 0.5 – 2.5, the larger number reflecting their highest recorded density. The authors noted that *“Without a density-dependent relationship, the crocodile subpopulation on Cape Sable grows quite large in comparison to the subpopulation of crocodiles in northeastern Florida Bay”*. It appears that density dependency was incorporated to prevent indeterminate growth in the projected population, though data to support the existence of density dependency appeared limited to anecdotal observations.
36. Estimates of hatchling survival rates were based on limited and highly variable data from Moler (1991) and estimates from Mazotti et al (2009). Hatchlings were modelled with very high mortality in the first four months of life, with survival rates of only about 10%. Crocodiles that survived longer than four months were presumed to have a first-year survivorship of 36.5%. Moler (1991) estimated that survival rates increased to ~65% in the second year, over 80% in crocodiles over 5 years old, and approaching 100% as adults because large animals had few/no natural predators (Kushlan & Mazotti, 1989).

Sensitivity analysis

37. Sensitivity analysis was conducted using ‘brute-force’/numerical methods. Salinity was varied while also varying estimates of hatchling and juvenile survival rates. The final size of the crocodile population after multiple simulations of the stochastic model, was used as the principal output from the model for sensitivity testing.

The Briggs-Gonzalez model

38. Briggs-Gonzalez et al (2017) constructed an age-structured population model for *C. acutus* up to 25 years old at the northern limit of their range in the Turkey Point nuclear power plant, Florida. The model was based on one of the very few long-term longitudinal studies of a crocodile population, covering a 35-year period.

39. Age-specific survival rates were estimated from extensive mark-recapture data, which also provided information to develop a length-age model. Age-specific fecundity was modelled from the proportion of females in the population with total length greater than 2.25m (the size at maturity). The model included no density-dependencies and no environmental or demographic stochasticity. The finite rate of population increase (λ) was estimated as the dominant eigenvalue of the Leslie matrix and the stable age distribution as the right eigenvector.

40. This age-structured model is of some interest because the detailed analysis of longitudinal data showed that age accounted for 26% of the variation in survival rates and also 85% of the variation in body size. The authors concluded that size was a suitable substitute for age when modelling crocodilians for which age-length relationships couldn't be determined.

Sensitivity analysis

41. In keeping with the relatively simple deterministic model employed, the authors estimated sensitivities and elasticities using analytical methods (Caswell, 2018) rather than numerical/brute-force methods. The population's finite rate of increase (λ) was found, somewhat unexpectedly, to be highly sensitive to juvenile survival – a pattern that has also been seen in *C. johnstoni* and the green turtle, *Chelonia mydas* (Tucker, 2001; Chaloupka, 2002 cit Briggs Gonzalez et al, 2017). Lambda was much less sensitive to variation in fecundity and sex ratio.

42. Interestingly, the authors did not find the high sensitivity to adult survival rates that has emerged in several crocodilian population models (Tucker, 2001; Dunham et al, 2014; Fukuda et al, 2020), except in declining populations where elasticity was three times higher for adult survival rates than for juvenile survival.

Australian freshwater crocodile models

The Smith & Webb model

43. Smith & Webb (1985) developed an age-structured model for a population of *C. johnstoni* on the north tropical coast of the Northern Territory based on an intensive but relatively short-term population study in the early 1980s. While the study area was favourable for detailed sampling of the population and estimation of various vital rates, the population modelling was made more challenging by the unstable age structure brought about by intensive hunting into the 1960s.

44. The population was modelled using an age-structured matrix over a 30-year period by tracking 50 age-classes year-by-year and applying estimates of age-specific survivorship, the proportion of females breeding as a function of age and the sex ratio of hatchlings. The model did not incorporate environmental stochasticity or possible density dependencies.

Sensitivity analysis

45. Sensitivity of model outputs to the vital rate estimates was tested by first deriving best estimates of the likely error in estimating various rates (see Table 1 in Smith and Webb, 1985) and then running the model while allowing the rates to vary by +/-1 standard error. Depending on the quality and extent of data available, errors were estimated as means with a calculated standard error or, more commonly, as a 'most likely range' derived from best estimates of parameters for which standard errors could not be calculated. Good distributional data allowed calculation of formal standard errors for clutch size, sex ratio of hatchlings and survivorship from 1-10 years of age. Estimates of age at maturity, proportion of females breeding, and survivorship of other age classes were less well defined.
46. As the population modelling exercise was particularly focused on the potential of the population to sustain a harvest, the sensitivity analysis focused on the rate of increase and the resultant population size after a fixed period under a number of harvest models.
47. The modelling estimated mean λ values for the unharvested population of 1.5% p.a. for the first 10 years and 2% over the next two decades. The predicted population size in 1983 closely matched results of population surveys. The modelled population increased exponentially for 10 years then linearly for a further 20 years as the age structure stabilised. It then reverted to exponential growth.
48. Rate of increase in the unharvested population was slow compared to *A. mississippiensis*, which lays many more eggs and whose eggs and hatchlings have higher survivorship. The low rate of increase suggested future hunting [of adults and/or subadults] would only be viable if there was a complementary program for rearing hatchlings and returning them to the wild. Modelling of egg and hatchlings harvests did suggest that up to 30% of eggs or hatchlings could be removed annually and even removal of 90% of eggs or hatchlings for 10 years would only reduce the population by half. The authors noted that field trials of these harvest model estimates would be essential.

The Tucker models

49. Tucker (1997a, 2001) used data from a Queensland Government study of *C. johnstoni* conducted by Colin Limpus over 25 years to construct detailed age- and stage-structured matrix models. This population occupies somewhat climatically marginal habitat towards the inland limits of the Lynd River, Queensland.
50. The deterministic age-based model was built using a Leslie matrix derived from a detailed life-table constructed from extensive mark-recapture, population census and ancillary studies of various aspects of the life history (Tucker et al, 1994, 1996, 1997a,b, 1998, 2006; Tucker and Limpus, 1997; Tucker, 2001). A stage-based model was constructed using the same data, using five post-hatching stages - yearlings, two-year olds, 3-11 year old juveniles, 12-22 year old adults and 23-55 year old adults. No stochastic or density-dependent influences were included.
51. Tucker was particularly focused on retrospective analyses of life history traits, comparing the Lynd River population with the NT McKinlay River population and five other crocodylians

(*A. mississippiensis*, *C. porosus*, *C. acutus* and *Caiman crocodilus*) using a life table response experiment (Tucker, 1997a, 2001).

52. Many of Tucker's findings are not especially relevant for this report. His analysis did identify important differences between the Lynd and McKinlay River populations, the Lynd River showing considerably delayed maturity compensated by higher juvenile survivorship relative to the McKinlay population. The highest elasticity values in the NT population and the other crocodilians examined were found for the survivorship of the oldest adults in Stage 5. The Lynd R population, on the other hand, showed higher elasticities for Stage 3 juveniles and Stage 4 young adults than for Stage 5, which were attributed to the late onset of maturity and the associated long duration of Stage 4.
53. The high elasticity of λ to survivorship for adult animals was also noted by Fukuda et al (2020) in their model for *C. porosus* but needs to be interpreted with caution as high elasticities are commonly associated with vital rates that have high values (Morris and Doak, 2002). In most crocodilians, survivorship in adults is known or assumed to be close to 100% and considerably greater than in smaller size classes.
54. Importantly, Tucker highlighted substantial differences between the life history traits of *C. johnstoni* from the Lynd and McKinlay Rivers and commented "*Prudent management plans should therefore consider demographic variability, as regional differences are likely to exist in stock structure. A precautionary approach is especially warranted in commercial harvests of crocodilians, particularly when high harvest levels are planned or if a local stock has low demographic resilience*". That is particularly relevant to Queensland given the very great physiographic and climatic differences across the State (Taplin, 1987) and genetic evidence that the estuarine crocodile population consists of several substantially isolated subpopulations, of which the NPEC population is one (Lloyd-Jones et al, submitted).

Sensitivity analysis

55. Tucker's used partial derivatives to estimate sensitivity and elasticity values for the stage-based matrices of the various species and populations. For intraspecific comparisons of *C. johnstoni* he used a one-at-a-time (OAT) approach, holding two of the population parameters constant while varying a third parameter by +/-10% from their initial values, which were set at the mean values for the Lynd and McKinlay River populations. Sensitivity of λ to different age-at-maturity in the Queensland and NT populations was tested while holding mean survival and fecundity constant. Similarly, sensitivity of λ to mean survivorship was tested while holding mean age-at-maturity and fecundity constant and of λ to fecundity by holding mean age-at-maturity and survival constant. Interspecific comparisons were based on the unperturbed matrix for *C. johnstoni* in NT and Queensland and best estimates of vital rates for the other species.

Estuarine crocodile models

The Webb model

56. Webb et al (1984) developed the first population model for *C. porosus* in the then well-studied Blyth-Cadell River system, for which spotlight survey data were available from 1974-84. The model was constructed in the same way as models of *A. mississippiensis* by Nichols et al (1976) and *C. johnstoni* by Smith & Webb (1985), applying key vital rates to an age-structured population matrix. It is not altogether clear, but it appears that animals over 5.3 years old were

either aggregated into a single stage or treated as a group with homogeneous vital rates and distributed across age classes between 5.3 and 70 years, the latter number being a rough estimate of longevity.

57. The model relied on a modest array of studies at that time from which estimates of survivorship, fecundity, age at maturity, and the proportion of females nesting in any one year could be estimated. No mark-recapture studies of survivorship were available at that time (and are still not today) so survivorship estimates for the younger age classes and the >5.3 year-old stage were calculated from 'retention rates'. Retention rates measured the proportion of animals remaining in the population in age class (i+1) from the preceding year's age class (i) and were recognized at the time to be problematical but unavoidable (see Appendix 3). Importantly, the retention rates were calculated from spotlight counts corrected for sightability using mark-recapture estimates from Bayliss et al (1986, 1987).
58. The modelling effort, including the detailed dissection of size-age relationships and trends in age classes over time, was used principally to gain insights into the pattern of population recovery in the first decade or so after protection that couldn't be gleaned from survey data alone. Importantly, it identified strong patterns of decline in 2-3 and 3-4 year old crocodiles aligned with increases in larger size classes that together suggested the operation of some density dependent population regulation.
59. The authors did note the paucity of data on survivorship to inform their model. It is telling that the 2020 Fukuda model has had to rely in part on much the same limited dataset.

Bradshaw's modelling of density dependence

60. Bradshaw et al (2006) analysed rates of increase of NT estuarine crocodile populations for evidence of density dependence, using helicopter and spotlight survey data from 19 river systems between 1972 and 2003. The number and type of surveys varied between rivers. Simple arithmetic rates of increase year-on-year were calculated from annual changes in density. Density was 'relative density' from helicopter or spotlight counts not corrected for sightability differences across size classes. Hatchlings and 'eyes-only' crocodiles were included in counts and density estimates.
61. They constructed five models of potential population dynamics based on variants of the generalised theta-logistic model:

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

where N_t = population size at time t , r = realized population growth rate, r_m = maximum intrinsic population growth rate, K = carrying capacity and θ is a parameter allowing non-linearity between rate of increase and abundance. ε_t represents environment-driven variation in r with mean zero and variance σ^2 .

62. They tested the survey data from each system against growth models incorporating (a) density independence with non-directional population fluctuations; (b) density independence with geometric growth; and (c) density dependence using a stochastic Ricker logistic function, a stochastic Gompertz model and a full generalised theta-logistic model. Model fits of r against density were made using linear or non-linear regression and model support compared using information theoretic approaches.

63. Fifteen of 19 river systems had sufficient data to assess support for the existence of density dependence and 8 of the 15 river systems showed over 50% support for a density-dependent model as the best approximation. Evidence for density dependence tended to increase as the number of data points for a river system increased. This finding appears robust notwithstanding later analysis showing that the theta logistic model could not be used to reliably estimate the shape of a growth curve from abundance data over time (Clark et al, 2010).
64. This study provided good support for some form of density dependence operating in NT estuarine crocodile populations but provided no insight into the life stages affected or the mechanisms giving rise to it.

The NT model

65. Fukuda et al (2020) have produced the most recent and detailed model of estuarine crocodile population dynamics. It is described in the main text.

Appendix 3: Issues with retention rates as estimates of annual survivorship

1. Retention rates (refer para 57 in the main report) have been used as a substitute for survival rates in estuarine crocodile population models. They are a necessary but imperfect substitute, having several shortcomings (Webb et al, 1984).
2. In addition to being influenced by net migration, retention rates can be affected by the extent to which a population has been perturbed away from its long-term equilibrium age structure and by the method used to calculate them. It is useful to examine this in a little depth and use Tucker's detailed longitudinal study of Australian freshwater crocodiles (Tucker, 1997) which gives a very detailed life table spanning 55 years. Tucker's life table provides a useful check on how retention rates perform in recovering underlying survival rates in a natural population that was growing slowly ($\lambda \sim 1.037$) and for which age- and stage-structured models are congruent (Tucker 1997).
3. Applying a deterministic age-structured model using Tucker's annual survivorship and fecundity rates and setting the initial population to the stable age distribution of the projection matrix, retention rates are stable over time and equal to the annual survival rates taken from Tucker's life table. This is as expected. If the modelled population is initiated a long way removed from its stable age distribution, then it can take many years to come to equilibrium (Figure 1) but the retention rates calculated from these data remain stable and equal to the annual survival rates throughout.
4. When age-class numbers are pooled into the stages defined by Tucker (1997)²⁰, the trajectories of the stage distributions show considerable fluctuations where multiple ages are pooled into a stage (Figure 2a) and the calculated stage-based retention rates also fluctuate strongly for many years (Figure 2b).
5. When we project the stage-structured version of the model, starting with an initial population far removed from the stable stage structure (Figure 3), much of the oscillation evident in the age-structured model is smoothed out because survival rates and fecundities are averaged across the duration of each stage (Figure 3a), but the retention rates for yearlings, juveniles and small adults still take a decade or so to stabilise (Figure 3b).

²⁰ Stage 1: hatchling (0-1yr); Stage 2: yearling (1-2yr); Stage 3: juvenile (3-11yrs); Stage 4: small adult (12-22yrs); Stage 5: adult (23-55yrs).

Figure 1. Convergence of a deterministic age-structured matrix model of *C. johnstoni* on its stable age class proportions when the initial population is a long-way removed from the stable age structure. ‘Ripples’ from the initial perturbation take many years to flow through the age structure because of the longevity and slow maturation of this species.

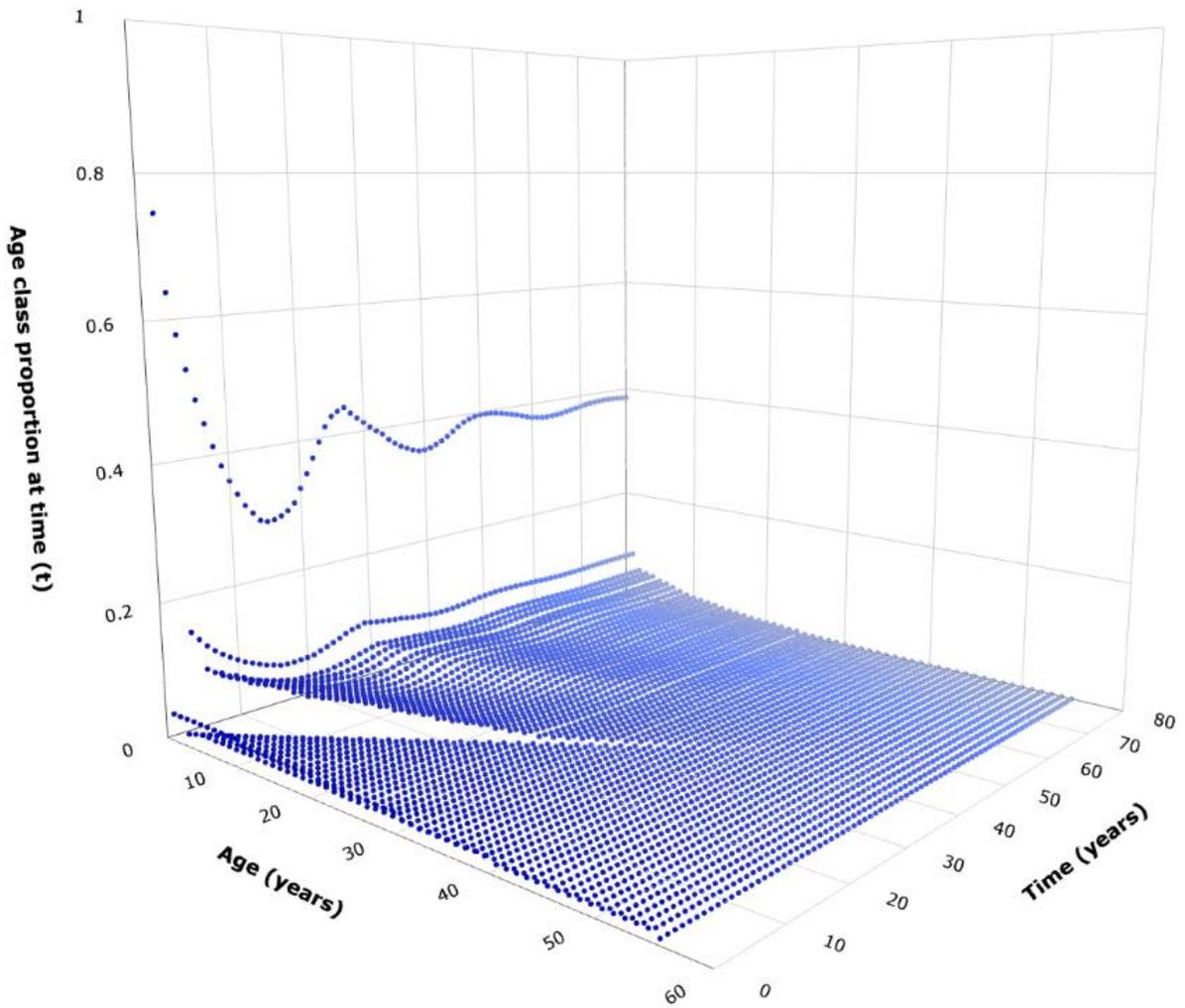
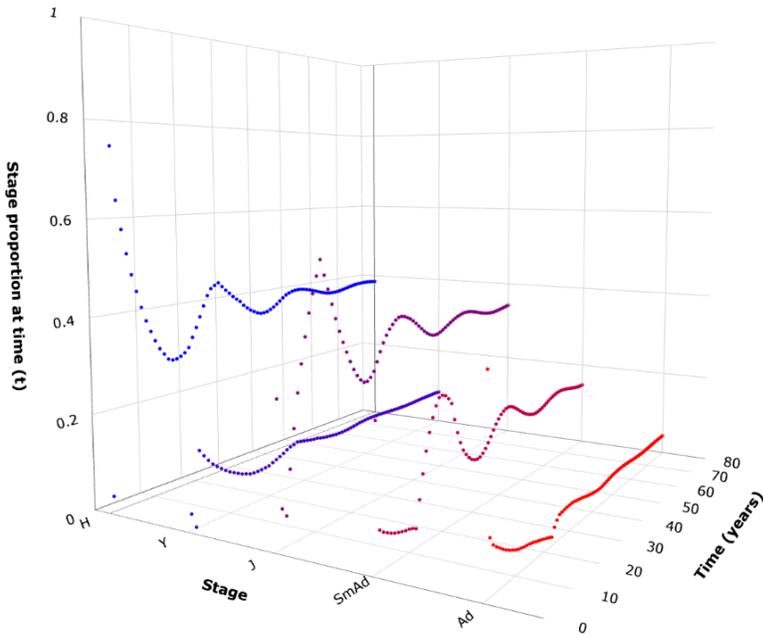


Figure 2: Consequences of superimposing five stages as defined by Tucker (2001) on the age-structured projections in Figure 1, showing (a) the trajectories of the proportion of animals in each stage and (b) the retention rates calculated for each stage as the population approaches the equilibrium consistent with the projection matrix. Retention rates oscillate over long periods despite constant underlying survival rates.

(a)



(b)

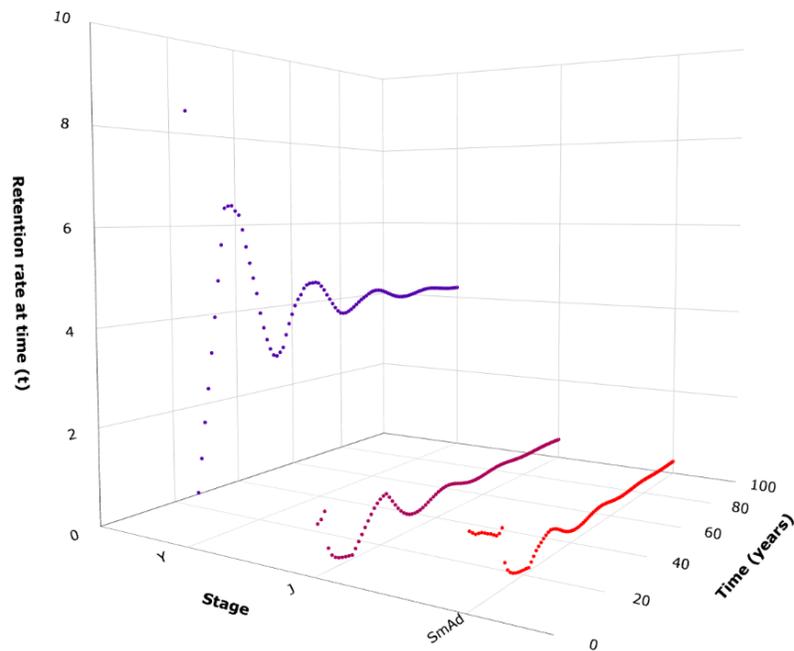
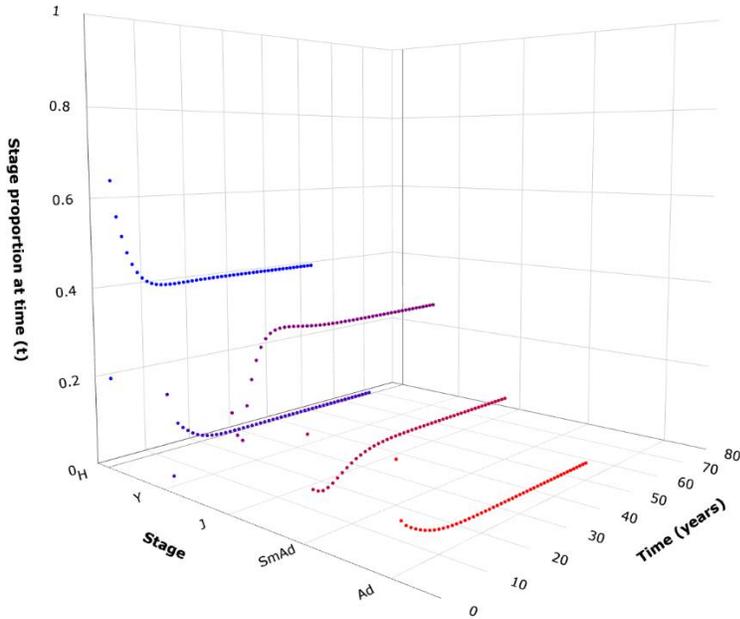
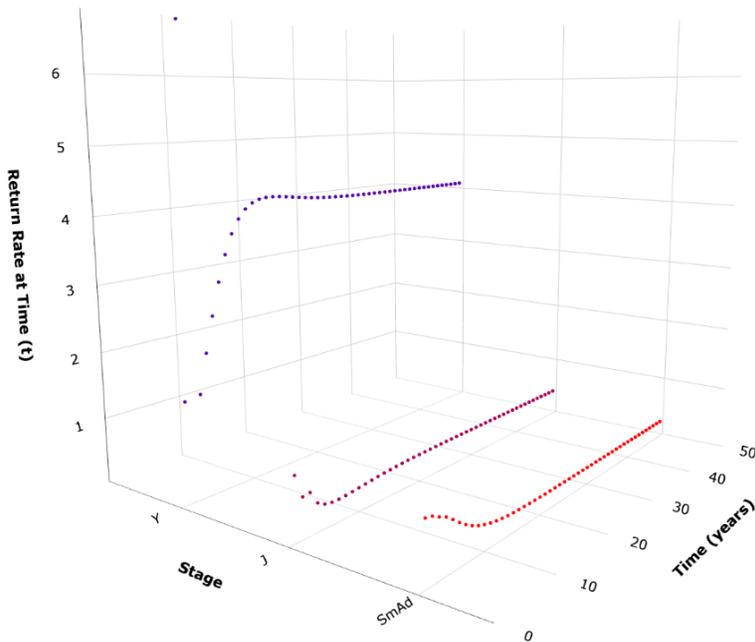


Figure 3: Trajectories of (a) the proportion of animals in each of five stages and (b) estimated retention rates in a stage-structured version of the Tucker model for *C. johnstoni* on the Lynd River, Queensland. The stage classes converge more rapidly on the stable stage distribution than do the underlying age classes (Figure 2) but estimates of retention rates for yearlings, juveniles and small adults take a decade or more to converge on their equilibrium values.

(a)



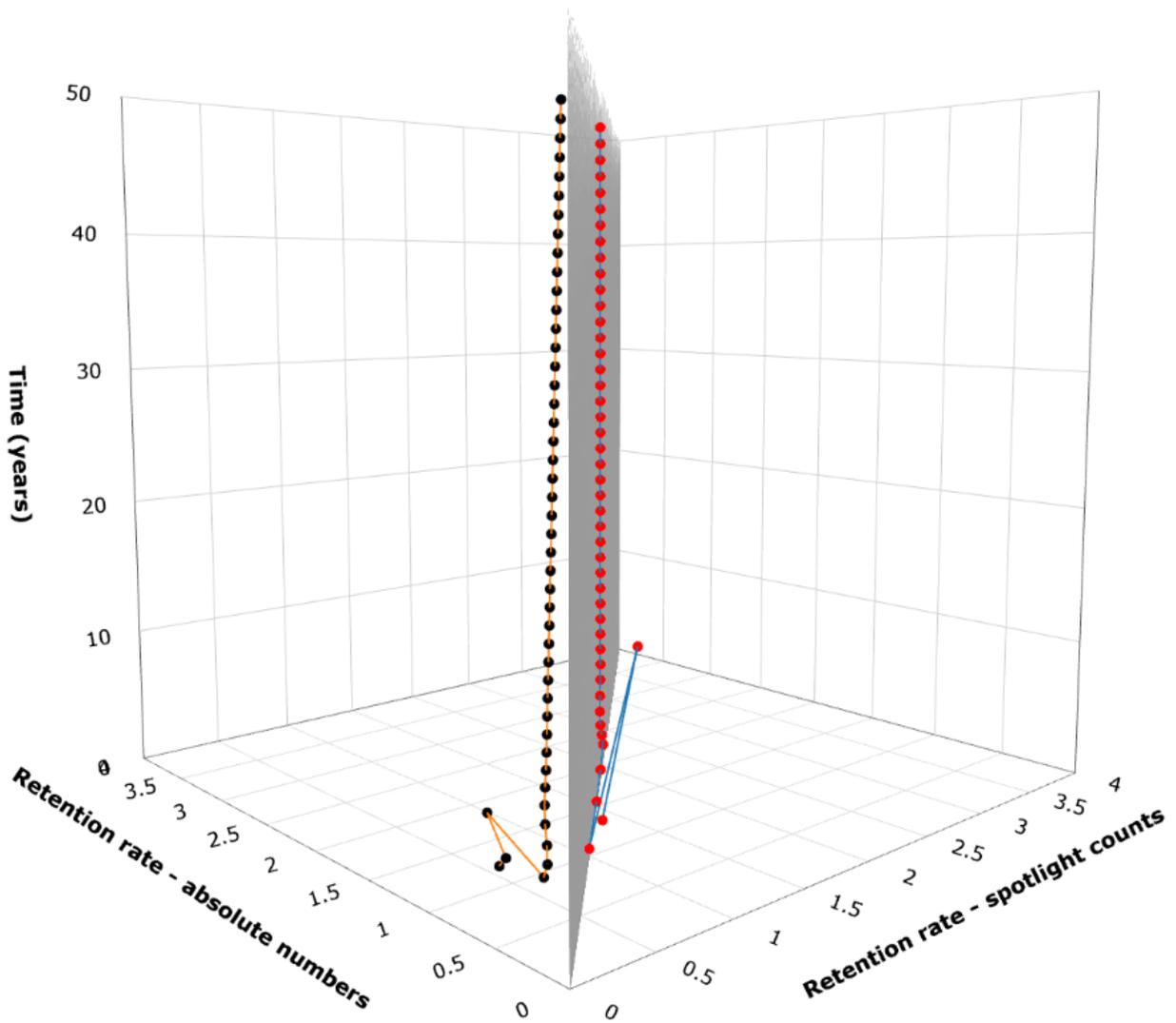
(b)



6. While it is not altogether clear from the description in Fukuda et al (2020) how retention rates were calculated in detail, their method appears to introduce some further uncertainty.
7. Use of relative rather than absolute densities means that some retention rates will be affected by differences in sightability between size classes. Sightability in adult crocodiles varies greatly with size. Bayliss et al (1986) estimated sighting probability for a single survey at 0.585 for 7-8ft, 0.469 for 8-9ft, 0.325 for 9-10ft and 0.153 for animals over 3m – but noted that captures/recaptures of animals over 3m were so few that values for larger animals couldn't be estimated.
 - 7.1. Calculating stage-based retention rates based on relative counts leads to estimates of retention rates that are higher or lower than those based on absolute densities by a factor reflecting the ratio of the sightability of Stage i to that of Stage $(i-1)$ (Figure 4). Thus, if the sightability of hatchlings is 0.693 and that of juveniles 0.737 (the simple arithmetic average of sightabilities of the size classes in the juvenile stage) then the calculated retention rates for hatchlings are 'inflated' by $0.737/0.693 = 1.063$. That is small in relation to other uncertainties inherent in the modelling.
 - 7.2. However, the retention rates for juveniles may be underestimated by as much as 57% if we estimate the sightability of crocodiles over 10-11ft to be 0.05 (one-third the level in the largest size class estimated by Bayliss et al (1986)) and thus estimate the arithmetic mean sightability for adult crocodiles to be 0.316. This under- or over-estimation of retention rates holds regardless of whether the modelled population is initiated at its stable age distribution or far removed from it. It also appears to hold regardless of whether the model is deterministic or incorporates density dependencies of the type included in the NT model. If this interpretation of the way retention rates have been calculated in the NT model is correct, then these approximations to stage-specific survival rates could be biased considerably.
 - 7.3. Figure 4 shows how estimates of retention rates based on absolute numbers and on spotlight counts are unstable before the population approaches its stable stage distribution and are not necessarily equal even when the stable stage distribution is reached.
8. A second and perhaps relatively minor issue is that the sightability of crocodiles in the different size classes may well not have remained constant over 30-40 years as new generations of adult crocodiles have matured without hunting pressure. There have been no mark-recapture or other experiments to test sightability since 1986 but it would be unsurprising to find large and very large crocodiles rather less wary in spotlight surveys than they were in the 1970s and 80s. If the sightability of adult crocodiles has increased relative to juveniles, the change in ratio would be reflected directly in changing estimates of retention rates over long periods.
9. Retention rates can therefore be quite problematical as estimates of annual survival rates for stage-based models when not based on absolute counts of numbers, when applied to populations that are in the early stages of recovery from severe perturbations, and when changes in sightability over time cannot be assessed. That casts some uncertainty over the regressions of log survivorship against abundance and the estimates of beta for the Ricker density dependency functions derived from them.

10. Notwithstanding these necessary cautions in using and interpreting retention rates, we have no information from Queensland to better inform the modelling exercise so we should accept the NT estimates of density dependency coefficients and intra-/inter-stage relationships as the best available.

Figure 4: Progressive estimates of retention rates in a version of the NT population model that excludes density-dependencies - calculated for a period of 45 years using spotlight counts directly and absolute numbers (spotlight counts adjusted for sightability). The initial stage distribution was far removed from the stable stage distribution for both the initial (1971) projection matrix and the final (2017) projection matrix. The vertical grey plane is the plane of equality for the two retention rates over time. The annually-calculated retention rates for hatchlings (red) and juveniles (black) each converge over time to a constant relationship (a vertical line of points) but do not necessarily converge on the plane of equality. At every time interval, the retention rates based on spotlight counts are related to those based on absolute numbers by the ratio of juvenile:hatchling and adult:juvenile detection probabilities respectively.



Addendum: Model revisions and refreshed findings following review

1. Independent review of the draft report constructed around the NT's four-stage model included several suggestions for improving or clarifying the analysis. The principal ones were:
 - 1.1. to model the egg and hatchling stages as a single stage with a duration of one year, consistent with the iteration interval for the model
 - 1.2. to incorporate density dependency in the proportion of females nesting each year (previously fixed at 75%);
 - 1.3. to handle estimation of the 1974 stage structure in the model differently; and
 - 1.4. to employ variance partitioning in the form of Sobol indices to explore the main effects of vital rates and density dependencies and their interactions and to inform judgements about which parameters might be set to fixed values;
 - 1.5. to incorporate sex in the model because removals are targeted largely at mature adult males and the impact of removing breeding males is likely to be very different from removing females;
 - 1.6. to model the duration of the juvenile stage as a boxcar train rather than a fixed stage duration.
 - 1.6.1. The boxcar train model would avoid the assumption of a stable age distribution within the juvenile stage and instead values for stage duration drawn from a negative binomial distribution (Caswell, 2018). The method is well-illustrated for a continuous time model of loggerhead turtle population dynamics by Chaloupka (2003) but relies on estimates of the distribution of age at first breeding which appear unavailable for *C. porosus*.
2. The first three suggestions have been adopted in a revised model. Incorporating sex in the model was rejected at this stage, despite being highly desirable, as there appears to be entirely too little information on the factors needed to inform a sex-based model, including such things as the existence and extent of multiple paternity, the role of senescence in old/large adult males and its impact on mating success, and the actual sex ratio in the adult stage of any Qld *C. porosus* populations. Variance partitioning has been explored but is not pursued here (see below). And boxcar train modelling has not been incorporated in the 3-stage model revision, but efforts to incorporate it will be employed in future revisions.
3. The results of the revised 3-stage model are presented in brief here.

Revising the immediate post-protection stage structure

4. Some review comments expressed difficulty with the initial (1974) population structure used in the 4-stage model, where the initial number of adults was allowed to vary between 20 and 200 while the numbers of eggs, hatchlings and juveniles were set arbitrarily at 1 for each stage. This initial stage structure is, for the most part, of no consequence because regardless of whether the counts are set unrealistically high or unrealistically low the stage structure will converge over time on the stable stage distribution inherent in the projection matrix.
 - 4.1. Convergence in the Qld model took something over a decade for the 4-stage model and manifested as an early decline in numbers as the adult size class declined through

mortality, while it took some years for recruitment to flow through the juvenile stage and generate new adults and increased egg/hatchling production (see Figure 15 in main report).

- 4.2. This initial decline was considered ‘unrealistic’ by some reviewers as the early post-protection years in the NT were marked by a rapid influx of hatchlings and juveniles from the remnant crop of breeding adults (Webb et al, 1984; Fukuda et al, 2020). A similar early flush of recruitment is likely to have occurred in Qld.
5. It was also argued that the 100-year time frame used for modelling was inappropriately long because it was unreasonable to expect the model to be capable of giving reliable “predictions” of the population trajectory beyond a horizon of perhaps 10-15 years.
6. Both of these concerns have at their root a misunderstanding of the critical difference between predictions/forecasts and projections, as discussed at some length in Caswell (2018, p. 616ff).
 - 6.1. The modelling exercise and sensitivity analysis undertaken here contains no predictions of what the NPEC crocodile population will or will not do in the future under the influence of variable environmental conditions.
 - 6.2. Each population trajectory displayed and analysed is a mathematical projection of what the population would do if a combination of vital rates and density dependencies was established in 1974 and held constant over time. That is an exercise in mathematics, the results of which will stabilise over time as the population reaches equilibrium and will be maintained whether run for 100 or 1000 years.
 - 6.3. And, as noted, the stage structure used to initiate any population projection has only a transient effect on the population trajectory.
 - 6.4. What we are trying to discover, through this exercise, is the extent to which the various vital rates and density dependencies affect the population trajectory and which of those population parameters, if varied, would likely have the greatest impact on the trajectory.
 - 6.5. It is not germane to the exercise that vital rates, density dependencies and interactions between them are extremely unlikely to remain constant in nature. It is germane to recognise that projections are not predictions.
7. That said, there is one element of the modelling that is likely affected by the initial stage distribution.
 - 7.1. The NPEC model/s are challenged by a dearth of information and therefore rely on identifying biologically realistic ranges for the vital rates and density dependency coefficients. The exercise defined biologically realistic ranges for each parameter based on knowledge from NT studies of *C. porosus* and, to a lesser extent, other crocodylians. But it is highly likely that some randomly selected combinations of population parameters that are individually realistic will combine to result in biologically unrealistic projection matrices.
 - 7.2. This phenomenon is manifested in the NPEC exercise by the very large number of parameter combinations that resulted in population trajectories tracking more or less rapidly to extinction and others which led to population numbers in the hundreds of thousands.

- 7.3. To filter out the array of ‘plausible’ parameter combinations, the known/estimated trajectory of the population from survey results was used to identify combinations that generated projections falling within the confidence limits of those estimates over time.
 - 7.4. The earliest period for which a population estimate and confidence limits are available is the late 1980s (termed the “1987 Era”), some 13 years after protection. The 13-year interval approximates the time it takes for the population projections to converge on their stable stage distribution and long-term trajectory. Because setting the initial stage structure to an arbitrary 1,1,1,100 (Eggs, Hatchlings, Juveniles and Adults) generates lags in convergence, the projected non-hatchling numbers for 1987 will tend to be biased to the low side.
 - 7.5. That issue can be avoided by setting the 1974 stage distribution to the stable stage distribution for the projection matrix – in which case convergence is immediate – but that poses two other issues. Firstly, there are some 10^6 matrices to be evaluated, each with its own stable stage distribution. Secondly, the 1974 population would have been perturbed from its stable stage distribution but there is inadequate information from which to derive a good estimate.
8. Therefore, in the revised 3-stage model the 1974 population structure was set as follows:
 - 8.1. Stage 3 (Adults): 100.
 - 8.2. Stage 1 (Eggs): 1328. Amounting to the production of 50 females (population sex ratio 0.5) at 26.55 female eggs per breeding female per year and assuming 100% of females nesting at the low density prevailing.
 - 8.3. Stage 1 (Hatchlings): Eggs * survivorship of eggs between laying and hatching.
 - 8.4. Stage 1 (Total): Eggs + Hatchlings
 - 8.5. Juveniles – Stage 1 * survivorship of eggs over 3 months * survivorship of hatchlings over 9 months.
 9. This structure assumes that in the year immediately before protection (1973) there was the same production of eggs, hatchlings and juveniles as in 1974. It has the advantage of lying closer to the stable stage distributions of the subset of projection matrices that generate plausible trajectories, hence should converge more quickly than the arbitrary (1,1,1,100) distribution. And it avoids the initial decline in numbers associated with that arbitrary population that troubled some reviewers.
 10. Importantly, despite Stage 1 now consisting of eggs and hatchlings, the numbers of hatchlings in Stage 1 had to be estimated continuously to estimate the important density dependent effect of hatchling numbers on hatchling survivorship.

Variance partitioning and Sobol indices

11. Variance partitioning analysis employed the R package sensobol (Puy et al, 2021; Puy et al. 2022). Three issues emerged in the course of the analysis.
12. Firstly, the package does not handle missing values in the output variable easily. In this case the output variable used for most of the analysis is the equilibrium numbers of non-hatchlings. This value is undefined for some combinations of parameters because equilibrium was not reached in 100 iterations – e.g. when very low values for density dependencies led to

continuing exponential growth (see Figure 12 in main report). This issue was handled by using the number of non-hatchlings at the 100th iteration as the output variable, after confirming that there is a precise and tight linear relationship between the two quantities.

13. Secondly, there is a high computational cost to generate the matrices needed to estimate first- and second-order interaction effects between the population parameters. This greatly reduces the viable sample size that can be employed across the parameter space.
 - 13.1. For example, an analysis of main effects and first order interactions for 5 vital rates (m4, S1, S2, S3, S4) and 3 density dependencies (beta2, beta4, beta5) required some 311,000 simulations, allowing for comparison of 8192 combinations of vital rates sampled randomly across the parameter space – compared to 10⁶ combinations for the main effects analysis used in the 4-stage NPEC model.
 - 13.2. Testing of second-order interaction effects multiplied the required simulations even further and reduced the number of combinations that could practically be tested and the capacity to detect significant effects.
14. The third and most salient issue is that sampling for the variance partitioning encompasses large numbers of parameter combinations that lead to population trajectories inconsistent with the known population trajectory. In analysing the 4-stage model these were filtered out, reducing the subset of combinations from 10⁶ to 11,706 ‘plausible’ models. But there are no well-defined constraints on the combinations of parameters that lead to ‘plausible’ projections (Figures 13 & 14 in the main report). So variance partitioning using the sensobol package samples parameter combinations and model outputs that dominate the sample numerically but are not of interest. And it is not possible to define simply a parameter space limited to combinations that are relevant.
15. It was concluded that calculation of Sobol indices would not add materially to the revised 3-stage model. Those Sobol indices that were calculated did lend weight to earlier decisions that the values of female fecundity and duration of the juvenile stage could reasonably be fixed at 26.55 female eggs per female per year and 8 years respectively. It also confirmed that the Beverton-Holt coefficient for the proportion of females nesting annually could reasonably be fixed at 0.45 (the value used in the NT model). Model outputs were not sensitive to any of these three parameters.
16. Further exploration of variance partitioning may prove worthwhile in the long-run, but is not pursued further for this report.

Effect of model revisions on the key results

17. The outputs of the revised 3-stage model did not differ markedly from the 4-stage model described in detail in the body of this report. The most important results are those showing the projected effects of future levels of removals of juveniles and hatchling.
18. Figure 1 is the 3-stage equivalent of Figure 25 in the main report after subsampling 11,706 random parameter combinations from the full data set of 28,876 (so as to make visual comparison of Figure 1 and Figure 25 easier). Figure 2 is the 3-stage equivalent of Figure 26 in the main report, again subsampled to 11,706 parameter combinations, and shows the same pattern of responses.

19. In light of these results, it is reasonable to conclude that adoption of the 3-stage structure and incorporation of density dependency in the proportion of females nesting have no material effect on the sensitivity analysis and that the conclusions derived from the 4-stage model in the main report are robust.

“Localised extinction” – a meaningful term for the NPEC?

20. Some reservations were expressed about use of the term ‘localised extinction’ in the report, arguing that it is not realistic or meaningful given Queensland’s crocodile management regime to discuss a potential consequence of removals that is unlikely to materialize in practice. The principal argument appears to be that, with ongoing monitoring of the population status, any emergence of serious population decline would be met with a management response to counter it.

21. If that is a correct representation of the issue, it confounds two very different matters. Both the 4-stage and the revised 3-stage model show that, as removals of adults (and to a lesser extent juveniles) increase, the proportion of projections that track to zero non-hatchlings in the population increases. This is not a prediction of localised extinction. It is an indication that, among the many population models/projection matrices that lead to plausible population projections, a higher proportion of projections results in localised extinction as the numbers of adults removed annually is increased.

21.1. It says nothing about whether any one of those projection matrices is a reliable representation of actual population processes. It simply says that the combination of population parameters, if held constant over time, would result in a plausible projection of population change up to 2022 and would result in the modelled outcome if the particular removal regime was adopted after 2022 and held constant over time.

21.2. Those modelled outcomes include localised extinctions and those results are important to inform judgements about the potential real-world impacts of management interventions.

22. To propose that management interventions could or would circumvent any prospect of localised extinction is to introduce an entirely extraneous factor. This is perhaps well illustrated by analogy to a generalised sensitivity analysis of the complex inputs to and outputs from a software program controlling the flight dynamics an aeroplane. One aim of the analysis is to identify combinations of plausible input values from sensors that could result in the aircraft flying into the ground – such things do happen. It is irrelevant to the sensitivity analysis that the aircraft’s pilots would intervene to try and prevent that happening. Their intervention is extraneous to the operation of the software model and tells us nothing about its internal workings. In the same way, management interventions to prevent localised extinction are extraneous to the operation of the population dynamics model.

23. Localised extinction, as an outcome of the model, is meaningful and relevant to the sensitivity analysis. There is no question it is an unlikely outcome of the current removal regime, which has seen the NPEC population grow slowly but consistently since its inception in 1987 and is reflected in the central blue graphs in Figure 1 and 2. But projections showing an increasing likelihood if removals of adults are increased and sustained are entirely relevant to management decisions.

Figure 1: Effects in the 3-stage model of implementing various levels of post-2022 adult (A) and juvenile (J) removals on the 28,876 models for which the 1974-2022 trajectory falls within the 95% CLs for the estimated NPEC population. A subsample of 11,706 projections has been used for easier comparison with Figure 25 in the main report. The blue histogram shows the results for a harvest that effectively continues the average removal rate of adults and juveniles from 2013-2022. The x-axis shows the proportion by which the unmanaged population would be reduced by the removals specified in the title. The vertical black line highlights the no-effect (0% change) line. As was the case for the 4-stage model, removal of adults has much bigger effects than removing juveniles and the proportion of trajectories that track to zero (i.e. localised extinction) within 100 years increases markedly with increased removals of adults

Figure 1(a)

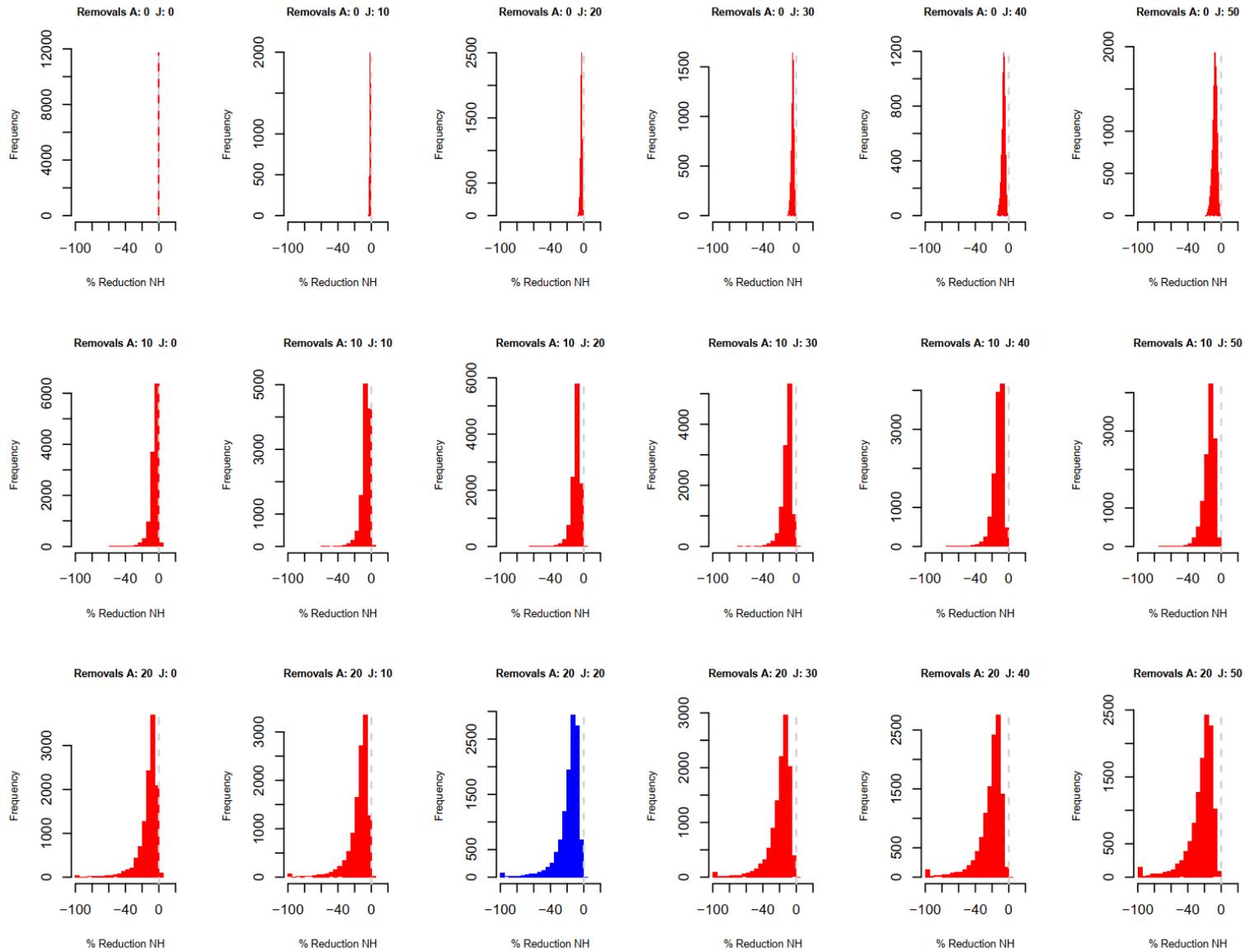


Figure 1(b)

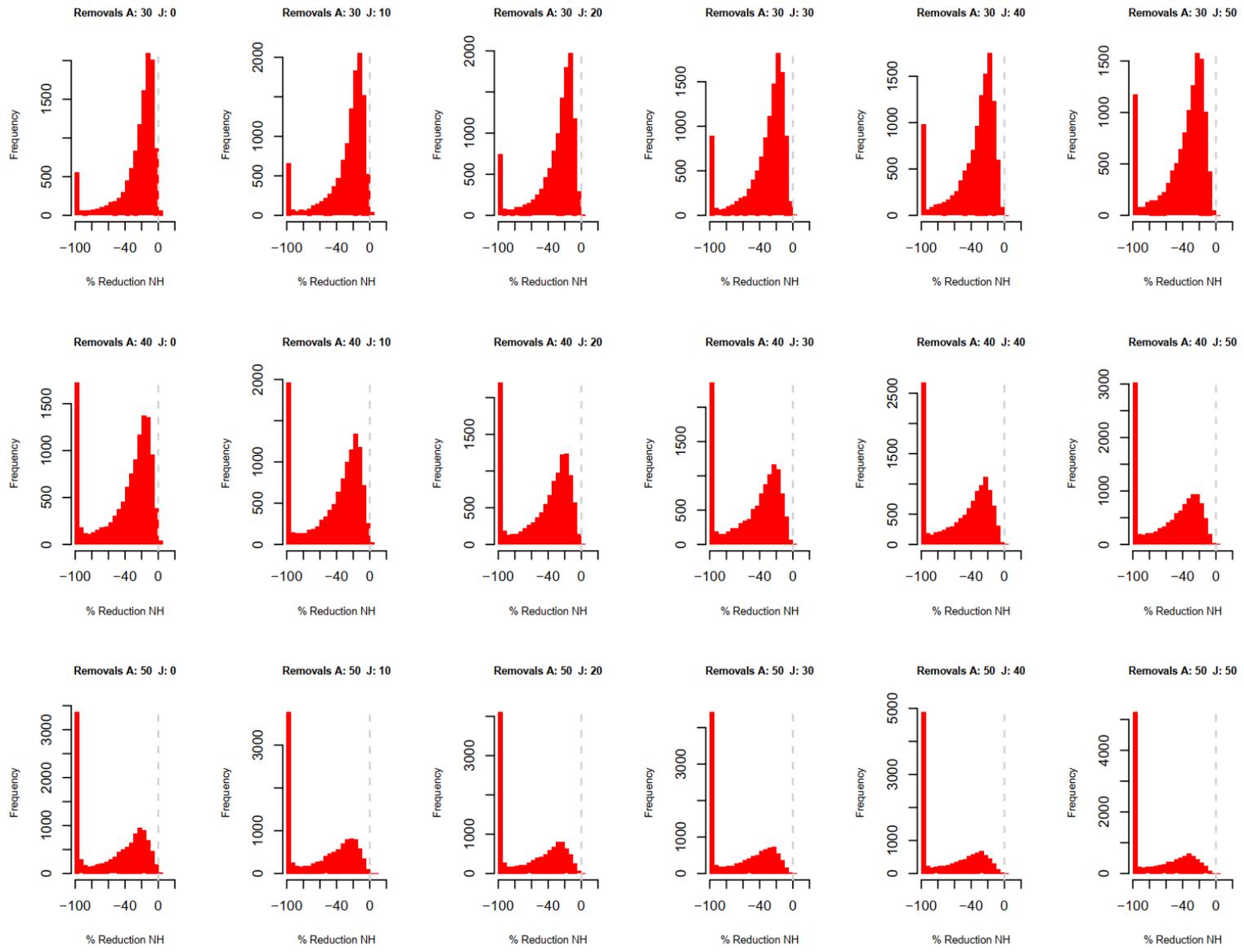


Figure 2: Effect of selected removal levels on the final (year 100) non-hatchling numbers and stage proportions in populations unmanaged after 2022 or subjected to different levels of adult and juvenile removals. The blue graph models continuation of the 2013-2022 removal program into the future, for 28,876 combinations of population parameters. The vertical gray line marks the lower limit of estimated non-hatchling numbers for the NPEC population. The upper-left graph shows results for a 'reference' population left unmanaged after 2022.

