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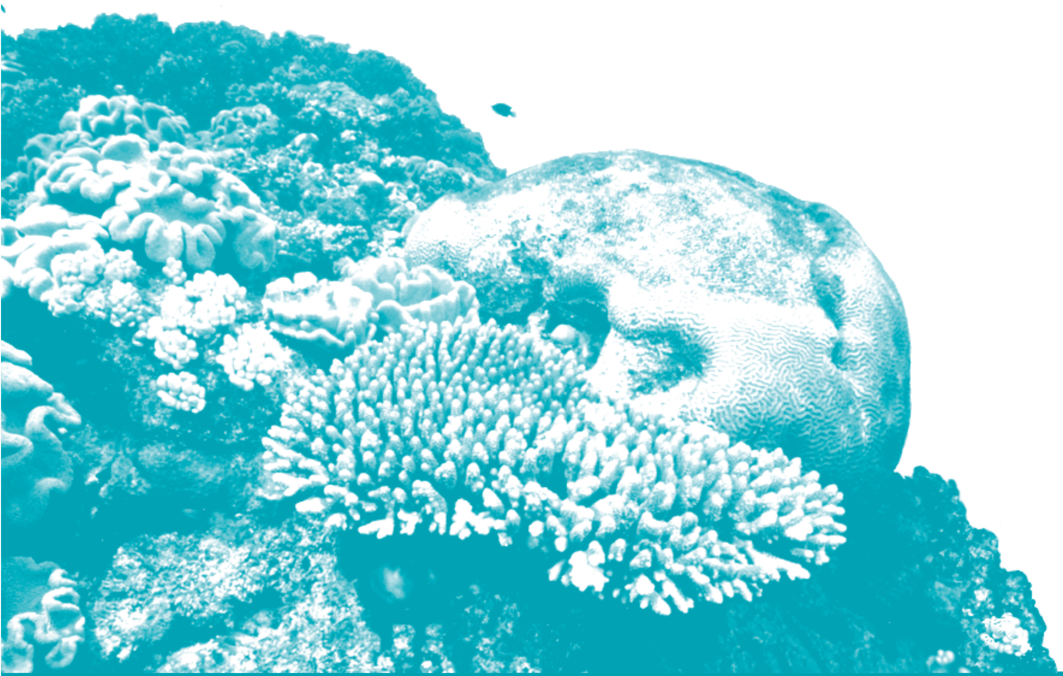
RESEARCH PUBLICATION NO. 81

Phase 2 - Development of a Population Model for the Southern Great Barrier Reef Green Turtle Stock

Dr Milani Chaloupka



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Dr Milani Chaloupka
UniQuest & CRC (Coastal Zone, Estuary & Waterway Management)

Report prepared for Queensland EPA, GBRMPA and EA

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Queensland
Government
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FOREWORD

The Great Barrier Reef Marine Park Authority (GBRMPA) and the Queensland Environmental Protection Agency (QEPA) are pleased to publish this second report on the development and validation of a population model for the southern Great Barrier Reef green turtle stock.

The QEPA data used for this model is the most comprehensive, long-term demographic study of green turtles in the world. As such it is a unique and valuable source of data to assist management for turtle conservation objectives. It is a tribute not only to QEPA staff, especially Dr Col Limpus, but also to the many hundreds of assistants and volunteers who have contributed to the research program over the past 30 years.

By using the data to develop this population model, wildlife management agencies have been provided with new insights into the population status of the southern Great Barrier Reef green turtle breeding stock, which nests primarily on the Capricorn/Bunker Group of islands and along the southern Queensland coast. The model will be a useful tool for developing and assessing appropriate conservation policies and strategies to address undesirable impacts on the long-term viability of the southern Great Barrier Reef green turtle stock.

The Great Barrier Reef Marine Park Authority and the Queensland Environmental Protection Agency are pleased to make this report generally available. Use of the population model to investigate risks and scenarios for management of the southern Great Barrier Reef green turtle stock will be restricted to projects and purposes approved by the GBRMPA and QEPA.

Hon Virginia Chadwick
Chair
Great Barrier Reef Marine Park Authority

James Purtill
Director General
Queensland Environmental Protection Agency

June 2003

ACKNOWLEDGEMENTS

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CONTENTS

FIGURES

TABLES

EXECUTIVE SUMMARY

A stochastic simulation model was developed for the southern Great Barrier Reef green sea turtle stock to foster better insight into regional metapopulation dynamics. The model was sex- and age class-structured linked by density-dependent, correlated and time-varying demographic processes subject to environmental and demographic stochasticity. The simulation model was based on extensive demographic information derived for this stock from a long-term sea turtle research program established and maintained by the Queensland Parks and Wildlife Service. Model validation was based on comparison with empirical reference behaviours and sensitivity was evaluated using multi-factor perturbation experiments and Monte Carlo simulation within a fractional factorial sampling design. The model was designed to support robust evaluation of the effects of habitat-specific competing mortality risks on stock abundance and also on the sex and ageclass structure. Hence, the model can be used for simulation experiments to design and test policies to support the long-term conservation of the southern Great Barrier Reef green sea turtle stock.

INTRODUCTION

The two common species of sea turtle resident in southern Great Barrier Reef (sGBR) waters are the green and loggerhead sea turtles (Limpus et al 1984). The sGBR green turtle stock is one of the major breeding metapopulations of green sea turtles in the southwestern Pacific region (FitzSimmons et al 1997b) with most nesting occurring on the coral cays in the sGBR region (see figure 1, Limpus et al 1984). The sGBR stock is not seriously exposed to any major hazards such as fisheries, disease, boat strikes or indigenous harvesting (Poiner & Harris 1996, Slater et al 1998). There is no evidence of population decline (see figure 2, Chaloupka & Limpus 2001) although this stock is exposed to subsistence harvesting in northern Australian waters (Kwan 1991). Yet robust management procedures have not been developed to support sustainable harvesting of the stock nor to evaluate the risk of exposure to other mortality factors such as incidental drowning in coastal trawl fisheries.

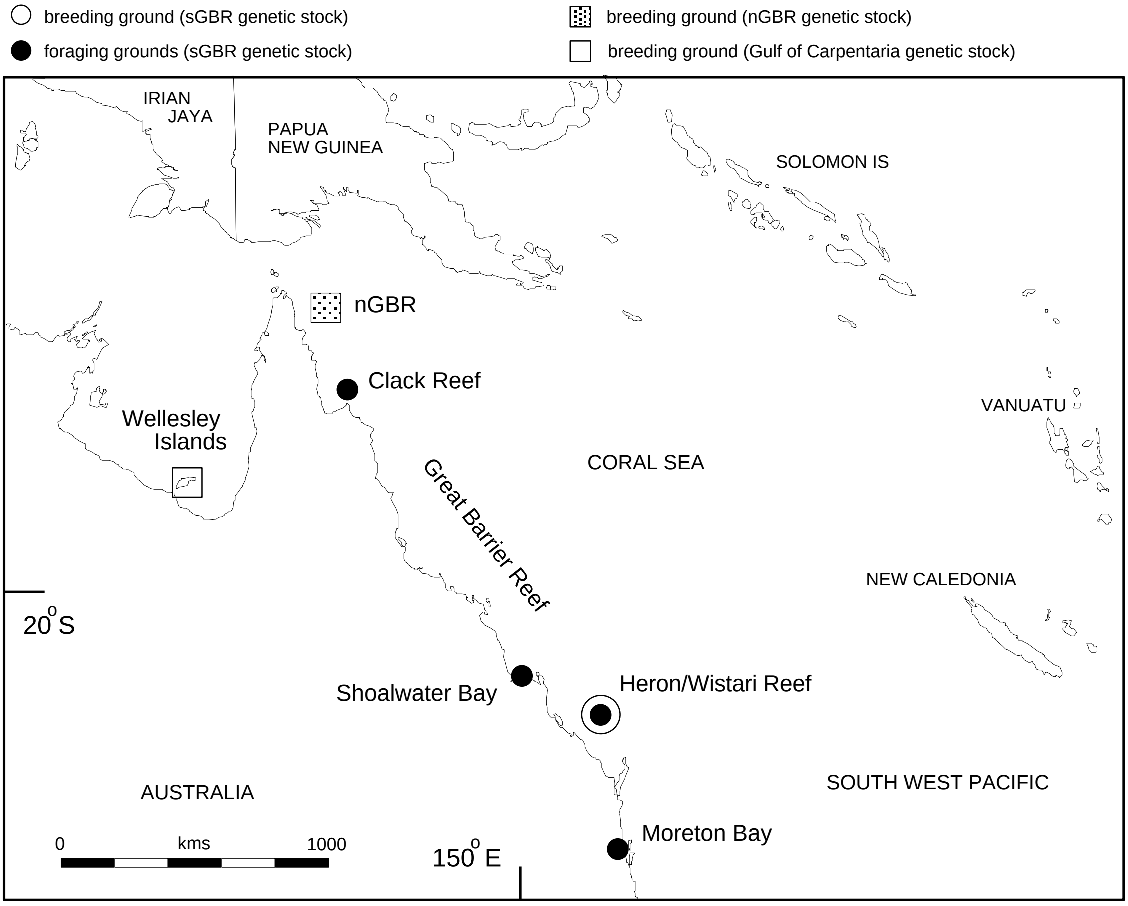

Figure 1. Location of the four foraging ground study sites for the sGBR genetic stock of green sea turtles resident in GBR and southern costal Queensland waters.

The study sites are: Clack Reef, Shoalwater Bay, Heron / Wistari Reef and Moreton Bay representing the estimated 15 675 km^2 of reefal (algae and / or seagrass) and coastal seagrass habitat occupied by the sGBR green turtle metapopulation. It was assumed that Clack Reef residents represent the northern Great Barrier Reef (nGBR) reefal habitat component of the sGBR metapopulation (26.8% of 15 675 km^2 of the metapopulation habitat), Shoalwater Bay represents a central coastal Queensland seagrass habitat component (16.3%), Heron / Wistari Reef the sGBR reefal component (47.7%) while Moreton Bay represent a southern coastal Queensland seagrass habitat component (9.2%). The major rookeries of the other two genetic stocks of Australian green turtles in the same region are also shown (nGBR, Wellesley Island group). Figure sourced from Chaloupka et al (in press).

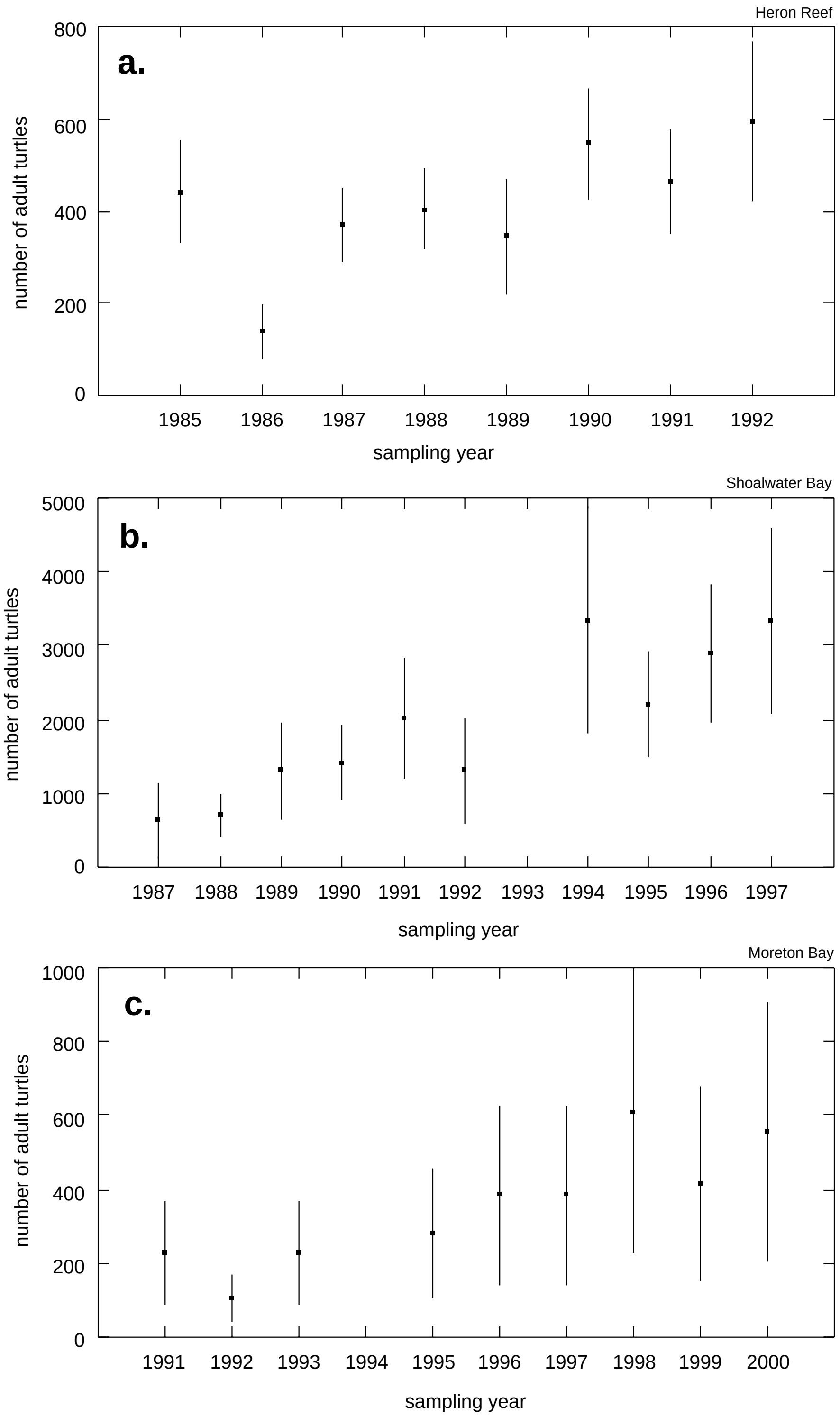

Figure 2. Annual population abundance estimates for green sea turtles from the sGBR genetic stock that were resident in the (a) Heron/Wistari Reef foraging ground, (b) Shoalwater Bay foraging ground and (c) Moreton Bay foraging ground.

Solid square = mean Horvitz-Thompson type abundance estimate, vertical bar = approx 95% confidence interval for Horvitz-Thompson estimate. See Chaloupka (2000), Chaloupka & Limpus (2001) or Chaloupka (2002) for details.

The development of such procedures depends on a reasonable understanding of sGBR green turtle demography and application of this information within a risk management framework. Risk comprises the following elements known as a risk chain (Merkhofer 1987)

1. hazard identification;
2. assessment of the likelihood of exposure to hazards;
3. assessment of the effects of exposure; and
4. social evaluation of the effects.

Risk assessment comprises the first three elements of the chain with stochastic simulation modelling being a useful tool to assess the risk to population viability given environmental stochasticity and management uncertainty. Therefore, a stochastic sex- and ageclass-structured simulation model of sGBR green sea turtle population dynamics was developed here that can be used to assess the viability of this stock given exposure to several competing mortality risk factors. The model is heuristic rather than predictive and is designed to help improve our understanding of green sea turtle population dynamics. The simulation model is based on the demographic information reviewed for this stock in Chaloupka (2002).

MODEL DESCRIPTION

A simulation model of the population dynamics of the sGBR green turtle genetic stock was developed using a system of > 100 ordinary differential equations linked by nonlinear, time varying and density-dependent demographic processes. The simulation model includes environmental and demographic stochasticity and some correlated demographic processes. See Engen et al (1998) for a discussion on environmental and demographic stochasticity and Burgman et al (1993) for discussion on correlated demographic processes. The model also includes a simple spatial configuration by accounting explicitly for four major habitat types assumed to represent the geographic range of the sGBR green turtle metapopulation or benthic habitat phase of the stock.

Environmental stochasticity was accounted for by sampling all the demographic rates from probability density or mass functions to reflect the temporal variability observed for this stock (Limpus & Chaloupka 1997, Chaloupka & Limpus 1998a, Chaloupka 2002). Demographic stochasticity was accounted for by using Poisson discrete event sampling (Gustafsson 2000) rather than a binomial sampling approach (Akçakaya 1991) because survival processes for this stock reflect significant over-dispersion including extra-Poisson sampling variation. Brillinger (1986) and Breslow (1990) provide important discussions on accounting properly for over-dispersion in demographic processes while Chaloupka & Limpus (1998a) addressed this issue in relation to the ageclass-specific survival processes for sGBR green sea turtles.

Compensatory sex-specific density-dependent processes were included in the model to account for the temporal variability in the proportion of females and males preparing to breed each year in response to major oceanographic anomalies (ENSO events) that is well known for this stock (Limpus & Nicholls 1994) and for green turtle stocks in northern Australian and southeast Asian waters (Chaloupka 2001a). Density-dependent somatic growth behaviour has also been shown for immature green turtles resident in Bahamian waters (Bjorndal et al 2000) but there is little evident so far of density-dependent growth behaviour for the sGBR stock (Limpus & Chaloupka 1997, Chaloupka et al in press).

Nonetheless, the density-dependent processes in the model are adjustable to account for variable functional form since density-dependence is not well understood and, importantly, Ginsburg et al (1990) have shown that risk assessment is sensitive to the functional form assumed for such processes. Depensatory density-dependent processes or Allee effects (Dennis 1989) were also included in the model by using a female mating success probability function that was dependent on the probability of finding at least one male mate, which is also adjustable to account for variable functional form.

MODEL SPECIFICATION

Demographic information sources

The model is based on extensive demographic information derived from various sources including the long-term Queensland Parks and Wildlife Service (QPWS) research program on green turtle populations resident in Great Barrier Reef waters and along the Queensland coast. See Limpus (1992, 1993, 1998), Limpus & Chaloupka (1997, 1998a), Limpus & Nicholls (1994), Limpus & Reed (1985), Limpus et al (1984, 1992, 1994a, 1994b), Brand-Gardner et al (1999), Chaloupka (2000, 2001b), Chaloupka & Limpus (2001), Chaloupka et al (in press), FitzSimmons et al (1997a, 1997b), Forbes (1994), Gyuris (1994), Slater et al (1998) and Whiting & Miller (1998). Further details were provided in Chaloupka (2002).

The QPWS sea turtle research program has focussed on four foraging ground populations of the sGBR green turtle stock. The foraging grounds are Clack Reef, Shoalwater Bay, Heron / Wistari Reef and Moreton Bay (see figure 1). Clack Reef is an offshore coral reef habitat in nGBR waters with extensive shallow water and deepwater seagrass meadows (Lee Long et al 1993). Shoalwater Bay is an inshore seagrass based coastal habitat with a significant tidal range in the sGBR region (Lee Long et al 1993). Heron / Wistari Reef is an offshore algal based coral reef habitat in sGBR waters (Limpus & Reed 1985, Forbes 1994). Moreton Bay is an inshore mixed seagrass and algal based coastal habitat in warm temperate southern Queensland waters (Limpus et al 1994a, Brand-Gardner et al 1999).

The green sea turtles resident in the Moreton Bay, Heron / Wistari Reef and Shoalwater Bay foraging grounds are from the sGBR genetic stock while the Clack Reef population comprises a mixture of sGBR and nGBR stocks (Limpus et al 1992, FitzSimmons et al 1997b).

Metapopulation structure

The benthic habitat component of the sGBR green turtle stock comprises a spatially disjunct metapopulation structure distributed over a substantial geographic range. (See Stith et al 1996 for discussion of metapopulation configurations). Green turtles from the sGBR stock are resident in foraging grounds distributed along the Queensland coast, Torres Strait, southern Papua New Guinea, Gulf of Carpentaria, Coral Sea and in southwestern Pacific waters around New Caledonia (see figure 1, Limpus et al 1992). The spatial dispersion of turtles throughout this range is patchy or disjunct, which presumably reflects the spatial and temporal distribution of suitable foraging habitat for sea turtles (Marsh & Saalfeld 1989).

Mature female and male green turtles resident in these foraging grounds migrate each year to a regional rookery in sGBR waters for courtship, mating and nesting before returning to the foraging grounds a few months later. Both capture-mark-recapture and genetic studies (Limpus et al 1992, FitzSimmons et al 1997a,b) have shown foraging ground fidelity for female and male sGBR green turtles so that foraging ground inter-change is negligible. Most of the benthic sGBR green turtles reside in foraging grounds in Great Barrier Reef (GBR) and east Queensland coastal waters (Limpus et al 1992).

Within this range, green sea turtles occupy two major habitat or foraging ground types (coral reef coastal seagrass meadows) along the east Queensland coast and throughout the GBR region. Seagrass is a major component of the green turtle diet in reefal and coastal habitats (Bjorndal 1997). However, algae are a major dietary component in reefal habitats such as Heron / Wistari Reefs (Forbes 1994) and can be an important component in inshore seagrass habitats such as Moreton Bay (Brand-Gardner et al 1999).

There is no apparent nutritional difference between algal and seagrass diets (Garnett et al 1985) and no growth differences between green turtles foraging on either algae or seagrass (Bjorndal 1997). Hence a combined estimate of coral reef (irrespective of whether the diet is mainly seagrass or algae) and inshore seagrass habitats along the east Queensland coast provides an estimate of suitable green turtle habitat throughout most of the geographic range of the sGBR metapopulation or benthic phase of the sGBR stock.

There is 20 000 km^2 of coral reef habitat in the Great Barrier Reef region (Hopley et al 1989) and it was estimated here that there is 5000 km^2 of coastal or inshore seagrass habitat along the east Queensland coast. Therefore, it was estimated that there is 25 000 km^2 of suitable inshore and offshore habitat for green sea turtles along the east Queensland coast where most of the sGBR genetic stock is also resident (Limpus et al 1992). The estimate of 5000 km^2 of inshore seagrass habitat was estimated as follows.

Firstly, Marsh & Saalfeld (1989, 1990) showed using aerial surveys that the inshore dispersion pattern of dugong and sea turtles along the east Queensland coast reflects quite well the known seagrass distribution (Lee Long et al 1993). Secondly, the three largest known areas of subtidal seagrass in the Queensland region occur in the Torres Strait ca 9^{0}S (3500 km^2, Poiner et al 1989), Barrow Point to Lookout Point in the nGBR region ca 15^{0}S (1600 km^2, Lee Long et al 1993) and Hervey Bay just south of the GBR ca 25^{0}S (1600 km^2, Preen et al 1995).

Green turtles from the sGBR stock are resident in these three areas but more so in the Barrow Pt-Lookout Pt area and predominantly in Hervey Bay (Limpus et al 1992). Green turtles from the nGBR stock are resident in foraging grounds along the east Queensland coast northward of Barrow Pt and in the Torres Strait and also display foraging ground fidelity (Limpus et al 1992, FitzSimmons et al 1997b). Hence the two major regional seagrass meadows (Barrow Pt-Lookout Pt, Hervey Bay) are major foraging grounds for the sGBR metapopulation.

Next, it has been estimated that there are 4600 km^2 of subtidal seagrass meadow along the east coast of Queensland between Cape York and Hervey Bay (see Lee Long et al 1993, Preen et al 1995). This is also considered an under-estimate because there were probably more extensive deep-water meadows near Barrow Pt-Lookout Pt and Hervey Bay than currently surveyed (Lee Long et al 1993). There are also other important seagrass meadows south of Hervey Bay within the habitat range of green turtles such as Moreton Bay around 27^0 S (Preen 1995).

The main green turtle and dugong foraging areas in Moreton Bay are located in the eastern portion near to Moreton and South Stradbroke Islands (Preen 1995). This area comprises 110 km^2 of subtidal seagrass and includes the Moreton Banks (Preen 1995), which is the main Moreton Bay green turtle sampling site (Limpus et al 1994a). The Moreton Banks comprise ca 63 km^2 of subtidal seagrass meadow (Limpus et al 1994a) or 57% of the eastern Moreton Bay seagrass meadows.

Therefore, it was estimated here that an additional 400 km^2 of inshore seagrass habitats exists along the east Queensland coast including Moreton Bay, deep-water meadows around Barrow Pt-Lookout Pt and Hervey Bay and the shallow-water area south of Hervey Bay to Moreton Bay (see figure 1). Hence the derived estimate here of 5000 km^2 (4600+400) of inshore seagrass habitat suitable for the sGBR metapopulation. However, most of the stock is resident along the east Queensland coast between 14^0-27^{0}S (Limpus et al 1992) so that the estimated 25 000 km^2 is an over-estimate of the sGBR green turtle metapopulation habitat.

Using the seagrass areal estimates in Lee Long et al (1995) it is apparent that around 80% of the coastal seagrass habitat along east Queensland occurs southward of 15^{o}S. So, it was assumed that 4000 of the estimated 5000 km^2 of the coastal seagrass habitat occurs within the main geographic range of the sGBR metapopulation. Similarly, using regional estimates in Hopley et al (1989), it was determined that 58% or 11 765km^2 of the 20 000 km^2 of reefal habitat in the GBR region occurs within the main geographic range of the metapopulation. Therefore, the sGBR metapopulation occupies a geographic habitat of 15 675 km^2 comprising 11 675km^2 of reefal habitat and 4000 km^2 of coastal seagrass habitat.

Recall that the QPWS sea turtle research program encompasses four major foraging grounds of the sGBR green turtle stock — Clack Reef, Shoalwater Bay, Heron / Wistari Reef, Moreton Bay. The Heron / Wistari and Clack Reef foraging ground populations are considered representative of coral reef habitats in the southern and northern geographic range of the metapopulation while the Shoalwater and Moreton Bay foraging ground populations are considered representative of the inshore seagrass habitat within the central and southern coastal Queensland range of the metapopulation.

Again using the reefal estimates in Hopley et al (1989), it was determined that 64% (7459 km^2) of the sGBR metapopulation reefal habitat occurs southward of 19^{o}S and was considered here to be represented by the Heron / Wistari population in the central and southern GBR regions. The Clack Reef population was considered representative of the remaining 36% or 4126 km^2 of metapopulation reefal habitat in the northern GBR region.

Similarly, using seagrass estimates in Lee Long et al (1993), it was determined that 64% (2560 km^2) of the metapopulation coastal seagrass habitat occurs along the central Queensland coast and was considered here to be represented by the Shoalwater Bay population in central coastal Queensland. The Moreton Bay population was considered representative of the remaining 36% or 1440 km^2 of seagrass habitat in the southern coastal Queensland region. Overall, the sGBR metapopulation was estimated to occupy four habitat types covering 15 675 km^2 in accordance with the configuration summarised in table 1.

Table 1. Metapopulation spatial configuration. mftbs = mean size (cm CCL) of first time female breeders resident in these habitat types (Limpus unpub.)

habitat type	**Area proportion**	**Area (km^2)**	**Representative substock**	**mftbs**
northern GBR coral reef habitat	0.268	4203	Clack Reef	105.3
central and southern GBR coral reef habitat	0.477	7472	Heron / Wistari Reef	103.4
central coastal Queensland seagrass habitat	0.163	2560	Shoalwater Bay	99.9
southern coastal Queensland seagrass habitat	0.092	1440	Moreton Bay	110.5
reefal habitats	0.745	11 675	Clack, Heron / Wistari	
coastal seagrass habitats	0.255	4000	Shoalwater, Moreton	

Initial abundance estimates

Given the 45 km^{-2} density estimate for green turtles resident in the sGBR reefal habitats (Chaloupka & Limpus 2001), it was determined that the reefal habitats summarised in table 1 account for ca 525 000 sGBR green turtles. Assuming similar densities in coastal habitats, it was estimated that the coastal seagrass habitats account for ca 160 000 sGBR green sea turtles. Therefore, the sGBR metapopulation, which is the benthic component of the stock, comprises ca 685 000 individual turtles resident in the four benthic habitats. It is important to note that green turtles spend the early development years in oceanic or pelagic habitats so that there are significantly more than 685 000 green turtles in the sGBR stock. These benthic substock abundance estimates were then used to initialise the 92 male and female ageclass abundances in the simulation model (see Demographic structure below).

The relative habitat proportions in table 1 were also used in the model to provide relative risk probabilities for the same proportion of the sGBR stock exposed to anthropogenic but habitat-specific risk factors. The age-at-maturity functions were also derived in accordance with the same habitat proportions since these estimates also represent relative abundance or habitat-specific population densities (see Demographic structure below). A simple but useful test of the validity of the relative habitat proportions derived for the sGBR metapopulation is shown by the following:

- The weighted average of mean size of first time female breeders from the 4 habitat types is 103.99 cm CCL derived by using the mean first time breeder size estimates and habitat proportions summarised in table 1.
- The mean of all first time female nesters is 104 cm CCL (Limpus unpub.) at the sGBR rookery in sGBR waters (see figure 1).

Demographic structure

The model is sex- and ageclass structured so that the main state variables in the model are the annual number of male and female green turtles from the sGBR genetic stock in each of 46 sex-specific ageclasses that reflect the 6 green turtle ontogenetic classes or ageclass groupings (see figure 3).

1. first year of life,
2. pelagic juveniles,
3. benthic juveniles,
4. immatures,
5. subadults and
6. adults.

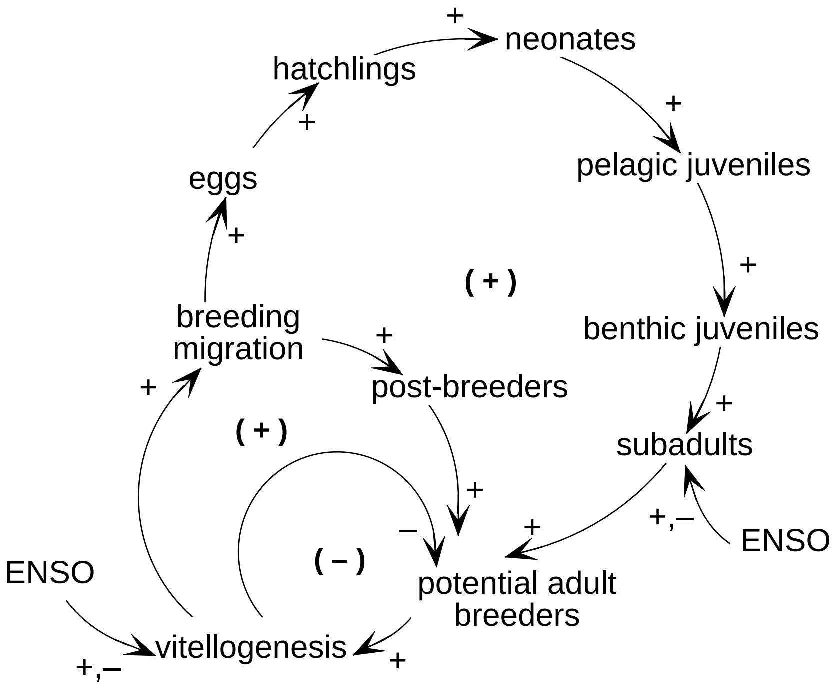

Figure 3. Conceptual or causal loop diagram for simulation model of the sGBR genetic stock of green sea turtles resident in GBR and southern coastal Queensland foraging grounds.

ENSO = El Niño-Southern Oscillation effect on immature growth (Limpus & Chaloupka 1997) and on breeding (Limpus & Nicholls 1994, Chaloupka 2001a). ± = causal loop polarity with + meaning 2 components move in same direction, - means they move in opposite directions; for instance, as more turtles breed and migrate then number of potential breeders decreases since females do not breed each year because of reproductive constraints. The concepts outlined here formed the basis for the demographic structure of the simulation model. See Puccia & Levins (1985) for details on causal loop modelling.

The simulation model was age-structured rather than developmental stage structured because most of the demographic processes are a function of age rather than size and it is important to capture the correct temporal delays in the sGBR green turtle demography that are a function of long age to maturity irrespective of how fast a turtle grows once it has recruited to the benthic habitat (see figures 4, 5 and discussion below). Simplistic stage-structured models have been commonly used to evaluate sea turtle demography (Chaloupka & Musick 1997) but these models have no developmental age structure within each stage so that turtles can enter a stage in one year and exit if alive the next year even if the stage duration was say 10 years. It is a design defect in most stage-structured models including sea turtle matrix projection models as discussed in Cochran & Ellner (1992) and Chaloupka & Musick (1997).

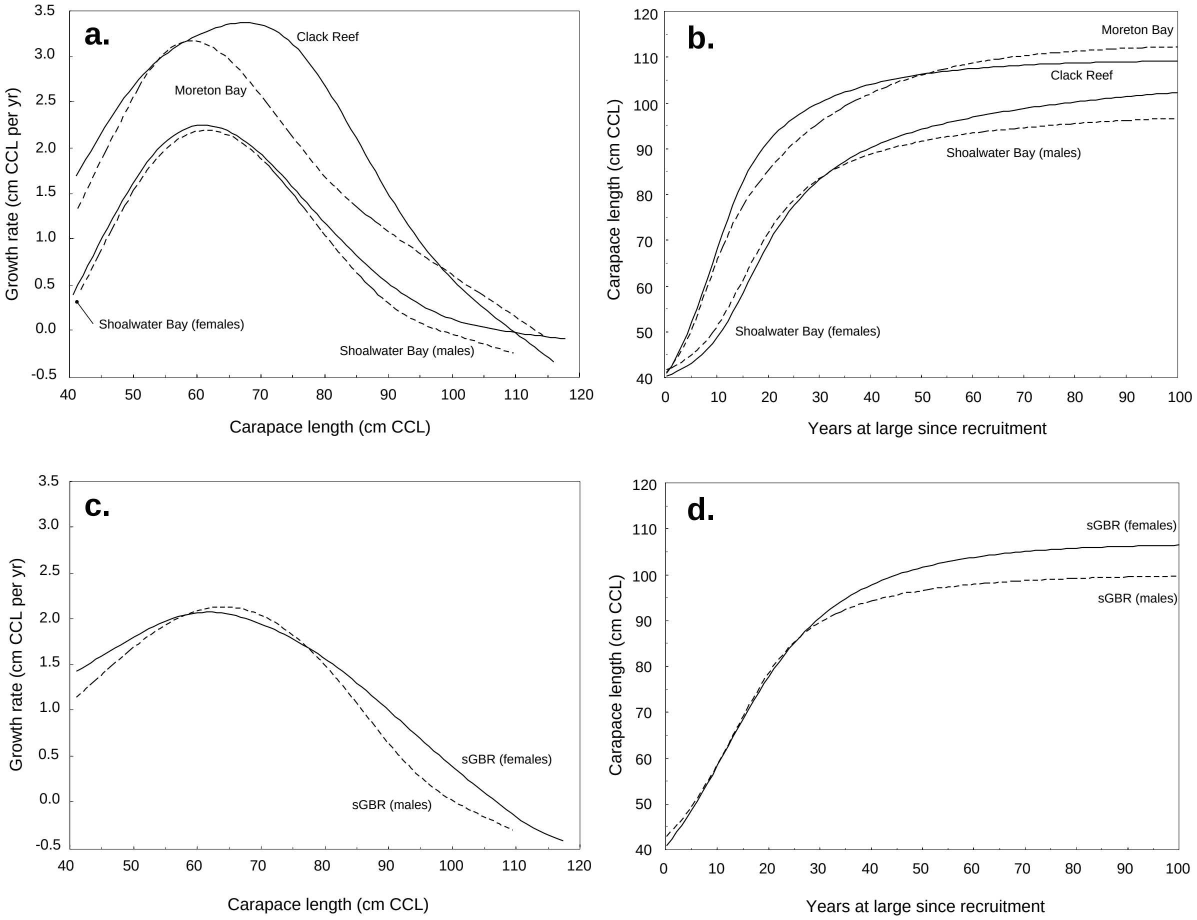

Figure 4. Estimated size-specific and size-at-age growth functions for 4 foraging ground subpopulations of the metapopulation comprising the sGBR genetic stock.

Growth functions for the Clack Reef, Shoalwater Bay and Moreton Bay subpopulations are shown in panels a. and b. corresponding functions for the Heron / Wistari Reef subpopulation in c. and d. are shown separately to avoid clutter. The size-specific growth functions in panels a. and c. were integrated numerically to give the expected size-at-age (age = years-at-large since recruitment) functions in panels b. and d. Growth models derived using nonparametric regression modelling and numerical integration of size-based growth rate functions (see Chaloupka & Limpus 1997, Limpus & Chaloupka 1997).

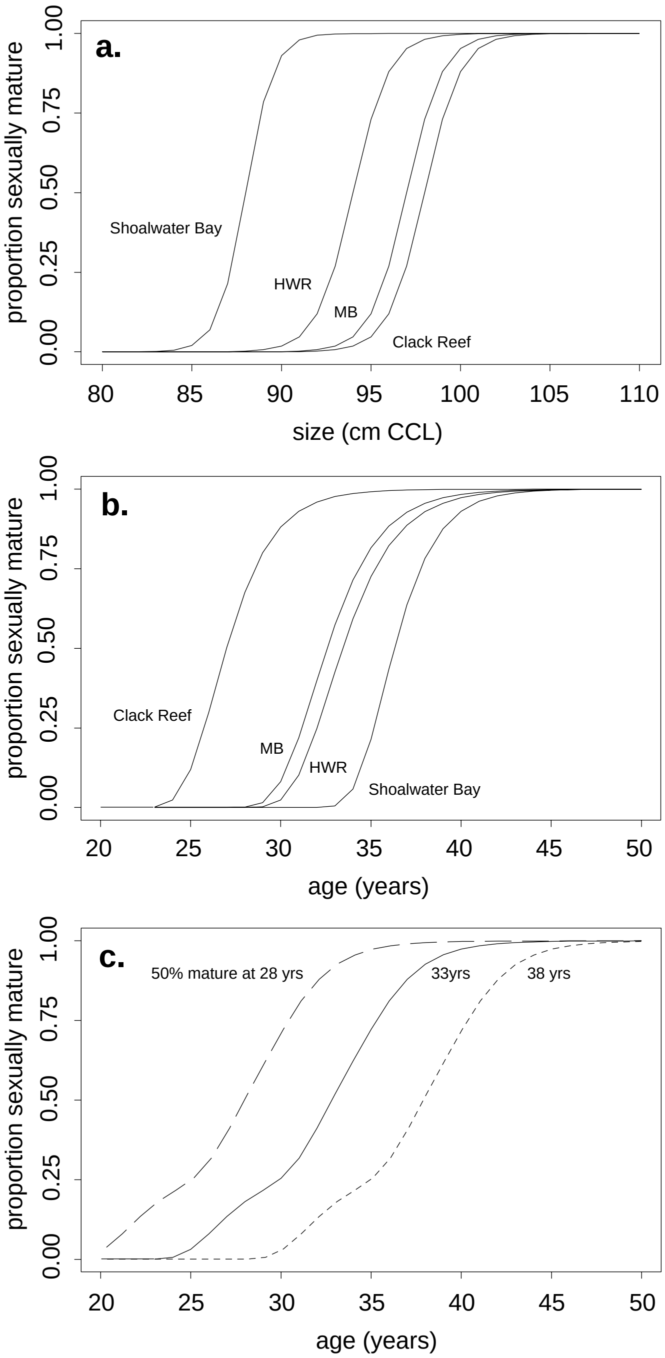

Figure 5. Expected size at maturity, age-specific functions and age at maturity estimated for the 4 sGBR green turtle foraging populations.

Panel a. shows expected size-at-maturity functions estimated for the four populations based on maturity estimates, mean size at nesting of first time breeders and courtship size for males derived from Limpus 1993, Limpus et al (1994), Limpus (1998), Limpus (unpub. for nGBR nesters) and size-specific growth functions (Limpus & Chaloupka 1997, Chaloupka et al in press). Panel b. shows estimated age-specific functions based on the size-specific functions in a. and Weibull type age-specific growth functions (Chaloupka 2001b).

Figure 5c. shows expected metapopulation age-at-maturity function (solid curve) by combining figure 5b functions in proportion to estimated relative turtle abundance in the 4 habitat types represented by the subpopulations (see figure 1). Dashed and dotted curves show expected age-at-maturity function assuming a 5 year decrease or increase in median age-at-maturity derived by adjusting the parameter values in the four curves shown in figure 5b. The functions in figure 5a were based on a logistic model fits while the functions in figure 5b were based on Gompertz model fits. Models fitted using the robust nonlinear regression procedures in SHAZAM (White 1997).

Several modelling approaches are possible to account for transition or maturation from one stage to the next including a distributed delay function based on a probability density function to control stage transition rates (see Blythe et al 1984). This method was used by Chaloupka & Limpus (1996, 1998b) to model sea turtle population dynamics within a stochastic simulation modelling framework. Caswell (1989) outlines a similar approach based on negative binomial transition probabilities for a deterministic matrix projection model (see also Lo et al 1995 for a fisheries example). Although well designed stage-structured population dynamic models are possible they are still only a simplified form of age-structured model unless the stages really reflect developmental behaviour such as metamorphosis in insects with temperature-dependent rather than time-dependent maturation.

Nonetheless, it is useful to assign the ageclasses to descriptive forms of stages or groupings of ageclasses for summary purposes in the model and for communicating model output in terms of the ageclass groupings. These groupings or stages were assigned as follows although assignment is approximate as there are differences in age-specific maturity between foraging ground population.

1. ageclass 1 comprising eggs, hatchlings and neonates (first year of life),
2. pelagic juveniles (1-6 years old),
3. benthic juveniles (5-15 years of age),
4. immatures (16-29 years of age),
5. subadults (30-45 years of age) and
6. adults (>=46 years of age).

Mean adult life expectancy was estimated ca 18-19 years using ageclass-specific survival probability estimates for this stock (Chaloupka & Limpus 1998a) but all adults were assigned to 1 ageclass with indistinguishable age and size characteristics (see discussion below).

Eggs hatch after ca two months and then the hatchlings escape the nesting beaches to recruit to the sea (Limpus et al 1994a). The hatchlings are then dispersed passively southward as neonates over the next six to nine months in the east Australian current and then dispersed eastwards into the southwestern Pacific Ocean (Walker 1994). The turtles now enter the pelagic juvenile phase that occurs in oceanic gyres or along convergence zones (Carr 1987, Polovina et al 2000). Pelagic juveniles then recruit to benthic habitats in foraging grounds along the east Queensland coastline or Great Barrier Reef region at a median size ca 44 cm CCL (Limpus & Chaloupka 1997).

The pelagic juvenile phase duration has been estimated ca four to seven years (Limpus & Chaloupka 1997, Zug & Glor 1998). Hence the model uses a more ecologically realistic distributed age rather than a knife-edge form of recruitment from the pelagic to the benthic habitat. The recruitment form in the model assumes that 25% of four year olds pelagic juveniles recruit to the benthic habitat as five year old benthic turtles while the remaining four year olds become five year old pelagic juveniles if still alive. Then 50% of five year old pelagic juveniles recruit to the benthic habitat as six year old benthic turtles while the remaining five year olds become six year old pelagic juveniles if still alive. Then all remaining six year old pelagic juveniles recruit to the benthic habitat as seven year old benthic turtles if still alive. The age distributed benthic recruitment function in the model is readily adjusted to handle other distributed age forms in light of new information.

Benthic juveniles then grow rapidly until 65-75 cm CCL, depending on foraging ground, when sex-specific growth becomes evident (see figure 4a and 4c, Limpus & Chaloupka 1997, Chaloupka et al in press). A detailed discussion of habitat utilization by juvenile sea turtles including green sea turtles was provided by Musick & Limpus (1997) while the feeding ecology of sea turtles was discussed in detailed by Bjorndal (1997). Mean benthic juvenile ontogenetic class duration was estimated ca eleven years for males and females, irrespective of size, using a system-of-equations age-specific growth model developed for this stock (Chaloupka 2001b). Hence the benthic juvenile ontogenetic class comprises eleven ageclasses.

Somatic growth slows rapidly after ca fifteen years of age (Limpus & Chaloupka 1997, Chaloupka et al in press), which marks the immature ontogenetic class prior to onset of sexual maturity and then adulthood ca 90-100 cm CCL (Limpus et al 1994a, Limpus & Chaloupka 1997, Chaloupka et al in press). Mean benthic immature class duration was estimated ca fourteen years for both males and females (Chaloupka 2001b) so that the immature ontogenetic class comprises fourteen ageclasses. Somatic growth is negligible from ca 90 cm CCL onwards but the maturing turtles or subadults represent a wide range of ages, sizes and maturity status because of foraging ground, year, cohort and individual heterogeneity effects (Limpus & Chaloupka 1997, Chaloupka et al in press). Hence a 105 cm CCL female might be a subadult determined using laparoscopy (Limpus & Reed 1985) while a 90 cm female could be mature and in its second nesting season.

Therefore, the extended maturing ontogenetic class was estimated using size- and age-specific maturation functions for each of the four foraging ground populations with subadult class duration estimated to span ca sixteen years depending on foraging ground. Subadult and adult ageclasses and ontogenetic class assignment were defined here using size-, age- and foraging ground specific growth functions (see figure 4) in conjunction with estimated age and size at first breeding and size-based reproductive criteria for adults from Clack Reef (Limpus unpub. for nGBR nesters), Heron / Wistari Reefs (Limpus & Reed 1985, Limpus 1993), Moreton Bay (Limpus et al 1994a) and Shoalwater Bay populations (Limpus 1998). The size-specific reproductive criteria included empirical estimates of minimum, mean and maximum breeding and courtship size for first time female and male breeders. The sex-specific growth functions were derived using the two stage nonparametric regression modelling procedure proposed by Chaloupka & Limpus (1997) and applied since to several green turtle stocks (Limpus & Chaloupka 1997, Bjorndal et al 2000, Chaloupka et al in press).

The size-specific reproductive criteria were used in conjunction with the growth functions (see figure 4) to derive some point estimates of size-specific maturation for each population using a logistic function that fitted the size-specific maturity estimates well. The logistic model used was given by $Y=1/(1+\exp(-a(X-b)))$ where Y=proportion mature, X=size, a= coefficient for rate of approach to asymptote and b=size at 50% probability of maturity (Ratkowsky 1990). These size-specific maturity functions are consistent with the size-specific maturity estimates derived using laparoscopic examination of a small sample of sGBR green turtles from the Moreton Bay population (Limpus et al 1994b) and the Shoalwater Bay population (Limpus 1998).

These derived size-specific maturity functions are shown in figure 5a with the corresponding age-specific maturity functions shown in figure 5b. The age-specific functions (see figure 5b) were derived by converting the size-specific functions in figure 5a into age-specific functions using the Weibull type age-specific growth functions developed for the sGBR green turtle stock (Chaloupka 2001b, eq 1 in Chaloupka & Musick 1997) to derive point estimates of age-specific maturation for each population. The following Gompertz function was found to be a good fit to the derived age-specific data series given by $Y=\exp(-\exp(-a(X-b)))$ where X=age, a= coefficient for rate of approach to asymptote and b= age at which the 50% probability of maturity occurs (Ratkowsky 1990).

The age-specific maturity functions (see figure 5b) were used in the model to determine the annual number of male and females that were sexually mature in each ageclass in accordance with the relative habitat proportion represented by each of the four foraging ground populations (see Table 1). For instance, the number of mature female 30 year olds in the metapopulation in any one year was determined as follows using the fitted Gompertz model parameters for age-specific maturity for females in each habitat types represented by the four foraging ground populations :-

$$
\begin{aligned}
&(\text{number of female 30 year olds})*\text{habitat1}*(\exp(-\exp(-0.56394*(30-26.338))))+\\
&(\text{number of female 30 year olds})*\text{habitat2}*(\exp(-\exp(-0.61313*(30-35.705))))+\\
&(\text{number of female 30 year olds})*\text{habitat3}*(\exp(-\exp(-0.49125*(30-32.678))))+\\
&(\text{number of female 30 year olds})*\text{habitat4}*(\exp(-\exp(-0.50284*(30-31.833))))
\end{aligned}
$$

where…

habitat1 = 0.268,
habitat2 = 0.163,
habitat3 = 0.477 and
habitat4 = 0.092 (refer table 1).

It was assumed here that males and females have the same age-specific maturity functions in each habitat type (see figure 5b) but the maturity functions in the model are readily adjusted to handle sex-specific maturity functions in light of new information. Combining all 92 sex-specific ageclasses shows the polyphasic maturity function realised in any one year in the model given the median-age parameter estimates (see figure 5c). A detailed description of polyphasic functions, parameter forms and robust estimation procedures with particular application to sea turtles can be found in Chaloupka & Zug (1997).

Wood & Wood (1993) found that most female green turtles raised in a Cayman Islands turtle farm were mature by 25 years of age. Sexual maturity is reached at significantly older ages for wild green turtles (Green 1993, Limpus & Chaloupka 1997, Limpus 1998, Bjorndal et al 2000, Balazs et al 2000) but the farm-based estimate provides a useful lower bound for age-specific maturity for the sGBR green turtle model. It is apparent from figure 5b that 100% maturity is assumed in the model to occur at all four foraging grounds by at least 45 years of age so that adults were defined as the ≥46 years old ageclass since growth is clearly negligible by this age (see figure 4b and 4d) and all individuals are assumed mature. Few turtles were assumed mature by 25 years of age in the simulation model, which are attributable to the Clack Reef population representing the reefal type habitat in nGBR waters.

All adults were included in the model in a single ageclass, which is appropriate assuming that there is no senescence or declining age-specific survival for adults. There is no evidence for declining survival probabilities for adult sGBR green turtles (Chaloupka & Limpus 1998a) nor is there any evidence of senescence for sea turtles nor for many other long-lived animals (Gaillard et al 1994, Nichols et al 1997, Chaloupka et al 1999) including freshwater turtles (Gibbons & Semlitsch 1982).

Survival probabilities

Ageclass-specific survival probability density function estimates for sGBR green turtles were derived from:

1. Known incubation and hatching related mortality probabilities (Limpus & Reed 1985);
2. Mortality estimates for sGBR green turtle hatchlings escaping to open water from the regional rookery (Gyuris 1994); and
3. Statistical modelling of survival probabilities for male and female benthic juvenile, immature and adult green turtles (Chaloupka & Limpus 1998a, Chaloupka 2002).

Chaloupka & Limpus (1998a, see also Chaloupka 2002) have shown that survival probabilities were neither sex-specific nor ageclass-dependent within each benthic ageclass grouping (benthic juveniles, immatures, adults) but that the survival probabilities were ageclass group dependent.

The expected annual sex- and age-group-specific survival and recapture probabilities for sGBR stock green turtles resident in the Heron / Wistari, Shoalwater Bay and Moreton Bay foraging grounds were derived from capture-mark-recapture histories for 5124 individual turtles. The probability estimates were derived using the Cormack-Jolly-Seber (CJS) statistical modelling approach (Cormack 1989, Lebreton et al 1992) and accounting for sampling effort, ageclass group, sex and potential transient behaviour. The CJS approach does not assume demographic closure and so is suitable for estimation of demographic parameters given an underlying stochastic birth, death and permanent emigration process between occasions. The statistical assumptions and limitations of the CJS approach for estimation of age-specific or time-dependent demographic probabilities are well known and discussed elsewhere (Cormack 1989, Lebreton et al 1992, Pradel et al 1997). The CJS derived capture probabilities were then also used to estimate age group specific abundance for the benthic component of the sGBR stock (Chaloupka 2000, Chaloupka & Limpus 2001, see also Chaloupka 2002). A similar approach has been used to estimated loggerhead turtle survival and abundance in sGBR waters (see Chaloupka & Limpus 2002).

The parameters and probability density functions assumed in the model for each ageclass group are summarised in table 2. There were no significant differences in the age group survival probability estimates between the foraging ground populations when sampling error was taken into account (see Chaloupka 2002). Therefore, the expected annual probabilities for the benthic age groups were sampled from probability density functions (pdfs) that cover the range and central tendency of the estimates for all foraging grounds summarised in table 6 in Chaloupka (2002). The expected age-group-specific survival probabilities for each year were also sampled from the ageclass-group-specific pdfs that reflect environmental stochasticity and measurement error in the probability estimates.

Table 2. Estimated ageclass-specific survival pdfs, parameter values and estimating equations.

ageclass	pdf	mean	mode	scale	estimates derived from
ageclass 0					
eggs (esp)	logistic	0.850		0.015	Limpus & Reed (1985), Chaloupka 2002
hatchlings (hsp)	logistic	0.550		0.015	Gyuris (1994), Chaloupka (2002)
neonate (nsp)	extreme value		0.950	-0.010	Chaloupka (2002), Chaloupka (unpub.)
pelagic juveniles (pjsp)	logistic	0.700 [a]		0.010	tuned in model
pelagic juveniles (pjsp)	logistic	0.672 [a]		0.010	tuned in model
benthic juveniles (bjsp)	logistic	0.850		0.010	Chaloupka & Limpus (1998), Chaloupka (2002)
immatures (imsp)	logistic	0.890		0.010	Chaloupka & Limpus (1998), Chaloupka (2002)
subadults (sasp)	extreme value [b]		0.890	0.010	Chaloupka & Limpus (1998), Chaloupka (2002)
adults (adsp)	extreme value		0.960	-0.010	Chaloupka & Limpus (1998), Chaloupka (2002)

ageclass 0 survival probability = (esp*hs*nsp)
esp = (mean-scale*(ln(((random(0,1))-1)-1)))
hsp = (mean-scale*(ln(((random(0,1))-1)-1)))
nsp = (MAX(0,(MIN((mode-(-scale)*(ln(-ln(random(0,1))))),1))))
pjsp = (mean-scale*(ln(((random(0,1))-1)-1)))
bjsp = (mean-scale*(ln(((random(0,1))-1)-1)))
imsp = mean-scale*(ln(((random(0,1))-1)-1)))
sasp = (MAX(0,(MIN((mode-(scale)*(ln(-ln(random(0,1))))),1))))
adsp = (MAX(0,(MIN((mode-(-scale)*(ln(-ln(random(0,1))))),1))))
Notes:
(a) if density-dependence switch on then 0.7 else 0.672;
(b) correlated with adult survival (Chaloupka 2002)

All pdfs in table 2 were sampled in the model using the inverse transformation method (Fishman 1996) with a uniform random variable in the interval [0,1]. For instance, the expected annual survival probability for adult females and males was sampled from a right skewed extreme value pdf as follows using the parameters in table 2.

$\bullet_{\text{adult}}$ = mode- scale*(ln(-ln(random(0,1))))

The corresponding functions for the other age groups are summarised in table 2 with some functions including constraints to ensure that sampled values fall within the [0,1] interval. This is important for the extreme value pdfs such as for the adult survival probability function shown above that are located near the upper bound. This constraint is not essential but was included to ensure no invalid parameter values were sampled during a large number of model runs. It is most unlikely that out of bounds or invalid values would be sampled but this trap is included as a precautionary measure.

Correlated processes might also be important for green sea turtle population dynamics. For instance, Doak et al (1994) used correlated survival probabilities in a simple stochastic matrix model of desert tortoise population dynamics and found that correlated demography in their model resulted in more uncertain estimates of population growth and abundance. Breininger et al (1999) also used correlated survival and fecundity in their Monte Carlo model of scrub-jay population dynamics given the suggestions in Burgman et al (1993) of the potential importance of correlated demography.

The adult and subadult survival processes were assumed in the model to be related due to the maturation process and onset of the reproductive migratory habit that could well expose these individuals to other mortality risks from shark predation and physical exhaustion since it seems that females do not feed in the courtship grounds (Limpus 1999). Therefore, the adult and subadult survival probability density functions were related using the random number tagging method outlined in Fishman (1996) to correlate nonnormal and/or differing pdfs.

This method is valid for correlating pdfs when the inverse transformation method is used for deriving a pdf from a uniform random variate in the [0,1] interval but it is not possible to vary the strength of the correlation using this method, which was assumed to be 100%. Simple methods exist for implementing normal pdfs with varying correlation strength (Burgman et al 1993) but this is no longer a trivial task when sampling from nonnormal and differing pdfs.

Pelagic juvenile mortality was unknown, which is the case for all sea turtle stocks, and so was derived here by tuning the simulation model to an estimate of pelagic mortality that resulted in a fluctuating but stable population. The expected annual pelagic juvenile survival probability was then sampled from a logistic pdf assuming the same scale parameter used for the benthic juvenile, immature and mature groups. All survival probability functions and parameters are readily adjustable in the model to account for new information or to test the effect of variable functional form on model performance or sensitivity.

Competing risks and cause-specific mortality

The age group specific survival functions outlined in table 2 reflect natural mortality sources. However, green sea turtles are also exposed to various significant anthropogenic mortality risks such as:

- Egg harvesting (Parson 1962, Frazier 1980, Chaloupka 2001a);
- Incidental capture and drowning in coastal otter trawl fisheries (Robins 1996, Poiner & Harris 1996, Slater et al 1998); and
- Indigenous harvesting of benthic habitat turtles in GBR and northern Australian coastal waters (Kwan 1991).

It was important to model simultaneously all anthropogenic hazards because of the problem of competing risks (Chiang 1991). The point is that a turtle cannot be killed twice and so mortality risks are not additive making it difficult to quantify cause-specific effects in the presence of competing risks. The model includes the capacity to account for cause-specific mortality using a multiplicative competing risks approach (see Chiang 1991). For instance, the multiplicative competing risks form applied to expected egg survival (esp) given natural and anthropogenic mortality is as follows:

esp = MAX(0,MIN((espn*(1-egg_harvest_mortality)),1))
{to ensure esp constrained to [0,1] interval since could be very close to boundary given high harvest rates};

espn = espn_norm-0.015*(logn(((random(0,1))$^{-1}$)-1))
{egg to hatching natural survival sampled from a logistic pdf accounting for environmental stochasticity}
espn_norm =0.85 { expected natural survival probability}; and

egg_harvest_mortality = egg_harvest_norm*egg_harvest_switch
{egg harvest switch = 1 if egg harvest duration > 0}
egg_harvest_norm = 0.75 {adjustable value to account for harvest mortality in [0,1] interval}.

The additional mortality risks included explicitly in the model include incidental capture and drowning of benthic turtles in coastal otter trawl fisheries and various forms of pelagic or benthic turtles harvesting. However, not all ageclasses have the same exposure probability to each hazard. For instance, larger turtles have a high probability of capture in the coastal otter trawl fisheries than smaller turtles (Robins 1995, Poiner & Harris 1996).

The assumed size-specific capture probabilities in the model are as follows, based on size-specific capture estimates (Robins 1995) and coastal habitat-specific probabilities of exposure to otter trawl fisheries in GBR and coastal Queensland waters (Slater et al 1998):

- Matures (0.073);
- Immatures (0.044); and
- Benthic juveniles (0.029).

The probability of drowning once captured in the trawl fishery is size-independent and was set at 0.1, which was based on estimates in Robins (1995) and Poiner & Harris (1996). The current settings in the model lead to the estimated number of green turtles captured and drowned each year in the East Coast Otter Trawl Fisheries (Robins 1995). All incidental capture and drowning parameters are adjustable in the model.

Besides egg harvesting, turtle harvesting is the main potential source of anthropogenic risk to green sea turtle stock viability (Parson 1962, Frazier 1980, Davenport 1988, Horikoshi et al 1994, Limpus et al 1994a, Bjorndal et al 2000). Three forms of harvest strategy are explicitly accounted for in the model:

- Constant rate;
- Constant offtake; and
- Threshold-based including pure and proportional forms.

Getz & Haight (1989) provide a discussion of the constant rate and constant offtake harvesting strategies. Constant rate strategies involve harvesting a prescribed proportion each year of the specified at-risk ageclass. Constant offtake strategies involve harvesting each year a prescribed number of the specified at-risk ageclass (a fulfilled quota). All harvesting strategies in the model can also address sex-biased harvesting options by adjusting the harvest sex ratio and is one of the reasons for including the depensatory mating success probability function in the model (see figure 6b).

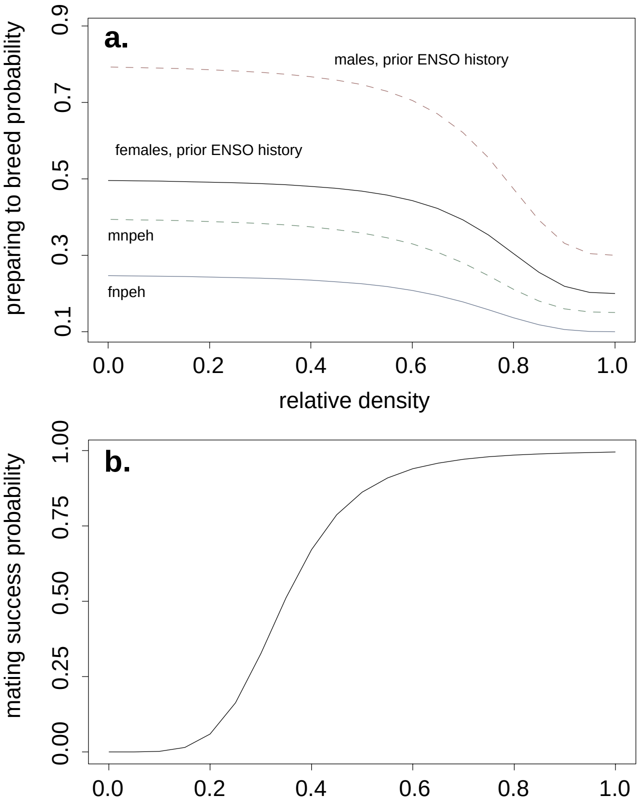

Figure 6. The sex-specific density-dependent nonlinear functional form assumed in the sGBR green sea turtle simulation model for (a) the scale parameter for sampling proportion of mature females and males preparing to breed each year given prior ENSO history from Weibull pdfs and (b) mature female mating success probability or probability of a mature female finding and mating with at least one male, which was used here to incorporate an assumed depensatory or Allee effect in reproductive capacity (see Dennis 1989).

Relative density in a. was derived from the ratio of benthic substock abundance to quasi-steady state or long-run benthic abundance each year constrained to the interval [0,1] while relative density in figure 6b was derived from the ratio of mature males to mature females each year constrained to the interval [0,1]. mnpeh = male function with no prior ENSO history, fnpeh = female function with no prior ENSO history.

Despite its simplicity, a constant offtake harvesting strategy can be very risky, leading to rapid decline for populations with slow growth potential (Milner-Gulland 1994). The constant offtake harvesting strategy was included in the model because it is the easiest strategy to apply and administer and is commonly used since it also requires no prior knowledge of stock abundance (Getz & Haight, 1989).

Threshold-based harvesting strategies involve harvesting a stock until it is reduced to a pre-specified fraction of unexploited stock abundance. The fraction of initial stock abundance is called a threshold. When a stock is above the threshold then all excess individuals (difference between stock abundance and threshold abundance) are harvested but when the stock declines below the threshold then harvesting is ceased until the stock recovers again above the threshold. This is known as a pure threshold harvesting strategy (Getz & Haight 1989).

Pulse-based harvesting strategies are a special case of the threshold-based harvesting approach. One major consequence of threshold harvesting is that there will be numerous occasions when there is little or no harvest (a zero or very low yield probability), which could have serious immediate economic consequences. Detailed discussions of various forms of threshold-based harvesting strategies can be found in Getz & Haight (1989), Zheng et al (1993), and Tufto et al (1999).

A recent variation of the pure threshold strategy is a proportional threshold strategy that involves harvesting a pre-specified fraction of the excess when stock abundance is above the threshold rather than the whole excess (Engen et al 1997, Lande et al 1997). Proportional threshold strategies are considered more efficient in terms of:

- Cumulative yield;
- Reducing the probability of no-harvest years when the stock falls below the threshold; and
- When the annual stock assessment used to determine whether the stock is above or below the threshold is subject to significant measurement error (Lande et al 1997).

The model includes the capacity to assess both pure and proportional threshold strategies. However, these threshold harvest strategies are only implemented in the model for evaluating adult ageclass harvesting. Extensive programming code would be required to apply this more complex strategy to the remaining 90 sex-ageclasses so has not been implemented in this version of the model.

Most strategies (except constant offtake) require reliable stock abundance assessment and this is fundamental to implementing a robust threshold harvesting scheme. However, assessing abundance is prone to substantial stock abundance assessment error (Zheng et al 1993, Engen et al 1997). This error can have a major impact on stock viability since harvesting might continue under the false impression that the stock abundance was high when in fact it was far lower than estimated. Assessment error in the annual estimate of adult abundance was implemented in the model by sampling adult abundance from a lognormal pdf with adjustable coefficient of variation in the [0,1] interval to reflect the prescribed level of assessment error (see also Zheng et al 1993). Meaningful levels of variation include 0, 0.1, 0.25, and 0.5.

Two main performance criteria are implemented in the model to evaluate the risks of exposure to various anthropogenic hazards:

1. The ‘15-year moving average’ stock growth rate was derived from a user-specified number of Monte Carlo trials (mean ± sd) and,
2. The cumulative biomass yield (million kg) derived from the Monte Carlo trials (mean ± sd) using the mean ageclass-specific weight estimates in Limpus et al (1994a).

It is also possible to estimate the probability of no annual yield derived from 1000 Monte Carlo trials if a 100 year simulation period is specified (mean ± sd).

The 15-year moving average is used to smooth the significant inter-annual variation that results for stochastic realisations (see figures 7a and 8a) and reflects a significant fraction of the 45 years to adulthood. The moving average parameter is adjustable to generate various moving average window smooths assuming a first order exponential annual growth rate trend that is then filtered using a first order exponential smooth of the trend.

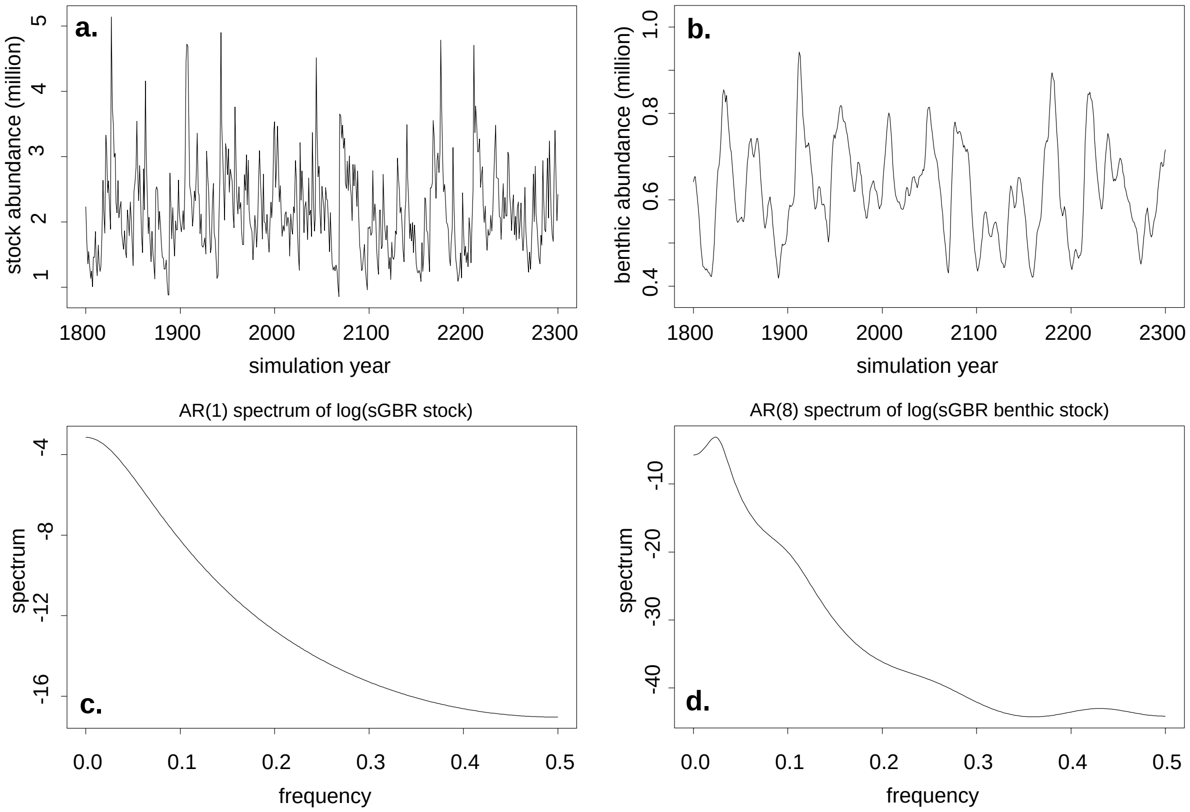

Figure 7. Simulation model temporal behaviour.
Figure 7a shows one sGBR green turtle stock abundance realisation for a 500 year simulation period with the power spectral density function (log scale y-axis = decibels) for that realisation shown as an autoregressive spectral density function (Bloomfield 1976) derived from the 1^{st} order autoregressive or AR(1) model fit in Figure 7c. Figure 7b shows one sGBR benthic substock abundance realisation for the same simulation period with the corresponding power spectral density function derived from an AR(9) model fit shown in Figure 7d. All autoregressive spectral density models were fitted using SPLUS (Venables & Ripley 1994) and AIC-based model selection criteria (Anderson et al 1998) to derive the appropriate autoregressive or AR order. The power spectra in figures 7c and figure 7d show a predominance of low frequency variability (reddened noise) that is indicative of temporal variability (environmental stochasticity) in simulated stock abundance. The sGBR green turtle model is capable of reproducing reddened spectra because of the strong environmental stochasticity incorporated in the model due to the lagged effects of major ENSO events on both female and male breeding behaviour.

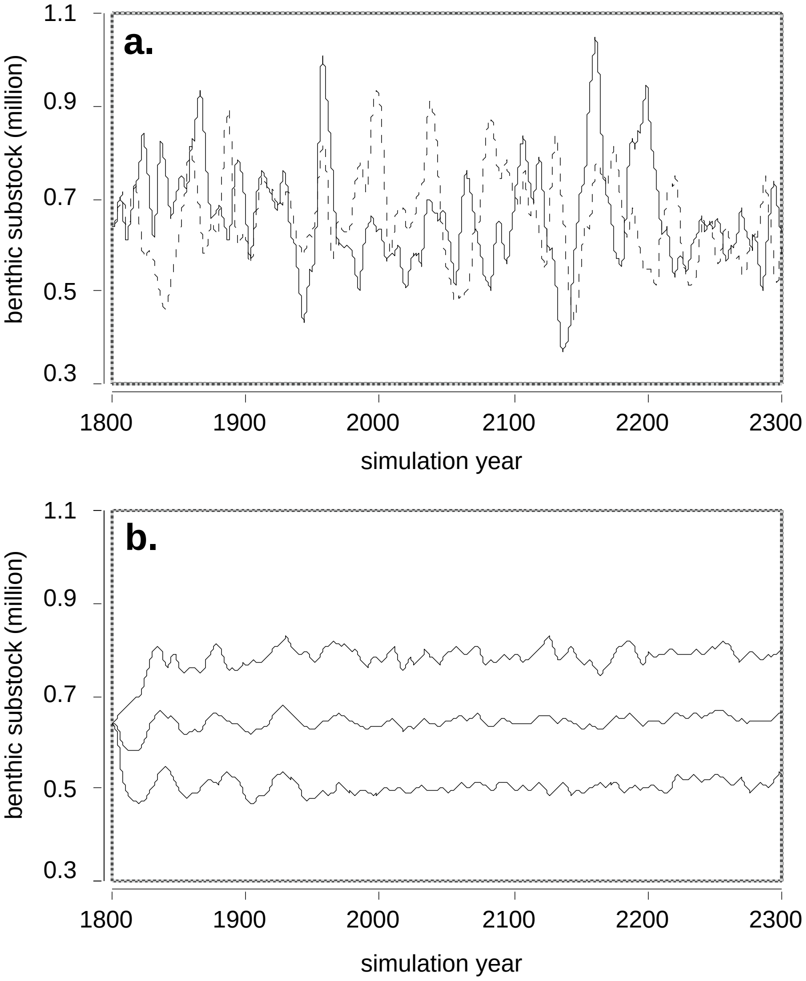

Figure 8. Expected model behaviour.
Panel a. shows two individual stochastic realisations of the model without any other anthropogenic risks. The long-run behaviour of the model for the same runs shown in panel a. is shown in b. as the mean±1 sd of 1000 runs of the model to show the expected or long-run model behaviour.

Other mortality sources such as boat strikes and incidental capture in crab pot fisheries are not significant and so have not been included in the model. However, such losses are easily tested by using the constant offtake functions to implement losses for these minor mortality sources.

Sex ratio, fecundity and demographic stochasticity

The primary sex ratio (PSR = 0.65 female) was sourced from Limpus et al (1984) and Limpus et al (1994a) and is consistent with Horvitz-Thompson type population abundance estimates for sGBR green turtle populations (Chaloupka 2000) and also with estimates derived from long-term studies of the annual variability in hatchling sex ratios for some other green turtle stocks (Godfrey et al 1996). The sex ratio is determined for hatchlings by the temperature profile experienced during egg incubation with females predominant at warmer temperatures and males at cooler temperatures (Limpus et al 1983).

The PSR for hatchlings was sampled in the model from a normal pdf (mean = 0.65, standard deviation = 0.025) to reflect the range of sex ratios observed in the metapopulation (Chaloupka & Limpus 2001). Demographic stochasticity was included here as suggested by Brook et al (2000) to derive the actual number of female and male hatchlings as follows by sampling expected number of female hatchlings from a Poisson pmf (see Gustafsson 2000).

- Female hatchlings = POISSON((eggs hatched)*normal(0.65,0.025))
- Male hatchlings = eggs hatched- female hatchlings.

Mean clutch size (EPC = 115.2 ± 7.9) was sourced from Limpus et al (1984) and Limpus & Reed (1985) and is consistent with mean estimates for other green turtle stocks (Mortimer & Carr 1987, Bjorndal & Carr 1989, van Buskirk & Crowder 1994). There is some evidence for seasonal variation in clutch size at other rookeries but the effect is limited (Mortimer & Carr 1987, Bjorndal & Carr 1989) and no such effect is apparent at the sGBR rookeries. There is some evidence for increasing clutch size with age at the Tortuguero rookery in Costa Rica (Bjorndal & Carr 1989) but any effect would be limited when discounted for annual survival of ageing females (Roff 1992).

The expected EPC was implemented in the model by sampling from a Poisson probability mass function (pmf) with $\mu = 115$ that was a good fit to the empirical distribution of clutch sizes for this stock and is a more appropriate sampling function than a normal probability density function (pdf). Mean number of clutches laid by a female per season (CPS = 5.1 ± 1.9, range 1-9, mode = 6) was sourced from Limpus et al (1984) and Limpus & Reed (1985) and is higher than mean estimates for some other green stocks (see Johnson & Ehrhart 1996).

The expected CPS was implemented in the model by sampling from a binomial pmf that was a good fit to the empirical distribution of clutches laid per season for this stock and is a more appropriate sampling function that a normal pdf. Expected annual fecundity per nesting female was then = (POISSON(115)*BINOMIAL(p=0.64,n=9)).

Density-dependent reproductive processes and environmental stochasticity

Expected fertility is a more complex function of the expected fecundity, expected proportion of females and males preparing to breed each season and the number that do breed in a particular season given that there are also sufficient males migrating to sGBR courtship areas to ensure female mating success. Fertility therefore comprises a combination of both environmental and demographic stochasticity with the environmental effects being predominant. The observed proportion of females and males preparing to breed each year in the various foraging grounds fluctuates significantly from year to year (Limpus & Nicholls 1994, Limpus 1999, see figure 4 in Chalopuka 2002).

Table 3. Estimated sex-specific proportion preparing to breed probability density functions given that either 'no prior ENSO' event in last 2 years or there was a major 'prior ENSO' event in the last 2 year. Data series sourced from Limpus (1999).

pdf	parameters	female		male	
		no prior ENSO	prior ENSO	no prior ENSO	prior ENSO
Weibull	location	0	0.05	0.05	0.25
	scale	0.125	0.333	0.10	0.45
	shape	1.2	2	1.2	6

The average recurrence interval (ari) of major ENSO events is 5 years so the expected female proportion preparing to breed was determined as follows using 1000 Monte Carlo trials:

wafpb = ((1 / ari).(Weibull(0.05,0.333,2))+((1-1 / ari).(Weibull(0,0.125,1.2)))=0.161, which gives a mean remigration interval = 1 / wafpb = 6.2 years.

For males: wampb = 0.249 or a mean remigration interval = 4 years. The expected proportions of females and males preparing to breed each year are in the same proportion as the foraging ground population sex ratio (norm(0.65,0.025) female) so that roughly equal numbers of males and females migrate each year to the breeding grounds in sGBR waters to ensure successful mating even though females in the foraging grounds outnumber males by ca 2:1.

This often results in very long periods between successive breeding seasons for most mature sGBR green turtles (Limpus 1993, Limpus et al 1994b, Limpus 1999) known as remigration intervals. A lognormal pdf (Fishman 1996) fitted the female Heron / Wistari Reef population remigration interval data well with maximum likelihood parameter estimates of the mean = 5.3 years and standard deviation = 1.6 years (see Chaloupka 2002), which is longer and more variable than estimates for other green turtle stocks (Hendrickson 1958, Mortimer & Carr 1987, van Buskirk & Crowder 1994). More recent updates from the QPWS mark-recapture program suggest that the remigration interval mean = 6 years (Limpus unpub.).

This significant temporal variability in proportion of females and males preparing to breed while resident in the foraging grounds is a two year lagged response to major ENSO events over the last two years (Limpus & Nicholls 1994, see also Chaloupka 2001a for similar response for green turtles nesting at southeast Asian rookeries). The mechanism for this delayed response is not well understood but is considered to be food related (Bjorndal 1997) as green turtles take one to two years to develop sufficient fat reserves to support vitellogenesis and the breeding migration from the foraging grounds to the courtship grounds and regional rookery in sGBR waters (Kwan 1994).

A more direct way to derive estimates of breeding likelihood for females and males is provided by visual examination of reproductive organs using laparoscopy (Limpus & Reed 1985, Limpus et al 1994a). Based on this method, Limpus (1999) provides time series estimates of the proportion of females and males breeding each year in the three foraging grounds of the sGBR genetic stock (see figure 4 in Chaloupka 2002). Probability density functions were fitted to these three series using maximum likelihood estimation (Fishman 1996) to derive sampling functions for use in the model of sGBR green turtle metapopulation dynamics.

These sampling distributions reflect environmental stochasticity due to prior ENSO history on both female and male breeding behaviour. Strong temporal correlations in breeding behaviour also occur between the foraging grounds that reflects the regional environmental forcing of the metapopulation breeding behaviour know as a spatially autocorrelated Moran effect (Chaloupka 2001a).

The best fit pdfs to the empirical estimates of both males and females preparing to breed each year in all foraging grounds given prior ENSO history are summarised in table 3. These sex- and ENSO-specific pdfs were incorporated in the model to determine the expected annual sex-specific breeding proportions. These pdfs give the expected remigration intervals ca six years for females and four years for males that are now recorded for the sGBR metapopulation (Table 3).

Importantly, the prior ENSO history comprises an assessment of the last two years but enhanced breeding can only occur if there was a major ENSO event two years previous (see Limpus & Nicholls 1994). A sequential run of two ENSO events, which happens, does not trigger the same response for the subsequent year because female green turtles cannot reproduce each year even if conditions are favourable. Hence the minimum remigration interval for females is two years and is why there are substantial fluctuations in the number of green turtles nesting each year at the sGBR regional rookery. Anomalous high nesting seasons are usually followed the next year by an anomalous low nesting season.

A sequential run of three events, which happens, will trigger the enhanced breed response two years later for the first year of the sequence and not for the second but will trigger the response again two years after the third year in the ENSO sequence. This same pattern of conditional ENSO triggered nesting anomalies is displayed by the other northern Australian and southeast Asian green turtle stocks (Chaloupka 2001a). The Markovian pattern of ENSO-triggered breeding behaviour is incorporated in the simulation model.

The expected breeding proportions were also assumed to be density-dependent by linking the Weibull pdf scale parameter for each sex given prior ENSO history to benthic metapopulation density. Density-dependent demography is a contentious issue (Strong 1986, Shenk et al 1998) but populations simply will not rebound or recover after a major perturbation unless some form of density-dependent demography occurs.

Bjorndal et al (2000) have shown evidence of density-dependent effects on green turtle growth that were assumed to be related to declining per capita food availability as the population increased. Moreover, there was a decline in the observed proportion of breeding females from the Heron / Wistari foraging ground (see figure 5 in Chaloupka 2002) that possibly reflects a density-dependent effect due to increasing population abundance in this foraging ground population (Chaloupka & Limpus 2001).

It was then reasonable to assume that food availability could also have an effect on green turtle breeding preparation in the sGBR metapopulation foraging grounds. Moreover, many marine vertebrate populations do recover from significant levels of harvesting (Smith et al 1998, Fromentin et al 2001) but this recovery can take a long time for sea turtles (Horikoshi et al 1994, Chaloupka 2001a) so that any density-dependent effects in the model need to be readily amended in light of new information. Hence, the model includes a switch to turn on or off any density-dependent functions to help evaluate the effect of including density-dependence and the assumed functional form of that dependence on model performance and sensitivity. All model runs here were based on the assumed density-dependent functions being in effect.

The functional form for each sex/ENSO combination is shown in figure 6a based on a Morgan-Mercer-Flodin function where $y = (a.b + c.X^{d})/(b + X^{d})$ and (a-d) are estimable or adjustable parameters, y = expected proportion preparing to breed each year and X = (1-relative density). The range of the density-dependent functions in figure 6a reflects the range of male and female breeding proportions recorded for the Heron/Wistari Reef, Moreton Bay and Shoalwater Bay populations (Limpus 1999).

The Morgan-Mercer-Flodin function is extremely flexible with good statistical fitting properties (Ratkowsky 1990) and is readily adjusted in the model to correct for new information or to evaluate the effect of different functional forms on model performance and sensitivity. Special cases of the Morgan-Mercer-Flodin function include the rectangular hyperbola, the Michaelis-Menten-Monod, the Holling Types I-III and the Hill functions that are used to reflect growth, nutrient uptake, predator consumption or density-dependent demographic functions.

The male and female Weibull pdf samplings are correlated to ensure that high probabilities for females occur simultaneously with high probabilities for males. The correlation was imposed in the model using the methods outlined in Fishman (1996) that are valid for correlating pdfs when the inverse transformation method is used for deriving a pdf from a uniform random variate in the [0,1] interval. All Weibull pdfs are derived using the inversion method but it is not possible to vary the strength of the correlation using the Fishman method, which was assumed to be 100% in the model.

For instance, the expected annual proportion of mature females preparing to breed each year given no prior ENSO history but with the capacity to turn off the Mercer-Morgan-Flodin form of scale parameter density-dependence (see figure 6a) was sampled from a Weibull pdf constrained to the empirical based interval [0.01,0.45] as follows:

> MAX(0.01,MIN((scale*(-ln(random(0,1)))$^{(1/shape)}$ +location),0.45))
>
> Where…
>
> location=0,
> scale= ndd_scale*(1-dd_switch)+dd_scale*dd_switch,
> shape=1.2,
> ndd_scale=0.125
> dd_scale = (a*b+c*(1-benthic stock density)^{d})/(b+(1-benthic stock density)^{d}),
> a=0.10, b=0.025, c=0.25, d=3

The actual proportion of males and females preparing to breed each year in the model is then calculated by first determining the Weibull pdf scale parameter for each sex given prior ENSO history and current relative benthic metapopulation density (see figure 6a) and then by sampling the expected proportion of males and females that will migrate that year to the breeding grounds from Weibull pdfs given that sampled scale parameter (Table 2). This procedure implements compensatory density-dependent environmental stochasticity into the sex-specific breeding behaviour that can be readily adjusted in the model to evaluate the effect of different forms of the flexible Morgan-Mercer-Flodin function on model performance and sensitivity.

The actual number of females breeding and then nesting depends not only on preparing to breed given prior ENSO history but also the probability of actually finding at least one male to mate with in the courtship grounds. For instance, if many females are ready to mate but there are too few males then many potential pregnancies will not be realised due to the male shortage. This is a form of depensatory density-dependence known as an Allee effect (Dennis 1989) that is an important demographic process affecting the recovery or rebound capacity of populations exposed to perturbations such as harvesting or a run of ecological catastrophes.

The mating success probability function used in the model was based on another Morgan-Mercer-Flodin function where: $y = (a.b + c.X^{d}) / (b + X^{d})$, (a-d) are adjustable parameters, y = probability of a female in the courtship grounds finding and mating with at least one male and X = relative density of mature males assuming they migrated that year to the courtship grounds. This form based on relative density is adopted here mainly to implement sex-biased harvesting potential in the model and assumes that it is the relative abundance of females to males that effects the probability of encountering a mate in the courtship grounds. It is also assumed here that there is some form of competion between females for mates. It is important to note that the functional form in the model shown in figure 6b is only an assumed form as there is no empirical information to derive such a function for the sGBR green turtle metapopulation. Nonetheless, the function is readily adjusted to reflect other forms if necessary and to evaluate the effect of various forms on model performance and sensitivity.

The expected number of nesting females was then a function of the age- and habitat-specific maturation probability (see figure 5b), the breeding preparation probability given prior ENSO history and benthic metapopulation density (see figure 6a) and the probability of finding at least one male mate given reproductive migration (see figure 6b). Demographic stochasticity was then included here in the model by sampling the expected number of females nesting on coral cays at the sGBR regional rookery from a Poisson pmf (see Gustafsson 2000) to determine the actual number of females nesting each year. The proportion of those nesting females that nested on Heron Island in the regional rookery was also determined to use as a reference check on model performance.

Environmental forcing function

The average recurrence interval (ARI) for major ENSO events is ca five years (Trenberth & Hoar 1997) but this parameter is adjustable in the model. The ENSO sequence is generated using a random uniform variate in the [0,1] interval conditional on a prescribed ARI threshold. Moreover, the frequency and magnitude of ENSO events has increased over the last 25 years (Trenberth & Hoar 1997) so the model also includes a switch to turn on or off the apparent Pacific basin regime shift from 1975 onwards. This switching capacity in the model is useful for testing the importance of a time-varying form of ENSO function on model performance and sensitivity. See Chaloupka (2001a) for a discussion of this major oceanographic regime shift on the nesting behaviour of southeast Asian green turtle stocks.

MODEL ESTIMATION

The model was implemented using a general purpose ordinary differential equation (ODE) solver using 4th order Runge-Kutta numerical integration with a one year sampling period and an integration step or dt=1 to reflect the seasonal birth pulse reproductive behaviour of the sGBR metapopulation (Caswell 1989), hence the differential equations are difference equations. The model was initialised with a stock of 1 199 433 green turtles comprising 558 171 pelagic juveniles, 480 475 benthic juveniles, 122 170 immatures, 25 986 subadults and 12 631 adults with the benthic substock abundance = 641 262 (see Chaloupka & Limpus 2001). These initialisation abundances are consistent with relative benthic abundance estimates for the sGBR foraging ground population of the sGBR metapopulation (Chaloupka & Limpus 2001). Many model control parameters and variables are linked to slider devices so they can be readily changed by the user. The model was implemented in MADONNA, which is a robust, fast and easy to use ODE solver.

MODEL EVALUATION

Evaluating model performance is a complex issue that usually requires a pragmatic approach to assessing model verification and validation (Oreskes et al 1994). Verification concerns the conceptual logic and quality of demographic information used in the model. The conceptual ecological logic used in constructing the sGBR green turtle simulation model is shown in figure 2 and was based on demographic information for this stock derived from the long-term QPWS sea turtle research program. See Limpus (1992, 1993, 1998), Limpus & Chaloupka (1997, 1998a), Limpus & Nicholls (1994), Limpus & Reed (1985), Limpus et al (1984, 1992, 1994a, 1994b), Brand-Gardner et al (1999), Chaloupka (2000, 2001b), Chaloupka & Limpus (2001), Chaloupka et al (in press), FitzSimmons et al (1997a, 1997b), Forbes (1994), Gyuris (1994), Slater et al (1998) and Whiting & Miller (1998). There is no reason to consider that the model formalism used here was conceptually incorrect.

On the other hand, model validation is concerned with evaluating whether the simulation model is acceptable for its intended use given various performance criteria (Rykiel 1996) and was assessed here using 2 approaches:

1. assessment of model capability to produce outputs that mimic qualitatively a range of empirical information including stock reference behaviours such as population trends or time series characteristics such as reddened spectra of annual nesting abundance; and

2. multi-factor sensitivity analysis to identify the demographic parameters that affect model behaviour the most and to determine whether those parameters were estimated with reasonable accuracy.

Reference behaviours

Quantile plots of some of the key model outputs are summarised in figure 9, which shows the distribution of specific projections or values sampled in model runs assuming a stable but fluctuating stock subject to environmental and demographic stochasticity but no anthropogenic risks. Figure 9a shows one realisation of survival probabilities sampled over a 500 year simulation period from a logistic pdf for eggs, a logistic pdf for pelagic juveniles (ca 1-6 yrs) and a logistic pdf for benthic juveniles (5-15 yrs). Figure 9b shows one realisation of survival probabilities sampled from a left-skewed extreme value pdf for adults (>= 46 yrs), a right-skewed extreme value pdf for subadults (30-45 yrs) and a logistic pdf for immatures (16-29 yrs) that was also correlated with subadult survival (high immature survival with high subadult survival).

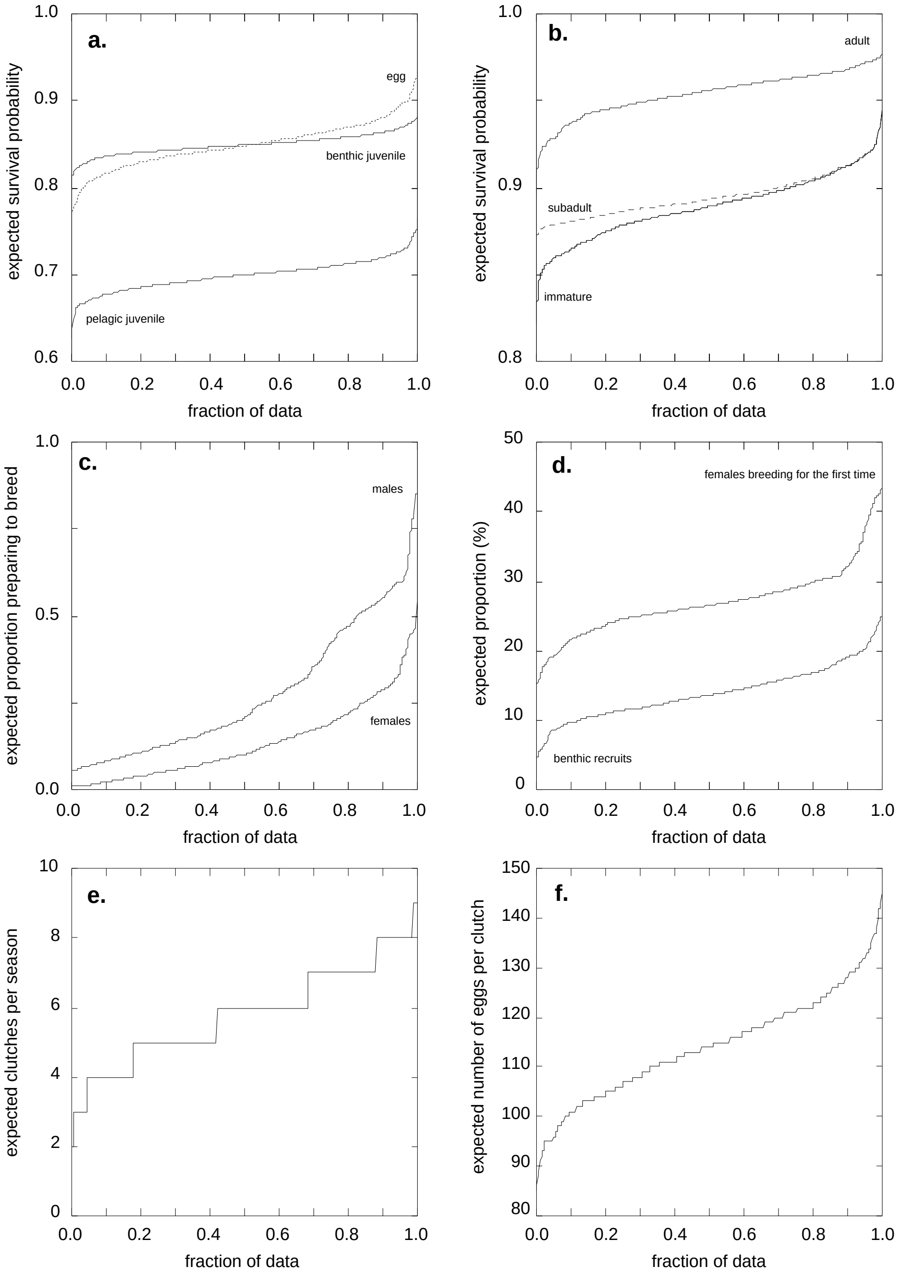

Figure 9. Quantile plots of some key model outputs showing distribution of specific projections or values sampled in model runs assuming a stable but fluctuating stock subject to environmental stochasticity but no anthropogenic risks.

Figure 9a shows one realisation of survival probabilities sampled over a 500 year simulation period from a logistic pdf for eggs, a logistic pdf for pelagic juveniles and a logistic pdf for benthic juveniles. Figure 9b shows one realisation of survival probabilities sampled from a left-skewed extreme value pdf for adults, a right-skewed extreme value pdf for subadults and a logistic pdf for immatures that was correlated with subadult survival. Figure 9c shows one realisation of the proportion of mature females and males actually breeding each year sampled from sex-specific Weibull pdfs that were dependent on benthic substock density and on ENSO history over previous two years (see figure 6a). Figure 9d shows one realisation of the proportion of first time female breeders and new recruits to the benthic habitat at ca 40 cm CCL. These are useful parameters to help assess stock viability since both parameters are readily measured in the field and so might be useful early warning metrics (see Limpus 1999). Figure 9e shows one realisation of the expected clutches per nesting female per season sampled from a binomial pmf that fitted the empirical estimates of clutches per season recorded for the stock. Figure 9f shows one realisation of expected eggs per clutch sampled from a Poisson pmf that fitted empirical estimates of eggs per clutch recorded for the stock. See Cleveland (1993) for description of quantile plots.

Autoregressive spectral analysis (Bloomfield 1976) was used to derive the spectral properties of the stochastic temporal model output. Spectral colour identified by specific patterns in the spectral density function is used to identify the scale of environmental variability that might be involved in the temporal fluctuations commonly observed in long-term ecological series (Cuddington & Yodzis 1999). More importantly, Cohen (1995) has shown that realistic ecological simulation models should be capable of producing reddened power spectra of model output while reddened spectra have been found for long time series of annual sea turtle egg production (Chaloupka 2001a).

Table 4. Summary of 3 level fractional factorial ($FF3^{11}$) design used to assess the sGBR green turtle model sensitivity given an ecologically realistic range of demographic parameter variability.

	parameter values											
run	**X1**	**X2**	**X3**	**X4**	**X5**	**X6**	**X7**	**X8**	**X9**	**X10**	**X11**	**masgr**
1	0.816	0.677	0.836	0.864	0.880	0.937	0.020	0.080	4	101	38	-0.0549
2	0.816	0.677	0.849	0.912	0.913	0.968	0.288	0.553	8	128	28	0.0552
3	0.816	0.677	0.864	0.890	0.893	0.956	0.100	0.208	6	115	33	-0.0048
4	0.816	0.699	0.836	0.912	0.913	0.968	0.100	0.208	6	101	38	-0.0017
5	0.816	0.699	0.849	0.890	0.893	0.956	0.020	0.080	4	128	28	-0.0314
6	0.816	0.699	0.864	0.864	0.880	0.937	0.288	0.553	8	115	33	0.0151
7	0.816	0.719	0.836	0.890	0.893	0.956	0.288	0.553	8	101	38	0.0094
8	0.816	0.719	0.849	0.864	0.880	0.937	0.100	0.208	6	128	28	-0.0029
9	0.816	0.719	0.864	0.912	0.913	0.968	0.020	0.080	4	115	33	-0.0179
10	0.848	0.677	0.836	0.912	0.893	0.937	0.288	0.208	4	128	33	0.0007
11	0.848	0.677	0.849	0.890	0.880	0.968	0.100	0.080	8	115	38	-0.0108
12	0.848	0.677	0.864	0.864	0.913	0.956	0.020	0.553	6	101	28	-0.0298
13	0.848	0.699	0.836	0.890	0.880	0.968	0.020	0.553	6	128	33	-0.0243
14	0.848	0.699	0.849	0.864	0.913	0.956	0.288	0.208	4	115	38	-0.0083
15	0.848	0.699	0.864	0.912	0.893	0.937	0.100	0.080	8	101	28	0.0158
16	0.848	0.719	0.836	0.864	0.913	0.956	0.100	0.080	8	128	33	-0.0061
17	0.848	0.719	0.849	0.912	0.893	0.937	0.020	0.553	6	115	38	-0.0338
18	0.848	0.719	0.864	0.890	0.880	0.968	0.288	0.208	4	101	28	0.0165
19	0.881	0.677	0.836	0.890	0.913	0.937	0.100	0.553	4	115	28	-0.0077
20	0.881	0.677	0.849	0.864	0.893	0.968	0.020	0.208	8	101	33	-0.0248
21	0.881	0.677	0.864	0.912	0.880	0.956	0.288	0.080	6	128	38	-0.0391
22	0.881	0.699	0.836	0.864	0.893	0.968	0.288	0.080	6	115	28	-0.0314
23	0.881	0.699	0.849	0.912	0.880	0.956	0.100	0.553	4	101	33	-0.0089
24	0.881	0.699	0.864	0.890	0.913	0.937	0.020	0.208	8	128	38	-0.0255
25	0.881	0.719	0.836	0.912	0.880	0.956	0.020	0.208	8	115	28	-0.0178
26	0.881	0.719	0.849	0.890	0.913	0.937	0.288	0.080	6	101	33	-0.0513
27	0.881	0.719	0.864	0.864	0.893	0.968	0.100	0.553	4	128	38	-0.0106

Eleven demographic parameters were fixed at 3 levels (10th, 50th, 90th percentiles) for each pdf sampled for X1-X10 or at 3 adjusted levels of the age parameter (–5, 0, 5 years) to yield median age-at-maturity of 28, 33 or 38 years for stock.

X1 = expected egg survival probability,
X2 = expected annual pelagic juvenile survival probability,
X3 = expected annual benthic juvenile survival probability,
X4 = expected annual immature survival probability,
X5 = expected annual subadult survival probability,
X6 = expected annual adult survival probability,
X7 = expected proportion of mature females preparing to breed each year,
X8 = expected proportion of mature males preparing to breed each year,
X9 = expected clutches per nesting female per season.
X10 = expected eggs laid per clutch,
X11 = expected median age-at-maturity for stock.

masgr = mean annual stock growth rate realised at the end of a 100 year simulation period derived from 1000 Monte Carlo trials for each of the 27 runs. Similar mean stock growth rates occur irrespective of whether model performance was assessed at 50, 75 or 100 years, during the 100 simulation period because mean growth was in quasi-steady state by year 50. Standard deviations were recorded for each run from the trials but there was negligible variability so not shown here to reduce clutter.

Unfortunately, there are no long-term time series of sGBR green turtle stock abundance or annual egg production. The longest series of benthic substock abundance derived from the QPWS sea turtle research program spans only a 10 year series (Chaloupka & Limpus 2001, Chaloupka 2002), which is not only too short for model calibration but the data were used to construct the initial model ageclass abundances. The most useful independent sGBR abundance series or abundance index is the annual census of female nesters on Heron Island (see figure 10a) that has been in place for the last 25 years.

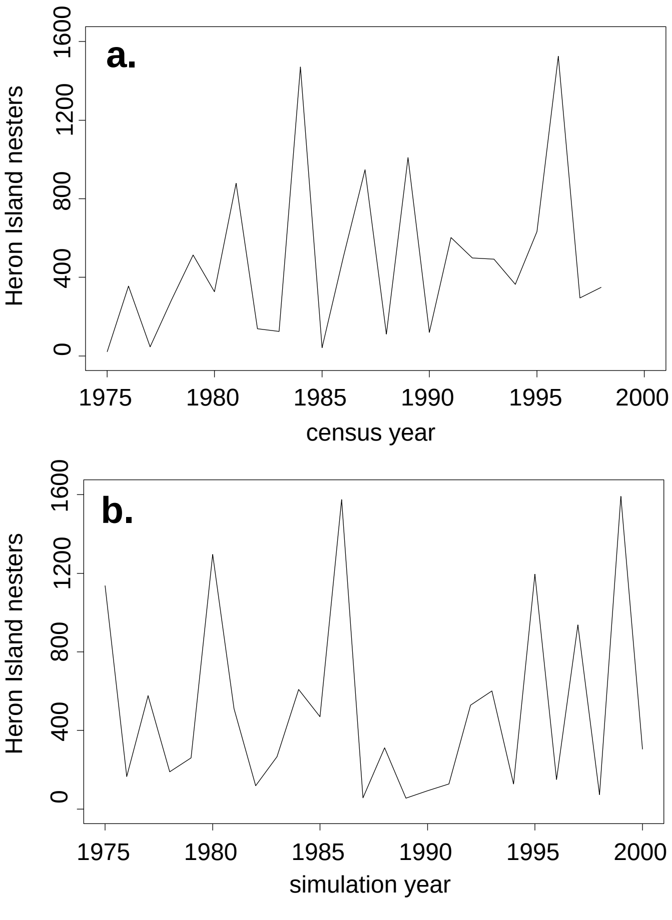

Figure 10. Nesting beach census reference behaviour.
Panel A shows the actual census of female green turtles nesting each year on Heron Island for the 1975 to the 1998 summer nesting seasons with mean = 485, sd = 417, median = 360 (source: Limpus unpub.). Panel B shows one realisation of the green turtle simulation model output for Heron Island nesters. The statistical summary for Heron nesters derived from 1000 Monte Carlo trials of the model was mean = 431, sd = 367 and median = 390. The two time series realisations do not match because the ENSO sequences are different although the statistical summaries (mean, sd, median) of the long run behaviour of the two series are similar. The simulation model is a heuristic

model intended to help develop a good understanding of sGBR green turtle population dynamics not a predictive or curve fitting model. It is of course possible to include the actual ENSO sequence to force the model to reflect the exact fluctuations between 1975 and 2000 shown in figure 10a, but then the model would no longer be a general purpose heuristic model capable for supporting broad ecological insights and would be of little general purpose use for designing and testing long-term conservation policies.

Figure 10a shows the observed census of females nesting on Heron Island since 1975 while one realisation of the model output for Heron Island nesting females is shown in Figure 10b. Note the similar qualitative and quantitative behaviour between figure 10a and figure 10b. Large occasional single year peaks with up to 1600 nesters followed usually by a substantial reduction in nesting the following season to as low as 30 nesters. These fluctuations are due to the Markovian effect of major ENSO events that are the key environmental forcing functions influencing sGBR green turtle reproductive behaviour.

Overall, the model produces temporal behaviour (see figures 9 and 10) that is fully consistent with the demographic information incorporated in the model. These data were sourced mainly from the long-term QPWS sea turtle research program.

Multi-factor parameter sensitivity analysis

It is common practice to use individual parameter perturbation to assess sea turtle population model sensitivity to small parameter changes (see Chaloupka & Musick 1997). This approach has several shortcomings and can result in seriously biased assessments because of nonlinear and parameter interaction effects (Bartell et al 1986, Breininger et al 1999, Mills et al 1999). A more robust approach is based on using experimental or sampling design principles to identify specific parameter combinations to be changed over a realistic ecological range. However, the stochastic simulation model developed here has many parameters and so sensitivity analysis would require an orthogonal factorial sampling design involving millions of combinations.

This many combinations can be reduced by selecting only those parameters presumed likely to have a major impact on model behaviour. Survival is usually considered the most important model parameter for sea turtle population dynamics while, interestingly, fertility has been considered least important (Crouse et al 1987, Crowder et al 1994, Siddeek & Baldwin 1996).

The parameters selected here for sensitivity analysis were the expected survival probabilities for eggs, pelagic juveniles, benthic juveniles, immatures, subadults and adults as well as the expected female and male preparing to breed probability, expected fecundity (eggs per clutch, clutches per season) and the expected metapopulation median age-at-maturity (see figure 5c). Ten of the eleven parameters were fixed at three ordinal levels defined by the three percentiles (10th, 50th and 90th) that summarised the best fit pdf for each parameter while median age-at-maturity was fixed at three ordinal levels by adjusting the mid-age parameter in the maturity functions to derive median age-at-maturity = 28, 33 or 38 years (see figure 5c).

Recall that egg, juvenile and immature survival probabilities were sampled from logistic pdfs, subadult and adult survival probabilities were sampled from correlated extreme value pdfs, sex-specific breeding proportions were sampled from correlated density. Prior ENSO history dependent Weibull pdfs and the fecundity parameters were sampled from binomial or Poisson probability mass functions. Sampling a parameter-specific pdf at the three percentile levels ensured that an ecologically realistic range of parameter variation was included in model evaluation (Breininger at al. 1999) while reducing the factorial combinations to a mere 3^{11} = 177 147.

Fractional factorial sampling enables further reduction in combinations needed to evaluate the impact of parameter changes on model performance (Steinhorst et al 1978, Henderson-Sellers & Henderson-Sellers 1996). The simplest fractional factorial sampling design possible for eleven elements sampled at three levels is a 3^{11} fractional factorial design ($FF3^{11}$) with limited replication (Cochran & Cox 1957). This particular FF3 design assumes only a main effects model with all multi-factor interactions confounded with the main effects. The FF3 sampling design used here to evaluate model sensitivity requires only 27 element combination sets or runs to estimate the eleven parameter effects on model performance (see table 4), which is a substantial reduction from the full factorial 3^{11} sampling design that would require 177 147 combination sets.

The performance criterion used here was a fifteen year moving average population growth rate smooth (±1 sd) derived for each of the 27 FF3 design runs from 1000 Monte Carlo trials sampled over a 100 year simulation period. An 11-factor main effects ANOVA accounting for quadratic functional form was fitted to the Monte Carlo derived mean and variance for each run using a variance-weighted generalised linear model (Nelder & McCullagh 1989). The $FF3^{11}$-ANOVA design and model were estimated using JMP (SAS Institute 1994). The parameter sensitivity model results were summarised using prediction profile plots that are used in quality improvement and industrial studies (Box et al 1978).

A prediction profile plot shows the predicted main effect of changing the eleven parameters on the simulated sGBR metapopulation growth, which are shown in figure 10. Recall that there were eleven parameters selected for sensitivity analysis but only seven were found to have a significant statistical effect on expected stock growth rate (see figure 11). Pelagic juvenile survival, benthic juvenile survival, subadult survival and expected eggs per clutch were all parameters found not to have a significant effect and so are not shown as the model was not sensitive to variation in those parameters given the functional form assumed in the model.

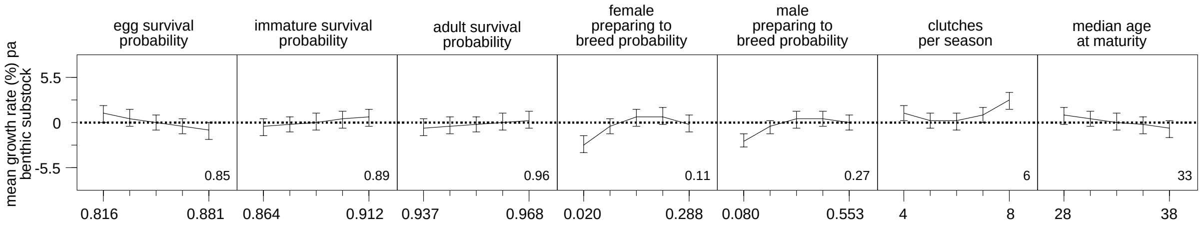

Figure 11. Parameter sensitivity analysis.
Prediction profile plot showing the effects of simultaneously changing eleven major demographic parameters on the predicted 'fifteen year moving average' stock growth rate smooth in accordance with a FF3[11] sampling design (Table 4). Only seven of the eleven parameters were found to have a significant statistical effect on expected stock growth rate and are shown here. Pelagic juvenile survival, benthic juvenile survival, subadult survival and expected eggs per clutch were not significant so not shown. The seven significant parameter-specific prediction traces shown above by solid curves and the 95% confidence intervals shown by error bars were derived from a weighted-variance ANOVA model with quadratic covariate functional form that was a good fit to 1000 Monte Carlo trials of the mean predicted growth rate for each of the 27 fractional factorial runs. Dashed line shows a specific combination of parameter levels that was predicted to yield a zero growth rate.

The seven significant parameter-specific prediction traces shown above by solid curves and the 95% confidence intervals shown by error bars were derived from a weighted-variance ANOVA model with quadratic covariate functional form. The model was a good fit to 1000 Monte Carlo trials of the mean predicted growth rate for each of the 27 fractional factorial runs (R^2 = 0.93, rmse = 0.008). The dashed line shows a specific combination of the 7 parameter levels that was predicted to yield a zero growth rate.

The model output is most sensitive to ecologically realistic variations in the annual proportion of females and males preparing to breed, expected number of clutches laid each season per female, expected median age-at-maturity and expected egg survival probability. All significant parameters were well estimated for the sGBR green turtle stock except for median age-at-maturity that requires further long-term field study although the maturity functions are based on the size- and age-specific somatic growth functions that are well estimated for this stock.

MODEL APPLICATION

Overall, the model is considered fit for use in conservation policy design and testing given the following model performance evaluation considerations:

- model based on data derived from the comprehensive long-term QPWS sea turtle research program (see Chaloupka 2002 and references therein);
- inclusion in the model of the major demographic processes affecting sGBR green turtle stock abundance subject to environmental and demographic stochasticity (see figure 2);
- most of the parameters that have a significant effect on model performance or sensitivity have been well estimated for the modelled stock (see figure 11);
- model capacity to support extensive parameter changes to test the effect of assumed functional forms and specific parameter values (see Tutorial below); and
- model capacity to account for various but limited empirical stock reference behaviours (see figures 7 & 10).

Some general simulation model runs are now presented to show the model behaviour and performance capabilities.

Figure 12a shows the relative ageclass proportions in the stock for one realisation of the model sampled over the 500 year simulation period from the arbitrary 1800-2300 simulation period. It is apparent from figure 11a that pelagic juveniles comprises ca 70% of the sGBR green turtle stock abundance but can fluctuate significantly between ca 45-90% of the stock and this is one of the reasons why the model is not sensitive to significant variation in pelagic juvenile survival as shown by the fractional factorial sampling design based parameter sensitivity analysis (see table 1 and figure 10). Benthic juveniles comprise ca 25% of the stock while immatures comprise ca 4.5% and matures ca 0.5% of the sGBR stock.

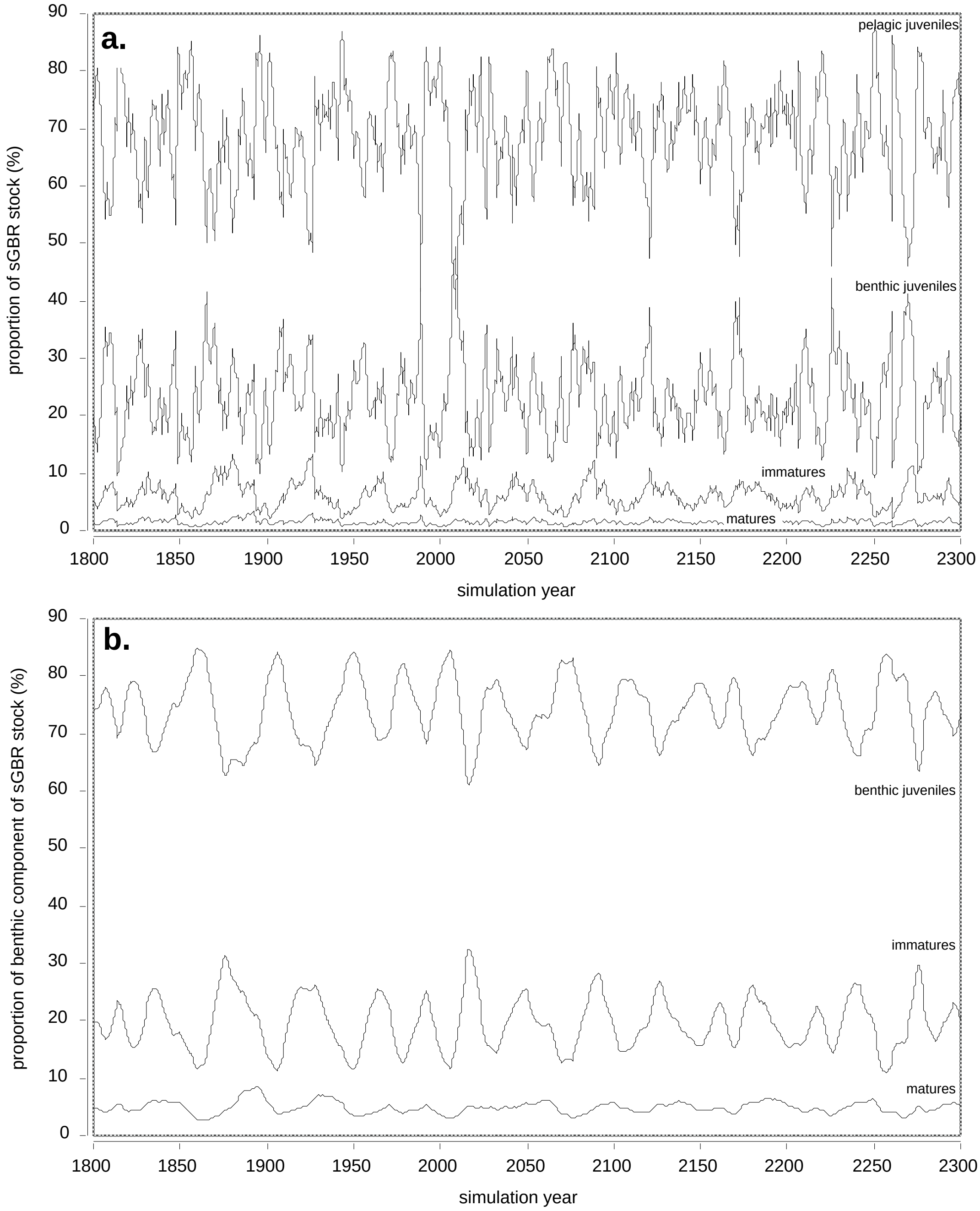

Figure 12. Simulation model behaviour.

Figure 12a shows the relative ageclass proportions in the stock for one realisation of the model sampled over the 500 year simulation period. Figure 12b shows the relative ageclass proportions in the benthic component of the sGBR stock for one realisation of the model sampled over the same period.

Benthic juveniles comprises ca 75% of the benthic substock abundance while immatures comprise ca 20% of the benthic substock and matures ca 5%. The benthic juvenile component of the sGBR benthic substock can fluctuate significantly between ca 60-85% of the benthic substock and this is also one of the reasons why the model is not sensitive to significant variation in benthic juvenile survival as shown by the fractional factorial sampling design based parameter sensitivity analysis (see table 1 and figure 11). The simulated benthic substock abundances are consistent with the empirical Horvitz-

Thompson abundance estimates for some foraging ground populations of the sGBR metapopulation (Chaloupka & Limpus 2001).

Figure 12 shows the results from a single model run over the 500 year simulation period but a stochastic simulation model produces time series behaviour that is highly variable with any one of the individual runs representing a possible stock abundance trajectory over the 500 year simulation period. For instance, two individual stochastic realisations of the model without any other anthropogenic risks are shown in Figure 12a, but which one is the most likely? In order to derive the expected long-run behaviour or most likely outcome it is necessary to run the model given any specific scenario a very large number of times. At least 100 times and at least 1000 times to generate the quasi-extinction curves that are useful for evaluating the potential risk to stock viability given some anthropogenic hazard.

Hence, the long-run behaviour of the model is shown in figure 12b as the mean (±1 standard deviation) derived from 1000 runs of the model. The expected behaviour of the model is now clear with the mean or expected sGBR benthic substock abundance ca 650,000 individuals but could vary between ca 500 000 to 800 000 individuals given the 67% confidence band represented by the mean ± 1 sd, which is consistent with the estimated abundance of green turtles in the GBR region derived by Chaloupka & Limpus (2001).

Some simulation model runs are now presented to show the model behaviour and performance capabilities to evaluate specific risks to stock viability given exposure to single or competing anthropogenic mortality risk factors or hazards. These scenarios are also used in the Tutorial.

Egg harvesting risks

The expected model behaviour given egg harvesting risks is summarised in figure 13 based on 1000 model runs. Figure 13a shows the expected or mean trend (± 1 sd) in mature sGBR green turtle abundance when subject to an egg harvesting risk as follows, 75% of all eggs (or 75% of all clutches) laid each nesting season are harvested for 100 years starting in 1975. The harvest period is shown by the stippled panel and shows the expected delay in the impact of egg harvesting on the mature substock abundance. Egg harvesting at this level clearly has a dramatic affect on stock abundance as discussed in some detail in Chaloupka (2001a) for southeast Asian green turtle stocks.

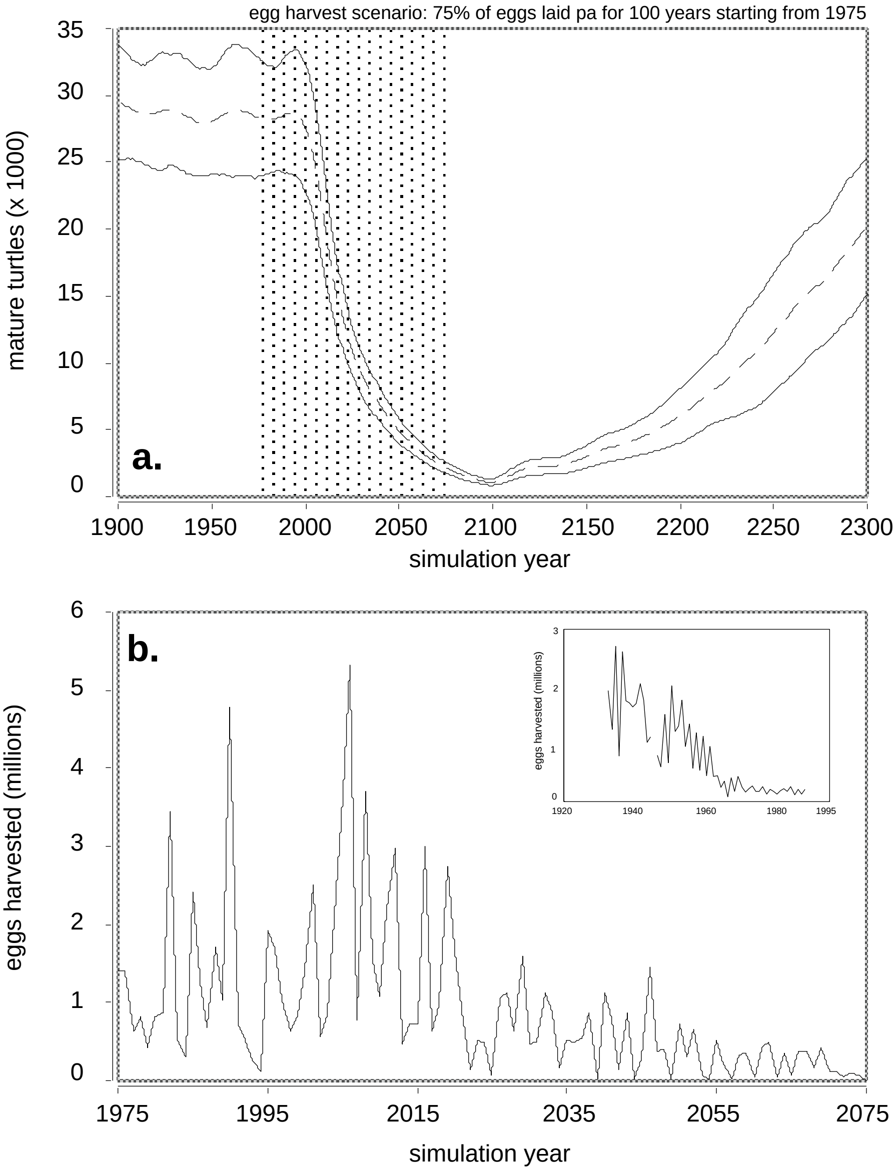

Figure 13. Expected model behaviour given egg harvesting risks.
Panel a. shows the expected or mean trend (± 1 sd) in mature sGBR green turtle abundance when subject to an egg harvesting risk as follows: 75% of all eggs (or 75% of all clutches) laid each nesting season are harvested for 100 years starting in 1975. The 75% egg harvest rate is purely arbitrary and used here for illustrative purposes. The harvest period is shown by the stippled panel and shows the expected delay in the impact of egg harvesting on the mature substock abundance.

The mature substock rebounds after cessation of the egg harvesting but takes on average ca 200 years to recover given the assumed density-dependent reproductive capacity in the model. Figure 13b shows one realisation of the number of eggs harvested each year over the 100 harvesting period (1975-2075) where the impact of egg harvesting is not evident for at least 40-50 years. The inset in figure 13b shows the actual decline in annual eggs harvested for the Sarawak Turtle Island rookery in southeast Asia monitored monthly from the 1930s to the late 1980s (see Chaloupka 2001a) where ca 90% of clutches laid each year were harvested from a year-round nesting stock. The model shows qualitatively similar behaviour (see figure 13b) to the observed long-term decline in eggs harvested as the stock declines for the Sarawak green turtle stock.

Constant rate harvesting risks

The expected model behaviour given constant rate harvesting risks is summarised in figure 14 based on 1000 model runs. Figure 14a shows expected or mean trend in sGBR pelagic juvenile abundance when subject to a constant annual subadult harvest rate as follows — 15% of all subadults across the 4 habitat types are harvested each year for 100 years starting in 1975. Subadult harvesting at this level has a dramatic effect on the stock abundance with the expected benthic substock trend shown in figure 14b and the expected adult substock trend shown in figure 14c. The mean or expected annual catch or landings of subadults is shown in figure 14d along with the expected cumulative biomass or landings weight from the annual harvests. The landings decline as the stock declines despite the slight rebound capacity due to the assumed density-dependent reproductive capacity in the model (see compensatory functional form in figure 6a but also the depensatory form or Allee effect shown in figure 6b).

For instance, figure 14f shows that there was a 40% probability that the adult substock had declined to < 5% of pre-harvest abundance within the 100 year harvesting period. Given this criterion it is apparent that the stock would most likely be well on the way to extinction given harvesting of 15% of subadults each year for 100 years. Further application of this use of cumulative threshold-based quasi-extinction profiles can be found in Akçakaya & Raphael (1998).

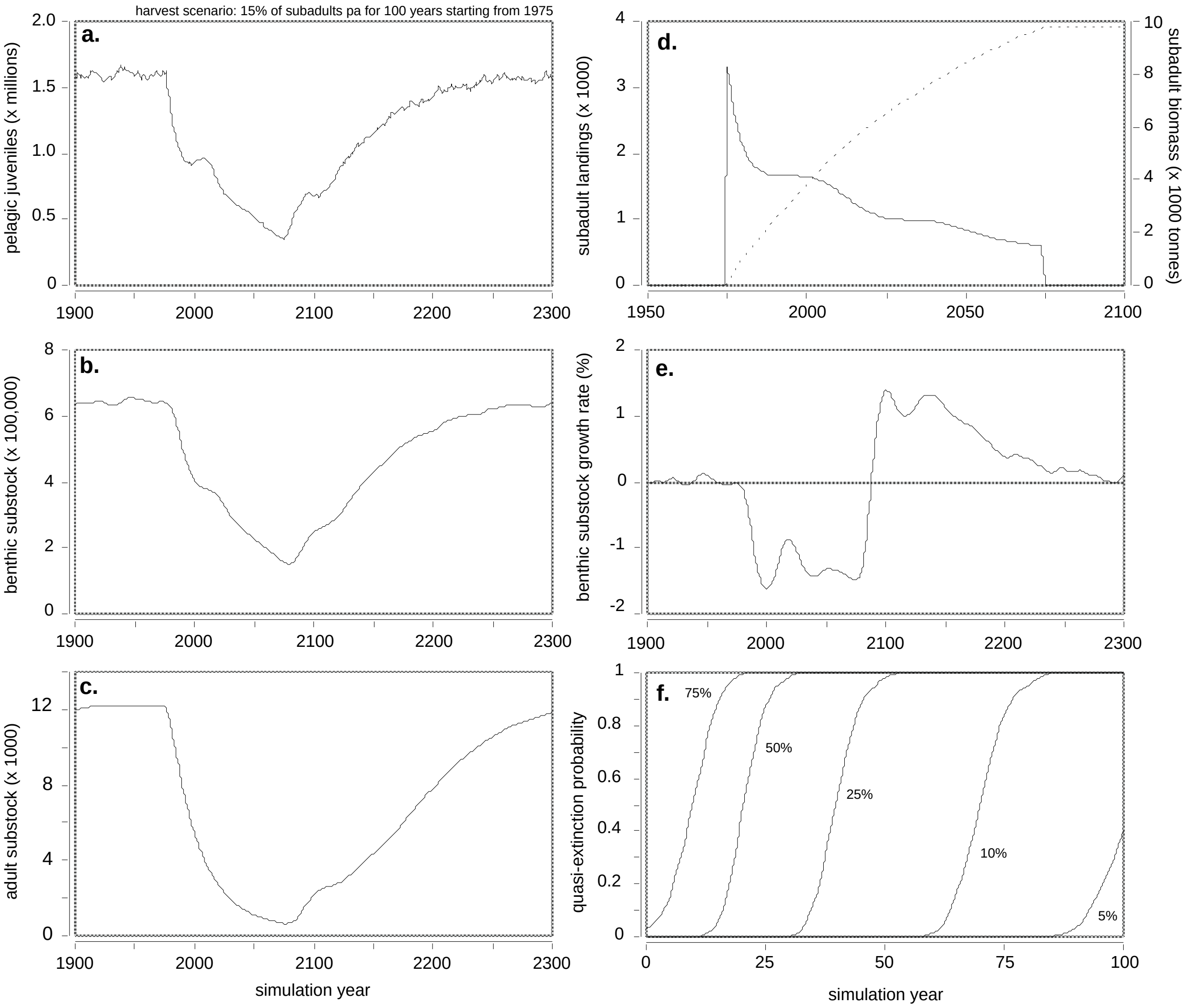

Figure 14. Expected model behaviour given a constant harvesting rate risk.

Constant offtake harvesting risks

The expected model behaviour given a constant harvest offtake rather than a constant harvest rate is summarised in figure 15 based on 1000 model runs. Figure 15a shows the expected or mean trend in pelagic juvenile abundance when subject to a constant annual offtake as follows — a constant quota of 4500 immatures (ca 16-29 yrs) across the four habitat types are taken each year for 100 years starting in 1975. Immature harvesting at this level has a dramatic effect on stock abundance with the expected benthic substock growth rate trend shown in figure 15b, the expected benthic substock abundance trend shown in figure 15c and the expected adult substock abundance trend shown in figure 15d.

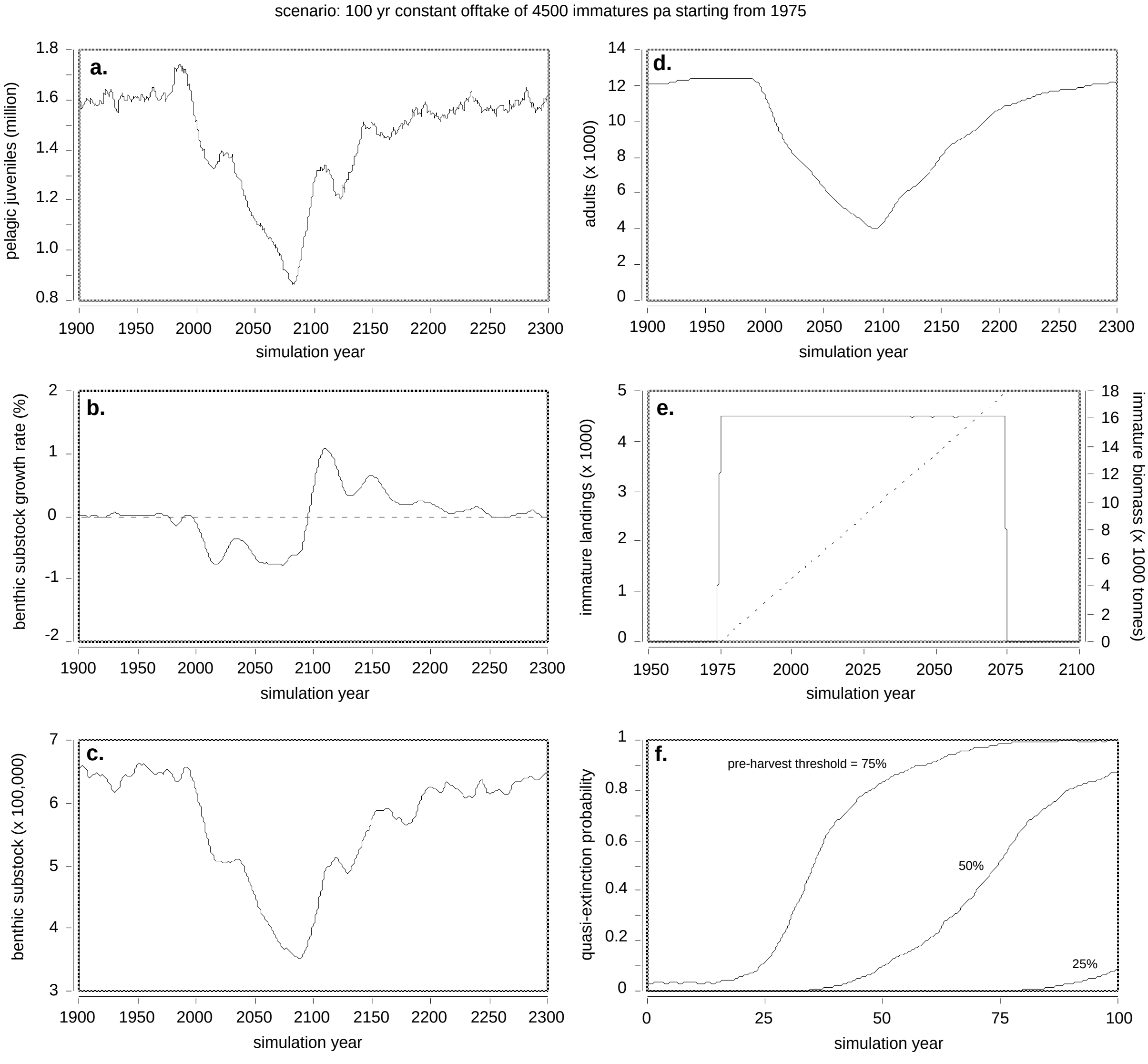

Figure 15. Expected model behaviour given a constant harvest offtake rather than a constant harvest rate.

The constant annual immature offtake is shown in figure 15e along with the expected cumulative biomass from the annual harvests. Panel 15f shows the cumulative quasi-extinction curves (see figure 14f) for reducing the adult substock to below 75%, 50% and 25% of pre-harvest adult substock abundance. There is ca a 10% probability that the adult substock had declined to less than 25% of pre-harvest abundance within the 100 year harvesting period. It has been estimated that 5000 green turtles, mainly from the nGBR stock, are harvested each year in northern Australian waters (Kwan 1991). It would appear given the sGBR model that an annual harvest of 5000 would not be sustainable unless the nGBR stock abundance was significantly greater than the sGBR stock and reproductive output was higher.

Proportional threshold based harvesting risks

The expected model behaviour given a proportional threshold harvesting strategy with moderate adult abundance assessment error (cv = 0.1) in the pre-harvest stock assessment is summarised in figure 16 based on 1000 model runs. Figure 16a shows the expected or mean trend in stock abundance when subject to a proportional threshold harvest as follows: Harvest 75% of the difference between the estimated current adult substock abundance and estimated pre-harvest period adult substock abundance each year across the four habitat types for 100 years starting in 1975. Maintain this harvest strategy so long as the adult substock remains above 50% of the pre-harvest abundance or else stop harvesting until the adult substock recovers above 50% of the pre-harvest period abundance.

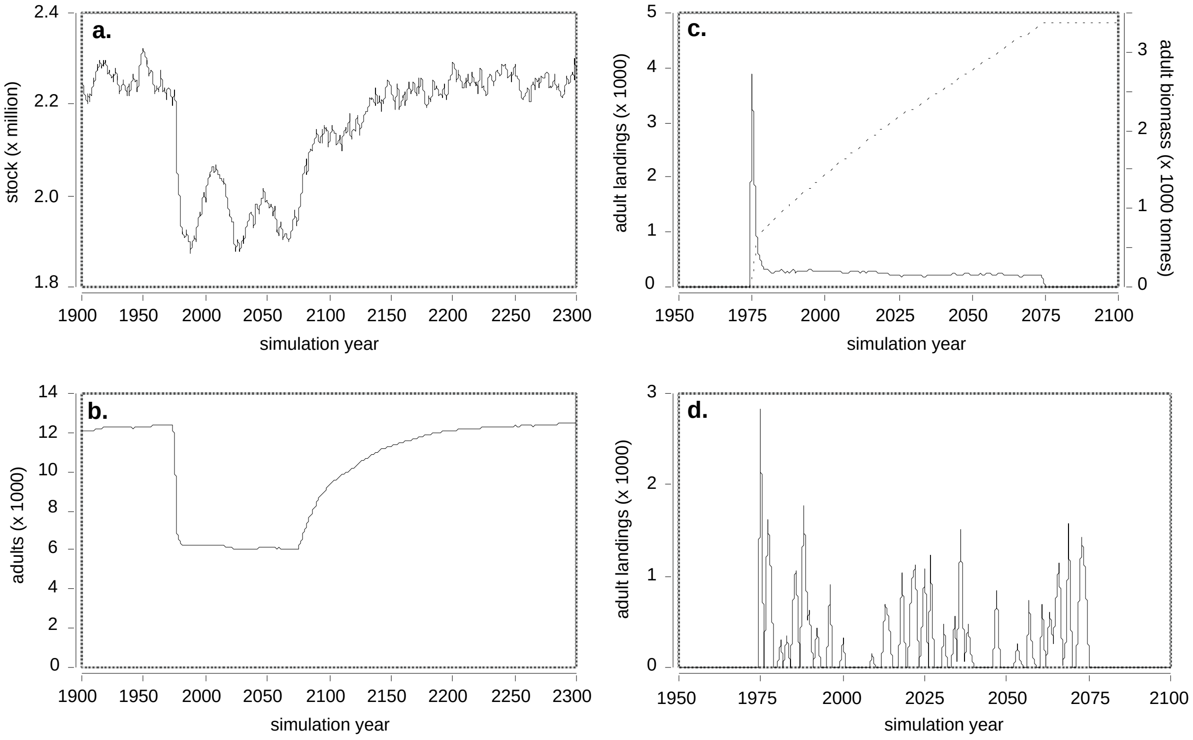

Figure 16. Expected model behaviour given a proportional rate threshold based harvesting strategy with uncertainty or measurement error in the annual pre-harvest stock assessment.

Harvesting under this strategy has less impact than either a constant rate or constant offtake strategy with the expected adult substock abundance trend shown in figure 16b where it is apparent that this strategy maintains the adult substock at a constant level. The expected annual landings and cumulative biomass are shown in figure 16c with a mean annual harvest ca 250 adults after the harvest levels off from 1980 onwards. The actual landings for an individual 500 year model run are shown in figure 16d that shows one of the major drawbacks of threshold based harvesting, which is that there are many years with little or no harvest at all.

As shown elsewhere (Lande et al 1997, Tufto et al 1999), harvesting under such a strategy has less impact than either a constant rate or constant offtake (quota) strategy with the expected adult substock abundance trend shown in figure 16b where it is apparent that this strategy maintains the adult substock at a constant level. The expected annual landings and cumulative biomass are shown in figure 16c with a mean annual harvest ca 250 adults after the harvest levels off from 1980 onwards. The actual landings for an individual 500 year model run are shown in figure 16d that shows one of the major drawbacks of threshold based harvesting, which is that there are many years with little or no harvest at all, especially if the abundance threshold is set to high such as 75% or 90% and the proportional harvest rate is set too low such as 10% or 20% (ie., a low risk aversion approach).

Competing risks (harvesting and incidental drowning)

The expected model behaviour given competing anthropogenic mortality risks is summarised in figure 17 based on 1000 model runs. Here the stock is subject to two simultaneous mortality risk factors for 100 years as follows:-

1. The same proportional threshold based harvesting strategy for adults shown in figure 16 starting in 1975; and
2. Incidental drowning of turtles from all benthic ageclasses resident in coastal habitats due to otter trawl fisheries starting in 1975.

The potential impact of incidental drowning in coastal otter trawl fisheries has been considered previously for the endangered loggerhead stock resident in sGBR waters (Chaloupka & Limpus 1998b).

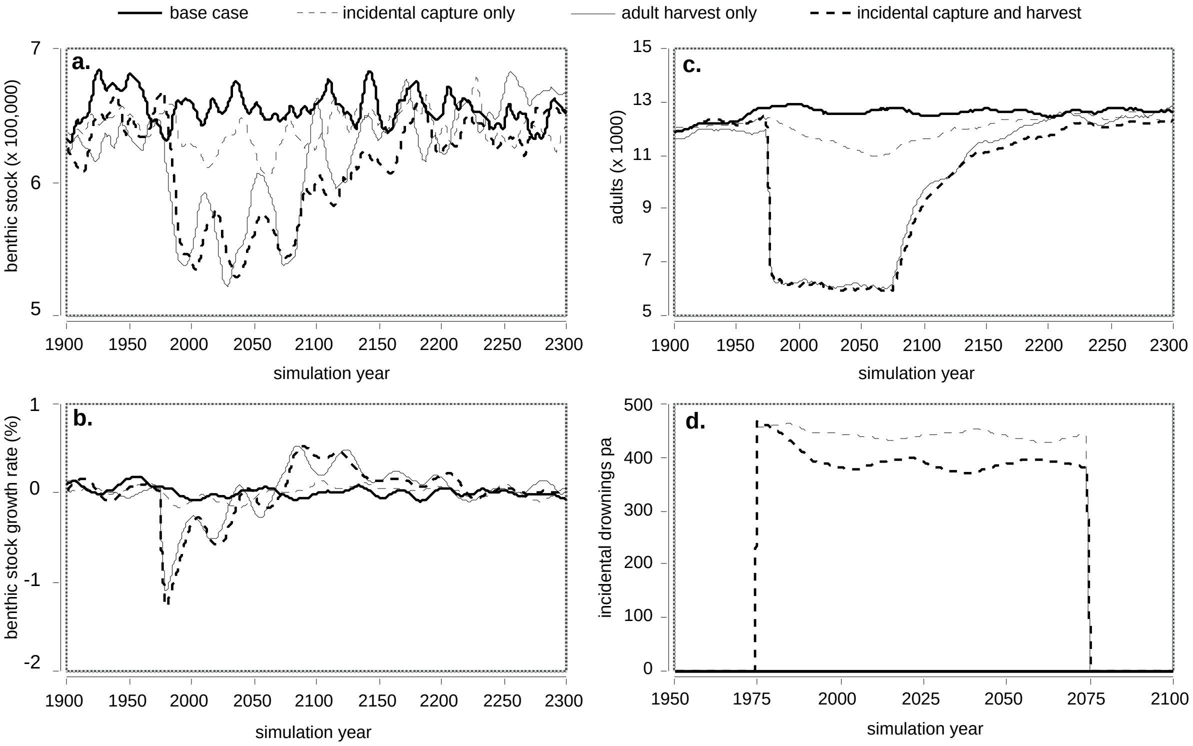

Figure 17. Expected model behaviour given competing anthropogenic mortality risks.

Panel a. shows the expected benthic substock abundance trend from 1000 runs when there were no anthropogenic mortality risks (thick solid curve) compared to:

- The expected incidental drowning trend but no threshold harvest (thin dashed curve;
- Proportional threshold harvest trend but no incidental drowning (thin solid curve); and
- Two anthropogenic risks operating (thick dashed curve).

Panel b. shows the expected benthic substock growth rate trend for the same scenarios shown in A where it is apparent that incidental drowning at the capture and drowning probabilities set for this scenario had relatively little effect on benthic substock growth b. which was also apparent for the adult substock abundance c. The competing risks effect is evident in panel d. that shows the decrease in drownings when the two risk factors are operating (thick dashed curve) because many adults were harvested and hence not alive to be captured in otter trawl fisheries operating in coastal seagrass habitats.

The coastal habitats comprise 25.5% of the 15 675 km^2 metapopulation habitat and represent habitats at-risk to otter trawling. The reefal habitats are not exposed to otter trawling so turtles occupying those habitats (ca 74.5% of the benthic metapopulation) are not at-risk to capture in the coastal otter trawl fisheries (Slater et al 1998).

Moreover, larger size green turtles (subadults, adults) have a higher probability of capture in otter trawl fisheries than do smaller turtles (Robins 1995) but once captured all ageclasses have the same 10% probability of drowning (Robins 1995, Poiner & Harris 1996). Larger turtles have a 7% probability of capture in the coastal habitats while smaller turtles have a 2-3% probability of capture in these habitats. Females have a higher probability of capture since they are more abundant than males in the sGBR stock and there is no evidence of any sex-specific avoidance behaviour (Slater et al 1998).

Figure 17a shows the expected benthic substock abundance trend (base case) when there were no anthropogenic mortality risks (thick solid curve) compared to the expected incidental drowning trend, but no threshold harvest (thin dashed curve) proportional threshold harvest trend, but no incidental drowning (thin solid curve) two anthropogenic risks operating (thick dashed curve).

Figure 17b shows the expected benthic substock growth rate trend for the same scenarios shown in figure 17a where it is apparent that incidental drowning at the capture and drowning probabilities set for this scenario had relatively little effect on benthic substock growth (figure 17b) which was also apparent for the adult substock abundance (Figure 17c).

The competing risks effect is now evident in figure 17d that shows the decrease in incidental drownings when the two risk factors are operating (thick dashed curve) because many adults were harvested and hence not alive to be captured in otter trawl fisheries operating in coastal seagrass habitats. Mortality from the two anthropogenic sources is not additive because some turtles that drowned would have died from natural causes anyway and similarly some turtles that were harvested also would have died from natural causes while some turtles that might have been captured had already been harvested. This is known as competing mortality risks (see Chiang 1991 for a detailed discussion of this important issue).

CONCLUSION

A stochastic simulation model was developed for the southern Great Barrier Reef green turtle stock to foster better insight into regional population dynamics. The model was sex- and ageclass-structured linked by density-dependent, correlated and time-varying demographic processes subject to environmental and demographic stochasticity.

The simulation model was based on extensive demographic information derived for this stock from a long-term sea turtle research program established and maintained by the Queensland Parks and Wildlife Service. (see Chaloupka 2002).

Model validation was based on comparison with long-term empirical reference behaviours such as the annual census of females nesting on Heron Island that has been ongoing for the last 25 years.

Model validation was also based on multi-factor perturbation experiments and Monte Carlo simulation within a fractional factorial sampling design. The model output was found to be most sensitive to ecologically realistic variations in the annual proportion of females and males preparing to breed, expected number of clutches laid each season per female, expected median age-at-maturity and expected egg survival probability. All these parameters were well estimated for the stock except for median age-at-maturity that requires further long-term field study.

The model was designed to support robust evaluation of the potential effects of habitat-specific competing mortality risks on stock abundance and sex-ageclass structure. The model has extensive adjustable devices called sliders that help the user to change parameter values and demographic process functional form to test model performance or for designing Monte Carlo based policy experiments or stochastic risk assessments.

Even though the model comprises more than 100 differential equations it is nonetheless extremely fast to run and so supports comprehensive Monte Carlo policy experimentation and extensive multi-factor parameter sensitivity based analysis. A User Guide has been completed to support application of the model for the design and testing of green sea turtle conservation policies.

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GLOSSARY

adults	fourth benthic phase ageclasses (>= 46 yrs, 100% mature)
ageclass	age interval of 1 year (365.25 days)
AIC	Akaike Information Criterion that is used to support statistical model selection from a suite of models fitted to the same data set (see Anderson et al 1998)
ANOVA	analysis of variance implemented here using variance-weighted least squares procedures
anthropogenic	human caused or sourced
AR(1)	linear model with first order autoregressive error while AR(9) means linear model with 9th order autoregressive error (see Judge et al 1985)
benthic juveniles	initial benthic phase ageclasses (ca 5-15 yrs)
benthic phase	shallow water habitat for turtles after recruitment from the pelagic habitat at ca 40 cm CCL (ca 4-6 yrs old) to coral reefs or coastal seagrass habitats where they spend most of their lives
biomass	ageclass abundance multiplied by mean ageclass weight (kg) divided by 1000 to yield biomass in metric tonnes
CCL	size estimate based on the mid-line curved carapace length in centimeters (cm CCL)
CJS	Cormack-Jolly-Seber
compensatory mechanism	demographic process such as reproductive output increases at low population levels due perhaps to increased availability of food per capita at lower abundance levels
CPS	Mean number of clutches laid by a female per season
demographic stochasticity	realised population variability in modelled survival, dispersal or reproductive output due to individual variability after accounting for any environmental stochasticity
depensatory mechanism	demographic process such as reproductive output decreases at low population levels due perhaps to decreased probability of finding a mate at lower abundance levels (also known as an Allee effect)

ENSO	El Niño-Southern Oscillation (ocean-atmosphere anomaly)
environmental stochasticity	expected population variability in modelled survival, dispersal or reproductive probabilities due to environmental effects
EPC	Mean clutch size
FF3	fractional factorial sampling design at 3 levels per variable or factor
FF3n	fractional factorial sampling design at 3 levels for each of “n” variables or factors
foraging ground	benthic habitat geographic residence
GBR	Great Barrier Reef
hatchlings	recently hatched turtle and escaping to sea from nesting beach
immatures	second benthic phase ageclasses (ca 15-29 yrs of age)
Monte Carlo trials	running a stochastic simulation model numerous times while sampling various demographic parameters from parameter-specific probability density or mass functions
neonates	post-hatchling but still less than 1 year old (0 ageclass)
nGBR	northern Great Barrier Reef
pdf	probability density function
pelagic juveniles	pelagic phase ageclasses (1-6 yrs of age, neonate = 0 ageclass)
pelagic phase	oceanic habitat for turtles from ca 4-45 cm CCL (0 to ca 6 yrs of age) in the southwestern Pacific Ocean prior to recruitment to the benthic habitat at ca 40 cm CCL (ca 4-6 yrs of age)
pmf	probability mass function
reefal	relates to a coral reef habitat
rmse	root mean square error (see Judge et al 1985)
sGBR	southern Great Barrier Reef
subadults	third benthic phase ageclasses (ca 30-45 yrs of age)