

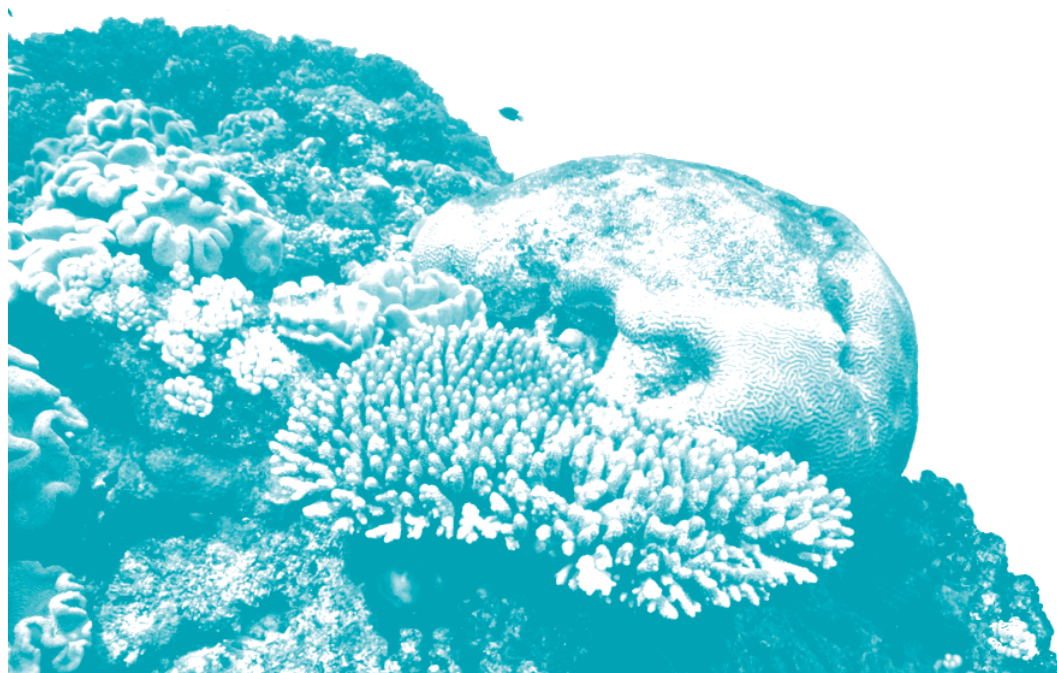


GREAT BARRIER REEF
MARINE PARK AUTHORITY

RESEARCH PUBLICATION NO. 74

**Phase 1 - Assessment of suitability of
Queensland Parks & Wildlife Service Sea
Turtle Data for use in models of the
population dynamics of the Southern
Great Barrier Reef Green Turtle Stock**

Dr Milani Chaloupka



let's keep it great

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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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FOREWORD

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

The QEPA data is now 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 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 very useful tool in 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.

In addition, the Report's recommendations for the development of sea turtle research in Queensland will be useful in considering the direction and funding of future research. The recommendations will be assessed against both agencies' research priorities. The GBRMPA and QEPA will work with other interested individuals, agencies and stakeholders, especially Indigenous people, to develop an overall green turtle conservation strategy for Queensland.

The Great Barrier Reef Marine Park Authority and the Queensland Environmental Protection Agency are pleased to make this report generally available.



Hon Virginia Chadwick
Chair
Great Barrier Reef Marine Park Authority



James Purtill
Director General
Queensland Environmental Protection Agency

March 2002

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EXECUTIVE SUMMARY

The sea turtle research program of the Queensland Parks and Wildlife Service (QPWS), which is part of the Queensland Environmental Protection Agency is the most comprehensive long-term program studying sea turtle demography in the world. The program provides substantial data sets on key aspects of sea turtle demography essential for developing an age-structured and sex-specific stochastic simulation model with some explicit spatial structure. This model would be suitable for helping to design conservation policies and strategies appropriate for addressing the potential impact of harvesting and other competing mortality risks on the long-term viability of the southern Great Barrier Reef (sGBR) green turtle stock. The statistical analyses to support such stochastic simulation model development are presented here using the extensive QPWS database. The data sets provide sufficient information to enable inclusion of environmental and demographic stochasticity on key demographic processes and for evaluating model performance against long-term stock abundance estimates. The key processes reviewed here include:

- (1) reproductive behaviour and environmental stochasticity;
- (2) sex-specific somatic growth and aging;
- (3) sex- and ageclass-specific survival probabilities; and
- (4) sex- and ageclass-specific population abundance estimates for foraging populations comprising the sGBR metapopulation.

Recommendations to guide future research on sGBR green sea turtle demography include:

- (1) Establishment of a concurrent annual nesting census program to provide a basis for simulation model calibration based on multiple sites rather than one site;
- (2) Establishment of a concurrent multi-site capture-mark-recapture (CMR) program in sGBR waters to support more robust estimates of ageclass-specific survival probabilities, ageclass-specific abundance and to investigate the possibility of sex-specific and/or ageclass-specific dispersal behaviour;
- (3) Expansion of the current CMR program to include important sGBR foraging grounds such as Hervey Bay and maintenance of the existing CMR study sites in Clack Reef, Shoalwater Bay, Heron/Wistari Reefs and Moreton Bay;
- (4) An increase in the number of researchers capable of performing laparoscopy to support the recommended expanded CMR program;
- (5) Promotion of the sea turtle research program as a major long-term ecological monitoring and research program of national and international significance and expansion of the application of this work and expertise into the neighbouring Southeast Asian region;
- (6) Establishment of a program to assess the pelagic turtle phase demography in the southwestern Pacific Ocean;
- (7) Development of a robust method to identify and monitor new turtle recruits settling from the pelagic phase into a benthic habitat in Great Barrier Reef and southern Queensland coastal waters;
- (8) Development of a skeletochronological methods to support reliable age estimation of biopsied sea turtles and stranded sea turtles in Great Barrier Reef and southern Queensland coastal waters; and
- (9) Maintenance of the annual nesting census on Raine Island to monitor the Great Barrier Reef wide spatial synchrony in nesting and reproductive behaviour of the sGBR and nGBR green sea turtle stocks.

INTRODUCTION

The two common species of sea turtle resident in southern Great Barrier Reef (sGBR) waters are the green and loggerhead sea turtles. The sGBR green turtle stock is not seriously exposed to major hazards such as fisheries and indigenous harvesting (Poiner & Harris 1996; Slater et al. 1998) and there is no evidence of population decline (Chaloupka & Limpus in press a). Nonetheless, the stock is exposed to extensive subsistence harvesting in northern Australian waters (Kwan 1991) although this harvest involves mainly the nGBR green stock (Figure 1). There is also increasing demand to allow traditional hunting of sGBR green turtles by local indigenous communities distributed along the Queensland coast (Limpus 1993a). Yet robust management procedures to support sustainable harvesting of the sGBR green turtle stock have not been developed. The development of such procedures depends in large part on a reasonable understanding of sGBR green sea turtle demography and the application of this information within a risk management based framework (Merkhofer 1987).

Therefore, UniQuest was commissioned to help develop a better understanding of sGBR sea turtle demography and to then use such information in a simulation model (Phase 2) suitable for risk-based conservation policy evaluation. The main purpose of Phase 1 of the consultancy was to "... assess suitability of QPWS sea turtle data for use in models of the population dynamics of the sGBR green turtle stock, including the strengths and limitations of models prepared from this dataset in responding to questions about population dynamics."

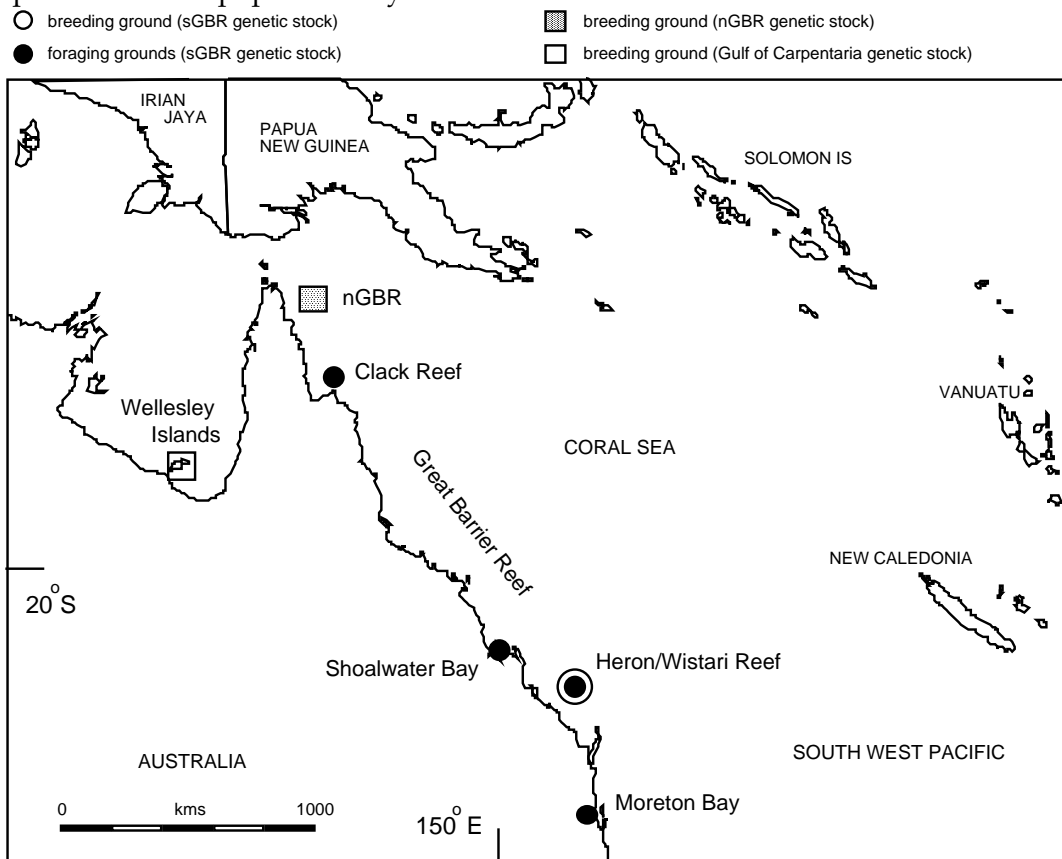


Figure 1. Location of the foraging ground study sites for the sGBR genetic stock of green turtles resident in GBR waters. The major rookeries of the other genetic stocks of Australian green turtles in the same region are also shown (nGBR, Wellesley Island group). Clack Reef comprises a mix of nGBR and sGBR stocks.

This task was addressed here by (1) a review of existing published literature relating to the sGBR green sea turtle stock and (2) extensive analysis of QPWS sea turtle datasets on the following major demographic processes (contact the QPWS for data set details):

- (1) foraging ground specific and sex-specific somatic growth behaviour for the southern Great Barrier Reef (sGBR) genetic stock
- (2) foraging ground specific and sex-specific survivorship for the southern Great Barrier Reef (sGBR) genetic stock
- (3) foraging ground specific temporal trends in population abundance for the southern Great Barrier Reef (sGBR) genetic stock
- (4) foraging ground specific temporal trends in the annual breeding behaviour for the southern Great Barrier Reef (sGBR) genetic stock

These processes provide the basis for the Phase 2 development of a spatially structured age- and sex-specific stochastic simulation model of the population demography of the sGBR green sea turtle stock. The simulation model would then function as a decision-support tool to help evaluate specific conservation policies.

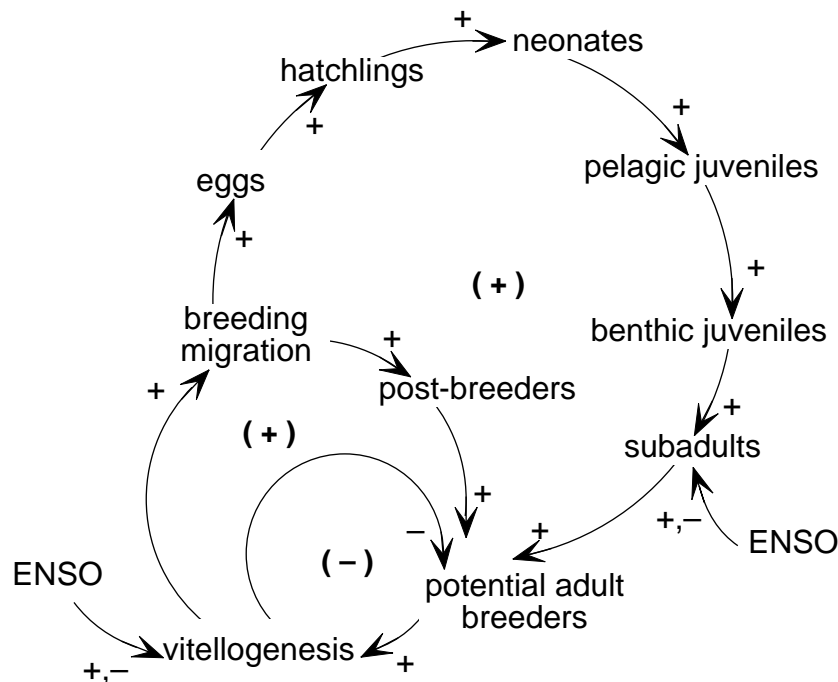


Figure 2. Life-cycle diagram for sGBR green turtles resident in sGBR foraging grounds (see Chaloupka & Limpus 1996). ENSO = El Niño-Southern Oscillation effect on immature growth (Limpus & Chaloupka 1997) and on breeding (Limpus & Nicholls 1994; Chaloupka 2001). \pm = causal loop polarity with + meaning 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 major ageclasses or developmental stages are shown here. There are 6 ageclasses defined here – egg/hatchling/neonate, pelagic juvenile, benthic juvenile, subadult, maturing adult, and adult. Potential adult breeders and post-breeders comprise the adult ageclass although some potential adults may still be immature and hence are maturing.

EXISTING MATERIAL REVIEW

Life history overview

The sGBR green turtle stock comprises 6 ontogenetic or developmental stages that can be derived using both size and reproductive status characteristics (Limpus & Chaloupka 1997). Stage 1 represents the first year cohort comprising eggs, hatchlings and neonates (Figure 2). Eggs hatch after ca 2 months and then hatchlings escape the sGBR nesting beaches to recruit to open water in the region (Gyuris 1994). The hatchlings are then dispersed southward as neonates over the next 6-9 months in the east Australian current and then eastwards into the southwestern Pacific Ocean (Walker 1994). Stage 2 comprises the pelagic juvenile phase that occurs in southwestern Pacific gyres or along convergence zones (Carr 1987). Excluding Stage 1, mean pelagic juvenile stage duration was estimated at ca 4-6 yrs (Limpus & Chaloupka 1997; Zug & Glor 1998).

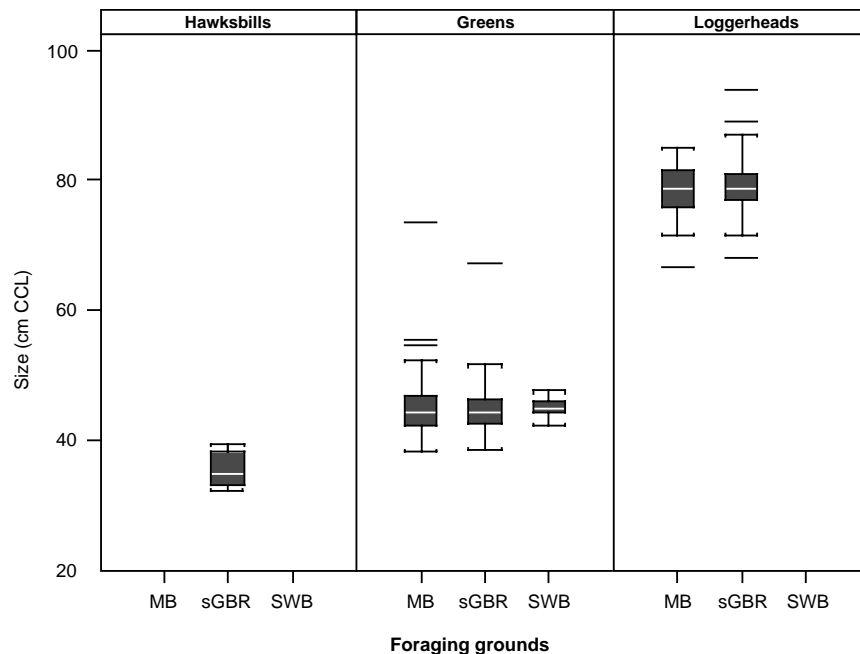


Figure 3. Box plots conditioned by species and foraging grounds of the benthic phase recruitment size distribution for sea turtles resident in sGBR and southern Queensland waters. MB = Moreton Bay, sGBR = Heron/Wistari Reefs in the southern Great Barrier Reef region, SWB = Shoalwater Bay. The greens are from the sGBR stock, loggerheads from the sGBR stock and hawksbills from the nGBR stock. The shaded boxes are the interquartile range (25th - 75th percentiles), hooked bars show 10th and 90th percentiles, white bar = median or 50th percentile. Unhooked bars shown extreme outliers. (Source: Limpus unpubl 1998).

Pelagic juveniles then recruit to the benthic juvenile development phase (Figure 2, Stage 3) in foraging grounds distributed along the Queensland coast (Figure 1) from ca 38 cm CCL (Limpus & Chaloupka 1997) with no significant difference in median recruitment size between foraging grounds for the sGBR green turtle stock (Figure 3).

Benthic green turtle juveniles then grow rapidly until ca 60 cm CCL when sex-specific growth is evident (Limpus & Chaloupka 1997). Mean benthic juvenile stage duration has been estimated ca 11 yrs using a system-of-equations age-specific growth model developed for this stock (Chaloupka in press). Somatic growth slows rapidly after ca 60-65 cm CCL (Limpus & Chaloupka 1997), which marks the subadult phase (Fig 2, Stage 4) prior to onset of sexual maturity and adulthood ca 90-100cm CCL (Limpus & Chaloupka 1997). Mean benthic subadult stage duration was estimated ca 19 yrs (Chaloupka in press). Mean nesting size at first or subsequent nesting is not a valid index of the onset of sexual maturity, although this appears to be a common misconception amongst sea turtle researchers.

Somatic growth is negligible from 90 cm CCL onwards (Limpus & Chaloupka 1997) but adults represent a range of ages, sizes and maturity status because of year, cohort and individual heterogeneity effects (Limpus & Chaloupka 1997). Hence a 105 cm CCL female might still be a maturing adult determined using laparoscopy (Limpus & Reed 1985) while a 93 cm female could be in its second nesting season. Therefore, adults are classified as maturing adults or mature adults using a size-specific maturity function derived for this stock (Limpus 1998). The maturing adult stage (Figure 2, Stage 5) was defined as size-classes > 91 cm CCL where the probability of sexual maturity was < 0.50. The adult stage (Figure 2, Stage 6) is defined for the sGBR stock using similar size-classes but with the probability of sexual maturity > 0.50.

The mean maturing adult stage duration was estimated at 5 yrs using maturity functions (Limpus 1998) and the age-specific growth functions developed for this sGBR stock (Chaloupka in press). Mean adult life expectancy has been estimated ca 18-19 yrs using stage-specific survival probability estimates for the Heron/Wistari Reefs foraging ground population of this stock (Chaloupka & Limpus 1998a).

Reproductive behaviour

The primary sex ratio (PSR = 0.65) for the sGBR stock was sourced from Limpus et al. (1984) and Limpus et al. (1994a) and is consistent with recent foraging ground population abundance and sex ratio estimates for this stock derived from a long-term capture-mark-recapture study (Chaloupka & Limpus in press a). The estimated foraging ground sex ratio suggests that there was no significant temporal variability for the Heron/Wistari population from the early 1980s onwards (Chaloupka & Limpus in press a). The estimated PSR for the sGBR green turtle stock is also consistent with estimates derived from long-term studies of the annual variability in hatchling sex ratios for other green turtle populations (Godfrey et al. 1996).

Mean clutch size or eggs per clutch (EPC = 115.2 ± 27.9) was sourced from Limpus et al. (1984) and Limpus & Reed (1985) and is consistent with 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 such effect would have limited demographic impact when discounted for survivorship of ageing females (Roff 1992). Mean number of clutches laid per season (CPS = 5.1 ± 1.9) was sourced from Limpus et al. (1984) and Limpus & Reed (1985) and is higher than estimates for other green turtle stocks

(Johnson & Ehrhart 1996). There are no other demographically informative data on nesting or fecundity that are relevant for modelling sGBR green sea population dynamics.

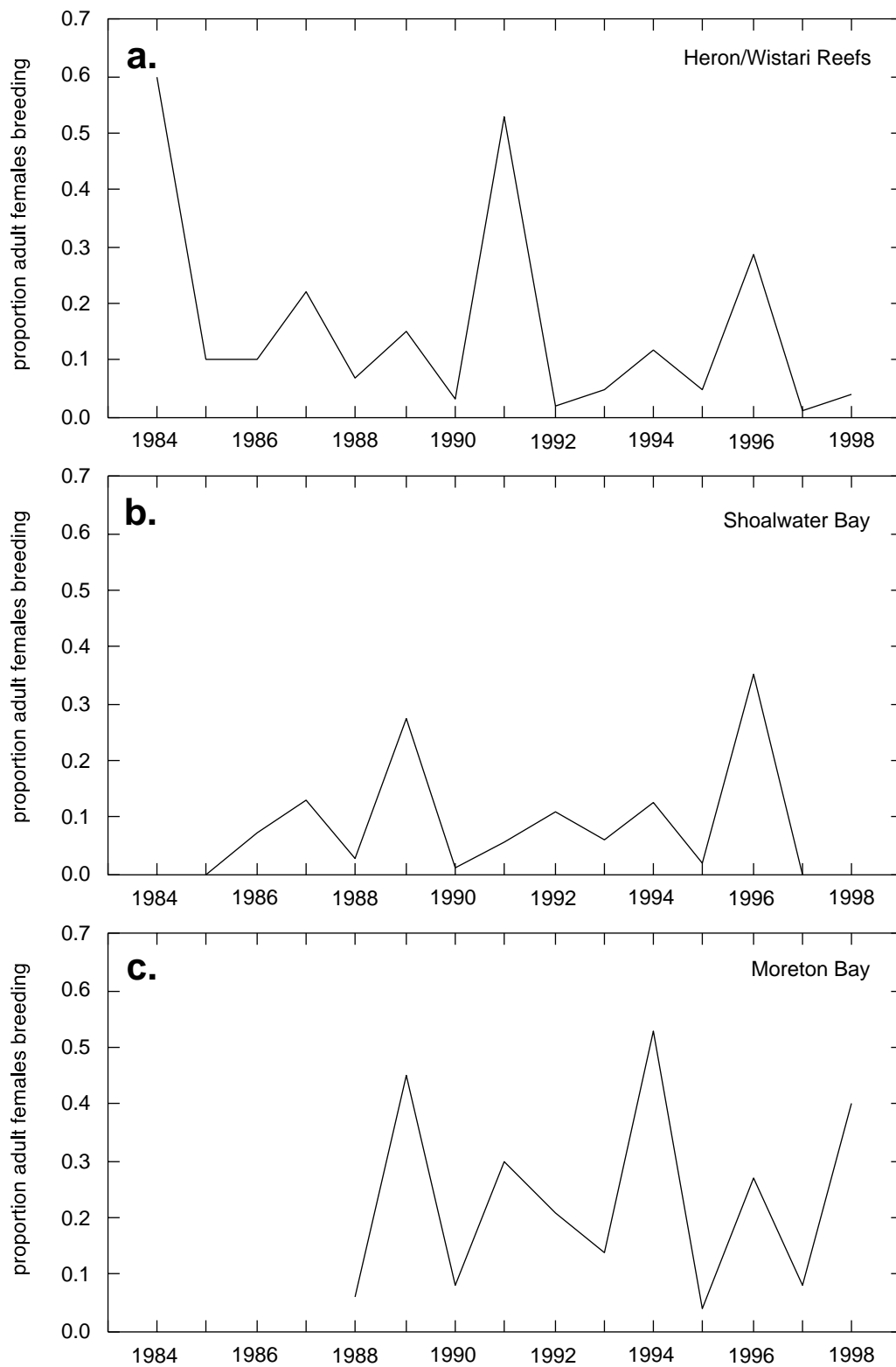


Figure 4. Temporal variability in the proportion of female green turtles breeding each year at 3 major foraging grounds of the sGBR genetic stock. Breeding status derived using laparoscopy. (Source: Limpus 2000a).

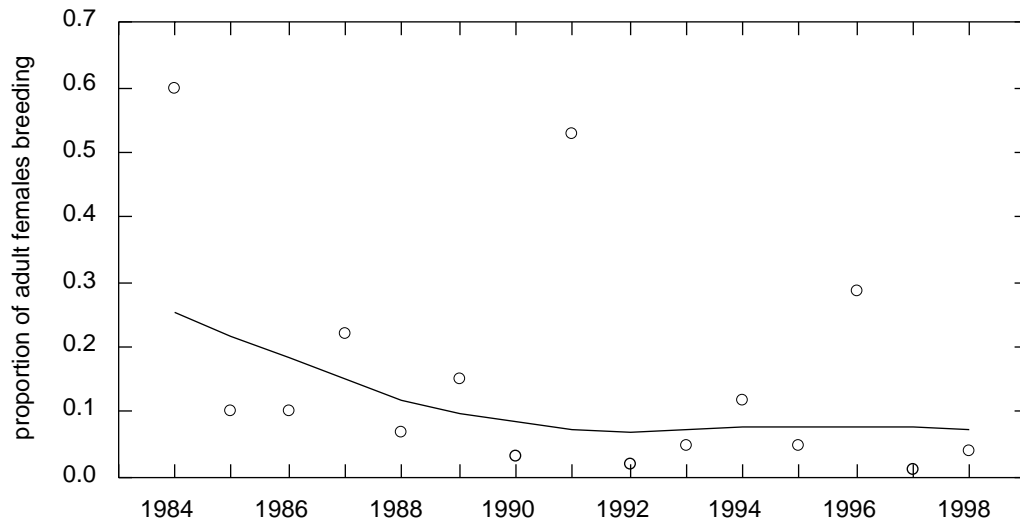


Figure 5. Long-term trend in the annual proportion of females breeding from the Heron/Wistari population. Trend shown by LOWESS smooth (solid curve). The 3 outliers (1984, 1991, 1996) indicate the anomalous breeding seasons associated with prior major ENSO events.

Breeding probabilities for both female and male sGBR green turtles can be derived from remigration intervals (RMI) that have been recorded for a large number of turtles tagged in sGBR waters (Limpus 1993b; Limpus et al. 1994b; Limpus 2000a). The remigration interval is the period between successive nesting seasons. A lognormal probability density function (Vose 1996) can be shown to fit the RMI data well for the female sGBR foraging ground population with maximum likelihood parameter estimates of the mean = 5.3 yrs and standard deviation = 1.6 yrs, which is longer and more variable than estimates for other green stocks (Hendrickson 1958; Mortimer & Carr 1987; van Buskirk & Crowder 1994).

Female breeding probability (FBP), which is the inverse of the remigration interval (RMI), can then be sampled in a simulation model using the following algorithm for deriving a stochastic lognormal variate from a normal probability density function or normal pdf (see Naylor et al. 1966):

$$FBP = (\exp(\text{normal}(\text{rmi_lnorm_mean}, \text{rmi_lnorm_sd}) + \text{rmi_lnorm_var}/2)) - 1 \dots (1)$$

where ...

```

rmi_lnorm_var=ln(((rmi_sd^2)/(rmi_norm^2))+1)
rmi_lnorm_mean=ln(rmi_norm)-0.5* rmi_lnorm_var
rmi_lnorm_sd=sqrt(rmi_lnorm_var)
rmi_norm=5.3 yrs
rmi_sd=1.6 yrs

```

Table 1. Summary of ageclass-specific survivorship for sea turtles. The estimates are annual survival probability estimates for all ageclasses except for the hatchlings where the estimates are for survival during the first few critical hours of escapement from inshore waters.

Species	Ageclass	Estimate	Method	Source
green	Hatchling	0.16-0.65	hatchling predation trials	<i>Gyuris 1994</i>
loggerhead	Hatchling	0.93	hatchling predation trials	<i>Witherington & Salmon 1992</i>
Kemp's ridley	Immature	0.30-0.76	enumeration	<i>Caillouet et al. 1995</i>
loggerhead	immature	0.69	size-based catch curve	<i>Frazer 1987</i>
flatback	adult female	0.93	enumeration	<i>Parmenter & Limpus 1995</i>
green	adult female	0.61	enumeration	<i>Bjorndal 1980</i>
Kemp's ridley	adult female	0.43	enumeration	<i>Marquez et al. 1982b</i>
loggerhead	adult female	0.81	enumeration	<i>Frazer 1983</i>
olive ridley	adult female	0.48	enumeration	<i>Marquez et al. 1982a</i>
green	immature-adult	0.84-0.94	Cormack-Jolly-Seber	<i>Chaloupka & Limpus 1998</i>
loggerhead	immature-adult	0.82-0.85	composite life table	<i>Frazer 1986</i>

Sampling FBP from a lognormal pdf for RMI with the specified parameters gives FBPs consistent with the empirical range of annual breeding rate estimates derived for several sGBR green turtle populations (Limpus & Nicholls 1994; Limpus et al. 1994a) that is also reflected in the temporal variability in annual nesting activity (Chaloupka & Limpus in press a). Equation (1) forms the basis for accounting for environmental stochasticity and variable interannual breeding probabilities in the stochastic simulation model that will be developed during Phase 2.

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). Limpus (2000a) provides time series estimates of the proportion of females and males breeding each year in the 3 foraging grounds of the sGBR genetic stock (see Figure 2 for females). Continuous probability density functions were fitted to these 3 series using maximum likelihood estimation (Vose 1996) to derive sampling functions for use in development of a simulation model of sGBR green turtle population dynamics. These sampling distributions reflect the affect of environmental stochasticity on breeding behaviour.

A Weibull probability density function (Vose 1996) fitted the data series in Figure 2 well ($\chi^2_{0.05,39} = 3.9$, $P > 0.42$) with the following ML parameter estimates of a Weibull pdf – location = 0, scale = 0.16, shape = 1. Strong correlations also occur between the foraging grounds evident in Figure 2 (spatial synchrony reflecting a Moran effect; see Chaloupka 2001). This demographic dependence in breeding behaviour for the sGBR metapopulation will also be included in the stochastic simulation to be developed in Phase 2.

Table 2. Demographic summary of the 1340 individual green turtles resident in 4 separate foraging grounds of the sGBR genetic stock used to estimate somatic growth functions.

Stage	Sex	Foraging ground increasing northwards (decreasing latitude)				Total
		Moreton Bay	Heron / Wistari Reef (sGBR)	Shoalwater Bay	Clack Reef (nGBR)	
Immature	Female	185	211	194	72	662
	Male	82	130	73	23	308
Adult	Female	9	50	98	8	165
	Male	3	146	50	6	205
Total		279	537	415	109	1340

There is also a significant decline apparent in the proportion of breeding females in the Heron/Wistari Reefs foraging ground (Figure 5) that possibly reflects a density-dependent effect due to increasing population abundance in this foraging ground population (Figure 8c). It is presumed here that any density-dependent effect on breeding behaviour in any of the foraging grounds is a function of declining per capita food availability as the population increases. Such an effect has been shown recently for an immature population of green sea turtles resident in a developmental habitat in Bahamian waters (Bjorndal et al. 2000). This density-dependent demographic process for the sGBR metapopulation will also be included in the stochastic simulation to be developed in Phase 2 to ensure some potential rebound capacity for the stock subject to harvesting pressures or other mortality risks such as boat strike and disease.

Survivorship

Age- or stage-specific survivorship is a key demographic component of population growth and evolutionary fitness (Fox 1993). Therefore, survival data are not only needed for the development of age- or state-dependent life history theories (McNamara & Houston 1996) but also for the heuristic modelling of demographic viability and ecological risk (Burgman et al. 1993). Despite the importance of survivorship there is a paucity of reliable data even for well studied vertebrate groups such as ungulates (Gaillard et al. 1998), squamate reptiles (Flatt et al. 1997), passerines (Martin et al. 1995), seabirds (Spendelov et al. 1995) and waterfowl (Nichols et al. 1997).

The lack of reliable survival data is particularly acute for turtles (Iverson 1991; Shine & Iverson 1995) and even more so for sea turtles (Chaloupka & Limpus 1998; Chaloupka & Limpus in press b). A summary of all known survival probability estimates for sea turtle stocks are shown in Table 1.

The hatchling trial studies were based on recording the known fate within a prescribed time interval of hatchlings released near to the nesting beach (Witherington & Salmon 1992; Gyuris 1994). The multiple trial study of Gyuris (1994) involved the release of tethered hatchlings under various conditions to derived survival probability estimates using logistic regression for green turtle hatchlings in sGBR waters. This study was especially useful for modelling the population dynamics of green turtles resident in sGBR waters (Chaloupka & Limpus 1996). The experimental design and sample size of both studies (Witherington & Salmon 1992; Gyuris 1994) were limited and more studies of this nature are needed to derive better estimates of hatchling survival under various environmental conditions.

Most attempts to estimate sea turtle survival used methods based on enumeration (Bjorndal 1980; Marquez et al. 1982a; Marquez et al. 1982b; Frazer 1983; Caillouet et al. 1995; Parmenter & Limpus 1995), composite life tables (Frazer 1986) or catch curve analysis (Frazer 1987) — see review in Chaloupka & Limpus (in press b). The relatively low estimates for annual survival derived from most of these 8 studies is hard to reconcile with the known longevity of sea turtle species (see Frazer 1986; Limpus & Chaloupka 1997; Bjorndal et al. 2000). For instance, the constant adult survival estimates in Table 1 imply that survival is an exponential random variate. The mean life expectancy derived from an exponential random variate is $(-\ln \phi)^{-1}$, where ϕ is mean annual survival probability and $\ln(\phi)$ is the instantaneous mortality or hazard rate (Lawless 1982). Using the mean annual survival probability proposed by Fraser (1983) for adult female loggerheads ($\phi_{\text{adult}} = 0.81$ from Table 1) implies that mean adult life span would be only ca 4.7 years for southeastern US female loggerheads.

All the estimates for females based on enumeration (Table 1), except for Parmenter & Limpus (1995), would suggest that adult sea turtles live on average for ca 2-5 years, which is incorrect (see Frazer 1986; Limpus & Chaloupka 1997; Bjorndal et al. 2000). The limitations of enumeration, catch curve and composite life table methods for estimation of survival probabilities are well known (Anderson et al. 1981; Seber 1982; Nichols & Pollock 1983; Martin et al. 1995; Chaloupka et al. 1999) prompting an advocacy for use of various Cormack-Jolly-Seber (CJS) based statistical modelling approaches instead (Pollock 1991; Lebreton et al. 1992; Cormack 1993). The ageclass-specific survival probabilities reported by Chaloupka & Limpus (1998), see also Chaloupka & Limpus (in press b) for sGBR green turtles were the first comprehensive estimates for a sea turtle species based on a capture-mark-recapture (CMR) study using CJS-based statistical modelling procedures.

SOMATIC GROWTH MODELLING FOR THE SGBR GREEN TURTLE METAPOPOPULATION

The green sea turtle is the most abundant large herbivore in marine ecosystems and feeds mainly on seagrass and soft algae (Bjorndal 1997). While the growth dynamics of this sea turtle are not well known (Chaloupka & Musick 1997) some recent studies provide important findings concerning environmentally induced temporal variability (Limpus & Chaloupka 1997) and variation due to regional differences (Bjorndal et al. 2000). An important source of growth variability that has yet to be considered is spatial or geographic variability within the same genetic stock, which is essential for developing a robust simulation model of sGBR green turtle population dynamics.

The sGBR genetic stock of green turtles comprises a spatially structured metapopulation with foraging grounds spanning 14° latitude and 1800 km ranging from tropical waters in the northern Great Barrier Reef to warm temperate waters in southern coastal Queensland (Figure 1). Adult turtles resident in these foraging grounds, and in some southwestern Pacific foraging grounds such as New Caledonia, migrate to breed in sGBR waters with females nesting on nearby coral cays (Figure 1). Hence the sGBR green turtle stock comprises a spatially disjunct metapopulation (see Stith et al. 1996 for discussion of metapopulation configurations). All sGBR rookeries comprise the same panmictic interbreeding stock, which is distinct genetically from the other Australian stocks (FitzSimmons et al. 1997). Therefore, the somatic growth dynamics of green turtles resident in four separate foraging grounds of the sGBR genetic stock were assessed using a nonparametric regression modelling. These foraging grounds represent the longer-term and more continuous study sites in the QPWS sea turtle research program.

Data sets

The QPWS data set comprised ca 2000 growth records for sGBR green turtles captured in 4 foraging grounds since 1974 in a long-term and spatially extensive mark-recapture program (Limpus & Reed 1985; Limpus et al. 1994a; Limpus & Chaloupka 1997). The foraging grounds were Clack Reef, Shoalwater Bay, Heron/Wistari Reef and Moreton Bay (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 greens resident in Moreton Bay, Heron/Wistari Reef and Shoalwater Bay foraging grounds are all 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. 1997).

The annual sampling periods varied between the foraging grounds with a 17 yr period (1974-1991) at Heron/Wistari Reef (sGBR), a 9 yr period (1986-1994) at Shoalwater Bay, a 6 yr period (1990-1995) at Moreton Bay and a 4 yr period (1987-1990) at Clack Reef. These periods represent the longest continuous series available and provide the minimum necessary data sets for demographic modelling – one-off and short-term

studies are of little utility for robust demographic modelling and simulation modelling of the population dynamics of long-lived marine species.

Capture and recapture was undertaken using the turtle rodeo technique with each turtle marked with coded titanium tags (Limpus & Reed 1985). Tag loss for this mark-recapture program is inconsequential (Limpus 1992a). The data included growth records for 827 females and 513 males spanning the post-recruitment phase from ca 40-120 cm CCL with 32% of turtles recaptured on 2 or more annual sampling occasions. The implicit sampling design was mixed longitudinal, which confounds year and cohort effects as age was unknown for all individuals (Chaloupka & Musick 1997).

Capture-recapture profiles for each of the 1340 turtles included:

- (1) CCL at first capture and at all recaptures (cm CCL);
- (2) sex and developmental stage (~ ageclass) determined using laparoscopic examination of reproductive organs (Limpus & Reed 1985; Limpus et al. 1994a);
- (3) year of first capture; and
- (4) years-at-large since first capture or previous recapture. Absolute growth rates were derived from the capture-recapture profiles with both negative and zero growth rates included since there is no valid reason to do otherwise (Chaloupka & Musick 1997).

A summary of the 1340 individual green turtles classified by sex and developmental stage (ageclass) at first capture within each of the 4 foraging grounds is given in Table 2. This data set extends significantly the single foraging ground data set used by Limpus & Chaloupka (1997) to study sGBR green sea turtle growth dynamics.

Statistical modelling approach

The standard approach to modelling sea turtle growth with unknown age has been the use of size-based analogues of age-based parametric growth functions, which has many shortcomings (Chaloupka & Musick 1997). Instead, the 2-stage statistical modelling approach of Chaloupka & Limpus (1997), Limpus & Chaloupka (1997) and Bjorndal et al. (2000) was used as follows:

- (1) a robust nonparametric regression model was fitted to the growth rate data to derive the expected size-specific growth rate function conditioned on informative growth predictors or covariates followed by;
- (2) numerical integration of the size-specific growth rate function using a difference equation and a 4th order Runge-Kutta integration method (Gerald & Wheatley 1994) to derive the expected size-at-age growth function. Numerical differentiation (Gerald & Wheatley 1994) of this function is then used to derive the age-specific growth rate function.

The growth rate predictors (covariates) used here were sex, calendar year, mean size (cm CCL) and recapture interval (yrs). Sex was determined along with developmental stage using laparoscopy. The year covariate reflects the growth year of the growth rate estimate and was included to account for the implicit time-dependent sampling design. Year effect is also a source of growth variability due to environmental factors but is confounded with cohort effects because of the mixed longitudinal sampling design with unknown age inherent in this study (Chaloupka & Musick 1997). The mean size covariate is the arithmetic mean of size at first capture and subsequent recapture and is

the appropriate metric for indexing size-specific growth assuming growth is locally linear within a sampling interval (Chaloupka & Limpus 1997). The functional relationship between absolute growth rates recorded for each turtle and the 4 growth predictors was modelled in the first stage of the 2-stage procedure using a generalized additive modelling approach (GAM: Hastie & Tibshirani 1990). GAM enables robust analysis of regression models with nonlinear covariate functional form and nonnormal error terms. The GAM regression models used here comprised:

- (1) an identity link;
- (2) a robust quasi-likelihood error function to minimise outlier effects and
- (3) cubic smoothing splines to model nonlinear functional form between growth rates and the covariates (year, mean size, recapture interval).

Major findings relevant to the consultancy

The major findings derived from this long-term and spatially extensive study of green turtle growth behaviour in GBR waters were:

- (1) nonmonotonic size-specific growth rate functions;
- (2) sex-specific growth;
- (3) immature growth variability due to environmental effects; and
- (4) geographical variability in immature growth.

The statistical modelling results are summarised for each foraging ground in Figure 6 and age-based growth functions shown in Figure 7.

Significant temporal variation (year effect) in growth rates was found for all 4 foraging ground populations that reflects local environmental variability (Figure 6b,f,j,n). Sex-specific growth differences were evident in the foraging grounds (Figure 6a,e) with females tending to grow faster than similar sized males after the juvenile growth spurt resulting in adult size dimorphism. The sGBR stock comprises mainly the same mtDNA haplotype so geographic differences are due to local environmental conditions rather than genetic factors. Limpus & Chaloupka (1997) suggested that an abrupt temporary increase in immature growth rates during the 1980s for the sGBR population (Figure 6j) was a function of El Niño-Southern Oscillation (ENSO) events that are believed to affect sGBR green turtle breeding behaviour (Limpus & Nicholls 1994).

Growth rates declined for all foraging ground populations during the late 1980s and early 1990s (Figure 6), which was coincident with the longest recorded series of ENSO events this century (Trenberth & Hoar 1997). Moreover, major local cyclone-induced flooding events occurred during the early 1990s that caused substantial seagrass loss along the southern Queensland coast (Preen et al. 1995). Similar local flooding events might also be responsible for temporary growth rate suppression apparent for the Shoalwater Bay and Moreton Bay foraging ground populations during the early 1990s (Figure 6f,n).

Given the temporal variability in growth rates at all foraging grounds it is proposed that the geographic variation evident for the sGBR stock is due to food stock dynamics subject to local environmental stochasticity resulting in differences in food availability (Garnett et al. 1985) and nutrient uptake rates (Bjorndal 1997). There is significant temporal and spatial variability in algal abundance around Heron Reef (Forbes 1994)

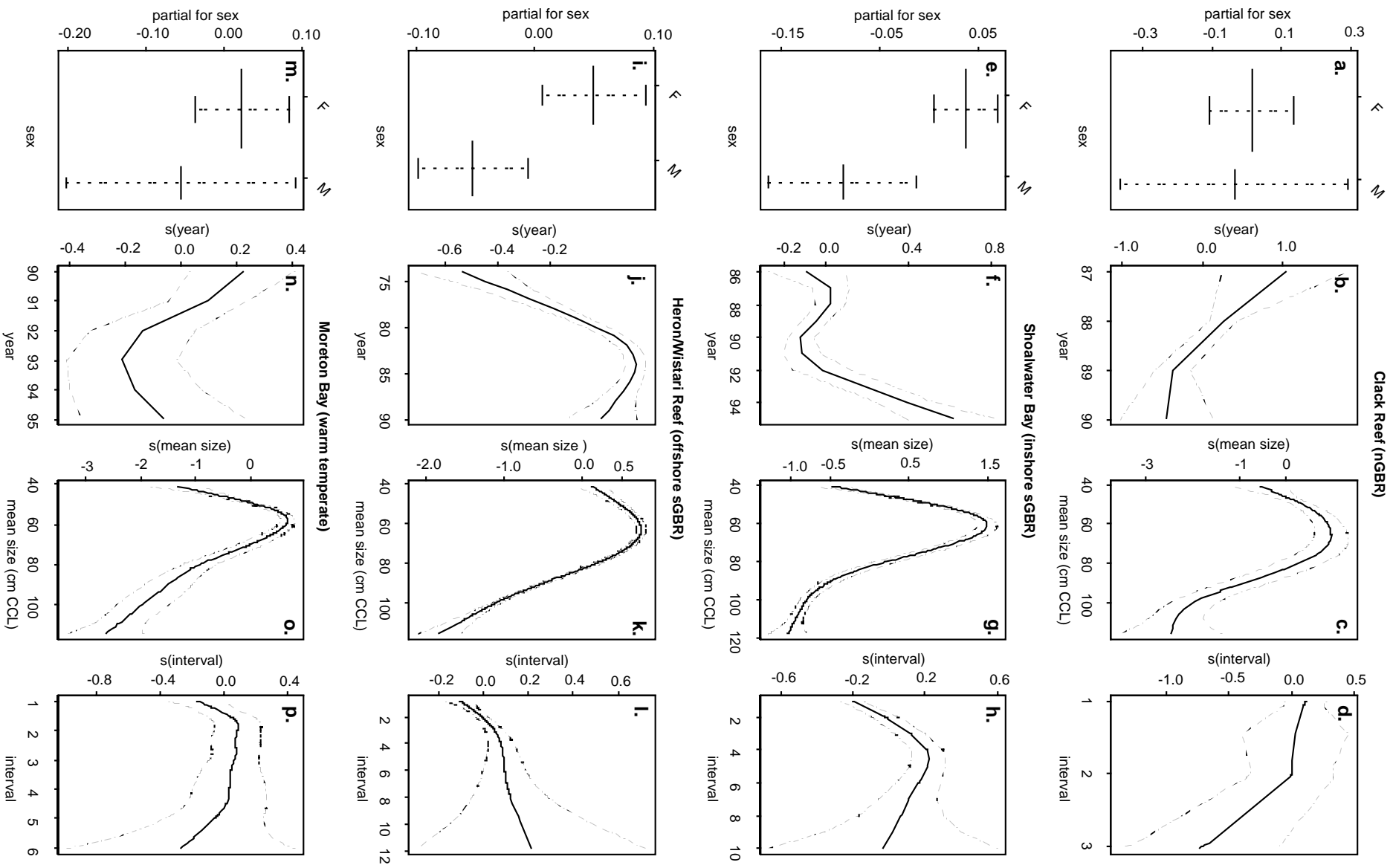
and also for seagrass along the Queensland coast (Lee Long et al. 1993; Lanyon & Marsh 1995) providing some circumstantial support for this view. Further support for this view is provided by a recent radio telemetry study that found unusually large foraging ranges for adult green turtles resident in sparse seagrass habitats in Repulse Bay northward of Shoalwater Bay (Whiting & Miller 1998).

The size-specific growth functions shown in Figure 6 (c,g,k,o) for each foraging ground were numerically integrated to derive the expected size-at-age functions and then numerically differentiated to derive the age-specific growth rate functions (for details see Limpus & Chaloupka 1997 and Bjorndal et al. 2000). The foraging ground specific expected size-at-age and age-specific growth functions are shown in Figure 7. Juveniles recruit to these foraging grounds at the same size but grow at different sex-specific rates that result in significant differences in size- or age-at-maturity for turtles in the same stock (Figure 7).

It is common practice to use the size-at-age curves (Figure 7b,e) to estimate the mean age at sexual maturity. The difficulty in using growth functions for this purpose is the lack of conclusive growth criteria to indicate onset of maturity. One criterion in the absence of maturity rate functions is the size at which the onset of negligible growth is apparent (Limpus & Chaloupka 1997), which is ca 95 cm CCL for all foraging grounds (Figure 7a,d). The onset of negligible growth by 95 cm CCL is also consistent with crude maturity rate estimates proposed by Limpus & Reed (1985) and Limpus et al. (1994a) for the sGBR genetic stock. Given this size criterion and the assumed epipelagic phase duration of ca 4-6 yr, the mean age at maturity was then estimated at ca 25 yr for the Clack Reef population, 30 yr for Moreton Bay, 40 years for Heron/Wistari Reef and more than 50 yr for the Shoalwater Bay population. Despite such local differences the expected size-specific growth rate function at all foraging grounds displayed a similar nonmonotonic growth pattern with a distinct juvenile growth spurt at ca 60-70 cm CCL or ca 15-20 years of age (Figure 7a,d,c,f).

Clearly, there is considerable variation in age and size at maturity for the various foraging ground populations that has not been reported for any other sea turtle stock, which has major implications for modelling the long-term population viability of the sGBR green turtle stock.

Figure 6. (NEXT PAGE) Graphical summary of GAM model fit for each of the 4 foraging grounds. Clack Reef growth model shown in panels (a) to (d), Shoalwater Bay model shown in (e) to (h), Heron/Wistari Reef shown in (i) to (l) and Moreton Bay model shown in (m) to (p). The response variable (growth rate) is shown on the *y*-axis in each panel as a centred smoothed function scale to ensure valid pointwise 95% confidence bands. Covariates shown on the *x*-axis: sex (a,e,i,m: F =female and M = male), year (b,f,j,n: growth year index), mean size (c,g,k,o: mean size between first and next capture in cm CCL), recapture interval in years (d,h,l,p). The width of the mean factor response (a,e,f,m) is proportional to sample size with the 95% confidence interval shown by cross bars. Solid curves in (b) to (d), (f) to (h), (j) to (l) and (n) to (p) are the cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAM model for each foraging ground. Dotted curves in (b) to (d), (f) to (h), (j) to (l) and (n) to (p) are pointwise 95% confidence curves.



SURVIVORSHIP MODELLING FOR THE SGBR GREEN TURTLE METAPOPULATION

The lack of reliable survival data is particularly acute for sea turtles (Chaloupka & Limpus 1998; Chaloupka & Limpus in press b) so the stage- and sex-specific survivorship for sGBR sea turtles resident in 3 major foraging grounds (Shoalwater Bay, Heron/Wistari Reefs, Moreton Bay) was assessed using robust mark-recapture based statistical modelling approaches (Lebreton et al. 1992). These 3 foraging grounds represent the major study sites in the QPWS sea turtle research program that were suitable for survival probability estimation – there are no useful data for survival probability estimation available for the Clack Reef foraging ground population. Also survival probability estimates for eggs, hatchlings and neonates were also derived here as well as an estimate of the survival probability for the pelagic phase (see Figure 2).

Early development stage survival estimates

Stage1 (eggs, hatchlings, neonates; see Figure 2) survival probability (\emptyset_1) was estimated here using Monte Carlo simulation (see Vose 1996) drawing from normal probability density functions (pdfs) as follows:

$$\emptyset_1 = (1-EM).(1-HM).(1-PHM) \dots\dots\dots(2)$$

where ...

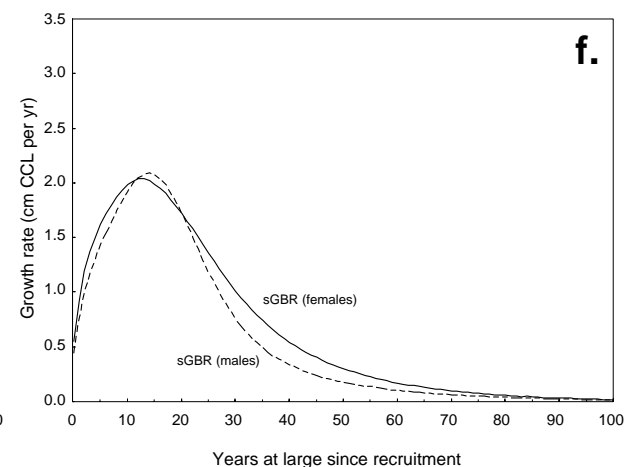
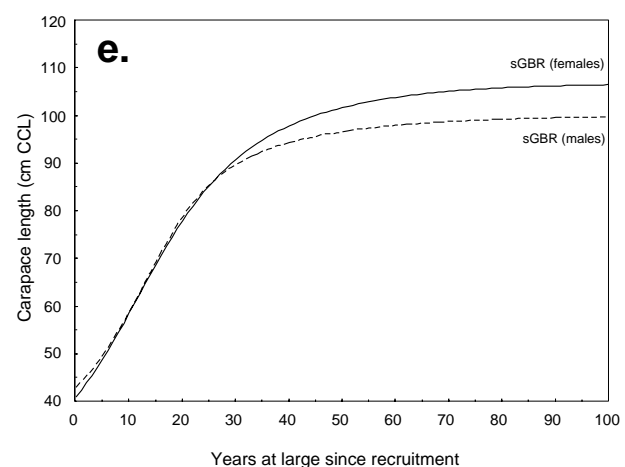
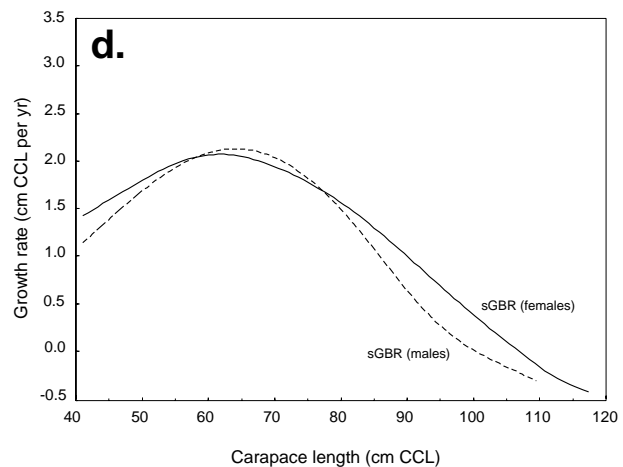
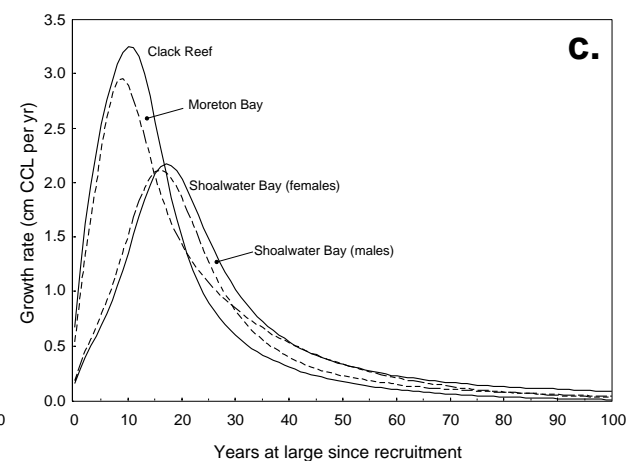
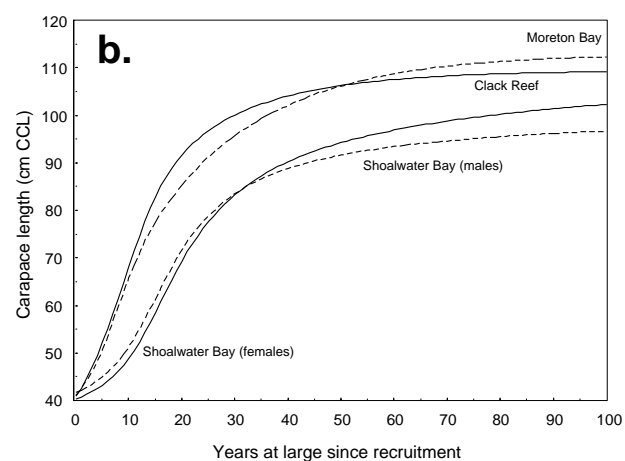
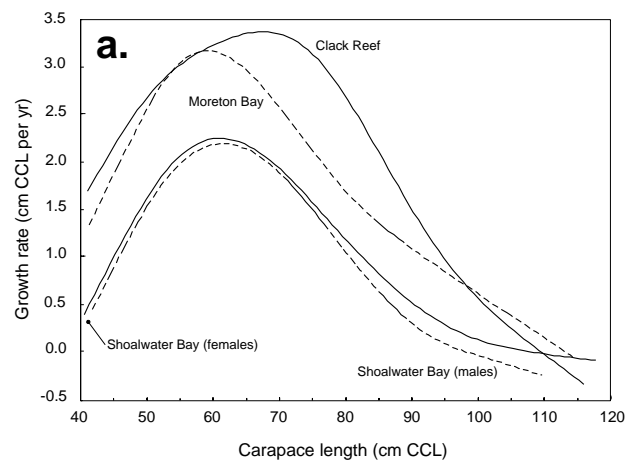
EM = egg mortality = normal pdf (mean = 0.159, standard deviation = 0.02)

HM = hatchling mortality = normal pdf (0.45, 0.05)

PHM = post-hatchling mortality = normal pdf (0.05, 0.01)

EM, HM and PHM were derived from Limpus & Reed (1985) and Gyuris (1994). Equation (2) was sampled 5000 times using Monte Carlo simulation (Vose 1996) with maximum likelihood (ML) estimates of pdf parameters. A normal pdf fitted the 5000 f_i samples best with ML mean = 0.4394 and standard deviation = 0.04. Stage 1 survival would then be sampled in simulation model from a normal pdf with those parameters. Stage 2 or pelagic juvenile mortality for all sea turtle stock is unknown and must be derived here by tuning a model to a stochastic estimate of pelagic mortality that results in a stable population. This approach will be adopted in the Phase 2 development of a stochastic simulation model for the sGBR green sea turtle population dynamics.

Figure 7. (NEXT PAGE) Estimated age- and size-specific growth functions for each foraging ground. Growth functions for Clack Reef, Shoalwater Bay and Moreton Bay foraging grounds shown in panels (a) to (c); corresponding functions for Heron/Wistari Reef foraging ground in (d) to (f) shown separately to avoid clutter. Panels (a), (d) reproduce size-specific growth rate functions derived using cubic B-spline fit to GAM predicted values (Figure 6c,g,k,o). Those functions were integrated numerically to give expected size-at-age (age ~ years-at-large since recruitment) functions in (b: Clack Reef, Shoalwater Bay, Moreton Bay) and (e: Heron/ Wistari Reef). The expected size-at-age functions (b) and (e) were differentiated to give expected age-specific growth rate functions shown in (c) and (f).



Benthic stage survival estimates

Expected sex-specific survival probabilities have been estimated for the benthic habitat ageclasses or developmental stages (benthic juveniles, subadults, maturing and mature adults) using a comprehensive capture-mark-recapture program (Chaloupka & Limpus 1998) and outlined below.

Data sets

The data set comprised the annual capture-mark-recapture (CMR) history profiles for 5124 sGBR green turtles sampled in 3 of the major sGBR foraging grounds since 1984 (Shoalwater Bay, Heron/Wistari Reefs, Moreton Bay — see Figure 1). The Heron/Wistari CMR dataset covers a 9 yr period from 1984-1992, the Shoalwater Bay dataset covers a 12 yr period from 1987-1998 and the Moreton Bay dataset covers a 11 yr period from 1990-2000. Capture and recapture was undertaken using the turtle rodeo technique with each turtle double-marked with uniquely coded titanium tags since 1984 (Limpus & Reed 1985). Titanium tag loss for this CMR study has been shown to be inconsequential (Limpus 1992a). Each CMR profile recorded whether or not a particular turtle was captured at least once during each of the annual sampling occasions. For instance, the CMR profile {#12345: 001101100} for the Heron/Wistari study site means a specific turtle was first captured, tagged (#12345) and released alive in the third sampling occasion of the study (1986). It was then recaptured alive and released at least once in 1987, again in 1989 and then again in 1990. The failure to recapture that turtle in 1991 and 1992 does not necessarily mean that the turtle died in 1991. The first “1” in each profile indicates not only initial capture but also the initial tagging cohort for each turtle. This CMR capture history form is known as “incomplete registration of survivors” data because recapture probability is less than 1 and so survival estimation requires simultaneous modelling of survival and recapture probabilities (Lebreton et al. 1993).

In addition to capture history, the CMR profiles recorded for each turtle included:

- size based on midline curved carapace length (cm CCL) at first capture and at each subsequent recapture or sampling occasion;
- sex and maturity status determined from visual examination of the reproductive organs using laparoscopy (Limpus & Reed 1985; Limpus et al. 1994a);
- sex-specific ontogenetic stage or ageclass classification assigned to each turtle at first capture derived from a combination of size-specific growth functions (Limpus & Chaloupka 1997) and maturity status.

A demographic classification of the 5124 individual CMR profiles used for estimation of sex- and stage-specific survival and recapture probabilities for the 3 foraging ground populations of the sGBR genetic stock is shown in Table 3. More details of this extensive CMR program can be found elsewhere (Limpus & Reed 1985; Limpus 1992b; Limpus et al. 1994a) while Chaloupka & Musick (1997) give an overview of the sampling and tagging protocols found in sea turtle CMR programs.

Table 3. Demographic summary of the 5124 CMR profiles for green turtles from the sGBR metapopulation that were resident in 3 major sGBR foraging grounds between 1984 and 2000. Turtles assigned to ontogenetic stage at time of first capture.

Site	Stage	Sex		Total
		Female	Male	
Heron/Wistari (954)	adults	93	142	235
	subadults	224	153	377
	juveniles	215	127	342
Shoalwater Bay (2584)	adults	627	301	928
	subadults	764	308	1072
	juveniles	396	188	584
Moreton Bay (1586)	adults	126	66	192
	subadults	292	186	366
	juveniles	599	317	916
Total		3336	1788	5124

Statistical modelling approach

Maximum likelihood estimates of the annual sex- and stage-specific survival and recapture probabilities for the green turtles resident in sGBR foraging grounds were derived from the 5124 foraging ground specific CMR profiles using the multinomial Cormack-Jolly-Seber (CJS) modelling approach advocated by Lebreton et al. (1992, 1993). 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 time-dependent demographic probabilities are well known and were discussed elsewhere (Cormack 1989; Pollock 1991; Lebreton et al. 1992; Brownie et al. 1993; Kendall et al. 1997; Pradel et al. 1997).

A major assumption of the time-dependent survival estimators of the CJS model is homogeneity of recapture likelihood. This assumption is addressed by including informative demographic covariates (age, sex), sampling occasion (sampling effort) covariates or multistate transitions in a CJS model to account for differences in survival and/or recapture probabilities (Cormack 1989; Lebreton et al. 1992; Brownie et al. 1993). Sex and ontogenetic stage (adults, subadults, juveniles) were the demographic factors used here by post-stratification of the 5124 CMR profiles into 3 sex-within-stage CJS models for each foraging ground to account for individual recapture heterogeneity. Each of these stage-specific models is referred to as a global CJS model for this study.

Age-specific models including the Brownie-Robson model (Pollock et al. 1990; Loery et al. 1997) were also fitted where the standard CJS model was found to be a poor fit to the dataset. Variable sampling effort is known to have a major affect on the reliable estimation of demographic probabilities such as survival probabilities through its effect on recapture likelihood (Lebreton et al. 1992). Sampling occasion covariates such as sampling effort has been assessed for the sGBR stock and found to have no significant effect on model fit or precision of parameter estimation (Chaloupka & Limpus 1998).

Table 4. Ageclass-specific CMR summary statistics for 5124 green sea turtle CMR profiles from the sGBR metapopulation resident in 3 major sGBR foraging grounds (1984-2000). Summary notation follows Pollock et al. (1990) where: year=sampling occasion, n_t = number of turtles (marked+unmarked) captured in t th year, m_t = number of marked turtles captured in t th year, R_t = number of n_t released after t th year = n_t since all turtles released alive following capture, r_t = number of R_t captured in t th year and recaptured in a subsequent year, z_t = number captured before and after t th year but not in t th year.

Year	Juveniles				Subadults				Adults			
	$n_t = R_t$	m_t	r_t	z_t	$n_t = R_t$	m_t	r_t	z_t	$n_t = R_t$	m_t	r_t	z_t
Heron/Wistari												
1984	61		48		86		46		42		18	
1985	85	32	48	16	108	26	41	20	41	4	16	14
1986	18	10	14	54	15	8	5	53	7	1	1	29
1987	84	31	43	37	43	13	20	45	31	6	15	24
1988	60	34	32	46	73	30	21	35	34	9	7	30
1989	95	51	33	27	71	35	18	21	39	14	8	23
1990	66	31	21	29	61	16	9	23	46	10	7	21
1991	54	23	9	27	40	18	7	14	32	13	2	15
1992	67	16			47	21			37	17		
Shoalwater Bay												
1986	3		3		3		2		33		20	
1987	55	0	15	3	47	0	14	2	98	5	42	15
1988	81	2	37	16	48	5	10	11	101	18	33	39
1989	136	25	66	28	130	2	22	19	89	14	23	58
1990	134	45	49	49	146	10	26	31	138	27	31	54
1991	131	51	26	47	179	23	16	34	116	22	28	63
1992	25	16	11	57	11	5	3	45	33	12	5	79
1993	0	0	0	68	0	0	0	48	0	0	0	84
1994	84	27	21	41	179	13	11	35	125	18	20	66
1995	88	39	10	23	195	21	11	25	136	36	10	50
1996	45	24	3	9	126	16	0	20	163	38	5	22
1997	43	12			123	20			113	27		
Moreton Bay												
1990	115		59		78		27		32		6	
1991	236	22	121	37	103	7	20	20	13	2	1	4
1992	125	60	69	98	34	4	6	36	6	1	1	4
1993	78	27	54	140	37	9	10	33	13	2	4	3
1994	123	57	60	137	16	5	6	38	0	0	0	7
1995	172	95	100	102	29	8	6	36	16	2	5	5
1996	155	83	58	119	58	13	14	29	22	5	2	5
1997	170	191	53	86	49	13	5	30	22	3	4	4
1998	112	78	34	61	65	22	12	13	35	4	0	4
1999	125	56	21	39	46	9	0	16	24	3	0	1
2000	134	60			69	16			32	1		

Table 5. Summary of best CJS model fits to the CMR data sets. QAICC = quasi-likelihood corrected form of the Akaike Information Criterion, nep = number of estimable parameters in model. Overall, best model fit selected for each site/ageclass indicated by underlined QAICC.

Model	Ageclass specific	Survival		Recapture		QAICC	Nep
		Sex- specific	Time- specific	Sex- specific	Time- specific		
Shoalwater Bay juveniles							
1	no	no	yes	no	yes	1561.1	14
2	no	no	no	no	yes	<u>1565.3</u>	10
3	no	yes	yes	no	yes	1565.9	21
Shoalwater Bay subadults							
1	no	no	no	no	yes	1041.5	9
2	no	yes	no	no	yes	1043.5	10
3	no	no	yes	no	yes	<u>1047.2</u>	12
Shoalwater Bay adults							
1	yes	no	no	no	yes	1679.2	12
2	no	yes	yes	no	yes	1679.6	15
3	no	no	no	no	yes	<u>1683.4</u>	11
Moreton Bay juveniles							
1	no	no	yes	yes	yes	3645.4	27
2	no	yes	no	no	yes	<u>3646.3</u>	12
3	no	no	yes	no	yes	3648.0	18
Moreton Bay subadults							
1	no	no	yes	no	yes	885.6	14
2	no	no	no	no	yes	<u>885.8</u>	11
3	no	no	no	no	no	886.5	2
Moreton Bay adults							
1	no	yes	yes	yes	no	199.1	9
2	no	yes	yes	no	no	199.3	8
3	no	no	no	no	no	<u>207.1</u>	2

All CMR modelling was implemented using a combination of RELEASE (Burnham et al. 1987) and MARK (Cooch & White 1998; White & Burnham 1999) for goodness-of-fit testing and MARK for model estimation and hypothesis testing. All models were based on the logistic link function (Lebreton et al. 1992) to ensure within-range but perhaps still inadmissible ($\emptyset = 1$) parameter estimates – see Cormack 1989 for a detailed discussion on this important issue. The 5124 CMR profiles have been summarised in Pollock et al. (1990) form for completeness in Table 4. The tabular summary for the Heron/Wistari Reefs population is from Chaloupka & Limpus (1998).

Goodness-of-fit and model selection

The goodness-of-fit (GoF) tests used here to assess compliance with CJS model assumptions were discussed in detail by Burnham et al. (1987), Pollock et al. (1990), Lebreton et al. (1992) and Pradel (1993) and included:

- TEST2+3 comprising a summation of all TEST2 (cohort effects) and TEST3 (subcohorts within cohort effects) component tests for an omnibus test of whether the global CJS model (time- and sex-specific survival and recapture probabilities) actually fitted before proceeding to further analyses (Burnham et al. 1987; Lebreton et al. 1992);

- the Brownie-Robson test for age/handling-effect or transients, which is equivalent to the TEST3.SR component test in RELEASE to help diagnose failure of global CJS model fit, if this occurred (Pradel et al. 1997; Loery et al. 1997);
- the Pradel ITEC test for specific behavioural patterns that mimic trap-dependence (eg., temporary emigration, recapture heterogeneity), which is also the TEST2.CT component test in some modified versions of RELEASE to help diagnose failure of CJS model fit, if this occurred (Pradel 1993; Pradel et al. 1995);
- TEST1 for an omnibus test for assessing any difference in survival and/or recapture probabilities between demographic subgroups (sex, stage, ageclass) or stratification of the CMR sample into treatment subgroups (Burnham et al 1987; Lebreton et al. 1992).

Once a satisfactory stage-specific global CJS model (time- and sex-specific survival and recapture probabilities) was found based on a GoF test (TEST2+3), then a number of reduced-parameter forms were fitted to find the most parsimonious model (Pollock et al. 1990; Lebreton et al. 1992). For instance, the standard CJS model (time-specific survival and recapture probabilities) is a reduced-parameter form and if it fitted the data as well as the global model then the parameter estimates would be based on the reduced model fit since there is no sex-specific difference in survival and recapture probabilities.

All model selection and statistical inference protocols relative to the global CJS model were based on the quasi-likelihood corrected form of the Akaike Information Criterion (QAICC), which is used for rapid screening of a large number of model fits (Burnham et al. 1995; Anderson et al. 1998). The most parsimonious model selected for each green turtle ontogenetic stage within each foraging ground was then used to derive maximum likelihood estimates of sex- and stage-specific survival and recapture probabilities.

Major findings relevant to the consultancy

A summary of the 3 best fit CJS models fitted to the 5124 CMR profiles is shown in Table 5. The best fit or preferred model compared to the global or full parameter CJS model is shown in Table 5 by the underlined QAICC value. The preferred model was selected on QAICC and admissible estimates. For instance, model 1 for Shoalwater Bay subadults was the best fit model but gave an inadmissible survival probability estimate (\emptyset greater than 1) so model 3 was used since it gave admissible parameter estimates. The adequacy of the global model assessed using (TEST2+3) was found to be good for the Heron/Wistari and Moreton Bay datasets and for the juvenile and adult Shoalwater Bay datasets because recapture probabilities were adequate. Global model fit for the subadult Shoalwater Bay datasets was poor and indicative of transient behaviour (see Pradel et al. 1997).

The GoF of the preferred fit model selected by QAICC relative to the global model was then assessed in absolute terms using a parametric bootstrap approach implemented in MARK (Cooch & White 1998). The bootstrap method enables an assessment of whether the preferred model fits the data set overall rather than just being the best fit compared to the model set summarised in Table 5. The bootstrap evaluation of the preferred models in Table 4 (underlined QAICC) were found to be good for the Heron/Wistari and Moreton Bay datasets and for the juvenile Shoalwater Bay dataset but marginal for Shoalwater Bay subadults and adults. There was some indication of apparent age-

specific survivorship for Shoalwater Bay adults but the recapture probabilities were too low to be conclusive so a simpler model was selected as the preferred model (Table 5).

Table 6. CJS survival probability estimates.

Site	Ageclass	Mean MLE estimate	95% confidence interval	
			Lower	Upper
Heron/Wistari	juveniles	0.8804	0.835	0.927
	subadults	0.8474	0.790	0.908
	adults	0.9482	0.919	0.978
Shoalwater Bay	juveniles	0.8290	0.777	0.871
	subadults	0.9389	0.878	0.999
	adults	0.9675	0.844	0.993
Moreton Bay	juveniles - females	0.8699	0.842	0.893
	juveniles - males	0.8131	0.771	0.848
	subadults	0.8858	0.806	0.935
	adults	0.8134	0.626	0.918

The ageclass or stage-specific survival and recapture probability maximum likelihood estimates derived from the preferred CJS models (Table 5) are summarised in Table 6 with the Heron/Wistari foraging ground estimates drawn from Chaloupka & Limpus (1998). The high annual survival probability estimate for sGBR green turtles is consistent with estimates for other long-lived vertebrates such as ungulates (Gaillard et al. 1998), manatees (Langtimm et al. 1998), pelagic seabirds (Russell 1999) and humpback whales (Chaloupka et al. 1999). The variability in the survival estimates reflects not only parameter estimation error but also environmental stochasticity and individual variation or demographic stochasticity (Engen et al. 1998), which is increasingly recognised as an important factor affecting population dynamics (Slade & Levensen 1984; McCarthy et al. 1994) and life history evolution (Fox 1993).

The survival probability estimates and estimated variability summarised in Table 6 forms the basis for including this demographic process in the stochastic simulation model to be developed in Phase 2, accounting for environmental and demographic stochasticity in survival probabilities.

POPULATION ABUNDANCE MODELLING FOR THE SGBR METAPOPOPULATION

Sex- and ageclass-specific abundance are key components of spatio-temporal population dynamics (Manly 1990). Reliable information on sex- and ageclass-specific abundance is essential for diagnosing trends (Thomson et al. 1997), assessment of population viability (Burgman et al. 1993) and development of recovery plans (Foin et al. 1998). Despite being subject to a long history of exploitation (Parsons 1962; Frazier 1980; Davenport 1988; Limpus et al. 1994a; Witzell 1994) there are few abundance estimates for any sea turtle population (Chaloupka & Limpus a).

Most assessments of sea turtle population trends have been based on monitoring of the beach nesting activity of adult females – for instance, hawksbill (Bjorndal et al. 1993), loggerhead (Limpus & Reimer 1994), flatbacks (Parmenter & Limpus 1995), leatherback (Chan & Liew 1996), olive ridley (Valverde et al. 1998), Kemp's ridley (Márquez et al. 1999), and green sea turtles (Bjorndal et al. 1999). However, monitoring only female nesting activity provides insufficient information for stock assessment because

- (1) adult females skip breeding seasons; and
- (2) no information is provided on demographic structure because the immature, adult male and non-breeding female components are not sampled.

Therefore reliable estimation of sea turtle abundance suitable for stock assessment and conservation management planning depends on sampling the demographic structure of a population resident in foraging grounds (Butler et al. 1987). I present here an assessment of sex- and stage-specific population abundance trends derived from a QPWS long-term CMR sampling program for 3 foraging populations comprising the sGBR metapopulation. These foraging ground specific and time-dependent population abundance estimates provide a basis for development of conservation plans for the sGBR green turtle stock and for development of the stochastic simulation model of green turtle population dynamics in Phase 2.

Statistical modelling approach

Huggins (1991), Pradel et al. (1997) and Pugesek et al. (1995) have shown the value of focussing on recapture behaviour where it is possible to model the effects of individual and/or sampling occasion covariates to derive recapture probability estimates. Leory et al. (1997) have then shown how it is possible to use such recapture probability estimates to derive population abundance estimates using the following approach. Chaloupka & Limpus (in press a) have used this approach to derive ageclass- and sex-specific population abundance estimates and ageclass-specific sex ratios for green and loggerhead sea turtles resident in the Heron/Wistari foraging ground of the sGBR genetic stock.

Assuming a good-fit CJS model to derive time-dependent recapture probabilities (ρ_i) for marked turtles, it is possible to estimate abundance using a Horvitz-Thompson type (Leory et al. 1997; Schwarz & Seber 1999) maximum likelihood estimator as follows:

$$N_i = (n_i / \rho_i) \dots\dots\dots (3)$$

where n_i is the number of turtles captured in i th year or sampling occasion (see Table 3), N_i is the number of turtles (both residents and transients) in the population in i th

year and p_i is the estimated capture probability in i th year derived from a CJS model (see Table 4). An approximate 95% confidence interval can then be derived from:

$$\{N_i \pm 1.96 * se(N_i)\} \dots\dots\dots (4)$$

where the conditional standard error $se(N_i) = [(n_i / \rho_i)^2 * (\text{var}(\rho_i) / (\rho_i)^2)]^{0.5}$ and $\text{var}(\rho_i)$ is the estimated capture probability variance in i th year (Loery et al. 1997 for details).

Major findings relevant to the consultancy

The Horvitz-Thompson (HT) type ageclass-specific population abundance estimates for each foraging ground derived from the recapture probability estimates listed above are summarised in Table 7. The abundance estimates were calculated using equations 3 and 4 using input from the previous CJS model evaluation to derive expected survival probabilities (Table 5). The Heron/Wistari population estimates were from Chaloupka & Limpus (in press a).

The population abundance estimates for 3 sGBR foraging populations are shown in Figure 8, which suggest increasing abundance of adults in all 3 foraging grounds and an increasing trend during the late 1980s/early 1990s for juveniles in the Heron/Wistari foraging ground. This is contrary to the recent suggestion of a declining sGBR green turtle stock (Limpus 2000b). The decline suggested by Limpus (2000b) was based on an apparent decline in mean nesting size for female sGBR green turtles. A decline in mean nesting size would be expected if the sGBR green turtle metapopulation was increasing in abundance, which would then result in a density-dependent somatic growth response due to reduce per capita food availability.

Just such a somatic growth response was found for an immature stock of green turtles in Bahamian waters (Bjorndal et al. 2000) and also for the recovering Hawaiian green turtle stock (Chaloupka & Balazs unpublished). The sGBR green turtle stock has been increasing in abundance since the mid 1980s in all sampled foraging grounds (Figure 8). Moreover, the nesting population on Heron Island has also been increasing at around 3% pa over the last 25 years (Chaloupka & Limpus in press a). All other ageclass abundance trends appear stable over the sampling period (Figure 8). However, population abundance trends need to be evaluated cautiously in conjunction with estimates of other relevant demographic parameters such as breeding rates and survival probabilities.

There are 5 approaches used to estimate sea turtle abundance or a related demographic indicator :

- (1) beach stranding counts (Epperly et al. 1996);
- (2) long-term beach census of nesting females (Bjorndal et al. 1999);
- (3) trawl- (Henwood 1987) or logbook- survey based (Witzell 1999) CPUE estimation;
- (4) aerial survey based density estimation using line- (Epperly et al. 1995) or strip-transects (Marsh & Saalfeld 1989); and
- (5) some form of CMR type estimation. The CMR approach provides an effective means to study ecological dynamics (Otis et al. 1978; Pollock et al. 1990; Lebreton et al. 1992) but there have been few CMR sea turtle abundance studies.

For instance, Mendonca & Ehrhart (1982) used closed population catch-effort (= Otis et al. 1978 model M_b) and Schnabel-type (= Otis et al. 1978 model M_l) estimators to determine immature green and loggerhead abundance in an east-central Florida coastal lagoon. Ross (1985) used a closed population Petersen estimator to determine green turtle abundance in foraging grounds off the Oman coast (northern Indian Ocean) while Le Gall et al. (1986) used a Jolly-Seber model (= Pollock et al. 1990 Model A) assuming no skipped breeding seasons to estimate nesting female abundance at 2 southern Indian Ocean green turtle rookeries.

In a well designed study, Butler et al. (1987) used a 2-stage approach comprising (1) trawl survey sampling and a closed population catch-effort or removal model (= M_b) to derive capture probabilities for (2) estimation of seasonal loggerhead abundance in Florida navigation channels over a 1 yr period. While not recognized as such, the capture-based abundance estimator used by Butler et al. (1987) was in fact an HT estimator such as used here and by Chaloupka & Limpus (in press a). Like Butler et al. (1987), the current multiple foraging ground study used a 2-stage approach comprising:

- (1) statistical modelling of the time-dependent capture probabilities for each stage, sex and foraging ground; and then
- (2) using those probabilities to derive HT type annual abundance estimates (see Figure 8).

The HT type abundance estimator was especially useful for the current project that was based on a assessment of survival and capture probabilities (Table 5). Huggins (1991) has shown the value of focussing on recapture likelihood where it is possible to model the effects of individual covariates (sex, size) and sampling occasion covariates (sampling effort) to derive better capture probability estimates. The time-dependent survival and capture probability models used in the current study (Table 6) included sex and developmental stage as informative individual covariates and annual sampling effort as a sampling occasion covariate has been previously assessed. This modelling approach provided robust estimates of the sex- and stage-specific capture probabilities for each foraging ground population of sGBR genetic stock that were suitable for deriving annual stage-specific abundance estimates.

Chaloupka & Limpus (in press a) have estimated that the sGBR green turtle genetic stock comprises at least 850,000 individuals resident in spatially disjunct coral reef habitat foraging grounds ranging from Heron/Wistari to Clack Reef in nGNR waters (Figure 1), which is the main geographic range of the sGBR genetic stock (Limpus et al. 1992). This estimate does not take into account abundance in major coastal foraging grounds such as Princess Charlotte Bay, Cleveland Bay, Repulse Bay, Shoalwater Bay, Hervey Bay and Moreton Bay (Figure 1) nor does it account for sGBR green turtles resident in other southwestern Pacific foraging grounds such as New Caledonia. Hence, the aerial survey estimate of Preen et al. (1997) that there were only ca 60,000 sea turtles of all species in the GBR region including inshore habitats is probably in error by a factor of 15 for green turtles in GBR coral reef habitats alone. The aerial survey estimate was drawn from Marsh & Saalfeld (1989) who had cautioned that their well designed sampling study provided precise but underestimates of turtle abundance. Marsh & Saalfeld (1989) noted that aerial surveys were probably inappropriate for estimating GBR turtle abundance because turtles were so difficult to sight from the air even in clear GBR waters.

The CMR modelling based population abundance estimates presented here are the most comprehensive estimates available for any sea turtle stock and provide the basis for evaluation of population structure of each foraging ground and for deriving estimates of metapopulation abundance essential for development of a stochastic simulation model of sGBR green turtle population dynamics in Phase 2.

Table 7. Summary of abundance estimates for green turtles in Shoalwater Bay and Moreton Bay populations. π_i = CJS model estimate of recapture probability in i th year, se = standard error of recapture probability, N_i = Horvitz-Thompson type population abundance estimate, LCL and UCL = lower and upper 95% confidence bound of abundance estimate. Missing rows show years with no sampling effort so recapture probability was zero. Summary for the Heron/Wistari foraging ground is given in Chaloupka & Limpus (in press a) and recall that there were no CMR data for the Clack Reef foraging ground population.

year	Juveniles					Subadults					Adults				
	π_i	se	N_i	LCL	UCL	π_i	se	N_i	LCL	UCL	π_i	se	N_i	LCL	UCL
Shoalwater Bay foraging ground															
1987											0.154	0.064	635	122	1147
1988	0.043	0.030	1879	0	4437	0.100	0.042	480	81	880	0.145	0.032	696	398	993
1989	0.245	0.045	555	357	754	0.022	0.015	6047	0	14315	0.069	0.018	1299	641	1957
1990	0.254	0.035	529	385	672	0.045	0.014	3230	1283	5177	0.098	0.018	1412	902	1923
1991	0.230	0.031	571	418	723	0.064	0.013	2780	1688	3871	0.057	0.012	2021	1200	2842
1992	0.064	0.016	391	198	583	0.010	0.004	1134	149	2119	0.025	0.007	1299	577	2021
1993	0.064	0.016													
1994	0.151	0.032	557	323	790	0.025	0.007	7160	3343	10977	0.037	0.009	3351	1819	4883
1995	0.199	0.037	442	281	604	0.031	0.007	6352	3675	9028	0.062	0.010	2204	1490	2918
1996	0.118	0.027	380	210	551	0.019	0.005	6774	3491	10058	0.056	0.009	2906	1972	3839
1997	0.065	0.020	665	256	1073	0.021	0.005	5971	3358	8584	0.034	0.007	3333	2061	4605
Moreton Bay foraging ground															
1991	0.227	0.043	1037	649	1426	0.100	0.036	1028	300	1756	0.058	0.018	226	84	369
1992	0.228	0.026	547	422	671	0.027	0.013	1250	34	2466	0.058	0.018	104	39	170
1993	0.096	0.017	805	514	1096	0.057	0.019	642	223	1062	0.058	0.018	226	84	369
1994	0.200	0.024	614	465	762	0.030	0.013	521	59	984					
1995	0.318	0.029	541	443	639	0.051	0.019	559	156	962	0.058	0.018	278	103	454
1996	0.256	0.026	605	484	727	0.083	0.025	691	279	1103	0.058	0.018	383	141	624
1997	0.269	0.027	632	507	756	0.073	0.022	668	268	1069	0.058	0.018	383	141	624
1998	0.220	0.024	507	395	619	0.116	0.029	557	277	837	0.058	0.018	609	225	993
1999	0.169	0.023	736	539	933	0.043	0.016	1050	298	1802	0.058	0.018	417	154	681
2000	0.176	0.023	760	559	961	0.074	0.022	926	383	1470	0.058	0.018	557	206	907

CONCLUSION

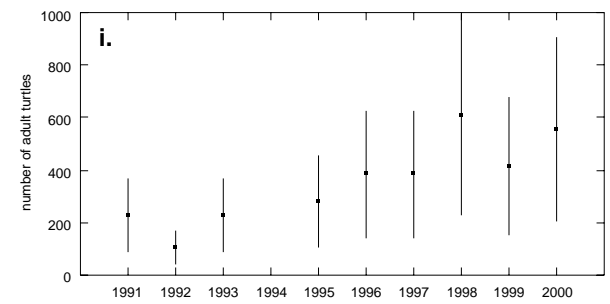
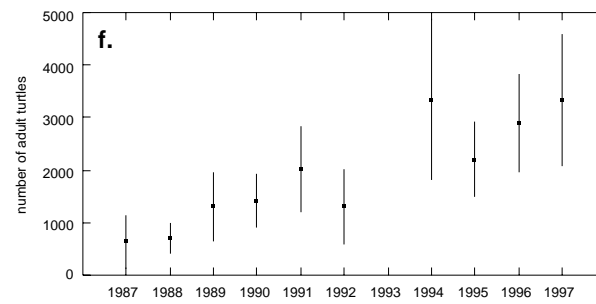
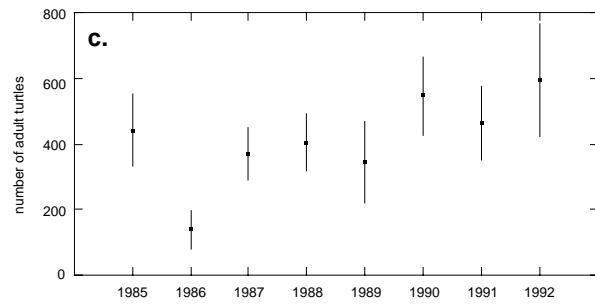
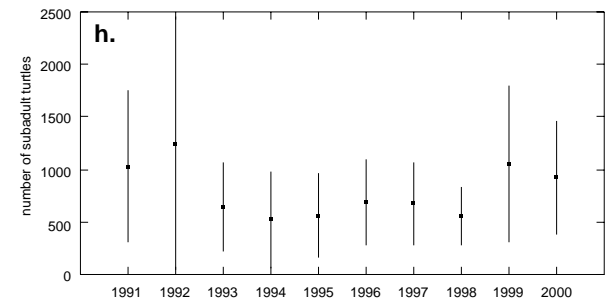
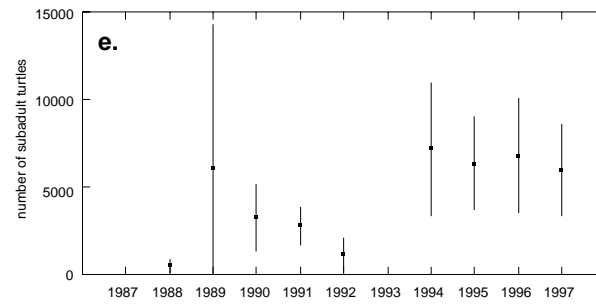
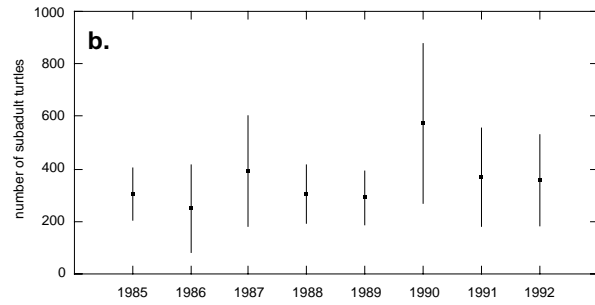
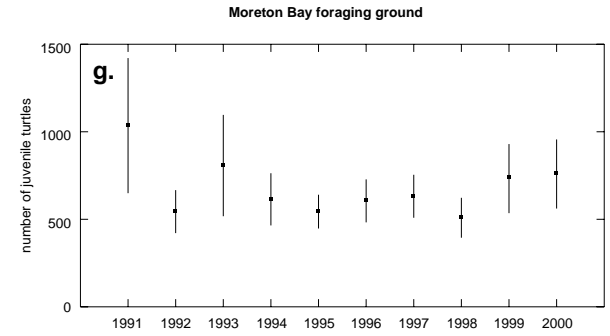
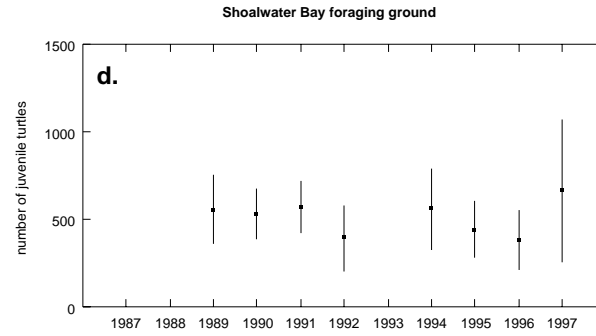
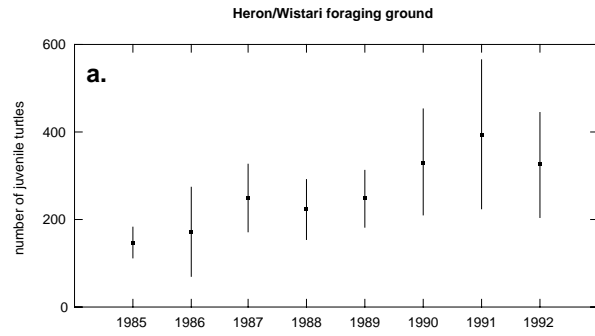
Significance of QPWS sea turtle program

It is important to recognise that there are no other sea turtle research programs that could provide the depth of data outlined above. For instance, there are no other sea turtle programs that have sex-specific data based on laparoscopy (Limpus & Reed 1985) and few with reliable long-term tagging protocols in the foraging grounds (Limpus 1992a; Chaloupka & Musick 1997). The capability for visual examination of reproductive organs using laparoscopy enables not only sex determination but also the capability to assess maturity and breeding status of individual turtles in the foraging grounds (Figure 4).

The long-term use of laparoscopy by the QPWS sea turtle research program is one of the many reasons that the QPWS program is the most comprehensive long-term study of sea turtle demography in the world. There are only 3 other major ongoing green sea turtle research programs in the foraging grounds – Hawaii (Balazs et al. 2000), Indian River lagoon in Florida (Mendonca & Ehrhart 1982) and in the Bahamas (Bjorndal et al. 2000). All these long-term studies provide the basis for comparative studies of sea turtle demography as shown recently by Bjorndal et al. (2000).

In summary, the QPWS sea turtle research program provides substantial data sets on many key aspects of sea turtle demography essential for developing a spatially and age structured sex-specific stochastic simulation model that would be suitable for designing conservation policies and strategies such as the potential impact of harvesting on long-term sGBR stock viability. The analyses to support model development are presented above using the extensive QPWS database on sea turtles. The data sets also enable inclusion of both environmental and demographic stochasticity for some demographic processes.

Figure 8. (NEXT PAGE) Annual stage-specific Horvitz-Thompson type population abundance estimates (solid squares) for green turtles resident in 3 major foraging grounds of the sGBR genetic stock. Panels (a-c) show population abundance estimates for Heron/Wistari foraging ground population, (d-f) for Shoalwater Bay and (g-i) for Moreton Bay. Panels (a,d,g) show abundance estimates for juveniles, panels (b,e,h) for subadults and panels (c,f,i) for adults. Vertical bar = approximate 95% confidence interval.



Recommendations for future directions

Although the QPWS sea turtle research program is by far the most comprehensive sea turtle research program in the world, there are nonetheless several areas that need to be considered to improve the program to further support the conservation of green sea turtles and their habitats in Great Barrier Reef waters.

The following recommendations for program improvement were derived after consideration of the information limitations identified in this report and elsewhere (Limpus & Chaloupka 1997; Chaloupka 2001; Chaloupka & Limpus in press a; Chaloupka & Limpus in press b) and following consultation with the QPWS sea turtle research program leader, Dr Colin Limpus:

- (1) Establish a concurrent annual nesting census program on Heron Island, Northwest, Wreck and Lady Musgrave Islands in the southern Great Barrier Reef for robust trend monitoring, to enable an assessment of dispersal within the regional rookery and also to provide a basis for simulation model calibration based on multiple sites rather than 1 site (Heron Island)
- (2) Establish a concurrent multi-site capture-mark-recapture (CMR) program in sGBR waters to support more robust estimates of ageclass-specific survival probabilities, ageclass-specific abundance and to investigate the possibility of sex-specific and/or ageclass-specific dispersal behaviour as suggested by Chaloupka & Limpus (in press b)
- (3) Expand the current CMR program to include important sGBR foraging grounds such as Hervey Bay and maintain the existing CMR study sites in Clack Reef, Shoalwater Bay, Heron/Wistari Reefs and Moreton Bay
- (4) Increase the number of researchers capable of performing laparoscopy throughout the State to support the recommended expanded CMR program
- (5) Promote the sea turtle research program as a major long-term ecological monitoring and research program of national and international significance and expand the application of this work and expertise into the neighbouring Southeast Asian region
- (6) Establish a program to assess the pelagic phase demography in the southwestern Pacific Ocean similar to the program established by Dr Alan Bolten (Archie Carr Centre for Sea Turtle Research, University of Florida)
- (7) Develop a robust method to identify and monitor new recruits settling from the pelagic phase into a benthic habitat in Great Barrier Reef and southern Queensland coastal waters
- (8) Develop skeletochronological methods to support reliable age estimation of biopsied sea turtles and stranded sea turtles in Great Barrier Reef and southern Queensland coastal waters
- (9) Maintain the annual nesting census on Raine Island to monitor the Great Barrier Reef wide spatial synchrony in nesting and reproductive behaviour of the sGBR and nGBR green sea turtle stocks as suggested in Chaloupka (2001)

The Great Barrier Reef Marine Park Authority research priorities (www.gbrmpa.gov.au) will be evaluated in the light of these recommendations.

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GLOSSARY

adults	fourth benthic phase ageclasses (≥ 46 yrs, 100% mature)
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
CCL	size estimate based on the mid-line curved carapace length in centimeters (cm CCL)
CJS	Cormack-Jolly-Seber
CMR	capture-mark-recapture
demographic stochasticity	realised population variability in modelled survival, dispersal or reproductive output due to individual variability after accounting for any environmental stochasticity
ENSO	El Niño-Southern Oscillation (ocean-atmosphere anomaly)
environmental stochasticity	expected population variability in modelled survival, dispersal or reproductive probabilities due to environmental effects
foraging ground	benthic habitat geographic residence
immatures	second benthic phase ageclasses (ca 15-29 yrs of age)
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)
QPWS	Queensland Parks and Wildlife Service
sGBR	southern Great Barrier Reef
subadults	third benthic phase ageclasses (ca 30-45 yrs of age)