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# Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters

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## Abstract

A mark-recapture study was used to estimate trends in annual abundance of green and loggerhead turtles resident in southern Great Barrier Reef (sGBR) waters between 1985–1992. Abundance was derived using a Horvitz–Thompson type estimator based on sex- and ageclass-specific recapture probabilities conditioned on annual sampling effort. The resident green turtle population increased over the 8 years by 11% pa and comprised 1300 individuals in 1992. The female nesting population also increased but more slowly at 3% pa and has continued to do so. The increase may be due to favourable environmental conditions affecting breeding behaviour. On the other hand, the resident loggerhead population declined at 3% pa and comprised < 40 adults by 1992. The female loggerhead nesting population also declined over the same period at 8% pa and has continued to do so. Yet loggerhead survival was high and constant so the decline may be due to recruitment failures resulting from (1) fox predation of eggs at mainland rookeries during the 1960s and (2) pelagic juvenile mortality from incidental capture in longline fisheries since the 1970s. The sGBR loggerhead stock is clearly endangered. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Sea turtles; Abundance; Sex ratios; Transients; Foraging grounds; Great Barrier Reef

## 1. Introduction

Sex- and age-specific abundance are key components of spatio-temporal population dynamics (Manly, 1990). Therefore, reliable information on sex- and age-specific abundance is essential for diagnosing population trends (Thomson et al., 1997), assessment of long-term population viability (Burgman et al., 1993) and development of species recovery plans (Foin et al., 1998). Yet despite being subject to a very long history of exploitation in traditional or commercial fisheries (Parsons, 1962; Johannes, 1978; Frazier, 1980; Davenport, 1988; Horikoshi et al., 1994; Limpus et al., 1994a; Witzell, 1994) there are few abundance estimates for any sea turtle population (Mendonca and Ehrhart, 1982; Ross, 1985; Butler et al., 1987).

Most assessments of sea turtle population trends have been based on long-term monitoring of the seasonal beach nesting activity of adult females — for instance, hawksbill (Bjorndal et al., 1993), loggerhead (Limpus

and Reimer, 1994), flatback (Parmenter and Limpus, 1995), leatherback (Chan and Liew, 1996), olive ridley (Valverde et al., 1998), Kemp's ridley (Márquez et al., 1999) and green sea turtles (Bjorndal et al., 1999). Unfortunately, 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 entire demographic structure of a population resident in the foraging grounds (Butler et al., 1987).

Two common species of sea turtle resident in the southern Great Barrier Reef (sGBR) foraging grounds are the green turtle (*Chelonia mydas*) and the loggerhead (*Caretta caretta*). The green turtle is recognised as under threat globally (National Research Council, 1990) with the sGBR stock exposed to a low mortality risk due to incidental capture in Australian coastal fisheries (Poiner and Harris, 1996; Slater et al., 1998) or from traditional

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harvesting in northern Australian and nearby South East Asian waters (Limpus et al., 1992). Just how serious these risks are to the long-term viability of the sGBR green sea turtle stock is not known at this stage. The loggerhead turtle is recognised globally as endangered (IUCN Red Data List) with the sGBR loggerhead stock exposed to a very high risk of incidental capture in Australian coastal fisheries (Poiner and Harris, 1996; Slater et al., 1998).

We present here a detailed assessment of sex- and ageclass-specific population abundance trends derived from a long-term capture-mark-recapture (CMR) sampling program for these two sea turtle species resident in sGBR foraging grounds (Fig. 1). These species-specific time-dependent population abundance estimates provide a basis for development of meaningful recovery and conservation management plans for green and loggerhead sea turtles resident in Australian waters.

## 2. Methods

### 2.1. Data summary

The data set comprised the annual capture-mark-recapture (CMR) history profiles for 954 sGBR green turtles and 271 sGBR loggerhead turtles sampled in the

Heron Reef/Wistari Reef complex in the sGBR foraging grounds (1984–1992). The Heron/Wistari Reefs study area is an offshore algal based coral reef habitat in southern Great Barrier Reef waters (Fig. 1, Limpus and Reed, 1985). Each CMR profile recorded whether or not a particular turtle was captured at least once during each of the nine annual sampling occasions between 1984 and 1992 (see Chaloupka and Limpus, 1998a for details). A demographic classification of the 1225 profiles is shown in Table 1.

Sex and ageclass for each of the 1225 individual turtles were determined using laparoscopy and growth functions (Limpus and Chaloupka, 1997; Chaloupka and Limpus, 1998a). Immature green turtles recruit to benthic habitats in sGBR waters at around 40 cm CCL after pelagic development in the southwestern Pacific Ocean (Limpus and Chaloupka, 1997). Pelagic green turtle ageclass duration is poorly known but estimated at ca. 5–6 years (Limpus and Chaloupka, 1997; Zug and Glor, 1998). Mean ageclass duration for sGBR green turtles is ca. 12 years for juveniles and ca. 18 years for subadults (Limpus and Chaloupka, 1997). Immature loggerhead turtles recruit to benthic sGBR habitats at ca. 80 cm CCL after pelagic development in the southwestern Pacific (Limpus, 1994b). Pelagic loggerhead ageclass duration is poorly known but ca. 7–10 years (Chaloupka, 1998; Bjorndal et al., 2000). Ageclass

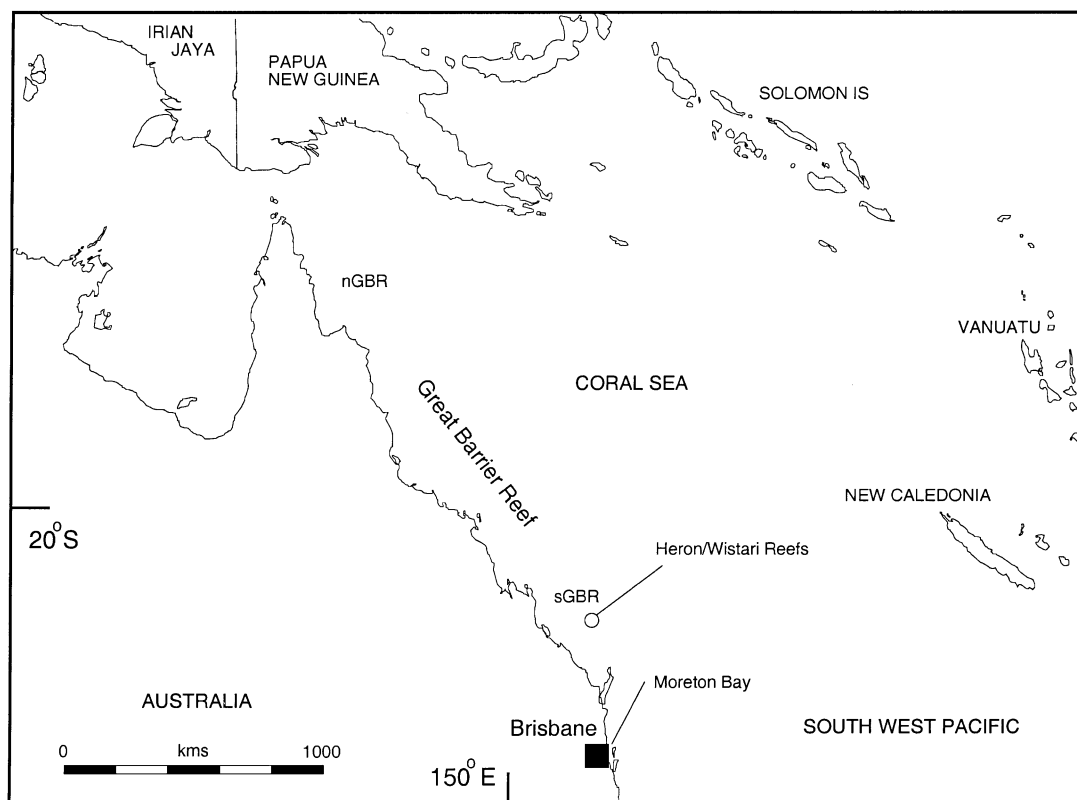


Fig. 1. Location of the Heron Reef/Wistari Reef foraging ground study site for the southern Great Barrier Reef (sGBR) genetic stocks of green and loggerhead sea turtles resident in sGBR waters.

Table 1  
Summary of the 1225 (954 green, 271 loggerhead) individual sea turtle CMR profiles used to derive CJS sex- and ageclass-specific recapture probabilities for each species

Species	Ageclass	Size range	Sex		Total
			Female	Male	
Green	Adult	(85–120 cm CCL)	93	142	235
	Subadult	(65–90 cm CCL)	224	153	377
	Juvenile	(40–65 cm CCL)	215	127	342
Loggerhead	Adult	(85–105 cm CCL)	25	62	87
	Immature	(69–104 cm CCL)	46	138	184

duration for immature sGBR loggerhead turtles is ca. 12–15 years (Limpus, 1992). Details of the CMR program and demographic structure of the sea turtle populations are provided in Limpus and Reed, (1985) and Limpus and Chaloupka, (1997).

## 2.2. Capture probability estimation

Sex- and ageclass-specific recapture probabilities were derived from the 1225 CMR profiles (Table 1) using the Cormack–Jolly–Seber (CJS) modelling approach (Lebreton et al., 1992). The recapture probabilities for the seven best fit models shown in Table 2 were estimated using SURGE (Lebreton et al., 1992) and sourced from Chaloupka and Limpus (1998b, 2001). Informative covariates such as indices of annual sampling effort and climatic factors were included in the CJS models. Annual sampling effort measured in field-days during the 4-month CMR sampling window (March–June) varied from year to year but had no effect on estimation of either survival or capture probabilities for the sGBR green or loggerhead sea turtle populations (Chaloupka and Limpus, 1998b; Chaloupka and Limpus, 2001).

The time-specific proportions of resident immature loggerhead turtles as opposed to transients were estimated from the CMR profiles summarised in Table 1 using TMSURVIV (Pradel et al., 1997). Transients are

regarded as individuals that are not resident in the sampling area but simply in transit across the area so that they are captured on one sampling occasion only and hence have zero probability of recapture even though they are still alive (Cormack, 1993a, Pradel et al., 1997). The annual fluctuations in the estimated proportion of transient immature loggerhead turtles was not a function of sampling effort but was most likely due to anomalous oceanographic conditions affecting immature dispersal (Chaloupka and Limpus, 2001). While there were nine annual sampling occasions (1984–1992) there are only eight estimable annual abundance estimates (1985–1992) using the CJS modelling approach with constant annual survival probability, since the first occasion provides no estimate of recapture probability.

## 2.3. Population abundance estimation

A Horvitz–Thompson type estimator  $\{N_i = (n_i/\rho_i)$ ; Seber, 1982} was used to derive sex- and ageclass-specific annual abundance estimates, where  $n_i$  is number of turtles captured in the  $i$ th year,  $N_i$  is number of turtles (residents + transients) in the population in the  $i$ th year and  $\rho_i$  is estimated recapture probability in the  $i$ th year (Table 3). Approximate 95% confidence intervals were then derived from  $\{N_i \pm 1.96 \times \text{S.E.}(N_i)\}$ , where  $\text{S.E.}(N_i) = \text{conditional standard error } \{ \text{S.E.}(N_i) = [(n_i/\rho_i)^2 \times (\text{var}(\rho_i)/(\rho_i)^2)]^{0.5} \}$  and  $\text{var}(\rho_i)$  is estimated recapture probability variance in  $i$ th year (Loery et al., 1997). Recapture probabilities and variances (Table 3) were derived from the CJS models in Table 2. It was assumed that all immature loggerhead turtles (residents and transients) had the same recapture probability in order to derive immature abundance estimates. The advantages of a Horvitz–Thompson (HT) estimator is that it is based on few assumptions (Seber, 1982) and is especially applicable to long-term CMR studies where the emphasis is on robust statistical modelling of recapture probabilities as an informative ecological process

Table 2  
Summary of the CJS models used to derive sex- and ageclass-specific recapture probability estimates for each species sourced from Chaloupka and Limpus (1998b, 2001)<sup>a</sup>

Species	Ageclass	Model description			GoF		
		Survival	Recapture	Transients	$\chi^2$	d.f.	$P$
Green	Adult	Constant	Effort-dependent		63.7	59	> 0.05
	Subadult	Constant	Time-specific		87.4	70	> 0.05
	Juvenile	Constant	Time-specific		65.2	50	> 0.05
Loggerhead	Adult	Constant	Sex-, time-specific		65.2	50	> 0.05
	Immature	Constant	Sex-, time-specific		117.8	54	< 0.05
	Immature	Constant	Time-specific (females)	Time-specific	15.6	47	> 0.05
	Immature	Constant	Time-specific (males)	Time-specific	53.1	47	> 0.05

<sup>a</sup> Goodness-of-fit tests (GoF) show that all models fitted satisfactorily in compliance with CJS model assumptions except for immature loggerhead turtles unless assumed transients were accounted for. Models that accounted for transients fit the immature data well.

Table 3

Summary statistics used for abundance estimation for green and loggerhead sea turtles resident in sGBR waters (1985–1992) J, juvenile; S, subadult; A, adult; I, immature;  $n_i$ , total number of turtles (marked + unmarked) captured at  $i$ th sampling occasion;  $R_i$ , number of  $n_i$  released after  $i$ th occasion =  $n_i$  as all turtles were released alive following capture;  $\rho_i$ , estimated recapture probability from best fit CJS models summarised in Table 2;  $\text{var}(\rho_i)$ , estimated  $\rho_i$  variance;  $\gamma_i$ , estimated proportion of residents so  $(1 - \gamma_i)$  is proportion of transients in sample

Species	Ageclass	Sex	Estimate	Sampling occasions								
				1985	1986	1987	1988	1989	1990	1991	1992	
Green	J	F	$n_i = R_i$	51	12	53	40	60	44	36	49	
		M	$n_i = R_i$	34	6	31	20	35	22	18	18	
		F,M	$\rho_i$	0.5791	0.1049	0.3379	0.2691	0.3823	0.1993	0.1369	0.2056	
		F,M	$\text{var}(\rho_i)$	0.0047	0.0010	0.0029	0.0018	0.0027	0.0014	0.0009	0.0015	
	S	F	$n_i = R_i$	70	8	24	48	42	35	22	21	
		M	$n_i = R_i$	38	7	19	25	29	26	18	26	
		F,M	$\rho_i$	0.3535	0.0605	0.1102	0.2385	0.2461	0.1061	0.1088	0.1322	
		F,M	$\text{var}(\rho_i)$	0.0035	0.0004	0.0009	0.0020	0.0020	0.0008	0.0008	0.0011	
	A	F	$n_i = R_i$	18	2	13	11	18	19	10	13	
		M	$n_i = R_i$	23	5	18	23	21	27	22	24	
		F,M	$\rho_i$	0.0929	0.0505	0.0841	0.0841	0.1131	0.0841	0.0688	0.0621	
		F,M	$\text{var}(\rho_i)$	0.0001	0.0001	0.0001	0.0001	0.0004	0.0001	0.0001	0.0001	
	Loggerhead	I	F	$n_i = R_i$	25	14	19	19	20	20	20	17
				$\rho_i$	1.0000	0.7587	0.9359	0.7047	0.9294	0.8257	0.8687	0.7687
				$\text{var}(\rho_i)$	0.0000	0.0115	0.0036	0.0115	0.0043	0.0083	0.0067	0.0113
			$\gamma_i$	0.3830	0.5000	0.3526	0.3494	1.0000	0.8337	0.7749		
M			$n_i = R_i$	47	23	37	38	54	49	63	44	
			$\rho_i$	0.6831	0.3221	0.4673	0.5129	0.6905	0.6643	0.794	0.6527	
			$\text{var}(\rho_i)$	0.0061	0.0041	0.0050	0.0047	0.0043	0.0047	0.0043	0.0054	
			$\gamma_i$	0.8637	0.5961	0.6315	0.6356	0.6917	0.5853	0.3482		
A		F	$n_i = R_i$	15	5	11	6	9	10	11	10	
			$\rho_i$	0.7774	0.3699	0.7762	0.4417	0.8029	0.8906	1.0000	1.0000	
			$\text{var}(\rho_i)$	0.0295	0.0186	0.0173	0.0201	0.0151	0.0102	0.0000	0.0000	
		M	$n_i = R_i$	39	21	22	22	18	16	16	14	
$\rho_i$			0.8267	0.4793	0.4946	0.5287	0.5435	0.4749	0.5702	0.4604		
		$\text{var}(\rho_i)$	0.0042	0.0063	0.0070	0.0069	0.0087	0.0118	0.0123	0.0154		

(Huggins, 1991; Pugesek et al., 1995) rather than using them only as nuisance parameters in survival estimation (Lebreton et al., 1992). The HT type estimator has found wide-spread application in a variety of forms in long-term CMR studies (Huggins, 1991; Loery et al., 1997; Chaloupka 2000a).

The HT annual abundance estimates for immature and adult green turtle were compared with mean annual abundance derived from another form of open population model using a Poisson likelihood modelling approach that also accounts for transients (Cormack, 1989, 1993a). It was of interest to compare the estimates as concurrence between different but assumption equivalent modelling approaches provides confidence in the annual HT estimates used here. The Cormack population abundance models were implemented with GLIM (Aitkin et al., 1989) using macros sourced from Cormack (1985, 1993a, 1993b, personal communication). Model selection was based on loglikelihood ratio tests (McCullagh and Nelder 1989) and assessment of parameter estimates and residual patterns suggested by Cormack (1985, 1993a).

The HT annual abundance estimates for adult green turtles were also compared with mean annual adult abundance derived from a closed population model ( $M_{t,bh}$ ) that accounts for any variation in individual recapture probability due to temporal variability ( $t$ ), behavioural response due to prior capture history ( $b$ ) and recapture heterogeneity ( $h$ ) modelled here using individual covariates (sex, size) and sampling occasion effort. Model  $M_{t,bh}$  has been discussed in detail elsewhere (Otis et al., 1978; Pollock et al., 1990) with some explicit estimators available (Lee and Chao, 1994). It is one of the more flexible classes of estimators available but assumes demographic closure so it will over-estimate abundance as the turtle population changes over the sampling period due to birth, death and possibly permanent dispersal. Nonetheless, it was of interest to compare the two estimates since it is well known that open population estimators can be sensitive to capture heterogeneity (Pollock et al., 1990) and transient behaviour (Cormack, 1993a) and so the closed model provides an upper bound on estimated abundance. The model was applied only to adult green turtles because

immature green turtles and loggerhead turtles are more likely to display transient behaviour and the loggerhead population was declining. The  $M_{tbh}$  equivalent was estimated using a logistic regression modelling approach (Buckland et al., 1993) developed for complex derivative forms of  $M_{tbh}$  (Huggins, 1989, 1991) and implemented with SHAZAM (White, 1997). Model selection was based on analysis-of-deviance tests (McCullagh and Nelder, 1989) but the full ( $M_{tbh}$ ) fitted better than any reduced parameter form such as ( $M_{tb}$ ).

#### 2.4. Population trend estimation

Variance-weighted linear regression models with log link and first order moving average error [MA(1); Judge et al., 1985] to account for any temporal correlation were used to estimate long-term linear trends in sex- or ageclass-specific sea turtle abundance. The response variable (HT annual abundance estimate) was in natural log form so that the parameter estimate for year (1985–1992) was interpretable as a constant annual population growth rate. The models used log (HT variance estimate) weights to account for measurement uncertainty and fitted using generalised least squares (GLS) by restricted maximum likelihood estimation (REML; McCullagh and Nelder, 1989) to account for non-standard error covariance structure due to variance weighting and the assumed autocorrelated error. These GLS/REML regression models were implemented with S-PLUS 2000 (MathSoft, 1999). For comparison, the annual number of female green and loggerhead turtles nesting on Heron Island within the study area over the last 25 years was also assessed using (1) LOWESS smooths to highlight graphically any nonlinear trend (Cleveland, 1993) and (2) estimation of linear trends using a moving average or MA(1) regression model for the loggerhead nesting time series and a moving average conditional heteroskedastic or MACH(1) regression model for the green turtle series. The annual number of nesting green turtles fluctuates significantly with an occasional period of stability so that accounting for a moving average conditional heteroskedastic (MACH) time series process was essential to derive robust parameter estimates (Judge et al., 1985). These MA(1) and MACH(1) regression models were implemented with SHAZAM (White, 1997).

### 3. Results

#### 3.1. Population abundance

The time-dependent capture probabilities, variance estimates, sampling summary statistics and estimates of the proportion of resident immature loggerhead turtles derived from the 7 CJS model fits (Table 2) are sum-

marised in Table 3. More details of the CJS model analyses are provided in Chaloupka and Limpus (1998a, 2001). These capture probability estimates and CMR summary statistics were then used to derive the Horvitz–Thompson type estimates (HT) of population abundance. The HT population abundance estimates and approximate 95% confidence intervals for the estimates are shown in Fig. 2(a–f) for the green sea turtles. Also shown in Fig. 2 are mean annual ageclass-specific population estimates from the Cormack model (Fig. 2d–f), mean annual abundance of resident juveniles from the Cormack model (Fig. 2d) and mean annual adult abundance derived from the Huggins ( $M_{tbh}$ ) model equivalent (Fig. 2f). The HT population abundance estimates and approximate 95% confidence intervals for the estimates are shown in Fig. 3 for loggerhead sea turtles. The total species-specific population estimates derived from the summed HT estimates are shown in Fig. 4. Also shown in Fig. 4 is the mean annual population estimate for green turtles derived from the Cormack model (Fig. 4a).

#### 3.2. Abundance trends

The GLS/REML regression models used to assess linear trends in annual population growth are summarised in Table 4. The loggerhead population declined significantly over the 8-year period (Fig. 3, Fig. 4b) at ca. 3% pa (95% CI: –3.9 to –2.2) with the adult component (Fig. 3c) declining at ca. 7.7% pa (95% CI: –8.1 to –7.3). There were no significant trends in immature abundance (Table 4, Fig. 3a,c) nor any sex-specific differences in immature (Table 4, Fig. 3a) or adult population growth rates (Table 4, Fig. 3b). Conversely, the green turtle population increased significantly over the 8-year period (Fig. 4a) at ca. 10.6% pa (95% CI: 9.0–12.2) due to increases in juveniles (Fig. 2a,d), adults (Fig. 2c,f) and male subadults (Fig. 2b,e) but not female subadults (Table 4, Fig. 2b). Adult green turtles (Fig. 2f) increased at ca. 14.4% pa (95% CI: 11.4–17.5) and there was no sex-specific difference (Table 4, Fig. 2c). The juvenile component (Fig. 2d) increased at ca. 14% pa (95% CI: 12.9–15.1) but the female juveniles increased more rapidly than males (Table 4, Fig. 2a). Subadult green turtles increased ca. 6% pa (95% CI: 4.3–7.8) but at a slower rate than either juveniles or adults (Table 4). There was no linear trend in female subadult abundance (Table 4, Fig. 2b).

#### 3.3. Trends in immature transients

The mean annual estimate of resident (as opposed to transient) juvenile green turtles is shown in Fig. 2d. Transients were defined as those sea turtles that were captured once only and presumed to be in transit across the study site enroute to somewhere else (Cormack,

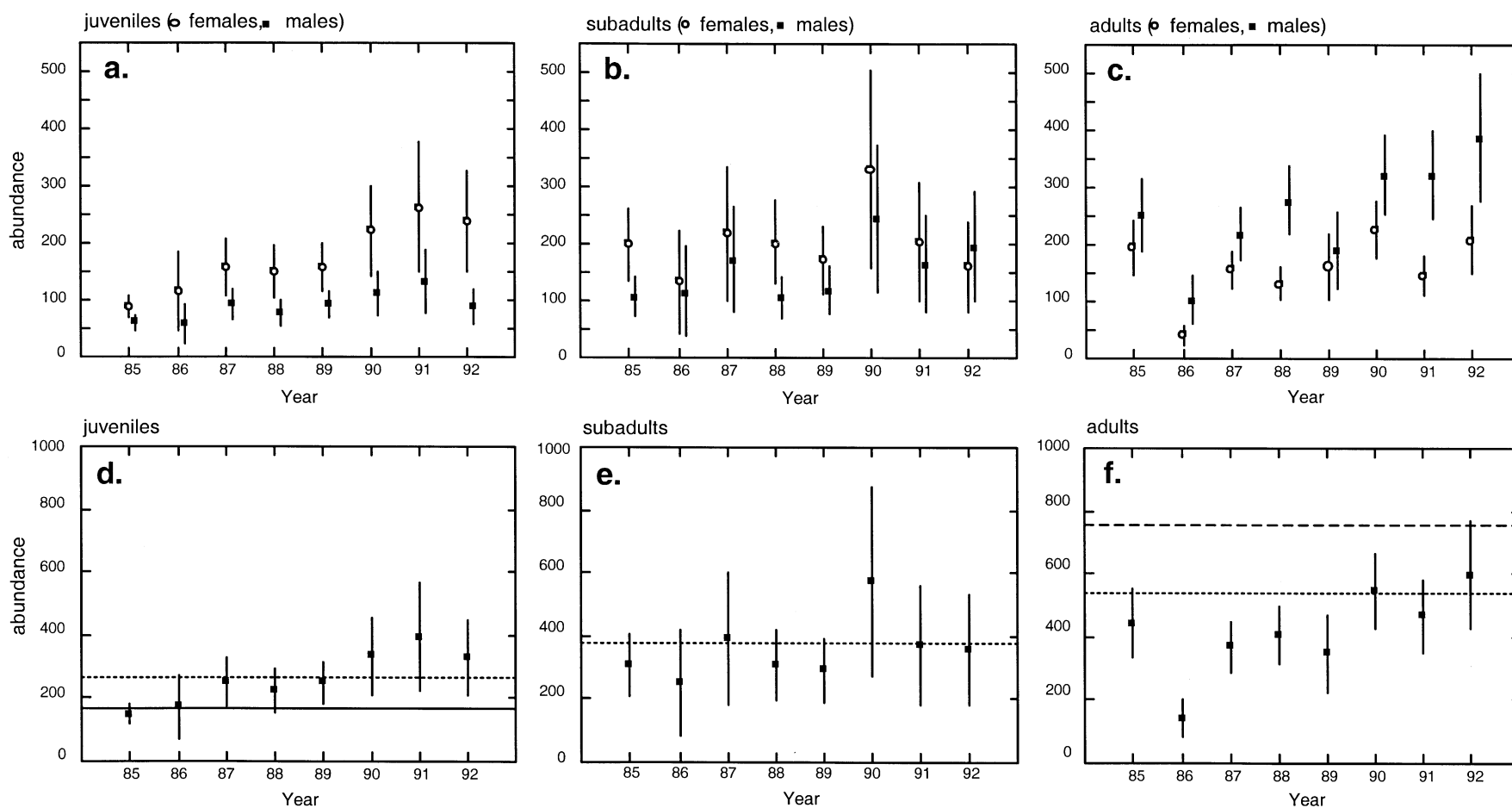


Fig. 2. Annual population abundance estimates for green turtles resident in waters around the Heron/Wistari Reefs study area (1985–1992). Sex-specific abundance estimates indicated by open circle (females) or solid square (males) in panels (a–c). Sex-pooled ageclass-specific abundance estimates (solid square) shown in panels (d–f). Vertical bar = approximate 95% confidence interval. Dotted horizontal line (panels d–f) = mean annual abundance (residents + transients) derived using a Poisson likelihood modelling approach (Cormack, 1993a) for comparison with Horvitz–Thompson estimates. Solid line (panel d) = Poisson likelihood mean annual abundance estimate for resident juveniles only (excluding assumed transients). Dashed line (panel f) = mean annual abundance derived using model  $M_{tbh}$  (Huggins, 1991) accounting for individual capture heterogeneity, prior capture history and individual and sampling occasion covariates.

1993a; Pradel et al., 1997). Recall that the proportion of transient turtles was estimated here from the 1225 CMR profiles summarised in Table 1 using TMSURVIV (see Pradel et al., 1997). It appears that the juvenile component comprises predominately residents and hence few

presumed transients as suggested previously in a study of juvenile green turtle survivorship (Chaloupka and Limpus, 1998b). The annual HT estimates for resident immature loggerhead turtles excluding transients is shown in Fig. 5a. The annual proportions of resident

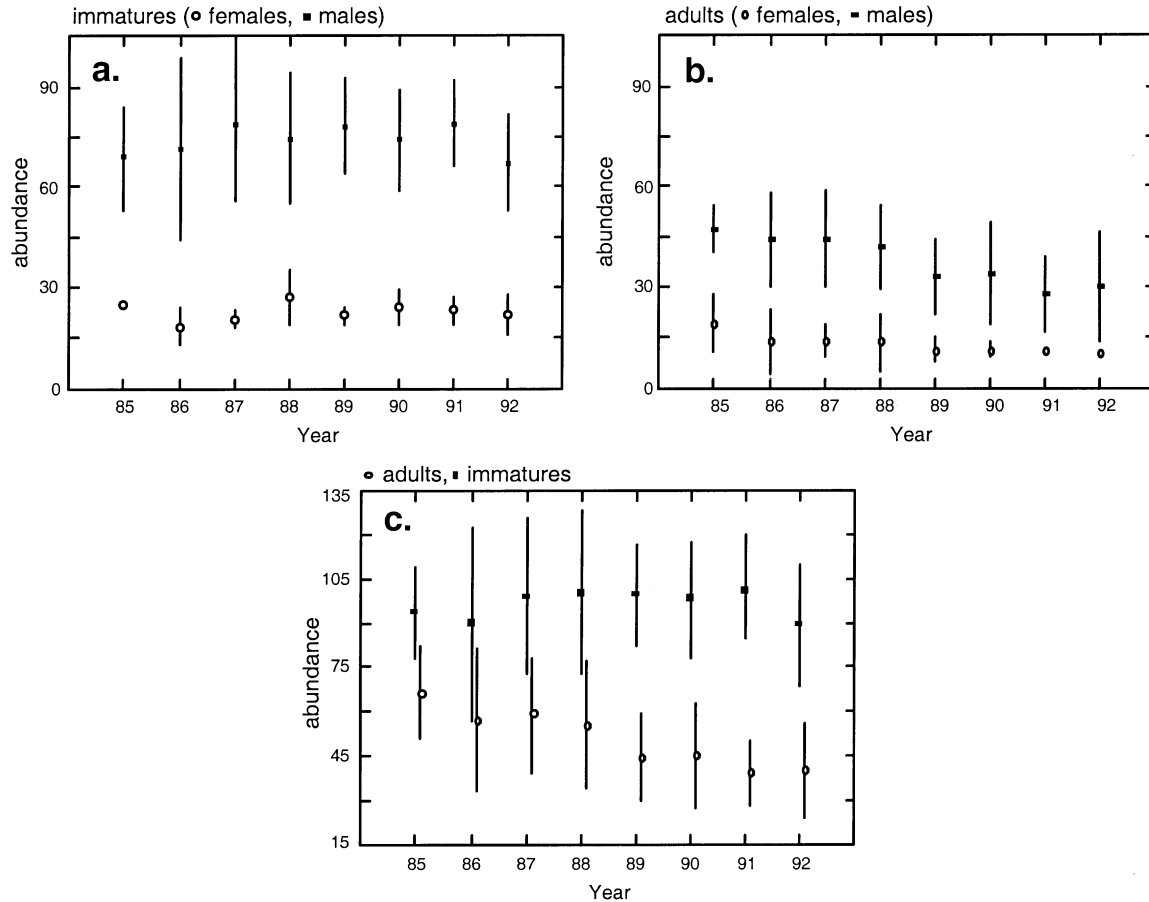


Fig. 3. Annual Horvitz–Thompson population abundance estimates for loggerhead turtles in waters around the Heron/Wistari Reefs study area. (a,b) Sex-specific estimates indicated by open circle (females) or solid square (males). (c) Sex-pooled ageclass-specific estimates (solid square). Vertical bar = approx 95% confidence interval.

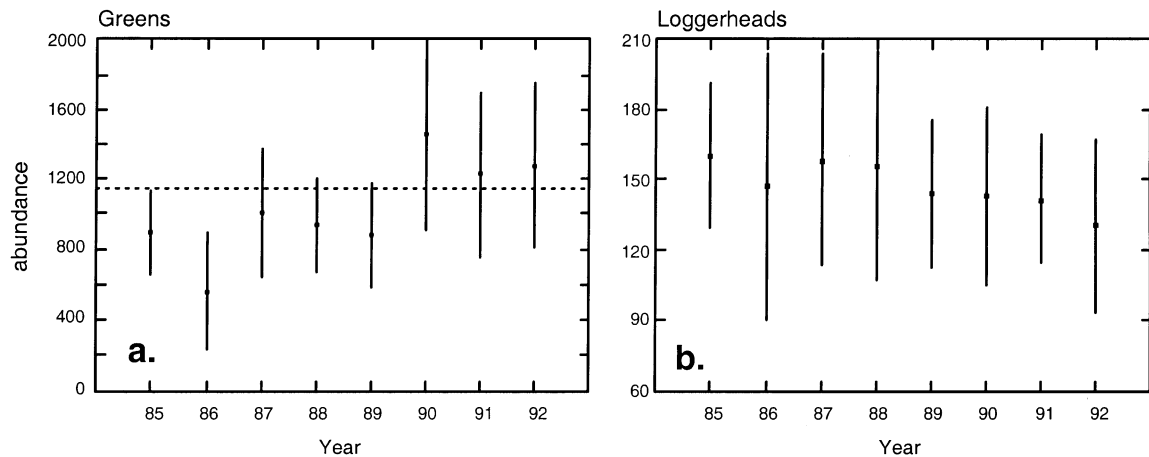


Fig. 4. Total annual population abundance derived from summed Horvitz–Thompson estimates for (a) green turtles and (b) loggerhead turtles (residents + transients) at the Heron/Wistari Reefs study area (1985–1992). Solid square = abundance estimate, vertical bar = approximate 95% confidence interval, dotted line (a) = mean annual abundance estimate using a Poisson likelihood modelling approach (Cormack, 1993a).



immature loggerhead turtles over the 7 years (1985–1991) for which transients can be estimated on an annual basis are shown in Fig. 5b.

There was a decline in male resident immature loggerhead turtles from 1987 onwards but any trend analysis lacks power. What is far more apparent is that the annual proportion of immature male residents declined

over the 7 years, or conversely, the proportion of male transients increased (Fig. 5b). Since the annual survival probabilities for immature sGBR loggerhead turtles was constant over the same period (Chaloupka and Limpus, 1998b, 2001) this resident male decline suggests a failure of juvenile recruits from the pelagic habitat — at least for males. The annual proportion of female immature

Table 4  
Summary of GLS/REML trend analysis<sup>a</sup>

Species	Ageclass	Sex	Year predictor				rse	Population growth (%)		
			Estimate	S.E.	t-Ratio	P		Mean	LCL	UCL
Green	Adult	Female	0.1444	0.0385	3.75	sig	0.198	15.53	11.2	20.1
		Male	0.1332	0.0231	5.76	sig	0.108	14.25	11.6	16.9
	Subadult	Female	0.0256	0.0327	0.78	ns	0.094	2.60	-0.7	6.0
		Male	0.0852	0.0235	3.62	sig	0.088	8.89	6.4	11.5
	Juveniles	Female	0.1458	0.0096	15.14	sig	0.046	15.70	14.6	16.8
		Male	0.1014	0.0148	6.87	sig	0.075	10.67	9.0	12.3
	Adult	Pooled	0.1343	0.0268	5.02	sig	0.118	14.37	11.4	17.5
	Subadults	Pooled	0.0586	0.0162	3.62	sig	0.068	6.04	4.3	7.8
	Juveniles	Pooled	0.1310	0.0099	13.23	sig	0.045	13.99	12.9	15.1
	Pooled	Pooled	0.1006	0.0142	7.11	sig	0.054	10.58	9.0	12.2
Loggerhead	Adult	female	-0.0942	0.0026	-36.38	sig	0.109	-8.99	-9.2	-8.8
		Male	-0.0782	0.0088	-8.92	sig	0.035	-7.52	-8.3	-6.7
	Immatures	Female	-0.0325	0.0172	-1.89	ns	0.136	-3.19	-4.8	-1.5
		Male	0.0032	0.0102	0.31	ns	0.033	0.32	-0.7	1.3
	Adult	Pooled	-0.0804	0.0044	-18.26	sig	0.027	-7.72	-8.1	-7.3
	Immature	Pooled	0.0012	0.0099	0.12	ns	0.027	0.12	-0.9	1.1
	Pooled	Pooled	-0.0309	0.0091	-3.42	sig	0.021	-3.04	-3.9	-2.2

<sup>a</sup> Mean annual population growth rate =  $((e^{\text{estimate}}) - 1) \times 100$  where “estimate” = GLS/REML parameter estimate for year = instantaneous growth rate. S.E., standard error of predictor estimate; sig, significant *P*-value at  $\alpha = 0.05$ ; ns, not significant; rse, model residual standard error; LCL, lower confidence interval bound; UCL, upper confidence interval bound.

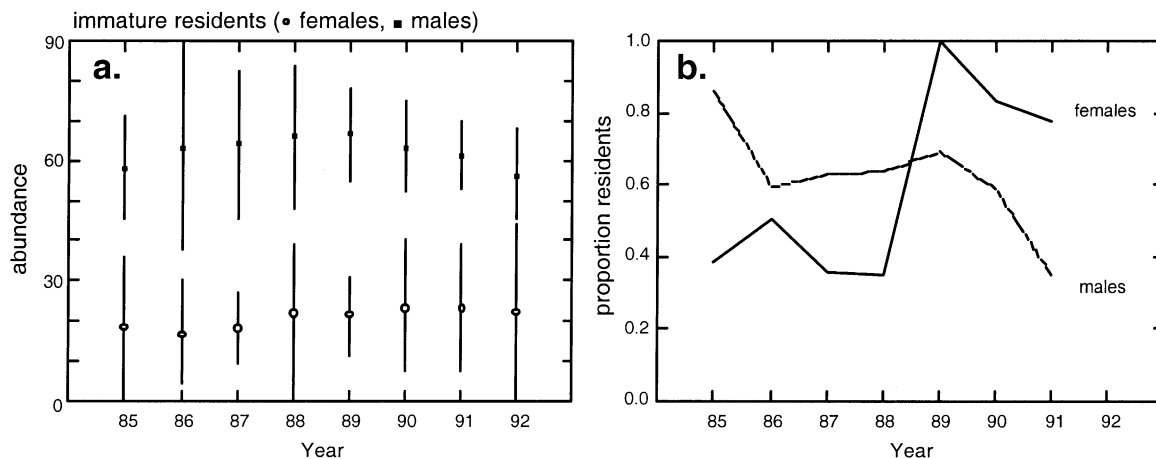


Fig. 5. Sex-specific abundance estimates for immature resident loggerhead turtles (excluding assumed transients) in (a) the Heron/Wistari Reefs study area. Open circle (females), solid square (males), vertical bar = approximately 95% confidence interval. Sex-specific estimates of the proportion of (b) immature residents.

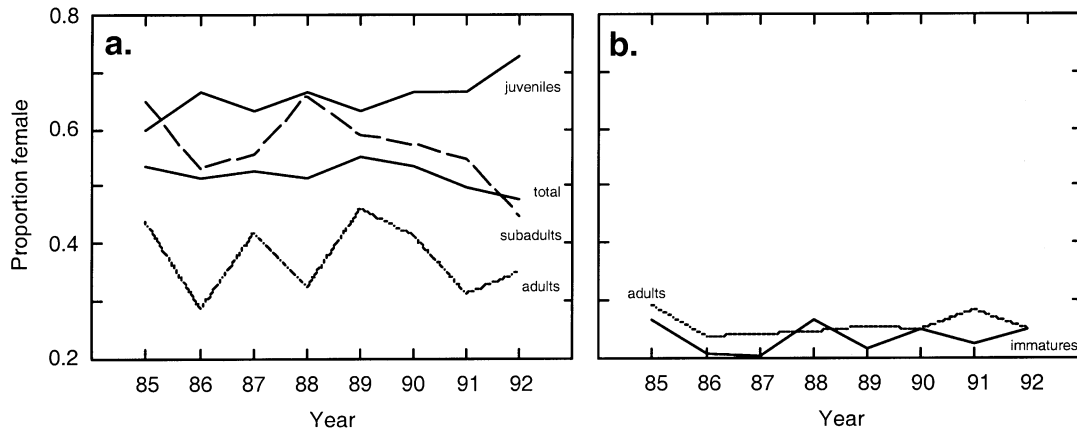


Fig. 6. Stage-specific time-dependent sex ratios derived from the mean Horvitz–Thompson estimates in Figs. 2 and 3 for (a) green sea turtles and (b) loggerhead sea turtles in the Heron/Wistari Reefs study area.

residents also suggests a decline prior to and after an anomaly in 1989 but the sample size is far too small to be meaningful (Fig. 5b).

### 3.4. Sex-ratio trends

The estimated long-term trends in ageclass-specific sex ratios are shown for the green sea turtle population in Fig. 6a and for the loggerhead turtles in Fig. 6b. Given measurement error in sex ratio estimation, there were no long-term trends apparent in the ageclass-specific sex ratios for either species. However, the proportion of female immature green turtles (juvenile, subadult) fluctuated over the 8 years and was significantly female-biased (Fig. 6a), contrary to earlier findings (Limpus and Reed, 1985). On the other hand, the adult green sex ratio fluctuated significantly but was male-biased (Fig. 6a). The overall green sea turtle population sex ratio remained relatively constant over the 8 years at ca. 50:50, which is consistent with earlier findings (Limpus and Reed, 1985). The sex ratio for the immature and adult loggerhead components remained relatively constant and was significantly male-biased for both components (Fig. 6b).

### 3.5. Nesting census trends

The annual number of green and loggerhead females nesting on Heron Island between 1974 and 1998 is shown in Fig. 7. These adult female nesting activity series are much longer and more easily obtained than the CJS estimates of absolute population abundance shown in Figs. 1 and 2 and hence may be useful indices of population trends in the absence of population estimates. The estimated long-term linear trend in green nesting (Fig. 7a) was well fit with a MACH(1) time series regression that suggests that nesting increased slowly over the 25 years at a mean rate ca. 3% pa (95% CI: 2.1–4.3). This nesting increase was consistent with the

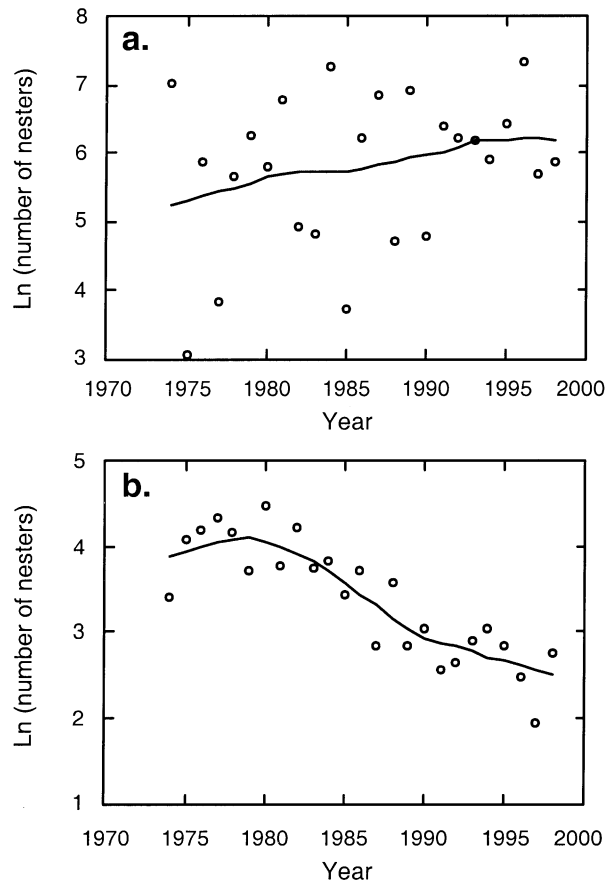


Fig. 7. Annual census of female (a) green and (b) loggerhead sea turtles nesting on Heron Island (sGBR foraging grounds) over the last 25 years (1974–1998). Open circles = number of nesters recorded each year, solid curves = locally weighted regression smooth (LOWESS — see Cleveland, 1993) to highlight any nonlinear trend in nesting activity. Note how volatile the green turtle nesting series is for most of the 25 years with a brief period of stability in the early 1990s. The LOWESS smooth for green turtles (a) suggests a linear functional form with the long-term linear increase estimated ca. 3% pa. The LOWESS smooth for (b) the loggerhead series suggests nonlinear functional form with a marked linear decline evident from 1984 onwards estimated ca. 8% pa.

estimated increase in green turtles resident year round in the surrounding foraging grounds (Fig. 2, Fig. 4a). The trend in loggerhead nesting was well fit with two separate MA(1) time series models suggested by the LOWESS smooth (Fig. 7b). There was no trend in nesting for the 11 years (1974–1984) but nesting declined markedly over the next 14 year period (1985–1998) at a mean rate ca. 8% pa (95% CI: –8.7 to –7.1). The long-term nesting decline was consistent with the estimated decline in loggerhead turtles in the surrounding foraging grounds (Fig. 3, Fig. 4b).

#### 4. Discussion

There are five approaches used to estimate sea turtle abundance or a related form of 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, 1998) CPUE estimation, (4) aerial survey based density estimation using line- (Epperly et al., 1995) or strip-transects (Marsh and Saalfeld, 1989) and (5) some form of CMR type estimation (Chaloupka, 2000a).

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 and Ehrhart (1982) used closed population catch-effort (see Otis et al., 1978 model  $M_b$ ) and Schnabel-type (see Otis et al., 1978 model  $M_t$ ) 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 (see Pollock et al., 1990 Model A) assuming no skipped breeding seasons to estimate nesting female abundance at two southern Indian Ocean green turtle rookeries.

In a well designed study, Butler et al., (1987) used a two-stage approach comprising (1) trawl survey sampling and a closed population catch-effort or removal model (see Otis et al., 1978 model  $M_b$ ) to derive capture probabilities for (2) estimation of seasonal loggerhead abundance in Florida navigation channels over a 1-year period. While not recognised as such, the capture-based abundance estimator used by Butler et al., (1987) was a Horvitz–Thompson type estimator. Like Butler et al., (1987), the current sGBR foraging ground CMR sea turtle study used a two-stage approach comprising (1) statistical modelling of the time-dependent capture probabilities for each species (Table 2) and then (2) using those probabilities to derive Horvitz–Thompson type annual abundance estimates over an 8-year period

for green and loggerhead turtles (Table 3). More details on the implementation of this CJS based population abundance estimation approach using Horvitz–Thompson estimators can be found in Chaloupka (2000a).

The HT abundance estimator was especially useful for the current study that was based on a prior assessment of sea turtle survival and capture probabilities (Chaloupka and Limpus 1998b, 2001). Huggins (1989, 1991) has shown the value of focussing on recapture likelihood where it is possible to model the effects of individual covariates (sex, age, size) and sampling occasion covariates (sampling effort, rainfall, temperature) to derive better capture probability estimates. The time-dependent survival and capture probability models used in the current study (Table 2) included sex and developmental stage (ageclass) as informative individual covariates and annual sampling effort as a sampling occasion covariate. This approach provided robust estimates of the sex- and ageclass-specific capture probabilities for each species suitable for deriving annual HT abundance estimates. The performance of the annual HT estimates for green turtles was qualitatively comparable with (1) the mean annual Jolly–Seber abundance estimates derived from a Poisson likelihood model (Figs 1d–f, Fig. 4a) and (2) the mean annual abundance derived from a  $M_{t,bh}$  equivalent that accounts for individual capture heterogeneity but assumes demographic closure (Fig. 2f).

##### 4.1. Local and regional abundance

Green sea turtles were abundant over the 8-year estimable period (1985–1992) in the Heron Reef/Wistari Reef study area (Fig. 1) that comprises ca. 28 km<sup>2</sup> of algal dominated coral reef habitat (Limpus and Reed, 1985). The HT estimate of the green sea turtle population resident in the study area in 1992 was 1278 (95% CI: 807–1748) with a density of ca. 45 turtles km<sup>-2</sup>. After 30 years of in-water field survey work in the GBR region there was no reason to consider that this study site was any more abundant in green sea turtles than most other reefal areas in the GBR (Limpus, unpublished). The Heron Reef/Wistari Reef study site is part of a larger sGBR coral reef region surrounding the Capricorn-Bunker coral cays that comprises ca. 368 km<sup>2</sup> of similar coral reef habitat (Hopley et al., 1989). It was estimated that there could be ca.  $368 \times 45 = 16,560$  green sea turtles resident in the Capricorn-Bunker region of the sGBR or ca. 855,000 (95% CI: 555,000–1,200,000) green sea turtles resident in the 19,000 km<sup>2</sup> of similar coral reef habitat (Hopley et al., 1989) in the GBR region. The sGBR green turtle foraging ground density estimates are comparable to density estimates derived for green turtles resident in foraging grounds off the Oman coast using a low flying helicopter survey (Ross, 1985).

It is important to note that this GBR coral reef habitat population estimate does not include any of the major inshore seagrass dominated habitats in the GBR region nor southern coastal Queensland that are also known to have large resident green sea turtle populations (Marsh and Saalfeld, 1989; Limpus et al., 1994a). The aerial survey estimate of Preen et al., (1997) that there were ca. 60,000 sea turtles of all species in the GBR region including inshore habitats is probably in error by a factor of  $>15$  just for green turtles in GBR coral reef habitats alone. The aerial survey estimate was drawn from Marsh and Saalfeld (1989) who had cautioned that their well designed sampling study provided precise but gross underestimates of turtle abundance. Marsh and Saalfeld (1989) also 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.

Loggerhead abundance in the Heron/Wistari Reefs study area was very low and declining over the 8-year period. The HT estimate of the loggerhead population in 1992 comprising adults and immatures (resident + transient) was 130 (95% CI: 93–167) with a density of ca. 4.5 turtles  $\text{km}^{-2}$ . Lower densities of the carnivorous loggerhead are expected given trophic considerations compared to the herbivorous green turtle in the same sGBR foraging grounds but density was also low due to the declining stock. The sGBR loggerhead density estimate was high compared with aerial survey based density estimates for immature loggerhead turtles resident seasonally in coastal habitats along the US Atlantic coast (Epperly et al., 1995). However, Butler et al. (1987) in a trawl survey study of sea turtle abundance found that there were ca. 700 loggerhead turtles overwintering in the Port Canaveral shipping channel so that densities in some seasonal habitats along the US Atlantic coast can be extremely high.

While by no means conclusive, it seems most likely that aerial survey sampling will seriously underestimate loggerhead foraging ground abundance. Loggerhead turtles are particularly difficult to sight from the air even in the clear GBR waters (Limpus, unpublished). Nonetheless, the aerial survey protocols developed by Marsh and Saalfeld (1989, see also Preen et al., 1997) and Epperly et al., (1995) could be a cost-effective means for deriving relative abundance indices for sea turtles if the indices were also ground-truthed with concurrent vessel based line- or strip-transect sampling surveys or a more demographically informative but costly CMR study.

#### 4.2. Abundance trends

The sGBR green sea turtle population increased significantly in abundance over the 8-year period from 1985–1992 (Fig. 4a) at ca. 10.6% pa (Table 4). The trend in increased abundance is also clear from the

annual beach census of nesting green females recorded over the last 25 years (Fig. 7a) that has increased at ca. 3% pa. Significant long-term increases in nesting sea turtles have been reported for leatherback turtles (Hughes, 1996) and green turtles (Bjorndal et al., 1999) where both stocks were recovering from over-exploitation. It is unclear why the unexploited sGBR green population has increased but it might be due to the increased frequency of ENSO climate-ocean anomalies over the last 25 year (Trenberth and Hoar, 1997; Guilderson and Schrag, 1998) that are linked to increased female breeding and nesting activity throughout the GBR (Limpus and Nicholls, 1994) and southeast Asian region (Chaloupka, 2001). What is clear is that the sGBR foraging ground population of the sGBR genetic stock was in a sound demographic state over the 8 year (1985–1992), despite exposure to coastal otter trawl fisheries (Slater et al., 1998), as annual survival of adult and immature green turtles was high and remained constant over the 8 years (Chaloupka and Limpus, 1998a).

Unfortunately, this was not the case for the sGBR foraging ground population of the sGBR loggerhead genetic stock that has declined over the 8 years at ca. 3% pa (Table 4). This trend is clear from the estimated annual abundance of adult (Fig. 3) and resident immature loggerhead turtles (Fig. 5a). A marked decline was also evident in the annual beach census of nesting loggerhead females recorded over the last 25 years (Fig. 7b), which has declined at ca. 8% pa since the mid-1980s. The ongoing long-term decline apparent in the annual beach census series is grounds for concern about the population viability of the sGBR loggerhead stock, which is one of the most important loggerhead stocks in the Pacific region (Limpus, 1994a; Limpus et al., 1994a; Limpus and Reimer, 1994). Substantial long-term declines in sea turtle nesting populations due to a range of anthropogenic factors have also been reported for hawksbill (Bjorndal et al., 1993), green (Limpus, 1994a), leatherback (Chan and Liew, 1996), Kemp's ridley (Márquez et al., 1999) and olive ridley sea turtles (Valverde et al., 1998).

It is unclear why the sGBR loggerhead population declined since annual survival probabilities for adults, immatures (resident + transient) and resident immatures were found to be constant or at least displayed negligible temporal variability over the 8-year period (Table 2). Demographic simulation models are useful here to help diagnose the demographic processes that could account for the observed loggerhead decline. For instance, the impact of egg production loss from fox predation during the 1960s on this stock has been shown in a stochastic simulation model of loggerhead population dynamics designed to evaluate competing mortality risk factors including incidental capture in coastal otter trawl fisheries (Chaloupka and Limpus,

1998b; Chaloupka, 2000b). The same model has also been used to evaluate the impact of pelagic juvenile mortality since the 1970s from incidental capture in oceanic longline fisheries.

The high risk of coastal otter trawl fisheries and oceanic longline fisheries to sea turtle survival is well known (Poiner and Harris, 1996; Slater et al., 1998; Witzell, 1998) with loggerhead turtles having a greater propensity than other sea turtle species to consume baited longline hooks (Witzell, 1998). Simulation-based evaluation of known sGBR loggerhead demography suggests that all three mortality risk factors (fox predation on eggs, incidental capture in coastal and oceanic fisheries) were implicated in the marked sGBR loggerhead population decline recorded since the early 1980s. More extensive testing of these simulation models needs to be undertaken to provide robust conclusions, but what is very clear is that for whatever the reasons, the sGBR loggerhead stock is in serious decline.

#### 4.3. *Transient immatures*

Adult and subadult green sea turtles did not display transient behaviour but there was some limited indication of juvenile transients over the 8 years (Chaloupka and Limpus, 1998b). Recall that transients were defined as individuals presumed to simply be in transit across the study area as they were captured on only one occasion (Cormack, 1993a; Pradel et al., 1997). This is only an operational definition of transience at this stage (apparent transience) and was not based on any assessment of local dispersal to identify actual individual transients. Given apparent transience, the mean annual abundance of transient juvenile green turtles was estimated to be negligible (Table 2) and hence unlikely to bias interpretation of juvenile green turtle abundance trends (Fig. 2d). While adult loggerhead turtles did not display transient behaviour, this was not the case for the immature loggerhead turtles (Table 2).

The annual proportion of resident immature loggerhead turtles showed significant temporal variation (Fig. 5b) with ca. 68% of new recruits in some years apparently transients (Chaloupka and Limpus, 2001). The annual proportion of apparent transient immatures was not a function of annual sampling effort but could be a function of annual fluctuations in pelagic juvenile loggerhead recruitment to the benthic habitat influenced by regional climatic-oceanographic anomalies related to feeding behaviour (Bjørndal, 1997). However, it is also apparent from Fig. 5 that transience as a consequence of the operational definition is also somewhat confounded with the declining immature abundance. It is impossible to distinguish here between a new immature recruit that dispersed permanently to another reefal area within 1 year of capture and was still alive (real transient) and a new immature recruit that simply died

within 1 year of capture (apparent transient). A multi-site CMR sampling study in sGBR waters is needed to estimate immature loggerhead dispersal and any effect on survival and population abundance estimation in order to support conclusive and ecologically informative interpretations about temporal transient behaviour of sea turtles.

#### 4.4. *Sex-biased population structure*

The green turtle population displayed significant temporal variability in foraging ground sex ratios over the 8 year (Fig. 2 a–c) but there was only negligible temporal variation in the loggerhead sex ratios (Fig. 3a,b). Not only did the sex ratios for the green population vary from year to year but contrary to earlier findings (Limpus and Reed, 1985) there were significant ageclass-specific differences in green turtle sex ratios. There can be significant temporal variation in the proportion of female green turtle hatchlings produced each season (Godfrey et al., 1996) and there can be significant differences in cohort sex ratios of juvenile green turtles recruiting to development habitats (Bolten et al., 1992). Moreover, Wibbels et al., (1993) found that the immature component of the Hawaiian Archipelago green population was ca. 1:1 for all immature size classes. Nonetheless, it is expected that the demographic structure in a green turtle population resident in the foraging grounds will usually be female-biased because hatchling production appears to be female-biased at many of the major green turtle rookeries (Spotila et al., 1987; Mrosovsky, 1994; Godfrey et al., 1996) including the sGBR rookeries (Limpus et al., 1984).

Therefore, the persistent male-biased adult component (Fig. 6a) of the sGBR resident green population appears unusual and is most probably a consequence of sex-biased migratory behaviour where adult males live closer to the sGBR genetic stock breeding grounds in sGBR waters than adult females (Limpus et al., 1992). Possible sex-biased dispersal behaviour of adult green turtles is an issue that warrants investigation as it has implications for demographic modelling of sea turtle population viability (Chaloupka and Musick, 1997) and for interpretation of migratory behaviours inferred from genetic studies (FitzSimmons et al., 1997).

Despite ageclass-specific differences, the green turtle population structure in this foraging ground was overall immature female-biased (Fig. 6a) while the loggerhead population structure was immature male-biased (Fig. 6b). Similar demographic structures occur in a warm temperate foraging ground in Moreton Bay (Fig. 1), which is 400 km south of the sGBR where the green turtle population is immature female-biased (Limpus et al., 1994a) and the loggerhead population is immature male-biased (Limpus et al., 1994b). Henwood (1987) also found a male-biased adult component for a

Florida loggerhead population but the juvenile component of most loggerhead populations resident along US Atlantic coast appear to be female-biased (Shoop et al., 1998). The loggerhead turtles in the sGBR and Moreton Bay foraging grounds are from sGBR genetic stock and nest at the same regional rookeries (Limpus et al., 1994b) but the mainland rookeries produce mainly female hatchlings while the sGBR coral cay rookeries produce mainly male hatchlings (Limpus et al., 1983). And yet the population structure of the immature and adult components of this stock are male biased in both of the major and widely separated foraging grounds (sGRR and Moreton Bay, Fig. 1).

These are only preliminary estimates of foraging ground specific sex ratios and any conclusions need to be considered with caution since more detailed studies of the primary sex ratios of the two species in the various foraging grounds are needed. There are clearly many complex issues here about sGBR sex-biased population structure that need to be resolved from the perspective of a regional metapopulation where a sea turtle stock comprises widely separated foraging grounds linked by adult mixing during periodic reproductive dispersal to a single stock-specific breeding ground. As previously mentioned, a multi-site CMR sampling study in sGBR waters is needed to further develop our understanding of the complex ecological dynamics of sea turtle populations resident in GBR waters. Meanwhile, the long-term nesting beach censuses undertaken at sGBR mainland and offshore coral cay rookeries over the last 25 years are useful indicators of long-term population decline in the sGBR sea turtle populations — especially in the absence of more informative long-term but costly CMR studies.

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