RESEARCH ARTICLE

Variation in adult annual survival probability and remigration intervals of sea turtles

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Abstract We analyzed a large dataset to quantify adult annual survival probability and remigration intervals for the Tortuguero, Costa Rica green turtle population. Annual survival probability was estimated at 0.85 (95% CI 0.75–0.92) using a recovery model and at 0.85 (95% CI 0.83–0.87) using an open robust design model. The two most common modes of remigration are 2 and 3 years. Annual survival probability is lower and remigration intervals are shorter than for other green turtle populations. Explanations for short remigration intervals include reproductive compensation due to historic population declines, availability of better quality food items, favorable environmental conditions, and short distance to the main foraging grounds. Variation in survival and remigration intervals have profound consequences for management and life history evolution. The short remigration intervals of Tortuguero green turtles partly offset mortality caused by turtle fishing in Nicaragua and mean that low juvenile survival represents a more urgent threat to the population than low adult survival. Low adult survival probability could result in selective pressure for earlier age at maturity.

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Introduction

Sea turtles are wide ranging marine species. Their complex lifecycle includes juvenile foraging, adult foraging and breeding habitats which can be geographically separated by thousands of kilometers. Sea turtles grow slowly and take decades to reach sexual maturity. Late age at maturity is a life history strategy that necessitates high adult survival probabilities to maintain populations (Congdon et al. 1993). Six of seven extant species of sea turtle are classified as Endangered or Critically Endangered (IUCN 2004), due to population declines caused by historical over-exploitation and more recently fisheries bycatch (Spotila et al. 2000; Seminoff 2004).

Sea turtle growth has been shown to be density dependent (Bjorndal et al. 2000), and both sea turtle growth and survival probability can vary between foraging grounds (Bjorndal et al. 2000; Balazs and Chaloupka 2004; Chaloupka et al. 2004a; Campbell and Lagueux 2005; Chaloupka and Limpus 2005). Female sea turtles are capital breeders and usually do not undertake reproductive migrations every year. The time between reproductive migrations, the remigration interval, varies between individuals and populations and may be related to individual quality, environ-

mental conditions and diet (Carr and Carr 1970; Solow et al. 2002; Rivalan et al. 2005). The distributions of five sea turtle species extend over several ocean basins with variation in marine productivity, in part linked to climatic cycles like the El Niño Southern Oscillation (Limpus and Nicholls 2000) and the North Atlantic Oscillation (Rivalan et al. 2004).

To find explanations for the variation in adult annual survival probabilities and remigration intervals, and to investigate consequences for management and life history evolution, we use the Tortuguero, Costa Rica green turtle *Chelonia mydas* nesting population as a case study. The Tortuguero rookery is the largest in the Atlantic Ocean (Carr et al. 1978; Seminoff 2004). Most adult turtles from the rookery forage in Nicaragua waters (Carr et al. 1978; Troëng et al. 2005) where they are subjected to capture by fishermen (Lagueux 1998). The annual take of green turtles in Nicaragua has been estimated to exceed 11,000 animals, mainly of size classes corresponding to large juvenile and adult turtles (Lagueux 1998; Campbell and Lagueux 2005). It has been suggested that low juvenile and adult annual survival probabilities resulting from the fishery may cause the Tortuguero rookery to decline (Campbell 2003; Campbell and Lagueux 2005). Green turtle nesting at Tortuguero, however, increased an estimated 417% between 1971 and 2003 (Troëng and Rankin 2005). Green turtle research and monitoring at Tortuguero began in 1955 (Carr et al. 1978). Since 1959, the Caribbean Conservation Corporation (CCC) has implemented an annual green turtle program at Tortuguero. Tagging data from this program, and subsequent tag recoveries from Nicaragua and other countries (Carr et al. 1978; Troëng et al. 2005) make the population an ideal case for the study of sea turtle survival probabilities and remigration.

In this paper, we: (1) improve on previous estimates of adult annual survival probability for Tortuguero green turtles using dead recoveries and live recaptures, (2) estimate remigration intervals for a sample of Tortuguero green turtles, (3) compare adult annual survival probability and remigration intervals for Tortuguero green turtles with published estimates from other populations, and (4) discuss sea turtle management and life history implications of variation in adult annual survival probability and remigration intervals.

Materials and methods

Between 1998 and 2004, a sample of female green turtles was double tagged at Tortuguero, Costa Rica during the main nesting season from mid-June until the end of October (Troëng and Rankin 2005). Inconel 681 tags (National Band and Tag Company, Newport, KY, USA) were attached to the front flippers of nesting turtles. Tag numbers of nesting turtles are recorded during night patrols, mainly conducted along 8 km of the 30 km nesting beach. Corroded, poorly placed and lost tags are replaced when possible. Tag loss (within season and between years) was estimated from observations of turtles returning to nest and still carrying one or two tags, using the method of Wetherall (1982) (Table 1).

Two different methods were used to estimate annual survival probability for adult female green turtles nesting at Tortuguero—a recovery model using tag data recovered from dead turtles and an open robust design model using data from females encountered on the nesting beach during nightly beach patrols.

Recovery model

A recovery matrix (Table 2), adjusted for tag loss (Table 3), was constructed with data pooled into calendar years, including a total of 8,408 tagged females and an estimated 438 dead recovered turtles. A large proportion (0.93) of the dead recoveries was reported by turtle fishermen in Nicaragua.

We used Program MARK, which estimates model parameters via numerical maximum likelihood techniques, to estimate annual survival (Φ) and detection (P) probabilities (White and Burnham 1999). Annual

Table 1 Number of turtles resighted after original tagging (n) and annual estimates of tag loss

Year	Within season		After 2 years		After 3 years		After 4 years		After 5 years		After 6 years	
	n	Tag loss ± 95% CI	n	Tag loss ± 95% CI	n	Tag loss ± 95% CI	n	Tag loss ± 95% CI	n	Tag loss ± 95% CI	n	Tag loss ± 95% CI
1998	292	0.019 ± 0.012	66	0.138 ± 0.068	186	0.167 ± 0.045	81	0.182 ± 0.072	48	0.157 ± 0.086	70	0.148 ± 0.069
1999	312	0.058 ± 0.020	39	0.130 ± 0.086	124	0.198 ± 0.061	27	0.286 ± 0.158	15	0.364 ± 0.240		N/A
2000	395	0.031 ± 0.013	110	0.128 ± 0.051	194	0.165 ± 0.044	66	0.245 ± 0.093		N/A		N/A
2001	362	0.033 ± 0.014	80	0.103 ± 0.053	130	0.250 ± 0.067		N/A		N/A		N/A
2002	243	0.030 ± 0.016	29	0.137 ± 0.103		N/A		N/A		N/A		N/A
2003	248	0.025 ± 0.014		N/A		N/A		N/A		N/A		N/A
2004	182	0.083 ± 0.031		N/A		N/A		N/A		N/A		N/A

Table 2 Recovery matrix for dead green turtle recoveries

Recovery year						
1998	1999	2000	2001	2002	2003	2004
18	29	14	11	12	15	9
	9	17	8	15	26	7
		6	22	13	11	21
			3	27	23	22
				8	20	22
					11	27
						12
Tagged turtles (n)						
1,232	1,052	1,278	1,207	1,249	1,268	1,122

Table 3 Recovery matrix for Tortuguero green turtles, adjusted for tag loss

Recovery year						
1998	1999	2000	2001	2002	2003	2004
18	29	14	11	12	15	9
	9	17	8	16	28	8
		6	22	13	11	22
			3	27	23	23
				8	20	22
					11	27
						12
Tagged turtles (n)						
1,232	1,052	1,278	1,207	1,249	1,268	1,122

survival parameters were divided into two classes—one for year of tagging and one for subsequent years. This is necessary as the nesting season takes place from mid-June to end of October and hence newly tagged turtles need to survive for a shorter time period to complete the year of tagging than to survive for an entire calendar year. Our recovery analysis differs from a previous analysis (Campbell and Lagueux 2005) in the definition of sampling periods [we use calendar years, Campbell and Lagueux (2005) used marking periods with 15 August mid-points] and in our adjustment for tag loss.

Akaike's Information Criterion (AICc) adjusted by the quasi-likelihood parameter $\hat{c}$ and small sample size (QAICc) was used to identify the most parsimonious recovery model (Table 4).

For the recovery model, we conducted a sensitivity analysis to evaluate the effect of varying detection probability and samples size by constructing recovery matrices from simulated data on individual turtles.

Three sets of data were simulated using an annual survival probability (Φ) of 0.85: (a) with the detection probability (P) half of that estimated for the Tortuguero green turtles, (b) with the detection probability (P) equal to that estimated for the Tortuguero green turtles, and (c) with the detection probability (P) double to that estimated for the Tortuguero green turtles. Data sets with sample sizes of 100, 1,000 and 10,000 turtles were simulated for each detection probability. Each detection probability and sample size combination was replicated ten times.

Open robust design model

Live recapture encounter histories were constructed for 7,161 female green turtles with year as the primary sampling periods and five 30-day secondary sampling periods beginning 12 June and ending 8 November each year. The resulting histories include a total of 9,932 encounters.

Female sea turtles skip years between reproductive migrations which means that not all females are available for sampling on the nesting beach each year. This necessitates the use of open robust design models to analyze live recapture data from nesting beaches (Kendall and Bjorkland 2001). We used the program ORDSURVIV to implement a model with temporary Markovian emigration to estimate annual survival ($\Phi*$), detection (P) and availability (β), (Φ), and (γ) probabilities (Kendall and Bjorkland 2001; Dutton et al. 2005). Based on the most common observed remigration interval of 3 years, we fixed the proportion of females not available for sampling on the nesting beach ($1 - \gamma$) to the biologically realistic value of 0.67.

We used Akaike's Information Criterion (AICc) adjusted by the quasi-likelihood parameter $\hat{c}$ (QAIC) to identify the most parsimonious open robust design model (Table 5).

Results

Recovery model

The most parsimonious recovery model has two classes (year of tagging, subsequent years) with constant sur-

Table 4 Most parsimonious recovery model and estimated annual survival probability

Annual survival (Φ)	Detection (P)	Parameters	QAICc[a]	QAICc weight	Annual survival probability ($\pm$95% CI)
Constant (two classes)	Time	9	2639.03	0.657	0.85 (0.75 – 0.92)

[a] Adjusted for $\hat{c}$ = 1.77

Table 5 Most parsimonious open robust design model and estimated annual survival probability

P	β	Φ	Φ*	1 − γ	Parameters	QAIC[a]	Annual survival probability (Φ* ± 95% CI)
Time	Time × Time	Constant	Constant	0.67	30	224.78	0.851 (0.832–0.870)

[a] Adjusted for $\hat{c} = 20.3$

vival probability and time varying detection rates (Table 4). This model is almost 2.5 times more parsimonious than the next model. Annual survival probability after the calendar year of tagging was estimated at 0.85 with 95% CI of 0.75–0.92 (Table 4).

Analyses of the recovery matrices derived from simulated data sets show that increased sample size (number of turtles) and increased detection probability improve the estimates of annual survival probability (Fig. 2).

Open robust design model

Data sparseness contributed to relatively low estimates of detection probability (P = 0.17–0.41) for the most parsimonious open robust design model. Annual survival probability for the adult female green turtles was estimated at 0.85 with 95% CI of 0.83–0.87 (Table 5).

Remigration intervals

The most common mode for observed remigration intervals was 3 years but a large proportion of Tortuguero green turtle females came back to nest already after 2 years (Fig. 1). The mean remigration interval for green turtles tagged 1998–2002 and observed nesting at Tortuguero during subsequent nesting seasons was 2.95 years (SD 0.88).
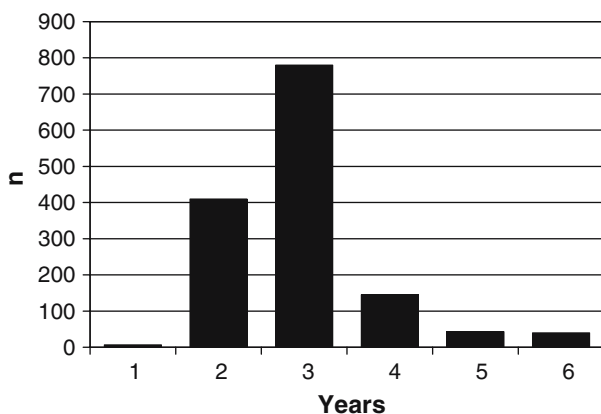

Fig. 1 Observed remigration interval for green turtles tagged in Tortuguero 1998–2001

Discussion and conclusions

There are some limitations to recovery and open robust design models. Currently, there are no good measures of model fit available. Bias in reporting of turtles captured by fishermen can affect the recovery model estimates (Bjorndal et al. 2003). The sensitivity analysis shows that annual survival probability estimates from the recovery model can be improved by increased detection probabilities. Increasing detection probabilities with regards to tags from dead turtles would require convincing more fishermen in Nicaragua and other countries in the Caribbean to report their captures of tagged turtles. Dispersal could be an issue for the open robust design model (Cilimburg et al. 2002). The mean spatial nesting range for green turtles at Tortuguero has been estimated at 10.1 km (Tiwari et al. 2005). Turtles tagged on the 8 km beach section may renest outside of the study area and hence will not be detected. The ad hoc approach to account for such transience (Pradel et al. 1997) cannot be applied due to the low detection probabilities which confound true transients with non-transients detected only once. New GPS satellite tags (Yasuda and Arai 2005) could potentially be used to quantify nesting dispersal for a sample of females so future analyses can be adjusted for transient nesters. Increased night patrols on the nesting beach would increase detection probabilities for the open robust design model and help in identifying transient nesters. High probabilities for detecting nesting females (preferably close to 1.0) will make the open robust design model a better candidate for estimating annual survival probability (Kendall and Bjorkland 2001). More night patrols would also contribute to a larger sample of tagged females for use in the recovery model. For these two reasons, increasing night patrol effort is the single action that would contribute most to improve the estimates of annual survival probability. The fixed estimate of the proportion of females not available for sampling each nesting season ($1 - \gamma$), used in the open robust design model, could be improved through laparoscopy of adult females on the foraging grounds in Nicaragua. Unfortunately, such a study would be very costly and it would be logistically challenging to capture a representative

Fig. 2 Annual survival probability estimated from simulated life histories (n = 100, 1,000, and 10,000) with annual survival probability (Φ = 0.85) and detection probability (P). Mean survival probability for each n indicated by *filled diamond*: **a** P = 0.078; **b** P = 0.156; **c** P = 0.312
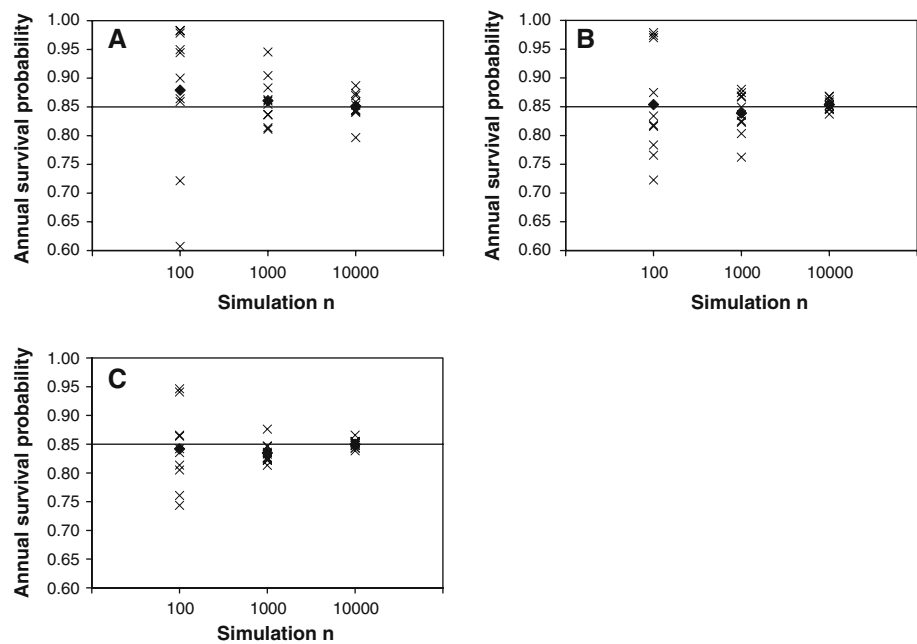
sample due to possible sex and size separation on the foraging grounds (Campbell and Lagueux 2005). Satellite telemetry data have also been used to estimate survival probability for sea turtles (Hays et al. 2003). Applying the method of Hays et al. (2003) to a dataset of ten adult female Tortuguero green turtles followed by satellite for a total of 2,653 days (Troëng et al. 2005) results in an estimate of annual survival probability of 0.87 (95% CI 0.67–1.00). Chaloupka et al. (2004b) have detailed the shortcomings of estimating survival probabilities from satellite telemetry data.

For the open robust design model, low detection probabilities and not being able to account for tag loss may weaken the parameter estimates. The large dataset of tagged females, the long-term consistent sampling effort and the very similar results of the recovery and open robust design models, however, compensate for the limitations and allow for reliable interpretations of parameter estimates while better modeling techniques are developed.

Previous annual survival probability estimates for adult female green turtles from Tortuguero (Bjorndal 1980; Campbell and Lagueux 2005) are lower (0.46–0.82) than our estimates (0.85). Although survival probability may have been lower in the past, most of the difference between the estimates is probably caused by tag loss. Tag loss may be low within season but will increase over time (Troëng et al. 2003) and results in lower annual survival probability estimates. From our study, it is clear that accounting for tag loss is crucial when estimating annual survival probability. Another alternative for sea turtle studies would be to

use passive integrated transponder (PIT) tags which many researchers believe are free from loss (Rivalan et al. 2005; Dutton et al. 2005). Fishermen, however, are unlikely to observe PIT tags on turtles they catch. Even if PIT tags are used, it would be prudent to double tag all turtles to confirm that there is no tag loss influencing the survival probability estimates. In view of the large fisheries take in Nicaragua (Lagueux 1998; Campbell and Lagueux 2005), it is not surprising that the annual survival probability for Tortuguero green turtles is lower than for less fished green turtle populations in Australia (Chaloupka and Limpus 2005). While Tortuguero green turtle survival probability is lower than for two other green turtle populations (Table 6), it is similar to the estimated adult annual survival probability of 0.89 (95% CI: 0.87–0.92) for a rapidly growing leatherback rookery in St Croix, US Virgin Islands (Dutton et al. 2005).

Observed remigration intervals of more than 3 years may represent females which were not detected during a previous breeding season (Carr and Carr 1970). This means observed remigration intervals overestimate the true remigration intervals (Rivalan et al. 2005). However, longer remigration intervals mean lower probability of surviving to return to nest and influence the observed remigration intervals in the opposite direction. The common modes of remigration of 2 and 3 years are consistent with previous studies of Tortuguero green turtles (Carr and Carr 1970; Carr et al. 1978), but are shorter than for other green turtle populations, with the exception of the Cyprus population (Table 6). Explanations for the short remigration intervals in-

Table 6 Key demographic parameter estimates for green turtle populations (adult life stage in bold)

Population	Age-at-maturity	Life stage	Annual survival probability (95% CI)	Remigration interval (most common modes)	Migration distance[a]
Atlantic Ocean					
Ascension Island, UK	**35 years (Frazer and Ladner 1986)**	**Adult**		**3–4 years (Mortimer and Carr 1987)**	**1,968 km (n = 6) (Luschi et al. 1998)**
Caribbean Sea					
Tortuguero, Costa Rica	**26 years (Frazer and Ladner 1986)**	**Adult**	**0.82 (0.73–0.89) (Campbell and Lagueux 2005) 0.85 (0.83–0.87) (This study)**	**2–3 years (Carr and Carr 1970; this study)**	**512 km (n = 10) (Troëng et al. 2005)**
RAAS, Nicaragua		Large juv./adult	0.55 (0.33–0.76) (Campbell and Lagueux 2005)		
Union Creek, Bahamas		Juvenile	0.51–0.81 (Bjorndal et al. 2003)		
Conception Creek, Bahamas		Juvenile	0.68 (0.63–0.73) (Bjorndal et al. 2003)		
Mediterranean Sea					
Cyprus		**Adult**		**2–3 years (Broderick et al. 2003)**	**1,076 km (n = 6) (Godley et al. 2002)**
Pacific Ocean					
Hawaii, USA	**30 years (Zug et al. 2002)** ~35–40 years (Balazs and Chaloupka 2004)	**Adult**		**3–4 years (Balazs and Chaloupka 2004)**	**1,100 km (n = 5) (Balazs 1994, Balazs et al. 1994)**
nGBR, Australia	~25 years (Chaloupka et al. 2004a)	**Adult**		**4–5 years (Limpus et al. 2003)**	few hundred to 2,773 km[b] (Limpus et al. 2003)
sGBR, Australia	**40 years (Chaloupka et al. 2004a)**	**Adult**	**0.95 (0.92–0.98) (Chaloupka and Limpus 2005)**	**5 and 7 years (Limpus et al. 1994a)**	**3,300 km (n = 1) (Spring 1994)**
Huyong Island, Thailand		**Adult**		**3 years (Yasuda et al. 2006)**	**836 km (n = 7) (Yasuda et al. 2006)**
Pacific coast, Mexico	**9–21 years[c] (Seminoff et al. 2002)**	**Adult**	**0.98 (0.84–0.99) (Seminoff et al. 2003)**		
Michoacan, Mexico		**Adult**		**3–4 years (Diaz et al. 2000)**	
sGBR, Australia		Subadult	0.85 (0.79–0.91) (Chaloupka and Limpus 2005)		
sGBR, Australia		Juvenile	0.88 (0.84–0.93) (Chaloupka and Limpus 2005)		
Pacific coast, Mexico		Immatures	0.58 (0.36–0.78) (Seminoff et al. 2003)		

[a] Distance from nesting beach to foraging grounds determined through satellite tracking of post-nesting females

[b] Based on tag recoveries

[c] After entering neritic habitat

clude better and more abundant food resources available for Caribbean green turtles, favorable environmental conditions in the Caribbean, and short distance between Tortuguero and the main foraging grounds in Nicaragua.

As capital breeders, sea turtles accumulate the energy needed for reproductive migrations and may breed when energy reserves reach a threshold value. In the Caribbean, adult green turtles feed mainly on turtle grass *Thalassia testudinum* (Mortimer 1981) that may be nutritionally superior to algae which dominates in the food intake of Pacific green turtles (Hirth 1997). If so, green turtles in the Caribbean reach the energy threshold needed to undertake reproductive migration more rapidly than green turtles in the Pacific. Also, density-dependent effects on growth have been observed in sea turtles (Bjorndal et al. 2000) and Limpus et al. (1994) suggested that remigration intervals should be shorter for severely reduced populations. Green turtle populations in the Caribbean are believed to have declined drastically as a result of overexploitation for meat, eggs and other products (Seminoff 2004). Current populations have been estimated at 3–7% of historical levels (Jackson et al. 2001). Historic decline in green turtle numbers can have freed up higher quality and/or more abundant food resources causing reproductive compensation by the remaining green turtles. Mediterranean green turtles have been called the most endangered green turtle population in the world, in great part due to historical declines (Broderick et al. 2002). Interestingly, green turtles on Cyprus in the Mediterranean also have short remigration intervals of 2–3 years (Broderick et al. 2003). Green turtle populations on Hawaii and in Australia which may not have suffered equally severe reductions have longer remigration intervals (Table 6). The Tortuguero green turtle rookery represents a recovering population (Solow et al. 2002; Troëng and Rankin 2005) and hence breeding output should be high as sea turtles do not appear to suffer from the Allee effect (Hays 2004). It may be that remigration intervals will increase as the population grows larger and density-dependent factors become increasingly important. A recent study showed that remigration intervals of Tortuguero green turtle have indeed become slightly longer since 1970 (Troëng and Chaloupka 2006).

Remigration intervals for sea turtles are also influenced by environmental conditions and climate cycles (Carr and Carr 1970; Hays 2000; Limpus and Nicholls 2000; Solow et al. 2002). Current environmental conditions and climate cycles influencing seagrass beds in the Caribbean may be conducive to rapid accumulation of energy reserves in adult green turtles.

Short distance between the major foraging ground and the nesting beach reduces the cost of reproductive migrations and contributes to short remigration intervals (Troëng et al. 2005). The distance between Tortuguero and the seagrass beds in Nicaragua is shorter than the distances documented for other green turtle rookeries and their main foraging grounds (Table 6). Shorter migration distance explains some of the difference in remigration intervals but does not account for all variation as demonstrated by the Hawaii and Cyprus green turtle populations which have very similar mean migration distances but different remigration intervals (Fig. 3).
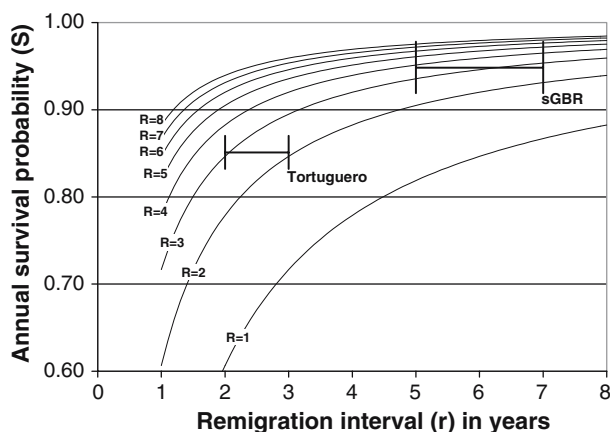
Reproductive output is influenced by remigration intervals, number of clutches per breeding season and eggs per clutch. We have only considered remigration intervals in this study. Rivalan et al. (2005) found a trade-off between current and future reproduction for leatherback turtles *Dermochelys coriacea* in French Guiana. Turtles with shorter remigration intervals laid slightly fewer clutches per active breeding season but had a higher estimated lifetime reproductive output (Rivalan et al. 2005). It appears that variation in remigration intervals is more important in determining lifetime reproductive output than clutches per breeding season or eggs per clutch. Lifetime reproductive output also depends on annual survival probability. Therefore, both adult annual survival probabilities and remigration intervals have profound management implications. This has been shown empirically using a stochastic simulation model of southern Great Barrier Reef green turtle population dynamics and demographic parameter sensitivity analysis based on fractional factorial sampling designs (Chaloupka 2002). Due to variability in survival probability and remigration interval, specific management interventions may
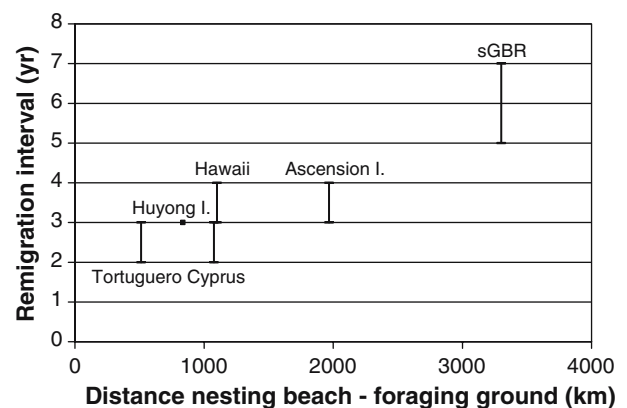
Fig. 3 Remigration intervals (most common modes) versus migration distance (nesting beach – foraging grounds). Data points from Table 6

be sufficient to maintain populations at one site but not at another. Also, if remigration intervals are influenced by climatic cycles, management interventions sufficient to maintain populations under favorable conditions may be insufficient when climatic conditions change. Management actions to conserve sea turtles therefore need to be tailored not only to local nesting trends but also to regional climatic cycles, anthropogenic threats, and natural conditions on the foraging grounds. Short remigration intervals make a rookery more susceptible to transient impacts which cause adult mortality on the nesting beach. In the unlikely event of all nesting females being killed on a nesting beach one year as a result of extreme weather or changes in the management regime, a larger proportion of adult females is eliminated from a population with short remigration intervals.

Concerns over the impact of the large Nicaragua fishery (Campbell and Lagueux 2005) are well founded in our current understanding of sea turtle life history and demography, especially the need to maintain high adult survival probability due to late age at maturity (Congdon et al. 1993). A comparison between the Tortuguero and the southern Great Barrier Reef (sGBR) green turtle populations, however, shows that the short remigration intervals of Tortuguero green turtles partly offset the lower annual survival probability (Fig. 4). Tortuguero green turtles have two to three expected breeding seasons and sGBR green turtles have three expected breeding seasons after first breeding (Fig. 4). The comparison shows that for sea turtle populations with long remigration intervals, a

small change in annual survival probability can greatly reduce the number of expected breeding seasons. Populations with short remigration intervals are less sensitive to small changes in annual survival probability. The importance of short remigration intervals in maintaining nesting populations can also be demonstrated by leatherback rookeries in the Atlantic (most common remigration interval 2 years; Rivalan et al. 2005) and the Pacific Ocean (most common remigration interval 3 years; Reina et al. 2002). Atlantic leatherback populations appear stable or increasing (Troëng et al. 2004; Dutton et al. 2005) while Pacific Ocean rookeries have declined dramatically in recent years (Spotila et al. 2000). Survival probabilities most likely differ between the two oceans but the difference in remigration intervals is also contributing to the nesting trends.

The Nicaragua green turtle fishery targets predominantly large juveniles and intensified during the early to mid-1990s (Lagueux 1998). It could be that instead of a rapid decline in nesting at Tortuguero, there will be a slow decline once recruitment of individuals into the adult population decreases. Alternatively, once the Tortuguero rookery grows and remigration intervals increase, the impact of the fishery will manifest itself in a slow nesting decline. Low juvenile survival probability may represent a more serious threat to the Tortuguero population than low adult survival probability. The estimated annual survival probability for large juvenile green turtles from the Tortuguero population is much lower (0.55; Campbell and Lagueux 2005) than for other populations (Table 6) but it is not known how representative this estimate is for Tortuguero green turtles. Further studies aimed at quantifying the survival probabilities of all life history stages would help in identifying the effects of fisheries-induced and other mortality on sea turtle population dynamics.

Additional factors to explain continued increases in nesting at Tortuguero include earlier maturation as a result of more rapid growth due to abundant food resources in the Caribbean (Bjorndal et al. 2000), and predation release caused by reduction in sharks (Shepherd and Myers 2005). Age-to-maturity and large juvenile survival probability for the entire population are the most urgently needed demographic parameters for determining the full impact of the Nicaragua fishery.

Low adult annual survival probability and short remigration intervals could have evolutionary consequences. It is feasible that shorter remigration interval is a response to selection resulting from high adult mortality rather than the result of abundant food resources. Low annual survival probability for adult

Fig. 4 Mean expected breeding seasons (R) after the first breeding season, as a function of annual survival probability (S) and remigration interval (r), $R = (1/{-}\ln S) \times (1/r)$. Adult annual survival probability (±95% CI) and the most common modes for remigration showed for Tortuguero and sGBR (data from Limpus et al. 1994; Chaloupka and Limpus 2005) green turtle populations

females may result in a strong selective pressure favoring shorter remigration intervals. Such an explanation is supported by trade-off between current reproductive effort and delay to next reproduction in sea turtles (Rivalan et al. 2005) but is contradicted by the rapidly declining leatherback nesting population with long remigration intervals in the Pacific Ocean (Spotila et al. 2000; Reina et al. 2002). Low survival probability for adult turtles instead is more likely to result in selective pressure for earlier age/smaller size at maturity. Continued monitoring of adult size at the Tortuguero rookery should detect any such change.

In conclusion, our study shows that short remigration intervals may be caused by reproductive compensation resulting from population reductions. Short remigration intervals partly offset low adult annual survival probability and could be an indicator both of marine productivity and of how well sea turtles fulfill their ecosystem roles. Researchers and managers interested in marine ecology and in defining sea turtle recovery goals may gain insights from comparing demographic parameters between sea turtle species and populations.

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