

Robust statistical modelling of hawksbill sea turtle growth rates (southern Great Barrier Reef)

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ABSTRACT: Growth rates recorded between 1974 and 1991 for 44 immature hawksbill sea turtles in the southern Great Barrier Reef foraging grounds were modelled using nonparametric regression methods. The implicit sampling design in this long-term mark-recapture program was mixed longitudinal and included growth records for both female and male hawksbills ranging between 39 and 85 cm CCL (curved carapace length). Distinct sex-specific growth patterns were found, with immature female hawksbills growing at ca 0.5 cm yr⁻¹ faster than male immature hawksbills at all recorded sizes. The mean-size specific growth rate function for females was nonmonotonic, rising rapidly from recruitment size (> 35 cm CCL) to a maximum growth rate of 2.2 cm yr⁻¹ at 60 cm CCL before declining to negligible growth approaching sexual maturity at a size ≥80 cm CCL. The mean-size specific growth rate function for males was also nonmonotonic, rising from the same recruitment size to a maximum growth rate of 1.7 cm yr⁻¹ at 60 cm CCL before declining to negligible growth approaching sexual maturity ≥80 cm CCL. No significant inter-annual variation in growth rates was found but the data set was too small to be conclusive. Size-specific growth rates were slower than observed for stocks from western Atlantic-Caribbean waters. Juvenile hawksbill growth spurts around 60 cm CCL, sex-specific growth and slow size-specific growth rates are distinct growth characteristics for immature hawksbill sea turtles resident in southern Great Barrier Reef waters.

KEY WORDS: Somatic growth · Nonparametric regression · Hawksbill turtles · Great Barrier Reef

INTRODUCTION

The hawksbill sea turtle *Eretmochelys imbricata* is an endangered and little-known marine turtle species with a broad circumtropical distribution (Witzell 1983). The hawksbill has been subject to a long history of extensive human exploitation for local egg harvests (Frazier 1980, Mortimer 1992) and for the commercial tortoiseshell trade (Frazier 1980). Hawksbill stocks are in serious decline in many regions (Hughes 1973, Carr & Stancyk 1975, Groombridge & Luxmoore 1989, Mortimer 1992, Bjørndal et al. 1993, Limpus 1993a) with the northwestern and northeastern Australian genetic stocks (Broderick et al. 1994) representing some of the few remaining stocks with seemingly viable breeding populations (Limpus 1992, Loop et al. 1995).

Australia shares its migratory hawksbill stocks with at least Indonesia and the Solomon Islands (Miller et al. in press), where there are widespread harvests for local consumption and trade (Groombridge & Luxmoore 1989). In northeastern Australian waters, hawksbills have a low probability of being caught incidentally in prawn fishery trawls but have quite a high probability of drowning once caught (Poiner & Harris 1996). The hawksbill is harvested for the local tortoiseshell market in neighbouring Papua New Guinea waters (Hirth & Rohovit 1992) with low levels of subsistence harvesting occurring in northern Australia (Limpus 1993a). The hawksbill sea turtle is clearly under threat globally (Groombridge & Luxmoore 1989) and increasingly in northern Australian waters so that improved knowledge of this species is needed to ensure the long-term viability of various regional stocks.

We present here a comprehensive statistical analysis of hawksbill growth rates obtained from a long-term

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mark-recapture program of hawksbill turtles resident in southern Great Barrier Reef (sGBR) foraging grounds (Limpus 1992). The hawksbills considered in this study comprised an indistinguishable mixture of genetic stocks, presumably including hawksbills from the northeastern Australian genetic stock (Broderick et al. 1994). The growth model presented here provides a basis for a better understanding of hawksbill growth dynamics in general, which is poorly known (Chaloupka & Musick 1997), and for modelling of regional hawksbill population viability.

Post-natal sea turtle somatic growth comprises separate ontogenetic growth compartments: (1) an epipelagic post-hatchling feeding phase followed by (2) a benthic feeding phase. These distinct ontogenetic phases (except perhaps for leatherbacks and flatbacks) are likely to have different growth characteristics (Chaloupka & Musick 1997). Therefore, this study considers only the benthic feeding phase for hawksbill sea turtles (>35 cm CCL, curved carapace length, to near onset of sexual maturity) resident in sGBR foraging grounds. Hawksbills <35 cm CCL have rarely been recorded from sGBR foraging grounds so the growth functions presented are not applicable to the unknown epipelagic phase (ca 4 to 35 cm CCL).

METHODS AND MATERIALS

Data set (hawksbill growth rates). The data set comprised 68 mark-recapture records for 44 immature hawksbill turtles tagged with monel and/or titanium tags in the sGBR foraging grounds between 1974 and 1991 (Limpus 1992). The data set included growth records for both female and male hawksbills ranging between 39 and 85 cm CCL. The 44 individual turtles comprised 30 females and 14 males providing 44 and 24 growth records respectively with 28% of individuals recaptured 2 or more times. All hawksbills in this data set were immature although some were larger than the mean size at sexual maturity at rookeries within the northern Great Barrier Reef (see Limpus 1992). Further details of this long-term mark-recapture program can be found in Limpus (1992), while Chaloupka & Musick (1997) provide an overview of the sampling and tagging protocols inherent in sea turtle mark-recapture programs.

Capture-recapture profiles recorded for each turtle included the following metrics: curved carapace length (cm CCL) at first capture and recaptures, sex and maturity determined from visual examination of gonads using laparoscopy (see Limpus 1992), year of first capture and time-at-large since first capture or previous recapture. Only turtles with recapture intervals ≥ 11 mo were included. Recapture intervals ranged

from 11 mo to 7 yr with a median recapture interval of 2 yr. Absolute growth rates were derived from these capture-recapture profiles, the growth rate metric being a standard first-order differential form ($dCCL/dt$), not to be confused with a specific growth rate ($1/CCL \cdot dCCL/dt$). Both negative and zero growth rates were included in the analysis because, as noted by Chaloupka & Limpus (1996), there is no statistically valid reason to do otherwise.

Sampling design. Demographic processes such as growth are complex time-dependent functions comprising 3 time effects (age, year, cohort). In other words there is natural variability in growth rates attributable to age-specific, inter-annual and cohort-specific factors (see Brillinger 1986). Year effect is considered an environmental factor while the cohort effect is considered a genetic factor. Confounded time effects result in biased growth estimates (Tucker et al. 1995) so growth analyses need to uncouple the time effects by accounting for age, year and cohort factors (see Chaloupka & Musick 1997). However, it is not always possible to uncouple the time effects in many studies because of limitations imposed by the mark-recapture sampling design and because of limitations in reliable aging of sea turtles (Chaloupka & Musick 1997).

The implicit sampling design in this study was mixed longitudinal sampling (sampling with partial replacement) with 28% of individual hawksbills recaptured 2 or more times. Mixed longitudinal sampling enables the age, year and cohort effects to be uncoupled, but only if age is known. Because age was unknown, as in most sea turtle studies, the implicit sampling design in this study confounds year and cohort effects. A full discussion of time-dependent demographic sampling designs in relation to sea turtle studies is presented in Chaloupka & Musick (1997).

Statistical modelling approach. The relationship between the absolute growth rates recorded for each hawksbill turtle and specific growth rate predictors or explanatory covariates was modelled statistically using a generalized additive modelling approach (see Hastie & Tibshirani 1990).

A generalized additive model (GAM) is a nonparametric regression model that allows (1) flexible specification of the error and link functions and (2) arbitrary specification of the functional form for each predictor included in the regression model. The GAM approach is a major extension of the familiar general linear model (GLM; Draper & Smith 1981, Cohen & Cohen 1983) and the recent generalized linear model (*glm*; McCullagh & Nelder 1989).

The GLM (parametric regression models such as linear regression, ANOVA, MANOVA) has many limiting assumptions including (1) normal error, (2) identity link of the response variable and (3) linear func-

tional form for each covariate included in the model. Linear form includes polynomial functional form. On the other hand, the *glm* approach supports more flexible link specification and relaxes the normality assumptions, but the constraint of linear predictor form still remains.

The GAM approach relaxes the normality assumptions and supports flexible link specification while the functional form (linear, nonlinear) for each predictor is estimated from the data using a scatterplot smoother conditioned on all other covariates included in the regression model. A GAM therefore includes additive (unlike nonlinear regression) and hence simple to interpret by comprising a separate function for each predictor in the regression model similar to the GLM and *glm* approaches. Examples of GAM models used in a variety of settings can be found in Hastie & Tibshirani (1987; ANCOVA-type field experiments, risks factors in heart disease), Swartzman et al. (1992; spatial analysis of fish stock distributions) and Chaloupka et al. (1994; epidemiology of ciguatera poisoning).

The GAM is complementary with modern statistical visualisation techniques (Cleveland 1993) that allow exploratory analysis of complex data sets including evaluation of the major assumptions of the GLM (normality, identity link, linear functional form). Preliminary analysis of the hawksbill growth data set based on data visualisation revealed that neither a GLM nor a *glm* approach to modelling the sGBR hawksbill growth would be worthwhile—in fact, as discussed below, a GLM would have resulted in erroneous conclusions about hawksbill growth.

The specific GAM regression model presented here used an identity link, a robust quasi-likelihood error function (Hastie & Tibshirani 1990) and reasonably stiff cubic smoothing splines to minimise small sample size and outlier effects on estimating nonlinear covariate form and regression parameter estimates. The robust estimator incorporated in the quasi-likelihood error function minimises the influence of outliers on parameter estimation (Hastie & Tibshirani 1990). Robust esti-

mators are important because sea turtles display considerable individual growth variability. A quasi-likelihood error function is quite general and precludes a need to assume a specific parametric error distribution (unlike the GLM) depending only on a mean-variance relationship derived from the data (McCullagh & Nelder 1989). The parameter estimates are therefore quasi-likelihood estimates modelled simultaneously with estimation of the mean-variance dispersion parameter. The dispersion parameter is used in computation of standard error and *t*-ratio values for each parameter and has a profound influence on statistical inference. The quasi-likelihood error function is also a means of accounting for potential correlated error due to the mixed longitudinal nature of the data (McCullagh & Nelder 1989).

The GAM fit and inference summary used here comprises 2 parts: (1) an estimate of the contribution of each predictor to the overall model fit using *t*-ratio statistical inference similar to the GLM and (2) an estimate of the nonlinearity for each continuous predictor using a Rao-type score or nonparametric *F*-ratio test statistic (Hastie & Tibshirani 1990). Both summary components were arranged into a single tabular format for ease of reporting and interpretation.

RESULTS

The GAM model comprised 1 response variable (absolute growth rates) and 4 potential growth factors (sex, mean.size, year, recapture.interval; see Table 1, Fig. 1). The sex factor is self evident (1 = female, 2 = male; Fig. 1a). Mean.size is the arithmetic mean of CCL at first capture and CCL at subsequent recapture. Mean.size is the appropriate size metric for indexing size-specific growth (see Fig. 1b) assuming that growth is locally linear or constant within the sampling interval (see Ricker 1979). This assumption is reasonable so long as relatively short sampling intervals are used. However, in long-term mark-recapture programs sam-

Table 1. Summary of parameter estimates for GAM model with robust quasi-likelihood error term and cubic smoothing splines (nominal df = 3) fitted to hawksbill turtle growth rates. Null deviance = 44.31, null df = 67, residual deviance = 17.69, residual df = 54.1, quasi-likelihood dispersion parameter = 0.2812, $R^2 = (44.31 - 17.69)/44.31 = 0.601$. npar: non-parametric (nonlinear) effects; df: degrees of freedom; ns: not significant; Prob(*F*) based on npar df and residual df

Parameter	Estimate	Asymptotic standard error	<i>t</i> -ratio	Prob(<i>t</i>)	Nonlinear effects (nonparametric)		
					npar df	npar <i>F</i>	Prob(<i>F</i>)
(constant)	4.1826	2.0675	2.0230	$p < 0.05$			
sex	-0.4759	0.1413	-3.3689	$p < 0.001$			
mean.size	-0.0130	0.0055	-2.3672	$p < 0.05$	3	13.238	$p < 0.0001$
year	-0.0205	0.0239	-0.8568	ns	3	1.177	ns
recapture.interval	0.0001	0.0001	0.9790	ns	3	1.657	ns

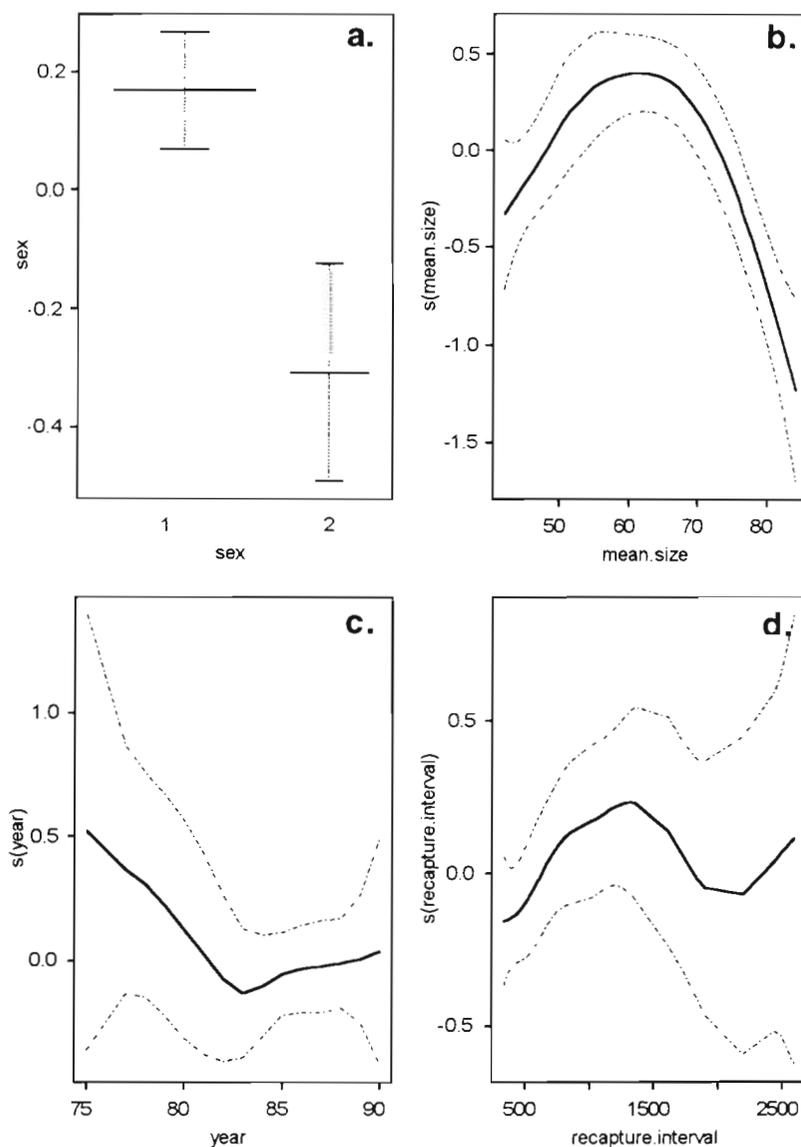


Fig. 1. Graphical summary of GAM model fit summarised in Table 1. Response variable (growth rate) shown on y-axis as a centred smoothed function scale to ensure valid pointwise 95% confidence bands. Covariate shown on the x-axis: (a) sex (1 = females, 2 = males), (b) year (year of growth record), (c) mean.size [mean CCL (cm) between first capture and next recapture] and (d) recapture.interval in years. The width of the mean factor response (a; sex) is proportional to sample size with the 95% confidence interval shown by cross bars. Solid curves in (b) to (d) are the cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAM model (see Table 1). Dotted curves in (b) to (d) are pointwise 95% confidence curves around the fits

pling intervals usually span a considerable time range. For instance, in the current study sampling intervals (recapture interval) ranged from 11 mo to 7 yr (median = 2 yr) so that this factor has been included in the model to account for potential bias due to variable sampling interval.

Year is the calendar year of the growth record and was included to account for the implicit time-depen-

dent sampling design (Fig. 1c). The year effect is a potential source of growth variability due to environmental factors but because of the implicit mixed longitudinal sampling design it was confounded with unknown cohort effects. If age for each turtle had been known (rarely the case for sea turtle studies), then it would have been possible to decouple the confounded year and cohort effects (see Chaloupka & Musick 1997). Whatever the year effect really measures in any particular study, it should always be included in a model because it is a time series sampling design constraint inherent in all mark-recapture programs—it is simply an unavoidable part of any growth study.

The GAM regression analysis suggested that immature hawksbill growth rates were dependent on both sex and mean.size effects (Table 1, Fig. 1a, b). Size-specific growth rates are referenced to mean.size between recaptures rather than initial size at capture. Mean.size is considered a more reliable approximation of a complex and instantaneous growth process (see Ricker 1979). Female growth rates were significantly different from male growth rates, with immature females growing on average about 0.5 cm yr⁻¹ faster than immature males (Table 1, Fig. 1a). Size was not only a significant covariate affecting growth rates but was also a significant nonlinear covariate (Table 1, Fig. 1b). On the other hand, hawksbill growth rates were independent of either year (Table 1, Fig. 1c) or recapture.interval effects (Table 1, Fig. 1d). Neither year nor recapture.interval effects displayed any nonlinearity (Table 1).

The GAM nonparametric regression model was a good fit to the growth data as shown by a small residual deviance relative to residual degrees of freedom (Table 1), acceptable nonparametric R² (Table 1) and no aberrant residual behaviour. The robust quasi-likelihood dispersion parameter (Table 1) suggests that an arbitrary error function was more appropriate than a normal or Gaussian error function (see McCullagh & Nelder 1989). However, the R² = 0.601 (Table 1) indicated that

while the GAM regression model accounted for at least 60% of the growth variance, immature hawksbills still displayed significant individual growth variation.

Covariate function plots for a GAM model fit (see Fig. 1) are centred on the response scale by subtracting a weighted mean to ensure valid pointwise 95% confidence bands (see Hastie & Tibshirani 1990). While essential for analytical purposes, centred plots are more difficult for the user to decode on the original response (i.e. growth rate) scale. To aid interpretation of the size-specific growth functions the predicted GAM model values were re-plotted on the uncentred growth rate scale for each sex with a cubic B-spline smooth superimposed to highlight the underlying nonlinear function (Fig. 2). Pointwise confidence bands are no longer valid in this format but the fitted model values provide a clear indication of the growth variability around the smoothed sex-specific growth functions in Fig. 2.

Distinct sex-specific growth patterns are clearly evident in Fig. 2, with immature female hawksbills growing about 0.5 cm yr⁻¹ faster than male immature hawksbills at all recorded sizes (compare Fig. 2a and 2b, see also Table 1). The fitted expected size-specific growth rate function for females was nonmonotonic, rising rapidly from the benthic phase recruitment size (>35 cm CCL) to a maximum growth rate of 2.2 cm yr⁻¹ at about 60 cm CCL before declining to negligible growth approaching sexual maturity at a size ≥80 cm CCL. The fitted expected size-specific growth rate function for males was also nonmonotonic rising from the same recruitment size to maximum growth of 1.7 cm yr⁻¹ at about 60 cm CCL before declining to negligible growth approaching sexual maturity at ≥80 cm CCL. The growth rate functions (Fig. 2) are monophasic (see Chaloupka & Musick 1997) displaying a single growth cycle with a growth peak or growth spurt for either sex at around 60 cm CCL.

The advantage of using a GAM model rather than a GLM model is quite apparent when the results of both approaches are compared. For instance, a linear regression model including a quadratic polynomial mean.size function accounted for only 31% of the variance compared to the GAM fit of 60% shown in Table 1. Yet the GLM model did not find the significant sex effect that was clearly evident in the data using data visualisation techniques (see Cleveland 1993) and supported by the GAM model analysis. Moreover, the

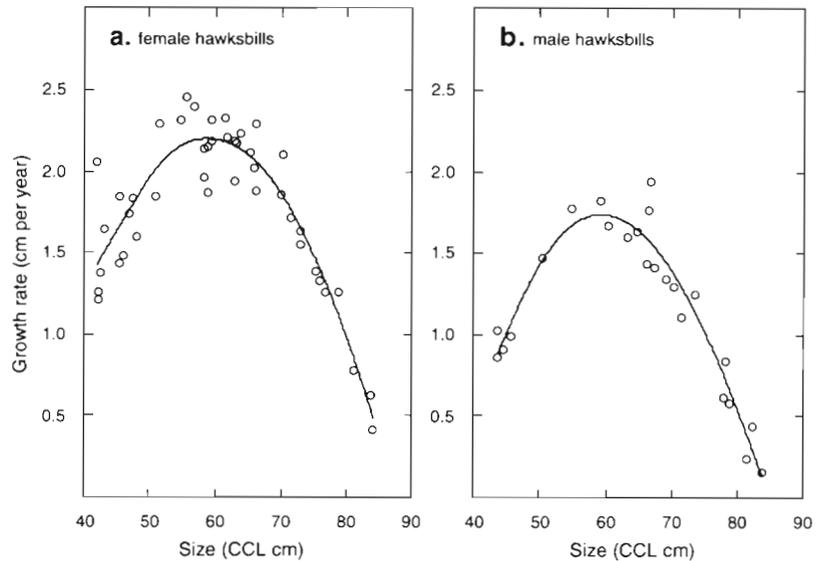


Fig. 2. *Eretmochelys imbricata*. Estimated size-specific growth rate functions for immature (a) female and (b) male hawksbills resident in southern Great Barrier Reef foraging grounds. (○) Fitted values from the GAM model (see Table 1); the solid curve in each panel is a cubic B-spline smooth fitted to the fitted GAM model values to highlight the underlying size-specific growth rate function

GLM model suggested that there was a significant year effect, an effect that was discounted by the GAM fit when the correct nonlinear functional form for the other covariates was used.

Whichever way you look at it, the GAM model is a good fit while the GLM model (with or without polynomial functional form) is a poor fit to these hawksbill growth data. It would seem that statistical modelling of sea turtle growth data might be more effective using nonparametric regression models that incorporate both nonlinear functional form and non-normal error structures. However, it is important to understand that since the sampling design was mixed longitudinal with unknown age, the growth model cannot account adequately for potential bias due to confounded year and cohort effects. How serious this potential bias would be is unknown but is an important issue rarely considered in biological growth modelling in general (see Chaloupka & Musick 1997).

DISCUSSION

Somatic growth of wild stock hawksbill sea turtles is poorly known (Chaloupka & Musick 1997). There are several compilations of growth rates of hawksbills reared in captivity (Witzell 1983, Zug et al. 1986, Godinez-Dominguez et al. 1993), but these data bear little resemblance to growth observed in wild stocks. For instance, hawksbill growth in captivity is much faster than growth in wild stocks (Limpus 1992). More-

over, captivity studies involve longitudinal sampling with known age, resulting in confounded age and year effects (Chaloupka & Musick 1997). On the other hand, wild stock growth studies invariably involve mixed longitudinal sampling with unknown age, confounding cohort and year effects. The 2 sampling designs lead to different sampling biases for time-dependent demographic processes such as growth (see discussion in Chaloupka & Musick 1997).

The hawksbills considered in this study were from an indistinguishable mixture of genetic stocks resident in southern Great Barrier Reef waters. Australia shares its migratory hawksbill stocks with at least Indonesia to the north and the Solomon Islands in the west (Miller et al. in press). The hawksbills were all immature, ranging from 39 to 85 cm CCL in size with both sex and maturity status confirmed using laparoscopy (Limpus 1992). Hawksbills ≤ 35 cm CCL have rarely been recorded from sGBR habitats so the growth functions presented here are not applicable for extrapolation to the poorly known epipelagic phase (ca 4 to 35 cm CCL). Moreover, mature adults were not included in this study because they have been poorly represented in samples from sGBR waters. The lack of adult hawksbills has been inferred to indicate a developmental migration to northern Australian waters (Limpus 1992). Hawksbill nesting for this stock occurs in the northern Great Barrier Reef, the Torres Strait, Solomon Islands and in Papua New Guinea waters (Limpus 1980, Limpus et al. 1983, Miller et al. in press).

The most comprehensive previous analysis of growth in wild hawksbills was presented by Limpus (1992) using data collected during the earlier years of the current study. Limpus (1992) used a growth interval method (see Chaloupka & Musick 1997) and concluded that immature hawksbill growth was nonmonotonic, peaking at 50 to 60 cm CCL then declining to very slow growth by 80 to 90 cm CCL. Limpus (1992) identified no sex-specific growth differences and presented no analytical growth functions.

The statistical growth rate modelling in the current study confirmed the nonmonotonic growth pattern suggested by Limpus (1992) but also found a significant difference in sex-specific growth rates (Table 1, Fig. 2). The distinct monophasic growth pattern with a growth spurt for both female and male immature hawksbills at around 60 cm CCL (see Fig. 2) or at any other size for that matter has not been recorded for any other hawksbill stock. On the other hand, Bjorndal & Bolten (1988) and Boulon (1994) have proposed a monotonic decreasing size-specific growth rate function for immature hawksbills resident in western Atlantic-Caribbean waters. A monotonic decreasing growth function suggests no growth spurt behaviour and infers a von Bertalanffy size-at-age growth func-

tion (see Chaloupka & Musick 1997). However, both studies were based on limited data sets and questionable sampling designs (see Chaloupka & Musick 1997).

Nonetheless, the apparent distinct regional growth patterns (monotonic vs nonmonotonic size-specific growth functions) might be real and due to distinct regional growth rate characteristics. Size-specific growth rates for the northeastern Australian genetic stock are much slower than stocks from western Atlantic-Caribbean waters where growth spurts are not evident (Bjorndal & Bolten 1988, Boulon 1994). For instance, Boulon (1994) found a mean growth rate for immature hawksbills in U.S. Virgin Island waters of 3.5 cm straight carapace length (SCL) yr^{-1} (SE = 0.52). Unfortunately, the hawksbill growth data in Bjorndal & Bolten (1988) are too limited for comparative purposes. For the current study in the sGBR region, the mean growth rate for immature females was 1.8 cm CCL yr^{-1} (SE = 0.12, median = 1.9 cm CCL yr^{-1}) and for immature males it was 1.2 cm CCL yr^{-1} (SE = 0.15, median = 1.3 cm CCL yr^{-1}). Even allowing for the transformation of SCL to CCL growth values, it would seem that immature hawksbills grow much faster in the western Atlantic-Caribbean region than in the sGBR region.

Inter-regional differences in immature growth rates could also explain why mature female hawksbills in northern Australian waters are apparently smaller than hawksbills nesting in the Caribbean and in the Seychelles (van Buskirk & Crowder 1994). The mean nesting female hawksbill size in northern Australia is about 83 cm CCL (range 76 to 93 cm CCL) or 76 cm SCL (Limpus et al. 1983, see also Loop et al. 1995). However, most hawksbill data sets are still too small for comparative growth analysis purposes. On the other hand, adult hawksbill growth is consistently recorded across regions as either negligible or perhaps having ceased altogether. For instance, Bjorndal et al. (1985) found that female hawksbills nesting at Tortuguero (Costa Rica) grew at about 0.3 cm yr^{-1} at a mean size of 83 cm SCL. Limpus (1992) found mature adult growth rates of 0.06 cm yr^{-1} at 80 to 90 cm CCL for hawksbills from the sGBR.

The size-specific growth functions developed here for immature hawksbills resident in sGBR waters are the first substantial growth functions presented for a wild hawksbill stock. Except for this data set, which is itself an extension of the data set in Limpus (1992), there are no other sex-specific growth data sets available for hawksbill sea turtles. The female and male immature hawksbill size-specific growth functions are significantly different, with immature females growing much faster at all sizes than immature males (Table 1, Fig. 2) implying sex-specific differences in size or age at maturity (i.e. adult size dimorphism). Nietschmann

(1981) has proposed adult size dimorphism for a mixed stock of hawksbills in Nicaraguan waters but Limpus (1993b) has questioned those data. The sex-specific growth functions presented here (Fig. 2) indicate that mature adult male hawksbills from the sGBR are most likely to be smaller on average than mature adult female hawksbills. For the moment, there are no valid data on mean mature male size for hawksbills resident in Australian waters although Limpus et al. (1983) recorded 1 mature male from the northern Great Barrier Reef at 82 cm CCL.

The size-specific growth functions for the sGBR hawksbills (Fig. 2) could be numerically integrated to yield size-at-age growth functions useful for estimating age-specific growth functions and age at sexual maturity for either sex (see Chaloupka & Limpus 1996). However, this hawksbill data set is currently too small and incomplete without mature adult records to warrant such further analysis. Nonetheless, it is clear from the size-specific growth functions (Fig. 2) that the onset of sexually maturity at a size ≥ 80 cm CCL for either sex will take decades, as proposed by Limpus (1992).

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