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Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation

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Abstract The growth dynamics of green sea turtles resident in four separate foraging grounds of the southern Great Barrier Reef genetic stock were assessed using a nonparametric regression modeling approach. Juveniles recruit to these grounds at the same size, but grow at foraging-ground-dependent rates that result in significant differences in expected size- or age-at-maturity. Mean age-at-maturity was estimated to vary from 25–50 years depending on the ground. This stock comprises mainly the same mtDNA haplotype, so geographic variability might be due to local environmental conditions rather than genetic factors, although the variability was not a function of latitudinal variation in environmental conditions or whether the food stock was seagrass or algae. Temporal variability in growth rates was evident in response to local environmental stochasticity, so geographic variability might be due to local food stock dynamics. Despite such variability, the expected size-specific growth rate function at all grounds displayed a similar nonmonotonic growth pattern with a juvenile growth spurt at 60–70 cm curved carapace length, (CCL) or 15–20 years of age. Sex-specific growth differences were also evident with females tending to grow faster than similar-sized males after the juvenile growth spurt. It is clear that slow sex-specific growth displaying both spatial and temporal variability and a juvenile growth spurt are distinct growth behaviors of green turtles from this stock.

Keywords *Chelonia mydas* · Green sea turtle · Great Barrier Reef · Somatic growth · Spatial variability · Nonparametric regression modeling

Introduction

The green sea turtle (*Chelonia mydas*) has a broad pantropical distribution and distinct regional population substructures (Bowen et al. 1992). The green turtle is also the most abundant large herbivore in marine ecosystems and feeds mainly on seagrasses and a wide range of soft algae (Bjorndal 1997). While the somatic growth dynamics of this ubiquitous sea turtle are not well known (Chaloupka and Musick 1997), some recent studies provide important new findings concerning environmentally induced temporal variability (Limpus and Chaloupka 1997) and variation due to regional stock-specific differences (Bjorndal et al. 2000). An important source of growth variability that has yet to be considered in any detail is spatial or geographic variability within the same genetic stock.

The southern Great Barrier Reef (sGBR) genetic stock of green turtles comprises a spatially disjunct metapopulation (Stith et al. 1996) with numerous foraging grounds spanning ca. 12° latitude and 1,800 km ranging from aseasonal tropical waters in the northern Great Barrier Reef (nGBR) to warm temperate seasonal waters in southern coastal Queensland. Juvenile green turtles recruit to these foraging grounds at ca. 40 cm CCL (curved carapace length) after pelagic development in the southwestern Pacific Ocean (Limpus and Chaloupka 1997). Pelagic green turtle stage duration is poorly known but estimated at ca. 5–6 years (Limpus et al. 1994; Limpus and Chaloupka 1997). Adult turtles resident in these foraging grounds then migrate every few years to breed in sGBR waters with females nesting on nearby coral cays. All the sGBR rookeries comprise the same panmictic interbreeding sGBR stock, which is distinct genetically from other Australian stocks (Norman et al. 1994; FitzSimmons et al. 1997).

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We present here a comprehensive statistical analysis of the temporal and spatial growth dynamics of green turtles resident in four major foraging grounds of the sGBR genetic stock (Fig. 1). These are not the only foraging-ground populations that comprise this stock, but are four of the major populations that have been extensively studied over the last 25 years. The analysis provides a basis for a better understanding of the temporal growth dynamics of a spatially structured population that spans a considerable geographic range and environmental conditions. This information has particular relevance for modeling the long-term viability of sGBR green turtle metapopulation population dynamics subject to various harvesting pressures throughout the Great Barrier Reef region (Chaloupka 2002, 2004).

Materials and methods

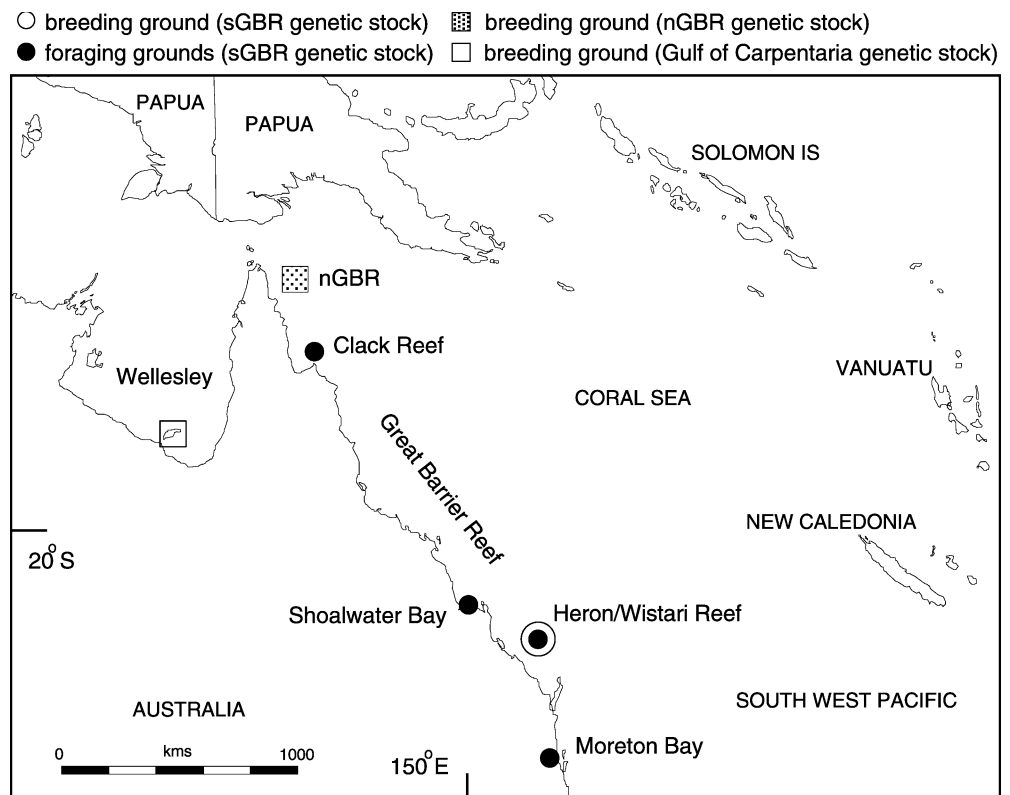
Data set and sampling design

The data set comprised 2,000 growth records for green sea turtles (principally sGBR genetic stock) captured in four foraging grounds since 1974 in a long-term and spatially extensive mark-recapture program (Limpus and Reed 1985; Limpus et al. 1994; Limpus and Chaloupka 1997). The foraging grounds were Clack Reef, Shoalwater Bay, Heron/Wistari Reef, and Moreton Bay (Fig. 1). Clack Reef is an offshore coral reef habitat in the warm nGBR waters with extensive shallow water

and deepwater seagrass meadows common in the area (Lee Long et al. 1993). Shoalwater Bay is an inshore, seagrass-based coastal habitat with a significant tidal range in the sGBR region (Lee Long et al. 1993). Heron/Wistari Reef is an offshore, algal-based coral reef habitat in southern Great Barrier Reef waters (Limpus and Reed 1985; Forbes 1994). Moreton Bay is an inshore, mixed seagrass- and algal-based coastal habitat in warm temperate southern Queensland waters (Limpus et al. 1994; Brand-Gardner et al. 1999). The green sea turtles resident in the Moreton Bay, Heron/Wistari Reef, and Shoalwater Bay foraging grounds are all from the sGBR genetic stock, whereas the Clack Reef population comprises a mixture of sGBR and nGBR stocks (Limpus et al. 1992; FitzSimmons et al. 1997).

The annual sampling periods varied between the foraging grounds; a 17-year period (1974–1991) at Heron/Wistari Reef, a 9-year period (1986 to 1994) at Shoalwater Bay, a 6-year period (1990–1995) at Moreton Bay, and a 4-year period (1987–1990) at Clack Reef. Capture and recapture was undertaken using the turtle rodeo technique with each turtle double-marked with uniquely coded titanium tags (Limpus and Reed 1985). Tag loss for this mark-recapture program has been shown to be inconsequential (Limpus 1992). The data included growth records for 827 females and 513 males spanning the post-recruitment phase from ca. 40 to 120 cm CCL with >32% of individuals recaptured on two or more annual sampling occasions. Hence, the implicit sampling design was mixed longitudinal or

Fig. 1 Location of the foraging-ground study sites for the sGBR genetic stock of green sea turtles resident in Great Barrier Reef waters. The major rookeries of the other two genetic stocks of Australian green sea turtles in the same region are also shown



sampling with partial replacement, which confounds year and cohort effects, since age was unknown for all individuals (Chaloupka and Musick 1997).

Capture-recapture profiles for each of the 1,340 individual turtles included (1) curved carapace length at first capture and at all recaptures (cm CCL); (2) sex and developmental stage (age class) determined using laparoscopic examination of reproductive organs (Limpus and Reed 1985; Limpus et al. 1994); (3) year of first capture; and (4) years-at-large since first capture or previous recapture. Only turtles with recapture intervals ≥ 12 months were used to minimize any measurement error on growth estimation where size was recorded as midline curved carapace length (cm CCL) using a fiberglass tape marked in 0.1-cm intervals (Limpus et al. 1994). Absolute growth rates were then derived from the 1,340 capture-recapture profiles (Chaloupka and Limpus 1997), with both negative and zero growth rates included since there is no valid reason to do otherwise (Chaloupka and Musick 1997; Limpus and Chaloupka 1997). A summary of the 1,340 individual green turtles classified by sex and developmental stage (age class) at first capture within each of the foraging grounds is given in Table 1. This data set extends significantly the single foraging ground data set used by Limpus and Chaloupka (1997) to study sGBR green sea turtle growth dynamics.

Statistical modeling approach

The standard approach to modeling sea turtle growth with unknown age has been the use of size-based analogues of age-based parametric growth functions, which has many significant shortcomings (Chaloupka and Musick 1997). Instead, the two-stage statistical modeling approach of Chaloupka and Limpus (1997) and Limpus and Chaloupka (1997) was used as follows: (1) a robust nonparametric regression model was fitted to the growth-rate data to derive the expected size-specific growth rate function conditioned on informative growth predictors or covariates, followed by (2) numerical integration of the size-specific growth rate function using a difference equation and a 4th-order Runge-Kutta

integration method (Gerald and Wheatley 1994) to derive the expected size-at-age growth function. Numerical differentiation (Gerald and Wheatley 1994) of this function is then used to derive the age-specific growth rate function. Hence, the expected size-at-age and age-specific growth functions were derived from a robust statistical modeling approach without recourse to any size-based growth analogues.

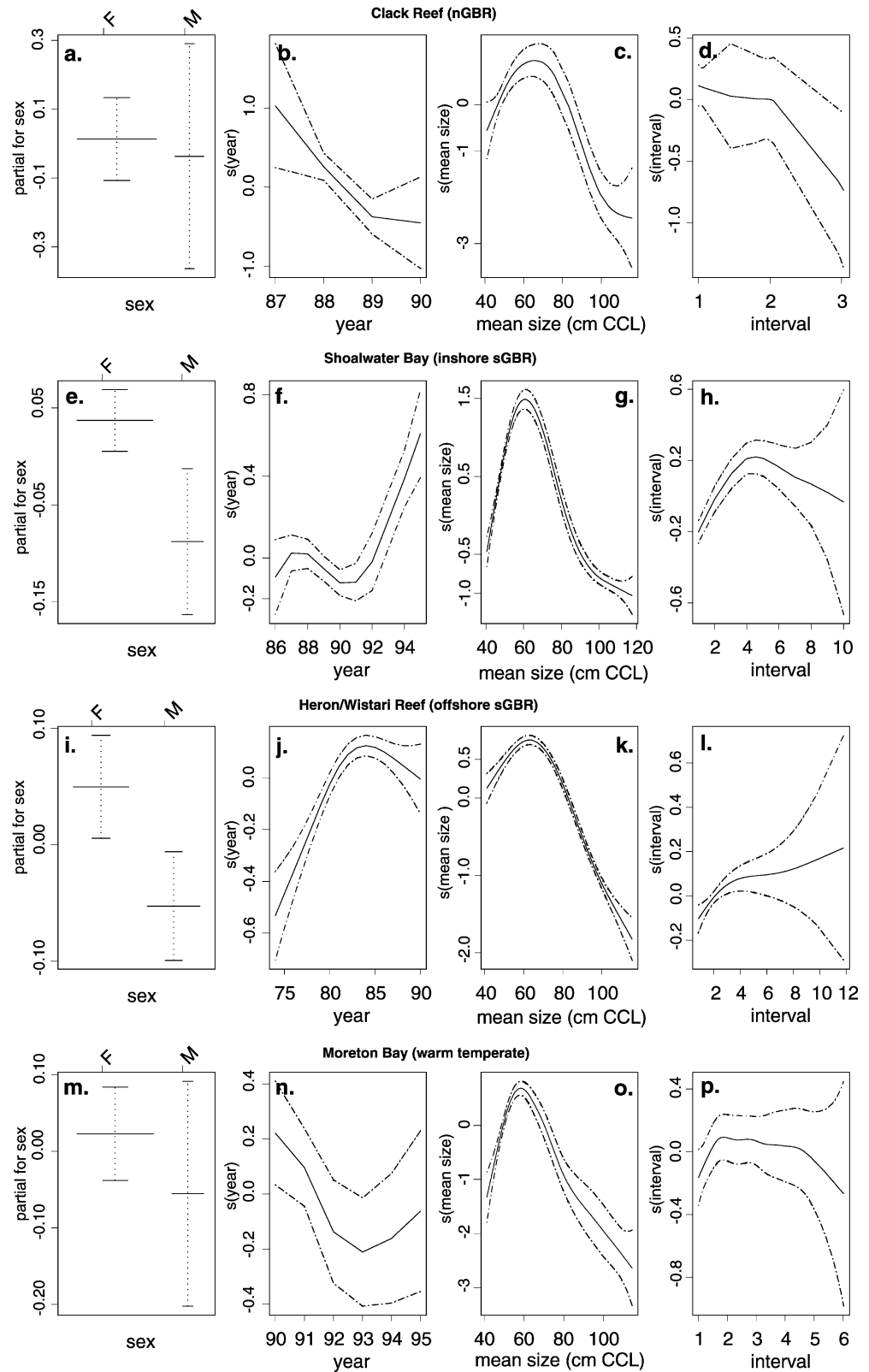
The growth rate predictors (covariates) used here were sex, calendar year, mean size (cm CCL), and recapture interval (years). Sex is a self-evident cofactor and was determined along with developmental stage using laparoscopy. The year covariate reflects the calendar year of the growth rate estimate and was included to account for the implicit time-dependent sampling design. Year effect is also a source of growth variability due to environmental factors, but is confounded with cohort effects because of the mixed longitudinal sampling design with unknown age inherent in this study (Chaloupka and Musick 1997). Moreover, year effect is imprecise, because not all growth records were for only 1-year duration. While the minimum growth or recapture interval was 1 year, the median recapture interval across all foraging grounds was 2 years. Hence, year effect was measured with a 2-year error, making assignment to a specific calendar year imprecise. Nonetheless, the year covariate as defined here is a useful proxy of the year effect and should be included because it is a sampling design constraint inherent in mark-recapture programs (Chaloupka and Musick 1997; Chaloupka and Limpus 1997; Limpus and Chaloupka 1997). The mean-size covariate is the arithmetic mean of size at first capture and subsequent recapture and is the appropriate metric for indexing size-specific growth assuming growth is locally linear within a sampling interval (Chaloupka and Limpus 1997). This assumption is reasonable if short sampling intervals are used. However, in mark-recapture programs, sampling intervals often span a considerable time range. For instance, recapture intervals here ranged from 1–12 years, so that this covariate should also be included in the models to account for potential bias due to variable sampling interval.

The functional relationship between absolute growth rates recorded for each of the 1,340 individual turtles and the four growth rate predictors was modeled in the first stage of the two-stage procedure using a generalized additive modeling approach (GAM: Hastie and Tibshirani 1990). GAM enables robust analysis of regression models with nonlinear covariate functional form and non-normal error terms. The GAM regression models used here comprised (1) an identity link since no other response transformation was necessary, (2) a robust quasi-likelihood error function to minimize outlier effects on parameter estimates, and (3) flexible cubic smoothing splines to model any nonlinear functional form between growth rates and the continuous covariates (year, mean size, recapture interval). A quasi-likelihood error function is

Table 1 Demographic summary of the 1,340 individual green turtles resident in four geographically separate foraging grounds of the sGBR genetic stock used to estimate somatic growth functions. Turtles assigned to sex and developmental stage (age class) at first capture using laparoscopic examination of reproductive organs

Stage	Sex	Foraging-ground population				Total
		Moreton Bay	Heron/Wistari Reef	Shoalwater Bay	Clack Reef	
Immature	Female	185	211	194	72	662
	Male	82	130	73	23	308
Adult	Female	9	50	98	8	165
	Male	3	146	50	6	205
Total		279	537	415	109	1,340

Fig. 2 Graphical summary of GAM model fit for each foraging ground summarized in Table 2. The Clack Reef growth model is shown in panels **a** – **d**; Shoalwater Bay model is shown in **e** – **h**; Heron/Wistari Reef is shown in **i** – **l**; and Moreton Bay model is shown in **m** – **p**. The response variable (growth rate) is shown on the y -axis in each panel as a centered smoothed function scale to ensure valid pointwise 95% confidence bands. Covariates shown on the x -axis: sex (**a**, **e**, **i**, **m**: where F female and M male), year (**b**, **f**, **j**, **n**: growth year index), mean size (**c**, **g**, **k**, **o**: mean size between first and next capture in cm CCL), and recapture interval in years (**d**, **h**, **l**, **p**). The width of the mean factor response (**a**, **e**, **f**, **m**) is proportional to sample size with the 95% confidence interval shown by *cross bars*. *Solid curves* in **b** – **d**, **f** – **h**, **j** – **l**, and **n** – **p** are cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAM model for each foraging ground (Table 2), while the *dotted curves* in the same panels are pointwise 95% confidence curves around the fits



extracted using a cubic B-spline smooth from the original data and is shown in Fig. 3a, d. Note that pointwise confidence bands are now no longer valid in this format (Chaloupka and Limpus 1997).

The functional form of the year effect was also significantly nonlinear at all foraging grounds (Table 2), except for Moreton Bay where the effect was evidently linear (Table 2, Fig. 2). The year effect indicates signif-

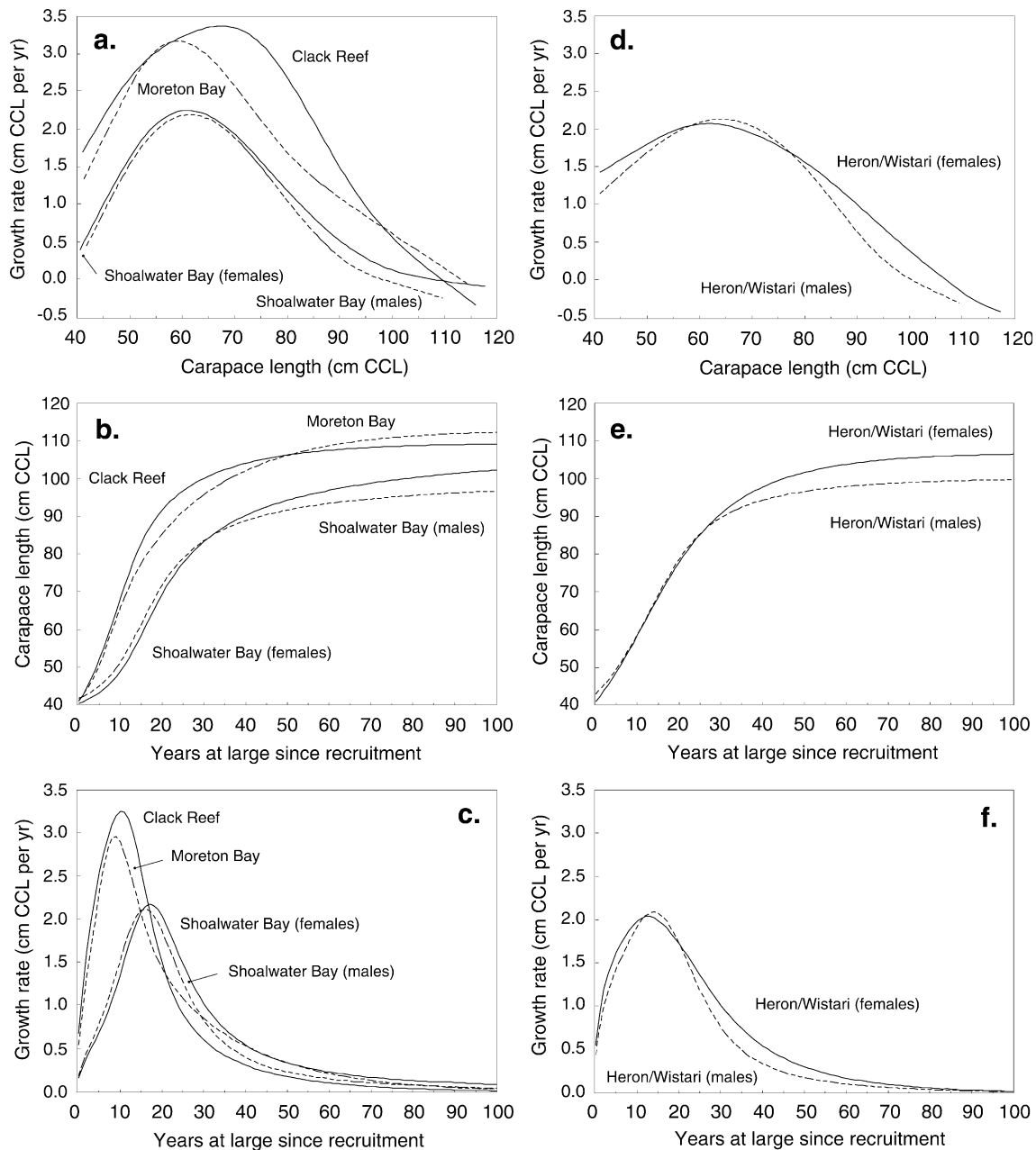


Fig. 3 Estimated age- and size-specific growth functions for each foraging ground derived from the GAM model fit conditioned on all covariates (Table 2). Growth functions for the Clack Reef, Shoalwater Bay, and Moreton Bay populations are shown in panels **a**–**c**; corresponding functions for the Heron/Wistari Reef population in **d**–**f** are shown separately to avoid clutter. Panels **a** and **d** reproduce the size-specific growth rate functions derived using cubic B-spline fit to GAM predicted values (Fig. 2c, g, k, o). Those functions were integrated numerically to give expected size-at-age (age = years-at-large since recruitment) functions in (**b**) Clack Reef, Shoalwater Bay, Moreton Bay, and (**e**) Heron/Wistari Reef, conditioned on all the covariates in the GAM model. The expected size-at-age spline functions **b** and **e** were differentiated numerically with respect to time to give the expected age-specific growth rate functions shown in **c** and **f**. 95% confidence curves are not included because the functions (**b**, **e**) are arbitrary smooth functions derived from other smooth functions (**a**, **d**), with no simple way to estimate valid pointwise standard errors

ificant inter-annual growth variability, inferring an environmental influence on immature growth, since turtles displayed constant negligible growth following the onset of sexual maturity (Fig. 2). Significant sex-specific growth rate differences were evident at the Shoalwater Bay and Heron/Wistari Reef foraging grounds (Table 2, Fig. 2), but there was no significant statistical difference at the Clack Reef or Moreton Bay grounds despite lower mean growth estimated for males at both sites (Fig. 2a, m). The recapture interval also was found to be a significant linear or nonlinear factor affecting growth variability except for Moreton Bay. Therefore inclusion of this predictor in growth models was warranted (Table 2).

Overall, growth rates for sGBR genetic stock green turtles resident in the four geographically separate for-

aging grounds in Great Barrier Reef waters were found to be sex, size, and year dependent. However, it is important to recall that the sampling design was mixed longitudinal with unknown age so that the models cannot account for any bias due to confounded year and cohort effects.

Age dependent growth behavior

The expected size-specific growth rate function for each foraging ground represented by cubic B-splines (Fig. 3a, d) was integrated numerically with respect to time (age estimate); separate sex-specific functions are shown if there was a significant sex-specific difference (see Table 2). The resulting monotonic growth function is then an empirical estimate of the expected size-at-age growth function for each foraging ground where age is years-at-large since recruitment to a benthic habitat in GBR waters ca. 40 cm CCL (Fig. 3b, e). We refer to years-at-large since recruitment rather than age because we modeled only the benthic growth phase (40 cm CCL to mature adult) without knowing the actual age of turtles since hatching ca. 5 cm CCL. Therefore, age (years-at-large since hatching) is the sum of the epipelagic developmental phase plus years-at-large since recruitment to a benthic habitat. Years-at-large since recruitment is then only an estimate of minimum age because we do not yet have a conclusive estimate of the duration of the epipelagic developmental phase for this stock, although it is currently estimated ca. 5–6 years (see Limpus et al. 1994; Limpus and Chaloupka 1997). The expected size-at-age functions were then differentiated numerically to derive the expected age-specific growth rate function for each foraging ground (Fig. 3c, f).

Discussion

Conventional definitions of metapopulations are at best vague (Thomas and Kunin 1999) and often refer to small-scale patch occupancy configurations that bear little relevance for marine or terrestrial vertebrates (York et al. 1996; Stith et al. 1996). We define a metapopulation here as a genetic stock comprising local independent populations resident in geographically dispersed and disjunct foraging grounds with dispersal between nearby populations more likely than dispersal between distance populations. The important issue of distance-dependent dispersal between various foraging populations comprising the sGBR green turtle metapopulation and the implications for stock viability was considered in Chaloupka (2004). This assemblage of spatially disjunct foraging ground populations from the same genetic stock is linked by annual reproductive migration to one panmictic interbreeding regional rookery in the southern Great Barrier Reef (Fig. 1). This definition is similar to the definition used by York et al.

(1996) for an Alaskan sea lion metapopulation and works well for describing both the sGBR and nGBR green turtle genetic stocks.

Here we have explicitly addressed the temporal and spatial (geographic) variability in somatic growth for green turtles from the sGBR metapopulation using samples drawn from four major foraging-ground populations that represent the entire east Australian geographic range of this stock. The major findings derived from this long-term and spatially extensive study of green turtle growth behavior in GBR waters were (1) nonmonotonic size-specific growth rate functions; (2) sex-specific growth, especially for the Heron/Wistari Reef and Shoalwater Bay populations in the sGBR region; (3) immature growth variability due to stochastic environmental effects; and (4) geographical variability in immature growth within the same genetic stock. Somatic growth rates within the sGBR green turtle metapopulation were found to be faster at all comparable sizes for the northern Great Barrier Reef population (Clack Reef) and also from the Moreton Bay population, which is well south of the Great Barrier Reef in warm temperate waters.

Nonmonotonic size-specific growth

The expected or mean size-specific growth rate function for each foraging ground conditioned on informative covariates (sex, year, recapture interval) was nonmonotonic, rising rapidly from recruitment size (40 cm CCL) to maximum growth rates ca. 60–70 cm CCL before declining to negligible growth approaching sexual maturity around 90–100 cm CCL (Fig. 3a, d). This finding is similar to the expected size-specific growth rate function derived by Limpus and Chaloupka (1997) for the Heron/Wistari population. All growth functions were monophasic (Chaloupka and Zug 1997), displaying a single growth cycle with a juvenile growth spurt indicated by a growth rate peak ca. 60–70 cm CCL. Hence, this pattern with a distinct juvenile growth spurt is characteristic of the spatially structured sGBR green turtle stock and may have a genetic basis.

Similar growth patterns have also been found for hawksbill sea turtles (Chaloupka and Limpus 1997) resident in sGBR foraging grounds, suggesting that such growth behavior might be characteristic of eastern Australian sea turtle species in general. General conclusions about size-specific sea turtle growth are not yet possible since there are few long-term studies of sea turtle growth behavior suitable for comparative analysis (Chaloupka and Musick 1997).

However, Bjørndal et al. (2000) recently found a monotonic declining size-specific growth pattern for immature green turtles resident in waters around the southern Bahamas using a similar GAM-type statistical modeling approach. Green turtles in sGBR waters grow much slower for the first 5–6 years following benthic

recruitment than do green turtles in the southern Bahamas, and this growth difference is most probably food-stock related (Bjorndal et al. 2000).

Sex-specific growth

Mean growth for female green turtles was higher than male growth at all four foraging grounds, but the difference was statistically significant only for the Heron/Wistari Reef and Shoalwater Bay populations (Fig. 2). The lack of a significant sex effect for the Clack Reef and Moreton Bay populations was due to smaller sample size, shorter study period, and juvenile-biased population structure compared to the Heron/Wistari Reef and Shoalwater Bay populations (Table 1).

A significant sex effect occurs because immature females grow faster than similar sized males after a juvenile growth spurt (> 60 cm CCL, Fig. 3a, d), resulting in the sexual dimorphism in adult size recorded for the sGBR genetic stock (Fig. 3d, e; see Limpus and Chaloupka 1997 for a more detailed analysis of the Heron/Wistari Reef population). However, the Clack Reef and Moreton Bay samples comprised $> 66\%$ of individuals smaller than 60 cm CCL, which is prior to the juvenile growth spurt that marks the onset of the sex-specific growth behavior for the sGBR genetic stock. On the other hand, the Heron/Wistari Reef and Shoalwater Bay samples comprised $< 40\%$ of individuals smaller than 60 cm CCL, resulting in far greater power for identification of the sex-specific growth behavior.

Significant sex-specific growth with relatively faster female growth also has been found for hawksbill turtles (Chaloupka and Limpus 1997) and green turtles (Limpus and Chaloupka 1997) resident in sGBR waters, suggesting that sex-specific growth behavior is a characteristic of these sea turtle species in GBR waters. However, there are no sex-specific differences in annual survival probabilities for sGBR sea turtles (Chaloupka and Limpus 2002), so the sex-specific growth behavior and sexual dimorphism in adult size for the sGBR green turtle stock cannot be attributed to differential survivorship. Moreover, there are no apparent sex- or age-specific dietary differences for green turtles resident in the Heron/Wistari Reef population (Forbes 1994). The ecological processes responsible for the sex-specific growth behavior of sGBR green turtles remain unknown, but are presumably related to size-dependent life history strategies (McNamara and Houston 1996).

Significant sex-specific growth has also been found recently for a population of immature green turtles resident in waters around the southern Bahamas, but this was probably due to an age- or sex-biased population structure (Bjorndal et al. 2000). More general conclusions about sex-specific sea turtle growth are not yet possible, since there are no other long-term studies of time-dependent sea turtle growth behavior that also include sex recorded for each individual (Chaloupka and Musick 1997).

Environmental effects on growth

Significant temporal variation (year effect) in growth rates was found for all four foraging-ground populations (Table 2, Fig. 2). This variation presumably reflects strong local environmental variability. Limpus and Chaloupka (1997) suggested that an abrupt temporary increase in immature growth rates during the 1980s for the Heron/Wistari Reef population (Fig. 2j) was a function of El Niño-Southern Oscillation (ENSO), events that are known to affect green turtle breeding behavior (Limpus and Nicholls 1994) and spatially synchronized nesting activity (Chaloupka 2001a). Therefore, it is interesting that growth rates declined for all foraging-ground populations during the late 1980s and early 1990s (Fig. 2), which was coincident with the longest recorded series of ENSO events this century (Trenberth and Hoar 1997).

The declining growth rates during the extended ENSO period of the late 1980s and early 1990s (Fig. 2b, f, j, n) is probably a direct consequence of the cooler-than-average sea surface temperatures experienced in the western Pacific Ocean during ENSO events (Lough 1994), and the decline in macroalgal diversity and biomass that occurs during such events in tropical waters (Carballo et al. 2002). Recall that macroalgae comprise a significant part of the sGBR green turtle diet (Forbes 1994; Brand-Gardner et al. 1999). However, it remains unclear as to why there is a discrepancy between increasing growth during the early 1980s shown for the Heron/Wistari Reef population following a single major ENSO event (Fig. 2j) and the declining growth rates for all populations during the extended period of ENSO events (Fig. 2b, f, j, n).

Moreover, major local cyclone-induced flooding events occurred during the early 1990s that caused substantial seagrass loss along the southern Queensland coast (Preen et al. 1995). Similar local flooding events might also be responsible for temporary growth rate suppression apparent for the Shoalwater Bay and Moreton Bay foraging ground populations during the early 1990s (Fig. 2f, n). Therefore, temporal variability in sGBR genetic stock green turtle growth behavior is probably a complex response to both local and regional environmental variability. The physiological and ecological mechanisms underlying such environmental effects on the long-term growth dynamics of sea turtles are not known, but are presumably food stock related, and warrant further investigation (Bjorndal 1997).

Geographic variability in growth

Significant geographical variation in growth rates was found with major differences in the long-term growth dynamics evident for each foraging-ground population comprising the sGBR genetic stock (Figs. 2 and 3). This is the first substantive report of geographic vari-

ation in sea turtle growth dynamics for the same stock, although some limited geographic variability also is evident for the Hawaiian stock (Balazs 1982). The various populations of the sGBR stock are characterized by having predominantly the same mtDNA haplotype with similar frequencies for the remaining haplotypes (Norman et al. 1994; FitzSimmons et al. 1997). Therefore, geographic differences in growth rates within the stock are possibly due to local environmental conditions rather than genetic factors.

Both the Clack Reef (nGBR) and Moreton Bay (southern Queensland) populations grew faster at all comparable sizes than the Heron/Wistari Reef or Shoalwater Bay populations located in the sGBR region (Fig. 3a, d). These foraging-ground, specific growth differences cannot be attributed to any latitudinal gradient in environmental variables such as sea-surface temperature, irradiance, or climatic regimes (Lough 1994). Moreover, the differences were not dependent on whether the foraging ground was an inshore embayment (Shoalwater Bay, Moreton Bay) or an offshore coral reef (Clack Reef, Heron/Wistari Reef), or if the food stock was mainly seagrass (Clack Reef, Shoalwater Bay) or algae (Heron/Wistari Reef, Moreton Bay). There are no digestive process differences needed for an algal or seagrass diet, although a mixed diet might lead to lower digestive efficiency (Bjorndal et al. 1991). There is also no known nutritional difference between algal and seagrass diets (Garnett et al. 1985), and no indication of growth rate differences between algal and seagrass feeders (Bjorndal 1997).

Given the temporal variability in green turtle growth rates at all foraging grounds, we propose that the geographic variation evident for the sGBR stock is due to food stock dynamics subject to local environmental stochasticity, resulting in differences in food availability (Garnett et al. 1985) and nutrient uptake rates (Bjorndal 1997). There is significant temporal and spatial variability in algal abundance around Heron Reef (Forbes 1994) and also for seagrass stocks along the Queensland coast (Lee Long et al. 1993; Lanyon and Marsh 1995), providing some circumstantial support for this view. Further support for this hypothesis is provided by a recent radio telemetry study that found unusually large foraging ranges for adult green turtles resident in sparse seagrass habitats in Repulse Bay just northward of Shoalwater Bay (Whiting and Miller 1998). Moreover, geographic variation in growth rates that has been attributed to algal food stock availability is also apparent for green turtles resident in Hawaiian waters (Balazs 1982).

It is also possible that the relatively faster growth for the Clack Reef and Moreton Bay populations (Fig. 3a, d) is attributable to an immature-biased population structure evident in these two foraging grounds (Table 1). Lower relative adult abundance might foster increased immature growth rates because of density-dependent growth behavior (Bjorndal et al.

2000), but density estimates for the foraging ground populations are not available, so it is impossible for the moment to evaluate such effects.

Age dependent growth

An important consequence of geographic variation in growth rates will be a substantial variation in size and age at sexual maturity for individual turtles within the stock. Recall that the age-specific growth functions for each foraging ground shown in Fig. 3 was (1) derived from a GAM regression model conditioned on the covariates summarized in Table 2, and (2) then derived by numerical integration of the curves in Fig. 3a, d and numerical differentiation of the curves in Fig. 3b, e without recourse to size-based growth analogues (see Chaloupka and Musick 1997).

The age-specific growth functions (Fig. 3c, f) show that the juvenile growth spurt occurs around 10–15 years after recruitment, depending on the particular foraging ground. Assuming that the epipelagic phase duration for the sGBR stock is ca. 5 years (Limpus and Chaloupka 1997), then the juvenile growth spurt occurs at ca. 15–20 years of age. Growth then slows rapidly following the juvenile growth spurt and so turtles from this sGBR stock take many years to reach sexual maturity, irrespective of the foraging ground. Chaloupka (2001b) presented a system-of-Weibull-equations growth model to describe and summarize the sex- and foraging-ground-specific growth behaviors of this stock based on these empirical age-specific growth functions. That system-of-equations model is especially useful for comparative demographic studies and further development of growth state theory (Chaloupka 2001b).

It is common practice to use the size-at-age curves (Fig. 3b, e) to estimate the mean age at sexual maturity. The difficulty in using growth functions for this purpose is the lack of conclusive growth criteria to indicate onset of maturity. One criterion in the absence of maturity rate functions is the size at which the onset of negligible growth is apparent (Limpus and Chaloupka 1997), which is ca. 95 cm CCL for all foraging grounds (Fig. 3a, d). The onset of negligible growth by 95 cm CCL is also consistent with crude maturity rate estimates proposed by Limpus and Reed (1985) and Limpus et al. (1994) for the sGBR genetic stock.

Given this size criterion and the assumed epipelagic phase duration, the mean age at maturity was then estimated at ca. 25 years for the Clack Reef population, 30 years for the Moreton Bay population, 40 years for the Heron/Wistari Reef population, and at least 50 years for the Shoalwater Bay population. Clearly, there is considerable variation in age and size at maturity for the various foraging-ground populations that has not yet been reported for any other sea turtle stock. This result has major implications for the design of stochastic simulations models useful for exploring the long-term viability of the spatially disjunct metapopulation com-

prising the sGBR green sea turtle genetic stock (Chaloupka 2004).

Overall, this study confirms the findings of Limpus and Chaloupka (1997) for somatic growth dynamics of green sea turtles from the Heron/Wistari Reef population (Fig. 1) and significantly extends that study to address the spatial structure of the sGBR genetic stock. It is now clear that slow sex-specific growth, displaying significant spatial and temporal variability, and a juvenile growth spurt are distinct growth behaviors of green sea turtles comprising the sGBR stock.

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