RESEARCH ARTICLE

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Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago

Abstract The somatic growth dynamics of green turtles (*Chelonia mydas*) resident in five separate foraging grounds within the Hawaiian Archipelago were assessed using a robust non-parametric regression modelling approach. The foraging grounds range from coral reef habitats at the north-western end of the archipelago, to coastal habitats around the main islands at the south-eastern end of the archipelago. Pelagic juveniles recruit to these neritic foraging grounds from ca. 35 cm SCL or 5 kg (~6 years of age), but grow at foraging-ground-specific rates, which results in quite different size- and age-specific growth rate functions. Growth rates were estimated for the five populations as change in straight carapace length (cm SCL year^{-1}) and, for two of the populations, also as change in body mass (kg year^{-1}). Expected growth rates varied from ca. 0–2.5 cm SCL year^{-1}, depending on the foraging-ground population, which is indicative of slow growth and decades to sexual maturity, since expected size of first-time nesters is ≥80 cm SCL. The expected size-specific growth rate functions for four populations sampled in the south-eastern archipelago displayed a non-monotonic function, with an immature growth spurt at ca. 50–53 cm SCL (~18–23 kg) or ca. 13–19 years of age. The growth spurt for the Midway atoll population in the north-western archipelago occurs at a much larger size (ca. 65 cm SCL or 36 kg), because of slower immature growth rates that might be due to a limited food stock and cooler sea surface temperature. Expected age-at-maturity was estimated to be ca. 35–40 years for the four populations sampled at the south-eastern end of the archipelago, but it might well be > 50 years for the Midway population. The Hawaiian stock comprises mainly the same mtDNA haplotype, with no differences in mtDNA stock composition between foraging-ground populations, so that the geographic variability in somatic growth rates within the archipelago is more likely due to local environmental factors rather than genetic factors. Significant temporal variability was also evident, with expected growth rates declining over the last 10–20 years, while green turtle abundance within the archipelago has increased significantly since the mid-1970s. This inverse relationship between somatic growth rates and population abundance suggests a density-dependent effect on somatic growth dynamics that has also been reported recently for a Caribbean green turtle stock. The Hawaiian green turtle stock is characterised by slow growth rates displaying significant spatial and temporal variation and an immature growth spurt. This is consistent with similar findings for a Great Barrier Reef green turtle stock that also comprises many foraging-ground populations spanning a wide geographic range.

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Introduction

The green sea turtle (*Chelonia mydas*) is a threatened marine turtle species with a broad pan-tropical distribution and distinct regional population substructures (Bowen et al. 1992). Green turtles are the most abundant large, long-lived marine herbivores (Bjorndal 1997) and have a long history of human exploitation for meat and eggs (Parsons 1962; Frazier 1980; Witzell 1994). Many green turtle stocks in the Pacific region are in serious decline (Seminoff 2002), with the populations resident in Great Barrier Reef and Hawaiian waters representing some of the few remaining stocks with apparently viable
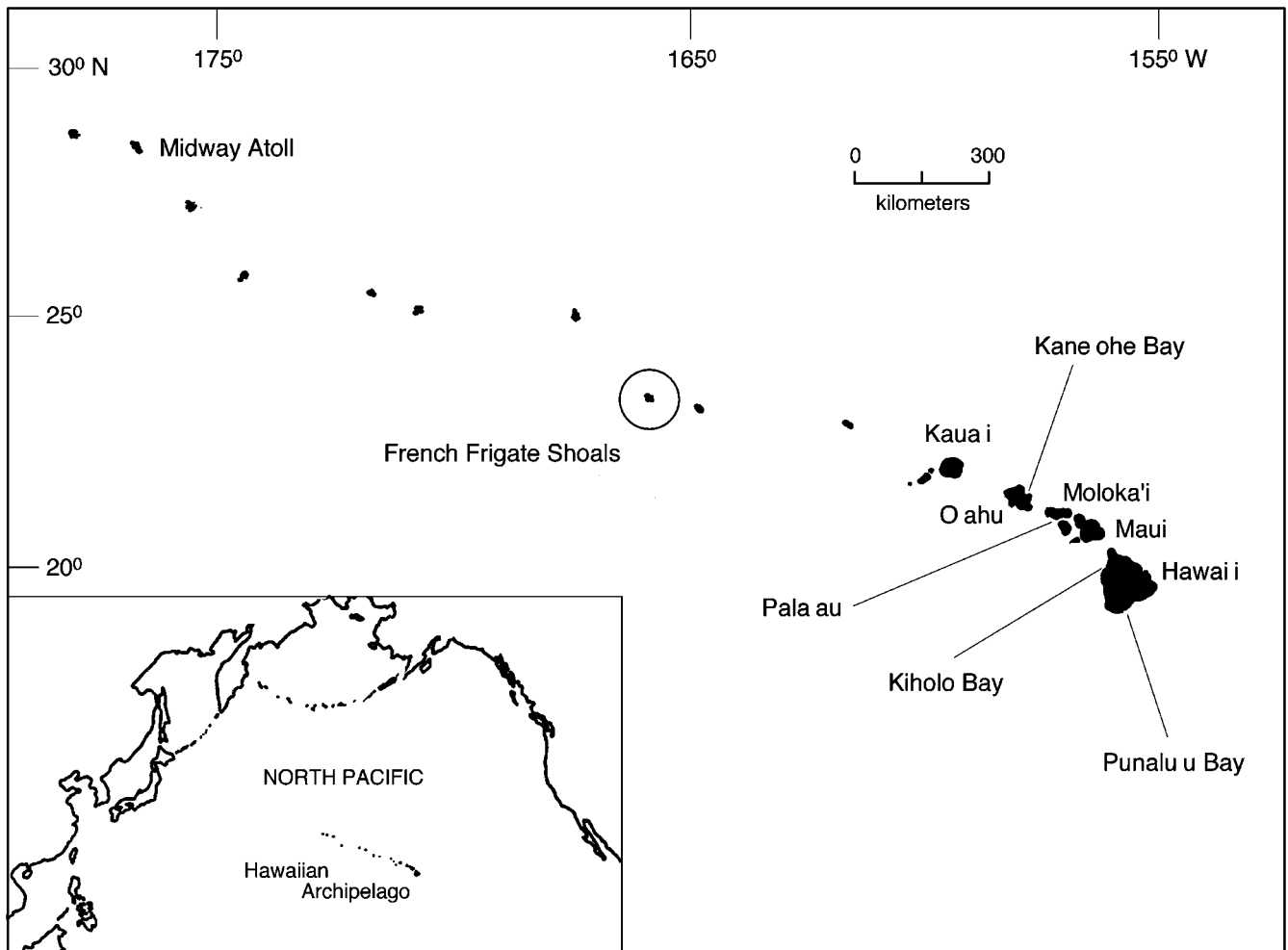
Fig. 1 *Chelonia mydas*. Location of the foraging-ground study sites for the Hawaiian genetic stock of green sea turtles resident in the Hawaiian Archipelago. The major rookery of this stock is at French Frigate Shoals located in the middle of the Hawaiian Archipelago

breeding populations (Chaloupka and Limpus 2001; Balazs and Chaloupka 2004).

A sound knowledge of the green turtle's somatic growth dynamics is essential for developing a better understanding of sea turtle population dynamics, especially when stocks are exposed to various anthropogenic hazards (Chaloupka 2002, 2004). The somatic growth dynamics of the green turtle are not well known (Chaloupka and Musick 1997); however, some recent studies provide important findings concerning environmentally induced temporal variability in growth (Limpus and Chaloupka 1997) and growth variation due to stock-specific differences (Bjorndal et al. 2000; Seminoff et al. 2002). A major source of growth variability that has received little attention is spatial or geographic variability within the same sea turtle genetic stock (Chaloupka et al. 2004).

The Hawaiian green turtle genetic stock comprises a spatially disjunct metapopulation, with numerous coral reef and coastal foraging grounds within the Hawaiian

Archipelago, which comprises 132 islands and reefs spanning 9° of latitude or ca. 2400 km (Fig. 1). Juvenile green turtles recruit to these foraging grounds from ca. 35 cm straight carapace length (SCL) onwards after pelagic development in the northern Pacific Ocean (Balazs 1982; Zug et al. 2002). The duration of this oceanic developmental phase (see Bolten 2003) is estimated to be ca. 6 years or more for Hawaiian green turtles (Zug et al. 2002). There is some permanent dispersal of immature green turtles between various nearby habitats and, in some cases, longer distance dispersal occurs when the immature turtle moves permanently to suitable coastal or neritic habitat elsewhere within the archipelago (Balazs 1980, 1996; Balazs et al. 2000b; Balazs, unpublished data).

Adult female turtles resident in these foraging grounds then migrate every few years to nest mainly at French Frigate Shoals (Balazs 1976), located in the middle of the archipelago (Fig. 1). Apparently there was also some nesting of green turtles at the south-eastern end of the archipelago prior to European settlement (Balazs 1985). The green turtles resident in Hawaiian waters comprise mainly one distinct genetic stock, but occasionally green turtles from the East Pacific stock are recorded in Hawaiian waters (Balazs, unpublished data).

Green turtles from the Hawaiian genetic stock are found only within the Hawaiian Archipelago (Balazs 1976; Dutton 2003), and so they are only exposed to a very low risk of incidental capture in pelagic longline fisheries operating in the North Pacific (Dutton et al. 1997). Exposure to local inshore fisheries, including recreational fisheries, occurs, but the incidental capture in these fisheries has not been investigated so far.

We present here a comprehensive statistical analysis of the temporal and spatial or geographic growth dynamics of green turtles resident at five major foraging grounds of the Hawaiian genetic stock (Fig. 1). The analysis provides a basis for better understanding of the temporal growth dynamics of a metapopulation that spans a considerable geographic range in the central northern Pacific Ocean. This information has particular relevance for modelling the long-term viability of green turtle stocks subject to anthropogenic hazards and for developing a better understanding of the effect of ecological processes on sea turtle population dynamics (Chaloupka and Musick 1997; Chaloupka 2002, 2003, 2004).

Materials and methods

Data set and sampling design

The data set comprised 1149 growth records for carapace size of 680 green turtles (Table 1) captured in five Hawaiian Archipelago foraging grounds in a long-term and spatially extensive capture–mark–recapture program (Balazs 1976, 1982; Balazs et al. 1994, 1998, 2000a, 2000b, 2004; Brill et al. 1995). The foraging-ground samples were from Midway Atoll, Kane'ohe Bay (O'ahu), Pala'au (Moloka'i), and from the island of Hawai'i at Kiholo Bay and Punalu'u Bay (Fig. 1). The data set also comprised 448 body mass growth records for turtles captured in the Kiholo and Punalu'u Bay foraging-ground populations (Table 1).

Midway is a small coral atoll at the north-western end of the Hawaiian Archipelago, with seagrass and algal habitat suitable for green turtle foraging (Balazs et al. 2004). Kane'ohe Bay is a large coastal algal and partial seagrass habitat on the island of O'ahu (Brill et al. 1995; Balazs et al. 2000a). Pala'au is an expansive coastal algal

and partial seagrass habitat on the island of Moloka'i (Balazs et al. 1987, 1998). Kiholo Bay is a small coastal algal habitat on the western side of the island of Hawai'i (Balazs et al. 2000b), while Punalu'u Bay is a small coastal algal habitat on the eastern side of the island of Hawai'i (Balazs et al. 1994). Details of the study sites and the Hawaiian Archipelago can be found in Balazs (1976, 1980, 1982).

The annual sampling periods varied between the five foraging grounds and ranged from 13 to 25 years (Table 1). Capture and recapture was undertaken using several methods including tangle set-nets, bullpen or pound nets, scoop nets, hand capture from small boats or with SCUBA. Additionally, some turtles were captured by hand while basking ashore at Kiholo, Punalu'u and Midway. More details of the capture, handling, measurement and tagging methods for this study can be found in Balazs (1982) and Balazs et al. (1998). Prior to 1996, turtles were double-marked with uniquely coded Inconel alloy flipper tags, but from 1996 onwards all turtles were double-marked with passive integrated transponder (PIT) tags. Tag loss from this capture–mark–recapture program is negligible (Balazs 1980; Balazs et al. 1998, 2000a, 2000b). Chaloupka and Musick (1997) provide a review of sea turtle tagging issues and potential sources of tag loss (see also Balazs 1999).

The data included growth records spanning the post-oceanic phase from ca. 28 to 95 cm SCL (or ca. 5–75 kg), with a variable proportion of turtles within each foraging ground recaptured on two or more annual sampling occasions. Hence, the implicit sampling design was mixed longitudinal sampling, which confounds year and cohort effects, since age was unknown for all individuals (Chaloupka and Musick 1997). Age can be known here only as years at large since recruitment from the oceanic developmental phase to the neritic development phase in coral reef or coastal habitats.

Capture–recapture profiles recorded for each turtle included the following: (1) carapace size recorded to the nearest millimetre as straight carapace length (cm SCL) at first capture and any subsequent recaptures using a high precision metal tree calliper marked in 0.1 cm intervals (or mass to the nearest 0.5 kg), (2) year of first capture and (3) the years at large since first capture or previous recapture. Straight line carapace length was defined as the straight line distance measured with a tree

Table 1 *Chelonia mydas.* Demographic summary of the 680 green turtles (1149 growth records) resident in five geographically separate foraging grounds of the Hawaiian genetic stock used to estimate somatic growth functions. There were 448 growth records for mass derived from the 246 individual turtles sampled from the Kiholo Bay and Punalu'u Bay populations that were weighed. Size and mass metrics are given as the number of turtles in each sample, with the number of growth records in *parentheses* (*SCL* straight carapace length)

	Foraging ground sample				
	Midway	Kane'ohe Bay	Pala'au	Kiholo Bay	Punalu'u Bay
Size (cm SCL)	20 (20)	142 (178)	172 (198)	240 (500)	106 (253)
Mass (kg)	–	–	–	160 (272)	86 (176)
Sampling period	1978–2001	1989–2001	1983–1998	1980–2000	1976–2000

calliper between the nuchal scute and the greatest extension of the post-central scutes. More details of the size and mass measurement protocols used in this capture–mark–recapture (CMR) study were described in Balazs (1980). Only turtles with recapture intervals ≥12 months were included to minimise measurement error on growth rate estimation, irrespective of whether it was for body size (cm SCL) or body mass (kg). Recapture intervals ranged from 1 to 13 years, with the median recapture interval for the various foraging-ground samples ranging from 1.5 to 3 years.

Absolute growth rates were derived from the CMR profiles for each foraging-ground sample, with negative or zero growth rates included, since these are part of the measurement error (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997). A summary of the 1149 green turtle growth records within each of the foraging grounds for the 680 individual turtles is given in Table 1—there were 448 body mass records for 246 of the turtles recorded for two of the five foraging-ground populations.

Statistical modelling approach

We used the following two-stage statistical modelling approach to model green turtle growth behaviour within each foraging ground (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997): (1) a robust non-parametric regression model for each foraging-ground sample was fitted to the absolute growth rate data (size or mass) 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 (but not the mass-specific function) using a difference equation and a fourth-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 modelling approach without any recourse to size-based growth analogues. More details of this approach can be found in Chaloupka and Limpus (1997), Limpus and Chaloupka (1997), Bjorndal et al. (2000), Seminoff et al. (2002) and Chaloupka et al. (2004).

The growth rate predictors (covariates) used here were year, mean size (cm SCL) or mass (kg), and recapture interval (years). Not all these covariates were used for the Midway Atoll sample, which was too small to enable temporal effects to be evaluated. Sex has also been used as an informative covariate in other sea turtle studies (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Chaloupka et al. 2004), but could not be determined for all individuals in this study. 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, the year effect is imprecise because not all growth increments were for a duration of 1 year and only 1 year. Recall that the median recapture interval ranged from 1.5 to 3 years, depending on the foraging-ground sample.

Nonetheless, the year covariate as defined here is a useful proxy of the year effect and should be included, as it is a sampling design constraint inherent in CMR programs (Chaloupka and Musick 1997). The mean size covariate is the arithmetic mean of the carapace size at first capture or previous recapture and then any 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 to 13 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 1149 individual body length growth records (or 448 mass-based growth records) and the growth rate predictors was modelled in the first stage of the two-stage procedure using a GAM or generalised additive modelling approach (Hastie and Tibshirani 1990). GAM enables robust analysis of regression models with non-linear covariate functional form and non-normal error terms. The GAM regression models used comprised: (1) an identity link, since no other response transformation was necessary; (2) a robust quasi-likelihood error function to minimise outlier effects on parameter estimates; and (3) flexible cubic smoothing splines to model any non-linear functional form between growth rates and the covariates (year, mean size, recapture interval). A quasi-likelihood error function is very general, depending only on an empirical mean–variance relationship derived from the data itself, and is useful in accounting for potential correlated error inherent in mixed longitudinal data (McCullagh and Nelder 1989). Where possible, the non-linear functional form was approximated by a simpler parametric form, such as a quadratic polynomial, to simplify model fit.

The models were fitted here using the gam() function in SPLUS (Hastie 1993), although these same models can be readily fitted using the vgam() supplementary library (Yee and Wild 1996) in R (Ihaka and Gentleman 1996). Local regression models (Loader 1999) were used to help support interpretation of some of the GAM models, especially to estimate the non-linear year effect on growth rates on the original growth rate scale (cm SCL year^{-1}) rather than on the centred GAM scale (see "Results"). Local regression models enable a non-linear

functional form for each growth rate predictor to be estimated like the GAM models, but, unlike GAM models, local regression models are not additive in the predictors and thus are more difficult to interpret in terms of the fit of each predictor (Hastie 1993; Loader 1999). On the other hand, local regression models are derived using the original response variable scale rather than the centred GAM form, which is more difficult to interpret. GAM and local regression modelling approaches are used here in a complementary way to help derive robust and interpretable estimates of the growth rate functional forms. These local regression models were fitted using the locfit() library (Loader 1999) for either SPLUS or R.

The GAM fit summary used here comprises two parts arranged in a tabular format for ease of reporting and interpretation: (1) an estimate of the contribution of each covariate to the model fit using t-ratio statistical inference and (2) an estimate of the non-linearity for each continuous covariate (non-parametric term) using non-parametric F-ratio tests. A more detailed discussion of the GAM approach, rationale for its use in sea turtle growth modelling and the summary format used here were given elsewhere (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Bjorndal et al. 2000).

Results

The GAM non-parametric regression model fits for the five foraging-ground population samples given the size-based growth metric are summarised in Table 2. The model fits for the Kiholo Bay and Punalu'u Bay populations given the mass-based growth metric are summarised in Table 3. Except for the Midway Atoll sample, each model comprised one response variable (absolute growth rates in either carapace length or body mass) and three growth predictors (mean size or mass, mean year, recapture interval). The Midway sample was too small with insufficient sampling years to warrant the inclusion of any covariates other than mean recapture size. The non-linear functional form could be replaced with a quadratic polynomial form for the Kiholo Bay population sample without any loss of model fit, so this parametric form for the relationship between expected growth rates (cm SCL) and mean recapture size was used in the model (Table 2).

The GAM regression models were adequate fits to the data, indicated by small residual deviances relative to residual degrees of freedom and adequate non-parametric R^2 values given the relatively small sample

Table 2 *Chelonia mydas*. Summary of generalised additive modelling (identity link, robust quasi-likelihood error, cubic smoothing splines or a quadratic polynomial function for body size) fitted to body size growth rates for the five-foraging ground populations. The (linear) and (quad) terms for the Kiholo Bay sample are the two terms in a polynomial function fitted to mean size to replace a cubic smoothing spline [*ase* asymptotical standard error; *npar* non-parametric (non-linear) effects; *df* degrees of freedom; *n.s.* not significant; *Prob(F)* based on npar *df* and residual deviance *df*; *SCL* straight carapace length]. A significant npar *F* means the covariate was non-linear. If the *t*-test for a covariate is not significant then the nonpar *F*-test for non-linearity is irrelevant

Parameter	Estimate	ase	*t*-ratio	Prob(*t*)	Non-linear effects (non-parametric)		
					npar *df*	npar *F*	Prob(*F*)
Midway Atoll, body size (cm SCL)							
Constant	0.4835	0.4524	1.07				
Mean size	0.0051	0.0074	0.68	n.s.	2.0	2.88	$P < 0.05$
(Null deviance = 15.68, null *df* = 19, residual deviance = 7.66, residual *df* = 15.9, R^2 = 0.58)							
Kane'ohe Bay, body size (cm SCL)							
Constant	−46.1385	71.8346	−0.64				
Mean size	−0.0189	0.0095	−1.99	$P < 0.05$	3.0	16.65	$P < 0.05$
Mean year	0.0246	0.0361	0.68	n.s.			
Recapture interval	0.0271	0.0643	0.42	n.s.			
(Null deviance = 346.2, null *df* = 177, residual deviance = 248.3, residual *df* = 169.9, R^2 = 0.28)							
Pala'au, body size (cm SCL)							
Constant	105.1472	37.2078	2.82				
Mean size	−0.0283	0.0062	−4.54	$P < 0.05$	3.0	4.75	$P < 0.05$
Mean year	−0.0511	0.0187	−2.72	$P < 0.05$	2.9	1.38	n.s.
Recapture interval	0.0242	0.0266	0.91	n.s.			
(Null deviance = 168.4, null *df* = 197, residual deviance = 123.2, residual *df* = 185.1, R^2 = 0.27)							
Kiholo Bay, body size (cm SCL)							
Constant	46.3408	18.4452	2.51				
Mean size (linear)	−0.2638	0.6921	−0.38				
Mean size (quad)	−4.5752	0.6893	−6.64	$P < 0.05$			
Mean year	−0.0225	0.0092	−2.43	$P < 0.05$	3.0	9.58	$P < 0.05$
Recapture interval	0.0076	0.0109	0.69	n.s.			
(Null deviance = 345.9, null *df* = 499, residual deviance = 253.3, residual *df* = 489.1, R^2 = 0.27)							
Punalu'u Bay, body size (cm SCL)							
Constant	232.3364	24.4598	9.49				
Mean size	−0.0883	0.0046	−19.07	$P < 0.05$	3.0	25.57	$P < 0.05$
Mean year	−0.1129	0.0122	−9.22	$P < 0.05$	3.0	9.51	$P < 0.05$
Recapture interval	−0.0192	0.0285	−0.67	n.s.			
(Null deviance = 405.1, null *df* = 252, residual deviance = 127.1, residual *df* = 240.1, R^2 = 0.69)							

Table 3 *Chelonia mydas*. Summary of generalised additive modelling (identity link, robust quasi-likelihood error, cubic smoothing splines) fitted to body mass growth rates for the Kiholo Bay and Punalu'u Bay populations [*ase* asymptotical standard error; *npar* non-parametric (non-linear) effects; *df* degrees of freedom; *n.s.* not significant; *Prob(F)* based on npar *df* and residual deviance *df*]. A significant npar *F* means the covariate was non-linear. If the *t*-test for a covariate is not significant then the nonpar *F*-test for non-linearity is irrelevant

Parameter	Estimate	ase	*t*-ratio	Prob(*t*)	Non-linear effects (non-parametric)		
					npar *df*	npar *F*	Prob(*F*)
Kiholo Bay, body mass (kg)							
Constant	157.6149	34.3309	4.59				
Mean mass	0.0361	0.0071	5.11	$P < 0.001$	2.9	7.98	$P < 0.001$
Year	−0.0786	0.0172	−4.57	$P < 0.001$	3.0	11.73	$P < 0.001$
Recapture interval	0.0081	0.0267	0.30	n.s.			
(Null deviance = 429.6, null *df* = 271, residual deviance = 270.9, residual *df* = 259.2, $R^2 = 0.37$)							
Punalu'u Bay, body mass (kg)							
Constant	647.5368	155.3787	4.17				
Mean mass	−0.1237	0.0203	−6.10	$P < 0.001$	2.9	4.25	$P < 0.01$
Mean year	−0.3203	0.0778	−4.12	$P < 0.001$	2.9	9.44	$P < 0.001$
Recapture interval	−0.0040	0.1625	−0.03	n.s.			
(Null deviance = 4033.7, null *df* = 175, residual deviance = 2233.6, residual *df* = 163.2, $R^2 = 0.45$)							

sizes. However, there was still significant variability remaining in the growth data for all five populations, indicating that other factors such as sex and individual variability were also important, but were not accounted for in these models. Sex is not a factor likely to be obtained for most green turtles from these sampled populations in the near future, so it will remain unaccounted. Meanwhile the apparent individual heterogeneity in somatic growth will be explored further elsewhere using a GAMM or generalised additive mixed modelling approach (see Fahrmeir and Lang 2001), although without the inclusion of potentially informative covariates such as sex this still might not result in significantly improved model fits.

Overall, the GAM models suggest that the growth rates (cm SCL year^{-1} or kg year^{-1}) were size or mass specific and year dependent (Tables 2, 3; Figs. 2, 3, 4, 5). However, it is important to recall that the sampling design was mixed longitudinal with unknown age, so the models cannot account for any bias due to confounding year and cohort effects (Chaloupka and Musick 1997). Recapture interval was not a significant covariate affecting growth variability for any of the populations, irrespective of whether the growth metric was carapace size (Table 2; Fig. 3c, f, i, l) or body mass (Table 3; Fig. 5c, f).

Size-specific growth

The GAM models for body length indicate that mean carapace size (cm SCL) had a significant effect on expected growth rates (cm SCL year^{-1}) for all five foraging-ground population samples (Table 2). Moreover, the mean size growth rate predictor was significantly non-linear for all five populations, reflecting a distinct immature growth spurt as shown in Fig. 2 for the Midway Atoll sample and in Fig. 3a, d, g, j for the Kane'ohe Bay, Pala'au, Kiholo Bay and Punalu'u Bay population samples, respectively. Note that there is a significant difference in the *y*-axis scale between Fig. 2 and Fig. 3. This is because covariate function plots for a GAM fit (see Figs. 3, 5) are centred on a response scale (growth rate per year) by subtracting a weighted mean to ensure valid pointwise 95% confidence bands and comparison between covariates (Hastie and Tibshirani 1990). While essential for analytical purposes, centred plots are more difficult for the user to decode on the original response scale. Therefore, to aid reader interpretation, the expected or mean size-specific growth rate function for each foraging ground was rescaled back to the original growth rate metric by adding the constant shown in Table 2 for each of the five sampled popula-
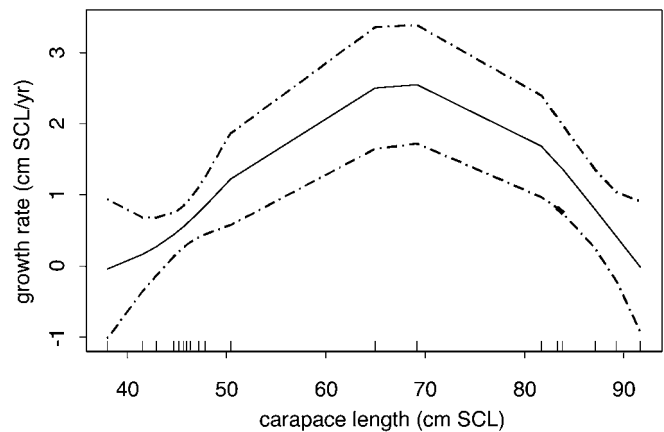
Fig. 2 *Chelonia mydas*. Graphical summary of the GAM (generalised additive modelling) model fit for straight carapace length growth (cm SCL year^{-1}) for the Midway Atoll foraging-ground population sample conditioned only on mean size. The response variable is shown here on the original growth scale (cm SCL year^{-1}) rather than on the centred GAM scale (see Fig. 3 caption for more details). The expected size-specific growth function is shown by the *solid curve*, while the 95% confidence bands are shown by the *broken curves*. The *vertical bars* on the lower *x*-axis are know collectively as a rug, which shows the data location to emphasise the data scarcity for this sampled population

tions. The expected size-specific growth function for the Midway Atoll population is shown in Fig. 2 on the original scale, while Fig. 4 shows the expected growth functions on the original scale (cm SCL year^{-1}) for the four populations that are shown in Fig. 3 (Kane'ohe Bay, Pala'au, Kiholo Bay, Punalu'u Bay) on the centred GAM scale.

The distinct immature growth spurt for the Midway Atoll turtles occurs at ca. 65 cm SCL, but there were too few data for this population to adequately define the growth spurt size range—given a larger sample size, the growth spurt might well be found to occur at a smaller carapace size. The immature growth spurt occurs at ca. 50 cm SCL for the Kane'ohe Bay and Pala'au populations (Fig. 4a, b) and at ca. 53 cm SCL for the Kiholo Bay and Punalu'u Bay populations (Fig. 4c, d). Overall, the size-specific growth rate functions for these five populations were non-monotonic functions, rising rapidly from post-oceanic recruitment size (ca. 35 cm SCL) to a maximum growth rate of between 1.5 and 2.5 cm SCL year^{-1} at ca. 50–52 cm SCL (south-eastern archipelago samples) or at 65 cm SCL (north-western archipelago), before declining to negligible growth approaching the onset of sexual maturity at a size >80 cm SCL (Figs. 2, 4). All these growth functions are monophasic (Chaloupka and Zug 1997), with a single immature growth spurt indicated by a single growth rate peak at ca. 50–53 or 65 cm SCL, depending on the foraging-ground population—a polyphasic growth function would comprise two or more growth spurts as proposed elsewhere for Kemp's Ridley sea turtle growth dynamics (Chaloupka and Zug 1997).

Mass-specific growth

The GAM models for body mass indicate that mean mass had a significant effect on expected growth rates (kg year^{-1}) for the two foraging-ground population samples (Kiholo Bay, Punalu'u Bay) that had sufficient mass measurements (Table 3). The mean mass growth rate predictor was significantly non-linear for both populations, reflecting an immature growth spurt at ca. 25 kg for the Kiholo Bay population (Fig. 5a) and at ca. 23 kg for the Punalu'u Bay population (Fig. 5d). The mass-specific growth rate functions for both populations are non-monotonic, rising rapidly from post-oceanic recruitment mass (ca. 5 kg) to a maximum growth rate at ca. 23–25 kg, before declining to negligible growth approaching the onset of sexual maturity at a body mass of >65 kg (Fig. 5a, d) or from ca. 80 cm SCL. The length–mass estimates for 209 green turtles sampled from nine foraging-ground populations of the Hawaiian stock are shown in Fig. 6, with a smoothing spline to highlight the underlying curvilinear functional form (solid curve).

Recall that the immature growth spurt for the Kiholo Bay and Punalu'u Bay populations occurred at ca. 53 cm SCL (Fig. 4c, d), which corresponds with ca. 23 kg mass according to the length–mass function

shown in Fig. 6 that was derived from an independent random sample of turtles. Hence, the immature growth spurt derived from the GAM models using either body size (cm SCL) or mass (kg) is shown to occur at a size or mass that is fully consistent with the expected length–mass function for the Hawaiian stock. The growth spurt for the Midway Atoll population, which occurs at ca. 65 cm SCL (Fig. 2), corresponds with a body mass of ca. 36 kg according to the expected length–mass function shown in Fig. 6. Similarly, the growth spurt for the Kane'ohe Bay and Pala'au populations, which occurs at ca. 50 cm SCL (Fig. 4a, b), corresponds with a body mass at ca. 18 kg (Fig. 6).

Temporal variability in growth

The GAM models for body size indicate that mean recapture year had a significant effect on expected growth rates (cm SCL year^{-1}) for the Pala'au, Kiholo Bay and Punalu'u Bay populations (Table 2). A significant year effect indicates significant inter-annual growth variability inferring an environmental influence on immature growth since turtles displayed constant negligible growth following the onset of adult size (Fig. 4). The year effect was not significant for the Kane'ohe Bay population (Table 2; Fig. 3b), probably because of the much shorter sampling period (ca. 10 years) for this population compared to 15–25 years for the Pala'au, Kiholo Bay and Punalu'u Bay populations, where size-based growth rates (cm SCL year^{-1}) have declined significantly since the late 1970s or early 1980s (Fig. 3e, h, k). The year effect was significantly non-linear for the Kiholo Bay and Punalu'u Bay populations located on the island of Hawaii (Fig. 3h, k), while a linear year effect was apparent for the Pala'au population on the island of Moloka'i (Fig. 3e). The year effect for the Kiholo Bay and Punalu'u Bay populations was also derived on the original growth rate scale (cm SCL year^{-1}) rather than the centred GAM scale (Fig. 3h, k), to aid interpretation of the magnitude of the long-term non-linear decline in growth rates since the late 1970s and early 1980s (Fig. 7). This was done using a local regression model (see "Statistical modelling approach" in "Materials and methods") comprising growth rates (cm SCL year^{-1}) as a non-linear function of mean size and mean year, but excluding recapture interval that was shown, using the GAM models, to have no effect on growth rates (Tables 2, 3). The local regression models were also fitted using significant smoothing to highlight the underlying long-term trend compared to the GAM model fits (compare for example Fig. 3h with Fig. 7a for the Kiholo Bay population sample). It is apparent from Fig. 7 that growth rates have declined significantly since the early 1980s for the Kiholo Bay population and especially so for the longer sampled Punalu'u Bay population since the late 1970s. A significant non-linear declining year effect was also apparent using mass-based growth rates (kg year^{-1}) for these two populations, for
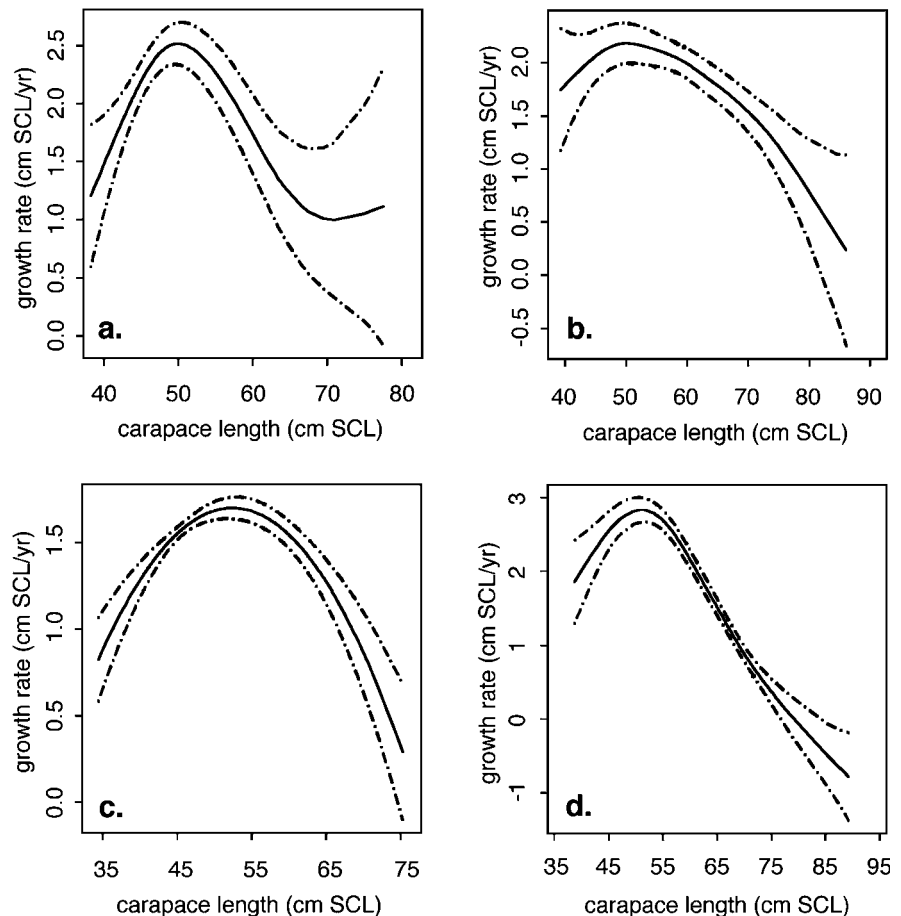
◀
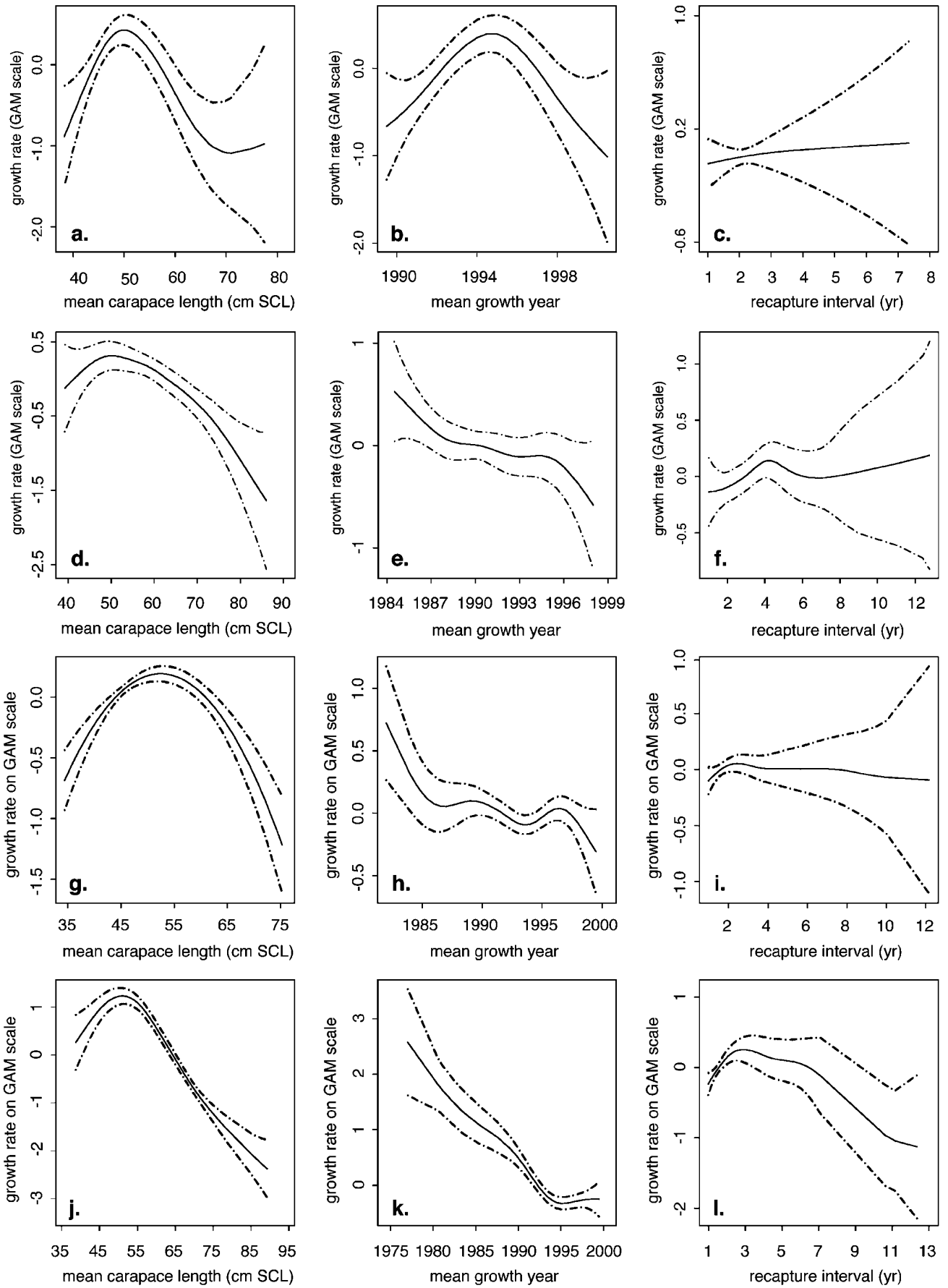
Fig. 3a–l *Chelonia mydas.* Graphical summary of GAM model fits for carapace length growth for the foraging grounds summarised in Table 2, except the Midway atoll sample. Growth models are shown for Kane'ohe Bay (O'ahu) (**a–c**), Pala'au (Moloka'i) (**d–f**), Kiholo Bay (Hawai'i) (**g–i**) and Punalu'u Bay (Hawai'i) (**j–l**). The response variable (growth rate in cm SCL year^{-1}) is shown on the *y*-axis in each panel as a centred smoothed function scale to ensure valid pointwise 95% confidence bands and comparison between the covariates for each population. Covariates shown on the *x*-axis: mean carapace length (**a, d, g, j**), mean growth year index (**b, e, h, k**) and recapture interval in years (**c, f, i, l**). *Solid curve* in each panel is a either a quadratic polynomial (panel a) or a cubic smoothing spline fit (panels b–l) for each covariate conditioned on all other covariates in the model for each foraging-ground sample, while the *broken curves* are pointwise 95% confidence curves around the fit. Recall that mean carapace length refers to the mean of the carapace length (in cm SCL) recorded at first capture (or next recapture) and the next recapture. Mean growth year index refers to the time interval (year fraction) between first capture (or next recapture) and the next recapture; for example if the capture–mark–recapture interval was 1973–1975 (a 2-year interval) then the index would be 1974

which body mass growth measurements were available (Table 3; Fig. 5b, e).

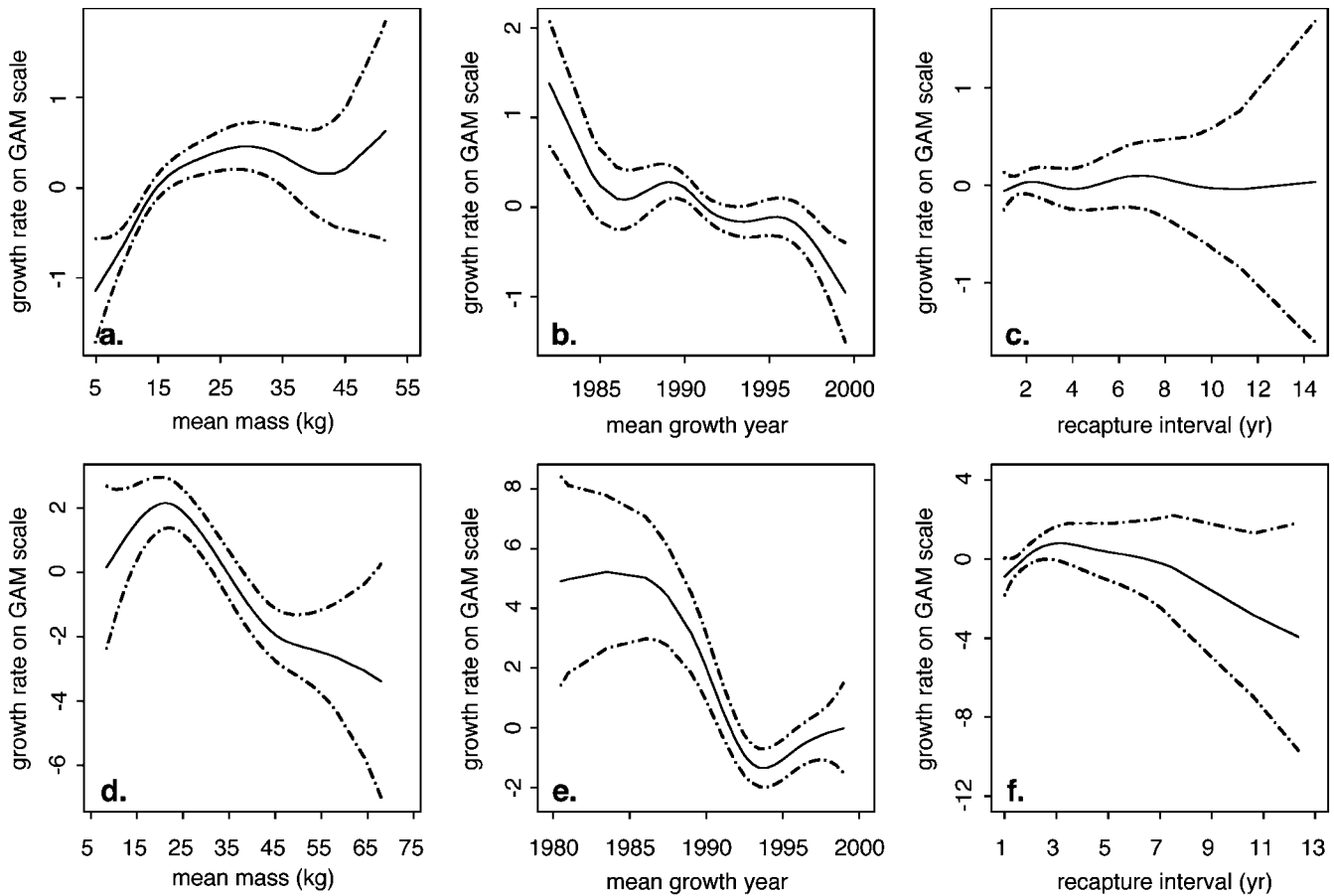## Geographic variability in size- and age-specific growth

The expected size-specific growth rate functions for the five foraging-ground population samples (Figs. 2, 4) are shown together in Fig. 8a to foster comparison between the expected size-specific growth rate functions on the same original growth rate scale (cm SCL year^{-1}). Figure 8a shows that the immature growth spurt for the four populations located at the main Hawaiian Islands of the south-eastern archipelago (Fig. 1) occurs at ca. 50–53 cm SCL ($\sim$18–23 kg) and that turtles from the Punalu'u Bay population on the island of Hawaii grow faster that turtles from the other populations at any comparative size up to ca. 65 cm SCL. From ca. 65 cm SCL onwards, the fastest comparative size-specific growth rates were apparent for the Pala'au population, which also comprised a greater proportion of larger turtles than the other populations. The growth spurt for the Midway Atoll population, located at the north-western end of the archipelago, occurs at a much larger carapace size (ca. 65 cm SCL, $\sim$36 kg) compared to the four other sampled populations (Fig. 8a). However, recall that the sample size for the Midway Atoll population was very small ($N=20$), so that the size-specific growth rate function derived for this population may not be well estimated (Fig. 2).

Since the Midway sample was so small, we have not attempted to derive any size-at-age or age-specific growth function for that population. The expected size-specific growth rate functions for the four other populations shown in Fig. 8a were then integrated
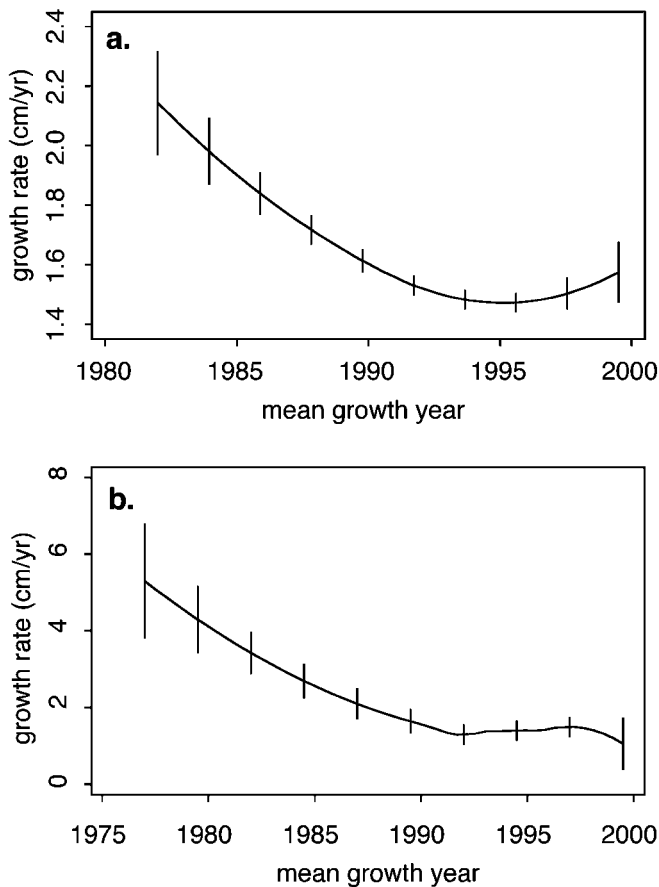
Fig. 4a–d *Chelonia mydas.* Estimated size-specific growth functions on the original growth rate scale (cm SCL year^{-1}) for four of the five green turtle populations summarised in Table 2 and shown in Fig. 3. This is done by adding the constant term from the GAM model to the plots shown in Fig. 3. The growth functions for foraging populations in Kane'ohe Bay (**a**), Pala'au (**b**), Kiholo Bay (**c**) and Punalu'u Bay (**d**) are shown

Fig. 5a–f *Chelonia mydas.* Graphical summary of GAM model fits (Table 3) for body mass growth for Kiholo Bay (**a–c**) and Punalu'u Bay (**d–f**). The response variable (growth rate in kg year^{-1}) is shown on the *y*-axis in each panel as a centred smoothed function scale to ensure valid pointwise 95% confidence bands. Covariates shown on the *x*-axis: mean mass (**a**, **d**) mean growth year index (**b**, **e**), recapture interval in years (**c**, **f**). *Solid curve* in each panel is a cubic smoothing spline fit for each covariate conditioned on all other covariates in the model for each foraging-ground sample, while the *dotted curves* in the panels are pointwise 95% confidence curves around the fit

numerically with respect to time. The resulting monotone growth function is an estimate of the expected size-at-age growth function for each sampled population (Fig. 8b), where age is years at large since recruitment from the oceanic habitat to a neritic or coastal habitat in Hawaiian waters from ca. 35 cm SCL. Note that we refer to years at large since recruitment rather than age. This is because we modelled only the neritic habitat growth phase (35 cm SCL to mature adult, Fig. 8a) without knowing the actual age of turtles since hatching (ca. 5 cm SCL). Therefore, age (i.e. years since hatching) is the sum of the oceanic developmental phase duration plus years at large since recruitment to a neritic 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 oceanic developmental phase for this stock although it is estimated at ca. 6 years (Zug et al. 2002).

Unlike the Pala'au sample, the upper bound of the expected size-at-age functions for the Kane'ohe Bay, Kiholo Bay and Punalu'u Bay samples were not as well defined, because there were too few adults in these
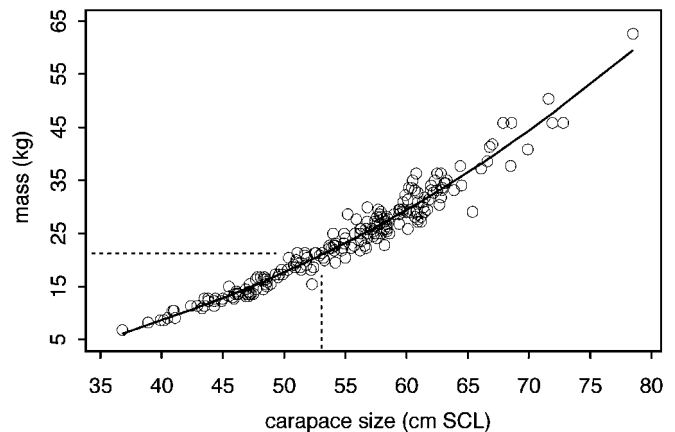
Fig. 6 *Chelonia mydas.* Estimated mass–size function for the Hawaiian green turtle stock drawn from nine different foraging-ground population samples. *Solid curve* shows a smoothing spline fit (degrees of freedom = 5) to 209 data values (*open circles*), see Hastie and Tibshirani (1990) for details of smoothing spline models. *Dashed lines* show that the estimated maximum size-specific growth rate in body mass (kg year^{-1}) at ca. 23 kg corresponds well with the estimated maximum size-specific growth rate in body size (cm SCL year^{-1}) at ca. 53 cm SCL—for instance, compare Fig. 4c with Fig. 5a or Fig. 4d with Fig. 5d

Fig. 7a,b *Chelonia mydas*. Estimated year-specific non-linear growth rate functions (cm SCL year^{-1}) for green turtles in the Kiholo Bay (**a**) and Punalu'u Bay (**b**) population samples, derived from a local regression model fit for two covariates (mean size, mean year) with 95% confidence intervals shown at ten equally spaced intervals—the wider the confidence intervals the fewer the data. Size-specific growth rate functions not shown here as they are similar to the GAM model functions shown in Fig. 3g, j. Note that unlike the GAM models (Fig. 3h, k), the response variable here is modelled on the original growth rate scale, see Loader (1999) for a detailed discussion of local regression models and the locfit() package for fitting such models using either SPLUS or R

samples (Fig. 8b). Nevertheless, the expected size-at-age functions for both the Pala'au and Kane'ohe Bay populations (Fig. 8b) are a close match with the expected size-at-age function derived for the Hawaiian stock using skeletochronological analysis of 104 humeri bones sampled mainly from O'ahu and Moloka'i green turtles (see Fig. 4b in Zug et al. 2002). The expected size-at-age functions (Fig. 8b) were differentiated numerically to derive the expected age-specific growth rate function shown in Fig. 8c for each of those four populations, which define the approximate age of the immature growth spurts evident in Fig. 8a.

Note that the age-dependent growth functions (Fig. 8b, c) for the four foraging-ground populations (Kane'ohe Bay, Pala'au, Kiholo Bay, Punalu'u Bay) were derived without having to resort to using any size-based growth analogue (see Chaloupka and Musick 1997 for detailed discussion). This was done here using

the following three-step process: (1) age-dependent growth functions derived from a GAM model conditioning on the covariates summarised in Table 2, (2) followed by numerical integration of the size-specific growth function (Fig. 8a) to derive the expected size-at-age functions shown in Fig. 8b and (3) followed then by numerical differentiation of the expected size-at-age function (Fig. 8b) to derive the expected age-specific growth rate functions (Fig. 8c).

Discussion

The major findings derived from this long-term and spatially extensive study of green turtle (*Chelonia mydas*) growth dynamics within the Hawaiian Archipelago were: (1) non-monotonic size- or mass-specific growth rate functions reflecting an immature growth spurt; (2) long-term decline in immature growth rates, possibly due to local density-dependent effects; (3) geographical or spatial variability in immature growth rates within the same genetic stock, possibly due to local food quality and supply dynamics; and (4) slow age-specific growth resulting in three to four decades to sexual maturity, depending on the particular foraging-ground population.

Non-monotonic growth rate functions

The green turtle populations sampled from the Hawaiian genetic stock display distinct dome-shaped size- and mass-specific growth rate functions that reflect an immature growth spurt: (1) at ca. 65 cm SCL or equivalently ca. 36 kg for the Midway Atoll population in the north-western archipelago (Fig. 2) or (2) at ca. 50–53 cm SCL or ca. 18–23 kg for the four populations sampled in the south-eastern archipelago (Figs. 4, 5). These dome-shaped or non-monotonic growth rate functions are similar to the size-specific functions shown for four foraging-ground populations sampled from the southern Great Barrier Reef (Australia) genetic stock (Limpus and Chaloupka 1997; Chaloupka et al. 2004). This non-monotonic pattern of size-specific growth has also been shown for a green turtle population resident in waters around the Galapagos Islands in the eastern tropical Pacific (Green 1993), a population resident in the temperate central Gulf of California, Mexico (Seminoff et al. 2002), as well as for several populations resident along the Atlantic coast of Florida, USA (Kubis and Chaloupka, unpublished data).

Green turtles from all these populations hatch at ca. 5 cm SCL and then spend a number of years in an oceanic habitat—estimated to be ca. 5 years for the southern Great Barrier Reef stock (Limpus and Chaloupka 1997) and ca. 6 years for the Hawaiian stock (Zug et al. 2002). Hawaiian green turtles then recruit to a neritic habitat from ca. 35 cm SCL and grow slowly for
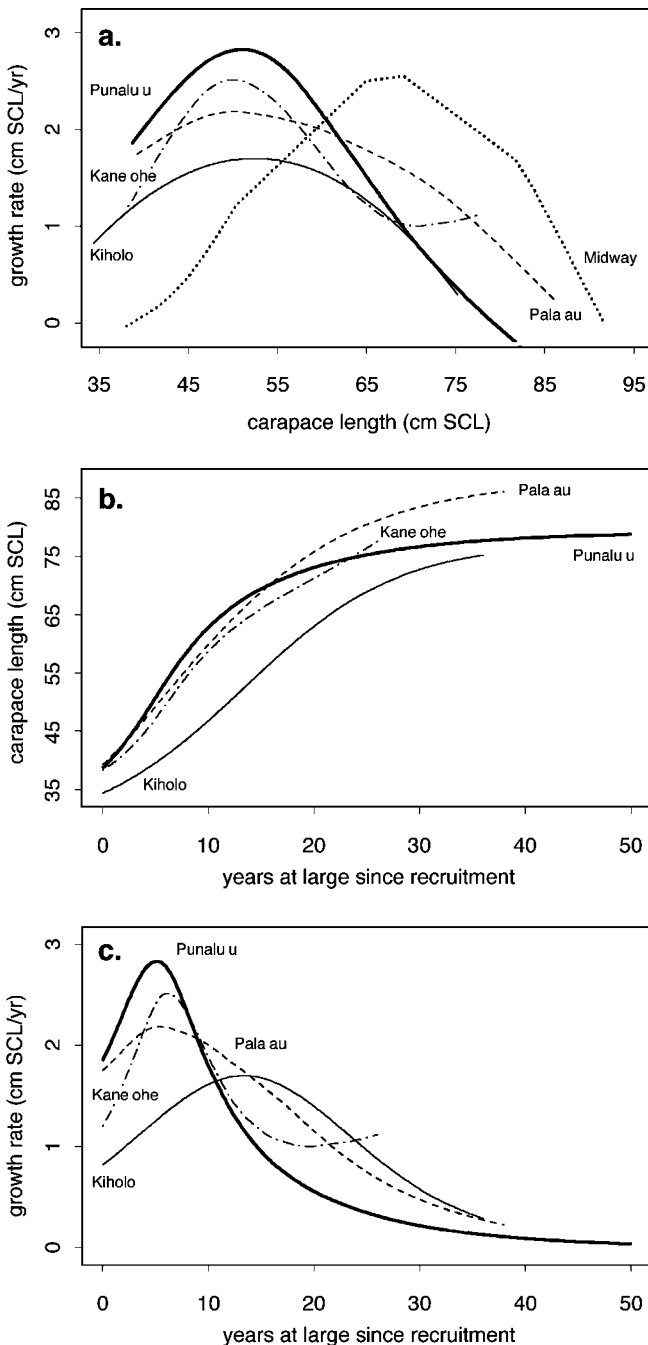
Fig. 8a–c *Chelonia mydas*. **a** Expected size-specific growth curves for green turtles resident in five foraging grounds (Midway Atoll, Kane'ohe Bay, Pala'au, Kiholo Bay, Punalu'u Bay). **b** Size-at-age growth curves for four of the foraging-ground populations, derived using numerical integration of size-specific growth curves in panel a. **c** Age-specific growth curves for the four populations, derived using numerical differentiation of the size-at-age curves in panel b. The size-at-age and age-specific growth curves for the Midway population are not shown as the sample ($N = 20$) was far too small

some time after recruitment. Growth rates then increase rapidly after a number of years in the neritic habitat (immature growth spurt), followed by declining growth rates approaching the onset of sexual maturity at a size

> 80 cm SCL. It is increasingly apparent that many green turtle populations in both the Pacific and Atlantic display this distinct non-monotonic somatic growth pattern, irrespective of whether the stock has been exposed to only limited human exploitation (Great Barrier Reef), or extensively exploited in the past but now protected and well on the way to recovery (Hawaii, Florida) or seriously depleted (Galapagos) and subject to ongoing anthropogenic hazards such as harvesting (Gulf of California). Non-monotonic size-specific growth functions have also been found for other sea turtle species such as hawksbills and loggerheads resident in coastal and coral reef habitats in the Great Barrier Reef region (Chaloupka and Limpus 1997; Chaloupka 2003) and for hawksbills resident in coral reef habitats around Puerto Rico in the Caribbean (Diez and van Dam 2002).

However, non-monotonic growth is by no means universal, since a monotonically declining growth rate function, implying no size-specific growth spurt, was found for a population of immature green turtles resident in waters around the southern Bahamas in the Caribbean (Bjorndal et al. 2000). The green turtles from the Bahamas population display maximum growth rates of ca. 7–8 cm year^{-1} at 30 cm SCL soon after recruitment to the neritic habitat (Bjorndal et al. 2000) compared to a maximum of ca. 2.5 cm year^{-1} long after recruitment at 50 cm SCL for the Kane'ohe Bay population (Fig. 4a), 2 cm year^{-1} at 60 cm SCL for turtles from the southern Great Barrier Reef stock (Limpus and Chaloupka 1997), or ca. 1.5 cm year^{-1} at 85 cm SCL for turtles resident in the temperate waters of the central Gulf of California (Seminoff et al. 2002). The reason for the difference in the size-specific somatic growth pattern between the Bahamas population and elsewhere (Great Barrier Reef, Hawaii, Galapagos, Gulf of California, Florida) remains unknown, but could be due to a high seagrass standing stock and low green turtle density in the Caribbean (Bjorndal et al. 2000).

Sex-specific differences in size-specific growth rate functions for the southern Great Barrier Reef green and hawksbill turtle stocks have been found, whereby females grow significantly faster than males at any comparable size for both species (Chaloupka and Limpus 1997; Limpus and Chaloupka 1997; Chaloupka et al. 2004). It was not possible to determine the sex of most of the 680 green turtles in the current study, so it was not possible to determine whether female Hawaiian green turtles also grow faster than males. Significant sex-specific growth rates were also found for the Bahamas population of immature green turtles, but this effect was most likely due to an age- or sex-biased population structure (Bjorndal et al. 2000). Unfortunately, more general conclusions about sex-specific sea turtle growth rate functions are not possible, as there are no other long-term studies of time-dependent sea turtle growth in which sex was recorded for each individual (Chaloupka and Musick 1997).

Long-term decline in growth rates

The significant long-term decline in size-specific growth rates (cm SCL year^{-1}) found for the Pala'au population on Moloka'i (Fig. 3e) and the Kiholo Bay and Punalu'u Bay populations on the island of Hawaii (Fig. 7) presumably reflects local foraging-ground factors such as food availability and possibly the nutritional quality of the food supply. The long-term decline was also clearly evident in mass-specific growth rates for the Kiholo Bay and Punalu'u Bay populations (Table 3; Fig. 5b, e), where turtle abundance has increased since the mid-1980s (Balazs et al. 1994; Rice et al. 2002). An increase in abundance has also been recorded at Pala'au (Balazs 2000) that corresponds with the declining trend in somatic growth rates for this population (Fig. 3e).

In fact, there has been a substantial increase in abundance throughout the Hawaiian Archipelago of this once seriously depleted stock following cessation of harvesting in the 1970s (Balazs et al. 1993; Balazs and Chaloupka 2004). In other words, it appears that growth rates have decreased in the various foraging-ground populations as the abundance of green turtles has increased throughout the archipelago. There has also been a significant increase in the incidence of terrestrial basking or onshore day-time resting in the main south-eastern islands since the early 1990s (Whittow and Balazs 1985; Balazs 1996; Rice et al. 2002, Balazs et al. 2004). Such behaviour might be one way to increase digestive efficiency given increasing abundance and reduced per capita food supply. The inverse relationship between somatic growth rates and the recovering stock abundance, and the increasing incidence of unusual behaviour such as basking, is suggestive of a density-dependent effect on the somatic growth of immature turtles. A similar inverse relationship between somatic growth rates and population abundance has also been shown recently for a population of immature green turtles resident in coastal habitat around the Bahamas (Bjorndal et al. 2000).

The Pala'au green turtle population is much larger than either the Kiholo Bay or Punalu'u Bay populations (Chaloupka and Balazs, unpublished data), but so is the area of habitat suitable for green turtle foraging. The decline in growth rates in the Pala'au population was linear and ongoing (Fig. 3e), which suggests that carrying capacity has yet to be reached for this population even as the Hawaiian stock recovers. On the other hand, the decline appears to have levelled off since the mid-1990s for the Kiholo Bay and Punalu'u Bay populations (Fig. 7), although the decline has been far greater for the Punalu'u Bay population, perhaps as much as 3 cm SCL since the late 1980s (Fig. 7b). The non-linear decline in growth rates in both the Kiholo Bay and Punalu'u Bay populations suggests that the carrying capacity of these two foraging grounds might have been reached by the mid-1990s. Density-dependent effects on sea turtle demography, including somatic growth dynamics (Bjorndal et al. 2000), are not well understood and

warrant further investigation, especially since density-dependent processes can have a profound effect on long-term stock viability such as increasing stock resilience to harvesting impacts (Chaloupka 2002, 2003, 2004).

Significant temporal variability in somatic growth rates has also been reported for the southern Great Barrier Reef green turtle stock (Limpus and Chaloupka 1997; Chaloupka et al. 2004), which has not been subject to extensive human exploitation (Chaloupka and Limpus 2001). Annual growth rates for immature green turtles in the Hawaiian stock fluctuated in response to major fluctuations in sea surface temperatures for offshore coral reef populations and to major coastal flooding events that caused substantial seagrass loss in coastal foraging grounds. The physiological and ecological mechanisms underlying such environmental effects on the long-term growth dynamics of sea turtles are not well understood, 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 differences in the expected size- and age-specific growth rate functions evident for the five populations sampled from the Hawaiian green turtle genetic stock (Fig. 8a, c). The foraging-ground-specific somatic growth rates result in different expected size-at-age functions (Fig. 8b) and, hence, foraging-ground-specific differences in expected age at maturity (see below). However, the Hawaiian stock comprises mainly the same mtDNA haplotype (Dutton 2003), with no difference in mtDNA stock composition between foraging-ground populations (Leroux et al. 2003; Dutton, personal communication). While individual variation in growth capacity undoubtedly has underlying genetic components, it is more likely that the differences found in growth rates between foraging-ground populations for this stock are most likely a function of environmental factors rather than genetic differences.

Green turtles from the Kane'ohe Bay, Pala'au and Punalu'u Bay populations grew faster at all sizes and ages than turtles from the Kiholo Bay population (Fig. 8a, c). All these populations are located in the south-eastern region of the archipelago (Fig. 1). The differences in somatic growth dynamics between these four populations cannot be attributed to the forage type differences. For instance, the Kiholo Bay and Punalu'u Bay foraging grounds comprise mainly algae rather than seagrass, yet turtles from the Punalu'u Bay population grew faster at all comparable size or ages than turtles from the Kiholo Bay population. The Kane'ohe Bay and Pala'au foraging grounds comprise a mix of algae and seagrass, yet turtles from these two populations grew at similar size-specific rates as the Punalu'u Bay population that forages exclusively on algae (Fig. 8a, c). Nonetheless, it is noteworthy that coastal habitats around O'ahu

and Moloka'i have been colonised recently by an introduced marine alga *Hypnea musciformis* (Russell and Balazs 1994). This alga has now become a significant food source for the green turtles resident in foraging grounds around O'ahu and Moloka'i, such as Kane'ohe Bay and Pala'au (Russell and Balazs 1994).

The slowest comparative size- or age-specific growth rates were found for the Midway Atoll population located in the north-western region of the archipelago. This remote coral reef habitat comprises a mix of seagrass and algae. There are no digestive process differences needed for an algal or seagrass diet although a mixed diet (Midway, Kane'ohe Bay, Pala'au) might lead to lower digestive efficiency (Bjorndal et al. 1991). Yet recall that the Kane'ohe Bay and Pala'au turtles displayed similar growth rates to the algal feeding Punalu'u Bay population (Fig. 8a, c). There is also no known nutritional difference between algal and seagrass diets for green turtles (Garnett et al. 1985), nor any difference in green turtle growth rates between algal and seagrass feeders (Bjorndal 1997). The only apparent environmental difference between the Midway Atoll habitat that supports the slowest somatic growth rates and the other four foraging grounds at the south-eastern end of the archipelago is mean winter sea surface temperature—Midway Atoll is a high-latitude coral reef habitat (Fig. 1) that experiences significantly cooler sea surface temperatures than coastal habitats in the southeast of the archipelago (Juvik and Juvik 1998). Yet green turtles from the southern Great Barrier Reef stock resident in cool temperate foraging grounds grow at comparable size-specific rates to turtles from the same genetic stock resident in tropical coastal seagrass or offshore coral reef algal habitats (Chaloupka et al. 2004).

Caution is also required here as the Midway Atoll sample was very small ($N = 20$), so that the expected size-specific growth rate function shown in Fig. 8a is not well defined—size-specific growth might not be quite as slow compared to the other four sampled populations if a much larger sample of growth rates were to be collected for the Midway Atoll population. Given these considerations, it is most likely that the geographic variation evident for the Hawaiian stock, which spans a wide geographic range, is due to local population density effects and fluctuations in the local forage stock resulting in differences in forage availability and nutrient uptake rates, irrespective of the forage type (Bjorndal 1997). A similar conclusion was made to explain the geographic variability in somatic growth rates for foraging-ground populations comprising the southern Great Barrier Reef green turtle stock, which also spans a wide geographic range (Limpus and Chaloupka 1997; Chaloupka et al. 2004). On a more local geographic scale, Diez and van Dam (2002) also found somatic growth rate variability between several small populations of hawksbill turtles (presumably from the same genetic stock) resident in Puerto Rican waters, which they attributed to variation in habitat quality and food availability.

Age-specific growth and expected age at maturity

An important consequence of geographic variation in somatic growth rates will be significant variation in size and possibly age at sexual maturity for individual turtles within the Hawaiian stock. The age-specific growth functions in Fig. 8c show that the immature growth spurt occurs ca. 7 years since recruitment to the neritic habitat for the Kane'ohe Bay, Pala'au and Punalu'u Bay populations and 13 years since recruitment for the Kiholo Bay population. Assuming that the oceanic phase duration for the Hawaiian stock is ca. 6 years (Zug et al. 2002), then it is estimated that the immature growth spurt occurs ca. 13 years of age for the Kane'ohe Bay, Pala'au and Punalu'u Bay populations and ca. 19 years of age for the Kiholo Bay population. Growth then slows rapidly following the immature growth spurt, and so turtles from this Hawaiian stock take many years to reach sexual maturity, irrespective of the foraging ground.

Green turtles resident in Hawaiian (Fig. 8c) and Great Barrier Reef waters (Limpus and Chaloupka 1997; Chaloupka et al. 2004) grow significantly slower for the first 6–7 years following post-oceanic recruitment to the neritic habitat than do green turtles in the southern Bahamas, and this growth difference might be due to differences in abundance and quality of the available forage supply (Bjorndal et al. 2000). Green turtles from the Bahamas stock have an early but short period of rapid immature growth (Fig. 6 in Bjorndal et al. 2000), while turtles from the Great Barrier Reef (Fig. 3 in Limpus and Chaloupka 1997) and Hawaiian stocks (Fig. 8c) have a later but longer period of rapid immature growth (growth spurt), so that the expected size-at-age functions are similar for the three green turtle stocks (cf. Fig. 8b and Figs. 3 and 6 in Limpus and Chaloupka 1997 and Bjorndal et al. 2000, respectively).

It is common practice to use size-at-age curves, as shown in Fig. 8b, to estimate the mean or expected age at sexual maturity. The difficulty in using such growth functions for this purpose is the lack of conclusive growth criteria to indicate the 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 ≥80 cm SCL for the Hawaiian foraging-ground populations (Fig. 8a). Given this size criterion and the assumed oceanic phase duration of 6 years (Zug et al. 2002), the expected age at maturity was estimated to be ca. 35 years for the Pala'au and Kane'ohe Bay populations (Fig. 8b), which is consistent with the estimate of >30 years derived by Zug et al. (2002). Recall also that the expected size-at-age functions (Fig. 8b) are consistent with the expected size-at-age function derived for the Hawaiian stock using skeletochronology on stranded turtles from the islands of O'ahu and Moloka'i (Zug et al. 2002). It is encouraging that these two different approaches (growth rate modelling based on CMR data and skeletochronology)

result in very similar size-at-age functions for the Hawaiian green turtle stock.

The expected age at maturity was estimated to be ca. 40 years for the Punalu'u Bay population and ≥40 years for the Kiholo Bay population. The Midway Atoll sample was too small to derive a robust estimate of the size-at-age function, but it could be >50 years if the expected size-specific growth rate function shown in Fig. 8a was any reasonable estimate of size-specific growth for this population. Clearly, there is significant variation in age at maturity for some of the populations that comprise the Hawaiian genetic stock of green turtles, which has major implications for simulation modelling of the long-term viability of this stock (see Chaloupka 2002, 2004).

This range of expected age at maturity (35–50+ years) for the Hawaiian green turtle stock is consistent with the range of age-at-maturity estimates for several foraging-ground populations comprising the southern Great Barrier Reef green turtle genetic stock, which also spans a wide geographic range (Limpus and Chaloupka 1997; Chaloupka et al. 2004). We are not aware of any other long-term studies of the somatic growth dynamics of sea turtles that comprise multiple foraging-ground samples from the same genetic stock spanning a wide geographic range. However, significant variability in expected age at maturity was proposed by Diez and van Dam (2002) for local hawksbill turtle populations resident in waters around Puerto Rico in the Caribbean.

Fibropapillomatosis

Fibropapillomatosis, a tumour-forming disease, is present in immature green turtles resident in some Hawaiian foraging grounds (Aguirre et al. 1998; Work et al. 2003). It is widely held that the disease could cause depressed growth rates for turtles resident in Hawaiian waters (Balazs et al. 1998; Zug et al. 2002), and many green turtles that wash ashore in the southern Hawaiian islands are emaciated and have the disease (Work et al. 2003). However, the foraging-ground-specific differences in somatic growth dynamics shown here for the Hawaiian green turtle stock (Fig. 8) do not appear to be a function of either the presence or severity of fibropapillomatosis.

Only a low incidence of the disease has been recorded for the Midway population (Balazs et al. 2004), which is located at the north-western end of the Hawaiian Archipelago (Fig. 1). Recall that the Midway Atoll population was found here to have the slowest somatic growth of the sampled foraging populations at any comparative size, at least up to ca. 65 cm SCL (Fig. 8a). At the south-eastern end of the archipelago around the island of Hawaii (Fig. 1), there has been no incidence of fibropapillomatosis recorded for the Kiholo Bay population (Balazs et al. 2000b) and only a very low incidence has been recorded for

the Punalu'u Bay population (Balazs et al. 1994). The Kiholo Bay population displayed the slowest growth at any size or age compared to the three other foraging-ground populations sampled around the main Hawaiian islands (Kane'ohe Bay, Pala'au, Punalu'u Bay). On the other hand, a high incidence of the disease has been recorded for both the Kane'ohe Bay and Pala'au populations (Brill et al. 1995; Balazs et al. 1998, 2002a). Yet the Kane'ohe Bay and Pala'au populations displayed both size- and age-specific growth functions (Fig. 8a–c) that were similar to the Punalu'u Bay population, which has a very low incidence of the disease.

Furthermore, the Kane'ohe Bay, Pala'au and Punalu'u Bay populations all displayed faster growth rates at any size compared to the Kiholo Bay population (Fig. 8a), which has no recorded incidence of the disease. Moreover, Balazs et al. (2000a), in an earlier study, found no difference in the expected growth rates between a small sample of tumoured and non-tumoured turtles resident in Kane'ohe Bay. It is apparent from both the current study and the study of Balazs et al. (2000a) that it is unlikely that fibropapillomatosis has a significant effect on population-specific somatic growth dynamics. However, this is not a strong inference, so that this issue should be investigated further using robust statistical modelling procedures and an appropriate data set comprising afflicted and non-afflicted turtles within each sampled population. This would be a useful extension of the growth modelling study presented here.

In summary, the Hawaiian green turtle stock is characterised by slow size- and age-specific growth rates, displaying significant geographic and temporal variation, and a distinct immature growth spurt (Fig. 8). These somatic growth characteristics are similar to those found for a Great Barrier Reef green turtle stock that also comprises many foraging-ground populations spanning a wide geographic range.

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