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SHORT NOTE

Using growth rates to estimate age of the sea turtle barnacle *Chelonibia testudinaria*

Sophie A. Doell[1] · Rod M. Connolly[1] · Colin J. Limpus[2] · Ryan M. Pearson[1] ·
Jason P. van de Merwe[1]

Abstract Epibionts can serve as valuable ecological indicators, providing information about the behaviour or health of the host. The use of epibionts as indicators is, however, often limited by a lack of knowledge about the basic ecology of these 'hitchhikers'. This study investigated the growth rates of a turtle barnacle, *Chelonibia testudinaria*, under natural conditions, and then used the resulting growth curve to estimate the barnacle's age. Repeat morphometric measurements (length and basal area) on 78 barnacles were taken, as host loggerhead turtles (*Caretta caretta*) laid successive clutches at Mon Repos, Australia, during the 2015/16 nesting season. Barnacles when first encountered ranged in size from 3.7 to 62.9 mm, and were recaptured between 12 and 56 days later. Fitting the growth measurements of these barnacles to a von Bertalanffy growth curve, we estimated the age of these barnacles as a function of their size. Length growth rate decreased over time in a nonlinear fashion, while basal area growth rate showed a linear relationship with age. The average estimated age of barnacles at first capture was approximately 6 months (barnacle length 30.3 ± 1.8 mm). The largest and oldest individual had a length of 62.9 mm when first measured, and was estimated to be 642 days old. The finding that *C. testudinaria* may live for up to 2 years, means that these barnacles may serve as interesting ecological indicators over this period. In turn, this information may be used to better understand the movement and habitat use of their sea turtle hosts, ultimately improving conservation and management of these threatened animals.

Introduction

Sea turtles are known to host diverse communities of plants and invertebrate animals (Caine 1986; Kitsos et al. 2005; Robinson et al. 2017). Past analyses of the size, abundance, and/or species composition of the organisms present on an individual turtle have provided insight into the health (e.g. Flint et al. 2009), habitat use (e.g. Pfaller et al. 2014), and movement (e.g. Killingley and Lutcavage 1983) of the host turtle. Hitchhiking barnacles present a particularly interesting epibiont, since their presence or absence, as well as the chemical information stored in their shells may be useful to obtain knowledge about the biology, life history and movement patterns of the host turtle (e.g. Hayashi and Tsuji 2008). Yet limiting the use of these barnacles as indicator species is the lack of basic life history information, such as growth rates and age estimates.

Understanding the growth of commensal barnacles could, for example, allow inferences about the length of stay in either neritic or oceanic habitats (e.g. Killingley and Lutcavage 1983). This could be achieved through the analysis of the size of commensal acorn barnacles (e.g. *Chelonibia* spp.), that tend to attach in coastal waters, versus the size of pedunculate barnacles (e.g. *Lepas* spp.), that are more oceanic in origin (Newman and Abbott 1980). Similar analyses of the relationship between size and lifespan of the barnacle could provide insights into the

✉ Jason P. van de Merwe
j.vandemerwe@griffith.edu.au

[1] Australian Rivers Institute-Coast and Estuaries, and School of Environment, Griffith University, Gold Coast, QLD 4222, Australia

[2] Threatened Species Unit, Department of Environment and Heritage Protection, Brisbane, QLD, Australia

scute sloughing frequency of sea turtles, with implications for understanding the community succession of hitchhiking biota, and also potentially improving satellite telemetry practices (e.g., to maximise the longevity of applied tags). Furthermore, chemical analyses of barnacle shell layers could allow turtles to be placed in time and space as they travel through water bodies of varying temperatures and/or salinities (e.g. Killingley and Lutcavage 1983). For example, Detjen et al. (2015) analysed isotopic signatures (in particular δ^{18}O) from the green sea turtle barnacles (*Platylepas* sp.) and found that barnacles could serve as proxies in regional movement studies. Ultimately, better understanding the growth rates of the hitchhikers on sea turtles could allow for the addition of a temporal component to each of the above analyses, thus furthering the understanding of these commensal relationships, and the conservation and management of threatened sea turtles.

Barnacles in the genus *Chelonibia* are commensal to sea turtles, manatees and crabs (Frick and Ross 2001; Frick et al. 1998; Zardus and Hadfield 2004; Zardus et al. 2014). Genetic analyses of *Chelonibia* barnacles has established that *Chelonibia patula, C. manati* and *C. testudinaria* are the same species (all now recognised as *C. testudinaria*) exhibiting host-specific phenotypic plasticity (Cheang et al. 2013; Zardus et al. 2014). In addition, the *C. testudinaria* found on sea turtles are morphologically distinct from those found on other living hosts (Ewers-Saucedo et al. 2015), and should be treated independently when investigating morphometrics, such as size and growth rate. *C. testudinaria* are most frequently encountered on the head, carapace and plastron of sea turtles, but are also found on the scales of the flippers and skin (Frick and Ross 2001). The persistence of *C. testudinaria* on its host is unknown, but is believed to be influenced by a number of external factors, including the frequency with which the host turtle sloughs its scutes and the active removal of epibionts by the host (Frick et al. 2000).

Two studies have previously looked at the growth rates of *C. testudinaria* attached to a range of substrates, including loggerhead turtle scutes, crab carapaces, slate tiles and Plexiglas, in both laboratory and field settings (Ewers-Saucedo et al. 2015; Sloan et al. 2014). These studies found that many factors can influence barnacle growth rate, including host origin, substrate type, laboratory or field conditions, and seasons. Both Sloan et al. (2014) and Ewers-Saucedo et al. (2015) presented linear growth rates, with *C. testudinaria* growing 4.28 mm^2 day^{-1} in basal area and 0.07 mm day^{-1} in rostro-carinal length. However, for acorn barnacles generally, shell formation is faster in young individuals, slowing progressively with age (Bourget and Crisp 1975). This trend matches the generalised animal growth model described by von Bertalanffy (1951). Indeed, Eckert and Eckert (1987) established the utility of this method for pedunculate barnacles by modelling the von Bertalanffy

growth of barnacles commensal to leatherback sea turtles (*Dermochelys coriacea*).

In this study, we used non-linear von Bertalanffy analysis to assess the natural growth rates of *C. testudinaria* attached to loggerhead turtles in the South Pacific population. This was done to provide an understanding of the growth rate of barnacles over time, and to provide an age estimate for barnacles at any given length. Understanding growth rates of *C. testudinaria* on turtles in this way will allow researchers to provide a temporal reference in future studies investigating the ecology of these barnacles and/or their host turtles.

Methods

Study site

Loggerhead turtles were encountered while nesting during the 2015/16 nesting season (November to February) at Mon Repos (24º48′S, 152º26′E), Queensland, Australia. This beach records more nesting loggerhead turtles than any other in the South Pacific.

Measuring barnacle size

Repeat photographs of barnacles attached to the head and carapace of nesting loggerhead turtles were taken throughout the nesting season, whenever the host was re-encountered and the same barnacle could be identified. A total of 78 barnacles from 41 loggerhead turtles (one to five barnacles on each turtle) were photographed. Barnacles covered in mud and algae were not used due to the potential impact of these coverings on growth rates. Similarly, barnacles on the midline of the carapace were avoided as they were likely to be removed by other researchers for the purpose of measuring turtle carapace lengths. A metric scale was placed next to each photographed barnacle to provide a size reference. Only barnacles on the head and carapace of the turtles were photographed, and its attachment position was recorded as head, or front/middle/back of carapace. To ensure repeated measures of the same barnacles, the position of each was recorded relative to the scute pattern of the host turtle (e.g. V4 for 4th ventral scute).

The rostro-carinal lengths (length through the centre of the barnacle from the rostral plate to the carinal plate) and basal areas of all photographed barnacles were measured using Image J software (v 1.49, Rasband 2015), using the adjacent metric scale as a size reference. For each barnacle, starting length (length when first encountered), length at recapture and the time between captures (to the

Fig. 1 Example photographs of two barnacles photographed 27 days apart. Left: 12-Dec-2015. Right: 8-Jan-2016. The larger barnacle recorded an increase in length of 2.8 mm, and a 13% increase in basal area over this time. Typical rostro-carinal length measurement shown in right panel
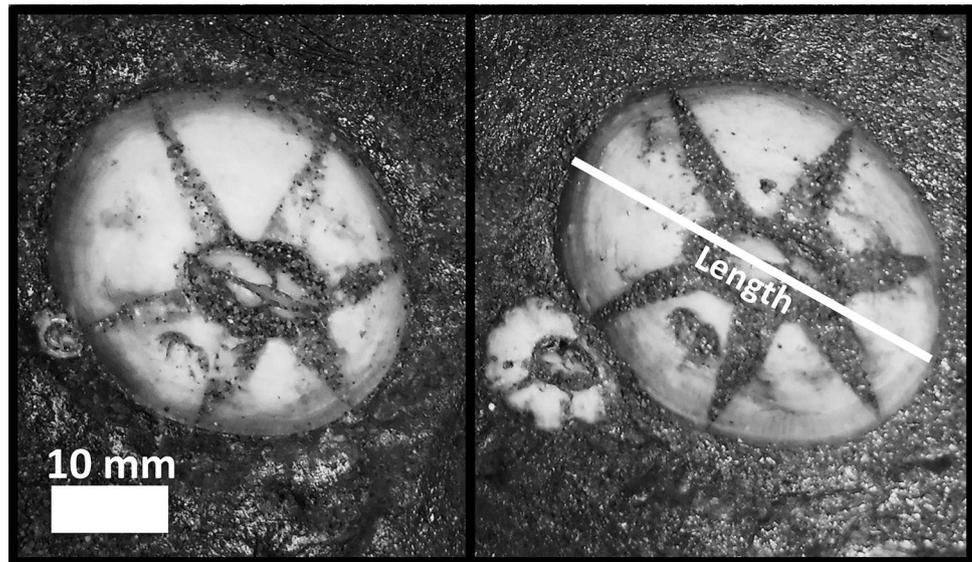
nearest whole day) were recorded (see Fig. 1 for example photographs).

Growth rate and age estimates

For length growth rates, a non-linear regression was analysed in R Studio (R Studio Inc, v1.0.136), using starting length, length at recapture and interval between measurements, to provide a maximum size (a) and intrinsic growth rate (k) for this sample of barnacles. As described by Eckert and Eckert (1987), the von Bertalanffy growth equation (Eq. 1) was then solved for b (relationship between the barnacle maximum size and the size at settlement) at the time of settlement ($t = 0$), where L was set to 0.634 mm—the mean length of the final larval stage (the cyprid) of *Chelonibia testudinaria* (Zardus and Hadfield 2004). With a, b and k solved in this way, a relationship between barnacle length (L) and time (t) was established using the von Bertalanffy growth equation (Eq. 1), from which the age of a barnacle of any given length could be estimated

$$L = a\left(1 - be^{-kt}\right) \tag{1}$$

Also, as described by Eckert and Eckert (1987), the predicted length at recapture (L_r) was calculated for each barnacle using the Fabens equation (Eq. 2):

$$L_r = a - \left(a - L_c\right)e^{-kt} \tag{2}$$

where a and k are the parameters from the von Bertalanffy growth model; t is the interval between measurements in days; L_r is the predicted length at recapture; and L_c is the observed length at first capture. To assess the accuracy of the von Bertalanffy model, the predicted and observed recapture lengths were correlated.

Given that all barnacles were measured on turtles during the same nesting season, it was expected that host behaviour and/or water physicochemistry had minimal influence on barnacle growth rate. However, to test for any effect of host turtle on barnacle growth rates, the von Bertalanffy growth analysis was repeated twice using different subsets of the full dataset, where only one barnacle from each turtle was included in the model ($N = 41$). While these alternative models provided similar relationships between length and age, the parameters described did not align well with our understanding of the biology of the species. For example, the two alternate models estimated parameter 'a' (maximum asymptotic length) as either smaller than, or more than twice the length (for the upper 95% CI), of the largest barnacle encountered. The model using the full dataset ($N = 78$) provided an estimate of maximum asymptotic length (69.3 mm) more similar to the largest barnacle we have encountered (length = 66.6 mm) during this study and > 400 barnacles collected from foraging and nesting loggerhead turtles in concurrent (unpublished) studies.

The alternative models also provided considerably wider 95% confidence limits and reduced predictability (i.e. lower r^2 when comparing predicted vs observed recapture lengths), compared to the model incorporating all the data. We also noted considerable variation in barnacle growth rates within turtles, with barnacles on the same turtle growing both faster and slower than predicted from the model. These observations further indicated minimal effect of turtle host on the barnacle growth rate. We thus considered individual barnacles to be independent, and presented the model described by the full dataset ($N = 78$).

The potential effect of the position of the barnacle on the turtle (head, front, middle or back carapace) on growth rate was tested using the difference between observed and

predicted values. The residuals for this metric were not normally distributed, and transformations failed to satisfy this assumption of ANOVA. Therefore, positions were compared using the non-parametric equivalent, Kruskal–Wallis test. Alpha was set to 0.05 for all tests.

To assess the change in basal area growth rate over time, the age of each barnacle at first capture was calculated using the starting length in Eq. 1 to solve for t (age in days), and then correlated with the basal area at first capture.

Results

Barnacle rostro-carinal lengths ranged from 3.7 to 62.9 mm (mean $\pm$ SE = 30.3 $\pm$ 1.8) when each barnacle was first encountered (start length). Maximum length at recapture was 66.6 mm. The mean rostro-carinal length was 30.3 mm (SE 1.8 mm). The period between photographs ranged from 12 to 56 days. The basal area growth rates for 75 barnacles from 39 loggerhead turtles were measured. Three barnacles were excluded from this analysis because photographs did not allow accurate assessment of the basal area. The starting basal area of barnacles ranged from 9.5 to 2535 mm^2.

Age estimation

The non-linear regression provided values for the parameters a (asymptotic size) and k (intrinsic growth rate) as 69.26 $\pm$ 6.35 (mean $\pm$ SE) and $3.68 \times 10^{-3} \pm 6.23 \times 10^{-4}$ (mean $\pm$ SE), respectively. The 95% confidence intervals for each parameter were: k, upper = 0.0049, lower = 0.0025; a, upper = 87.12, lower = 59.37. Using the mean value for a in Eq. 1, and the size at settlement as described in the methods, provided a value for the b parameter of 0.9907. This resulted in a *Chelonibia testudinaria* specific von Bertalanffy growth relationship between barnacle length and time (Eq. 3; Fig. 2), from which barnacle age could be calculated for any given barnacle length. From this relationship, the age at first capture of barnacles measured in this study was calculated to range from 12.4 to 642 days (approx. 21 months). The average age of the sampled barnacles was 181 days (SE 15 days)

$$L = 69.26\left(1 - 0.9907e^{-0.003678t}\right) \tag{3}$$

There was a significant correlation ($p < 0.001$, $r^2 = 0.97$) between predicted and observed recapture lengths (Fig. 3). Kruskal–Wallis analysis detected no difference in growth rates between barnacles encountered on different positions on the turtle ($H = 4.89$; $df = 3$; $p = 0.180$).

There was a significant linear correlation (Fig. 4; $p < 0.001$; Pearson's $R = 0.992$; $r^2 = 0.985$) between age and basal area at first capture, with a linear basal area growth rate of 4.86 mm^2 day^{-1} (Table 1).

Discussion

The results of this investigation into the growth rate of *C. testudinaria* are consistent with those of previous studies, with the growth rate (in length) of acorn barnacles decreasing with size, and thus also with age (e.g. Bourget and Crisp 1975). For the two studies that have investigated linear growth rates (length and area) of *C. testudinaria*

Fig. 2 von Bertalanffy growth curve describing the relationship between rostro-carinal length and age of *Chelonibia testudinaria* attached to loggerhead turtles in the southwest Pacific Ocean (solid line) with 95% confidence intervals (dashed lines)
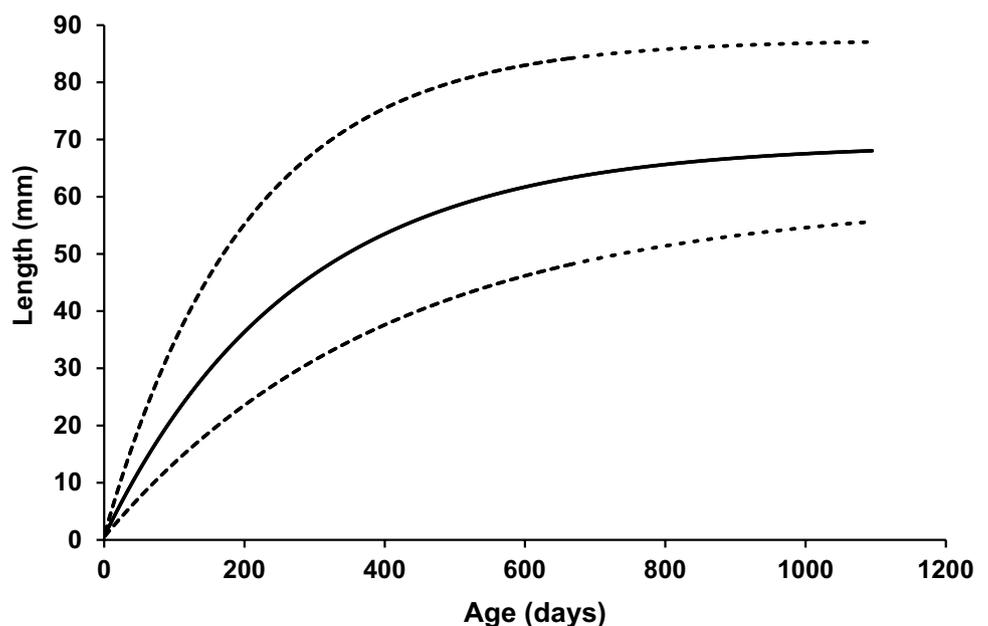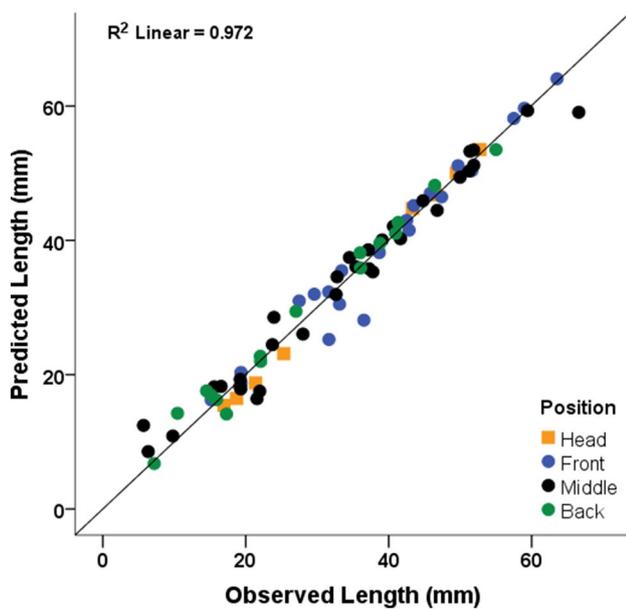
Fig. 3 Linear correlation of observed length at recapture versus the length predicted by the model for all barnacles measured. Colours represent the position in which the barnacle was growing on the turtle carapace, and shapes separate samples from the head vs carapace
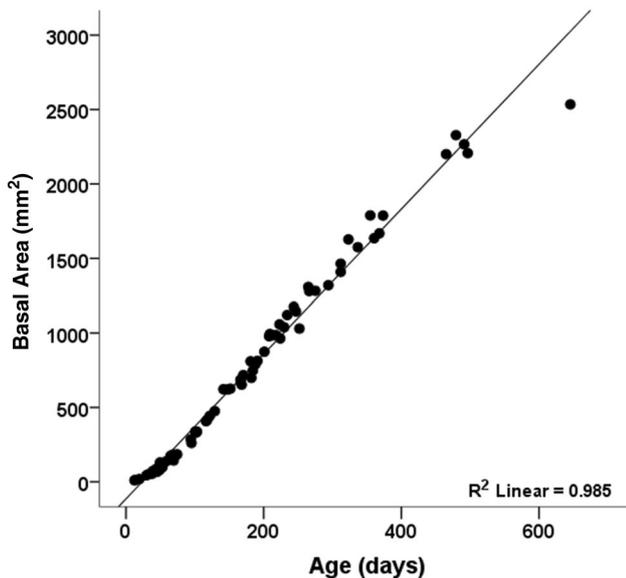

Fig. 4 Linear relationship between age (days) and basal area (mm^2) for 75 barnacles. Age estimated using von Bertalanffy growth model

(Sloan et al. 2014; Ewers-Saucedo et al. 2015), variations in their reported growth rate estimates can be explained by our growth curve (Table 1). For example, the current study identified a linear relationship between age and basal area at a rate of 4.86 mm^2 day^{-1}, which is comparable to the rate of 4.28 mm^2 day^{-1} reported by Sloan et al. (2014) for

the first four weeks of growth post-settlement. Similarly, the median length growth rate reported by Ewers-Saucedo et al. (2015) was 0.074 mm day^{-1}, not markedly different to our average linear growth rate calculated using all the barnacles (0.097 mm day^{-1}; Table 1). However, given their barnacles were recaptured over large intervals (up to one year), rates closer to those reported by Ewers-Saucedo et al. (2015) can be replicated by our curve by averaging daily growth rates over a similar period, in this case, through months 7–18, 0.072 mm day^{-1} (Table 1). While the size distribution of the barnacles used by Ewers-Saucedo et al. (2015) was not clearly reported for the capture–recapture analysis we are comparing to, it is possible that they measured a higher proportion of larger barnacles, and thus skewed the growth rate towards this smaller value.

Barnacles from this study and those from Ewers-Saucedo et al. (2015) were obtained from *C. testudinaria* attached to loggerhead turtles, while growth estimates from Sloan et al. (2014) came from *C. testudinaria* attached to inanimate substrata. This may have affected food supply and respiration, and hence influenced growth. However, despite these differences in growth conditions and morphology, growth rates predicted by the von Bertalanffy growth model in the present study closely resemble those described by Sloan et al. (2014) and Ewers-Saucedo et al. (2015). These similarities in growth rates suggest that environmental conditions such as current flow, food availability and the habitat of the host do not appear to affect growth rates in *C. testudinaria*.

This in-depth knowledge about the growth rates of commensal barnacles such as *C. testudinaria* can prove beneficial in understanding the ecology of the host turtles. The size of barnacles (as a proxy for age), for example, may provide an indication of the frequency of scute sloughing in the host, and allow for estimates of the age of the underlying keratin layer. This information could prove useful in terms of improving satellite tagging practices (e.g., for estimating the length of time a transmitter might stay attached, which would guide the programming to maximise battery life). Estimation of the age of underlying keratin layers could also improve the ecological contribution of studies analysing the chemical composition (e.g. stable isotopes) of host scute layers (e.g. Vander Zanden et al. 2010). In addition, the number of barnacles on the turtle, as well as their size (and age), may assist in estimating the time of reduced activity of the host turtle, as a proxy for the timing of health deterioration (e.g. Flint et al. 2009).

The ability to estimate *C. testudinaria* age from their size may also allow for assessments of habitats used by the host turtles. These barnacles settle most commonly in coastal areas (Newman and Abbott 1980), thus, by estimating the age of attached barnacles, it may be possible to identify when a turtle moved from the ocean to settle in the neritic environment. Furthermore, age estimations may prove

Table 1 Comparison of methods and findings for field studies measuring growth rates of *Chelonibia testudinaria*

Metric	Current study				Sloan et al. (2014)	Ewers-Saucedo et al. (2015)
N	78				83	38
Recapture interval (days; mean ± SE)	29.2 (± 1.19)				28[a]	Unknown < 365[b]
Size range (length; mm)	3.7–62.9				0–23	0.5–60[c]
Period for growth rate estimates (months)	Total (< 21)	1–12	7–18	10–21	Total (< 1)	Total (< 12)
Length						
Growth rate (linear; mm day^{-1})	0.097[d]	0.141[d]	0.072[d]	0.052[d]	N/A	0.074[e]
Relationship	Non-linear (von Bertalanffy)					Linear
Area						
Growth rate (mm^2 day^{-1})	4.86[f]				4.28	N/A
Relationship	Linear				Linear	

[a] Recapture interval was weekly, but reported growth rates were averaged across 4 weeks given linear rate

[b] Ewers-Saucedo et al. 2015 measured barnacles from five turtles; three recaptured in same season, two recaptured in following season. Unreported interval but likely to be considerably longer than the current study

[c] Size range represents range across the entire study, range in specific capture-recapture on loggerhead turtle component not reported

[d] Mean from predicted growth rates per day based on von Bertalanffy model

[e] Median rate, no clear mean offered for capture-recapture method on loggerhead turtles

[f] Slope of linear fit line between observed basal area and modelled von Bertalanffy age calculation

particularly useful for analytical studies using the barnacle shell, where chemical tracers (e.g. stable isotopes) in individual shell layers could be related to varying water temperatures and salinities, and thus provide information about the movement patterns of the host through water bodies of differing characteristics (e.g. Killingley and Lutcavage 1983; Detjen et al. 2015). However, the temporal scale at which barnacles can provide information on host turtle ecology is limited by scute sloughing, with barnacles (and the information they contain) disappearing as scutes are sloughed. Age estimates from this study suggest that *C. testudinaria* can live for up to 21 months, thus potentially providing information on the ecology of the host across one or more nesting seasons. However, the barnacles in this study were all attached to adult female loggerhead turtles, which grow at a slower rate (and hence slough scutes less frequently) compared to juveniles and sub-adults (Bjorndal et al. 2013). More rapid scute sloughing rates in juvenile and sub-adult turtles (during this more rapid growth stage) may reduce the temporal scale at which barnacles can provide ecological information about their hosts.

The growth of barnacles can be affected by the presence of other epibiotic organisms, generally decreasing when covered with other organisms (Barnes 1955). Given barnacles that were covered in algae were not included in our analysis, it is possible that our growth curve will over-estimate the growth rate of individuals exposed to this or another type of stressor. However, this remains untested for *Chelonibia testudinaria*.

Food available to *C. testudinaria* when attached to a turtle may be affected by the turtle's activity level, diet and feeding behaviour. During migration, sea turtles may move over very large distances between their feeding and breeding grounds (Limpus and Limpus 2003), increasing water flow and nutrient availability and thus providing potentially enhanced feeding conditions for barnacles (Trager et al. 1990), which may promote rapid growth. Barnacle growth may change when turtles are at foraging or nesting grounds, due to a potential change in host activity and movement. In case that the growth rate does change during turtle nesting season, this study may have under- or over-estimated the potential growth rates of *C. testudinaria* throughout host migration, but this also remains untested.

Compliance with ethical standards

Conflict of interest The authors declared that they have no conflict of interest.

Ethical approval All barnacles were collected from nesting loggerhead turtles following procedures approved by the Griffith University Animal Ethics Committee under permit ENV/06/15/AEC.

References

Barnes H (1955) The growth rate of *Balanus balanoides*. Oikos 6:109–113

Bjorndal KA, Schroeder BA, Foley AM, Witherington BE, Bresette M, Clark D et al (2013) Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (*Caretta caretta*) in the northwest Atlantic. Mar Biol 160:2711–2721

Bourget E, Crisp DJ (1975) An analysis of the growth bands and ridges of barnacle shell plates. J Mar Biol Assoc UK 55:439–461

Caine EA (1986) Carapace epibionts of nesting loggerhead sea turtles: Atlantic coast of USA. J Exp Mar Biol Ecol 95:15–26

Cheang CC, Tsang LM, Chu KH, Cheng I-J, Chan BKK (2013) Host-specific phenotypic plasticity of the turtle barnacle *Chelonibia testudinaria:* a widespread generalist rather than a specialist. PLoS One 8:e57592

Detjen M, Sterling E, Gómez A (2015) Stable isotopes in barnacles as a tool to understand green sea turtle (*Chelonia mydas*) regional movement patterns. Biogeosciences 12:7081–7086

Eckert KL, Eckert SA (1987) Growth rate and reproductive condition of the barnacle *Conchoderma virgatum* on gravid leatherback sea turtles in Caribbean waters. J Crust Biol 7:682–690

Ewers-Saucedo C, Arendt MD, Wares JP, Rittschof D (2015) Growth, mortality, and mating group size of an androdioecious barnacle: implications for the evolution of dwarf males. J Crust Biol 35:166–176

Flint M, Patterson-Kane JC, Limpus CJ, Work TM, Blair D, Mills PC (2009) Postmortem diagnostic investigation of disease in free-ranging marine turtle populations: a review of common pathologic findings and protocols. J Vet Diagn Invest 21:733–759

Frick MG, Ross A (2001) Will the real *Chelonibia testudinaria* please come forward: an appeal. MTN 94:16–17

Frick MG, Williams KL, Robinson M (1998) Epibionts associated with nesting loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. Herpetol Rev 29:211–214

Frick MG, Williams KL, Veljacic DX, Jackson JA, Knight SE (2000) Epibiont community succession on nesting loggerhead sea turtles, *Caretta caretta*, from Georgia, USA. Science 64:185–188

Hayashi R, Tsuji K (2008) Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*. Ecol Res 23:121

Killingley JS, Lutcavage M (1983) Loggerhead turtle movements reconstructed from ^{18}O and ^{13}C profiles from commensal barnacle shells. Estuar Coast Shelf Sci 16:345–349

Kitsos M-S, Christodoulou M, Arvanitidis C, Mavidis M, Kirmitzoglou I, Koukouras A (2005) Composition of the organismic assemblage associated with *Caretta caretta*. J Mar Biol Assoc UK 85:257–261

Limpus CJ, Limpus DJ (2003) Loggerhead turtles in the equatorial and southern Pacific Ocean: a species in decline. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington DC, pp 199–209

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. Intertidal invertebrates of California. Stanford University Press, Stanford

Pfaller JB, Alfaro-Shigueto J, Balazs GH, Ishihara T, Kopitsky K, Mangel JC, Peckham SH, Bolten AB, Bjorndal KA (2014) Hitchhikers reveal cryptic host behavior: new insights from association between *Planes major* and sea turtles in the Pacific Ocean. Mar Biol 161:2167–2178

Rasband WS (2015) ImageJ. U. S. National Institutes of Health, Bethesda. www.imagej.nih.gov/ij. Accessed 16 Oct 2015

Robinson NJ, Lazo-Wasem EA, Paladino FV, Zardus JD, Pinou T (2017) Assortative epibiosis of leatherback, olive ridley and green sea turtles in the Eastern Tropical Pacific. J Mar Biol Assoc UK 97:1233–1240

Sloan K, Zardus JD, Jones ML (2014) Substratum fidelity and early growth in *Chelonibia testudinaria*, a turtle barnacle especially common on debilitated loggerhead (*Caretta caretta*) sea turtles. Bull Mar Sci 90:581–597

Trager GC, Hwang J-S, Strickler JR (1990) Barnacle suspension-feeding in variable flow. Mar Biol 105:117–127

Vander Zanden HB, Bjorndal KA, Reich KJ, Bolten AB (2010) Individual specialists in a generalist population: results from a long-term stable isotope series. Biol Lett 6:711–714

von Bertalanffy L (1951) Metabolic types and growth types. Am Nat 85:111–117

Zardus JD, Hadfield MG (2004) Larval development and complemental males in *Chelonibia testudinaria*, a barnacle commensal with sea turtles. J Crust Biol 24:409–421

Zardus JD, Lake DT, Frick MG, Rawson PD (2014) Deconstructing an assemblage of "turtle" barnacles: species assignments and fickle fidelity in *Chelonibia*. Mar Biol 161:45–49