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ORIGINAL PAPER

Growth rates of the epibiotic barnacle *Chelonibia testudinaria* reveal habitat use of pre-nesting green turtles in Costa Rica

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Abstract

The barnacle *Chelonibia testudinaria* is arguably the most common and conspicuous epibiont on sea turtles. As evidence suggests that *C. testudinaria* settles on turtles in coastal areas, this barnacle could serve as an indicator of habitat use. The utility of *C. testudinaria* for this purpose is, however, limited by a lack of information on its growth rate. Here, we estimated growth curves for *C. testudinaria* on green turtles (*Chelonia mydas*) nesting on Cabuyal (10° 40 N, 85° 39 W) and Playa Grande/Ventanas (10° 20 N, 85° 51 W) in northwest Costa Rica. Growth rates of 106 barnacles from 38 green turtles were measured during the 2023/24 turtle nesting season and then incorporated into a von Bertalanffy growth model. The mean intrinsic growth rate (rostro-carinal length) was 0.0091 d^{-1} and the asymptotic length was 59.5 mm. We detected a statistically significant effect of beach and turtle identity on growth rates, and growth rates were almost double those reported from *C. testudinaria* on loggerhead turtles in Australia. Our results indicate that barnacle larvae settled a mean of 76 d before turtles begin nesting, and thus pre-nesting turtles likely also inhabit coastal habitats. In addition, we provide the first measurements of barnacle detachment rates in wild sea turtles with 24.1% of barnacles detaching after a single internesting period (9–21 d). Our study reinforces the utility of *C. testudinaria* as indicators of coastal habitat use in sea turtles, although further studies into the variables driving barnacle growth are still required.

Keywords *Chelonia mydas* · Epibiosis · Growth curve · Migration · Von Bertalanffy

Introduction

Sea turtles host a diverse range of epibionts (Robinson and Pfaller 2022), which are organisms living on the external surfaces of other organisms. As epibionts inherently experience the same environmental conditions as their host (Frick and Pfaller 2013), they can reveal habitat use by that host (Casale et al. 2004; Pfaller et al. 2014; Ten et al. 2019). For example, measuring epibiont life-history traits (such as growth, settlement, or survival rates) that are influenced by environmental conditions (such as temperature or salinity) can reveal the previous habitats occupied by the epibiont and, in turn, its host. To this extent, epibionts can provide an inexpensive alternative to more common methods for studying habitat use such as satellite transmitters or biologging devices (Robinson et al. 2023). Currently, however, a lack of basic information on the life-history of sea turtle epibionts limits their use as ecological indicators.

Chelonibia testudinaria, often referred to as the sea turtle barnacle, is arguably the most conspicuous and universally

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present macro-epibiont on sea turtles (Zardus 2021). It is a large acorn barnacle that can reach a diameter of up to 86 mm (Zambrano et al. 2022). While *C. testudinaria* is typically sessile in the adult stage (although see Chan et al. 2021), it passes through six actively swimming and planktonic larval stages before progressing to a cyprid stage during which surface exploration and settlement occurs (Zardus and Hadfield 2004). These planktonic life stages facilitate the settlement of larval *C. testudinaria* on any potential hosts that they opportunistically encounter while in the water column.

Previous studies have indicated that *Chelonibia* spp. spawn and settle in coastal waters (Casale et al. 2004, 2012; Ten et al. 2019). In addition, once a barnacle has settled on a host, it may survive and grow for several months (Doell et al. 2017). Consequently, the presence of *C. testudinaria* could indicate that the host turtle has previously passed through coastal habitats. Based on this information, Ten et al. (2019) proposed that knowledge of both barnacle size and growth rates could be used to calculate when a turtle has previously inhabited coastal waters. Such information could be particularly interesting when looking at nesting turtles as this provide information on the pre-nesting migration and habitat use.

To measure barnacle growth rates on sea turtles, the same turtle must be encountered multiple times over a barnacle's lifespan. A practical way to achieve this is to measure barnacles on nesting turtles, since sea turtles return to the same general area to nest and lay multiple clutches over a nesting season (Miller 1997). To date, however, growth rates of *C. testudinaria* have been predominantly measured on sea turtles under captive conditions (e.g., Bromwell 1991; Chan et al. 2021) or when attached to non-living substrates (e.g., Perspex sheets or dead turtle carapaces: Sloan et al. 2014; Ewers-Saucedo et al. 2015). Only a single published study has measured growth rates of *C. testudinaria* on wild sea turtles and this was on loggerhead turtles (*Caretta caretta*) nesting in Australia (Doell et al. 2017). Consequently, it is uncertain if growth rates of *C. testudinaria* are consistent across different host taxa or geographic locations.

In many barnacle species, growth is strongly influenced by temperature and food availability (e.g., Inatsuchi et al. 2010). Specifically, warmer water temperatures are often correlated with faster growth, but only within each species' tolerable temperature range and when food availability is not limited (Sanford and Menge 2001; Goehlich et al. 2024). In turn, food availability is often dependent on water flow dynamics as barnacles are typically filter feeders (Sanford et al. 1994). Specifically, low water velocities reduce encounter rates with suspended food particles but high water velocities can exceed the mechanical stiffness of barnacle cirri, causing them to buckle and render the capture of food impossible (Miller 2007; Nishizaki and Carrington 2015).

For epibiotic barnacles, water flow dynamics can change dramatically across a host's body (Ten et al. 2025). Because of this, *C. testudinaria* barnacles typically settle on the anterior and central vertebral scutes of the carapace where the current flow is greatest (Pfaller et al. 2008). There is even evidence to suggest that *C. testudinaria*, which has the unique capacity among barnacles to actively translocate after settling on the carapace, will move toward areas of higher current flow (albeit at movement rates of <0.3 mm d^{-1}; Chan et al. 2021). Such an adaptation may be particularly essential considering that *C. testudinaria* is a passive filter feeder and thus cannot feed in the absence of a current (Lane et al. 2021).

If temperature and food availability influence growth rates of *C. testudinaria*, we can hypothesize that *C. testudinaria* growth rates will vary based on both local environmental conditions and host taxa. For example, green turtles during the internesting period (IP; the time elapsed between consecutive nesting events) typically inhabit warmer temperature waters than loggerhead turtles (Robinson et al. 2022). Internesting green turtles seem also to exhibit a greater tendency towards active behaviors than loggerhead turtles (Enstipp et al. 2011; Fossette et al. 2012), which increases water flows and consequently, facilitates increased feeding opportunities for epibiotic barnacles (Lane et al. 2021). Consequently, we might expect *C. testudinaria* on internesting green turtles to grow faster than those on loggerhead turtles. In addition, green turtles seem to spend more time self-cleaning, typically observed as rubbing their carapace against hard substrate, than loggerhead turtles (Bjorndal 2003). Thus, barnacles on green turtles may detach more frequently than on loggerhead turtles although no studies to date have examined detachment rates for epibiotic barnacles on sea turtles.

Here, we had five key objectives: (1) to measure growth rates of *C. testudinaria* on green turtles nesting on the northwest Pacific coast of Costa Rica, (2) to compare the calculated growth rates to those on loggerhead turtles in Australia as reported in Doell et al. (2017), (3) to examine whether growth rates of *C. testudinaria* on green turtles are influenced by water temperature, nesting beach, barnacle position on the turtle carapace and host turtle identity, (4) to estimate time of barnacle settlement relative to the onset of the green turtle nesting season, and (5) to quantify detachment rates from the carapace of green turtles.

Materials and methods

We conducted this study at two green turtle nesting sites in Northwest Costa Rica: (1) Cabuyal (10° 40 N, 85° 39 W) and (2) Playa Grande/Ventanas (10° 20 N, 85° 51 W). Sampling was conducted between October 2023 and March 2024 to coincide with the green turtle nesting season in the area (Santidrián Tomillo et al. 2015). Cabuyal is a 1.4 km sandy beach, within the Gulf of Papagayo. Playa Grande/Ventanas are 3.6 km and 1.0 km sandy beaches, respectively, that are separated by a rocky headland and are part of Parque Nacional Marino Las Baulas.

We conducted night patrols to encounter nesting turtles at Cabuyal as described in Santidrián Tomillo et al. (2015) and at Playa Grande/Ventanas as described in Reina et al. (2002) and Dornfeld et al. (2015). All encountered green turtles were checked for inconel metal tags and Passive Integrated Transport (PIT) tags and were tagged accordingly if none were found. To avoid interfering with the nesting process, tagging and data collection began after each turtle had completed oviposition.

Measuring Chelonibia testudinaria growth

We measured *C. testudinaria* exclusively and no other barnacle species were observed on green turtle carapaces during this study. We exclusively sampled barnacles attached to the carapace and not to other body-parts as body-location may affect growth rates. We also excluded “clusters” of barnacles (considered here as a group of five or more individuals in direct contact with each other) as we assumed that this could also affect growth rates.

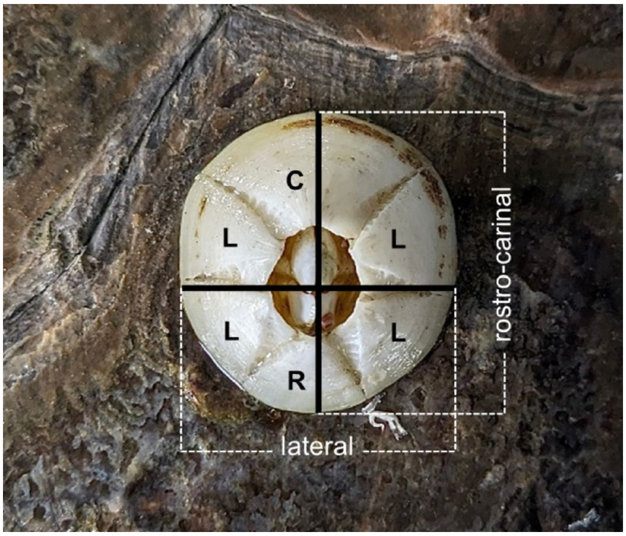


Fig. 1 Image in dorsal view of *C. testudinaria* on the carapace of a green turtle indicating how size was measured, “R” refers to the rostral plate, “C” to the carinal plate and “L” to the lateral plate

Before measuring *C. testudinaria*, we removed all sand from the carapace of the turtle to ensure that the outline of each scute was clearly visible. Next, we assigned an arbitrary identification number to up to 10 barnacles, recording their location on a datasheet that included a diagram of a green turtle carapace and taking care to align the location of each barnacle correctly with the diagram of the turtle’s scutes. Finally, we used a digital calliper (± 0.1 mm) to measure the length of each selected barnacle, both inline (rostro-carinal) and perpendicular (lateral) to the dividing line of the feeding appendages, which are located between the carinal and rostral plates (Fig. 1). Barnacles for data collected were selected haphazardly.

To ensure that the same barnacles were measured on subsequent encounters with the same nesting turtle (as identified via the metal and PIT tags), on night patrols we carried photocopies of the datasheets illustrating the barnacles’ location on each turtle. Upon reencountering a nesting turtle, we could directly compare the location of the barnacles previously recorded to those currently being observed. While adult *C. testudinaria* can translocate, such movements are slow enough (< 0.3 mm d^{-1}) (Chan et al. 2021) that they would not confound barnacle identification. If an identified barnacle had detached between encounters, we noted its loss and selected a new individual barnacle, if present, for measuring.

Growth rates

We followed the same methodology as Doell et al. (2017) to determine growth rates of *C. testudinaria*. In short, we calculated growth rates using both the rostro-carinal and lateral shell lengths and the non-linear growth equation described in von Bertalanffy (1951):

$$L = a(1 - b\, e^{-k\, t}) \tag{1}$$

where L was length, t was time since settlement and b was the relationship between asymptotic length and settlement length (when $t = 0$) of *C. testudinaria* (Eq. 2).

$$b = \frac{(a - settlement\ length)}{a} \tag{2}$$

For the settlement lengths, we used the mean rostro-carinal and lateral lengths of the last larval stage of *C. testudinaria*, which were 0.643 mm and 0.286 mm respectively, based on Zardus and Hadfield (2004). To avoid pseudo-replication, we only used a single pair of measurements per barnacle (e.g., one capture and one recapture). We chose the measurements that were separated by the longest time interval (e.g., the first and last encounter with each barnacle) to minimize the effects of measurement error associated with small growth windows. To complete Eq. 1 required knowledge of an organism's size at a known age; however, we only knew the growth time of each barnacle relative to its first encounter. To address this limitation, we used the growth interval equation in Fabens (1965) (Eq. 3) to generate growth curves based solely on the observed growth rates between capture and recapture:

$$L_r = a - (a - L_c)\ e^{-k\, t_{cr}} \tag{3}$$

where L_r was the length at recapture, L_c was the length at capture, t_{cr} was the time interval between capture and recapture, k was the intrinsic growth rate and a was the asymptotic length. To obtain estimates of the parameters a and k, we performed a non-linear least squares regression analysis by fitting the Eq. 3 to the observed data.also estimated the growth rate of the basal area of *C. testudinaria* by applying the following formula to calculate the area of an ellipse (Eq. 4) using both rostro-carinal and lateral measurements:

$$A = \pi\ c\, d \tag{4}$$

where A was the basal area, π was the constant pi, c was the rostro-carinal length and d was the lateral length. Next, we calculated the time since settlement of each barnacle using its rostro-carinal length at the time of capture in a rearranged form of the von Bertalanffy equation (already solved with rostro-carinal lengths) designed to solve for t (Eq. 5).

$$t = \frac{Ln\left(\frac{a-L}{a\, b}\right)}{-k} \tag{5}$$

We correlated the time since settlement with the observed basal area at first capture and extracted the slope of the regression line as an estimate of the linear growth rate of the basal area.

Variables influencing growth rates

We compared predicted and observed rostro-carinal lengths at recapture of *C. testudinaria* to assess the influence of daily Sea Surface Temperature (hereafter SST), nesting beach (Cabuyal, Playa Grande/Ventanas), barnacle position on the turtle carapace (front, middle, or back), and/or host turtle identity on growth rate. We obtained the predicted lengths using Eq. 3.

The mean SST for the time interval between the first and last measurement within green turtle internesting habitats was obtained at a 0.01° x 0.01° spatial resolution and a daily temporal scale from the NASA spacecraft Multiscale Ultra-high Resolution (MUR) sensor (JPL MUR MEaSUREs Project 2015). For Cabuyal, we used internesting areas identified in Clyde-Brockway et al. 2019 and previously used in Valverde-Cantillo et al. (2019) (Fig. 2). As tracking data on the internesting habitats used by turtles nesting on Playa Grande/Ventanas were not available, we defined an area of equivalent size (25 km^2) to that used for Cabuyal (Fig. 2).

To categorize each barnacle's position on the carapace, we divided the carapace into three sections: "front", extending from the anterior most point of the nuchal scute to the boundary defined by the posterior end of the first costal scute; "middle", extending from the posterior end of the first costal scute to the boundary defined by the posterior end of the third costal scute; and "back", extending from the posterior end of the third costal scute to the posterior most point of the supracaudal scutes (see Online Resource 1 for a visual representation).

As we had fixed effect variables (SST, beach, and barnacle position) and a random effect variable (host turtle identity), we first assessed the influence of the random effect variable to determine whether it should still be included in the final model. To do this, we used the gls() function from the "nlme" package (Pinheiro and Bates 2000) to build a linear model including all fixed effect variables but excluding the random effect variable and then used the lme() function from the same package to build a linear mixed model with all fixed effect and random variables. To simplify the models, we did not include interactions between the fixed effect variables. Both models were fitted using Restricted Maximum Likelihood (REML), which is appropriate for comparing models that differ only in their random component (Cayuela and de la Cruz 2022). We then performed a likelihood ratio test (LRT) to determine whether the inclusion of the random effect variable (host turtle identity) significantly improved model fit. As this comparison revealed a statistically significant difference ($P< 0.001$), we included the host turtle identity in the subsequent models to assess the fixed effect variables on growth rates. Specifically, we used the dredge() function from the "MuMIn" package (Bartoń 2023) to build thirteen linear mixed models, accounting for all possible combinations of fixed effect variables (including interactions) (Table 1). This time, these models were fitted using Maximum Likelihood (ML), which is appropriate when comparing models with different fixed-effect variables (Cayuela and de la Cruz 2022). To compare models, we used the Akaike Information Criterion corrected for small sample size (AICc) and selected the most parsimonious models based on the lowest AICc value. We used ANOVA to test the significance of all fixed effect variables on the most parsimonious model. Tests were conducted in R version 4.3.1 (R Core Team 2023).

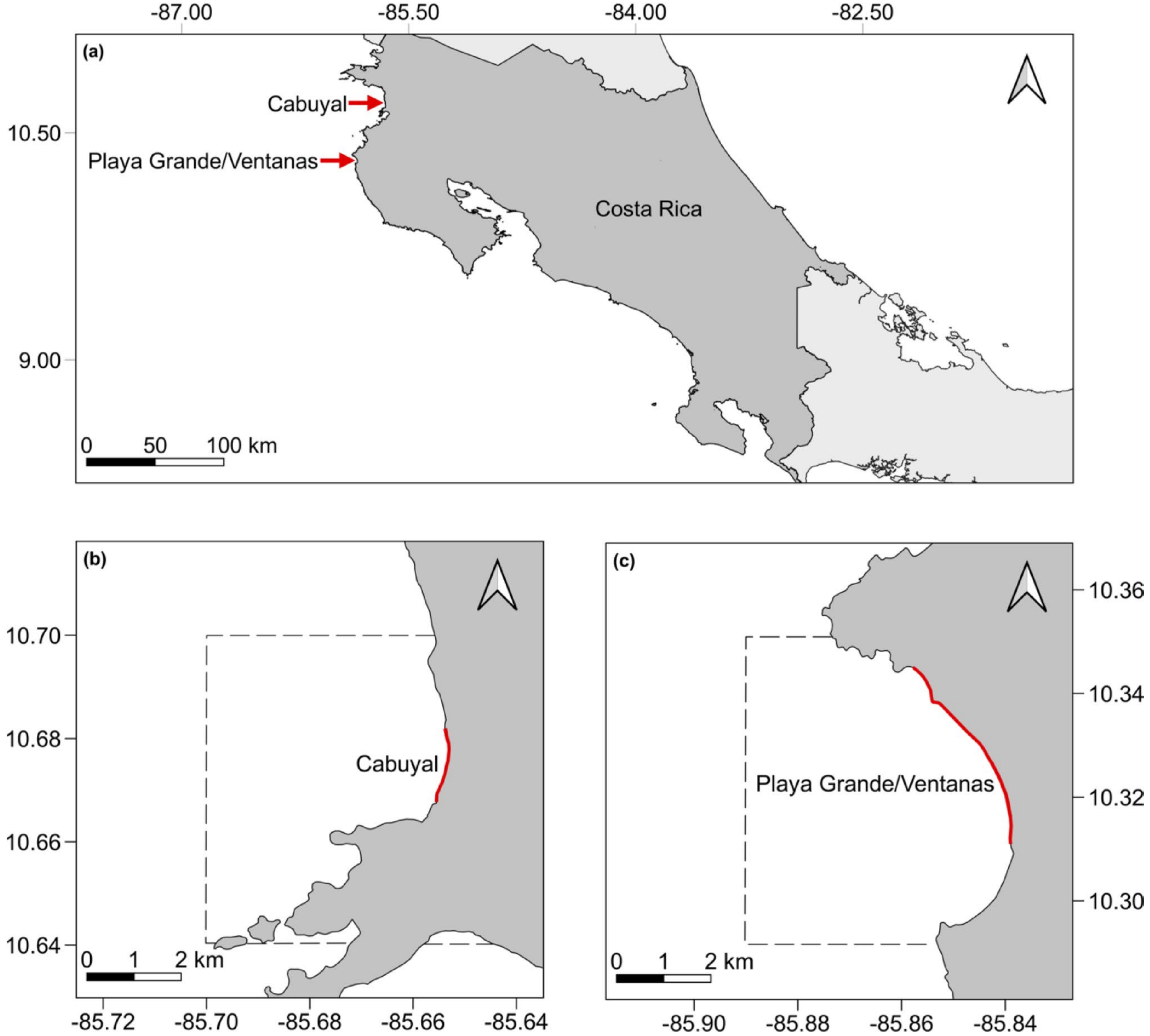


Fig. 2 Location of Cabuyal and Playa Grande/Ventanas on the northwestern coast of Costa Rica (a) and the presumed internesting habitats (dashed black lines) for green turtles nesting at (b) Cabuyal and (c) Playa Grande/Ventanas. Red lines indicate the nesting beaches

Time from barnacle settlement to the turtle's first nesting event

To estimate when *C. testudinaria* settled relative to the start of the turtle nesting, we input the rostro-carinal length measurements of the largest *C. testudinaria* found on turtles encountered nesting for the first time that season into Eq. 5. Consequently, since we only included turtles for which we recorded its first nesting event of the season without the need for subsequent encounters, the number of turtles included here differed from the number used to estimate growth rates. We used the length of the largest barnacle because its time since settlement would represent the most accurate estimate of the minimum time (elapsed) since a turtle arrived to the coastal habitat.

Since beach coverage (i.e., the proportion of nesting activity recorded) was not 100% and turtles sometimes move between nesting beaches (Miller 1997), we could not guarantee that our first encounter with each turtle corresponded to their first nesting event for that season. To account for this, we adjusted our estimate of time since settlement to account for the probability of missing a nesting event. At Cabuyal, green turtles have a 65% nesting success (i.e., 65% of nesting attempts result in a successful nest) and we maintained a 70% beach coverage in 2023/24 (Santidrián Tomillo unpubl. data). Thus, we did not observe 30%

Table 1 All tested linear mixed models and their associated AICc value as determined using the maximum likelihood method

Model	Variables	AICc
1	SST, Beach, Position, SST: Position, Turtle	523.2
2	SST, Beach, Position, SST: Beach, SST: Position, Turtle	525.4
3	Turtle	526.5
4	Beach, Turtle	526.7
5	SST, Beach, Turtle	526.8
6	SST, Position, SST: Position, Turtle	528.1
7	SST, Turtle	528.7
8	SST, Beach, SST: Beach, Turtle	528.9
9	SST, Beach, Position, Turtle	529.2
10	Beach, Position, Turtle	529.3
11	Position, Turtle	529.5
12	SST, Beach, Position, SST: Beach, Turtle	531.3
13	Position, SST, Turtle	531.7

[a] Interactions are indicated with ":"

of turtle activity, resulting in a 19.5% probability of missing a successful nesting event. To correct this, we applied the 19.5% probability to the mean IP for green turtles at Cabuyal (14.3 days; Valverde-Cantillo et al. 2019) and subtracted it from our estimated settlement time. The probability of missing a nesting event at Playa Grande/Ventanas was 45.1%. Consequently, we considered this value too high to warrant estimating the time since barnacle settlement relative to the turtle's first nesting event at Playa Grande/Ventanas.

Detachment rates

To calculate barnacle detachment rates, we used data from turtles encountered between two sequential nesting events (i.e., without an additional nesting event between measurements). To avoid including turtles that may have laid additional nests between encounters, we only used data from turtles reencountered between 9 and 21 d, which is the IP of green turtles in Cabuyal (Valverde-Cantillo et al. 2019). As there is no published data on typical IPs for green turtles at Playa Grande/Ventanas, we also used the Cabuyal IP range for this nesting site too. For all barnacle that were not present on turtle recapture after a IP, we used Eq. 5 to estimate the time since settlement based on their rostro-carinal length at the last observation before detachment.

Results

Size data

We estimated growth rates for 106 *Chelonibia testudinaria* barnacles from 38 green turtles (Cabuyal: 92 barnacles, 32 turtles; Playa Grande/Ventanas: 14 barnacles, 6 turtles). The time between the first and last measurements ranged from 11 to 66 d. The mean (± SD) rostro-carinal length on first encounter was 20.3 ±8.7 mm (range: 6.1–52.8 mm) and the lateral length was 17.2 ±6.8 mm (range: 4.9–41.7 mm). In contrast, the maximum rostro-carinal and lateral lengths at last recapture were 53.7 mm and 45.8 mm, respectively. The mean starting basal area of *C. testudinaria* was 325.9 ±307.3 mm^2 (range: 23.8–1728.4 mm^2), while the basal area at last recapture was 611.4 ±350.8 mm^2 (range: 107 to 1901.9 mm^2).

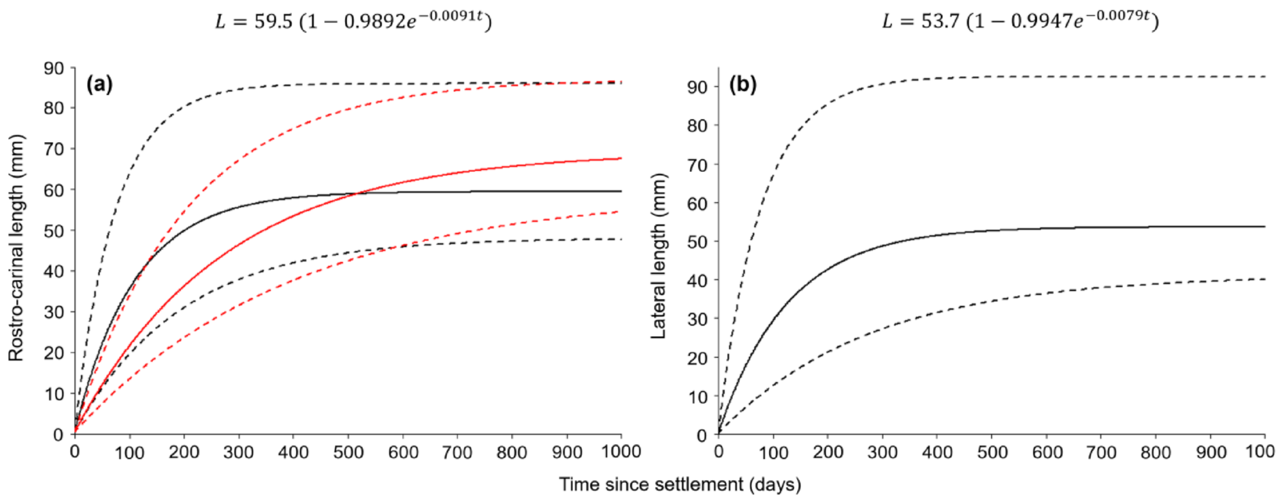
Growth rates

For the rostro-carinal length, the mean values (± SE) for k(intrinsic growth rate) and a(asymptotic length) were 0.0091 ±0.0022 d^{-1} and 59.5 ±8.2 mm, respectively. For the lateral length, the parameters k and a were 0.0079 ±0.0024 d^{-1} and 53.7 ±9.7 mm, respectively. Using the mean values for a and the settlement lengths (mean lengths of the last larval stage of *C. testudinaria*), b was estimated as 0.9892 for the rostro-carinal length and 0.9947 for the lateral length. The resulting von Bertalanffy growth curves and respective equations are shown in Fig. 3.

There was a statistically significant linear correlation between basal area and time since settlement at first encounter (Pearson's correlation, $R = 0.991$, $r^2 = 0.982$, $N = 106$, $P < 0.001$) with a linear growth rate of 8.6 $\text{mm}^2\ \text{d}^{-1}$ (Fig. 4; Table 2).

Variables influencing growth rates

We found a statistically significant correlation (Pearson's correlation, $R = 0.901$, $r^2 = 0.813$, $N = 106$, $P < 0.001$) between predicted and observed recapture lengths (Fig. 5). According to the AICc values, the most parsimonious model included SST, beach, barnacle position, and the interaction between SST and barnacle position as variables with fixed effect (Table 1). Considering that any model with an ΔAICc >2 relative to the best model is considered less suitable (Cayuela and de la Cruz 2022), we considered all other models less parsimonious. In the most parsimonious model, 66.4% of the variance in growth rates was explained by the host turtle (random effect variable SD =2.767, residual SD =1.967). ANOVA results for this model indicated that growth rates were significantly affected by beach (ANOVA, $F_{(1,36)} = 4.903$, $P = 0.033$) and the interaction between SST and barnacle position (ANOVA, $F_{(2,63)} = 5.385$, $P = 0.007$). Although the model improved when SST and barnacle position were included, suggesting a potential effect on growth rates, this effect was not statistically significant for either SST (ANOVA, $F_{(1,63)} = 0.034$, $P = 0.855$) or barnacle position (ANOVA, $F_{(2,63)} = 0.786$, $P = 0.459$).


$L = 59.5\,(1 - 0.9892e^{-0.0091t})$

$L = 53.7\,(1 - 0.9947e^{-0.0079t})$

Fig. 3 Von Bertalanffy growth curves illustrating the relationship between length and time since settlement of *C. testudinaria* on green turtles in northwest Costa Rica (black solid line) with 95% confidence intervals (black dashed lines). (a) corresponds to rostro-carinal length and (b) corresponds to lateral length. The red solid line in (a) represents the growth curve of *C. testudinaria* attached to loggerhead turtles in the South-west Pacific Ocean with 95% confidence intervals (red dashed lines), as reported in Doell et al. (2017)

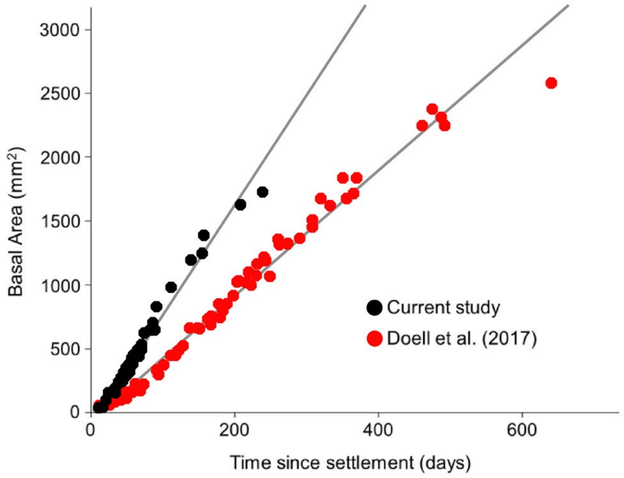


Fig. 4 Linear correlation between basal area and time since settlement (from the von Bertalanffy growth model) from this study and Doell et al. (2017)

Table 2 Comparison of our results with those reported in Doell et al. (2017). Both studies measuring growth rates of *C. testudinaria* on sea turtle hosts in the wild

Metric	Current study	Doell et al. (2017)
N (barnacles and turtles)	106 and 38	78 and 41
Mean recapture interval (± SD) (d)	29.6 (± 13.7)	29.2 (± 10.6)
Mean length (± SD) on first encounter (rostro-carinal length; mm)	20.3 (± 8.7)	30.3 (±15.9)
Size range on first encounter (basal area; mm^2)	23.8–1728.4	9.5–2535
Rostro-carinal length		
Mean intrinsic growth rate (± SE) (d^{-1})	0.0091 (±0.0022)	0.0037 (±0.0006)
Mean asymptotic length (± SE) (mm)	59.5 (± 8.2)	69.3 (±6.4)
Relationship	Non-linear	Non-linear
Basal Area		
Growth rate (mm^2 d^{-1})	8.6	4.9
Relationship	Linear	Linear

Time from barnacle settlement to the turtle's first nesting event

To estimate the time when barnacle settlement occurred relative to each turtle's first nesting event that season, we used the rostro-carinal length measurements from the largest *C. testudinaria* found on 34 green turtles nesting at Cabuyal. Our measurements revealed a mean length (± SD) of 29.3 ±8.6 mm (range: 15.9–49 mm) (Fig. 6). Using Eq. 5, we estimated that these *C. testudinaria* had settled a mean of 79 ±37 d (range: 33–190 d) before the first recorded turtle nest (Fig. 6). After accounting for a 19.5% probability of missing a nesting event, the adjusted time was 76 days.

Detachment rates

Of the 106 *C. testudinaria* barnacles used for the growth rate calculation, 83 barnacles from 22 turtles were suitable for the detachment analysis. Of these, 20 barnacles (24.1%) were absent (i.e., detached) after one IP. The mean rostro-carinal length of detached barnacles (± SD) was 22.9 ±10.7 mm (range: 6–54.4 mm). Based on these data, we estimated the mean time since settlement for detached barnacles to be 61 ±54 d (range: 10–269 d).

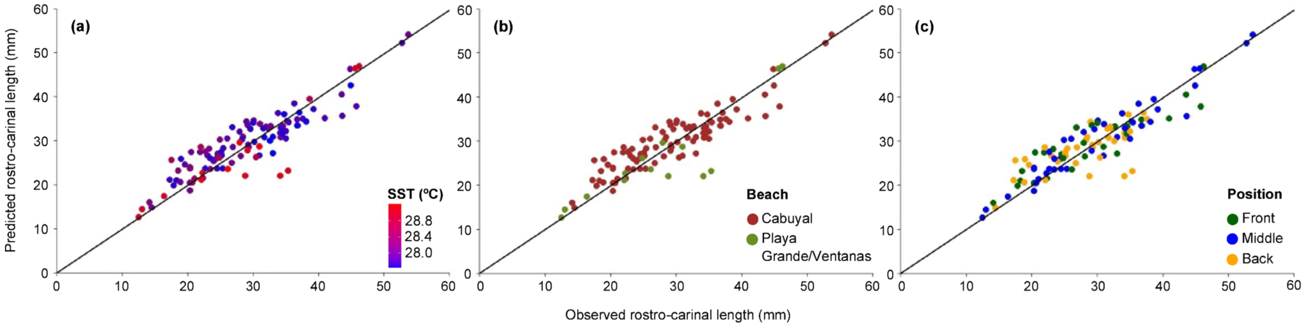


Fig. 5 Linear correlation between predicted and observed recapture lengths. Black line corresponds to the regression line. Colours indicate: (a) SST over the measured period of barnacle growth, (b) the beach where barnacles were measured and (c) the position on the carapace where the barnacles were growing

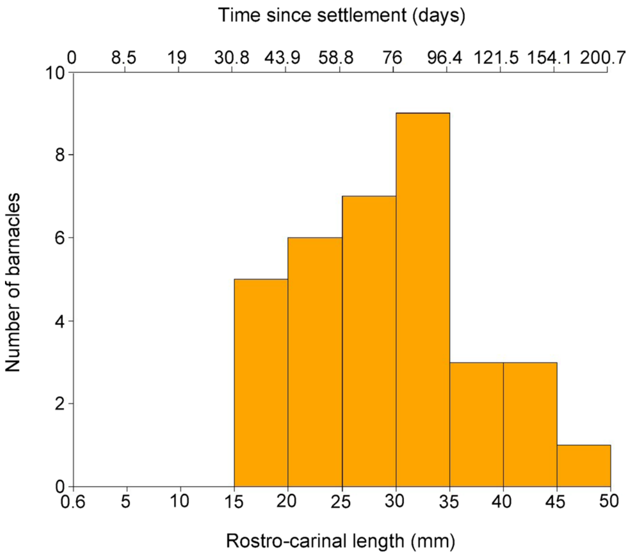


Fig. 6 Frequency histogram of rostro-carinal lengths and estimated times since settlement of the largest *C. testudinaria* found on the first recorded turtle nest

Discussion

Variables influencing growth rates of *Chelonibia testudinaria*

Host identity significantly influenced growth rates, with 66.4% of the variance attributed to this variable, indicating a strong individual effect. This influence is likely due to differences in turtle behavior (e.g., activity patterns, swim speed) or thermal habitats. Moreover, a previous study has shown that inter-nesting green turtles from Cabuyal nesting beach may exhibit unique movement patterns, with individual variation in dive duration and depth (Clyde-Brockway et al. 2019) and/or inhabit different temperature waters (Robinson et al. 2022). Thus, this could help explain why the effect of SST on barnacle growth rates was not statistically significant, despite its inclusion in the two best-fitting models (Table 1). Given that temperature influences growth rates of many other barnacle taxa (Sanford and Menge 2001; Goehlich et al. 2024), a lack of a significant effect here could be driven by the lack of resolution of the SST data. For example, the SST within our bounding boxes may not accurately reflect the local thermal conditions at the exact location inhabited by individual sea turtles. Similarly, we calculated the mean SST over repeat turtle encounters, but such averaging may obscure temporal variations in temperatures which could be key for influencing growth. It should also be noted that we only observed a range of 27.6 to 29.2 ºC for SST per IP and such a narrow temperature range may not have strong influence on growth. Indeed, growth rates remain relatively stable in *Balanus glandula* under temperature changes < 2 °C (Sanford and Menge 2001).

After host identity, the next most influential variable was the beach. Specifically, growth rates were higher in barnacles collected at Playa Grande/Ventanas than at Cabuyal. Two possible hypotheses to explain this are either that turtle behavior differs between sites, or that environmental conditions vary across sites. However, this difference could also be driven by differences in the sizes of barnacles found at either site. Specifically, the three smallest *C. testudinaria* (6.2, 6.1, 7.8 mm) were all measured on Playa Grande/Ventanas and each had observed growth rates exceeding the predicted values. The lack of representation of small barnacles at Cabuyal could therefore explain the slower growth rate at this location. The lack of small barnacles in our study, which could be driven by their absence or by a human bias towards measuring only the larger barnacles on each turtle, is a limitation of our study and could alter our estimated growth rates.

Our reported growth rates of *C. testudinaria* on green turtles in Costa Rica were almost double those previously observed by Doell et al. (2017) for *C. testudinaria* on loggerhead turtles in Australia (Fig. 3). One hypothesis to explain this difference is the variation in host species behaviour. Green turtles are generally more active and prefer warmer waters than loggerhead turtles (Enstipp et al. 2011; Fossette et al. 2012; Robinson et al. 2022), which may promote faster barnacle growth. Another hypothesis is that environmental conditions in the internesting habitats differ between the two regions. For example, mean SST in the internesting habitats in Costa Rica during the 2023/2024 green turtle nesting season was approximately 3 ºC higher than in the coastal zone near the nesting beach on the Pacific coast of Australia, where data were collected in Doell et al. (2017) during the 2015/2016 season (Poyatos, unpubl. data). This, combined with potential differences in food availability, may have contributed to the observed differences, as these environmental variables are known to strongly influence barnacle growth (Sanford and Menge 2001; Inatsuchi et al. 2010; Nishizaki and Carrington 2015).

Finally, it should be noted that another variable potentially influencing growth rates between *C. testudinaria* sampled at different locations might be genetic variation. At present, some studies have indicated genetic differentiation between *C. testudinaria* on opposite sides of the Pacific Ocean (Rawson et al. 2003) while other studies have found no such varation (Zardus et al. 2014). Whether *C. testudinaria* settling on green turtles on the Pacific coast of Costa Rica or on loggerhead turtles in Australia exhibit identifiable genetic separation, and whether this is enough to influence growth rates, would require more fine-scale genetic studies on the global phylogeny of *C. testudinaria*.

Epibiotic barnacle detachment rates

We provide the first quantitative assessment of epibiotic barnacle retention/detachment rates on wild sea turtles. Our results showed that 24.1% of *C. testudinaria* detached after a single IP. This selective pressure could be influencing the life cycle of these organisms, potentially favouring faster growth in these individuals compared to non-epibiotic barnacles living in more stable conditions. This hypothesis, however, relies on the assumption that epibiont barnacles such as *C. testudinaria* detach more frequently than barnacles living on inanimate substrates.

A potential explanation for barnacle detachment is that individuals detach upon reaching a critical size due to senescence. If this were the case, larger individuals would exhibit higher detachment rates. However, the mean length of detached *C. testudinaria* individuals was 22.9 mm, substantially smaller than the maximum length observed in our dataset (53.7 mm). In addition, the estimated time since settlement for detached barnacles exhibited high variability (mean ± SD: 61 ± 54 days), further suggesting that detachment is unlikely to be primarily driven by senescence. These observations instead point toward host behavioral factors as a more likely driver of barnacle detachment. Self-cleaning behavior has been reported in sea turtles (e.g., Heithaus et al. 2002; Schofield et al. 2006) and may contribute to barnacle detachment by mechanically dislodging individuals from the carapace. Green turtles have been suggested to exhibit self-cleaning behavior more frequently than loggerhead turtles (Bjorndal 2003) and bio-logging devices affixed to green turtle carapaces using epoxy typically remain attached for shorter periods compared to those on loggerhead or hawksbill turtles (Smith et al. 2019; Hart et al. 2021). These observations suggest that detachment rates may be higher in green turtles compared to other species. However, detachment rates across turtle species have not yet been reported, and this hypothesis needs to be confirmed.

C. testudinaria as an indicator of habitat use in sea turtles

We used *C. testudinaria* growth rates to estimate how long green turtles had occupied coastal habitats prior to nesting. Based on our growth rate estimations and the length of the largest *C. testudinaria* encountered on the first recorded turtle nest, our findings suggest that *C. testudinaria* settled a mean of 76 days before turtles laid their first clutch. If we accept that *C. testudinaria* only settles in nearshore habitats then this could suggest that green turtles spend an extended period in nearshore reproductive habitats before laying their first clutch. Confirming this would require satellite tracking of turtles on departure from their foraging areas and such data are not yet available for the green turtles nesting at Cabuyal. A similar, yet slightly modified, explanation could be that some green turtles nesting on Cabuyal remain year-round in nearshore waters close to the nesting beach as has already been confirmed from post-nesting satellite telemetry studies on green turtles at Cabuyal (Clyde-Brockway 2014) and other nearby nesting beaches (Blanco et al. 2012). Observations from Unoccupied Aerial Vehicles have also shown that turtles in the waters near Cabuyal are feeding (Robinson et al. 2024), further supporting evidence that several individuals occupy these habitats year-round. Finally, it could also be that even those turtles that conduct more extensive migrations away from Cabuyal still primarily occupy coastal habitats where settlement of *C. testudinaria* can still occur. It would therefore be particularly valuable to repeat this study at green turtle nesting sites where individuals are known to occupy oceanic pre-nesting habitats, such as Ascension Island (Koch et al. 1969) to assess whether barnacle settlement times differ under these migratory conditions. Such a study could also be further validated using stable isotope analyses of δ^{18}O in the calcite deposited in barnacles shell to assess how pre-migrating animals have passed through different thermal habitats (Pearson et al. 2020).

While we postulate that the size and growth rates of *C. testudinaria* could provide an estimate of coastal habitat use in sea turtles, these estimates are constrained by the lifespan of the barnacles. Specifically, if barnacles can be easily detached from the host, as indicated by reported detachment rates, barnacles may generally reflect habitat use over short periods. However, in some cases, such as the barnacle with the maximum observed rostro-carinal length in this study (i.e., 53.7 mm), they could indicate habitat use over a longer duration (potentially spanning around one year). Another key knowledge gap for using *C. testudinaria* as an indicator of habitat use is the lack of information on the timing of larval spawning in *C. testudinaria*. If *C. testudinaria* only spawn during specific times of the year, then even if a turtle arrives at coastal habitats, where *C. testudinaria* likely spawns (Casale et al. 2004, 2012; Ten et al. 2019), it will only be settled by these barnacles if this coincides with the timing of larval settlement. Knowledge of *C. testudinaria* spawning cycles is also essential for the use of *C. testudinaria* as indicators of coastal habitat use in sea turtles.

Conclusions

We present the first growth curve for *C. testudinaria* on green turtles in the wild, revealing that growth rates for this species are not consistent between individuals and potentially also species and geographic regions. Thus, the use of *C. testudinaria* growth rates as indicators of sea turtle habitat use on a global scale still requires further investigation into the variables influencing *C. testudinaria* growth. If such data are generated though, the resolution of this indicator could be refined, and barnacles may offer a cost-effective method to reveal sea turtle habitat use.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author.

Declarations

Competing Interests The authors do not have any financial or non-financial competing interests to declare.

Ethical approval All research undertaken during this study was conducted in full compliance with the ethical standards of Costa Rican environmental governing authorities such as MINAE and SINAC.

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