Growth of the coconut crab *Birgus latro* estimated from mark-recapture using passive integrated transponder (PIT) tags

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ABSTRACT: Determination of the growth pattern of a harvested species is an important step toward a proper assessment and suitable management of the stock. Although coconut crab *Birgus latro* populations in most regions have been severely depleted, few reliable biological data are available. We assessed the growth of *B. latro* using a mark-recapture method based on the use of passive integrated transponder (PIT) tags on Hatoma Island, located southwest of Okinawa, Japan. Of 781 crabs tagged (337 males, 444 females; 14.89 to 58.03 mm thoracic length [ThL]), 17 males and 20 females were recaptured. The application of PIT tags provided field data for growth of individuals for up to 2326 d and confirmed that coconut crabs molt during the winter dry season on Hatoma Island. The curves relating ThL with age, estimated from data of 29 crabs that had spent one or multiple winter dry seasons at liberty, showed that the coconut crab is an extremely slow growing species, with males showing much higher mean asymptotic ThL (69.87 mm) than females (42.79 mm). The Brody growth coefficient (K) was 0.061 yr^{-1} for males and 0.091 yr^{-1} for females. This study is the first to provide growth estimates of wild coconut crabs based on mark-recapture over multiple years. Potentially long-lived, slow growing species such as coconut crabs may be susceptible to overharvesting, and a cautious approach is recommended to the determination of resource management regimes for *B. latro*.

KEY WORDS: Coconut crab · *Birgus latro* · Growth rate · Japan · Mark-recapture · Passive integrated transponder tag

INTRODUCTION

The knowledge of the growth parameters of a harvested species is important for understanding population dynamics (Courtney et al. 2001), providing stock assessment (Punt 2003), and developing resource management (Brandão et al. 2004). However, determination of the growth parameters of crustaceans is difficult because (1) their exoskeletons, together with any attached mark or external tag, are almost always

lost by molting (although T-bar tags are generally well retained, e.g. Stewart & Kennelly 2000) and (2) as far as we know, crustaceans possess no detectable annually marked physical structures that they retain throughout their life span (but see Kilada et al. 2012). There are currently 2 methods of age estimation for crustaceans, size frequency analysis (e.g. France et al. 1991) and lipofuscin assays (e.g. Kodama et al. 2006); however these methods are subjected to various limitations and require further validation (Hartnoll 2001).

The coconut crab *Birgus latro* (Linnaeus 1767), also known as robber crab or palm thief, lives in coastal areas of the tropical Indo-Pacific region. Individuals can weigh up to 4 kg (Brown & Fielder 1991) and live up to 40 to 60 yr, with a mean of about 50 yr (Fletcher et al. 1991a). Populations in most habitats have been severely depleted (Brown & Fielder 1991), due primary to overharvesting (Fletcher 1993) and habitat destruction (Eldredge 1996). In 1981, the IUCN Red List classified the coconut crab as a vulnerable species. In 1996 the listing was downgraded to the 'data deficient' category, not because the species had recovered but because of the lack of available data (Eldredge 1996). Although coconut crabs have been traditionally eaten by local people, there have been few serious attempts to manage stocks in most regions and there are few reliable biological data on the species (Drew et al. 2010). A mark-recapture study to determine the growth rate of *B. latro* (Fletcher et al. 1990) had limited success, due to the difficulties of long-range marking and identification of individuals—difficulties also encountered in studies of other species of crustacean (see Drew et al. 2010). Consequently, the study by Fletcher et al. (1990) was limited to a single intermolt period, reducing the ability to accurately estimate growth rates. In addition, little was found out about the growth of *B. latro* females, due to a deficiency of female growth data (Fletcher et al. 1990).

A newer tagging method, using passive integrated transponder (PIT) tags, which alleviates the problems associated with mark-recapture methods, has recently been developed and applied to some crustaceans (e.g. Donaldson et al. 1992, Bianchini et al. 2001, Bubb et al. 2002, Diele & Koch 2010, O'Malley 2011, Drew et al. 2012). Because the tags are implanted into the body of animal, there is a markedly lower risk of tag loss at molting. PIT tags display a unique identification number when energized from external antennae, offering the possibility of detecting and identifying tagged animals without destructive sampling. PIT tags may be a suitable tagging system for coconut crabs since tag implantation causes no mortality or adverse behavior, and the rate of tag loss is low. PIT tags therefore have the ability to provide biological information over a long period of time (Drew et al. 2012). We utilized the PIT tag marking method to assess the growth of a wild population of coconut crabs.

MATERIALS AND METHODS

A field investigation was conducted on Hatoma Island (24° 28′ N, 123° 49′ E) in the Sakishima archipelago, located southwest of Okinawa, Japan. Hatoma Island is a small island, approximately 4 km in circumference, and with an area of 0.96 km². Inland, the island displays a mix of dense and sparse vegetation; coastal areas are characterized by jagged limestone pinnacles and sand beaches. Coconut crabs are distributed throughout the island and migrate between inland and coastal areas (Sato & Yoseda 2013). On Hatoma Island, crab sizes at 50% sexual maturity were estimated to be 22.2 mm thoracic length (ThL) in males (Sato et al. 2008) and 24.5 mm ThL in females (Sato & Yoseda 2008). The reproductive season starts around early June and ends in late August (Sato & Yoseda 2008). Most mature females extrude eggs by mid-July, with ovigerous females found until late August on Hatoma Island (Sato and Yoseda 2008). Local people selectively harvest larger males (based on their own understanding of the biology of the species, since there is no regulation of harvesting for *B. latro*), skewing the sex ratio toward females (Sato & Yoseda 2010).

Since the coconut crab is nocturnal, crabs were captured during night by hand without baits at inland and coastal areas of Hatoma Island from March to October in each year from 2005 to 2009. Captured crabs were sexed based on the presence of pleopods on the left ventral surface, which are possessed exclusively by females to support external egg masses (Fletcher 1993). The ThL of each crab was measured to the nearest 0.01 mm using Vernier calipers (Mitutoyo Corporation, CD-20PM). A PIT tag was implanted in each crab using a large gauge (diameter 2.8 mm) single shot implanter. A PIT tag consists of an electronic microchip encased in a biocompatible material; the tag can be pre-programmed with an infinite number of unique codes. Tags used in this study (Item TX-1400L, Destron, South St. Paul, MN) measured 11.0 × 2.1 mm and weighed approximately 0.067 g in air. All tags were implanted into the right hand side of the pleon near the second tergal plate (Drew et al. 2012).

In a preliminary laboratory experiment, 10 coconut crabs (28.7 to 53.5 mm ThL) were implanted with PIT tags and reared for 6 mo to examine rate of tag loss and mortality due to tag implantation. In this period, no tag loss was observed, and all crabs stayed alive and showed no adverse behavior caused by tag implantation. Although 3 crabs molted within the period, PIT tags were retained in their respective pleons (T. Sato unpubl. data). Immediately after implantation to captured crabs, the tags were scanned using a mini portable reader (HS5900L-F, Destron) and the crabs were released at their site of capture.

From March to September in each year from 2006 to 2013, the crabs with implanted PIT tags were recaptured at inland and coastal areas of Hatoma Island and their ThL was measured to the nearest 0.01 mm. Coconut crabs usually exhibit clear sexual size dimorphism, with the mean body size of females being 20 to 25% smaller than males (Fletcher et al. 1991b), implying that growth and likely mortality rates would differ between the sexes. Males and females were therefore treated separately in our analyses.

As crustaceans grow in a stepwise fashion, if molting occurs between the times of capture and recapture this may result in abnormally large estimations of growth rates. In contrast, the growth rate may appear to be zero if no molting has occurred. Because the coconut crab is suggested to molt during the winter dry season in holes or crevices (Fletcher et al. 1990)—this includes crab populations in the Sakishima archipelago (T. Sato unpubl. data)—we analyzed only those individuals that had grown and wintered for at least one winter season, from November to February, between the times of capture and recapture. The relationship between the numbers of winters from tagging to recapture and their ThL increments was analyzed separately in males and females by linear regression. Both regressions were forced to origin.

Tag-recapture data were fitted to the von Bertalanffy growth function (VBGF, von Bertalanffy 1938) with Francis's (1988) maximum likelihood method. Fitting was done using the GROTAG program designed by Simpfendorfer (2000) for the Microsoft Excel (version 7) solver function. Growth trajectories were compiled from the length at initial capture (i.e. the release ThL) (L_1), the time at release (T_1), the time at recapture (T_2), the change in length (ΔL) from L_1 to the length at recapture (L_2), and the duration in years between release and recapture (ΔT). T_1 and T_2 were measured in years from the arbitrarily chosen point in time, 1 January 2005.

Table 1. Model scenarios (Models 1 to 4) applied to tag-recapture data on the growth of coconut crabs *Birgus latro* on Hatoma Island, Japan, to evaluate optimal model parameterization, using incremental combinations of parameters estimated by GROTAG (Francis 1988)

Model	Estimated parameters
1	g_α, g_β, s
2	g_α, g_β, s, v
3	g_α, g_β, s, v, m
4	g_α, g_β, s, v, m, p

A total of 6 parameters were estimated by GROTAG and 4 model scenarios (Models 1 to 4) were applied using incremental combinations of these parameters (Table 1): mean annual growth rates (g_α and g_β) in mm yr^{-1} for 2 release sizes (α and β mm ThL, respectively, where $\alpha < \beta$); standard deviation of the growth increment (v); mean measurement error (m); standard deviation of the measurement error (s); and outlier contamination probability (p). The majority of L_1 values must fall within the range of reference lengths α and β (Francis 1988), so these were chosen to span the range of L_1. The estimated growth increment (ΔL) for a crab tagged at length L_1 at liberty for time ΔT is given by:

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T} \right] \quad (1)$$

The growth model was fitted using the likelihood function (λ) (Francis 1988):

$$\lambda = \sum_i \ln \left[(1-p)\lambda_i + \frac{p}{R} \right] \quad (2)$$

where

$$\lambda_i = \exp \frac{-0.5(\Delta L_i - \mu_i m)^2/(\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{0.5}} \quad (3)$$

R is the range of the observed growth increments, μ_i is the expected value of growth increment of the ith individual, and σ_i is the standard deviation of the growth variability.

In present study, σ_i was assumed to be proportional to μ_i, with v as the estimated scaling factor of individual growth variability around the mean growth increment; v is assumed to increase with increasing expected growth (Francis 1988), i.e. $\sigma_i = v\mu_i$.

The GROTAG methodology cannot accurately determine m and s and cannot distinguish between variability in growth and measurement error because individuals with very short times at liberty were removed from the analysis. Therefore, m and s were determined based on independent estimates from

differences in ThL at release and ThL at recapture for crabs that had not wintered between the times of capture and recapture, i.e. had not molted and grown (see 'Results') (male: n = 4, mean liberty period 45.8 d; female: n = 4, mean liberty period 67.3 d). The mean and standard deviation of these differences represents an exact measure of measurement error, which was estimated (mean ± SD) to be 0.01 ± 0.06 mm ThL for males and 0.03 ± 0.01 mm ThL for females.

After maximizing the likelihood function for each of Models 1 to 4, the likelihood ratio test (LRT) was then used to determine the final model which produced the highest value for λ, and the lowest value for Akaike's Information Criteria corrected for small sample size (AICc) (Burnham & Anderson 2002). A significant improvement in fit (at the 5% level), was indicated if the addition of one parameter increased λ by at least 1.92 (Francis 1988).

Variability in growth estimates was assessed with bootstrap simulations of each sex's raw tag-recapture data, thereby enabling the calculation of 95% confidence intervals (CI) for the optimized GROTAG growth parameter estimates. Raw data quadruples (T_1, T_2, L_1 and ΔL) for each sex (with n samples) were re-sampled (1000 iterations) with replacement to generate 1000 bootstrap data sets (with n samples) for each sex. The optimized GROTAG model was then applied to each of the 1000 bootstrap data sets to generate 1000 bootstrap-derived growth parameter estimates. For each sex, variability was subsequently quantified by calculating the 95% CI for the 1000 estimates of each growth parameter.

The 2 growth rate parameters were used to estimate the von Bertalanffy parameters for the Brody growth coefficient (K) and mean asymptotic length (L_∞):

$$K = \ln(1 + (g_\alpha - g_\beta)/(\alpha - \beta)) \qquad (4)$$

$$L_\infty = (\beta g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta) \qquad (5)$$

These parameters were then used to plot the VBGF; the value of t_0 (theoretical age at zero ThL) was estimated by constraining the y-axis intercept. The y-axis intercept was assigned a value of 0.51 mm ThL for both sexes, based on the mean ThL of first instar coconut crabs in other laboratory studies (ThL = 0.51 ± 0.05 mm [mean ± SD], n = 10; Hamasaki et al. unpubl. data). The estimates of L_∞, K and t_0 were used to create an age-length curve following the VBGF.

To compare the growth between sexes, the growth performance index (φ') (Pauly & Munro 1984) was calculated by the equation:

$$\varphi' = \log_{10} K + 2\log_{10} L_\infty \qquad (6)$$

This index is preferred for growth comparison, rather than using L_∞ and K independently, because these 2 parameters are often inversely correlated (Pauly & Munro 1984). The mean annual growth rate of all sizes (g_γ) was determined from the final model outputs for each sex data set by the equation of Francis (1988):

$$g_\gamma = ((\gamma - \alpha)g_\beta + (\beta - \gamma)g_\alpha)/(\beta - \alpha) \qquad (7)$$

The longevity (t_{max}) that individuals of a given population would reach was estimated by the equation of Taylor (1958): $t_{max} = t_0 + 3/K$. The age where 95% of L_∞ is reached (t_{ThL95}) was estimated using the inverse VBGF. The age at which 50% of individuals are sexually mature (t_{SM50}) was calculated by transforming data from Hatoma Island on size at sexual maturity of male (Sato et al. 2008) and female (Sato & Yoseda 2008) crabs to age using the inverse VBGF of each sex.

RESULTS

Of 781 coconut crabs tagged (male ThL = 32.63 ± 8.19 mm [mean ± SD], range 16.26 to 58.03 mm, n = 337; female ThL = 29.88 ± 4.66 mm, range 14.89 to 41.49 mm, n = 444), 37 (17 males and 20 females) were recaptured (approximately 5% recapture rate) (Fig. 1), with each recaptured only once. The period between tagging and recapture ranged from 9 to 2326 d (corresponding to 0.02 and 6.37 yr). Of the 20 recaptured females, all individuals recaptured during mid-July to mid-August (n = 7) were ovigerous.

Of the 37 crabs recaptured, 29 (13 males and 16 females) had spent one or multiple winter seasons from the time of capture to recapture (Table 2). The others (4 males and 4 females) were recaptured 9 to 96 d after tagging, and had spent no winter season during their liberty (Table 2). They showed little growth increment. These 8 crabs were excluded from analysis of growth. Incremental ThL of recaptured crabs was significantly associated with increased numbers of winters from initial capture, both in males (linear regression forced to origin, increment of ThL = 2.21 (number of winters between capture and recapture), $r^2 = 0.87$, n = 17, $F_{1,16} = 105.9$, p < 0.001) and females (increment of ThL = 0.81 (number of winters between capture and recapture), $r^2 = 0.81$, n = 20, $F_{1,19} = 79.5$, p < 0.001) (Fig. 2).

To analyze growth, we utilized data from the 29 individuals, 13 males and 16 females, recaptured after at least one winter at liberty (Table 2). Of the
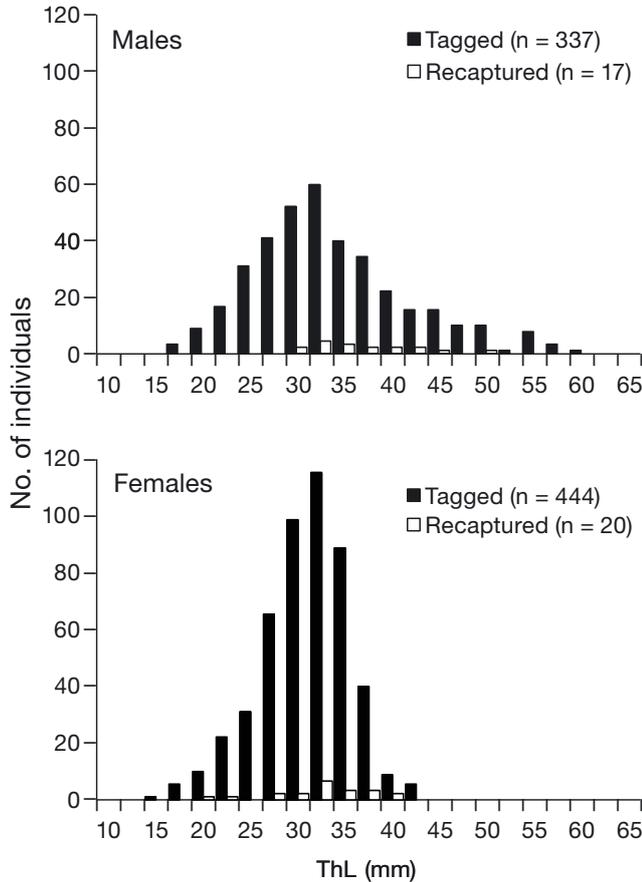
Fig. 1. *Birgus latro.* Thoracic length (ThL) frequency distributions of tagged and recaptured males (top) and females (bottom) on Hatoma Island, Japan

Table 2. *Birgus latro.* Thoracic length (ThL) at tagging (L_1) and recapture (L_2), number of days from L_1 to L_2 (ΔT), absolute increment in ThL at liberty, and number of winters at liberty. Only individuals recaptured after at least one winter season, from November to February, were analyzed

L_1 (mm)	L_2 (mm)	ΔT (d)	Increment (mm)	No. of winters at liberty
Male				
28.40	30.26	370	1.86	1
29.80	29.83	66	0.03	0
30.10	30.10	59	0	0
31.76	32.82	415	1.06	1
32.04	46.94	1450	14.90	4
32.38	32.28	9	−0.10	0
33.30	33.34	49	0.04	0
33.11	42.02	1496	8.91	4
33.77	36.80	879	3.03	3
35.28	43.50	1060	8.22	3
36.51	37.60	398	1.09	1
37.80	41.30	724	3.50	2
38.29	42.29	777	4.00	2
40.78	47.26	1184	6.48	3
40.90	46.91	1397	6.01	4
42.72	45.00	392	2.28	1
48.00	49.11	362	1.11	1
Female				
18.00	18.51	301	0.51	1
21.40	27.19	1030	5.79	3
26.65	31.67	2326	5.02	7
27.20	29.49	351	2.29	1
28.28	28.28	81	0.03	0
30.00	32.26	693	2.26	2
30.11	30.81	300	0.70	1
30.79	33.70	1209	2.91	3
31.00	32.26	1084	1.26	3
31.48	33.89	398	2.41	1
31.81	35.06	1383	3.25	4
32.34	32.71	581	0.37	2
32.74	33.42	785	0.68	2
33.57	33.60	70	0.03	0
33.98	33.99	96	0.01	0
35.41	36.81	1003	1.40	3
35.77	39.50	1455	3.73	4
35.84	38.08	1093	2.24	3
37.90	38.81	858	0.91	2
39.27	39.30	22	0.03	0

4 models, Model 2 containing g_α, g_β, s, and ν provided the best fit to the male data (Table 3). Although AICc indicated that Model 3, containing g_α, g_β, s, ν, and m, was the best fit to male data, applications of the LTR indicated no significant improvement in fit by Model 3 over Model 2. Both LRT and AICc indicated that Model 3 was the best fit to female data (Table 3). The bootstrapped mean von Bertalanffy estimates were highly consistent with the original optimized GROTAG outputs for each sex (Table 4). The estimated values of ν indicated that coconut crab exhibits substantial individual variability in growth in both sexes (Table 4). Growth curves generated using the estimated VBGF parameters in Table 4 are presented in Fig. 3, showing that growth patterns differ between males and females, with L_∞ being 39% smaller and K being 33% higher in females than in males (Table 4). The growth performance index (φ') was higher in males than females (Table 3), and the calculated mean annual growth rate (mm yr^{-1}) of
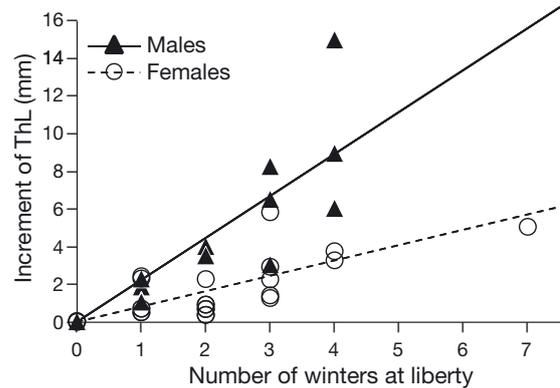

Fig. 2. *Birgus latro.* Relationship between number of winters from tagging to recapture and increment of thoracic length (ThL)

Table 3. *Birgus latro.* Likelihood values (λ) from Francis (1988) method and Akaike's Information Criterion corrected for small sample size (AICc) for different combinations of parameters. Values in bold indicate the optimal parameterization for each sex of *Birgus latro* and best AICc. The significance of additional parameters was tested with the likelihood ratio test (see text for details)

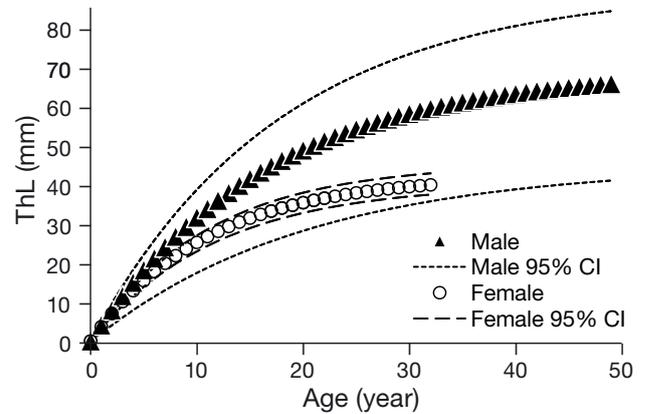| Model	λ	AICc
Males (n = 13, g_α = 28, g_β = 48)		
g_α, g_β, s	−27.41	72.38
g_α, g_β, s, ν	**−22.94**	65.98
g_α, g_β, s, ν, m	−22.93	**65.94**
g_α, g_β, s, ν, m, p	−22.93	70.27
Females (n = 16, g_α = 18, g_β = 38)		
g_α, g_β, s	−34.80	87.13
g_α, g_β, s, ν	−31.28	84.62
g_α, g_β, s, ν, m	**−24.04**	**54.50**
g_α, g_β, s, ν, m, p	−27.04	84.09

Fig. 3. *Birgus latro.* Thoracic length (ThL) at age for males (mean asymptotic length $[L_\infty]$ = 69.87 mm, Brody growth coefficient $[K]$ = 0.061) and females (L_∞ = 42.79 mm, K = 0.091). The growth curves are plotted up to the age at which 95% of the maximum asymptotic size (t_{ThL95}) is reached (see Table 5)

males was also higher than that of females over the entire life span (Fig. 4).

Estimated longevity, based on age estimates at t_{ThL95} calculated by inversed VBGF, indicated that the coconut crab has a long life span (Table 5). Males and females reached 95% of L_∞ in 48.84 and 32.65 yr, respectively, whereas t_{SM50} was 6.15 yr in males and 9.21 yr in females (Table 5).

Table 4. *Birgus latro.* Parameter estimates for each sex based on tag-recapture data using GROTAG (Francis 1988) and growth performance index, φ′ (Pauly & Munro 1984). Mean estimates (Mean BS) and 95% confidence intervals (95% CI) represent 1000 bootstrapped simulations for each sex. Male s was fixed at 0.06. Female s and m were fixed at 0.01 and 0.03, respectively. ThL: Thoracic length; VBGF: von Bertalanffy growth function; L_∞ mean asymptotic length; K: Brody growth coefficient; t_0: theoretical age at zero ThL

	Males (n = 13, α = 28, β = 48)			Females (n = 16, α = 18, β = 38)		
	Data	Mean BS	95% CI	Data	Mean BS	95% CI
GROTAG parameters						
g_α	2.47	2.40	2.36–2.45	2.16	2.10	2.06–2.14
g_β	1.29	1.32	1.29–1.35	0.42	0.44	0.42–0.46
s	0.06	–	–	0.01	–	–
ν	0.38	0.34	0.34–0.35	0.55	0.51	0.50–0.52
m	–	–	–	0.03	–	–
VBGF parameters						
L_∞ (mm)	69.87	68.20	45.62–90.77	42.79	43.30	40.66–45.95
K (yr^{-1})	0.061	0.053	0.049–0.056	0.091	0.087	0.085–0.090
t_0 (yr)	−0.12	−0.14	−0.22 to −0.10	−0.13	−0.13	−0.15 to −0.12
Growth performance index						
φ′	2.47			2.22		

DISCUSSION

With application of PIT tags to coconut crabs, the present study provided the first field data for growth of the species, following individuals for up to 2326 d in which tagged individuals molted multiple times. The results indicate that PIT tagging is a suitable long-term tagging method for individual identification of coconut crabs and has the potential to address numerous questions relating not only to growth of the species as in this study but also to e.g. its behavior, movements and habitat use. Furthermore, all females recaptured during mid-July to mid-August after tagging were ovigerous, indicating that PIT tagging had no apparent negative effects on their reproductive activities. However, the recapture rate in this study was rather low (approximately 5%), even though a preliminary laboratory experiment indicated that implanted PIT tags had no adverse effects on retention rate, mortality rate or behavior (n = 10), and were retained in their respective pleons even after a molting (n = 3) (T. Sato unpubl. data). In another tag-recapture study of coconut crab with PIT tags, 15% of tagged crabs were recaptured (Drew et al. 2012). It was not possible to determine why the recapture rate was lower in this study.

Although Fletcher et al. (1991a) suggested the adult coconut crabs molt in
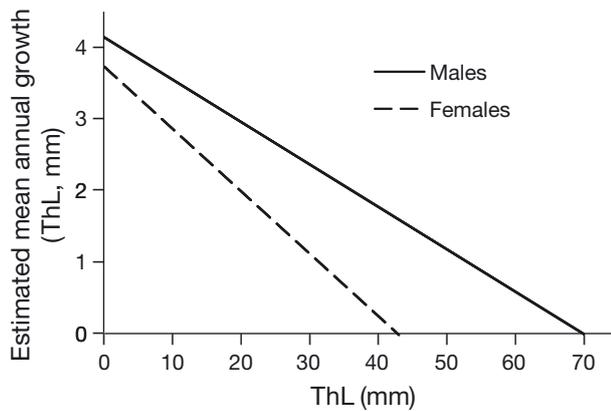
Fig. 4. *Birgus latro.* Estimated mean annual growth rates of males and females, plotted against the size of individuals. ThL: Thoracic length

Table 5. *Birgus latro.* Age at size estimates (yr) based on tag-recapture data. t_{max}: longevity estimated by Taylor (1958); t_{ThL95}: age where 95% of mean asymptotic length (L_∞) is reached; t_{SM50}: age at size of 50% sexual maturity; number in brackets: thoracic length in mm at 50% sexual maturity for males (Sato et al. 2008) and females (Sato & Yoseda 2008)

	t_{max}	t_{ThL95}	t_{SM50}
Males	49.06	48.96	6.15 (22.2)
Females	32.84	32.78	9.21 (24.5)

the dry season based on temporal variation of abdominal expansion, there are few direct data on the period of molting of coconut crab, especially in females (Drew et al. 2010). Fig. 2 shows that (1) incremental ThL of recaptured crabs positively increased with numbers of winters from initial capture, and (2) individuals of both sexes that had spent no winter season, from November to February, between tagging and recapture showed little growth increment. These results confirmed that coconut crabs on Hatoma Island molt during the winter dry season.

The curves relating ThL with age showed that the coconut crab is an extremely slow growing species with molt increment decreasing with increasing size (Fig. 4, Table 4). The pattern of decreasing molt increment with increasing size is reported for most other decapods (Hartnoll 1982), although little is known about the mechanism regulating this pattern in crustaceans (Hartnoll 1983). The general opinion on the growth of land crabs is that they grow slowly and live long (Hartnoll et al. 2006). Molting on land may constrain the amount of increase possible, particularly as body size increases, because a certain threshold level of rigidity must be maintained by the

new exoskeleton to avoid distortion due to the force of gravity (Fletcher et al. 1991a). Restricted access to water at the molting site might also partly account for small molt increments (Hartnoll 1988).

The curves relating ThL with age also show that *Birgus latro* has a long life span (Table 5). Fletcher et al. (1991a) suggest that individuals of *B. latro* live up to 40 to 60 yr, with a mean of about 50 yr, almost consistent with results of males in the present study. Although females were expected to have a shorter life span than males in this study, so far there is no report indicating a sex-specific longevity of *B. latro*. Tag-recapture experiments over longer periods and the use of absolute age determinations derived from counting endocuticle growth bands (Kilada et al. 2012) could provide more exact estimations of the life span of *B. latro* and evidence of sex-specific longevity.

Our data show that growth patterns differ between males and females (Fig. 3). Both L_∞ and φ' were much higher in males than in females (Table 4). Differences in growth patterns between sexes (sexual size dimorphism) are common in many other species of crabs (Hartnoll 1982). In crustaceans, growth and reproduction are antagonistic process competing for the same energy resources (Hartnoll 1985). After reaching sexual maturity, females allocate more energy to reproduction than males of the same age (Hartnoll 1985, Hartnoll et al. 2006), and thus growth rates of females can decrease (e.g. Annala & Bycroft 1988, McGarvey et al. 1999), according to the 'reproductive drain hypothesis' (Pauly 1998). Mature female coconut crabs extrude one clutch of eggs per year (Sato & Yoseda 2008), with each clutch accounting for as much as one-third of their body weight (Helfman 1973). In addition, coconut crab females have to spend a longer period of time than males in coastal areas, where food supply is scarce, while they are incubating eggs and releasing larvae (Sato & Yoseda 2013), reducing the period when females can feed compared with males. These energetic costs may explain the smaller L_∞ and slower growth rate of females (Fig. 3 & 4).

However, the present study also provided unexpected evidence of a difference in sex-specific growth during the juvenile stage. Female juveniles (at 50% sexual maturity) were smaller than males of the same age (Fig. 3). Thus growth was already differentiated between the sexes, prior to females reaching sexual maturity and allocating energy to reproduction. Fletcher (1993) also reported sex-specific growth of juvenile coconut crabs in the northern part of the Vanuatu archipelago, although his study pro-

vided no accurate data on female growth. Similar slower growth of females during juvenile stage was reported for *Jasus edwardsii* by Linnane et al. (2012) who suggested that female somatic growth can be slowed by the internal development of reproductive organs before sexual maturity. Coconut crab females may require larger amounts of energy to reach sexual maturity due to the larger investment in energy needed to develop the reproductive organ that produces the huge masses of eggs. The internal development of reproductive organs before sexual maturity may be a reason why coconut crab females reach sexual maturity much later than males (Table 5). Females of *J. edwardsii* also reach sexual maturity later than males (Turner et al. 2002, Linnane et al. 2008).

However, the reproductive drain hypothesis does not hold in all cases. Females can become larger, or much larger, than males in some crustaceans (e.g. Bergström 1992, Stewart & Kennelly 2000, Béguer et al. 2011, Ahamed & Ohtomi 2012, Baeza & Asorey 2012) and most fishes (Pauly 1994). The faster growth in females is considered to be a life history strategy, enabling females to attain a larger size and increase egg production (Berglund 1981). Differences in growth patterns between sexes (sexual size dimorphism) are associated with not only the energetic costs but also sexual selection. Male sexual competition is considered an important evolutionary force driving sexual dimorphism in body size (Baeza & Asorey 2012). When male sexual competition for receptive females is intense, males are expected to attain larger body sizes than females, and this increasing investment in body size by males augments their resource holding potential and, thus, their capacity to access and defend receptive females from rival males (Baeza & Thiel 2007). In the coconut crab, a larger size confers advantage in struggles with other individuals for physical control, regardless of sex (Helfman 1979). Furthermore, Sato & Yoseda (2010) revealed that larger coconut crab males are preferred by females as a mate in laboratory experiments. The female preference for larger males is one of the main causes of size-assortative mating (larger males mate with larger females) in wild populations (Sato & Yoseda 2010).

We found that the estimated L_∞ (69.87 mm) of males (Table 4) was lower than previously reported for coconut crabs in the northern part of the Vanuatu archipelago ($L_\infty = 80.00$ mm) (Fletcher et al. 1991a). Estimated L_∞ of females in the present study was also about 10 mm smaller than as described by Fletcher (1993). Growth in decapods is usually described in

terms of 2 components: (1) the frequency of molting (intermolt period) and (2) the size increment at each molting (molt increment) (Aiken 1980). Growth rates of crustaceans can be affected by several factors, with temperature being a major environmental factor (Hartnoll 1982). Warm temperatures increase growth rates by shortening intermolt periods (e.g. Hazell et al. 2001). Port Vila, the capital of Vanuatu, has an average temperature of 25°C with August being the coolest month (averaging 23°C) and February the warmest (27°C) (Vanuatu Climate Center, www. meteo.gov.vu). Temperatures at Hatoma Island are lower: the annual average is 23.7 ± 3.7°C (mean ± SD), and monthly temperatures range between 18.2 ± 2.0°C and 27.9 ± 0.5°C in the coolest and warmest months, respectively (T. Sato unpubl. data). In coconut crabs, molting frequency has been reported to change in response to sexual maturity, from several times to once per year. For example, in Vanuatu, juvenile coconut crabs molt up to 3 times per year, whereas adults molt once per year (Fletcher et al. 1990). On Hatoma Island, adult crabs molt once per year, as shown by the relationship between wintering and ThL (Fig. 2), but there are no data about juveniles. The difference in temperature between the 2 study sites may affect juvenile molting frequency and/or the degree of molt increment, resulting in the different growth pattern.

Molt increments of crustaceans are affected by nutrition (Aiken 1980, Melville-Smith et al. 1997). Food supply can influence crustacean growth, affecting both maximum size attained and the growth rate (Mason 1963, Hartnoll 1982, Gu et al. 1996). Growth of coconut crabs has been suggested to be strongly linked with food supply (Drew et al. 2010). Different kinds of diets can also influence crustacean growth rates (Mayfield et al. 2000, Gendron et al. 2001). The differences in abundance and/or variability of foods between Vanuatu and Hatoma Island may result in the different growth patterns observed. Population density can also influence growth rate through competition for food. In addition, population density can be affected by, for example, harvesting pressure. At present, it is difficult to determine the causes of the differences in growth rate and L_∞ observed in coconut crabs resident on Vanuatu and Hatoma Island because there is no comparable data on food availability, population density, or harvesting pressure on Vanuatu. Investigations into these topics would provide insights into the differences in growth patterns between regions.

However, the results presented here should be considered preliminary. Although interindividual dif-

ferences in observed growth were high in the present study (Fig. 2, Table 2), the numbers of recaptured individuals were small and the ranges of size of recaptured crabs were narrow in both sexes, which made it difficult to accurately estimate L_∞ and K for males and females of *Birgus latro*. Especially in males, the 95 % CI showed a wide range (Fig. 3). A larger sample size would enable more accurate estimates of growth rate, as well as providing insights into the reasons underlying interindividual differences. Data on juveniles are also required to provide more accurate information on growth over the life span of the coconut crab, and thereby improve the accuracy of resource assessments. Future long-term mark-recapture studies using PIT tags may identify resource-specific differences in growth patterns and identify the causes of the large variations in observed growth.

To our knowledge, this study is the first to provide growth estimates of a wild population of coconut crabs based on mark-recapture over multiple years using PIT tags. Potentially long-lived, slow growing species, such as coconut crabs, are susceptible to overharvesting, justifying a cautious approach to resource management of *Birgus latro*. Slot size limits with male-only harvesting (Sato & Yoseda 2010, Sato et al. 2010, Sato & Suzuki 2010, Sato 2011), seasonal (Sato & Yoseda 2009) and area closures (Sato & Yoseda 2013), and conservation of suitable habitats (Sato & Yoseda 2013) have been recommended to maintain the reproductive rate of coconut crabs. Combinations of these and other management measures should be considered (Sato 2012) in order to limit exploitation and maintain the viability of this vulnerable resource.

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