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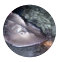

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ORIGINAL PAPER

Change in population structure, growth and mortality rate of juvenile green turtle (*Chelonia mydas*) after the decline of the sea turtle fishery in Yaeyama Islands, Ryukyu Archipelago

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Abstract The Yaeyama Islands provide habitat for juvenile green turtles originating from various rookeries in the western Pacific. The sea turtle fishery has been declining since 2004 due to the retirement of sea turtle fishermen in the region. We investigated the population ecology of green turtles based on capture–mark–recapture data from 1995 to 2016. The effect of the past sea turtle fishery on the green turtle population was analyzed by comparing the population structure, growth and mortality rates during 1995–2003, with those of the population in 2004–2016. Mean straight carapace lengths of green turtles in 1995–2003 were 51.5 cm (SD = 10.9, range 34.0–102.4, $N = 838$), annual growth rates were 2.7 cm year^{-1} (SD = 1.31, range 0.09–5.32, $N = 50$), and mortality rates were 0.25 year^{-1} (95% CI 0.20–0.30). In comparison, mean straight carapace length of green turtles in 2004–2016 was 55.5 cm (SD = 12.1, range 6.2–96.5, $N = 595$), growth rates were 2.24 cm year^{-1} (SD = 0.78, range 0.79–4.17, $N = 67$) and mortality rates were 0.15 year^{-1} (95% CI 0.11–0.19). Carapace size increased and annual growth and mortality rates decreased after 2004. The increase in the number of larger-sized green turtles and the decrease in mortality rates were likely effects of the decline in the sea turtle fishery.

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Introduction

The green turtle (*Chelonia mydas*) has a circumglobal distribution, mainly occurring in tropical and subtropical waters, and is listed as globally endangered on the IUCN Red List (IUCN 2008). Several studies have investigated the population structure, migration, growth and mortality rates of juvenile green turtles based on long-term capture–mark–recapture data during long-term monitoring, for example, the Great Barrier Reef (Limpus and Chaloupka 1997; Chaloupka and Limpus 2005), Hawaii Islands (Balazs et al. 2015), Baja California (Seminoff et al. 2003; Koch et al. 2007; López-Castro et al. 2010), Galápagos Islands (Zárate et al. 2015), Colombian Pacific (Sampson et al. 2015), Bahamas (Bjorndal et al. 2000, 2003), Puerto Rico (Patrício et al. 2014) and Brazil (Colman et al. 2014). In western North Pacific including Japan, the genetic structure of juveniles (Hamabata et al. 2009), migration patterns (Shimada et al. 2014; Fukuoka et al. 2015) and size distribution (Cheng and Chen 1997; Suganuma et al. 2010; Kameda et al. 2013a) of green turtles have been investigated previously. Tanaka (2009) reported the growth rates of green turtles on the Ogasawara

Islands; however, sample size was limited to juveniles released by the Head Start program in the region. Consequently, growth and mortality rates of green turtles in the western North Pacific are not completely understood.

The Yaeyama Islands are located at the southern end of the Ryukyu Archipelago in Japan and belong to the Okinawa Prefecture. This region is also the main green turtle nesting beach in Japan (Kamezaki 1989). Juvenile and mature green turtles inhabit these coastal areas, originating from various Pacific rookeries in the Yaeyama, Ogasawara and western Pacific (Nishizawa et al. 2013). Sea turtles have been captured in this region for consumption, as well as for taxidermy and sale to tourists and local peoples. Licensed sea turtle fishermen can legally catch sea turtles for local consumption in Okinawa Prefecture, and juvenile green turtles have been heavily harvested for food from after end of the World War II. The sea turtle fishery has been declining due to a decrease in consumption of turtle meat caused by cultural changes in diet and awareness of sea turtle conservation. Sea turtle fishing was active in the Yaeyama Island region until the 1990s, with more than 90% of sea turtles being caught by fisheries (Abe et al. 2003). When most fishermen retired in 2003, the number of harvested sea turtles in Okinawa Prefecture decreased from 200 (1989–2003) to 40 (after 2004) (Okinawa Prefectural Government; http://www.pref.okinawa.jp/site/norin/suisan/kaiku/index.html). Additionally, the number of green turtle spotted by local divers and fishermen has increased in recent years (Ishihara et al. 2014).

Kuroshima Research Station (formerly Yaeyama Marine Research Center) has been monitoring green turtle coastal foraging areas on the Yaeyama Islands since 1995. The main objective of the present study was to investigate the population ecology of green turtles in this region. The effect of the past sea turtle fishery on the green turtle population was analyzed by comparing population structure, growth and mortality rates of the population in 1995–2003 with those of the population in 2004–2016.

Methods

Study area

The Yaeyama Islands are located at the southern end of Ryukyu Archipelago and have one of the largest coral reefs in Japan (N24°00′–N24°40′; E122°45′–E124°30, Fig. 1). Water depth of the inner reef is 2–6 m, and that of the outer reef is >20 m. Tidal range is about 2 m during the spring tide. Average annual water temperature was 26.0 °C, and seasonal range was 20.8–29.8 °C at a depth of 5 m in the inner reef (Ministry of the Environment; http://www.e-monitoring.jp/). The islands are surrounded by coral reefs, although sea grass and sea algae flourish in the sandy regions of the inner reefs. The fishing industry is flourishing, including spear fishing, small set and gill nets, and however does not include large set nets or round haul nets (Ministry of Agriculture, Forestry and Fisheries; http://www.maff.go.jp/j/tokei/census/fc/). This region is also a popular tourist destination for diving and snorkeling.

Sea turtle capture and data collection

Turtles were captured by several local fishermen with a license from Fisheries Adjustment Commission of Okinawa Prefecture from January 1995 to March 2016. Local fishermen searched for resting sea turtles in the outer reef area by snorkeling and dive capturing. In addition, surveys using entanglement nets (200 m long, 2 m high, 40 cm mesh size) have been conducted since 2009. The net was set in the inner reef area. Green turtles in this region move from the outer reef area to the inner reef area to forage on sea grass (Okuyama et al. 2013). Therefore, captured sea turtles were not clustered into outer reef and inner reef groups.

The turtles were transported to an outdoor flow-through saltwater tank at the Kuroshima Research Station, Sea Turtle Association of Japan (N24°14′24.0″ E123°59′36.4″), where they were retained for 1 day to up to 1 month to conduct research. Straight carapace length (SCL) was measured using metal calipers to the nearest 0.1 cm (Kamezaki and Suganuma 1991), and turtles were tagged with an Inconel tag (Style 681; National Band and Tag Company, Newport, KY, USA) or a plastic tag (Jambo Tag; Dalton Tags, Nottingham, England) from the Sea Turtle Association of Japan (nonprofit organization; http://www.umigame.org/) proximal to the first large scale on both rear flippers.

Population structure

Size data from the first capture were used for the data analysis, even when the same sea turtle was recaptured, in order to prevent data bias. The population structure in 1995–2003 (group 1) and 2004–2016 (group 2) was compared using the Chi-square test. A turtle with SCL of 93 cm was considered an adult, which was an intermediate size between mature males (91 cm) and females (95 cm) captured near the Ogasawara Islands (Tachikawa 1991).

Growth rate

Annual growth rates were calculated as (SCL final−SCL initial)/recapture interval, which is the time interval in days between the first and last captures of a given turtle. Growth based on mean SCL was set as the mean value between the final and initial SCL. For example, if a 50-cm turtle was captured and recaptured after 900 days, with a size of 60 cm, the SCL value would be 55 cm (mean between 50

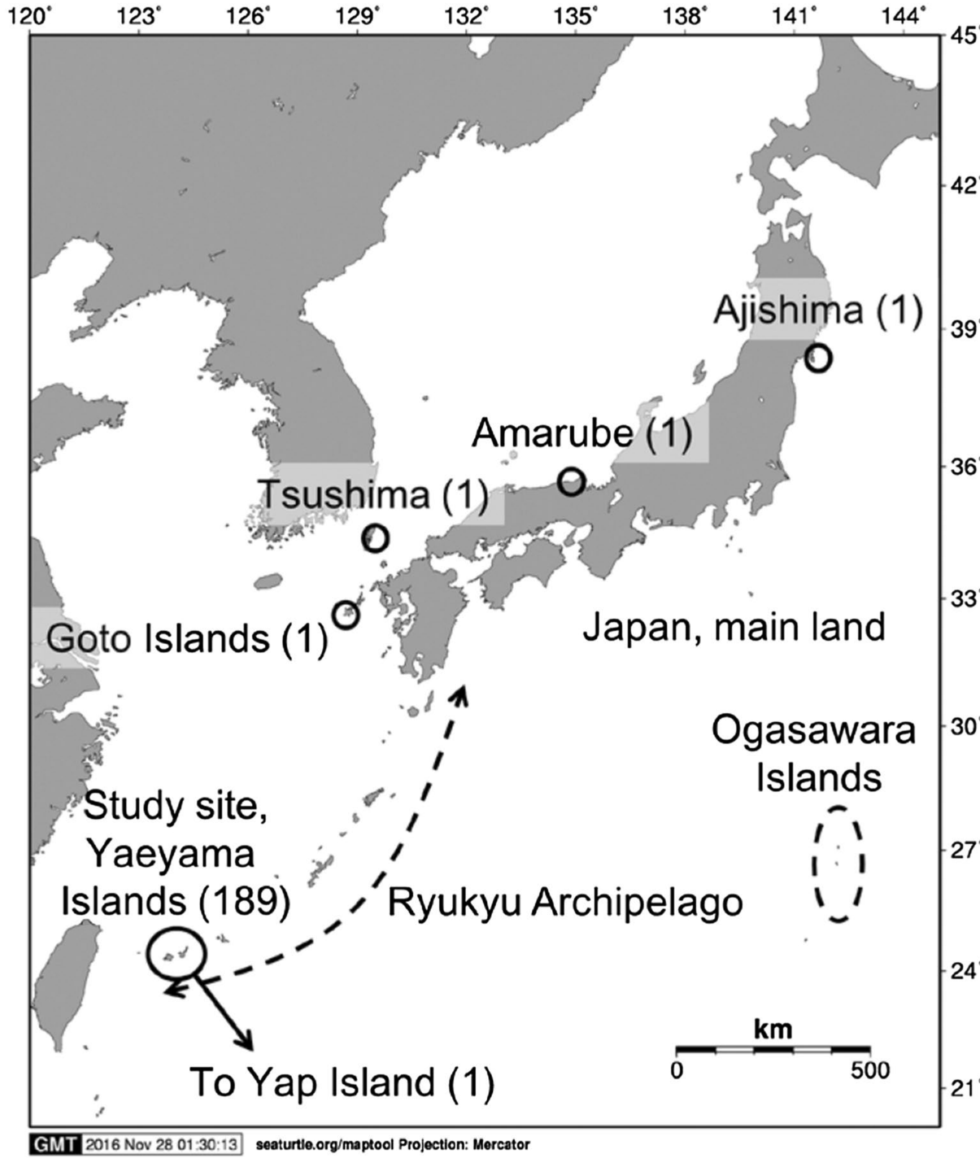

Fig. 1 Map of the Yaeyama Islands and the recapture points showing number of recaptured green turtles

and 60 cm). Thus, growth rate would be: [(60 − 50 cm)/900 days × 365] = 4.05 cm. If the recapture interval is short, the annual growth rate estimate can be dramatically affected by measurement error and seasonal effect (Chaloupka and Musick 1997; Seminoff et al. 2002). Therefore, in this study, only turtles recaptured >11 months after being released were used in analyses (Bjorndal et al. 2000). Furthermore, the turtles were classified into two groups, 1995–2003 and 2004–2016, according to the years they were recaptured. For example, if a turtle was released in 1998 and recaptured in 2005, it was classified into the 1995–2003 group because years spent before recapturing were longer in period of 1995–2003 (1998–2003: 5 years) compared to 2004–2016 (2004–2005: 1 year). Turtles were retained up to 1 month, and the possibility of artificial change in growth cannot be denied. Therefore, growth rates analysis were conducted by linear regression analysis to confirm the influence of retained days to growth rate. A two-sample unequal variance *t* test was used to calculate statistical differences using Excel (Microsoft Inc., Redmond, WA, USA).

Mortality

Green turtle mortality rates (Z) were estimated by the linearized length converted catch curve (Sparre and Venema 1998). Growth rates were used to estimate the growth parameter (K), and the value was inserted into the von Bertalanffy growth function (VBGF):

$$\mathrm{SCL}t = \mathrm{SCL}\infty \times \left(1 - \exp^{(-k \times t)}\right),$$

where SCLt is the straight carapace length at time (t); SCL∞ is asymptotic SCL; K is the von Bertalanffy growth constant, and exp is an exponential function.

The age of each size class was estimated by the VBGF. Mortality rate of each size class was estimated by the age of each size class and the size frequency distribution of the population. Mortality rates (Z) were expressed using the following equation:

$$\mathrm{Ln}(N/t\Delta) = C - Z \times \mathrm{Age},$$

where Ln is the natural logarithm, N is number of individuals from SCL$t2$ to SCL$t1$, $t\Delta$ is age from SCL$t2$ to SCL$t1$, Age is age of midsize turtles from SCL$t2$ to SCL$t1$, and C is the intercept.

The slope test was used to compare mortality rates between the 1995–2003 (group 1) and 2004–2016 (group 2) (Tomikawa and Uchiyama 2004). The slope test was used to detect significant differences in the two regression lines of slope (b), using the following equations:

Group 1; $y = a_1 + b_1 x$, group 2; $y = a_2 + b_2 x$

$$S_1 = S_{y1}(1 - R_1^2),$$

$$S_2 = S_{y2}(1 - R_2^2),$$

$$S = \sqrt{\frac{S_1 + S_2}{n_1 + n_2 - 4}},$$

$$t_1 = \frac{|b1 - b2|}{S\sqrt{1/S_{x1} + 1/S_{x2}}},$$

$t_2 = t$ value of $P < 0.05$, $df\,[(n_1-2) + (n_2-2)]$

where Sx_1, Sx_2, Sy_1 and Sy_2 are the sum of squared deviations for groups 1 and 2, R_1^2, R_2^2 are the correlation coefficients for groups 1 and 2, n_1 and n_2 are the sample sizes for groups 1 and 2, and b_1 and b_2 are the slopes for groups 1 and 2. If t_1 was larger than t_2, slope (b_1) and slope (b_2) were considered significantly different.

Results

Turtle captures and recapture locations

A total of 1433 turtles were caught in water off Yaeyama Islands. We measured 838 turtles that were dive-captured by several local fishermen from 1995 to 2003; from these, 318 turtles were tagged and released, and 520 sea turtles were used as food or to stuffed. From 2004 to 2016, 595 turtles were tagged and released; of these, 317 were caught by local fishermen and 278 turtles were captured using entanglement nets.

Out of 194 recaptured turtles, 189 were recaptured in the Yaeyama Islands (Fig. 1). One hundred and forty-five of these were recaptured once, 35 were recaptured twice, 8 were recaptured three times, and 1 turtle was recaptured 4 times. Other recapture locations were the Goto Islands (distance to 1040 km), Tsushima (distance to 1206 km), Amarube (distance to 1620 km), Ajishima (distance to 2305 km) and Yap Island (distance to 2330 km). One turtle was recaptured once in each region. Recapture intervals varied from 13 to 5025 days.

Population structure

The size distribution of turtles was strongly skewed toward smaller turtles on both periods (1995–2003 and 2004–2016), and the 40.0–49.9-cm size class was predominant (Fig. 2). The majority of turtles (99%) were immature (<93 cm SCL). Mean SCL was 51.5 cm (standard deviation [SD] = 10.9, range 34.0–102.4, $N = 838$) in 1995–2003 and 55.5 cm (SD = 12.1, range 36.2–96.5, $N = 595$) in 2004–2016. The mean size of turtles captured was >55.0 cm in 2004–2016 (Fig. 2), which is larger than the turtles caught in 1995–2003. The catch frequency of turtles >55.0 cm SCL was higher in 2004–2016 than in 1995–2003 (Chi-square test $\chi 1 = 43.4$, $P < 0.01$). In total, 612 sea turtles (73%) were <54.9 and 226 (27%) were >55.0 cm SCL in 1995–2003, whereas 335 turtles (56%) were <54.9 cm and 260 sea turtles (44%) were >55.0 cm in 2004–2016.

Growth rates

A total of 117 turtles were recaptured at intervals >11 months; 50 were recaptured in 1995–2003 and 67

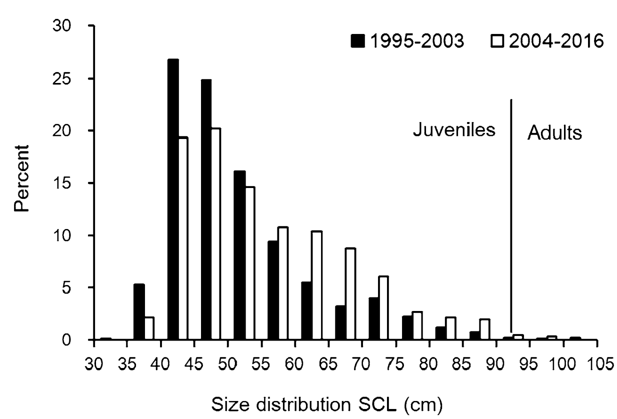

Fig. 2 Size distribution of green turtles caught in the Yaeyama Islands. Measurement data are values taken from the first capture ($N = 838$ in 1995–2003, $N = 595$ in 2004–2016)

were recaptured in 2003–2016. Those growth rate dates did not sufficiently correlate with retained days in this study ($r2 = 0.0018$, $F115 = 0.20$, $P = 0.65$, Fig. 3). Mean growth rates were 2.7 cm year^{-1} (SD = 1.31, range 0.09–5.32) in 1995–2003 and 2.2 cm year^{-1} (SD = 0.78, range 0.79–4.17) in 2004–2016. Negative growth rate was not confirmed in this study. Growth rates differed significantly between the two periods ($t74 = 2.34$, $P < 0.05$). A third-order polynomial equation was used to determine the maximum growth of 3.31 cm year^{-1} at 59.2 cm SCL in 1995–2003 and 2.47 cm year^{-1} at 60.8 cm SCL in 2004–2016 (Fig. 4). Growth rates of similar-sized turtles varied considerably, which resulted in a low correlation coefficient ($r^2 = 0.195$ in 1995–2003, $r^2 = 0.019$ in 2004–2016).

Mortality rates

The Gulland and Holt (1959) plot method did not produce a usable regression line for L∞.

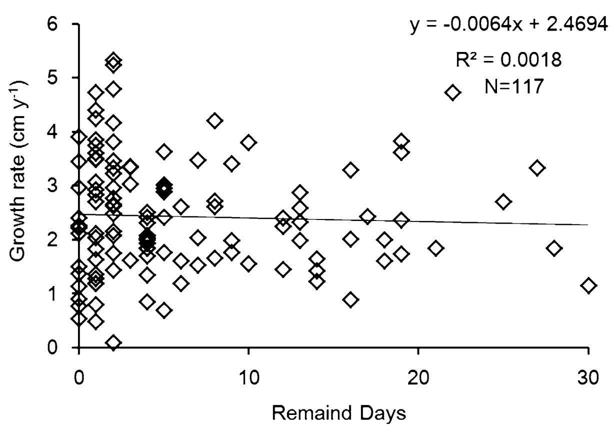

Fig. 3 Correlation between remained days and growth rate

Accordingly, the von Bertalanffy growth constant (K) was calculated based on the assumption that L∞ was 102.4 cm SCL in 1995–2003 and 96.5 cm SCL in 2004–2016, which is the maximum size in both groups (known as a forced Gulland and Hot plot; Pauly 1983). As a result, the K values were 0.067 in 1995–2003 and 0.054 in 2004–2016. Therefore, the VBGF was defined as $SCLt = 102.4\ (1-\exp^{-0.067 \times t})$ in 1995–2003 and $SCLt = 96.5\ (1-\exp^{-0.054 \times t})$ in 2004–2016. The length converted catch curve was calculated using VBGF and the size distribution (Table 1). To calculate the estimated total mortality rate, the three points on the right side of the graph were excluded from the regression since the age calculation was unreliable in large individuals. The points used in the regression analysis were $Z \times \Delta t < 1$ (Sparre and Venema 1998). The three points on the left side were excluded due to the increase in the number of turtles (Table 1). Total mortality rates derived from the length converted catch curve were 0.25 year^{-1} (95% confidence interval [CI] 0.20–0.30) in 1995–2003 and 0.15 year^{-1} (95% CI 0.11–0.19) in 2004–2016 (Fig. 5). Total mortality rates in 1995–2003 were greater than that in 2004–2016 (Slope test, $t11 = 4.8$, $P < 0.01$), which corresponded to an estimated annual survival rate of 0.75 (95% CI 0.70–0.80) and 0.85 (95% CI 0.81–0.89) in 1995–2003 and 2004–2016, respectively.

Discussion

Size distribution

The life cycle of green turtles begins with hatchlings swimming out to pelagic waters. After inhabiting that environment until they grow to juvenile size, they migrate to more shallow waters near the coast (Hirth 1997). The size of

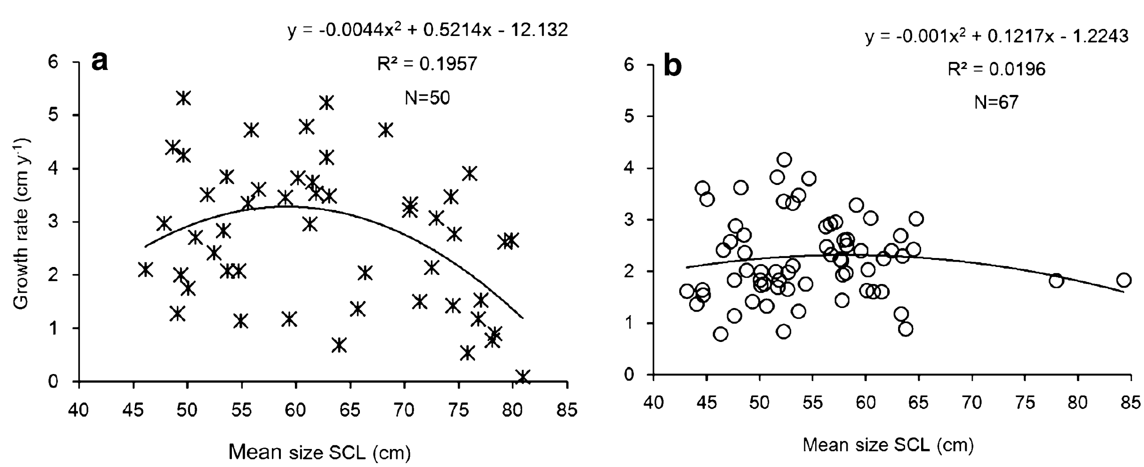

Fig. 4 Annual growth rates of green turtles from 1995–2003 (**a**) and 2004–2016 (**b**). A third-order polynomial was fitted to show the data trend

Table 1 Linearized catch curve based on length composition data for green turtle in the Yaeyama Islands from (a) 1995 to 2003 and (b) 2004 to 2016

SCL(L1–L2)	*N*	Age of L1	*t*Δ	Age of mean size *L*1 and *L*2	Ln (*N*/*t*Δ)	*Z*	95% confidence limit	Remarks
(a) 1995 to 2003								
30.0–35.0	1	5.14	1.06	6	−0.1			Not used; not decline of number
35.0–39.9	44	6.202	1.143	6.773	3.651			
40.0–44.9	224	7.345	1.238	7.964	5.198			
45.0–49.9	208	8.583	1.351	9.259	5.036			Portion used in the regression analysis
50.0–54.9	135	9.934	1.487	10.678	4.509			
55.0–59.9	79	11.421	1.653	12.248	3.867	0.392	0.134	
60.0–64.9	46	13.074	1.861	14.005	3.208	0.388	0.021	
65.0–69.9	27	14.935	2.128	15.999	2.541	0.374	0.024	
70.0–74.9	34	17.063	2.485	18.306	2.616	0.290	0.116	
75.0–79.9	19	19.548	2.988	21.042	1.850	0.264	0.077	
80.0–84.9	10	22.536	3.745	24.409	0.982	0.254	0.051	
85.0–89.9	6	26.281	5.023	28.793	0.178	0.240	0.037	Not used; too close to SCL∞
90.0–94.9	2	31.305	7.654	35.132	−1.342	0.235	0.025	
95.0–99.9	1	38.959	16.696	47.307	−2.815	0.207	0.025	
100.0<	2	55.656						
(b) 2004 to 2016								
35.0–39.9	13	8.368	1.575	9.155	2.11			Not used; not decline of number
40.0–44.9	115	9.943	1.721	10.803	4.20			
45.0–49.9	120	11.664	1.897	12.612	4.15			
50.0–54.9	87	13.561	2.113	14.617	3.72			Portion used in the regression analysis
55.0–59.9	64	15.674	2.385	16.866	3.29			
60.0–64.9	62	18.058	2.736	19.426	3.12	0.123	1.240	
65.0–69.9	52	20.795	3.210	22.400	2.78	0.114	0.234	
70.0–74.9	36	24.005	3.884	25.947	2.23	0.124	0.104	
75.0–79.9	16	27.889	4.916	30.347	1.18	0.152	0.048	
80.0–84.9	13	32.805	6.705	36.158	0.58	0.146	0.036	
85.0–89.9	12	39.511	10.597	44.809	0.12	0.127	0.038	Not used; too close to SCL∞
90.0–94.9	3	50.108	27.236	63.726	−2.21	0.120	0.026	
95.0–99.9	2	77.344						

N number of individuals from L1 to L2, *Age* estimated age from the von Bertalanffy growth function, *t*Δ years to grow from L1 to L2; *Ln* natural logarithm, *Z* mortality rate

recruited sea turtles in this study was 35.0–44.9 cm, which is consistent with the size of pelagic juvenile turtles at the stage of switching to a neritic lifestyle in other Pacific regions, such as the Hawaiian Islands, the Great Barrier Reef and Mantanani, Malaysia (Balazs and Chaloupka 2004; Limpus and Chaloupka 1997; Pilcher 2010). The size distribution of green turtles at the Yaeyama Islands showed that 99% of them were juvenile and >90% of the recapture locations were at the Yaeyama Islands, suggesting that green turtles at the Yaeyama Islands settle in this foraging ground until they reach maturity. The size distribution of sea turtles captured in 2004–2016 was larger than those captured in 1995–2003. The larger-sized turtles during the most recent period may have resulted from a decline in local green turtle harvesting and a decreased mortality rate, allowing larger individuals to forage within the area.

Growth rates

Mean growth rates in 1995–2003 were 2.7 cm year^{-1}, and the maximum growth rate calculated was 3.31 cm year^{-1} at 59.2 cm SCL in this study. This value was higher than the rates reported for other Pacific regions before 2004, such as in the Great Barrier Reef, where the growth rate was 2.2 cm year^{-1} (Limpus and Chaloupka 1997) and 2.1 cm in the Hawaiian Islands (Balazs and Chaloupka 2004). Mean growth rates in the Gulf of California were 1.4 cm year^{-1} (Seminoff et al. 2002) and 1.62 cm year^{-1}

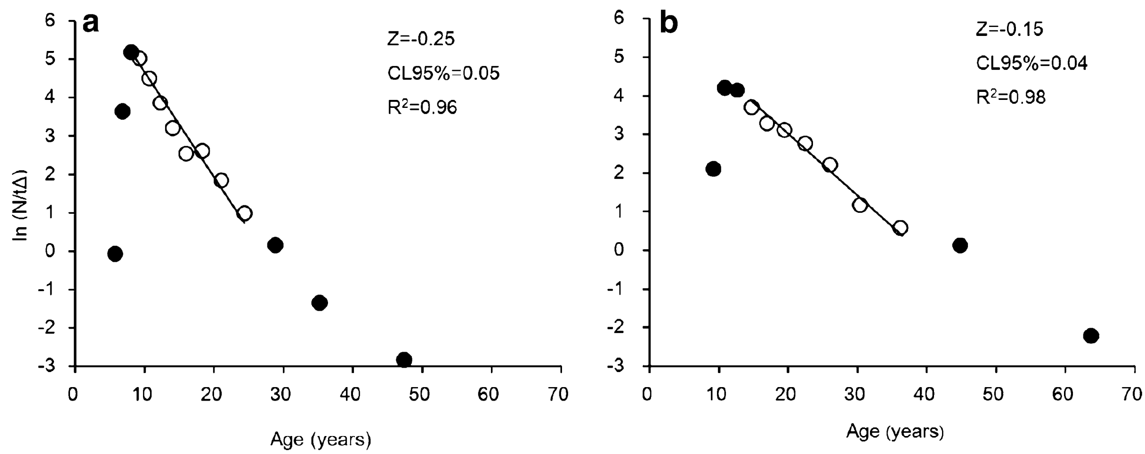

Fig. 5 Length-converted catch curve for green turtles on the Yaeyama Islands, 1995–2003 (**a**) and 2004–2016 (**b**). *Open circle* used in regression, and *closed circle* not used in regression. The rightmost two to three points in the graph were excluded because they were too close to asymptotic straight carapace length (SCL∞). The left most two to three points were not used because the turtles in those areas are not being exploited (Sparre and Venema 1998)

in Bahia Magdalena, Mexico (Koch et al. 2007). Mean growth rate in 2004–2016 was 2.2 cm year^{-1} in this study. This value was higher than Galápagos Islands where the growth rate was 0.8 cm year^{-1} (Zárate et al. 2015) and 0.74 cm year^{-1} the Gorgona National Park (Sampson et al. 2015). One possible explanation is that the water around the Yaeyama Islands might be superior foraging grounds, leading to faster growth rates for green turtles in the Pacific.

The growth rate of green turtles is reportedly affected by water temperature, sea turtle density, food quality and abundance (Kubis et al. 2009; Bjorndal et al. 2000; Balazs and Chaloupka 2004; Eguchi et al. 2012). Among those factors, water temperature is strong effecter of growth rate (Eguchi et al. 2012). During winter, water temperatures of Yaeyama Islands fall to about 21 °C, but Bahia Magdalena falls to about 16 °C. Growth rates of green turtles in Bahia Magdalena declined to 0.08 month^{-1} into winter season (Koch et al. 2007). In addition, green turtles in Yaeyama feed on sea grass and algae (Kameda and Ishihara 2008, Shimada et al. 2014) while green turtles in Gorgona National Park feed on algae and tunicates (Amorocho and Reina 2007). Reports have been made on turtles foraging more on jellyfish, fish carcass and floating vegetation having slower growth rates compared to turtles feeding primarily on algae (Kubis et al. 2009). Availability of algae might have been low in Gorgona National Park due to its geographical feature, resulting in slower growth rate (Sampson et al. 2015). Therefore, this difference of growth rates between Yaeyama Island and Magdalena/Gorgona National Park is likely to be caused by difference of water temperature and food abundance. Food resources of green turtle in Hawaii Islands and Great Barrier Reef are sea grass and algae (Fuentes et al. 2006; Arthur and Balazs 2008; Arthur et al. 2009), similar to Yaeyama Islands, but growth rate in Yaeyama Island was higher than both region. Green turtles of Yaeyama Island have been heavily harvested after the World War II, resulting in richer amount of food resource for each green turtle. This abundance in food and low green turtle density may have contributed to higher growth rate. Sea turtle growth rate is affected by various factors, and further comprehensive study is required.

Growth rates in 2004–2016 were slower than in 1995–2003. Large-scale disappearance of sea grass and seaweed beds has not been reported in the Yaeyama Island region. Therefore, the loss of foraging grounds itself is difficult to consider as an explanation for slower growth rates. Juvenile green turtles in this area originate from various Pacific rookeries in the western Pacific, particularly Iriomote Island and Ishigaki Island in the Yaeyama and Ogasawara Islands (Nishizawa et al. 2013), and the number of nests in those green turtle rookeries has increased (Abe et al. 2003; Chaloupka et al. 2008; Kameda et al. 2017). Accordingly, the decline of growth rates in 2004–2016 may be due to a higher density of juvenile green turtles within the area, resulting from an increase in the number of green turtles from the Yaeyama and Ogasawara Islands swimming to this region as well as a decline in mortality rates.

Mortality rates

The use of the VBGF model to sea turtle is thought to be unsuitable for estimating age, because growth rates of sea turtles changes through the postnatal development phase (Chaloupka and Musick 1997). However, the actual differences among a variety of growth models in same phase were rather small (Bjorndal et al. 2000). In addition, VBGFs is standard assessment method of calculating mortality rate (Sparre and Venema 1998). VBGFs in this study was calculated from capture–mark–recapture data of juvenile size (size range about 45–80 cm, Fig. 4). Estimated years required for juveniles to grow from 45 to 80 cm are 13.9 years in 1995–2003 and 21.1 years in 2004–2016 (Table 1). Collaborating with mortality rates, the survival number was only 1.8 out of 100 turtles (survival rate 0.75 ^ 13.9 years) before 2003, and 3.2 out of 100 turtles (survival rate 0.85 ^ 21.1 years) after 2004 past sea turtle fishery. Because green turtles return to natal beach for reproduction (Bowen and Karl 2007) and green turtles in this area come from various Pacific rookeries in the western Pacific (Nishizawa et al. 2013), decline of mortality rate in Yaeyama Islands may contribute to the recovery of the number of nesting sea turtle in western Pacific rookeries.

Several studies have estimated the survival probability of juvenile green turtles worldwide. The numbers are 0.85 $year^{-1}$ in Bahia Magdalena, Mexico (Koch et al. 2007), 0.88 $year^{-1}$ in the south Great Barrier Reef (Chaloupka and Limpus 2005), 0.89 $year^{-1}$ in Union Creek, Bahamas (Bjorndal et al. 2003), 0.56 $year^{-1}$ in Nicaragua (Campbell and Lagueux 2005) and 0.85 $year^{-1}$ in Brazil (Colman et al. 2014). Among these, Union Creek is considered the most pristine site, as the area is unaffected by human activities. On the other hand, the mortality rate in Nicaragua is high due to the sea turtle fishery. The survival probability of 0.75 $year^{-1}$ in 1995–2003 was lower than the ones observed in Bahia Magdalena, Great Barrier Reef or Union Creek, which may be a result of the sea turtle fishery on the Yaeyama Islands, and similar to what has caused the high mortality rate in Nicaragua. The survival probability recovered from 0.75 $year^{-1}$ in 1995–2003 to 0.85 $year^{-1}$ in 2004–2016. However, the value did not reach the survival probability seen on Union Creek. Recovery may have been triggered by the decline in the sea turtle fishery. Moreover, large-sized pound nets increase sea turtle by-catch, but are not used in the Yaeyama Islands (Ishihara et al. 2014). This may also have contributed to improve survival probability. However, the juvenile green turtles in this area were by-caught in small gill and set nets (Kameda et al. 2013b), which is probably why survival did not approach the value at Union Creek.

Conclusion

Our study provides the first analysis on biological data from the green turtle population on the Yaeyama Islands, based on long-term capture–mark–recapture data. Monitoring growth and mortality rates is important for the conservation of the green turtle population, since they ultimately reflect population density and fishing pressure, including by-catch. Our study suggests the recovery of green turtle population after the decrease in fishing activity. This is also supported by indirect evidence of decrease in growth rate and increase in number of nest at rookeries in this region. However, by-catch is still on going even with the smallest set nets and gill net. Concrete confirmation of population recovery is possible after obtaining catch per unit effort and abundance data. Meanwhile, green turtles that have not demand as food are obstacle to the fishermen because sea turtles break fishing gear and decrease the size of sea grass beds. Local fishermen see no advantage in protecting the sea turtles since increase in sea turtle number may affect their income. Future conservation efforts should consider the development of novel by-catch prevention technique, and spread of those newly developed methods. Local fishermen should also be educated the importance of sea turtle conservation.

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Compliance and ethical standards

Conflict of interest The authors declare no conflicts of interest. All turtles were captured with permission from the Okinawa Prefecture Government.

References

Abe O, Shibuno T, Takada Y, Hashimoto K, Tanizaki S, Ishii H, Funakura Y, Sano K, Okumura Y (2003) Nesting populations of sea turtle in Ishigaki Island, Okinawa. In: Proceedings of the 4th SEASTAR2000 Workshop. Graduate school of Informatics, Kyoto University, pp 40–43

Amorocho DF, Reina RD (2007) Feeding ecology of the East Pacific green sea turtle *Chelonia mydas* agassizii at Gorgona National Park, Colombia. Endang Species Res 3:43–51

Arthur KE, Balazs GH (2008) A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the Main Hawaiian Islands. Pac Sci 62(2):205–217

Arthur KE, McMahon KM, Limpus CJ, Dennison WC (2009) Feeding ecology of green turtles (*Chelonia mydas*) from Shoalwater Bay, Australia. Mar Turt Newsl 123:6–12

Balazs G, Chaloupka M (2004) Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. Mar Biol 145:1043–1059

Balazs GH, Van Houtan KS, Hargrove SA, Brunson SM (2015) A review of the demographic features of Hawaiian Green Turtles (*Chelonia mydas*). Chelonian Conser Biol 142(2):119–129

Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. Ecol Appl 10(1):269–282

Bjorndal KA, Bolten AB, Chaloupka MY (2003) Survival probability estimates for immature green turtles *Chelonia mydas* in the Bahamas. Mar Ecol Prog Ser 252:273–281

Bowen BW, Karl SA (2007) Population genetics and phylogeography of sea turtles. Mol Ecol 16:4886–4907. doi:10.1111/j.1365-294X.2007.03542.x

Campbell C, Lagueux C (2005) Survival probability estimates for large juvenile and adult green turtles (*Chelonia mydas*) exposed to an artisanal marine turtle fishery in the western Caribbean. Herpetologica 61(2):91–103

Chaloupka M, Limpus C (2005) Estimates of sex-and age-class-specific survival probabilities for a southern Great Barrier Reef green sea turtle population. Mar Biol 146:1251–1261

Chaloupka MY, Musick JA (1997) Age, growth, and population dynamics. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC, Boca Raton, pp 233–276

Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB, Ehrhart LM, Limpus CJ, Suganuma H, Troëng S, Yamaguchi M (2008) Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Global Ecol Biogeogr 17:297–304. doi:10.1111/j.1466-8238.2007.00367.x

Cheng I-J, Chen T-H (1997) The incidental capture of five species of sea turtles by coastal setnet fisheries in the Eastern waters of Taiwan. Biol Conserv 82:235–239

Colman LP, Patrício ARC, McGowan A, Santos AJB, Marcovaldi MA, Bellini C, Godley BJ (2014) Long-term growth and survival dynamics of green turtles (*Chelonia mydas*) at an isolated tropical archipelago in Brazil. Mar Biol 162(1):111–122. doi:10.1007/s00227-014-2585-5

Eguchi T, Seminoff JA, LeRoux RA, Prosperi D, Dutton DL, Dutton PH (2012) Morphology and growth rates of the green sea turtle (*Chelonia mydas*) in a northern-most temperate foraging ground. Herpetologica 68(1):76–87

Fuentes MMPB, Lawler IR, Gyuris E (2006) Dietary preferences of juvenile green turtles (*Chelonia mydas*) on a tropical reef flat. Wildl Res 33:671–678. doi:10.1071/WR05081

Fukuoka T, Narazaki T, Sato K (2015) Summer-restricted migration of green turtles *Chelonia mydas* to a temperate habitat of northwest Pacific Ocean. Endang Species Res 28:1–10. doi:10.3354/esr00671

Gulland JA, Holt SJ (1959) Estimation of growth parameters for date at unequal time intervals. J Cons CIEM 25(1):47–49

Hamabata T, Nishida S, Kamezaki N, Koike H (2009) Genetic structure of populations of the green turtle (*Chelonia mydas*) in Japan using mtDNA control region sequences. Bull Grad Sch Soc Cult Stud Kyushu Univ 15:35–50

Hirth HF (1997) Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Fish and Wildlife Service US Department of the Interior, Washington

Ishihara T, Kamezaki N, Matsuzawa Y, Ishizaki A (2014) Assessing the status of Japanese coastal fisheries and sea turtle bycatch. Wildl Hum Soc 2(1):23–35 **(in Japanese with English Abstract)**

IUCN (2008) The IUCN red list of threatened species. ISSN2307-8235 (online). http://www.redlist.org Accessed 27 November 2016

Kameda K, Ishihara T (2008) Gut contents analysis of green turtles (*Chelonia mydas*) in Japan. Umigame News Lett 81:17–23 **(in Japanese with English abstract)**

Kameda K, Asari Y, Sugitani K, Wakatsuki M (2013a) Stranding status of sea turtles at Iriomote Island, Okinawa Prefecture, Japan. Umigame Newsl 96:2–8 **(in Japanese with English abstract)**

Kameda K, Wakatsuki M, Kamezaki N (2013b) Population structure and growth rate of the green turtle *Chelonia mydas*, on feeding ground at Kuroshima Island, of Yaeyama group, Ryukyu Archipelago. Biol Mag Okinawa 51:93–100 **(in Japanese with English abstract)**

Kameda K, Wakatsuki M, Iwase F, Kuroyanagi K, Shima T, Kondo T, Misaki H, Asai Y, Sato F, Kotera Y, Kamezaki N (2017) Green turtle track trends and possible nesting threats in Ubu and Sazare hama (Iriomote Island, Japan) from 1984 to 2016. Umigame News Lett 105:13–20 **(in Japanese with English abstract)**

Kamezaki K (1989) The Nesting Sites of Sea Turtles in the Ryukyu Archipelago and Taiwan. In: Matsui M, Hikida T, Goris R (eds) Current Herpetology in East Asia. The Herpetological Society of Japan, pp 342–348

Kamezaki N, Suganuma H (1991) Summary of the first Japanese sea turtle meeting in Kaogoshima, 23–24 Nov., 1990. Umigame Newsl 7:114–119 **(in Japanese)**

Koch V, Brooks LB, Nichols WJ (2007) Population ecology of the green/black turtle (*Chelonian mydas*) in Bahia Magdalena, Mexico. Mar Biol 153:35–46. doi:10.1007/s00227-007-0782-1

Kubis S, Chaloupka M, Ehrhart L, Bresette M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Mar Ecol Prog Ser 389:257–269. doi:10.3354/meps08206

Limpus C, Chaloupka M (1997) Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). Mar Ecol Prog Ser 149:23–34

López-Castro MC, Koch V, Mariscal-Loza A, Nichols WJ (2010) Long-term monitoring of black turtles *Chelonia mydas* at coastal foraging areas off the Baja California Peninsula. Endang Species Res 11:35–45. doi:10.3354/esr00264

Nishizawa N, Naito Y, Suganuma H, Abe O, Okuyama J, Hirate K, Tanaka S, Inoguchi E, Narushima K, Kobayashi K, Ishii H, Tanizaki S, Kobayashi M, Goto A, Arai N (2013) Composition of green turtle feeding aggregations along the Japanese archipelago: implications for changes in composition with current flow. Mar Biol 160:2671–2685. doi:10.1007/s00227-013-2261-1

Okuyama J, Nakajima K, Noda T, Kimura S, Kamihata H, Kobayashi M, Arai N, Kagawa S, Kawabata Y, Yamada H (2013) Ethogram of immature green turtles: behavioral strategies for somatic growth in large marine herbivores. PLoS One 8(6):1–12. doi:10.1371/journal.pone.0065783 **(e65783)**

Pauly D (1983) Some simple methods for the assessment of tropical fish stocks. FAO, Rome, fish tech paper 234

Patrício R, Diez CE, van Dam RP (2014) Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. Endang Species Res 23(1):51–62

Pilcher N (2010) Population structure and growth of immature green turtles at Mantanani, Sabah. Malays J Herpetol 44(1):168–171

Sampson L, Giraldo A, Payán LF, Amorocho DF, Eguchi T, Seminoff JA (2015) Somatic growth of juvenile green turtle (*Chelonia mydas*) morphotypes in the Colombian Pacific. Mar Biol 162(8):1559–1566. doi:10.1007/s00227-015-2692-y

Seminoff JA, Resendiz A, Nichols WJ (2002) Growth rate of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf California, Mexico. Copeia 3:610–617

Seminoff JA, Jones TT, Resendiz A, Nichols WJ, Chaloupka MY (2003) Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices describe population status. J Mar Biol Assoc UK 83:1355–1362

Shimada T, Aoki S, Kameda K, Hazel J, Reich K, Kamezaki N (2014) Site fidelity, ontogenetic shift and diet composition of green turtles *Chelonia mydas* in Japan inferred from stable isotope analysis. Endang Species Res 25:151–164. doi:10.3354/esr00616

Sparre P, Venema SC (1998) Introduction to tropical fish stock assessment part 1. manual. FAO, Rome, Fish Tech Paper 306.1, Rev. 2

Suganuma H, Tanaka S, Inoguchi E, Narushima K (2010) Understanding from the stranded sea turtles. Aquabiology 32(5):407–412 **(in Japanese with English abstract)**

Tachikawa H (1991) Carapace length and body weight of adult green turtle in Ogasawa. Umigame Newsl 8:128–131 **(in Japanese)**

Tanaka E (2009) Estimation of temporal changes in the growth of green turtles *Chelonia madas* in waters around the Ogasawara Islands. Fish Sci 75:629–639. doi:10.1007/s12562-009-0095-z

Tomikawa Y, Uchiyama T (2004) Statistics for biomechanisms using excel (3). J Soc Biomech Jpn 28(4):221–225 **(in Japanese)**

Zárate PM, Bjorndal KA, Seminoff JA, Dutton PH, Bolten AB (2015) Somatic growth rates of green turtles (*Chelonia mydas*) and hawksbills (*Eretmochelys imbricata*) in the Galápagos Islands. J Herpetol 49(4):641–648. doi:10.1670/14-078