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Apparent survival probability and abundance of juvenile green turtles in the foraging ground at Kuroshima Island, Ryukyu Archipelago

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ABSTRACT: An understanding of the survival probability and abundance of endangered species is critical for their effective conservation and management. In this study, long-term capture–mark–recapture data were used to estimate the apparent survival probability and abundance of green turtles *Chelonia mydas* at Kuroshima Island in the Yaeyama Islands, Japan. A total of 453 turtles were captured from 2009 to 2020 using entangling nets. All captured turtles were juveniles and subadults; no adult turtles were captured during this study. The estimated apparent survival rate of this aggregation was 0.82 (95% CI = 0.76–0.86) using the Cormack-Jolly-Seber model, which accounts for both permanent emigration and death. Annual abundance was estimated using the Horvitz-Thompson estimator. Estimated abundance increased from 234 (95% CI = 182–286) in 2009 to 418 (95% CI = 325–510) in 2020. This trend in abundance for green turtles in the foraging ground may result from the increasing nesting population in this region. Our study provides information for understanding the life cycle of green turtles in the Yaeyama Islands and for the conservation and management of marine ecosystems in this region.

KEY WORDS: *Chelonia mydas* · Abundance trend · Cormack-Jolly-Seber model · Capture–mark–recapture · Japan

1. INTRODUCTION

Estimating survival probability and abundance is critical for endangered species conservation and management plans. For example, the green turtle *Chelonia mydas* is globally categorized as Endangered on the International Union for Conservation of Nature Red List of Threatened Species (Seminoff 2004). Green turtle hatchlings in the Pacific region swim out to pelagic waters, growing to ca. 35 cm straight carapace length (SCL), and then migrate to neritic foraging grounds (Zug et al. 2002, Balazs & Chaloupka 2004), where they typically spend over 30 yr while they grow to maturity (Balazs & Chaloupka 2004, Balazs et al. 2015). Accordingly, neritic foraging grounds are vitally important in the life cycle of green turtles.

Nesting female abundance is monitored by counting the number of females or nests on nesting beaches (e.g. Kamezaki et al. 2003, Chaloupka et al. 2008, Shimada et al. 2021). Abundance of juvenile turtles is linked to the number of nesting females (Chaloupka 2000, Bjorndal et al. 2005); however, knowledge on demographic structure of sea turtles at foraging grounds is limited. Additionally, estimating the survival probability in juvenile life stages is important for assessing the threats and dangers green turtles face in the water (e.g. by-catch, ghost net mortality, and

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sea turtle fisheries). Monitoring juvenile sea turtles at sea can provide additional indications of regional population trends and help detect potential dangers in foraging grounds (Bjorndal et al. 2005).

There are multiple methods used to assess foraging sea turtle populations (Bjorndal & Bolten 2000). The Cormack-Jolly-Seber (CJS) models use long term capture–mark–recapture (CMR) data to provide estimates of apparent survival and capture probabilities, where apparent survival probability includes permanent emigration and survival. These approaches can be applied to assess sea turtle populations at foraging grounds (Chaloupka & Limpus 2001, 2005, Bjorndal et al. 2003, 2005, Patrício et al. 2011, 2014, Colman et al. 2015). The estimated capture probabilities from the CJS models can be used to estimate the abundance via the Horvitz-Thompson estimator. The effectiveness of using the estimator to assess in-water sea turtle populations has been discussed by Chaloupka (2000).

The Yaeyama Islands are located at the southern end of the Ryukyu Archipelago, Japan. The northern area of Ishigaki Island and the southern area of Iriomote Island are major nesting areas in this region (Kamezaki 1991, Okuyama et al. 2020). Juvenile and subadult green turtles inhabit the coastal waters of this region (Kameda et al. 2017). They originate from various Pacific rookeries, including the Yaeyama and Ogasawara Islands (Nishizawa et al. 2013). Staff from the Kuroshima Research Station on Kuroshima Island in the Yaeyama Islands conduct sea turtle CMR surveys along the island's coast. Based on this CMR data, we estimated the survival rate and abundance of juvenile green turtles in the coastal waters of Kuroshima Island.

2. MATERIALS AND METHODS

2.1. Study area

The Yaeyama Islands are located in a subtropical region and have one of the largest coral reefs in Japan (Fig. 1). This study was conducted off the coast of Kuroshima Island (24° 14′ 13″ N, 124° 00′ 35″ E), one of the Yaeyama Islands. Kuroshima Island is surrounded by coral reefs, and seagrass and algae flourish on the inner reef. The water depth of the inner reef is 2–3 m at low tide, and that of the outer reef is 10–20 m. The tidal range is about 2 m during the spring tide. The main industries on Kuroshima Island are cattle livestock and tourism. Set net and gillnet fishing, which can result in sea turtle by-catch, are not conducted around Kuroshima Island.

2.2. Sampling method

The study was conducted over an 11 yr period, between August 2009 and November 2020. Turtles were captured using an entanglement net (200 m long ×

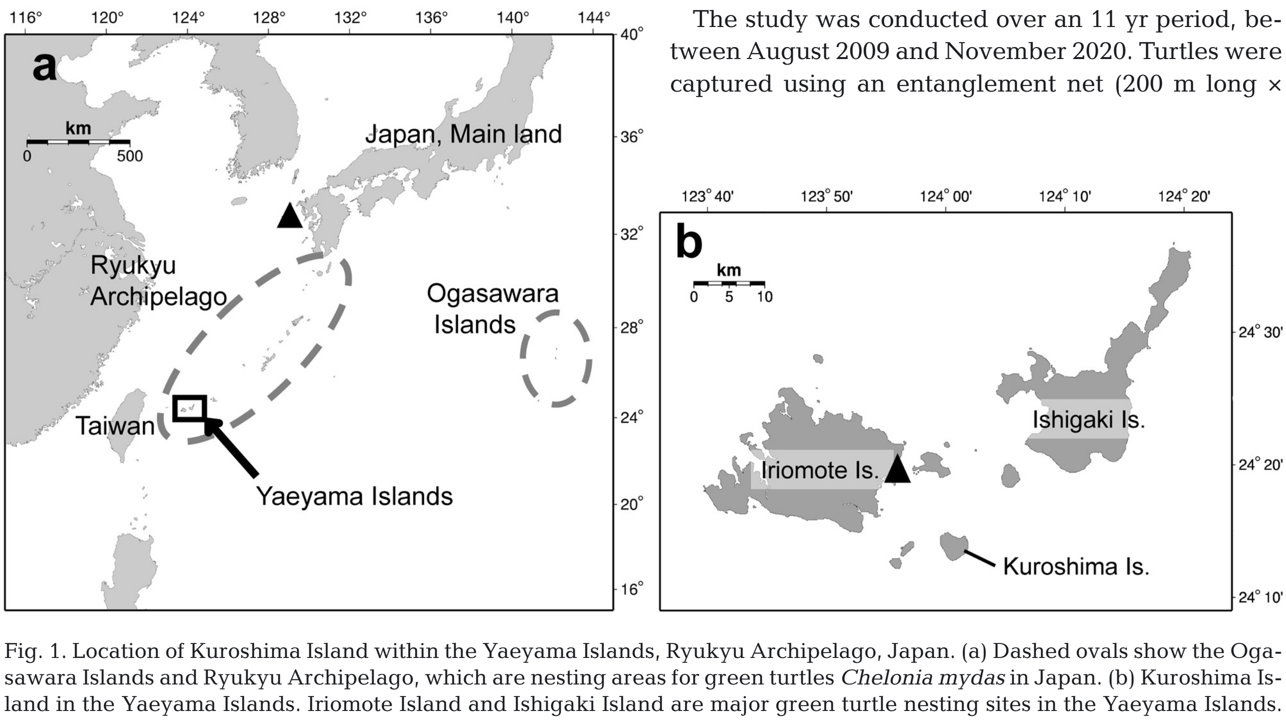

Fig. 1. Location of Kuroshima Island within the Yaeyama Islands, Ryukyu Archipelago, Japan. (a) Dashed ovals show the Ogasawara Islands and Ryukyu Archipelago, which are nesting areas for green turtles *Chelonia mydas* in Japan. (b) Kuroshima Island in the Yaeyama Islands. Iriomote Island and Ishigaki Island are major green turtle nesting sites in the Yaeyama Islands. ▲: Recapture points other than Kuroshima Island

2 m high, mesh size = 40 cm). The net was set in the inner reef area at 3 different sites: the northeast, west, and south sides of Kuroshima Island. The nets were checked for turtles and other species hourly by snorkelers. Turtles were captured year-round at 1- or 2-mo intervals: each capture session was conducted at one of the 3 sites on a rotation basis. Each capture session lasted 12–48 h, and the annual capture effort ranged from 12 to 22 d. The total effort in hours was converted to days.

Captured turtles were transported to an outdoor flow-through saltwater tank at the Kuroshima Research Station, Sea Turtle Association of Japan, where they were retained for between 1 d and 1 mo to conduct other research. First, the SCL was measured to the nearest 0.1 cm using metal calipers. Then, 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, UK) proximal to the first large scale on both rear flippers. Tags were replaced as needed upon recapture to maintain individual identification of turtles.

This study was approved by the Marine Fisheries Coordinating Committee of Okinawa Prefecture, Japan (Approval numbers: Oki-cho K21-16, K22-6, K23-1, K23-30, K24-1, K25-2, K25-24, K26-4, K27-3, K28-4, K29-4, K30-28, K31-20, K2-21, K3-3, K3-28).

2.3. Estimates of survival and recapture probabilities

The CJS model, which is based on live-captures only, was used to estimate apparent survival and recapture probabilities using the program MARK (Cooch & White 2019). The apparent survival probability is the probability that a marked turtle in the study population at capture occasion *i* survives until capture occasion *i* + 1, while acknowledging that permanent emigration from the study area is possible. Recapture probability is the probability that a marked turtle in the study population at capture occasion *i* is recaptured during capture occasion *i* + 1. The CJS model has the following assumptions: (1) every marked turtle present in the population at capture occasion *i* has the same recapture probability at capture occasion *i* + 1; (2) every marked turtle in the population immediately after capture occasion *i* has the same survival probability at capture occasion *i* + 1; (3) tags are not lost or missed; (4) all samples are instantaneous, relative to the interval between capture occasions *i* and *i* + 1 (Cooch & White 2019).

The program RELEASE was used to test the goodness-of-fit (GoF) of the full parameter CJS model to our data (Cooch & White 2019). The probability results of Tests 2 and 3 were used to validate the fit of the CJS model to the data. Test 2C and Test 3SR in the program RELEASE were used to test for equal recapture and survival probabilities to meet assumptions (1) and (2), respectively (Patrício et al. 2011). Double-tagging and non-corrosive tags were used to ensure assumption (3) was met (Chaloupka 2000). Captures spread over 1 yr were redefined as captures from 1 sample to meet assumption (4). That is, multiple captures of any specific turtle in the same year were counted as a single capture, and captures in the following years were defined as a recapture.

Following the examination using the program RELEASE, we developed 4 models based on the assumption that survival and recapture probabilities were time-dependent or constant. The 'median c-hat' procedure implemented in MARK was used to calculate the variance inflation factor ($\hat{c}$).

Where $\hat{c}$ was >1, we used the estimated value to adjust the model of Akaike information criterion, and converted to quasi-likelihood Akaike information criterion (QAICc) (Table 1). The model with the smallest QAIC value was selected (Cooch & White 2019).

2.4. Population size and abundance trend

The Horvitz-Thompson estimator was used to estimate the annual abundance of juvenile green turtles in foraging grounds (Chaloupka 2000, Bjorndal et al. 2005). The number of turtles in the sampling population (N_i) was calculated as $N_i = (n_i / p_i)$, where n_i is the number of turtles captured on capture occasion *i*, and

Table 1. Capture–mark–recapture models in this study. Φ: apparent survival probability; ρ: recapture probability; No. par.: number of parameters; QAICc: quasi-likelihood Akaike information criterion adjusted for small sample size; ΔQAICc: QAICc − minQAICc; QAICc weight: relative likelihood of model (normalized to sum to 1)

Model no.	Φ	ρ	No. par.	ΔQAICc	QAICc weight
1	Constant	Constant	2	0.00	0.65
2	Time-dependent	Constant	12	2.07	0.23
3	Constant	Time-dependent	12	3.56	0.11
4	Time-dependent	Time-dependent	21	8.78	0.01

p_i is the recapture probability for capture occasion i. The 95% confidence intervals for N_i were then derived by calculating the standard error of N_i as $SE(N_i) = \{(n_i / p_i)^2 [var(p_i) / (p_i)^2]\}^{0.5}$, where $var(p_i)$ is the recapture probability variance for capture occasion i. The 95% confidence intervals for N_i were calculated as 95% CI = $N_i \pm 1.96$ SE(N_i). It should be noted that the CJS model does not compute an estimation of recapture probability for the first year (2009), so we estimated abundances from 2010 onwards.

Trends in juvenile green turtle abundance were evaluated using variance-weight linear regression models with a log link and first-order moving average process (Bjorndal et al. 2005). We employed a first-order moving average structure because there was a substantial overlap of individual turtle data between successive years (Bjorndal et al. 2005). Assuming a constant rate of change for the study period, the slope of the regression (b) was an estimate of population change: Population growth (%) = $\{[(e^b) - 1] \times 100\}$. The 95% confidence intervals were calculated as 95% CI of population growth (%) = $\{[(e^b \pm 1.96 \text{ SE})] - 1\} \times 100$, where e is the base of the natural logarithm, b is the slope of the regression model, and SE is the standard error of the slope estimate. The Microsoft Excel Solver add-on and data analysis functions were used to perform the Horvitz-Thompson annual abundance estimates and trend analysis.

3. RESULTS

A total of 122 capture sessions were conducted between May 30, 2009, and November 19, 2020. The total capture effort was 201 days, with 12–22 capture-days per year. The total number of captures was 621, corresponding to 453 unique individuals. Of the 168 recaptures, 87 turtles were recaptured once, 21 were recaptured twice, 9 were recaptured 3 times, and 3 were recaptured 4 times. Turtles classified as juveniles (SCL < 60 cm at first capture) totalled 362 unique individuals and 154 recaptures, and subadults (60 cm ≤ SCL < 93 cm at first capture) represented 91 unique individuals and 14 recaptures (Fig. 2). Of the 168 recaptured sea turtles, the tag loss rate was 13.7% for Inconel tags and 2.4% for plastic tags. Tag loss left easily identifiable scars on the flippers, but no individual with scars on both flippers was recaptured during our study periods. Therefore, we assume that there were few or no cases of recaptured individuals misidentified as new captures. Therefore, tag loss was not adjusted in our analysis. The recapture interval ranged from 1 to 7 yr. Of the 168 recaptured turtles, 166 were caught around Kuroshima Island. Other recapture locations were Iriomote Island and the Japanese mainland (Fig. 1). The mean SCL was 51.6 cm (SD = 9.4, range = 33.7–90.0; Fig. 3). The average size-at-maturity in this region is >93 cm (Kameda et al. 2017), which strongly implies that no adult green turtles were captured in this study.

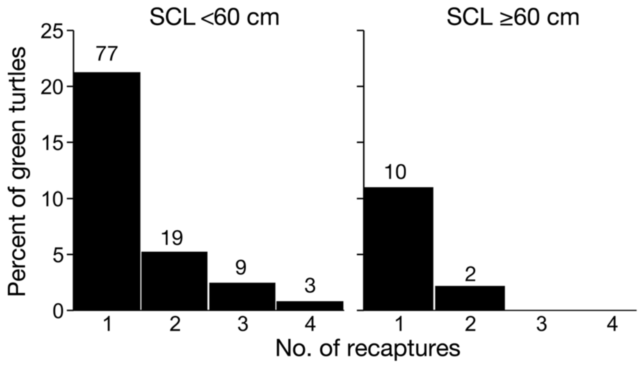

Fig. 2. Percentage and number of recapture times for juvenile (SCL < 60 cm at first capture) and subadult (SCL ≥ 60 cm at first capture) green turtles at Kuroshima Island. Number of individuals is indicated above each column

We fitted the 4 models to the capture–recapture data using the program MARK. The GoF test on the time-dependent full parameter CJS model showed that our global dataset complied with the assumptions of the model (Tests 2 and 3; $\chi^2 = 39.0$, df = 37, p = 0.37). GoF tests suggested that the assumptions of equal recapture and equal survival probabilities were met (Test 2C, $\chi^2 = 23.1$, df = 18, p = 0.18; Test 3SR, $\chi^2 = 13.0$, df = 10, p = 0.22). The $\hat{c}$ value was calculated to be 1.13, and this $\hat{c}$ value was used to compute QAIC values.

The model with the best fit based on the QAIC was a constant CJS model for survival and recapture probabilities. The annual apparent survival probability was 0.82 (95% CI = 0.76–0.86), and the recapture probability was 0.15 (95% CI = 0.12–0.19).

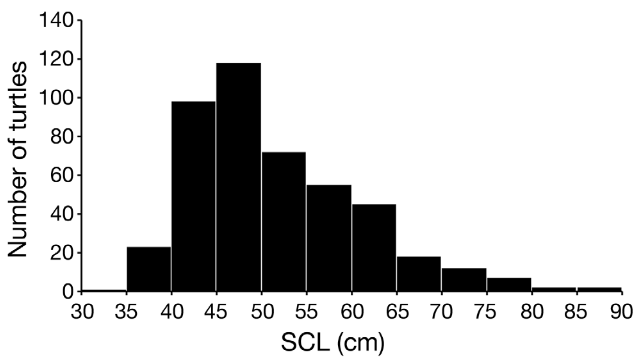

Fig. 3. Size distribution of green turtles in the waters surrounding Kuroshima Island

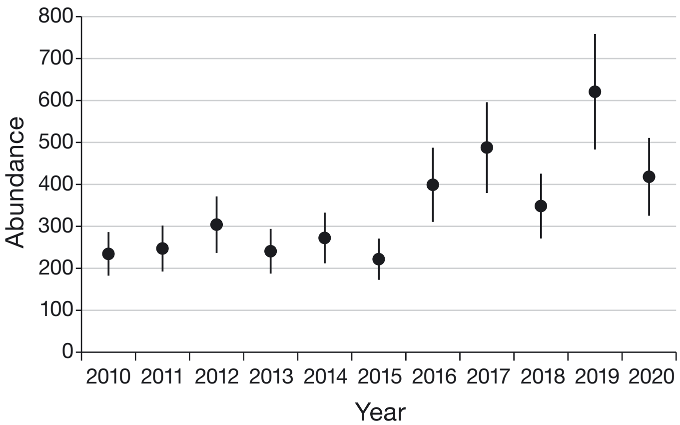

Fig. 4. Estimated abundance of green turtles at Kuroshima Island from 2010 to 2020. Data are means ± 95% CIs

The Horvitz-Thompson annual abundance estimates of green turtles around Kuroshima Island ranged from 234 (95% CI = 182–286) in 2010 to 418 (95% CI = 325–510) in 2020 (Fig. 4). Green turtle abundance showed a significant increasing trend from 2010 to 2020 (regression analysis, slope = 0.086, $t = 8.32$, $p < 0.01$), and the growth rate was 9.0% per year (95% CI = 6.8–11.2%).

4. DISCUSSION

The present study estimated apparent survival probability and abundance trends in the northwest Pacific. Currently, sea turtle nesting beach monitoring is being conducted in Japan, but there are no reports of long-term monitoring of juveniles and subadults in foraging grounds. Therefore, our results may provide new information regarding green turtle ecology in their foraging grounds. Our findings are an important resource when discussing future conservation activities for sea turtles in this region.

4.1. Survival probability

The apparent survival probabilities of green turtles in the foraging ground on Kuroshima Island were similar to those found in other foraging grounds around the world (Table 2), except for juveniles in Conception Creek, Bahamas and for subadults in Culebra, Puerto Rico, where the apparent survival probabilities were 0.68 and 0.53, respectively. Those lower survival values have been attributed to mortality from occasional poaching of turtles in Bahamas (Bjorndal et al. 2003), and ontogenic migrations, where turtles move to different habitats as they grow, in Puerto Rico (Patrício et al. 2011).

Sea turtle fishing in the Yaeyama Islands, including Kuroshima Island, has not been conducted since 2004 (Kameda et al. 2017). Gillnet and fixed net fishing, which can result in bycatch of green turtles, were also not conducted around Kuroshima Island during the study period (Sea Turtle Association of Japan, unpubl. data). Furthermore, large sharks, which predate on sea turtles (Heithaus et al. 2005), were harvested by the Yaeyama Local Fisheries Cooperative to protect fishery resources (Kakuma 2009). Therefore, the presumed relatively low turtle mortality at Kuroshima Island likely results from factors other than fishing or significant predation.

Instead, apparent survival probabilities of green turtles in the foraging ground around Kuroshima Island could be mainly influenced by permanent emigration with growth. Such ontogenic movements of foraging green turtles have been reported in Mexico, Bahamas, Puerto Rico and Brazil (Koch et al. 2007, Bresette et al. 2010, Patrício et al. 2011, Colman et al. 2015). The size distribution of green turtles captured around Kuroshima Island, and the very low recapture of subadult turtles, indicate that it is a feeding ground mostly used by juvenile green turtles, while subadult and adult turtles are likely to move to

Table 2. Apparent survival probabilities (Φ) based on Cormack-Jolly-Seber model for different green turtle aggregations from foraging grounds worldwide. Values in parentheses correspond to 95% confidence limits. SCL: straight carapace length; CCL: curved carapace length

Size class	Carapace length (cm)	Location	Φ (95%CI)	Reference
Juvenile	SCL 22–64	Conception Creek, Bahama	0.68 (0.63–0.73)	Bjorndal et al. (2003)
Juvenile	CCL 24–65	Culebra, Puerto Rico	0.83 (0.79–0.87)	Patrício et al. (2011)
Juvenile	CCL 40–65	Southern Great Barrier Reef, Australia	0.88 (0.84–0.93)	Chaloupka & Limpus (2005)
Juvenile and subadult	CCL 27–87	Fernando de Noronha, Brazil	0.85 (0.59–1.00)	Colman et al. (2015)
Juvenile and subadult	SCL 34–90	Kuroshima Island, Japan	0.82 (0.76–0.86)	Present study
Subadult	CCL 65–90	Culebra, Puerto Rico	0.53 (0.39–0.67)	Patrício et al. (2011)
Subadult	CCL 65–90	Southern Great Barrier Reef, Australia	0.85 (0.79–0.91)	Chaloupka & Limpus (2005)

different areas, or use deeper waters not surveyed during this study. Therefore, it is possible that true survival probability in green turtle aggregations around Kuroshima Island is higher than found in this study. Future research investigating this would require a model which treats survival probability as a function of size class.

4.2. Population size and abundance trend

The observed increase in green turtles at Kuroshima Island reflects a similar trend at nesting beaches in this region. Green turtles that forage around the Yaeyama Islands originate from various Pacific rookeries in the western Pacific Ocean, including several Japanese rookeries (Nishizawa et al. 2013). Okuyama et al. (2020) reported an increase in the number of green turtle nests on the Ishigaki Islands (Yaeyama Islands) between 1992 and 2008. The reasons for this increase were unclear, but it is possible that one factor was the decline in the custom of sea turtle harvesting in Japan, especially after 2004 (Kameda et al. 2017). In addition, Kondo et al. (2017) reported that between 1975 and 2015, the number of turtles nesting on the Ogasawara Islands increased. Recovery of nesting females on the Ogasawara Islands is attributed to the temporary suspension of the turtle harvest after World War II, and the introduction of harvest regulations in 1994 (Kondo et al. 2017). It takes approximately 5 yr for juvenile green turtles to move from the outer pelagic habitats to the neritic area (Turner Tomaszewicz et al. 2022). Therefore, the increasing nest numbers and nesting female trends of Ishigaki Island and the Ogasawara Islands could have positively influenced the abundance of green turtle populations in the Yaeyama Islands, including Kuroshima Island.

The association between an increase in the green turtle population and a decline in seagrass meadows has been observed in the Derawan Islands, Indonesia (Christianen et al. 2014), and in Bermuda (Fourqurean et al. 2010). Declines in seagrass coverage due to overgrazing by green turtles has been observed on the west side of Iriomote Island, which is close to Kuroshima Island. Furthermore, seasonal changes in seagrass cover on turtle-grazed beds have been associated with changes to the local fish ecology (Inoue et al. 2021). Similarly, the increase in green turtle populations and declines in seagrass have resulted in changes in the local green turtle ecology. For example, reductions in the size-distribution of green turtles were associated with declines in the foraging site areas (Meylan et al. 2022). Additionally, shark harvests are conducted around the Yayeama Islands each year, and juvenile green turtles are often observed in the stomachs of harvested tiger sharks (Ishigaki local government, unpubl. data). The shark harvests may have also contributed to the increase in the foraging green turtle population which our results show. Future conservation plans for the Yaeyama Islands should consider the entire food chain in marine ecosystems.

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