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Factors Affecting the Long-Term Population Dynamics of Green Turtles (*Chelonia mydas*) in Ogasawara, Japan: Influence of Natural and Artificial Production of Hatchlings and Harvest Pressure

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Abstract. – The Ogasawara Islands in Japan represent an important rookery for green sea turtles (*Chelonia mydas*) in the Pacific Ocean. The marine turtle population in these islands was severely depleted due to overexploitation in the 1800s; however, continuous nesting surveys starting in 1975 showed signs of a gradual recovery, and an upward trend of nesting females has been observed in recent years. The Japanese government undertook a "hatch and release project" to recover the turtle stock in 1910 as the world's first attempt of a sea turtle hatchery. A total of more than 251,000 hatchlings were released into the wild as a part of the project; however, its contribution to the recent increase in nesting females is not well understood. The increase in nesting females may be attributed to the temporary suspension of the turtle harvest and reduction of catch from 1942 to 1968, which allowed for stable production of hatchlings from natural beaches. This study documents the levels of harvest, number of nesting females, and hatchling production at Ogasawara and explores, for the first time, their influence on population dynamics of Ogasawara's green turtles.

Key Words. – Cheloniidae; long-term study; sea turtle harvesting; artificial hatching; Ogasawara Islands

The Ogasawara Islands, located approximately 1000 km south of Tokyo on the mainland of Japan, are globally recognized as one of the most important rookeries for green turtles, *Chelonia mydas* (Chaloupka et al. 2007). Ogasawara is the most northern breeding habitat among the range of major green turtle rookeries (Chaloupka et al. 2007). The Ogasawara Islands were uninhabited until 1830, at which time a group of native Hawaiians and a few Caucasians organized by the first British consul to the Sandwich Islands (Hawaii) arrived and established a colony (Kramer and Kramer 2013). After the first settlement, the islands played an important role as a junction port for Western whalers to fill depleted food supplies (Kramer and Kramer 2013). Turtle harvesting by settlers began around this time and the meat was an important source of protein. In addition to this local consumption, green turtles were sold to whaling ships visiting the area (Kurata 1983). Ogasawara became a Japanese territory in 1876 and the population gradually increased to over 4000 people by 1895 (Kurata 1983). As the population increased, so did the number of turtles harvested (Kurata 1983). Moreover, the Japanese Ministry of Agriculture and Commerce encouraged turtle harvest for economic growth, and approximately 3000 turtles were caught in the next few years, which led to a drastic decline of Ogasawara's green turtle population (Kurata 1983). Turtle harvesting and catch records have been documented by the islanders for more than a century (Kurata and Hirose 1969). Understanding historical backgrounds and information can be a great contribution to population assessments including definition of targets and conservation goals to ensure effective population recovery from previous human exploitation (Van Houtan and Kittinger 2014).

The first attempt to recover the severely exploited Ogasawara green turtle population came in the form of a "hatch and release project" that was experimentally conducted in 1877 in Chichi-jima; this was the world's first effort of this kind (Kurata 1983). The Japanese Ministry of Agriculture and Commerce officially commenced the project in 1910, which had been unofficially conducted in small scale until then (Kurata and Hirose 1969). The hatch and release project was suspended during World War II (WWII) when the United States occupied the islands; it was restarted in 1972 with expanded facilities at the hatchery and the turtle captive pool.

The human population continued to grow on the islands, reaching more than 7000 inhabitants in 1940 (Kurata 1983). Most of the islanders, however, were forced to evacuate from Ogasawara in 1944 due to WWII (Kurata 1983). After WWII, from 1946 through 1968, the Ogasawara Islands were occupied by the United States and only descendants of western settlers who inhabited the islands before they became Japanese territory were

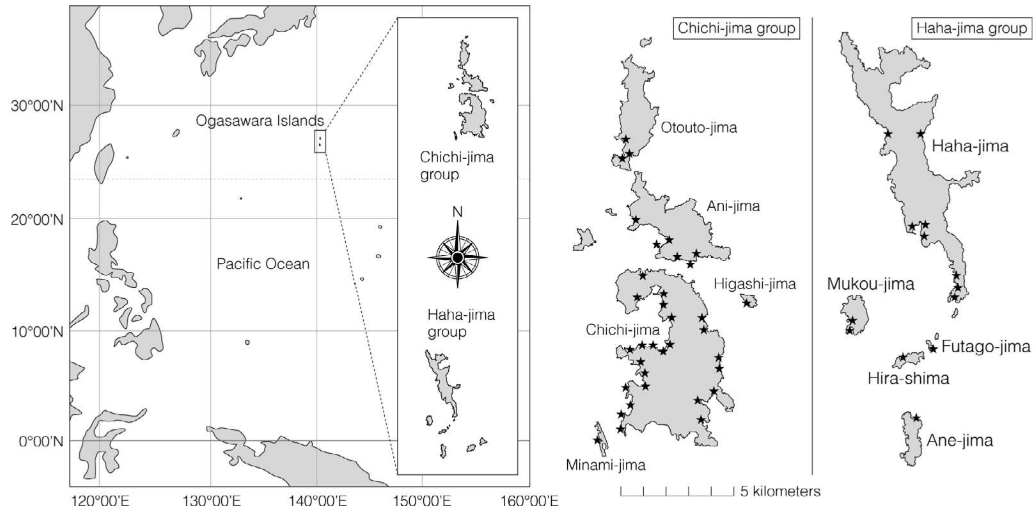

Figure 1. Location of Chichi-jima Group and Haha-jima Group in the Ogasawara Islands where nest surveys, turtle harvest, and the hatch and release project were conducted. Star-shaped characters idicate nesting beaches. (Chichi-jima: lat 27°5′N, long 142°12′E.)

allowed to return. The Islands were returned to the Japanese government in June 1968; only 345 people inhabited the islands at that time. By 1990, the population had increased to about 2000 people and has since increased to approximately 2500 current residents (The Tokyo Metropolitan Ogasawara Island Branch Office 2016).

In current times, the seasonal migration of green turtles is closely attached to islanders' lives, businesses, education, and culture. Turtle meat is still consumed within the islands under a strictly regulated harvest and green turtles play an important cultural role among island residents. It should be noted, however, that the harvest of turtle eggs has been prohibited since 1898 to increase the sustainability of the turtle harvest. Also, long-term nesting surveys have been conducted since 1975, and the Ogasawara islands are one of the few breeding regions among green turtle rookeries worldwide where continuous harvest records are available (Horikoshi et al. 1994; Chaloupka et al. 2007).

In this article, we aim to document the level of green turtle harvest, the number of nesting females, and hatchling production at Ogasawara. We also explore the influences of these parameters on the abundance of Ogasawara's green turtle population. The relationships among these parameters will assist in the prediction of the future population trends and assessment of the effectiveness of management strategies.

METHODS

Study Area. — Ogasawara is an archipelago with 4 main island chains consisting of 2 inhabited islands (Chichi-jima in the Chichi-jima group and Haha-jima in the Haha-jima group) and over 30 uninhabited islands (Fig. 1). This study focused on both the Chichi-jima (consisting of Chichi-jima, Ani-jima, Otouto-jima, Higashi-jima, and Minami-jima) and the Haha-jima (consisting of Haha-jima, Hira-shima, Futago-jima, Ane-jima, and Mukou-jima) groups. The main nesting beaches are located within these 2 island groups and also where turtle harvesting and the hatch and release project have taken place. High-energy waves and winds surround the edge of the islands, forming numerous pocket beaches of < 1 km in length in small inlets and caves between the cliffs. These pocket beaches are the main nesting beaches for green turtles in Ogasawara. Nesting activity has been observed at 37 beaches in the Chichi-jima group and at 13 beaches in the Haha-jima group. The only beach on Minami-jima has a single narrow entrance at a cave with an opening < 5 m in width. Nesting turtles swim through the cave and emerge on the beach. People, including researchers, usually arrive from another side of the island by climbing a rocky cliff where a boat can be moored to access the beach. The majority of the beaches consist of coral rubble sand, pebbles, and boulders. Nesting green turtles sometimes crawl more than 30 m from the shoreline to avoid boulders while looking for an adequate nesting location.

Turtle Harvesting Levels. — Catch data before WWII are given by Kurata and Hirose (1969), whereas the data during the United States occupation were referred to in Horikoshi et al. (1994) and also reproduced from interviews with residents who lived on the island during this period. Interviews with residents were conducted soon after the islands returned to Japanese control. At this time, green turtle harvest levels were recorded in increments of 10 turtles. Catch data for Chichi-jima after the islands returned to the Japanese government have been gathered through port sampling surveys and interviews with fishermen right after landing harvested turtles. Catch records and statistics for Haha-jima were obtained from The Haha-jima Fishery Association.

Currently, most of the harvested turtles are taken during the breeding season from March through the end of May by fishermen with permission from the governor of the Tokyo metropolitan area; harvest is prohibited in June and July during the peak nesting season. Green turtles are mostly harvested using a harpoon while snorkeling. In addition, during almost every year prior to 1995, a few nesting females were caught while on the nesting beaches regardless of whether the turtle had already nested or not. Therefore, most of the nests are deposited by female turtles that are not captured during the harvest season. Any turtle encountered during the harvest season is caught, including mating couples. However, the overall take ratio is slightly biased toward females due to the capture of nesting turtles.

The annual harvest pressure on female turtles was calculated for both Chichi-jima and Haha-jima from 1975 to 2015. Harvest pressure was estimated by dividing the number of harvested females by a sum of harvested females and the total estimated nesting females.

Sex ratio data for harvested turtles were not obtained for 1997–2002, and thus the number of harvested females during those years was estimated from the total annual catch using sex ratio data from 1992–1996 and 2003–2007 (female:male = 1.1:1.0).

Number of Nesting Females. — Nesting surveys on nesting beaches have been conducted during the nesting season (early May to late September) since 1975 on the Chichi-jima group and since 1988 on the Haha-jim group. Survey periods and frequency varied over the years depending on available resources and weather conditions. The majority of beaches were only accessible by a boat; thus, the surveys were incomplete for some years due to safety reasons.

Nesting surveys were conducted by searching the beaches for nests, using visual inspection of adult turtle emergence tracks, and body pits. The exact nest location was determined using a steel stick, measured from fixed marks on the beach to the exact nest location using a measuring tape, and recorded to avoid double counting. Once a nest was found, a few eggs were excavated to determine the nesting date. The nesting date was estimated from the appearance and distibution of a chalky white patch on the upper surface of the egg shell. The white spot frequently appears in the egg within 3 d after oviposition and spreads downward to cover the entire egg within 10 d (Miller 1985). In this study, the eggs were classified into Day 1 to Day 14 or more based on examination of this white spot. For example, a whole egg shell which had pink beige color was classified as Day 1 and an egg shell with the white spot less than approximately 1 cm was classified as Day 2. An egg with the white spot expanding to half of the entire egg was categorised as Day 7 and an entire egg of chalky white color was determined to be Day 14 or more. Because 50 nesting beaches are interspersed on 8 islands, where access to some of the beaches is limited due to rough seas, this method was applied to estimate the nesting date instead of direct observation at nighttime nesting surveys. The surveys were usually conducted during daytime with intervals between surveys usually no more than 2 wks. In addition, night surveys were conducted at some major nesting beaches during the peak nesting season, and exact location of the nests were determined through direct observation during these surveys. Nesting surveys were not conducted in 1976, 1977, and 2009 in either the Chichi-jima group or the Haha-jima group.

Because there were no data on nest counts in Haha-jima for 1975 and from 1978 to 1987, numbers of nests for the 11 yrs were estimated using a mean ratio of the number of nests in Chichi-jima group compared with that of Haha-jima group from 1988 to 1997 (Chichi-jima group:Haha-jima group = 2.2:1.0). This was done because there was a correlation in number of nests from 1988 to 2015 between those 2 island groups (Spearman's rank correlation $r = 0.61$, $p < 0.05$). Then, the estimated nest counts were used to determine the number of nesting females.

Calculation of Total Females.— The total number of nesting females was estimated by dividing the number of nests counted each year by a mean clutch frequency of 5.3 nests per female per season in 2008 ($n = 10$), derived from turtles that were held captive as part of the hatch and release project. Every nesting activity was observed and the nesting frequency for each turtle was recorded during nightly observations. However, because captive green turtles may occasionally release eggs in water, it was difficult to determine if nightly observations documented all clutches for each female. Therefore, the highest annual mean nesting frequency among all turtles was used for the calculation.

Artificial Hatchling Production. — The hatch and release project entailed capturing mature female turtles from the wild during mating season by a harpoon while snorkeling. By this method, the fishermen speared only the surface of their carapace with the harpoon; therefore, the turtles were not deeply injured and did not bleed. The turtles were then tied with a rope and carried to the enclosure for nesting. The enclosure where captive turtles were kept had an adjoining beach and the turtles were able to emerge on the beach to nest (Fig. 2). The eggs were collected for incubation while turtles were laying, and most hatchlings were released during the night onto a natural nesting beach soon after emergence. A very small portion of the hatchlings were raised in captivity for a period of time before release; eggs were never transferred from the natural beaches to hatcheries. From 1910 through 1939, turtles were kept in an enclosure of approximately 473 m^2 until laying eggs at least once before being slaughtered for meat (Kurata 1983). Some eggs were also collected from the oviduct at the time of slaughter and transported to the experimental turtle farm for incubation (The Tokyo Metropolitan Fisheries Experiment Station 1986). After hatchling emergence, the hatching and emergence success of each nest was calculated.

The hatch and release project was suspended during WWII and the United States occupation of the islands. Ogasawara was returned to the Japanese government in 1968, and the project restarted its activities in 1972

Figure 2. The enclosure for the hatch and release project where harvested females were kept and nested on an adjoining beach.

following 32 yrs of suspension. In 1975, when the project was fully implemented, an enclosure pool measuring 10×15 m was built in the ocean with iron pipes where turtles were kept until they laid eggs multiple times before being slaughtered. The facilities were reconstructed in 1981 with a beach area measuring 15×12 m and an adjacent enclosure pool measuring 30×35 m. Around this time the Ogasawara government began purchasing some of the turtles from fishers to be kept in captivity and released after nesting. The project was discontinued in 2008, almost 100 yrs after its start, owing to difficulties in maintenance of the facilities and increased numbers of nests on natural beaches, which were considered to produce more hatchlings than those from the project.

There were no hatchlings released in 1912 and 1974, and only data for the number of eggs relocated to hatcheries was obtained for 2001; thus, number of hatchlings released in 2001 is missing.

Natural Hatchling Production. — We analyzed data from hatching surveys conducted since 1993 in the Chichi-jima group to examine influences of both artificial and natural hatching on abundance of females. We also considered how hatchlings from the hatch and release project on Chichi-jima compared with all natural hatchling production.

Hatching surveys were conducted after the predicted hatching date. In this study, approximate hatching date was predicted to be 60 d after the estimated nesting date based on data from French Frigate Shoals, one of the closest insular rookeries to Ogasawara (Balazs 1980). Hatching surveys occurred from July to the end of November. During these efforts, nests were excavated, all egg shells removed, and emergence success was examined for each clutch. We classified each clutch as being either not damaged, washed out, inundated, dug out by other turtles, or depredated. Each egg shell recovered from the nest was categorized as successfully hatched, not hatched (undeveloped embryo and 4 developing stages), depredated, or damaged by a steel stick during nesting survey, and each recovered hatching was recorded as dead or alive. We calculated emergence success following Miller (1999): emergence success = [(number of empty shells − number of hathlings remaining in the nest that did not emerge)/estimated clutch size derived from the nest inventory]. If a nest recorded during the nesting survey was not found during the hatching survey for unknown reasons, the nest was counted as uninvestigated and the nest was excluded from emergence success calculation.

Hatching surveys in 1999, 2001, and 2009 were incomplete; therefore, data of natural hatchling production of these years are missing. Number of hatchlings and emergence success from 1983 to 1990 were reported in Suganuma et al. (1994), and the data from 1991 to 1998 were included in annual reports prepared by The Tokyo Metropolitan Marine Environment Conservation Association (1992–1999). To calculate the total number of hatchlings produced on the natural nesting beaches each year from 2000 to 2008 (except 2001 when only 65.7% of nests were examined), the number of hatchlings from uninvestgated nests was estimated by multiplying the total

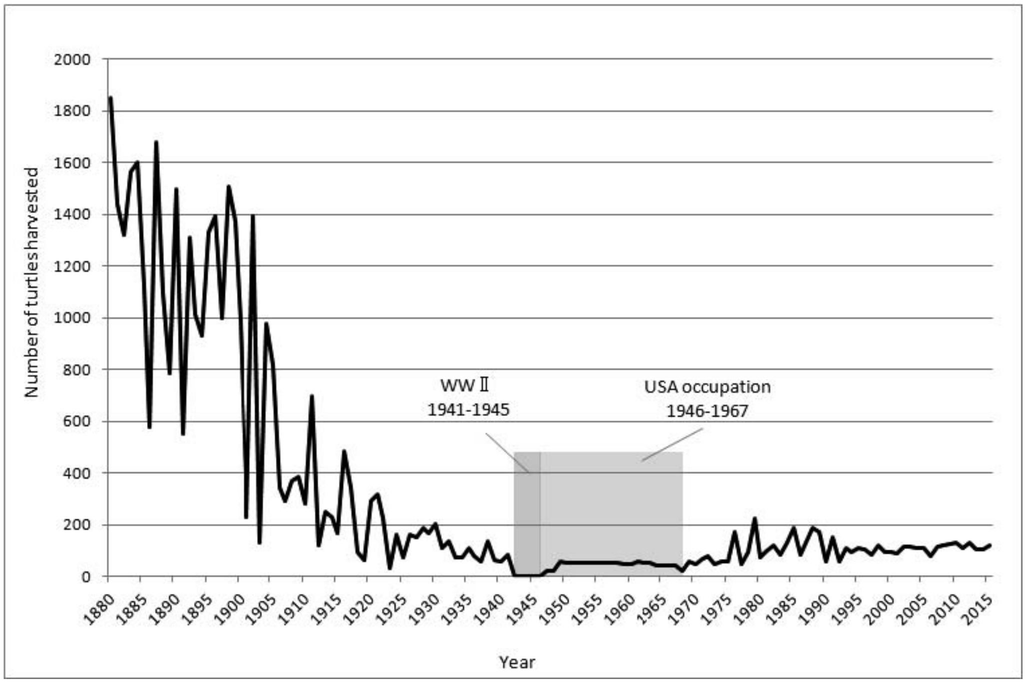

Figure 3. Number of harvested turtles from 1880 to 2015 in Ogasawara including male and female turtles.

nest numbers for that year by the mean cluch size and calculated emergence success for the captive turtles. From 2010 to 2015, hatching surveys were conducted on almost all of the clutches (annual mean of 96.9%), with the remaining clutches uninvestigated owing to loss most likely from being washed out or depredated.

RESULTS

Turtle Harvest Levels. — Long-term data on turtle catch recorded continuously over 134 yrs are shown in Figure 3. The catch was reported to be 1852 turtles captured in 1880, and dropped to 32 turtles in 1923, although sharp fluctuations were observed during these first 43 yrs (Kurata and Hirose 1969). The fluctuation became more moderate during the next 2 decades until WWII, when the number of turtle catches was low. After 1923, the highest annual catch was 205 turtles (in 1930; Kurata and Hirose 1969). Turtle harvest was suspended during WWII and no catch was reported from 1942 to 1946. Small-scale harvest resumed when island residents of western descent were permitted to return after WWII during the United States occupation; the catch during this time ranged between 20 and 60 turtles (annual mean of 44.5 turtles). Full-scale harvest resumed when the Ogasawara Islands were returned to the Japanese government in 1968 and, after that, the catch temporarily increased. Harvest levels stabilized after a Fisheries Adjustment Regulation was implemented in 1994 by the Tokyo Metropolitan, which put the maximum annual catch limit at 150 turtles. The limit was revised in 1997 to the current 135 turtles per year.

The highest estimated harvest pressure was in 1978, when 88.3% of the female nesting population was harvested, with the pressure gradually decreasing over the next 37 yrs (Fig. 4). From 2005 to 2015, the harvest pressure ranged from 10% to 15% of the nesting population, except in 2006 and 2009 with a harvest pressure of 25.6% and 29.1%, respectively.

Number of Nesting Females. — There has been an increasing trend in the annual number of nesting since nesting surveys began in 1975 (Fig. 4). Chaloupka et al. (2007) estimated that the abundance of nesting turtles in Ogasawara increased at an annual growth rate of 6.8% from 1978 to 2003. A further increase in annual nesting females occurred from 2005 and 2015, with a maximum of 582 nesting females in 2008.

Artificial Hatchling Production. — From 1910 to 2008, a total of 2115 adult female turtles were kept in captivity to collect eggs for the hatch and release project (The Tokyo Metropolitan Fisheries Experiment Station 1986). From 1910 to 1939 prior to WWII, a total of 1259 females were kept in captivity and 38,702 hatchlings (annual mean of 1331 hatchlings) were released (Fig. 5; The Tokyo Metropolitan Fisheries Experiment Station 1986). When the project resumed in 1972, 77 hatchlings were released into the wild, and the highest number of hatchlings (23,249) was released in 1979 (The Tokyo Metropolitan Fisheries Experiment Station 1986). A total of 212,763 hatchlings were released from 1972 to 2008 (annual mean of 5750 hatchlings; The Tokyo Metropolitan Fisheries Experiment Station 1986). The mean emergence success (total number of live hatchlings/total number of eggs) in the hatcheries was 26.9% per year before WWII (The Tokyo Metropolitan Fisheries Experiment Station

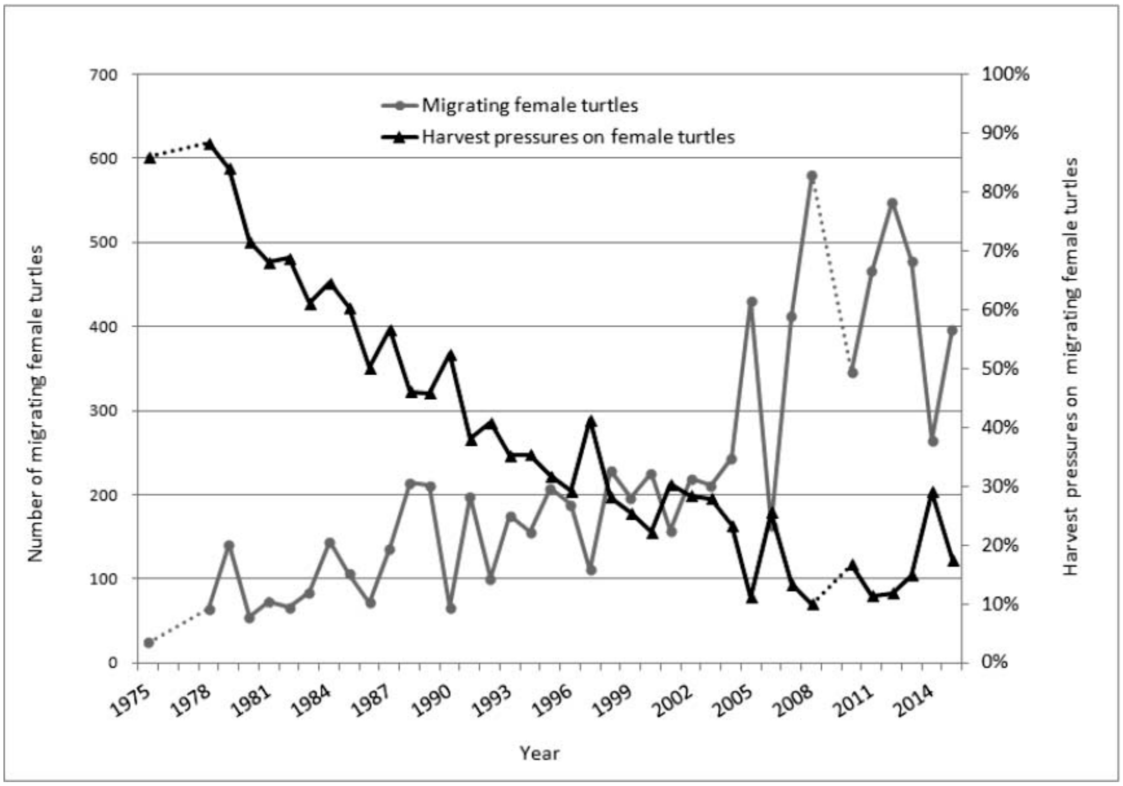

Figure 4. Sum of estimated nesting and harvested female turtles from 1975 to 2015 in Chichi-jima and Haha-jima groups combined, and harvest pressures on the female turtles from 1975 to 2015. Dashed line represents years when nesting surveys were not conducted in either Chichi-jima or Haha-jima.

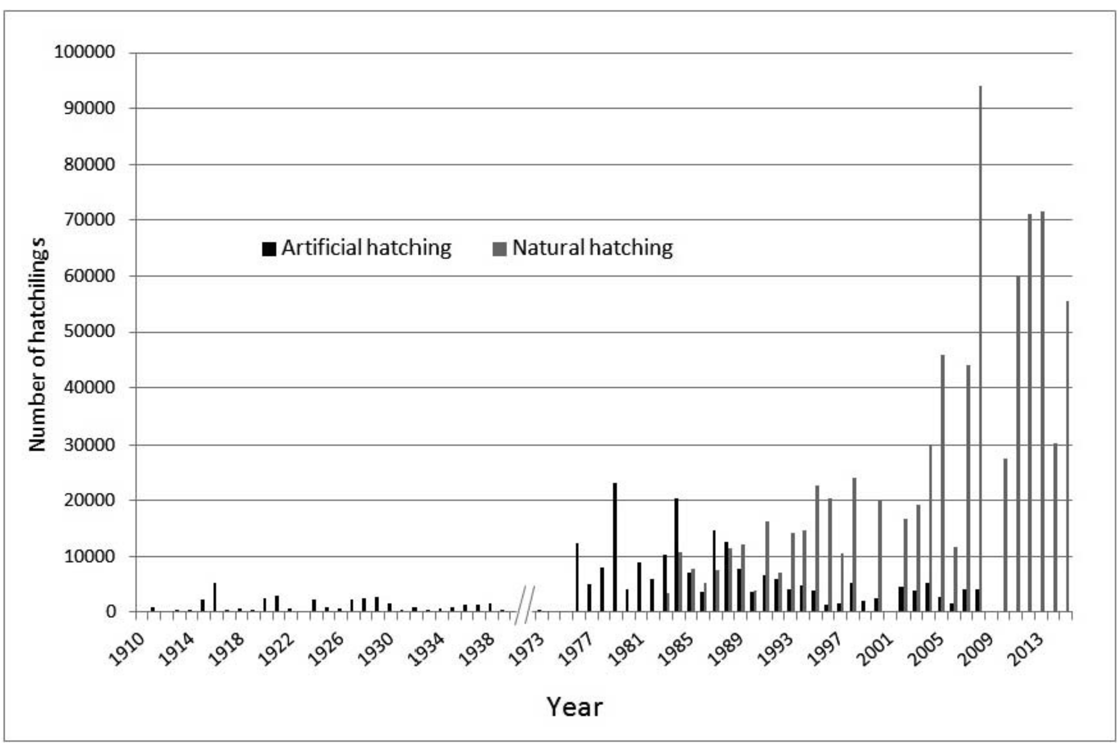

Figure 5. Number of hatchlings produced by the hatch and release project from 1910 to 1939 and 1972 to 2008 and number of hatchlings produced on the natural beaches in Chichi-jima from 1983 to 2015.

1986) and it improved to 70.8% for the period between 1975 and 2008 after the project was fully implemented when the post-WWII United States occupation ended.

Natural Hatchling Production. — Hatching surveys were conducted on an average of 76.3% of all clutches on each season from 1983 to 2015 excluding 1999, 2001, and 2009; this amounts to roughly 550 nests being surveyed every year. From 2010 to 2015, more than 1400 clutches were excavated on average each season. The annual mean emergence success of clutches on natural beaches was 33.6% (range = 18.6%–51.8%).

Natural Hatching Versus Artificial Hatching. — A total of 98,137 hatchlings were produced by the hatch and release project from 1975 to 1984, when it was assumed more hatchlings were being produced by artificial hatching than from the natural beaches. From 1975 to 1982, hatching surveys were not conducted; however, our supposition of more hatchlings via the hatch and release program is based on the fact that 1071 nests were collected for incubation during that period, whereas only 489 nests were observed on natural nesting beaches during the same period. Moreover, emergence success of the artificial hatching was always higher (annual mean of 70.8%) than that on natural nesting beaches (annual mean of 33.6%) in a given year. In 1983 and 1984, 30,748 hatchlings were produced by the hatch and release project whereas 14,243 hatchlings emerged from the natural beaches. From 1985 to 1990, the number of hatchlings artificially produced decreased to almost equal the number of hatchlings emerging from natural beaches, with 49,463 hatchlings produced from the captive program and 48,277 hatchlings from natural beaches. In 1991, the production of natural hatchings (16,235) exceeded those produced by the hatch and release project (6604) and continued to increase in subsequent years. In the mid-2000s there was a dramatic increase in the ratio of natural versus artificial hatchlings, with a total of 395,546 hatchlings (annual mean of 23,267) from natural beaches versus 58,133 hatchlings (annual mean of 3633) from artificial hatching from 1992 to 2008. The estimated number of hatchlings from natural beaches reached over 90,000 in 2008, when the hatch and release project ceased. During 2011 to 2015, 30,000 to 70,000 hatchlings were produced on the natural beaches every year (Fig. 5).

DISCUSSION

Ogasawara's green turtle population has experienced an increase in the annual number of nesting females, nest counts, and number of hatchlings being produced on natural beaches, indicating that the population is recovering from its near extirpation caused by years of overharvesting. Bjorndal et al. (2005) suggested that long-term monitoring surveys are necessary for assessing abundance trends on long-lived species. Long-term studies, such as the present one, are key to understanding population dynamics and species recovery, and the trend of Ogasawara's green turtle population would not have been known without the 40+ yrs of study summarized here.

We highlight that the number of nesting females has increased even though the legal turtle harvest has continued in smaller numbers. This indicates that sustainable harvest of sea turtles is possible under limited and regulated level. There are other examples of sustainable traditional use and trade of sea turtles. For example, sustainable, regulated harvest of hawksbill turtles, *Eretmochelys imbricata*, has been reported in Cuba, and this harvest has provided benefits to local artisans (Mrosovsky 2000; Webb 2002). Webb (2002) also provides an example of successful management programs through sustainable harvest on saltwater crocodiles, *Crocodylus porosus*, in the Northern Territory of Australia. Webb (2002) stated that conservation is linked to values of wild species, and sustainable use of wildlife can increase the value of wildlife to local communities, which ultimately promotes conservation of a species and its habitat. Also, Webb (1997) noted that scientific data collection is necessary for monitoring and assessment to achieve sustainability of a wild species. We suggest that sustainable use should be evaluated based on the results of such surveys rather than be influenced by the biases of sustainable harvest skepticism. Indeed, understanding the values of all peoples, cultures, and traditions is required for a successful conservation through sustainable use (Webb 1997). Nevertheless, the long-term monitoring of nesting females and regulation of green turtle harvest based on these demographic data has promoted sustainable use of green turtles in Ogasawara.

When comparing the 2 groups of islands, turtle harvest numbers have been much higher in Haha-jima than in Chichi-jima. From 1975 to 1987, the total reported catch was 149 turtles in Chichi-jima, whereas 608 turtles were reported captured in Haha-jima. Conversely, nest numbers have been lower in Haha-jima than in Chichi-jima, and thus it might be indicative that the turtle harvest in Haha-jima has had a substantial impact on the population.

No data are available on nest counts before 1975; however, it is assumed that fewer females nested during this period. Thus, the number of hatchlings produced on natural beaches for several decades before WWII was limited and probably similar to the number of hatchlings produced in the hatch and release project up to 1939. Our assumption is based on the significant decrease of turtle catch prior to WWII, which occurred despite no harvest limits, and the increasing demand of turtle meat as a result of the increased population of islanders. There was high variation in turtle catch numbers before versus after 1923 (Fig. 3), and the lower catch numbers with a smaller fluctuation after 1923 may indicate that the population was facing local extirpation. The sudden decrease in catch was likely caused by overharvesting, and it is assumed that the greater portion of the green turtle population migrating to Ogasawara during the breeding season had been harvested.

A small number of hatchlings were produced on natural beaches when emergence success surveys began in 1983 (Fig. 5), suggesting that the natural production of hatchlings as well as the hatch and release project before WWII were insufficient to result in an increase in the nesting population. Conversely, the hatch and release project was not conducted from 1940 to 1971, and the number of harvested turtles was also very low during a similar period (from 1942 to 1968), suggesting that the natural production of hatchlings might have increased significantly during this time. We assume that the low harvest levels led to increased production of natural hatchlings during this period and most likely contributed to the recent overall recovery of the nesting population in the region.

Age at reproductive maturity is currently unknown for Ogasawara green turtles; however, we could derive an estimate for age at maturity based on the temporal nature of population trends. For example, if the production of hatchlings during the period of low harvest levels is the main contributor to the gradual increase seen for a couple of decades in the early periods of nest surveys starting in 1975, it suggests that Ogasawara green turtles reach sexual maturity in approximately 30 yrs. This is consistent with the studies regarding age at first nesting of green turtles, which ranges 9–58 yrs in Hawaii (Balazs 1982; Zug et al. 2002; Balazs et al. 2015), 25–50 yrs in Australia (Limpus and Walter 1980; Chaloupka et al. 2004), 18–27 yrs in Florida (Frazer and Ehrhart 1985), and 27–33 yrs in the Atlantic (Frazer and Ladner 1986). Moreover, a recent study by Van Houtan et al. (2014) suggested that Hawaiian green turtles reach sexual maturity at an age of 23 yrs, which seems plausible and may explain the 40-yr recovery of green turtles in Hawaii. Thus, there is a great possibility that green turtles in Ogasawara become sexually mature in fewer than 30 yrs, as the population in Chichi-jima showed a higher growth rate than did the green turtle population at East Island in the Northwestern Hawaiian Islands (Chaloupka et al. 2007).

The harvest pressure on female turtles, which was estimated by dividing the number of harvested females by the sum of harvested females and total estimated nesting females, has remained relatively low since 2005. An annual mean of 16.2% females were harvested among all migrating female turtles since 2005, which is assumed to be directly brought about by increasing numbers of nesting females during the same period (Fig. 4). The number of female turtles captured each year has been similar after the islands were returned to the Japanese government in 1975, with even greater consistency starting in 1994 when new harvest restrictions were implemented (Fig. 3). However, a decrease of the harvest pressure was observed during the same period. The total number of female turtles caught in 11 yrs from 2005 to 2015 was 656 turtles, whereas in the 11 yrs from 1975 to 1985 a total of 644 female turtles were caught with a mean annual harvest pressure of 69.1%.

If green turtles take up to 50 yrs to reach maturity as suggested by Balazs (1982) for Hawaiian green turtles, it is possible that the significant increase observed since 2005 may be from maturing offspring from turtles that nested during the low harvest level period during WWII and the United States occupation. We note that the harvest pressure was critically high during a couple of years after 1975, when only a small number of hatchlings were produced, thus it is unlikely that the increases are from turtles hatched during these years. Nevertheless, recruitment of nesting females during the last 40 yrs is likely to have contributed to the increase in number of nesting females.

Hatchlings produced by the hatch and release project during all these years could have been a contributor for the increase seen in the number of nesting females over the past 10 yrs. It is known, however, that numerous threats and predators exist at different stages (Georges et al. 1993), which may result in low juvenile survivorship for long-lived, slow-growing green turtles. Limpus (1985) and Frazer (1986) also noted that survivorship is low in hatchling loggerhead turtles, *Caretta caretta*. It is estimated that at least 1 of 100 hatchling sea turtles must survive to adulthood to maintain a stable population (Hirth and Schaffer 1974; Bjorndal 1980). A total of 136,061 artificial hatchlings were produced during 13 yrs from 1976 to 1988, which represents more than 60% of all artificial hatchlings produced after the project was resumed in 1972. If those hatchlings had reached adulthood with a survival rate of 1%, then 1361 individual turtles would have survived to breed.

Any turtles encountered during mating season are captured, and there is no preference for either sex, thus results from the harvest records during 1975 to 2015 ($n = 4002$) indicate that the breeding sex ratio of waters around Ogasawara was 52.8% females to 47.2% males. Based on the apparent sex ratio of captured turtles, this means that of the aforementioned 1361 individuals that would have been expected to survive, 719 would have been adult females. With a 4-yr remigration interval for Ogasawara green turtles (Suganuma 1989), the lowest total number of nesters for any 4 successive years during the significant increase of nesting females from 2005 to 2015 was 1590 females (from 2005 to 2008). Thus, the estimated number of adult females produced by the project during those years reflects only half the total number of nesting females during the years of the significant increase (Fig. 4). Thus, our hypothesis does not fully explain the increase and suggests that survival to adulthood of Ogasawara green turtle hatchlings is greater than 1%.

The gradual increase in the number of nesting females was observed since the 1990s and became more significant in 2005, showing an increasing trend of about 24 yrs. The 27 yrs of stable production of hatchlings on natural beaches from 1942 to 1968 seem to be the most likely reason for the increasing trend for the nesting population. Further, it is likely that the long-term prohibition of egg harvest (since 1898) has contributed to the increasing trend, as it has allowed the continued production of hatchlings under natural conditions.

In conclusion, long-term monitoring of nesting activity is key to understand population dynamics and trends. Analyses of harvest pressure on the Ogasawara green turtle population are also essential for facilitating the sustainable use of green turtles and conserving the population for future generations. The harvest pressure on the nesting females the past few years has ranged between 10% and 30% with existing regulations on the annual harvest limit. The increase in the number of nesting females is likely due to natural production of hatchlings during the periods of no harvest. However, it is unknown whether the current harvest pressure is sufficient for maintaining a sustainable use of the Ogasawara's sea turtle population in the long-term. Continuous monitoring for a few more decades to half a century will be necessary to better understand the interactions between green turtle population dynamics and turtle consumption. Further studies are also necessary to estimate the age at maturity and the reproductive longevity of green turtles in Ogasawara and to further assess the effectiveness of artificial hatching programs, including estimating survival rates for both natural and artificially produced green turtles. Moreover, other parameters that are not discussed in this study, such as conditions on feeding grounds, recruitment of head started turtles released from Ogasawara, and indirect human activities including coastal development, could have had more-intense impacts on green turtle abundance and trends. Research in these areas will contribute to a better understanding of appropriate conservation and management of green turtle populations, both local and globally.

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