Ontogenetic habitat shifts of green turtles (*Chelonia mydas*) suggested by the size modality in foraging aggregations along the coasts of the western Japanese main islands

Tomoko Hamabata[a], Tsutomu Hikida[a], Kei Okamoto[b], Saya Watanabe[c] and Naoki Kamezaki [d, e]

[a] Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo, Kyoto 606-8502, Japan

[b] Orido, Shimizu, Shizuoka, Shizuoka 424-0902, Japan

[c] Sea Turtle Association of Japan, 5-17-18 Nagaomotomachi Hirakata, Osaka 573-0163, Japan

[d] Suma Aqualife Park Kobe, 1-3-5 Wakamiyacho Suma, Kobe, Hyogo 654-0049, Japan

[e] Faculty of Biosphere-Geosphere Science, Okayama University of Science, 1-1 Ridai-mae Kita, Okayama, Okayama 700-0005, Japan

Corresponding author: T. Hamabata
E mail: hamabata@zoo.zool.kyoto-u.ac.jp
Phone: +81-75-753-4091; Fax: +81-75-753-4114

Abstract

To understand the life histories and ontogenetic habitat utilization of green turtles along the coasts of the western Japanese main islands, we collected size frequency and genetic data of green turtles captured by pound nets in three foraging grounds (FG): Nomaike (n = 38), Muroto (n = 93), and Kumano-nada (n = 31), and compared their natal origins among different size classes. Population genetic analyses based on an 820-bp fragment of mitochondrial DNA showed that the three FG were part of a single multiple-coast FG. Although turtles from all size classes originated mainly from rookeries in the Ogasawara Group, the size distributions clearly exhibited bimodality, with low occurrences of turtles in the 50–70-cm straight carapace length (SCL) range. The bimodal size distributions could not be attributed to demographic shifts in rookeries, because the number of female green turtles in Ogasawara has exhibited an increasing trend since 1979. We also examined whether factors such as seasonality and predation risk could have caused the size bimodality. There were, however, no strong relationships between sea-surface temperatures when turtles were captured and the sizes of the turtles ($r^2 < 0.2$), and it appeared that predation risk could not result in the size modality observed in the FG. Our results strongly suggest that after switching from a pelagic to a neritic lifestyle, the green turtles in the neritic FG along the western Japanese main islands undergo another ontogenetic habitat shift upon reaching ~50-cm SCL. Here, we explore the possibility that developmental growth might stimulate a

habitat shift, resulting in habitat differentiations by size and growth phase in the long-lived green turtle.

Keywords

Size distribution, Foraging ground, Ontogenetic habitat shift, Green turtle, Developmental change

Abbreviations

FG: Foraging ground

MSA: Mixed Stock Analysis

mtDNA: Mitochondrial DNA

SCL: Straight carapace length

SST: Sea surface temperature

RMU : Regional Management Unit

1. Introduction

The green turtle (*Chelonia mydas*) has a circumglobal distribution and is highly migratory and long-lived. It is believed that in its typical life cycle, after hatching on beaches the green turtle spends several years in the oceanic environment in its pelagic stage before moving back into the neritic zone (neritic stage), where its major food sources, seagrass and sea algal beds, are distributed (Bolten, 2003). Although this typical life cycle suits some populations, several studies have revealed that green turtles have non-homogenous

lifestyles, and may exhibit diversity or plasticity in behavior, food resources, and timing of ontogenetic dietary and habitat shifts among populations, regions, and individuals (e.g., Burkholder et al., 2011; Cardona et al., 2009; González Carman et al., 2012; Hatase et al., 2006; Hays et al., 2002; Parker et al., 2011). This lifestyle diversity suggests that the ecologies and life histories of green turtles may vary depending on their local environments, the availability of resources, and their biological requirements.

Foraging grounds (FG), where green turtles aggregate and spend the vast majority of their life spans, are some of the most important areas for understanding their ecology, migration, and life history. Previous studies have constructed hypothetical scenarios of the foraging aggregation processes of marine turtles by using mixed-stock analysis (MSA), estimating the contributions of various source rookeries to FG based on the haplotype compositions of mitochondrial DNA (mtDNA) in rookeries and FG (reviewed by Jensen et al., 2013). Many studies have focused on the early passive recruitment to neritic FG after the pelagic stage and proposed factors that might influence foraging aggregation, such as distance from rookeries (Bass and Witzell, 2000), relative sizes of rookeries (Lahanas et al., 1998), and oceanic currents (Bass et al., 2006). Yet in some FG, immature turtles were thought to have migrated from their initial FG to suitable FG closer to their natal rookeries (Luke et al., 2004).

As suggested by several mechanisms proposed above, green turtle size distribution

85 data in FG have also demonstrated that the timing of habitat shifts and patterns of habitat use
86 are varied and complex across regions, even after the shift from a pelagic to a neritic
87 lifestyle. For example, in Atlantic sites many green turtle FG are dominated by immature
88 turtles, and some FG are shared seasonally with migratory adults (Meylan et al., 2011). Also,
89 evidence from the direct tracking of the developmental migrations of large immature green
90 turtles in the Atlantic has shown that they can actively swim among different FG (Godley et
91 al., 2003). In contrast, the FG in Pacific sites have well mixed compositions of adult and
92 immature turtles year-round (Balazs, 1980; Limpus et al., 2005; Sterling et al., 2013). These
93 mixed-size compositions were believed to be a result of their long-term strong fidelity to
94 their foraging areas based on mark and recapture studies that showed limited movement
95 between FG (Limpus et al., 1992). One study conducted MSA in the green turtle FG of the
96 Torres Strait, in the southwestern Pacific, however, demonstrated that the contributions of
97 source rookeries varied between the juveniles and the adults, suggesting either
98 developmental migration by juveniles, or demographic shifts due to reduced hatching
99 success at source rookeries (Jensen, 2010). Moreover, at Palmyra Atoll, in the central
100 Pacific, discrepancies between the directions of oceanic currents and the distributions of
101 haplotype data suggested that biological processes may be important factors driving green
102 turtle foraging aggregation (Naro-Maciel et al., 2014). These results indicate that foraging
103 aggregations were not always governed by the passive early recruitments. Thus, detailed

104 investigations of the composition and dynamics of each foraging aggregation, as well as
105 information on the source rookeries, are critical for revealing the main influences on the
106 lifestyle, ecology, and migration of this species.

107 Distributions of foraging green turtles on the coasts of the Japanese main islands in
108 the northwestern Pacific, were determined based on incidental catch by coastal net fisheries,
109 direct observation, and coastal stranding data (Kameda and Ishihara, 2009; Kamezaki et al.,
110 2007; Okamoto et al., 2011; Shimada, 2009). Previous studies using MSA have revealed
111 that green turtles in foraging aggregations along the Japanese main islands originate
112 primarily from rookeries in the Ogasawara Group, the largest nesting site in Japan
113 (Nishizawa et al., 2014, 2013). Foraging aggregations, however, have been described
114 without regard to population dynamics, because available data on the size compositions of
115 foraging green turtles around the Japanese main islands were limited (e.g., Okamoto et al.,
116 2011). Here we describe the size compositions of green turtle foraging aggregations around
117 the western Japanese main islands, discuss how these foraging aggregations were formed,
118 and provide new insights into foraging aggregation dynamics and the factors affecting the
119 ontogenetic habitat shifts of green turtles.

120

121 **2. Materials and methods**

122 *2.1. Descriptions of the study sites and sample collection*

123 The Japanese main islands are all situated beyond the northern limit of the female green
124 turtles' nesting sites in the North Pacific, and green turtles distributed along these coasts are
125 therefore considered to be aggregated for the purpose of foraging. Our data set consists of
126 the aggregations from three FG located in the coastal areas of the western Japanese main
127 islands: Nomaike FG (31°25'N, 130°08'E), Muroto FG (33°15'N, 134°11'E), and
128 Kumano-nada FG (34°07'N, 136°27'E) (Fig. 1A). The Nomaike FG was located on the
129 southwestern coast of Kyushu Island. The pound net used at Nomaike was set at a depth of
130 27 m in the inner bay. The Muroto FG was located on the southeastern coast of Shikoku
131 Island. Our samples from the Muroto FG were taken from individuals captured in three
132 pound nets located within an 8-km area near the tip of the Cape. These pound nets were set
133 at depths ranging from 35–78 m, near the edge of the narrow continental shelf. The
134 Kumano-nada FG was located at the west side of the Kii Peninsula, in the central part of the
135 Pacific coast of the Japanese main island. These pound nets were set at depths of ~60 m in
136 the ria coasts.

137 Tissue samples were collected from green turtles captured from the three FG from
138 2004 to 2012 (Table 1, n = 162): 38 turtles from the Nomaike FG, 93 turtles from the Muroto
139 FG, and 31 turtles from the Kumano-nada FG. All turtles from the Nomaike FG and 59
140 turtles from the Muroto FG were previously examined by Hamabata et al. (2009). Twelve
141 turtles previously examined by Hamabata et al. (2009) that were listed as samples from

142 Owase were regarded as samples from the Kumano-nada FG in this study, as Owase is a part
143 of Kumano-nada. Two turtles from the Muroto FG and two from the Kumano-nada FG were
144 the same individuals as used in a morphological study by Okamoto and Kamezaki (2014);
145 these four turtles correspond to ID nos. 8–11 in Okamoto and Kamezaki (2014; Appendix 1).
146 Living turtles were released after the attachment of plastic tags, Inconel tags, or both, and
147 multiple samples from the same individual were avoided. Size frequency structures were
148 constructed based on the straight carapace length (SCL). The relationship between water
149 temperature and the sizes of turtles aggregating in FG were examined by regression analysis.
150 Sea surface temperature (SST) data were used for water temperature. We obtained the SST
151 data from the Japan Oceanographic Data Center website
152 (http://www.jodc.go.jp/index_j.html), the Kochi Prefectural Fisheries Experiment Station
153 (http://www.suisan.tosa.pref.kochi.lg.jp/kaikyo_inf/show), and the Mie Prefectural
154 Fisheries Research Institute (http://www.mpstpc.pref.mie.lg.jp/SUI/kaikyo/index.htm). For
155 size analyses, the turtles from each FG were grouped into three size classes: i) SCL < 50 cm;
156 ii) 50 cm ≤ SCL < 70 cm; and iii) SCL ≥ 70 cm. These size groupings were arbitrarily
157 defined, with consideration of the shapes of the size distributions.
158
159 *2.2. Molecular techniques and haplotype determination*
160 Skin or muscle samples were preserved in 99% ethanol until laboratory analysis. We

isolated DNA from skin or muscle samples by phenol/chloroform extraction or DNeasy Blood and Tissue Kits (QIAGEN). Polymerase chain reaction (PCR) was performed using the primers LCM15382 and H950 (Abreu-Grobois et al., 2006), designed to target an 820-bp fragment containing partial sequence of the $tRNA^{Pro}$ gene and the 5' end of the control region of the mtDNA genome. For each PCR, 1–2 μl of template DNA was used in a 12.5- or 15.0-μl reaction volume under the following conditions: hot start at 94°C for 3 min; 35–40 cycles of 94°C for 30 s, 55°C for 30 s, and 72°C for 60 s; a final extension at 72°C for 3 min; and then storage at 4°C. Sequences were obtained using an ABI model 3130xl (Applied Biosystems Inc.) sequencer, with all variable positions confirmed by comparing sequences from the forward and reverse strands. Sequences were assembled using DNA BASER (Heracle Biosoft S.R.L), and aligned with Muscle in MEGA 6 (Tamura et al., 2013). We sequenced all 162 samples, because short fragments of haplotypes (500-bp) were used in the previous study by Hamabata et al. (2009). Sequences were compared to previously described haplotypes based on 380-bp, 500-bp, and >700-bp fragments of the mtDNA control region reported by Chassin-Noria et al. (2004), Cheng et al. (2008), Dethmers et al. (2006, 2010), Dutton et al. (2008), Hamabata et al. (2009, 2014), Nishizawa et al. (2010, 2011, 2013, 2014), and Norman et al. (1994). The standardized haplotype names for the Indo-Pacific region were assigned to new sequences.

180 *2.3. Population genetic analyses*

181 Haplotype diversity (*h*) and nucleotide diversity (π) were estimated for each FG and each
182 size class of the FG using ALREQUIN V.3.5. (Excoffier and Lischer, 2010) based on
183 380-bp sequences, to compare our results with FG from previous studies. Annual variations
184 were examined in the Muroto and Kumano-nada FG (Muroto FG: n = 37 in 2005, n = 9 in
185 2006, n = 25 in 2007, and n = 17 in 2008; Kumano-nada FG, n = 14 in 2004, n = 3 in 2005,
186 n = 6 in 2008, and n = 8 in 2009). Five turtles in the Muroto FG (n = 1 in 2004, n = 2 in 2009,
187 and n = 2 in 2011) were excluded from this analysis due to the small sample sizes for annual
188 comparisons. Annual variations were not examined in the Nomaike FG because all samples
189 were collected in 2004. To examine seasonal variations within the FG, turtles were grouped
190 based on two different SST as follows: i) SST < 20°C (n = 15 in the Muroto FG, n = 9 in the
191 Kumano-nada FG) and SST ≥ 20°C (n = 78 in the Muroto FG, n = 22 in the Kumano-nada
192 FG), and ii) SST < 25°C (n = 6 in Nomaike FG, n = 56 in Muroto FG, n = 16 in
193 Kumano-nada FG) and SST ≥ 25°C (n = 32 in Nomaike FG, n = 37 in Muroto FG, n = 15 in
194 Kumano-nada FG). In the Nomaike FG, only one turtle was captured at a SST < 20°C.
195 Therefore, the Nomaike FG was excluded from the former analysis. Annual and seasonal
196 variations were examined by exact tests of population differentiation (Raymond and
197 Rousset, 1995) using a Markov chain length of 500,000 steps with 10,000 dememorization
198 steps, implemented in ARLEQUIN.

199 Genetic data from the three FG examined in this study were also compared by
200 exact tests with data from four other FG around Japan: Yaeyama and Ginoza in the Ryukyus,
201 and Kanto and Sanriku in the eastern Japanese main islands (Nishizawa et al., 2013, 2014).
202 The comparisons were conducted using shorter sequences, truncated to ~380 bp. The
203 p-values of the multiple comparisons were corrected using the B-Y method (Benjamini and
204 Yekutieli, 2001).
205
206 *2.4. Mixed-stock analyses*
207 We performed MSA on pooled size group data from the Nomaike, Muroto, and
208 Kumano-nada FG, because no significant differences were observed between the same size
209 classes among the three FG. Following Naro-Maciel et al. (2014), potential source rookeries
210 outside of the northwestern Pacific were classified under the following regional
211 management units (RMU) developed by Wallace et al. (2010): Hawaii, Eastern Pacific,
212 Western and South Central Pacific, Southwestern Pacific, Eastern Indian, and Southeast
213 Asia. The Northwestern Pacific RMU was divided into the following four regions for a
214 more detailed investigation: the Taiwan and Hong Kong, Yaeyama, Central Ryukyu, and
215 Ogasawara regional groups of rookeries (Fig. 1B). Haplotype data for the above rookeries
216 were derived from Dethmers et al. (2006), Dutton et al. (2008), Chassin-Noria et al. (2004),
217 Cheng et al. (2008), Hamabata et al. (2014), Nishizawa et al. (2011, 2013), Ng et al. (2014),

and Naro-Maciel et al. (2014). Additional data from four female turtles nested on the northwestern Amami Oshima Island, Central Ryukyus, in 2013, were also included for analysis (all four females possessed haplotype CmP39.1). The rookery size data for the MSA were obtained from Amorocho et al. (2012), Cheng et al. (2008), Dethmers et al. (2006), Maison et al. (2010), and Hamabata et al. (2014). Following Nishizawa et al. (2013, 2014), MSA estimations were conducted in two ways using Bayesian methods: many-to-one (M2O) analysis using the program BAYES, which examines each size class of the combined FG independently (Pella and Masuda, 2001), and many-to-many (M2M) analysis using the software package R which enables the estimation of multiple FG simultaneously (Bolker et al., 2007). In the M2M analyses we included the data from four other FG around Japan: the Yaeyama, Ginoza, Kanto, and Sanriku FG (Nishizawa et al., 2013, 2014). Both methods were carried out under two priors: (1) uninformative priors assumed that each rookery had the same likelihood of contributing individuals to the foraging aggregations ($M2O_1$ and $M2M_1$), and (2) informative priors incorporated the relative size of each rookery ($M2O_2$ and $M2M_2$). For the M2O analyses, six chains, corresponding to potentially contributing sources, were run with 20,000 Markov chain Monte Carlo (MCMC) steps and a burn-in of 10,000 runs to calculate the posterior distribution. For the M2M analyses, six chains were run with 50,000 MCMC steps and a burn-in of 25,000 runs. The Gelman and Rubin shrink factor diagnostic was calculated to

test that the posterior probability distribution of all chains had converged (shrink factor < 1.2). Orphan haplotypes, defined as haplotypes observed only in the foraging grounds and not in any of the nesting rookeries, were removed from the analyses.

3. Results

3.1. Size compositions

The sizes of turtles in the Nomaike, Muroto, and Kumano-nada FG ranged from 40.6 to 96.7, 37.2 to 105.2, and 37.3 to 95.4 cm SCL, respectively. All size distributions (three individual distributions and one pooled distribution), plotted in 5-cm increments, did not exhibit bell-shaped curves, but bimodal size distributions, with peaks in the 45–49.9-cm range, and either the 70–74.9- or 75–79.9-cm range (Fig. 2). There was no strong relationship between SST and SCL ($r^2 < 0.2$, Fig. 3).

3.2. Haplotype composition, genetic diversity, and differentiation

Twenty-seven 820-bp haplotypes were identified from a total of 162 samples from green turtle FG around the Japanese main islands (Table 1). Twenty-three haplotypes matched previously reported shorter haplotypes (380- or 500-bp), and 16 matched previously identified longer haplotypes (>700-bp). Two haplotypes did not match any previously identified sequences, and were assigned standardized haplotype designations. One new

256 haplotype, found in the Kumano-nada FG, differed from CmP50.1 by one base pair, and was
257 assigned the name CmP210.1 (GenBank accession no. **AB896707**). The other new
258 haplotype, found in the Muroto FG, was characterized by a 10-bp insertion difference from
259 CmP39.1, and has been assigned the name CmP208.1 (GenBank accession no. **AB896708**).
260 The Hawaiian and Eastern Pacific haplotypes (CmP4.1, CmP6.1, and CmP15.1) were
261 observed in the Muroto and Kumano-nada FG (Table 1). Orphan haplotypes (CmP51.1,
262 CmP79.1, CmP93.1, CmP122.1, CmP131.1, CmP208.1.1, CmP210.1.1, CmP213.1) made
263 up 6.8% (n = 11) of the total sample population. Both the haplotype and nucleotide diversity
264 in the Muroto FG and the haplotype diversity in the Kumano-nada FG were highest in the
265 50–70-cm SCL class despite the smaller sample sizes than the other size classes; however,
266 the nucleotide diversities of the 50–70 cm SCL classes in the Nomaike and Kumano-nada
267 FG were lower than those of the other size classes, showing no consistent pattern in
268 diversity indices (Table 2). The diversity of the total sample population was similar to that
269 of the Sanriku FG, and lower than the other FG in the Ryukyus and Kanto (Table 2).
270 Neither annual nor seasonal variations were observed in any of the FG (annual: $p >$
271 0.055, and seasonal $p > 0.482$). Exact tests revealed that significant population
272 differentiation occurred between the FG in the Ryukyus (Yaeyama and Ginoza) and the
273 Muroto and Kumano-nada FG, but no significant differences were observed among the
274 Nomaike, Muroto, and Kumano-nada FG (Table 3). In addition, significant population

differentiations were supported between the Kumano-nada and Kanto FG by the exact tests, even after the correction for multiple comparisons (Table 3), but no significance was observed among the three FG of the present study and the Sanriku FG, which was more distant than the Kanto FG. Although a significant difference was observed between the 50–70-cm SCL class of the Muroto FG and the >70-cm SCL class of the Kumano-nada FG, the difference was absent after correction for multiple comparisons (Table 4).

3.3. Mixed-stock analyses

All estimations by MSA indicated that in the FG of the western Japanese main islands, many turtles in all size classes originated from rookeries in the Ogasawara Group, although the proportion decreased in M2M analyses, especially in M2M of the 50–70-cm SCL classes (Fig. 4). While the contributions from the Northwestern Pacific rookeries (the Taiwan, Hong Kong, Yaeyama, and central Ryukyu rookeries) were very small in the M2O analyses (the lower limits of 95% probability intervals included zero), in M2M the 95% probability intervals of these rookeries were larger (Fig. 4). The probability intervals were broader in the M2M of the 50–70-cm SCL classes (Fig. 4).

4. Discussion

4.1. Genetic structure of the foraging aggregations along the Japanese coasts

The non-differentiation of genetic compositions among the three FG examined in the present study suggests that turtles migrate among the coasts of the western Japanese main islands as if they constitute a single foraging site. This is supported by a report that one turtle tagged at the Kumano-nada FG on 3 November 2005 was recaptured at the Muroto FG eleven days later (Okamoto and Kamezaki, 2014). Our additional population genetic analyses highlighted significant differences between the Yaeyama FG and all FG along the Japanese main islands. Yet, the extent of the multiple-coast foraging site was unclear, because the significant differences did not show a clear pattern. For example, the Kumano-nada FG was not significantly differentiated from the Sanriku FG, but was significantly differentiated from the closer Kanto FG. These results suggested that the boundaries among the FG were complex or that more samples are needed to reveal the boundaries conclusively.

4.2. Size compositions in the FG and population trends in the natal region

The range of SCL in the present study indicated that green turtles in various growing stages aggregate around the Japanese main islands. The mixed-size compositions of all three FG in the present study were consistent with size ranges from other FG in the Pacific. The smallest turtles in the three FG were ~40 cm SCL. This size is similar to that at which pelagic juveniles in the Pacific appear to switch to a neritic lifestyle (e.g., Balazs, 1980; Limpus et

313 al., 2005). The size distributions of the three FG, however, clearly demonstrated a
314 characteristic bimodality with a low frequency of turtles of 50–70 cm SCL, similar to
315 reports from FG in Shoalwater Bay in eastern Australia (Limpus et al., 2005), and in eastern
316 Taiwan (Cheng and Chen, 1997). Bresette et al. (2010) also reported a bimodal size
317 distribution of pooled green turtles from Mooney Harbor and the eastern Quicksands, west
318 of Key West, Florida, USA, although the bimodality was not noted in their study.
319 Interestingly, the peak sizes of the present size distributions were consistent among all three
320 FG. Some FG in the Atlantic are seasonally shared by immature and adult green turtles, and
321 their size compositions could change temporarily to be similar to a bimodal distribution
322 (Meylan et al., 2011). The bimodality of the present study, however, was not a result of
323 seasonal sharing among turtles in different life stages, as both smaller and larger turtles were
324 captured in various sea surface temperatures.

325 One of the most important factors affecting the population demographics was the
326 number of births in the rookeries. The estimations by MSA indicated that in the three FG of
327 the present study, the main natal origin of turtles of all size groups was the Ogasawara
328 Group, although some turtles from the central Ryukyu and Yaeyama rookeries were also
329 observed in the FG. Therefore, variations in the numbers of births in Japan, especially
330 Ogasawara, the largest nesting site in Japan and the predominant source for the present FG,
331 would substantially affect the demographics of these foraging aggregations. The number of

nests in the Ogasawara Group has been monitored since 1979 and demonstrated an increasing trend up to 2005 (Chaloupka et al., 2008; Yamaguchi et al., 2005). The precise age to reach ~50 cm SCL has not been estimated for wild green turtles born in the Ogasawara Group; however, based on estimates from other Pacific regions that females reach sexual maturity at around 20–40 years (Zug et al., 2002), an increasing number of nests over the past 25 years would not result in such SCL bimodality. In addition, although mortality during the pelagic life stage or in the FG could influence the size compositions of foraging aggregations, in the past decades no specific factors that could have increased the mortality of green turtles in the pelagic stage or in the FG are known. Therefore, there is no reason to believe that the bimodal size compositions of the three FG reflects skewed population demographics in which green turtles of 50–70 cm SCL were less abundant in the wild. Presumably, the size modality is attributable to location shifts by turtles of ~50-cm SCL into habitats that were not sampled, as indicated by data from the Shoalwater Bay, where over 18 years of sampling adults were captured at a higher frequency than late-stage juveniles (Limpus et al., 2005).

4.3. Possible factors contributing to the bimodal size distributions

What factors could cause green turtles to choose their habitat locations according to their sizes? In several FG, green turtles were known to demonstrate size-partitioning of habitats

as a result juveniles inhabiting shallower waters, and larger turtles inhabiting deeper water (Balazs, 1980; Bresette et al., 2010; Koch et al., 2007; Limpus et al., 2005; López-Mendilaharsu et al., 2005). Such size-partitioning of habitats has been explained by the minimization of predation risk. Yet, all pound nets in our study sites were set at depths deep enough (> 27 m) for large predators such as sharks to approach turtles of all sizes. Thus, the differences in predation risk among sizes probably did not cause the bimodality.

We speculate that a developmental change, which commonly occurs in green turtles, could have stimulated habitat shifts in some FG based on the evidence that low occurrences of turtles in the 50–70-cm SCL range were common in all of the FG exhibiting bimodal size distributions. The size range of 50–70 cm SCL corresponds to an accelerated somatic growth phase that occurs before the sub-adult stage (Chaloupka et al., 2004). The requirement for food resources at this stage is probably increased compared to younger stages, resulting in increased competition within the habitat. Meylan et al. (2011) surmised that in the Atlantic, FG dominated by immature turtles formed because immature green turtles were avoiding intraspecific competition with adults, as green turtles showed density-dependent growth, indicating that intraspecific competition can limit the growth rate (Bjorndal et al., 2000). Similarly, in some FG, the developmental change that is characteristically observed in green turtles upon reaching ~50-cm SCL may drive them to depart to other FG, where they can maintain their growth rate by avoiding intraspecific

competition with turtles of other size classes. The possibility of habitat shifts corresponding to developmental growth has been reported in Kemp's ridley turtles, *Lepidochelys kempii* (Schmid et al. 2003). At present, there is no evidence to support this hypothesis or data showing conditional differences, such as higher intraspecific competition in the three FG from the present study than in other FG with unimodal size distributions. Future studies examining to which location the 50–70-cm SCL turtles move and evaluating differences in the growth rates between unimodal and bimodal FG are needed to verify size-specific habitat preferences and ontogenetic habitat shifts. Nevertheless, our results strongly suggest that developmental growth in green turtles can cause shifts in habitat selection. It is likely that the green turtle foraging aggregations along the coasts of the western Japanese main islands are not maintained by long-term residents, but by periodic and continually dynamic populations resulting from ontogenetic habitat shifts.

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590

591

592 **Table 1.** Frequencies of 820-bp mtDNA haplotypes for each size class in the FG. The size

593 classes are denoted as follows: i, SCL < 50 cm; ii, 50 cm ≤ SCL < 70 cm; and iii, SCL ≥ 70

594 cm.

Haplotype name	Nomaike FG			Muroto FG			Kumano-nada FG			GenBank
820-bp	i	ii	iii	i	ii	iii	i	ii	iii	Accession no.
CmP4.1									1	**KC306666**
CmP6.1					1					**KC306657**
CmP15.1						1				**KC306649**
CmP18.1				1						**AB896713**
CmP20.1			1							**AB819806**
CmP20.3						1				**KF311745**
CmP32.1			2							**KF311749**
CmP39.1	3	6	12	19	3	27	7	3	7	**AB819807**
CmP39.2						1				**AB896709**
CmP49.1		1	1	1						**AB819808**
CmP50.1	1		2	5	4	9	3			**AB819809**
CmP51.1				1						**AB896706**
CmP53.1			1				1		1	**AB819810**
CmP54.1			2	1	1	3				**AB819811**
CmP79.1		1				2				**AB896712**
CmP93.1								1		**FJ917194**
CmP95.1						2		1		**FJ917196**
CmP121.1						2	1		1	**AB819813**
CmP122.1						1	1		1	**AB896710**
CmP126.1				1						**AB819815**
CmP127.1	1		1			1		1		**AB856321**
CmP128.1		1		1						**AB896711**
CmP130.1	1			1						**AB973567**
CmP131.1				1						**AB973568**
CmP208.1						2				**AB896708**
CmP210.1									1	**AB896707**
CmP213.1			1							**AB973569**
Total	6	9	23	32	9	52	13	6	12	

595

596

597 **Table 2.** Haplotype (*h*) and nucleotide (π) diversities of green turtles in FG along the
598 Japanese coasts. Values were calculated for both the total samples from each FG and the
599 three size groups from each FG and regional FG based on 380-bp haplotypes. Data for the
600 Yaeyama, Ginoza, and Kanto FG were from Nishizawa et al. (2013), and data for the
601 Sanriku FG were from Nishizawa et al. (2014).

Foraging ground		N	*h*	π
Nomaike	total	38	0.6913 ± 0.0823	0.02363 ± 0.01236
	< 50 cm	6	0.8000 ± 0.1721	0.02721 ± 0.01672
	50–70 cm	9	0.5833 ± 0.1833	0.01073 ± 0.00668
	> 70 cm	23	0.7273 ± 0.0971	0.02717 ± 0.01434
Muroto	total	93	0.6746 ± 0.0477	0.02320 ± 0.01193
	< 50 cm	32	0.6351 ± 0.0915	0.02106 ± 0.01116
	50–70 cm	9	0.7500 ± 0.1121	0.03248 ± 0.01838
	> 70 cm	52	0.6825 ± 0.0642	0.02189 ± 0.01140
Kumano-nada	total	31	0.6946 ± 0.0888	0.02450 ± 0.01284
	< 50 cm	13	0.6923 ± 0.1187	0.02747 ± 0.01505
	50–70 cm	6	0.8000 ± 0.1721	0.01839 ± 0.01160
	> 70 cm	12	0.6818 ± 0.1482	0.02722 ± 0.01504
Combined	total	162	0.6785 ± 0.0385	0.02324 ± 0.01189
	< 50 cm	51	0.6525 ± 0.0691	0.02257 ± 0.01175
	50–70 cm	24	0.7391 ± 0.0891	0.02391 ± 0.01268
	> 70 cm	87	0.6855 ± 0.0528	0.02352 ± 0.01209
Yaeyama	-	142	0.8355 ± 0.0215	0.03343 ± 0.01675
Ginoza	-	20	0.8789 ± 0.0432	0.03473 ± 0.01819
Kanto	-	47	0.7438 ± 0.0448	0.03054 ± 0.01563
Sanriku	-	39	0.6478 ± 0.0745	0.02313 ± 0.01210

602

603

604 **Table 3.** P-values from exact tests based on the 380-bp haplotypes identified in FGs around
605 Japan. Data for the Yaeyama, Ginoza, and Kanto FGs were from Nishizawa et al. (2013),
606 and data for the Sanriku FG were from Nishizawa et al. (2014).
607

	Yaeyama	Ginoza	Nomaike	Muroto	Kumano-nada	Kanto
Ginoza	0.3725					
Nomaike	< 0.001**	0.0469*				
Muroto	< 0.001**	0.0110**	0.2683			
Kumano-nada	< 0.001**	0.0063**	0.3074	0.1422		
Kanto	< 0.001**	0.1433	0.0166*	0.1981	0.0090**	
Sanriku	< 0.001**	0.0059**	0.0869	0.3910	0.1623	0.0547

608 *P < 0.05, **P < 0.0137 in B-Y method for 21 simultaneous tests
609
610

611 **Table 4.** P-values from exact tests of comparisons of FG size classes based on the 380-bp
612 haplotypes.
613

Size class	Nomaike FG			Muroto FG			Kumano-nada FG	
	< 50 cm	50–70 cm	> 70 cm	< 50 cm	50–70 cm	> 70 cm	< 50 cm	50–70 cm
Nomaike								
50–70 cm	0.474							
> 70 cm	0.716	0.702						
Muroto								
< 50 cm	0.532	0.537	0.485					
50–70 cm	0.472	0.053	0.373	0.368				
> 70 cm	0.461	0.320	0.216	0.340	0.497			
Kumano-nada								
< 50 cm	0.633	0.278	0.672	0.611	0.405	0.771		
50–70 cm	1.000	0.474	0.468	0.225	0.118	0.267	0.177	
> 70 cm	0.566	1.000	0.426	0.201	0.032*	0.157	0.647	0.568

614 Significant differences were absent after correction for multiple comparisons ($P < 0.01198$
615 in B-Y method for 36 simultaneous tests).
616 *$P < 0.05$
617

618 **Figure Legends**

619 **Fig. 1.** Locations of the FG (A), and rookeries (black dots) and regional groups of rookeries
620 (dashed circles) used in this study (B). Stars indicate the FG analyzed in this study. Circles
621 indicate the referenced Sanriku, Kanto, Ginoza, and Yaeyama FG. Rookery location data
622 were from Chassin-Noria et al. (2004), Dethmers et al. (2006), Cheng et al. (2008), Dutton
623 et al. (2008), Naro-Maciel et al. (2014), Nishizawa et al. (2011 and 2013), and Hamabata et
624 al. (2014).

625

626 **Fig. 2.** Size frequency distributions of straight carapace lengths (SCL) in the FG: Nomaike
627 (A, n = 38), Muroto (B, n = 93), Kumano-nada (C, n = 31), and the combined data of the
628 three FG (D, n = 162). The minimum sizes considered to be adults in male and female of the
629 Ogasawara Group are 79.4 and 82.1 cm SCL, respectively (Tachikawa, 1991).

630

631 **Fig. 3.** Sea surface temperatures (SST) and sizes (SCL) of green turtles captured at each FG:
632 Nomaike (A), Muroto (B), and Kumano-nada (C). Each point represents an individual.

633

634 **Fig. 4**. Estimated mixed-stock analysis (MSA) of green turtle foraging aggregations along
635 the coasts of the western Japanese main islands. Circles and triangles represent M2O and
636 M2M analyses, respectively. Bars indicate 95% probability intervals. Uninformative prior

637 estimations ($M2O_1$, $M2M_1$) are indicated in black, and informative prior estimations ($M2O_2$,
638 $M2M_2$) are indicated in white. Abbreviations of location and RMU are as follows: HK =
639 Hong Kong, SW Pacific = Southwestern Pacific, W & SC Pacific = Western and South
640 Central Pacific, and SE Asia = Southeast Asia. Size classes are as follows: A, SCL < 50 cm;
641 B, 50 cm ≤ SCL < 70; C, SCL ≥ 70 cm.
642

Fig. 1.

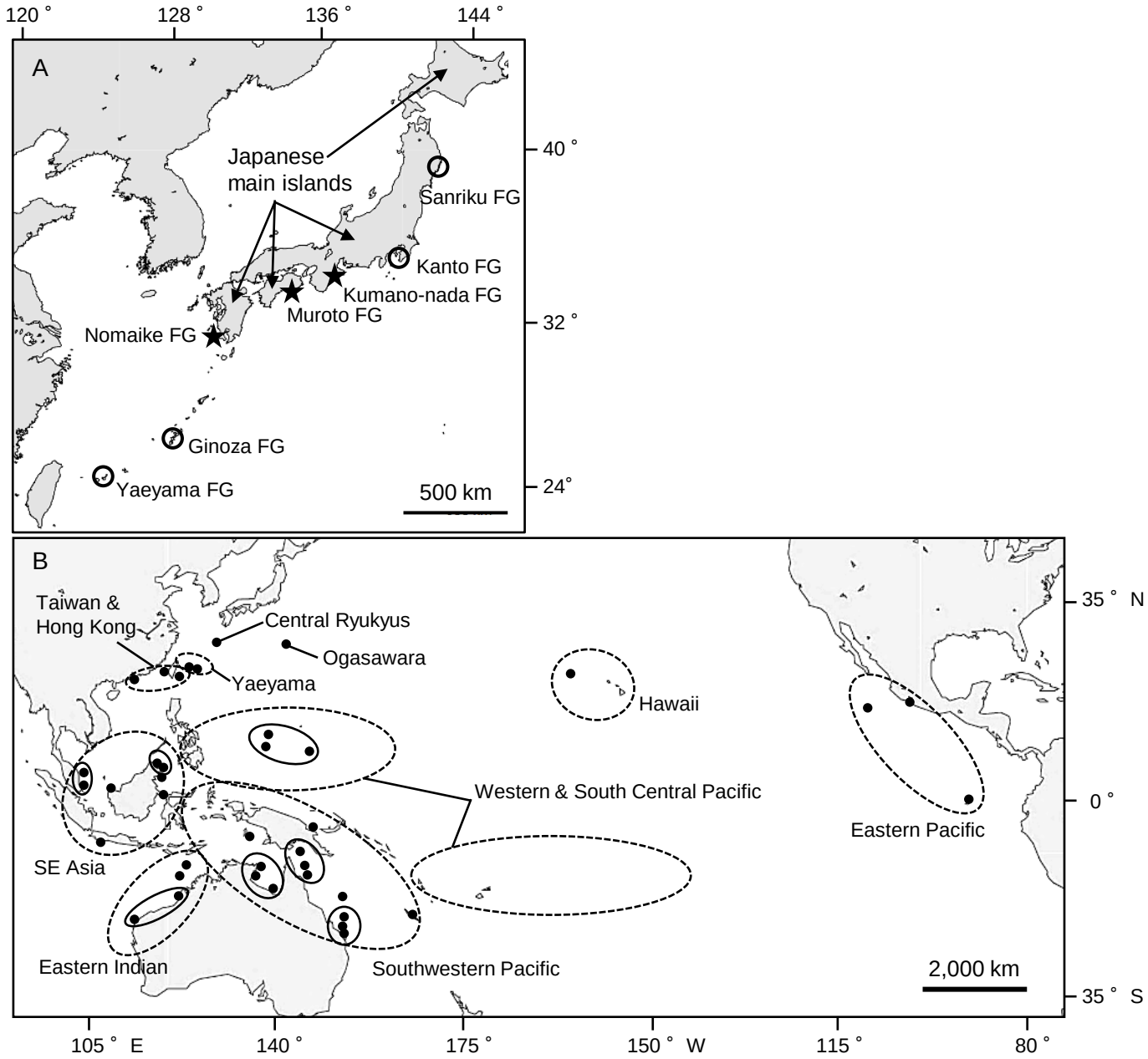

A
120 °
128 °
136 °
144 °
40 °
32 °
24°
Japanese
main islands
Sanriku FG
Kanto FG
Kumano-nada FG
Muroto FG
Nomaike FG
Ginoza FG
Yaeyama FG
500 km
B
Taiwan &
Hong Kong
Central Ryukyus
Ogasawara
Yaeyama
Hawaii
Western & South Central Pacific
Eastern Pacific
SE Asia
Eastern Indian
Southwestern Pacific
2,000 km
35 ° N
0 °
35 ° S
105 ° E
140 °
175 °
150 ° W
115 °
80 °

Fig. 2

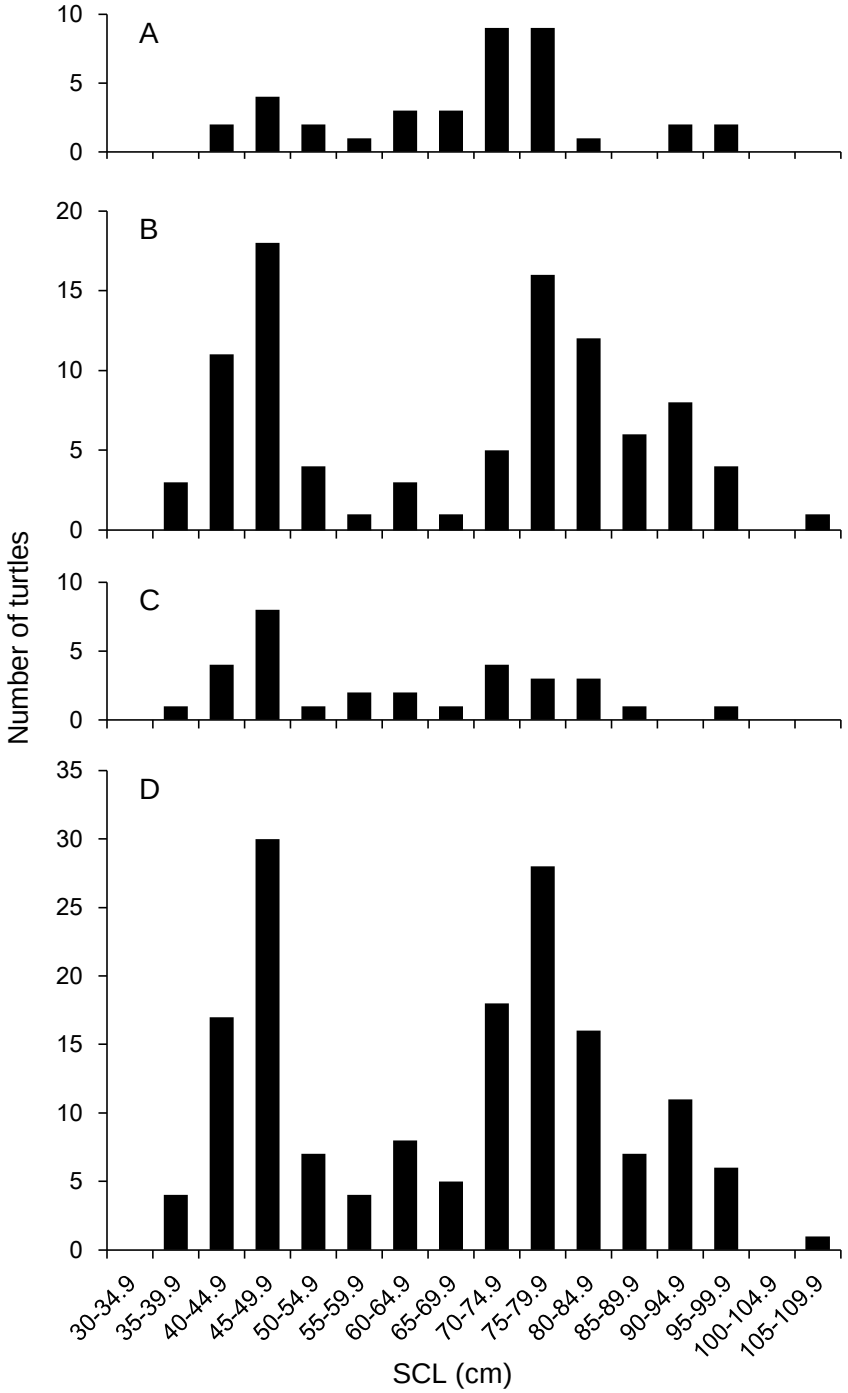

A
B
C
D
Number of turtles
SCL (cm)
30-34.9
35-39.9
40-44.9
45-49.9
50-54.9
55-59.9
60-64.9
65-69.9
70-74.9
75-79.9
80-84.9
85-89.9
90-94.9
95-99.9
100-104.9
105-109.9

Fig. 3

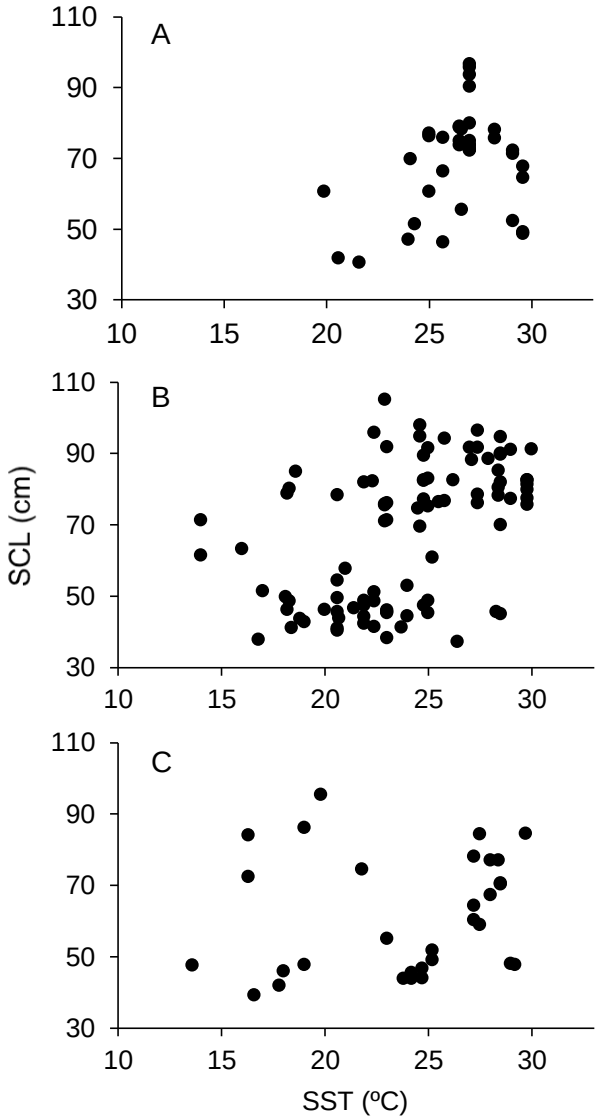
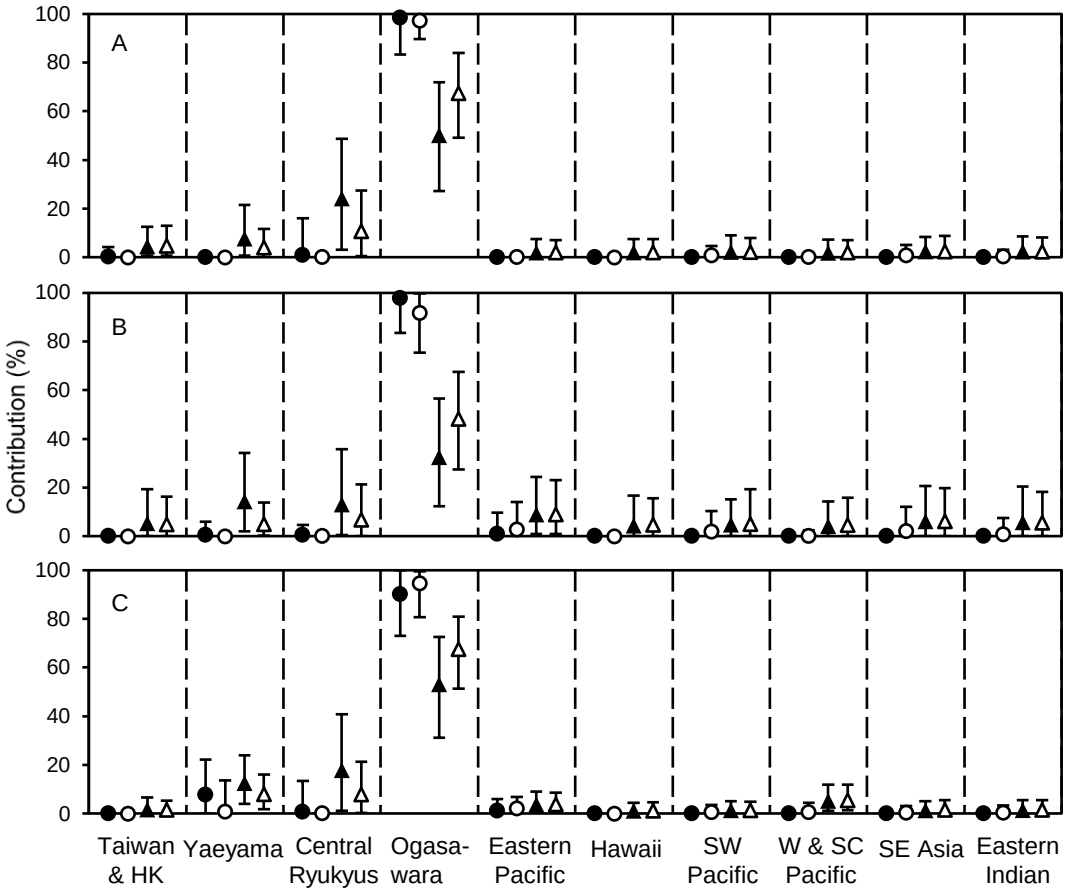


Fig. 4


A
B
C
Contribution (%)
100
80
60
40
20
0
Taiwan & HK
Yaeyama
Central Ryukyus
Ogasa-wara
Eastern Pacific
Hawaii
SW Pacific
W & SC Pacific
SE Asia
Eastern Indian