Composition of green turtle feeding aggregations along the Japanese archipelago: implications for changes in composition with current flow

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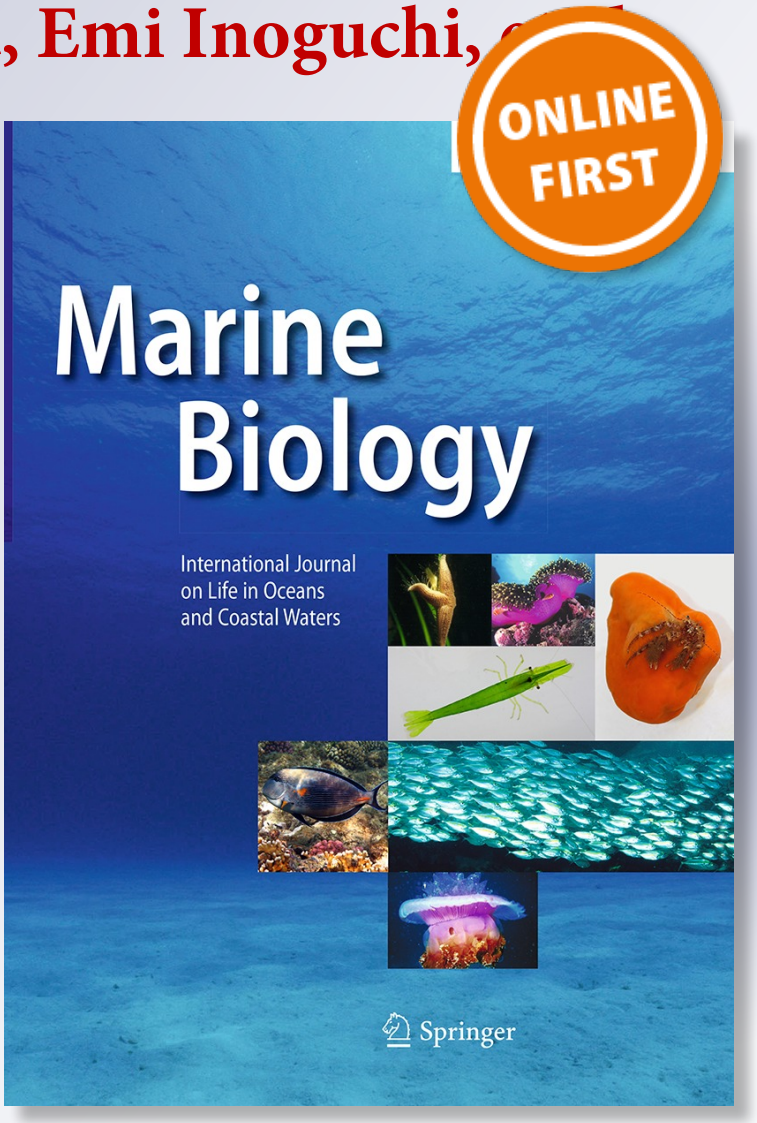
Marine Biology
International Journal on Life in Oceans and Coastal Waters

ISSN 0025-3162

Mar Biol
DOI 10.1007/s00227-013-2261-1



Springer

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ORIGINAL PAPER

Composition of green turtle feeding aggregations along the Japanese archipelago: implications for changes in composition with current flow

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Received: 25 February 2013 / Accepted: 10 May 2013

Abstract In order to develop effective conservation strategies for endangered migratory species, the link between feeding and breeding grounds needs to be clarified. In this study, the genetic compositions of consecutive Japanese feeding aggregations of green turtles (*Chelonia mydas*) along the Kuroshio Current were examined by mixed-stock analyses of mitochondrial DNA control-region sequences. The results indicated that the southern feeding aggregation around Yaeyama (24.3°N, 124.0°E) was sourced from various Pacific rookeries in the Yaeyama, Ogasawara, Western Pacific, and Indian Oceans and Southeast Asia. Among northern feeding aggregations, the Ginoza (26.5°N, 128.0°E) aggregation was also sourced from the Western Pacific Ocean, but the Nomaike (31.4°N, 130.1°E), Muroto (33.2°N, 134.2°E), and Kanto (35.6°N, 140.5°E) aggregations were contributed mostly by the closer Ogasawara rookeries. The reduced contribution from tropical Pacific rookeries to northern feeding aggregations and the significant correlation between genetic differentiation and geographical distance matrices of feeding aggregations indicated that most hatchlings from these regions transported by the Kuroshio Current settle in upstream feeding grounds along the Japanese archipelago, implying that current flow influences the composition of feeding aggregations. Differences in the composition of relatively close neritic feeding aggregations have important conservation implications, for which both regional and multinational conservation strategies are needed.

Communicated by M. I. Taylor.

H. Nishizawa (✉) · J. Okuyama · N. Arai
Department of Social Informatics, Graduate School of Informatics, Kyoto University, Kyoto 606-8501, Japan
e-mail: nishiza@bre.soc.i.kyoto-u.ac.jp

Y. Naito · A. Goto
Laboratory of Breeding Science, Graduate School of Fisheries Sciences, Hokkaido University, Hakodate 041-8611, Japan

H. Suganuma · S. Tanaka · E. Inoguchi · K. Narushima
Everlasting Nature of Asia, Acty Part II 4F Nishi-Kanagawa 3-17-8, Kanagawa-ku, Yokohama, Kanagawa 221-0822, Japan

O. Abe · M. Kobayashi
Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute, Fisheries Research Agency, 148 Fukaiohta, Ishigaki, Okinawa 907-0451, Japan

O. Abe
National Research Institute of Far Seas Fisheries, Fisheries Research Agency, 5-7-1 Orido, Shimizu, Shizuoka 424-8633, Japan

J. Okuyama
Protected Resource Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

K. Hirate
Okinawa Prefectural Fisheries and Ocean Research Center, 1-3-1 Nishizaki, Itoman, Okinawa 901-0305, Japan

K. Kobayashi
Program in Environmental Management, Graduate School of Agriculture, Kinki University, 3327-204 Nakamachi, Nara 631-8505, Japan

H. Ishii · S. Tanizaki
Ishigaki Island Sea Turtle Research Group, 2357-11 Arakawa, Ishigaki, Okinawa 907-0024, Japan

Published online: 22 May 2013

Introduction

Many vertebrates spend discrete phases of their lives in widely separated geographical areas, complicating research and management. In particular, understanding the migration of an endangered species can assist in the development of effective conservation and management strategies for that organism (Boyle et al. 2009). Therefore, migratory connectivity between feeding grounds and spawning or breeding grounds needs to be clarified (Webster et al. 2002). For migratory marine species, oceanic currents have been suggested to influence these migrations, especially when undertaken at a very young age (McConnell et al. 2002; Clarke et al. 2003), and therefore, patterns of recruitment and settlement to feeding grounds are hypothesized to vary regionally.

The movements of migratory marine vertebrates from their natal sites and the composition of feeding aggregations have historically been difficult to elucidate. Recently, however, examination of differences in mitochondrial DNA (mtDNA) haplotype frequencies caused by genetic isolation among nesting populations has afforded an opportunity to link feeding populations back to their rookery of origin and to estimate the contributions of genetically differentiated nesting populations to foraging assemblages using mixed-stock analysis (MSA) (Pella and Masuda 2001; Bolker et al. 2003). Therefore, the results of MSA are expected to be useful for understanding the migrations of marine vertebrates.

Sea turtles are marine vertebrates that spend most of their lives in the sea, and most sea turtle species generally migrate for long distances. Most of these migratory events are thought to be influenced by oceanic currents, especially in smaller juveniles. After hatching in terrestrial habitats, they undertake a mostly passive pelagic drifting that may last several years, followed by the recruitment to neritic habitats as feeding grounds (Musick and Limpus 1997; Reich et al. 2007). On the other hand, when growing up, active swimming is thought to play an important role in forming the settlement patterns of feeding sea turtles during the recruitment of young juveniles (Okuyama et al. 2011; Scott et al. 2012) or migration of older juveniles that may move preferentially toward feeding grounds in the region of their natal beach (Bowen et al. 2004).

Using MSA, previous research has indicated that most feeding aggregations of sea turtles have geographically diffuse sourcing (Lahanas et al. 1998; Luke et al. 2004; Roberts et al. 2005; Bass et al. 2006; Bowen et al. 2007; Naro-Maciel et al. 2007; Blumenthal et al. 2009; Amorocho et al. 2012), whereas some feeding aggregations may be much more locally sourced (Dutton et al. 2008). Ocean currents are thought to be important drivers of the patterns of genetic diversity observed in feeding aggregations (Blumenthal et al. 2009; Godley et al. 2010; Monzón-Argüello et al. 2010). Therefore, knowledge of the genetic compositions of feeding aggregation along the ocean current and estimation of settlement patterns of sea turtles would improve our understanding of their migration and the effect of the oceanic current.

The coastal waters of the Japanese archipelago provide feeding grounds for the green turtle (*Chelonia mydas*) along the strong Kuroshio Current (Hamabata et al. 2009). Major green turtle nesting assemblages in Japan are located at the northern edge of their Pacific nesting habitat, Ogasawara Islands and Ryukyu Archipelago (Fig. 1). Feeding habitats in Japan may be occupied by individuals from these Japanese rookeries, but also carried by the Kuroshio Current from multiple tropical rookeries in the Pacific. Japanese feeding grounds are good sites to investigate the settlement pattern of green turtles because of the large number of these feeding grounds and their closeness to the oceanic current. The pattern would have important conservation implications for this endangered species (IUCN 2010). The necessity of regional management strategies would be emphasized if the contribution from the Japanese rookeries was high, whereas the necessity of multinational management strategies would be emphasized if the contribution from multiple tropical rookeries was found to be significant.

In order to understand the genetic composition of Japanese feeding aggregations and conduct MSA, it is first necessary to obtain information about the genetic structures of the rookeries. The genetic structure of Yaeyama nesting populations, major nesting populations in the Ryukyu Archipelago, has been recently characterized (Nishizawa et al. 2011), but that of the largest nesting population of green turtles in Japan, namely the population in the Ogasawara Islands (Hatase et al. 2006), is not understood. Therefore, we first identified mtDNA sequences from nesting green turtles in the Ogasawara Islands. Then, by determining mtDNA haplotype frequencies, we investigated and compared the genetic structures and compositions of several feeding aggregations in Japan. Thus, this study (1) describes the genetic structure of the Ogasawara nesting population, (2) estimates the stock composition of multiple feeding aggregations along the Japanese archipelago based on potential source rookeries from around the Pacific, and (3) compares the differences in origins of the feeding aggregations.

Materials and methods

Source and mixture samples

In order to determine the genetic structure of Ogasawara nesting populations, samples were collected during 2002

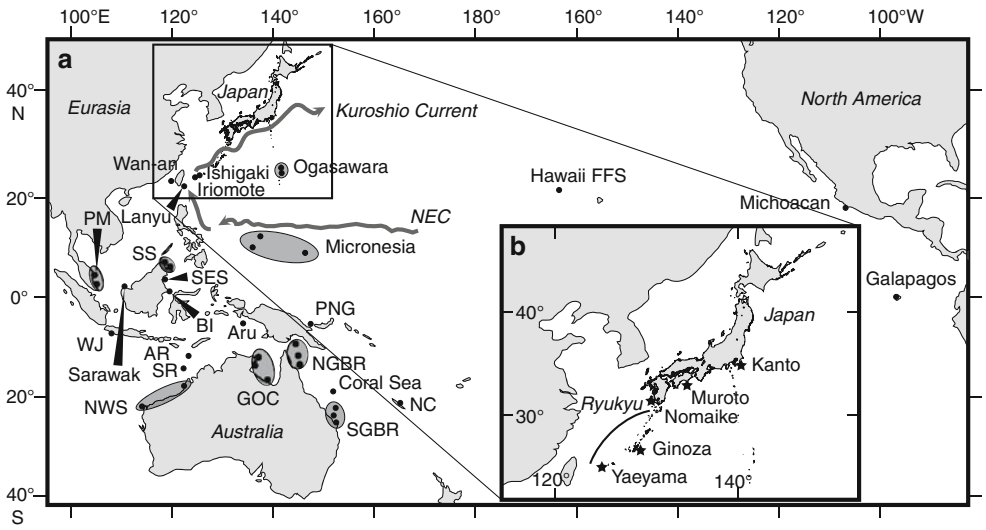

Fig. 1 **a** Locations of 25 breeding stocks as inferred from mtDNA variants in previous studies: Iriomote, Ishigaki, Ogasawara, Wan-an, Lanyu, Michoacan, Galapagos, Hawaii French Frigate Shoals (*FFS*), northern Great Barrier Reef (*NGBR*), Coral Sea, southern Great Barrier Reef (*SGBR*), New Caledonia (*NC*), Micronesia, Papua New Guinea (*PNG*), Gulf of Carpentaria (*GOC*), Aru, Berau Islands (*BI*), Southeast Sabah (*SES*), Sulu Sea (*SS*), Sarawak, Peninsular Malaysia (*PM*), Ashmore Reef (*AR*), Scott Reef (*SR*), West Java (*WJ*), Northwest Shelf (*NWS*), and **b** locations of feeding grounds along the Japanese archipelago marked by *stars*. *Arrows* indicate oceanic currents, including the Kuroshio Current and the North Equatorial Current (*NEC*)

and 2003 from 103 nesting green turtles. Additionally, published data of 24 nesting populations of green turtles were used in the MSA, providing for a total of 25 geographically or genetically separated rookeries in the Pacific and eastern Indian Ocean regions (Fig. 1), including the Japanese rookeries of Yaeyama (Nishizawa et al. 2011) and Ogasawara, Taiwanese rookeries (Cheng et al. 2008), the eastern Pacific rookeries of Mexico (Chassin-Noria et al. 2004), Hawaii, the Galapagos (Dutton et al. 2008), and 17 Australasian rookeries defined in Dethmers et al. (2006). These populations, which were used as the source populations in MSA, were geographically and phylogenetically grouped into six regions: Yaeyama, Ogasawara, Taiwan, eastern Pacific, western Pacific, and Indian and Southeast Asia (Table 1).

Japanese feeding aggregations in Yaeyama, Ginoza, Nomaike, Muroto, and Kanto were used as mixture samples in MSA (Fig. 1). Sequence data of Nomaike ($n = 38$; straight carapace length [SCL]: 40.6–96.7 cm) and Muroto ($n = 60$; SCL: 33.0–105.2 cm) were from Hamabata et al. (2009). For genetic analyses of feeding aggregations at Yaeyama, Ginoza, and Kanto, samples were collected from green turtles captured around or stranded at Yaeyama ($n = 142$; SCL: 33.0–95.6 cm) from 1995 to 2008 and at Ginoza ($n = 20$; SCL: 37.5–90.1 cm) and Kanto ($n = 47$; SCL: 37.1–92.4 cm) from 1995 to 2005 (Fig. 1). Because of the scarcity of samples, we pooled the samples across years and size classes, but later discussed the testing of interannual differences and differences in size classes for the Yaeyama feeding aggregation, which contains the largest number of samples. Blood or skin samples secondarily recovered while punching for tagging were collected from living turtles. From dead animals, samples were collected from the pectoral muscle after autopsy. Whole blood was stored at −20 °C, and tissue samples were stored in 99 % EtOH.

DNA sequence analysis

Details of the DNA extraction, amplification, and sequencing analyses from Yaeyama feeding green turtle samples are available in Nishizawa et al. (2010). In brief, a ~520-bp segment of the mtDNA control region was amplified using the primers CMMTF1 (Nishizawa et al. 2010) and TCR6 (Norman et al. 1994). From Ogasawara nesting green turtle samples and Ginoza and Kanto feeding green turtle samples, DNA was extracted and prepared for PCR using the PUREGENE Genomic DNA Purification Kit (Gentra/Qiagen, Valencia, CA, USA). A 488-bp segment of the mtDNA control region was amplified using the primers LTCM2 (Encalada et al. 1996) and TCR6. PCR with Ex Taq polymerase (Takara, Shiga, Japan) included 35 cycles of denaturing at 95 °C for 30 s, annealing at 58 °C for 30 s, and extension at 72 °C for 30 s. PCR products were purified using ExoSAP-IT (GE Healthcare Bio-Sciences K. K., Tokyo, Japan). The sequencing reactions were performed using a Big Dye Terminator version 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) or Thermo Sequenase II Dye Terminator Cycle Sequencing Premix Kit (GE Healthcare

Table 1 Locations of samples, sample sizes (*N*), frequencies of mtDNA control-region haplotypes from Japanese feeding aggregations, and possible source populations. The feeding grounds are ordered from south to north

Region	Location	*N*	Haplotype[a]																References
			AB 472301/ 07/13/ 485791 CMJ2/8/ 14/33 CMP2/ A30	AB 472324 CMJ25 CMP50	AB 472317 CMJ18 CMP39	AB 472305 CMJ6 CMP54	AB 472308 CMJ9 CMP32	AB 472311 CMJ12 CMP6/ E21	AB 472325 CMJ26 CMP53	AB 472310 CMJ11 CMP77/ A4	AB 472330 CMJ31 CMP5/ D27	AB 472302 CMJ3 CMP22	AB 472329 CMJ30 CMP49/ C3	AB 485794 CMJ36 CMP4	AB 485793 CMJ35 CMP19	AB 485792 CMJ34	AB 472318 CMJ19	AB 472314 CMJ15	AB 472315 CMJ16	
Feeding aggregation																			
	Yaeyama	142	47	27	16	10	6	5	4	4	4	3	2	2	2	2	1	1	1	This study
	Ginoza	20	4	4	5	2	–	1	1	–	–	–	–	–	–	–	–	–	–	This study
	Nomaike	38	1	3	21	2	2	–	1	–	–	–	2	–	–	–	2	–	–	Hamabata et al. (2009)
	Muroto	60	1	10	35	5	–	–	–	–	–	–	1	–	–	–	2	2	–	Hamabata et al. (2009)
	Kanto	47	2	16	18	2	–	–	2	–	–	–	–	–	–	–	–	–	2	This study
Source population																			
Yaeyama																			
	Iriomote	26	1	10	–	14	–	–	–	–	–	–	–	–	–	–	–	–	1	Nishizawa et al. (2011)
	Ishigaki	41	5	2	5	24	–	–	–	2	–	–	–	–	–	–	–	–	3	Nishizawa et al. (2011)
Ogasawara																			
	Ogasawara	103	–	13	53	1	–	–	2	–	–	–	4	–	–	–	12	3	4	This study
Taiwan																			
	Wan-an	40	13	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	Cheng et al. (2008)
	Lanyu	14	–	–	–	–	–	–	–	–	–	–	14	–	–	–	–	–	–	Cheng et al. (2008)
Eastern Pacific																			
	Michoacan	123	–	–	–	–	–	–	–	–	–	–	–	82	–	–	–	–	–	Chassin-Noria et al. (2004)
	Galapagos	98	–	–	–	–	–	–	–	–	–	–	–	95	–	–	–	–	–	Dutton et al. (2008)
	Hawaii FFS	229	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Dutton et al. (2008)

Table 1 continued

Region	Location	*N*	Haplotype[a]																References
			AB 472301/07/13/485791 CMJ2/8/14/33 CMP2/A30	AB 472324 CMJ25 CMP50	AB 472317 CMJ18 CMP39	AB 472305 CMJ6 CMP54	AB 472308 CMJ9 CMP32	AB 472311 CMJ12 CMP6/E21	AB 472325 CMJ26 CMP53	AB 472310 CMJ11 CMP77/A4	AB 472330 CMJ31 CMP5/D27	AB 472302 CMJ3 CMP22	AB 472329 CMJ30 CMP49/C3	AB 485794 CMJ36 CMP4	AB 485793 CMJ35 CMP19	AB 485792 CMJ34	AB 472318 CMJ19	AB 472314 CMJ15	AB 472315 CMJ16	
Western Pacific																			
	NGBR	52	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Dethmers et al. (2006)
	Coral Sea	41	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	Dethmers et al. (2006)
	SGBR	102	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Dethmers et al. (2006)
	New Caledonia	10	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	Dethmers et al. (2006)
	Micronesia	49	26	–	–	–	–	12	–	2	–	–	–	–	–	–	–	–	–	Dethmers et al. (2006)
	PNG	18	16	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	Dethmers et al. (2006)
Indian and SE Asia																			
	GOC	132	1	–	–	–	–	–	–	–	–	–	45	–	–	–	–	–	–	Dethmers et al. (2006)
	Aru	28	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Dethmers et al. (2006)
	Berau Islands	29	–	–	–	–	–	–	–	–	7	–	7	–	–	–	–	–	–	Dethmers et al. (2006)
	SE Sabah	30	–	–	–	–	–	–	–	–	8	–	18	–	–	–	–	–	–	Dethmers et al. (2006)
	Sulu Sea	67	–	–	–	–	–	–	–	–	53	–	13	–	–	–	–	–	–	Dethmers et al. (2006)
	Sarawak	22	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	Dethmers et al. (2006)

Table 1 continued

Region	Location	*N*	Haplotype[a]																References
			AB 472301/07/13/485791 CMJ2/8/14/33 CMP2/A30	AB 472324 CMJ25 CMP50	AB 472317 CMJ18 CMP39	AB 472305 CMJ6 CMP54	AB 472308 CMJ9 CMP32	AB 472311 CMJ12 CMP6/E21	AB 472325 CMJ26 CMP53	AB 472310 CMJ11 CMP77/A4	AB 472330 CMJ31 CMP5/D27	AB 472302 CMJ3 CMP22	AB 472329 CMJ30 CMP49/C3	AB 485794 CMJ36 CMP4	AB 485793 CMJ35 CMP19	AB 485792 CMJ34	AB 472318 CMJ19	AB 472314 CMJ15	AB 472315 CMJ16	
	PM	28	–	–	–	–	–	–	–	–	–	–	23	–	–	–	–	–	–	Dethmers et al. (2006)
	Ashmore Reef	20	9	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	Dethmers et al. (2006)
	Scott Reef	19	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	Dethmers et al. (2006)
	West Java	23	–	–	–	–	–	–	–	–	–	–	17	–	–	–	–	–	–	Dethmers et al. (2006)
	NW Shelf	45	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	Dethmers et al. (2006)

Region	Location	*N*	Haplotype[a]																References
			AB 472312 CMJ13 CMP67/A6	AB 472327 CMJ28 CMP91/C14	AB 472326 CMJ27 CMP1	AB 485795 CMJ37 CMP44/B1	AB 472321 CMJ22	AB 472319 CMJ20	AB 661780 CMJ38	AY 955215 CMP76/A1	AB 472331 CMJ32	AB 472320 CMJ21	AB 472322 CMJ23 CMP95	AB 472323 CMJ24	AB 661781 CMJ39	AB 661782 CMJ40	AB 661783 CMJ41	NA CMP37/JPNa	Others[b]	
Feeding aggregation																			
	Yaeyama	142	1	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	This study
	Ginoza	20	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	This study
	Nomaike	38	–	–	–	–	1	1	–	–	1	1	–	–	–	–	–	–	–	Hamabata et al. (2009)
	Muroto	60	–	–	–	–	–	1	–	–	1	–	1	1	–	–	–	–	–	Hamabata et al. (2009)
	Kanto	47	–	–	–	–	–	1	–	–	1	–	–	–	1	1	1	–	–	This study
Source population																			
Yaeyama																			
	Iriomote	26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Nishizawa et al. (2011)
	Ishigaki	41	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Nishizawa et al. (2011)
Ogasawara																			
	Ogasawara	103	–	–	–	–	–	3	3	–	2	–	2	–	–	–	–	1	–	This study

Table 1 continued

Region	Location	*N*	Haplotype[a]																	References
			AB 472312 CMJ13 CMP67/ A6	AB 472327 CMJ28 CMP91/ C14	AB 472326 CMJ27 CMP1	AB 485795 CMJ37 CMP44/ B1	AB 472321 CMJ22	AB 472319 CMJ20	AB 661780 CMJ38	AY 955215 CMP76/ A1	AB 472331 CMJ32	AB 472320 CMJ21	AB 472322 CMJ23 CMP95	AB 472323 CMJ24	AB 661781 CMJ39	AB 661782 CMJ40	AB 661783 CMJ41	NA CMP37/ JPNa	Others[b]	
Taiwan																				
	Wan-an	40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	Cheng et al. (2008)
	Lanyu	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Cheng et al. (2008)
Eastern Pacific																				
	Michoacan	123	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	41	Chassin-Noria et al. (2004)
	Galapagos	98	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	Dutton et al. (2008)
	Hawaii FFS	229	–	–	156	–	–	–	–	–	–	–	–	–	–	–	–	–	73	Dutton et al. (2008)
Western Pacific																				
	NGBR	52	–	–	–	42	–	–	–	–	–	–	–	–	–	–	–	–	10	Dethmers et al. (2006)
	Coral Sea	41	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	40	Dethmers et al. (2006)
	SGBR	102	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	102	Dethmers et al. (2006)
	New Caledonia	10	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	5	Dethmers et al. (2006)
	Micronesia	49	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	2	Dethmers et al. (2006)
	PNG	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	Dethmers et al. (2006)
Indian and SE Asia																				
	GOC	132	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	85	Dethmers et al. (2006)
	Aru	28	–	27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Dethmers et al. (2006)
	Berau Islands	29	1	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	Dethmers et al. (2006)
	SE Sabah	30	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	Dethmers et al. (2006)
	Sulu Sea	67	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	Dethmers et al. (2006)
	Sarawak	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	Dethmers et al. (2006)
	PM	28	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	Dethmers et al. (2006)
	Ashmore Reef	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	Dethmers et al. (2006)

Table 1 continued

Region	Location	*N*	Haplotype[a]																References
			AB 472312 CMJ13 CMP67/ A6	AB 472327 CMJ28 CMP91/ C14	AB 472326 CMJ27 CMP1	AB 485795 CMJ37 CMP44/ B1	AB 472321 CMJ22	AB 472319 CMJ20	AB 661780 CMJ38	AY 955215 CMP76/ A1	AB 472331 CMJ32	AB 472320 CMJ21	AB 472322 CMJ23 CMP95	AB 472323 CMJ24	AB 661781 CMJ39	AB 661782 CMJ40	AB 661783 CMJ41	NA CMP37/ JPNa	Others[b]	
	Scott Reef	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	Dethmers et al. (2006)
	West Java	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	Dethmers et al. (2006)
	NW Shelf	45	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	41	Dethmers et al. (2006)

[a] Haplotype classification was based on a 380-bp mtDNA fragment: upper strand, GenBank accession numbers; middle strand, nomenclatures following Hamabata et al. (2009) and Nishizawa et al. (2010); lower strand, nomenclatures of the CMP system found on the SWFSC Web site (http://swfsc.noaa.gov/), Norman et al. (1994), and Dethmers et al. (2006)

[b] 'Others' indicate that the haplotypes were not detected in the Japanese feeding aggregations and Ogasawara nesting population

Bio-Sciences K. K.). The primers TCR5 (forward) (Norman et al. 1994) and TCR6 (reverse) were used in the reactions. An ABI Prism 3100, 310 genetic analyzer or ABI Model 373 (Applied Biosystems) was used to determine the sequences of 380-bp products.

Genetic analyses

The sequence datasets were truncated for subsequent analyses to include only the 380-bp region of the control region for comparison with the earliest studies of green turtles (Chassin-Noria et al. 2004; Dethmers et al. 2006). The haplotype diversity and nucleotide diversity of the Ogasawara nesting population and each feeding aggregation were estimated using ARLEQUIN version 3.1 (Excoffier et al. 2005). The exact tests for population differentiation (500,000 steps in a Markov chain with a 10,000-step dememorization) implemented in ARLEQUIN were used to detect genetic differentiation between the Ogasawara nesting population and other Pacific nesting rookeries.

The haplotype frequencies among feeding aggregations along the Japanese archipelago were compared by the exact test in ARLEQUIN with sequential Bonferroni correction. Correlations between genetic differentiation (Φ_{ST} values) and the log-transformed geographical distances among these feeding aggregations were tested with Mantel tests as implemented in ARLEQUIN. The correlation between these two matrices was evaluated with 10,000 permutations.

For examining the temporal variation and differences among size classes, the haplotype frequency of the Yaeyama feeding aggregation was analyzed more closely. During the sampling period in Yaeyama, most samples were collected in 2003 ($n = 31$), 2004 ($n = 27$), and 2005 ($n = 40$), while 10 or fewer samples were collected in other years. Therefore, differences in haplotype frequencies among these years were examined by the exact test in ARLEQUIN. In the Yaeyama feeding aggregation, most specimens were immature juveniles with SCLs of less than 50 cm and estimated to be in the early juvenile stage ($n = 97$); however, some specimens were larger juveniles with SCLs between 50 and 70 cm ($n = 28$) or mature turtles with SCLs of 70 cm or more ($n = 11$). The SCL was unknown in six samples. Haplotype frequencies were also compared among these size classes by the exact test in ARLEQUIN. Because of small sample sizes, comparisons that took into account both size class and year or those in other feeding aggregations were not made in this study.

Mixed-stock analyses

The Bayesian MSA was used to estimate relative contributions of nesting (source) populations to feeding

aggregations. In the Bayesian analysis, checking the robustness of the results by different approaches is important (Karl et al. 2012). We compared two methods of MSA to check robustness of the estimates: traditional Bayesian MSA using BAYES (Pella and Masuda 2001) and the more recent 'many-to-many' MSA developed by Bolker et al. (2007). The former is 'many-to-one' analysis where multiple mixtures are analyzed independently of each with all sources or representative sources assumed sampled, whereas the latter jointly estimates the origins of multiple mixtures as well as a possible unsampled mixture.

Both Bayesian analyses use Markov chain Monte Carlo (MCMC) to simulate unknowns from the posterior distribution. Six MCMC chains of 50,000 samples were run, each chain corresponding to a potentially contributing nesting group. The first 25,000 samples of each chain were discarded as burn-into remove dependence on starting values. Remaining samples were pooled and summarized. The convergence of MCMC sampling to the posterior distribution was assessed using the Gelman–Rubin shrink factor (Gelman and Rubin 1992). This shrink factor provides an indication of convergence by comparing the variation within a single chain to the total variation among all chains. Shrink-factor values greater than 1.2 indicate lack of convergence in both Bayesian analyses. If the convergence was not achieved, we increased the number of samples of each chain up to 100,000 with half burn-in steps. Individual chains were started with 95 % of the mixed sample initially contributed by each group of source populations, and the remaining 5 % was divided equally among the remaining populations. The Dirichlet prior distribution was set in two ways. One was an uninformative prior giving all population proportions equal weights and the other was an informative prior considering the effect of distance and population size. In the latter case, the prior was weighted by the population size multiplied by the inverse of straight distance in the traditional Bayesian MSA, whereas the prior was weighted by the inverse of straight distance and population size was separately set in the program in the 'many-to-many' analysis. Population size was based on Moritz et al. (2002), Dethmers et al. (2006), and Amorocho et al. (2012).

Results

Genetic structures

Thirteen haplotypes were identified from the Ogasawara nesting population (Table 1). Four of these haplotypes contained the same sequences detected in Yaeyama nesting populations (CMJ6/CMP54, CMJ16, CMJ18/CMP39, and CMJ25/CMP50) (Nishizawa et al. 2011), one haplotype of CMJ30 was identical to C3/CMP49, a widely observed haplotype in rookeries of Australia and Southeast Asia (Dethmers et al. 2006), and another haplotype was identical to JPNa/CMP37, which had been detected previously in Japan (Norman et al. 1994). Six haplotypes (CMJ15, CMJ19, CMJ20, CMJ23, CMJ26, and CMJ32) were previously found only in feeding aggregations (Hamabata et al. 2009), and one haplotype (CMJ38) did not match any previously found sequences. The haplotype frequency of the Ogasawara nesting population was significantly different from those of other Pacific nesting populations ($p < 0.00001$). Haplotype diversity (h) and nucleotide diversity (π) estimates for the Ogasawara nesting population were $h = 0.706 \pm 0.044$ and $\pi = 0.0174 \pm 0.0092$.

In the feeding aggregations, 24 haplotypes from Yaeyama (Nishizawa et al. 2010), nine haplotypes from Ginoza, and eight haplotypes from Kanto were identified (Table 1). The longer control-region fragment from Yaeyama identified five new polymorphic sites at the 5′ end of the control region and increased the genetic resolution relative to the previous 380-bp region. When sequence data were truncated to the 380-bp region, four haplotypes (CMJ3, CMJ9, CMJ22, and CMJ34) from 12 specimens were not observed at previously surveyed nesting locations. Additionally, three haplotypes detected in Kanto (CMJ39, CMJ40, and CMJ41) have never been observed in previous studies to our knowledge. The genetic diversity indices of the feeding aggregations were estimated as $h = 0.836 \pm 0.022$ and $\pi = 0.0334 \pm 0.0167$ in Yaeyama, $h = 0.879 \pm 0.043$ and $\pi = 0.0347 \pm 0.0182$ in Ginoza, and $h = 0.707 \pm 0.046$ and $\pi = 0.0288 \pm 0.0148$ in Kanto. Exact tests indicated that the haplotype frequency of the Yaeyama feeding aggregation was significantly different from those of the Nomaike, Muroto, and Kanto aggregations ($p < 0.00001$; Table 2a). Some of the other comparisons were significant at the 0.05 level of probability, but were not significant after sequential Bonferroni correction (Table 2a).

In the Yaeyama feeding aggregation, comparisons in haplotype frequencies among years showed a significant difference between 2003 and 2004 ($p < 0.03$), but sequential Bonferroni correction did not support this significance (Table 2b). There was no significant difference observed among size classes (Table 2c).

Contribution of nesting rookeries to feeding aggregations

Bayesian estimates of the nesting colony origins of feeding aggregations are provided in Figs. 2 and 3. The Gelman–Rubin shrink factors for Bayesian estimates in 'many-to-many' MSA with sources of 25 rookeries indicated a lack of convergence, even if the samples of each chain were

Table 2 Differences in haplotype frequencies (p-values) among (a) feeding aggregations, (b) years, or (c) size classes within the Yaeyama aggregation

Location	N	Yaeyama	Ginoza	Nomaike	Muroto	Kanto
(a)						
Yaeyama	142					
Ginoza	20	0.372				
Nomaike	38	**<0.00001**	0.042			
Muroto	60	**<0.00001**	0.020	0.444		
Kanto	47	**<0.00001**	0.147	0.019	0.030	
Years	N	2003	2004	2005		
(b)						
2003	31					
2004	27	0.029				
2005	40	0.353	0.770			
Size	N	SCL $\leq$ 50 cm	50 < SCL $\leq$ 70 cm	70 cm < SCL		
(c)						
SCL < 50 cm	97					
50 $\leq$ SCL < 70 cm	28	0.098				
70 cm $\leq$ SCL	11	0.404	0.736			

Values in bold indicate significant differences after sequential Bonferroni correction

increased up to 100,000; therefore, the results are not shown. Other Bayesian estimates, including estimates in 'many-to-many' MSA with sources of six groups of rookeries, had Gelman–Rubin shrink factors of 1.08 or lower, indicating convergence among MCMC estimates. Traditional MSA with 25 rookeries demonstrated that feeding habitats in the Yaeyama Islands were used extensively by turtles originating from multiple locations, including Iriomote, Ogasawara, and Micronesia, whether or not the informative prior was considered (Fig. 2). The feeding aggregation at Ginoza was significantly attributed to Ogasawara and Micronesia, but aggregations at Nomaike, Muroto, and Kanto were attributed mostly to Ogasawara (Fig. 2). Group estimates for both traditional MSA and 'many-to-many' MSA supported the significant contribution from various rookeries of Yaeyama, Ogasawara, Western Pacific, and Indian and Southeast Asia to the Yaeyama feeding aggregation, from Ogasawara and Western Pacific to the Ginoza feeding aggregation, and from Ogasawara to aggregations at Nomaike, Muroto, and Kanto, although 'many-to-many' MSA indicated additional significant contributions from Taiwan and eastern Pacific to Yaeyama, from Yaeyama and Taiwan to Ginoza and Nomaike, and from Yaeyama to Muroto and Kanto aggregations (Fig. 3). A Mantel test revealed a significant correlation between genetic differentiation measured by Φ_{ST} values and geographical distance measures ($r = 0.734$, $p = 0.034$).

Discussion

Genetic structure of the Ogasawara nesting population

The haplotype frequency of the Ogasawara nesting population presented in this study was significantly different from those of other Pacific rookeries, including the closest Ishigaki or Iriomote populations. This is consistent with the natal philopatry of green turtles (Bowen et al. 1992; Encalada et al. 1996; Dethmers et al. 2006; Cheng et al. 2008; Nishizawa et al. 2011). The relatively high genetic diversity values indicate that the Ogasawara nesting rookery, one of the northernmost rookeries in the Pacific Ocean, might have been formed by historical introgressions by individuals with divergent haplotypes or multiple colonization events, as was the case with the Yaeyama nesting rookeries (Nishizawa et al. 2011).

Estimated migration and implications for the influence of ocean current

MSA indicated that the feeding aggregation in the Yaeyama Islands is sourced from various rookeries in Yaeyama, Ogasawara, Western Pacific, and Indian Oceans and Southeast Asia, although the 'many-to-many' analysis estimated a higher contribution from the local Yaeyama and less from Western Pacific. Whereas the Ginoza feeding aggregation also showed contributions from Western

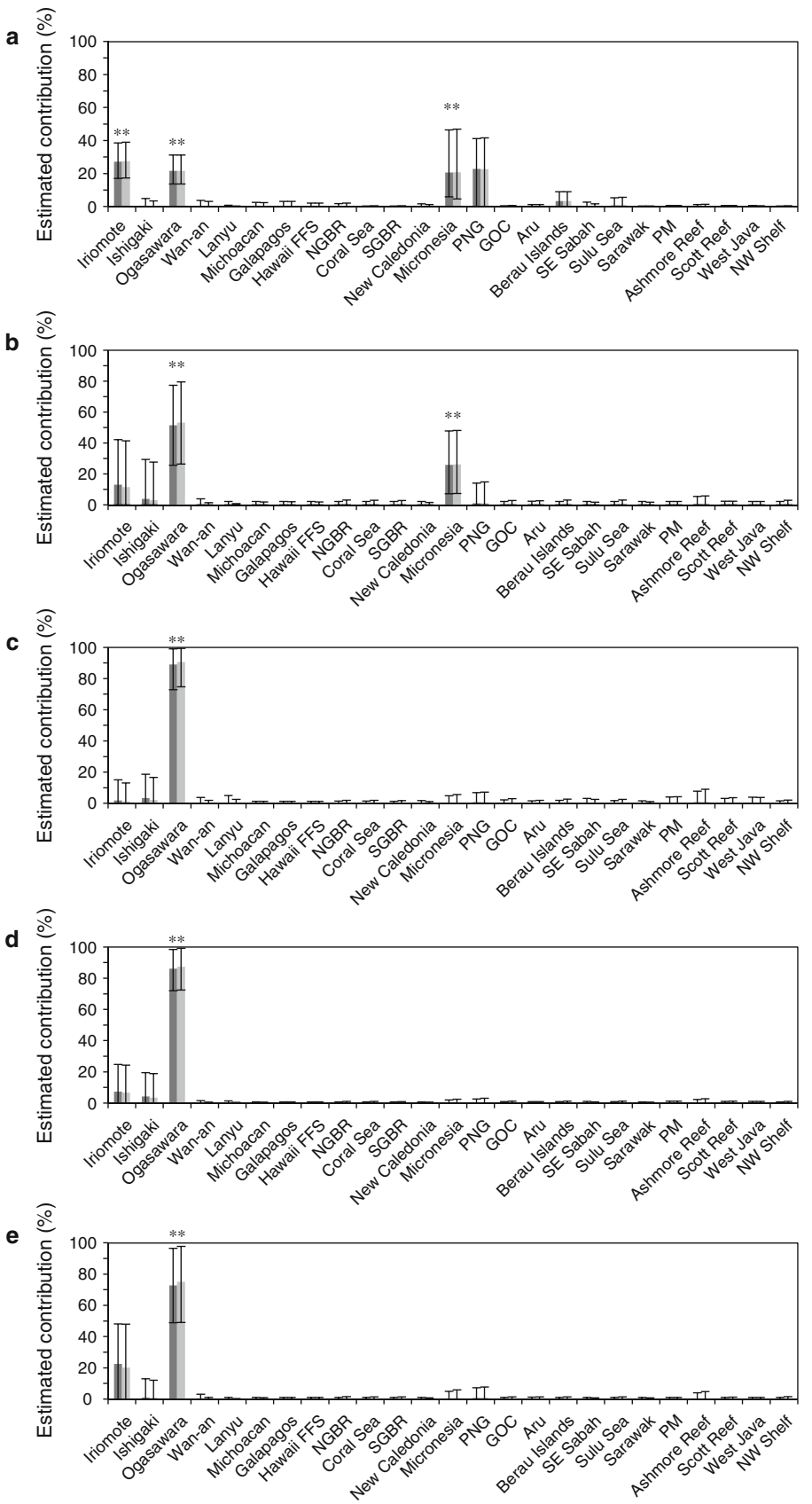

Fig. 2 Estimated contributions (%) of source populations to green turtles on Japanese feeding grounds in **a** Yaeyama, **b** Ginoza, **c** Nomaike, **d** Muroto, and **e** Kanto. Results using uninformative priors (*black bars*) and informative priors (*gray bars*) are represented. *Error bars* represent 95 % probability intervals and *asterisks* represent that the intervals do not include zero

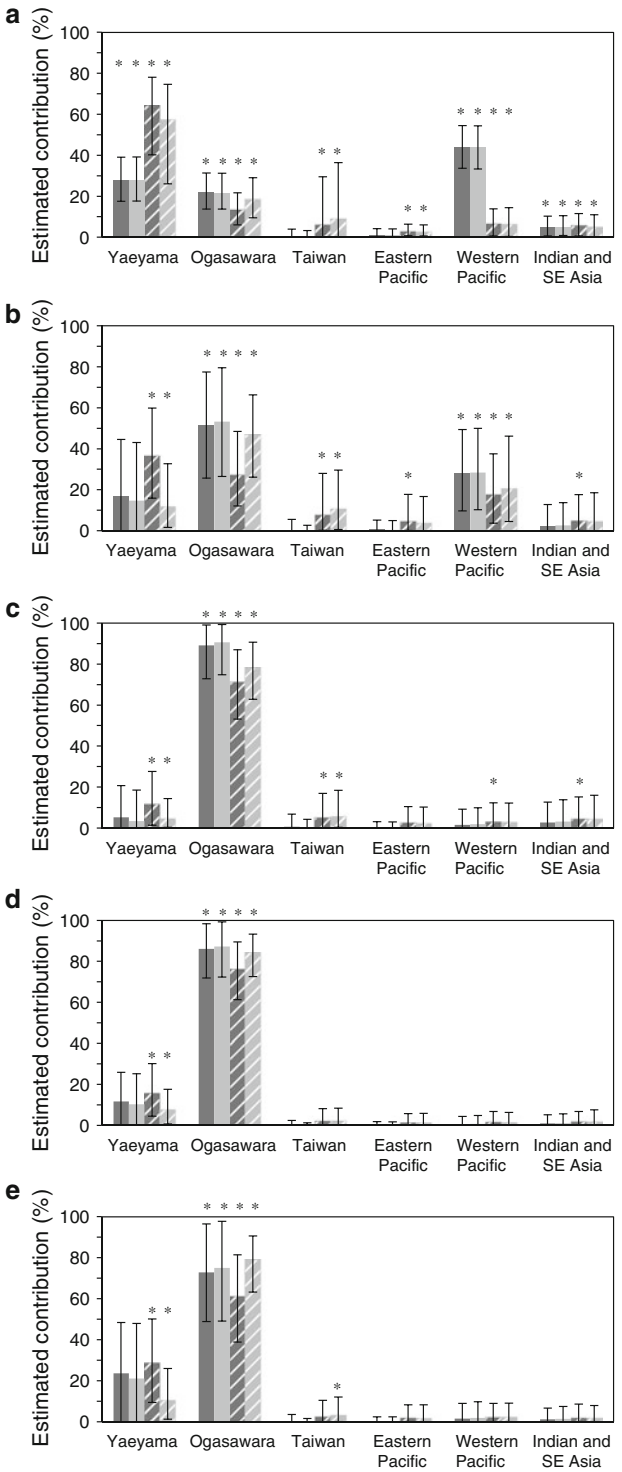

Fig. 3 Estimated contributions (%) of groups of source populations to green turtles on Japanese feeding grounds in **a** Yaeyama, **b** Ginoza, **c** Nomaike, **d** Muroto, and **e** Kanto. Results are represented in the same manner as in Fig. 2, but the *left* two *bars* indicate the results of traditional Bayesian estimates and the *right* two *striped bars* indicate the 'many-to-many' estimates

Pacific, the other aggregations involved little contribution from Western Pacific, but high contribution from the Ogasawara nesting colonies located closer to these feeding grounds. In all estimations, different prior distributions resulted in similar results, probably reflecting that the data are sufficiently informative and that there are many haplotypes specific to the rookeries (Karl et al. 2012).

Since hatchling turtles undertake passive drifting in oceanic gyre systems after hatching and entering the sea (Musick and Limpus 1997), oceanic currents influence the composition of juvenile feeding aggregations (Bass et al. 2006; Bowen et al. 2007; Blumenthal et al. 2009; Godley et al. 2010; Monzón-Argüello et al. 2010). Hatchlings born in the western Pacific, especially in Micronesia, would drift toward the west in the NEC and then toward the north in the Kuroshio Current into Japanese feeding grounds. The significant correlation between genetic differentiation and geographical distance matrices may reflect a decrease in the contribution from Western Pacific rookeries and an increase in the contribution from Ogasawara since the current flows from southwest to northeast. Higher haplotype and nucleotide diversities also indicated that the Yaeyama feeding ground, located upstream of the Kuroshio current, contains turtles originating from several rookeries. The reduced contributions from nesting colonies in tropical Pacific regions to northern feeding aggregations indicated that most hatchlings from these regions transported by the Kuroshio Current settle in upstream feeding grounds in the Japanese archipelago.

One haplotype detected in the Yaeyama feeding aggregation, CMP4, has only been identified in eastern Pacific 'black turtles' (Chassin-Noria et al. 2004). This supports the existence of 'black turtles' (Pritchard 1999) around the Yaeyama Islands (Abe and Minami 2008) and invokes the likelihood of occasional transoceanic migrations from eastern Pacific rookeries, perhaps reflected in a small but significant contribution estimated by 'many-to-many' MSA.

The estimated contributions of rookeries to feeding grounds may vary temporally (Bjorndal and Bolten 2008). Because we pooled the mixture samples over several years, the estimated sources are considered to be averaged over the years. In the Yaeyama feeding aggregation, however, no strong evidence of temporal variation was detected during the sampling period from 2003 to 2005. Additionally, in the Yaeyama feeding aggregation, the hypothesis that older juveniles move preferentially toward the feeding ground in the region of their natal beach (Bowen et al. 2004) was not supported because of no significant difference in haplotype frequencies among size classes. These results indicate the stability of the feeding aggregation at least in the Yaeyama.

Nine haplotypes (CMJ3, CMJ9, CMJ21, CMJ22, CMJ24, CMJ34, CMJ39, CMJ40, and CMJ41) detected in feeding aggregations were not observed at previously surveyed nesting locations, indicating the existence of unknown rookeries or incomplete sampling (Bowen et al. 2007). Nonetheless, the results illustrate differences in the composition of Japanese feeding aggregations between southern and northern locations and the mixing of green turtles with multiple origins in the south, with significant contributions from restricted rookeries in the north.

Conservation and management implications

The management of green turtles based on linkages between their feeding aggregations and rookeries will be needed for their conservation (Bowen et al. 2007). In the Pacific Ocean, the Hawaiian feeding aggregation of green turtles was estimated to originate mostly from Hawaiian rookeries, indicating a distinct regional population for management (Dutton et al. 2008). On the other hand, the Colombian feeding aggregation in the eastern Pacific was estimated to be recruited from distant sites, indicating the importance of multinational conservation strategies (Amorocho et al. 2012). In Japanese feeding aggregations, both of these types of sourcing were observed. The estimated compositions of Japanese feeding aggregations have conservation implications. The Ogasawara nesting rookery was estimated to contribute significantly to all Japanese feeding aggregations analyzed in this study. Among them, northern feeding aggregations from Japan, Nomaike, Muroto, and Kanto were estimated to have contributions primarily from Ogasawara. Therefore, hazards that affect declining nesting populations in Ogasawara may also affect a wide range of Japanese feeding aggregations, especially northern feeding aggregations. This indicates the importance of regional management in Japan. On the other hand, the Yaeyama and Ginoza feeding aggregations of Japan are estimated to have migrated from remote Pacific rookeries. Therefore, any source of mortality in nesting rookeries in the tropical Pacific is likely to affect remote feeding aggregations in Japan. Conversely, effects on feeding aggregations in Japanese waters could affect nesting populations in other countries because of natal philopatry. It emphasizes the necessity for multinational conservation strategies for green turtles in the western Pacific, as in other regions (Amorocho et al. 2012) and for other sea turtle species (Bowen et al. 2007).

Conclusions

This is the first intensive study revealing the genetic structures of green turtle feeding aggregations in the northwest Pacific. Changes in the composition of consecutive neritic feeding aggregations from south to north along the ocean current seem to support the hypothesis that patterns of recruitment and settlement to feeding grounds in sea turtles are influenced by oceanic currents. Our findings are consistent with the hypothesis that ocean currents drive the geographical distributions of feeding aggregations of sea turtles (Blumenthal et al. 2009; Godley et al. 2010; Monzón-Argüello et al. 2010; Amorocho et al. 2012). Further studies such as simulations investigating changes in ocean current and migration will clarify the results' implications. The changes in the composition of the relatively close consecutive neritic feeding aggregations that were identified in this study have important conservation and management implications and may be applicable to other migratory marine vertebrates, such as fish (e.g., eels; Tsukamoto 1990; Kimura et al. 1994), birds (e.g., penguins; Clarke et al. 2003), and mammals (e.g., seals; McConnell et al. 2002).

Acknowledgments We would like to acknowledge the followings for providing information about the stranded turtles on Ishigaki Island and field sampling assistance in Yaeyama Islands: the member of the Ishigaki Island Sea Turtle Research Group; K. Okuzawa and the staff of the Ishigaki Tropical Station and Yaeyama Station, Seikai National Fisheries Research Institute; D. Imakita (Faculty of Agriculture, Kinki University); and Y. Kawabata, T. Yasuda, K. Ichikawa, and H. Watanabe (Graduate School of Informatics, Kyoto University). The staff of the Ogasawara Marine Center and fisheries cooperative associations in Hahajima Island and Chichijima Island and M. Kaneko (Club Noah Hahajima) kindly helped with sampling in Ogasawara Islands. Sampling in Ginoza was supported by N. Kamezaki and the Sea Turtle Association of Japan. M. Kinoshita, H. Sawada (Graduate School of Agriculture, Kyoto University), R. Matsuoka, and T. Nishizawa (IREIIMS, Tokyo Women's Medical University) provided assistance with the DNA extraction, amplification, and sequencing analyses. T. Hamabata and H. Koike (Graduate School of Social and Cultural Studies, Kyushu University) kindly provided data on the Muroto and Nomaike aggregations. We thank the two anonymous reviewers for valuable comments on this manuscript. This study was partly supported by a Grant-in-Aid for JSPS Fellows (J.O. 17-1976), for Research Activity Start-up (J.O. No. 19880017), for Young Scientists B (J.O. No. 22710236), and the Global COE Program, Informatics Education and Research for a Knowledge–Circulating Society.

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