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Occurrence and diet analysis of sea turtles in Korean shore



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Abstract

Background: Sea turtles, which are globally endangered species, have been stranded and found as bycatch on the Korean shore recently. More studies on sea turtles in Korea are necessary to aid their conservation. To investigate the spatio-temporal occurrence patterns of sea turtles on the Korean shore, we recorded sampling locations and dates, identified species and sexes and measured sizes (maximum curved carapace length; CCL) of collected sea turtles from the year 2014 to 2020. For an analysis of diets through stomach contents, we identified the morphology of the remaining food and extracted DNA, followed by amplification, cloning, and sequencing.

Results: A total of 62 stranded or bycaught sea turtle samples were collected from the Korean shores during the study period. There were 36 loggerhead turtles, which were the dominant species, followed by 19 green turtles, three hawksbill turtles, two olive ridley turtles, and two leatherback turtles. The highest numbers were collected in the year 2017 and during summer among the seasons. In terms of locations, most sea turtles were collected from the East Sea, especially from Pohang. Comparing the sizes of collected sea turtles according to species, the average CCL of loggerhead turtles was 79.8 cm, of green turtles was 73.5 cm, and of the relatively large leatherback turtle species was 126.2 cm. In most species, the proportion of females was higher than that of males and juveniles, and was more than 70% across all the species. Food remains were morphologically identified from 19 stomachs, mainly at class level. Seaweeds were abundant in stomachs of green turtles, and Bivalvia was the most detected food item in loggerhead turtles. Based on DNA analysis, food items from a total of 26 stomachs were identified to the species or genus level. The gulfweed, *Sargassum thunbergii*, and the kelp species, *Saccharina japonica*, were frequently detected from the stomachs of green turtles and the jellyfish, *Cyanea nozakii*, the swimming crab, *Portunus trituberculatus*, and kelps had high frequencies of occurrences in loggerhead turtles.

Conclusions: Our findings support those of previous studies suggesting that sea turtles are steadily appearing in the Korean sea. In addition, we verified that fish and seaweed, which inhabit the Korean sea, are frequently detected in the stomach of sea turtles. Accordingly, there is a possibility that sea turtles use the Korean sea as feeding grounds and habitats. These results can serve as basic data for the conservation of globally endangered sea turtles.

Keywords: Sea turtle, Stranding, Stomach contents, Diet analysis, Korean shore

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Background

Sea turtles are keystone species in coastal ecosystems (Stringell et al. 2016). Globally, seven sea turtle species belonging to six genera of two families exist, which are distributed from the Arctic Ocean (70 °N) to the Tasman Sea (45 °S) (Márquez 1990; Klemens 2000; Lee et al. 2014). All sea turtle species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) because of their declining population caused by overhunting, habitat destruction, pollution, and climate change (Moon et al. 2009). In addition, the International Union for Conservation of Nature (IUCN) classified six sea turtle species as critically endangered (CR), endangered (EN), or vulnerable (VU). However, flatback turtles (*Natator depressus*) were not classified because of insufficient data (IUCN 2021). Among these classified turtles, green turtles (*Chelonia mydas*) and leatherback turtles (*Dermochelys coriacea*) were first reported in the 1930s (Hironobu 1936a; 1936b), and loggerhead turtles (*Caretta caretta*) were reported in the 1960s (Won 1971) on the Korean coast. Additionally, hawksbill turtles (*Eretmochelys imbricata*) have been recorded (Jung et al. 2012a). Recently, olive ridley turtles (*Lepidochelys olivacea*) were reported for the first time from the coastal waters of South Korea (Kim et al. 2019). Following international efforts to protect sea turtles, these five species were designated as “Marine Organisms under Protection” by the Conservation and Management of Marine Ecosystems Act in Korea (MOF (Ministry of Oceans and Fisheries) 2021).

Studies on the ecology of sea turtles in Korea are limited because of their low occurrence frequency, which in turn is because Korean shores are not the main habitats and nesting areas for these species as compared with other warm temperate and tropical countries (Wallace et al. 2010; Haywood et al. 2019). Studies on the status of stranding and bycatch of sea turtles, including their distribution, satellite tracking, and nesting places, in Korea began in the late 2000s (Moon et al. 2011; Jung et al. 2012b). Lee et al. (2014) comprehensively described the morphology of loggerhead turtles from the Yellow Sea of Korea. Koo et al. (2014) reported hybridization between loggerhead and green turtles from Jeju Island, South Korea. Further, Jang et al. (2018) investigated the spatiotemporal movements of green turtles in the Jeju Island Sea, Korea. Recently, the number of dead-stranded sea turtles on the Korean shore has been increasing, and there is growing concern about the protection of this species in the nation. However, comprehensive research on sea turtles is still lacking and more studies are needed on the status of sea turtles in Korea to conserve them (Kim et al. 2017).

Understanding animal feeding ecology provides information about their habitat requirements, thereby

promoting scientific conservation (Prior et al. 2015). Monitoring sea turtles through direct observation and indirect monitoring methods, such as observing feeding signs and using video or radio telemetry are not often undertaken, because more than 99% of their lives are spent at sea, thereby making them largely inaccessible (Tomas et al. 2001). Thus, their feeding ecology has been mainly studied globally by sampling the stomach and esophagus of dead individuals from strandings, fishery bycatch, or by direct collection (Mortimer 1981; Shaver 1991; Plotkin et al. 1993; Tomas et al. 2001; Stringell et al. 2016), or by lavages of the stomach and esophagus of live individuals (Forbes and Limpus 1993; Carrión-Cortez et al. 2010; Prior et al. 2015). Accordingly, green turtles have been reported to feed primarily on algae, especially *Ulva* spp. and/or seagrass such as *Thalassia testudinum*, and their diet varies depending on their habitats (Carrión-Cortez et al. 2010). Further, loggerhead turtles primarily feed on fish and benthic invertebrates, such as crustaceans and mollusks (Plotkin et al. 1993; Tomas et al. 2001). To date, few studies on sea turtle diets have been conducted in Korea. Moon et al. (2009) reported the occurrence of sea turtles in Korean waters and dissected their digestive tracts. They observed seaweed, such as *Ulva* spp., *Sargassum* spp., and *Gelidium* spp. in the digestive tracts of three green turtles and animal food sources such as mackerel, hairtail, squid, and crab, in the stomach of a loggerhead turtle. In most studies, researchers directly identified food remains in the digestive tract with the naked eye and/or indirectly through a microscope using morphological characteristics. Although these conventional methods are easily accessible, there is a possibility of misidentification, which poses further limitations (Reynolds and Aebischer 1991; Pires et al. 2011). Therefore, complementary methods, such as molecular analysis, can be applied to dietary studies of marine predators (Deagle et al. 2005; Dunn et al. 2010). Diet analyses using DNA can provide substantive and accurate information regarding food sources, which cannot be obtained through direct observation and radio telemetry (Kim et al. 2021). Furthermore, this approach is efficient in terms of labor and time requirements compared with the morphological and microhistological analyses of digestive contents (Joo et al. 2014). Additionally, it has higher resolution than conventional approaches by the identification of prey to the genus or species level (Zhao et al. 2020).

In this regard, this study aimed to provide information about the occurrence patterns and feeding ecology of sea turtles in South Korea to enable their conservation. This information can help identify important food resources and foraging areas necessary for establishing regulations and policies regarding the management of endangered sea turtle populations (Bjørndal 1999; Behera et al.

2015). Specifically, we investigated (1) the spatiotemporal patterns of sea turtles found stranded or as bycatch on the Korean shore and (2) the diets of sea turtles through stomach analysis.

Materials and methods

Sample collection

Dead sea turtles occurring on the South Korean shores due to stranding or bycatch events from August 2014 to September 2020 were collected and transferred to the National Marine Biodiversity Institute of Korea (MABIK) from other research institutes and government agencies, which primarily collected the sea turtle after receiving observation reports by a finder. A total of 62 sea turtles in the form of carcasses, skeletons, and stuffed specimens were transferred with relevant information, such as the location and date of stranding/bycatch, turtle species, and sex. According to the condition of the samples, maximum curved carapace length (CCL), sexual maturity, and wet weight were measured and recorded except for skeleton and highly decayed carcasses of samples. Subsequently, fresh frozen carcasses were moved to the National Institute of Ecology (NIE) for necropsy and dissected to separate food items in stomach contents according to a veterinarian's guidelines for sea turtles (Flint et al. 2009). Determination of sexual maturity was based on CCL size at sexual maturity: 95 cm in *C. mydas*, 66.5 cm in *C. caretta*, and 125 cm in *D. coriacea* (Avens and Snover 2013). However, sexual maturity of some individuals and species was determined by veterinary examination through necropsy.

Morphological and molecular analysis of stomach contents

The stomach contents of the sea turtles, except for skeleton and highly decayed carcasses of samples, were sieved with a 1 mm mesh, and items, such as shell, carapace, and seaweed, which were larger than the mesh size and could be sorted with the naked eye, were collected

and washed with distilled water. Items that appeared as food were separated into plant and animal food items. Subsequently, we identified the items morphologically at the class level with a taxonomic reference (Hong et al. 2006) and recorded non-food objects (stone and anthropogenic materials, among others) in green ($n = 3$), loggerhead ($n = 15$), and olive ridley turtles ($n = 1$, Table 2).

Tissues under good conditions were selected for further molecular analysis in green ($n = 9$), loggerhead ($n = 16$), and leatherback turtles ($n = 1$, Table 3). Genomic DNA was extracted from the tissue samples using the QIAamp® Blood & Tissue Kit (Qiagen, Germany) following the manufacturer's instructions with a flexible duration for lysis from 3 h to overnight depending on the sample conditions.

All polymerase chain reaction (PCR) amplifications were conducted using 20 µl sample solution, containing 1 µl of extracted DNA, 0.25 µM of each primer, and 1 U of FastMix/Frenche™ PCR (i-StarTaq) premix (iNtRON, Korea). The PSf/Ur primer pair and the Uf/PSr pair (Stiller and McClanahan 2005) were used to amplify the plastid 16S gene to identify herbivorous food items, such as terrestrial plants and macroalgae (Table 1). The PCR mixture was denatured at 95 °C for 4 min, followed by 35 cycles of 30 s at 94 °C, 30 s at 60 °C, and 90 s at 72 °C, and a final extension at 72 °C for 7 min. To identify the animal-based food items, the mitochondrial-encoded cytochrome oxidase subunit I (COI) region was amplified using LCO1490 and HCO2198 primers (Vrijenhoek 1994), and the 12S rRNA gene was amplified using MiFish-U/E primers (Miya et al. 2015), especially for fish. PCR was performed in a thermal cycler (Applied Biosystems, USA) using the following conditions: initial denaturation for 3 min at 94 °C, followed by 45 cycles at 94 °C for 45 s, 50 °C for 1 min, and 72 °C for 1 min, and a final extension for 5 min at 72 °C to amplify the COI region. PCR conditions for the 12S region were set as follows: initial denaturation at 95 °C for 5 min, followed by 40 cycles of denaturation at 95 °C for 15 s, annealing at

Table 1 Information on primer set used in this study

Target	Primer	Sequence (5'– 3')	Reference
Algae (16S)	PSf	GGGATsTAGATACCCCWGTAGTCCT	Stiller and McClanahan 2005
	Ur	TACGGYTACCTTGTTACGACTT	
	Uf	GAGAGTTTGATCCTGGTCAG	
	PSr	AGGACTACWGGGGTATCTAATCCCC	
Fish (12S)	MiFish-E-F	GTTGGTAAATCTCGTGCCAGC	Miya et al. 2015
	MiFish-E-R	CATAGTGGGGTATCTAATCCTAGTTTG	
	MiFish-U-F	GTCGGTAAACTCGTGCCAGC	
	MiFish-U-R	CATAGTGGGGTATCTAATCCCAGTTTG	
Animal (COI)	LCO1490	GGTCAACAATCATAAAGATATTGG	Vrijenhoek 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	

58 °C for 30 s, and elongation at 72 °C for 30 s, followed by a final extension at 72 °C for 7 min.

The PCR products were purified using an AccuPrep® PCR Purification Kit (Bioneer, Korea). Sequencing was performed using a commercial sequencing service company (Genotech, Korea). For ambiguous sequencing results, purified PCR products were inserted into the pGEM®-T Easy Vector (Promega, USA) and transformed into competent DH5α cells. The cells were spread on Luria-Bertani agar + ampicillin medium with 2% X-gal (w/v) solution to facilitate antibiotic selection and blue-white screening. After cloning, the cell colonies were selected and amplified using the M13F and M13R primers. Each resultant sequence was identified by BLASTN analysis using the GenBank database.

Data analysis

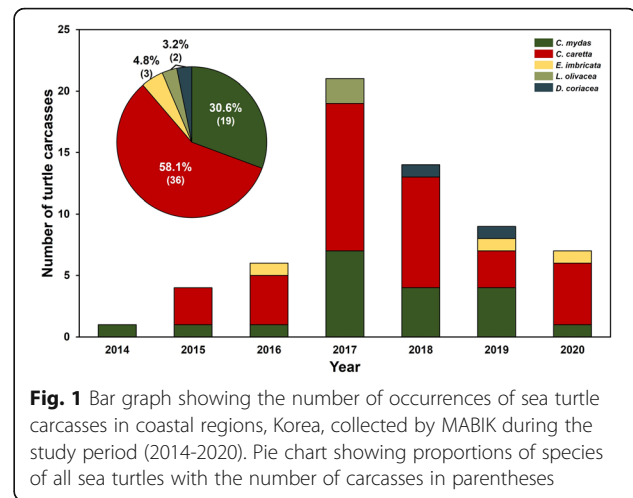
We conducted Chi square tests to determine seasonal differences in the number of stranded and bycaught turtles. To understand the relationship between water temperature and sea turtle occurrence, we analyzed water temperature records in the stranding/bycatch areas during the sampling period using data from the Korea Hydrographic and Oceanographic Agency (KHOA). Dietary analysis results using morphological and molecular methods were presented as frequency of occurrence (% FO), representing the percentage of individuals in which a food item was found among analyzed sea turtles by each method. In addition, information on the sampling sites of seaweeds and marine algae in Korea (Lee and Kang 2001; Kim et al. 2013), the distribution map acquired from the Marine Bio-Resource Information System (MBRIS, www.mbris.kr), and Ocean Biodiversity Information System (OBIS, www.obis.org) were used to investigate the local distribution of seaweeds among the observed food items.

Results

Spatio-temporal occurrence patterns of sea turtles

A total of 62 sea turtles were collected during the entire study period. Loggerhead turtle, *C. caretta*, was the most dominant species (36 individuals, 58.1%), followed by green turtle, *C. mydas* (19 individuals, 30.6%), hawksbill turtle, *E. imbricata* (three individuals, 4.8%), and olive ridley, *L. olivacea*, and leatherback turtle, *D. coriacea* (two individuals each, 3.2%) (Fig. 1). In terms of years, most sea turtles were collected in 2017, with 21 individuals (33.9%), followed by 14 individuals (22.6%) in 2018 and nine individuals (14.5%) in 2019. Since 2016, three or more species were collected, and olive ridley turtles were collected only in 2017 (two individuals).

Regarding collection months, sea turtles were most frequently collected in October, followed by June. In addition, green turtles and loggerhead turtles (relatively



high number of individuals) were collected throughout the study period, except in January, February, and April (Fig. 2). To investigate the difference in the numbers of the pairs of species according to the sampling months, we conducted a chi-square test; however, no statistically

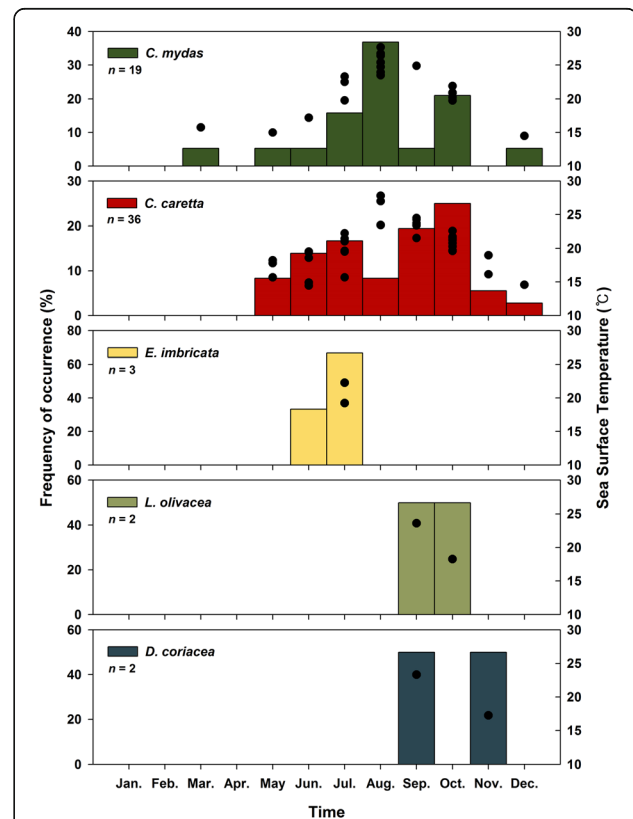
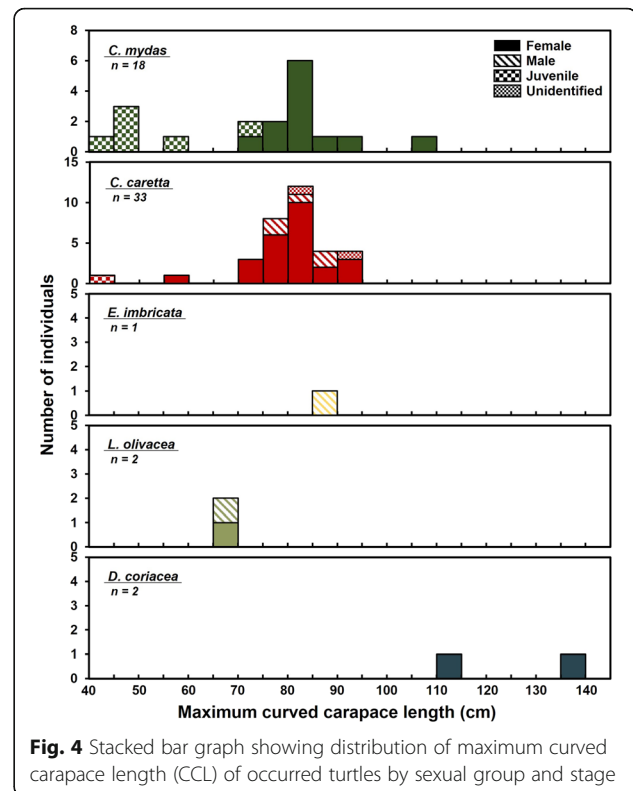
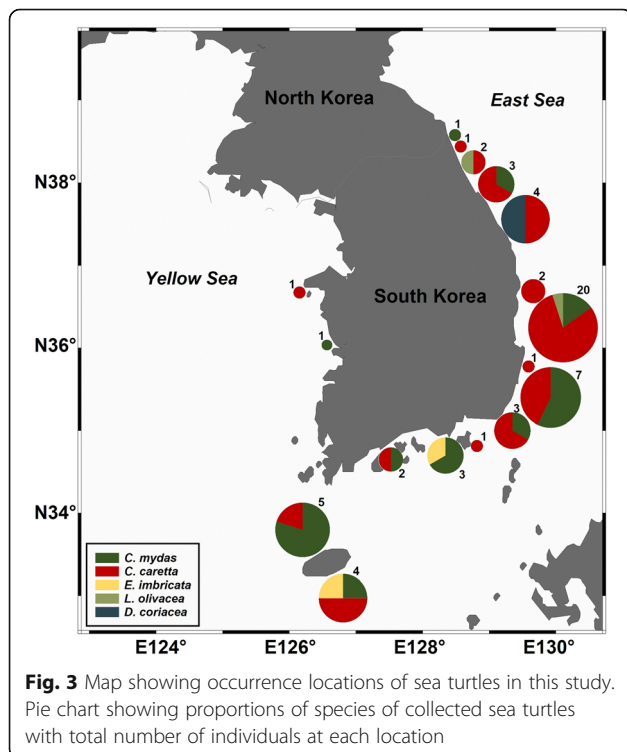


Fig. 2 Bar graph showing the monthly distribution of occurred sea turtles during the study period (2014-2020). Closed circles indicating daily mean of sea surface temperature (SST) for 15 days before collection, measuring near the stranding site based on data from the Korea Hydrographic and Oceanographic Agency (KHOA)

significant difference was observed ($\chi^2 = 11.54$, $p = 0.173$). Further, three hawksbill turtles were collected in June and July, two olive ridley turtles in September and October, and two leatherback turtles in September and November.

Of the 61 individuals (data missing for one individual), the highest number of sea turtles ($n = 20$, 32.8%) was collected from the East Sea, specifically near Pohang, followed by Jeju Island ($n = 9$, 14.8%) (Fig. 3). Green turtles and loggerhead turtles were collected from all Korean waters, including the West Sea. Hawksbill turtles were collected only from the South Sea, olive ridley turtles were collected only from the East Sea, while leatherback turtles were collected only from Samcheok in the East Sea.

We measured the size of 56 individuals among the samples, considering their condition. The average CCL of green turtles was 73.5 cm ($n = 18$, juveniles: 43.3–74.0 cm; adults: 74.8–106.6 cm) and that of loggerhead turtles was 79.8 cm ($n = 33$, juveniles: 42.0 cm; adults: 58.8–93.5 cm) (Fig. 4), while that of a hawksbill turtle individual was 88.8 cm. Moreover, the CCL of the two olive ridley turtles were 65.1 and 66.2 cm, and those of the relatively large leatherback turtles were 114.0 and 138.4 cm ($n = 2$). The size thresholds for CCL between adults and juveniles have been reported to be 95, 66.5, and 125 cm (green, loggerhead, and leatherback turtles, respectively; Avens and Snover 2013). However, the size at sexual maturity in species was determined by



measuring methods (straight or curved carapace length), techniques (mark-recapture, length frequency, skeletochronology, among other methods), and populations. In our study, the sizes were approximately 75 cm in green turtles, 59 cm in loggerhead turtles, and 114 cm in leatherback turtles through the necropsy method. Consequently, the proportion of females was more than 70% in sea turtles. Among the 18 green turtle individuals, 12 were females and six were juveniles. A total of 33 loggerhead turtle individuals comprised 25 females, 5 males, and 1 juvenile. One male hawksbill turtle was recorded, and two female leatherback turtles were identified. A male and a female were identified in the two olive ridley turtle individuals (Fig. 4).

Dietary composition of the sea turtles found stranded or as bycatch on the Korean shores

Morphological analysis of stomach contents revealed the presence of a few animal-based food items, but several plant-based food items were found in all three green turtle individuals (Table 2). Based on morphological identification, various seaweed species such as *Grateloupia* spp., *Chondrus* spp., and *Sargassum* spp. were also observed (Fig. 5A). Bivalves such as Veneridae were most frequently detected in the stomachs of 15 loggerhead turtles, followed by Polychaeta and Osteichthyes representing animal-based food items (Fig. 5B), and plant-based food items were also detected. However, only

Table 2 Stomach contents of green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and olive ridley (*Lepidochelys olivacea*) sea turtles identified by morphological analysis at class level, and the percentage frequency of occurrence (% FO), with the number of stomachs the item occurred in *n*. Plant materials included all items of plant origin and macroalgae, and synthetic flotsam included plastics, styrofoam, and nylon cord/string

Stomach content	Green turtles		Loggerhead turtles		Olive ridley turtles	
	% FO (<i>n</i> = 3)	<i>n</i>	% FO (<i>n</i> = 15)	<i>n</i>	% FO (<i>n</i> = 1)	<i>n</i>
Synthetic flotsam	67	2	87	13	100	1
Phylum Cnidaria						
Cl. Anthozoa			7	1		
Phylum Arthropoda, sub ph. Crustacea						
Cl. Malacostraca			40	6	100	1
Cl. Cirripedia	33	1	13	2	100	1
Phylum Mollusca						
Cl. Gastropoda			20	3		
Cl. Bivalvia			73	11	100	1
Cl. Cephalopoda			20	3		
Phylum Chordata						
Cl. Osteichthyes	33	1	47	7		
Cl. Ascidiacea			7	1		
Phylum Brachiopoda						
Cl. Articulata			7	1		
Phylum Annelida						
Cl. Polychaeta			53	8		
Plant	100	3	53	8		
Stone			7	1		

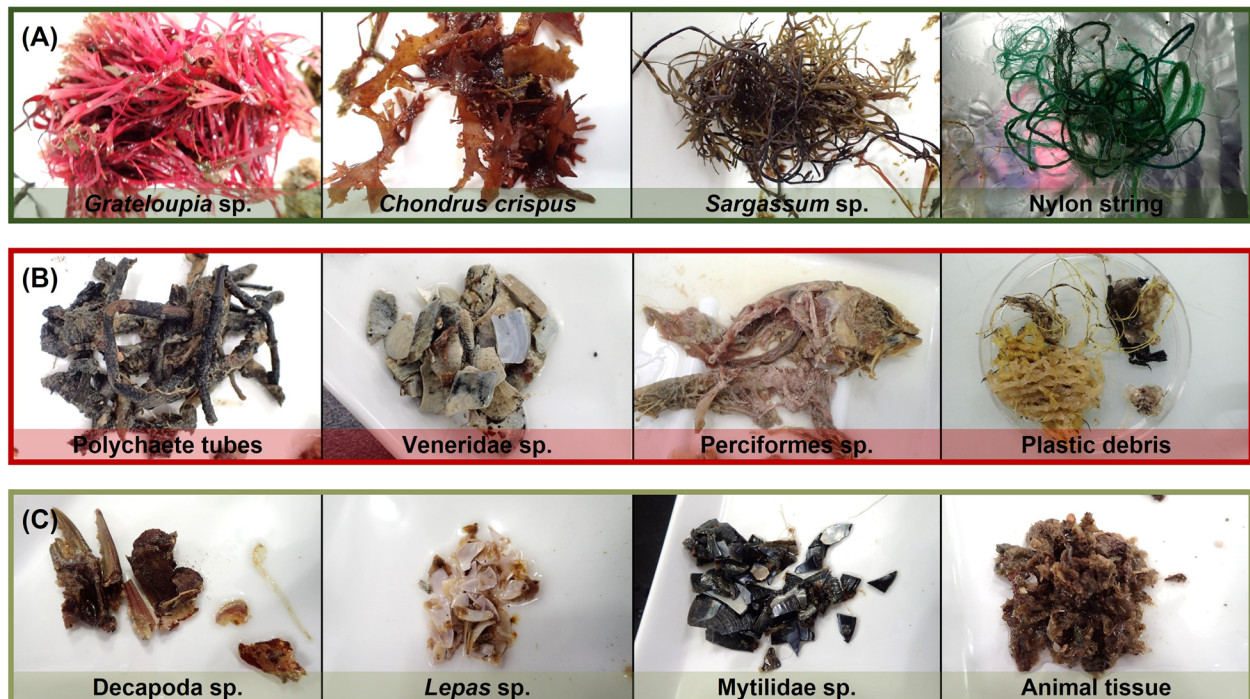


Fig. 5 Images of stomach contents of green turtles, *Chelonia mydas* (A), loggerhead turtles, *Caretta caretta* (B), and olive ridley turtles, *Lepidochelys olivacea* (C), in this study

animal-based food items, such as animals belonging to Cirripedia (*Lepas* spp.) and Bivalvia (Mytilidae spp.), were observed in an olive ridley turtle (Fig. 5C). Synthetic flotsams, including plastics, styrofoam, and nylon cords/strings, comprised most of the other collected objects from the turtle stomachs (Table 2).

To supplement the resolution of morphological analysis to identify food items, DNA analysis was performed. Our results showed that 44 taxa of 33 genera and 34 species were observed in the stomach samples of the sampled turtles (Table 3). The gulfweed, *Sargassum thunbergii* (55.6% FO, $n = 9$), and the kelp species, *Saccharina japonica* (44.4% FO, $n = 9$), were frequently detected in the stomachs of green turtles. Furthermore, the jellyfish, *Cyanea nozakii*, and the swimming crab, *Portunus trituberculatus* (each 25% FO, $n = 16$), were found most frequently in loggerhead turtles. In addition, *S. japonica* (25% FO, $n = 16$) was the most frequently detected plant-based food item. In the stomach of the leatherback turtle, *P. trituberculatus*, and the species of Gastropoda, *Nassarius sinarus*, were detected; however, these results may not reflect the food preference of leatherback turtles because of the insufficient number of analyzed samples.

Among the 41 sequences detected from the stomach contents of nine green turtles, which included four juveniles and five females, 90.2% comprised plant-based items and 9.8% comprised animal-based items (Table 4). The analyzed sequences from the stomachs of 15 loggerhead turtles, which included one juvenile, nine females, and five males, indicated that plant-based and animal-based items comprised 30.6% and 69.4%, respectively.

Discussion

Spatio-temporal occurrence patterns of sea turtles

According to the results of our study (Fig. 1) and those of previous studies (Moon et al. 2011; Jung et al. 2012a; Kim et al. 2017), sea turtles have been continuously observed due to their declining populations caused by stranding and bycatch in the coastal regions of Korea in the last two decades. Kim et al. (2017) assessed the number of dead or alive sea turtles in the Korean coastal regions from the year 1949 to July 2016 by referring to diverse data sources (e.g., newspaper articles, published reports, and research data). They reported that occurrence of approximately 1–9 sea turtles per year was due to stranding and bycatch in the past 20 years. Our study recorded 21 carcasses in 2017. MABIK initiated the study of sea turtles, including necropsy, and received a higher number of sea turtle carcasses from research groups and government agencies, such as the Cetacean Research Institute (CRI), the Hanwha Aqua Planet Yeosu, and the Korea Coast Guard, Korea, in 2017 than in other years. Consequently, the largest number of

samples was collected in 2017, after which a decreasing trend was observed. In this study, we considered the number of sea turtle samples collected only by MABIK; thus, more sea turtles could be stranded annually than the number recorded in Korea during the study period.

The trends in the occurrence of sea turtles from 1949 to July 2016 in the Korean coastal waters analyzed by Kim et al. (2017) showed that green turtles (58.8%) were more prevalent than loggerhead turtles (31.5%), especially on Jeju Island. Based on satellite tracking data, green turtles were mainly observed to remain on Jeju Island (Moon et al. 2011; Jung et al. 2012a; Jang et al. 2018). In this study, we collected more loggerhead turtles (58.1%) than green turtles (30.6%), and most individuals of the former species originated from Pohang (Figs. 1 and 3). The collection of sea turtle carcasses from Jeju Island has been limited because of transportation difficulties. Despite the limitation of sampling, our results showed that the distribution of stranded or bycaught turtles in Korean shores differed according to the species. Green turtles had a higher proportion in the South Sea than other species, while loggerhead turtle numbers increased in the East Sea (Fig. 2). These results are consistent with those reported by Kim et al. (2017). This distribution pattern might be related to the habitat and habits related to migration and foraging. Rasmussen et al. (2011) suggested that the distribution of sea turtles, Cheloniidae and Dermochelyidae, was primarily along tropical coasts and across oceans, including all Korean coasts. Loggerhead and green sea turtles migrate to a comparable range of oceans, such as the Atlantic, Mediterranean, Indian, and Pacific oceans (Wallace et al. 2010). However, the nesting sites and foraging habits are dissimilar between the two species. Nesting sites of green sea turtles are reported to be distributed from 30 ° N to 23 ° S (e.g., coasts of Australia, Philippines, and Vietnam) (Wallace et al. 2010; Figgenger et al. 2019). In addition, they show a dietary shift through the development stage, consuming Gastropoda, Scyphozoa, and Malacostraca as juveniles and expanding to mainly plant food sources such as seagrass and mangrove materials as adults (Jones and Seminoff 2013). However, loggerhead sea turtles mainly nest in the northwestern Atlantic, Mediterranean, and northern Pacific regions, including Japan, and principally have animal diets such as Cephalopoda, Actinopterygii, and Bivalvia with seagrass and algae (Wallace et al. 2010; Jones and Seminoff 2013). Some records have described that they arrived on Korean breeding grounds located on Jeju Island and the coasts of the East Sea (Kim et al. 2017). Loggerhead sea turtles, which had a high proportion of adults in this study, could migrate to the East Sea for breeding with foraging activity, thus increasing the possibility of occurrence in the eastern areas. Fishes, such as *Scomber* spp.

Table 3 Stomach contents of green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and leatherback (*Dermochelys coriacea*) sea turtles identified by DNA analysis at species or genus level, and the percentage frequency of occurrence (% FO), with the number of stomachs the item occurred in *n* (* represents the species detected from stomach contents of leatherback turtle, *n* = 1)

Stomach content			<i>C. mydas</i>		<i>C. caretta</i>	
			Green turtle		Loggerhead turtle	
			% FO (<i>n</i> = 9)	<i>n</i>	% FO (<i>n</i> = 16)	<i>n</i>
Phylum Cnidaria						
Cl. Scyphozoa	<i>Cyanea nozakii</i>		22.2	2	25.0	4
Phylum Arthropoda						
Cl. Malacostraca	<i>Portunus trituberculatus</i>	*			25.0	4
	<i>Portunus sanguinolentus</i>				6.3	1
	<i>Pagurus</i> spp.				6.3	1
Phylum Mollusca						
Cl. Gastropoda	<i>Nassarius sinarus</i>	*	11.1	1	6.3	1
	<i>Rapana venosa</i>				6.3	1
	<i>Turbo cornutus</i>				6.3	1
Cl. Bivalvia	<i>Mytilus</i> spp.				6.3	1
	<i>Mytilus galloprovincialis</i>				12.5	2
Cl. Cephalopoda	<i>Octopus vulgaris</i>		11.1	1		
	<i>Todarodes pacificus</i>				6.3	1
Phylum Chordata						
Cl. Actinopterygii	<i>Scomber</i> spp.				6.3	1
	<i>Scomber japonicus</i>				6.3	1
	<i>Scomberomorus niphonius</i>				6.3	1
	<i>Decapterus maruadsi</i>				12.5	2
	<i>Psenopsis</i> spp.				6.3	1
	<i>Sphyræna pinguis</i>				6.3	1
	<i>Hippocampus</i> spp.				6.3	1
	<i>Ascidia aspersa</i>				6.3	1
Phylum Rhodophyta						
Cl. Florideophyceae	<i>Grateloupia</i> spp.		22.2	2		
	<i>Grateloupia turuturu</i>		22.2	2		
	<i>Grateloupia angusta</i>		11.1	1		
	<i>Grateloupia filicina</i>		11.1	1		
	<i>Grateloupia lanceola</i>		11.1	1		
	<i>Grateloupia taiwanensis</i>		11.1	1		
	<i>Prionitis abbreviata</i>		22.2	2		
	<i>Polyopes constrictus</i>		11.1	1		
	<i>Ceramium sungminbooi</i>		11.1	1		
	<i>Melanothamnus harveyi</i>		11.1	1		
	<i>Gelidium elegans</i>		11.1	1		
	<i>Pterocladia capillacea</i>		11.1	1		
	<i>Chondrus crispus</i>		11.1	1		
	<i>Gracilaria textorii</i>		11.1	1		
	<i>Scinaia undulata</i>		11.1	1		

Table 3 Stomach contents of green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and leatherback (*Dermochelys coriacea*) sea turtles identified by DNA analysis at species or genus level, and the percentage frequency of occurrence (% FO), with the number of stomachs the item occurred in *n* (* represents the species detected from stomach contents of leatherback turtle, *n* = 1) (Continued)

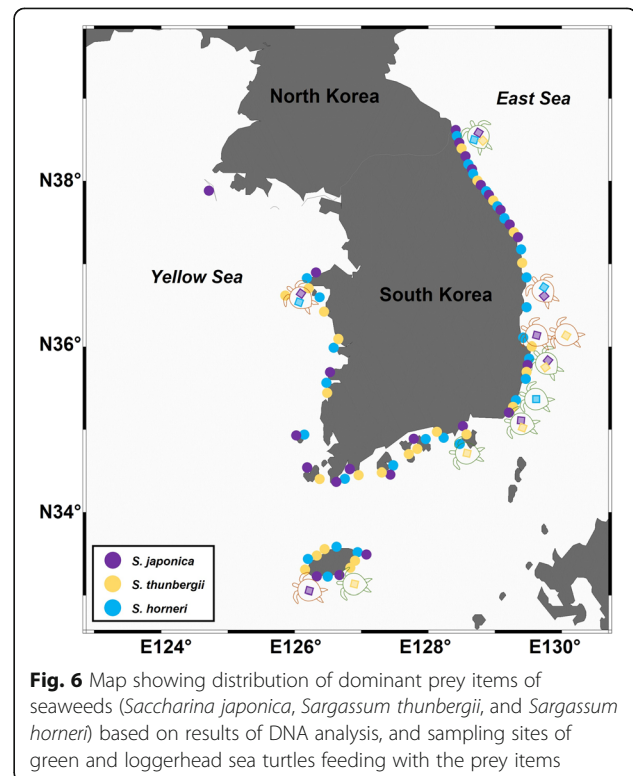
Stomach content		<i>C. mydas</i>		<i>C. caretta</i>	
		Green turtle		Loggerhead turtle	
		% FO (<i>n</i> = 9)	<i>n</i>	% FO (<i>n</i> = 16)	<i>n</i>
Phylum Ochrophyta					
Cl. Phaeophyceae	<i>Sargassum</i> spp.	22.2	2	12.5	2
	<i>Sargassum thunbergii</i>	55.6	5	6.3	1
	<i>Sargassum horneri</i>	22.2	2	12.5	2
	<i>Saccharina japonica</i>	33.3	3	25.0	4
Cl. Ulvophyceae	<i>Codium fragile</i>	11.1	1		
	<i>Ulva</i> spp.	11.1	1		
Phylum Magnoliophyta					
Cl. Liliopsida	<i>Zostera marina</i>	22.2	2		
	<i>Alisma plantago-aquatica</i>	11.1	1		
Cl. Magnoliopsida		11.1	1		
	Family. Tamaricaceae			6.3	1
Phylum Pinophyta					
Cl. Pinopsida	<i>Pinus</i> spp.	11.1	1	6.3	1

and *Decapterus maruadsi* which are distributed in the Korean sea (Lee et al. 2018; Zhao et al. 2021), were detected in the stomachs of loggerhead turtles (Table 3). Moreover, the distribution of sessile seaweed (Lee and Kang 2001; Kim et al. 2013), such as *S. japonica*, *S. thunbergii*, and *Sargassum horneri*, which occur frequently in the stomach contents, overlapped with the collected locations of sea turtles (Fig. 6). This suggests that sea turtles can feed on animals and seaweeds on the Korean shore.

Leatherback sea turtles have a wider range of movement than other species and nesting distribution from 38 °N to 34 °S (Wallace et al. 2010; Figgenger et al. 2019). Based on satellite telemetry data, leatherback turtles

Table 4 Relative frequencies of plants and animal food sources sequences detected from stomachs of green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*) at life stage or sex

	No. of analyzed individuals	No. of sequences	Relative frequency	
			Plants	Animals
Green turtle	9	41	90.2	9.8
Juvenile	4	8	75.0	25.0
Female	5	33	93.9	6.1
Loggerhead turtle	15	36	30.6	69.4
Juvenile	1	2	50.0	50.0
Female	9	26	34.6	65.4
Male	5	8	12.5	87.5



moved along the East Sea of Korea, a transit zone, in November and December (Benson et al. 2011). Our results showed a relevant distribution pattern; leatherback turtles were found only on the eastern coast in September and November (Figs. 2 and 3). Loggerhead, green, and leatherback turtles have been reported to appear on the eastern and southern coasts of Korea (Kim et al. 2017). On the western coast, however, accidentally captured live loggerhead turtles were found in a waste fishing net (Lee et al. 2014). In this study, a loggerhead turtle and a green turtle were stranded on the western coast. Chan et al. (2007) reported that leatherback, loggerhead, green, and hawksbill turtles were observed in the Yellow Sea, China. Based on the reference, both leatherback and hawksbill turtles are likely to be observed on the western coast of Korea in the future.

In our study, olive ridley turtles were found only in the eastern coastal region, while hawksbill turtles were found in southern coastal regions, including Jeju Island. These two species have a narrow range of in-water distributions and nesting distribution, concentrated in tropical regions, compared with other species (Wallace et al. 2010; Figgner et al. 2019), and the turtles were observed in lower latitudinal regions than those of other species observed in the Yellow Sea, China (Chan et al. 2007). Olive ridley turtles, which were recently found in Korean waters, were reported to be stranded in the East China Sea (Chan et al. 2007) and in Japanese waters, including the western coast of the East Sea (Fukuoka et al. 2019). However, there is insufficient information regarding the distribution of this species along the Korean shore (Kim et al. 2019).

The distribution and behavior of sea turtles are influenced by the water temperature. Cold water reduces their activity, resulting in a cold-stunned state due to physiological effects (Williard et al. 2013). In loggerhead turtles, locomotor abilities are weakened below 15 °C, and turtles may be cold-stunned below 10 °C (Mansfield and Putman 2013). In this study, the occurrence of sea turtles was concentrated during the summer and autumn. We calculated the average water temperature near the sampling sites for 15 days before turtle sampling using data from KHOA. However, some values were missing from the KHOA dataset. We assumed that the estimated time of death is within 15 days considering drifting time and carcass decomposition of the sea turtles referred to a study by Santos et al. (2018) despite different environmental conditions. The average and minimum temperatures were found to be 20.5 °C (SD = 3.4 °C) and 13.5 °C, respectively. Only five individuals (8.2%) were observed at temperature below 15 °C. Our results indicated that most sea turtles in the Korean shores possibly had not reduced their activity because of the cold environments in the collection months.

Regarding the proportion of occurrence, most sea turtles, especially loggerhead turtles, were found in the eastern coasts of Korea during the study period. The eastern coasts maintain a relatively high water temperature even in winter because of the influence of the East Korean Warm Current, a branch of the Tsushima Warm Current (TWC) (Choi et al. 2012). Moreover, the TWC is known to affect marine ecosystems, dissolved inorganic nutrients (Won and Lee 2015), and the composition of fish assemblages (Lee et al. 2008) on the Korean coast. Furthermore, the distribution of sea turtles is influenced not only by physical phenomena, such as ocean currents and water temperature but also by the movement and distribution of food sources (Jung et al. 2012a). In this study, the occurrence of omnivorous loggerhead turtles in the East Sea was believed to be due to the flow of ocean currents and food sources. In our satellite tracking study, loggerhead turtles were observed to move along the coast of the East Sea and toward Japan (data not shown, manuscript in preparation), supporting the possibility of turtle appearance on the Korean coast by swimming, and not by drifting of the carcass.

Dietary composition of the sea turtles stranded or as bycatch on the Korean shores

In this study, we elucidated the diet of sea turtles through morphological and molecular analyses of stomach contents. Morphological analysis of food items is limited by the difficulty in accurate identification because of damage during capture, ingestion, and digestion (Jarman et al. 2004). However, DNA-based diet analysis methods generally have higher resolutions than morphological methods (Zhao et al. 2020), and are less laborious and use prior knowledge (Valentini et al. 2009). Based on the genetic analysis of the prey collected from the stomach samples of the sampled sea turtles, we identified the prey to the species or genus level, thereby resulting in 31 families, 33 genera, and 34 species, whereas morphological analysis identified the diet at higher taxonomic levels, such as class level.

Moreover, various plant food items were observed in the stomachs of three green turtle individuals using the morphological method (Table 2, Fig. 5A). Cirripedia, barnacle, and osteichthyes could also be directly identified with the naked eye. We detected 41 sequences of 18 genera and 21 species in nine green turtle stomachs by molecular analysis (Table 3). Green turtles are generally omnivorous, with a strong carnivorous tendency during young and juvenile life stages in open ocean pelagic habitats (Bjørndal 1985; Jones and Seminoff 2013; Vélez-Rubio et al. 2016; Burgett et al. 2018). Dietary reports from small pelagic green turtles are few, but some records show that their diet consists of seagrass and small species of Ctenophora and Mollusca (Hughes 1974; Frick

1976; Fuentes et al. 2006). However, they shift to a herbivorous diet and occupy a unique feeding niche when they enter benthic foraging areas (Lutz et al. 2002; Howell et al. 2016). Many studies have been conducted on the food sources of green turtles in various oceans and countries (Esteban et al. 2020). The findings of these studies suggested that feeding primarily on seagrasses and algae was common, although they also consumed animals, particularly jellyfish, salps, and sponges (Mortimer 1981; Fukuoka et al. 2019; Piovano et al. 2020). The main food of green turtles stranded in Hong Kong was red algae such as *Grateloupia filicina*, *Gelidium pusillum*, and *Pterocladia tenuis* (Russell and Balazs 2009; Russell and Balazs 2015; Ng et al. 2016), which are also distributed along the coast of Korea (Guiry and Guiry 2016; NIBR 2020). In Australia, red algae were dominant, followed by brown and green algae in green turtle stomachs (Garnett et al. 1985; André et al. 2005). In addition, gelatinous animal tissues, such as those of *Physalia* and mollusk eggs, were observed in the stomach lavage (Forbes and Limpus 1993). Algae comprised the diet of sea turtles in Japan (Kurata et al. 1978), and 56 species of algae were included in the diet of green turtles in the Hawaiian Archipelago (Balazs 1980). Furthermore, digestive tracts of green turtles stranded on the Korean shore consisted of seaweed such as *Ulva* spp., *Sargassum* spp., and *Gelidium* spp. (Moon et al. 2009). In our study, various plant materials were detected in the stomachs of most green turtles. Brown algae were predominant, particularly *Sargassum* spp. and *S. japonica*. Similar to previous studies, the proportion of red algae was also high, among which 14 species were identified, including five *Grateloupia* spp. Furthermore, *C. nozakii* and Mollusca, such as *Nassarius sinarus* and *Octopus vulgaris*, were also identified, although their frequency was low.

Although the number of juvenile green turtles studied was insufficient, the frequency of plant-based food items was higher than that of animal-based food items (Table 4). Similarly, the proportion of plant sequences was higher in the female samples. Although bias in the amplification and digestibility differences may occur, a sufficient number of samples and well-planned analysis can facilitate the understanding of dietary differences in juveniles and adults using molecular methods.

In the loggerhead turtles, stomach contents comprised various taxa, with the frequency of Mollusca being the highest based on morphological analysis (Table 2). Further, DNA analysis revealed 37 sequences of 18 genera and 16 species in 16 loggerhead turtle stomachs (Table 3). Loggerhead turtles are considered generalists and versatile predators of slow-moving or sessile prey (Dodd Jr 1988; Plotkin et al. 1993; Tomas et al. 2001), thus, contributing to diverse diets across geographical localities (Burke et al. 1993; Plotkin et al. 1993; Thomson

et al. 2012). Therefore, to date, various prey taxa have been identified for this turtle species in many regions. The diets range widely from marine animals and plants to terrestrial insects, such as ants, planthoppers, and beetles (Richardson and McGillivray 1991). Crustaceans, especially crabs, and gelatinous animals (medusae and ctenophores) are important prey for this species (Burke et al. 1993; Tomas et al. 2001). In addition, pelagic coelenterates, salps, gastropods, barnacles, anemones, and sargassum have been identified as dietary components of loggerhead turtles in many studies (Brongersma 1972; Van Nierop and den Hartog 1984). In Korea, the stomach contents of loggerhead turtles mainly consisted of animal-based food materials such as mackerel, hairtail, and squid (Moon et al. 2009), with crabs and jellyfish as the major food sources (Table 3). Brown algae, such as *Saccharina* and *Sargassum*, were dominant plant-based food items in the loggerhead turtle stomachs, similar to green turtles, along with a high frequency of animal content. Arthropoda, including crabs, and Chordata, including fishes, were diverse, and Mollusca and Cnidaria with soft tissue were also detected in the stomachs. There is a dietary shift in loggerhead turtles among seasons (Bjornedal 2017). They feed mainly on sea pens in spring and crabs in summer and autumn when the abundance of crabs increases (Plotkin et al. 1993). However, turtle stomach samples for dietary analysis in this study were collected only in summer and autumn from June to October; therefore, we could not determine the dietary shifts. A difference in the number of detected sequences between female and male turtles was observed, but the frequency of animal sequences was higher than that of plant sequences, regardless of the sex of the loggerhead turtles (Table 4).

Our results showed that diverse food items were consumed by turtle species, similar to the findings of previous studies. For example, loggerhead turtles were generally omnivores (Fukuoka et al. 2016), and green turtles were classified as herbivores on maturity (Stringgell et al. 2016) based on morphological and molecular methods. The diets of olive ridley and leatherback turtles were analyzed from only one sample each using morphological and molecular methods, respectively. Arthropoda and Mollusca were commonly found in the stomachs of the two species; however, the results may not reflect their respective food preferences due to an insufficient number of analyzed samples.

Sea turtles mainly contained *Sargassum* spp., *S. japonica*, and *Zostera marina* in plant items, and *P. trituberculatus* and *C. nozakii* in animal items in Korean shores based on our results (Table 3), although we could not verify that the stomach remains were preferences or merely remained in the stomachs among consumed items. Among the main diets, some species are

consumed as seafood by humans in Korea. Such marine organisms have been directly and indirectly threatened and their populations have reduced due to marine pollution, coastal development, and overexploitation (Park and Lee 2007; Oh 2011). For the conservation of sea turtles, which are part of marine ecosystems, it is critical to sustain food sources and habitats by the designation of marine protected areas, restoration of habitats, and management of fisheries resources.

In addition, we suggest that water pollution by plastic debris should be managed for sea turtles. Synthetic flot-sam, including plastics, styrofoam, and nylon cords/strings, were found in 16 of the 19 stomach samples (Table 2). It was not confirmed whether these pollutants caused stranding and death of the turtles; however, these results show that water pollution by plastic debris is a growing environmental issue worldwide. It affects at least 267 species, including 86% of all sea turtle species (Laist 1997). However, the problem is prone to be underestimated because it is difficult to find a majority of the victims across the vast ocean (Wolfe 1987). The ingestion of plastic debris by marine organisms occurs in every region of the world and in all the studied seven turtle species (Schuyler et al. 2014), with the probability of mortality and plastic concentration in the digestive tract being positively correlated (Wilcox et al. 2018). In particular, polythene bags floating on the ocean look similar to the prey of turtles (Mattlin and Cawthorn 1986; Gramentz 1988; Bugoni et al. 2001; Derraik 2002). Intake of plastic is the main cause of non-natural death of these animals (NMFS 1998), inducing intoxication, obstruction of the esophagus, or perforation of the bowel (Mascarenhas et al. 2004). Young sea turtles are particularly vulnerable to plastic pollution (Carr 1987).

For over 50 years, long-term monitoring and protection of nesting sites in some locations have resulted in stabilization or an increase in sea turtle populations (Kelle et al. 2009; Delcroix et al. 2014; Laloë et al. 2020; Mortimer et al. 2020; Godley et al. 2020). These projects have emphasized the importance of protecting nesting and foraging habitats and promoting the participation of local communities, citizens, volunteers, and tourists (Godley et al. 2020). In addition to these international efforts, many studies on the ecology of sea turtles, including our research on feeding ecology, could promote awareness regarding the necessity of sea turtle conservation.

Conclusions

In summary, we investigated the occurrence patterns and feeding ecology of sea turtles on the coasts of Korea. Our findings showed that sea turtles are steadily appearing in the Korean sea, and the dietary analysis of the stomach contents indicated that they may be utilizing

the sea as a feeding ground. These results can serve as baseline data for the conservation of globally endangered sea turtles. In future studies, stable isotope analysis of tissues can provide more information regarding the food preferences and trophic positions of sea turtles in the Korean sea. In addition, research on the migration route of sea turtles through satellite telemetry is required to understand the spatial ecology and habitat use of sea turtles in the Korean and neighboring waters.

Abbreviations

CCL: Maximum curved carapace length; CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora; IUCN: International Union for Conservation of Nature; KHOA: Korea Hydrographic and Oceanographic Agency; MABIK: Marine Biodiversity Institute of Korea; MBRI: Marine Bio-Resource Information System; NIE: National Institute of Ecology; OBIS: Ocean Biodiversity Information System; SD: Standard deviation; SST: Sea surface temperature

Acknowledgements

We would like to thank Dr. Hye Seon Kim, Dr. Chang Ho Yi, In-Young Cho, Seong Joon Bae, and Ji Min Kim in MABIK, and Sugil Lee, So Jin Jeon, Young Hae Jang, Ji Yeon Park, and Se Rim Chin in NIE for assisting the necropsy and this study, and anonymous reviewers for their valuable and constructive suggestions.

Authors' contributions

JK performed the analysis, and wrote the manuscript. IHK and MSK designed and organized a project including this study. HRL and YJK organized and conducted the necropsy. SP reviewed and edited the manuscript. DY planned this study, performed the analysis, and wrote/reviewed the manuscript. All authors read and approved the final manuscript.

Funding

This study was supported by a grant from the National Marine Biodiversity Institute of Korea (2021 M00300).

Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 4 October 2021 Accepted: 4 November 2021

Published online: 21 November 2021

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