Polymorphic foraging tactics in a marine reptile: insight from horizontal movement and dive behavior analyses

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ABSTRACT: Life-history polymorphism in habitat use has been widely reported in aquatic migratory animals. Adult loggerhead sea turtles *Caretta caretta* in the North Pacific exhibit foraging-habitat polymorphism, showing a 2.4-fold greater reproductive output for neritic foragers than for oceanic ones. However, knowledge of how turtles in each habitat behave and what effect this has on reproduction remains limited. We combined horizontal movement and dive behavior analyses to explore foraging behavior and habitat utilization in adult female loggerheads in the North Pacific. Between 2016 and 2018, satellite relay data loggers were attached to 10 females nesting in Japan. The turtles were tracked for 219.2 ± 185.0 d (±SD) within the range of 10 to 521 d. Three foraging destinations were revealed, with different foraging tactics in each habitat: (1) the neritic East China Sea (ECS), (2) neritic coastal areas of mainland Japan (CMJ), and (3) oceanic North Pacific Ocean (NPO). ECS females mainly foraged on benthic prey with foraging-site fidelity; however, some turtles alternately preyed on benthos and plankton along with their seasonal migration. CMJ females also foraged on benthic prey with site fidelity, whereas NPO females foraged on plankton by drifting eastward with the oceanic currents. Dive-type analyses revealed that the proportion of time spent presumably foraging was similar among the 3 habitats, suggesting that the nutrient richness of prey items and the migration distance between foraging and breeding grounds may cause differences in reproductive outputs among different life-history types of loggerhead turtles.

KEY WORDS: Behavioral polymorphism · Foraging dichotomy · Intrapopulation variability · Loggerhead sea turtle · North Pacific · Satellite relay data logger · Satellite tracking · State-space modeling

1. INTRODUCTION

Life-history polymorphism in habitat use has been widely reported in aquatic migratory animals (eels: Tsukamoto et al. 1998, Daverat et al. 2006; salmon: Groot & Margolis 1991; sea turtles: Hatase et al. 2002). Life-history polymorphism in habitat use can result in differences in the reproductive output between life-history types. For instance, Salmonidae species exhibit 2 life-history types: the anadromous-type that undertakes oceanic migration for feeding purposes and remains at sea for several years, and the nonanadromous-type that remains in freshwater streams for its entire life cycle. The anadromous-type

matures to a larger size and is considerably more successful at breeding (e.g. larger egg size and higher fecundity) than the nonanadromous-type (e.g. Hutchings & Jones 1998, Healey 2001). It is assumed that this difference is generated by the differences in prey abundance and quality between foraging habitats (e.g. freshwater vs. marine). As empirical evidence has been reported in Salmonidae species (Aas et al. 2010, Quinn 2018), knowledge of foraging behavior and habitat utilization is important to help understand what causes the variations in growth rate and reproductive output among different life-history types.

To investigate the foraging behavior of migratory animals, the typical horizontal movement pattern has frequently been used as an index of foraging behavior such as area-restricted search (ARS) because animals deliberately search for prey at specific sites by decreasing their speed and/or increasing their turning frequency and angle when encountering areas with sufficiently abundant prey (Kareiva & Odell 1987, Turchin 1991). Conversely, animals encountering unsuitable habitats typically travel fast and have infrequent and small turning angles (Kareiva & Odell 1987, Turchin 1991). A Bayesian switching state-space model (SSSM) estimates the probability of the behavioral states of migratory animals: ARS vs. transiting (Jonsen et al. 2007). This statistical analysis enables researchers to identify habitat use and extrapolate foraging hotspots of marine migrant animals (e.g. seabirds: Powers et al. 2017; whales: Silva et al. 2013; sea turtles: Benson et al. 2011, Bailey et al. 2012, Iverson et al. 2019).

As marine animals forage in a 3-dimensional environment, collecting information on their vertical as well as horizontal movement patterns along with the utilization of depth zones is essential to understand their behavior and ecology. Particularly for air-breathing divers, dive behavior and dive pattern have been the center of attention for ecologists (e.g. seals: Davis et al. 2003; whales: Tyack et al. 2006; sea turtles: Houghton et al. 2002, Hochscheid 2014). A popular approach to the study of dive behavior has been to classify dive patterns based on the characteristics of dive parameters (Schreer et al. 2001). The identification of different types of dive behavior is useful for comparing behavioral patterns and activity budgets between individuals and in different spatial and temporal contexts, and thus for understanding their underwater behavior (Schreer et al. 2001).

Some sea turtle species have been known to exhibit foraging-habitat polymorphism during the foraging period after the reproductive season (loggerhead sea turtle *Caretta caretta*: Hatase et al. 2002, Hawkes et

al. 2006, Rees et al. 2010, Reich et al. 2010, Eder et al. 2012; leatherback turtle *Dermochelys coriacea*: Benson et al. 2011, Seminoff et al. 2012). In particular, the North Pacific and Western African loggerhead populations exhibit a size-related difference in foraging-habitat use: large turtles utilize neritic areas (water depths <200 m), whereas small turtles utilize oceanic areas (water depths >200 m) (Hatase et al. 2002, Hawkes et al. 2006), despite there being no known significant genetic difference between the individuals utilizing these neritic and oceanic habitats (Watanabe et al. 2011). Stable isotope and dietary analyses indicate that neritic females mainly forage on benthic prey such as mollusks and crustaceans, whereas oceanic females mainly forage on plankton such as gelatinous zooplankton and *Lepas* spp. (Hatase et al. 2002, 2007, Parker et al. 2005). Neritic females have larger and more frequent clutches and higher breeding frequency but a shorter remigration interval than oceanic females, generating a 2.4-fold difference in reproductive output (defined as the number of emergent hatchlings) between the 2 types of foraging dichotomies (Hatase et al. 2013). Feeding on nutrient-rich prey in neritic habitats likely results in turtles needing less time to accumulate energy and nutrients for reproduction, thereby yielding a higher reproductive output for neritic females (Hatase et al. 2002, 2013), while feeding on nutrient-poor prey in an oceanic habitat results in a lower reproductive output. However, knowledge remains limited about how the turtles exhibiting each foraging type behave in each habitat, how much time they spend foraging, and how these behaviors are related to their reproductive output.

In this study, we combined the horizontal movement and dive behavior analyses to explore both horizontal and vertical habitat utilizations during the post-nesting foraging period in North Pacific loggerhead females exhibiting foraging-habitat polymorphism. Okuyama et al. (2022) demonstrated that some neritic loggerhead females utilize not only the East China Sea (ECS) but also the coastal areas of mainland Japan (CMJ) after nesting, indicating a third type of post-nesting foraging habitat in addition to the neritic ECS and oceanic North Pacific Ocean (NPO). However, they focused on how frequently the 3 types occurred and did not mention the horizontal and dive behavior of turtles in each habitat type during the foraging period after nesting. The objective of the present study was to characterize the horizontal and vertical habitat utilization of loggerhead turtles in each of the foraging habitats (ECS, CMJ, and NPO) based on horizontal movement patterns, be-
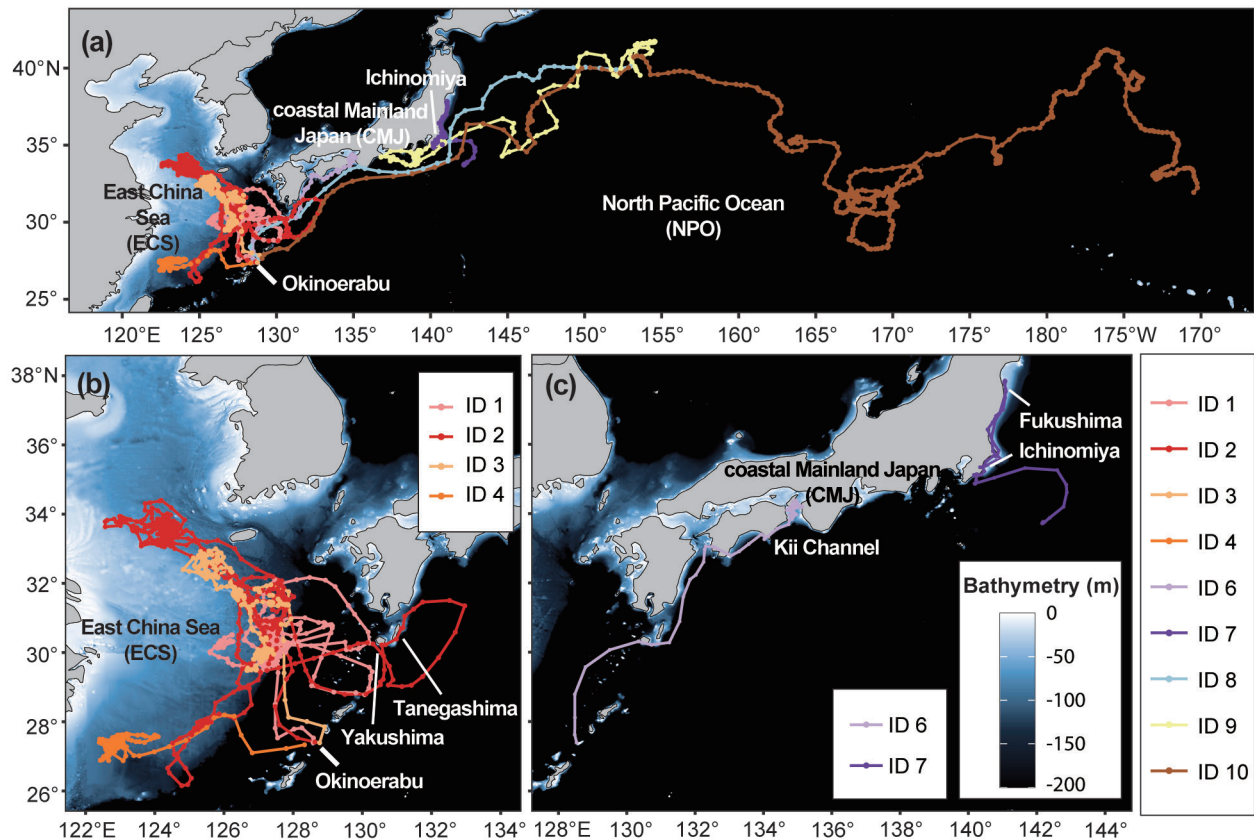
Fig. 1. Migration routes for (a) 9 loggerhead turtle females, (b) 4 neritic females utilizing the East China Sea, and (c) 2 neritic females utilizing coastal mainland Japan

havioral states determined by the SSSM, and dive patterns. By comparing these behavioral patterns among 3 foraging habitats, we can explore the behavioral factors contributing to the differences in fitness (reproductive output).

2. MATERIALS AND METHODS

2.1. Data collection

A satellite relay data logger (SRDL; Sea Mammal Research Unit) was used to track both the horizontal movement and dive behavior of adult female loggerhead turtles during the post-nesting and foraging periods. The tags were deployed on 8 turtles nesting at Okinoerabu Island (27.37° N, 128.57° E) and 2 turtles nesting at Ichinomiya (35.36° N, 140.38° E), located in the southern and the eastern parts of Japan, respectively (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m707p115_supp.pdf). We patrolled the nesting beaches each night to find turtles at these 2 sites during the 2016–2018 nesting seasons (May–August). After the turtles had finished nesting, we measured their straight carapace length, cleaned the carapace with sandpaper, and attached the SRDLs securely to the carapace using epoxy resin and fiberglass cloth (Konishi Co.). After the resin had completely dried, the turtles were released into the sea. The 10 turtles in this study were included in those tracked by Okuyama et al. (2022).

The SRDLs provide location data as well as a dive profile. Data were transferred and downloaded via the Argos satellite system. Each SRDL was equipped with a saltwater switch that identified a haul-out when it was continuously dry for 10 min. Haul-outs were used to detect the time of landing for nesting turtles. We determined the post-nesting and foraging periods of each turtle based on the criterion that (1) data did not contain haul-outs and (2) positional data indicated the departure of the turtle from its nesting site. Only data during post-nesting and foraging periods were used in this study. Sea surface temperature (SST) was defined as the temperature at 2 m depth, which was the shallowest point of the temper-

ature–depth profile obtained by SRDL. One SRDL deployed in 2016 was physically retrieved in 2018 when the turtle returned to the same nesting beach (Kishida et al. 2022); therefore, detailed data on dives deeper than the limit of depth measurement (340 m) were retrieved via satellite transmission (Text S1 in the Supplement).

To explore turtle movements in relation to geographical and environmental features in the sea, bathymetry data were extracted from the General Bathymetric Chart of the Oceans (https://www.gebco.net/) 2020 grid data with 15 arc-second resolution, and monthly means of surface chlorophyll data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS).

2.2. Horizontal movement analysis

We used R v.3.6.3 (R Development Core Team 2020) for the following analyses. We applied hierarchical SSSM (hSSSM) for positional data with Argos location classes of 3 to B during the post-nesting and foraging periods to estimate the daily behavioral state as well as the unobserved true locations (Jonsen et al. 2007, Jonsen 2016). The R package 'bsam' (Jonsen 2016) was used to fit the hSSSM via a Markov chain Monte Carlo (MCMC) sampler executed in JAGS (Plummer 2003). An hSSSM estimates parameters jointly across multiple individual tracking data sets, reducing uncertainty of parameter estimates at the individual level (Morales et al. 2004). We constructed 2 models: one for the neritic females utilizing the ECS or CMJ and another for the oceanic females utilizing the NPO since the travel ranges differed greatly between both areas (Fig. 1). Each model was estimated in a Bayesian framework that ran 2 parallel chains of MCMC, each of which contained 180 000 samples. The first 120 000 samples were discarded as a burn-in, and every 30th sample was retained from the remaining samples to reduce sample autocorrelation. Convergence and sample autocorrelation were assessed by visually inspecting trace and autocorrelation plots (Silva et al. 2014).

The discrete behavioral state is represented by a parameter, b, that can be 1 or 2. Because the posterior mean of the b value at each location ranges continuously from 1–2, we delineated the 2 behavioral states by cut-off values at 1.4 and 1.6 based on their distribution. Thus, b-values <1.4 were categorized as 'transiting,' whereas b-values ≥1.6 were considered as 'ARS.' All values between 1.4 and 1.6 were treated as 'uncertain.'

2.3. Classification of dive types

The SRDLs provided dive profiles with the time and depth of 5 prominent points of inflection during each dive based on the compression algorithm described by Photopoulou et al. (2015). We defined dives as any submergences with a maximum depth of ≥3 m for >30 s in duration. The dives were categorized into 5 types following Minamikawa et al. (1997), Houghton et al. (2002), Seminoff et al. (2006), and Okuyama et al. (2021) (Fig. 2). Type 1 dives are U-shaped dives characterized by a steep descent phase, a flat bottom phase, and a steep ascent phase. Type 2 dives are V-shaped dives with a steep descent phase and a steep ascent phase. Type 3 dives are identified as having a steep descent phase, a gradual ascent phase, and a steep final ascent phase. Type 4 dives are very shallow dives. Type 5 dives are W-shaped dives with up-and-down undulations (termed a 'wiggle') in depth during the bottom phase of the dive.

Because the number of dives extracted from the SRDLs was quite large (N = 15 013), a random forest was used to automatically classify the dive types by using the R package 'randomForest' (Liaw & Wiener 2002). We used 36 parameters for constructing a
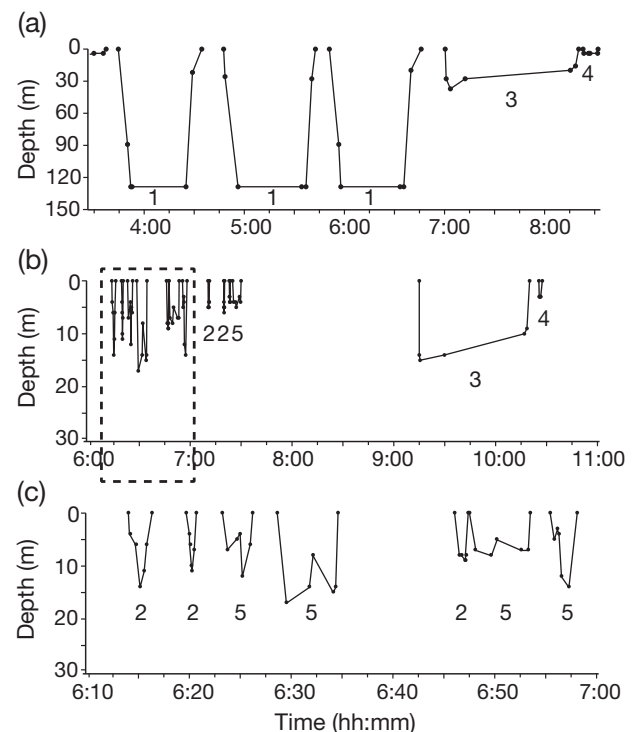

Fig. 2. Typical loggerhead turtle dive profile for 5 h periods at depths (a) 0–150 m and (b) 0–30 m. (c) Enlarged view of the dashed line in (b). Numbers below the profile indicate the dive types (see Section 2.3)

random forest classifier. These parameters included maximum depth, dive duration, the ratio of the dive duration to the maximum depth, the ratio of the duration until reaching the bottom to the maximum depth, and the time ($T_1–T_5$), and depth ($D_1–D_5$) of the 5 prominent points of inflection during the dive. Furthermore, we measured the ratios of $D_1–D_5$ to the maximum depth ($Dr_1–Dr_5$) as well as the ratios of $T_1–T_5$ to the dive duration, the difference of the depth and the velocity between 2 neighboring points, the mean of $Dr_1–Dr_5$, and the SD of the 5 points. The training data set of 1862 dives was prepared by visual inspection of the dive shape using Igor Pro v.6.0.3.1 (WaveMatrics).

2.4. Statistical analyses

The difference in the proportion of time spent in ARS and transiting among 3 foraging habitats (ECS, CMJ, and NPO) and the difference in temporal composition of dive types between ARS and transiting in each of the foraging habitats were tested using a chi-squared test. Here, the behavioral state was assigned per day. The temporal composition of dive types was also compared between daytime and nighttime to understand the diel change in dive behavior. There are latitudinal environmental variations in the ECS, such as upwelling in the northern ECS (Dunxin 1984), resulting in more zooplankton and jellyfish blooms in the summer than in the winter (Chen et al. 2011, Zhang et al. 2012, Peng et al. 2014); thus, the temporal composition of dive types was compared among 3 latitudinal areas — southern area (<28° N), middle area (28–32° N), and northern area (>32°N) — to infer the difference in dive behavior within the ECS.

The same dive types may have different behavioral meanings in different foraging habitats; therefore, the difference in the maximum dive depth of each dive type between day/night and between foraging habitats was examined by linear mixed modeling that assumed habitat and day/night as fixed effects and individual differences as a random effect. Similarly, the duration of each dive type was compared between day and night for each habitat. Likelihood ratio tests were conducted using these models and the reduced models for statistical testing. There were differences in the time zones where the data were recorded because the turtles migrated between 122°E and 170°W longitude. Therefore, daytime and nighttime were corrected using each time zone. The detailed method is described in Text S2.

To examine the seasonal pattern of foraging dives in the water column for the 2 turtles that were tracked for more than 500 d (ID 2 in ECS and ID 10 in NPO), we focused on the dive depth of W-shaped Type 5 dives that relate to foraging in the water column. A 1-way ANOVA was used to test the difference in the monthly dive depth of Type 5 dives for each of the 2 turtles.

3. RESULTS

3.1. Horizontal movements

Post-nesting and foraging movements of 10 loggerhead turtles were tracked for a mean (±SD) of 219.2 ± 185.0 d within the range of 10 to 521 d (Table S1). As reported by Okuyama et al. (2022), 3 destinations of post-nesting migration were identified: (1) 5 of 10 females (IDs 1–5) migrated to the neritic ECS, (2) 2 females (IDs 6 and 7) migrated to and stayed around the CMJ, and (3) 3 females (IDs 8–10) migrated into the NPO. One turtle (ID 5) reached the ECS but was tracked for only 10 d during the post-nesting period, so this individual was omitted from the following analyses on horizontal movement and dive behavior, except for constructing the model for the dive-type classifier.

Two ECS turtles (IDs 2 and 3) moved to the northern ECS after their nesting season, while turtles ID 1 and 4 migrated to the middle and southern ECS, respectively (Fig. 1b). Each of the ECS turtles utilized a single area with frequent ARS states (77.6 ± 8.7 %), but the areas that they utilized differed among individuals. Intensive utilization of the same habitat by each turtle lasted until the data transmission was terminated, except for 2 turtles (IDs 2 and 3) that exhibited seasonal migration. The 2 turtles migrating to the northern ECS stayed there until the onset of winter (October), and thereafter moved southward and utilized the middle or southern ECS with frequent ARS states in winter (Figs. 1b & 3). Data transmission of ID 3 stopped during winter. ID 2 left the southern area, headed northward in February, and stopped in the middle area until April. In April, she approached the sea around Yakushima and Tanegashima Islands; however, there was no 'haul-out' data during this period, and therefore it was assumed that this turtle did not come onshore to nest (Fig. S1). She then finally moved back to the same northern foraging habitat the following summer (July).

The 2 CMJ turtles (IDs 6 and 7) also showed strong site fidelity in the neritic habitats after a transiting
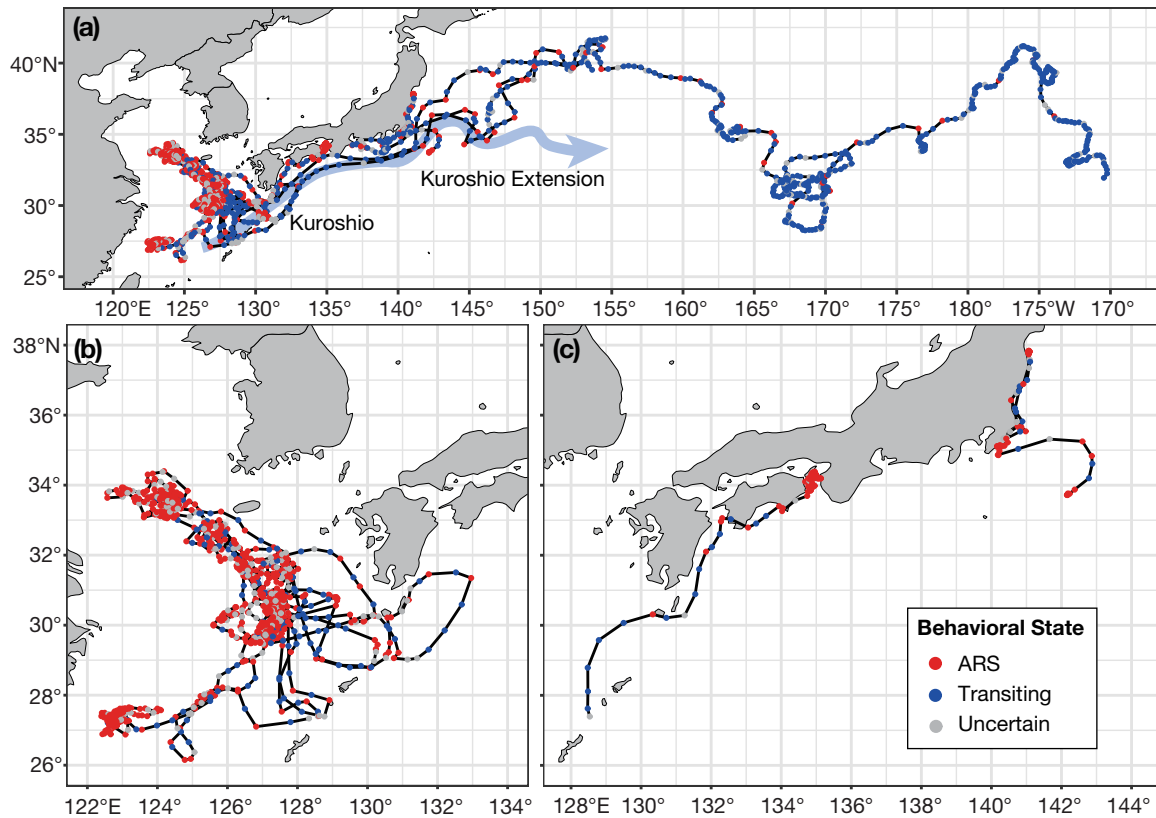
Fig. 3. Behavioral states of (a) 9 loggerhead turtle females, (b) neritic females utilizing the East China Sea, and (c) neritic females utilizing coastal mainland Japan estimated by hierarchical switching state-space modeling. ARS: area-restricted search

phase of a few weeks. ID 6 frequently exhibited ARS at the narrow area in the Kii Channel (Figs. 1c & 3) until December. After that, she moved out to the open ocean, but no dive data (continuous haul-out data) were observed so she was assumed to have died (Okuyama et al. 2022). ID 7 stayed at the Fukushima coastal area in a frequent ARS state (Figs. 1c & 3). However, in mid-October, she migrated southward along the coastal line when SST decreased to approximately 20°C (Fig. S2) and reached Katsuura City (35.1° N, 140.25° E), located approximately 30 km south of Ichinomiya, where she stayed for 1.5 mo (November–December). She then left the coastal area where the SST had decreased to approximately 20°C and headed southward to the open ocean. Transmission terminated immediately after she left the coastal area.

The 3 NPO turtles (IDs 8–10) continued to wander and travel eastward, exhibiting frequent clockwise/counterclockwise rotations (Fig. 1a). ID 10 also showed seasonal migrations from around 40° N in summer and fall and around 30° N in winter along the Transition Zone Chlorophyll Front (TZCF); how-

ever, the migration was not associated with a decrease in water temperature, unlike that of the neritic females (Figs. S2 & S3). During the tracking period, the NPO turtles spent 73.5 ± 6.1 % in the transiting state (Fig. 3). ID 10 started her post-nesting migration on 8 July 2016, and finally crossed the international date line on 26 June 2017. The direct distance from the nesting site at Okinoerabu Island to the farthest location (32.25° N, 170.23° W) was 5854 km.

Mean displacements from the release locations were 490 ± 194, 506 ± 399, and 3321 ± 1765 km for the ECS, CMJ, and NPO females, respectively. There were significant differences in the proportion of estimated behavioral states (ARS vs. transiting) between the 3 foraging habitats ($\chi^2 = 1084.9$, df = 4, p < 0.001).

3.2. Dive classification and performance

In total, 14 963 dives were observed from the 9 turtles during the post-nesting and foraging periods (Tables S2 & S3). The total dive duration obtained by

SRDLs was 5213 h. The overall accuracy of the random forest classifier constructed from the training data set of the 1862 dives was 93.8%. The classification accuracies for each dive type were 92.5% (Type 1), 87.0% (Type 2), 90.0% (Type 3), 100.0% (Type 4), and 97.3% (Type 5).

The maximum depth of Type 1 dives was significantly different among the 3 foraging habitats (likelihood ratio test, $\chi^2 = 16.7$, $p < 0.001$; Table S2); Type 1 dives in the ECS (mean ± SE: 103.5 ± 0.9 m) were considerably deeper than in the other 2 regions (CMJ: 36.0 ± 0.6 m, NPO: 38.8 ± 3.1 m). The maximum depth of Type 1 for the ECS and CMJ turtles corresponded to the seafloor depth (ECS: approximately 100 m, CMJ: 20–40 m; Fig. 1b,c). Type 1 dives of the oceanic foraging turtles were mainly observed in the coastal area around their nesting beaches before they departed to the oceanic area. Thus, the depth of Type 1 in the NPO turtles corresponded to the bottom depth of the coastal area. For the other 4 types, there were no significant differences in dive depth among the 3 foraging habitats (Type 2: $\chi^2 = 1.5$, $p = 0.47$, Type 3: $\chi^2 = 0.7$, $p = 0.72$, Type 4: $\chi^2 = 3.7$, $p = 0.16$, Type 5: $\chi^2 = 3.7$, $p = 0.16$; Table S2). The retrieved tag from ID 2 showed that the maximum dive depth throughout the entire dive data in this study was 379.5 m in a Type 2 dive when this turtle approached Yakushima Island (Fig. S4, Text S1).

Dive classification revealed that the ECS turtles spent considerable time performing deeper Type 1 (42.6%) followed by W-shaped Type 5 (31.4%) dives in the daytime, while using Type 3 dives (60.9%) at night (Fig. 4a). In the CMJ, they spent most of their time engaging in longer Type 1 dives in both daytime (77.5%) and nighttime (73.2%) (Fig. 4b). In the NPO, Type 5 (73.8%) dives were the most common in the

daytime, while Type 3 (44.9%), Type 4 (30.9%), and Type 5 (21.6%) were common at night (Fig. 4c). In the 3 foraging habitats, there were significant differences in the proportion of time spent performing each dive type between day and night (chi-squared test, ECS: $\chi^2 = 2569318.8$, df = 4, $p < 0.001$; CMJ: $\chi^2 = 104526.2$, df = 4, $p < 0.001$; NPO: $\chi^2 = 1982856.7$, df = 4, $p < 0.001$).

A comparison of the behavioral states (ARS vs. transiting) demonstrated that there were significant differences in the time spent performing each dive type (ECS: $\chi^2 = 166595.8$, df = 4, $p < 0.001$; CMJ: $\chi^2 = 538745.7$, df = 4, $p < 0.001$; NPO: $\chi^2 = 33114.1$, df = 4, $p < 0.001$). In the ECS, Type 1 (29.9%) and Type 3 (38.8%) dives were mainly exhibited in the ARS period, while Type 3 (49.5%) and Type 5 (28.1%) were most common in the transiting period (Fig. 4a). In the CMJ, turtles mostly exhibited Type 1 (79.2%) in the ARS period, while Type 3 (52.2%) was the most prevalent in the transiting period, followed by Type 5 (20.2%) (Fig. 4b). In the NPO, although there was a significant difference between the behavioral states, the common dive types (Types 3 and 5) were similar between the ARS (37.1 and 43.0%) and transiting (27.6 and 49.5%) periods (Fig. 4c).

For ECS and NPO turtles, the difference in dives was greater between daytime and nighttime than between behavioral states (ARS vs. transiting), whereas for the CMJ turtles, behavioral states had a far greater impact, while daytime vs. nighttime showed a very similar spread of dive types (Fig. 4). In the ARS period, the ECS turtles mainly performed deeper Type 1 dives (47.5%) followed by Type 5 (28.4%) during the daytime and Type 3 (61.1%) at night, whereas the CMJ turtles mainly performed Type 1 (day: 81.0%; night: 77.5%) during both day-
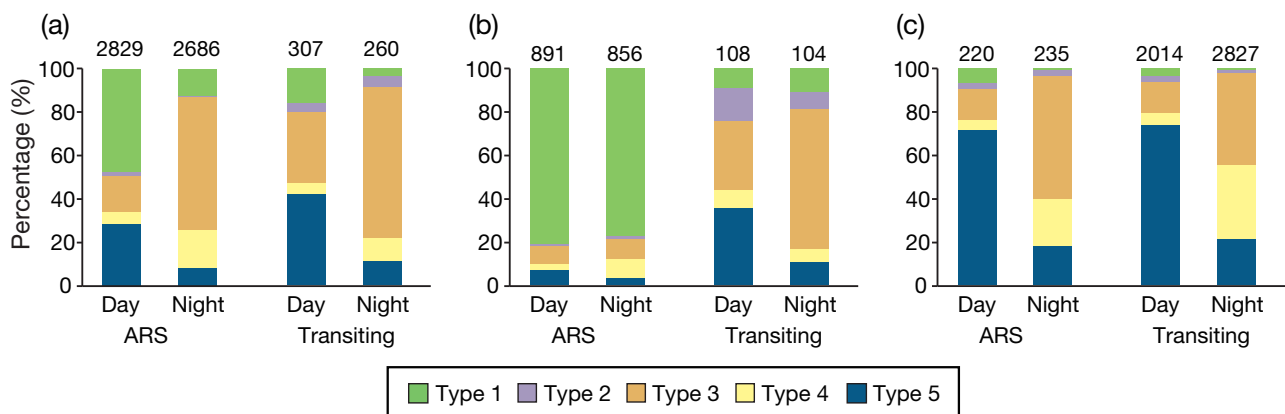

Fig. 4. Diel changes in loggerhead turtle dive composition during area-restricted search (ARS) and transiting in 3 foraging habitats: (a) East China Sea, (b) coastal mainland Japan, and (c) North Pacific Ocean. Numbers above the bars show number of dives; see Section 2.3 for description of dive types
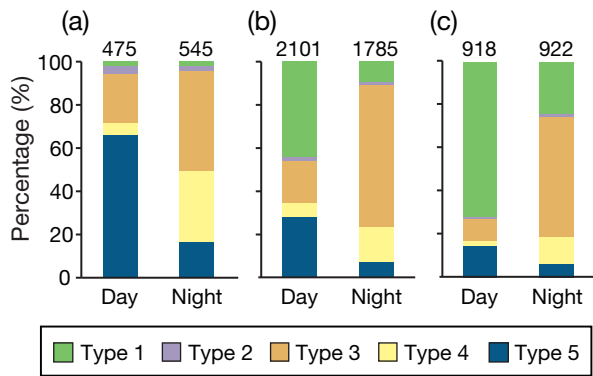
Fig. 5. Latitudinal changes in dive composition of neritic female loggerhead turtles utilizing the East China Sea. Dives were divided into 3 areas: (a) northern area (>32°N), (b) middle area (28–32°N), and (c) southern area (<28°N). Numbers above the bars show number of dives; see Section 2.3 for description of dive types

time and nighttime. The NPO turtles mainly performed Type 5 (ARS: 71.8%; transiting: 74.0%) during daytime, and Type 3 (42.5%) and Type 4 (33.9%) at night.

As for the turtles in the ECS, the proportion of time spent diving was significantly different among the latitudinal areas ($\chi^2 = 1038308.0$, df = 8, p < 0.001). In the northern part of the ECS (>32°N; bathymetry: 60–100 m), the turtles mainly performed Type 5 dives (65.9%) to the mid-water during the daytime, while Type 3 (46.9%) and Type 4 dives (32.6%) were made at night (Fig. 5a). In the southern area (<28°N; bathymetry: approximately 100 m), turtles mainly engaged in Type 1 dives (71.9%) during the daytime and Type 3 dives (55.8%) at night (Fig. 5c). Turtles staying in the middle area (28–32°N; bathymetry: 60–150 m) showed an intermediate pattern between the northern and southern areas (Fig. 5b). These geographical differences in the composition of dive patterns correlated well with the changes in dive patterns along with the seasonal migration. Two ECS females (IDs 2 and 3) and a CMJ female (ID 7) changed their dive types along with their seasonal migration (Fig. 6, Text S3).

Depth utilitzation patterns were affected in neritic (ID 2) and oceanic (ID 10) turtles in the months in which thermoclines occurred (Fig. 7, Text S4). When thermoclines were present, both turtles remained in water just above or in the thermocline (ECS: between 30 and 60 m; NPO: between 30 and 70 m). ID 2 (ECS) performed deeper Type 5 dives during months where no thermocline was present (December–May), whereas ID 10 (NPO) showed shallower Type 5 depth utilization.

4. DISCUSSION

4.1. Foraging-site fidelity and seasonal migration

Intraseasonal site fidelity to their foraging habitat observed in all neritic (ECS and CMJ) females was not surprising because sea turtles reportedly exhibit foraging-site fidelity (loggerhead turtle: Hatase et al. 2007, Hawkes et al. 2011, Saito et al. 2015; green turtle *Chelonia mydas*: Stokes et al. 2015). Neritic foragers utilize the same areas that they previously used unlike pelagic foragers, likely because of the predictability of food resource quality and the risks associated with relocating to an alternative site (Shimada et al. 2020). Therefore, utilization of the foraging habitat with intraseasonal site fidelity is likely a common foraging tactic in neritic turtles.

In contrast with the intraseasonal residency, seasonal migration from north to south was observed in 2 ECS females and 1 CMJ female when the SST decreased to approximately 20°C. Water temperature has a significant effect on the migration and habitat suitability of sea turtles (McMahon & Hays 2006, Hawkes et al. 2007, Kobayashi et al. 2008, Witt et al. 2010); the seasonal migration observed in our study may be triggered by colder water temperatures.

Unlike neritic loggerhead turtles, the NPO females did not show site fidelity but continued to migrate eastward, presumably by drifting with the Kuroshio and Kuroshio Extension currents with typically clockwise/counterclockwise rotations. One female finally reached the Central North Pacific (160°E–160°W longitude), which has been known to be an important developmental foraging ground for young juvenile loggerhead turtles (Polovina et al. 2006, Briscoe et al. 2016). Although this female did not clearly show the returning movement to the west before the data transmission was terminated, our results indicate that Central North Pacific is also an important foraging ground for mature female loggerheads. Clockwise/counterclockwise movements were associated with cyclonic and anti-cyclonic eddies, respectively, at the edge of which subsurface prey is concentrated at shallow depths during the fall, winter, and spring (Polovina et al. 2006). This corresponds with shallow-water foraging by the NPO female during this period when clear thermoclines were not observed. Furthermore, the NPO female showed north–south movement along the TZCF, where chlorophyll is concentrated (Polovina et al. 2001, 2017). The TZCF moves seasonally within a range of 45°N in summer and 30°N in winter (Polovina et al. 2001, 2017), and juvenile loggerheads
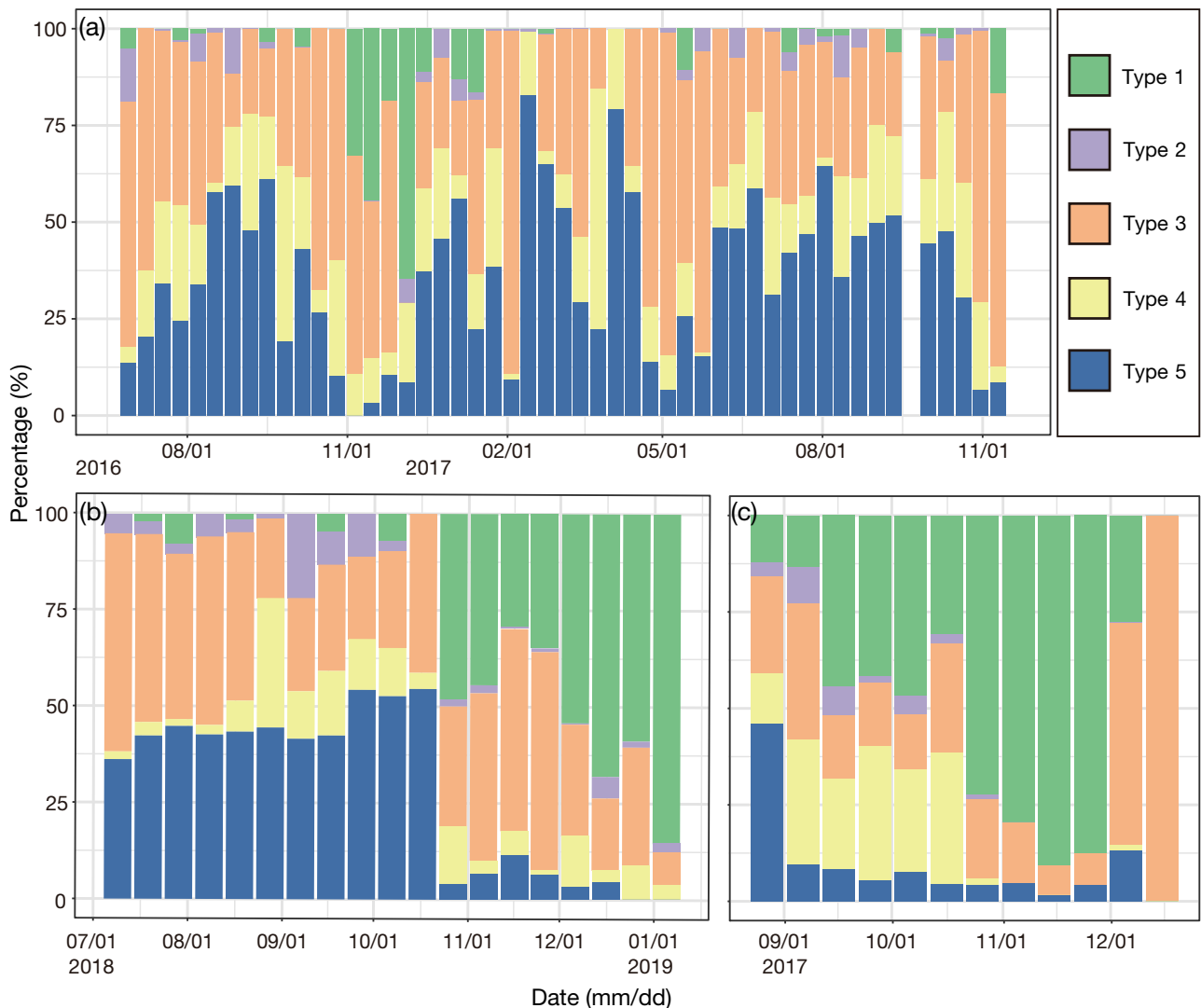
Fig. 6. Seasonal changes in dive composition of loggerhead turtles (a) ID 2, (b) ID 3, and (c) ID 7. The composition of dive types based on dive duration is shown every 10 d; see Section 2.3 for description of dive types

observed there, as well as other marine species, seasonally migrate within the 30–45° N latitude range (Murata 1990, Polovina et al. 2001, 2004, 2006, Watanabe et al. 2006).

4.2. Foraging tactics

Dive behavior analyses suggested that the foraging behaviors differed among the 3 habitats: loggerhead turtles were benthic foragers in the middle/southern ECS and CMJ and mid-water foragers in the northern ECS and NPO. Foraging methods were flexible depending on location, especially in the ECS.

Benthic foraging of loggerhead turtles in the middle/southern ECS was supported by U-shaped Type 1

dives dominant during daytime and ARS (Fig. 5). Type 1 dives have been presumed to relate to bottom feeding or resting (Houghton et al. 2002, Seminoff et al. 2006). However, Type 1 dives observed in the middle/southern ECS likely reflect benthic (seafloor) foraging as opposed to resting for the following reasons. First, the depths of Type 1 observed in the ECS were considerably deeper than the depth at which sea turtles can attain neutral buoyancy (~20 m; Hays et al. 2004). Second, the resting dive duration can be maximized when turtles rest at the depth of their neutral buoyancy when they fully inhale air-volume (Hays et al. 2004). Therefore, resting on such a deep seafloor seems unlikely because they have to spend extra energy and time shuttling between the surface and deep seafloor. Foraging on the seafloor is consis-
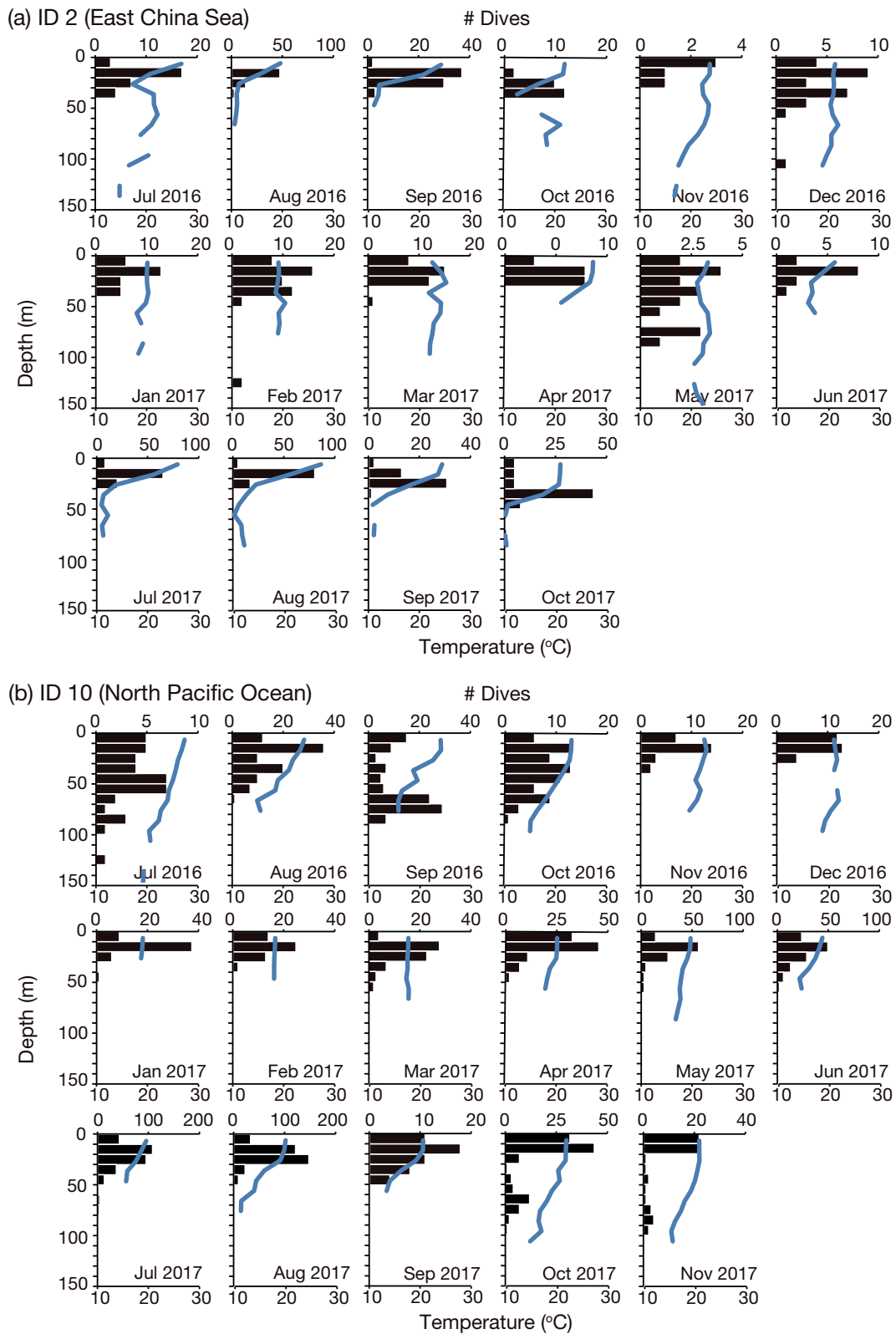
Fig. 7. Monthly comparisons of the depth of Type 5 dives and temperature–depth profile for loggerhead turtles (a) ID 2, migrating to the East China Sea and (b) ID 10, migrating to the North Pacific Ocean. Black horizontal bars: depth distribution of Type 5 dives in each month (upper axes); blue lines: monthly mean temperature at 10 m intervals in depth (lower axes)

tent with previous stable isotope analyses that suggested benthic foraging of ECS females (Hatase et al. 2002, Okuyama et al. 2022).

Type 1 dives in CMJ were shallower than those in ECS; thus, it is difficult to discriminate foraging and resting from the dive depth. However, dominant Type 1 dives indicate that CMJ turtles forage for benthic prey on the seafloor at a depth of 20–30 m. A CMJ turtle (ID 7) moved from the northern foraging habitat, which juvenile loggerhead turtles also utilized in the summer (Narazaki et al. 2015), to the southern habitat. In the northern habitat, this female typically engaged in Type 4 dives as well as Type 1 dives, indicating that she also foraged for plankton in the shallow water column (4–6 m).

Mid-water foraging in the northern ECS was indicated, as wiggle dives into the mid-water column (Type 5) were dominant during the daytime. Wiggle dives are common in diving animals and are associated with foraging behaviors such as searching for and feeding on prey resources (penguins: Hanuise et al. 2010; sea turtles: Salmon et al. 2004, Fossette et al. 2007, Wallace et al. 2015, Okuyama et al. 2021). Similar wiggle movement during dives was observed in subadult loggerhead turtles (T. Narazaki unpubl. data). The depth of Type 5 dives in the northern ECS was shallower than that of the seafloor, indicating that they are foraging on the plankton in the mid-water.

The 2 turtles showing seasonal migration between the northern and southern ECS regions presumably changed their diet with this seasonal habitat shift. This shift in prey items and foraging habitats may be triggered by the abundance of prey resources. Benthic animals are distributed over the entire ECS throughout the seasons (e.g. Lü et al. 2007, Yamamoto & Nagasawa 2015). Meanwhile, the northern ECS (north of 32° N) has zooplankton and jellyfish blooms in summer, with fewer blooms occurring in winter (Chen et al. 2011, Zhang et al. 2012, Peng et al. 2014). The observed depth of Type 5 dives in the northern ECS region was just above or in the thermoclines (30–60 m) when they clearly occurred (June–October). Thus, this evidence suggests that during summer they utilized the northern ECS, where there was more biomass in the mid-water than in the middle and southern areas, where benthic items were available. The ECS females presumably foraged on benthic prey on the seafloor by diving to a depth of >100 m in the south/middle areas or planktonic prey in the mid-water of 0–70 m in the northern area.

The NPO females were thought to forage on planktonic prey while showing nomadic movement in the North Pacific, as the dominant Type 5 dives during the daytime likely reflect feeding on planktonic items within the water column (Salmon et al. 2004, Wallace et al. 2015, Okuyama et al. 2021). This planktonic foraging was supported by dietary analysis (Parker et al. 2005) and stable isotope analyses (Hatase et al. 2002, Okuyama et al. 2022). The depth of Type 5 dives was concentrated around the depth of thermoclines when the thermocline occurred (June–November), whereas the turtles utilized shallow waters (<30 m) when the thermoclines were not clearly observed (December–May). Similar foraging behavior — changing depth utilization in correspondence with the depth of the thermocline — was also reported in juvenile loggerhead turtles (Polovina et al. 2004, Howell et al. 2010) and leatherback turtles foraging in the pelagic North Pacific (Okuyama et al. 2021). Moreover, a similar influence of vertical thermal structure on dive behavior has been observed in marine mammals and seabirds (Takahashi et al. 2008, Kuhn 2011). These changes in utilization of vertical habitat may be due to differences in the vertical distribution of prey items, such as gelatinous zooplankton whose aggregations are typically most concentrated around sharp density discontinuities of thermoclines or haloclines (Graham et al. 2001). Therefore, the NPO turtles may change their foraging depth in response to the vertical distribution of gelatinous zooplankton, likely influenced by thermocline depth.

Our results demonstrate that loggerhead females can change their foraging behavior and prey items (from plankton or benthos) depending on the marine environmental conditions, including prey abundance and water temperature. Such changes in foraging behavior within individuals have been reported in large marine predators (e.g. seabirds: Garthe et al. 2011; mammals: Watanabe et al. 2004, Breed et al. 2009). Moreover, the seasonal change in the depth of mid-water foraging on planktonic prey is probably a behavioral response to changes in the vertical distribution of prey. Therefore, flexible changes in prey utilization and foraging place/depth may constitute a common tactic in loggerhead turtles.

4.3. Resting tactics

As the ECS and NPO females mainly performed Type 3 dives at night, they were likely undertaking mid-water resting. Although our SRDLs were not equipped with acceleration, motion, or image sensors to determine activity and actual behavior (e.g.

Houghton et al. 2008, Fossette et al. 2012, Okuyama et al. 2013), the mean depth of Type 3 dives (23.9 m in the ECS; 21.3 m in the NPO) was assumed to be around the depth at which mature loggerhead females can achieve neutral buoyancy (Hays et al. 2004). Therefore, the ECS and NPO turtles probably achieved neutral buoyancy for resting during the Type 3 dives.

Bottom resting was indicated in the CMJ females. They predominantly performed Type 1 dives to the seafloor during the day and night in ARS. The duration of Type 1 dives was longer during the night than in the day (Table S3, Text S5), indicating that the function of CMJ Type 1 dives at night was resting in contrast with foraging during the daytime. Green turtles are known to maximize their period of submergence during resting dives while not foraging by depleting the oxygen stored in their bodies (Okuyama et al. 2014). Moreover, foraging and subsequent digestion reportedly consume oxygen, resulting in a decrease in dive duration (Houghton et al. 2002, Seminoff et al. 2006, Jones et al. 2009). Bottom resting of female loggerheads is commonly observed in shallow areas during the inter-nesting period (Minamikawa et al. 1997, Houghton et al. 2002) and may also be common in post-nesting loggerhead turtles foraging in the shallow coastal area.

Our results indicate that mature loggerhead females may be flexible in their behavioral tactics for resting (bottom vs. mid-water resting) in response to the depth of seafloor in their habitat. This depth-related resting flexibility is first reported in our study, although these 2 types of resting styles (mid-water and bottom resting) have been observed in loggerhead turtles (Minamikawa et al. 1997, Houghton et al. 2002, Hatase et al. 2007, Hawkes et al. 2007) and other sea turtle species (Hays et al. 2001, Reina et al. 2005, Seminoff et al. 2006).

4.4. Implications for different reproductive outputs among three life-history polymorphisms

The percentage of time spent in presumed foraging dives during the daytime was similar in all 3 foraging habitats, with a range of 70–80%: a total of 74.0% for the ECS (Type 1: 42.6% and Type 5: 31.4%), 77.5% for the CMJ Type 1, and 73.8% for the NPO Type 5. Therefore, time spent foraging is an unlikely factor affecting the differing reproductive outputs among the 3 foraging habitats. On the other hand, prey quality may affect reproductive output, as neritic benthic prey is more nutrient-rich than oceanic

planktonic prey (Hatase et al. 2002). However, further studies investigating, for example, the energy spent and feeding amount per foraging dive are required to better understand the effect of foraging tactics on reproductive outputs.

In addition to the difference in prey items, the energy costs of traveling most likely have an impact on reproductive output, as observed in leatherback turtles (Okuyama et al. 2021). In the present study, an NPO turtle (ID 10) traveled 5854 km directly from the nesting site, Okinoerabu Island, to the farthest location (32.25° N, 170.23° W). Nichols et al. (2000) reported that an adult loggerhead turtle was observed traveling 11 500 km in 368 d with an average speed of 1.3 km h^{-1} to reach Japan from Baja California, Mexico. Given that NPO females move at the same speed, it would take approximately 188 d to return to their nesting or breeding grounds. Meanwhile, the ECS loggerheads can return within 10 d. These facts suggest that the return migration of oceanic turtles to their breeding ground would require more energy than that required for neritic turtles, which may result in the longer remigration interval to the nesting site and lower reproductive output of oceanic turtles (Hatase et al. 2013). It is possible that pelagic foraging occurs during the return migration like during the transiting period in the NPO; however, oceanic females may have less time to store energy for reproduction than neritic turtles, as they must start the breeding migration earlier to coincide with mating and nesting seasons. These time and energy costs may contribute to the longer remigration interval of oceanic turtles than that of neritic turtles (Hatase et al. 2013).

In conclusion, despite the limitations of a small number of individuals tracked, loggerhead females in the North Pacific population changed their foraging tactics depending on the environment and prey abundance in polymorphic habitats. As the amount of time spent in presumed foraging behavior was similar among the 3 habitats, the nutrient richness (quality) of prey items and the total distance between foraging and breeding grounds may cause differences in reproductive outputs among the different life-history types of loggerhead turtles.

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