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Seasonal Distribution and Behavior of Loggerhead Sea Turtles in the North Pacific

- statistical analysis in relation to environmental oceanographic parameters

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Abstract

Loggerhead sea turtles *Caretta caretta* nesting off coasts of Japan are known to travel an immense distance throughout their life, however much of their behavior in the open ocean is still not clear. Argos transmitters were attached to 30 turtles, which were either postnesting, headstarted, or bycaught, and their tracks were recorded spanning several months to over a year. Location data were low in quality with nearly 70% of the points having error radii that could not be estimated. As an initial step, the noisy data were smoothed under a systematic set of criteria to remove redundant information and obtain the most reasonable paths taken, controlling both location and average velocity. Smoothed turtle tracks were obtained for all individuals with average velocities no greater than 250 cm/s.

Behavior was categorized into three groups; 1) remaining, 2) returning and 3) departing, among which significant differences were found in straight carapace lengths (SCLs), being largest for remaining turtles and smallest for departing turtles. Logistic regression estimated the pivotal range of SCL to be 725 to 783 mm dividing coastal (remaining and returning) and non-coastal (departing) turtles. Longitudinal distributions were clearly different between behaviors and also within the returning turtles being west of 135°E from May to July due to mating and nesting, which took place near the coast. During the same season, departing turtles were in regions as far as 170°E. In latitudinal distribution, all turtles were seasonally variable, being in latitudes higher than 30°N during warmer months. Behavioral differences were examined based on relative velocity of the turtle with respect to ocean current, where geostrophic current velocity was obtained from optimally interpolated satellite data (J-OFURO). Regression analysis was undergone comparing relative velocity to current velocity, along with other oceanographic parameters, such as sea surface temperature (SST) from AVHRR satellite data and nutrient concentrations from WOA01 climatological data. Turtle paths were divided into specific stages and comparisons were made between returning and departing turtles. In regions with strong Kuroshio currents, all turtles were drifted, however returning turtles were swimming in the opposite direction of the current more often than the departing turtles, which were reacting more to cooler SST. This indicates that returning turtles were unintentionally drifted into the direction of the strong currents. Frequently, turtles made roaming or circular movements in the open ocean, just off of the Kuroshio extension, possibly being drifted into circular currents or eddies, however in all cases, turtles confronted regions with plenty of prey during the roaming stage. After this stage, turtles either moved farther east to the Kuroshio extension bifurcation region, a “hotspot” for juvenile turtles, or changed their directions and headed back to nesting grounds. Deciding moments were characterized by a difference in current velocity magnitude and direction, which was mainly due to the turtles being at different latitudes, in which returning turtles were located south of the Kuroshio mainstream, being closer to cyclonic currents and nutrient-high cold rings, whereas departing turtles were closer to the center of the mainstream. When returning turtles initiated their long journeys back to the coast spanning several months, they headed southward into regions of relatively weaker currents and with a lower chance of finding prey. Initially, they were swimming more actively in the opposite direction of the current, but were less active as they headed south towards the end of their returning path. Hence, they seemed to have been extremely cautious concerning energy consumption, by swimming slower even in warmer SST, only swimming opposite of weak currents to head towards high silicate regions. They may have also been making frequent shallow dives in order to sense subsurface water temperatures as a cue to returning back to familiar waters near Japan. Departing turtles in the bifurcation region were continuously influenced by the currents and constantly headed towards prey abundant regions, remaining in this area until transmissions ended.

It has been verified that ocean currents and other environmental factors influenced the horizontal movement and behavior of loggerhead sea turtles in the North Pacific at different stages of their tracks. Abrupt environmental changes causing SST increase, distributional change in plankton and intensification of the Kuroshio and its countercurrent could have an impact on their behavior, however the degree of the impact would depend on the adaptability of the turtles. These effects as well as those related to human activity are the determinant factors for their survival to endangerment.

Acknowledgments

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Chapter 1

Introduction

Many marine animals are known to migrate in the course of a lifetime, whether they are relocating themselves for purposes of foraging, mating, or due to seasonal aspects. However, the underlying mechanism behind migrating behavior is still unknown for many species. Unlike animals that migrate in groups, sea turtles exhibit solitary migration and are especially difficult to examine each individual's oceanic path that is never identical to any other's. As technology has improved over the years, tracking of sea turtles has become possible with the use of satellite telemetry and, thus, providing researchers with new tools to investigate behaviors that could not even be considered in the past. In one of the previous studies involving satellite telemetry, it was reported that loggerhead sea turtles (*Caretta caretta*) have the ability to make transpacific migrations from Mexico to Japan [40]. Although findings were for one specific individual, many researchers began to find interest in discovering the unknown behaviors and abilities of the sea turtles along coastal waters and also in the open ocean.

Sea turtles in different life stages have different habitats, those being terrestrial, neritic and pelagic [44]. However, with the ocean as their main habitat, sea turtles have the ability to move to other regions allowing them to explore new environments and foraging grounds or interact with other individuals. Nesting grounds of loggerhead sea turtles are distributed in temperate and subtropical waters around the world, covering a wide range of water temperatures [37]. Based on stable isotope analysis and tracks obtained by satellite telemetry, feeding habits and habitat areas in adult female loggerheads near Japan are known to differ, with smaller individuals of low isotope level being planktonic and pelagic, and larger ones of high isotope level being benthic and neritic [15]. These differences are thought to influence the life history of these turtles in relation to remigration and their growth rates, in which smaller individuals have longer intervals of remigration and lower remigration rates [13].

Sea turtles are also subject to numerous environmental factors, much of them affecting their survival and way of life. Constantly being present in the ocean directs attention to the effects of ocean currents on the turtles [35]. Tracks of loggerhead and leatherback turtles (*Dermochelys coriacea*) superimposed onto sea surface temperature and geostrophic current fields seem similar in shape and hint a possible effect of these factors on the turtles' paths [36, 46, 45]. However, recent studies have not been able to show significant relationships between their behavior and ocean currents. For example, displaced green turtles (*Chelonia mydas*) in the Mozambique Channel were found to be distracted by the currents and, thus, causing the turtles to experience longer wandering periods and disorientation before finding their way back to homing grounds [11, 33]. Loggerhead behavior in the Mediterranean basins has also been investigated in relation to ocean currents, however it was clearly stated that the turtles' traveling speeds were not dependent on the current's speed or direction [4].

In many cases, a sufficient sample size is an issue due to the accumulating costs to undergo satellite tracking, however a small number of tracked individuals would only provide uniquely characterized journeys, and are not adequate for investigating general behaviors of the turtles. This is the reason why many of the past studies have resulted in providing specific findings by focusing on similar regions and making comparisons within a specific type of behavior. In addition, data filtering is a mandatory step when handling data that are low in quality, noisy, highly dense or sparse, and should be designed accordingly depending on one's objectives. However, this step cannot be taken lightly, since inadequate filtering processes can result in false outcomes and, therefore, lead to misinterpretations of underlying characteristics of the data. Past studies in relation to ocean currents have failed to show clear results using filtering processes and analysis methods of their choice and, hence, they make reference to other possible factors that might be the cause of the variability in behavior, e.g. geomagnetic forces. However, it may simply be the location of the study site being difficult to relate to turtle behaviors. For instance, the currents in the Mozambique Channel and Mediterranean basins are seasonally variable, however not as distinct as, say, the Gulf Stream in the North Atlantic having a strong meandering mainstream. Lastly, short tracking periods have a limit as to what can be said and, hence, longer periods are usually more ideal when considering behavioral changes during the year, making reference to mating and nesting seasons. This can be optimally obtained when satellite tracking devices are properly set in order to maximize battery life and, thus, ensure longer tracking periods. With such precautions, and proper transmitter attachment [2], turtles can be tracked for periods spanning well over a year, consisting of a few points per day, and possibly covering a wider spatial range of points in the coastal region and/or open ocean. Furthermore, sufficient temporal and spatial resolutions of oceanographic parameters, with efficient interpolation methods supplied, would be required when estimating corresponding values at the locations of the turtles.

The Kuroshio current is known to be the strongest current in the Pacific, flowing northeastward and carrying warm tropical waters from the western Pacific. Its width is about 100-200 km with a depth of about 200 m. Maximum current velocities reach up to 200 cm/s near the center of the current. Its presence is constantly felt all year round, although its path and strength are variable seasonally and yearly [26, 20, 51]. It is characterized not only by its relatively warmer temperatures but also by fronts that supply favorable environments for many species, such as anchovy and sardine larvae in the Kuroshio front and juveniles in the Kuroshio extension and Kuroshio-Oyashio transition region [29]. There are some organisms abundant in the North Pacific, like albacore [27] and chum salmon [1], that are known to make use of the currents during migration, however unlike sea turtles, they migrate in groups. Furthermore, between longitudes 155 and 160°E, considerable water turns south and southwest, forming part of the Kuroshio countercurrent, which initiates a large scaled clockwise circulating current [57].

Also, at the Shatsky Rise, currents become more complex at locations east of the Kurohio extension bifurcation region, at which meandering currents create many eddies on adjacent sides of the mainstream [29].

The objectives of this research are to investigate distributional patterns of loggerhead sea turtles captured near Japan, and it is also of interest to determine whether environmental factors have a significant effect on their behavior. This is the first study to simultaneously and objectively examine multiple factors aiming to clarify the reasons for the horizontal movements of loggerheads in the North Pacific. Chapter 2 will describe the data used in this study, the data filtration method, the oceanographic databases and methods of interpolation. Chapter 3 divides the results and discussions into three separate sections. Section 3.1 concerns general behaviors categorized into three different groups, comparing seasonal distribution and size of the turtles. In section 3.2, turtle movement will be examined by their relative velocity with respect to the ocean current and compared between behaviors. Turtle tracks are divided into several stages and described separately. These are 1) the initial stage, 2) roaming stage, 3) behavior-deciding stage and 4) returning or departing stage. Section 3.3 explains the regression method involving multiple factors affecting their movement, followed by interpretations of the regressions for each stage. Finally, chapter 4 will involve final remarks.

Chapter 2

Material and Methods

2.1 Turtle data

Argos transmitters were used to track horizontal surface movements of loggerheads (straight carapace length (SCL) mean=787 mm, SD=83, n=30). These individuals were found nesting on beaches, raised and headstarted, or released after being caught by commercial fishnets near coasts of Japan. The sex ratio of females to males was 16:7 based on whether the individual was found during nesting or carried eggs, and by the length of its tail, being larger for males. However, the distinction between females and immature males could not be made for a total of seven individuals and, hence, they were categorized as “unknown” [49]. Transmission dates ranged from May 17, 2000 to April 28, 2006, in which each turtle was tracked for different periods ranging from 27 to 493 days. The total distance traveled for each turtle ranged from 915 to 21,383 km. Transmission locations ranged from 114-174°E and 18-44°N. Causes of transmissions to end may have been due to battery exhaustion, salt-water switch failure, accidental detachment, dysfunction of the device or animal mortality [16]. In the Appendix, Table A.1 shows further information describing the status of these turtles.

All points are categorized by the Argos satellite system [54, 10], in which accuracy radius of the points are estimated based on the number of messages transmitted by the satellite. The points are then divided into seven classes, 3, 2, 1 and 0, representing an accuracy radius of each location of <150m, <350m, <1000m and >1000m, respectively, A and B for locations with error that cannot be estimated, having only three or two messages, and Z for points that fail in location processing. The data consist of 4.1, 10.2, 15.2, 14.0, 18.5, 28.8 and 9.1% of classes 3, 2, 1, 0, A, B and Z, respectively, resulting in nearly 70% of the points being categorized lower than “0” and, therefore, having no upper limit on the error estimate (Fig. 2.1). Points were transformed into Cartesian coordinates (x, y) with equations of Great circle distance, and average velocities V_{av} are calculated as,

$$V_{av} = \frac{\sqrt{\triangle x^2 + \triangle y^2}}{\triangle t} \tag{2.1}$$

where $\triangle t$ is a segment of time between two points. This velocity represents the magnitude of the turtle based on its displacement from point to point of the Argos data.

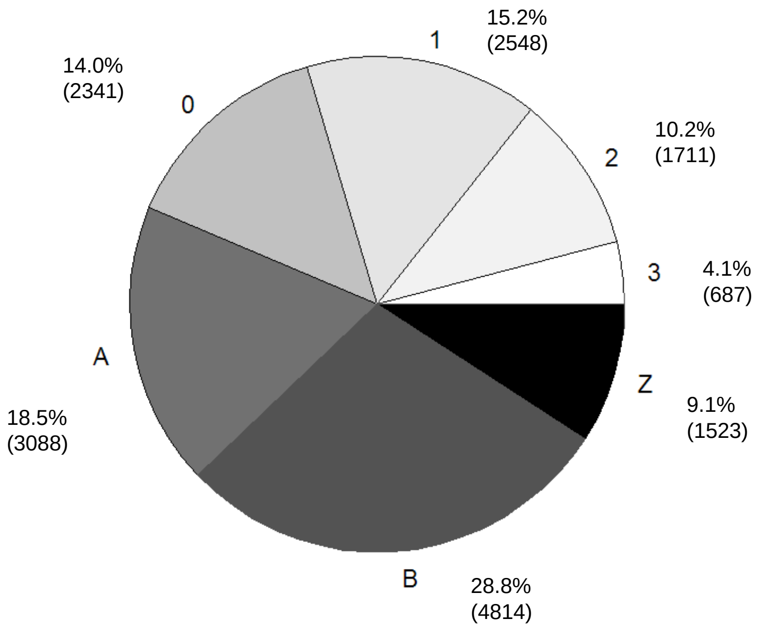

Figure 2.1: Pie chart of raw data categorized by classes (3,2,1,0,A,B,Z). Low classes account for over 70%.

2.2 Filtration method

Many past studies have introduced methods of data filtration and smoothing for noisy Argos data. The use of only high classed data points (e.g. [15, 6]) is most simple, but not appropriate when the majority of the points is low classed. Lately, more involved filtering processes have been introduced, resulting in better estimates for locations and presumably more reliable paths (e.g. [22, 47]). The method used in [47] (referred to as the “Polovina filter”) was applied to one individual, “Fujiko” (ID29976), to verify its effectiveness on the data quality seen in this study. This method considers selecting specific points mainly based on the Argos classes, and is explained as follows:

- In a single day, in which several transmissions are available, the point with the highest classification is used.
- When there are several points of the same class within that day, the point closest to noon is used (due to reasons of daylight visibility).
- When only one point is available during the entire day, that point is used.

The raw data of Fujiko's path are both sparse and dense in certain areas (Fig. 2.2) . The quality of the data is quite low, with 72.9% of the points being below "0" (Fig. 2.3). After the points were filtered by the above method, the obtained path became much smoother, containing only a ninth of the original points, with more distinctly visible loops near the coast. Although the method shows its reliability in terms of location (Fig. 2.4), V_{av} calculated from the smoothed locations showed heavy-tailed distributions with extremely high values (Fig. 2.5) and, therefore, unreasonable in the sense of turtle mobility in the water [34].

The poor outcome of this filtering method is thought to have occurred due to the simple removal of low classed points and the majority of the Fujiko's track being low classed. These points, despite being regarded as less accurate, still have the possibility of providing important information. However, this would depend on the surrounding points and the velocity that the individual displaces itself from that location to the next. Although the error estimates correspond to each point, a more dependable data filtering method would have to consider not only the point of concern relying solely on its error radius and its average velocity but also the relation with these

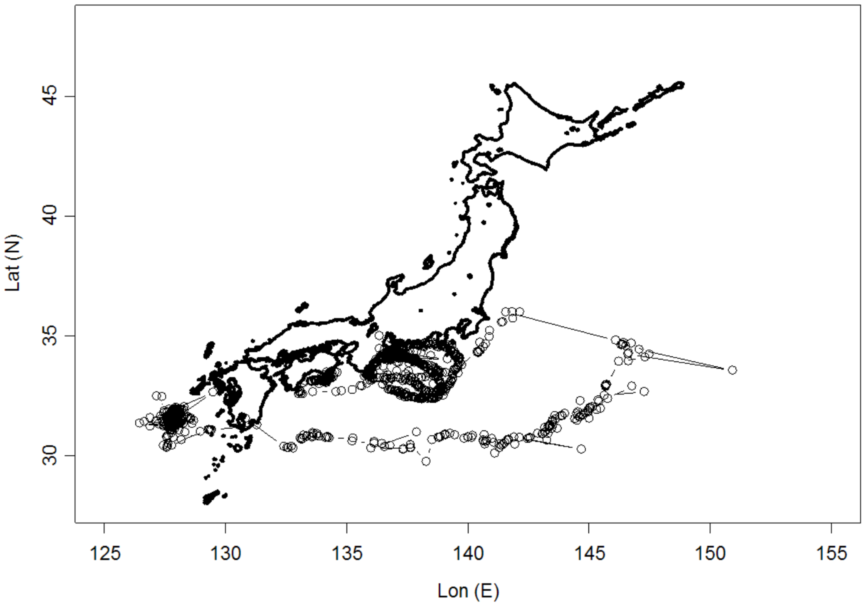

Figure 2.2: Raw data of Fujiko's track.

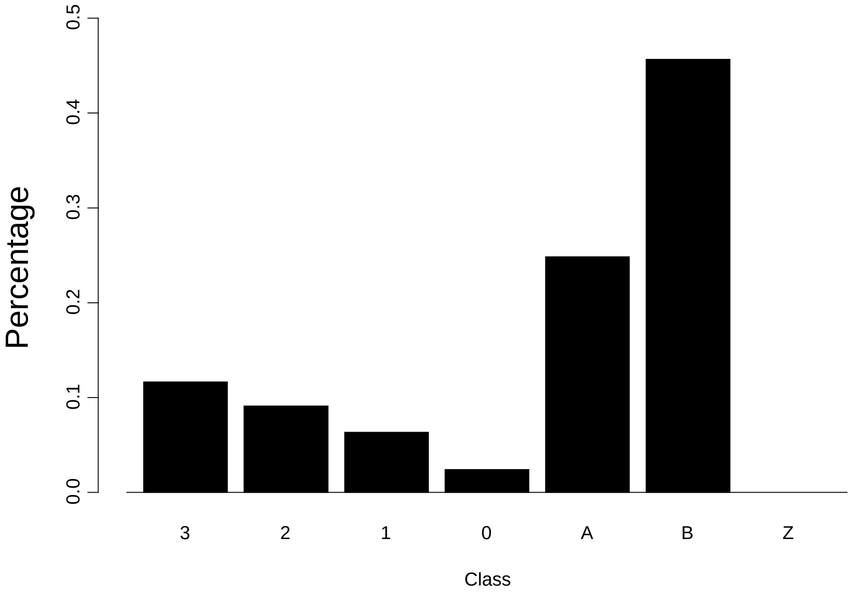

Figure 2.3: Histogram of Fujiko's location classifications.

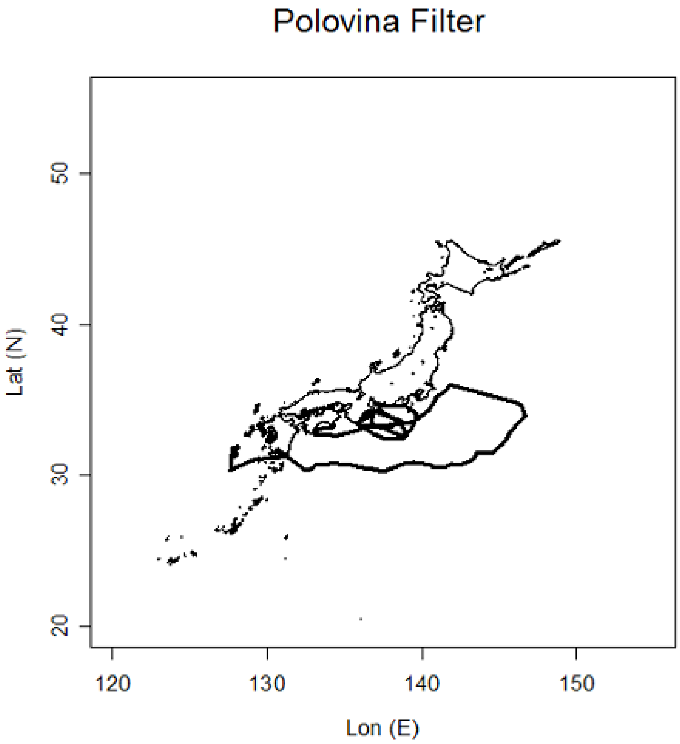

Figure 2.4: Fujiko's smoothed track based on Polovina's method.

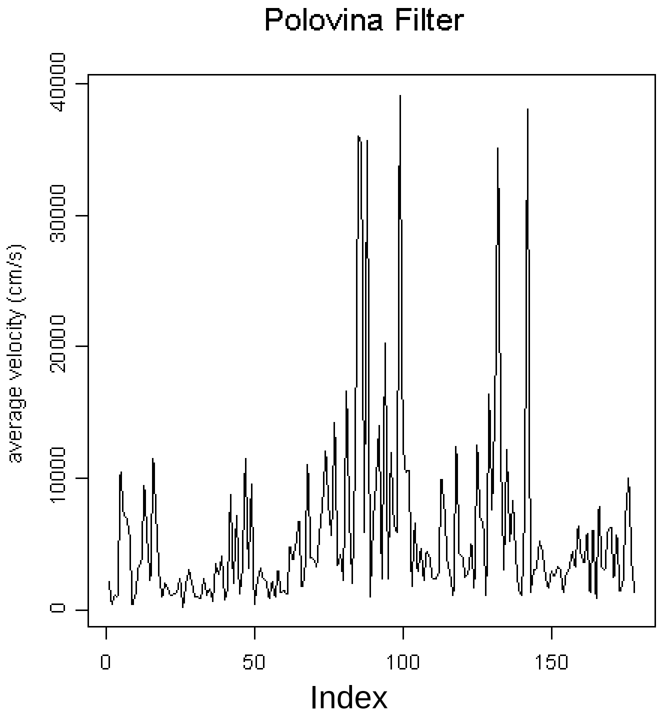

Figure 2.5: Fujiko's average velocity based on Polovina's method.

neighboring points. Hence, rather than simply removing a low classed data point, the verification of its surrounding points should be considered in the criteria for data filtration before estimating the most reliable point for a given day.

The need for an adaptable data filtering method is crucial when handling low quality data, since the use of redundant data could lead one to inaccurate results and false conclusions, however the removal of such data should not be overlooked. To improve on past filtration methods, we introduce a set of criteria consisting of three systematic steps focusing on not only the turtle's location but also its average velocity. The steps are detailed as follows:

- Step 1. Remove all points of class "Z" - error estimates cannot be estimated for data points classed as "Z" due to unpredictable accuracy.
- Step 2. Remove the latter point of two consecutive average velocities greater than 300 cm/s - sudden unrealistic movements occurring in the track are recognized and points are removed based on their distance with respect to neighboring points.
- Step 3. Take daily averages of time and location with the remaining points - minor movements within a day are not significant when dealing with overall behavior of the turtle. Furthermore, the error for each averaged point is lower compared to those of the original points.

The new set of points and recalculated average velocity values are shown in Figures 2.6 and 2.7. Comparing with the results from the previous method in [47], the filtered tracks are nearly identical, however V_{av} with

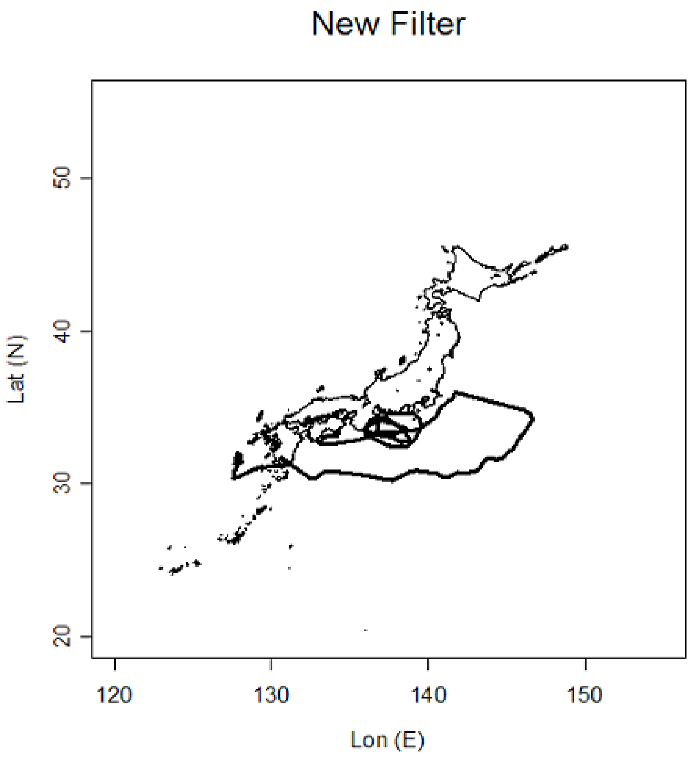

Figure 2.6: Fujiko's smoothed track based on the new method.

the new method are maintained at more realistic values and, thus, making this a trustful filtering method when handling low classed data. Therefore, data of all remaining individuals were filtered in the same manner (individual paths are shown in the Appendix). The distribution of average velocity for all individuals is skewed to the right, with mean 42 and standard deviation (SD) 33 cm/s, with a maximum of 236 cm/s (Fig. 2.8). The slightly high upper limit is thought to be caused by the effect of ocean currents, namely the Kuroshio, and other strong currents in the North Pacific.

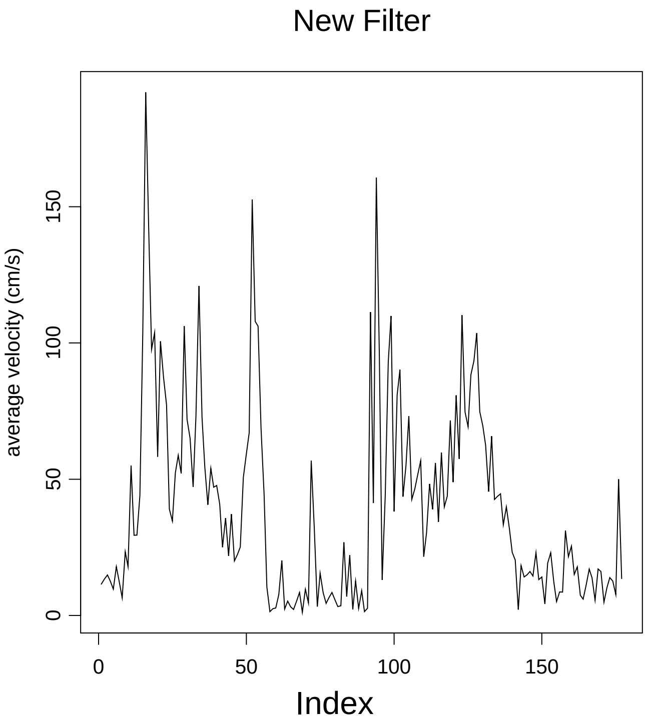

Figure 2.7: Fujiko's average velocity based on the new method.

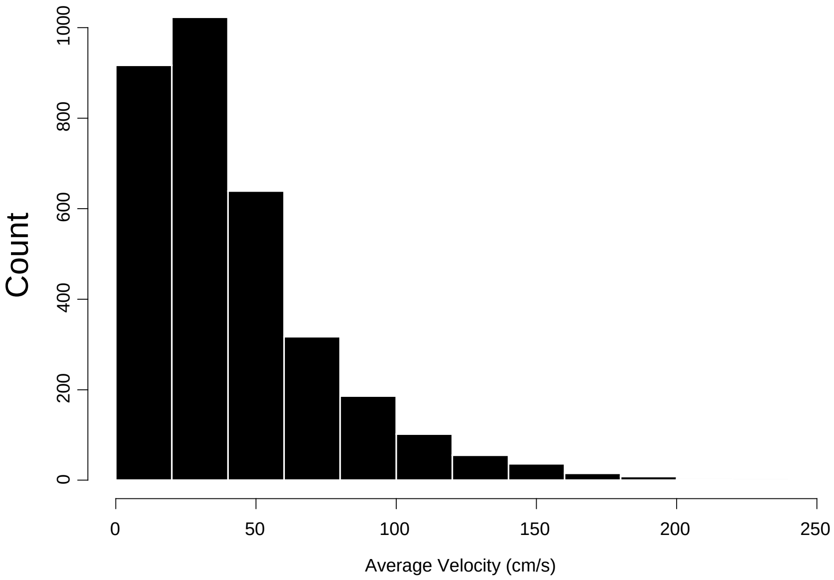

Figure 2.8: Average velocity for all 30 individuals after data filtration with the new method.

2.3 Oceanographic parameters and interpolation method

Several data sources have been used to investigate oceanographic parameters. This subsection will list and briefly explain the data used in this analysis, also with references provided for further details.

A) J-OFURO (Japanese Ocean Flux data sets with Use of Remote sensing Observations):
Altimeter data of surface dynamic topography and geostrophic velocity data fields calculated by optimally interpolated satellite data from TOPEX/Poseidon, Jason-1, ERS-1, ERS-2, and Envisat. Spatial resolution is at 0.25° with a 10-day cycle. Gridded data are available from October 8, 1992 to January 4, 2005. Details are in [31].

B) AVHRR (Advanced Very High Resolution Radiometer) Pathfinder Oceans:
Sea surface temperature data measured by AVHRR thermal imagery aboard the National Oceanic and Atmospheric Administration (NOAA) satellite, at 18km grids with a weekly cycle from August 29, 2001 to October 26, 2005. MODIS Aqua data (spatial resolution 9.26km, at 8-day cycles) were used to replace intervals with missing data.

C) WOA 2001 (World Ocean Atlas):
Climatological data consisting of temperature, salinity, dissolved inorganic nutrient concentrations, chlorophyll a and oxygen levels, objectively-analyzed

on grids of spatial resolution 1° covering the entire globe. Timescales are annual, seasonal or monthly, with 33 depth intervals from the surface to 5500m. For further details, refer to [5].

D) ETOPO5 (Earth Topography at 5 arc-minutes):
Topographical data including sea depth and land elevations at 5-minute grids covering the entire globe. They are described in [41].

To achieve optimal values for the above data (Z) in correspondence to filtered turtle locations (T) occurring at inter-grid points, the following interpolation method was carried out. Suppose a certain point is denoted by $Z_{i,j} \in R$, in which $(i, j) \in I$ are coordinates on an xy-plane. Let S be a set of four points $(Z_{i,j}, Z_{i+1,j}, Z_{i,j+1}, Z_{i+1,j+1})$, forming a square section within the plane. $T_{m,n}$ is a location at which a Z value is to be estimated, say Z_T. At any location $T_{m,n}$, estimation of Z_T depends on m and n in relation to S:

- If $(m, n) = (i, j)$, then $Z_T = Z_{i,j}$.

- If one coordinate is equal, say $m = i$, then $Z_T = \frac{Z_{i,j}+Z_{i,j+1}}{2}$.

- If $(m, n) \neq (i, j)$ but within S, Z_T is calculated by a geographic mean of S, i.e. Z values closer to (m, n) are weighted more heavily.

- If less than three points in S are missing, Z_T is calculated by a geographic mean of the available points.

- If all points in S are missing, Z_T is estimated by the average of the available points of the surrounding eight squares.

Chapter 3

Results and Discussions

3.1 Distribution

Turtle paths for all individuals showed temporal and spatial variability, but they could be categorized into three behavioral groups: 1) “Remaining” - those that do not swim out to the North Pacific staying near the coasts, 2) “Returning” - those that head out to the open ocean but migrate back to the coasts, and 3) “Departing” - those that do not migrate back and reside in far east regions until transmission ends (Figs. 3.1 to 3.3, respectively).

Seasonal distributions are shown for returning and departing turtles (remaining turtles were only tracked for short periods and, hence, they are not shown) based on longitude and latitude (Figs. 3.4 and 3.5, respectively). Calendar months were divided into the following four seasons: November to January, February to April, May to July, and August to October, corresponding to inactive, mating, mating/nesting, and nesting seasons, respectively. Returning turtles were mostly at longitudes west of 150°E throughout

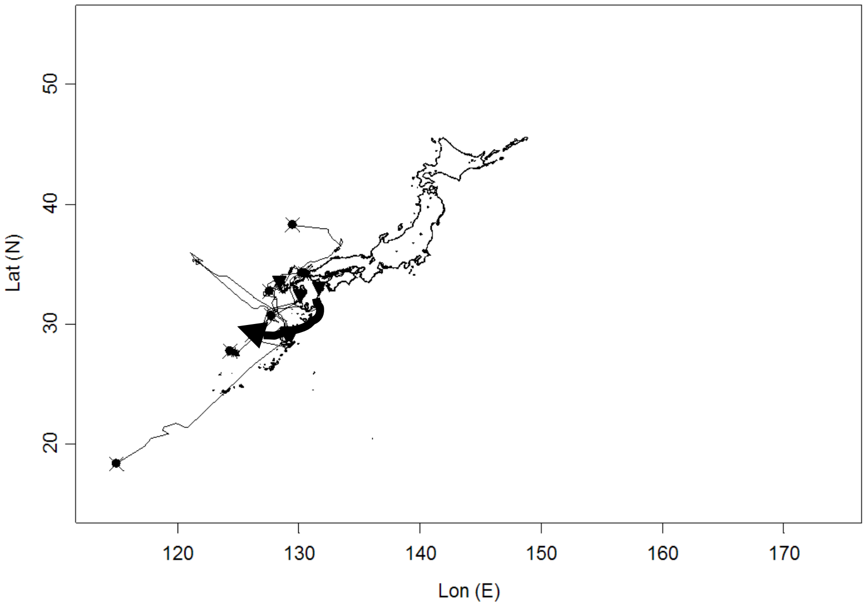

Figure 3.1: Tracks of "Remaining" turtles.

the year, with a positively skewed distribution, and were very densely located near the coast during peak mating season in early summer. During May-July, they were even more west, locating themselves closer to the coasts (Fig. 3.4, top row). Their latitude ranges became narrower from winter to fall, centering in on warm waters north of 30°N (Fig. 3.5, top row). Since all turtles do not reproduce every year [39], there were some individuals that showed completely different paths during these seasons. As for departing turtles, longitudes were far more spread out for all seasons, not showing much preference in coastal waters during mating and nesting seasons (Fig. 3.4, bottom row). However, a clear bimodal distribution was seen from February to April, with peaks at approximately 140°E and 160°E. The two peaks occurred at

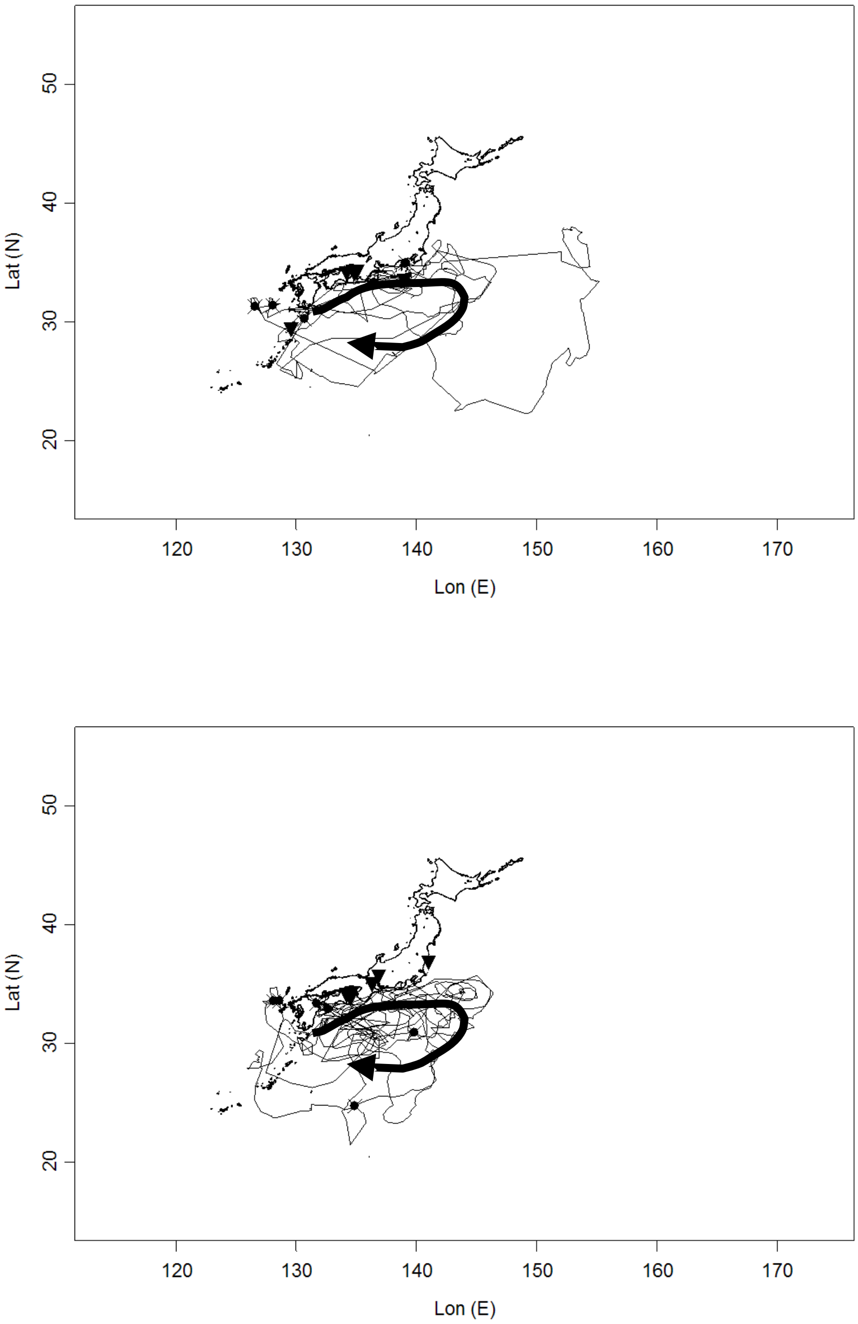

Figure 3.2: Tracks of “Returning” turtles.

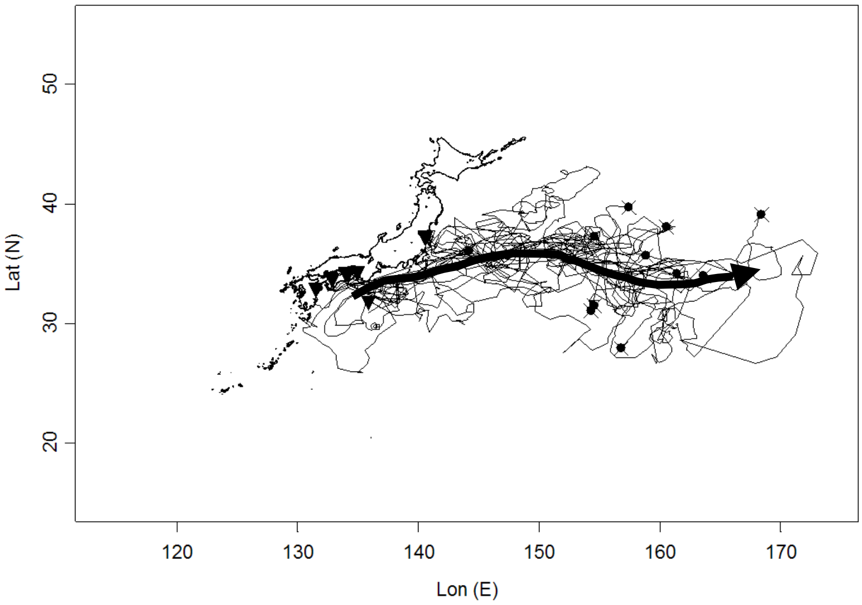

Figure 3.3: Tracks of "Departing" turtles.

locations, in which returning turtles were densely located and the edge of the Kuroshio extension bifurcation region [50]. Latitudinal ranges gradually shifted to the north from winter to fall, in which turtles eventually ended up in waters north of 30°N (Fig. 3.5, bottom row), much like the returning turtles. However, on average, departing turtles were found in regions further north compared to returning turtles (Wilcoxon rank-sum test (W-test): Z=19.90, $p<0.001$).

Two individuals, "Leo" (ID20822) and "Tomoyo" (ID20114), were head-started individuals, released at (32.60°N, 128.40°E) on September 15, 2002 and (30.89°N, 135.9°E) on July 31, 2003, and lasting a total of 44 and 493 days, respectively. The two individuals differed in transmission period and

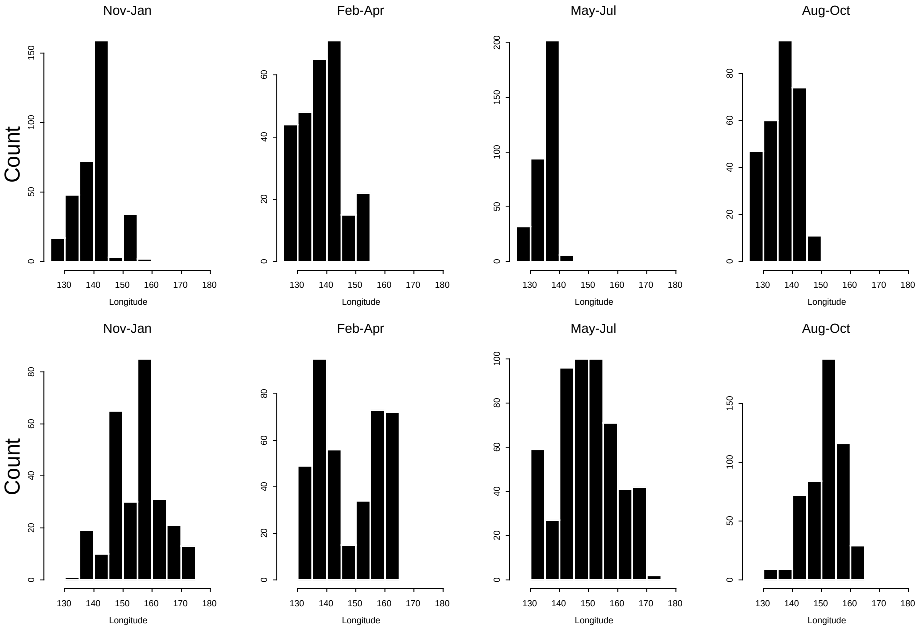

Figure 3.4: Seasonal distributions of longitude for returning (top) and departing (bottom) turtles.

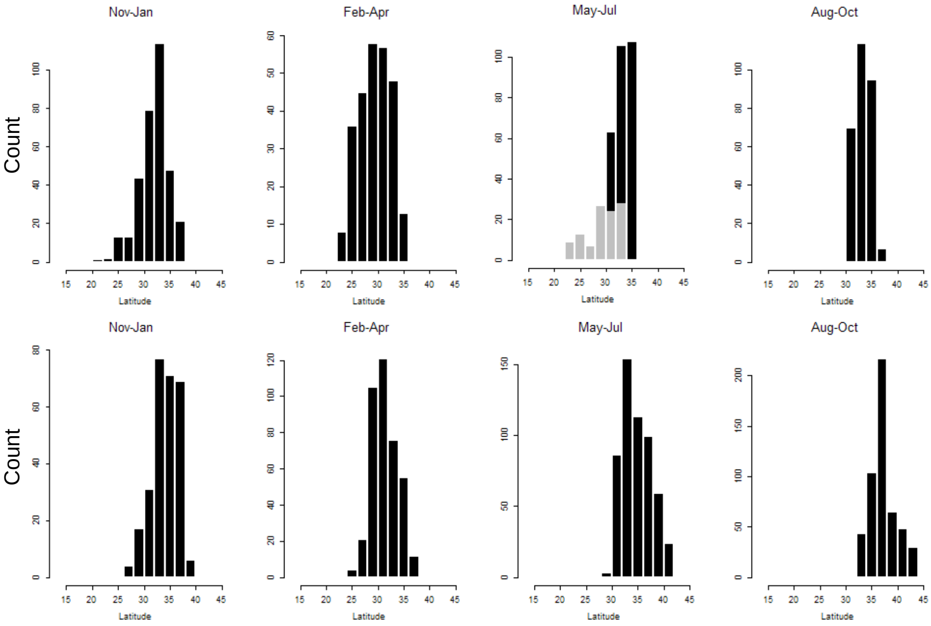

Figure 3.5: Same as Fig. 3.4 but for latitude. Gray bars indicate latitudes for Umira.

also total displacement distance and, thus, a comparison between the two was difficult. According to the two individuals' tracked paths (Figs. A.15 and A.26), they were categorized as remaining and departing turtles, respectively. Just after the release of Tomoyo, she remained in the northern branches of the Kuroshio current from around May to November, reaching latitudes as high as 43.15°N and in cold waters (mean 16.9, SD 2.7°C). Compared to all other individuals during the same months, Tomoyo was found roaming in much colder temperatures (W-test: $Z = -20.84$, $p<0.001$). After an extensive roaming period in these cold waters, she moved back south and close to the Kuroshio mainstream. Finally at the end of November, she headed out to the east similar to the other departing turtles, moving in the direction of the Kuroshio. This wandering stage could be an indication that headstarting can cause turtles to behave differently compared to those brought up in the wild.

In addition to distributional characteristics, differences based on body size were also of interest, as seen in [15]. Sex ratios (Female:Male:Unknown) for remaining, returning and departing turtles were 3:4:1, 6:2:3 and 7:1:3, with 95% confidence intervals for SCL of (814, 935), (763, 824), (688, 750) mm, respectively, each consisting of 8, 9 and 11 turtles (due to missing data). Significant differences were seen in all behaviors (Fig. 3.6, Tukey's comparison test for unequal sample sizes, $p<0.05$), with remaining, returning and departing turtles each greater in size compared to the next. This result was comparable to that by [15], in which body size differences were seen in turtles showing different paths, but also provided a statistically significant comparison due to a sufficiently sized sample for each behavior group. From this result, the pivotal range of SCLs was also calculated based on a logistic regression for which turtles show different behaviors, with 0 being individuals that do not stay in coastal regions (departing turtles) and 1 for those that mostly do (remaining and returning turtles). Figure 3.7 shows the resulting curve from the regression (deviance=18.19, df=1, $p<0.001$), with dashed lines representing the interquartile range intersecting with the regression curve, resulting in an estimate of the pivotal range of 725 to 783 mm. This range was reasonable in comparison to SCLs of loggerheads that have nested on the Japan coast being at least 741 mm [15].

Significant differences were seen concerning the three basic track patterns taken by the turtles. This leads one to the question of whether there is a reason for the differences and, hence, to further examine the data in relation to physical and chemical oceanographic parameters that characterize the environment of the turtle. Although turtles exhibit highly variable track patterns, there are however similarities within certain stages of the tracks. The next two sections will each be divided into subsections looking at different stages of the turtles' tracks.

3.2 Ocean currents

Adult loggerheads are known to make frequent submerges ranging from depths of 0 to 250 m, however most of their dives are between 0 and 25 m in oceanic and neritic regions [14]. Therefore, optimally interpolated altimeter data of surface dynamic topography (J-OFURO) were used to examine the effects of ocean currents on turtle behavior. Effects of wind in relation to

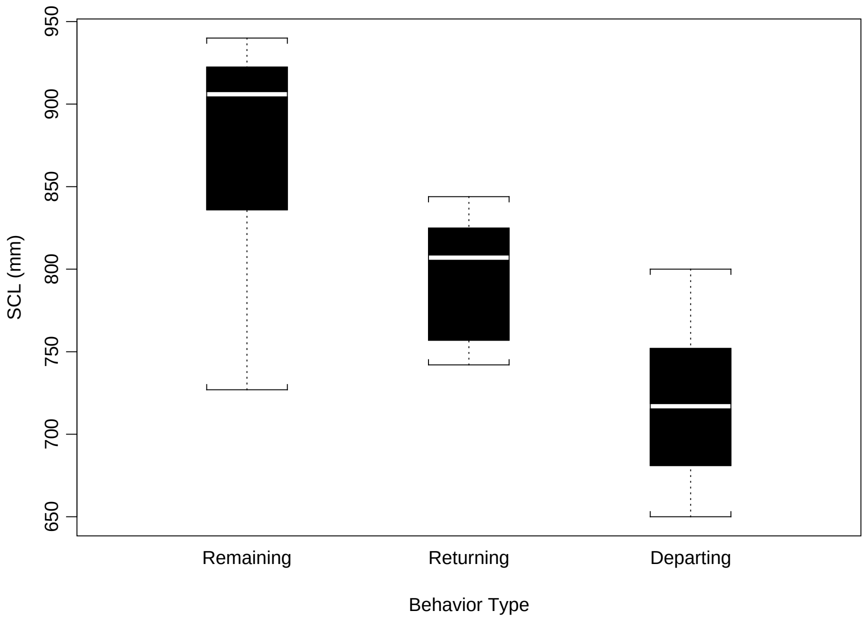

Figure 3.6: Boxplot of straight carapace length (SCL) for each behavior type. Significant differences between all types (Tukey's comparison test for unequal sample sizes, $p<0.05$).

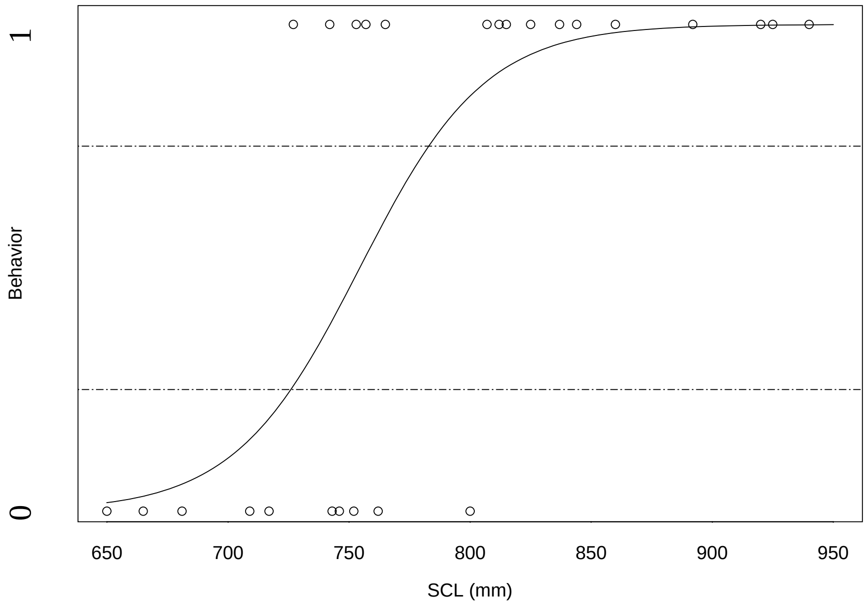

Figure 3.7: Logistic regression curve of turtle behavior (0=coastal, 1=open ocean) vs. SCL (deviance=18.19, df=1, $p<0.001$). Dashed lines indicate interquartile range based on predicted values corresponding to 725–783 mm.

Ekman transport, in which wind stress in combination with the Coriolis force moves water to the right of the wind's direction [48], were not considered in the calculation of geostrophic current velocity. Since wind forces become weaker as depth increases, loggerheads swimming in subsurface waters are considered not to be affected by the wind when making their displacements. Fifteen turtles (indicated by asterisks in Table A.1) were considered, eight of which were categorized as returning turtles and seven as departing turtles. The remaining turtles were not considered in the analysis because of tracks covering only a short period of time, making displacements that were too small or too sparse. The J-OFURO database covers dates up to January 2005 and, hence, data collected for individuals after this date were also not included in this analysis.

3.2.1 Initial stage

After turtles were released into the ocean with their transmitters attached, most of them were found roaming near the coasts, making small scale movements. This sort of behavior can be expected just after release, since they could either be wandering around investigating the environment of the release point (especially if it is different from the captured location and/or a fair amount of time had passed since its capture), or hunting for prey at the sea floor in the shallow depths of the coastal region. In any case, these movements were not of major interest when dealing with the overall behavior extending over a wider scale both temporally and spatially. Therefore, the "initial stage" focused on the moment just after turtles had headed out of

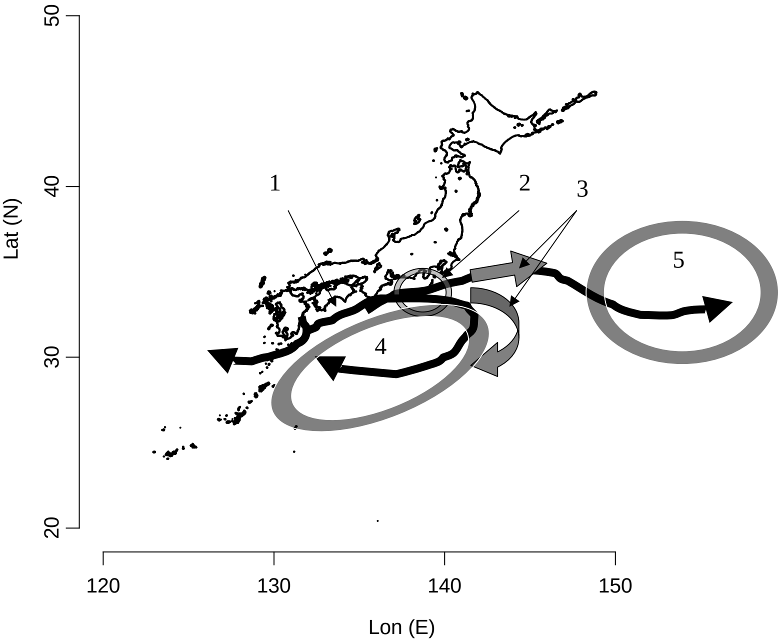

Figure 3.8: Generalized turtle tracks (black bold arrows) with regions of 1) initial, 2) roaming, 3) behavior-deciding, 4) returning and 5) departing stages indicated accordingly with lighter shaded arrows and circles.

waters deeper than 200 m until the moment in which they were subject to decide on whether they should head back to the coast or further east (Fig. 3.8).

Average velocities, V_{av}, in the initial stage are plotted in Figure 3.9 for both returning and departing turtles, in which nearly 70% of the points were in the eastern direction and in the higher magnitudes. This was expected due to the effects of the Kuroshio current having a strong impact on the overall displacement of the turtles in these areas. In Figure 3.10, current velocity magnitudes, $|V_c|$, calculated for locations at which returning and departing turtles were present show different distributions (Kolmogorov-Smirnov test

(KS-test): KS=0.211, $p<0.01$), however there was no significant difference in median values (W-test: Z=0.786, $p>0.1$). The high values of V_c indicated that turtles were present near the Kuroshio current's mainstream and at times close to the center where velocities were the fastest. Horizontal and vertical components of V_c, $(u, v)_c$, plotted in polar coordinates show the magnitude and direction of the currents at each location (Fig. 3.11). Returning and departing turtles were swimming in currents directed eastward 77 and 86% of the time, respectively. Significant differences were not seen in both components between the two behaviors (KS-test: KS=0.158 and 0.153, $p>0.05$, respectively), and because of these percentages being high, similar to those of V_{av}, it implies that, in the initial stage, all turtles were present in strong currents. However, when $(u, v)_c$ are plotted by season (Fig. 3.12), there was an imbalance in the number of points depending on the season, even though both returning and departing turtles were released in similar seasons (Table A.1). This is an indication that returning turtles were in the fast Kuroshio currents less often during spring, which can be expected if they were to be active during mating season.

Since turtles were constantly in a moving environment and located near the Kuroshio's mainstream, V_{av}, which was calculated from the filtered Argos data locations, would be better thought as a composite of the turtle's actual movement within the water and the effects of the ocean current. The actual velocity mentioned here is referred to as the relative velocity (V_{rel}) of the turtle in reference to the current, and was calculated by the following,

$$V_{rel} = V_{av} - V_c, \tag{3.1}$$

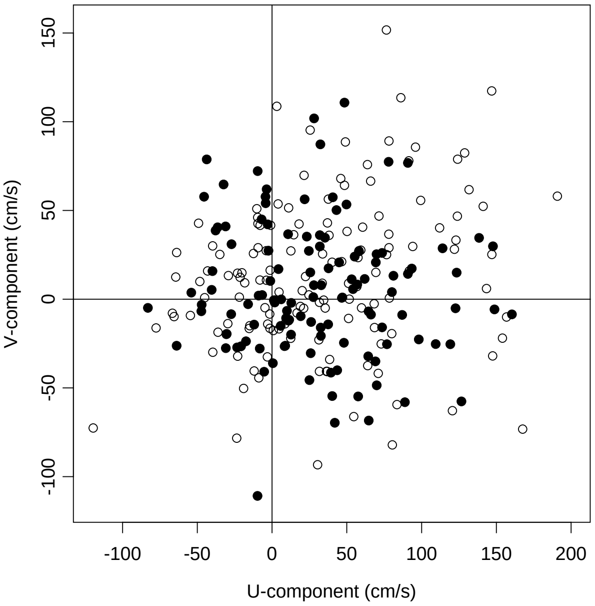

Figure 3.9: Average velocity of departing (white) and returning (black) turtles at initial stage.

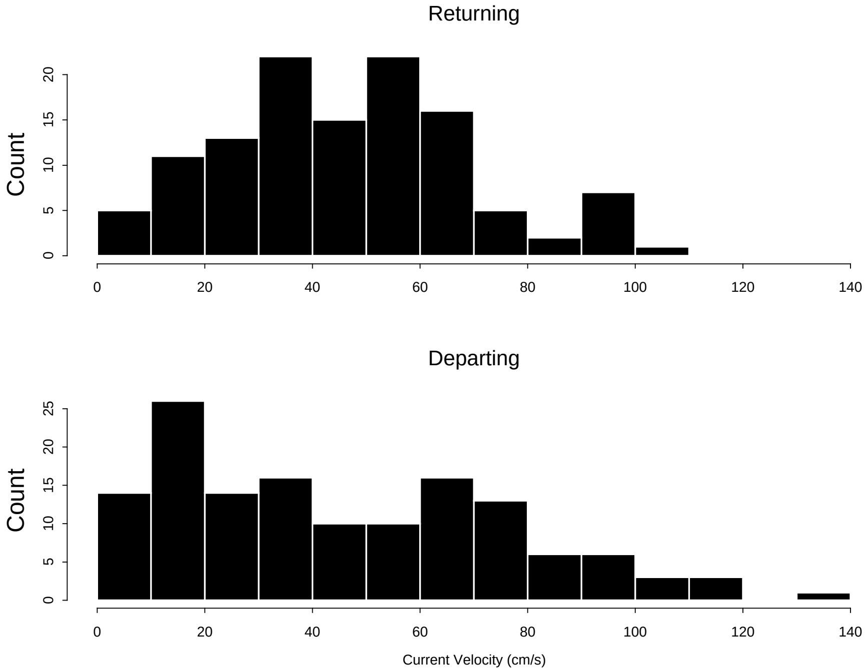

Figure 3.10: Histogram of current velocity magnitude for returning and departing turtles during the initial stage of the track with significant difference between behaviors (KS-test: KS=0.211, p<0.01).

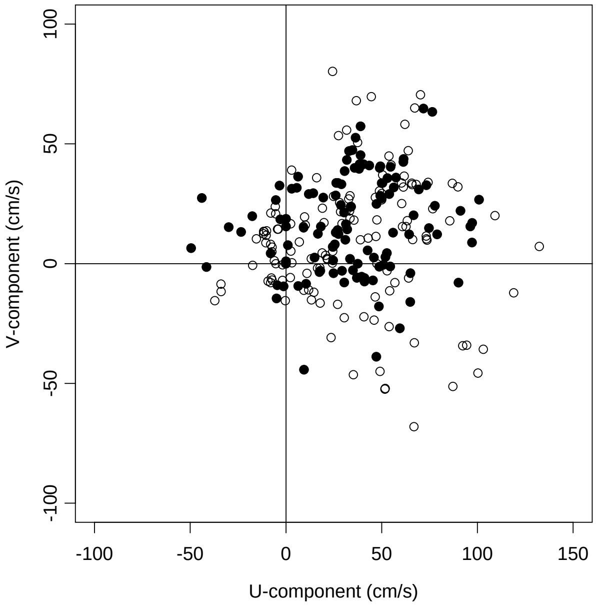

Figure 3.11: Current velocity in polar coordinates for returning (black circles) and departing (open circles) turtles during the initial stage of the track. Both u- and v-components were not significantly different between behaviors (KS=0.1575 and 0.1525, respectively, p>0.05).

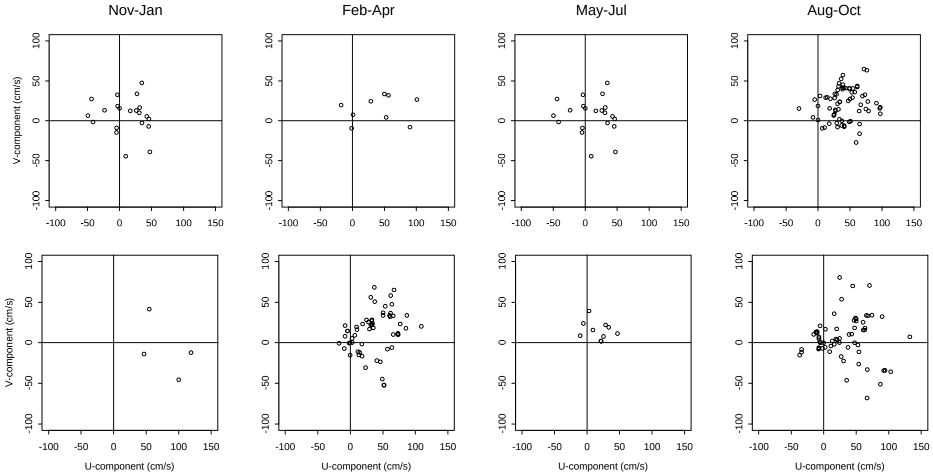

Figure 3.12: Current velocity in polar coordinates plotted by season for returning (top row) and departing (bottom row) turtles during the initial stage of the track.

in which V_{av} and V_c are vectors with u- and v-components. This is comparable to the calculation in [11]. Mean±SD values for V_{av}, V_c and V_{rel} are 46.7±37.6, 28.7±22.8 and 41.2±29.9 cm/s, with ranges of (0.201 262),(0.211, 133) and (0.137, 200) cm/s, respectively. Figure 3.13 shows the distributions of V_{rel} magnitude for returning and departing turtles. Upper limit values for V_{rel} for both turtles were smaller than those of V_{av} and there were no significant differences between returning and departing turtles for either V_{av} or V_{rel}, as well as within returning turtles between V_{av} and V_{rel} (all KS- and W-tests had p>0.1). However for departing turtles, V_{av} and V_{rel} were different (KS-test: KS=0.1739, p<0.05; W-test: Z=2.611, p<0.01) with medians of 54.21 and 45.51 cm/s, respectively.

Smaller V_{rel} could mean that the turtles depended on the current's force in order to assist their movement and lower energy consumption, however this was not necessarily true in all instances, since the direction of the current was a key factor in deciding whether the currents had a positive or negative influence on the turtles. Hence, to clarify this issue, u- and v-components of V_{rel} were again plotted in polar coordinates, but rotated at angles with current velocity, α, i.e. making the x-axis to point in the direction of the current at all times. Figure 3.14 shows $V_{rel,\alpha}$ for both returning and departing turtles, forming a circular cluster of points at the center. This indicates that turtles were moving in a variety of directions within the current, however significant differences were only seen when comparing the u-component of $V_{rel,\alpha}$ between returning and departing turtles (KS-test: KS=0.1748, p<0.05), with returning turtles swimming opposite of direction of the current more often than those departing (W-test: Z = -1.954, p<0.05, median = -8.190 and 3.343

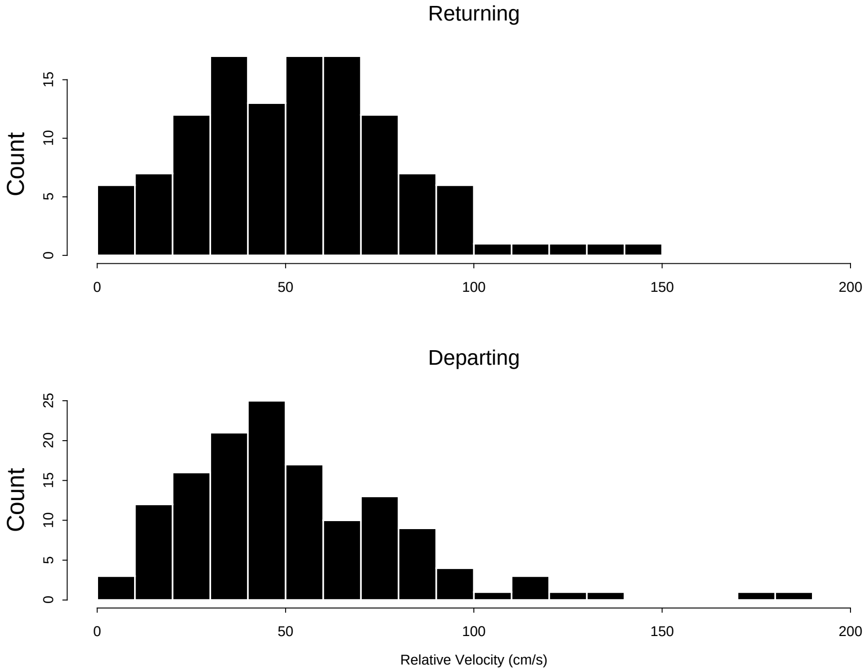

Figure 3.13: Relative velocity magnitude for returning and departing turtles during the initial stage of the track. No significant difference in distributions between behaviors (KS-test: KS=0.1042, p>0.1).

cm/s, respectively). It is also interesting to note that, although rare, the highest V_{rel} moments occurred in directions exactly opposite and perpendicular to the direction of the current. Furthermore, seasonal plots of $V_{rel,\alpha}$ indicated that the returning turtles were swimming in the opposite direction of the currents more often in August to October (Fig. 3.15).

Although there were some differences in relation to relative velocity between returning and departing turtles, it can be said that the currents played an important role in turtle movement in the initial stage near coastal regions. This can also relate to many of the tracks being shaped very similar to the Kuroshio current's mainstream.

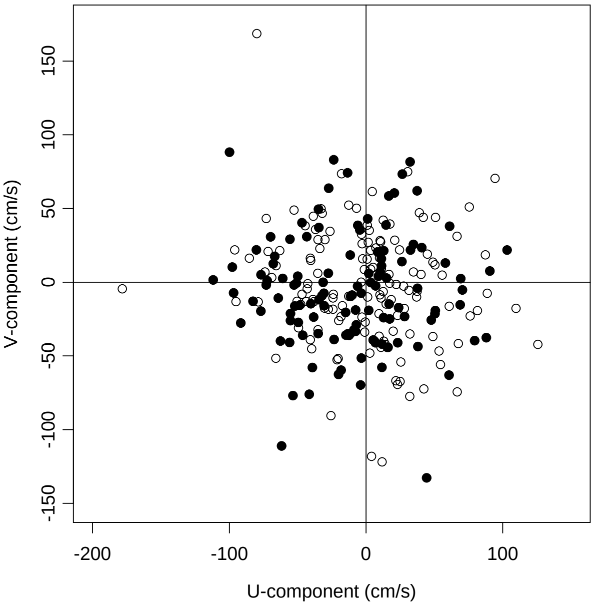

Figure 3.14: Relative velocity plotted at angles with current velocity for returning (black) and departing (white) turtles during the initial stage of the track. Significant difference was seen in u-components between behaviors (KS-test: KS=0.1748, p<0.05, W-test: Z = -1.954, p<0.05).

3.2.2 Roaming stage

During a turtle's track, there were many instances in which the turtle was found making circular movements or roaming in a similar location, whether it be near the coast or in the open ocean. However after the initial stage, all returning and departing turtles exhibited these movements just before heading south or farther east, at which they were divided into their respective behavior categories (Fig. 3.8). Further investigation of these instances was carried out in order to describe these regions.

Figure 3.16 shows an example of one turtle ("Midori", ID16090) exhibit-

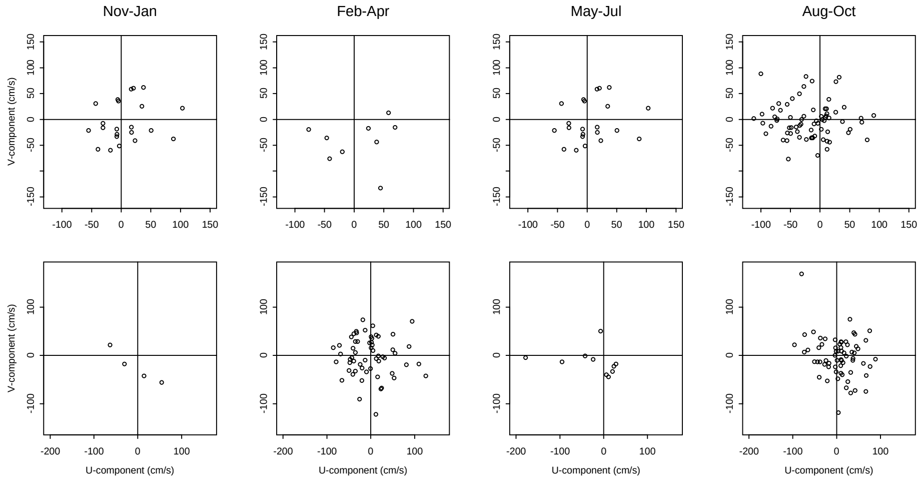

Figure 3.15: Relative velocity plotted at angles with current velocity for returning and departing turtles during the initial stage of the track by season. Significant differences were seen in v-component during Feb-Apr and u-component during Aug-Oct (KS-test: KS=0.561 and 0.313, $p<0.01$).

ing a circular counterclockwise path at longitudes between 150 and 160°E from November 8 to December 22, 2002, before making her southward motion and eventual return to the coast. The location of the circling path coincided well with the complex currents of the meandering Kuroshio caused by the Shatsky Rise [29]. This can be examined in more detail with the geostrophic currents supplied by J-OFURO. An up-close view of the roaming path superimposed with the current velocity vectors (rescaled to km/day and appropriately resized according to Great circle distance) at each location showed that the path was indeed in the direction of the current during the entire course of the loop (Fig. 3.17).

Focusing on the north end of the loop, points were most dense with weaker currents. The availability of prey within this region can be of concern, looking at levels of nutrients or chlorophyll a. Since this segment of the track only covered a little over a month, climatological data, even with interpolation, could not supply reasonable estimates for these points. However, near the Kuroshio in winter, sea surface temperatures (SSTs) and chlorophyll a levels are negatively correlated [59]. Therefore, with the use of the weekly SST data, weekly chlorophyll a levels could be estimated accurately (Fig. 3.18, Spearman's rank correlation ρ = -0.848, Z = -4.57, $p<0.001$), and superimposed onto Midori's looping path (Fig. 3.19). The points gathered densely at the northern part of the loop were estimated to contain high levels of chlorophyll a; thus increasing amounts of potential prey for the turtle within this region.

Furthermore, since turtle locations are estimated by daily averages and current velocity in Fig. 3.17 is in units of km/day, a segment connecting two consecutive points and the current velocity vector pointing from the first point are comparable by length and direction and, therefore, allows one to also picture daily averaged relative velocity at each location. With this in mind, it can be said that Midori was relatively moving inward as she headed to northern regions during the initial part of the loop but outward as she made her way south. The anticyclonic eddy in which she was present contains cold nutrient-rich waters from the northern side of the Kuroshio. Hence, this suggests that she may have initially been heading towards prey and/or drifted by the eddy currents, entering a nutrient-rich region and, thus,

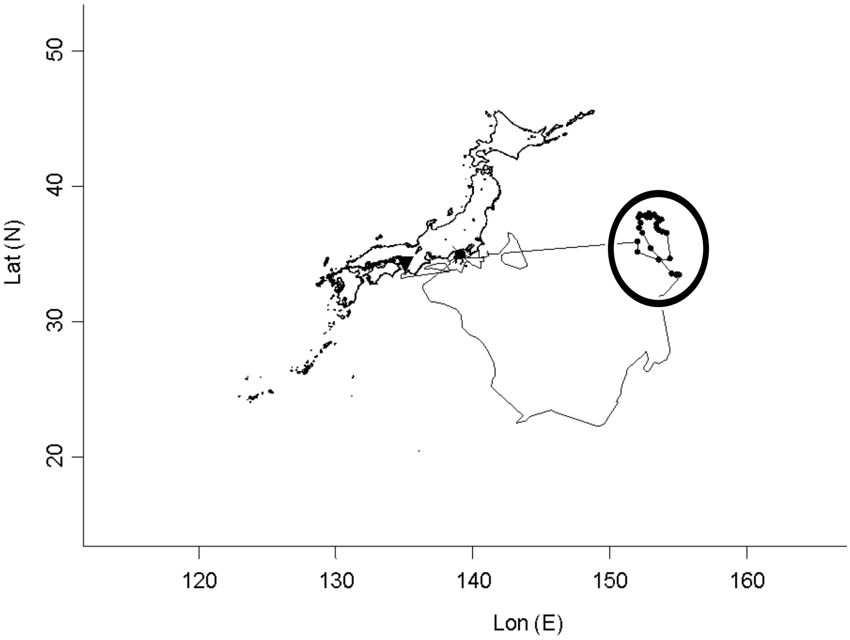

Figure 3.16: Track of Midori, leaving coastal region and roaming counter-clockwise from Nov. 8 to Dec. 22, 2002, before heading south and returning to Japan.

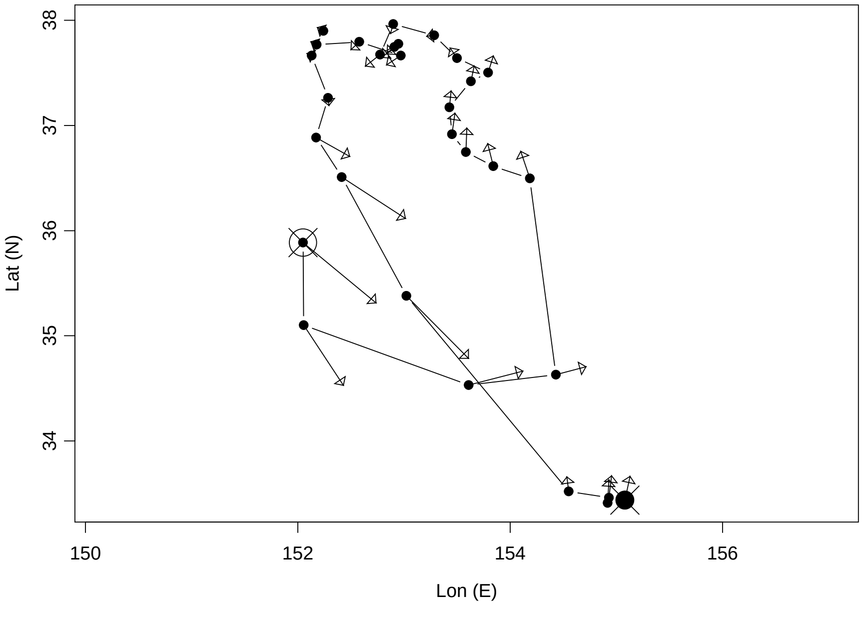

Figure 3.17: Vector plot of current velocity superimposed on the roaming stage of Midori's track. White circle indicates start of the loop. Length of arrows correspond to magnitude of velocity and re-scaled at km/day.

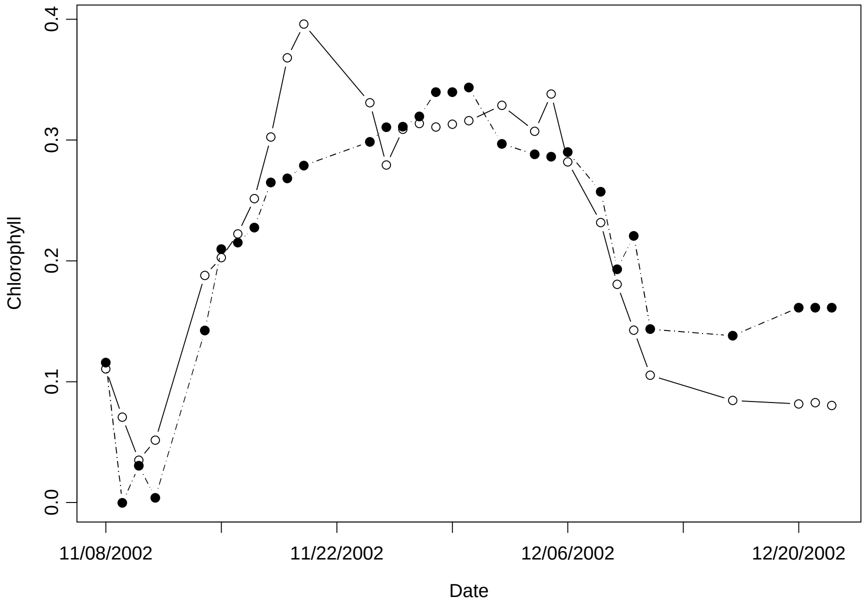

Figure 3.18: Time series of chlorophyll a concentration from seasonal climatology averages (white) and predicted values from weekly SST (black). Significant high correlation is seen between the two (Spearman's rank correlation: ρ = -0.848, Z = -4.57, p<0.001).

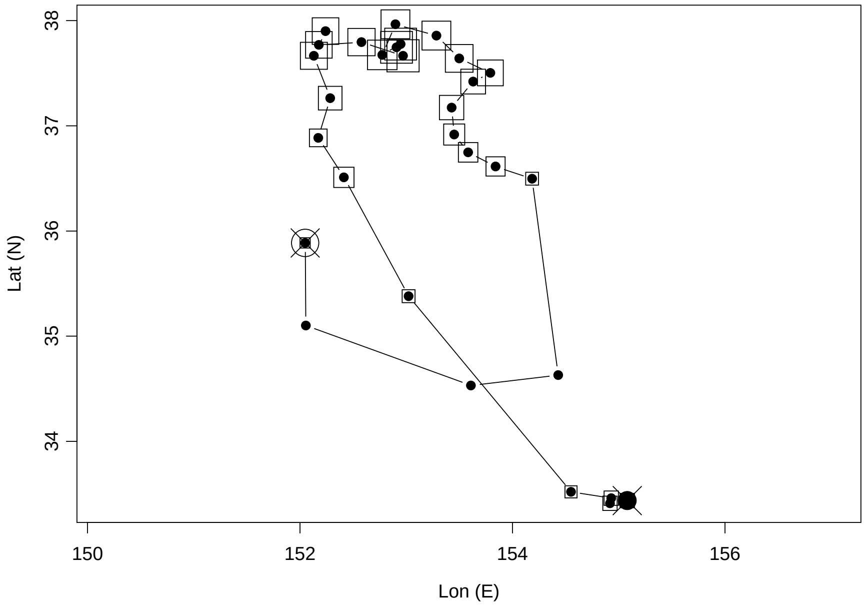

Figure 3.19: Predicted chlorophyll a concentrations superimposed on track of Midori's roaming location. White circle indicates start of the loop. Larger squares correspond to relatively higher amounts of chlorophyll a.

could have a high probability of confronting plenty of prey, which was also drifted by the current, such as jellyfish and larvae.

Near the end of the roaming stage, she initiated her distant displacement southward, in which the currents were relatively stronger. Compared to all other returning turtles, Midori's turn back to the coast was farthest to the east. However, Midori's track contains missing data from (142.3°E, 35.1°N) to (152.0°E, 35.9°N), which lasted nearly 20 days. During this time, within the longitudinal range of her missing segment, the Kuroshio mainstream was at latitudes ranging from 33.5 to 36.0°N, with very little meandering currents (not shown). There is a chance that she was on or north of the mainstream and, thus, not accessible to the Kuroshio countercurrent or the anticyclonic eddies until later on in her track.

Other turtles made looping and roaming patterns during their track just before heading either south or farther east (four examples in Fig. 3.20 a) Umira, ID28938, b) Sagi, ID29060, c) Sanae, ID16089 and d) Yasuko, ID28409), in which current velocity seemed to have an effect on the turtles' paths. However, this was seen only for these specific individuals and, thus, it cannot be clarified whether all roaming turtles had been making use of the current's force or if they were just being drifted. A similar relationship between SST and chlorophyll a was not seen in all cases due to segments taking place during non-winter seasons, but in any case, the current had an influence on the circular paths taken.

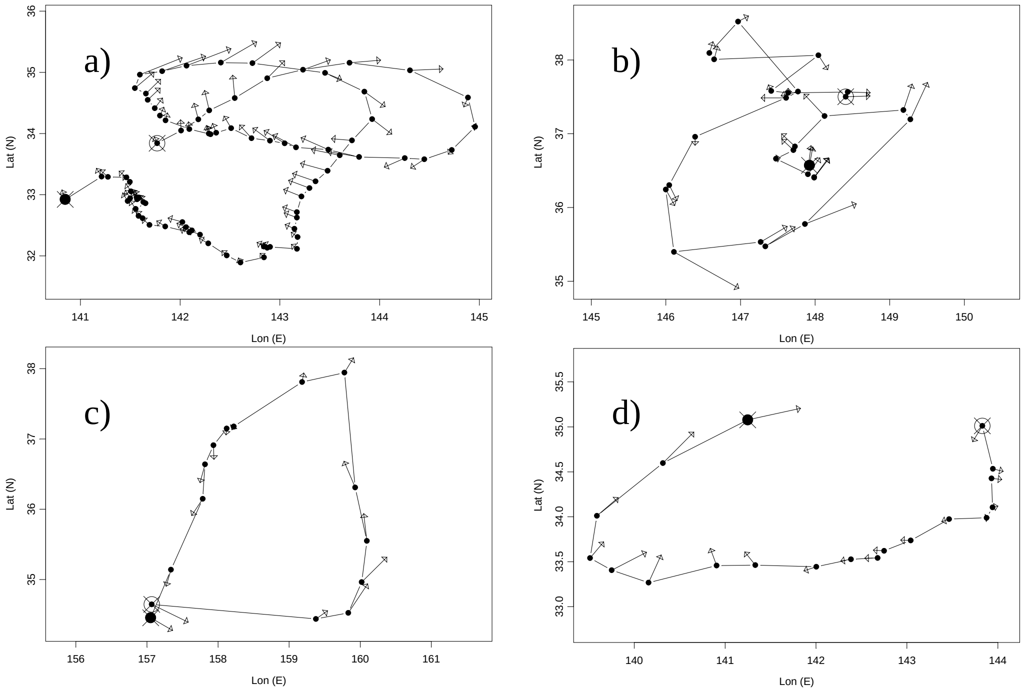

Figure 3.20: Same as Fig. 3.17 but for a) Umira, b) Sagi, c) Sanae and d) Yasuko.

3.2.3 Behavior-deciding stage

The "behavior-deciding stage" was considered as the most critical moment during the turtle tracks, in which turtles either headed south to return to the coast or further east into regions beyond the Kuroshio extension bifurcation region. This stage is just after the roaming stage, at which turtles initiated distinct movements toward their resulting destination until they reached another location in which they roamed again (Fig. 3.8). Comparisons were again made between returning and departing turtles.

Similar to the initial stage explained previously, average, current and relative velocities were examined. Figure 3.21 shows distinct differences in average velocity magnitude and u- and v-components, being faster and more widely ranged for departing turtles. This was thought to be affected by the magnitudes of current velocity at which the turtles were present, similar to the initial stage, being remarkably faster for departing turtles (Fig. 3.22), pointing mostly in the direction of the turtles' displacements (Fig. 3.23).

However, another difference was seen between latitudinal distributions of the two behaviors (Fig. 3.24), in which returning turtles were in lower latitudes than those departing (W-test: $Z=-9.352$, $p<0.001$). The pattern of meandering currents near the Kuroshio extension is variable, which causes the Kuroshio mainstream to alter in latitude [51]. Therefore, during the behavior-deciding stage, comparisons were made between latitude values of the Kuroshio mainstream (based on J-OFURO) and those of returning and departing turtles. Firstly, returning turtles were found to be south of the Kuroshio mainstream (Welch modified two-sample t-test: $t=-5.80$, $df = 17.62$, $p<0.001$). However, for departing turtles, there was no significant difference in latitude values with those of the mainstream ($t = 0.89$, $df = 17.19$, $p>0.3$). This suggests that the returning turtles had easier access to the Kuroshio countercurrent and cold rings south of the Kuroshio [57] than those departing. It cannot be concluded whether the returning turtles intentionally located themselves in such regions, however this latitudinal difference may be an important factor relating to the path of the turtles heading back to the coast.

Relative velocity magnitudes for the two behaviors were significantly different as well (Fig. 3.25, KS-test: $KS=0.361$, $p<0.001$), however component-

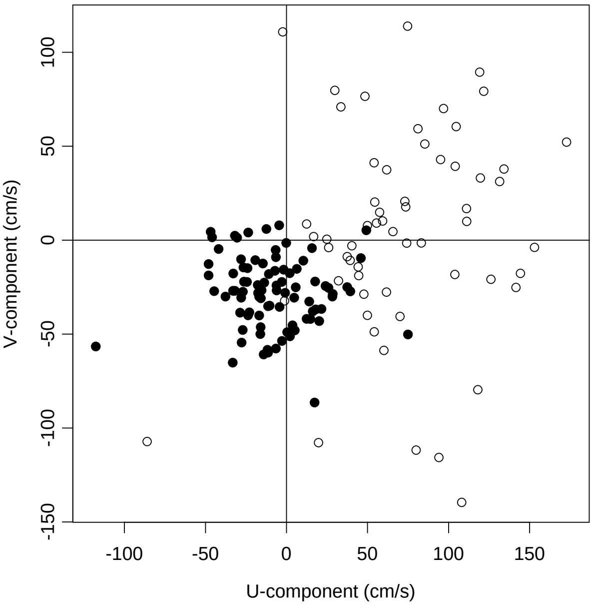

Figure 3.21: Average velocity in polar coordinates at the behavior-deciding stage, with significant differences between returning (black) and departing (white) turtles (KS-test: KS=0.721, p<0.001).

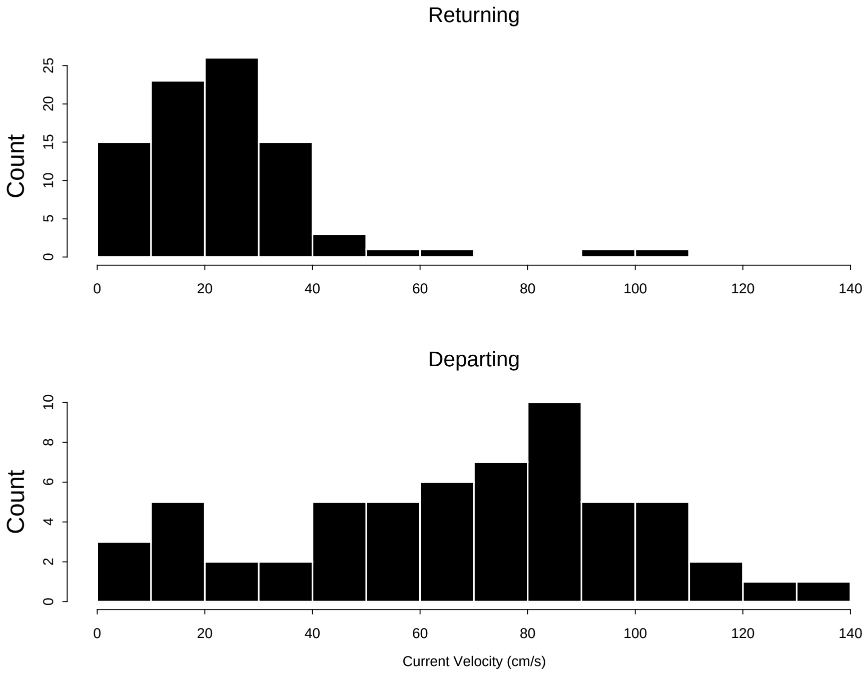

Figure 3.22: Current velocity for returning (top) and departing (bottom) turtles at the behavior-deciding stage. Significant difference was seen between the two behaviors (KS-test: KS=0.727, p<0.001), with departing turtles being in faster currents than those returning.

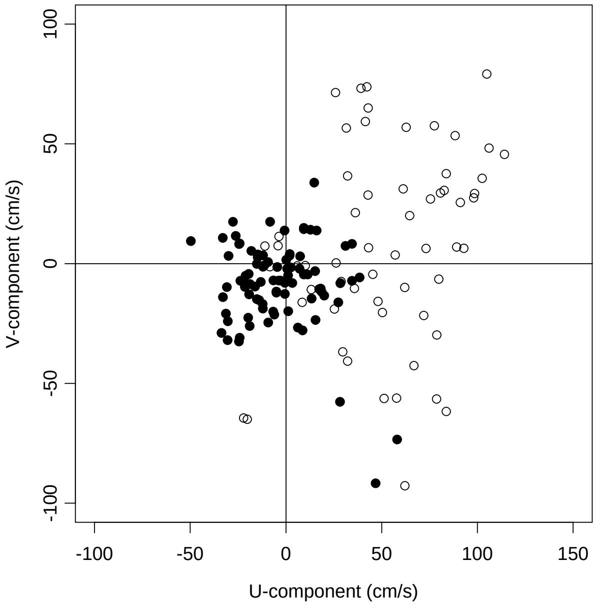

Figure 3.23: Current velocity in polar coordinates for returning (black) and departing (open) turtles at the behavior-deciding stage. Significant differences were seen between both u- and u-components (KS-test: KS=0.726 and 0.412; p<0.001).

wise in reference to α (Fig. 3.26), they were only different in the u-component (KS=0.331, p<0.001) with median=-5.34 cm/s (compared to that of departing turtles being 13.2 cm/s, W-test: Z=-2.87, p<0.005), indicating that returning turtles were relatively swimming more often in opposite directions of the current, similar to the initial stage. The lack of a significant difference in the v-component showed that both returning and departing turtles had been slightly on the warmer side of the current (medians are -2.28 and -1.63 cm/s, respectively). Figure 3.27 shows seasonal plots of $V_{rel,\alpha}$ with no significant differences in both components between returning and departing turtles (possibly due to the imbalance of the number of points).

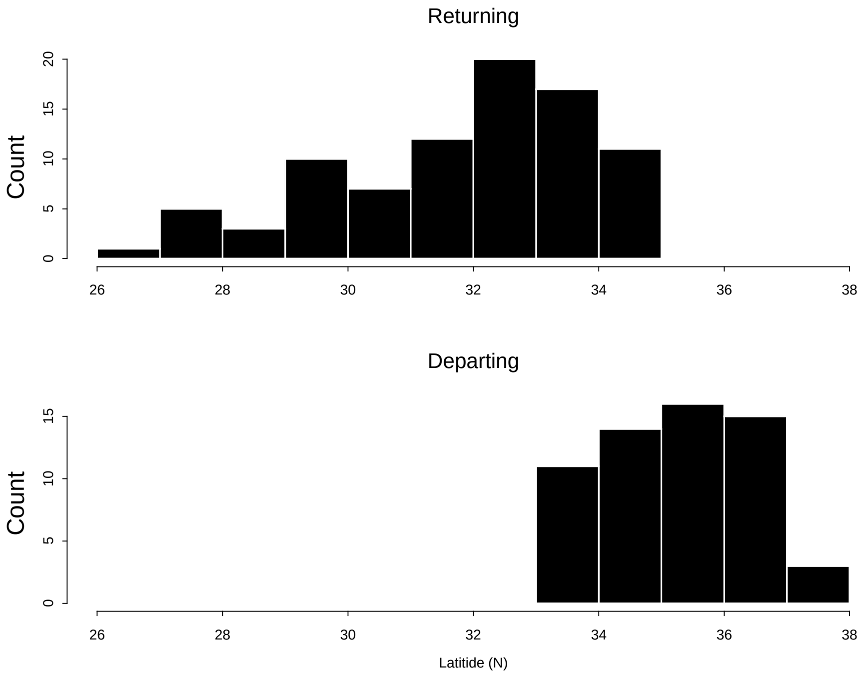

Figure 3.24: Latitudes for returning (top) and departing (bottom) turtles at the behavior-deciding stage. A significant difference was seen between the two behaviors (KS-test: KS=0.7873, p<0.001), with departing turtles being at higher latitudes in the mainstream and returning turtles south of the mainstream, more in the Kuroshio recirculation (W-test: Z=-9.352, p<0.001).

However to get a better glimpse of what might have been going on within each season, percentages on current ($V_{rel,\alpha}$ falling between $|\alpha| < \frac{\pi}{4}$) and those in colder regions ($0 < \alpha < \pi$) were examined. In Table 3.1, it can be verified that departing turtles were relatively on the current more often in every season than those returning, while both turtles in winter months were relatively swimming more on warmer sides of the current.

Since this stage was designed to involve the critical moment, differences characterizing the ocean currents of the two behaviors were easily recognizable, as expected, but surprisingly, differences in relative velocity magnitude

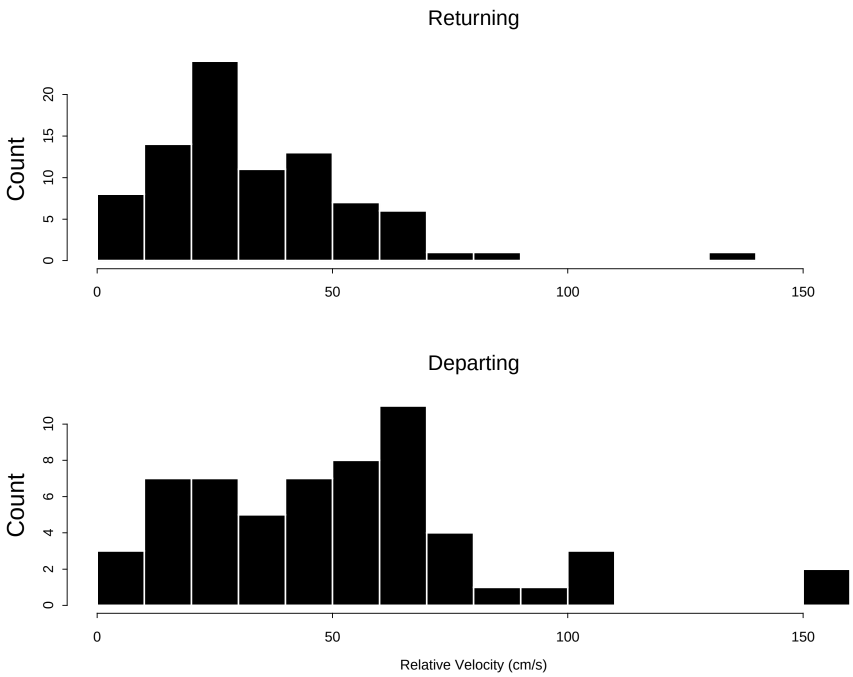

Figure 3.25: Relative velocity for returning and departing turtles at the behavior-deciding stage. Significant difference was found between the two behaviors (KS=0.361, p<0.001).

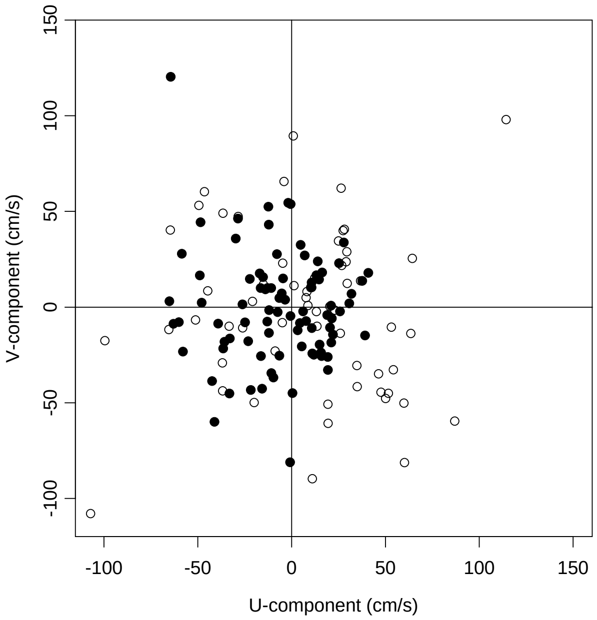

Figure 3.26: Relative velocity plotted at angles with current velocity for returning (black) and departing (white) turtles at the behavior-deciding stage. Significant differences were seen for u-components (KS=0.331, p<0.001), but no difference in v-components (KS=0.172, p>0.1).

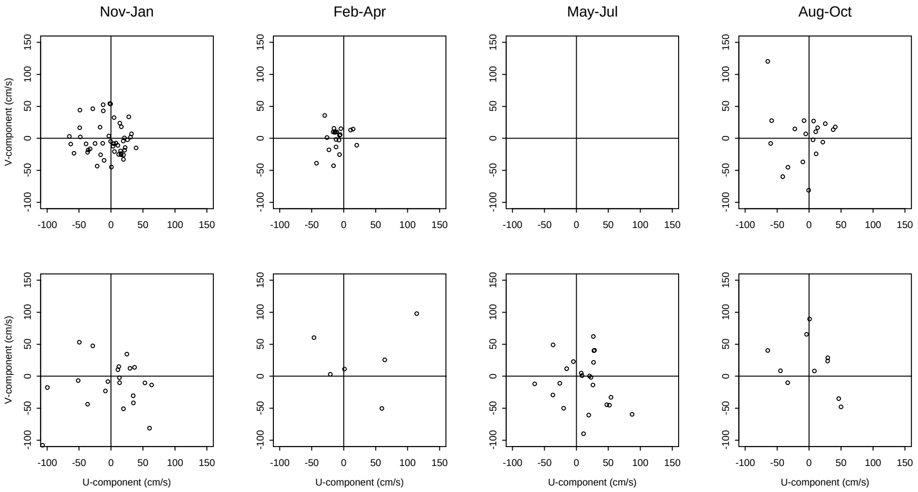

Figure 3.27: Relative velocity plotted at angles with current velocity by season for returning (top) and departing (bottom) turtles at the behavior-deciding stage. Significant differences were seen in relative velocity magnitude in Nov-Jan (KS-test: KS=0.354, $p<0.05$) and Feb-Apr (KS=0.667, $p<0.05$). u- and v-components were not different in all seasons ($p>0.1$).

were not as apparent. This once again gathers attention towards the possibility that there may be underlying reasons that cause the difference between returning and departing turtles based on their relative movements with respect to the current, especially since those returning were again found to be relatively swimming opposite to the current.

3.2.4 Returning or departing stage

This stage looks at either the returning or departing paths taken by the turtles after the behavior-deciding stage until returning to presumably fa-

Table 3.1: Seasonal percentages of relative velocity in direction of current and in cold regions for returning and departing turtles.

%	Behavior	Nov-Jan	Feb-Apr	May-Jul	Aug-Oct
On current	Returning	19.1	10.0	NA	31.6
	Departing	38.1	50.0	45.5	50.0
In colder regions	Returning	38.3	60.0	NA	57.9
	Departing	33.3	83.3	45.5	70.0

miliar regions of shallower depths (in this case, less than 1000 m), or farther east just before transmission ends (Fig. 3.8).

Both returning and departing turtles were present in weaker currents (Fig. 3.28), displacing themselves away from the Kuroshio's mainstream. These currents were very much weaker than those in the initial stage (W-test: Z=-11.99 and -6.213, $p<0.001$, respectively). Returning turtles made their way back to the coasts through the Kuroshio recirculation region [7]. Even though the effect of these weaker cyclonic currents might seem minor to the turtles themselves, they are important currents for smaller organisms, such as larvae of crustacean species [21], and presumably for krill, which are often found in stomach contents of loggerheads [43]. On the other hand, departing turtles were found in the Kuroshio extension bifurcation region, a region known to be foraging grounds for juvenile loggerheads [47].

Figure 3.29 shows that both turtles were relatively swimming slower than in their respective initial stages (W-test: Z=-3.828 and -6.388, $p<0.001$, respectively). As for the direction of their relative velocity, there were no significant differences between behaviors for either u- or v-component (Fig. 3.30, KS-test: KS=0.0787 and 0.0722, $p>0.1$, respectively) and almost for

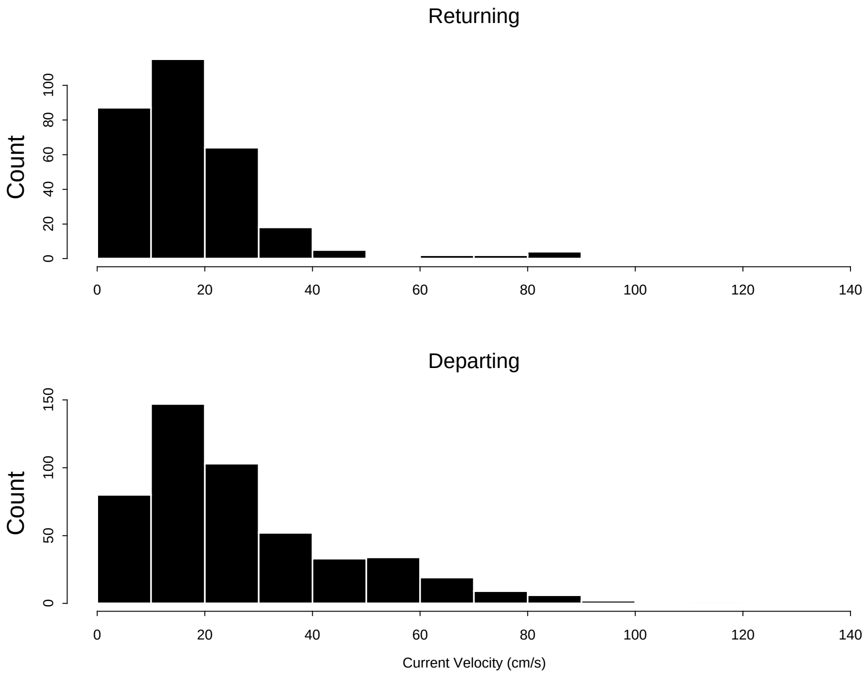

Figure 3.28: Current velocity magnitudes for returning (top) and departing (bottom) turtles after behavior-deciding stage, with returning turtles being in weaker currents (W-test: Z=-7.371, p<0.001).

every season (Fig. 3.31).

It is interesting to see that returning and departing turtles showed little differences in relative velocity, whether it be in magnitude or by component, even though they were in totally different locations. Despite the fact that both regions were characterized by weaker currents, there were obvious differences in other oceanographic parameters, such as SST and nutrient richness, and should therefore be considered simultaneously.

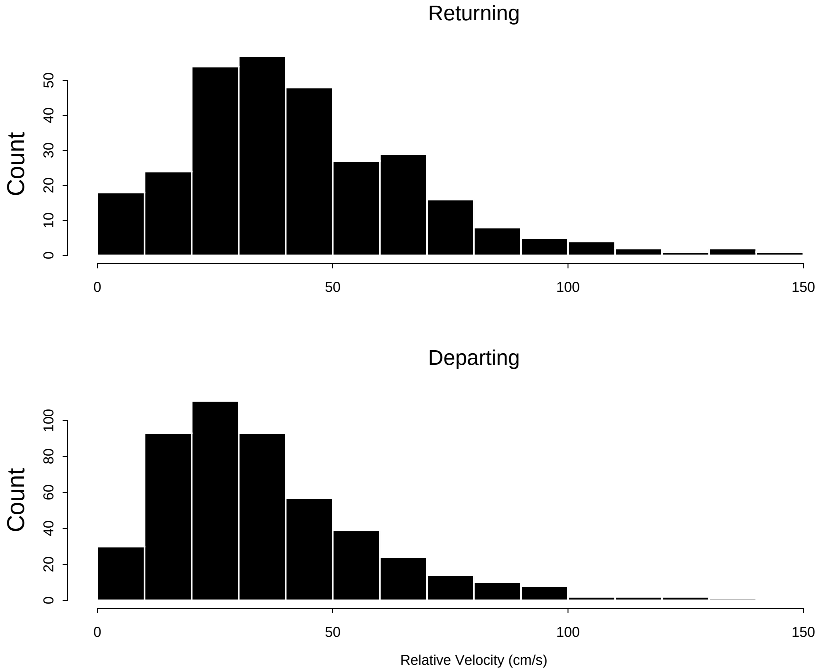

Figure 3.29: Relative velocity magnitudes for returning (top) and departing (bottom) turtles after behavior-deciding stage, with returning turtles relatively swimming significantly faster than departing turtles (W-test: Z=4.412., p<0.001).

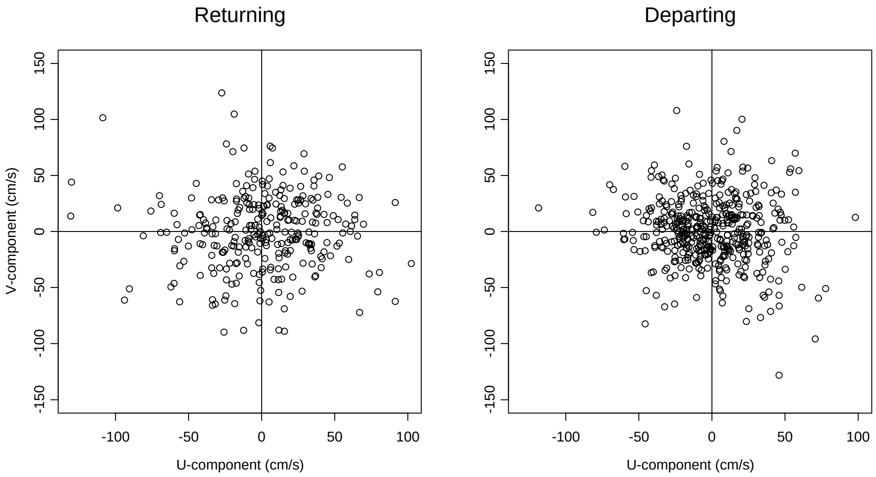

Figure 3.30: Relative velocity for returning (left) and departing (right) turtles after behavior-deciding stage. There were no significant differences between behaviors for both u- and v-components (KS-test: KS=0.0787 and 0.0722, p>0.1, respectively).

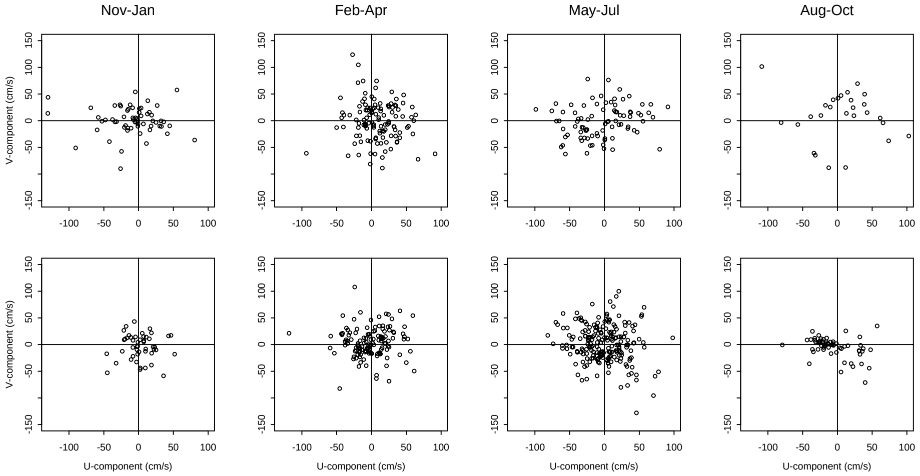

Figure 3.31: Relative velocity plotted at angles with current velocity by season for returning (top) and departing (bottom) turtles after behavior-deciding stage. Significant difference was seen in v-component in Aug-Oct (KS-test: KS=0.443, p<0.001).

3.3 Regression

Detailed investigations of each stage were carried out in the previous section by dividing the turtles' behaviors into four separate stages (initial, roaming, behavior-deciding and returning or departing), however it is still of interest to see whether there remain any differences that could not be detected by graphical methods. It is well understood that the ocean's system behaves under numerous factors simultaneously and, thus, a reasonable approach would be to objectively investigate these factors together rather than separately. Are there any underlying relationships between turtle behavior and oceanographic parameters? This is the question of concern in the following subsections, in which specific stages and moments are examined in further detail, making use of multiple oceanographic parameters and benefiting from the relationships among them.

Regression analysis was undergone to further investigate the behaviors seen within each stage. Dependent variables (Y) were chosen to be relative velocity $|V_{rel}|$, which indicates how fast the turtle was swimming relative to the current, and u-component of $V_{rel,\alpha}$, which involves additional information concerning its direction (i.e. positive/negative meaning on/opposite of current) to describe the turtles' movement. $|V_{rel}|$ and $u_{rel,\alpha}$ had Gamma and Gaussian distributions, respectively (with the KS-test, p>0.1 for all cases). However, the v-component, which represents whether the turtle had moved to the right/left-hand side of the current, was not of interest since geostrophic currents are characterized by pressure and temperature differences on adjacent sides, in which currents in the northern hemisphere are cooler on the left-hand side of the current. Furthermore, these locations, referred to as fronts, are ideal environments for many organisms, including sea turtles [46].

Many oceanographic parameters are multi-correlated and, hence, three representative parameters were chosen as independent variables (X): 1) current velocity $|V_c|$, 2) sea surface temperature (SST) and 3) silicate concentration (SIL) from J-OFURO, AVHRR and WOA01, respectively. Each parameter had a different temporal and/or spatial resolution and, thus, were handled differently. Y_i depends only on $|V_c|_i$, however since Y_i was derived by the average velocity between two consecutive points, it could be influenced not only by SST_i and SIL_i but also those at adjacent points. Therefore, to incorporate these possible effects, three additional configurations were supplied:

1. $\triangle_1 X = X_{i+1} - X_i$, to distinguish an increase/decrease in X with a future point,

2. $\triangle_2 X = X_{i+1} - X_{i-1}$, to distinguish an increase/decrease in X for surrounding points,

3. $X_m = \frac{1}{3}\sum_{j=1}^{3} X_j$, to examine the average effect including adjacent points.

Furthermore, SIL was obtained from monthly means of interpolated climatological data, which show little variability when viewed at short timescales and, therefore, the differences and mean are also meant to compensate for this low resolution. Inclusion of silicate also allows for an indirect view of other variables that are highly correlated with it ($|r| >$0.7), such as nitrate, phosphate, subsurface temperatures, salinity and chlorophyll a. Since all independent variables were not mean-centered, the resulting intercept becomes weighted and, hence, it does not reflect the mean signal of the dependent variable (denoted by “null” in all tables). Regression was undergone for every combination of the three parameters (significance verified with Type II likelihood ratio tests) and the “best” fit was chosen based on highest deviance percentage (i.e. $\%_D =$ (null deviance - total residual deviance)/null deviance) or correlation coefficient.

3.3.1 Initial stage

When comparing returning and departing turtles in the initial stage, there was no significant difference in $|V_{rel}|$ between the two (Fig. 3.13); therefore the two behaviors were pooled in the regression for $|V_{rel}|$. Significant parameters included $|V_c|$ with a negative coefficient and $\triangle_2 SIL$ with a positive coefficient (Table 3.2). This indicated that in faster currents with low silicate levels, turtles made smaller movements, or in other words, were less active. This could be related to the turtles being present in relatively faster currents of the Kuroshio in the beginning of the initial stage when near the coast. However, once they approached areas with higher silicate (i.e. prey abundance), such as in the Kuroshio extension or Kuroshio-Oyashio mixed region, currents gradually became weaker farther from the coast. In combination with the $u_{rel,\alpha}$ regression again having $|V_c|$ negative for returning turtles, they seemed to have been swimming in the opposite direction of the faster currents (Table 3.3). However for departing turtles, they were swimming opposite of the currents when they approached regions of colder SST despite the current's speed. This result was comparable to what was mentioned earlier, in which returning turtles were swimming opposite of the current more often than departing turtles, however it also indicated that these instances had occurred in the faster currents, in which case, $|V_{rel}|$ would also become low and, thus, minimizing its rate of energy loss.

Returning turtles seemed to not have been significantly dependent on SST possibly due to most of them being present during August to October (Fig. 3.15), in which the ocean surface became completely warmed up and, thus,

Table 3.2: Regression results for relative velocity magnitude $|V_{rel}|$ (cm/s) for pooled turtles during the initial stage. $|V_c|$, SST and SIL are current velocity (cm/s), sea surface temperature (°C) and silicate concentration (μmol/L), respectively. $\triangle_1 X = X_{i+1} - X_i$, $\triangle_2 X = X_{i+1} - X_{i-1}$ and $X_m = \frac{1}{3}\sum_{j=1}^{3} X_j$. 'Value' and 'SE' are corresponding coefficients of explanatory variables and standard error, respectively, in units of 10^{-4}. df is degrees of freedom. Type II likelihood ratio (LR) tests were used to calculate p-values, with non-significance (NS) occurring at probabilities greater than 0.1.

$\|V_{rel}\|$		Value	SE	df	LR	P(χ)
Pooled	null			212		
	SST_m	2.38	1.98	1	1.42	NS
	$\triangle_2 SIL$	1.21	1.16	1	19.3	<0.0001
	$\|V_c\|$	-1.10	0.230	1	21.0	<0.0001

Table 3.3: Regression results for component $u_{rel,\alpha}$ (cm/s) for returning and departing turtles during the initial stage. 'SS' denotes sum of squares.

$u_{rel,\alpha}$		Value	SE	SS	df	F	P(F)
Returning	null				81		
	SST_m	-2.98	1.83	4920	1	2.64	NS
	$\triangle_2 SIL$	-0.178	0.795	93.5	1	0.0501	NS
	$\|V_c\|$	-0.700	0.213	20233	1	10.8	<0.005
Departing	null				97		
	SST_m	4.32	1.28	23105	1	11.4	<0.005
	$\triangle_1 SIL$	1.10	0.958	2677	1	1.32	NS
	$\|V_c\|$	0.0579	0.158	274.1	1	0.135	NS

becoming less variable. Overall, during this stage, the strong currents had a great influence on the paths of the turtles. To lower energy consumption, turtles may have been eagerly swimming only opposite of weaker currents when present in high prey regions, and for the most part, they were being drifted by the strong currents. However, their relative directions were dependent on different factors, indicating that returning turtles may have already been moving differently within the fast Kuroshio currents compared to departing turtles reacting only to SST.

3.3.2 Roaming stage

In the roaming stage, instances of turtles either swimming in circular tracks or in one location before heading towards their resulting paths were examined. Currents seemed to have been influencing the circular path taken (Fig. 3.17), but it could not be specified how the turtles were moving, whether they had been swimming with the current or simply being drifted, and only for specific individuals. In the Kuroshio extension, in which the meandering Kuroshio creates complex currents and eddies, the results showed that $|V_c|$ had a negative effect on $|V_{rel}|$ and $u_{rel,\alpha}$ (Tables 3.4 and 3.5). This indicated that in stronger currents, they were not swimming as active and were drifted by the current. Furthermore, turtles were relatively swimming faster in weaker currents when approaching warmer regions. Results suggested that there may have been a higher chance of them being drifted by the circular currents, since changes in silicate levels did not influence their movements, and currents closer to the mainstream were stronger than those farther away.

Tomoyo was considered separately as a special case, since she showed a different roaming pattern compared to all other turtles, wandering into colder regions and remaining in high latitudes for a relatively long period. A verification of both $|V_{rel}|$ and $u_{rel,\alpha}$ showed that they were significantly different from the other roaming turtles (KS-test: KS=0.144 and 0.189, $p<0.05$, respectively). Regression results showed distinctly different parameters affecting her roaming behavior as well. While not being drifted by the current, she was actively swimming when approaching higher silicate regions, even though she had reached higher latitudes with cold water temperatures. Her extended period in the Kuroshio-Oyashio mixed region may have been the key to her survival, since even at cold temperatures, she was present in nutrient-rich regions, possibly during months in which other organisms, such as squid, migrate to the Kuroshio-Oyashio transition zone to forage [25]. Compared to other roaming turtles, Tomoyo was in a region with weaker currents (W-test: Z=-8.23, $p<0.001$), and since her behavior seemed to have been mostly dependent on food, her lack of knowledge in the wild may have been the reason for her wandering and lengthy roaming stage.

3.3.3 Returning turtles

At the behavior-deciding stage, returning turtles initiated their long journey back to coastal regions and continued to swim in the open ocean for several months. Currents away from the Kuroshio mainstream were indeed weaker, but not negligible, especially in the Kuroshio countercurrent, and

Table 3.4: Same as Table 3.2, but for pooled turtles and Tomoyo separately, during the roaming stage.

$\|V_{rel}\|$		Value	SE	df	LR	P(χ)
Pooled	null			150		
	$\triangle_2 SST$	15.0	10.5	1	13.5	<0.0005
	SIL_m	2.56	2.61	1	0.97	NS
	$\|V_c\|$	-2.28	0.383	1	25.9	<0.0001
Tomoyo	null			99		
	SST_m	-22.4	5.41	1	14.4	<0.0005
	$\triangle_1 SIL$	16.1	2.74	1	24.0	<0.0001
	$\|V_c\|$	-1.16	0.702	1	2.28	NS

Table 3.5: Same as Table 3.3, but for pooled turtles and Tomoyo separately, during the roaming stage.

$u_{rel,\alpha}$		Value	SE	SS	df	F	P(F)
Pooled	null				185		
	SST_m	-0.377	0.541	356.4	1	0.485	NS
	SIL_m	0.123	0.380	77.5	1	0.105	NS
	$\|V_c\|$	-0.356	0.0974	9835	1	13.39	<0.0005
Tomoyo	null				186		
	$\triangle_2 SST$	1.29	1.32	721.3	1	0.952	NS
	SIL_m	0.544	0.258	3363	1	4.44	<0.05
	$\|V_c\|$	-0.506	0.103	18371	1	24.2	<0.0001

Table 3.6: Same as Table 3.2, but for returning turtles heading back to coast from the behavior-deciding stage.

$\|V_{rel}\|$		Value	SE	df	LR	P(χ)
Returning	null			265		
	SST_m	-8.96	3.68	1	5.66	<0.05
	SIL_m	2.88	1.94	1	2.37	NS
	$\|V_c\|$	-0.695	0.476	1	1.97	NS

can possibly guide the turtles back to their home grounds.

Results from the $|V_{rel}|$ regression showed only a significantly negative relationship with SST_m (Table 3.6). Furthermore, in relation to direction, the $u_{rel,\alpha}$ regression indicated two factors affecting their movement (Table 3.7); SIL_m having a significantly negative effect, and $|V_c|$ having a marginally positive effect. Most turtles were present in this region during non-summer months (Fig. 3.31), meaning that water temperatures at the surface, as well as silicate distribution, were variable latitudinally. Hence, turtles were in colder nutrient-rich regions in the northern segment of their returning path, and gradually entered warmer nutrient-poor regions as they headed south. This indicates that the turtles may have been swimming more actively in the opposite direction of the current in the beginning of their return and less actively as they headed south towards the end. This could suggest that turtles returning to the coast were minimizing energy costs due to the long traveling distance and less frequent confrontation with prey.

It was found that when turtles entered relatively faster currents, such as the Kuroshio countercurrent, they swam faster in the direction of the current, presumably to lower energy costs. However, it is somewhat questionable

Table 3.7: Same as Table 3.3, but for returning turtles heading back to coast from the behavior-deciding stage.

$u_{rel,\alpha}$		Value	SE	SS	df	F	P(F)
Returning	null				312		
	SST_m	1.82	0.488	1291	1	2.22	NS
	SIL_m	-0.372	0.250	8092	1	13.9	<0.0005
	$\lvert V_c \rvert$	1.168	0.0921	1948	1	3.34	<0.1

whether they are capable of sensing the current being in the open ocean and in a less distinct region compared to the Kuroshio mainstream. It is also important to note that SST, even collected at a weekly rate, can be less informative than climatological data due to temporal and spatial factors. For instance, during summer months, SST can be heated up causing a less variable or nearly constant temperature field at latitudes south of 35°N. In such cases, water temperature at deeper depths is seasonally less variable and, thus, maintains information concerning previously formed ocean fronts. With silicate levels being highly correlated with subsurface temperature (in this stage, ρ = -0.795, Z = -13.7, p<0.001), the direction of returning turtles may be inversely correlated to changes in subsurface temperature rather than those in silicate concentration. This can be further related to the diving behavior of sea turtles, in which they are known to make frequent shallow dives while swimming to help minimize energy consumption [12], however in addition, these frequent dives could be related to the turtles sensing water temperatures below the surface. Since information on vertical behavior is not available for these individuals, it would certainly be of interest to verify in further studies whether they are making use of these dives for purposes not only related to energy cost.

3.3.4 Departing turtles

The Kuroshio extension bifurcation region is known to supply major foraging grounds for juvenile turtles [47]; thus the smaller departing turtles in this study may have reached this region for similar reasons. However, it could not be verified in the previous section whether they had intentionally headed towards these areas or whether they were drifted by the currents and arrived there as a result.

Regression results were similar to those of the roaming stage in relation to currents, in which $|V_c|$ had a negative effect on both $|V_{rel}|$ and $u_{rel,\alpha}$ (Tables 3.8 and 3.9). This indicated that departing turtles were not swimming as active in stronger currents, making only small movements and, thus, being drifted by the currents. If this is the case, it could be somewhat similar to what is seen through simulations of floating marine debris accumulating north of the Hawaiian Islands due to westerly winds, geostrophic currents and Ekman drift [30]. However, in weaker currents, such as in regions of the weakened Kuroshio, turtles were swimming more eagerly toward higher silicate levels, which can relate to the nutrient-rich foraging grounds attracting juvenile turtles [47]. Unfortunately, all transmissions ended for departing turtles while they were in the foraging area. Further discussions are made in the following chapter.

Table 3.8: Same as Table 3.2, but for departing turtles after the behavior-deciding stage.

$\lvert V_{rel}\rvert$		Value	SE	df	LR	P(χ)
Departing	null			356		
	$\triangle_1 SST$	-3.76	10.7	1	0.123	NS
	$\triangle_1 SIL$	-4.06	2.18	1	3.18	NS
	$\lvert V_c\rvert$	-2.03	0.381	1	24.8	<0.0001

Table 3.9: Same as Table 3.3, but for departing turtles after the behavior-deciding stage.

$u_{rel,\alpha}$		Value	SE	SS	df	F	P(F)
Departing	null				312		
	SST_m	-0.216	0.762	64.8	1	0.0801	NS
	SIL_m	0.730	0.360	3320	1	4.11	<0.05
	$\lvert V_c\rvert$	-0.264	0.0826	8235	1	10.2	<0.005

Chapter 4

Conclusion

Analysis of loggerhead sea turtle distribution and movement was undergone, making use of turtle location data and other oceanographic databases. The initial step considered the handling of a low-quality data set produced by the Argos satellite tracking system. Rather than relying on only the classifications supplied by Argos, additional criteria were stated, not only to provide another measure of accuracy of the points but also to extract information in the form of average velocity of the turtle, which is simultaneously verified for accuracy in the same process. Although information on location seemed to have not changed depending on the filtering method (compared to the method in [47]), the recalculation of average velocity showed a clear difference in the accuracy of the derivative values (Fig. 2.4). The derivative is a trustful index to examine when concerning locational information, but at the same time, provides additional information which further describes underlying behaviors. Distributional and size differences categorized the turtles into three distinct groups referred to as remaining, returning, and departing individuals. When comparing the latter two, four stages during their tracking period were set to investigate whether there were differences in the effects of several oceanographic parameters between them; initial, roaming, behavior-deciding and returning or departing stages. Initial analyses indicated that turtles were in different environments, such as geographic location, season and current velocity and direction and, therefore, seemed to have been affected differently by them, however differences in their relative velocity with respect to the current were not as noticeable and, thus, lead to further investigation in reference to multiple oceanographic parameters.

Regression analyses were carried out for relative velocity magnitude and the u-component of relative velocity parallel to current velocity. These two variables were used to explain the turtles' actual movement and direction with the effects of the ocean current removed. Differences and mean values were also taken to treat the temporal and spatial resolution in the independent parameters. Highly correlated parameters were not included in the analysis, but were considered when making interpretations of the results. Comparisons were made between returning and departing behaviors in specific stages of the turtles' tracks. All turtles were mostly found drifting with the current when the currents were stronger, but actively swimming when weaker. However, returning turtles were swimming within the strong currents differently compared to departing turtles, in which returning turtles were found to be swimming opposite to the current more frequently. Furthermore, turtles were also affected by temperature and silicate levels. Roaming behavior was most significantly affected by current velocity, causing some turtles to be swept into circular currents or eddies adjacent to the mainstream, however all turtles would have a high chance of being guided towards regions of nutrient-high waters and highly abundant with prey, such as floating organisms. Returning turtles were found in lower latitudes compared to departing turtles, being in relatively weaker currents and, thus, thought to have a greater ease in accessing the Kuroshio countercurrent and eddies south of the mainstream before starting their return to the coast. Low energy consumption may have been the key factor for returning turtles to having a successful journey back to their homing grounds, since they were not swimming faster in warmer temperatures, only swimming opposite of the current for food when weak, and swimming in the direction of fast currents. Turtles are known to make short and frequent dives in the open ocean, in which this type of behavior may be connected to the verification of subsurface temperatures, which contain past information on ocean fronts. On the other hand, departing turtles were found roaming, while drifting on the current, but often swimming eagerly while reacting to high nutrient levels.

In conclusion, all results indicate that currents and other oceanographic parameters have a significant influence on the turtles within different stages. Previous studies ([11, 33, 4]) could not state whether there was a clear relationship possibly due to their study sites being in regions such as the Mediterranean Sea and Mozambique Channel, in which currents are seasonally variable but enclosed in a smaller area and rather weak. This study shows that the strength and variability of the currents influence the turtles differently. When turtles were frequently in strong currents, they were found making small movements or drifting, and as a result, they were forced to flow in the direction of the current.

It could not be shown for sure whether the currents had a physical influence on the turtles and if the turtles were making use of them for mobility purposes, or whether they were drifted as a result of being present in a strong current. Moments of complete drifting could only be distinguished when relative velocities are zero, but a small enough relative velocity, which relates to small movements, can be very similar to drifting behaviors, depending on how fast the surrounding currents are moving. Graphically, turtle tracks are indeed influenced by the currents, often being very similar in shape and direction, but with the regression analysis, since $|V_c|$ has mostly a significantly negative effect on $|V_{rel}|$ and/or $u_{rel,\alpha}$, the turtles relative movements and directions depend on the current's velocity at that time. However, in many cases, there were other significant parameters, such as temperature and nutrient level having either a positive or negative effect on its relative movements. This suggests that turtles may have been sensing temperatures in order to remain in the fast currents, while making only small movements to lower energy consumption and, thus, resulting in their paths to be shaped similarly to the currents. When currents are weak, turtles are actively swimming, but still reacting to temperatures and also amounts of prey when available. In any case, being close to the Kuroshio may be an important cue for the turtles, whether it be intentional or not, as they can lower energy loss, frequently encounter regions of high prey, be in ideal temperatures and mature turtles can win their ticket back home on the Kuroshio countercurrent.

The climatological data used in this study have a few disadvantages. The overall mean trends of the parameters can be examined and they are sufficient for most regions examined in the analysis, however in regions with meandering currents that interannually or seasonally vary with the Kuroshio, such as near the Kuroshio extension, these data are not able to represent the fronts of nutrient concentrations formed by the currents. As a potential substitute, the readily available SST data can supply reasonable predictions of chlorophyll a concentration for regions such as the Kuroshio extension, as seen in Fig. 3.18. However, the use of in-situ data of nutrient concentrations would be an optimal solution to strengthen the regression models.

Transmission periods end for departing turtles in foraging grounds in the central North Pacific, however it is certainly of interest as to how they return to their home grounds after their developmental migration. Returning turtles are larger and, thus, more mature, which is an indication that they may have a higher chance of being active in mating than those departing. They may also be more knowledgeable concerning the nature of the Kuroshio, by which they are aware that being on its south side allows easier access to the Kuroshio countercurrent while the nutrient-rich eddies provide them with enough food to consume before returning back to the coast and, thus, ensuring a higher mating success rate. However, for smaller departing turtles, this may not be the case, in which they may or may not be as knowledgeable, but more concerned with finding prey, growing and eventually taking part in mating. Unfortunately, departing turtles could not be distinguished between old juveniles and young adults and, therefore, further discussion on differences between life stages is limited.

Furthermore, all possible parameters affecting turtle behavior cannot be included in the analysis and, therefore, discovering underlying behaviors is a difficult task. The inclusion of other unstudied factors would improve the reliability of the regression models. Recently, many studies show the possibility of sea turtles being capable of sensing geomagnetic fields as a way to guide them back to natal grounds and/or locate themselves in the open ocean [32, 33]. A combination of such geomagnetic cues, phenological behavior, such as mating and nesting, and information from physical and biological environmental factors could be the key elements to explaining the unknown behaviors of sea turtles.

As for headstarting of turtles, many studies have argued over the past few years whether it is an effective method for conservation purposes [28, 19, 55, 17, 56, 3]. It can be considered advantageous for the individual to be raised until reaching a size to maximize survival, however there is a downside in which it may be less experienced in the wild. In any case, the procedure should be well planned before undergoing, since it may cause certain individuals to behave differently, much like Tomoyo and her extensive wandering in the Kuroshio-Oyashio mixed region, and possibly lower their chance of survival.

Since turtles were influenced by several oceanographic factors, it is of interest to predict whether they are capable of adapting to environmental changes, especially abrupt ones caused by global warming or El Niño/La Niña events. Many studies predict future states of the ocean on a global scale focusing on numerous aspects. For instance, studies with numerical models have shown that the Kuroshio and the Kuroshio extension will be accelerated, intensifying overall Sverdrup transport and strengthening the Kuroshio countercurrent [52]. The change in the countercurrent is most certainly capable of influencing the turtles present in these regions, either by providing a stronger more distinct current for returning turtles, or some confusion for departing turtles heading out to foraging grounds in the central North Pacific. However, these foraging grounds could also be affected by the changes in biochemical processes, in which distributions of large plankton species and all other organisms in the food chain would be affected [58]. A numerical model simulated a decrease in chlorophyll a in the North Pacific due to the effects of global warming [53] and, thus, it is most probable that there would be a negative effect on the availability of prey for the turtles and possibly obligate them to search for new foraging grounds. Sea level rise and increase of SST are also of concern for nesting turtles by decreasing the number of nesting beaches or rushing their timings of nesting [9, 38] and, thus, both could result in turtles changing their migration route destinations. Predictions at high spatial resolution by the Earth Simulator provide information on what could be expected from these abrupt environmental events [42] and, thus, should be considered when predicting future survival rates of sea turtles.

Difficulties are experienced in this study when examining solely the relationship with ocean current and, therefore, additional analyses with other oceanographic parameters are carried out, suggesting that a combination of environmental factors play important roles in deciding the behavior of sea turtles. The possibility that all sea turtle species around the world are being influenced by ocean currents can be examined fully once turtle data and oceanographic data are both readily available. There are numerous strong currents flowing in different parts of the world's ocean, in which sea turtle species inhabit [8]. Investigation of these effects is an ongoing process and there is no guarantee that all sea turtles in all life stages exhibit behaviors that are comparable to ocean currents and oceanographic parameters as seen in this study. Future analysis concerning loggerhead sea turtle movement in the North Pacific should consider usage of Bayesian methods, state-space models [23, 24] and information theoretic parameter selection theory [18] extended to investigate turtle velocities. Collection of vertical behavior and ambient temperatures would be most useful for further discoveries. Many studies in relation to sea turtles movement in the open ocean are very recent and, therefore, new findings can be expected providing more information on their unknown behaviors. In any event, environmental changes are occurring at a rapid pace and they are surely capable of affecting the turtles in some significant way, however the degree of the effect would depend on the adaptability of the turtles, accustoming themselves to their new environment in order to prevent further endangerment and avoid extinction.

Appendix A

Turtle Information and Tracks

Thirty individuals were used in this analysis. Information and tracks of each individual are given here. All tracks were smoothed based on the refined filtering method explained in Section 2.2. The starting location of a track is represented by a triangle. Each point of the track represents a daily-averaged location, however when data were scarce, it would represent the average location of a few days.

Table A.1: Information on each turtle, including PTT ID, name, sex, start and end dates, total number of tracked days, SCL (mm), and weight (kg). Missing information is noted as "NA". "∗" indicates whether geostrophic current information exists for that turtle. Supplementary information: 1 = nesting on beach; 2 = caught in fishnet; 3 = caught in fishnet with eggs; 4 = headstarted; 5 = in captive.

ID	Name	Sex	Start Date	End Date	♯days	SCL	Wt	Suppl.
21861	Amami-1	M	05/17/00	10/09/00	145	812	65	2
21862	Amami-2	M	05/17/00	08/29/00	104	920	124	2
21868	Amami-3	M	05/17/00	03/03/01	290	940	100	2
21934	Amami-4∗	F	06/01/00	09/14/00	105	892	115	2
21935	Amami-5	M	05/21/00	07/12/03	157	925	102	2
28940	Aya ∗	F	07/06/03	08/29/04	420	807	NA	1
28411	Eiko	F	07/19/02	08/15/02	27	920	NA	1
29976	Fujiko ∗	F	04/21/03	11/16/2003	209	844	95	3
52590	Gemini	U	10/05/04	08/31/2005	330	753	NA	2
22168	George∗	M	06/25/03	12/30/03	386	765	NA	-
52588	Haruko	F	04/13/05	11/09/2005	210	860	NA	2
20823	Kagetsu∗	M	11/02/02	07/11/03	251	825	83	2
26250	Kameko ∗	F	09/19/01	04/16/02	209	NA	NA	-
33054	Kofuji	U	02/18/05	10/16/2005	240	681	NA	2
20822	Leo	M	09/15/02	10/29/02	44	727	43	4
16090	Midori∗	F	08/13/02	05/25/03	285	815	NA	2
21873	Mihali∗	F	10/21/02	11/23/03	398	NA	NA	2, 5
17929	Mika∗	F	04/07/03	09/12/03	158	837	103	2
17816	Otome∗	F	05/19/03	06/29/04	407	746	68	2
29060	Sagi ∗	U	08/01/03	05/31/04	304	681	46	-
23538	Sakura	F	12/02/04	03/26/06	479	752	NA	-
16089	Sanae∗	F	08/12/02	04/13/03	244	743	68	2
19608	Sanaejr∗	F	03/18/03	08/12/03	147	665	NA	-
23001	Taro	M	03/06/05	12/28/05	297	717	NA	-
52589	Taurus	U	11/06/04	05/28/2005	203	757	NA	2
20114	Tomoyo∗	F	03/25/02	07/31/03	493	650	NA	4
28938	Umira ∗	U	10/27/03	09/17/04	326	742	64	2
22270	Virgo	U	02/18/05	04/28/06	434	709	NA	-
28409	Yasuko ∗	F	02/10/03	10/01/03	233	762	61	3
28410	Zooko ∗	F	06/21/02	10/21/02	122	800	NA	1

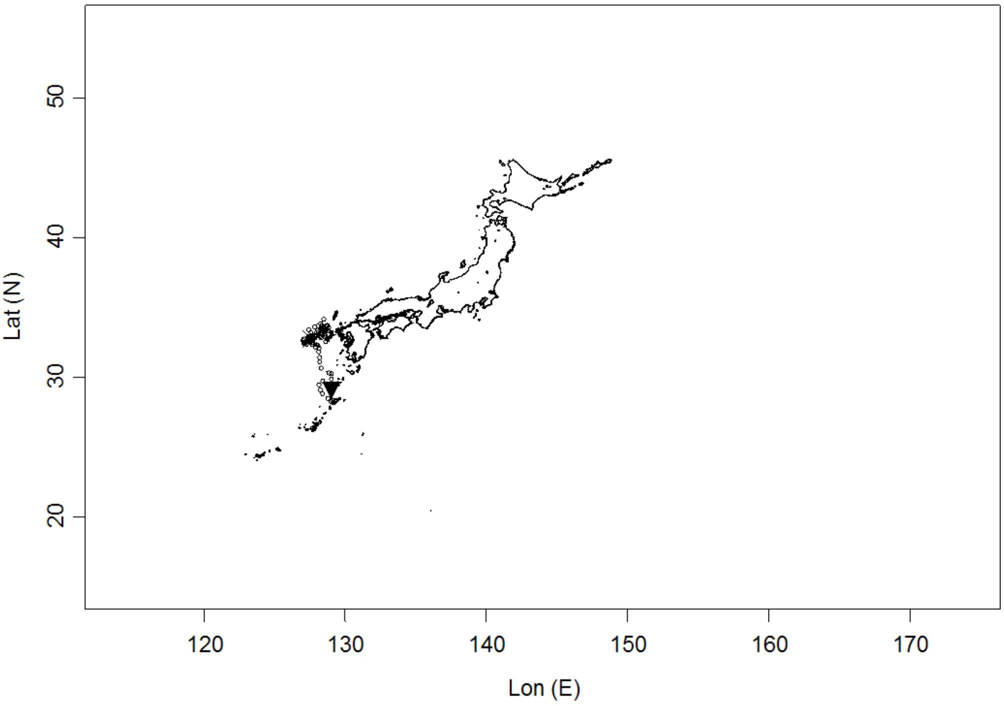

Figure A.1: Track of Amami-1.

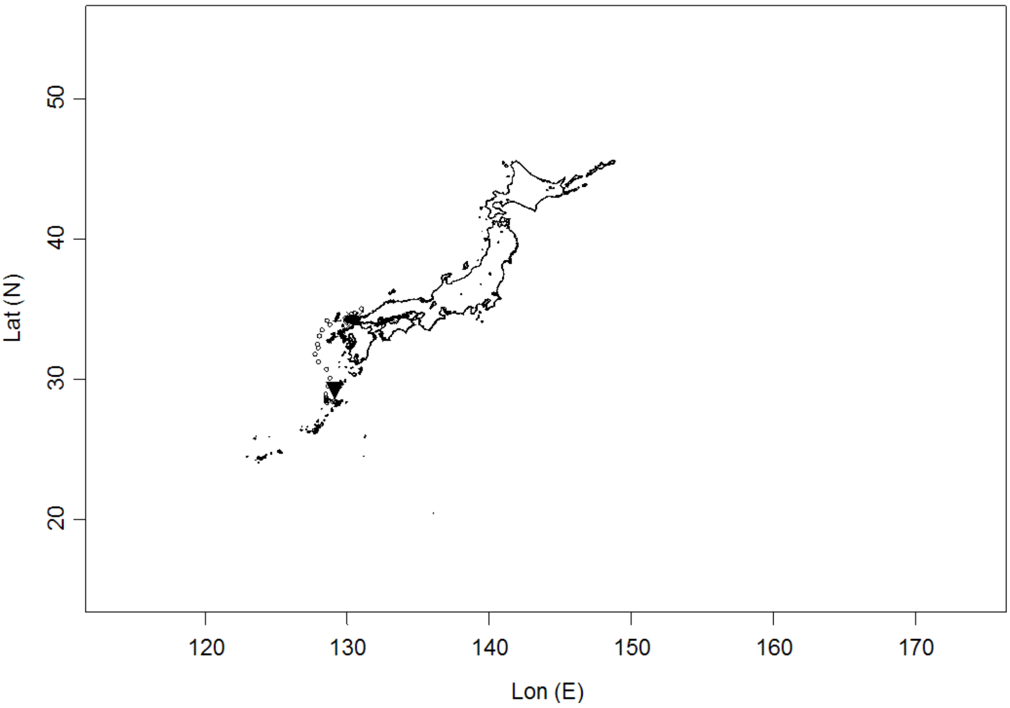

Figure A.2: Track of Amami-2.

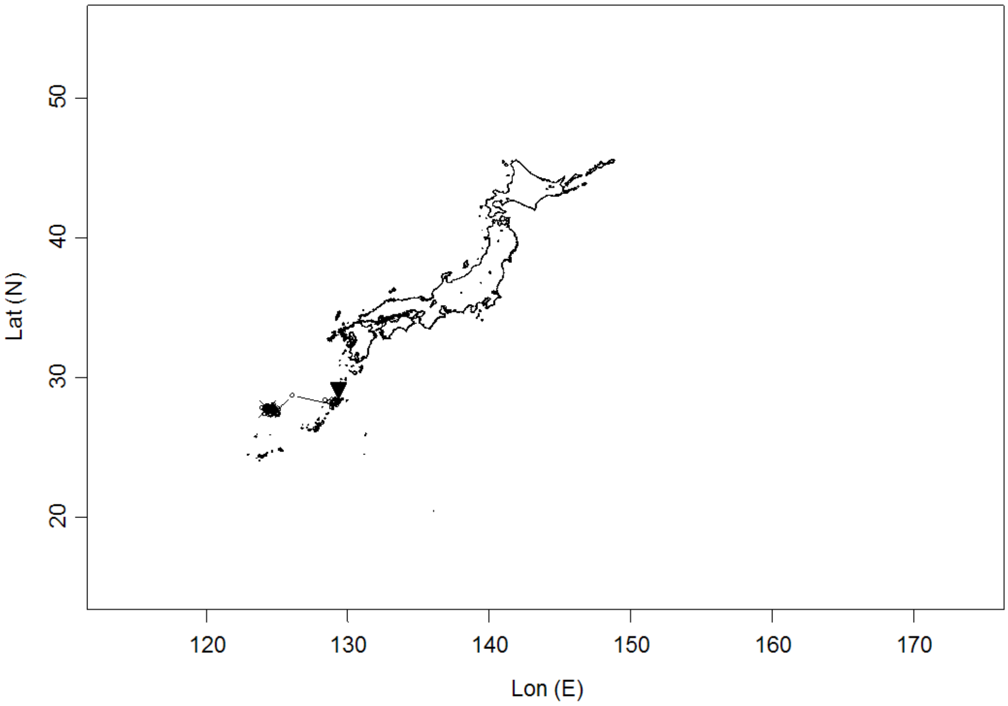

Figure A.3: Track of Amami-3.

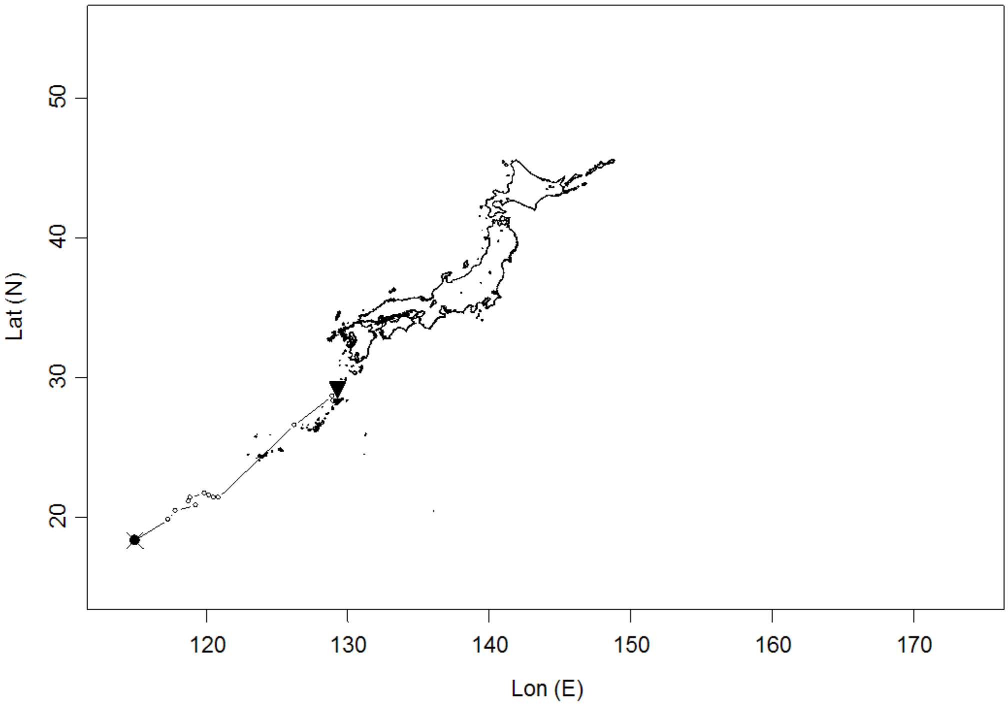

Figure A.4: Track of Amami-4.

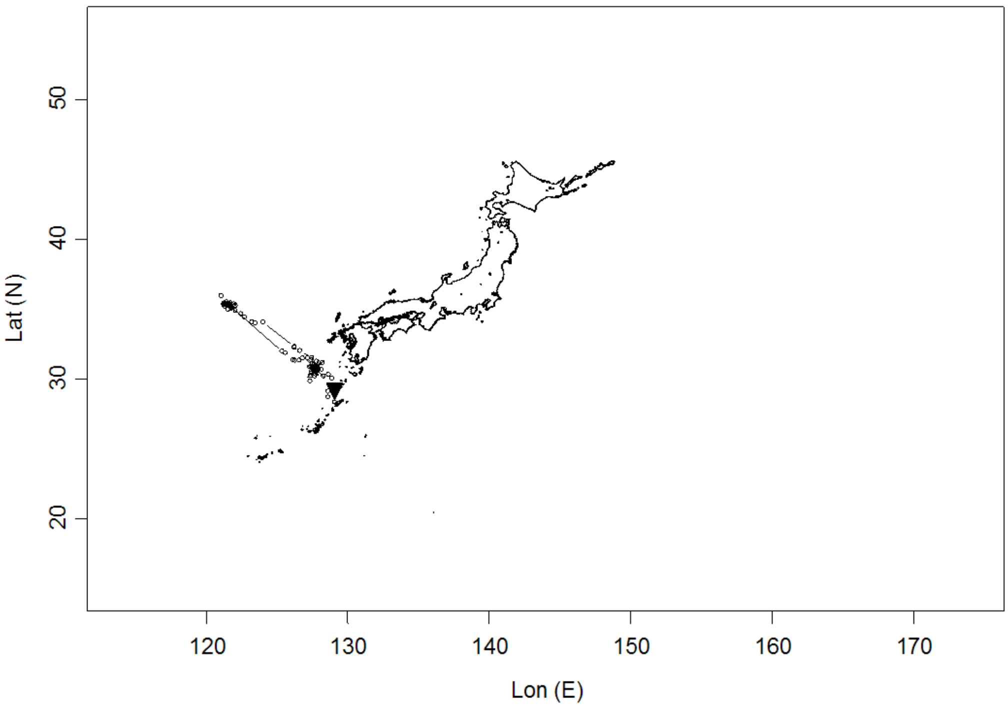

Figure A.5: Track of Amami-5.

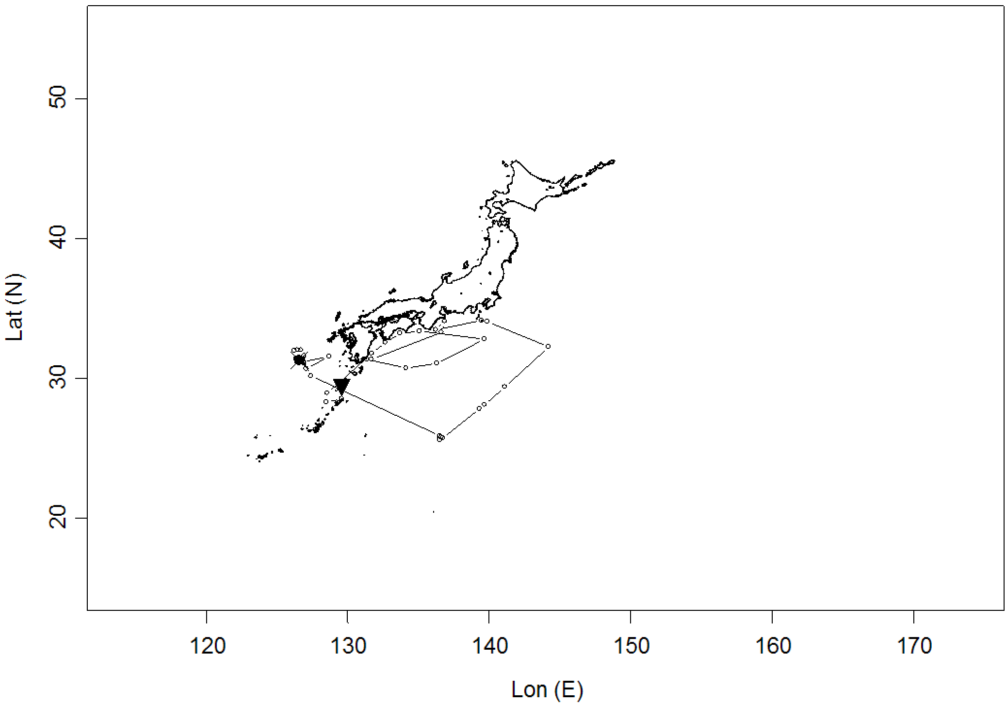

Figure A.6: Track of Aya.

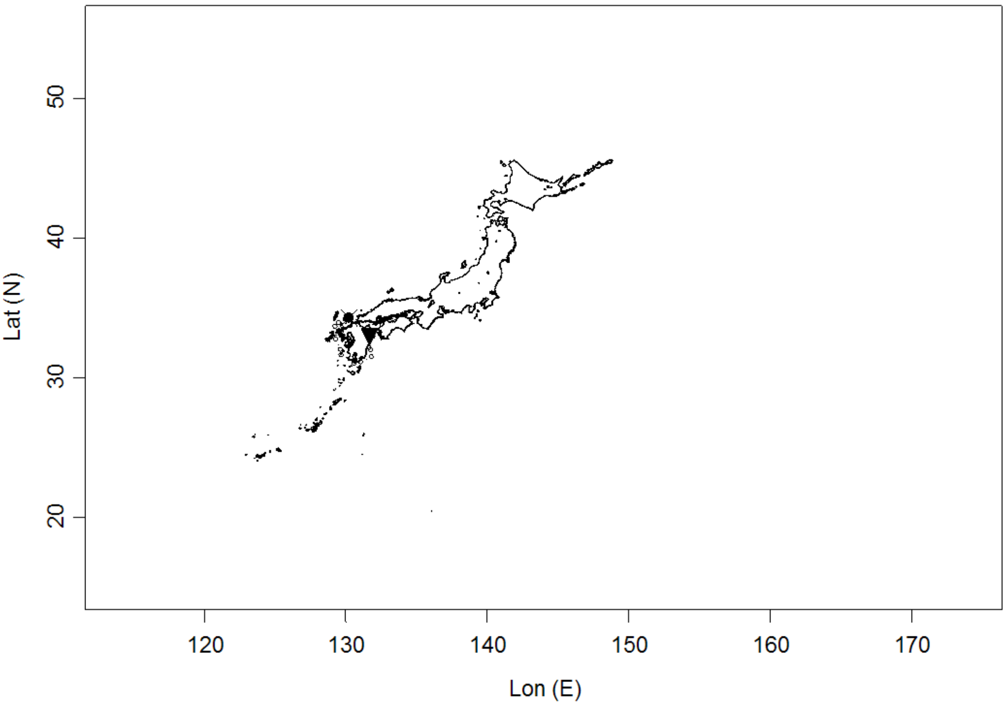

Figure A.7: Track of Eiko.

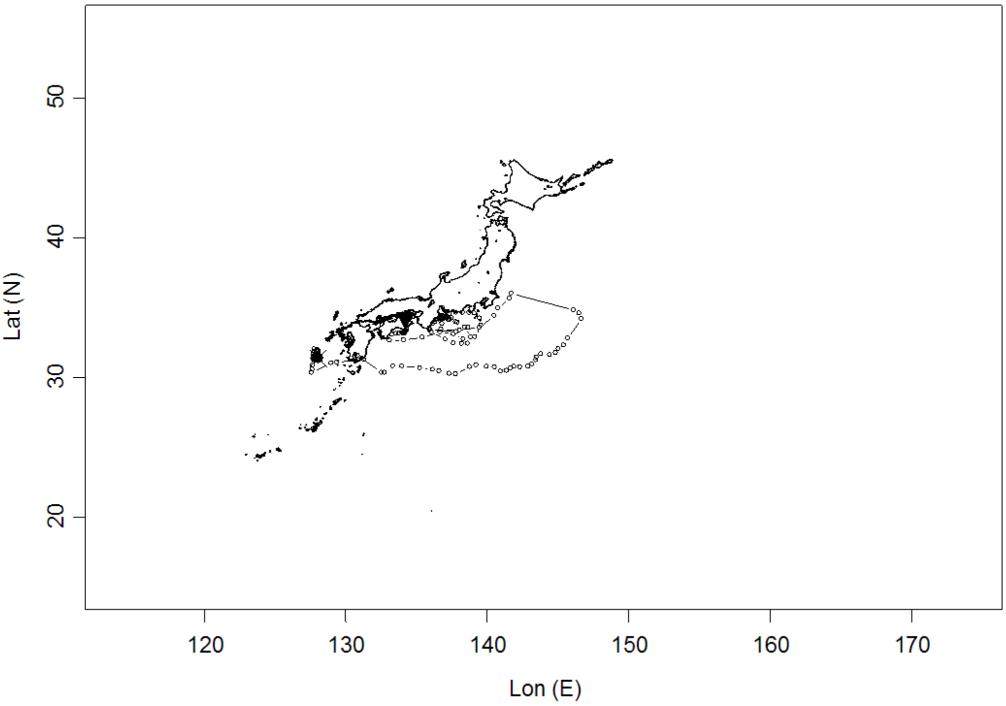

Figure A.8: Track of Fujiko.

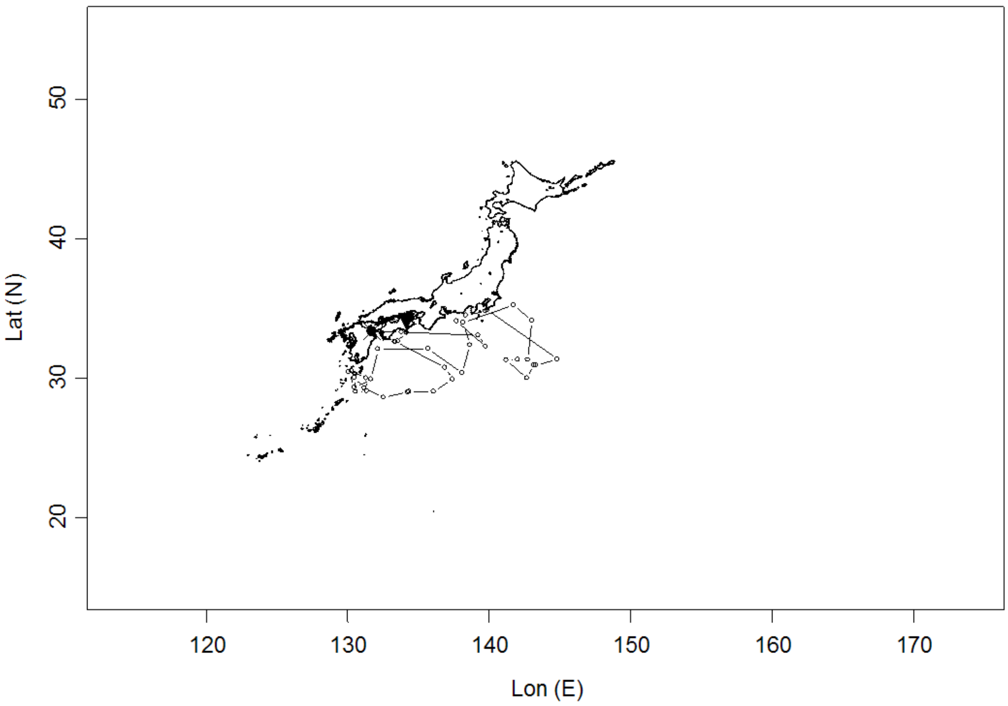

Figure A.9: Track of Gemini.

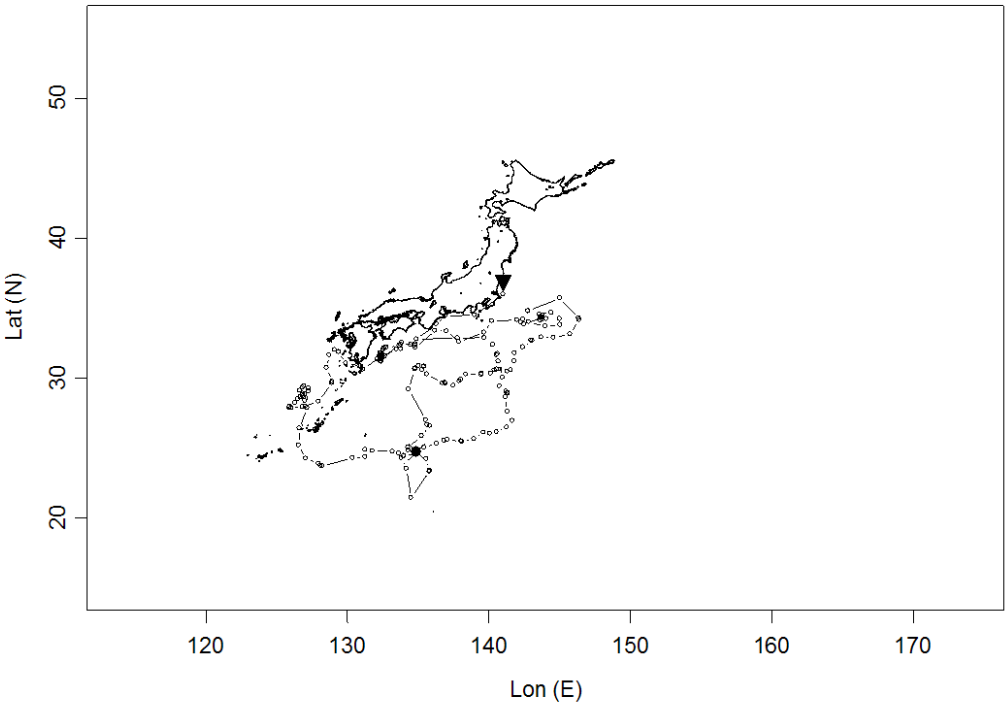

Figure A.10: Track of George.

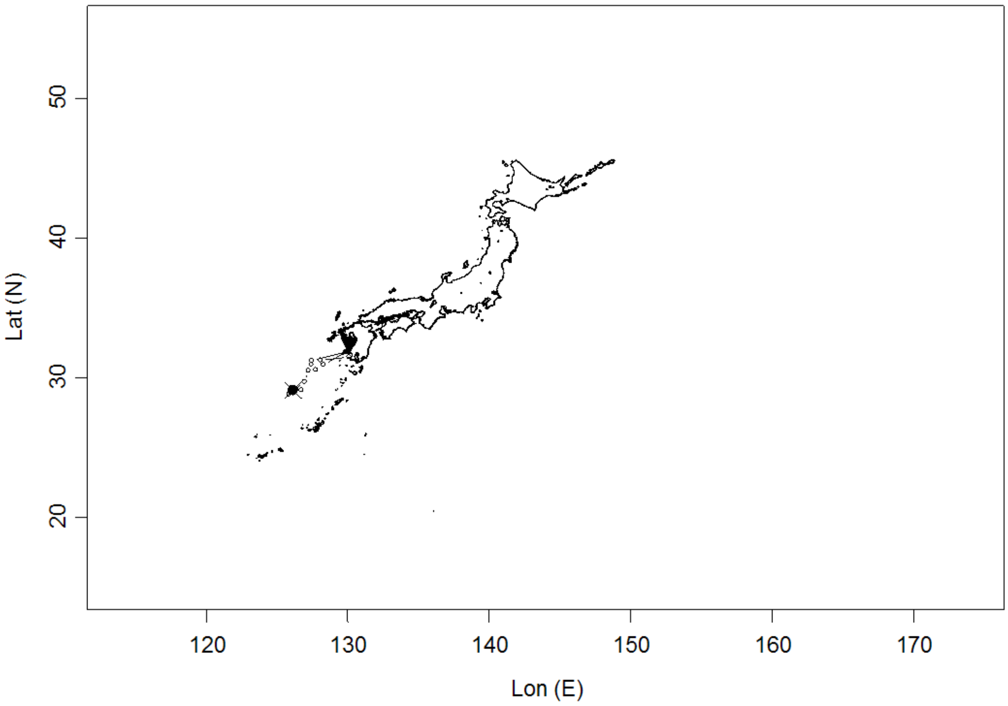

Figure A.11: Track of Haruko.

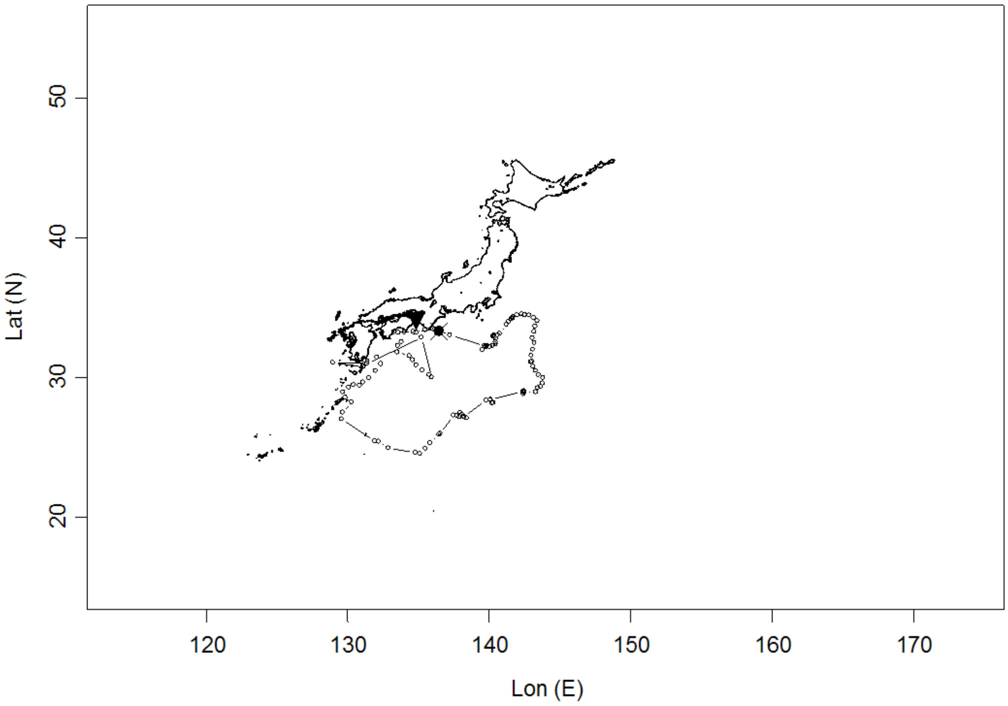

Figure A.12: Track of Kagetsu.

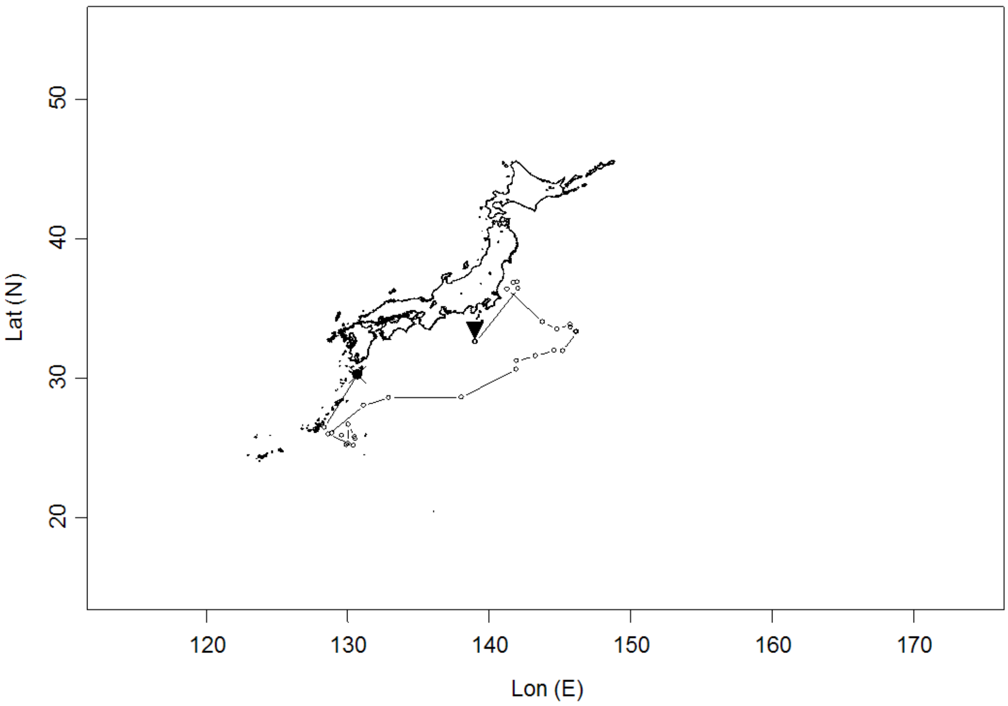

Figure A.13: Track of Kameko.

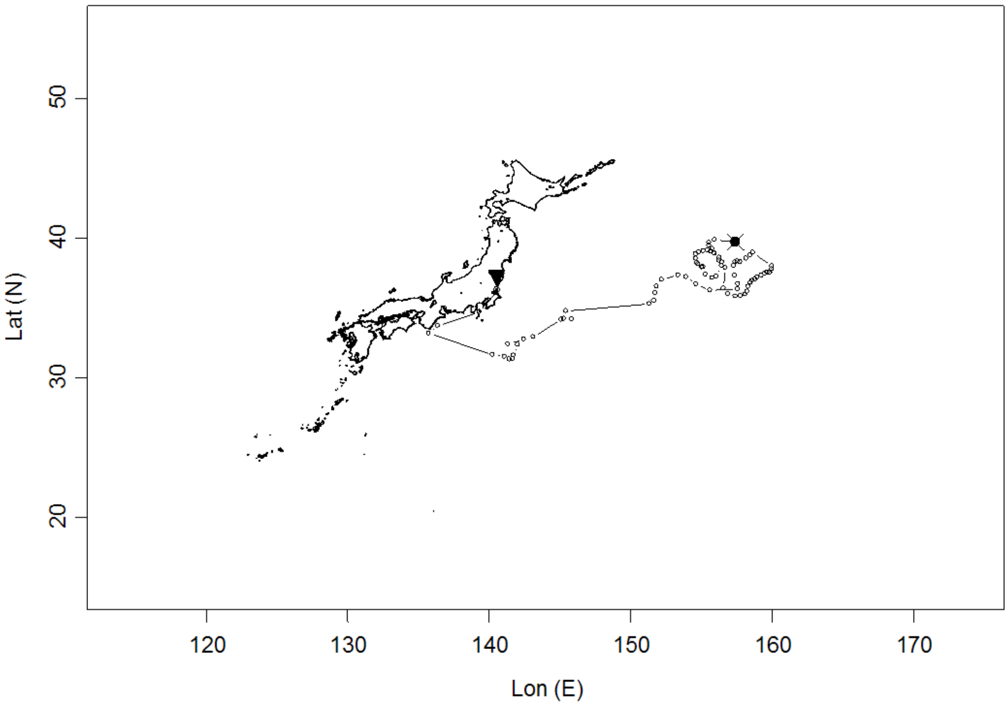

Figure A.14: Track of Kofuji.

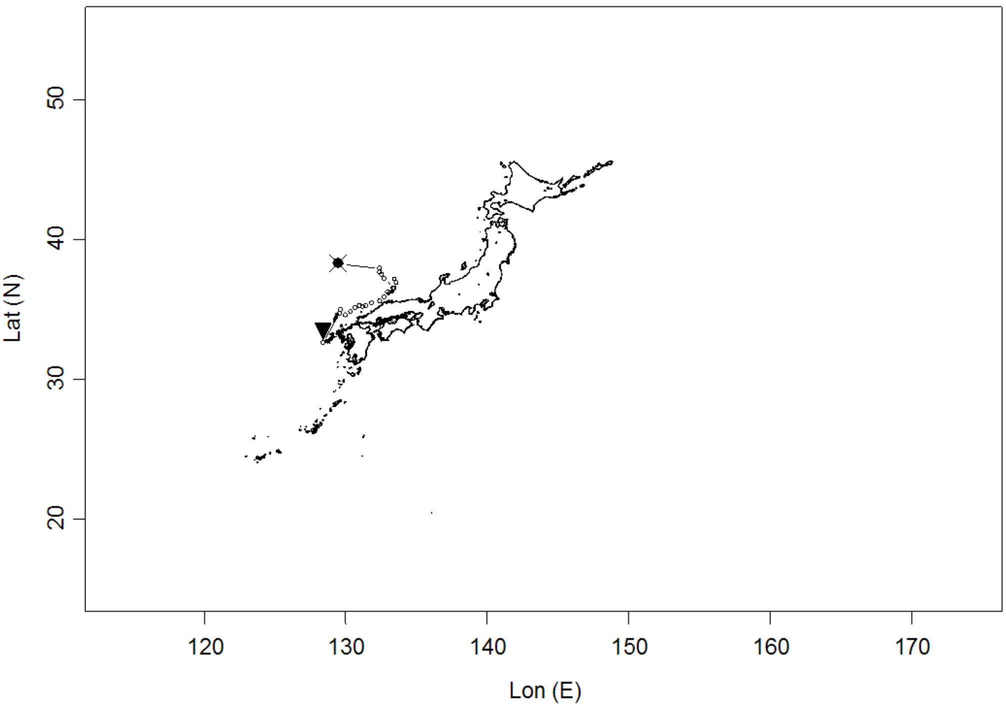

Figure A.15: Track of Leo.

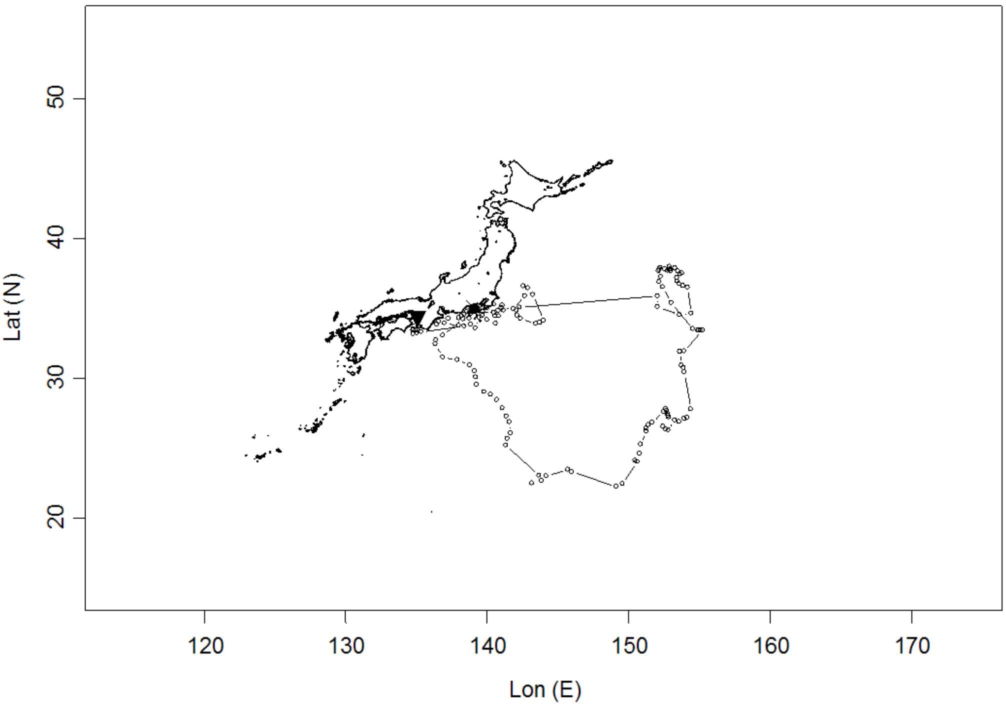

Figure A.16: Track of Midori.

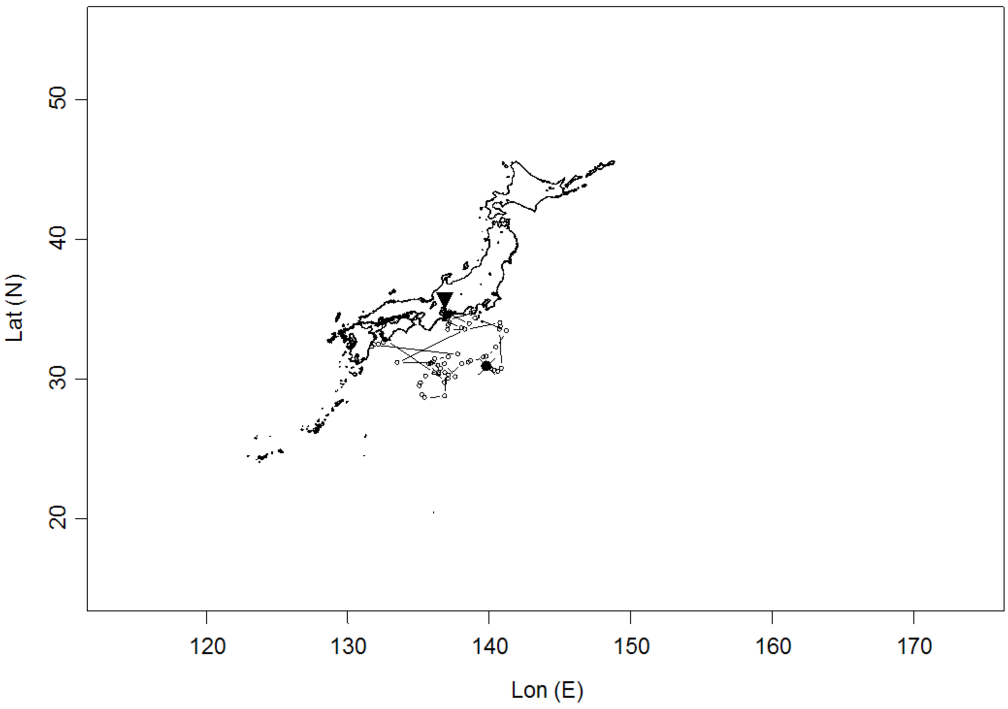

Figure A.17: Track of Mihali.

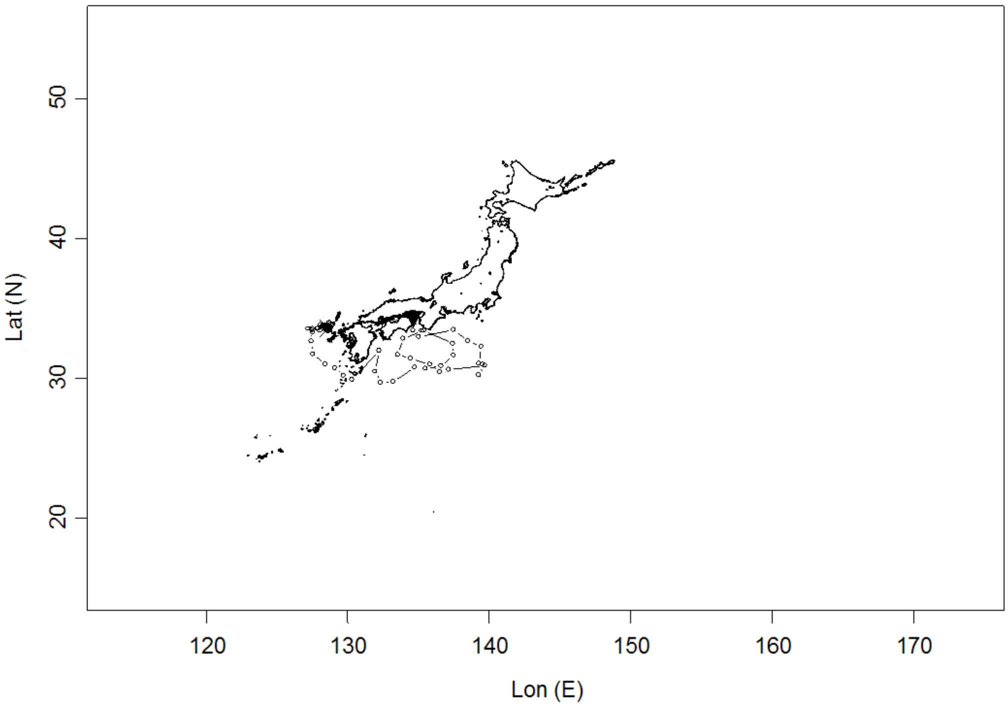

Figure A.18: Track of Mika.

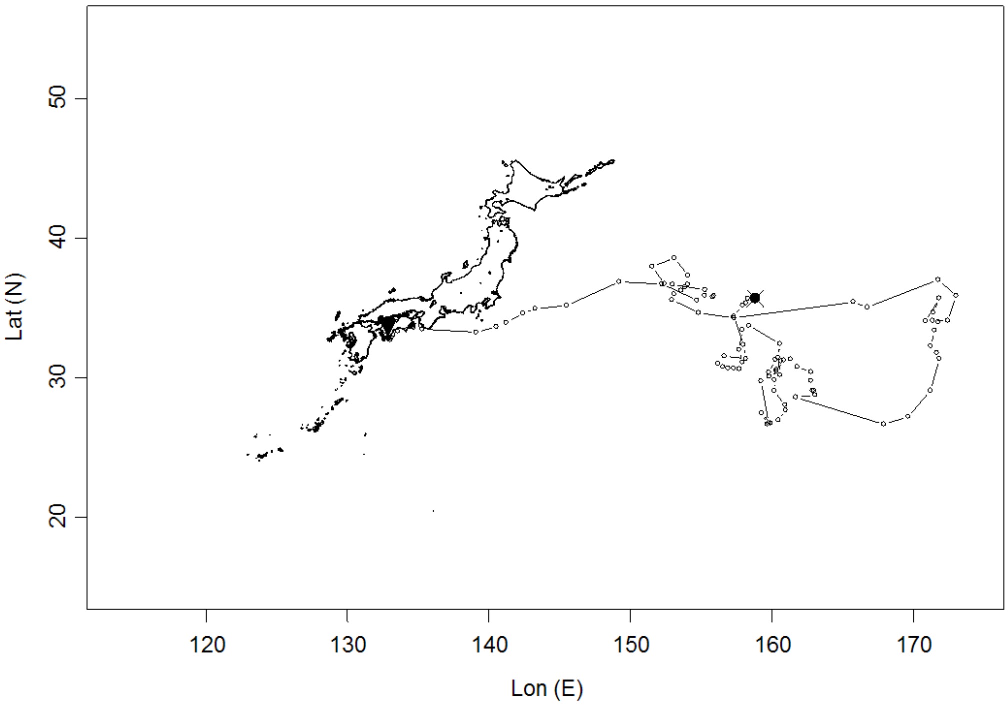

Figure A.19: Track of Otome.

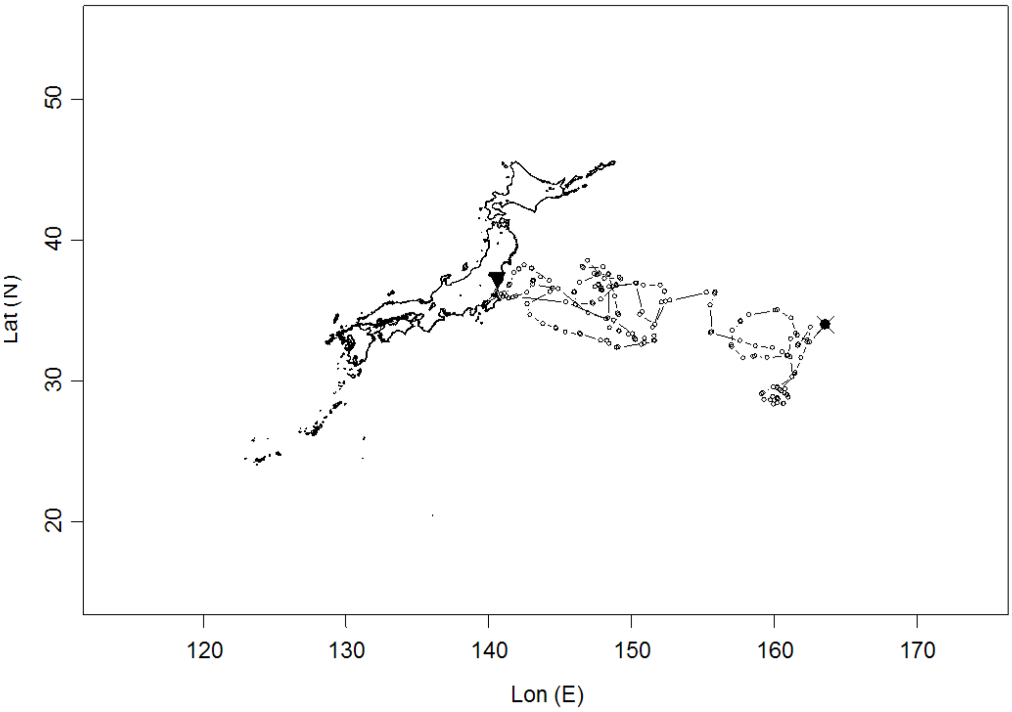

Figure A.20: Track of Sagi.

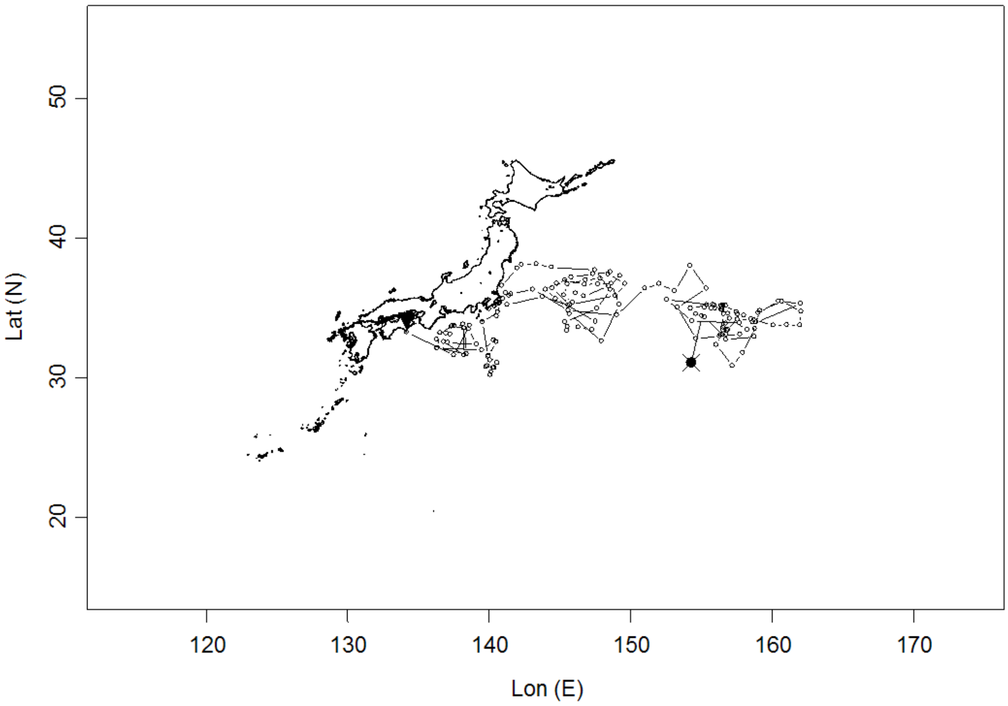

Figure A.21: Track of Sakura.

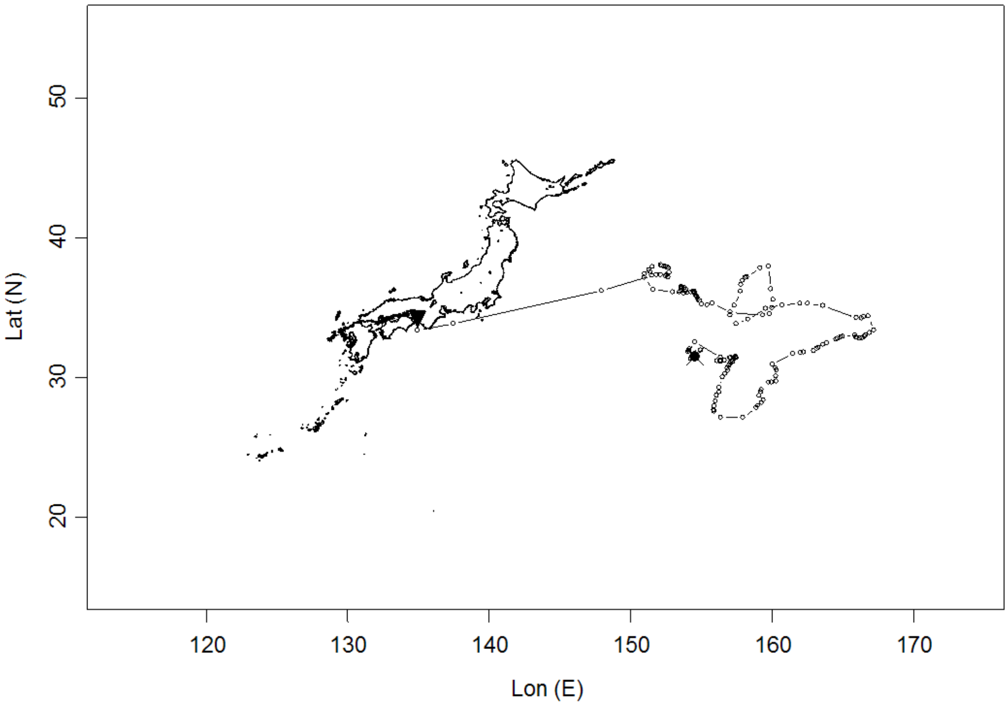

Figure A.22: Track of Sanae.

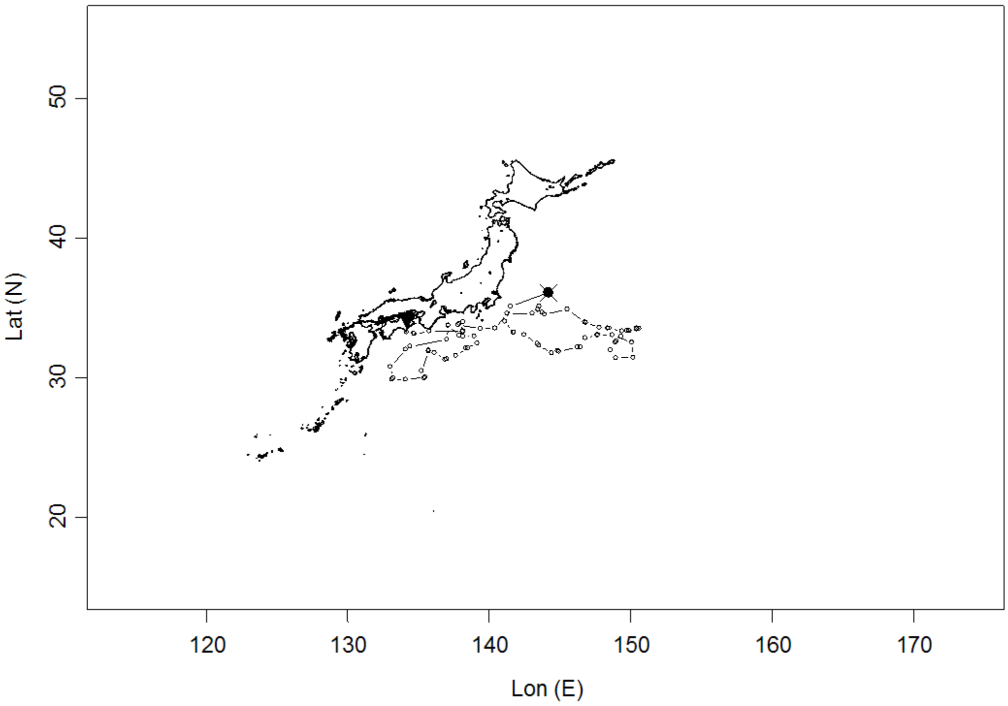

Figure A.23: Track of Sanaejr.

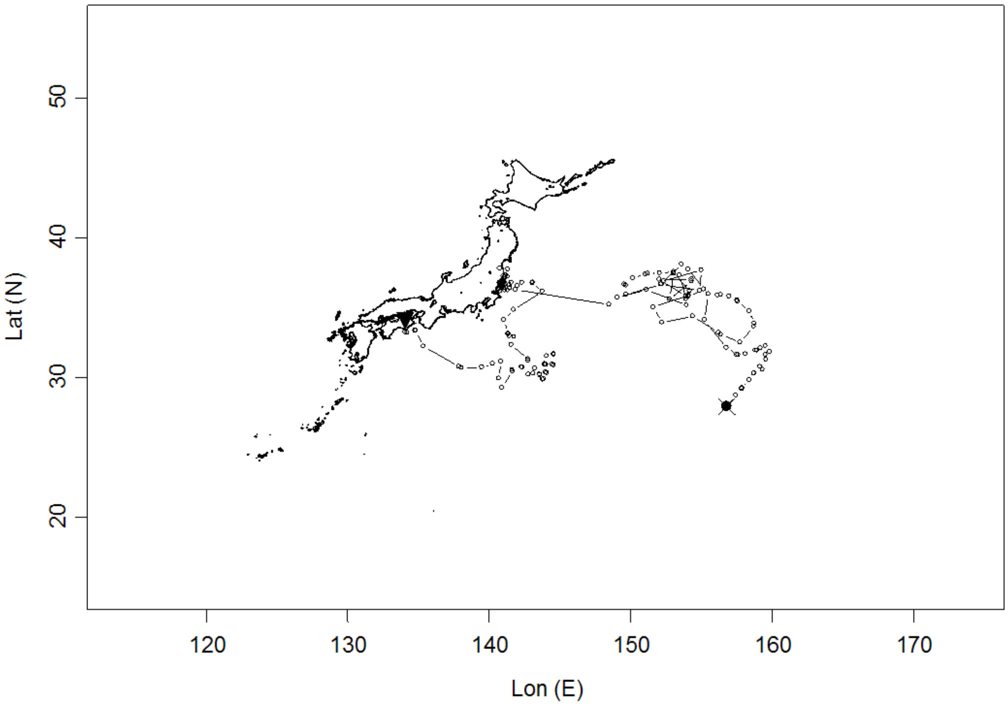

Figure A.24: Track of Taro.

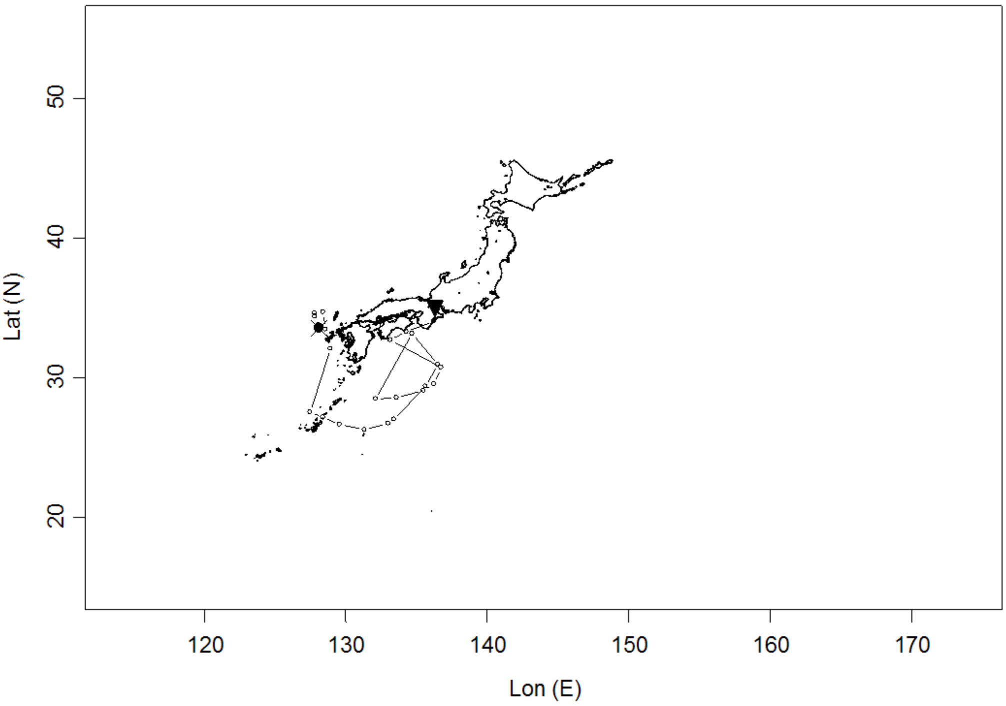

Figure A.25: Track of Taurus.

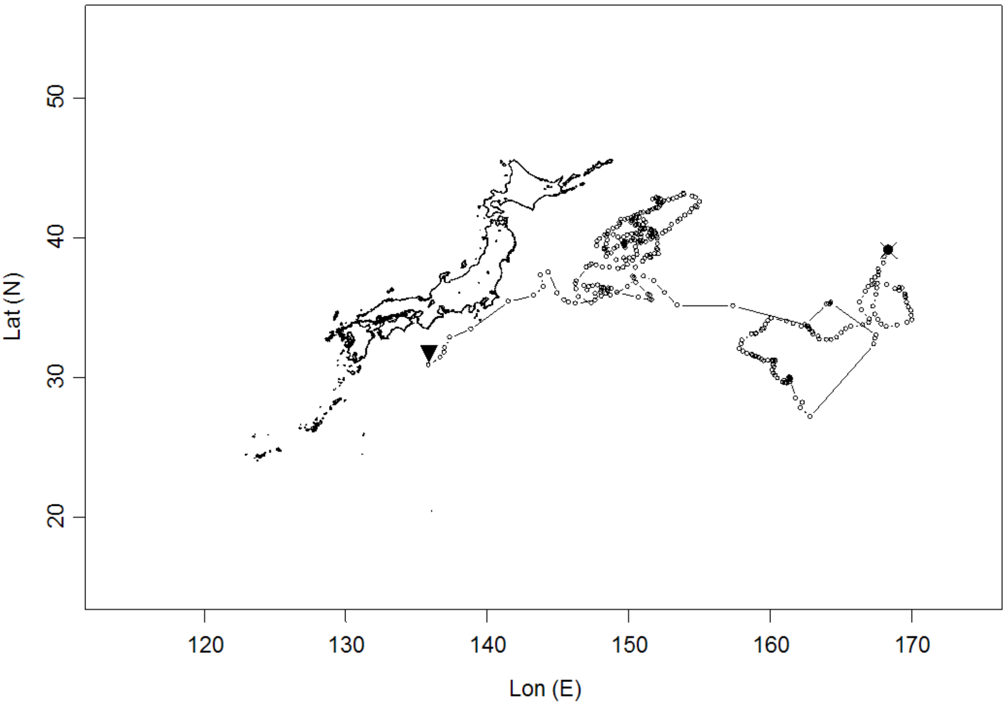

Figure A.26: Track of Tomoyo.

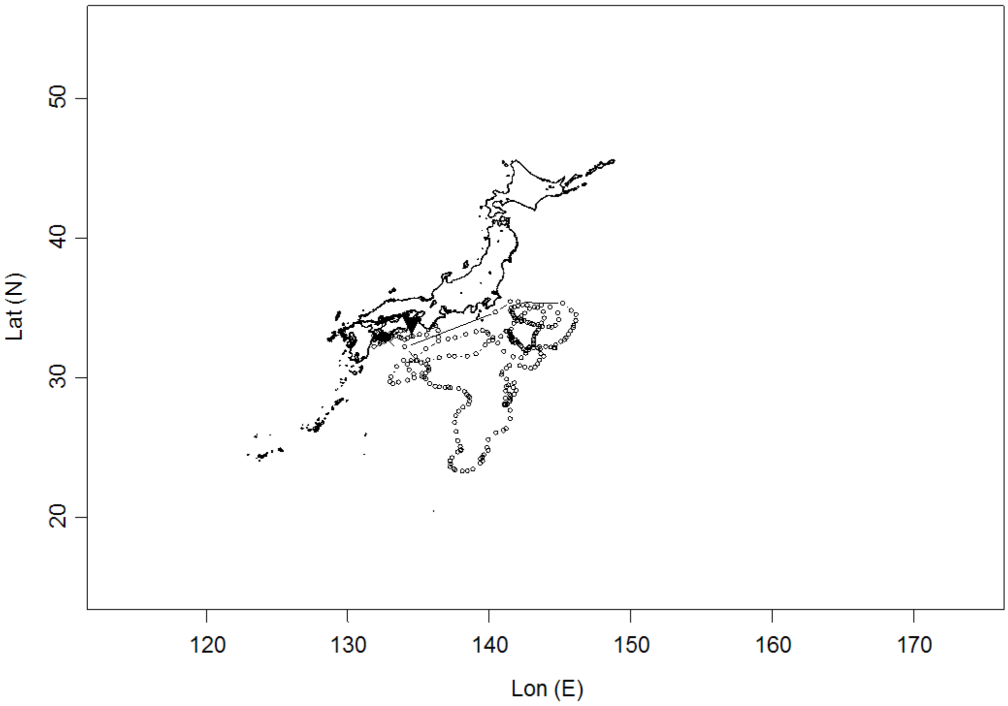

Figure A.27: Track of Umira.

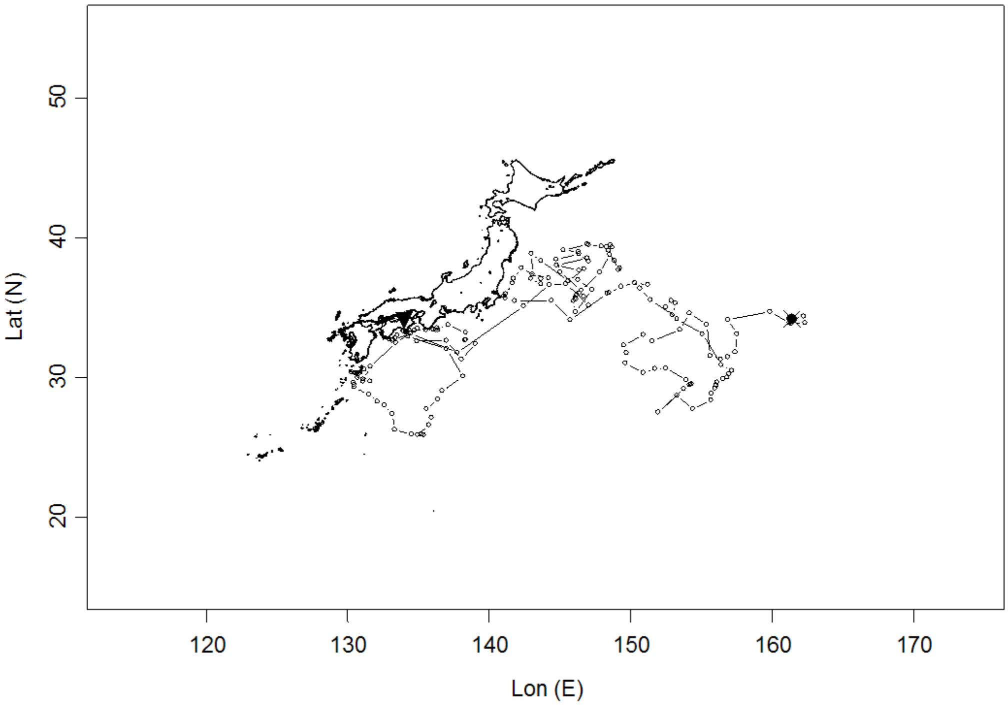

Figure A.28: Track of Virgo.

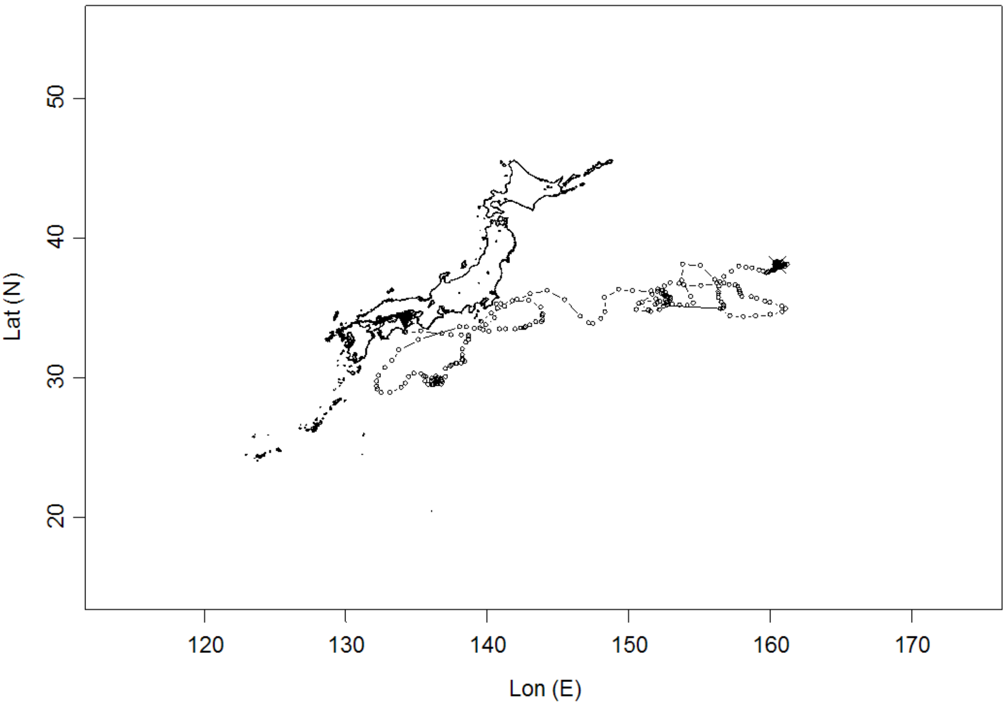

Figure A.29: Track of Yasuko.

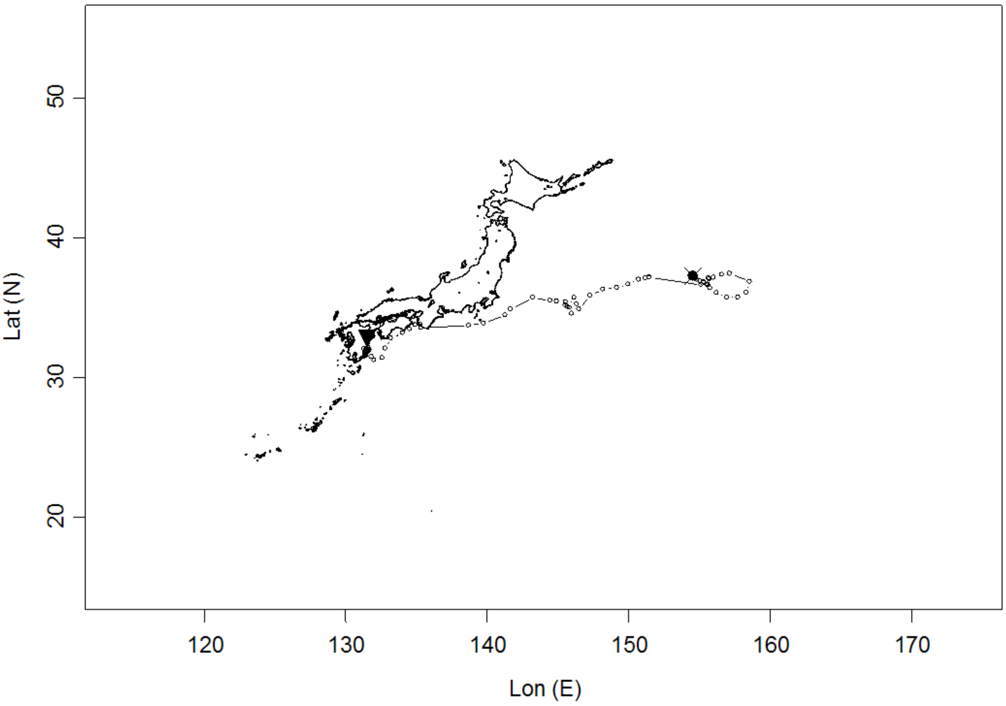

Figure A.30: Track of Zooko.

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