Satellite telemetry elucidates migratory pathways and foraging areas for hawksbill sea turtles,

Eretmochelys imbricata, in the Caribbean

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1   **ABSTRACT**—Adult female sea turtles are highly migratory, moving between foraging and

2   nesting areas that can be thousands of kilometers apart. Conserving sea turtles and their habitats

3   therefore depends on knowledge of space use across these migration-linked environments. Here,

4   we describe migratory behavior of hawksbill sea turtles (*Eretmochelys imbricata*), a globally

5   imperiled species. We used satellite telemetry to characterize the movements of females from

6   nesting areas in Jamaica (n = 4) and Antigua (n = 4), West Indies, over 1998–2001. We mapped

7   migrations and summarized space use during inter-nesting and foraging periods with kernel

8   utilization distributions (UDs) and minimum convex polygons. Seven of eight turtles made post-

9   nesting migrations, with paths ranging 56–1324 km in length, representing straight-line

10   displacements of 68–1206 km. Two turtles sampled in southern Jamaica made short-range

11   migrations within southern Jamaican waters, whereas two from northern Jamaica migrated

12   further to foraging areas in the waters of Belize and Honduras. Three migrants sampled at Long

13   Island, Antigua migrated to St. Eustatius, St. Kitts, and Redonda, respectively, with a fourth

14   individual remaining resident in northeastern Antigua. Inter-nesting movements observed for

15   three turtles produced 50% UDs ranging 12–44 km^2, with centroid depths between 4–13 m.

16   Foraging UDs for seven turtles spanned 8–111 km^2 and 2–161 m in depth. Our results reveal

17   variable migratory strategies, demonstrate international connectivity between hawksbill foraging

18   and nesting habitats, and provide important information for Caribbean conservation efforts such

19   as the design of protected areas or fisheries policies.

20

21   **Keywords** Satellite tracking, inter-nesting, foraging, switching state space model, platform

22   terminal transmitter

INTRODUCTION

23

24

25   Adult sea turtles (Cheloniidae) spend the majority of their lives at sea in foraging habitats

26 where they are often difficult to locate and observe. After accumulating sufficient energy

27 reserves, females periodically migrate to their nesting beaches where observation is much easier.

28 Studies based at nesting beaches form the foundation for most population monitoring programs,

29 but these habitats are visited only briefly by adult females during the nesting season every ~2–4+

30 years (Lutz and Musick 1997). A better understanding of marine habitat use is essential for

31 conservation strategies such as protected area design and threat management (e.g., fisheries

32 bycatch reduction), as well as research efforts, e.g., evaluating the relationship between foraging

33 habitat quality and population dynamics (Ceriani et al. 2017; Hays and Hawkes 2018; Hart et al.

34 2019).

35   The advent and growth of satellite telemetry technology over the past several decades

36 have helped to address knowledge gaps surrounding the movement ecology of sea turtles (Hays

37 and Hawkes 2018). Adult females can be outfitted with satellite transmitters on nesting beaches

38 and then tracked to foraging areas. However, to date, satellite-tracking research has been

39 disproportionately concentrated on certain populations, regional management units (RMUs;

40 Wallace et al. 2010), and species. For example, Hays and Hawkes (2018) synthesized sea turtle

41 satellite tracking research to find that almost half of all transmitters deployed have been placed

42 on loggerhead sea turtles (*Caretta caretta*; Linnaeus, 1758), with the other six species lagging

43 well behind.

44   Hawksbill sea turtles (*Eretmochelys imbricata*; Linnaeus, 1766) in the Caribbean present

45 a clear situation in which more satellite tracking research would be beneficial. Hawksbills nest

46 on nearly all land masses in the Caribbean Sea, often in low densities on relatively small beaches

47 (Eckert and Eckert 2019). Yet, satellite-tracking records documenting post-nesting migrations

48 from regional rookeries have been published for only 85 individual females from 12 nations or

49 insular territories (Horrocks et al. 2001; Troëng et al. 2005; van Dam et al. 2008; Moncada et al.

50 2012; Esteban et al. 2015; Revuelta et al. 2015; Nivière et al. 2018; Hart et al. 2019; Uribe-

51 Martínez et al. 2021; Soanes et al. 2022). As individuals are tracked from additional nesting

52 locations, connectivity with new foraging areas is often revealed, underscoring the need for

53 wider geographic representation in tracking research. Nonetheless, previous work has revealed a

54 preliminary pattern in the distribution of regional foraging areas, and it is apparent that

55 hawksbills can migrate thousands of kilometers and cross through multiple exclusive economic

56 zones (EEZs). This combination of highly migratory behavior and a relatively large number of

57 management authorities makes the management of sea turtles in the Caribbean particularly

58 complex.

59   In the present article, we describe the movements of post-nesting hawksbills tracked from

60 Antigua and Jamaica over 1998–2001. This work was coordinated by the United States National

61 Oceanic and Atmospheric Administration (NOAA) and hinged on collaboration with several sea

62 turtle monitoring programs in the Caribbean region. We revisit this project, part of the Caribbean

63 Hawksbill Tracking Consortium, to disseminate key data and extract as much information as

64 possible for the benefit of hawksbill conservation. The eight satellite tracks represent an

65 important contribution to the regional knowledge base regarding hawksbill habitat use, providing

66 a ~9% increase in the number of post-nesting females tracked from Caribbean nesting beaches.

67 Our goals were to model and map post-nesting movements, characterize habitat use during

68 foraging periods and inter-nesting intervals (i.e., during a nesting season, before migrating), and

69 put results in the context of related work in the region.

70

71 **MATERIALS AND METHODS**

72

73 *Study areas and transmitter deployment*

74

75 We deployed eight satellite transmitters (hereafter platform terminal transmitters; PTTs)

76 during this study—four in Antigua and four in Jamaica. Antiguan hawksbills were outfitted with

77 PTTs (Telonics ST-14 1.0 watt) at Pasture Bay on Long Island (17° 09' 31" N, 61° 45' 19" W), a

78 barrier island to the northeast of mainland Antigua where the Jumby Bay Hawksbill Project

79 (JBHP) has conducted yearly monitoring since 1987 (e.g., Richardson et al. 1999; Kendall et al.

80 2019). Transmission records for these four turtles began when PTTs were deployed in 1998, on

81 12 September (PTT 8455), 16 October (PTT 8456), 25 October (PTT 8552), and 12 November

82 (PTT 8553). Two individuals had nested at Long Island several years previously and were

83 therefore remigrants (Table 1). The other two turtles were observed for the first time in the year

84 of PTT deployment.

85 Two of the Jamaican turtles were outfitted with PTTs in 1998 in the vicinity of Portland

86 Bight (77° 07' 42" W, 17° 43' 31" N) in southern Jamaica. Both turtles were intercepted after

87 nesting on the night of 19 September, one at Little Portland Cay (PTT 8442) and the other at Big

88 Half Moon Cay (PTT 8443). Available transmission records for both began later, on 6 October

89 (preceding data may have been lost during long-term storage, however, we still observed inter-

90 nesting behavior for both turtles). The other two individuals were outfitted with PTTs in 2000 in

91 St. Mary Parish on the northern coast of Jamaica, in the vicinity of Oracabessa and Port Maria.

92 PTT 7677 was deployed on 19 July and PTT 7665 was deployed on 13 September.

93 Information on turtle Inconel flipper tag numbers and nesting histories, where available,

94 is provided in Table 1, along with the number of raw and model-fit locations used in subsequent

95 analyses. Methods for PTT attachment followed those outlined by Balazs and Parker (1998).

96 Researchers waited for a turtle to finish laying eggs and covering its nest, then safely detained it

97 in a wooden box or frame in order to affix the PTTs with polyester resin and fiberglass cloth.

98

99 *State-space modeling*

100

101 We performed all data analyses in program R (version 3.5.2; R Core Team 2018) using

102 RStudio (version 1.1.463; R Team 2015). State-space movement models additionally used JAGS

103 (version 4.2.0; Plummer 2003). Location data from satellite transmitters were provided by the

104 ARGOS satellite system. ARGOS fixes result when turtles surface and expose a PTT's sensors

105 and antenna to air, with longer periods at the surface generally corresponding to more signals

106 sent to satellites and thus better location accuracy. Location fixes additionally depend upon

107 satellites being in position overhead. As a result, transmitted locations are temporally irregular

108 and are each assigned a class representing estimated spatial accuracy (from highest accuracy to

109 lowest: class 3, 2, 1, 0, A, B, and Z; numbered classes range < 250 m to >1500 m in estimated

110 accuracy and lettered classes have no associated estimate for spatial accuracy).

111 We used a Bayesian, hierarchical state-space model (SSM) to accommodate inaccuracy

112 and irregularity in observations and estimate true locations at regular timesteps. Specifically, we

113 fit a switching, first difference correlated random walk (DCRWS) model that uses Markov Chain

114   Monte Carlo (MCMC) sampling to estimate locations and assign each location one of two

115   behavioral states. This type of model focuses on the differences between consecutive locations

116   (i.e., distance and turning angle) as described by Jonsen et al. (2005). The model assumes two

117   distinct behavioral states, each with different movement parameters, and discriminates (i.e.,

118   switches) between the two states based largely on patterns in swimming speed and direction.

119   This SSM approach is useful for quantitatively differentiating between migratory and non-

120   migratory states—migrations are associated with straighter paths and higher swim speeds (state

121   1), whereas non-migratory behavior entails high turning angles and slower speeds (state 2). The

122   switching SSM has been used extensively to model movement data for sea turtle migrations

123   (e.g., Jonsen et al. 2007; Hart et al. 2019, 2020).

124   We first used the R package 'argosfilter' to filter raw location data by removing

125   erroneous satellite fixes that would produce swimming speeds above a conservatively high

126   velocity of 2.5 m s^{-1} (Freitas 2012). We then used the remaining data to implement the SSM with

127   the R package 'bsam' (Jonsen et al. 2005; Jonsen 2016). The eight tracks were modeled in a

128   single, hierarchical run. This joint approach entails the estimation of identical movement

129   parameters for all individuals and can significantly improve state estimation by pooling statistical

130   power (Jonsen 2016). We specified the model to estimate locations every eight hours. MCMC

131   settings were designated for an adaptation and burn-in phase of 10,000 samples each followed by

132   10,000 posterior samples that were thinned by five. We evaluated model convergence by

133   assessing stationarity in the posterior samples and monitoring for well-mixed MCMC chains,

134   low within-chain sample autocorrelation, and sufficiently low Brooks–Gelman–Rubin shrink

135   factors (below 1.1; Brooks and Gelman 1998).

136

137   *Summarizing space use*

138

139   We characterized patterns in movement during migratory and non-migratory periods

140   based on the SSM-generated dataset of model-fit locations for the eight turtles. We first used the

141   median behavioral state (either 1 or 2) from the model posterior samples to assign each location

142   to a turtle's inter-nesting, migratory, or foraging period. To summarize movements during

143   migratory periods, we calculated the distance each hawksbill traveled along its migratory path.

144   Additionally, we computed the straight-line distance (i.e., displacement) between the centroids of

145   each turtle's foraging and inter-nesting range; if no inter-nesting behavior was observed, we

146   instead used the first location of the migratory path.

147   We characterized space use during inter-nesting and foraging periods with home range

148   analyses from the R package 'adehabitatHR' (Calenge 2006). For all non-migratory periods, we

149   computed 50% and 95% utilization distributions (UDs) with kernel density estimation, in

150   addition to 95% minimum convex polygons (MCPs). Kernel UDs use a smoothing parameter to

151   estimate the true area of use based on all observed locations (i.e., satellite fixes), accounting for

152   where fixes are most concentrated (Worton 1989). Here, we used a 50% UD to represent the

153   inner core area of use and the 95% UD for the full extent of home range movements (excluding

154   5% to reduce bias from outliers). In contrast, a MCP more simply bounds a polygon to the

155   outermost locations, here after excluding the outer 5% to remove outliers. Thus, MCPs provide a

156   less-manipulated (i.e., no smoothing function) representation of the full home range and are also

157   useful for comparing results to previous studies utilizing this method. We did not delete model-

158   fit locations on land before computing UDs and MCPs to avoid introducing user bias, as these

159   locations could be closer to true turtle positions than a given point in water. When generating

160   maps, we excluded UD and MCP areas that overlapped land by placing home range polygons

161   underneath land polygons. We computed centroids for the 50% UDs (both inter-nesting and

162   foraging) to measure straight-line migration distances. We also used these centroids to examine

163   water depth, extracting depth data from the 2020 General Bathymetric Chart of the Oceans (15

164   arc-second resolution; GEBCO Compilation Group 2020). At this resolution, the depth data

165   presented are a coarse representation of bathymetry in these areas. In one case, UD geometry

166   resulted in an inter-nesting centroid located on land (PTT 7665); we assigned this centroid the

167   value from the nearest raster cell containing a depth below sea level.

168

169   **RESULTS**

170

171   *Transmitter deployments*

172

173   Satellite transmissions for the eight hawksbills spanned a mean ± SD of 353 ± 103 days

174   per turtle (Table 1). Transmissions began on the start date of the inter-nesting period for turtles

175   that exhibited this behavior, otherwise the start of the migration represents the beginning of

176   transmissions (Table 2; Table 3). PTT 8553 is the exception, because we assigned all locations to

177   the foraging period for this individual (Table 3). Three of the six PTTs deployed in 1998 ceased

178   transmitting on 3 December 1999, when service was stopped due to financial considerations. All

179   other PTTs, including the two from 2000, ceased transmitting on their own, likely due to loss of

180   battery power, damage, or failure (although mortality cannot be ruled out).

181   PTT 8553 did not provide usable satellite location data over two stretches of >50 days

182   (e.g., 1 July–28 August 1999). During these times it provided only locations of quality Z, the

183 highest error designation, and no associated coordinates. Therefore, we split this track into three

184 segments and modeled each separately so that the SSM would not estimate locations during long

185 stretches with no raw data to inform the model. We then combined the three sets of model-

186 estimated behavioral states and locations for further analysis.

187

188 *Migrations*

189

190   Seven of the eight hawksbills exhibited post-nesting migrations, with paths ranging 56–

191 1324 km in length (mean ± SD = 357 ± 488 km; Table 2). One turtle tagged in northern Jamaica

192 exhibited two distinct migrations (PTT 7665), first traveling 321 km to forage in Jamaican

193 waters for ~71 days and then migrating another 403 km to a destination in Nicaragua's EEZ (Fig.

194 1). For migratory summary statistics presented here, we summed the two resulting path lengths

195 and computed an overall straight-line distance to its final foraging home range. Notably, the two

196 individuals tagged in northern Jamaica had straight-line migration distances >600 km, whereas

197 all other individuals had migratory distances <140 km (Table 2; Fig. 1; Fig. 2; Fig. 3). Of the

198 seven migrants, three did not exhibit inter-nesting behavior (detailed below), and therefore we

199 calculated their straight-line migration distances using the first location of the migratory path

200 (not the inter-nesting centroid); these three first locations were <200 m from shore and thus did

201 not introduce appreciable bias as compared to using centroids to compute migration distances.

202   The two long-range migrants from northern Jamaica established foraging areas in

203 southern Belizean and eastern Honduran waters (Fig. 1). The double migrant from northern

204 Jamaica (PTT 7665) first foraged in an area in the northwestern portion of Pedro Bank, Jamaica,

205 and made its second migration to an area approximately 200 km west of Serranilla Bank,

206 Colombia. The other female from northern Jamaica (PTT 7677) foraged near Placencia, Belize,

207 easternly adjacent to Lark Caye. The two individuals tagged in Portland Bight remained in

208 southern Jamaican waters, migrating to the relatively shallow areas of Blossom Bank and

209 northeastern Pedro Bank (Fig. 2). The migrations of all four Jamaican turtles were contained

210 within the Nicaraguan Rise, an oceanic ridge that begins in eastern Honduras and northern

211 Nicaragua and stretches northeast to Jamaica. The three hawksbills the migrated from Antigua

212 traveled relatively short distances to coastal areas near St. Eustatius, St. Kitts, and Redonda,

213 respectively (Fig. 3). Redonda is an uninhabited, small island (< 3 km^2) located to the southwest

214 of Antigua and is part of the nation of Antigua and Barbuda.

215   The fourth turtle tracked from Antigua remained resident in northeastern waters around

216 Long Island (Fig. 4). The SSM did not detect any switches in behavior for this individual and

217 therefore estimated a non-migratory state for all locations. Biologically speaking, over 318 days

218 the turtle must have transitioned from a nesting state to a foraging state, as the nesting season for

219 hawksbills does not exceed three months (Bjorndal et al. 1985; Kendall et al. 2019). Model-fit

220 locations revealed that the turtle stayed around Long Island, Antigua during the whole period of

221 satellite transmissions. Thus, we infer that this was a resident turtle, and any small migration

222 went unobserved, perhaps occurring during a gap in transmissions. We assigned all model-fit

223 locations as the foraging period because the turtle was sampled on 14 November, which is at the

224 end of the nesting season (Hart et al. 2019). However, it is likely that this period hosted both

225 inter-nesting and foraging behavior (Table 3).

226

227 *Inter-nesting and foraging areas*

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229   Three turtles were outfitted with transmitters at the end of their nesting season and SSM

230   results suggested that they immediately migrated, so no information on their inter-nesting

231   movements was available (Table 3). Given modeling results, we did not observe inter-nesting

232   movements for a fourth, nonmigratory individual from Antigua (PTT 8553). The four individuals

233   with inter-nesting data—three from Jamaica and one from Antigua—exhibited inter-nesting

234   behavior for a mean of 41 ± 19 days (Table 3; Fig. 4; Fig. 5). Hawksbills deposit clutches

235   approximately every two weeks within a nesting season (Bjorndal et al. 1985; Kendall et al.

236   2019), so these turtles likely transmitted over periods spanning 1–4 clutches before migrating.

237   Inferences into the inter-nesting home range of the single northern Jamaican individual with

238   inter-nesting behavior (PTT 7665) were limited by sample size. This turtle's 50% UD was larger

239   than its 95% MCP, potentially indicating an insufficient sample size for reliable home range

240   estimation; we present these inter-nesting data but excluded them from summary statistics

241   reported here. For the three other turtles with inter-nesting information, we observed

242   considerable variation in home range sizes; 50% kernel UDs averaged 27.1 ± 16 km^2, while 95%

243   UDs covered a mean of 133 ± 69 km^2 and 95% MCPs had a mean area of 90.9 ± 49 km^2. Mean

244   depth at the three inter-nesting UD centroids was 7.33 ± 4.9 m.

245   We documented nine foraging periods for the eight hawksbill females, with one

246   individual from northern Jamaica exhibiting two distinct foraging phases. Foraging periods,

247   including that of the non-migratory Antiguan individual, spanned a mean of 286 ± 144 days. We

248   note that observed foraging and inter-nesting durations were constrained by transmitter function,

249   and not necessarily turtle behavior (i.e., true foraging durations before a subsequent migration

250   would be much longer). The nine foraging areas that we documented had a mean 50% UD area

251   of 39.2 ± 38.5 km^2 (Table 3). Much of the variation in 50% UD area was driven by three

252   individuals with exceptionally large UD sizes: the two long-range migrants from northern

253   Jamaica and the non-migratory individual from Antigua. When excluding these three turtles,

254   50% UDs averaged 11.5 ± 3.4 km^2. The nine foraging 95% UDs averaged 272 ± 260 km^2, while

255   95% MCPs covered a mean of 210 ± 200 km^2. Mean depth at the nine foraging centroids was

256   31.8 ± 50 m. Eight of the nine foraging UDs had centroids with a depth of <35 m, but one

257   individual (PTT 8456) foraged near Redonda with a centroid depth of 161 m. The bathymetry

258   around Redonda features a rapid drop-off running north-south on the island's western side, and

259   the centroid was located in this steep area (Fig. 3).

260

261   **DISCUSSION**

262

263   *Migratory behavior*

264

265   Our results provide the first published information for hawksbill sea turtles making post-

266   nesting migrations from Jamaica and Antigua. We tracked eight turtles, of which four remained

267   to forage within the EEZ in which they nested, two crossed a single international boundary, and

268   two crossed two boundaries (Fig. 6; Fig. 7). These data inform management efforts along

269   migratory corridors and at nesting or foraging locations, especially in the context of previously

270   published satellite tracking data for the region (discussed below). For example, identifying home

271   ranges can facilitate investigation of overlap with regional fishing effort (Dunn et al. 2010),

272   which may inform the design of fisheries policies and marine protected areas. The migratory

273   behavior we documented also was characterized by considerable variation. Whereas five of

274   seven migrants made relatively short-range migrations (path lengths <130 km), two exhibited

275   substantially longer movements (>700 km), with one turtle traveling >1300 km. Interestingly, all

276   seven migrations featured a strong westward heading (with variation on the north-south axis),

277   adding support to the idea that post-nesting females make use of prevailing currents when

278   returning to foraging habitats (van Dam et al. 2008; Horrocks et al. 2011).

279   The two long-range migrants were both tagged in northern Jamaica. One stopped to

280   forage for over two months in Pedro Bank, within Jamaica's EEZ, before migrating to a final

281   destination in the EEZ of Honduras (Fig. 1). This site lies within a large area of the Nicaraguan

282   Rise that may represent a regional foraging hotspot given the significant proportion of female

283   hawksbills tracked to date that have migrated there (Nivière et al. 2018; Hart et al. 2019; Uribe-

284   Martínez et al. 2021). The other long-range Jamaican migrant traveled to southern Belize, where

285   individuals of multiple sea turtle species are known to forage, including hawksbills (Uribe-

286   Martínez et al. 2021). It is interesting that both long-distance migrants from our study were

287   tagged in the same area of northern Jamaica and represent all individuals sampled from that site.

288   Future satellite tracking efforts may be merited in this location to determine whether this reflects

289   a more general trend or is an artifact of small sample size. In contrast, short-range migrants

290   tracked from southern Jamaica remained in the national EEZ. While hawksbills of varying sizes

291   have long been known to forage in Jamaican waters (Haynes-Sutton et al. 2011), these satellite

292   tracks provide the first evidence of post-nesting hawksbills remaining to forage as national

293   residents. The three turtles completing migrations from Antigua also exhibited relatively short-

294   range movements—two migrated to another potential foraging hotspot in the Leeward Islands,

295   spanning Anguilla to Nevis (Hart et al. 2019; Soanes et al. 2022), and the third established

296   migratory connectivity between Antigua and the island of Redonda (still within Antigua and

297   Barbuda's EEZ), where hawksbill foraging has long been known to occur (Fuller et al. 1992).

14

298   In the context of previous satellite-tracking work, our study adds resolution to a spatial

299   pattern emerging for foraging post-nesting females in the Caribbean, which may reflect patterns

300   of adults more broadly. Hart et al. (2019) described the movements of 31 nesting females tracked

301   from St. Croix, U.S. Virgin Islands and summarized foraging destinations for 33 other females

302   across six studies (see Figure 6 in Hart et al. 2019). Nivière et al. (2018) contributed information

303   for another 11 adult females tracked from Martinique, French West Indies, Uribe-Martínez et al.

304   (2021) tracked three individuals from Quintana Roo, Mexico, and Soanes et al. (2022) tracked

305   seven from Anguilla. Satellite-tracking research is complemented by studies analyzing flipper

306   tag returns, where tag numbers are physically observed and movements inferred based on where

307   turtles were originally tagged (Meylan 1999; Horrocks et al. 2011; Barrios-Garrido et al. 2020).

308   Combined, these studies establish a pattern of adult female hawksbills inhabiting neritic areas

309   that fringe the deeper waters of the Caribbean Basin to the west, north, and east (Hart et al.

310   2019). Moreover, they suggest highly variable migratory patterns. Many hawksbills migrate

311   >2,000 km between nesting and foraging habitats, crossing through several EEZs. For instance,

312   three hawksbills from St. Croix migrated west across the Caribbean Sea to an apparent foraging

313   hotspot in the Nicaraguan Rise (Hart et al. 2019), and tags from females nesting in Barbados

314   have been returned from Nicaragua and Honduras (Horrocks et al. 2011). In contrast, many other

315   individuals have been recorded making shorter migrations in the range of hundreds of kilometers

316   or less (e.g., Horrocks et al. 2001) and/or remain resident near the island where they nest (e.g.,

317   Hart et al. 2019; Moncada et al. 2012). Similar short-range migrations have been documented in

318   areas of the Pacific (Mortimer and Balazs 2000; Parker et al. 2009). In the present study, we

319   observed migratory behavior that spanned this continuum.

320

321   *Inter-nesting and foraging home ranges*

322

323   The characteristics of the inter-nesting and foraging home ranges that we described for

324   eight individuals provide useful insight into patterns in habitat use for adult female hawksbills in

325   the Western Atlantic. Here we focus discussion on 50% UDs, as these should be less sensitive to

326   outlier behavior than 95% MCPs or UDs. We documented inter-nesting 50% UDs for three

327   turtles, one from southern Jamaica and two from Antigua. UD sizes ranged 12–44 km^2, with a

328   mean of 27 km^2. Mean depth at the centroids of the three inter-nesting UDs was 7 m, with a

329   maximum of 13 m. These home range sizes fall squarely within the range of two previous studies

330   that provide a basis for comparison. Using the same modeling methods (i.e., a switching SSM),

331   Hart et al. (2019) documented inter-nesting 50% UDs between 9.6 and 77.7 km^2 for 25 turtles

332   from St. Croix, with a mean depth of 16.2 m. Revuelta et al. (2015) did not use comparable SSM

333   methods, but used ARGOS data to describe inter-nesting 50% UDs for seven individuals from

334   the Dominican Republic with a mean area of 13.2 km^2.

335   Our sample size for foraging UDs was larger because we observed this behavior in all

336   eight turtles. The nine foraging 50% UDs we documented spanned from 8 to 111 km^2, with a

337   mean of 39 km^2. With the exception of one turtle whose foraging centroid had a depth of 161 m,

338   all centroids were shallower than 35 m. It is interesting that the three largest foraging UDs were

339   produced by the two longest-distance migrants (from northern Jamaica), including both UDs

340   exhibited by the turtle exhibiting two migrations. It is possible that longer-ranging migrants

341   require more time to locate their preferred foraging home range after switching to nonmigratory

342   behavior in the vicinity of their foraging area, which could result in an expanded home range

343   estimate. This potential association between long migrations and large foraging home ranges

344   may merit further investigation. Our results were largely consistent with the previous studies by

345   Hart et al. (2019) and Revuelta et al. (2015), although the largest foraging 50% UD that we

346   documented fell outside the range of the cited work. Hart et al. (2019) described foraging 50%

347   UDs for 31 individuals, ranging in area from 6.3 to 95.4 km^2 and with a mean depth of 65.8 m.

348   Revuelta et al. (2015) described eight foraging UDs with a mean area of 16.2 km^2.

349   Our results from home range analyses add to a body of evidence suggesting that variation

350   in both inter-nesting and foraging area sizes is common. Future work elucidating the drivers of

351   this variation would be valuable to the management of hawksbill habitat in the region, as clearly

352   some hawksbills occupy much larger areas while nesting or foraging and thus would benefit

353   from expanded habitat protection measures compared to turtles with smaller ranges. Drivers of

354   home range variation could include factors such as site-specific availability and distribution of

355   food sources and shelter areas, as well as potential competitive interactions with other turtles and

356   marine fauna. Individual behavior (i.e., movement tendencies and habitat preferences) likely also

357   plays a role in documented variation. Building on ARGOS datasets with higher accuracy, GPS-

358   enabled transmitters would help to refine our understanding of home range behavior (Dujon et al.

359   2012). For instance, Walcott et al. (2012) used GPS data to examine fine-scale movement

360   patterns of hawksbills in Barbados during intervals between successive nests, identifying distinct

361   phases of movement during which nesting females moved to and from small residency areas that

362   ranged only 0.01–0.40 km^2. Expanding knowledge of these finer scale movement patterns,

363   including within foraging areas, would be highly useful to site-specific management and lend

364   insight into drivers of behavioral variation.

365

366   *Conclusions*

367

368   Our findings from satellite tracking eight individuals are consistent with an emerging

369   spatial pattern for the migratory and foraging behavior of adult female hawksbills in the

370   Caribbean. We also described post-nesting migratory connectivity to three foraging locations to

371   which hawksbill had not been tracked in previous literature (Blossom Bank, Jamaica; Pedro

372   Bank, Jamaica; Redonda, Antigua and Barbuda). This result highlights the need for tracking

373   from additional nesting areas to better characterize connectivity between hawksbill nesting and

374   foraging areas in the Caribbean. Extremely little is known about the distribution of adult males in

375   this region due to the difficulty of accessing this population sector, but we speculate that the

376   foraging distribution of adult females may serve as a useful proxy for adult males given similar

377   habitat preferences. Whether males exhibit similar migratory patterns merits further study.

378   Hawksbills are highly imperiled in this region (Mortimer and Donnelly 2008) and face threats

379   from human activities and global environmental change (Hamann et al. 2013; Maurer et al. 2015,

380   2021a, 2021b, 2022). Because the recovery of the Caribbean population will depend in part upon

381   survival of adults, especially considering their high reproductive value (Crouse et al. 1987),

382   identifying and protecting adult migratory and foraging habitats should be among our top

383   priorities for conserving this species.

384

385   **ACKNOWLEDGEMENTS**

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396

397 **LITERATURE CITED**

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591   **TABLES AND FIGURES**

592

593 TABLE 1. Summary of satellite transmitter deployments. A "•" denotes information was not

594 available. Days tracked indicates the span of satellite transmissions rounded to the nearest whole

595 day. Raw fixes refer to the number of ARGOS locations (post filtering) that were used to model

596 movements. IN (inter-nesting), migration, and foraging points display the number of switching

597 SSM model-estimated locations assigned to each period (three points estimated per day).

PTT ID	Days tracked	Raw fixes	IN points	Migration points	Foraging points	Flipper tag no.	Annual nesting history
7665[a]	133	179	46	73	282	•	•
7677	288	300	0	106	759	•	•
8442	423	1211	131	7	1131	•	•
8443	404	930	176	13	1025	•	•
8455	438	1353	145	10	1160	PPN-011	1987, 1989, 1991, 1993, 1995, 1998, 2001, 2004, 2007
8456	413	843	0	10	1230	PPC-946	1998, 2000, 2002, 2004, 2006
8552	404	1140	0	19	1194	PPN-058	1988, 1990, 1992, 1994, 1996, 1998, 2003, 2005, 2007, 2010, 2012, 2015
8553[b]	318	139	0	0	653	PPC-943	1998, 2002

598 [a] This turtle made an initial migration to forage for ~71 days before making a second migration to its final foraging
599 destination; we summed migration and foraging points for the two migratory and two foraging periods
600 [b] Because of two large gaps in usable transmissions, this individual's track was split into three for modeling (and
601 then combined); this resulted in < 3 model locations estimated per day of deployment

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609 TABLE 2. Migration information for eight hawksbill sea turtles (*Eretmochelys imbricata*)

610 tracked from Caribbean nesting beaches in 1998 and 2000. Migratory durations are rounded to

611 the nearest half-day. A "•" denotes the parameter is not applicable due to no observed migration.

PTT ID	Nesting location	Start	Duration (days)	Path (km)	Straight-line distance (km)	Foraging location	Coordinates
7665[a]	N Jamaica	28 Sep 00	13	320.5	235.7	Jamaica	78.8867° W, 17.4434° N
7665[a]	N Jamaica	22 Dec 00	10.5	403.2	372.0	Honduras	82.0968° W, 16.1233° N
7677	N Jamaica	19 Jul 00	35	1323.7	1205.5	Belize	88.2168° W, 16.5465° N
8442	S Jamaica	19 Nov 98	2	55.7	100.9	Jamaica	77.7782° W, 17.0891° N
8443	S Jamaica	3 Dec 98	4	90.5	95.4	Jamaica	77.9641° W, 17.8888° N
8455	Antigua	30 Oct 98	3	120.6	139.3	St. Eustatius	62.9993° W, 17.5205° N
8456	Antigua	16 Oct 98	3	59.4	67.6	Redonda	62.3499° W, 16.9495° N
8552	Antigua	25 Oct 98	6	126.5	119.1	St. Kitts	62.8386° W, 17.4415° N
8553[b]	Antigua	•	•	•	•	Antigua	61.7784° W, 17.1474° N

612 [a] This turtle made an initial migration to a foraging area, remaining for ~71 days before making a second migration
613 to a final foraging destination; straight-line distance from IN centroid to final foraging area centroid was 607.3 km
614 [b] No migration observed, individual remained local to NE Antigua
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625 TABLE 3. Summary of inter-nesting and foraging home ranges for eight hawksbill sea turtles

626 (*Eretmochelys imbricata*) tracked from Caribbean nesting beaches in 1998 and 2000. Durations

627 of observation (i.e., satellite transmissions) are rounded to the nearest half-day. UD denotes

628 utilization distribution as computed with kernel density estimation, and MCP denotes minimum

629 convex polygon. Depths are provided for the centroid of 50% UDs. A "•" notes that we did not

630 observe that behavior.

	Inter-nesting period						Foraging Period					
PTT ID	Start	Duration (days)	50% UD (km²)	95% UD (km²)	95% MCP (km²)	Depth (m)	Start	Duration (days)	50% UD (km²)	95% UD (km²)	95% MCP (km²)	Depth (m)
7665[a]	13 Sep 00	15	41.7	207.3	31.0	5	11 Oct 00	71	110.5	861.0	618.7	31
7665[a]	•	•	•	•	•	•	2 Jan 01	22.5	56.8	284.2	127.1	32
7677	•	•	•	•	•	•	23 Aug 00	252.5	90.2	466.0	384.2	3
8442	6 Oct 98	43.5	12.1	54.8	35.6	5	21 Nov 98	376.5	8.1	56.7	45.1	10
8443	6 Oct 98	58.5	44.3	158.7	110.3	13	8 Dec 98	341.5	12.0	109.0	100.4	19
8455	12 Sep 98	48	25.0	185.2	126.9	4	2 Nov 98	386.5	16.9	135.0	76.5	2
8456	•	•	•	•	•	•	19 Oct 98	409.5	11.4	108.3	107.1	161
8552	•	•	•	•	•	•	31 Oct 98	397.5	9.3	59.7	54.0	24
8553[b]	•	•	•	•	•	•	12 Nov 98	317.5	37.8	367.9	377.2	4

631 [a] After migrating away from the nesting beach, this turtle stopped to forage for ~71 days before making a second
632 migration to its final foraging destination; information is shown for both foraging periods. Sample size limited
633 inference into IN home range behavior; atypically, 50% UD area > 95% MCP, so these data were excluded from
634 summary statistics
635 [b] No migration observed, information listed likely spans both inter-nesting and foraging movements
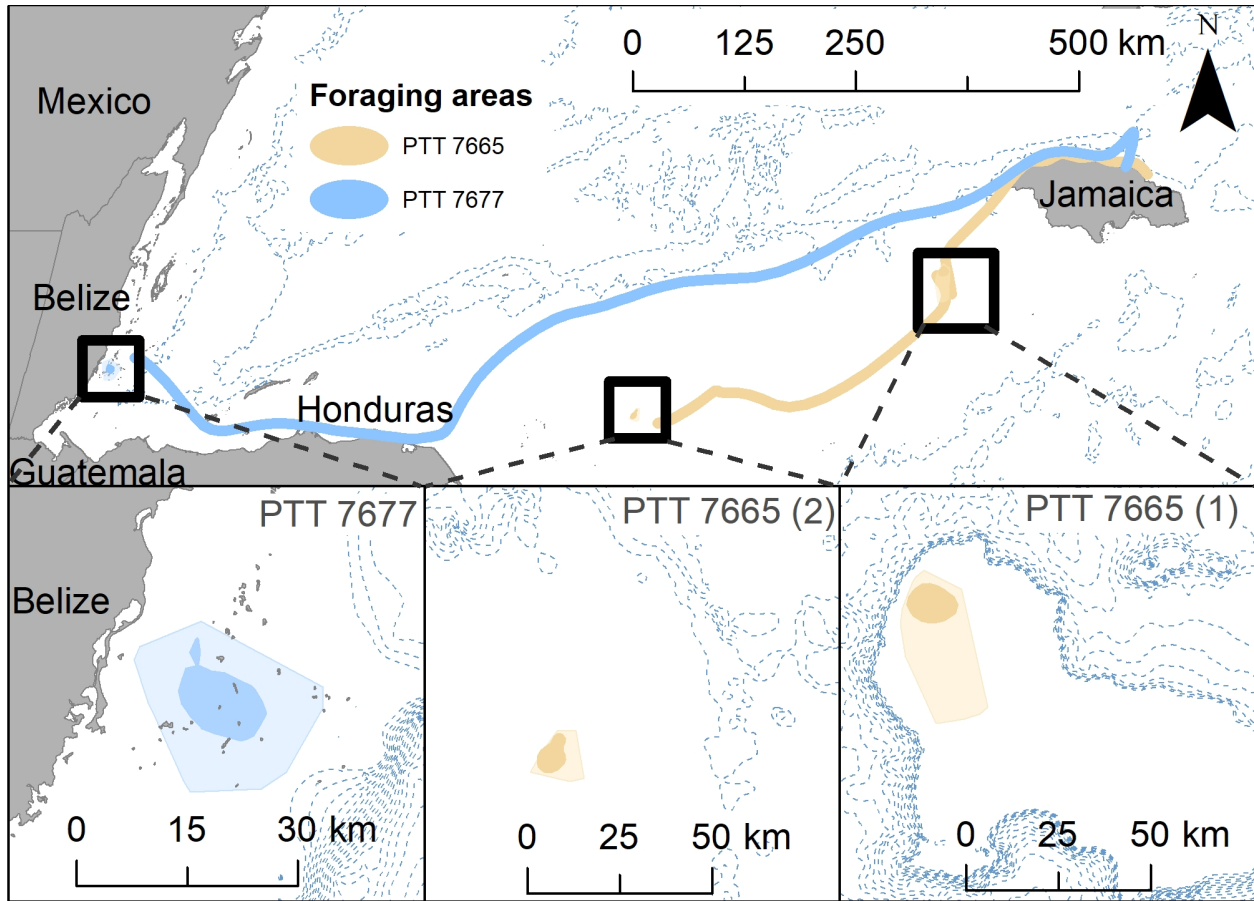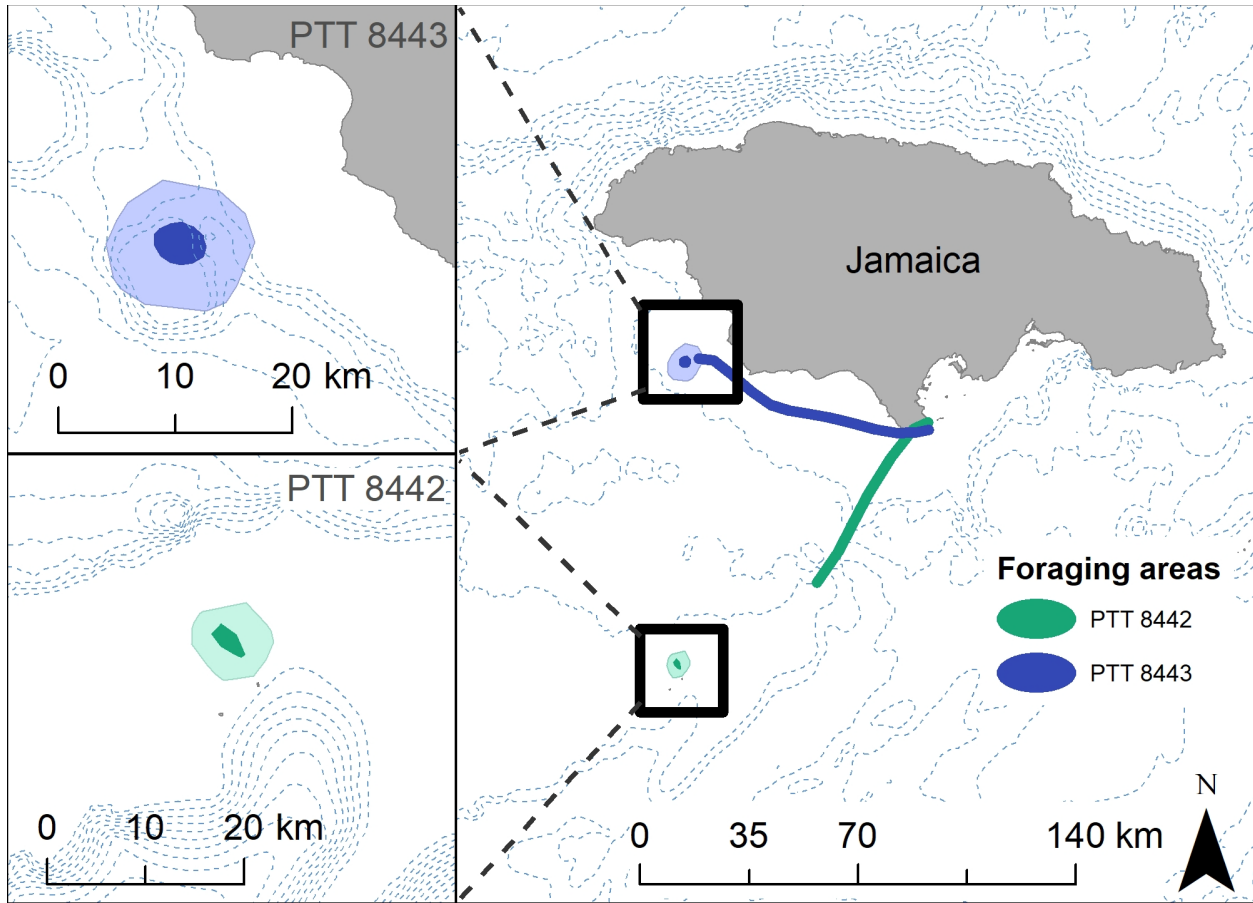636

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FIG. 1. Migrations and foraging home ranges for two hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in St. Mary Parish, northern Jamaica in 2000. Darker polygons in the insets show 50% kernel utilization distributions and are paired with larger, lighter 95% minimum convex polygons. Dashed lines display 2000-m depth contours in the large map and 100-m contours in the insets.
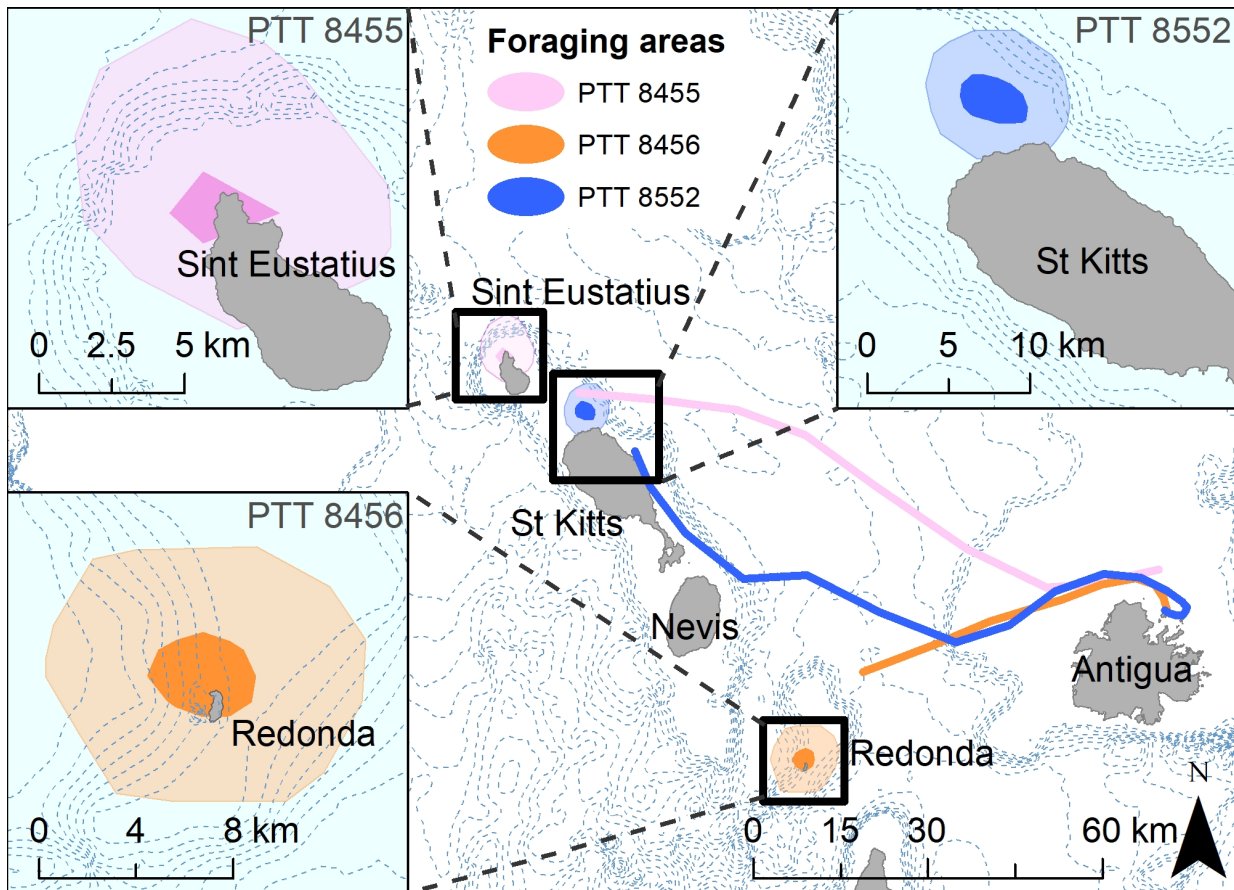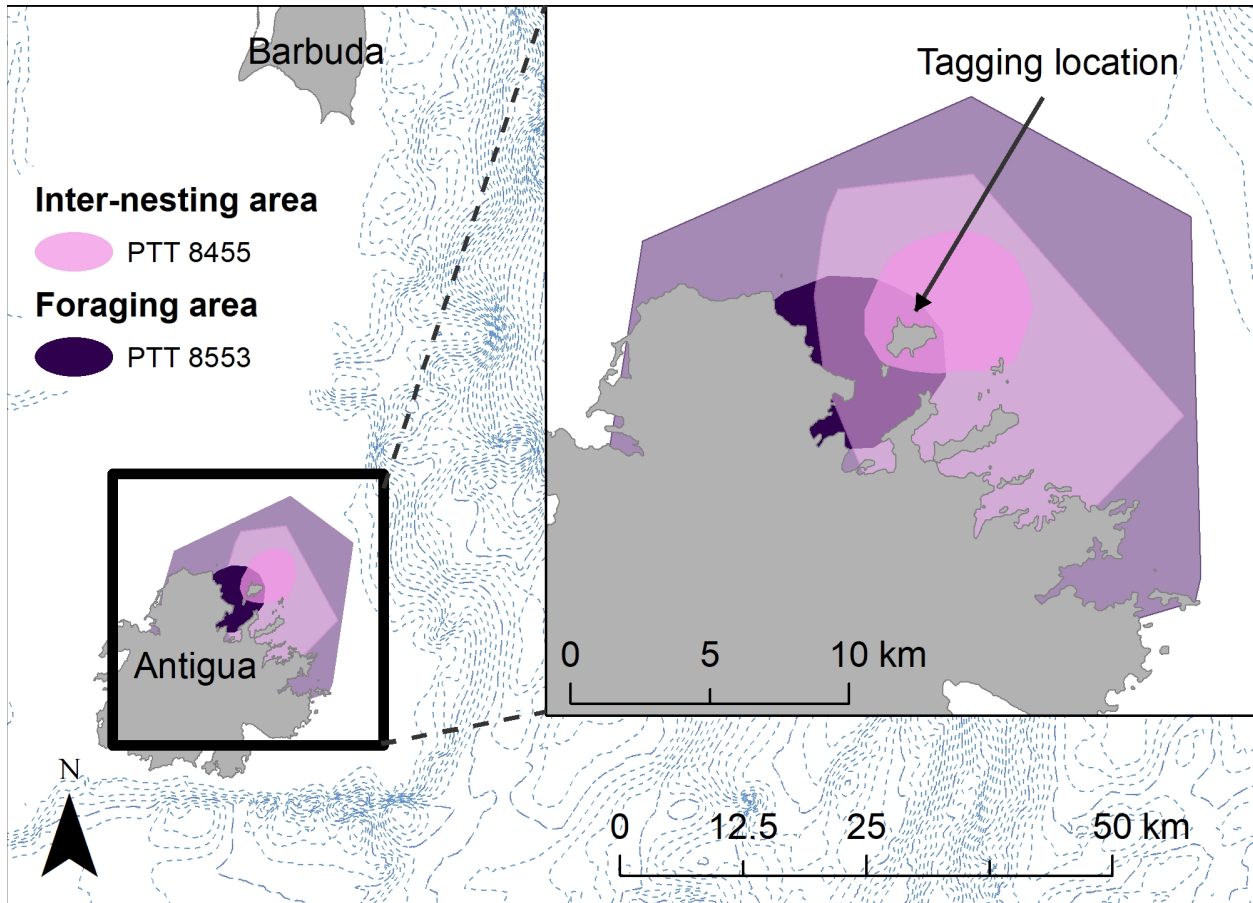
FIG. 2. Foraging home ranges for two adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in Portland Bight, Jamaica in 1998. Lines show post-nesting migrations and polygons display foraging home ranges, with darker polygons providing 50% kernel utilization distributions paired with larger, lighter 95% minimum convex polygons. Dashed lines display 500-m depth contours in the large map and 100-m contours in the two insets.
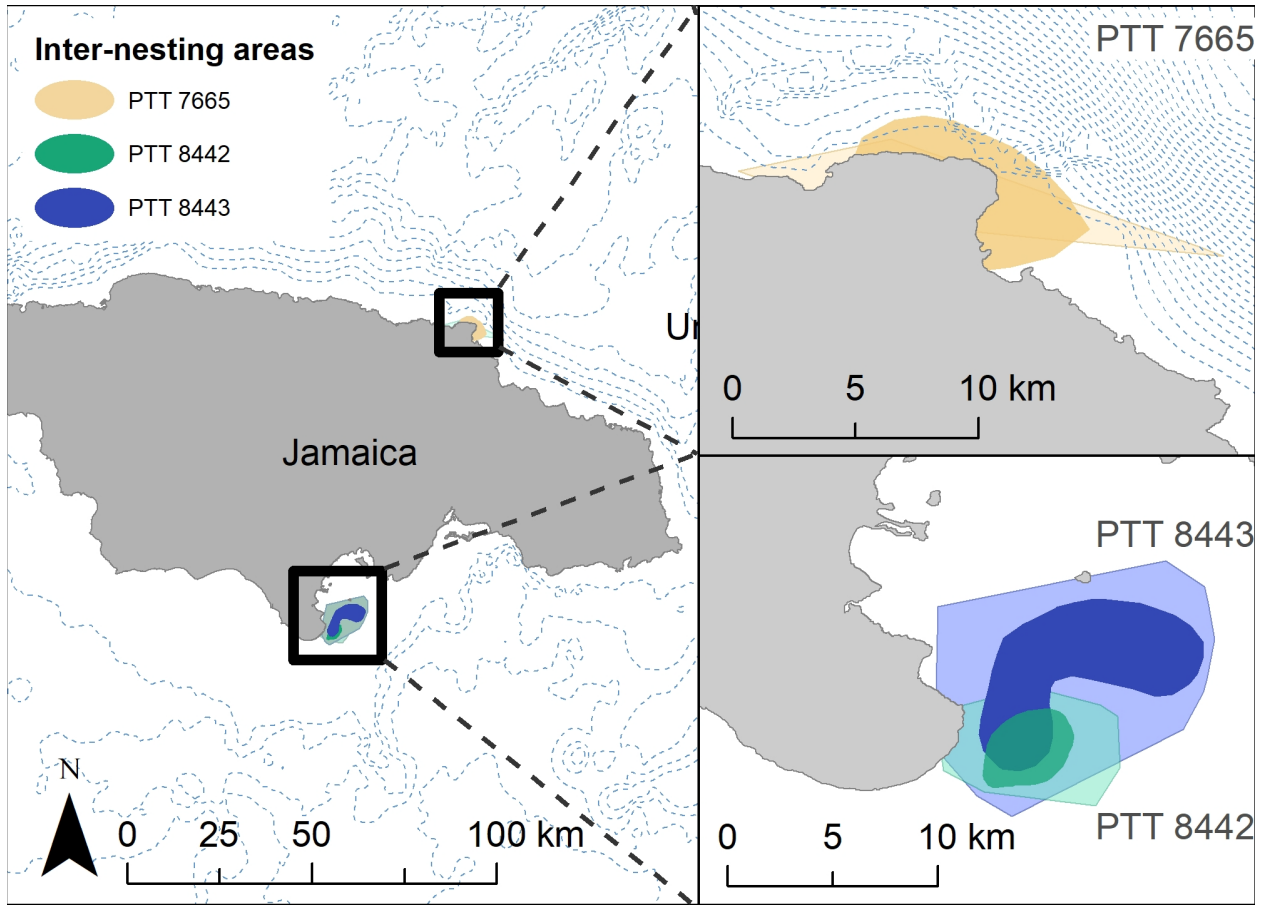
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658   FIG. 3. Migratory movements and foraging home ranges for three adult female hawksbill sea

659   turtles (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting at Long

660   Island, Antigua in 1998. Lines show post-nesting migrations and polygons display foraging

661   areas, with darker polygons providing 50% kernel utilization distributions paired with larger,

662   lighter 95% minimum convex polygons. Dashed lines display 100-m depth contours.

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FIG. 4. Resident and inter-nesting Space use of two adult female hawksbill sea turtles

(*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) in northeastern Antigua in

1998. Dark polygons provide 50% kernel utilization distributions and are paired with larger,

lighter 95% minimum convex polygons. Dashed lines show 100-m depth contours. For PTT

8455 the inter-nesting home range is shown. For PTT 8553, a home range is shown for all

movements observed; we expect this turtle was resident and that this area may encompass both

inter-nesting and foraging behaviors.

FIG. 5. Inter-nesting home ranges for three adult female hawksbill sea turtles (*Eretmochelys imbricata*) outfitted with transmitters (PTTs) in Jamaica over 1998–2000. Dark polygons provide 50% kernel utilization distributions (UDs) and are paired with lighter 95% minimum convex polygons (MCPs). Dashed lines display 500-m depth contours in the large map and 100-m contours in the two insets. Inferences into the home range for the individual with PTT 7665 were limited by sample size, with a 95% MCP smaller than the corresponding 50% UD.

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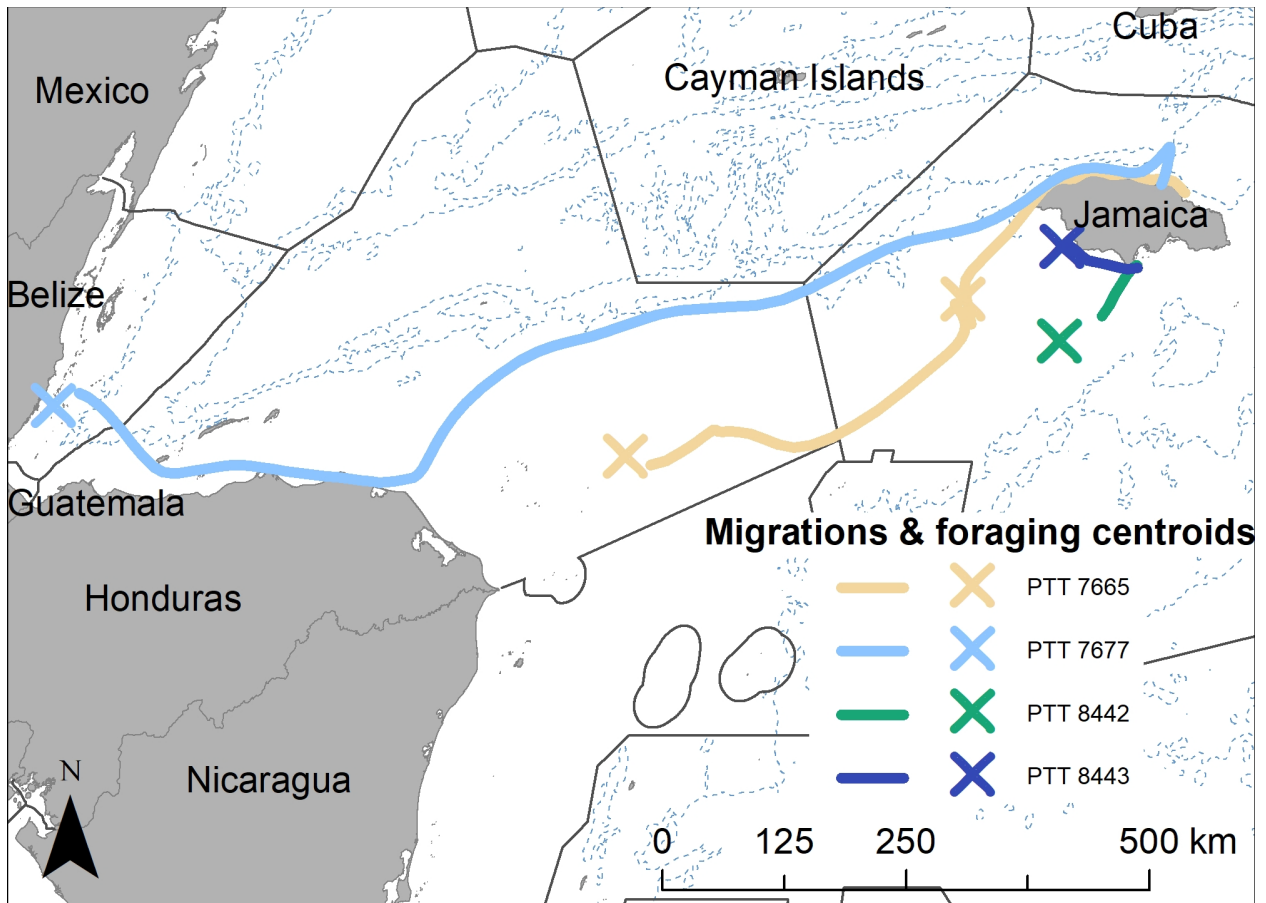
FIG. 6. Migrations and foraging area centroids for four adult female hawksbill sea turtles

(*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting in Jamaica.

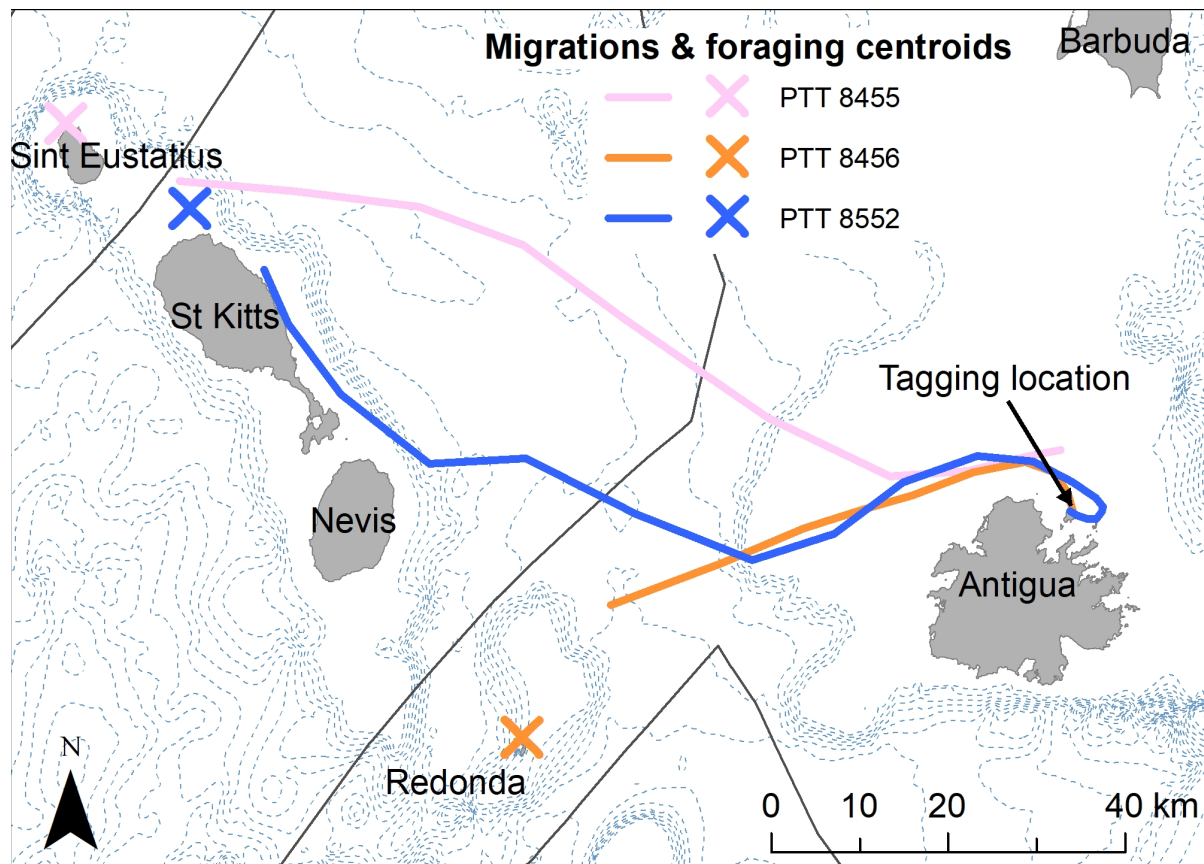Black lines display national exclusive economic zones. Dashed lines show 2000-m depth

contours and indicate that all individuals generally moved over the relatively shallow Nicaraguan

Rise (an area extending from northern Nicaragua and eastern Honduras northeast to Jamaica).

Solid black lines display national exclusive economic zones.

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693   FIG. 7. Migrations and foraging area centroids for three adult female hawksbill sea turtles

694   (*Eretmochelys imbricata*) outfitted with satellite transmitters (PTTs) after nesting at Long Island,

695   Antigua. Migratory tracks do not intersect with centroids because turtles ceased migrating at the

696   edge of their foraging home ranges. Solid black lines display national exclusive economic zones,

697   and dashed lines show 100-m depth contours. A fourth individual tracked from Long Island did

698   not migrate.

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