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High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information

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Abstract The movements and behavior of nine female leatherback sea turtles, *Dermochelys coriacea* (L.) were monitored for up to 370 days from their nesting beaches on the Caribbean island of Trinidad between 1995 and 2004 using satellite-linked time and depth recorders. During the inter-nesting period (typically March–July) turtles ranged widely, but frequented the area around Galera Point on the NE corner of Trinidad. Diving depths were typically < 51 m. Upon leaving Trinidad, the three longest tracked turtles moved to higher latitude foraging areas, NE of the Flemish Cap; along the continental shelf of the Iberian peninsula to the Bay of Biscay; and along the N. Atlantic subtropical front, where they remained until the end of November. Dives were initially deep (100–300 m) and long (> 26 min) as the turtles left the Caribbean, but became very shallow (> 50 m) and short at high latitudes. Between mid-October and mid-November, the turtles left high latitudes for a presumed foraging area in the Mauritania upwelling where they resided until their tracking records ended. Diving remained relatively shallow. It is proposed that movements of these turtles from one foraging area to another are driven by the opportunity to forage in areas of distinct oceanic structure which serve to

concentrate their gelatinous prey (e.g., salps, Scyphomedusae, Siphonophora) either at or below the surface.

Introduction

The leatherback sea turtle, *Dermochelys coriacea* is the largest marine turtle and has the widest geographic range of any reptile (Pritchard and Trebbau 1984). It is generally considered completely pelagic, but is also observed in coastal waters when food is available (Leary 1957; Duron and Duron 1980; Duguy and Duron 1984; Shoop and Kenney 1992; Eckert et al. 2006). Historically, information on the distribution, movements, and migratory pathways for this pelagic species was limited primarily to anecdotal observations, fishery bycatch data, flipper tag returns, or coastal aerial surveys (Leary 1957; Carr and Ogren 1959; Pritchard 1976; Duron and Duron 1980; Pritchard 1980; Duguy and Duron 1984; Shoop and Kenney 1992; Starbird et al. 1993). These studies showed that female leatherbacks migrated between north temperate foraging areas and tropical nesting beaches every 2 or 3 years. Movements of males were virtually unknown. However, the use of satellite telemetry on leatherbacks has enabled a better understanding of this species' movements and use of oceanic environments (Duron-Dufrenne 1987; Morreale et al. 1996; Eckert and Sarti 1997; Eckert 1998; Hughes et al. 1998; Eckert et al. 2006). In some studies, male and female leatherbacks tracked for more than a few months in the Atlantic made annual high latitude migrations (Eckert 1998; Eckert et al. 2006; James et al. 2005a, b). Other studies using satellite telemetry on leatherbacks in the Atlantic have delineated foraging areas, or have illustrated egress routes from low latitude nesting colonies or high latitude foraging areas (Eckert 1998; Ferraroli et al. 2002, 2004; Hays et al. 2004b; Eckert et al. 2006; James et al. 2005c).

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Information on how leatherbacks utilize oceanic areas away from the nesting beaches is also very limited. While diving, swimming, and movements of female leatherbacks near nesting colonies is well studied (Eckert et al. 1986, 1989, 1996; Southwood et al. 1999; Eckert 2002) habitat use by leatherbacks away from nesting areas has rarely been documented. Such data are usually limited to a description of the environment in which the turtles were observed, and what their behavior was at the surface (Duguy and Duron 1984; Stinson 1984; Shoop and Kenney 1992; Starbird et al. 1993). Two exceptions were studies by Standora et al. (1984) and Hays et al. (2004a). Standora et al. (1984) monitored dive activity of a leatherback off Rhode Island on the U.S. Atlantic coast. Data were recorded on dive depth, dive duration, surface time, and location. Hays et al. (2004a) monitored by satellite the dive activity of two female leatherbacks as they moved away from their nesting colony on the Caribbean Island of Grenada and partially across the mid-tropical Atlantic Ocean. Dive activities of these turtles were similar to what was recorded for leatherbacks near deep water nesting beaches, with dive behavior influenced by time of day and turtles occasionally exceeding 500 m in dive depth.

In the present study I tracked and monitored the dive behavior of nine female leatherbacks by satellite for up to 370 days after they were equipped with satellite transmitters on the southern Caribbean island of Trinidad between 1995 and 2003. Trinidad supports one of the largest nesting populations of leatherbacks in the world with approximately 6,000 turtles nesting annually (S.A. Eckert et al., unpublished data). As elsewhere in the Caribbean, nesting begins in March, and continues through August with individual turtles laying eggs in as many as 12 nests per season. Because of the large population size and an ongoing conservation and research program on Trinidad's east coast, this colony was ideally situated for a telemetry study to monitor inter-nesting movements and post-nesting migration and oceanic habitat use by female leatherback sea turtles.

Materials and methods

Satellite transmitters used in this project were SSC3 Platform Transponder Terminals (PTT), SPOT 3 PTT's (Wildlife Computers, Redmond, Washington, USA) and a Kiwisat PTT (Sirtrack, New Havelok, New Zealand). These three instrument types work with the ARGOS CLS satellite system, which is commonly used in wildlife tracking studies (Argos 1996). Both transmitters have an electronics package and batteries embedded in polyester resin to pressure and waterproof them as leatherbacks are known to dive to depths > 1,000 m (Eckert et al. 1989). The Wildlife Computers' model SSC3 transmitter (14×14×5 cm³) weighs 1,100 g in air. It contains a user-programmable microprocessor which controls data acquisition and transmission protocols and a pressure sensor for monitoring dive depth. Data gathered by the

sensors are summarized every 6 h as a frequency distribution, and four of these frequency distributions (= 24 h) are broadcast each time the turtle surfaces. Data include number of dives to user-programmed depth bins, number of dives of user-programmed duration bins, and the proportion of time spent at user-programmed depth bins (time-at-depth). For one of the SSC3 transmitters, time spent at user-programmed temperature was also reported. Data are regularly transmitted on the maximum dive depth during the previous 24 h, the proportion of time spent on the surface during the two previous 6-h periods, and on the status of the transmitter including battery condition and number of transmissions to date. Transmission schedules can be set by day and by hour by the user. To prevent non-diving surface activities from being interpreted as dives, the SSC3 uses a user programmed pressure (i.e., depth) threshold which must be exceeded for the event to be recorded as a dive (Appendix 1). The SPOT 3 PTT (15×5×5 cm³) was used only for determining location; it also reported on its battery condition and number of transmissions. The Kiwisat (25×8×6 cm³) weighs 750 g in air and also was used only to monitor turtle location.

Data from the PTTs were distributed using ARGOS' Automatic Distribution System via email. ARGOS classifies the accuracy of reported locations as location classes (LC) Z, B, A, 0, 1, 2, 3 in increasing order of accuracy. While ARGOS provides assurances about the accuracy of LC's > 0, no such assurances are made for LC's < 0 which tend to be less reliable. However, by applying filter algorithms to the data many of the poorer quality locations can be used (Eckert et al. 2006). A filtering program developed by Dave Douglas (United States Geological Survey—Anchorage, Alaska, USA) was used in this study. The Douglas filter extracts locations from the Argos diagnostic format files and provides output as a number of filtered data sets including all locations (no filtering), minimum redundant distance (MRD) filtered locations, distance angle rate (DAR) filtered locations, and a hybrid of both. The MRD algorithm allows the user to set a maximum distance from each location beyond which all other locations are rejected within a set time frame. The DAR algorithm determines whether to accept a location by determining the angle of divergence away from a path created by connecting three consecutive locations with the location under evaluation. The hybrid filter uses both the MRD and DAR algorithms. User inputs include a limit on the plausible rate of travel, and the acceptable angle of divergence. The filter does not remove LC 3 locations and this limit may be set lower. In this study the hybrid filter was used with the LC limit set to 2 and the maximum rate of travel was determined by using the 95 percentile of all rates of travel calculated for the turtles (Eckert et al. 2006).

GIS plotting software (ArcView 3.2, Environmental Systems Research Institute, Inc.) was used to plot turtle movements and calculate high use areas. High use areas

were delineated by 50% fixed kernel utilization distributions (UDs) (Eckert et al. 2006) as assessed with the Animal Movement Analyst module for Arcview (Hooge et al. 1999). Kernel smoothing parameters were set based on least squares cross validation. For assessments of high use, including the primary inter-nesting habitats, temporal auto-correlation and sampling bias were reduced by using only a single best location per day. For the inter-nesting home range analysis, each inter-nesting period was treated as an independent event because in this study individual turtles did not repeat their previous inter-nesting movement patterns. Mean rates of travel (km h^{-1}) were determined by extracting a single best location per day, then dividing the distance between consecutive points by the time elapsed.

Two of the turtles (DC1, DC2) were also equipped with a Wildlife Computer Mk5 Time-Depth-Recorder (TDR), and an Ultramarine Velocity Recorder (Ultramarine Instruments Inc., Galveston, TX, USA). The TDRs are accurate to 2 m with a maximum depth range of 550 m, and the UVR's are accurate to 0.005 m s^{-1} and have a stall speed of $<0.25 \text{ m s}^{-1}$. A further description of these instruments and their application can be found in Eckert (2002).

Attaching transmitters to leatherback sea turtles (*D. coriacea* L.) is challenging due to the fragile skin covering their carapace and their flexible morphology (Eckert and Eckert 1986). Transmitters can be mounted to a polyvinyl plate attached to a harness (Eckert and Eckert 1986). For the present long-term deployments the harness was modified substantially. Instead of rubber bands to secure the harness, silicon tubing was used because it is far less prone to degradation in sea water and UV light than rubber. To guarantee release of the harness where the turtle was not re-encountered a corrodible steel link was integrated into the tubing. Laboratory tests showed that this link breaks apart after approximately three years in flowing sea water (S. Eckert, unpublished data). The harness consisted of 3.75-cm flat webbing and 316 stainless steel D-rings to join the straps and ease harness adjustment. The shoulder straps were inserted through thick vinyl tubing to prevent chafing to the turtle's shoulders. Harnesses and trans-

mitters were coated with ULTRA-KOTE antifouling paint (Interlux Yacht Paint Inc., Union, NJ, USA) to reduce biofouling.

Results

Nine satellite transmitters were deployed on female *D. coriacea* between 1995 and 2003, three on turtles nesting on the north coast of Trinidad at Grande Riviere beach and six at Matura Beach on the east coast (Table 1).

Tracking duration ranged from 35 to 370 days. Number of transmissions reported ranged from 8,602 to 125,440 (Table 1). The reason for cessation of transmissions was often unknown, but four of the turtles (DC2, 4, 8, 9) were caught in gillnets on the north coast (DC2 and DC8 at Galera Point, DC4 and DC9 between Grande Riviere and Matelot). The transmitter and harness on DC2 were damaged as the turtle was extracted from a net (Said Mohammed, personal communication) and the transmitter failed or fell off within 3 week of the turtle's capture. The other three turtles were killed, and the transmitters returned. The transmitter on DC1 reported low battery voltage after 44,027 transmissions just before transmissions stopped; the transmitter on DC3 reported 2 days before it quit that its battery voltage was within operational limits and that it had made 29,639 transmissions. DC6 and DC7 reported battery voltage also within operational ranges when they quit. DC6 sent an extraordinary 125,440 transmissions in 370 days and DC7 sent 22,272 transmissions in 24 days. Interesting locations of nine turtles are shown in Electronic appendices 1–9.

The first transmitter was deployed on DC1 while nesting on 17 May 1995 at Matura Beach. She re-nested on 25 May at Matura, and again on 5 and 15 June, on Fishing Pond beach (Appendix 2). The turtle remained in Trinidad waters until 16–21 June (no location data were received on these days) when she moved northeast and left the Caribbean passing 50–80 km south of Barbados (Fig. 1). This turtle moved east across the Atlantic Ocean between 15 and 20°N latitude directly against the North Equatorial Current, until 30°W lon-

Table 1 *Dermochelys coriacea*. Information on nine leatherback sea turtles nesting at Matura or Grande Riviere (Gr. Riv.) beaches, Trinidad and the performance of satellite transmitters placed on those turtles

Turtle ID	Length (cm CCL)	Tag type	Deployment nesting beach	Date deployed	Date of last location	Days tracked	Minimum distance traveled (km)	Date of last transmission	Number of transmissions
DC1	155.0	SSC3	Matura	17/05/95	20/05/96	369	13,909	22/05/96	44,027
DC2	140.0	SSC3	Matura	17/05/95	11/07/95	55	1,303	11/07/95	8,602
DC3	166.0	SSC3	Matura	26/05/95	25/03/96	304	11,285	24/05/96	29,639
DC4	162.0	SSC3	Matura	26/03/99	29/04/99	34	1,065	29/04/99	21,120
DC5	154.0	Kiwisat	Gr. Riv.	24/06/02	27/07/02	33	2,118	27/07/02	–
DC6	155.0	SPOT3	Matura	18/04/03	22/04/04	370	8,734	27/04/04	125,440
DC7	140.0	SPOT3	Matura	18/04/03	15/06/03	58	1,604	15/06/03	22,272
DC8	166.0	SPOT3	Gr. Riv.	20/04/03	14/05/03	24	1,034	14/05/03	11,264
DC9	154.0	SPOT3	Gr. Riv.	20/04/03	13/05/03	23	561	13/05/03	12,032

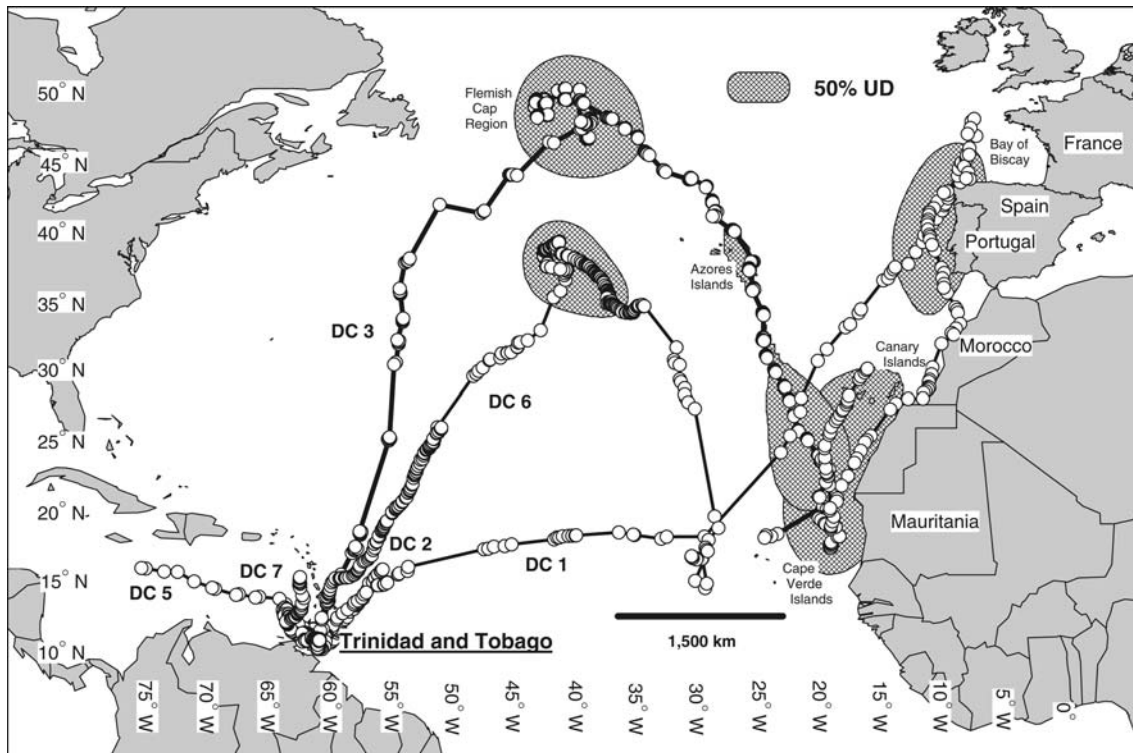


Fig. 1 *Dermochelys coriacea*. Post nesting movements of six leatherback sea turtles monitored using satellite telemetry. High use or foraging areas delineated using 50% utilization distribution

(UD) of Kernel Home Range estimation. Three high-use, high-latitude and one low-latitude area were described

gitude when she turned northeast and swam 3,600 km to the Bay of Biscay. Between 15 and 28 November she turned south and traveled down the coast of Spain, to the coast of Morocco, Africa. She continued moving south to a point midway between the Cape Verde Islands and the coast of Mauritania. On about 25 March, she turned north and moved to the vicinity of the Canary Islands, where the transmitter quit. The entire route spanned a minimum of 13,909 km over 370 days.

DC2 nested and was satellite-tagged at Matura on 17 May 1995 but was accidentally caught in a gillnet off northeast Trinidad near Galera Point on 22 May (Appendix 3). After release this turtle nested three more times before moving NE along the same trajectory as DC1 passing 120 km south of Barbados into the Atlantic (Fig. 4). Transmissions were received up to 11 July 1995. When the transmissions ceased DC2 had traveled a minimum of 8,602 km.

DC3 was satellite-tagged on 26 May 1995. This turtle then moved to the north coast of Trinidad where she was next detected on 30 May. DC3 probably nested on the north coast between 3 and 10 June (most likely around 6 June), but this event was missed because the transmitter was programmed to be off 3 days out of every four. On 10 June DC3 was detected 35 km east of Galera Point, and over the next 5 day, she moved southwest and back toward the nesting beach at Matura and probably nested at Matura Beach on 16 June before departing Trinidad waters (Appendix 4). After leaving Trinidad, DC3

moved north past Barbados into the Atlantic Ocean, then proceeded north between 50 and 60°W to an area near the Flemish Cap, bounded at 35°–45°E and 45°–50°N (Fig. 1). The turtle remained in this vicinity for approximately 2 months. Between 18 and 22 November DC3 moved southeast past the Azores and Canary Islands to an area between the Cape Verde islands and Mauritania arriving on 25 March. This turtle resided in the general area, moving only a few hundred kilometers to the west over the next 6 weeks until data transmissions became erratic and ceased. Total distance traveled was at least 11,285 km.

On 26 March 1999 a transmitter was deployed on DC4 nesting at Matura Beach. After nesting, DC4 moved offshore to the northeast approximately 100 km, then circled south to Matura Beach where she nested again on 5 April. She then moved 60 km north of Trinidad and circled to the west to nest at Grande Riviere beach on 15 April. From there she moved north approximately 80 km then east along the north side of Tobago, and circled to the west and along the north coast of Trinidad when transmissions ceased (Appendix 5). Total distance traveled was at least 1,065 km.

DC5 was satellite-tagged on 24 June 2002 on the north coast beach of Grande Riviere. After nesting the turtle moved 60 km north, then 150 km southwest arriving off the coast of Venezuela on 28 June. She then moved east along the coasts of Venezuela and Trinidad and arrived back at Grande Riviere on 6 July to nest

again (Appendix 6). After nesting she departed along the same trajectory as she had after her previous nesting but after moving 90 km from Grande Riviere, she turned northwest and continued traveling in this direction until 27 July when transmissions ceased (Fig. 1). Minimum distance traveled was 2,118 km.

DC6 was satellite-tagged while nesting at Matura beach on 18 April 2003. This turtle nested at Matura eight more times until the final nesting on 7 July. The entire inter-nesting period was spent within 24 km of the coast from Matura to the north side of Galera Point (Appendix 7). Upon completion of nesting DC6 moved NE and left the Caribbean 120 km north of Barbados continuing this trajectory until early October when she reached 39°N, 41.6°W, approximately 1,000 km west of the Azores Islands and along the North Atlantic subtropical front, then turned southeast traveling to the west of the Cape Verde Islands, where transmissions ceased (Fig. 1).

On 18 April 2003 at Matura Beach, a satellite transmitter was attached to DC7 during nesting. Much like DC6 this turtle remained between Galera Point and Matura beach for the next inter-nesting interval, returning to Matura to nest again. However, after nesting DC7 moved to the north coast and remained

there for the duration of the season, nesting three times at Grande Riviere beach before departing to the NW (Appendix 8). This turtle continued along this trajectory until reaching 13°N, 63°W when she diverted to the SW for 110 km, then turned NE and continued on a course parallel to the Lesser Antilles (Fig. 1). The signal was lost 100 km west of Dominica.

Two turtles (DC8, DC9) were satellite-tagged while nesting on Grande Riviere beach on 20 April 2003. After nesting, DC8 moved approximately 100 km NNW and 180 km west and then south to the coast of Venezuela, traversing east along the coast of the Paria Peninsula, Venezuela and the north coast of Trinidad to Paria Beach, Trinidad where she nested again on approximately 2 May. This turtle repeated the loop and nested at Madamas beach, Trinidad on approximately 13 May (Appendix 9). By 17 May DC8 had moved east of Galera Point where she was entangled and killed in a gillnet on 28 May. After transmitter deployment, DC9 moved to the northeast coast of Tobago, then returned to Grande Riviere to nest on 30 April. The next inter-nesting movements were similar to those of DC8 as DC9 moved north 100 km and west approximately 120 km, and then south to within approximately 7 km of the coast of the Paria Peninsula (Appendix 10). She moved

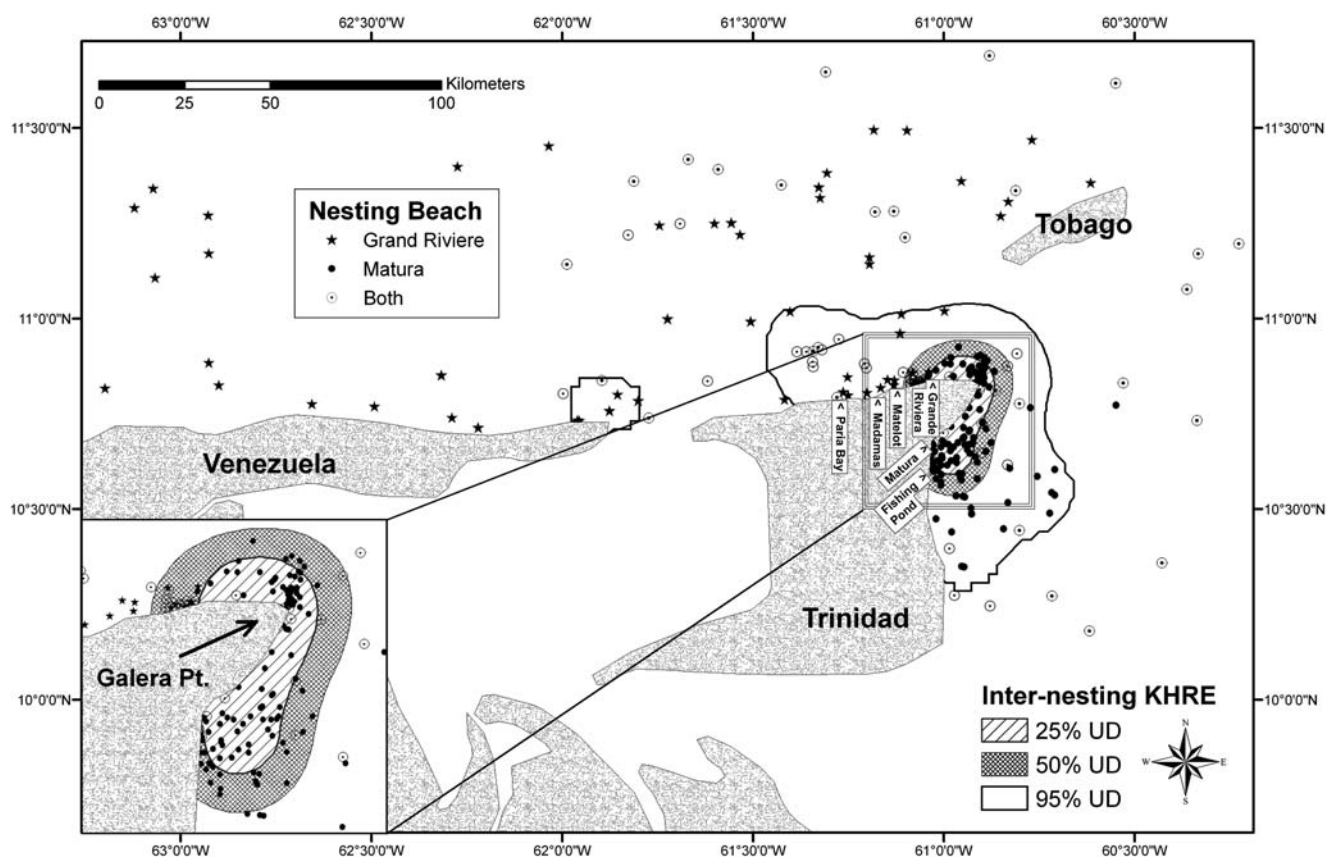


Fig. 2 *Dermochelys coriacea*. Inter-nesting habitat use areas delineated by Kernel-Home Range estimation for nine leatherback sea turtles around Trinidad. Point locations coded by where the turtles nested, either Grande Riviere on north coast, Matura Beach on

east coast, or both. Primary inter-nesting usage areas extended from nesting beaches toward Galera Point, an (exceptionally) important residence area

east along the north coast of Venezuela and Trinidad and was killed in a gillnet on approximately 14 May off Grande Riviere.

Delineation of primary inter-nesting habitat use by these female leatherbacks using a 95/50/25% UD formed an area from Grand Riviere to Fishing Pond beach, extending ~20 km from shore (at the 50% UD) (Fig. 2). Zones of highest use included the region around Galera Point and directly off the nesting beaches. Post-nesting foraging areas using the 50% UD delineated four areas in the North Atlantic (Fig. 1), two north of 35°N and bounded by 35°–45°W, a third along the western Iberian coast, and a fourth off the western side of the African coast in the Mauritania upwelling region.

Mean distance traveled per hour for each turtle ranged from 1.09 to 1.51 km h⁻¹ with an overall mean of 1.37 km h⁻¹ (Table 2). However, for all turtles their rate of travel varied, based on the time period in which it was recorded (Table 2, Fig. 3). Inter-nesting rates of travel were lowest, and post-nesting travel rates were highest (Kruskal–Wallis test, $P < 0.0001$) (Table 2).

Swim speed and distance data were recorded from 17 May to 25 May (between nestings) for DC1. Due to fouling of the speed impeller, no speed record was available for DC2. Mean swim speed for DC1 was 0.53 m s⁻¹ (SD = 0.18, $n = 191,098$), which approximates 1.9 km h⁻¹ (Appendix 11). Total distance traveled during this period was 404.2 km and mean distance covered was 44.9 km day⁻¹ (SD = 6.98, $n = 9$, range = 33.5–55.7 km day⁻¹). Using only the filtered satellite telemetry data from this same time period, the mean swim speed was 0.568 km h⁻¹ and calculated distance traveled was 190.2 km and represent a substantial underestimate of this turtle's swim speed.

For DC1, DC2, DC3, and DC4, dive depths, dive durations, time spent at specific depths, maximum depth for the previous 24 h, and proportion of time spent at the surface were recorded. For DC4, time spent at specific temperatures was reported as well (Appendix 14).

Frequency distributions of the dive depths for each turtle indicated that most dives were to 6–51 m (Appendix 12). For three of the turtles dive depths were evenly divided between 6 to 12 m and 13 to 51 m, with DC3 an exception. Most of DC3's dives were 6–12 m. For all turtles the proportion of time spent at specific depths was highest between 6 and 51 m. Two of the

turtles (DC1 and DC3) exceeded the maximum depth recording capacity of their PTTs at 747 m.

Dive durations were most frequently <2 min (Appendix 13). However, all turtles also had a large proportion of dives of 8–12 min similar to previous values recorded for this species (Eckert et al. 1986, 1989; Southwood et al. 1999). DC1 was distinct however in having a significant proportion of its dives (10%) >26 min.

DC4 was tagged with a SSC3 transmitter that also reported temperatures. A frequency distribution of this turtle's temperature record indicated that the turtle remained in waters 26.0–27.9°C >50% of the time (Appendix 14).

While frequency distributions provide a valuable perspective on leatherback behavior, a continuous record of dive activity combined with locations allowed estimates of turtle habitat use. Data were reported as 6 h frequency distributions and usually four distributions were reported each day (=24 h). Data for each 24 h period were averaged over 10 days to reduce the influence of missing data (occasionally a 6 h period might not be reported within a 24 h time block) and plotted as contour plots in which the x axis represents data summed over 10 days, the y axis represents the variable (depth or duration), and the contour shading (z axis) represents the proportion of dives or time that the turtle spent within each bin (depth, time, or temperature category) of the frequency distribution. Contour plots were created by fitting a spline smoothed surface fit to each data point represented in two dimensions (Statistica 1994).

Contour plots were used to illustrate changes in dive depth and dive duration for the two longest records, DC1 and DC3 (Fig. 4a, b). DC1 made most dives to 12–51 m during the nesting season (17 May 1995–15 June 1995) but as the turtle left the Caribbean some dive depths increased to >100 m (Fig. 4a). From 16 June to 14 August 1995, as DC1 moved across the Atlantic, dive depths were somewhat bimodal with most dives 51–102 m or 150–201 m. During this same period dive durations became very long with most dives exceeding 26 min. Between 14 September and 3 October as this turtle moved north between the Cape Verde Islands and the Canary Islands, the dives became gradually shallower, initially with the largest

Table 2 *Dermodochelys coriacea*. Mean (SD) and sample sizes for travel rates (km h⁻¹) for five leatherback sea turtles monitored for up to 1 year. Travel rates reported separately for inter-nesting period, post-nesting travel, high-use (presumed foraging) areas, and overall. High-use areas were delineated by Kernel home-range estimated 50% utilization distributions

Turtle number	Inter-nesting (km h ⁻¹)		Travel (km h ⁻¹)		Forage (km h ⁻¹)		All (km h ⁻¹)	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
DC 1	0.510 (0.380)	29	1.90 (0.590)	69	1.50 (0.670)	101	1.50 (0.750)	199
DC 2	0.610 (0.570)	29	1.80 (0.510)	21	–	–	1.10 (0.790)	50
DC 3	0.460 (0.450)	6	1.90 (0.980)	42	1.20 (0.720)	55	1.40 (0.910)	103
DC 6	0.420 (0.460)	79	1.70 (0.830)	83	1.20 (0.650)	53	1.10 (0.860)	214
DC 7	0.780 (0.660)	37	1.90 (0.870)	22	–	–	1.20 (0.930)	59

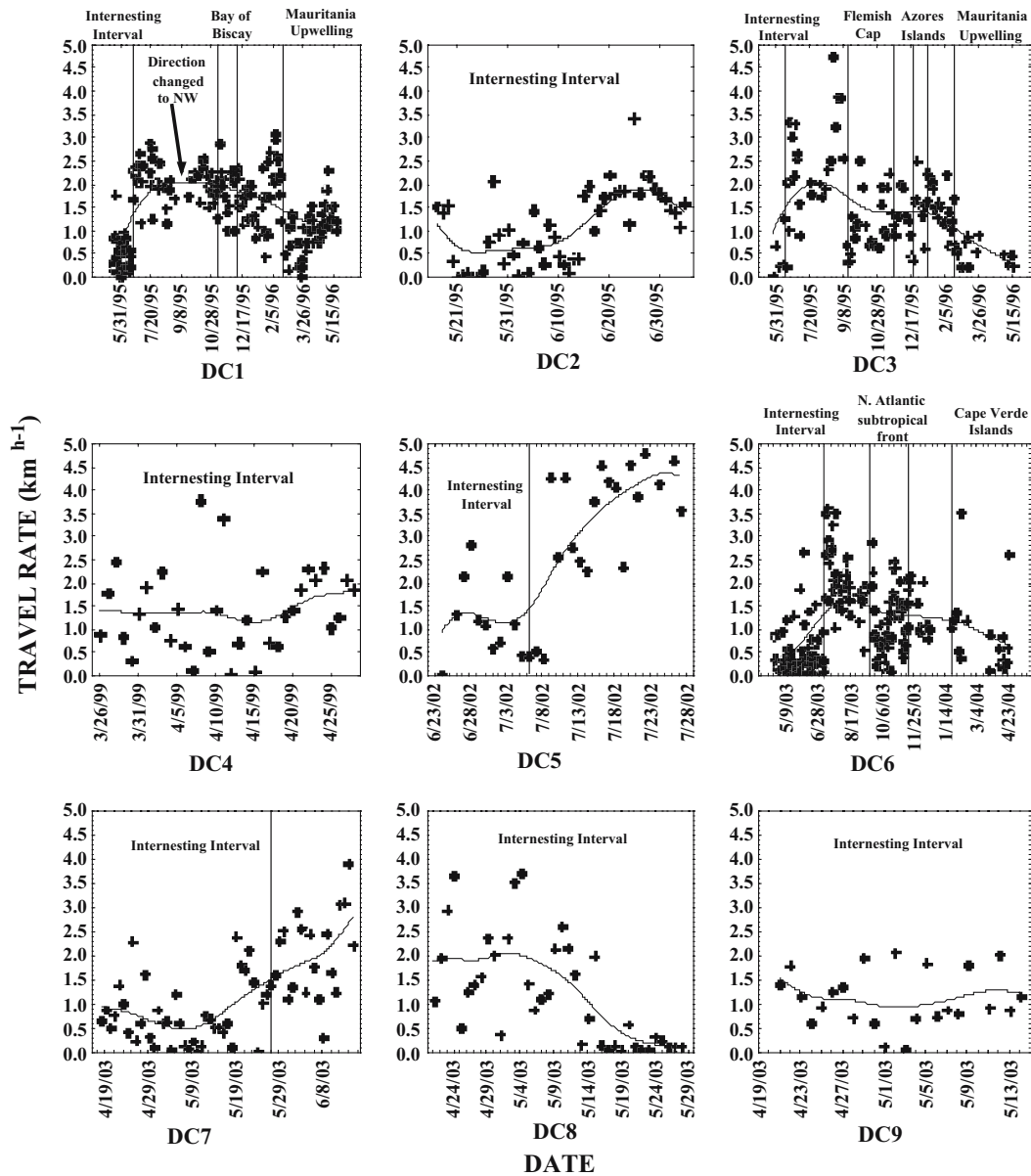


Fig. 3 *Dermochelys coriacea*. Scatterplot of travel rates of nine leatherbacks determined by measuring distance between locations and dividing by the elapsed time interval. Travel rates substantially under-estimated swim speeds, but recorded the average time for a

leatherback to move from one location to another. Rates changed over the records being slowest during inter-nesting and highest during migration. Least squares lines were fitted to the data

proportion to 102–150 m, and as the turtle approached the Canary Islands most commonly to 51–102 m. Dive durations continued to be >26 min. As the turtle moved north of 30°N, dives were shallower and substantially shorter and by 13–22 November >50 of DC1's dives were 12–51 m and most <4 min in duration. DC1 turned south at the end of November and moved along the coast of Morocco. Dives remained short and 12–51 m deep. However, as DC1 moved south of 30°N (ENE of the Canary Islands), most dives were more shallow (6–12 m). This pattern continued until completion of the record. No locations were reported for this turtle during the final 19 days.

DC3's dive depth record was initially similar to DC1 (Fig. 4b). Dive depths of 12–51 m were most frequent during the nesting season. After leaving the Caribbean and during the northward transit to the Flemish Cap, the proportion of dives >102 m increased until the turtle passed north of 30°N when most dives were <12 m. Dive durations reflected this same pattern, often exceeding 26 min until the turtle reached 30°N. Upon reaching the Flemish Cap, dives rarely exceeded 51 m with >90% of dives to 6–12 m. This pattern continued as the turtle left the Flemish Cap region and began moving southeast at the end of November. As DC3 moved south of the Azores Islands, dive depths became

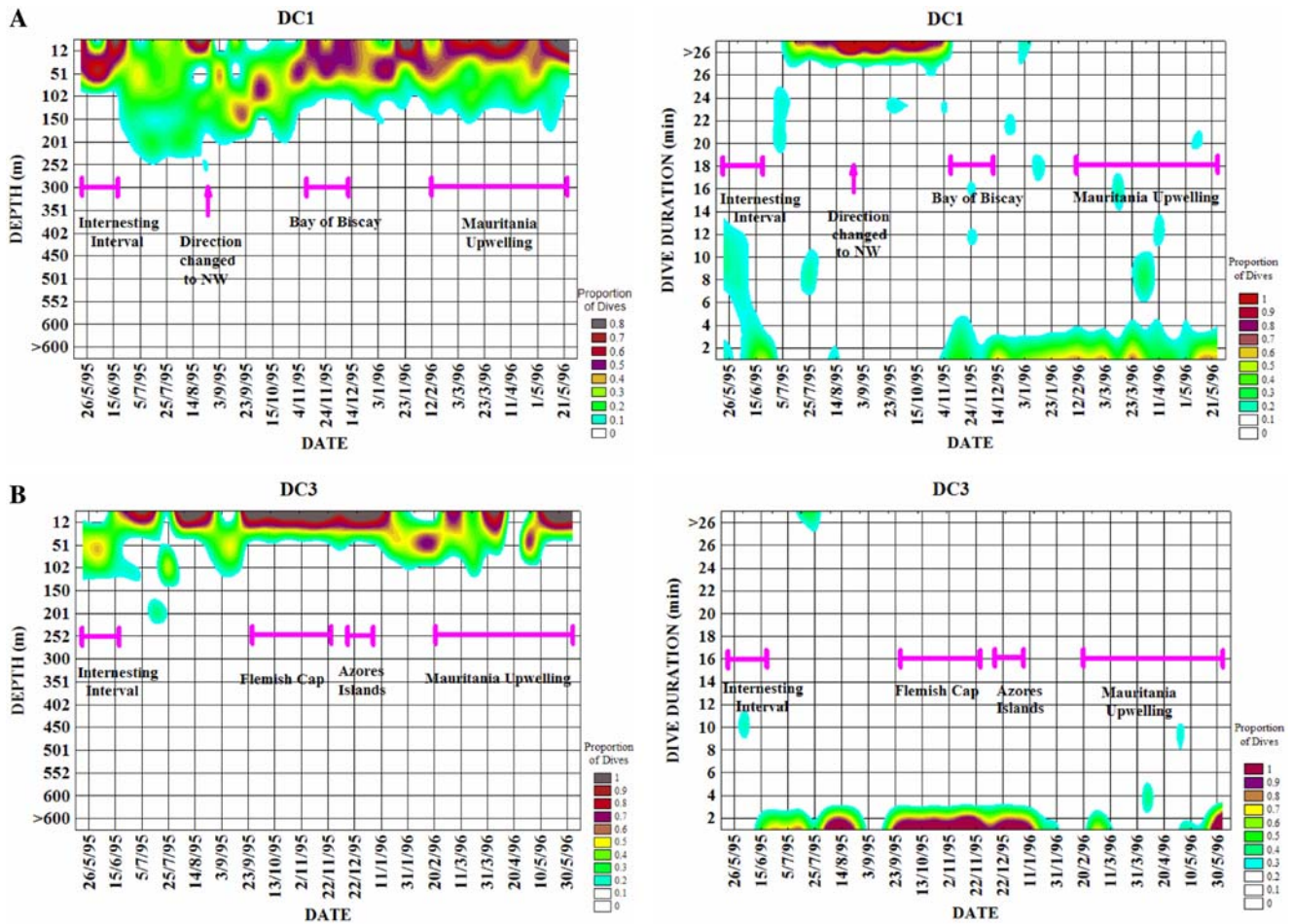


Fig. 4 a, b *Dermochelys coriacea*. Contour plots of proportion of dives to specific depth ranges (*left*), and for specific time ranges (*right*) within 10 day intervals, for DC1 and DC3. Data used to

generate plots consisted of 6 h frequency distributions combined into 10 day blocks to reduce the influence of missing blocks

progressively deeper until most were to 51–102 m. However, in late February, as DC3 entered the region of the Mauritania upwelling, most dives were to 6–12 m and remained so until the end of the record.

Because the SSC3 also provided information on the maximum dive depth per 24 h, it can be plotted over the year for each turtle and compared to location Appendix 15). For DC1 most maximum dive depths were < 100 m until 19 June 1995 after the turtle left Trinidad. Between 19 June and 13 October 1995, the turtle's maximum dive depths remained between 200 and 450 m and exceeded 747 m (the maximum range of the PTT) on two occasions (13 September, 13 October 1995). After 13 October, maximum dive depths were < 250 m except on 28 December 1995 when DC1 dove to 350 m. DC2's maximum dive depths were also < 100 m until 15 June 1996 when the maximum dive depths gradually increased until the end of the record. DC3's maximum dive depths were < 100 m until the turtle left Trinidad on 15 June 1995. Maximum dive depths then increased to > 300 m and for the next 100 days were deeper than 100 m. On two occasions (19 August and 20 September 1995) DC3 exceeded the maximum capacity of the PTT (> 747 m).

However, after 28 October 1995 DC3's maximum dive depths rarely exceeded 150 m and this pattern continued until the end of the record. DC4's dive record did not extend beyond the inter-nesting period in Trinidad waters. However, unlike the other leatherbacks DC4's maximum daily dive depths regularly exceeded 100 m. The deepest dives were during the first inter-nesting period when this turtle gradually increased the maximum dive depth up to 31 March 1995 (at 350 m) and then later on 23–24 April 1995 when the maximum dive depth was 550 m.

Finally, it was possible to monitor the percent of time *D. coriacea* females spent in surface waters (< 3 m). The SSC3 PTT logged the number of seconds spent at < 3 m for two 6 h time blocks every 24 h, and reported that information every 20th uplink. The mean percent time spent at < 3 m ranged from 25.4 to 42.3% (range 1–91%) for DC1, DC2, DC3, and DC4. However, the percent time spent near the surface varied over the course of each turtle's record. The two longest records (DC1, DC3) were scatter-plotted against date and a least squares line was fitted to the data (Fig. 5). Both turtles spent approximately 30% time near the surface during

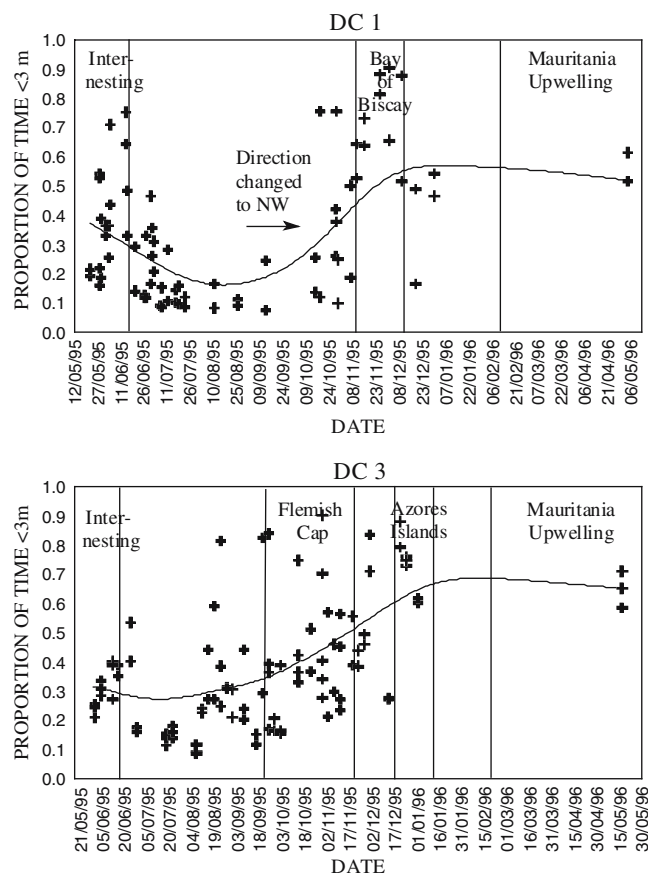


Fig. 5 *Dermochelys coriacea*. Proportion of time spent > 3 m for four leatherback sea turtles by date. A least squares line is fit to the data

inter-nesting. As DC1 moved across the Atlantic, time near the surface decreased, to as low as 10% as might be expected from the deep dive depths and long dive durations. However, as the turtle turned NW and moved to higher latitudes time near the surface gradually increased to 90% in the highest latitudes. As DC1 moved south to lower latitudes, time near the surface decreased to $\sim 50\%$ in the Mauritania upwelling. Turtle DC 3 had a similar pattern with increasing time near the surface as it moved to higher latitudes. The highest proportion of time near the surface was also 90% while in the Flemish Cap region and it decreased to $\sim 60\%$ in the Mauritania upwelling. Only limited uplink messages were received from DC1 and DC3 while they were in the Mauritania upwelling, so that region was under-represented in the scatterplots.

Discussion

This study describes an entire year of movements and dive activities for reproductive female leatherback sea turtles (*D. coriacea*). Two of five turtles swam at least 11,000 km in 1995–1996 confirming that female leatherbacks make longer post-nesting movements than any other species of sea turtle. As for males in the North

Atlantic Ocean (James et al. 2005b), reproductive females make annual north/south migrations. Prior to the use of satellite telemetry, such movements were suspected only to occur every 2 or 3 years, and exclusively for reproduction because Atlantic leatherback females are encountered on nesting beaches every 2 or 3 years. Satellite telemetry data demonstrates that females return to low latitudes annually, however do not nest during intervening years.

The present study also provides a clear picture of the important inter-nesting areas for female leatherback sea turtles around Trinidad. As might be expected from previous studies (Chan et al. 1991; Eckert 2002; Eckert et al. 2005), female leatherbacks spent much of their time directly off the nesting beaches and up to 30 km offshore. Less anticipated was the importance of the area directly off Galera Point, Trinidad. Turtles from both the Grande Riviere and Matura nesting beaches spent extended time in this area between nestings.

Why Galera Point is particularly significant to inter-nesting females is unclear. However, two long-shore currents intersect at Galera and this confluence may serve to concentrate jellyfish prey thus providing an important foraging area if these turtles feed during the nesting season as has been proposed for nesting leatherbacks at other colonies (Eckert et al. 1989). That Galera Point is important to leatherbacks is confirmed by other studies. In 2003, James et al. (2005b) tracked a leatherback male from Nova Scotia, Canada to Galera Point where it resided from 28 February to 12 April 2004. This male turtle remained within a relatively small geographic area during its residency, and when it left it moved directly back toward Nova Scotia. In 2005, this male returned to the same location off Galera Point. The presence of this male off Galera Point early in two nesting seasons and the importance of this area to reproducing females is unlikely to be coincidental. Galera Point represents an area for mating and possibly for foraging.

Given the importance of Galera Point to leatherback sea turtles as a mating area and an inter-nesting refuge, perturbations such as commercial developments or commercial fishing operations should be limited. There have been plans to develop the nearby township of Toco as a trans-shipment point for ferry and cargo service to Tobago, or for servicing oil industry vessels (<http://www.toco.interconnection.org/history.htm>). Given the critically endangered status of *D. coriacea* (IUCN 2004) and the importance of the region around Galera Point to the Trinidad nesting population, development of a Toco port facility may be inadvisable.

Turtles DC1, DC3, and DC6 moved to North Atlantic areas at the completion of nesting, and their routes and destinations were similar to those of leatherbacks leaving other southern Caribbean nesting colonies (Ferraroli et al. 2004; Hays et al. 2004b). DC1 spent much of its high latitude period along the continental shelf break off the Iberian peninsula or in the Bay of Biscay. Turtle DC 3 moved just NE of the Flemish Cap at the confluence of the North Atlantic and Lab-

rador Currents (Colbourne and Foote 2000) and resided there from October through mid-November. Turtle DC6 moved along a route similar to DC3, but instead of residing near the Flemish Cap this turtle remained in an area along the Atlantic subtropical front (Pingree et al. 1999) for 2 months. These records confirm that leatherbacks frequent distinct oceanic features such as frontal zones which are commonly found where currents converge or along their margins (Shoop and Kenney 1992; Lutcavage 1996).

While in high latitudes, leatherback dive depths became dramatically shallower and short, and surface waters were more heavily used than the tropical inter-nesting or migratory periods. This change in behavior may parallel the vertical distribution of their soft-bodied prey. In deep Caribbean or southeast Atlantic waters, leatherbacks forage in the deep scattering layer (DSL) (Eckert et al. 1986, 1989; Hays et al. 2004a). Turtles monitored in this study dove deeply and for long periods at latitudes below 35°N. In high latitudes leatherback have been observed foraging at the surface (James et al. 2005b). It is tempting to conclude that deep diving or deep foraging is the norm in tropical waters and that shallow diving is typical in high latitudes. However, subsequent dive data for DC1, DC3, and DC6 challenge this conclusion.

Turtles DC1, DC3, and DC6 left high latitudes during the between mid-October and mid-November, and moved directly to the west coast of Africa around the Cape Verde Islands and off the coast of Mauritania, previously identified as an important hotspot for leatherbacks (Eckert et al. 2006). The wind driven Mauritania upwelling occurs each year in February or March (Mittelstaedt 1991). Turtles arriving in this tropical region, did not dive deeply. Dives remained relatively shallow and short, closely resembling high latitude dive patterns.

The seasonal upwelling may provide increased primary and secondary production, and may provide increased prey production resulting in increased prey abundance for the turtles. However, because turtles arrived at the very beginning of the upwelling season, it is doubtful that gelatinous zooplankton production of the species which might support leatherbacks could have increased quickly enough to represent an abundant food source (Graham et al. 2001).

I propose an alternate theory that the initiation of upwelling is responsible for the formation of local convergences and frontal zones, which concentrate jellyfish prey in surface waters (Graham et al. 2001), thus providing higher density food patches in these surface waters. Turtle DC1 resided near surface currents that flow poleward off the Iberian peninsula in an area of distinct oceanic structuring (Frouin et al. 1990) and then moved south to the Mauritania upwelling. DC3 remained in the confluence of two significant currents near the Flemish Cap and then moved to the Mauritania upwelling region. DC6 resided in the region of the North Atlantic subtropical front before moving to the west of the Cape Verde islands.

That leatherbacks forage along frontal zones or other oceanic features is not new information. Surveys of leatherbacks by air or ship have shown leatherbacks concentrating in such areas (Shoop and Kenny 1992; Lutcavage 1996) and in one study using satellite telemetry (Luschi et al. 2003). However, that they move on large regional scales to take advantage of such features was not previously demonstrated. Given the near simultaneous movements of leatherbacks from widely separated high latitude high-use areas to the west coast of Africa in time to access a seasonally driven increase in foraging opportunities suggests that the species may time its long distance movements to enhance foraging opportunities within high-density prey patches. What cues the turtles use for this timing is unclear. The turtles left high latitudes prior to changes in sea surface temperatures so it is unlikely that cooling water temperatures initiate the movement. Food resources may have declined, but this cannot be determined from our data. What is clear is that the turtles began movement to lower latitudes 3–4 months prior to the initiation of seasonal upwelling off Africa and that it took 3–4 months to travel to this destination.

This study suggests that leatherbacks are patch feeders, relying on the concentrating effects of oceanic structuring to provide high density prey patches and that some of these feature may be predictable, though ephemeral. The long distance movements and foraging of leatherbacks is governed by the need to find these food patches and they must anticipate where and when such high density patches will occur. It also must be considered that features which concentrate prey into patches cannot always be observed from the surface. Thermoclines, salinity, hydrostatic pressure, and light level have all been shown to influence the vertical distribution of jellyfish (Graham et al. 2001). Thus, tracking studies which hope to understand leatherback movements and do not account for subsurface gelatinous zooplankton concentrating features will be incomplete. Work is ongoing to develop analytical approaches to confirm this theory, but it is a logical foraging strategy for a large pelagic predator feeding on low energy, geographically dispersed prey.

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Electronic Appendices

Electronic appendix descriptions

Appendix Table 1: Table of Transmitter Parameters: *Dermochelys coriacea*. Programmed dive data acquisition parameters for Wildlife Computer's SSC3 satellite linked, time-depth-recorders, Wildlife Computers' SPOT 3 satellite transmitter, and Sirtrack's "Kiwisat" satellite transmitter used for this project

Appendix Figures 2, 3, 4, 5, 6, 7, 8, 9, 10: Inter-nesting Maps: *Dermochelys coriacea*. Inter-nesting movements of nine leatherback sea turtles around Trinidad determined using satellite telemetry (9 figures)

Appendix Figure 11: Frequency Distribution - Swim Speed : *Dermochelys coriacea*. Frequency distribution of swim speeds for DC1 during inter-nesting (1 Figure)

Appendix Figure 12: Frequency Distributions - Dive Depths: *Dermochelys coriacea*. Frequency distributions of number of dives to specific depth ranges for four leatherbacks for up to one year. For DC4 the x axis scale is different than for DC1, DC2, and DC3 with the addition of depth bin 51 - 78 m (4 Figures)

Appendix Figure 13: Frequency Distributions - Dive Durations: *Dermochelys coriacea*. Frequency distributions of number of dives of specific duration ranges for four leatherback sea turtles for up to one year (4 Figures)

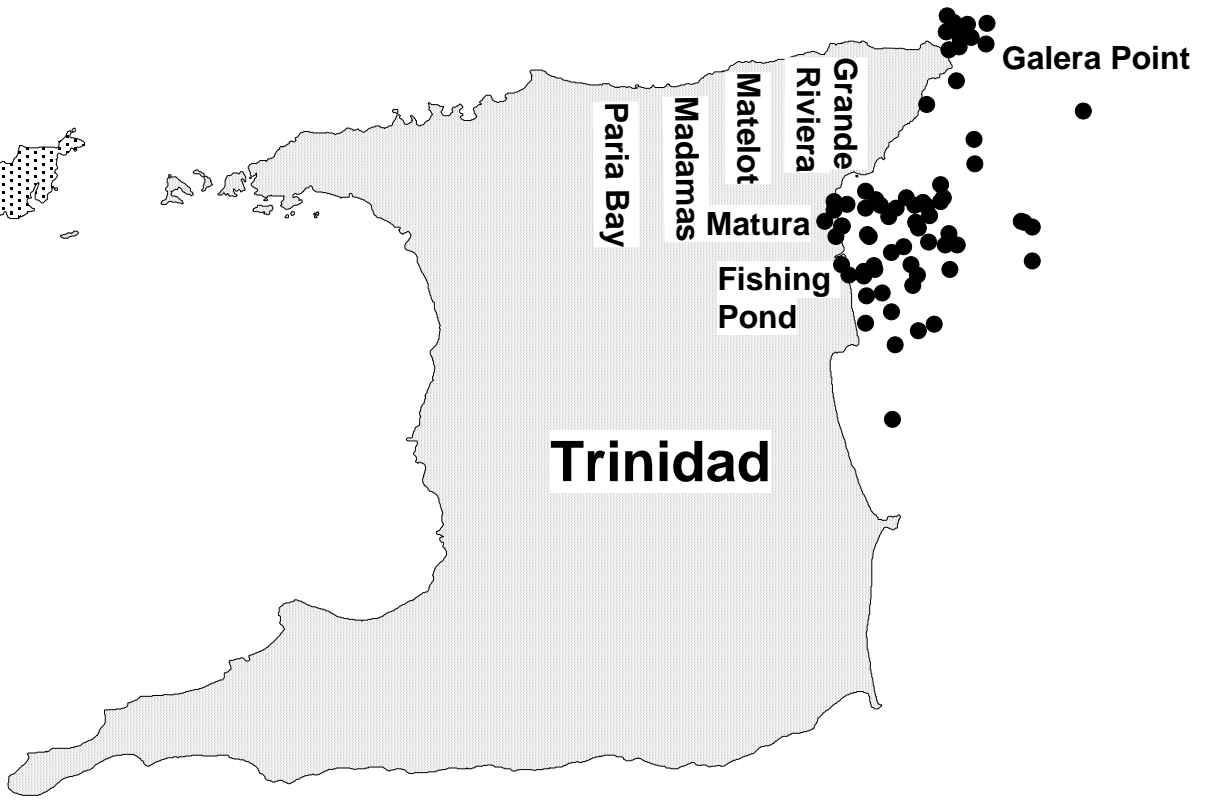
Appendix Figure 14: Frequency distribution - Temperature: *Dermochelys coriacea*. Frequency distribution of the proportion of time spent by DC4 at specific temperature ranges (1 Figure)

Appendix Figure 15: Scatterplots: *Dermochelys coriacea*. Maximum dive depth per 24 h for four leatherback sea turtles. For two turtles, maximum dive depth exceeded the capacity of the instruments at 747 m (4 Figures)

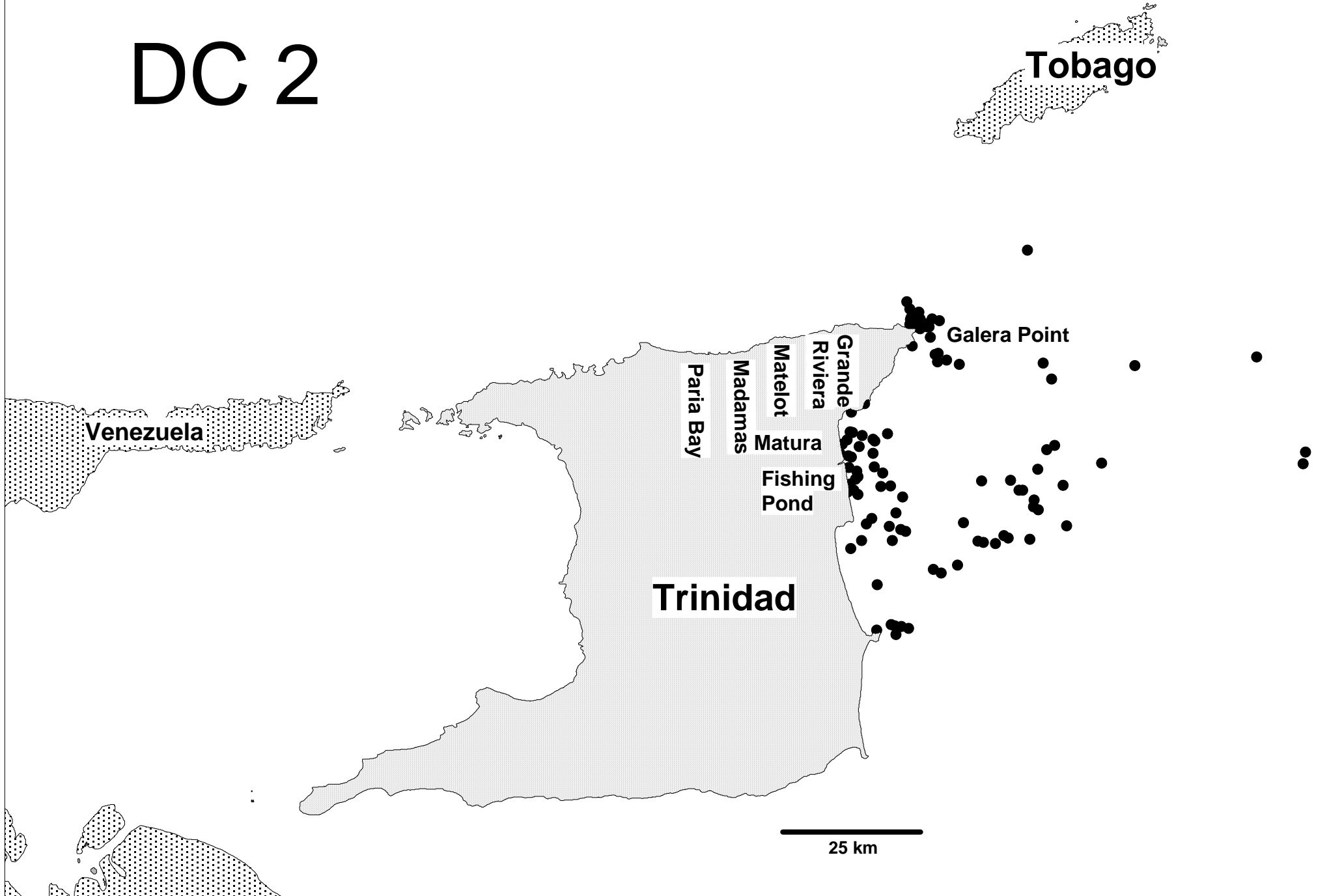
Satellite transmitter parameters

Turtle ID	Max Depth Range (m)	Depth Resolution (m)	Minimum depth recorded as "at surface"	Duty Cycle (days)	Duty Cycle (hours on)	Histogram depth limits (m)	Histogram duration limits (min)	Histogram time at depth limits (m)
DC1	0-747	3	3	on 1 - off 2	0-2, 11-14, 23	12, 51, 102, 150, 201, 252, 300, 351, 402, 450, 501, 552, 600, ∞	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, ∞	51, 102, 150, 201, 252, 300, 351, 402, 450, ∞
DC2	0-747	3	3	on all	0-2, 11-14, 23	12, 51, 102, 150, 201, 252, 300, 351, 402, 450, 501, 552, 600, ∞	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, ∞	51, 102, 150, 201, 252, 300, 351, 402, 450, ∞
DC3	0-747	3	3	on 1 - off 3	0-2, 11-14, 23	12, 51, 102, 150, 201, 252, 300, 351, 402, 450, 501, 552, 600, ∞	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, ∞	51, 102, 150, 201, 252, 300, 351, 402, 450, ∞
DC4	0-747	3	3	on all	0-23	12, 51, 78, 102, 150, 201, 300, 351, 402, 450, 501, 552, ∞	2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 24, 28, 32, ∞	12, 51, 78, 102, 150, 201, 300, 351, 402, 450, 501, 552, ∞
DC5, DC6, DC7, DC8, DC9	-----	-----	-----	on all	0-23	-----	-----	-----

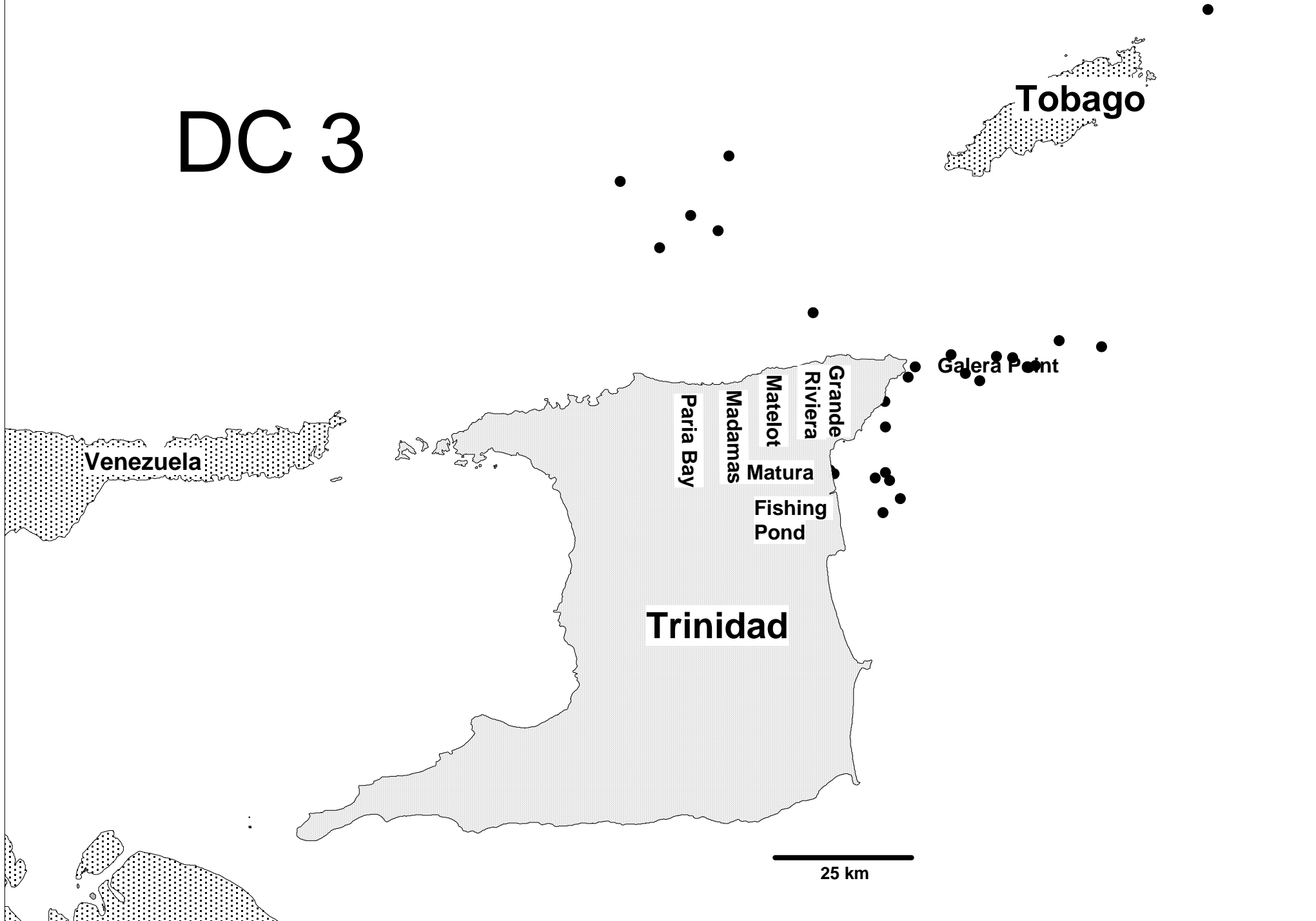
DC1



DC 2



DC 3



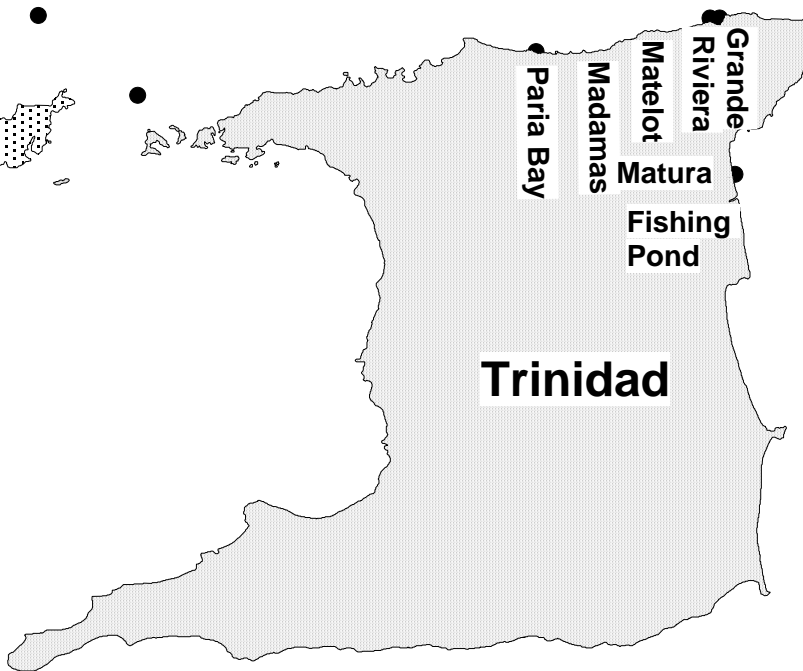
DC 4



Tobago



Venezuela



Trinidad

Paria Bay

Madamas

Matelot

Riviera

Grande

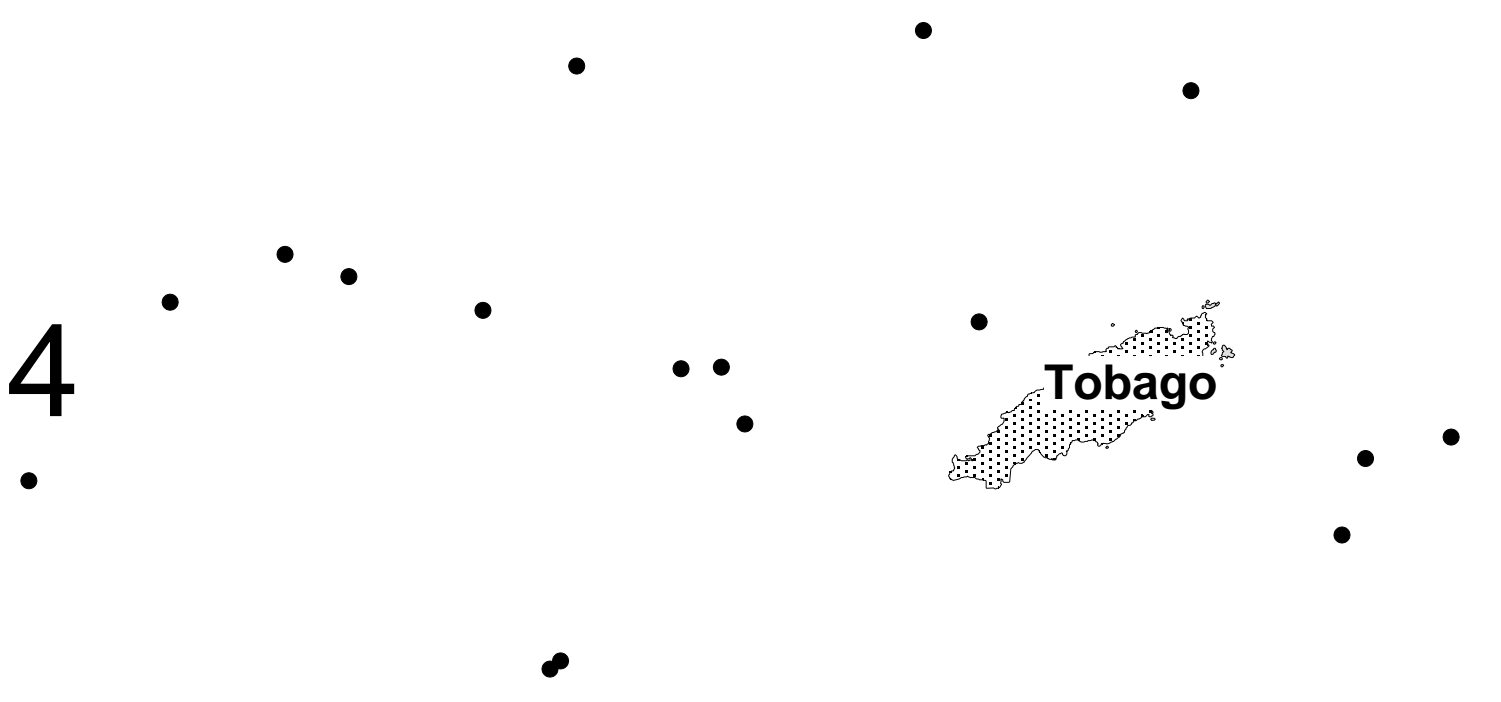
Matura

Fishing Pond

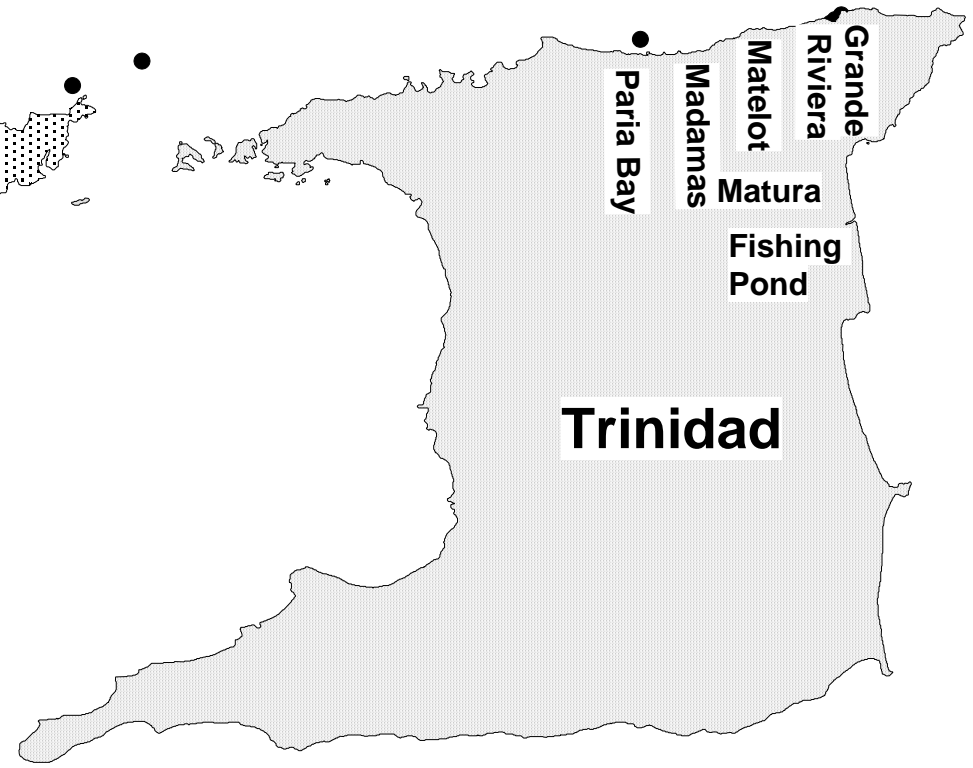
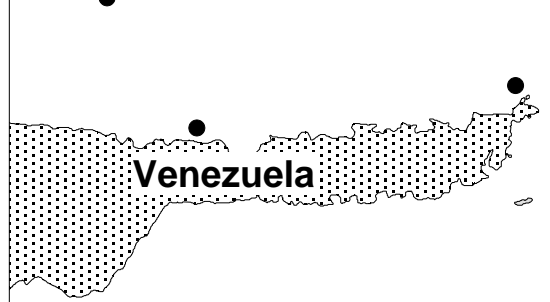
Galera Point



25 km



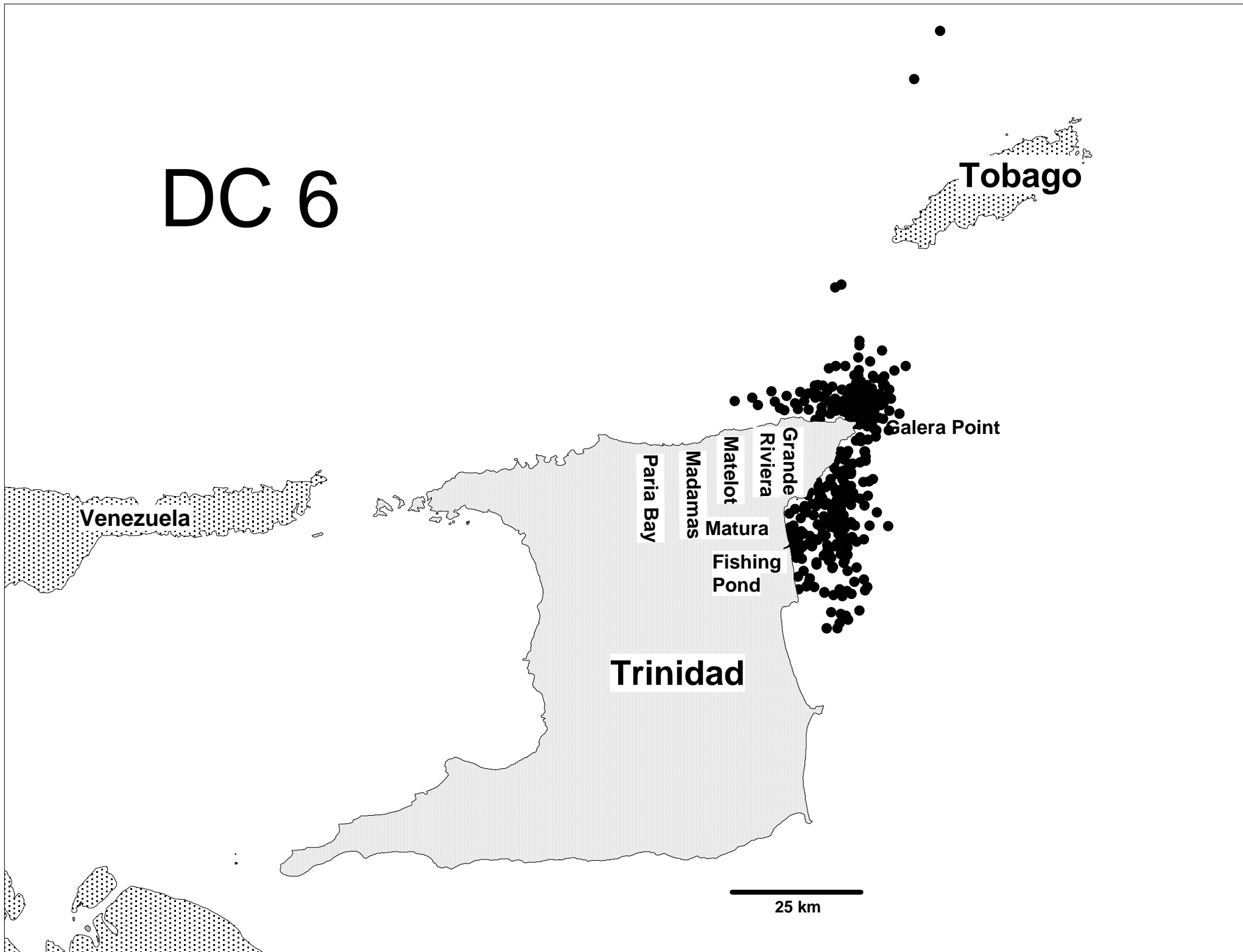
DC 5



Galera Point



DC 6



DC 7

Tobago

Venezuela

Paria Bay

Madamas

Matelot

Riviera

Grande

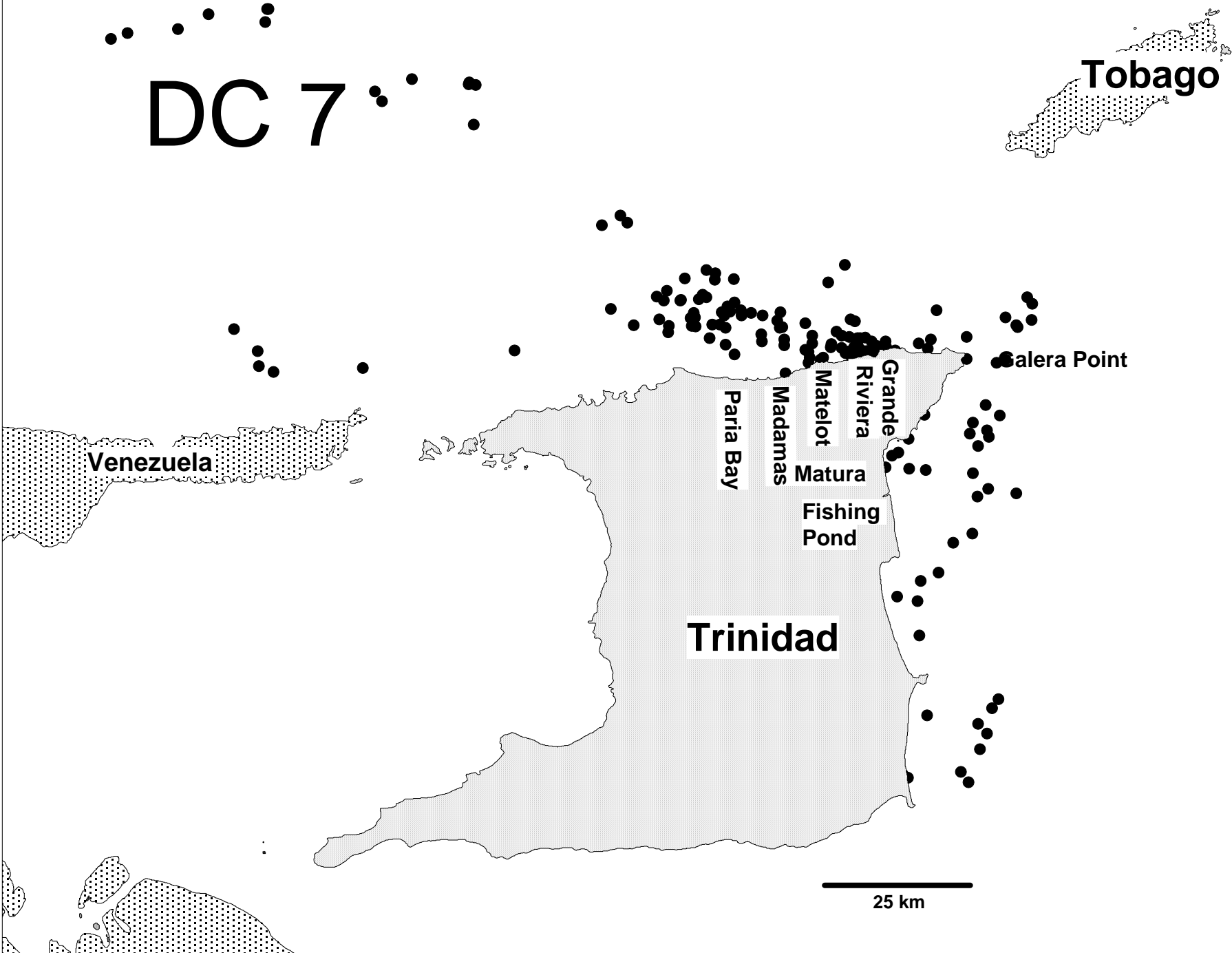
Matura

Fishing Pond

Salera Point

Trinidad

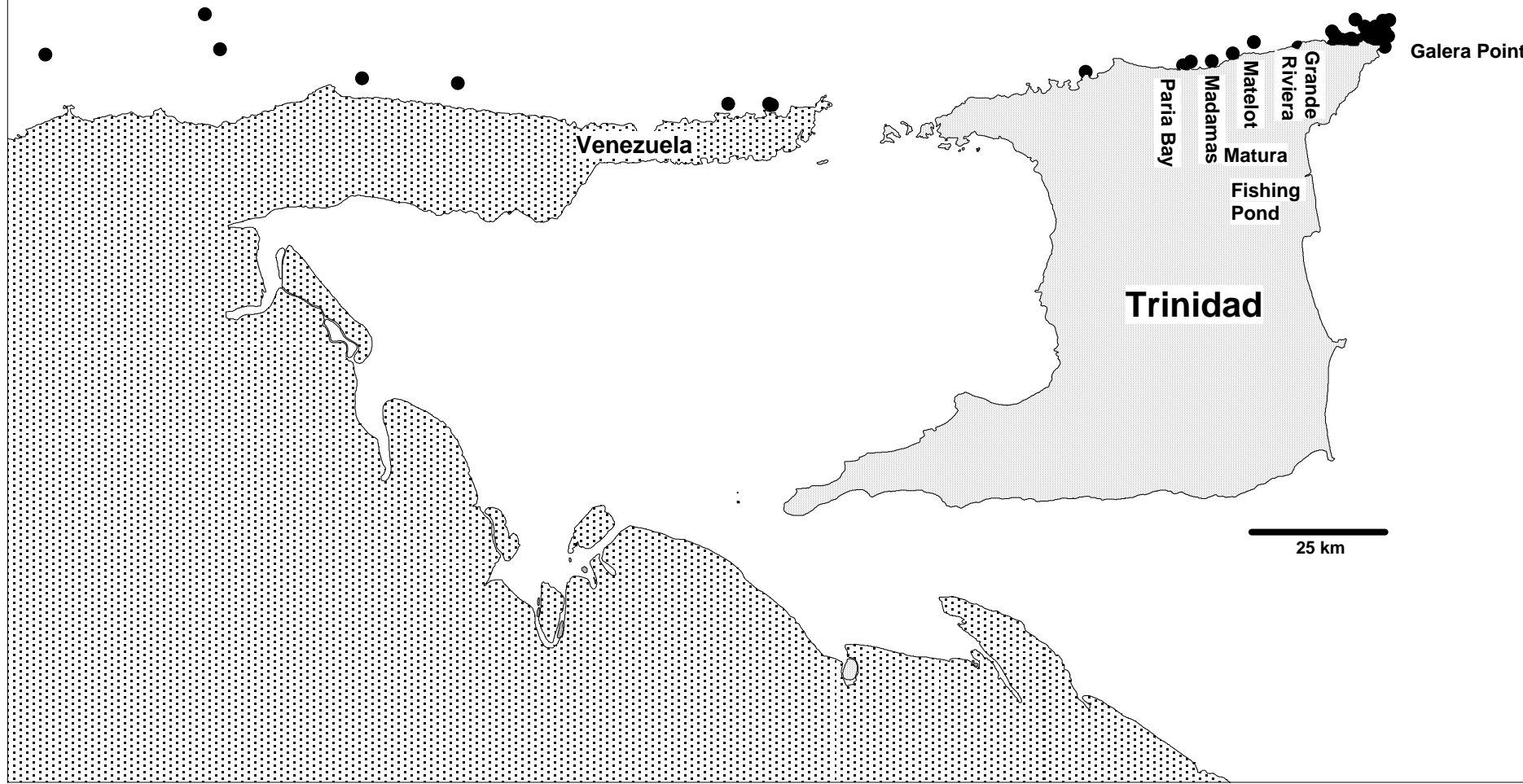
25 km



DC 8



Tobago



Venezuela

Trinidad

Paria Bay

Madamas

Matelot

Grande
Riviera

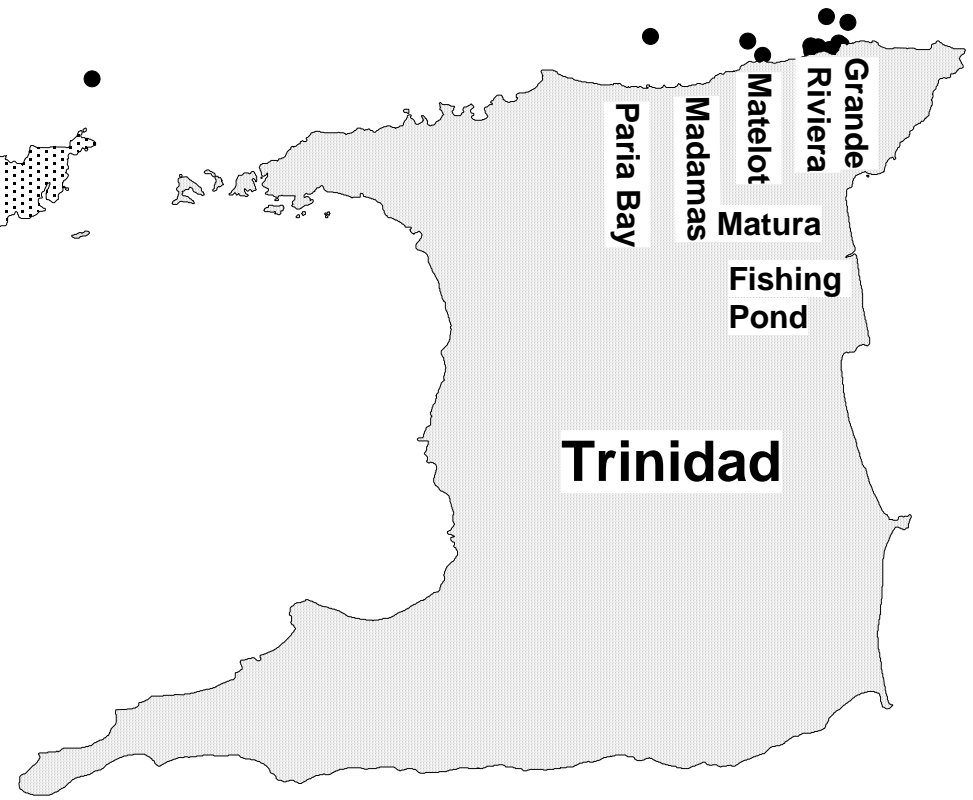
Matura

Fishing
Pond

Galera Point

25 km

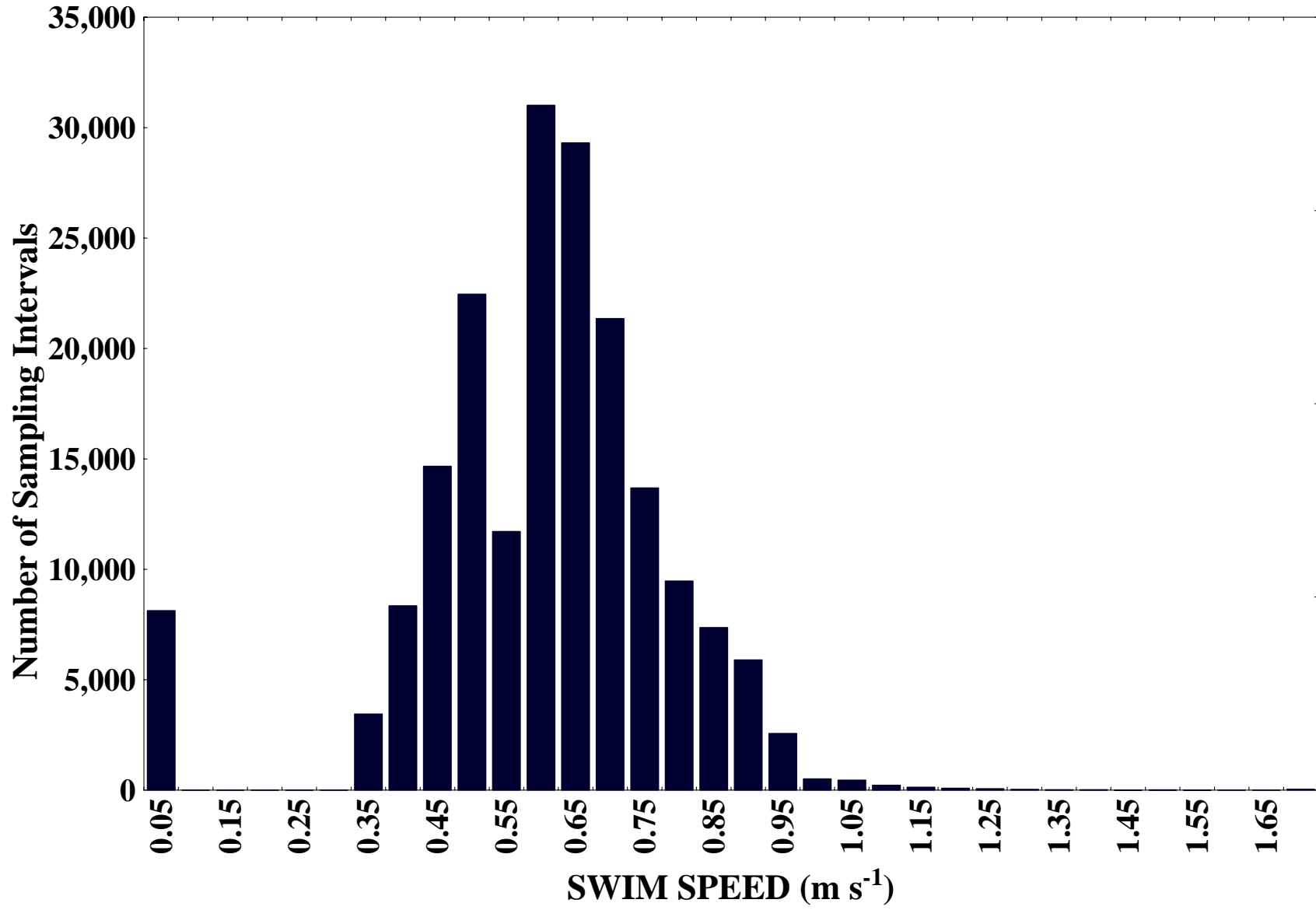
DC 9



Galera Point

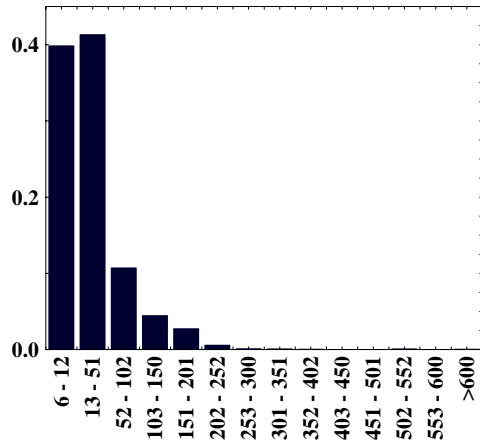
25 km

DC1

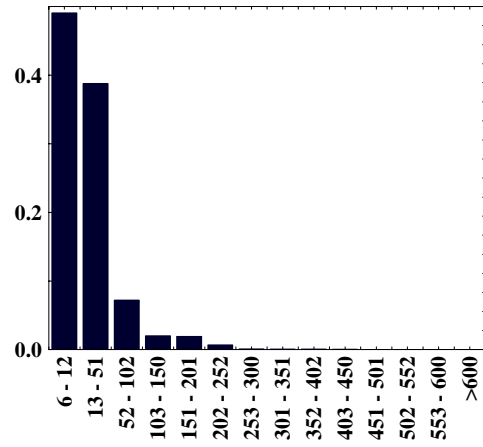


PROPORTION OF DIVES

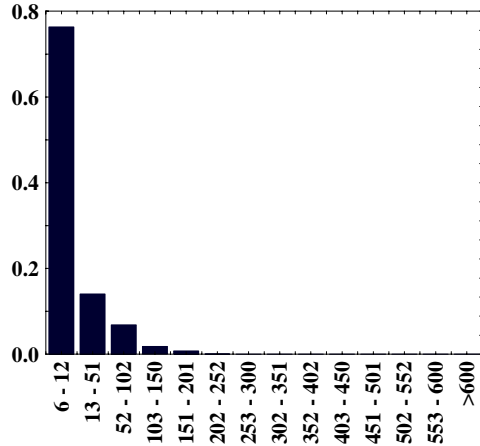
DC1



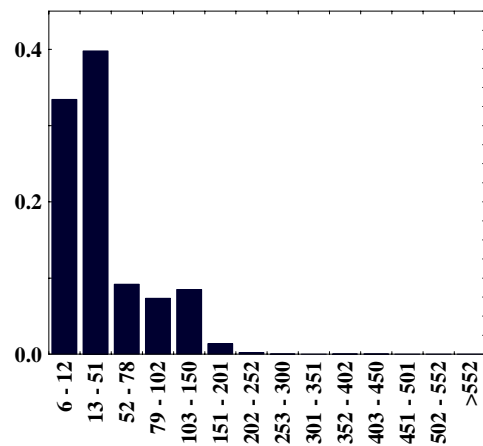
DC2



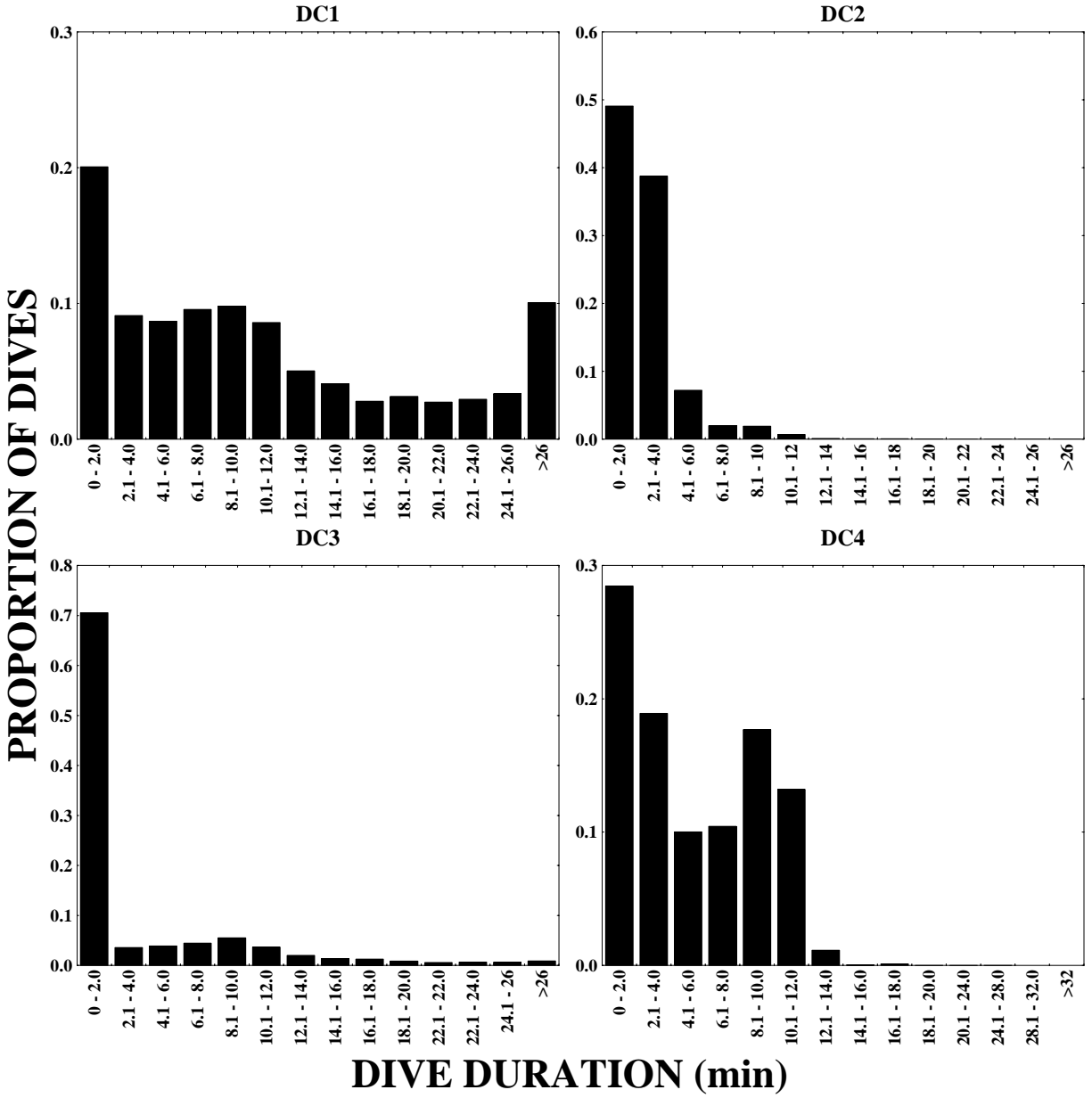
DC3



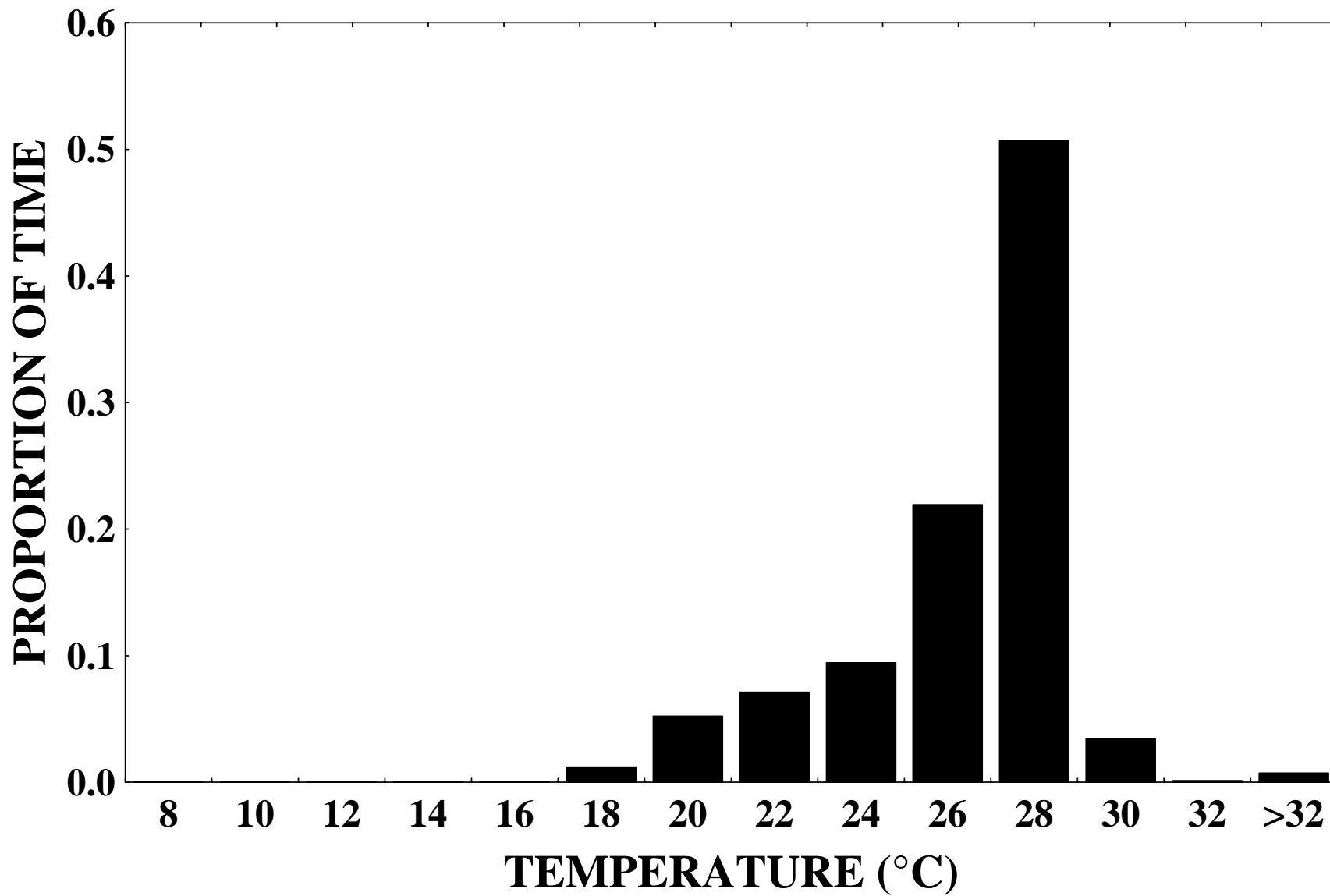
DC4



DIVE DEPTH (m)



DC4



MAXIMUM DIVE DEPTH (m)

