

Water mass characteristics and solar illumination influence leatherback turtle dive patterns at high latitudes

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Citation: Hamelin, K. M., D. E. Kelley, C. T. Taggart, and M. C. James. 2014. Water mass characteristics and solar illumination influence leatherback turtle dive patterns at high latitudes. *Ecosphere* 5(2):19. <http://dx.doi.org/10.1890/ES13-00158.1>

Abstract. Eastern Canada hosts one of the largest seasonal aggregations of leatherback turtles (*Dermochelys coriacea*) in the Atlantic Ocean, and is considered critical foraging habitat. Explaining distributional variation of leatherbacks in this three-dimensional habitat is relevant to the recovery strategy for this endangered species as human activities are a leading cause of mortality. We identify high-resolution spatial and temporal patterns in leatherback movements, and associated environmental variables shaping leatherback habitat use in Atlantic Canadian foraging waters. Data loggers were deployed on three female leatherbacks off Halifax, Nova Scotia, and were recovered during subsequent nesting in South and Central America. Time (0.5 Hz), depth (± 1 m), water temperature ($\pm 0.1^\circ\text{C}$), and location data were recorded and analyzed for the period when the turtles were resident in their Canadian foraging domain. We demonstrate that leatherback dives are primarily restricted to the main thermocline, suggesting a food-related water mass association. We also identified low- and high-frequency periodicities in turtle depth-at-time, reflecting a diel pattern triggered by nautical twilight and dive periods of 8–10 minutes. We further demonstrate that dive frequency is a function of seasonal change in daylight. Our findings illustrate that solar illumination influences leatherback diving in north temperate waters, consistent with turtles using visual cues for foraging.

Key words: Atlantic Canada; *Dermochelys coriacea*; dive behavior; foraging; leatherback sea turtle; oceanography; solar illumination; thermocline.

Received 3 May 2013; revised 26 August 2013; accepted 9 September 2013; final version received 13 January 2014; **published** 13 February 2014. Corresponding Editor: R. R. Parmenter.

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INTRODUCTION

The study of the biology and behavior of marine organisms has been greatly advanced through the use of electronic tags that allow researchers to collect detailed data on the movements of free-ranging animals and their local environment (Bograd et al. 2010). Whether

such data are collected remotely (e.g., via wireless telemetry), or through the recovery of archival data loggers, the results yield insight into relations among animal distributions, behavior, and their environment (Gaspar et al. 2006, Bograd et al. 2010, Costa 2012)

The leatherback sea turtle, *Dermochelys coriacea*, is the largest turtle species and is a highly

migratory and globally distributed animal (Bleakney 1965). Partly because of their global decline in number, and their designation as endangered (Sarti Martinez 2000, COSEWIC 2012), leatherbacks have been the subject of numerous tagging studies (e.g., Ferraroli et al. 2004, Hays et al. 2004).

In summer, the Atlantic coast of Canada hosts one of the largest seasonal aggregations of leatherbacks in the world (James et al. 2006a). The turtles typically arrive in Atlantic Canada in late spring and early summer, with a portion of the population migrating along the Scotian Shelf to foraging areas off Cape Breton Island, southern Newfoundland, and the southern Gulf of St. Lawrence (GSL) (Appendix: Fig. A1). Most leatherbacks depart the region in October when they migrate southward (James et al. 2005b).

Leatherbacks specialize on a diet of jellyfish (scyphozoan medusae), with lion's mane jellyfish, *Cyanea capillata*, representing their primary prey in Atlantic Canadian shelf waters (James and Herman 2001, Heaslip et al. 2012). Leatherback turtles resident in their north temperate foraging domain sequester food to enable their southward migrations, with infrequent feeding, from the northern foraging areas to the southern breeding areas, as evidenced by the fact that average body mass is ~33% higher for high latitude turtles than those on nesting beaches (Eckert et al. 1989, Morgan 1990, James et al. 2005a, James et al. 2007). The food energy value of Canadian waters to leatherbacks, and the relatively high concentration of turtles that seasonally occur there, attest to the importance of Atlantic Canadian foraging habitat for this endangered species (James et al. 2006b).

Throughout their summer-autumn range in Atlantic Canadian waters and elsewhere, the leatherbacks are vulnerable to injury and death due to entanglement in fishing gear (James et al. 2005a, Lee Lum 2006, Wallace and Saba 2009). Assessing the influence of oceanographic features on the time and space distributions of marine animals may contribute to the design and implementation of protection strategies (Żydelis et al. 2011, Bailey et al. 2012).

Leatherback turtles may fine-tune their foraging patterns according to local conditions (Hays et al. 2006), but only limited relationships between foraging and remotely sensed sea-surface characteristics, such as chlorophyll-*a*

concentration and Ekman upwelling, have been demonstrated (Bailey et al. 2012). The environmental variables that may shape leatherback distribution in their three-dimensional habitat through time have not been clearly identified. Given that leatherbacks are actively diving animals that spend most of their time at depth (James et al. 2005b), it should be informative to study their movements in the context of the depth-structured characteristics of the waters they occupy.

Instruments deployed on nesting female leatherbacks in subtropical and tropical waters have revealed diel dive patterns (Eckert et al. 1989, Ferraroli et al. 2004, Hays et al. 2004) and Casey et al. (2010) propose that this constitutes an energy-saving strategy used by a visual predator to maximize foraging during daylight hours when prey might be most effectively captured. In contrast to the tropics, only general conclusions have been drawn regarding dive patterns at north temperate latitudes (e.g., James et al. 2005b, 2006a). Nevertheless, there is some evidence that dives become progressively shorter and shallower as turtles migrate northward (Eckert 2006, Hays et al. 2006, Fossette et al. 2008), though low-resolution telemetry data indicate that dive patterns do not appear to vary predictably in Atlantic Canada until the onset of southward migration (James et al. 2005b). Most long-term leatherback tag-data studies suffer from limitations associated with a reliance on Argos satellite telemetry. Such data are typically classified (binned) into categories of dive depth or duration, or enumerated in terms of dive type, but only rarely are individual dive characteristics reported due to limitations in Argos transmission capabilities (James et al. 2005b). Furthermore, geographic position estimates from Argos can be uncertain due to limitations in the number of transmissions received by satellites during a single orbit.

To overcome some of the above limitations, in the present study we rely on the analysis of high-resolution (high-frequency) archival dive data, and location data from both Argos and Fastloc Global Positioning System (GPS) and retrieved from satellite tags that were deployed on female turtles off Nova Scotia and subsequently recovered from the turtles on their nesting beaches. We use the data to assess high-resolution (HR)

spatial and temporal variation in leatherback movements in their north temperate foraging domain. The data offer us the ability to assess patterns at scales from minutes to weeks, and in relation to local variation in the water masses occupied by the turtles. We focus on the foraging domain around eastern Nova Scotia, the Cabot Strait, southwest Newfoundland and the southern GSL where leatherbacks are annually resident from July to September (James et al. 2005a, James et al. 2006b). We first describe the geographic distribution of the turtles and the generalized variation in their dive patterns in relation to local water mass structure. We then quantify temporal variation in dive patterns, and their associations with short- and long-term variation in solar illumination.

METHODS

Data collection

Archival satellite-linked temperature-depth recording tags (SLTDRs: models MK10A [Argos] and MK10AF [Argos plus Fastloc GPS]; Wildlife Computers, Redmond, WA, USA) were deployed on three female leatherback turtles near Halifax, Nova Scotia (44° N 64° W); two in July 2008 (MK10A and MK10AF) and one in July 2009 (MK10AF). Tag deployment was similar to that described by James et al. (2005b), except that the tags were attached directly to the carapace (Byrne et al. 2009). The tags were later recovered from each of the turtles (FG, CL, and PN) on their nesting beaches located in French Guiana (FG; 2008, MK10A), Colombia (CL; 2008, MK10AF), and Panama (PN; 2009, MK10AF).

The HR time (FG: 0.25Hz, 1 sample/4 seconds; CL, PN: 0.5Hz, 1 sample/2 seconds), depth (0.5-m resolution, $\pm 1\%$), temperature (0.05°C resolution, $\pm 0.1^\circ\text{C}$), and location (Argos for FG, and Fastloc GPS for CL and PN) data were recovered from the tags. Depth data were zero-corrected for a pressure sensor offset such that the surface values corresponded to a depth of 0 m. To focus on the 'foraging domain' (James et al. 2005a, James et al. 2006b), we limited our analysis to the data associated with turtle movements on the eastern extent of the Scotian Shelf, the Cabot Strait, the south coast of Newfoundland, and the southern GSL (Appendix: Fig. A1). Unless stated otherwise (e.g., coordinated universal time, UTC)

all time references are 'local' (ADST; Atlantic daylight savings time).

Data analyses

Our analyses rely on using 'R' Statistical Computing Software (R Development Core Team 2008). We confined our analyses to the data beginning with the entry of each turtle into the foraging domain and ending when it was apparent that the turtle had initiated directed migration out of the region, though still within the domain. Surface location data, collected less frequently than the HR time, depth, and temperature data, were interpolated through time and space using 'R' to generate matching HR locations (latitude, longitude). The more accurate and frequently sampled GPS data (average 24 GPS records/day) from CL and PN were linearly interpolated. The Argos data from FG (transmitted on alternating days) were spline-interpolated to provide an optimum between smoothing the track and retaining movement detail. Statistical outliers for each of the three turtles, defined by adjacent locations separated by a translocation speed that differed by >2 standard deviations (SD) of the overall mean translocation speed between points, were not used for interpolation. Though the location estimates for FG have a higher margin of error relative to CL and PN (Witt et al. 2010), the uncertainties associated with geographic position should not affect the integrity of the dive data and have limited impact on our interpretation of the leatherback movement patterns.

We developed an algorithm to detect dives within each turtle-specific data-series using a threshold descent-depth of 5 m. The algorithm was used to identify data records that constituted the beginning, maximum recorded depth, and end of each turtle dive to determine the time, temperature, depth, and approximate geographic location associated with each of these dive stages. The depth threshold served to eliminate dive noise associated with the turtle being at or near the surface between dives. We defined dive duration as the time difference between the start and the end of a dive, and inter-dive translocation distance as the horizontal distance between geographic locations at the start and end of a dive.

Averages and standard deviation ($\pm\text{SD}$, or in

parentheses) were compared for the maximum dive depth, dive duration, and inter-dive translocation distance among the turtles. For visual examination purposes, the time- and depth series for each turtle were graphically prepared as color-scaled temperature-at-depth over time superimposed with sun angle below and above the horizon (proxy for magnitude of ambient light at the surface) estimated for each time, date, and location using the *oce* package in 'R' (Kelley 2011).

Associations between turtle dive patterns and thermal structure of the water column were illustrated using contours of the observed probability density of a turtle being found at a particular temperature-at-depth across its entire ambit within the domain. The probability contours were compared with similar ones generated using archival conductivity-temperature-depth (CTD) profile data (Fisheries and Oceans Canada, Integrated Science Data Management, ISDM database, 12W082-200 Kent Street, Ottawa, Ontario, Canada, K1A 0E6) that were coincident with the time and space ambit of the turtles. The CTD and turtle-tag profiles available for 2008 and 2009 were classified among $1^\circ \text{N} \times 1^\circ \text{W}$ grid-cells, each $\sim 111 \times 74$ km, within the domain. This resulted in using 317 different CTD profiles collected in 2008 over the period 3 July through 28 September, and 308 profiles in 2009 over the period 1 July through 30 September to construct the temperature-at-depth probability contours.

Dominant temporal patterns in dive depth variation among the three turtles were estimated using autocorrelation analyses at hour- and day-scale lags (FG, $n = 209,661$; CL, $n = 3,014,760$; PL, $n = 1,584,780$). The context of these temporal periodicities was examined as dive depth, dive duration, and inter-dive translocation distance among 24 h time-of day (local) classes. However, two of the turtles, CL and PN, provided tag-data over many days (>10), a scale over which seasonal changes in solar illumination and day-length are substantial at high latitudes. Therefore, we also examined the maximum dive depth in relation to regional sun-elevation (10° class intervals) relative to the horizon (-45° through 65° with sunrise at 0°). We also investigated daily dive frequency in relation to seasonal changes in the number of daylight hours; i.e., the number of hours in the local nautical inter-twilight period

(beginning and ending with the sun 12° below the horizon).

Partitioning of day-to-night changes in dive depth, in relation to sun elevation, was assessed using conditional inference trees in 'R' (Hothorn et al. 2006). As sun elevation is a proxy for ambient light conditions at any given time, we also examined dive depth variation based on subsets of the data using only those dates and times when we could be reasonably confident there was little or no cloud cover over the region. Suitable dates were determined by examining archived infrared satellite (GOES, AVHRR) day-time images for the region (US National Oceanic and Atmospheric Administration, National Weather Service; Unisys archive: <http://weather.unisys.com/archive/index.php>), and we assume the images would be valid for a period ± 3 h of the time the image was taken.

RESULTS

FG (curved carapace length, CCL, 174.5 cm, curved carapace width, CCW, 123.5 cm) was tagged on 24 July 2008, entered the study domain on 2 August, initiated her outward migration on 11 August, and provided only 10 days of data while in the foraging domain (Appendix: Fig. A1). CL (CCL 152.4 cm, CCW 111.7 cm) was tagged on 17 July 2008, began her southward migration on 5 October, and provided 71 days of data while in the domain. PN (CCL 159.0 cm, CCW 115.2 cm) was tagged on 15 July 2009, entered the domain on 20 July, and departed on an eastward trajectory on 26 August, providing 38 days of data while in the domain.

Dive patterns and water mass associations

The average maximum dive depths for FG (20.7 ± 8.9 m) and CL (20.6 ± 10.3 m) in 2008 were similar but highly variable, with ~ 10 m differences in the average depth of the thermocline in occupied waters (~ 35 m for FG and ~ 46 m for CL; Fig. 1a, b, Fig. 2). In 2009, PN typically performed shallower dives (14.0 ± 6.4 m) than either FG or CL, though the average depth of the thermocline in the waters occupied was intermediate at ~ 37 m (Fig. 1c, Fig. 2). All three turtles tended to spend most of their time in the warm surface mixed layer ($>10^\circ\text{C}$), sometimes entering $5\text{--}10^\circ\text{C}$ water, and occasionally descending to

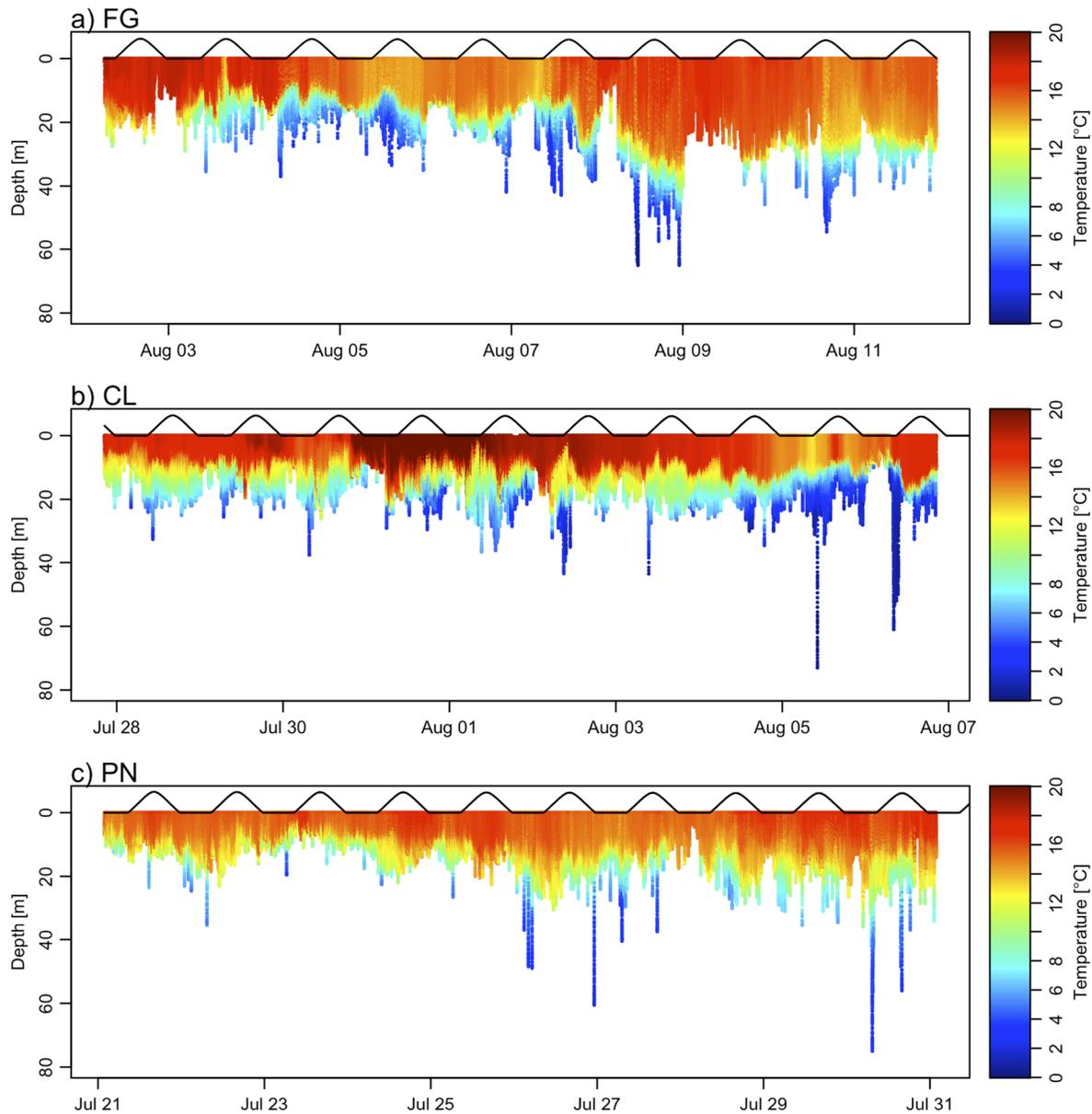


Fig. 1. Representative example 10-d temperature ($^{\circ}\text{C}$) -at-depth (m) time-series from each of the (a) FG, 2008; (b) CL, 2008 and (c) PN, 2009, leatherback sea turtle archival tag-data. Daily sun angle associated with each turtle and date is represented by a black line superimposed above each panel and varies between zero (below horizon) and maximum elevation above horizon.

depths with temperatures of $<5^{\circ}\text{C}$ (Fig. 1). Changes in the maximum dive depths appeared to exhibit periodic patterns with occasional abrupt changes to deeper dives, often at or before sunrise, with a tendency for shallower dives during the night. The CTD-profile data (Fig. 2) indicated that

the thermal structure of the waters associated with the ambits of the turtles was consistent with the thermal structure derived from the turtle-tag profiles, and that the dives were, for the most part, restricted to depths at or above the depth of the main thermocline (surface layer).

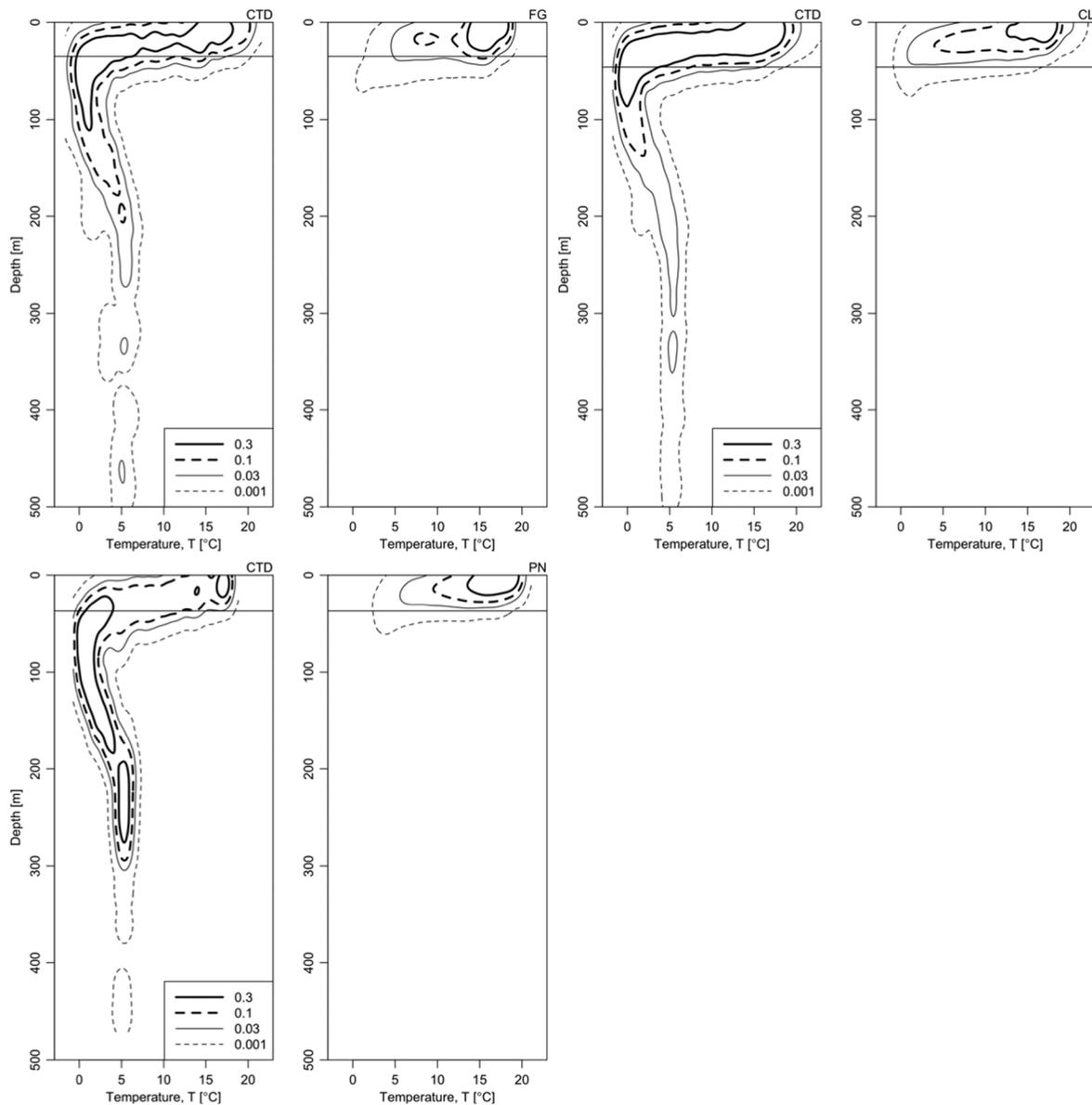


Fig. 2. Temperature ($^{\circ}\text{C}$) -at-depth (m) probability density contours (inset) illustrating the thermal structure of the water column as provided by the CTD profiles (left panel) in 2008 and 2009 in water masses that were occupied by each turtle and as provided by their associated tag temperature-at-depth data for each of the FG (2008), CL (2008), and PN (2009) turtles (right panels) in the water masses. The horizontal line references the approximate depth of the surface thermocline.

Average dive duration for FG was 7.2 ± 3.2 min, while that for CL was 4.6 ± 1.7 min. PN exhibited shallower dives and shorter dive durations, averaging 3.5 ± 1.8 min. FG covered greater average inter-dive translocation distance (312 ± 211 m) relative to CL (186 ± 149 m) and PN (142 ± 178 m), though all were highly

variable (coefficient of variation, CV: 68%, 80%, 125%, respectively).

Dive frequency variation

The autocorrelation analyses of the turtle depth series showed clear high-frequency periodicity at ~ 10 minutes for FG and ~ 8 minutes

for CL and PN (Fig. 3a, c, e), as well as a clear diel periodicity for all three turtles (Fig. 3b, d, f).

Solar illumination

When examined by hour-of-day, and as exemplified by FG (Appendix: Fig. A2a, b, c), the turtles exhibited deeper dives of shorter duration and inter-dive translocation distance during the daylight period (~06:00 to ~20:00 h local), and maximum dive depth was slightly more variable during the day (CV = 42%) than during the night (CV = 38%). Night dives (~21:00 to ~05:00 h local) were characterized by shallower depth, longer duration, and longer translocation distance. Consistent with the above, dive depth began to change in relation to daily changes in solar illumination as measured using regional sun-elevation, our proxy for solar illumination. For both FG and CL, dive depth began to increase in the morning and decrease in the evening when the sun was ~15° below the horizon, an angle that is intermediate between astronomical (−18°) and nautical (−12°) twilight (Fig. 4). This change in depth was less apparent for PN. There was also some evidence that each turtle tended toward shallower depths when the sun reached its zenith at 65°.

Conditional inference trees used to partition dive depth in relation to sun elevation angle, revealed relatively sensitive night vs. day dive depth dependence for each of FG and CL (Appendix: Fig. A3). Primary partitions ($p < 0.001$) occurred at −13° for each of FG and CL, indicating a change from shallow to deep dives just before morning nautical twilight (12°), and from deep to shallow dives just after evening nautical twilight (−12°). Secondary and marginal ($p = 0.039$ and 0.011) partitions occurred at −18° and −34° for each of FG and CL, respectively. For FG, this indicated even shallower dives with a change from evening nautical twilight (−13°) to evening astronomical twilight (−18°) and vice versa for morning. We have no simple explanation for the partition at −34° for CL, which is related to a secondary increase then decrease in depth at around −35° (Fig. 4), though given the length of the series (71 d), we can speculate that moonlight and (or) cloud cover might be involved. There were no statistically significant partitions identified for PN.

When the dive depth variation was examined

based only on those dates and times when we could be reasonably confident there was little or no cloud cover over the region (Appendix: Fig. A4), the influence of solar illumination became more apparent (Appendix: Fig. A5a). Though there was only one cloud-free image for FG (18:00 to 00:00 ADST, 11 August 2009; Appendix: Fig. A4), and thus a limited number of dives to assess, the influence of sun elevation was reflected as a sequential decrease in dive depth from ~35 m at 5°, just before sunset, to ~20 m at −25° near midnight. Conditional inference trees indicated a partition ($p < 0.001$) at −9°, near nautical twilight for FG (Appendix: Fig. A6). For CL, there were more clear or marginally clear days (Appendix: Fig. A4), and the change from shallow to deeper dives was apparent from 17 to 20 m at −45°, −35° and −25° to ~25 m just after sunrise or before sunset, and, as above, there was a decrease in dive depth when the sun was at its zenith (Appendix: Fig. A5b). Similar to FG, there was a significant ($p < 0.001$) partition for CL at −8°, just before nautical twilight (Appendix: Fig. A6). For PN, dive variation patterns were limited (Appendix: Fig. A5c), and no significant partitions were identified (Appendix: Fig. A6).

Further evidence that solar illumination influences dive behavior was provided by an examination of dive frequency variation as a function of day-to-day seasonal variation estimated using the period of daylight hours between morning and evening nautical twilight. Both CL and PN performed more dives on days with more hours of solar illumination (Fig. 5). The notable minimum exhibited by CL at ~14.5 h corresponds to dates when she occupied an area west of Prince Edward Island in the GSL and was traveling at a greater-than-average speed (see Appendix: Fig. A1).

DISCUSSION

Dive patterns and water mass associations

Our analyses demonstrate that three leatherback turtles, following different horizontal trajectories over tracking durations of 10 to 70 days in a north temperate, coastal foraging domain, exhibited variable dive behavior, but were remarkably consistent in some specific dive characteristic patterns. As reported elsewhere (James et al. 2005b, Eckert 2006, Hays et al. 2006),

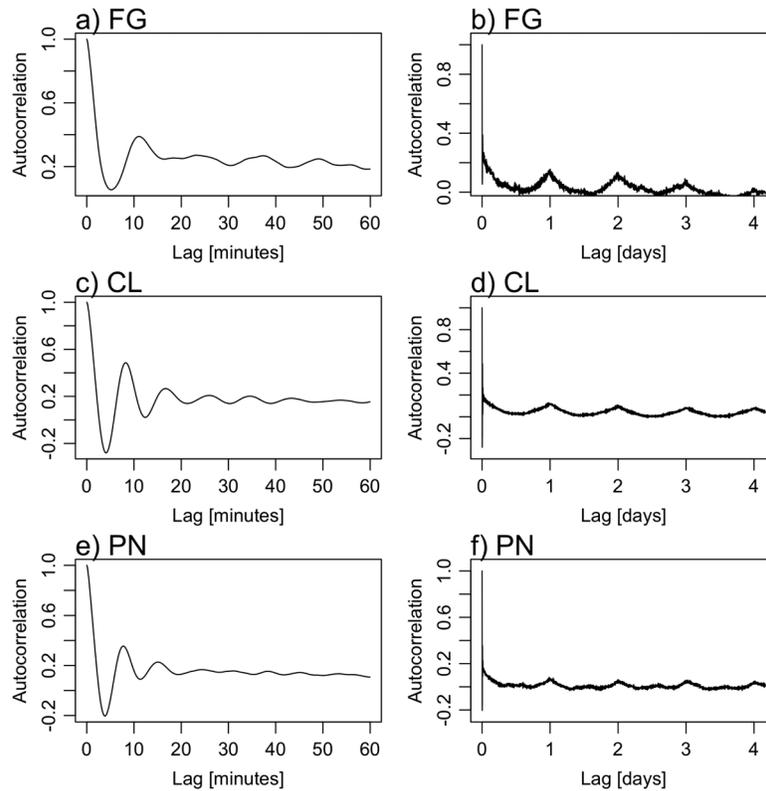


Fig. 3. Auto-correlograms of the depth time series for each of the FG, CL, and PN leatherback sea turtles at minute and hourly lags illustrating dominant dive periodicities near 9 to 10 minutes (a, c, e) and at 24 hours (b, d, f).

the turtles exhibited near-continuous diving in the foraging domain, where they performed relatively short (~ 6 min) and shallow (~ 20 m) dives that are typical of leatherbacks at north temperate high latitudes. Hays et al. (2006) speculated that this is related to the availability of jellyfish. Although FG and CL had very similar average maximum dive depths (~ 21 m), all three turtles exhibited different and variable dive durations that were proportionately reflected in different inter-dive translocation distances. We can also speculate that this variation is related to variation in the prey fields encountered by the different turtles as they traveled within and among different water masses.

Our results indicate that diving patterns of leatherbacks in this northern temperate foraging domain correspond to the thermal structure of the water column. Despite subtle differences in the depth of the thermocline, all three turtles restricted the majority of their dives to depths at or above the depth of the main thermocline (Fig.

2), in this case at or above the pycnocline with densities $\leq 25.3 \text{ kg m}^{-3}$ (Appendix: Fig. A7). There were infrequent departures from this pattern when the turtles entered higher density waters of 5°C or less at greater depth (Fig. 1). Although we have not addressed specific discontinuities in the dive record corresponding to encounters with different water masses, leatherbacks may be adjusting their dive patterns in response to changes in oceanographic conditions, particularly the depth of the thermocline and (or) pycnocline.

It is clear that leatherbacks use the stratified waters of Atlantic Canada as foraging grounds and thus their dive patterns may reflect jellyfish concentration and distribution. Strong density gradients associated with the pycnocline often reflect high concentrations of planktonic animals, including gelatinous plankton (Gallager et al. 1996, Brodeur 1998, Daunt et al. 2003, Bastian et al. 2011). Such gradients may provide leatherbacks with concentrated food and the dive

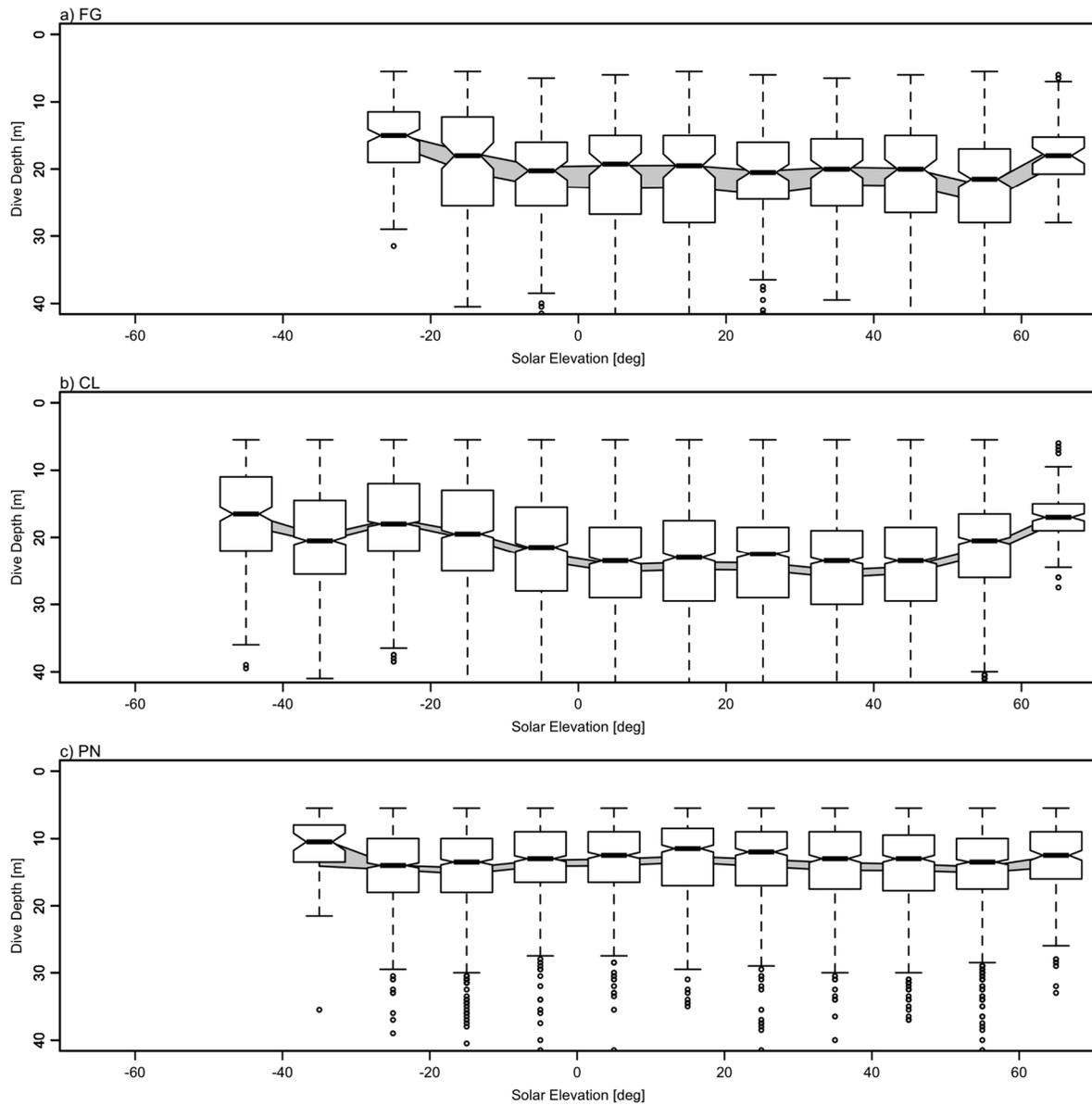


Fig. 4. Maximum dive depth (m) box plots, in 10° class increments of sun elevation (night $< 0^\circ >$ day), showing the median (black bar), 95% confidence interval (CI) around the median (waist), 95% CI around the average (grey shading), top whisker (dashed line and bar) indicating largest observed value within 1.5 inner quartile range (IQR) of the upper quartile (similar for bottom whisker indicating lowest value within 1.5 IQR lower quartile), and statistical outliers (open circles) > 1.5 IQR, for each of the FG, CL, and PN leatherback sea turtles.

patterns we identified may reflect a strategic foraging behavior.

Jellyfish are believed to accumulate around discontinuities such as the pycnocline as a result of their density and buoyancy, behavior, and the local hydrodynamic conditions (Graham et al. 2001, Graham et al. 2003, Alvarez Colombo et al.

2009). However, recent studies propose that some species of jellyfish eaten by leatherbacks, including *Rhizostoma octopus* and *Cyanea capillata*, are not passive in the water column, but are capable of meter-scale vertical oscillations and more advanced swimming behaviors than previously thought (Hays et al. 2012, Moriarty et al.

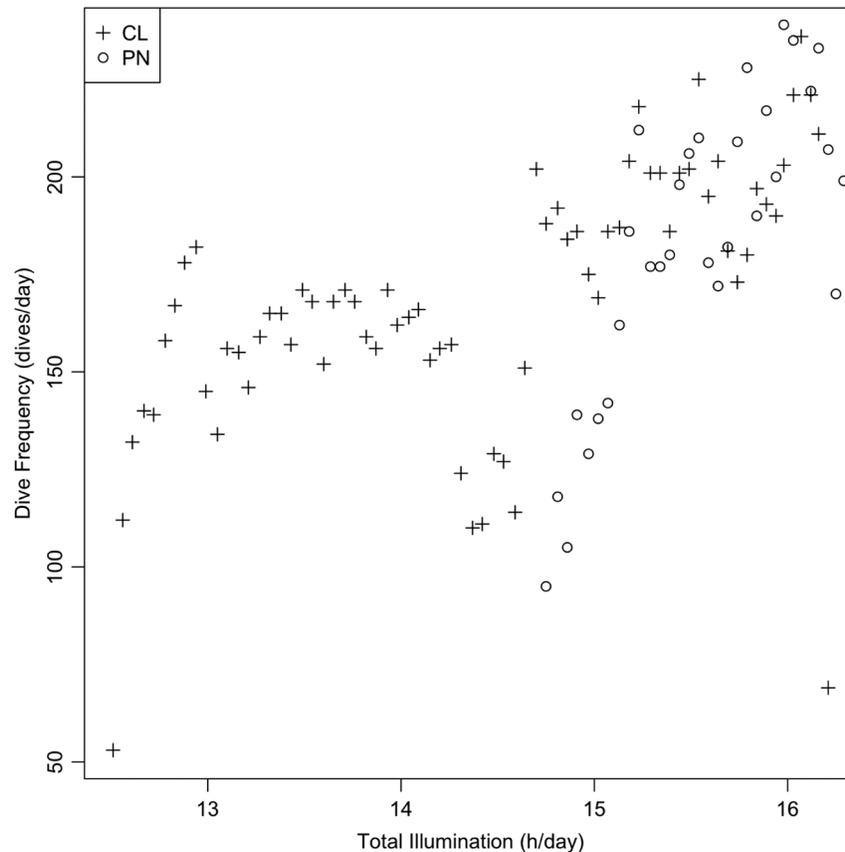


Fig. 5. Scattergram of daily dive frequency as a function of nautical inter-twilight period (h d^{-1}) for each of the CL (plus signs; 27 July to 5 October 2008) and PN (open circles; 20 July to 26 August 2009) leatherback sea turtles.

2012). Although it appears that leatherbacks are exhibiting prey-related water mass associations, and are perhaps focusing on those depths where food resources are concentrated, the literature regarding distribution and behavior of gelatinous plankton in the temperate, coastal waters of the northwest Atlantic region is very limited. Research focused on assessing jellyfish distribution at depth in leatherback foraging areas is essential to verify the prey-related water mass associations suggested here.

It is also possible that the warmer surface mixed layer has a role in the physiology of food energy acquisition for the leatherbacks. The increase in biochemical rates in the warmer water may allow for enhanced energy assimilation from their prey, and thus enhanced growth. This would help to ensure sufficient stores for successful southward migration and subsequent nesting, evidenced by large increases in leather-

back mass (James et al. 2005a), and changes in carapace shape (Davenport et al. 2011) while feeding in Atlantic Canadian waters.

The role of occasional dives to colder, deeper waters may be related to exploratory diving for food, or thermoregulation related to cooling after extended periods in the warmer surface waters.

Dive frequency variation

All three turtles showed dive patterns with two dominant and consistent periodicities. The first reflects a dive periodicity of 8 to 10 min, a relatively consistent pattern compared to their average dive duration that varied from 3.5 to 7.2 min. The second reflects a systematic diel periodicity that was associated with shallower dives during the night and deeper dives during the day.

The diel cycle has been reported elsewhere for leatherbacks during southward migrations and

while resident in the tropics (Eckert et al. 1989, James et al. 2005a, James et al. 2006a, Casey et al. 2010). However, only with the HR archival data presented here is the consistency so clearly evident for turtles in their Canadian foraging domain, and so clearly triggered by solar illumination.

The most frequently proposed explanation for diel dive patterns among planktivorous animals, such as leatherbacks, is that the animals track a postulated diel vertical migration in their prey field (Eckert et al. 1989, Eckert 2002, Hays 2003). Similar thinking has been used to explain the diel behavior of leatherbacks in the tropics (Eckert et al. 1989, Hays et al. 2004). Using coarser resolution data, James et al. (2006a) did not detect diel variation in leatherback dive patterns in north temperate coastal areas and suggested this might reflect foraging on relatively high concentrations of shallowly distributed prey during the day and night. In contrast, using finer-resolution diving data, we found marked diel dive patterns for leatherbacks in these same areas, suggesting that foraging is light-mediated. Heaslip et al. (2012) demonstrated that foraging during daylight hours in Atlantic Canada is restricted to the photic zone. Moreover, while leatherbacks clearly dive throughout the night throughout their range, Casey et al. (2010) provide evidence from stomach temperature telemetry that food ingestion rates in waters adjacent nesting beaches are significantly lower during the night than during the day.

The HR data we examined leads us to the simplest conclusion that the strictly diel dive depth periodicity is explained by leatherbacks being visual predators that are reliant on adequate ambient light to effectively forage (Casey et al. 2010). This idea has been proposed before for diving marine predators, including penguins, which have been recorded diving more deeply during daylight hours and remaining in shallow waters, with infrequent feeding, throughout the night (Wilson et al. 1993). To date, there is no evidence for diel patterns in the depth-distribution of the leatherback's north temperate prey field. Indeed, for many marine predators exhibiting diel dive patterns (e.g., whale shark, *Rhincodon typus*; ocean sunfish, *Mola mola*), there is a paucity of data on corresponding prey distribution and behavior

(Cartamil and Lowe 2004, Graham et al. 2006, Sims et al. 2009). Linking foraging behavior of marine mega-fauna at depth to the three-dimensional spatio-temporal distribution of their prey is an important future direction for marine wildlife telemetry (Cartamil and Lowe 2004). Until corresponding results are available for leatherbacks, we suggest that visual, and therefore light-mediated foraging behavior offers the most parsimonious explanation for the diel dive depth periodicity we observed among northern leatherbacks.

Solar illumination

The above 'visual predator' interpretation of the dive depth periodicity is consistent with differences in dive properties exhibited by the turtles at different hours of the day. All three turtles exhibited shorter and deeper dives with smaller inter-dive translocation distances during the day (~05:00 to ~20:00 h local). In contrast, with low ingestion rates at night, simultaneous long, shallow dives during the night may be related to resting and a conservation of energy for times when prey detection and capture is more probable and profitable (Casey et al. 2010).

For two of the turtles, we were able to identify clear divisions between day and night dive patterns as a function of solar illumination (sun angle), with sharp discontinuities associated with morning and evening nautical twilight. The use of sun angle eliminated confounding factors associated with seasonal changes in daylight hours and we were able to show that the seasonally decreasing light levels result in fewer dives per day, by as much as 50% or more, providing further evidence of light-mediated foraging. The various influences of solar illumination on dive patterns lead us to speculate that changes in light levels at the northern latitudes of the foraging habitat may reach a threshold that triggers southward migration at a time when the days are too short to allow energy efficient foraging. Such a threshold would vary seasonally with latitude and may explain the observed variation in the initiated dates of southward migration that increase with decreasing latitude (Sherrill-Mix et al. 2007). Many of our above interpretations and postulations could be validated through the deployment of

light meters on turtle satellite tags that would provide measures of ambient light at depth over time and latitude. Finally, it is not surprising that the dive behavior of leatherbacks is influenced by solar illumination given the prominent de-pigmented spot on the dorsum of the leatherback head, located above the light-sensitive pineal gland of the leatherback brain (McDonald et al. 1996).

Policy considerations

Our findings have implications for conservation, as we have begun to define the three-dimensional foraging habitat for leatherback turtles in northern coastal and shelf waters where turtle entanglement in fishing gear is a serious threat to this species (James et al. 2005a). While leatherback high-use areas exist in the Atlantic Canadian region, their use varies among individual turtles. Thus time and (or) space fishery closures may not reduce entanglement and subsequent mortality if fishing effort shifts elsewhere (James et al. 2005a). Changes to fishing practices may offer alternative reduction in risk. It appears that in their foraging domain, the turtles limit their diving much of the time to the upper mixed layer and thus potentially entangling fixed gear could be set below the thermocline (pycnocline) to minimize the probability of entanglement. Buoy lines pose a particular risk for turtle entanglement (James et al. 2005a), perhaps because they intersect the surface mixed layer. More sinking and rigid buoy lines, at least in the upper mixed layer, could serve to reduce the risk of turtle injury and mortality.

ACKNOWLEDGMENTS

Satellite tags and associated field research were funded by Conservation International, National Geographic, and World Wildlife Fund Canada grants to M. C. James and the Canadian Sea Turtle Network (CSTN). K. M. Hamelin was supported by an NSERC-USRA, a VEMCO scholarship, and a Canadian Wildlife Federation grant to C. T. Taggart. We thank the CSTN, S. Craig, B. Fricker, H. Fricker, P. MacDonald, K. Martin, B. Mitchell, and M. Nicholson for assistance with fieldwork. We are grateful to the Centre National Scientifique (French Guiana), Grupo GILA (Colombia), and Sea Turtle Conservancy (Panama) nesting beach field teams for satellite tag recovery. We also thank two reviewers for their helpful comments on the manuscript.

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SUPPLEMENTAL MATERIAL

APPENDIX

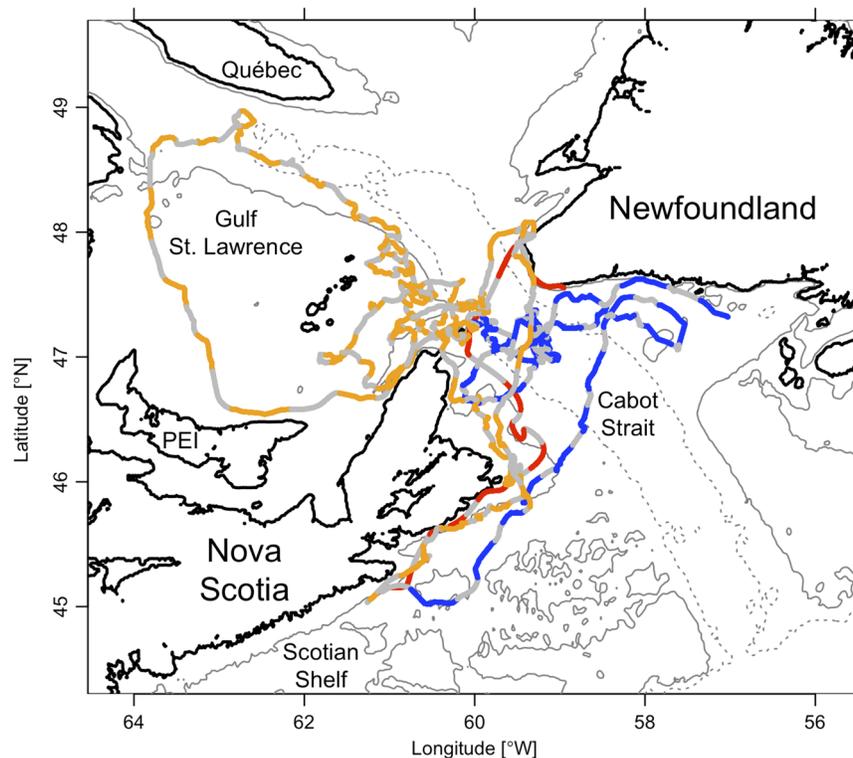


Fig. A1. Bathymetric chart (100 and 400 m isobath increments) of eastern Canada illustrating the southern Gulf of St. Lawrence, Cabot Strait, eastern Scotian Shelf, southwest extent of the Grand Banks, and the color-coded line trajectories of each leatherback sea turtle (FG, red; CL, orange; PN blue) within the north temperate summer foraging domain. The alternating color portions of the line trajectories denote sequential day (color) and night (grey) portions of the ambit of each turtle.

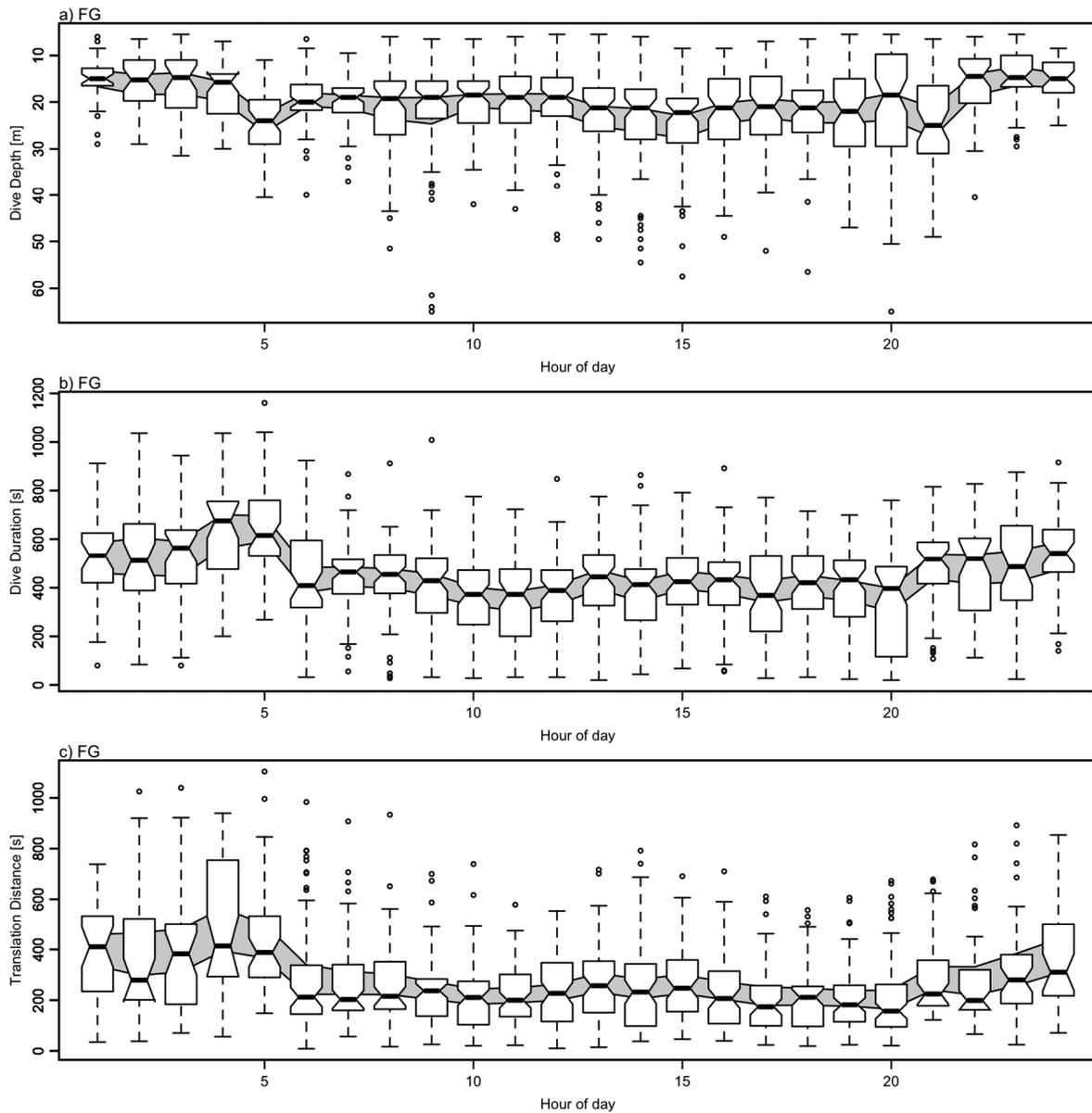


Fig. A2. Box plots of (a) maximum dive depth (m), (b) dive duration (in seconds), and (c) inter-dive translocation distance (m) for hour-of-day classes (12 = local noon), showing the median (black bar), 95% confidence interval around the median (waist), 95% CI around the average (grey shading), top whisker (dashed line and bar) indicating largest observed value within 1.5 inner quartile range (IQR) of the upper quartile (similar for bottom whisker indicating lowest value within 1.5 IQR lower quartile), and statistical outliers (open circles) >1.5 IQR, for the FG leatherback sea turtle.

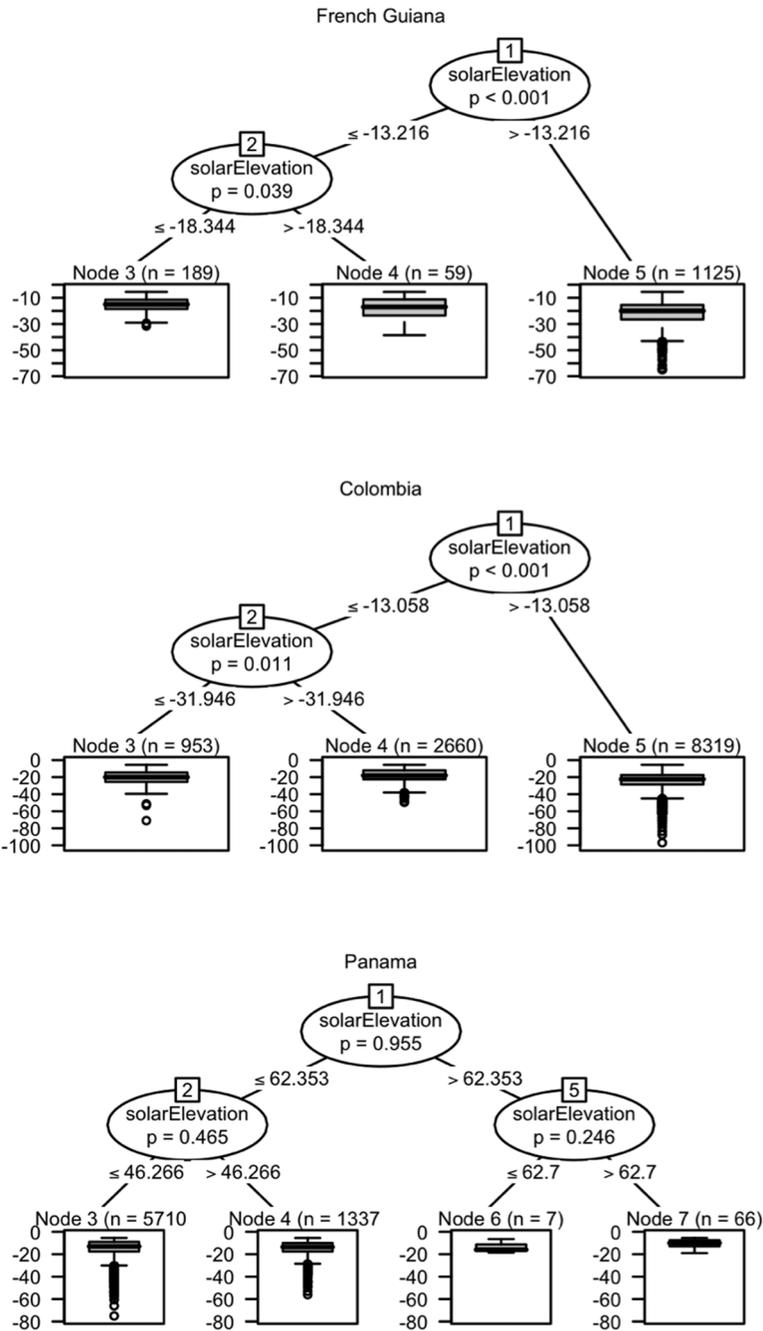


Fig. A3. Conditional inference tree partitioning of maximum dive-depth in relation to the solar elevation (sun angle) where a partition was identified and the associated significance (p-value) of the partition is provided for each of the FG, CL, and PN leatherback sea turtles.

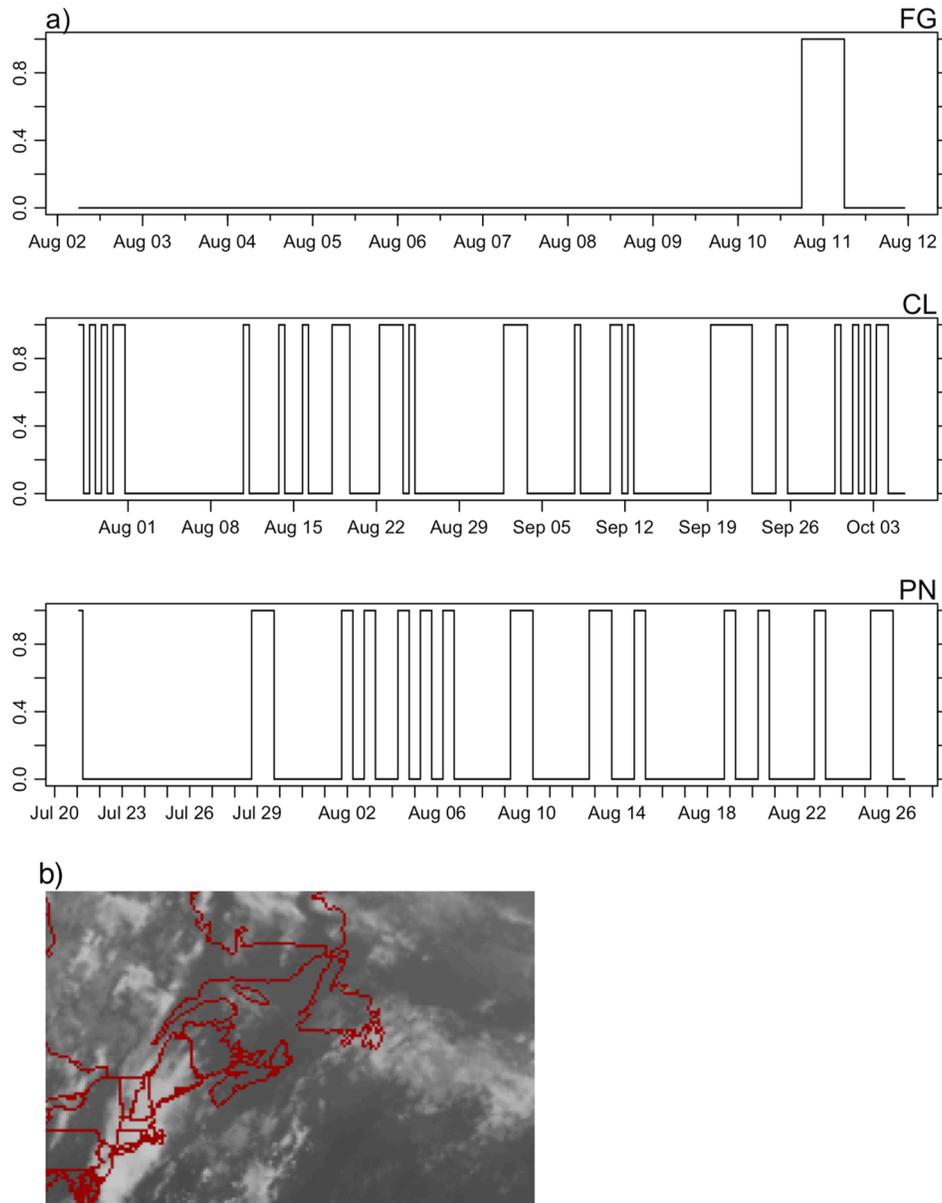


Fig. A4. (a) Binary plot illustration of the dates and times (00:00 h and 12:00 h satellite-pass images) of the resident period for each of the FG, CL, and PN leatherback sea turtles when we could be reasonably confident there was little or no cloud cover over the region as determined by examining the archived infrared (11- μ m) satellite (GOES, AVHRR) images for the region. A suitable image is scored 1 and unsuitable 0 and the width of the bar indicates the number of images where the narrowest bar indicates 1 image only per day, and (b) is an example of a suitable image dated 00:00 GMT, 28 July 2008.

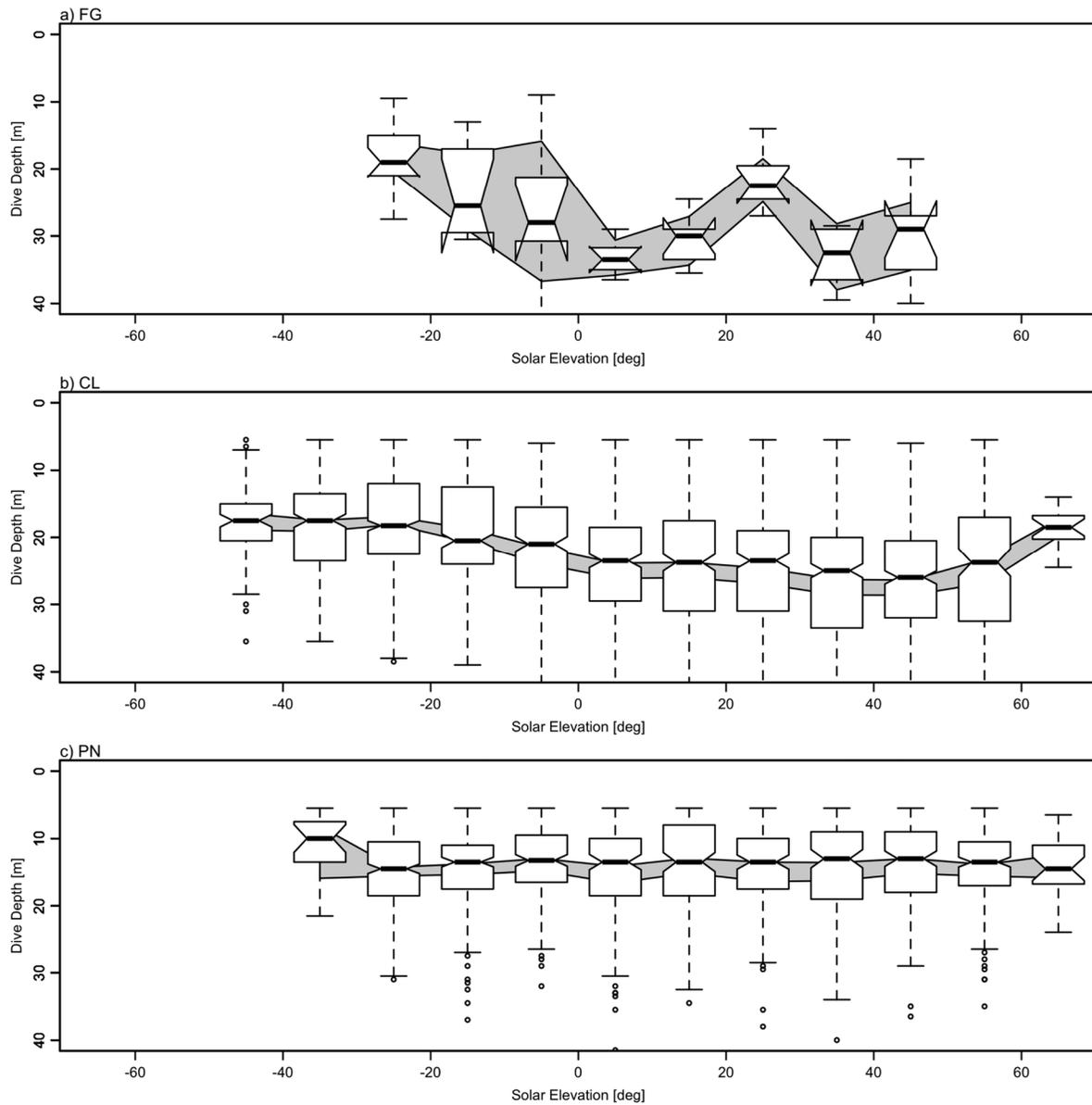


Fig. A5. Maximum dive depth (m) box plots, in 10° class increments of sun elevation (night $< 0^\circ >$ day), showing the median (black bar), 95% confidence interval (CI) around the median (waist), 95% CI around the average (grey shading), top whisker (dashed line and bar) indicating largest observed value within 1.5 inner quartile range (IQR) of the upper quartile (similar for bottom whisker indicating lowest value within 1.5 IQR lower quartile), and statistical outliers (open circles) >1.5 IQR, using only those data where cloud cover was considered absent or marginal for each of the FG, CL, and PN leatherback sea turtles.

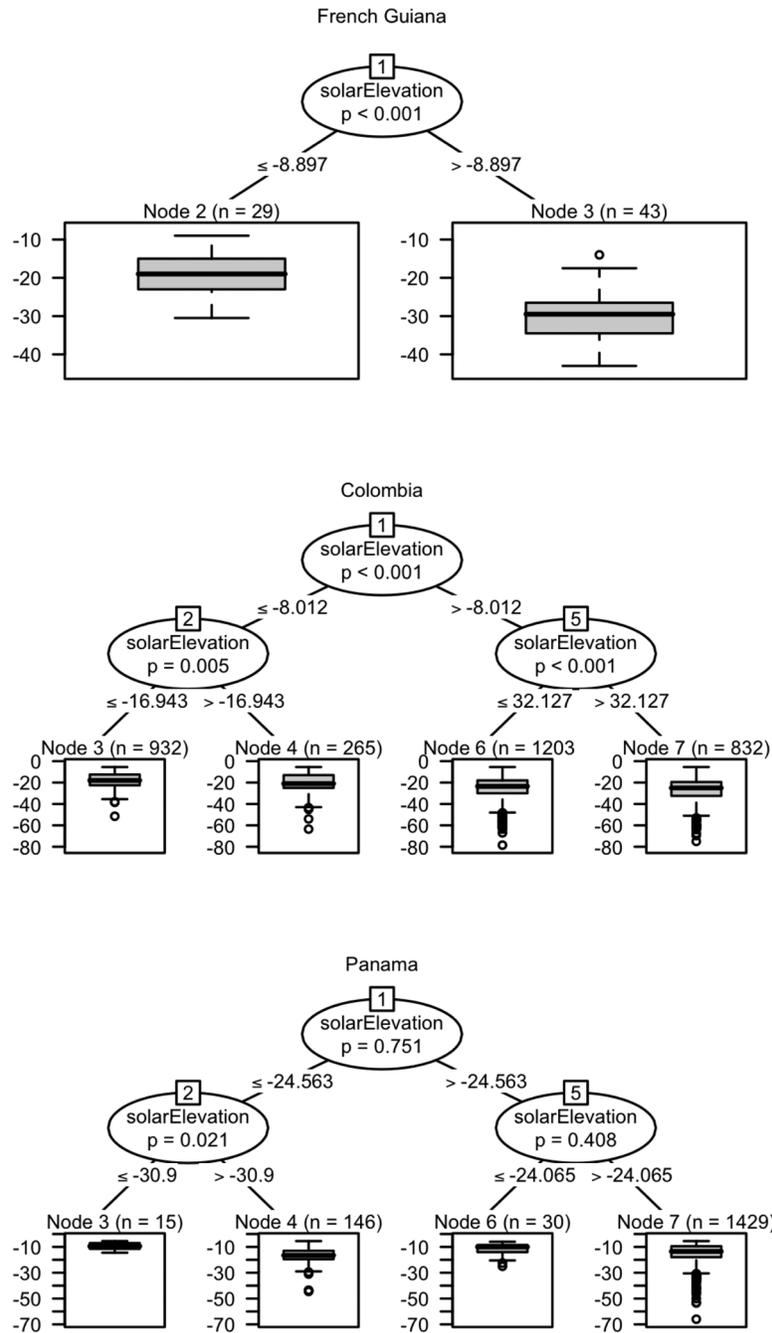


Fig. A6. Conditional inference tree partitioning of maximum dive-depth in relation to the solar elevation (sun angle), using only those data where cloud cover was considered absent or marginal, where a partition was identified and the associated significance (p-value) of the partition is provided for each of the FG and CL and PN leatherback sea turtles.

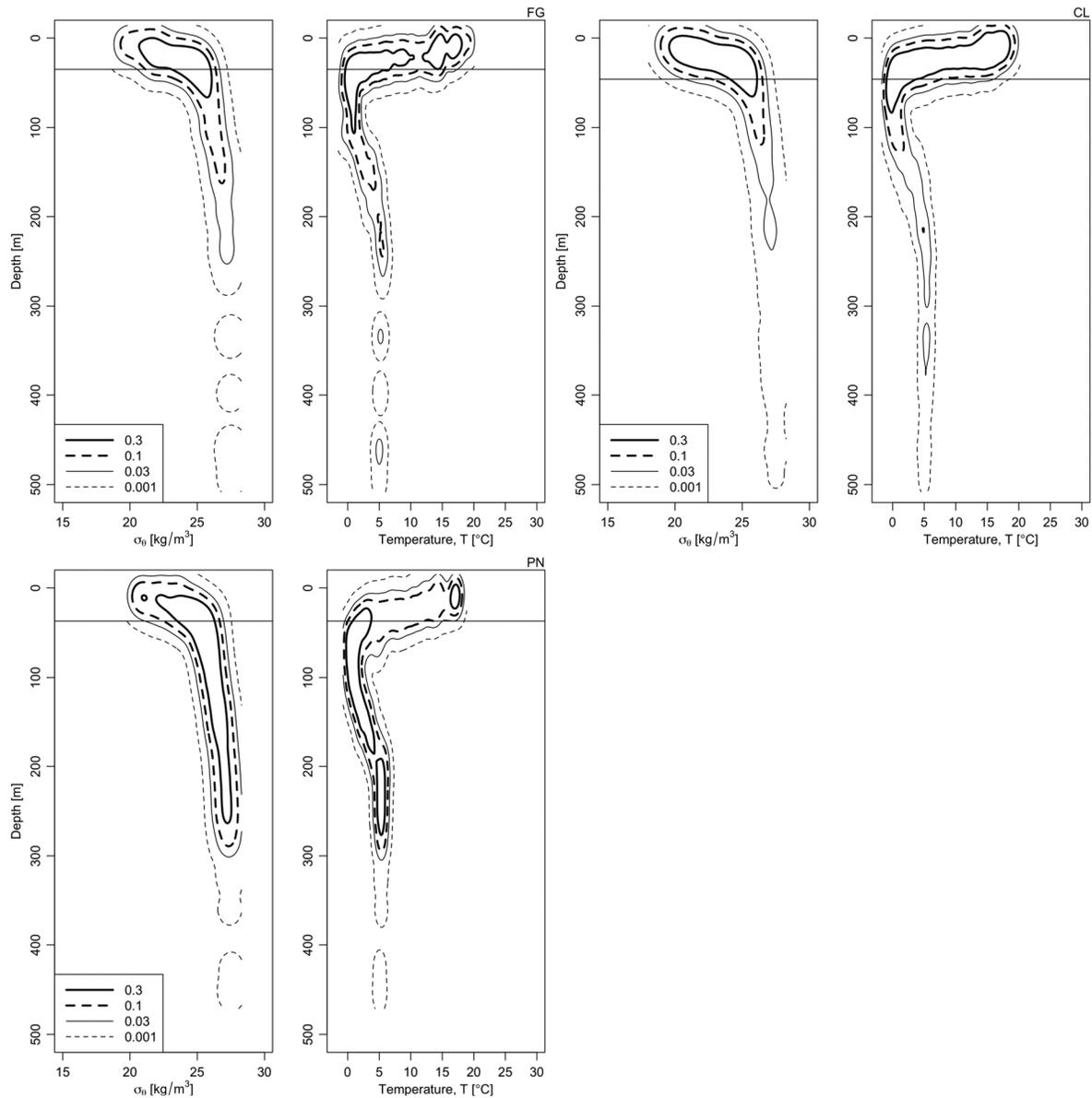


Fig. A7. Probability density contours of temperature ($^\circ\text{C}$; right panel) and potential density (kg m^{-3} ; left panel) at depth (m), based on data from the CTD profiles associated with water masses occupied by each turtle of the FG (2008), CL (2008), and PN (2009) leatherback sea turtles shown in Fig. 2. The figures illustrate that the thermal structure of the water column in the foraging domain of the turtles generally reflects the density structure and that the location of the main thermocline generally parallels the location of the pycnocline. The solid horizontal lines show the depth of the thermocline.