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Characterizing response of East Pacific green turtles to changing temperatures: using acoustic telemetry in a highly urbanized environment

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Abstract

Background: Ocean water temperature is changing as a result of anthropogenic influences on the marine environment. Highly mobile marine ectotherms, such as sea turtles, may be particularly susceptible to these changes. However, our current understanding of location-specific thermal tolerances, especially at coastal foraging or over-wintering areas, is limited. Human-induced changes, such as thermal effluent from power plants, appear to have a suite of influences on species that reside in affected areas. Here, we describe a study of green turtle habitat use related to changing water temperature at a coastal foraging site that has recently experienced a power plant closure, leading to a transition to cooler ambient water temperature. We used a combination of active and passive acoustic telemetry to monitor green turtle distribution in relation to water temperature in this dynamic thermal environment.

Results: Both before and after closure of the power plant, turtles were distributed in significantly warmer waters than surrounding environments during winter months (December–February). Turtles in winter were rarely detected in water temperatures lower than 14.5 °C. Body size was negatively correlated with water temperature after closure of the power plant, with larger turtles found in cooler waters, while smaller turtles remained within warmer areas. There was not a significant relationship between body size and water temperature before closure of the power plant as water temperature was more constant during operation.

Conclusions: Green turtles in San Diego Bay experienced a shift in water temperature following the loss of thermal effluent from a power plant. The effects of this shift were particularly evident during winter months, when ambient water temperatures were coolest. Water temperatures in the southern region of San Diego Bay were significantly warmer during winter before the closure of the power plant, and turtles were detected in significantly warmer water. Turtles in San Diego Bay may associate with or seek out thermal refugia, when possible, to avoid low water temperatures. The cold water temperature inactivity threshold for East Pacific green turtles may be lower than previously thought. There was a significant negative relationship between turtle size and water temperature after power plant closure. East Pacific green turtles exhibit clear responses in habitat use to changes in water temperature at a foraging site near the edge of their geographic range.

Keywords: Temperature, Behavior, Green turtle, Power plant, Anthropogenic

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Background

Globally and locally, water temperatures are changing at unprecedented rates and these changes are likely already impacting animals [6, 20, 42]. Although considerable uncertainty remains as to how exactly marine ecosystems will be affected by global temperature change [9], understanding how marine ectotherms respond to thermal dynamics is a necessary element for effective conservation and management. Marine ectotherms reliant on particular thermal conditions for proper physiological and behavioral functions are particularly susceptible to changes in environmental temperature.

Marine turtles represent one such group of marine ectotherms whose relationship with water temperature has been particularly well studied. Environmental temperature directly affects rates of marine turtle metabolism and other physiological processes, i.e., circulation, respiration, feeding and digestion, osmoregulation and pH balance [17, 19, 33]. As environmental temperature increases, and in turn body temperature, so does the rate of these bodily processes [17, 33]. Likewise, metabolic and physiological processes of marine turtles, like other ectotherms, slow at lower environmental temperatures [52, 59]. For adult marine turtles at foraging habitats, water temperature is a key environmental factor that influences behavior. Marine turtles have been found to decrease activity levels and become torpid in response to water temperatures below 15 °C as a means to direct energy to basic physiological maintenance; metabolic rates, heart rate and respiration rates are all lower in cooler water temperatures [18, 46, 48].

For marine turtles, temperature changes will likely affect local and migratory movement, as well as the availability of adequate resources at breeding and foraging areas [16, 20, 42]. Marine turtles may be able to contend with changes in the thermal environment by expanding their ranges and/or utilizing thermal refugia. However, new areas may not have the appropriate food resources or the environmental conditions previous habitats offered. Access to thermal refugia is likely most important for marine megafauna at the boundaries of their range [22, 50] where they must contend with thermal conditions outside of their preferred thermal optima [30]. As a result, these populations may be able to tolerate greater variability in water temperature and/or may acclimate to variability by changing their behavior.

Size also plays an important role in distribution related to water temperature. Larger organisms maintain a higher degree of thermal inertia and are more equipped to contend with cooler water temperatures due to their reduced surface area to volume ratio. Because of their large body mass marine turtles are able to maintain stable core body temperature through metabolic heat production [5, 38, 52]. This thermal inertia allows diving ectotherms to maintain internal body temperature warmer than the external environment for extended periods of time—further increasing dive duration and/ or depth [33, 37, 45]. However, thermal inertia is ineffective at maintaining core body temperature even in larger turtles after prolonged exposure to water temperatures below 8–10 °C [35, 41, 61].

The general thermal ecology of marine turtles has been fairly well described. Species-specific temperature preferences have been found in both pelagic and coastal waters [14, 15, 46, 47, 50–52]. Marine turtle species experience different thermal conditions across their ranges; hence, understanding location-specific tolerance is crucial. Aggregations in temperate marine ecoregions [49], especially near the thermal extremes of a given species, are more susceptible to extreme water temperatures approaching potentially lethal levels, i.e., 8–10 °C [4].

One major anthropogenic influence on local marine environments is thermal effluent from power plants, which use once-through cooling (OTC) systems. OTC power stations discard waste heat, a by-product of the plant cooling process, into nearby aquatic environments, thus altering the thermal conditions of the environment. These plants are most commonly found in temperate climates, where ambient environmental water temperature is low enough to be utilized for the cooling process [23, 28]. Average water temperature discharged from OTC power stations between 1996 and 2005 was 37 °C (± 6.5 – 6.8 °C) and 9.5–10 °C (±4.8–5.0 °C) higher than ambient temperatures in summer, when ambient temperatures are highest [28]. Since the early 1970s, studies of mobile aquatic organisms have demonstrated physiological and behavioral changes across taxa in response to the heated effluent from power plants [12, 50, 55, 57]. Marine turtle species in Brazil, Chile and the USA have also demonstrated high aggregations in the thermal effluent areas of industrial plants [10, 11, 57, 7, 13, 43, 56].

Understanding the thermal ecology of marine turtles in the natural environment is critical to the management of these species. Although considerable work has been done in the laboratory studying responses by marine turtles to temperature change [36, 39, 52, 59], the results of these studies may have limited application to how ectothermic vertebrates contend with shifts in environmental temperature in situ, where other environmental variables are also factors [2]. Because of the shifts away from OTC power plants in the USA [8], these plant closures have provided an opportunity to study how marine ectotherms such as marine turtles respond behaviorally to shifts in environmental temperature.

We used acoustic telemetry to monitor the response of green turtles (*Chelonia mydas*) to temperature in the northern extreme of their foraging aggregation [10, 11]. The behavior and movements of green turtles were described before and after closure of an OTC fossil-fuel power plant. We also explore how this relationship varies with turtle size. Although local and global scale changes may be driven by different factors, changes to the thermal environment at the local level provide insights as to how animals may react to longer-term changes in global environmental temperature.

Methods

Study site

San Diego Bay (SDB) is a narrow, 22.5-km-long natural harbor near the US-Mexico border along the west coast of the USA that is the terminus of three watersheds encompassing over 660 km² (Fig. 1). SDB is bordered by several municipalities, including San Diego (population: 1.3 million), Chula Vista (population: 257,000), National City (population: 60,000) and Coronado (population: 24,000). The area affected by thermal effluent from the South Bay Power Plant (SBPP; Dynegy, Inc.) was located in the southern section of SDB, known as South Bay, in the 2300-acre San Diego Bay National Wildlife Refuge [58]. South Bay is designated as the region south of the Sweetwater Channel in San Diego Bay (Fig. 1). The SBPP was in operation from the 1960s until its full decommissioning on December 31, 2010. A foraging aggregation of green turtles has been documented in SDB since the 1800s, with ongoing research on these turtles beginning in the 1970s [32, 53]. From the 1960s, green turtles in SDB were almost exclusively observed in South Bay, near the power plant effluent area and adjacent eelgrass beds, and this area is recognized as the home range for this aggregation (Fig. 1; [10, 11, 26, 27, 31, 53]).

Turtle capture

Turtles were captured in years 2009–2012 during months November–May (before closure; 2009–2010) and December–June (after closure; 2011–2012) in the effluent and intake areas of the SBPP following protocol outlined in Eguchi et al. [10] and Lemons et al. [24]. Sampling methods were adjusted slightly and extended until June after the closure of the SBPP.

Entanglement nets (100 m long by 5 m deep, mesh size 0.6 m stretched) were placed in the water and were continuously monitored from land. Nets were physically checked for entanglement at 30-min intervals or more frequently when turtles or other organisms were observed in the net, following established protocols for turtle capture in this area [10, 11, 26, 27]. Nets were placed in the effluent area, the intake channel and openwater areas adjacent to the SBPP (Fig. 1). Upon capture,

sex of adult turtles was determined, if possible, based on the presence or absence of male secondary sexual characteristics: elongated tail extending beyond the carapace edge, curvature of the front claws and softened plastron [60]. Life stage of turtle was categorized as juvenile (juvenile and subadult) or adult, based on straight carapace length (SCL): juveniles and subadults <80 cm and adults \geq 80 cm [1, 25]. Turtles were weighed, tagged, fitted with telemetry devices and released back into San Diego Bay near the site of capture within 60 min.

Acoustic telemetry

Both active (via boat-based survey) and passive (via underwater receiver stations) acoustic telemetry were used to monitor green turtle movement. Tagged turtles were equipped with an ultrasonic transmitter (Sonotronics, Inc., Tucson, Arizona, CT Series). To reduce hydrodynamic drag [21], transmitters were affixed to the rearmost lateral scute of each turtle using fiberglass mesh and resin, following a modified procedure from Balazs et al. [3]. Each transmitter had a unique combination of frequency, pulse burst and pulse burst interval. Active tracking was conducted using an omnidirectional hydrophone (Sonotronics, TH-2), a directional hydrophone (Sonotronics, DH-4) and an ultrasonic receiver (Sonotronics, USR-08) from aboard a 17-ft Boston Whaler 170 Montauk ("Wanda") with an 85 horsepower outboard motor. Submersible ultrasonic receivers (Sonotronics, SUR) were used for passive tracking.

A turtle detection was defined as any location where an acoustic receiver (either active or passive) positively detected a tagged turtle. Data were collected actively via grid surveys and passively via SUR stations, each of which represented different spatial and temporal scales (Fig. 2). The combination of active and passive telemetry allowed for near-constant monitoring of turtle movement across the home range of this population.

Active monitoring

Active tracking of turtles occurred via a semi-monthly boat-based survey across SDB. The range of frequencies for all tagged turtles (35–40 kHz) was scanned via hydrophone and receiver using a 500-m latitude/longitude grid and covering the expanse of SDB (Fig. 2a). When a tagged turtle was detected, a directional hydrophone was employed to exact a more accurate location of the turtle. A turtle was considered in close proximity (approximately 10 m) when the acoustic signal could be heard loudly at the receiver's lowest gain setting, or if the turtle was sighted [26, 27]. While actively tracking, water temperature was monitored using a handheld multiparameter instrument calibrated using ice water (556MPS,



YSI Incorporated, Yellow Springs, Ohio) and data were collected at each grid point on every survey, regardless of whether a turtle was detected.

Passive monitoring

For passive tracking, turtles were detected by autonomous ultrasonic receivers (SURs). The range of detection for the SURs was up to approximately 100 m, based on range tests from a previous study in SDB [27]. SURs (n = 10) were deployed throughout South Bay in SDB: the intake channel, effluent area and eelgrass pastures (Fig. 1). An additional set of SURs (n = 5) were deployed following closure of the SBPP to extend the spatial range of possible turtle detection beyond the vicinity of the SBPP. The SURs were deployed in South Bay, as in previous studies [26, 27], with the addition of several SURs in central and northerly locations in SDB (Fig. 2b). When a tagged turtle was within the detection range of the SUR, the date and time were recorded. Attached to each SUR was a temperature logger (HOBO Water Temperature Pro v2, Onset Computer Corporation, Bourne, MA), which monitored water temperature at intervals of



3–5 min, depending on site; temperatures were recorded more frequently (3-min intervals) in the effluent area of the SBPP to capture changes in temperature dependent on plant operation. These data permitted water temperature to be matched with turtle detections at SUR locations, as well as creating a thermal profile at each site.

Analyses

Water temperature

To determine whether turtle behavior in winter months changed in response to a decrease in water temperature, we use data on ambient water temperature and turtle distribution. We used a *t* test to compare changes in the mean ambient water temperature before (2009–2010) to after (2011–2012) the plant closure during winter months (December–February), when ambient water temperature was coldest. We used ArcGIS 10.3 (ESRI, Inc., Redlands, CA) to map water temperatures in south San Diego Bay before and after SBPP closure. Kriging was used to interpolate among data to create an estimated surface of winter water temperature.

Turtle detections and associated thermal conditions

Turtle detections and water temperature collected during winter months were compared before and after the SBPP decommissioning. A binary logistic regression was used to determine the relationships between turtle detection/ non-detection and potential predictors: SBPP operational status (before/after), water temperature and the interaction between them.

Association between size and thermal conditions

We used a generalized linear model (GLM) to determine whether there was a relationship between continuous variables of turtle size (weight) and water temperature (at detection), before SBPP closure and after SBPP closure. Turtle size data were collected for 21 individual turtles before SBPP closure and 26 individual turtles after SBPP closure.

Statistical analyses were performed using SYSTAT 13 [54], SAS software [44] and R [40] and evaluated at significance levels of alpha = 0.05. Mean values and standard errors (\pm SE) are reported.

Results

Tagged turtles

A total of 35 individuals were tagged and tracked during this study. Of these, 9 turtles were monitored only before the SBPP closure, 14 turtles were monitored only after the SBPP closure, and 12 turtles were monitored both before and after the SBPP closure (Fig. 3). The study group was comprised of 14 female turtles, 13 male turtles and 8 turtles that were juvenile/unknown sex. During SBPP operation, turtles aggregated in the effluent area (outfall) and nets were almost exclusively placed in this channel. Following the SBPP closure, turtle capture in the outfall area was inconsistent as turtles ceased to aggregate in the absence of



the thermal effluent. Consistent successful turtle captures occurred almost exclusively in the intake channel following SBPP closure. Tag retention varied among individuals with a minimum of 1 day and a maximum of 396 days. Weights of tagged turtles ranged from 18 to 192 kg; when an individual was captured more than once, the weights were averaged across the study period (Fig. 3).

Water temperature

Average water temperatures in winter months were not significantly different between 2009 and 2010 (before SBPP closure) and were not significantly different between 2011 and 2012 (after SBPP closure). Therefore, we grouped temperature based on SBPP operational status: before (2009, 2010) and after (2011, 2012). Both before and after SBPP closure, the warmest water temperatures in South Bay were recorded in the effluent area (Fig. 4). Mean winter water temperature in the effluent area of the SBPP was significantly colder after closure of the SBPP (t = -8.945, df = 976, p < 0.001). Mean winter water temperature during SBPP operation was 17.8 °C (\pm 1.9 SE), and mean winter water temperature after SBPP closure was 16.6 °C (\pm 2.1 SE).

Turtle detections and associated thermal conditions

Turtles in this study were detected exclusively in the South Bay region of SDB: in and around the SBPP intake channel, effluent area and adjacent eelgrass beds (Fig. 1). Results from the binary logistic regression revealed that water temperatures at the locations of turtle detections were significantly warmer than where turtles were not detected, both before (Z = 2.569, p = 0.010) and after SBPP closure (Z = 5.477, p < 0.001). Before SBPP closure, the mean water temperature where turtles were detected was 18.0 °C (± 0.1 SE) with a range of 14.5–25.6 °C (Fig. 5a). Mean water temperature was 17.4 °C (± 0.2) at locations where turtles were not detected, with a range of 11.3–29.1 °C (Fig. 5a). After SBPP closure, the mean water temperature at turtle detections was 17.0 °C (± 0.1 SE) with a range of 12.5–22.4 °C (Fig. 5b). Mean water temperature was





15.9 °C (\pm 0.2) with a range of 11.54–21.86 °C at locations where turtles were not detected (Fig. 5b).

Association between size class and thermal conditions

The GLM revealed no significant relationship between mean water temperature at turtle detection locations and turtle size before SBPP closure (F = 0.324; df = 1; p = 0.569; y = -0.003x + 20.134). However, following the closure of the SBPP turtle size had a significant negative

relationship with mean water temperature. Larger turtles were found in the coldest waters and smaller turtles in the warmest waters (F = 4.858; df = 1; p = 0.028; y = -0.011x + 17.934).

Discussion

In San Diego Bay, we found that green turtles responded to shifts in water temperature by inhabiting warmer than average areas in winter months. Water temperatures in San Diego Bay during winter frequently dropped to levels that are physiologically challenging for green turtles; however, tagged turtles were not detected in water temperatures <12.5 °C. This temperature is lower than that suggested for green turtle survival, as Seminoff [46] recorded an approximate minimum water temperature at detection of about 15 °C of green turtles in the nearby Gulf of California.

Turtles in San Diego Bay utilized the thermal effluent from the SBPP as a means of thermal refuge when water temperatures were at or below the inactivity threshold for this population. Turtles aggregated in the effluent area when water temperatures were cooler (at night; in winter) and then would move out into adjacent eelgrass pastures for foraging during the day and in summer [27]. However, after the SBPP closure, resident turtles were still able to find pockets of warm water, despite the loss of thermal effluent. Although not considered here, it is also possible that turtles in SDB and other foraging sites altered their activity levels as well as their spatial distribution (i.e., changing patterns of resting or diving) in response to temperature shifts [29].

Green turtles in San Diego Bay are some of the largest on record in the Eastern Pacific Ocean, potentially an indirect result of the year-round warmer water temperatures during SBPP operation; turtles were able to forage year-round instead of entering torpor as is typical in other foraging populations [10, 11]. Prior to the closure of the SBPP, turtles of all sizes were distributed in similar average water temperatures. However, after closure of the SBPP, we found a negative relationship between sea turtle size and water temperature.

Conclusions

Understanding the relationship of marine megafauna and water temperatures is critical given the ongoing and rapid shifts in local and global thermal conditions [30]. These environmental changes will continue to impact resident and migratory animals in coastal environments [6]. Because logistical constraints make monitoring highly mobile species with complex life histories problematic, biotelemetry plays an important role in characterizing marine species responses to changing thermal conditions in the ocean. Human-induced changes to water temperature at the local level provide a relevant, model system to monitor behavioral and physiological responses to temperature shifts that can help predict likely responses to marine temperature shifts for long-lived, highly mobile marine megafauna.

Green turtle presence in San Diego Bay preceded the operation of the SBPP [53], and our research demonstrates the turtles' continued use of this foraging area even with the decrease in winter water temperatures.

The habitat use of turtles was affected by the power plant operation with turtles aggregated in the effluent area. Following the plant decommissioning, we observed a shift in habitat use in response to the loss of warm-water effluent. Our findings suggest that foraging turtles can identify and associate with thermal refugia and that these areas may be outside of the former local home range for this aggregation [26]. MacDonald et al. [26] found that green turtle home range in San Diego Bay was limited to waters within the San Diego Bay National Wildlife Refuge, where turtles were afforded protection in the form of limited boat traffic and speed restrictions [58]. Turtles venturing northerly in San Diego Bay to associate with possible thermal refugia will encounter greatly increased commercial and recreational boating activity from the US Navy, cruise ships, cargo ships and recreational users. Continued monitoring of movement and habitat use of this aggregation is necessary to describe how foraging turtles, like those found in San Diego Bay, will continue to respond to thermally dynamic environments and other direct human impacts (e.g., boat strikes, debris entanglement, fisheries bycatch and contamination). Conservation and management of this foraging aggregation will be critical, especially as the ecosystem in San Diego Bay recovers in the years following the power plant closure.

Other studies have demonstrated similar aggregations of marine turtles in the thermal effluent of power plants that utilize once-through cooling systems [10, 11, 57, 7, 13, 43, 56]. However, to the best of our knowledge, this study is the first to document turtle response during both power plant operation and in the time immediately following plant decommissioning. As energy needs continue to change and new technology eliminates the need for once-through cooling systems [8], these power plant closures will become increasingly common. Power plant closures provide an experimental in situ opportunity to explore the response of a large vertebrate marine species to changing thermal conditions. In light of current and future changes to the thermal environment from anthropogenic influences, behavioral plasticity of coastal organisms will play an important role in whether these organisms can acclimatize to increased thermal variability. Characterizing the responses of coastal fauna to rapid shifts in thermal conditions addresses a gap in ecological knowledge-understanding how populations of long-lived marine vertebrates will be affected by a thermally dynamic environment that is changing at a rapid rate.

Abbreviations

GLM: generalized linear model; OTC: once-through cooling; SBPP: South Bay Power Plant; SCL: straight carapace length; SDB: San Diego Bay; SUR: submersible ultrasonic receiver.

Authors' contributions

This study was conducted as part of the doctoral dissertation of SVM in the Joint Doctoral Program in Ecology through San Diego State University and University of California, Davis. SVM developed methodology, conducted acoustic telemetry and monitoring, performed the statistical analyses and drafted the manuscript. RLL secured funding for the research, participated in study design, helped to draft the manuscript and served as academic advisor and dissertation committee chair for SVM. JAS participated in study design and field research, assisted in securing funding, provided edits for the manuscript and served on the dissertation committee of SVM. TE participated in study design and field research, assisted in securing funding, and provided guidance in statistical analyses and edits for the manuscript. The study was conceived by JAS and TE and further developed by RLL and SVM. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and/or analyzed in this study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

All research and animal handling were carried out under National Marine Fisheries Service Permit #1591 and #16803 and were in compliance with IACUC protocol at San Diego State University.

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