Vol. 683: 157–168, 2022
https://doi.org/10.3354/meps13940

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 3

Effects of ambient temperature on dive behavior of East Pacific green turtles before and after a power plant closure

Sheila V. Madrak[1,*], Rebecca L. Lewison[2], Tomoharu Eguchi[3], A. Peter Klimley[4], Jeffrey A. Seminoff[3]

[1]San Diego Miramar College, 10440 Black Mountain Road, San Diego, CA 92126, USA
[2]San Diego State University, 5500 Campanile Drive, San Diego, CA 92181, USA
[3]National Marine Fisheries Service, Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA
[4]University of California, Davis, 1 Shield Avenue, Davis, CA 95616, USA

ABSTRACT: Water temperature plays a critical role in mediating energy budgets and influencing the behavior of marine ectotherms. Previous research has demonstrated that marine ectotherms such as sea turtles conserve energy by decreasing activity levels in colder water — often at or near the latitudinal limits of their range. San Diego Bay is near the northern edge of the range for eastern Pacific green turtles and is home to a year-round foraging population. Turtles in San Diego Bay experienced a significant decrease in ambient water temperature following the closure of a fossil-fuel-based power plant and corresponding loss of the plant's warm-water effluent. Time–depth recorders were placed on 13 turtles before (n = 5) and after (n = 8) the closure of this plant to determine how changing water temperature influenced dive duration. Deployments lasted 2–25 d, with a mean deployment of 7.5 d. Green turtle behavior in different thermal regimes revealed a strong relationship between dive duration and water temperature; dive duration was significantly longer when water temperatures were colder, especially when water was below 14.4°C. Establishing the inactivity threshold for this population is critical to future management in light of temperature variability in coastal habitats and the impacts this may have on sea turtle energetics. Understanding organismal response to relatively rapid shifts in thermal conditions is relevant to assessments of the direct and indirect anthropogenic effects on aquatic environments.

KEY WORDS: Sea turtle · Water temperature · Diving behavior · Archival tags · Marine ecology · Movement

1. INTRODUCTION

Animals move within and among their habitats to acquire resources needed for survival and reproduction (Dingle 2014). Within an animal's home range, these movements reflect responses to the biotic and abiotic factors in their environment (Dingle 2014): resource availability, interaction with conspecifics, predator avoidance, temperature, and more. Highly mobile marine vertebrates contend with environmental challenges in both the spatial distribution (latitude and longitude) and depth (Butler & Jones 1997, Hochscheid et al. 1999). The study of dive behavior in mobile marine animals provides critical information to understand how these species respond to their environments while maintaining physiological processes (Kramer 1988, Kooyman 1989, Butler & Jones 1997, Hochscheid et al. 1999, Southwood & Avens 2010). Substantial research has focused on the behavior of deep-diving animals in pelagic environments, revealing previously unknown depth extremes, behavioral responses, and unexpected trophic relationships (Block et al. 2002, Fossette et al. 2010, Schorr et al. 2014). Comparatively less research has been

*Corresponding author: smadrak@sdccd.edu

conducted on diving animals in the more variable abiotic conditions of shallow coastal environments, despite growing evidence of significant human impacts (e.g. pollution, recreational and commercial use) on marine animals in shallow coastal zones (Harley et al. 2006, Doney et al. 2012, IPCC 2014).

Dive frequency, duration, and depth may change as rates of respiration — the rate at which oxygen stores are utilized — are affected by environmental variation and/or the animal's level of activity (Butler & Jones 1997, Hochscheid et al. 1999). Two categories of diving organisms have been identified based on respiratory strategy. 'Divers' are those animals that spend most of their time at the water's surface with diving bouts below for foraging purposes (e.g. seabirds, sea lions). In contrast, 'surfacers' are animals that spend most of their time below the water, generally surfacing for respiratory purposes (e.g. marine reptiles, whales, seals) (Kramer 1988, Kooyman 1989, Hochscheid et al. 1999). Poikilothermic ectotherms such as sea turtles have internal body temperatures that closely reflect the external environment and generally fall into the category of surfacers. These air-breathing surfacers spend much of their time in the epipelagic zone of the ocean and demonstrate prolonged subsurface periods.

As with many surfacers, there is a strong negative relationship between sea turtle dive duration and water temperature (T_w): turtle dive duration increases as T_w decreases (Hays et al. 2002b, Southwood et al. 2003b, Hazel et al. 2009). Decreased energetic demands from slower metabolic, heart, and respiratory rates in colder T_w extends oxygen stores and leads to longer dives (Hays et al. 2002a,b, Southwood et al. 2003b, Hazel et al. 2009). Turtles have been found to respond to T_w changes by changing their dive behavior (i.e. longer dives in cooler water) and altering their spatial distribution (Mendonça 1983, Hochscheid et al. 2007). Sea turtles may change their distribution locally or regionally in response to variable environmental conditions (Southwood et al. 2003b, Hazel et al. 2009, MacDonald et al. 2013, Madrak et al. 2016). Because of the strong influence of temperature on metabolism and other physiological processes (Hofmann & Todgham 2010), both natural and anthropogenic influences on environmental T_w can have considerable effects on diving behavior of sea turtles.

One source of direct anthropogenic influence on coastal T_w is from power plants that utilize once-through cooling (OTC) systems. OTC power plants use environmental water to remove excess heat generated during energy production and discharge the heated water, i.e. thermal effluent, back into the adjacent habitat (Madden et al. 2013). The heated effluent significantly increases the T_w at the discharge site (the outfall) on average 9–10°C above maximum intake T_w during summer (Madden et al. 2013). The effects of OTC systems on the adjacent environment are localized, with the most acute increases in T_w directly proximate to the source; however, slight temperature increases may be detected away from the source as water dissipates downstream, and even minor changes can affect inhabitants in these areas (Madden et al. 2013, Madrak et al. 2016). Thermal effluent from OTC power plants can have direct and indirect effects on the physiology and behavior of resident marine animals. Documented responses to thermal effluent include increased growth rates, larger body sizes, increased metabolic rates, and changes in dispersal and other movements (Gibbons & Sharitz 1981, Avery et al. 1993, Eguchi et al. 2010, 2012). In some documented cases, thermal effluent can negatively affect resident animals through exhaustive physiological demands due to increased metabolic rates and associated energy requirements that exceed available food resources, resulting in emaciation and increased susceptibility and prevalence of disease (Gibbons & Sharitz 1981).

Effluent can also create thermal refugia, leading to site fidelity and range expansion, sometimes resulting in ecological traps (Schlaepfer et al. 2002). Ecological traps occur when organisms respond to unnatural, often human-induced, cues like temperature change and choose a suboptimal habitat (Schlaepfer et al. 2002, 2010) and have been observed in Florida manatees *Trichechus manatus latirostris* in response to OTC plants (Laist & Reynolds 2005a,b) where natural thermal springs have been lost. As a result, Florida manatees have become dependent on the thermal effluent from OTC plants for warm-water refugia in winter despite the risks that these areas may pose (Laist et al. 2013). Organisms attracted to thermal effluents may continue to exhibit site fidelity after OTC power plant closures, even when T_w is at sub-optimal levels, with potentially negative consequences such as increased prevalence of disease and phenological mismatches (Laist & Reynolds 2005a, Laist et al. 2013, Madrak et al. 2016).

Sea turtles that utilize thermal effluent from OTC plants near the latitudinal (and thus physiological) limits of their ranges may face a heightened risk of 'cold-stunning' events as these power plants are decommissioned (Laist & Reynolds 2005a,b, Lyon et al. 2006, Guerra-Correa et al. 2008, Eguchi et al. 2010, Turner-Tomaszewicz & Seminoff 2012, Sarmiento-

Devia et al. 2015). Cold stunning occurs with prolonged exposure to water at or below 10°C, which induces a hypothermic reaction whereby the turtles become extremely lethargic with markedly reduced circulatory and respiratory functions and can face mortality at 5–6°C (Spotila et al. 1997, Shaver et al. 2017). Between 10 and 15°C, sea turtles have been found to reduce activity and, in some studies, have been found to enter a state of torpor (Felger et al. 1976, Seminoff 2000, Southwood et al. 2003a).

San Diego Bay, one of the largest natural bays on the California coast, is a highly urbanized environment with anthropogenic influence from military, industrial, commercial, and recreational users. It is also home to a well-studied foraging aggregation of East Pacific green turtles (Dutton & Dutton 1999, Eguchi et al. 2010, 2012, MacDonald et al. 2012, 2013, Madrak et al. 2016). From 1960–2010, San Diego Bay was the locale of a fossil fuel-based power plant that utilized an OTC system and generated thermal effluent — the South Bay Power Plant (Dynegy). The energy produced by the South Bay Power Plant was deemed unnecessary for the region and so, in compliance with the OTC policy in the state of California, the plant was scheduled for decommissioning (Duke Energy South Bay 2004). On 31 December 2009, 2 of the power plant's 4 generators were permanently shut down; complete decommissioning of the plant occurred on 31 December 2010.

The South Bay Power Plant thermal effluent provided a thermal refuge for green sea turtles in San Diego Bay, with aggregations of individuals throughout most of the year and during all seasons (Eguchi et al. 2010). Its closure presented an *in situ* experiment to explore the behavioral responses of green turtles to changes in T_w when an artificial thermal refuge is removed. MacDonald et al. (2013) demonstrated that during South Bay Power Plant operation, turtles demonstrated high usage of eelgrass beds in South Bay during the day and strong fidelity to the South Bay Power Plant outfall at night. In another study, Madrak et al. (2016) observed a significant relationship between turtle size and T_w after the South Bay Power Plant closure; larger turtles were found in the coldest water, with the inverse true for smaller turtles. The T_w in which turtles were detected was significantly warmer than that of the surrounding environment, suggesting that turtles compensated behaviorally by moving to an area with warmer T_w when the South Bay Power Plant was operational. Both of these studies provide insight into the spatial distribution of turtles before and after South Bay Power Plant closure; however, data on the turtles' dive behavior is needed to fully appreciate the behavioral effects.

Here, we characterized the relationship between turtle dive duration and T_w before versus after the closure of an OTC power plant. We affixed time–depth archival recorders (TDRs) on sea turtles and recorded their dive behavior before and after the closure of the OTC system power plant to investigate changes in dive behavior with the associated shifts in T_w. We also examined whether any observed behavioral changes suggested a thermal activity threshold for this species — a temperature below which active dive behavior declines significantly. Monitoring the dive activities of a marine ectotherm provides insight into how these organisms respond to large and relatively rapid shifts in T_w that exceed typical seasonal variability. As OTC systems become increasingly outdated, more coastal power plants will be closed in the near future. Consequently, understanding how sea turtles respond to these closures will be important for effective management of this and other coastal species that utilize these outfall areas. Our study is the first to examine the effects of thermal effluent on dive duration, providing insight through an *in situ* natural experiment on how sea turtles may respond to future changes in T_w in coastal areas. More broadly, the insights obtained from this study may contribute to our understanding of how increased variability in coastal T_w due to climate change might affect the distribution and behavior of green turtles in the coming years.

2. MATERIALS AND METHODS

2.1. Study site and turtle capture

San Diego Bay is a narrow, 22.5 km long natural harbor near the USA–Mexico border and is the terminus of 3 watersheds encompassing over 660 km^2 (Fig. 1). San Diego Bay 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 outfall area from the South Bay Power Plant was located in the southern section of San Diego Bay, known as South Bay, in the San Diego Bay National Wildlife Refuge. Use of San Diego Bay by recreational boaters, commercial shipping vessels, the US military, and cruise ships increases substantially north of the South Bay region, and usage is particularly high in the northwest region of San Diego Bay (Fig. 1).

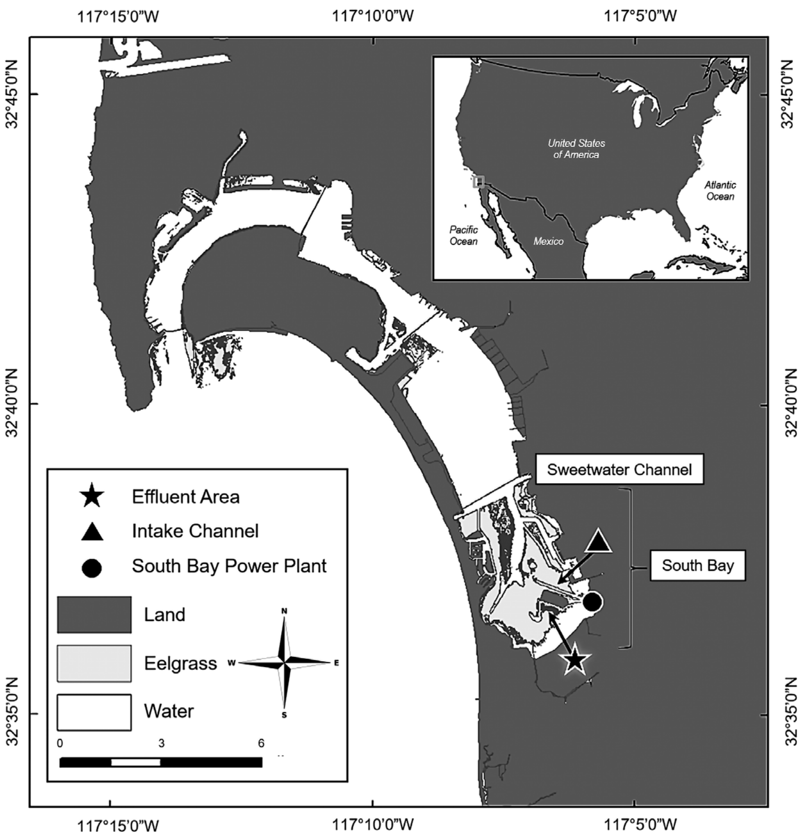

Fig. 1. San Diego Bay, near the border of the USA and Mexico in Southern California (inset). Green turtles in San Diego Bay primarily inhabit the southern portion of the Bay (South Bay)

Green turtles in San Diego Bay were routinely observed in the effluent of the power plant from the 1960s until the plant's closure (Stinson 1984, Dutton & McDonald 1990, Eguchi et al. 2010, 2012, MacDonald et al. 2012, 2013). We monitored T_w in San Diego Bay beginning in 2009 (Fig. 2); in the outfall, T_w ranged from approximately 12–40°C during plant operation (Eguchi et al. 2012, Madrak et al. 2016). This temperature range was reflective of variable plant operation dependent on local energy demands and the status of plant operation. Turtles were captured in or adjacent to the outfall of the South Bay Power Plant following protocol outlined in Eguchi et al. (2010) and Lemons et al. (2011). Entanglement nets (100 m long by 5 m deep, mesh size 0.6 m stretched) were placed in the water and checked at approximately 30 min intervals, or more frequently when turtles or other animals were observed in or near the nets. Upon capture of a turtle, sex was determined if possible and turtles were measured, weighed,

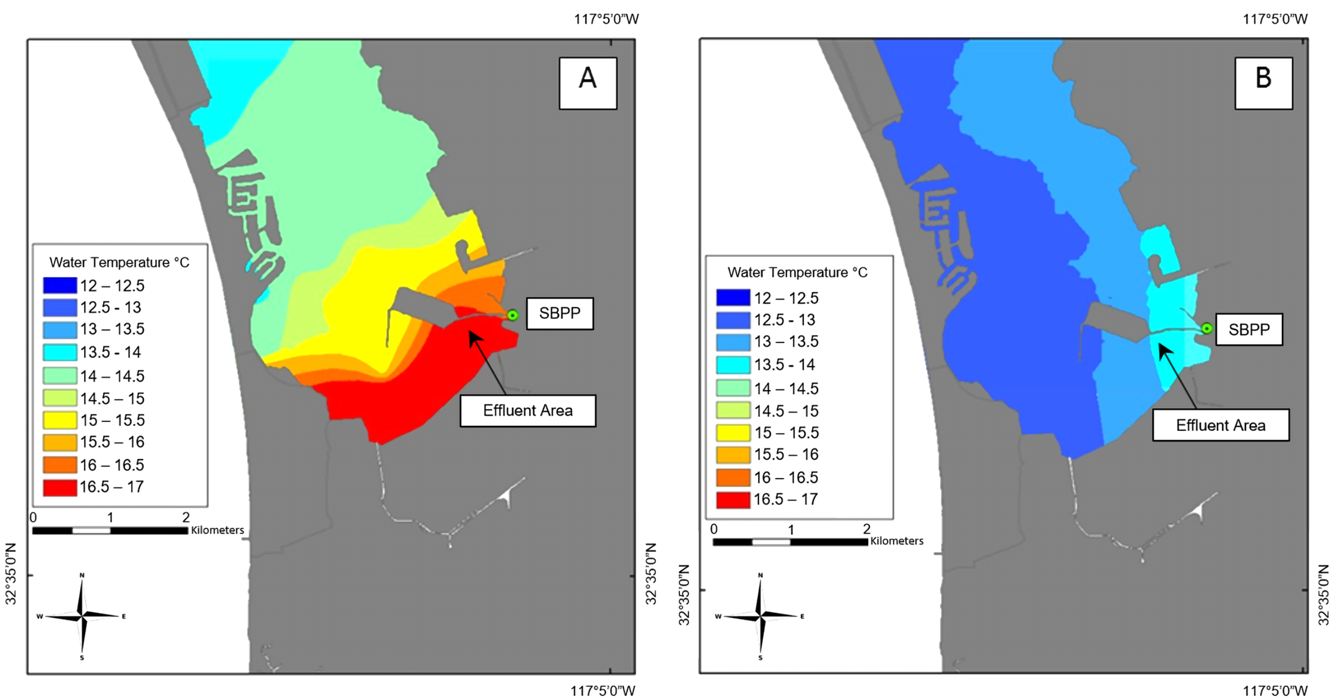

Fig. 2. Water temperature (T_w) in the outfall area of the South Bay Power Plant (SBPP) before and after cessation of operations, showing striking temperature differences in the winter months (December through February) before and after the plant closure. (A) Winter T_w before closure, demonstrating a diminished effect with increased distance from the thermal effluent source with pronounced thermal effects in the outfall area and adjacent eelgrass. (B) Winter T_w after the closure, showing a more 'natural' thermal regime. Originally published in Madrak et al. (2016)

tagged, fitted with telemetry devices, and released back into San Diego Bay near the site of capture within 60 min of capture.

2.2. TDRs

To monitor dive behavior, we used TDRs (MK-9, Wildlife Computers) that recorded date, time, pressure (depth), light level, and T_w at a sampling rate of 5 s and a depth sensor resolution of 0.5 m. Each TDR was housed in an incompressible syntactic foam drogue with a VHF transmitter (MOD 050, Telonics; Fig. 3A). For deployment on a turtle, we affixed a TDR drogue to the crown of the carapace using a 2-plate system described in Seminoff et al. (2006). For this attachment, the top plate was connected to the TDR drogue via hose clamps and the bottom plate was fitted with a nylon-mesh apron and glued to the turtle's carapace using West System G5 5-Minute Epoxy (West System; Fig. 3B). A magnesium link connecting these 2 plates (Fig. 3A) was designed to corrode after a period of approximately 5–14 d, depending on the size of the link, after which the 2

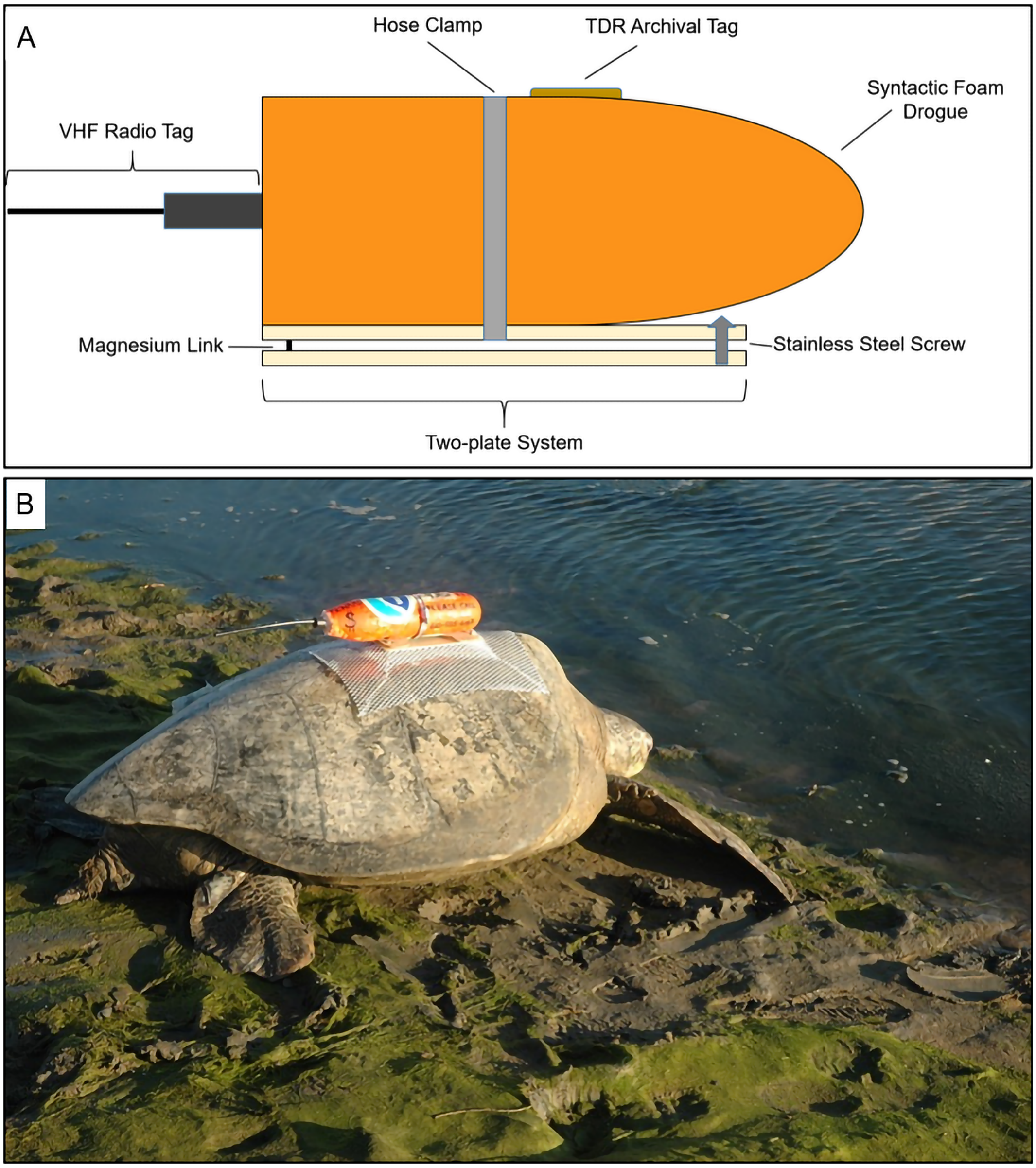

Fig. 3. Time–depth recorder (TDR) drogues affixed to carapaces of green turtles to monitor dive behavior. (A) TDR 2-plate system, designed to separate via corrosion in saltwater after 5–14 d. (B) Plates were attached to the carapace using a mesh skirt and marine epoxy (Photo: S. V. Madrak; NMFS permit nos. 1591 and 16803)

plates would separate and the detached TDR drogue would float to the surface. A lead counter-weight ensured that the antenna of the VHF transmitter was above the surface of the water to allow the TDR drogue to be retrieved by radio telemetry.

Only large sub-adult and adult turtles were studied, to minimize the effects of drag on turtles from the TDR drogue attachment. The smallest turtle tracked in this study measured 62.8 cm straight carapace length (SCL) and 38 kg in body mass; all other turtles were ≥78.3 cm SCL and ≥63 kg in body mass (see Table 1). Considering the neutral buoyancy and hydrodynamic form of TDR drogues and the limited tracking durations (mean: 7.5 d), we reasoned that impacts on dive behavior and energetic performance of turtles were minimal as per recommendations in Jones et al. (2013).

2.3. Dive data

Archived data from TDR deployments were downloaded using the Wildlife Computers HexDecode and viewed using Wildlife Computers Instrument Helper (Wildlife Computers). We applied a zero-offset correction (ZOC) to correct for error in depth recording in relationship to the surface of the water. Following the application of ZOC, dive data were viewed using MT-Dive (Jensen Software Systems) for extraction of discrete dive events. The ZOC was adjusted in MT-Dive when the surface baseline did not appear to be appropriately determined by Wildlife Computers Instrument Helper. A minimum dive threshold parameter was set at 1 m; i.e. dives with a maximum depth <1 m were not included in the analyses. The allowable surface error was set at ±0.5 m. MT-Dive classifies discrete dives based on set criteria, which represents dive types outlined in previous sea turtle literature (Hochscheid et al. 1999, Hochscheid & Wilson 1999, Seminoff et al. 2006). One observer visually verified all extracted dives and categorized each dive by type; only one observer was used for these analyses for consistency of dive categorization across TDR deployments.

Dives were broadly categorized as either 'resting' or 'active.' We classified resting dives as any dive that exceeded 1 m depth and had a uniform bottom phase (i.e. a near constant, sustained depth coincident with the substrate), following established criteria (Hochscheid et al. 1999, Hays et al. 2004, Seminoff et al. 2006). We focused on resting dive behavior because of the importance of resting dive duration for determining overall activity patterns. McMahon et al. (2007) noted that differentiating whether the function of 'U-shaped dives' (resting or foraging) is a challenge in the benthic zone, and noted that resting bouts (sequences of long-form dives) help to better distinguish dive function. Accounting for this difference, we utilized depth records from TDRs to identify 2 measures of resting behavior: individual resting dives (episodic resting; Seminoff et al. 2006) and resting bouts (continuous resting; Seminoff et al. 2006). A resting bout reflects a prolonged period of rest (2 or more individual resting dives, each separated by <1 min; Fig. 4). Seminoff et al. (2006) observed that episodic resting and continuous resting were not statistically different in duration or depth and suggested that both episodic and continuous resting may provide the same energetic conservation. As a conservative approach to differentiate horizontal benthic foraging from actual resting behavior, we included only those uniform bottom phase dives or dive bouts that exceeded 10 min.

Time spent resting per time period was also calculated in order to understand circadian behavior. Dawn and dusk were considered ±1 h of sunrise and sunset, respectively. Episodic (individual dives) and continuous (dive bouts) resting durations were calculated for a given period (i.e. dawn, day, dusk, or night) and divided by the number of minutes available in that period to compute a proportion of time spent resting per time period.

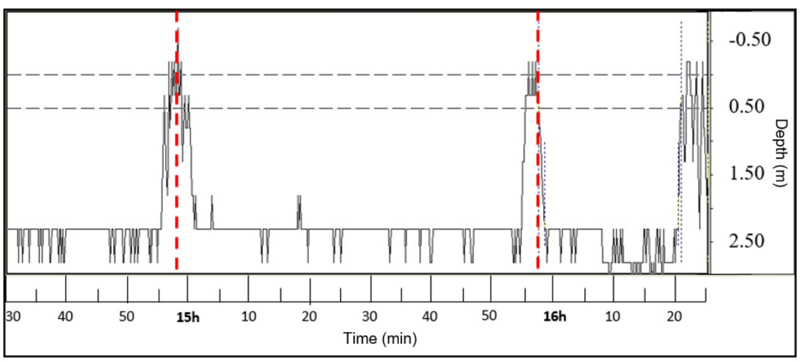

Fig. 4. Individual green turtle resting dive (between red dashed lines), defined as a discrete descent, bottom phase, and ascent by a turtle over a period of 10 min or greater. A resting bout constitutes 2 or more individual resting dives in a row, each separated by <1 min. The vertical axis is reversed: positive values indicate below surface. Horizontal dashed lines represent the water surface accounting for potential instrumental error (0–0.5 m)

2.4. Data analyses

To consider how changes in T_w may have affected dive behavior, we used T_w from TDRs to monitor the thermal environment of each tagged turtle. To determine whether there were detectable differences in dive-associated temperatures, we used a generalized linear model to compare mean T_w before and after the South Bay Power Plant closure during (1) individual resting dives and (2) resting bouts. We used linear regression analysis to determine the relationship between resting dive duration and T_w. Finally, we determined whether turtles in San Diego Bay have an inactivity threshold relative to T_w. We compared individual resting dives with T_w < 18.0°C for all TDR deployments to determine if there was a temperature below which turtles spent a significantly greater time engaged in resting behavior, using a broken-line, piecewise regression. Two methods of broken-line regression were used to identify the relationship between dive duration and T_w: (1) iterative searching and (2) the R package 'segmented' (Muggeo 2003, 2008). Statistical analyses were performed using SYSTAT 13 (SPSS), SAS software (SAS Institute), and R version 3.2.0 (R Core Team 2015).

3. RESULTS

Turtles were captured in the water adjacent to the South Bay Power Plant (Fig. 1). During power plant operation, turtles aggregated in the outfall area, and capture nets were almost exclusively placed in this area. Following power plant closure, turtles were observed less frequently in the outfall area and so capture attempts were made in the outfall (during high tides only), the intake channel, and open-water areas adjacent to the South Bay Power Plant outfall and intake.

A total of 13 TDRs were deployed on 12 turtles (Table 1). We deployed 5 TDRs prior to the closure of the South Bay Power Plant between November 2004 and May 2005. After the power plant closure, we deployed 8 TDRs between May 2011 and May 2012, of which 7 were recovered. Deployments before and after closure were coincident to seasonal capture efforts in San Diego Bay and so were subject to logistical constraints. However, deployments both before and after power plant closure occurred during seasons with the coolest average T_w: winter (November, December, January) and spring (March, April, May). Only one deployment after closure occurred outside of these seasonal windows, in July (Table 1); however, the recorded temperature range was comparable to other deployments from winter and spring.

T_w ranged from 12.9–43.3°C on all TDR records. The mean (±SE) T_w from all deployments was 18.6 ± 4.3°C. For individual resting dives (episodic resting), we analyzed 397 dives (>10 min dive duration) before the South Bay Power Plant closure; these dives had a mean T_w of 21.2 ± 0.2°C. We analyzed 575 individual resting dives from TDR deployments after the power plant closure; these dives had a mean T_w of 16.9 ± 0.1°C. For resting bouts, the average T_w was 23.4°C before the South Bay Power Plant closure

Table 1. Time–depth recorder drogues deployed before (n = 5) and after (n = 8) closure of the South Bay Power Plant. SCL: straight carapace length; F: female; M: male; J: juvenile

Date	Turtle ID	Sex	Weight (kg)	SCL (cm)	Days tracked	Resting dives analyzed	Dive depth (m) Mean	Dive depth (m) Max.	Dive time (min) Mean	Dive time (min) Max.	Temperature range (°C)
Before closure											
January 2004	2070	F	87[a]	82.9	2	174	2.63	5.50	9.22	157.75	12.30–35.25
November 2004	12 114	J	38	62.8	13	1376	2.94	9.00	9.88	137.42	13.44–26.14
March 2005	8367	F	104[a]	89.2	3	516	3.04	5.00	3.03	28.58	16.80–36.85
April 2005	8356	M	115[a]	92.8	8	1278	2.24	5.65	4.64	107.08	13.90–42.30
May 2005	5806	M	118[a]	94.1	6	283	1.97	3.50	5.61	71.00	14.60–35.90
After closure											
May 2011	5806	M	138	96.7	5	555	2.21	6.50	5.94	91.83	16.95–26.80
July 2011	5868	F	150	100.3	2	333	2.10	7.00	2.89	46.17	18.10–26.00
November 2011	3025	M	112	90.0	2	74	1.89	4.00	9.42	60.67	13.75–17.40
December 2011	1304	M	121	97.2	25	407	2.75	12.00	34.10	297.83	12.74–17.00
January 2012	4546	F	134	95.8	18	952	2.42	6.50	18.96	180.33	13.45–17.84
May 2012 (L)	3004	F	133	100.1	3	176	2.14	3.50	3.48	13.00	22.45–27.05
May 2012 (S)	33 149	J	63	78.7	3	229	1.79	3.00	4.02	15.75	22.55–26.50

[a]Weights estimated based on turtles captured between 22 Oct 2009 and 24 Jul 2014 with known SCL using the linear regression equation: $y = 2.838x - 148.250$ (n = 58)

(n = 497) and 19.0°C after the South Bay Power Plant closure (n = 571). Generalized linear models revealed that T_w during resting behavior (episodic/dives and continuous/bouts) was significantly warmer for turtles before the closure than after (dives: $F = 228.253$, df = 1, $p < 0.001$; bouts: $F = 271.026$, df = 1, $p < 0.001$). Thus, turtles in San Diego Bay experienced significantly cooler T_w during periods of rest after the South Bay Power Plant closure.

Turtles spent a significantly longer time resting after the power plant closure, when T_w was significantly colder. For both individual dives and resting bouts, we found that turtles engaged in resting behavior for significantly greater amounts of time after the closure of the plant. Generalized linear models revealed that individual resting dives ($F = 60.304$, df = 1, $p < 0.001$) and resting bouts ($F = 26.421$, df = 1, $p < 0.001$) after the closure were significantly longer and in colder water.

Individual resting dives showed a strong negative correlation between T_w and duration of resting dives. As T_w decreased, time spent resting increased. This pattern was particularly pronounced for resting dives greater than 90 min and at T_w below about 15°C. Broken-line regression via iterative searching revealed that dive duration was significantly longer below 14.4°C (iterative searching, $F = 23.57$, n = 98, $p < 0.001$; Fig. 5).

4. DISCUSSION

Anthropogenic impacts on coastal waters are increasing as the number of humans living along coastlines grows. One impact to urbanized coastlines is power plant operations that employ OTC systems to cool plant machinery and release heated effluent into adjacent aquatic environments, altering the thermal regime of these habitats. Organisms inhabiting these effluent areas have acclimated to or become dependent on these anthropogenically altered thermal refugia and show strong fidelity to these locations. As energy technologies like fossil-fuel-based power plants become outdated due to changes in energy demands and advancements in technology (Jaske et al. 2009, Wong & Lee 2019), there is an immediate need to understand how these organisms will respond (Laist et al. 2013, MacDonald et al. 2013). The December 2010 closure of the South Bay Power Plant in San Diego Bay, at the northern end of the range for foraging green turtles, provided a unique opportunity to monitor the behavior of a foraging aggregation of green sea turtles before and after the loss of the thermal effluent site, which previous research (Eguchi et al. 2010, Eguchi et al. 2012) identified as a thermal refuge, particularly in winter and spring when adjacent ambient temperatures were much colder.

During South Bay Power Plant operation, the T_w recorded during TDR deployments in 2004 and 2005 was upwards of 40.0°C, well outside the range of naturally occurring temperatures in San Diego Bay and representative of T_w of thermal effluent in the outfall area. Thus, these data suggest that turtles were occupying areas in and around the outfall. Following the decommissioning and subsequent closure of the power plant, T_w recorded during TDR deployments was significantly colder than during plant operation — even including records from the summer (July 2011) deployment. With the loss of the thermal effluent, turtles in the area were faced with overall colder ambient T_w and the absence of a thermal refuge historically utilized by turtles during plant operation throughout winter and spring months. These results indicate that green turtles in San Diego Bay experienced a significant and relatively rapid shift in ambient T_w. Post-closure deployments suggest that turtles did not find an alternative thermal refuge during cooler months and may have instead compensated with their level of activity.

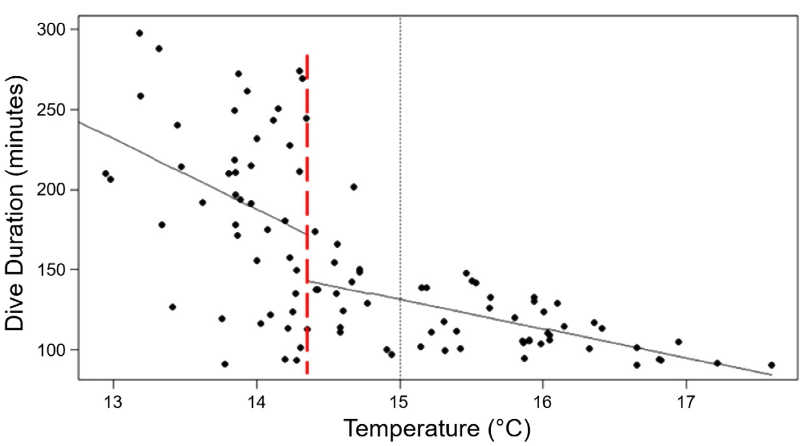

Fig. 5. Results of 2 broken-line regression analyses between water temperature (T_w) (<18°C) and resting dive duration, longer than 90 min. Vertical red dashed line: estimated temperature at which regression slopes change; black dotted line: previously established inactivity threshold for green turtles (Seminoff 2000)

Following the South Bay Power Plant closure, we found a significant change in turtle resting dives. Dive durations were longer in colder water, supporting findings from other diving behavior studies of an inverse relationship between dive duration on a single breath and T_w (Hays et al. 2002b, Southwood et al. 2003b, Reina et al. 2005, Hazel et al. 2009). A study conducted in parallel with this one revealed that San Diego Bay turtles in winter months (December–February) were distributed in significantly warmer water than average both before and after the closure (Madrak et al. 2016), with turtles retaining a lesser degree of site fidelity to the outfall area following the loss of thermal effluent. These results, paired with the shifts in dive patterns observed in this study, suggest that green turtles respond to changes in temperature by altering both their horizontal distribution and dive duration activity level.

Given the importance of ambient conditions for maintaining physiological functions in ectothermic organisms, some behavioral plasticity is expected to allow for acclimation to environmental conditions (Komers 1997). In the case of green turtles in San Diego Bay, Madrak et al. (2016) observed that the turtles continued to use the South Bay area after the South Bay Power Plant closure — even when the thermal regime was strikingly different (Fig. 2). This continued site fidelity by turtles to the outfall area in the absence of thermal refuge led to a shift in dive behavior seen in this study to contend with less than favorable T_w; the turtles significantly increased time spent resting in response to significantly colder T_w.

Sea turtles in San Diego Bay are located relatively near the latitudinal northern extent of this population's geographic range (Crear et al. 2016, Madrak et al. 2016), where T_w naturally falls to 10–15°C during winter and spring months. Thus, turtles in the northerly extent of this range are most likely to demonstrate a behavioral response to temperature shifts given the proximity to the northern limit to their habitat range. Previous research estimated a temperature threshold of 15°C, below which turtles are largely inactive (Felgar et al. 1976, Seminoff 2000). Results from this study confirm this previously observed temperature threshold for green turtles and suggest the threshold may even extend lower, to approximately 14.4°C for adult green turtles.

Green turtles are capable of dive durations exceeding 60 min (Brill et al. 1995, Southwood et al. 2003b, Seminoff et al. 2006). Dive duration is affected by total oxygen store and metabolic rate, the latter of which varies with body size, activity, temperature, and hormonal and dietary status (Lutcavage & Lutz 1997, Southwood & Avens 2010). Although capable of extended breath-hold dives, green turtles only require approximately 2–3 s to empty and refill their lungs (Berkson 1966, Tenney et al. 1974). Longer resting dives coincide with greater depths, when accessible (Hays et al. 2000, 2002a, 2004, Okuyama et al. 2014); however, given the overall shallow depths of green turtle habitat in San Diego Bay, resting dive depth was not a response to oxygen stores but instead largely limited by the depths of their habitat.

In San Diego Bay, the activity level of green turtles appears to be related to T_w, with longer periods of rest in colder T_w following the loss of the thermal refuge. In previous research, green turtles in more tropical habitats demonstrated dive durations similar to those for green turtles in San Diego Bay before the South Bay Power Plant closure (Table 2). However, in the years following the closure, when T_w was significantly colder, green turtles made significantly longer resting dives, similar to green turtles in other temperate locations. In a controlled laboratory study, Moon et al. (1997) found that captive juvenile green turtles

Table 2. Previous green turtle dive data versus San Diego Bay water temperature. Dive temperature and duration are means across all turtles in each study. na: not available

Location	Age class	No. of turtles	Dive temp. (°C)	Dive duration (min) Mean	Dive duration (min) Max.	Reference
San Diego Bay, CA, USA	Adult	5	21.2	24.4	157.8	Before closure
San Diego Bay, CA, USA	Adult	8	16.9	49.6	297.8	After closure
Moreton Bay, Queensland, AUS	Juvenile/ adult	19	22.1 (mean across turtles)	na	161 (mean across depths)	Hazel et al. (2009)
Heron Island, AUS	Juvenile	13	23.8 (mean across turtles, n = 10)	15.9 (avg. across turtles, n = 8)	na	Southwood et al. (2003b)
Bahia de Los Angeles, MEX	Juvenile/ adult	19	na	12.6	130.9 (episodic); 288.2 (continuous)	Seminoff et al. (2006)
Biology Department, Texas A&M University	Juvenile	5	<15 (laboratory controlled)	na	>180	Moon et al. (1997)

rested for periods in excess of 180 min in temperatures below 15°C (Table 2). While these dives are shorter than green turtles in San Diego Bay at similar T_w, it must be noted that the maximum allowable dive depth in Moon et al.'s (1997) study was 0.75 m — coincident with the bottom of the tank. These turtles very likely would have demonstrated longer periods of rest if greater depths were available.

Our study indicates that green turtles exhibited behavioral plasticity in response to shifts in T_w, an important finding for future research on how environmental changes from direct and indirect anthropogenic impacts may affect sea turtle populations in coastal areas. Although these ectothermic organisms may be able to contend with shifts in ambient temperature by altering their behavior, changing T_w paired with projected changes in sea level may also impact food availability for these and other coastal species. Additionally, increased variability in T_w from climate change may lead to habitat range expansion by green turtles to more northerly regions where increases in overlap with human activities are likely. Understanding how ectotherms contend with major changes to their coastal environments is critical for their conservation and management in light of continued direct and indirect anthropogenic stressors in coastal zones.

Acknowledgements. The authors acknowledge members of the Conservation Ecology Lab at San Diego State University and members of the Marine Turtle Ecology and Assessment Program. We thank the following individuals for their tremendous support in the field: J. Bredvik, J. Brower, S. Coates, C. Coppenrath, A. D'Amico, A. Gaos, S. Graham, T. Grimes, D. Ho, C. Jackson, G. Lemons, N. Magana, D. Mahoney, B. MacDonald, R. Moens, N. Nourn, K, Ritchie, A. Miller, D. Prosperi, J. Okuyama, C. Turner-Tomaszewicz, and the entire NOAA-NMFS team that assisted with turtle capture. Our gratitude is also extended to R. LeRoux for the invaluable assistance in sonic transmitter attachment, permitting, and coordination of turtle capture. Financial and logistical support was provided by San Diego State University, San Diego State University Research Foundation, NOAA Service Southwest Fisheries Science Center, Unified Port of San Diego, the United States Navy, Sonotronics Inc., and South Bay Power Plant LLC.

LITERATURE CITED

Avery HW, Spotila JR, Congdon JD, Fischer RU, Standora EA, Avery SB (1993) Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta*. Physiol Zool 66:902–925

Berkson H (1966) Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). Comp Biochem Physiol 18:101–119

Block BA, Costa DP, Boehlert GW, Kochevar RE (2002) Revealing pelagic habitat use: the tagging of Pacific pelagics program. Oceanol Acta 25:255–266

Brill RW, Balazs GH, Holland KN, Chang RKC, Sullivan S, George JC (1995) Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L.) within a foraging area in the Hawaiian Islands. J Exp Mar Biol Ecol 185:203–218

Butler PJ, Jones DR (1997) Physiology of diving of birds and mammals. Physiol Rev 77:837–899

Crear DP, Lawson DD, Seminoff JA, Eguchi T, LeRoux RA, Lowe CG (2016) Seasonal shifts in the movement and distribution of green sea turtles *Chelonia mydas* in response to anthropogenically altered water temperatures. Mar Ecol Prog Ser 548:219–232

Dingle H (2014) Migration: the biology of life on the move. Oxford University Press, Oxford

Doney SC, Ruckelshaus M, Duffy JE, Barry JP and others (2012) Climate change impacts on marine ecosystems. Annu Rev Mar Sci 4:11–37

Duke Energy South Bay (2004) South Bay Power Plant cooling water system effects on San Diego Bay, Vol 1: compliance with Section 316(1) of the Clean Water Act for the South Bay Power Plant. San Diego Regional Water Quality Control Board, San Diego, CA

Dutton DL, Dutton PH (1999) Accelerated growth in San Diego Bay green turtles? In: Epperly SP, Braun SP (eds) Proc 17th annual symp sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC-415. US National Marine Fisheries Service, Miami, FL, p 164–165

Dutton P, McDonald D (1990) Status of sea turtles in San Diego Bay: 1989-1990 Final Report. Sea World Research Institute Tech Rep #90-225

Eguchi T, Seminoff JA, LeRoux RA, Dutton PH, Dutton DL (2010) Abundance and survival rates of green turtles in an urban environment: coexistence of humans and an endangered species. Mar Biol 157:1869–1877

Eguchi T, Seminoff JA, LeRoux RA, Prosperi D, Dutton DL, Dutton PH (2012) Morphology and growth rates of the green sea turtle (*Chelonia mydas*) in a northernmost temperate foraging ground. Herpetologica 68: 76–87

Felger RS, Cliffton K, Regal PJ (1976) Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. Science 191: 283–285

Fossette S, Gleiss AC, Myers AE, Garner S and others (2010) Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. J Exp Biol 213: 4074–4083

Gibbons JW, Sharitz RR (1981) Thermal ecology: environmental teachings of a nuclear reactor site. Bioscience 31: 293–298

Guerra-Correa C, Guerra-Castro C, Bolandos P, Silva A, Garfias P (2008) Sea turtle congregations in discrete temperate shoreline areas in cold northern Chilean coastal waters. In: Rees, AF, Frick M, Panagopoulou A, Williams K (eds) Proc 27th annual symp sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC-569. Southeast Fisheries Science Center, Miami, FL, p 211–212 (Abstract)

Harley CDG, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000) The diving behaviour of green turtles at Ascension Island. Anim Behav 59: 577–586

Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002a) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. Mar Biol 141:985–990

Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002b) Water temperature and internesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. J Therm Biol 27:429–432

Hays GC, Metcalfe JD, Walne AW (2004) The implications of lung-regulated buoyancy control for dive depth and duration. Ecology 85:1137–1145

Hazel J, Lawler IR, Hamann M (2009) Diving at the shallow end: green turtle behaviour in near-shore foraging habitat. J Exp Mar Biol Ecol 371:84–92

Hochscheid S, Wilson RP (1999) A new method for the determination of at-sea activity in sea turtles. Mar Ecol Prog Ser 185:293–296

Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. Mar Ecol Prog Ser 185: 101–112

Hochscheid S, Bentivegna F, Bradhai MN, Hays GC (2007) Overwintering behaviour in sea turtles: dormancy is optional. Mar Ecol Prog Ser 340:287–298

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. Annu Rev Physiol 72:127–145

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Jaske MR, Peters DC, Strauss RL (2009) Implementation of once-through cooling mitigation through energy infrastructure planning and procurement. https://efiling.energy.ca.gov/GetDocument.aspx?tn=52577&DocumentContentId=10414

Jones TT, Van Houtan KS, Bostrom BL, Ostafichuk P and others (2013) Calculating the ecological impacts of animal-borne instruments on aquatic organisms. Methods Ecol Evol 4:1178–1186

Komers PE (1997) Behavioural plasticity in variable environments. Can J Zool 75:161–169

Kooyman GL (1989) Diving physiology: marine mammals. In: Lenfant C (ed) Comparative pulmonary physiology: current concepts. Marcel Dekker, New York, NY, p 721–734

Kramer DL (1988) The behavioral ecology of air breathing by aquatic animals. Can J Zool 66:89–94

Laist DW, Reynolds JE III (2005a) Influence of power plants and other warm-water refuges on Florida manatees. Mar Mamm Sci 21:739–764

Laist DW, Reynolds JE III (2005b) Florida manatees, warm-water refuges, and an uncertain future. Coast Manage 33:279–295

Laist DW, Taylor C, Reynolds JE III (2013) Winter habitat preferences for Florida manatees and vulnerability to cold. PLOS ONE 8:e58978

Lemons G, Lewison R, Komoroske L, Gaos A and others (2011) Trophic ecology of green sea turtles in a highly urbanized bay: insights from stable isotopes and mixing models. J Exp Mar Biol Ecol 405:25–32

Lutcavage ME, Lutz PL (1997) Diving physiology. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 276–296

Lyon B, Seminoff JA, Eguchi T, Dutton PH (2006) *Chelonia* in and out of the Jacuzzi: diel movements of East Pacific green turtles in San Diego Bay, USA. In: Frick M, Panagopoulou A, Rees AF, Williams K (eds) Proc 26th annual symp sea turtle biology and conservation. International Sea Turtle Society, Crete, p 101 (Abstract)

MacDonald BD, Lewison RL, Madrak SV, Seminoff JA, Eguchi TE (2012) Home ranges of East Pacific green turtles, *Chelonia mydas*, in a highly urbanized temperate foraging ground. Mar Ecol Prog Ser 461:211–221

MacDonald BD, Madrak SV, Lewison RL, Seminoff JA, Eguchi T (2013) Fine scale diel movement of the east Pacific green turtle, *Chelonia mydas*, in a highly urbanized foraging environment. J Exp Mar Biol Ecol 443: 56–64

Madden N, Lewis A, Davis M (2013) Thermal effluent from the power sector: an analysis of once-through cooling system impacts on surface water temperature. Environ Res Lett 8:035006

Madrak SV, Lewison RL, Seminoff JA, Eguchi T (2016) Characterizing response of East Pacific green turtles to changing temperatures: using acoustic telemetry in a highly urbanized environment. Anim Biotelem 4:22

McMahon CR, Bradshaw CJA, Hays GC (2007) Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. Mar Ecol Prog Ser 329:239–252

Mendonça MT (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copeia 1983:1013–1023

Moon DY, Mackenzie DS, Owens DW (1997) Simulated hibernation of sea turtles in the laboratory: I. Feeding, breathing frequency, blood pH, and blood gases. J Exp Zool 278:372–380

Muggeo VMR (2003) Estimating regression models with unknown break-points. Stat Med 22:3055–3071

Muggeo VMR (2008) Segmented: an R package to fit regression models with broken-line relationships. R News 8: 20–25

Okuyama J, Tabata R, Nakajima K, Arai N, Kobayashi M, Kagawa S (2014) Surfacers change their dive tactics depending on the aim of the dive: evidence from simultaneous measurements of breaths and energy expenditure. Proc R Soc B 281:20140040

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reina RD, Abernathy K, Marshall GJ, Spotila JR (2005) Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. J Exp Mar Biol Ecol 316: 1–16

Sarmiento-Devia RA, Harrod C, Pacheco AS (2015) Ecology and conservation of sea turtles in Chile. Chelonian Conserv Biol 14:21–33

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480

Schlaepfer MA, Sherman PW, Runge MC (2010) Decision making, environmental change, and population persistence. In: Westneat DF, Fox CW (eds) Evolutionary behavioral ecology. Oxford University Press, New York, NY, p 506–509

Schorr GS, Falcone EA, Moretti DJ, Andrews RD (2014) First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. PLOS ONE 9:e92633

Seminoff JA (2000) Biology of the East Pacific green turtle, *Chelonia mydas agassizii*, at a warm temperate feeding area in the Gulf of California, México. PhD thesis, University of Arizona, Tucson, AZ

Seminoff JA, Jones TT, Marshall GJ (2006) Underwater behaviour of green turtles monitored with video–time–depth recorders: What's missing from dive profiles? Mar Ecol Prog Ser 322:269–280

Shaver DJ, Tissot PE, Streich MM, Walker JS and others (2017) Hypothermic stunning of green sea turtles in a western Gulf of Mexico foraging habitat. PLOS ONE 12: e0173920

Southwood A, Avens L (2010) Physiological, behavioral, and ecological aspects of migration in reptiles. J Comp Physiol B 180:1–23

Southwood AL, Darveau CA, Jones DR (2003a) Metabolic and cardiovascular adjustments of juvenile green turtles to seasonal changes in temperature and photoperiod. J Exp Biol 206:4521–4531

Southwood AL, Reina RD, Jones VS, Jones DR (2003b) Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. Can J Zool 81: 1014–1024

Spotila JR, O'Connor MP, Paladino FV (1997) Thermal biology. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 297–314

Stinson ML (1984) Biology of sea turtles in San Diego Bay, California, and the northeastern Pacific Ocean. MSc thesis, San Diego State University, San Diego, CA

Tenney SM, Bartlett D Jr, Farber JP, Remmers JE (1974) Mechanics of the respiratory cycle in the green turtle (*Chelonia mydas*). Respir Physiol 22:361–368

Turner-Tomaszewicz C, Seminoff JA (2012) Turning off the heat: impacts of power plant decommissioning on green turtle research in San Diego Bay. Coast Manage 40: 73–87

Wong L, Le A (2019) California Energy Commission - tracking progress: once-through cooling phase-out. https://www.energy.ca.gov/sites/default/files/2019-12/once_through_cooling_ada.pdf

Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia
Reviewed by: R. D Reina, A. Williard and 1 anonymous referee

Submitted: January 18, 2021
Accepted: October 20, 2021
Proofs received from author(s): January 27, 2022