

1 **No rest for the weary: restricted resting behavior of green turtles (*Chelonia***
2 ***mydas*) at a deep-neritic foraging area influences expression of life history**
3 **traits**

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22 **Running head:** Life history implications of green turtle resting behavior

23
24 **Abstract**

25 For breath-holding marine animals, tradeoffs between ‘active’ and resting behaviors
26 during periods of submergence can have consequences for acquisition and allocation of energy to
27 vital life history requirements. In this study, we fitted 18 green turtles (*Chelonia mydas*) with
28 detachable time-depth recorder (TDR) systems to obtain and analyze fine-scale dive behavior
29 and daily activity—with a focus on resting dive bouts—at Bahía de los Angeles (BLA), a warm-
30 temperate foraging area in the Gulf of California, México. Our results showed that resting bout
31 durations increased with water depths among all turtles, but patterns of resting bout durations

32 and depths varied widely among individuals. To evaluate potential consequences to green turtles
33 of tradeoffs between time spent ‘active’ *versus* resting, we also compared behavioral parameters
34 (e.g., time spent resting, home range sizes) and life history traits (e.g., growth rates, body size at
35 maturity) of green turtle populations from around the world, including BLA. We found that BLA
36 green turtles spend less time resting, spend more time actively swimming and diving, occupy
37 larger home ranges, and exhibit slower growth rates and smaller adult body sizes compared to
38 their counterparts in other parts of the world. Unique characteristics of the BLA foraging habitat
39 (e.g., patchy resources and temperature extremes) appear to require increased diel movements
40 and foraging activity and decreased resting opportunities. These interactions between habitat and
41 turtle behavior not only influence expression of life history traits, but can also increase turtles’
42 exposure to human activities (e.g., vessel traffic and fisheries bycatch) as they move throughout
43 the area.

44

45 **Key Words:** black turtle, diving, Gulf of California, Mexico, sea turtle, time-depth recorder

46

47 **Introduction**

48 Studies of dive behavior by breath-holding marine animals tend to focus on ‘active
49 behaviors’ such as transit, foraging, and predator evasion (Block et al. 2005, Ropert-Coudert et
50 al. 2009, Rutz and Hays 2009, Hochscheid 2014). However, a critical—yet often overlooked—
51 component of diving animal energy budgets is resting behavior during periods of submergence
52 (but see Mitani et al. 2010). Tradeoffs in time spent between ‘active’ behaviors and periods of
53 rest have consequences for efficiency of acquisition and allocation of energy to vital life history
54 requirements such as growth and reproductive output (Nagy et al. 1999, McNab 2002). Further,
55 identifying patterns of rest versus activity can help pinpoint the specific habitats and times where
56 animals might be most susceptible to human impacts such as coastal fishing and vessel traffic
57 (Hart et al. 2016, Shimada et al. 2017). In addition, improved quantification of time spent at the
58 surface versus diving is critical to population estimates based on aerial survey data (Benson et al.
59 2007, Fuentes et al. 2015).

60 Marine turtles have been subjects of numerous studies of underwater behavior using a
61 range of biologging devices, including time-depth recorders (TDRs), acoustic and satellite
62 telemetry, and animal-borne video systems (e.g. Reina et al. 2005, Godley et al. 2008, Thomson

63 et al. 2018). Using time *versus* depth relationships of dives, researchers have characterized up to
64 six archetypal dive types to make inferences about sea turtle time-activity patterns (Houghton et
65 al. 2002, Seminoff et al. 2006) (Fig. 1). These inferences become more powerful when multiple
66 tools are combined; for example, video footage recorded from a “turtle’s-eye view” or by tags
67 that also record tri-axial body movements using accelerometers can provide a much fuller picture
68 of what turtles are interacting with and reacting to in their underwater habitats, thus reducing
69 potential errors when inferring specific behaviors—and collective behavior patterns over time
70 and among individuals—from dive data alone (Wallace et al. 2015, Hart et al. 2016). For
71 example, Seminoff et al. (2006) used video footage to discriminate active versus resting behavior
72 by green sea turtles (*Chelonia mydas*) based on Type 1 (i.e., U-shaped) dives detected by TDR
73 data, which allowed the authors to refine parameters that could be used to improve identification
74 of true ‘resting’ dives within TDR data.

75 Green turtles use a wide range of habitats throughout their lifetime (for review see Hirth,
76 1997), but primarily occupy neritic, coastal habitats where they maintain a largely herbivorous
77 diet of marine algae and seagrass (Bjorndal 1997). However, omnivory including invertebrate
78 prey is common in some locations, particularly in the eastern Pacific Ocean (EP) (Jones and
79 Seminoff 2013). The EP green turtle subpopulation—sometimes referred to as the ‘black turtle’
80 because of its distinct morphology despite belonging to the single global species—experienced a
81 significant population decline from the 1960s through 1990s, but in recent years it has shown
82 signs of recovery (Delgado-Trejo and Alvarado-Díaz 2012, Seminoff et al. 2015). Despite the
83 recent positive population trend, ongoing threats persist throughout the region (Delgado-Trejo
84 and Alvarado Díaz 2012, Tiburcio Pintos and Cariño Olvera 2017). Improved characterization of
85 spatio-temporal habitat use by green turtles could inform efforts to reduce threats from human
86 activities. For example, a greater understanding of the habitats and depths at which green turtles
87 most frequently occur can be useful for mitigating impacts present in near shore environments
88 such as fisheries bycatch and boat strikes (Balazs et al. 1987, Snape et al. 2016, Shimada et al.
89 2017).

90 Among the most important foraging areas for green turtles in the EP is Bahía de los
91 Angeles (BLA), a warm-temperate bay in the Gulf of California, México, which was the former
92 green turtle fishery capital of México during the era of legal harvest (Caldwell 1963, Seminoff et
93 al. 2003; 2008). Whereas green turtles in other foraging areas often focus time and energy in

94 single, discrete localities within their foraging grounds (Hart and Fujisaki 2010, Hazel et al.
95 2013, Griffin et al. 2019, 2020), BLA green turtles tend to move among multiple foraging
96 localities separated by up to 8 km over the course of several days (Seminoff et al. 2002a,
97 Seminoff and Jones 2006). Home ranges of green turtles in BLA tend to be larger, and activity
98 centers of individual turtles more dispersed, than those of green turtles in other parts of the world
99 (Seminoff et al. 2002a, Okuyama et al. 2013; Table 3). Large home ranges are likely because of
100 the relatively small area of coastal shallows areas and patchily distributed food resources
101 (Seminoff et al. 2002a, Seminoff and Jones 2006). In addition, BLA green turtles tend to perform
102 deeper foraging dives, on average, than their counterparts in other parts of the world (Seminoff et
103 al. 2006, Ballorain et al. 2013, Okuyama et al. 2013, Hart et al. 2016). Whereas water
104 temperatures are generally stable year-round in tropical areas inhabited by most green turtle
105 populations (e.g. Ballorain et al. 2013), BLA is characterized by marked seasonality in ambient
106 water temperatures. Extended cold periods can limit green turtle activity (Southwood et al. 2003,
107 Hazel et al. 2009), and green turtles in the Gulf of California have been observed in seasonal
108 torpor during winter months (Felger et al. 1976, Seminoff et al. 2003). Collectively, these factors
109 likely translate to more time and energy spent by BLA green turtles actively searching—both
110 vertically and horizontally—for food resources as a relatively high proportion of their overall
111 time-energy budgets compared to processing and assimilating those resources, which could have
112 consequences for critical life history requirements such as physiological maintenance and
113 somatic growth (Niewiaroski 2001, McNab 2002).

114 In the context of overall time-energy budgets, variations in diving activity, foraging
115 behaviors, and habitat use by green turtles in different parts of the world suggest that time spent
116 resting should also vary substantially. Generally, green turtles are more active during the day
117 than at night (Ogden et al. 1983, Blumenthal et al. 2010, Hazel et al. 2009; 2013, Makowski et
118 al. 2013, Hart et al. 2016, Dujon et al. 2017), and sometimes show bimodal peaks in diurnal
119 activities (Mendonça 1983, Okuyama et al. 2013). Immature green turtles foraging and growing
120 in BLA, an area characterized by marked seasonality in ambient temperatures as well as patchily
121 distributed resources (Seminoff et al. 2002a; 2006, Seminoff and Jones 2006), may spend more
122 time actively transiting and foraging—and less time resting—than their counterparts in areas
123 with more consistent ambient temperatures and resource availability. This tradeoff in energy

124 expenditure to acquire resources and time spent resting, presumably to enhance nutrient
125 assimilation, could have consequences for vital functions such as somatic growth.

126 In this study, we analyzed diving activity data collected over multiple years from BLA
127 green turtles to build on previous studies at this location (Seminoff and Jones 2006, Seminoff et
128 al. 2006), with a focus on resting activity. Our goal was to use parameters of resting dives
129 described using paired TDR and video data (Seminoff et al. 2006) to identify individual and
130 collective dive characteristics, and use them to investigate resting activity time and allocation
131 among depths at this warm temperate foraging habitat in the Gulf of California. We hypothesized
132 that 1) the duration and depth of resting dives would be longer and deeper than non-resting dives,
133 2) resting bout durations would increase with resting depths, and 3) green turtles in BLA would
134 rest for less time and less frequently than green turtles in other locations around the world.

135

136 **Methods**

137 *Study site*

138 The study was conducted in June and July, from 1999 to 2002 at BLA (28°58' N,
139 113°33'W; Fig. 2), a NNE-oriented bay along the western coast of the Baja California peninsula
140 and in the Gulf of California, Mexico (Seminoff et al. 2003). BLA is 60 km² in area, and
141 characterized by strong tidal mixing and upwelling, which supports a diverse assemblage of
142 marine life (Álvarez-Borrego 2007). A series of 17 islands line the northeastern portion of the
143 bay and separate this foraging area from pelagic offshore waters of the central Gulf of California.
144 Benthic habitats at these islands are characterized by boulder fields that steeply descend 40 to 50
145 m to the soft-bottomed sea floor. Marine invertebrates such as gorgonians, sponges, and soft
146 corals are abundant (Brusca 1980). Marine algae, primarily red and brown algae, dominate the
147 marine vegetation in the bay. A small town also named Bahía de Los Angeles is located along
148 the western shore of BLA. The local economy for the community of approximately 500 persons
149 during the time of data collection was based on artisanal fisheries, sport fishing, and nature
150 tourism.

151

152 *Turtle capture and measurement*

153 We attached time-depth recorders (TDRs) to 18 individual green turtles (Table 1)
154 captured with entanglement nets (100 m x 8 m, mesh size = 50 cm stretched) as part of a long-

155 term study of green turtles at BLA (Seminoff et al. 2003). We measured straight carapace length
156 (SCL; ± 0.1 cm) from the nuchal notch to the posterior-most portion of the rear marginal scutes
157 using a forester's caliper and mass (± 1 kg) with a 150-kg spring balance. The maturity status of
158 each turtle was assigned, based on the mean nesting size (MNS) of females at the closest major
159 rookery (77.3 cm SCL at Colola, Michoacán, México; Figueroa et al., 1993). Green turtles with
160 $SCL < MNS$ were considered putative immatures, whereas those with $SCL \geq MNS$ were
161 considered putative adults. We measured tail length (TL; ± 1.0 cm) from the tip of the tail to the
162 trailing edge of the carapace using a flexible tape. Among adult-sized turtles, individuals with an
163 elongated tail ($TL \geq 25$ cm) were classified as adult males, while all others were classified as
164 putative adult females. All turtles were marked with Inconel flipper tags (#681; National Band
165 and Tag Co.) in the first large proximal scale of each rear flipper. TDR-fitted turtles ranged from
166 57.5 to 92.5 cm (mean = 71.4 ± 10.4 cm) in straight carapace length (SCL) and from 27.2 to
167 102.1 kg (mean = 53.5 ± 22.6 kg) in body mass (Table 1), and were typically released at the site
168 of initial capture within 24 hours of capture.

169

170 *Data logger attachment*

171 TDRs (MK-7, Wildlife Computers, Redmond, Washington) were seated in tubular-
172 shaped syntactic foam drogues (20-cm length, 7-cm diameter). TDRs logged time-of-day, depth
173 (resolution = 0.5 m), temperature ($^{\circ}\text{C}$), and light levels (lumens). All devices had integrated Very
174 High Frequency (VHF) radio (MOD 050, Telonics, Inc. Mesa, Arizona) and ultrasonic (DT-96,
175 Sonotronics, Tucson, Arizona) transmitters to enable recovery. Units weighed 0.5 kg out of
176 water, were slightly positively buoyant in water and were affixed with counterweights to achieve
177 neutral buoyancy while attached to the turtle. The drogue was shaped to minimize hydrodynamic
178 drag, although this is less of a concern for short-term, local biotelemetry deployments in this
179 study compared to studies of long-term migratory behavior, where drag reduction has significant
180 energetic consequences (Jones et al. 2011, 2013).

181 We used an automatic release mechanism consisting of two interlocking plates; one
182 (which included the counterweight) fixed to the turtle's carapace with a 5-minute quickset epoxy
183 and the second attached to the TDR drogue with two stainless steel hose clamps. A screw-and-
184 groove assembly linked the anterior portion of these plates. The rear portion was connected with
185 a galvanic (magnesium) link that slowly dissolved upon immersion in seawater. Upon dissolving,

186 a spring mechanism forced the rear of the top plate upwards, thereby disengaging the front
187 portion. The slight buoyancy caused the units to float to the surface, thus enabling retrieval by
188 conventional VHF and sonic telemetry.

189

190 *Data Analysis*

191 In order to distinguish active from resting dives, we first used Jensen software's Multi-
192 Trace Dive™ program (hereafter MT Dive) to identify and classify Type 1 or U-dives from
193 among all *ca.* 10,000 discrete dive events. MT-Dive scans the recorded depth data and searches
194 dive events according to the 'Parameters for the dive analysis' set by the user. Thus, we used
195 several specific parameters to inform MT Dive's analysis. Type 1 dives or U-shaped dives (Fig.
196 1) are defined as having a sharp descent followed by an extended flat bottom phase and a sharp
197 ascent. Type 1 dives are the least ambiguous in terms of indicating a specific behavior and are
198 commonly accepted as representing resting behavior (e.g. Hochscheid et al. 1999, Hays et al.
199 2000, Southwood et al. 2003). However, not all Type 1 dives are resting dives; previous studies
200 have described activities such as benthic traveling and stationary foraging during Type 1 dives
201 (Hochscheid et al. 1999; Seminoff et al., 2006, Thomson et al. 2011). Therefore, we set
202 additional criteria for a dive to be classified as a resting dive: a maximum depth ≥ 2 m, a duration
203 ≥ 4 min, steep descent and ascent phases (Houghton et al. 2002), and no systematic depth change
204 during the bottom phase. Green turtle-borne cameras paired with TDR dive data at BLA showed
205 that Type 1 dives that occurred within a sequence of ≥ 2 such dives were for resting and not
206 stationary foraging (Seminoff et al. 2006). Therefore, in the present study, a U-dive was
207 classified as part of a resting bout instead of a stationary foraging bout if it occurred within a
208 sequence of ≥ 2 consecutive dives meeting the aforementioned depth, duration, and
209 ascent/descent criteria. This set of criteria for identifying resting dives should be considered
210 conservative because it excludes 'episodic resting dives' described by Seminoff et al. (2006),
211 which can account for ~10% of Type 1 dives.

212 We also performed visual inspection to evaluate the MT-Dive output (n=607 Type 1
213 dives) and to include in our analyses dives that the program misidentified as non-Type 1 dives.
214 Two observers experienced in dive profile analysis were in agreement with each other on 91% of
215 reviewed resting dives, and this visual inspection resulted in identification of 30 additional dives

216 to the MT-Dive output. After including these additional dives, our analysis comprised resting
217 dives (n=637) as determined by both MT-Dive and visual observers.

218 We also compared log-transformed (to reduce heteroscedasticity) resting dive depth and
219 duration among individuals using mixed-effects models (R package nlme; Pinheiro et al. 2017).
220 We treated each dive event as an individual data point and turtle IDs as the random effect
221 (Thomson et al. 2011). For the majority of data analyses, dives were pooled across all individual
222 turtle data sets and categorized as resting dives and all other dives. Resting dives were divided by
223 hour of the day and categorized as “day” (05:45 to 19:30 local time) or “night” (19:30 to 05:45
224 local time) dives to identify diel trends; these time periods reflected the mean sunrise and sunset
225 times during the study periods. Not all turtles performed resting dives during day and night, so
226 we used the pooled data to perform a chi-squared test for differences in number of resting dives
227 among individual turtles during the day and night. Variance around central tendency values are \pm
228 1 standard deviation, and ranges (minimum and maximum values) are also presented for dive
229 parameters.

230

231 *Comparison of behavior and life history among green turtle populations, including BLA*

232 Our third hypothesis was that green turtles at BLA might spend less time resting—and
233 thus more time actively transiting and foraging—than green turtles in other locations around the
234 world that have more consistent ambient temperatures and/or resource availability. To evaluate
235 our third hypothesis, we compiled published data on resting behaviors (e.g. time spent resting,
236 resting bout durations and depths), home range sizes, and ambient temperature ranges from
237 numerous studies of green turtle underwater behaviors (Table 3). Further, to examine whether
238 observed relationships between activity *versus* resting were related to potential consequences for
239 green turtle life history traits, we also compiled information on somatic growth rates and size at
240 sexual maturity for each regional subpopulation.

241

242 **Results**

243 We obtained a combined total of 1,343 hours (mean = 60.2 hours/turtle, range = 9.9 to
244 271.9 hours/turtle) of TDR data (9,855 total dives) among 18 turtles (Table 1). Maximum dive
245 depth among turtles was 57.0 m, and averaged $9.7 \text{ m} \pm 6.3 \text{ m}$ (range of averages = 2.0 – 29.1 m).
246 Mean dive duration was $5.4 \text{ min} \pm 5.2 \text{ min}$, and dive duration ranged between 0.2 min to 51.5

247 min. Including all dives, turtles occupied median water temperatures of 25.4 ± 1.7 °C (range =
248 17.7 to 34.9°C).

249 In total, 637 resting bouts across 12 turtles accounted for 172.2 hours (~12.8%) of the
250 cumulative dive record. Of the total deployment time analyzed, cumulatively these individuals
251 spent 25.0% in depths < 2 m and 75.0% diving in waters >2 m. Of dive time in depths >2m, the
252 12 turtles spent 17.6% of dive time performing resting bouts.

253 Among individual turtles, average resting dive bouts were longer and deeper than non-
254 resting dives (Fig. 3). Average duration of resting dives was $18.5 \text{ min} \pm 7.8$ (range = 4.1 – 44.8
255 min) and average depth was $10.8 \text{ m} \pm 2.6 \text{ m}$ (range = 2.0 – 44.4 m), whereas non-resting dives
256 lasted $5.2 \pm 4.4 \text{ min}$ (range = 0.2 – 51.5 min) and occurred at depths of $6.3 \text{ m} \pm 6.2 \text{ m}$ (maximum
257 = 5.0 m), on average. Mean dive temperature did not affect non-resting dive duration
258 ($R^2=0.0003$), resting dive duration ($R^2=0.0009$), non-resting dive depth ($R^2=0.0013$), or resting
259 dive depth ($R^2=0.0011$). Turtle size (SCL, CCL, mass) did not affect dive depth ($R^2=0.0000$,
260 $R^2=0.0004$, $R^2=0.0103$, respectively) or duration ($R^2=0.3437$, $R^2=0.3371$, $R^2=0.3421$,
261 respectively) for resting and non-resting dives.

262 Green turtles consistently (Wilcoxon rank sum test, p -value = <0.0001) rested at mean
263 dive depths greater during the day ($11.5 \text{ m} \pm 6.2 \text{ m}$) than at night ($7.9 \text{ m} \pm 5.9 \text{ m}$). Turtles
264 performed more resting dives at night ($n=380$) than during the day ($n=257$, $\chi^2 = 23.75$, p -value =
265 <0.0001), and diel resting patterns varied among individuals ($\chi^2 = 185.58$, p -value = <0.0001).

266 Among individuals, turtles showed wide variation in time allocated to resting, as well as
267 depths occupied while resting (Table 2; Fig. 4). Six turtles did not perform any resting bouts
268 during their data recording periods, which lasted between 19 hr and 56 hr (Table 2). Among the
269 turtles that did perform resting bouts during recorded periods of at least 24 hr, time spent resting,
270 normalized for a 24-hr period, ranged from 5% per day (~1.1 hr/day, BLA 314) to 36% per day
271 (8.7 hr/day, BLA 704). Similarly, bottom depth during resting bouts varied among individuals
272 (Table 2; Fig 4). For example, one individual (BLA 604) remained within 5.5 m to 8.8 m over
273 3.5 hours of resting time and 20 resting bouts, while another turtle (BLA 709) performed 27
274 resting bouts totaling 10.3 hr, but occupied depths of 12.0 m to 16.0 m (Fig 4A). Average resting
275 dive depth and dive duration also varied widely among individuals, and the two parameters were
276 positively correlated (Fig. 4B).

277 Compared to other green turtle subpopulations, green turtles in BLA have larger home
278 ranges, are more active (i.e., higher proportion of submerged time performing active behaviors),
279 and conversely rest for shorter periods and often at deeper depths. In addition, EP green turtles—
280 the subpopulation to which BLA green turtles belong—tend to have slower growth rates and
281 mature at smaller body sizes than green turtles from other parts of the world (Table 3).

282

283 **Discussion**

284 Diving animals perform active underwater behaviors for several reasons vital to their
285 survival, including resource acquisition, interactions with other individuals, and predator
286 avoidance (Hochscheid 2014). Time spent resting is also critical for efficient physiological
287 performance, including assimilation of resources acquired during active foraging (Okuyama et
288 al. 2013), yet resting is often overlooked in evaluations of time-energy budgets and their
289 ecological consequences for diving animals (Campbell and Tobler 1984). In the present study,
290 data on free-swimming green turtles at the BLA foraging area in the Gulf of California, México
291 (Fig. 2), confirmed our first two hypotheses by showing that 1) non-resting dives were shallower
292 and shorter than resting bouts (Fig. 3), and 2) resting bout durations increased with resting depths
293 (Fig. 4). These results illustrate how distinct active and resting behaviors are, and thus how
294 profoundly tradeoffs in time spent in each phase can affect time-energy budgets. Key factors that
295 influence these active *versus* resting tradeoffs typically include resource availability and
296 distribution (Okuyama et al. 2013), ambient conditions (e.g. temperature) (Hazel et al. 2013),
297 presence of predators (Heithaus et al. 2007), and human disturbance (Balazs et al. 1987).

298

299 *Inter-individual variation in resting behaviors*

300 Duration and depth of resting bouts were positively correlated, but varied widely among
301 individuals (Fig. 4). As initially reported by Seminoff et al. (2006), our study confirms that green
302 turtles at BLA do not exhibit submergence patterns of depth and durations that correspond to use
303 of lung volume to achieve neutral buoyancy as described in other studies (Milsom and Johansen
304 1975, Hays et al. 2004). Rather, BLA green turtle resting bout duration and depths are size-
305 independent, and reflect the varied bathymetry and patchy distribution of food resources
306 (Seminoff et al. 2002a; 2006).

307 The high inter-individual variation in resting bouts likely represents ‘snapshots’ of
308 natural behavior that were possible with the available technology; i.e., high-resolution dive data
309 that could only be stored for short periods of time. BLA green turtles tend to move among
310 multiple activity centers within large home ranges over the course of several days (Seminoff et
311 al. 2002a, Seminoff and Jones 2006), so the inter-individual patterns of active *versus* resting
312 behaviors in this study reflect brief segments of these multi-day circuits that turtles tend to
313 undertake. Where turtles were tracked relative to their individual foraging circuits within BLA
314 explains both the inter-individual variation in resting bout duration and depths as well as the fact
315 that six of 18 instrumented turtles showed no resting bouts during their deployments. However,
316 the absence of resting bouts for these six turtles does not imply that no resting occurred; rather, it
317 is likely an artifact of the conservative definition of ‘resting bout’ we used to identify resting
318 behavior. For example, analysis of simultaneously recorded dive data and video footage of BLA
319 green turtles confirmed that resting also occurs during single extended dives or in water ≤ 2 m
320 (Seminoff et al. 2006), both of which are excluded in the current analysis. As such, it is possible
321 that **the mean resting depth reported here** (10.8 ± 2.6 m) is an overestimate. However,
322 considering that green turtle diving and resting depths are shaped by local conditions (Okuyama
323 et al. 2013, Hart et al. 2016), and that BLA is a deep-water basin (~ 50 -m maximum depth) with
324 sparse shallow-water habitat, it is reasonable to believe that green turtles do not spend significant
325 periods in areas with water depths < 2 m. In support, local tracking efforts show that green turtle
326 home ranges and activity hotspots in BLA tended to be in waters ≥ 10 -m deep (Seminoff et al.
327 2002a). Nevertheless, we encourage additional green turtle tracking efforts that simultaneously
328 record time at depth to further clarify the potential for resting in shallow, nearshore habitats of
329 BLA.

330 Considering the challenges of inferring an individual’s underwater behavior from dive
331 profiles that have been described previously (Seminoff et al. 2006, Hagihara et al. 2011), the
332 pairing in this study of human- and machine-based dive evaluation using conservative criteria
333 minimized these potential errors. Furthermore, as deployment duration increased, total amount of
334 time resting as well as average resting bout duration increased (Table 2). For example, turtles
335 that only performed short resting bouts in shallow waters also tended to have shorter deployment
336 periods than turtles with wider ranges of resting bout durations and depths. Thus, longer
337 deployments likely captured greater proportions of turtles’ foraging circuits within BLA, which

338 included more variation in characteristics of habitats visited (e.g. bathymetry, food availability).
339 However, the potential effect of capture stress cannot be ruled out (e.g., Thomson and Heithaus
340 2013).

341 Tradeoffs between fine-scale resolution of behavioral observations and overall duration
342 of observation periods is a common challenge in animal tracking studies (Ropert-Coudert et al.
343 2009, Rutz and Hays 2009). Regardless, granular analyses of natural animal behaviors outweigh
344 the limited observation periods when the insights gained from such analyses shed new light on
345 behaviors that are otherwise inferred (i.e. not directly observed) across multiple, non-continuous
346 time-steps, as is typically the case with satellite tracking data (Block et al. 2005, Ropert-Coudert
347 et al. 2009, Rutz and Hays 2009). Fortunately, technology currently available for tracking free-
348 ranging animals allows researchers to record multiple types of information that, when analyzed
349 together, can provide a fuller, richer motion picture of how animals behave in their natural
350 environments (Seminoff et al. 2006, Ropert-Coudert et al. 2009, Wallace et al. 2015).

351

352 *Comparison of behavior and life history among green turtle populations, including BLA*

353 Our synthesis of data on green turtle activities and vital rates show that BLA green turtles
354 appear to be distinct in several ways from their counterparts around the world (Table 3). Green
355 turtles in BLA—a foraging area with patchy resource distribution and marked seasonality in
356 water temperatures (Seminoff et al. 2003, Álvarez-Borrego 2007)—have larger home ranges
357 (409–3231 ha, Seminoff et al. 2002), are more active (i.e., higher proportion of submerged time
358 performing active behaviors), and conversely rest for shorter periods (17.6% of measured dive
359 time) and at deeper depths (mean resting depth = 10.8 m ± 2.6 m) compared to green turtles in
360 other parts of the world (Table 3). In several other locations, immature green turtles maintain
361 small home ranges (10s to 100s of hectares [e.g. Hazel et al. 2013]), and forage in shallow waters
362 (generally much less than 8 m [e.g. Makowski et al. 2006, Hart et al. 2016]), while annual
363 temperature fluctuations are relatively small (e.g. Ballorain et al. 2013) (Table 3). In turn,
364 average growth rates of BLA green turtles are generally lower than those of other green turtles at
365 several locations (Australia: Limpus and Chaloupka 1997; Florida: Zug and Glor 1998; Hawaii:
366 Zug et al. 2002; Bahamas: Bjorndal et al. 2000; Peru: Velez-Zuazo et al. 2014). In addition, the
367 EP green turtle subpopulation mature at the smallest body sizes of any green turtle subpopulation
368 in the world (Table 3; Hirth 1997). Taken together, these patterns suggest that BLA green turtles

369 must move farther distances more frequently to access patchy food resources, often in deeper
370 waters and cooler temperatures, which limits their time spent resting and assimilating and
371 allocating acquired resources to somatic growth. Consequently, environmental limitations (e.g.,
372 low water temperature, limited activity season) on resource acquisition and assimilation might
373 constrain growth trajectories of BLA green turtles, resulting in smaller maximum body sizes
374 compared to green turtles in other areas.

375 Variation in sea turtle life history traits such as growth rates and reproductive output have
376 been linked to quality and availability of resources in foraging areas (e.g., Zug and Glor 1998,
377 Bjorndal et al. 2000, Saba et al. 2008). For example, faster growth rates have been reported for
378 green turtles in Atlantic Ocean/Caribbean Sea locations compared to Pacific locations, which
379 some authors linked to variation in available food resources (Zug and Glor 1998, Chaloupka and
380 Limpus 2004). Seminoff et al. (2002b) also highlighted that growth rates of BLA green turtles
381 were lower than Atlantic green turtle growth rates, but were higher than growth rates of green
382 turtles in the Galápagos Islands, which support foraging as well as reproduction of EP green
383 turtles (Zárate et al. 2015). Because most turtles in the present study were large immature or
384 adult turtles, it is understandable that their growth rates are lesser than those for small juveniles
385 due to predictable decreases in growth rate with size (Ramirez et al. 2021). Nevertheless, BLA
386 green turtles of the size class most consistent with the turtles in this study (70–80 cm SCL) still
387 had a slower growth rate ($1.2 \pm 0.65 \text{ cm yr}^{-1}$, Seminoff et al. 2002b) as compared to green turtles
388 of the same size class in Florida USA ($2.2 \pm 1.1 \text{ cm yr}^{-1}$, Mendonca 1981). It would be
389 informative to conduct a systematic analysis of somatic growth rates in the context of foraging
390 habitat type, turtle movements, and dive patterns to explore the potential influence of extrinsic
391 factors and behavior on green turtle demography.

392 The patterns we report here for green turtles reflect a broader biogeographic pattern in
393 intraspecific life history variation in the Eastern Pacific Ocean region compared to other ocean
394 basins that has been documented for taxa at multiple trophic levels, including sea turtles (Suryan
395 et al. 2009, Seminoff et al. 2012). In particular, the EP region has been characterized by high
396 variability in environmental conditions over both ecological and geological time periods, which
397 has led to cycles of contractions and expansions of sea turtle populations over time (Bowen and
398 Karl 2007). These environmentally driven cycles have appeared to manifest in novel life history
399 traits in EP sea turtle populations compared to their conspecifics in other regions (Saba et al.

400 2008, Gaos et al. 2012, Jones and Seminoff 2013). For example, EP leatherback sea turtle
401 (*Dermochelys coriacea*) foraging areas tend to have more highly variable and overall lower
402 productivity than foraging areas for leatherbacks in other regions, resulting in reduced breeding
403 probabilities, smaller body sizes, lower reproductive outputs, and negative population trends for
404 EP leatherbacks compared to conspecifics (Saba et al. 2008, Wallace and Saba 2009, Wallace
405 and Jones 2015, Wallace et al. 2018). Likewise, EP hawksbill sea turtles (*Eretmochelys*
406 *imbricata*) were thought to be regional extirpated, but a small regional population persists across
407 ~2,000 km of sheltered coastal and inshore habitats including mangrove estuaries, in contrast to
408 tropical coral reef systems typically occupied by hawksbills in other regions of the world (Gaos
409 et al. 2012; 2017). These examples indicate that the EP region provides marginal habitat for
410 multiple sea turtle species that are sufficient for populations to exist, but appear to be suboptimal
411 for achieving life history traits considered more typical for these species (Zug and Glor 1998,
412 Seminoff et al. 2002, Saba et al. 2008; Wallace and Saba 2009, Gaos et al. 2012; 2017).

413 We acknowledge that our data compilation does not demonstrate causative, mechanistic
414 relationships between activity patterns and life history traits. In-depth analysis of environmental
415 factors, resource distribution and quality, and bioenergetics would help to draw more definitive
416 conclusions. Nonetheless, available data for several green turtle populations around the world
417 indicate that: 1) green turtles in BLA show increased activity over larger areas, likely to achieve
418 resource acquisition requirements (Seminoff et al. 2002a); 2) they must do so in a location
419 characterized by fewer, smaller shallow-water foraging areas and limited periods of favorable
420 environmental periods (Seminoff et al. 2003), which; 3) reduces their opportunities to garner
421 energetic benefits of extended resting bouts (this study), and; 4) this tradeoff between increased
422 activity at the expense of resting could influence vital rates such as somatic growth and size- and
423 age-at-maturity (Table 3).

424

425 *Conclusions*

426 Our study ties together multiple threads of research to connect fine-scale behavior,
427 habitat characteristics, and their potential influence on life history of the regional population.
428 We relied on previously defined characteristics of green turtle resting dive behavior obtained by
429 a combination of TDR and video data (Seminoff et al. 2006) to quantify fine-scale patterns of
430 resting bouts across multiple years at an important foraging area for a depleted sea turtle

431 population. Collective patterns of resting behaviors exhibited by green turtles over several years
432 at BLA show that, during the summer, when water temperatures are more favorable to green
433 turtle physiological performance, turtles maximize activity to search for and acquire resources
434 across larger areas than green turtles in other locations characterized by more readily available
435 resources in more favorable conditions. This increased activity occurs at the expense of resting,
436 which likely reduces efficient assimilation of acquired resources into somatic growth demands
437 (Table 3). Consequently, BLA green turtles tend to grow more slowly and reach sexual maturity
438 at smaller body sizes than green turtles in other areas. These findings reflect the uniqueness of
439 sea turtle habitats and populations in the EP.

440 In addition, BLA's foraging habitat is not only critical to EP green turtle population
441 dynamics, but also contributes to the vulnerability of green turtles to human pressures from
442 increasing tourism, vessel traffic, harvest for consumption, and incidental capture by fisheries
443 throughout BLA (Seminoff et al. 2003; 2008). Because turtles travel large distances and are
444 actively foraging > 80% of the time they are submerged to access patchy marine algae pastures
445 scattered around BLA (Seminoff and Jones 2006, Seminoff et al. 2002a; 2006), they are likely
446 more susceptible to interactions with humans in the water for ecotourism, as well as with local
447 artisanal set-net fisheries gear soaking throughout shallow coastal margins of BLA during
448 summer months (Table 3). BLA area hosts a small-scale artisanal fleet of *ca.* 30 outboard skiffs
449 that uses bottom-set gillnets to target a variety of finfish species (Danemann et al. 2007).
450 Interactions between fishing gear and sea turtles is commonplace in BLA (Seminoff et al. 2003),
451 and has worsened in recent years due to the influx of illegal fishing for totoaba (*Totoaba*
452 *macdonaldi*). Thus, local conservation efforts must scale to broad—rather than discrete—areas
453 of BLA to adequately address threats to turtles.

454

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467

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Table 1. Individual capture data: Turtle ID Bahía de los Angeles (BLA) and individual turtle number, straight carapace length (SCL), mass, maturity status / sex (I = immature, F = adult female, M = adult male; all assignments are putative; see Methods for maturity status / sex assignment criteria), capture location (see Fig. 2), start and end dates of data recording, and whether turtles performed resting bouts during the deployment.

Turtle ID	SCL (cm)	Mass (kg)	Maturity Status / Sex	Capture/Release Locality	Start Date	Stop Date	Data recording duration (hours/min)	Resting bouts during deployment (Y/N)
BLA 407	92.5	101.4	F	3. El Bajo	25 June 99	26 June 99	21 / 02	Y
BLA 408	87.0	84.0	F	3. El Bajo	28 June 99	9 July 99	271 / 55	Y
BLA 314	72.1	49.9	I	3. El Bajo	2 July 99	9 July 99	124 / 11	Y
BLA 410	78.0	57.6	F	3. El Bajo	11 July 99	12 July 99	25 / 38	N
BLA 411	77.4	62.7	F	6. Playa Blanca	14 July 99	15 July 99	19 / 32	N
BLA 604	70.0	49.9	I	1. El Barco	29 June 01	22 June 01	47 / 30	Y
BLA 605	59.1	29.0	I	2. La Silica	25 June 01	27 June 01	42 / 33	N
BLA 607	63.4	-	I	5. Ped Blanca	3 July 01	4 July 01	26 / 10	N
BLA 609	70.5	52.2	I	3. El Bajo	9 July 01	11 July 01	45 / 25	Y
BLA 615	62.7	33.1	I	1. El Barco	26 July 01	28 July 01	53 / 52	N
BLA 616	64.5	35.4	I	1. El Barco	28 July 01	30 July 01	41 / 01	Y
BLA 704	75.5	55.9	I	6. Playa Blanca	15 June 02	19 June 02	86 / 33	Y
BLA 707	57.5	27.2	I	1. El Barco	19 June 02	20 June 02	09 / 54	Y
BLA 709	68.5	49.9	I	1. El Barco	30 June 02	2 July 02	38 / 51	Y
BLA 711	84.4	68.0	M	1. El Barco	2 July 02	6 July 02	91 / 01	Y
BLA 715	65.2	37.2	I	4. El Cardon	20 July 02	21 July 02	28 / 34	N
BLA 716	73.0	47.6	I	6. Playa Blanca	22 July 02	24 July 02	43 / 24	Y
BLA 717	64.5	38.6	I	6. Playa Blanca	26 July 02	29 July 02	69 / 58	Y

Table 2. Summary of resting behaviors for 12 green turtles at Bahía de Los Angeles, Baja California, Mexico.

TURTLE ID	total deployment time (hours)	number resting dive bouts	Total resting time (hours)	proportion resting time / deployment time	resting time/24 hr	Dive duration (min)	Dive duration range (min)	Bottom depth (m)	Bottom depth range (m)
BLA 314	124.2	19	5.7	0.05	1.1	17.9 ± 4.5	6.3 – 28.0	20.0 ± 4.5	14.5 – 28.5
BLA 407	21.0	34	8.3	0.39	9.5	14.7 ± 4.0	5.0 – 21.5	3.7 ± 0.9	2.5 – 6.9
BLA 408	271.9	305	63.7	0.23	5.6	12.5 ± 5.2	4.3 – 30.5	7.9 ± 6.4	2.0 – 44.4
BLA 604	47.5	20	3.5	0.07	1.7	10.4 ± 3.0	4.3 – 15.7	7.3 ± 0.9	5.5 – 8.8
BLA 609	45.4	24	7.5	0.17	4.0	18.9 ± 5.1	5.3 – 26.7	10.5 ± 5.5	6.9 – 24.2
BLA 616	41.0	8	3.4	0.08	2.0	25.4 ± 8.7	9.2 – 33.0	10.8 ± 2.8	7.0 – 13.9
BLA 704	86.6	83	31.4	0.36	8.7	22.7 ± 3.7	4.3 – 30.5	9.7 ± 1.2	7.4 – 12.6
BLA 707	9.9	31	3.0	0.30	7.2	5.7 ± 1.1	4.1 – 8.3	5.0 ± 0.4	4.3 – 5.5
BLA 709	38.9	14	6.4	0.16	3.9	27.3 ± 3.7	21.6 – 32.6	13.7 ± 1.1	12.0 – 16.0
BLA 711	91.0	27	10.3	0.11	2.7	23.0 ± 5.3	14.8 – 36.5	9.3 ± 2.0	4.6 – 14.4
BLA 716	43.4	45	14.8	0.34	8.2	31.7 ± 6.3	9.2 – 44.8	19.7 ± 3.4	7.1 – 27.2
BLA 717	70.0	27	5.3	0.08	1.8	11.8 ± 3.7	5.1 – 19.3	12.7 ± 1.7	10.4 – 16.8

Table 3. Comparison of resting dive behaviors, home ranges, ambient temperatures and life history traits among green turtle foraging areas around the world. Data on resting behaviors were included only if the original source specifically described as resting behaviors, unless otherwise noted; several studies reported implied resting behavior (i.e., fewer, longer, deeper dives at night than during the day). Growth rate data included if original studies provided average size-specific growth rates. Size at maturity typically reported as mean size of adult females observed on nesting beaches. ^ Combines times spent in both 'shallow' (<2m) and 'deep' (> 2m) resting behaviors as described by the authors of the original papers; * adult females during internesting periods, other studies are in foraging areas, and mostly immature animals; ** % of time spent submerged in summer and winter.

Location	size class (SCL, cm)	% resting time	average resting bout duration (min)	average resting depth (m)	home range (ha)	annual temp. range (°C)	growth rate (cm/yr)	size at maturity (SCL, cm)	Reference(s)
<u>East Pacific Ocean</u>									
BLA, Mexico	57.5 – 92.5	16.4% ± 11.0%*	18.5 ± 7.8*	10.8 ± 2.6*	1,662 ± 323	14.5 – 30.0	1.4 ± 0.9	mean: 77.3	* = this study; Seminoff et al. 2002a; 2003; 2006; Seminoff and Jones 2006; Figueroa et al. 1993
4 sites on Baja California Peninsula, Mexico	30 – 95.5	-	-	-	-	-	2.3 ± 1.4	-	López Castro et al. 2010
Orange County, California, USA	50.8 – 74.3	12.1% of day 32.0% of night	-	-	2.4 – 4.6	-	-	-	Crear et al. 2017
San Diego Bay, California, USA	85 ± 17.3	-	-	-	-	-	1.03	-	Eguchi et al. 2014

Location	size class (SCL, cm)	% resting time	average resting bout duration (min)	average resting depth (m)	home range (ha)	annual temp. range (°C)	growth rate (cm/yr)	size at maturity (SCL, cm)	Reference(s)
Galapagos, Ecuador	40 – 90	-	-	-	-	-	0.4 – 0.11	-	Green 1983; Zarate et al. 2015
El Niño, Peru	43.7 – 101.1	-	-	-	-	-	2.8 ± 1.5	-	Velez-Zuazo et al. 2014
<u>Central Pacific Ocean</u>									
Hawaiian Islands	30 – 90	-	-	-	-	-	2.0 – 2.5	mean: 92 (86 – 106)	Zug et al. 2002
Kaneohe Bay, Oahu, Hawaii	mean: 51.3	-	-	-	262 ± 96	-	-	-	Brill et al. 1995
<u>North Atlantic/Caribbean Sea</u>									
Palm Beach, Florida, USA	27.9 – 48.1	-	-	5.2 – 6.2#	238 ± 178	-	-	-	Makowski et al. 2006
Indian River Lagoon, Florida, USA	28 – 74	-	-	-	-	-	3.0 - 5.2	-	Zug and Glor 1998
Mosquito Lagoon, Florida, USA	mean: < 65.0	-	-	-	288 ± 146	-	-	-	Mendonca 1983
Dry Tortugas, Florida, USA	41.1 ± 7.7	25% of day^ 90% of night	-	0.3 – 12.5#	-	-	-	-	Hart et al. 2016

Location	size class (SCL, cm)	% resting time	average resting bout duration (min)	average resting depth (m)	home range (ha)	annual temp. range (°C)	growth rate (cm/yr)	size at maturity (SCL, cm)	Reference(s)
South Padre Island, Texas, USA	mean: 34.5	-	-	-	77 ± 90	-	-	--	Renaud et al. 1995
Grand Cayman	48.9 ± 4.4	-	-	0.9 – 12.4#	-	-	4.1 ± 2.2	-	Blumenthal et al. 2010
Union Creek, Bahamas	25.3 – 82.3	-	-	-	-	-	4.2	> 95	Bjorndal et al. 2000
<u>South Atlantic</u>									
Ascension Island	103.0 – 121.2*	31.7% – 67.5%	two turtles: 28.6 ± 13.2 36.0 ± 11.7	12.1 ± 5.2 14.3 ± 3.6	-	-	-	-	Hays et al. 2000
<u>Southwest Indian Ocean</u>									
Mayotte	79.9 – 98.2	81% – 90%**	31.9 – 69.9	8.9 – 11.6	-	25.7 – 29.3	-	-	Ballorain et al. 2013
<u>Northwest Pacific</u>									
Japan	49.2 – 79.5	69%	-	8.9 ± 3.8	54 – 354	-	-	-	Okuyama et al. 2013
<u>Southwest Pacific Ocean</u>									
Low Isles, Australia	65.5 – 80.6	-	-	-	47 – 104	-	-	-	Hazel et al. 2013

Location	size class (SCL, cm)	% resting time	average resting bout duration (min)	average resting depth (m)	home range (ha)	annual temp. range (°C)	growth rate (cm/yr)	size at maturity (SCL, cm)	Reference(s)
Moreton Bay, Australia	45.1 – 111.7	-	~20 – ~120	2.8 – 7.9	660 ± 294	13.8 – 30.3	-	-	Hazel 2009; Hazel et al. 2009
Repulse Bay, Australia	mean: 105.4	-	-	-	315 ± 272	-	-	-	Whiting and Miller 1998
southern Great Barrier Reef, Australia	36 – 110	-	-	-	-	-	max at 2.1 (at ~56 SCL)	89.5	Limpus and Chaloupka 1997

Figure Captions

Figure 1. Generalized profiles for the six dive types as defined by Seminoff et al. (2006)

Figure 2. Map of Bahía de los Angeles study area along the eastern coast of the Baja California Peninsula, Mexico (inset); 10 m bathymetric contours represented by dashed lines; Capture sites: 1. El Barco, 2. La Silica, 3. El Bajo, 4. El Cardon, 5. Pedregal de la Blanca and 6. Playa Blanca.

Figure 3. Dive depth vs. dive duration for (A) all non-resting dives by all turtles ($R^2=0.26$, slope = 0.72) and (B) all resting dives by all turtles ($R^2=0.31$, slope = 0.43)

Figure 4. Depth versus duration of resting bouts for (A) each individual turtle ($n=12$), and (B) average dive depth vs. dive duration for all resting dives by each individual turtle ± 1 standard deviation ($R^2=0.36$)

Figure 1

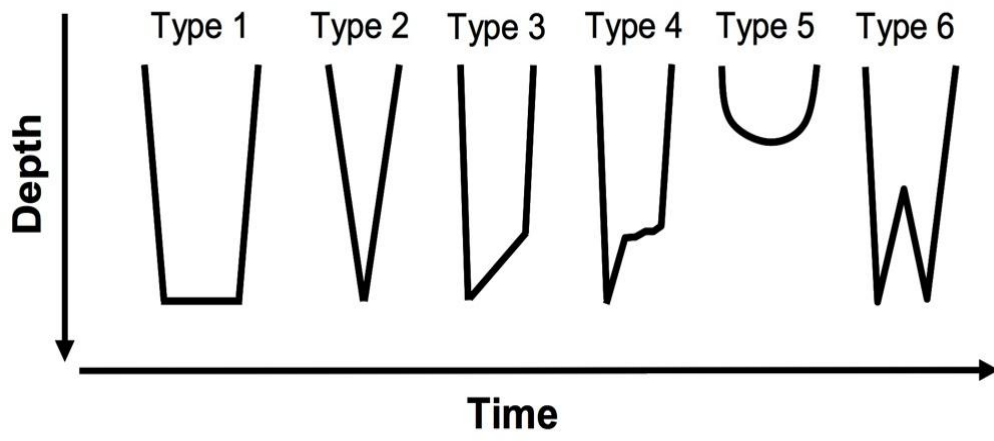


Figure 2

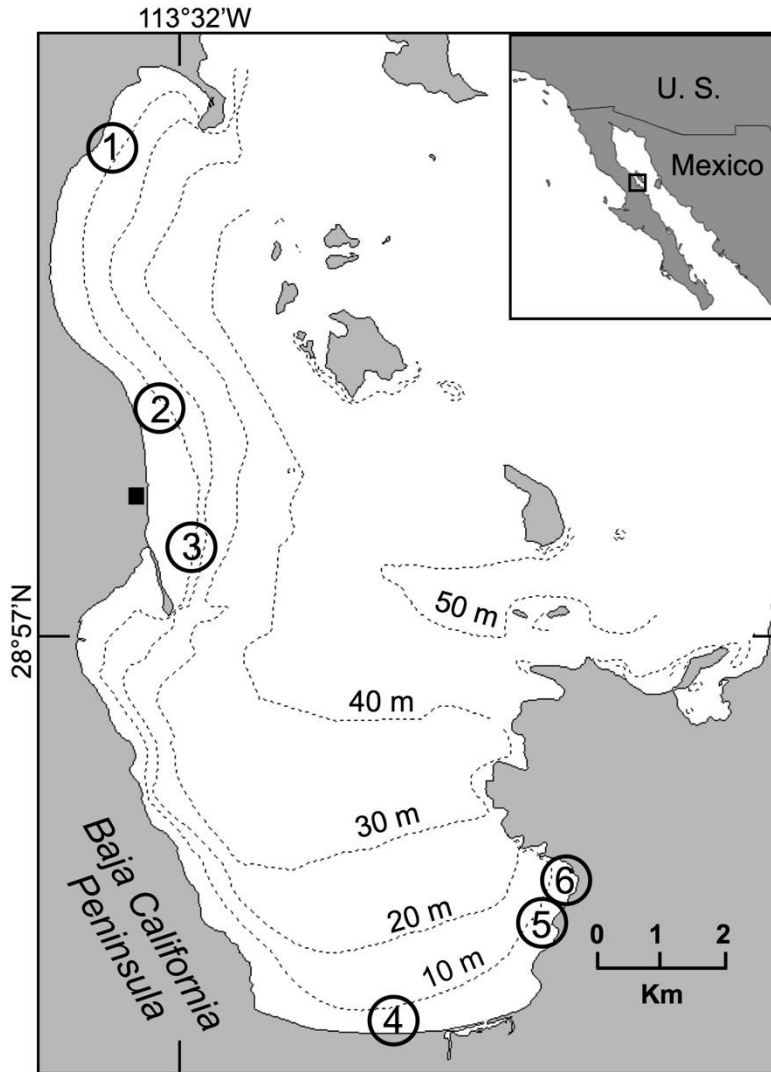


Figure 3

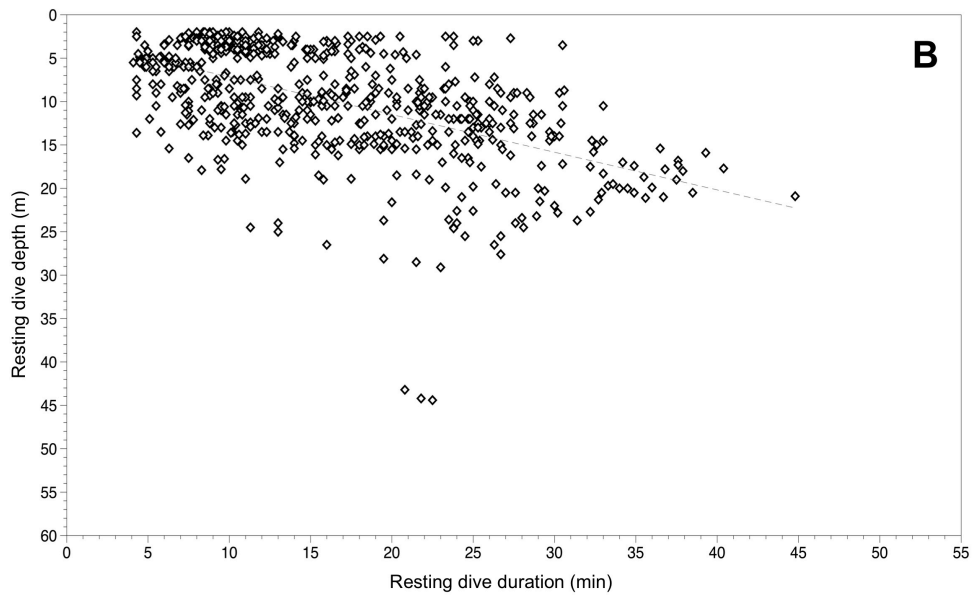
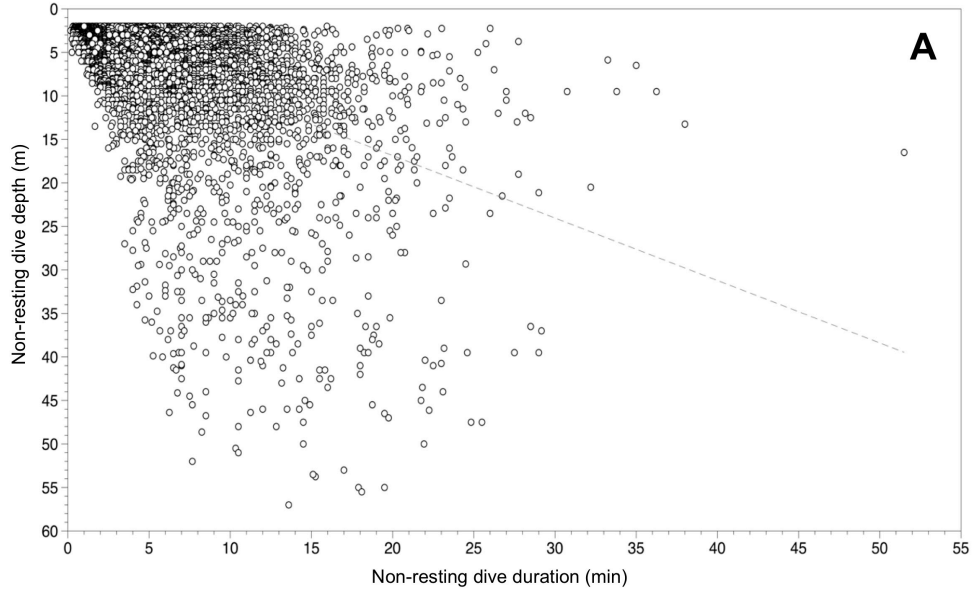


Figure 4

