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Changes in ocean conditions and hurricanes affect porbeagle *Lamna nasus* diving behavior

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ABSTRACT: Recovered archival satellite tags afford a rare opportunity to evaluate diving behavior relative to ocean conditions at fine spatiotemporal scales. Ocean temperature and mixed layer depth (MLD) were strongly related to daily and seasonal patterns in diving behavior of an adult female porbeagle shark *Lamna nasus*. The shark remained below MLD when waters were strongly stratified in summer or in the Gulf Stream; the daily timing of dives was associated with local sunrise and sunset. In the presence of a hurricane, diving activity abruptly increased, coincident with upwelling causing an abrupt decrease in surface temperature. Our first report of the behavioral response to a hurricane as well as the seasonal patterns in depths, occupied temperatures, and vertical speeds suggest environmental preferences of porbeagle are not static and individuals may use horizontal, as well as vertical, movement to take advantage of areas with specific characteristics.

KEY WORDS: Ocean conditions · Hurricanes · Porbeagle · Diving behavior

1. INTRODUCTION

Understanding porbeagle *Lamna nasus* behavior in relation to ocean conditions is important to predict responses of this at-risk shark to climate change. Their primary habitats in the Gulf of Maine (GOM) and Scotian Shelf (SS) (Fig. 1; Campana et al. 2010) are in the confluence zone of the North Atlantic's subtropical and subpolar gyres, an area that has undergone significant warming over the past half century (Greenan et al. 2019). Habitat loss (Hazen et al. 2013) may result from shifting temperatures given the limited thermal tolerance of porbeagle (Campana & Joyce 2004). To support future species distribution modeling (e.g. Rogers et al. 2019), correlating dive behavior with oceanographic or atmospheric variation may help elucidate relevant environmental predictors.

Archival satellite tagging has revolutionized what is known about the spatial ecology of pelagic sharks (e.g. Haulsee et al. 2018), and porbeagle exhibit high temporal and spatial variability in dive characteristics (Pade et al. 2009, Francis et al. 2015). However, the temporal resolution of typical satellite tag transmissions can obscure immediate behavioral responses to proximate ocean conditions. Data are summarized over multiple hours (up to 24) when transmitting over the ARGO system, while recovered tags store information at 10 s intervals for the entire deployment duration (Wildlife Computers). Recovered tags afford a rare opportunity to evaluate diving behavior at fine spatiotemporal scales, which could improve our understanding of habitat use and likely behavioral responses to ocean variation and may ultimately contribute to protection of this species.

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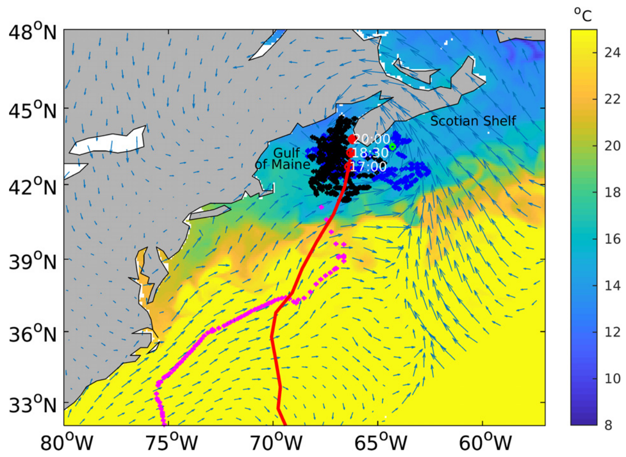

Fig. 1. Porbeagle movement track from July 6, 2008 to April 14, 2009, overlain with daily mean sea surface temperature (°C) and wind quivers at 20:00 h AST from Hurricane Kyle on September 28, 2008. The movement track is separated into 3 time periods to help show temporal changes in position. P1: blue (Jul 6–Oct 20, 2008); P2: black (Oct 21, 2008–Feb 25, 2009); P3: magenta (Feb 26–Apr 14, 2009). Solid red line: track of Hurricane Kyle; cluster of light green circles: locations of the shark between Sep 27 and 30, 2008. White text: time in h AST that the hurricane was at the adjacent point

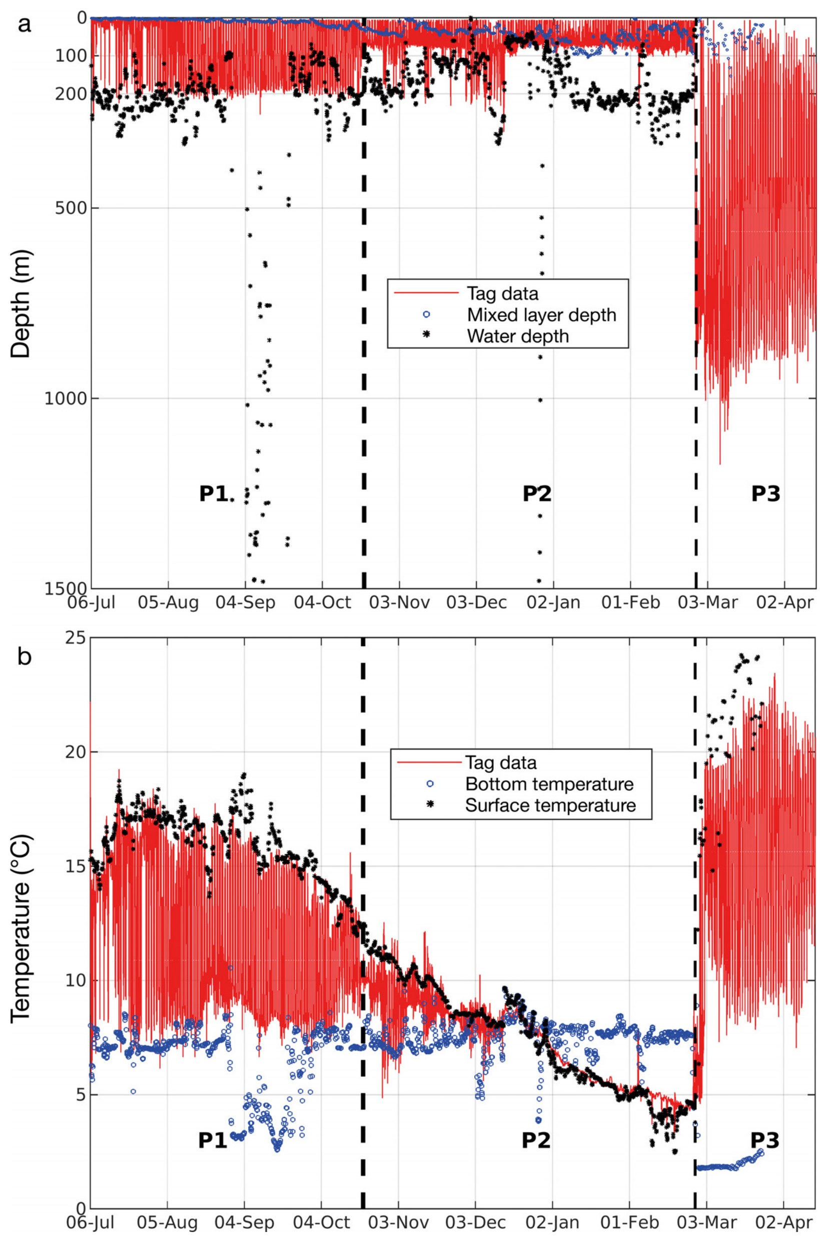

Fig. 2. (a) Time series of dive depth (red) relative to total water depth (black) and mixed layer depth (blue). (b) Time series of occupied temperatures (red) relative to sea-surface temperature (black) and bottom temperature (blue). P1: Jul 6–Oct 20, 2008; P2: Oct 21, 2008–Feb 25, 2009; P3: Feb 26–Apr 14, 2009

2. MATERIALS AND METHODS

The recovered satellite tag (Model Mk10; Wildlife Computers) was originally deployed on an adult female porbeagle shark *Lamna nasus* (217 cm fork length) on July 6, 2008 and recorded for 283 d (Text S1 in the Supplement at www.int-res.com/articles/suppl/m654p219_supp.pdf). Measurements of depth (resolution = 0.5 m ± 1.0%) and temperature (resolution 0.05 ± 0.1°C) were made every 10 s and stored in flash memory. Post-processing to estimate position from associated light level readings used the state-space model in GPE3 software (Wildlife Computers; Text S1). The number and quality of location estimates from light data decrease when a shark remains at depth (Francis et al. 2015, Braun et al. 2018), which reduced track resolution while offshore. Maximum likelihood position estimates were used to determine the timing of sunrise, sunset, and nautical twilight at the real-time location of the shark.

The shark spent most of the time near the surface or at depth, so the least-occupied intermediate depth was used as a threshold (92, 33.5, and 528.5 m for the 3 periods reported in Section 3) to identify dives. The depth time series was smoothed using a robust LOESS smoother (10 min smoothing window). The start and end times of a dive were defined as the nearest time points before and after the threshold depth for which the 5 min change in depth was smaller than 5 m in the raw (unsmoothed) data. The time difference between consecutive raw depth measurements was used to calculate vertical speed.

Daily sea surface temperature (SST) and bottom temperature (BT) data were obtained from GLORYS12V1 data product (Text S1). Daily mixed layer depth (MLD) was calculated from GLORYS12V1 temperature and salinity. The MLD represents the depth above which active turbulence has homogenized oceanic properties; temperature and salinity will be approximately constant within the mixed layer (Text S1; Fig. S1). Hurricane Kyle (Category 1) was the only hurricane that passed over the GOM and the SS in 2008 and provided a rare opportunity to examine behavioral response to a hurricane. The estimated track of hurricane Kyle was provided by the Hurricane Research Division of the Atlantic Oceanographic and Meteorological Laboratory (https://www.aoml.noaa.gov/hrd/data_sub/hurr2008.html), and 3 h wind came from the Canadian Meteorological Centre (https://weather.gc.ca/grib).

3. RESULTS

The shark exhibited 3 distinct periods of diving behavior: P1 (early July to October 20, 2008); P2 (October 21, 2008 to February 25, 2009); and P3 (February 26 to April 14, 2009, the end of the record) (Fig. 2). During both P1 and P2, the porbeagle *Lamna nasus* remained on the continental shelf, except for 2 forays offshore of the shelfbreak (Aug 30–Sep 26, 2008 and Dec 27–Dec 28, 2008). Dive patterns differed markedly in the 2 periods despite similar geographical locations. The shark remained between ~5–200 m depth in P1 and ~20–100 m in P2. Note that the shark often dove to the bottom in P1 but rarely did in P2 (Fig. 2a). When the shark moved off the continental shelf and into the Gulf Stream region in P3, occupied depths increased significantly to ~400–800 m (Fig. 2a). Occupied temperatures were highly variable in P1 (~7–15°C) yet had a decreasing range over time (Fig. 2b). The shark remained within a restricted temperature range in P2, and occupied waters were progressively colder (~9 dropping to ~4°C). In P3, variability as well as temperature suddenly increased to a large range (~10–20°C). Although occupied depths changed seasonally (Fig. 3a), a daily descent/ascent cycle was present in all 3 periods, with the shark occupying shallow warmer water during nighttime and colder deeper waters in daytime (Fig. 3b).

The shark tended to stay below the MLD in P1, when the ocean was well stratified and SST was high. In the beginning of P2 (October to early December), the MLD deepened due to cooling air temperatures and strong winds, which enhanced vertical mixing. The shark began to frequently ascend into the mixed layer (Fig. 2a). In the latter half of P2, the shark stayed completely within the mixed layer. When the shark entered the warm, salty Gulf Stream in P3, it stayed below the MLD, apparently diving deeper to reach colder water masses.

Diel dive behavior was strikingly different among P1, P2 and P3, yet all patterns were closely related to the timing of local sunrise and sunset (Fig. 4). In P1, multiple daytime dives were common in late July and early August, yet nighttime dives rarely occurred. The porbeagle tended to descend near sunrise and ascend progressively

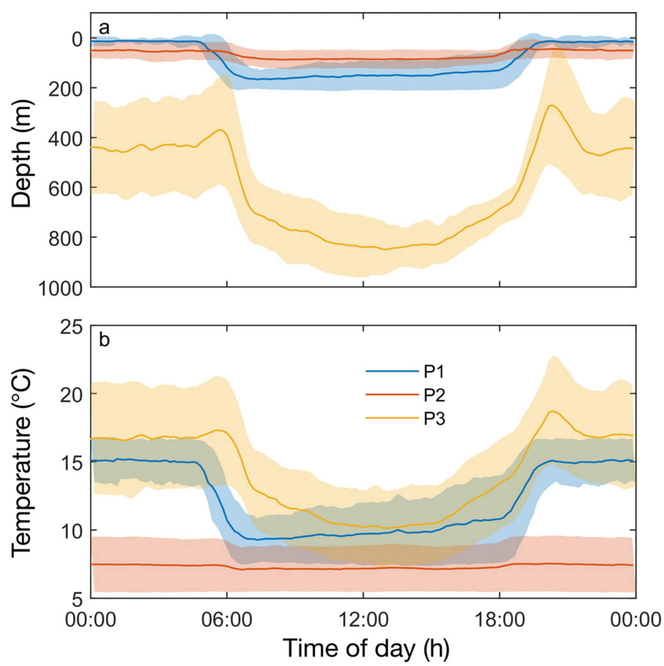

Fig. 3. Average (a) depth and (b) temperature versus time of day during P1 (July 6 to October 20, 2008), P2 (Oct 21, 2008–Feb 25, 2009) and P3 (Feb 26–Apr 14, 2009). Shading represents ± 1SD. These averages and SDs were computed by 10 min increments of time of day

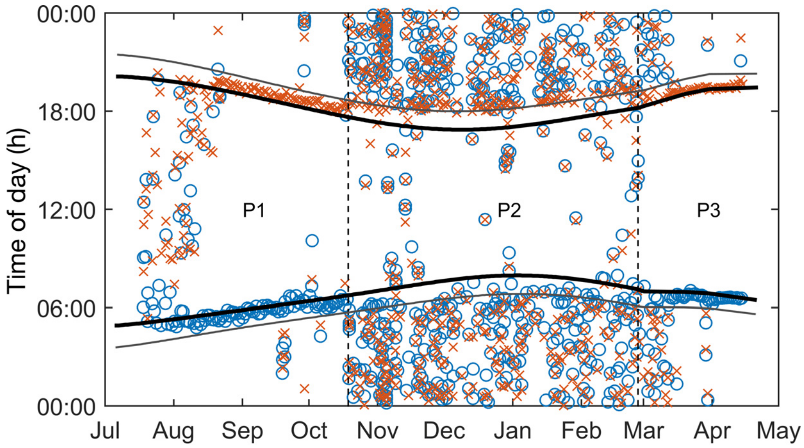

Fig. 4. Timing of dive descents and ascents relative to local time of sunrise and sunset. P1: Jul 6–Oct 20, 2008; P2: Oct 21, 2008–Feb 25, 2009; P3: Feb 26–April 14, 2009

later in the day. After mid-August, the porbeagle displayed a well-defined descent/ascent pattern, descending shortly before sunrise and ascending shortly after sunset, with almost no daytime excursions. In contrast, the shark regularly performed several nighttime dives in P2, with occasional irregularly timed daytime dives. These nighttime dives were bounded by twilights rather than sunrise and sunset (Fig. 4). In P3, frequent dives occurred exclusively during nighttime until mid-March, when a descent/ascent pattern established with a single descent shortly before sunrise and a single ascent shortly after sunset, similar to later in P1. Multiple descent/ascent cycles during nighttime were observed when temperature in the shelf waters cooled from October to February. The shark was very active at night during this period (Fig. 4).

Vertical speeds during descents and ascents were nearly symmetric (Fig. 5) and were slowest in P2. Maximum 1 min averaged speeds were 2.52 m s^{-1} on ascent and 3.12 m s^{-1} on descent. While in the GOM and SS, the warmer conditions in P1 were associated with faster vertical speeds as compared to P2 (Figs. 3 & 5). Although the shark undertook multiple dives during nighttime in P2, vertical speeds were slower. Conversely, daytime vertical speed was slower than nighttime speed when the shark was in the Gulf Stream in P3.

The porbeagle broke from its regular daily dive cycle when the hurricane was passing over, undertaking rapid descent/ascent cycles during a nighttime period when it had been habitually close to the surface (Figs. 4 & 6). Surface waters cooled by ~2°C when Hurricane Kyle passed over, consistent with the expected upwelling caused by cyclonic atmospheric systems (Zhu & Zhang 2006). Although temperature at depth also decreased, the shark dove to a similar depth (~180 m) as on its previous descent/ascent cycle. The increased dive frequency during the hurricane was transitory. Beginning at ~18:30 h AST, the shark ascended at the habitual time while seemingly in a region affected by the hurricane. Upon reaching the surface layer, it immediately dove to 120 m, and then immediately ascended again. It undertook several very shallow dives until 20:30 h when it returned to ~180 m, remaining for ~ 1 h, before undertaking 3 descent/ascent cycles in quick succession. From 01:00 h on September 29, it started to remain at the surface with occasional, shallow dives, and resumed regular dive activity by 06:30 h. Although dive frequency markedly increased when the shark was in the surface layer during the hurricane period, vertical speeds remained the same. Compared to the single nighttime ascents seen from mid-August to mid-October in P1 (Fig. 4; high resolution examples shown before and after the hurricane period in Fig. 6), the increased dive frequency was sufficiently uncommon to be attributable to the hurricane.

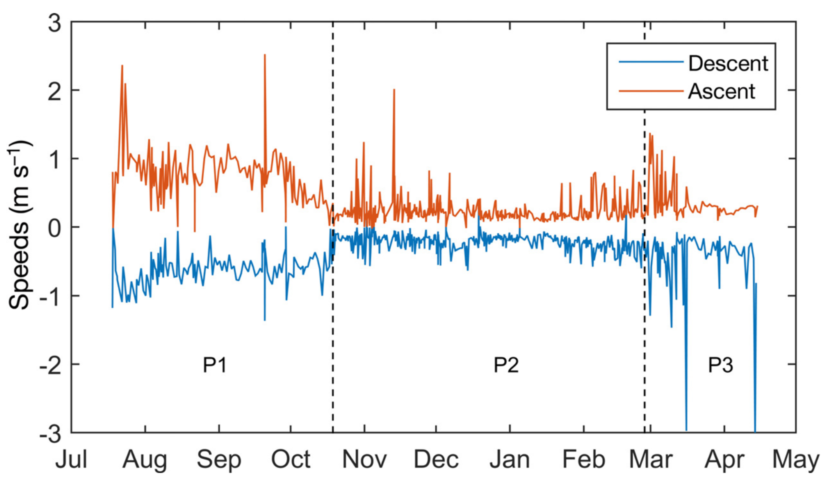

Fig. 5. Maximum 1 min vertical speeds for dive descents (blue) and ascents (orange). P1: Jul 6–Oct 20, 2008; P2: Oct 21, 2008–Feb 25, 2009; P3: Feb 26–April 14, 2009

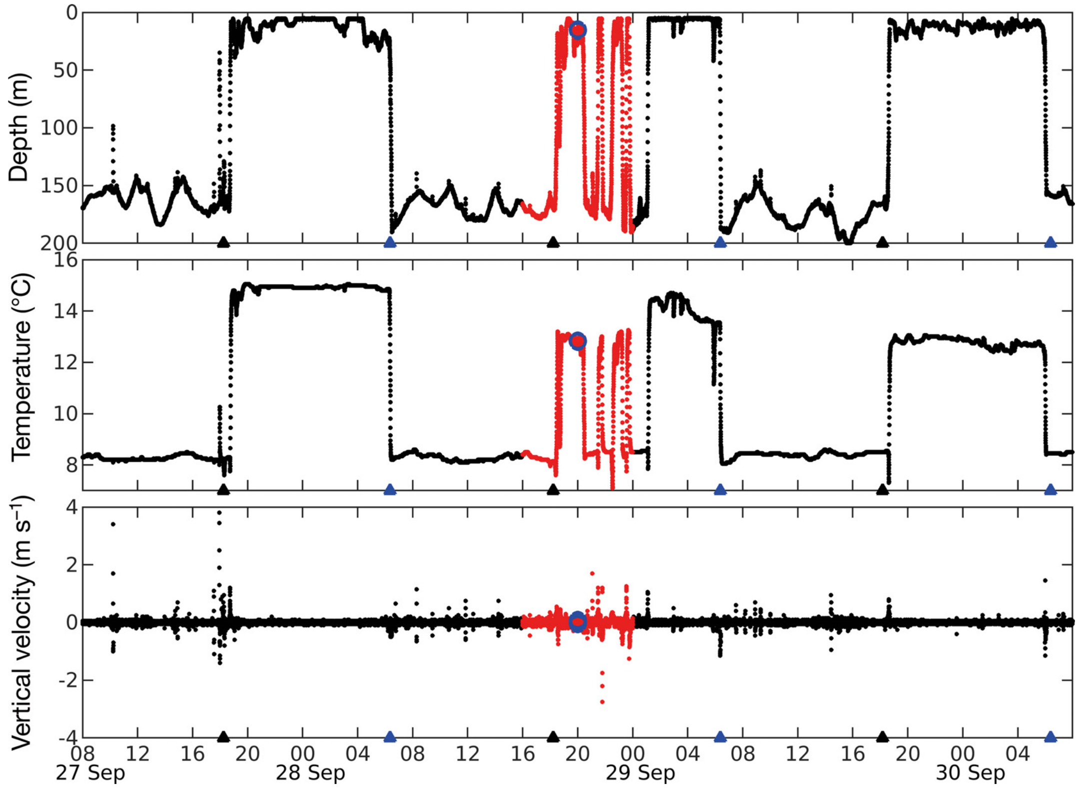

Fig. 6. Time series of depth (top), temperature (middle), and vertical velocity (bottom; positive on ascent) before, during (coloured segments) and after Hurricane Kyle. Sunrise (blue triangles) and sunset (black triangles) are given for reference. The blue circle at 20:00 h AST, September 28, 2008 indicates the time of the available wind data plotted in Fig. 1

4. DISCUSSION

The remarkable consistency in dive behavior exhibited at different periods for this female porbeagle shark *Lamna nasus* demonstrates a fine-tuned behavioral response to proximate ocean conditions (Pade et al. 2009, Campana et al. 2010, Francis et al. 2015). Seasonal patterns were separable relative to the depths and temperatures occupied, as were associated patterns in vertical speed and the timing of descents/ascents. As opposed to a static preferred temperature or depth range (Campana & Joyce 2004), this individual actively sought distinctly different oceanographic conditions throughout the year. In particular, dive depth was strongly related to the difference between SST and BT, as well as MLD while on the continental shelf. When the waters were strongly stratified due to high SST in P1, the shark tended to inhabit the top 200 m of the water column, below the MLD. As SST declined during the fall and into winter while BT showed little change, the shark remained in the upper ~100 m, mostly within the mixed layer in waters <10°C. The dive depths observed during P2 (Fig. 2a) demonstrate that the shark didn't merely change location to inhabit shallower water, and similar reductions in dive depths during winter have been observed in other pelagic species (Andrzejaczek et al. 2018). It seems counter-intuitive that the shark would restrict diving behavior to remain in the coldest part of the water column if diving was more energetically efficient than surface-oriented swimming (Watanabe et al. 2019). Alternately, high variability in dive frequency and timing has been hypothesized to result from foraging behavior (e.g. Cartamil et al. 2010). During the winter months in P2, dive variability increased as this shark undertook frequent shallow dives during nighttime (Fig. 4). Further research is required to determine the relative importance of energetics and/or predator–prey dynamics on diving behavior of porbeagle sharks.

The movement patterns in relation to MLD, ocean temperature and geographical location (GOM and SS to the Gulf Stream) strongly suggest that porbeagle exhibit spatiotemporal changes in habitat use and may use horizontal as well as vertical movement to take advantage of areas with specific characteristics (Kubisch et al. 2014). The shark's short-term response to Hurricane Kyle indicates that it was able to respond rapidly to a disturbance, albeit in a different way than the flight response previously observed for teleosts (Bailey & Secor 2016) and other elasmobranchs (Udyawer et al. 2013). The North Atlantic has been undergoing significant changes; in particular, there have been increases in SST (Loder & Wang 2015) and BT (Brickman et al. 2018) in the GOM and SS, and an increase in summertime stratification of shelf waters (Li et al. 2015). Our results suggest that these changes in temperature and MLD could affect porbeagle distribution. Future studies should pay careful attention to the timing of tagging and proximate ocean conditions, as both may influence the strength of association with oceanographic characteristics at the population level. Also, research incorporating oceanographic predictors into species distribution models (e.g. Rogers et al. 2019) may need to account for temporal changes in environmental preferences when trying to predict porbeagle distribution.

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