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BRIEF COMMUNICATION

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Observations of a species-record deep dive by a central Pacific female scalloped hammerhead shark (*Sphyrna lewini*)

James M. Anderson[1,2] | Patrick T. Rex[1] | Kelsey Maloney[2] | Mark Johnston[2] | Deron Verbeck[2] | Neil Allen[3] | Kim Holland[2]

[1]Department of Biology, California State University Long Beach, Long Beach, California, USA

[2]Hawaii Institute of Marine Biology, Kaneohe, Hawaii, USA

[3]Point Defiance Zoo and Aquarium, Tacoma, Washington, USA

Correspondence
James M. Anderson, Dept. of Biological Sciences – HSCI 1250 Bellflower Blvd. Long Beach, CA 90840
Email: james.anderson@csulb.edu

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Dr. Holly Reed Conservation Fund, Point Defiance Zoo Society

Abstract

A female scalloped hammerhead shark (*Sphyrna lewini*) conducted a species record deep dive to 1240 m in coastal-pelagic waters off Hawaii Island. This extends the deepest known depth range of the species by over 200 m (650 ft) and highlights the question of the extent to which deep-diving activity is mediated by physiological constraints, such as temperature and oxygen availability.

The scalloped hammerhead (*Sphyrna lewini*) is a large-bodied shark, known to occur in coastal, pelagic and semi-oceanic environments, with a circumglobal distribution in warm-temperate and tropical waters (Compagno, 2002; Gallagher & Klimley, 2018; Miller *et al*., 2013). Throughout their range, scalloped hammerheads are known to exploit a variable vertical habitat range, from the epipelagic (< 200 m) through mesopelagic (< 1000 m) depths (Bezerra *et al*., 2020; Diemer *et al*., 2011; Gallagher & Klimley, 2018; Harry *et al*., 2011; Jorgensen *et al*., 2009; Ketchum *et al*., 2014b; Klimley & Nelson, 1984; Nalesso *et al*., 2019) with the deepest recorded depth being 1042 m (Moore & Gates, 2015). This deep-diving behaviour likely facilitates exploitation of mesopelagic prey resources, such as cephalopods, which have been documented in the stomach contents of adult scalloped hammerheads in Hawaii, as well as other locations within the species' distribution (Clarke, 1971; Galván-Magaña *et al*., 2013; Vaske Júnior *et al*., 2009). The species is also known to show fidelity to (and aggregate seasonally around) seamounts and oceanic islands throughout its range (Aldana-Moreno *et al*., 2020; Bessudo *et al*., 2011a; Hoyos-Padilla *et al*., 2014; Ketchum *et al*., 2014b; Klimley & Nelson, 1984; Rojas *et al*., 2014). These aggregations and assemblages are often polarised/sexually segregated (Aldana-Moreno *et al*., 2020; Bessudo *et al*., 2011b; Drymon *et al*., 2020; Ketchum *et al*., 2014a; Klimley, 1987; Klimley & Nelson, 1984), but may also be heterogeneous (Torres-Rojas *et al*., 2006; pers. obs.). In Hawaii, female scalloped hammerheads are known to seasonally aggregate at locations along the leeward coast of Hawaii Island. As part of a study examining movement and space-use patterns of these aggregations, a pop-up archival satellite tag (miniPAT 348 k, Wildlife Computers Inc., Redmond, WA, USA) was deployed on a 274 cm individual in February 2020. The tag was physically recovered after a 180 day deployment period, allowing access to the full suite of archived temperature and depth data, which were measured with 5 s resolution.

In total, the shark undertook 1098 deep dives (≥ 500 m) across the tag deployment period. Maximum deep-dive depths ranged from 500 m (our nominal classification of a deep dive) to a species-record of 1240 m (4068 ft). With the exception 14 dives (one of them being the deepest dive recorded), no deep dives took place between 7 am and 5 pm (HST). Individual total dive durations ranged from 6 to

49 min, with a mean of 24 ± 8 min. Overall, deep dives were characterised by fast descent rates (3.8 ± 0.9 m s^{-1}) to the maximum depth, and slower ascents (0.81 ± 0.60 m s^{-1}), until the shark reached a transition point (inflection point) in the dive profile whereby the ascent rate slowed down to 0.30 ± 0.07 m s^{-1} (black arrows in Figure 1a–d,f). This behavioural transition point has also been identified as a feature of dive profiles in oceanic white tip sharks (*Carcharhinus longimanus*) when undertaking dives to mesopelagic depths (Howey *et al*., 2016). The function behind this feature is as-yet unclear, but may well represent the initiation of a physiological recovery period. Notably, the ascent rate following the transition point was remarkably consistent regardless of dive depth, or time at depth (mean = 0.299 m s^{-1} ± 0.061). Mean transition point occurrence was at 256 m depth (± 56.2), with a mean remaining ascent period of 5.54 (± 2.83) min.

On 24 July 2020, the shark initiated a deep dive to bathypelagic depths (> 1000 m) at approximately 08:07 am (HST), reaching a maximum depth of 1240 am (4068 ft), *c*. 1.6 times greater than the mean dive depth (Figure 1f). This dive followed a shallow period (time between initiation of current dive and end of previous dive) of 56 min, and followed a total of 12 deep dives over the course of the previous evening. Dive duration (from initiation to return to surface/shallow swimming) was 29 min, with a dive profile that best fit the "V" characteristics (Figure 1f). The shark initially descended to approximately 750 m depth, at a rate of *c*. 1.62 m s^{-1}, where it remained (including some minor vertical excursions) for approximately 2 min before a second distinct descent was initiated, descending an approximate 490 m further, at a rate of *c*. 1.42 m s^{-1}. Time at depth (time at max depth prior to initiating a distinct ascent) was *c*. 4 min. The shark then began an initial pronounced ascent at a rate of 0.10 m s^{-1} from 1223 m for 4.55 min, before increasing its ascent rate to 1.08 m s^{-1} at 1100.5 m, until it reached a depth of 386 m, the transition point at which ascent rate slowed down to *c*. 0.3 m s^{-1}. This ascent rate was maintained until the shark returned to its shallow swimming depth *c*. 5 min later. GPE3 estimation of the shark's location that day would suggest this activity occurred in the vicinity of the edge of the insular shelf, approximately 8.3 nautical miles south of South Point, Hawaii Island (white star in Figure 1e).

Spaet *et al*. (2017) characterised the dive profiles of a deep-diving scalloped hammerhead shark based on time spent at deepest depths. Dive profiles were classed as "V" dives (immediate ascent after

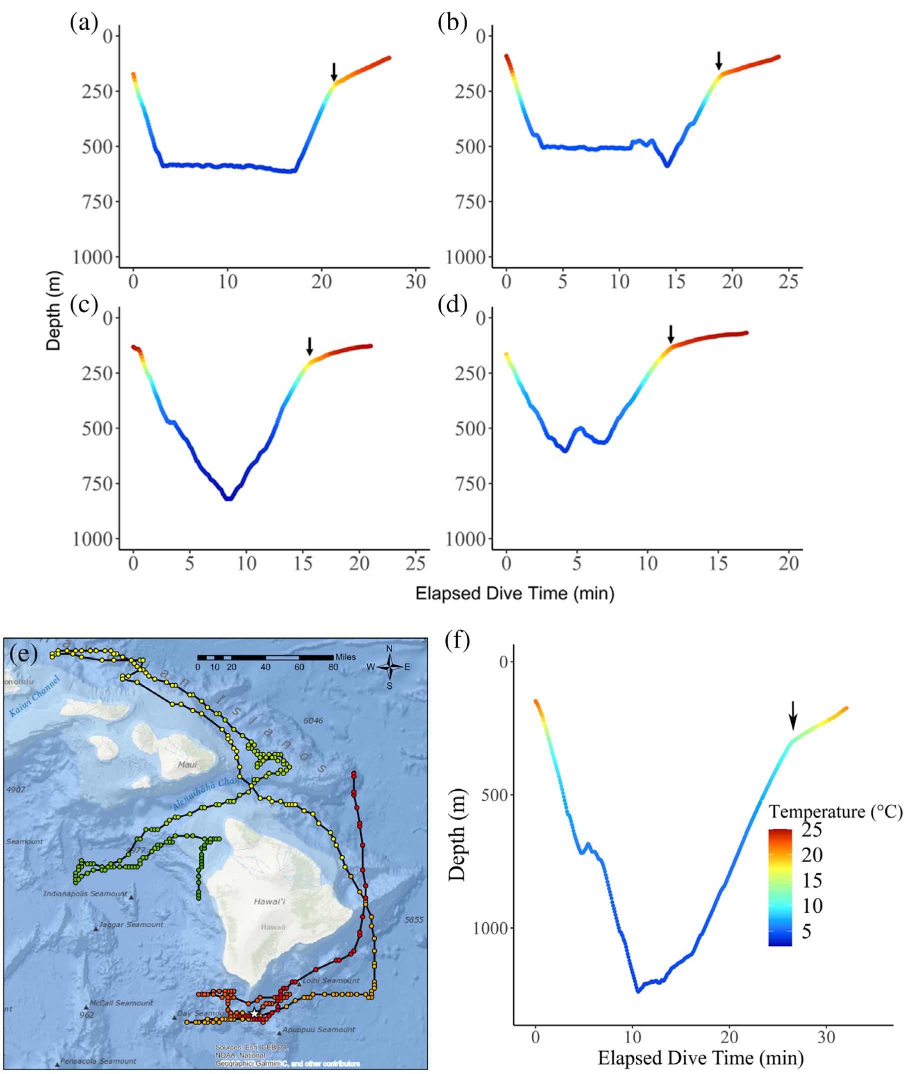

FIGURE 1 (a–d) Characteristics of the four observed dive profile classifications: (a) U dive, (b) Uv dive, (c) V dive, (d) W dive. Black arrows show ascent rate transition point initiation. (e) Reconstruction of horizontal movements (track) based on maximum likelihood estimates (MLE) derived from light-geolocation estimates. Coloured points (green through red) transition sequentially from day of tagging to day of tag release. White star marks MLE location of the deepest dive. (f) Dive profile of deepest recorded dive

reaching max. depth), "U" dives (characterised by long periods at max depth) and "Uv" dives (extended bottom times with one or more vertical excursions during the ascent phase of the dive). Analysis of dive profiles exhibited by the shark in this study revealed four broad classes of diving behaviour: three classes that follow those described by Spaet *et al.* (2017) (Figure 1a–c) and a fourth class, which is referred to as a "W" dive (Figure 1d). "W" dives were characterised by an extended period at depth, punctuated with a pronounced departure and return to the same approximate depth (Figure 1d). The authors postulate that the identification of this fourth dive profile is likely facilitated by the higher sampling rate of the miniPAT used in this study, compared with that in the Spaet *et al.* (2017) study (5 s *vs.* 15 s). Overall, "Uv" dives were exhibited most frequently (Figure 2).

A change point analysis [broken-stick regression, based on the analyses described by Howey *et al.* (2016)] identified two distinct clusters of diving behaviour that appeared seasonally mediated (Figure 2). Cluster 1 was from 22 February (day of deployment) through 6 June. Cluster 2 was from 6 June to 20 August. In both clusters, "Uv" dives were the most common dive profile exhibited (Figure 2c). Dive profiles in cluster 1 were generally shallower and shorter, with fewer dives per night (mean = 6 ± 3). Mean dive depth was 675 m ± 118.5. Dive profiles in cluster 2 were generally slower, longer-duration, deeper dives (mean 784 m ± 67.5), with less variation in dive type, and an average of seven deep dives per night (± 2). Deep diving (> 500 m deep) was observed within 24 h of tagging and likely reflects the shark moving offshore from the tagging location (*c.* 90 m deep) to forage at the edge of the nearby insular shelf. A reconstruction of the daily horizontal movements of the animal using maximum likelihood estimates *via* the WC-GPE3 hidden Markov model (Wildlife Computers: Redmond, WA, USA) suggests that the gradual pattern of dive-depth increase over time was associated with the increased use offshore/pelagic habitat across the duration of the tag deployment (Figure 1e).

Without a measure of activity rate (*e.g.*, *via* an accelerometer), it is impossible to understand exactly why the shark undertook such a deep dive, but it is possible that when at the first descent stop (*c.* 750 m) the shark encountered a rich-prey source, or a potential predator, which it then either pursued or fled from. Although time at depth and post transition point ascent rate for this dive did not differ from the mean for deep dives, total dive time (29 min) was greater than the average deep dive time (24 min), and observed ascent and descent rates were markedly greater than the averages for the previous 12 dives undertaken that night. Undoubtedly, dives to such depths are likely to be metabolically expensive, particularly given the low temperatures and low oxygen levels associated with such depths. Although the average deep-dive maximum depth was probably within

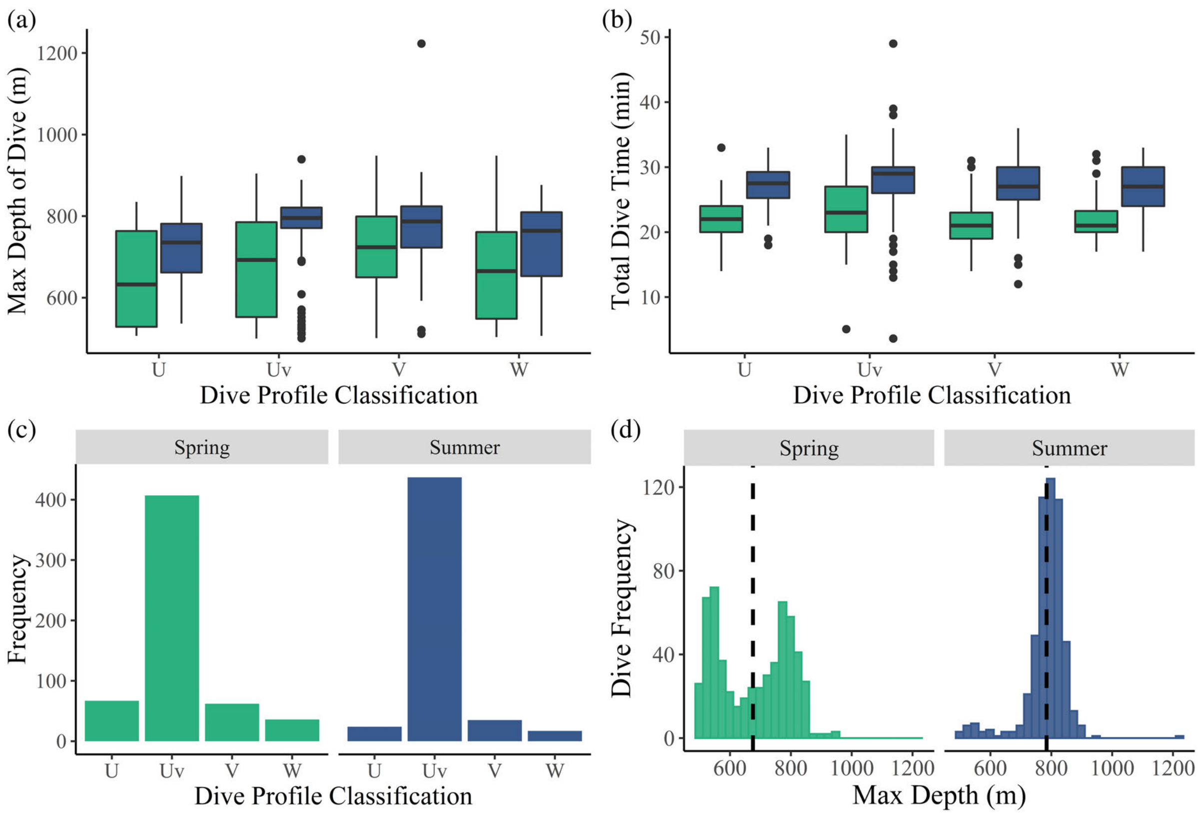

FIGURE 2 Depths, durations and frequencies by dive type. Seasonal differences (spring/summer) identified *via* broken stick regression analysis are demonstrated by colour. (a, b) Box and whisker plots showing dive type according to maximum depth (a) and total dive time (b). Black horizontal lines show median values. (c) Bar chart showing frequency of dive type, and differences by season. (d) Histogram of dive depth frequency, broken down by season. Black dashed vertical lines show mean depth according to season. Cluster ■ Spring, ■ Summer

oxygen minimum zones (OMZ) [500–1000 m (Coffey *et al*., 2020; Yeh & Drazen, 2009)], the profile of this record-breaking dive may well be facilitated by the shark actually diving below the OMZ, thus helping to mitigate metabolic (oxygen consumption) costs associated with the dive. Thus, further investigation is needed into the species' behavioural and physiological adaptations (activity rates and associated metabolic costs) that allow it to tolerate such environmental extremes and exploit meso and bathypelagic resources.

AUTHOR CONTRIBUTIONS

J.M.A. conceived the study, led data collection and wrote the manuscript. P.T.R. participated in data collection, analysed the data and produced the figures. K.M, M.J. and D.V. participated in data collection and contributed towards edits made to the manuscript. N.A and K.H. contributed towards edits made to the manuscript.

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ETHICS STATEMENT

Sharks were not collected or killed and did not experience significant distress during this research. All tagging activities were carried out in accordance with University of Hawaii IACUC protocol # 05–053-15.

ORCID

James M. Anderson https://orcid.org/0000-0002-4900-5916

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