DR. FREDERICK GOETZ (Orcid ID : 0000-0002-6300-1655)

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What goes up must come down: Diel vertical migration in the deep-water sablefish (*Anoplopoma fimbria*) revealed by pop-up satellite archival tags

FREDERICK W. GOETZ[1], ANDREW J. JASONOWICZ[2] AND STEVEN B. ROBERTS[2]

[1]*Environmental and Fisheries Sciences Division*

Northwest Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

7305 Beach Dr. East, Port Orchard, WA 98366 USA

rick.goetz@noaa.gov

[2]*School of Aquatic and Fishery Sciences*

University of Washington

Seattle, WA, USA

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andyj1@uw.edu
sr320@u.washington.edu

Corresponding Author: Frederick Goetz
NOAA Manchester Research Station
7305 Beach Dr. East
Port Orchard, WA 98366
rick.goetz@noaa.gov
360-871-8322

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Running Title: Depth selection in sablefish

ABSTRACT

The sablefish (*Anoplopoma fimbria*) is a long-lived species with wide distribution throughout the North Pacific Ocean. While adult sablefish are considered a deep-water fish, diet analyses suggest that they undergo vertical migrations that could be related to prey movement and feeding. Pop-up satellite archival tags (PSATs) were used to observe the fine-scale depth selection behavior of adult sablefish tagged off the Washington coast during the summer from June to August. Tags were physically retrieved after they surfaced using direction-finding equipment so that complete datasets over the entire deployment were obtained from 14 tags. PSATs that recorded depth and temperature every four minutes during the deployment confirm that sablefish inhabit depths of 750 m or greater. However, a majority of the tagged fish underwent extensive vertical migrations that averaged 254.4 m overall and occurred at a 24-hour periodicity. Variations were observed among individuals in the amount of the deployment during which vertical migrations occurred, ranging from 12.37 to 63.48% of the time. During the vertical migration, fish ascended towards the surface at night and descended prior to daylight (i.e., diel vertical migration). Sablefish generally inhabited temperatures of 5^{o}C but during the vertical migrations were found at temperatures from 6-10^{o}C. Sablefish are opportunistic feeders with a large proportion of their diet being fish, euphausiids and cephalopods. Because these prey

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items also exhibit diel vertical migrations, it is possible that the vertical migratory behavior displayed by the sablefish was in response to the movements or the location of their prey.

KEYWORDS
sablefish, *Anoplopoma fimbria*, diel vertical migration, pop-up satellite tags, archival tags

INTRODUCTION

Sablefish are a long-lived marine species with wide distribution extending from Baja California to Alaska, the Bering Sea and through to the eastern coast of Japan. Even though their range is extensive, no distinct genetic population structure is evident (Jasonowicz *et al.*, 2016). This may be a result of the potential to move great distances as adults (Hanselman *et al.*, 2015) as well as movements that are part of the life history of younger sablefish (Maloney and Sigler, 2008). Adults are considered deep-water inhabitants (Sasaki, 1985) and there appears to be a relationship between depth and size with larger fish living at greater depths (Laidig *et al.*, 1997; Sogard and Berkeley, 2017; Afanasyev *et al.*, 2014). There also appears to be seasonal movement of adults to deeper water in the winter and shallower in the summer (Karinen *et al.*, 2010). Spawning sites are unknown for sablefish but are proposed to be deep (Mason *et al.*, 1983) with developing larvae ascending gradually to the surface (Alderdice *et al.*, 1988; Mcfarlane and Beamish, 1992). There is a pelagic larval phase and in southeast Alaska, juveniles have been shown to inhabit inshore areas (Rutecki and Varosi, 1997).

Studies on sablefish diets suggest that they are opportunistic feeders and that fish generally comprise the largest part of their diet (Laidig *et al.*, 1997; Buckley *et al.*, 1999; Yang *et al.*, 2006). While deep-water fish species (e.g., thornyhead (*Sebastolobus* sp.)) are observed in the stomachs of adults, fish species (e.g. Pacific hake (*Merluccius productus*)) and invertebrates (e.g., euphausiids) that would be considered off-bottom inhabitants and that undergo diurnal vertical migration (daily migrations up and down in the water column) are also observed in sablefish stomachs (Laidig *et al.*, 1997). This would suggest that sablefish may not remain on the bottom but could undergo vertical migrations that are related to prey movement and feeding. However, there have not been any direct recordings or observations of vertical migratory behavior in adult sablefish. A way to test this hypothesis would be to use archival tags that

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record depth at sampling intervals frequent enough to determine the precise depth profile of individuals on a daily basis.

Internally-implanted archival tags have been deployed in sablefish (Echave *et al.*, 2013) but, as far as we know, depth distribution data from those tags have not been reported. Another form of archival tag, the pop-up satellite archival tag (PSAT), have also been used on sablefish, primarily to determine spawning locations and the methods to deploy these tags on sablefish have been extensively described (Echave, 2016). However, success rates in obtaining data from these tags appear to have been lower than expected (Echave, 2016). Pop-up satellite archival tags are composed of a data-logger and battery, and a float with attached antenna. The tag is tethered to the fish and the data logger is programmed to continually collect depth, temperature and light for a specified duration (weeks to months). At the end of the programmed time, a detachment mechanism is automatically activated that releases the data logger/float and antenna from the tether. The float carries the data logger to the surface where the antenna transmits the environmental data to an orbiting satellite of the Argos System (http://www.argos-system.org/) and the tag's location is determined by the satellite via the Doppler shift of the received signal. The satellite then relays the tag data and location estimates back to the researcher. There are several manufacturers of PSATs and these tags have now been used on a number of marine fish including tuna, marlin, sailfish, halibut and sharks and have provided detailed information about their geographic and vertical (depth) movements (Sims *et al.*, 2003; Loher and Seitz, 2006; Shepard *et al.*, 2006; Musyl *et al.*, 2011).

In the current study, PSATs were deployed on sablefish in the summer of 2016 for 2.5 months off the Washington coast. Sablefish could be easily collected and tagged at this time of the year and because of weather and sea conditions, PSATs that had surfaced could also be easily tracked. For some PSATs, relying on transmission to the satellite results in poor and incomplete data recovery. Thus, radio direction-finding equipment, combined with locations provided by Argos, were used to physically retrieve the surfaced tags. This resulted in immediate and complete access to all of the data archived in the tags and the depth and temperature profiles obtained from these fish provided a very detailed view of their microhabitat selection. The depth data were analyzed using signal-processing techniques to identify periodic vertical migratory behavior. We observed a significant number of the fish undergoing diurnal vertical migrations that may help explain the feeding habits of this species.

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METHODS

Animals

Sablefish were collected on June 8 and 9, 2016 using demersal longlines set in the Quinault Canyon off the coast of Washington (Fig. 1). Longlines were soaked for 2-3 hours before retrieval. Fish that were caught and subsequently used for tagging were held for up to 4 hours prior to tagging in a tote (122 x 122 x 91 cm) containing seawater maintained at 4-5^{o}C that was aerated with a pump (Sweetwater Linear II; Pentair Aquatic-Ecosystems, Apopka, FL) and constantly filtered with a submerged, indwelling filtration system (Pondmaster PM24; Danner Manufacturing Inc., Icelandia, N.Y. fitted with a Pentek 150237 #10 Big Blue Filter Housing; Pentek Inc., Coraopolis, PA). During collection, larger fish were selected for tagging and a total of 25 fish (Mean = 753.75, SD = 75.52 mm, range 680-950 mm) were tagged over the two-day period with 11 and 14 fish tagged and released on June 8 and 9, respectively (see Appendix 1).

Sexing fish

Male and female sablefish cannot be differentiated externally. To noninvasively determine the genetic sex of each fish, a polymerase chain reaction (PCR) assay of the sablefish sex marker *gsdf* (Rondeau *et al.*, 2013) was conducted on DNA isolated from fin clips (taken during tagging) using the DNeasy Blood & Tissue Kit (Qiagen, Germantown, MD, USA). PCRs for genetic sexing had a total volume of 25 µL consisting of 1 µL of DNA template, 12.5 µl of Amplitaq Gold master mix (Applied Biosystems, Foster City, CA), and 80 nM each of a forward (6FAM-GTGCAGCCAAATATTGCRTA) and reverse primer (TGTCAACATTATGTTTTGAGGTGT) for *gsdf* (Luckenbach and Fairgrieve, 2016). For reaction analysis, 9.75 µL of Hi-Di formamide and 0.25 µL of Genescan-1200 LIZ size standard (LT) were combined with 1 µL of PCR product. The reaction was incubated at 96^{o}C for 3 min for thermal denaturation and then immediately placed into a -20^{o}C freezer to cool. An ABI 3730 DNA analyzer was used to separate the PCR products and the genotypic sex was determined by the presence or absence of a male-specific band (Rondeau *et al.*, 2013).

Tags and Tagging

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Desert Star SeaTag-MODs were used as the pop-up satellite archival tags for this study. The tags were programmed to record pressure (depth), temperature, photocell voltage (light) and magnetic field strength every 4 minutes throughout deployment. SeaTag-MODs can use the magnetic field data in a geolocating mechanism (http://www.desertstar.com/page/improved-geo-positioning-accuracy-via-magnetic-lig). However, this mechanism still requires the reception of light during the day for the determination of noontime. Because sablefish resided during the day at depths where light penetration was too low for light reception, we were not able to track the geographic movements of the fish during deployment nor do we report data for light in the Results.

After the longlines were retrieved and all of fish that were going to be tagged were placed in the holding tote, the water temperature of the tote was decreased to 1-2^{o}C using ice. The lower holding temperature immobilized fish and enabled tag attachment without chemical anesthesia. For tagging, each fish was held in a plastic V board and fork length was recorded. A small fin clip was taken and used later to determine sex as described above. Pop-up satellite archival tags were harnessed to the sablefish exactly as described by Lacroix (2013) for Atlantic salmon (*Salmo salar*). Briefly, a fluorocarbon monofilament (90 lb test - Jinkai; Burns Fishing Supplies, Poulsbo, WA) harness was fixed to the tags several days prior to the tagging trip using chafe tubing (1.3, 1.6 and 2.2 mm - Chafe Gear; Trophy Fishing Tackle, West Babylon, NJ) (Lacroix, 2013). On board, veterinarian needles (16 gauge x 3" - Cadence Science, Cranston, RI) were used to insert the monofilament line through the epaxial muscle approximately an inch below the dorsal fin in two places. After needle insertion, the monofilament line was fed through the needle bore and the needle was then removed leaving the line in place. This harness was fixed through two places in the muscle and the ends were held together on the harness by aluminum alloy crimps ("J" - Jinkai; LMR, Fort Lauderdale, FL) in two places. A small piece of latex tubing (1/16 ID x 1/32 Wall - 1/8 OD) was slipped over the crimp to protect the fish from possible chaffing by the crimps. Lengths of the harness were adjusted prior to crimping so that the dorsal fin did not touch the base of the tag when extended. Immediately following the attachment of the harness, the four points where the needle entered or exited the muscle were swabbed with 10% betadine and the fish was placed first in a large cooler of 1-2^{o}C seawater for rinsing and then transferred after a few minutes back into the holding tote containing 1-2^{o}C water. The entire tagging procedure required approximately four minutes for each fish. After

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all of the fish were harnessed, the water temperature of the holding tote was increased to 4-5^{o}C by adding ambient seawater, and the fish were held for 20 minutes and then released within 1-2 miles of the collection site. A GoPro (Hero4; GoPro, San Mateo, CA) camera was used underwater to ensure that fish swam downward and appeared to be swimming without distress (https://www.youtube.com/watch?v=ARcEIbmgh_U).

Tag retrieval

Tags were programmed to release from the fish and surface on August 21, 2016. After this time, the Argos-transmitted locations for all surfaced tags were tracked, and on August 23 and 24, two boats were deployed for retrieving tags. The most recent Argos locations were used to guide boats to tag sites off the Washington coast (Fig. 1). When the boats were within 2-3 miles of the reported location of the tags, radio direction-finding equipment (Goniometer - CLS America; Lanham, MD and Model DFR-1000B - RDF Products; Vancouver, WA) was activated. Usually when the boat was within 1-2 miles of the tag, a signal (tag transmitting to the Argos satellite) was detected and the relative position of the tag in relationship to the boat was assessed and the direction of the boat adjusted if required. SeaTag-MODs use a photocell to generate power for satellite transmissions when they are at the surface and, depending on the individual tag and environmental conditions, the frequency of this transmission can vary from 1-5 minutes. Thus, the speed of the boat moving towards the tag was adjusted to the transmission frequency so that the tag was not overtaken. Visual scanning of the water for the tag was initiated based on the intensity of the signal from the direction-finding equipment and the distance traveled from the first signal of the tag. Tags could usually be seen in the water within 50 meters of the boat. While the time for tag retrieval varied, in every case in which a tag signal was detected by the direction-finding equipment on the recovery vessel, the tag was eventually located and retrieved.

Processing of tag data

Pop-up satellite archival tag locations were identified as the first Argos message received from a location in the Pacific Ocean (Fig. 1). If a tag did not produce an integer location class estimate (http://www.argos-system.org/manual/3-location/34_location_classes.htm) soon after transmission began, the Argos positions for the first day of transmissions were visually inspected and the most likely position was chosen based on the duration of time from the beginning of

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transmission and the proximity to other Argos positions. From our experience recovering tags at sea, we have found that lower quality positions can be reliably used to recover tags when they are close to other low quality positions. Displacement between the release sites and pop-up locations were calculated by using the geodesic length function in spatialite (version 4.3.0a, Furieri, 2015).

The amount of time for a tagged fish to reach the bottom after release was estimated by calculating the elapsed time between when the fish began its descent from the surface to when it reached the depth at the site it was released at. To reduce bias that might result from behavioral patterns of an individual adjusting to the attachment of the tag and to allow behavior to normalize, the first seven days of data after release were discarded prior to data analysis. Sunrise, civil dawn, civil dusk and sunset time were estimated for Quinault Canyon (47.2723, -124.862) using the python package astral (version 1.3.1, Kennedy, 2016). Observations were then categorized as one of day, night, dawn or dusk.

Periodic patterns of depth selection

Smoothed periodograms were calculated using fast Fourier transformation (FFT) (spec.prgam function, R version 3.3.1, R Core Team, 2016) in order to examine the overall frequency spectrum of the depth data for each retrieved PSAT. Periodograms generated using FFT have also been successfully used to investigate behavioral patterns in depth data collected from archival data storage tags in other fish species (Graham *et al.*, 2006; Shepard *et al.*, 2006; Graves *et al.*, 2009). The magnitude of the peaks in the periodogram indicate the strength of the periodicities present in the time series (Shepard et al. 2006) and, in this case, they correspond to the periodic intervals at which rhythmic patterns associated with depth selection occurred.

Detection and characterization of diurnal patterns of depth selection

The continuous wavelet transformation was used to analyze the depth data from each tag to identify regions of periodic behavior. Wavelet analysis uses functions referred to as wavelets to localize specific frequencies as a function of time (e.g., Fig. 2; Figures for all fish given in Appendix 2) (Torrence and Compo, 1998; Cazelles *et al.*, 2008). Briefly, the wavelet transformation can be thought of as the cross-correlation of different time points in a signal with wavelet functions of varying scale (Cazelles et al. 2008). We used the Morlet ($\omega_0 = 6$) (Fig. 2d)

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wavelet function for this analysis. To correct bias that favors large scales (low frequencies) present in the signal, the raw values of the local wavelet power spectra were divided by the scale with which they were associated (Liu *et al.*, 2007).

Significance of the wavelet spectrum was assessed by generating 5,000 simulated time series for each individual by resampling the observed depth data based on a Markov process with similar properties as the original data (Cazelles and Stone, 2003; Cazelles *et al.*, 2008). The wavelet spectra from the simulated time series were then used to generate a null distribution of wavelet quantities on which to test hypotheses against (Cazelles and Stone, 2003; Cazelles *et al.*, 2008). This type of resampling scheme is often preferred over others as it preserves the distribution of values and short-term autocorrelation structure of the original time series and it provides a framework for testing the null hypothesis that *the observed wavelet spectrum and related quantities are due to a random process with similar Markov properties* (i.e., the frequencies observed in the depth data are not due to random vertical movements in the water column) (Cazelles *et al.*, 2008; Cazelles *et al.*, 2014). Statistical significance was assessed by comparing the local, global, and scale-averaged wavelet power spectra to this distribution. Values exceeding the bootstrapped 95% confidence levels were considered statistically significant and were used to identify regions of the time series that were a result of non-random vertical migratory behavior.

For each fish, the global wavelet spectrum was calculated to display the dominant periods present in the signal (Fig. 2e) (equation 22; Torrence and Compo, 1998). To determine if an individual underwent significant diurnal vertical migrations, the global wavelet power spectrum was examined for a significant peak at the 24-hour period (Fig. 2e). If a significant peak was detected, a scale averaged wavelet spectrum and associated 95% confidence levels (equation 24; Torrence and Compo, 1998) were subsequently calculated for the 22 - 26 hour band of the local wavelet power spectrum (Fig. 2c). Significant regions of the 22 – 26 hour scale-averaged time series indicated when the individual was exhibiting vertical migratory behavior occurring on a diurnal basis (Fig. 2c).

To characterize the range of depth and temperature that individuals were subject to during periods of diurnal periodicity, we estimated 'baseline' trends using asymmetric least squares (R package ptw, Bloemberg *et al.*, 2010; Wehrens *et al.*, 2015) that describe the lower and upper limits of the depth distribution. An average of the distance between the two baselines

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was used to estimate the approximate range of vertical travel during periods of diurnal behavior. We defined the bottom of a vertical migration as periods when the depth sensor readings were less than 10 m shallower than the estimated bottom baseline and the top of a vertical migration when the depth sensor readings where less than 10 m deeper than the estimated upper baseline. To evaluate the time at which vertical movements occurred, patterns of depth change during vertical migrations were examined by averaging the overall hourly change in depth each day across individuals and visualized as a contour plot. Also, the average time of day at which the fish were at the top and bottom of the migrations was estimated by converting the timestamps at the top and bottom periods of the vertical migrations to angular measurements and then taking their mean and standard deviation (R package circular, Agostinelli and Lund, 2013). The angular metrics returned were then converted back to units of time.

RESULTS

Tag release and retrieval

Of the 25 tags originally harnessed to fish in June, four released prior to the programmed release date, 14 released on the programmed release date (August 21), one released late, and six did not report (Appendix 1). Of the tags that released early, one did so because a commercial trawler had captured the fish. Although this tag was returned, the data for this fish were not included in the analyses because they did not extend over the complete deployment time. Additionally, one tag that had reported as scheduled was not recovered and therefore was not included in the analyses. However, a single tag that did not report was found on a beach and returned. After downloading, its dataset was found to be complete over the deployment time and was, therefore, used in the analysis. As a result, full data from 14 tags were available and these comprise the analyses that will be reported subsequently.

Tags surfaced from approximately 139.1 km (48.31°N) to the north to 126.9 km (46.14°N) to the south of the release sites (Fig. 1 and 3). Of the tags that surfaced on the programmed date (n=14), half surfaced within 50 km of the original tagging site and the remaining tags surfaced >75 km (Fig. 3). Of the 25 fish originally tagged, 20 were females and 5 were males. Of the retrieved tags, 12 were from females and 2 from males.

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Depth

All fish appeared to reach the bottom soon after tagging (mean = 2.97 hours, SD = 3.26 hours, max = 11 hours). Depending on the time of day, fish were found from depths of greater than 750 m to the surface (Fig. 4a, Online Supplement). However, fish tended to reside deeper during the day than at night (Fig. 4a, Online Supplement) and this was a result of the vertical migrations that many of the fish underwent at night (see below). The FFT periodograms indicated that there was a dominant periodicity of 24 hours in the vertical movements of most fish (Fig. 5). Wavelet analysis indicated that of the 14 tags for which complete deployment data were obtained, 13 fish exhibited significant, nonrandom vertical migratory behavior that occurred on a 24-hour period (Figs. 3 and 6 and Appendix 2). For those fish that exhibited significant diurnal periodicities, the vertical migratory behavior occurred on average 37.63% (range: 12.37 to 63.48%) of their days at large. Vertical migrations extended on average from a depth of 466.30 m (SD = 119.45) at the bottom to 201.63 m (SD = 74.74) at the top (Fig. 7). The extent of vertical displacement during periods of vertical migration was on average 254.53 m (SD = 87.55), ranging from as little as 43 m to as much as 668 m (Fig. 7). Sablefish were at the top of their vertical migrations at night (mean = 01:46, SD = 42 minutes) and at the bottom during the day (mean = 13:23, SD = 66 minutes) (Fig. 8). These movements are consistent with diel vertical migration (DVM); that is, where an organism ascends at night and descends to lower depths in the day. The greatest changes in depth during periods of DVM occurred near both sunrise and sunset, indicating that the upward movement of fish occurs near sunset and the downward movement near sunrise (Fig. 9).

Temperature

Temperatures recorded by the tags ranged from 3.65°C to 11.84°C but were generally colder during the day and warmer at night (Fig. 4b, Online Supplement). This shift in temperature was correlated with the DVM exhibited by many of the fish. Of those fish that exhibited significant DVM, temperatures were cooler (mean = 5.17°C, SD = 0.57) at the lower limits and higher (mean = 6.57°C, SD = 0.59) at the upper limits of the DVM (Fig. 7).

DISCUSSION

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Sablefish are considered a deep-water marine species (Sasaki, 1985) and are commercially fished by bottom trawls, longlines and pots. The results of the present study confirm that sablefish inhabit deep water of up to 750 m or greater. However, the most interesting observation was the extensive vertical migrations observed for many of the fish that could at times be considered DVMs. While both the FFT periodograms and wavelet analysis identified a 24-hour periodicity in the depth selection behavior of sablefish, individual behavior patterns varied substantially. Wavelet analysis provides a framework on which periods of significant DVM can be identified; however, some key considerations should be kept in mind when interpreting the periods of significant DVM identified in this analysis. There are a variety of mother wavelets available and a range of null models may be used to identify significant regions of the wavelet spectrum. Sometimes there is a trade-off between the time and frequency resolution of the wavelet spectrum that is often determined by the choice of mother wavelet (Cazelles *et al.*, 2008). Because we were interested in detecting sustained patterns of activity that occurred at a consistent 24-hour periodicity, we chose the Morlet ($\omega_0 = 6$) wavelet because its features make it well suited to isolate frequencies that comprise a signal while maintaining a good compromise between both time and frequency resolution (Torrence and Compo, 1998; Cazelles *et al.*, 2008). We felt that the wavelet analysis employed here generally did a good job identifying periods of significant DVM, especially when vertical migrations occurred over great depths and consecutive days. However, in some cases this method may be conservative in detecting periods of DVM. There were some periods where DVM behavior appeared to be present in the depth profiles yet were not identified as significant (e.g., TagSN: 1474, 1397 – Fig. 6, Appendix 2). Qualitatively it appeared that during these periods the vertical movements were less extensive (<~ 150 m) when compared to periods of significant DVM or the fish did not remain at a relatively consistent depth during deep and shallow phases of vertical movements. These periods often had higher wavelet power in the 22 – 26 hour band than adjacent frequencies and, while they were not found to be statistically significant, they may represent smaller biologically meaningful vertical movements. While data-driven resampling techniques such as the method used here to generate a null model are often preferred over other methods, significant regions of the power spectrum may vary as a consequence of the statistical test that is chosen (Cazelles *et al.*, 2014).

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Diurnal vertical migrations are common in marine organisms, especially zooplankton (Hays, 2003). The most common form is DVM where organisms ascend at night and descend to lower depths in the day and one of the adaptive advantages of this is believed to be the avoidance of visual predators by prey (Hays, 2003; Williamson *et al.*, 2011). In turn, predators of these organisms can undergo DVM that could facilitate prey capture (Nielson and Perry, 1990). Reports on sablefish stomach contents indicate that they are very opportunistic feeders. In the Gulf of Alaska and along the Pacific coast from California to Canada, the top prey items were fish, cephalopods and euphausiids (Buckley *et al.*, 1999; Yang *et al.*, 2006). The main difference between locations was the prey fish species. For example, in the Gulf of Alaska this was walleye pollock (*Gadus chalcogrammus*) (Yang *et al.*, 2006) whereas off the Canadian and Washington coasts it included Pacific hake (Buckley *et al.*, 1999). Throughout the eastern Pacific, fishery offal was also found to be a major portion of the diet (Buckley *et al.*, 1999; Yang *et al.*, 2006), substantiating the opportunistic feeding of these fish. In prior studies, diets have also varied considerably with the size of the fish and the depth at which collections were made. For example, larger fish had higher contributions of fish in their stomachs (Laidig *et al.*, 1997). The fish that we tagged were large and, therefore, likely to be feeding primarily on fish.

Euphausiids, cephalopods (e.g., squid) and hake are all reported to exhibit DVM (Alverson and Larkins, 1969; Alton and Nelson, 1970; Bailey *et al.*, 1982; Mackas *et al.*, 1997; Watanabe *et al.*, 2006). Thus, given the diets reported for sablefish on the Pacific coast, it could be that the DVMs exhibited by the fish tagged in this study are related to the DVMs exhibited by their prey; or, simply, that prey species are located at shallower depths than sablefish occupy during the day and sablefish may ascend to those depths during night when light levels are low. However, DVM was not prominent in all individuals in the study and even in sablefish that did exhibit significant DVM, it was not continual. This may have been related to the opportunistic nature of their feeding behavior. Those individuals exhibiting reduced or no DVM may have been feeding predominantly nearer to the bottom. It may also be related to where the sablefish were located in relation to the availability of different prey. Nielson and Parry (1990) indicate that there can be a number of environmental factors that entrain, promote or modify vertical migratory behavior. In fish there appears to be significant plasticity in DVM behavior suggesting that multiple oscillators could be involved (Nielson and Perry, 1990). If sablefish undergo DVM to facilitate prey capture, is it an endogenous biological rhythm or is the behavior

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promoted by the DVM of the prey or some environmental cue such as photoperiod? If it were merely a result of a biological rhythm then we might expect DVM to be more continuous. However, prey movement and success in capture could initiate or reinforce a diel vertical migratory behavior and this could be modified/entrained by photoperiod or other environmental drivers.

To our knowledge, evidence of diurnal vertical migratory behavior in sablefish using archival tags has not been previously reported. Based on fishing effort throughout a 24-hour period, Kulikov (1965) reported that sablefish catch by bottom trawl was greater at night than during the day. They concluded that fish migrated away from the bottom during the day and towards the bottom at night. This observation is directly opposite to what we observed but a potential problem with the study by Kulikov (1965) could be differences in the way the trawl fished on the bottom during the day versus the night. Even at the depth they were fishing, the fish may have been able to avoid the trawl more effectively during the day. Doya et al. (2014) observed "a diel swimming pattern" of sablefish in the Barkley Canyon off Vancouver Island with cameras that were part of the NEPTUNE (North-East Pacific Time-Series Undersea Networked Experiments) Ocean Networks Canada Observatory. They interpreted the activity to be movement off and onto the bottom on a diurnal basis. However, the cameras used to collect video were stationary and positioned on the seafloor at 892-987 m deep and, therefore, would not have captured movements up and down in the water column or along the bottom. Finally, Sullivan (1982 in Norris, 1997) indicated that an individual sablefish was tracked by a sonic tag in La Jolla Canyon over a 44 hour period and found to migrate between 206 and 610 m, moving into shallow water at night and back into deeper water during the day. This would be the type of vertical migration that we observed. While DVM was frequently observed in the fish in the present study, it should be pointed out that these sablefish were collected at relatively shallow depths compared to the range of depths that sablefish inhabit. In tagging studies of sablefish off the coast of Oregon, Sogard and Berkeley (2017) found that there was an increasing proportion of females as depth increased and a progressive decrease in growth. As depth increases, environmental conditions and food resources may alter the behavior of the sablefish and, thus, it is unclear whether sablefish inhabiting deeper water would exhibit the types of depth selection behavior as those shown here.

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In the current study, the success rate for tags that remained on the fish until their programmed pop-off date and successfully transmitted their release locations, was 56% for tags that surfaced and transmitted their location on the programmed day of release. It was higher (67%) if we include tags that surfaced earlier than the programmed release date but successfully transmitted their location to Argos. The SeaTag-MOD has an automatic release incorporated into the tag when depths of >2000 m are exceeded. Thus, it is possible that some of the tags that surfaced prior to the programmed release date were on fish that descended to depths >2000 m. Premature release could also have resulted from the harness being shed or from predation. (Echave, 2016) used several methods to attach Desert Star PSATs to sablefish and the methods resulted in different success rates ranging from 15 to 58%. We have observed a higher success rate (78%) for the same tags when deployed on lake trout in Lake Superior, USA (Goetz, unpublished results). This could be due to the fact that predation would not be a concern since lake trout are the apex predator in those lakes. SeaTag-MODs use an explosive release mechanism for detachment and failure to release could result from the explosive chamber seal leaking and the gunpowder getting wet, or an electronic/programming problem such that the release mechanism was not activated. In other studies with SeaTag-MODs, we have retrieved tags in the water after the programmed release date that had the harness attached with the release section intact, suggesting that the failure to separate is a real possibility and may account for some missing tags.

While we could not determine the geographic location of the tagged fish during their times at large, the location at which tags surfaced provided some estimate of the movement of the fish away from the tagging site. Based on these locations, we found that most fish appeared to stay within 100 km of the tagging and release site; however, a few fish did move a substantial distance north and south along the coast. Regardless of the distance that fish may have moved from the tagging site, all tags that surfaced on the correct day and transmitted to Argos were located on the shelf break (intersection of shelf and slope) similar to where the fish were tagged and released. The shelf break would provide complex bathymetry that would allow fish to move extensively up or down. Aggregations of Pacific hake and euphausiids were observed on the shelf break off Vancouver Island between 50 and 200 m (Mackas *et al.*, 1997) reinforcing the shelf break as a likely site for feeding. We could imagine sablefish residing at 400-500 m near the bottom on a significant slope where they could ascend or descend further along the gradient

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of the slope. This could explain the depth behavior of some individuals (e.g., TagSN 1554; Fig. 6 and Appendix 2, Online Supplement) that appear to be on the bottom but show upward and downward displacement around this point.

The temperature at which sablefish were found varied and changes in the temperature coincided with changes in depth. As expected, temperatures were generally low when fish were deep but many of the fish that underwent vertical migrations experienced temperatures of 7-8^{o}C when they ascended towards the surface at night. One fish underwent vertical migrations that at times were at the surface or just below the surface where the tag recorded temperatures of 9-11^{o}C. Juvenile sablefish can live in temperatures as high as 22^{o}C (Sogard and Olla, 2001) but these fish would be assumed to inhabit shallower water where temperatures could be as high as 18^{o}C (Sogard and Olla, 2001). As sablefish get older they inhabit deeper water (Maloney and Sigler, 2008) where temperatures would be colder. As far as we know, the temperature range of adult sablefish has not been reported. At the NOAA Manchester Research Station (Port Orchard, WA, USA) we have held adult sablefish in netpens where temperatures can be as high as 15^{o}C at certain times of the year (Goetz, unpublished results). With one exception, it appears that the fish in the present study ascended into water of 8^{o}C (based on upper whiskers in Fig. 7) but generally not higher. The fish in the current study could have been avoiding temperatures higher than 8^{o}C; however, if their migratory behavior was related to feeding, the thermal ranges may have been related to the upper depth at which the prey that they were following were located. Unfortunately, detailed information on the depth selection behavior of Pacific hake is not available to accurately compare the extent of the vertical migration with what we observed in sablefish. It would be interesting to tag hake with PSATs to determine at what depth and temperature they reside at night versus day.

Diurnal vertical migrations have been recorded in other deep-water marine fish species tagged with archival or acoustic tags including Pacific (*Gadus macrocephallus*) and Atlantic (*Gadus morhua*) cod (Arnold and Walker, 1992; Nichol *et al.*, 2013) and saithe (*Pollachius virens*) (Armannsson and Jonsson, 2012). However, a major difference between these species and sablefish is that sablefish do not have a swimbladder (Rummer *et al.*, 2010) and, therefore, physiological constraints related to the inflation or deflation of the swimbladder in relation to the speed and extent of vertical migrations would not be a concern. Sablefish have moderate levels (~14%) of lipid in their muscle (Sullivan and Somero, 1983; Karinen *et al.*, 2010) but have large

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lipid reserves in their bones (Lee *et al.*, 1975) and they may use lipid as a means to help maintain buoyancy at depth. However, given that sablefish do not have a swimbladder and the lipid levels cannot be rapidly altered, the energetic cost of DVM would be a result of the locomotory activity necessary to ascend and descend in the water column or along the slope.

In summary, the data from the PSATs indicate that while sablefish can inhabit great depths, they are also capable of extensive vertical migrations that frequently occur at a 24 hour periodicity. These migrations may be used to facilitate the capture of prey such as Pacific hake. It will be interesting to tag fish over the winter to determine at what depth they reside during the reproductive season and if they undergo vertical migratory behavior at other times of the year.

FIGURE LEGENDS

Fig. 1. Map showing the displacement of pop-up satellite archival-tagged (PSAT) sablefish (*Anoplopoma fimbria*) in June 2016 between the site of release and the tag pop-up location. Blue pop-up locations indicate PSAT tags that reported on the expected pop-up date (Aug 21, 2016), red locations indicate tags that reported prior to their expected pop-up date, and the orange dot indicates a tagged fish that was caught by a commercial trawler. Dashed lines connect release and pop-up locations and do not represent the actual path of travel. Sources: GEBCO, NOAA.

Fig. 2. Steps of the analysis used to quantify diurnal vertical migrations of pop-up satellite archival-tagged (PSAT) sablefish (*Anoplopoma fimbria*). Fish exhibiting high levels (tag 1465) of diurnal vertical migratory behavior and no (tag 1518) diurnal vertical migratory behavior were chosen as examples. A) Raw depth data downloaded from the tag. Dark grey shaded regions indicate nighttime. B) Bias-corrected local wavelet power spectrum of the depth data. Wavelet power is color-coded (red – high wavelet power; blue – low wavelet power), black lines show the 95% confidence level and gray shading represents the cone of influence. D) The Morlet wavelet ($\omega_0 = 6$). E) The global wavelet power spectrum (solid black line) and associated 95% confidence level (dashed line) was used to determine whether or not an individual exhibited significant diurnal vertical migrations during the deployment. C) The observed scale-averaged wavelet spectrum for the 22 – 26 hour band of the wavelet power spectrum (solid black line) was compared to its associated 95% confidence level (dashed line) to determine when an individual underwent diurnal vertical migrations. Regions shaded in red in A and C indicate when

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significant diurnal vertical migrations were identified (Note: no regions are shaded red for tag 1518 because significant diurnal vertical migrations were not identified in the global wavelet power spectrum). The red dashed lines in A indicate the top and bottom baselines used to determine when an individual was near the top (yellow points) and bottom (blue points) of the diurnal vertical migratory cycle. Similar figures for all tags are provided in Appendix 2.

Fig. 3. Displacement (distance between release site and first Argos message received) of pop-up satellite archival-tagged (PSAT) sablefish (*Anoplopoma fimbria*) for which the tag reported on time (N=14).

Fig. 4. Depth (A) and temperature (B) probability density functions for sensor readings during the day and night from all recovered sablefish (*Anoplopoma fimbria*) tags for which complete datasets were available (N=14).

Fig. 5. Smoothed fast Fourier transformation (FFT) periodograms for depth data from all recovered tags for which complete datasets were available (N=14).

Fig. 6. Summaries of diurnal vertical migrations for each sablefish (*Anoplopoma fimbria*) tag analyzed. Complete raw sensor data is displayed and the periods where significant diurnal vertical migrations were identified by wavelet analysis are shaded in red. The orange portion of the depth profile represents data that was omitted from analysis to allow behavior to normalize prior to analysis (see Methods) and the black portion of the profile is the data used to detect diurnal vertical migrations using wavelet analysis. The arrow on the y axis represents the depth of water at the site of release. Gray shaded regions indicate nighttime. Tags 1576 and 1622 are males, the rest are female. Please see the online supplemental material for interactive charts containing the depth and temperature data for each fish.

Fig. 7. Box and whisker plots summarizing the depth (left) and temperature (right) data at the tops and bottoms of the diurnal vertical migrations for all sablefish (*Anoplopoma fimbria*) where significant diurnal vertical migrations were detected (N=13). The box dimensions represent

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the interquartile range (25th to 75th percentiles), the whiskers represent the highest and lowest values within 1.5* interquartile range of the 75th and 25th percentiles, and the dots are outliers.

Fig. 8. Circular histogram of the times at which fish were at the top and bottom of a diurnal vertical migration for those sablefish (*Anoplopoma fimbria*) where significant diurnal vertical migrations were detected (N=13). Blue bars represent the bottom and yellow the top. The lines indicate the mean time at which fish were at the top (solid) and bottom (dashed) of a diurnal vertical migration with the times indicated next to the line. The shaded region indicates when night occurs for Quinault Canyon at this time of year.

Fig. 9. Contour plot of average hourly change in depth by date and hour of the day for pop-up satellite archival-tagged (PSAT) sablefish (*Anoplopoma fimbria*) showing significant diurnal vertical migrations (N=13). Blue regions indicate an increase in depth (downward movement) and red regions indicate decreases in depth (upward movement). Solid lines indicate sunrise and sunset and dashed lines indicate dawn and dusk. Shaded region indicates when night occurs for Quinault Canyon.

DATA ACCESIBILITY

Supplemental data files are available online in a GitHub repository (https://github.com/ajasonowicz/what-goes-up) which is archived with the Zenodo research data repository at https://zenodo.org/record/801771.

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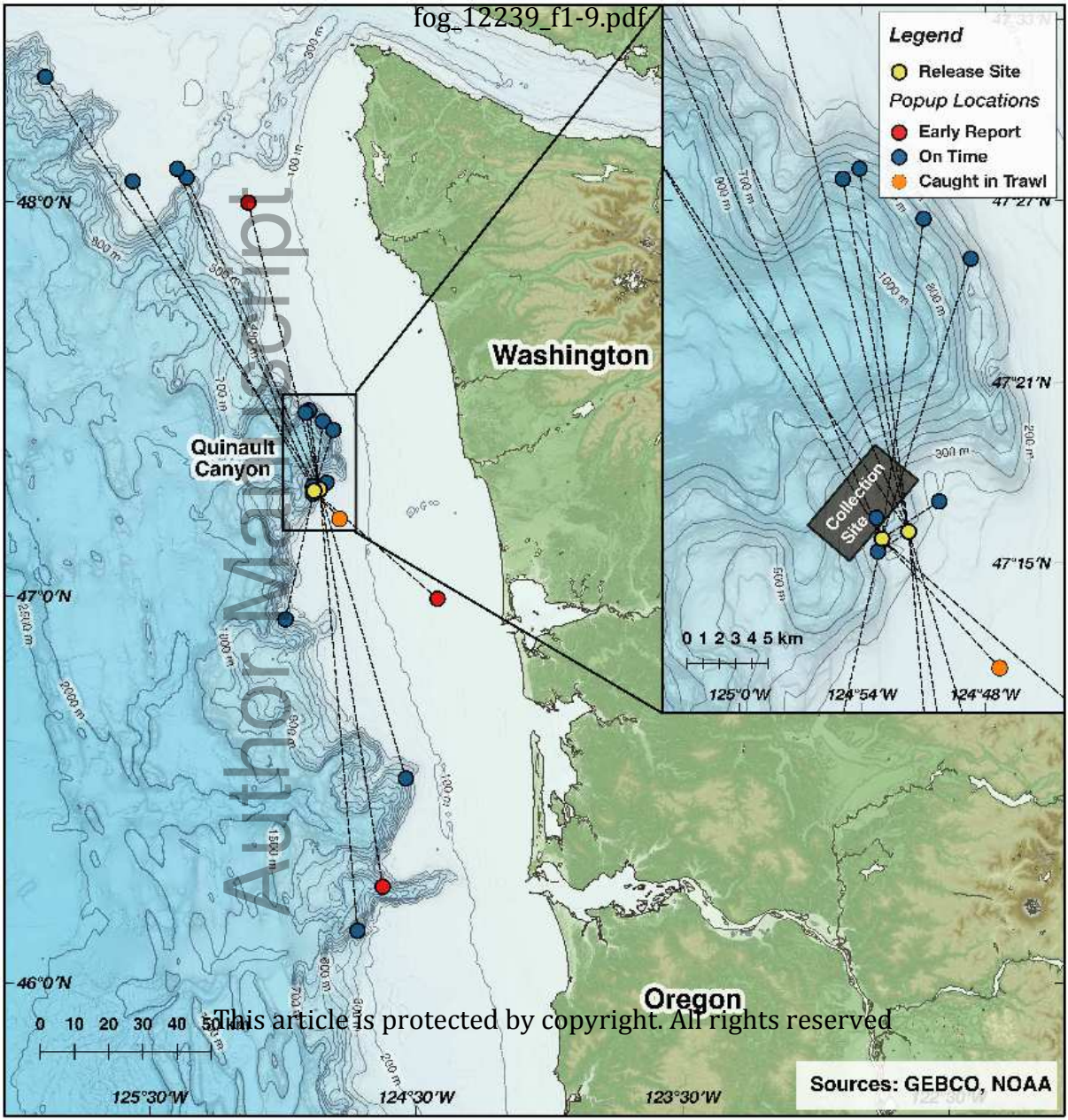

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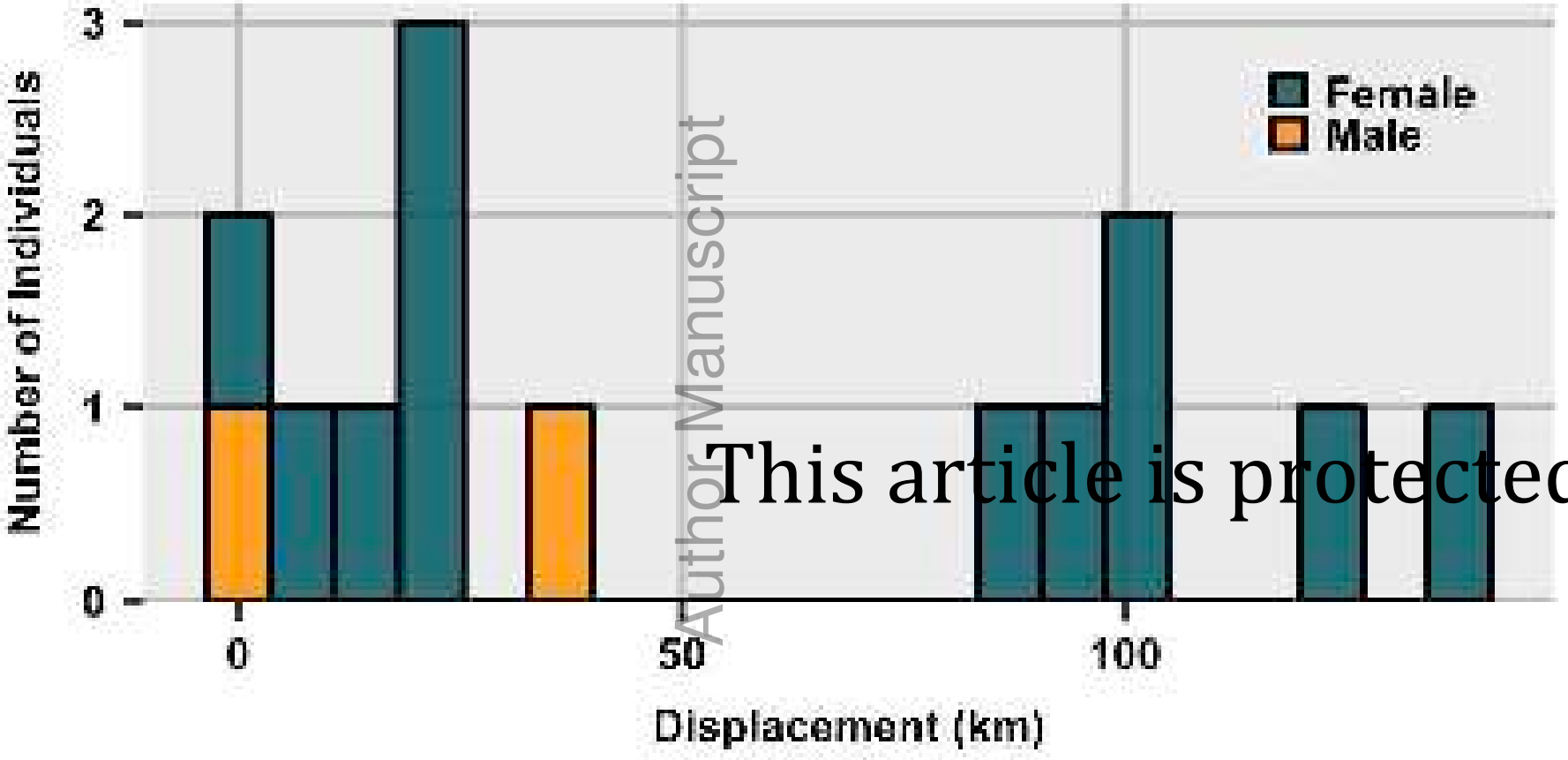

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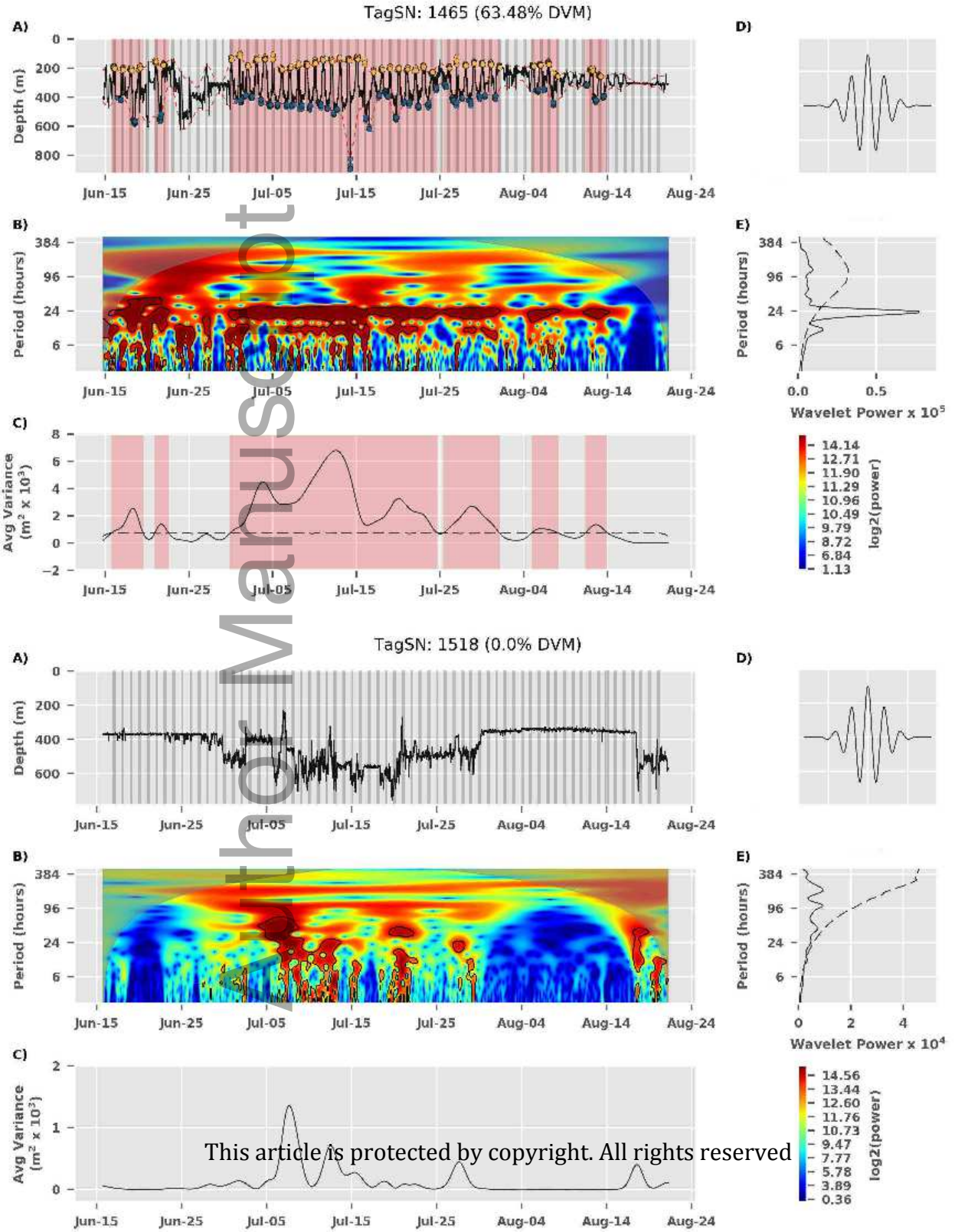

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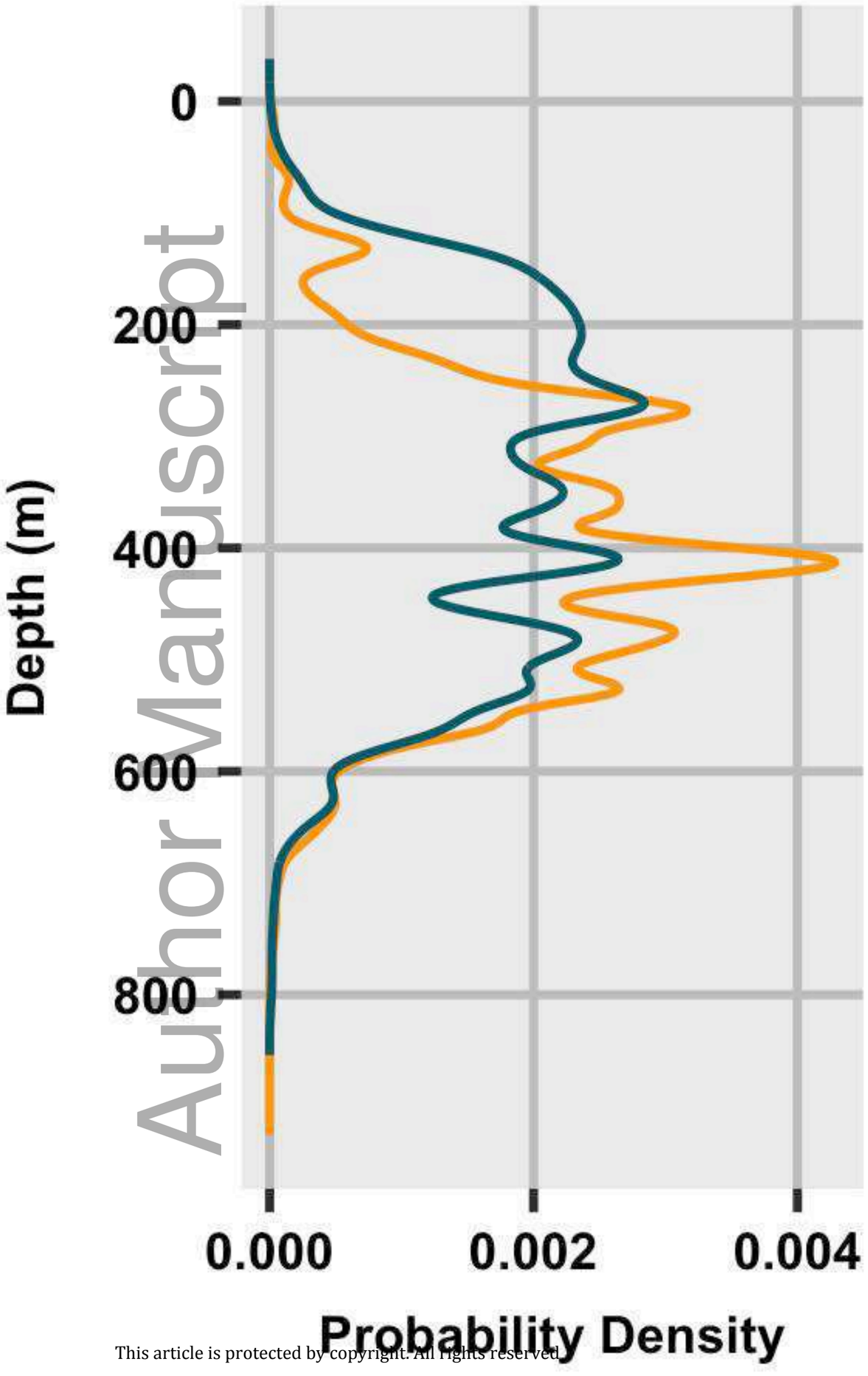

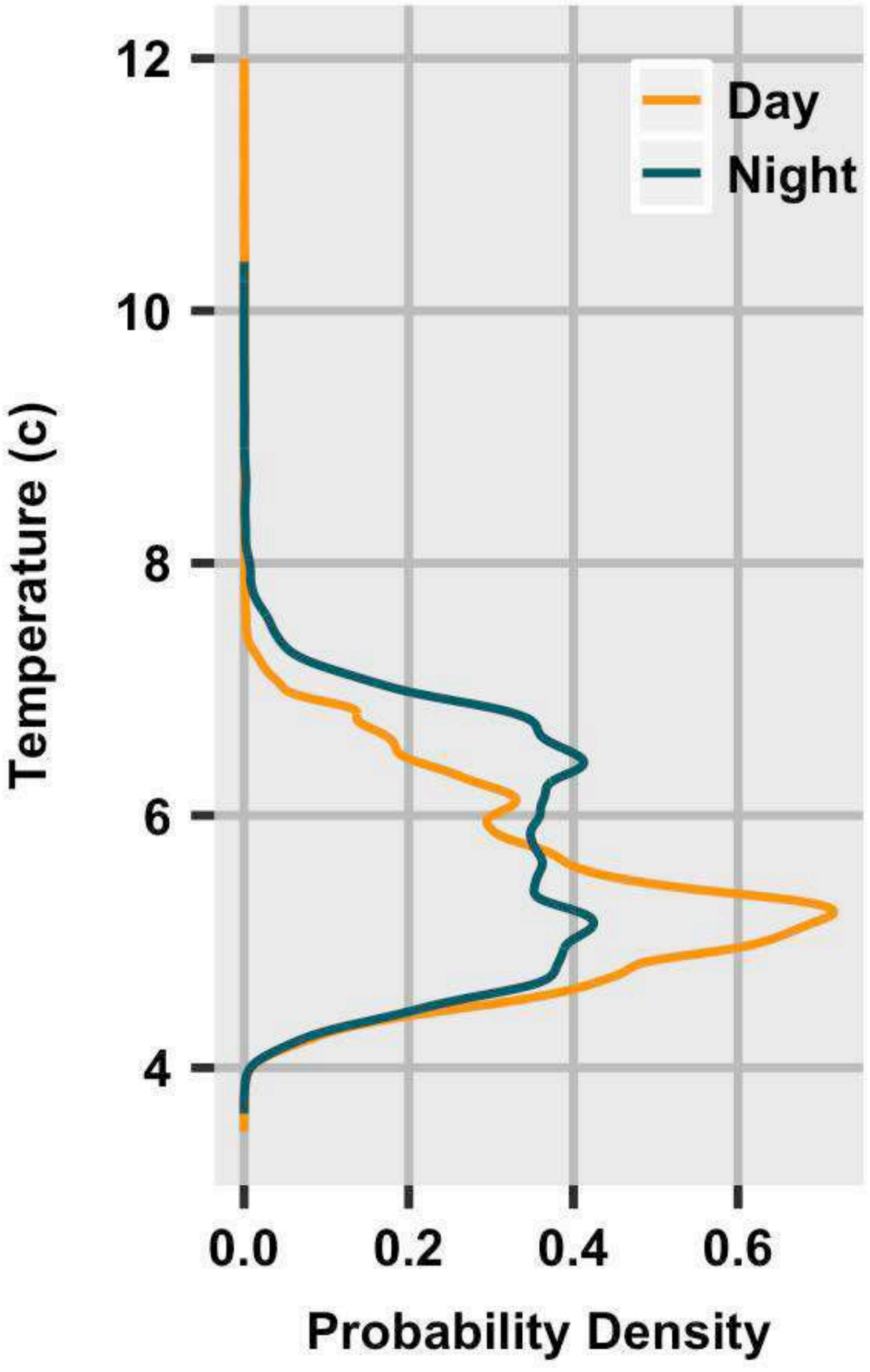

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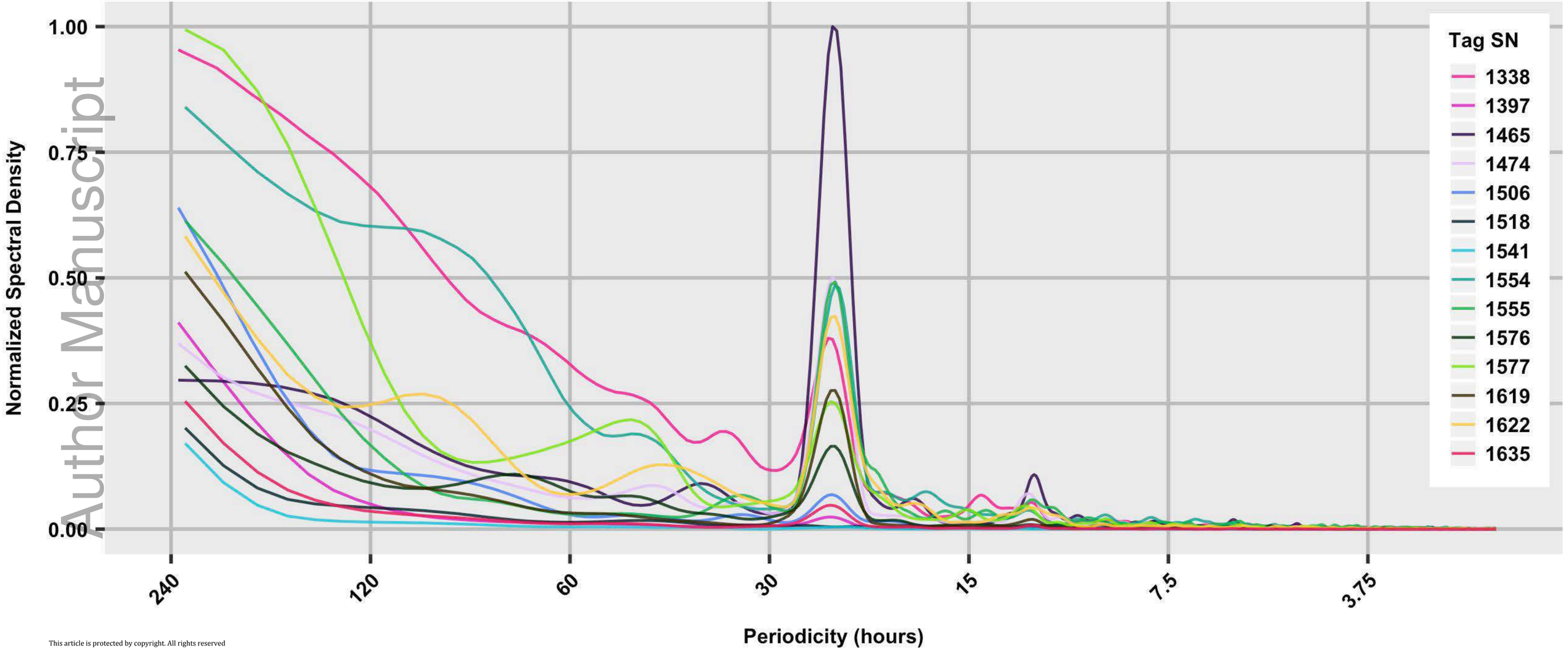

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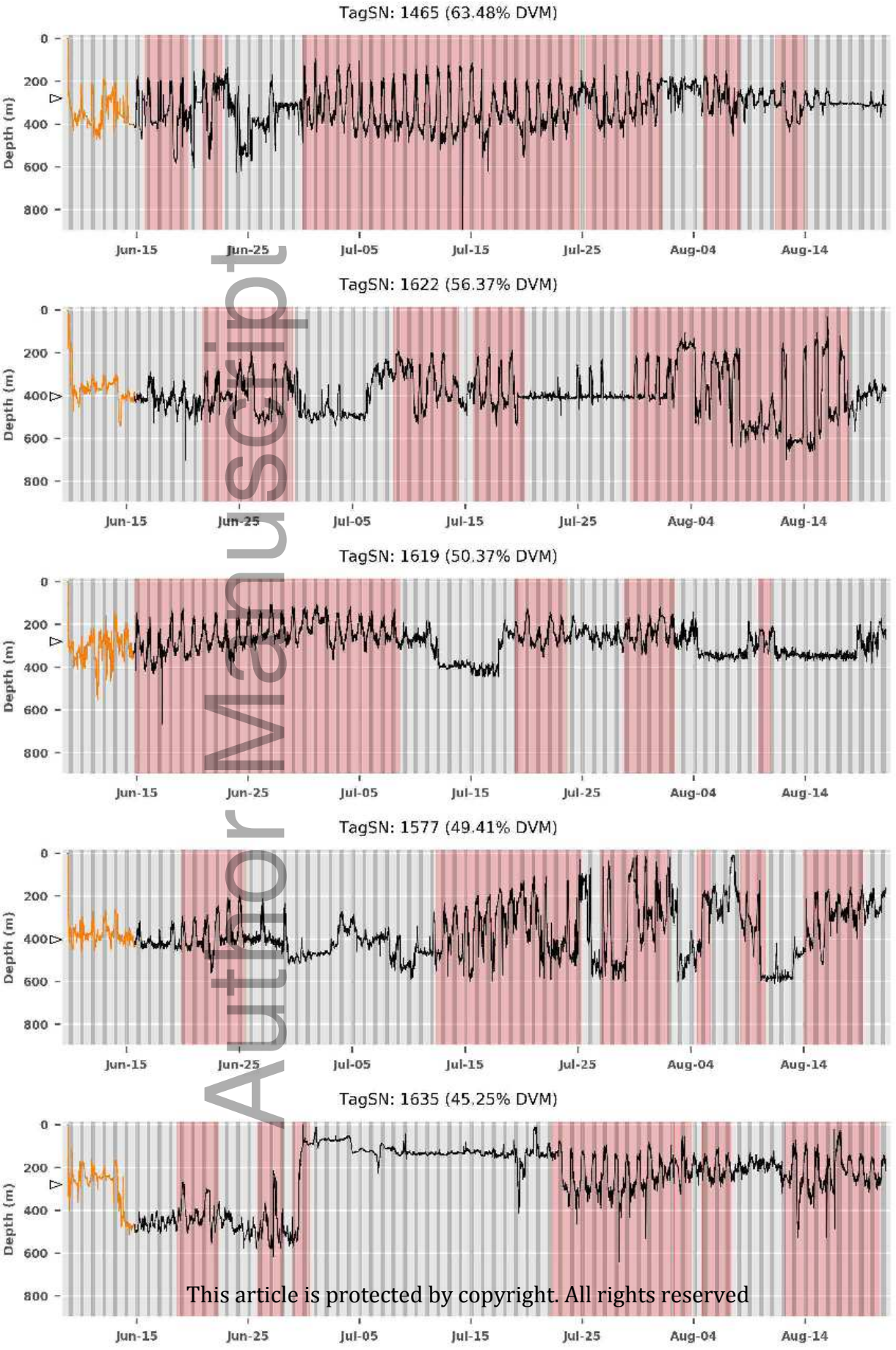

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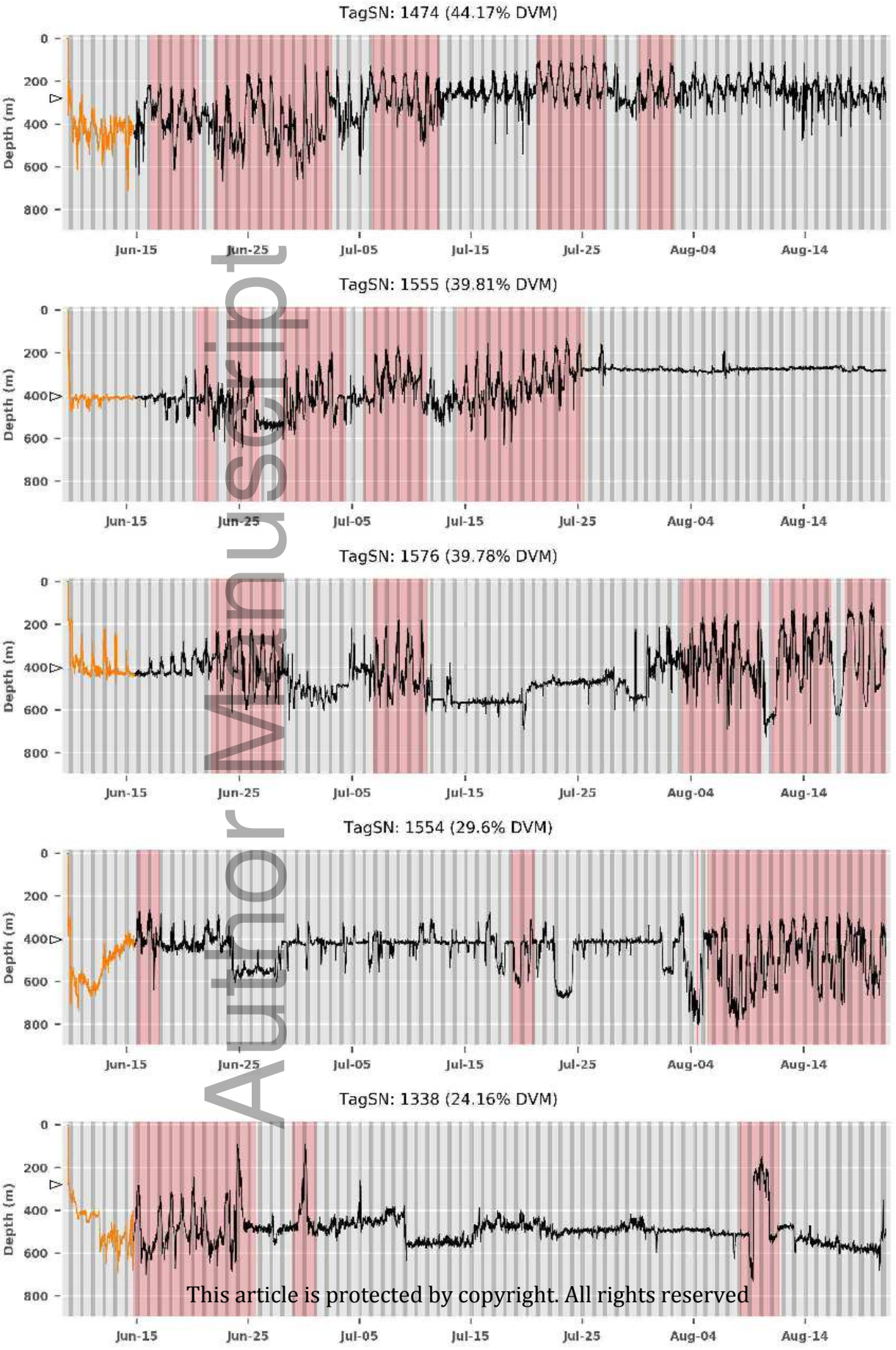

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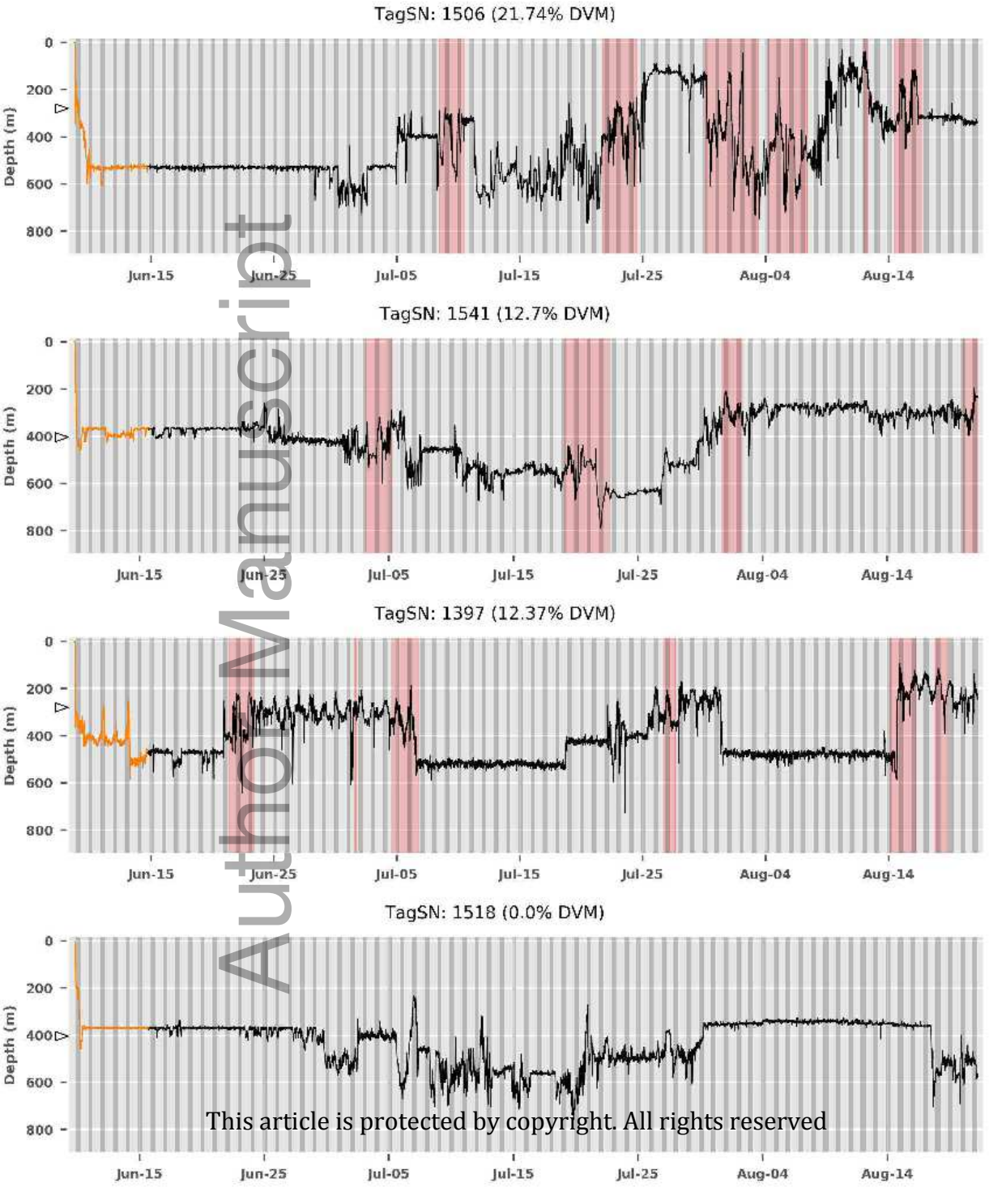

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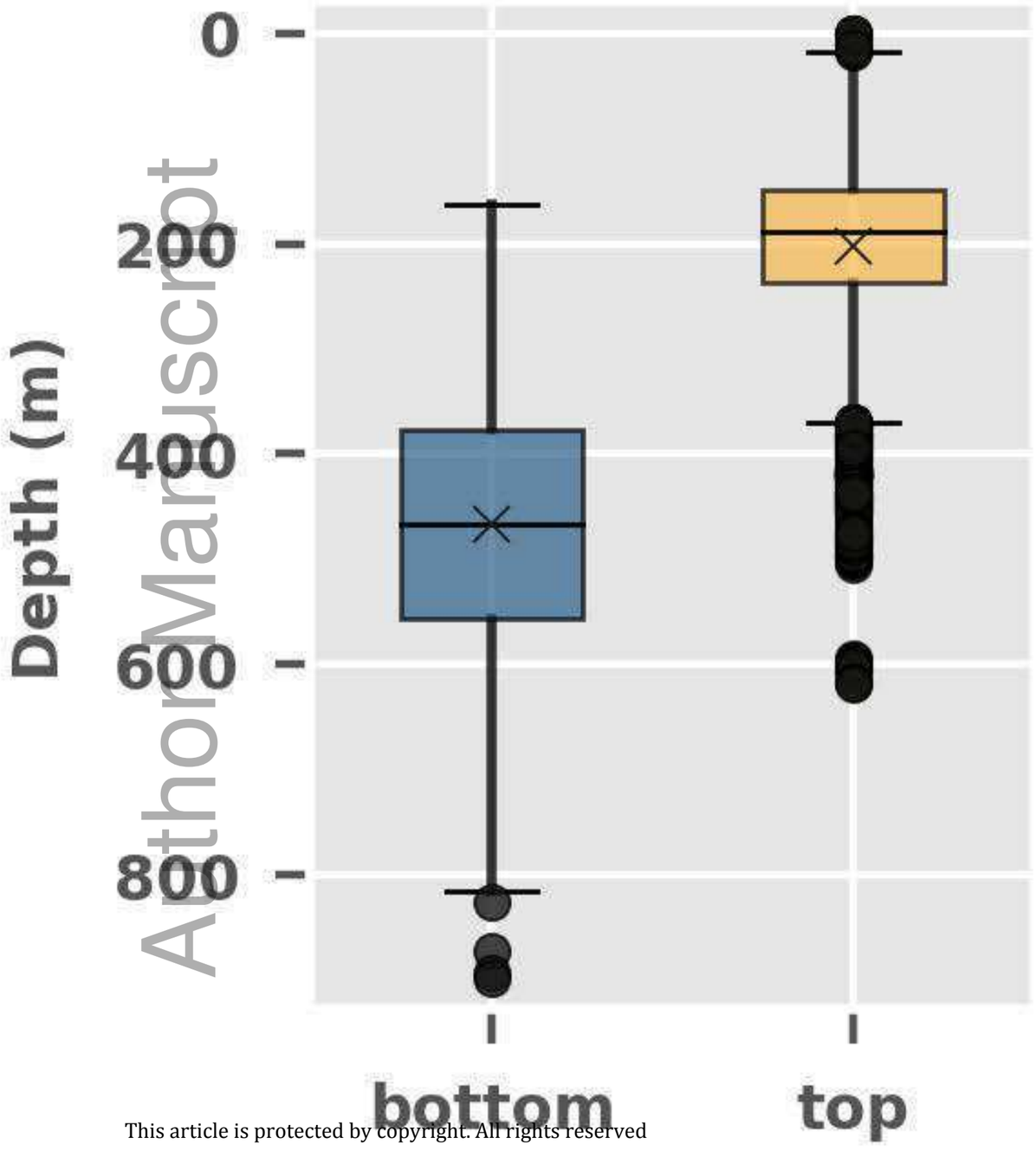

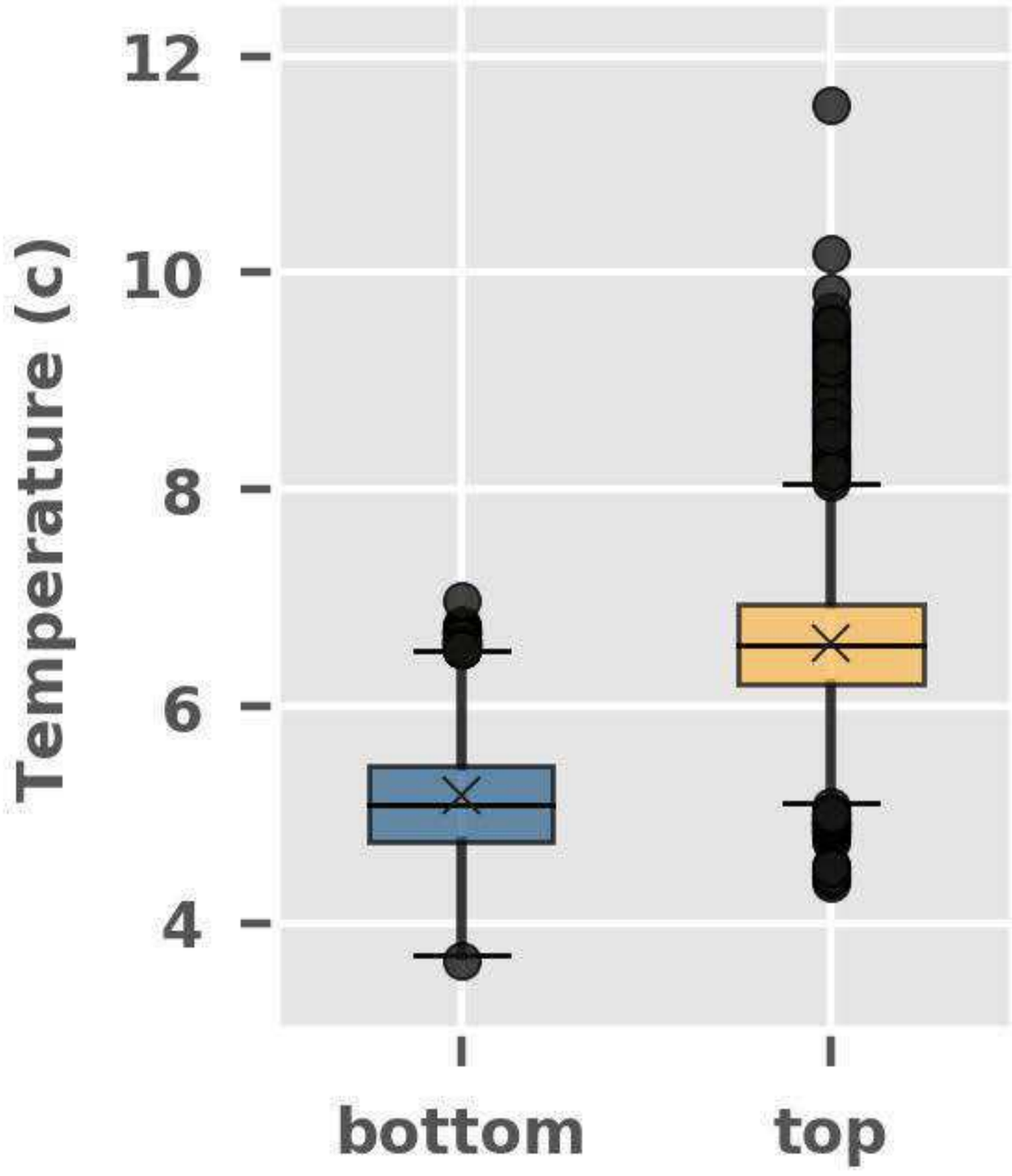

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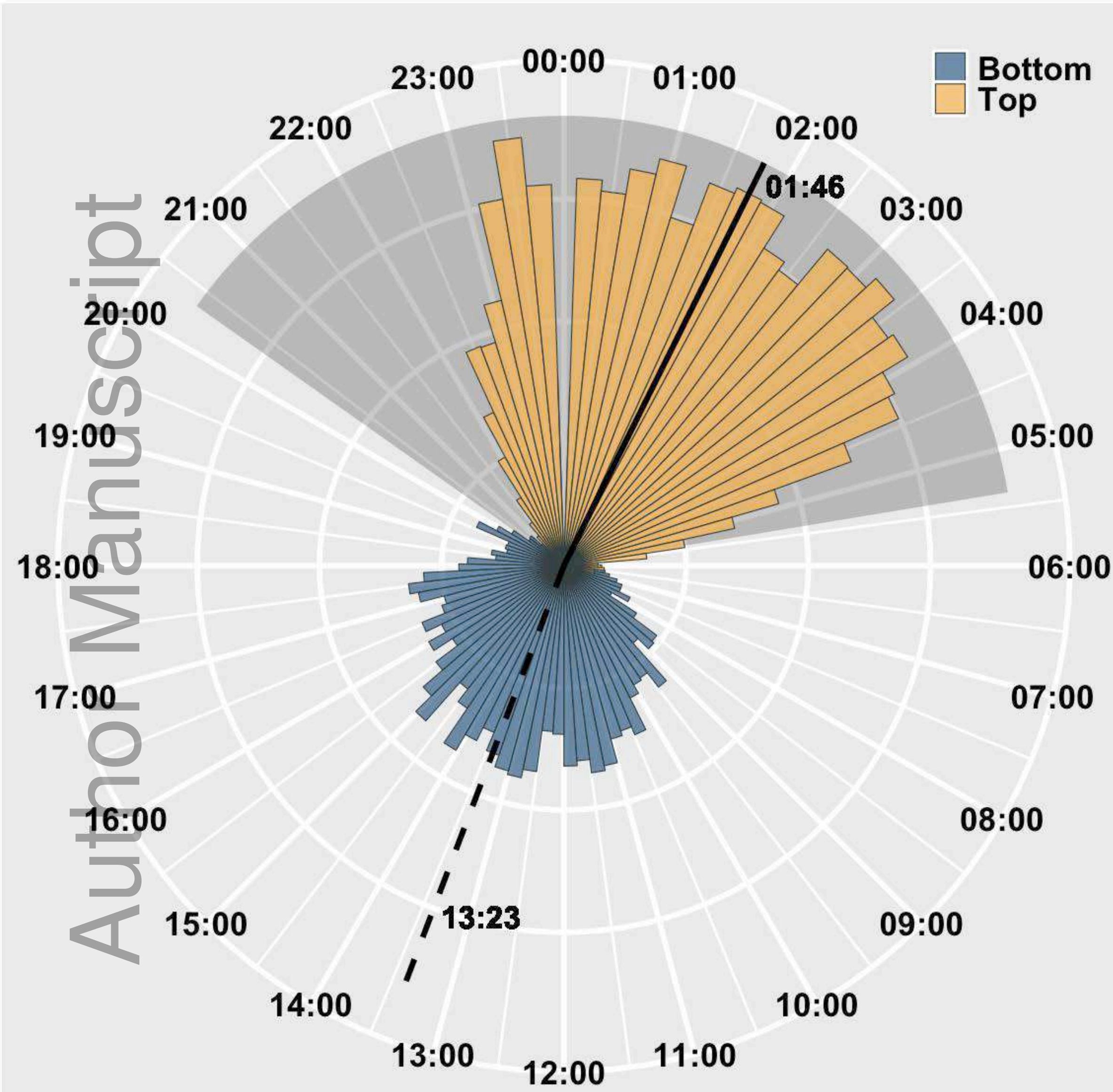

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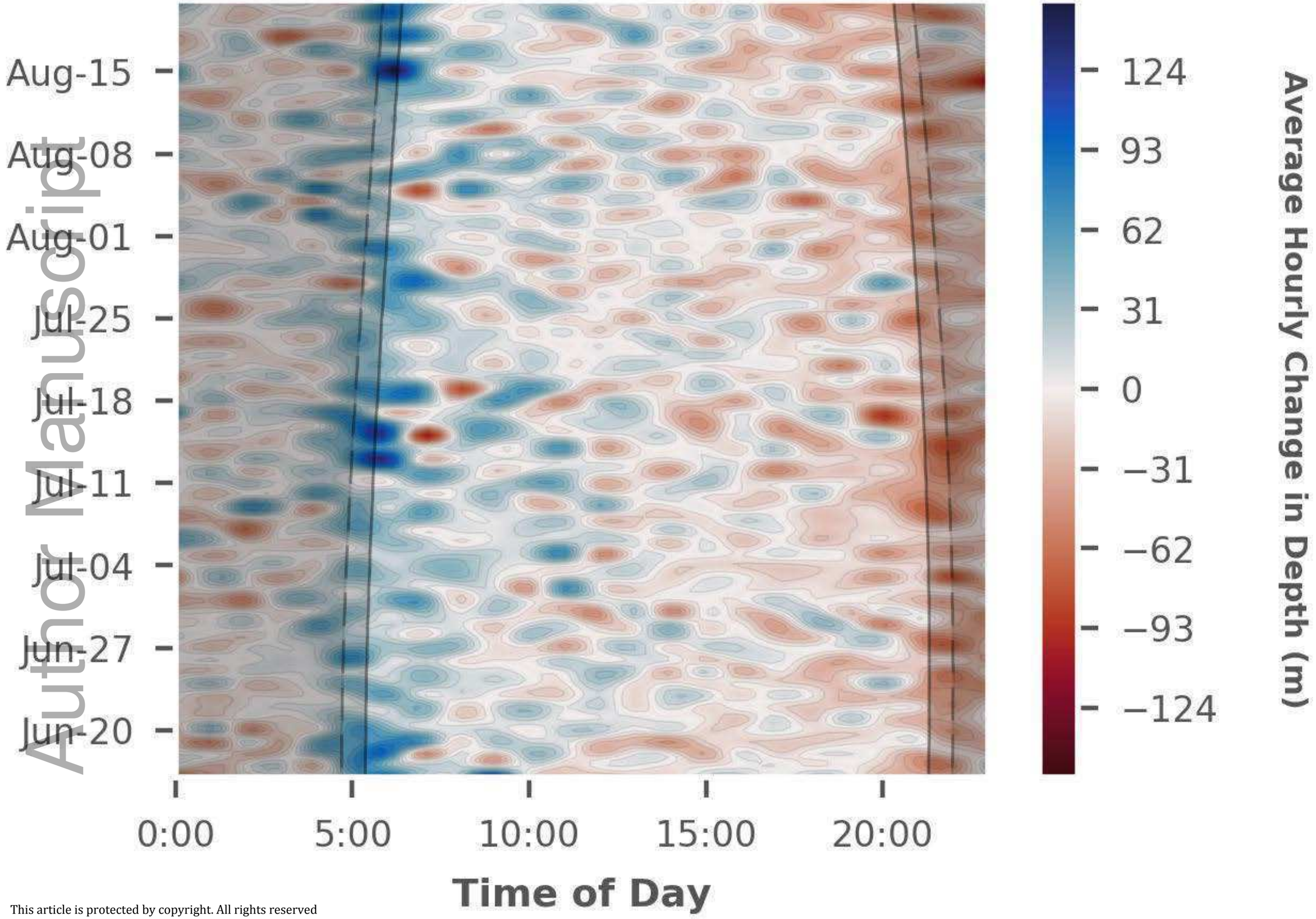

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