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COASTAL AND MARINE ECOLOGY

Diurnal vertical movements in black sea bass (*Centropristis striata*): Endogenous, facultative, or something else?

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Citation: Secor, D. H., H. Bailey, A. Carroll, V. Lyubchich, M. H. P. O'Brien, and C. J. Wiernicki. 2021. Diurnal vertical movements in black sea bass (*Centropristis striata*): Endogenous, facultative, or something else? Ecosphere 12(6):e03616. 10.1002/ecs2.3616

Abstract. Fishes commonly exhibit diel rhythms in movements with consequences to feeding, reproduction, predator evasion, and resting. Such behaviors are conceived as plastic, persisting for phases (days to weeks), and then becoming disrupted, masked, and altered by changed environmental or ecological conditions. In telemetered black sea bass *Centropristis striata* (family Serranidae), we documented a remarkable 4-month record of persistent diurnal vertical movements. Within the U.S. Mid-Atlantic Bight June–October 2019 setting, biotelemetry data of 31 fish were examined through time series analysis and generalized additive modeling. Sun altitude played a dominant role throughout the series, where movements were diurnal. Thermal conditions were uniform until a September hurricane caused a 10°C rise in inhabited waters within the span of six hours, the result of water column mixing. This and other storms caused short-term disruptions (<2 d) to diel rhythmicity. Daytime vessel traffic, but not dolphin presence, caused ≤1 h refuge-seeking excursions. The discovery of pelagic behaviors (up to 15 m off the seabed) requires revision to the species' natural history, which was previously conceived as exclusively demersal. Spring-autumn movement functions included reef recruitment and evacuation, courtship and spawning, and seasonal changes in feeding ecology and predator fields. Throughout these phases, the cycle of daytime movement and nighttime inactivity persisted. We hypothesize that during the nocturnal period these visual specialists become immobile and thus evade predation and mobilize energy toward growth, reproduction, and storage. Because this function does not change from spring through autumn, we speculate that nocturnal quiescence serves as the proximate control for the diurnal activity cycle.

Key words: biotelemetry; black sea bass; Cold Pool; diel movement; diel vertical migration; hurricanes; movement ecology; offshore wind energy; reef fish.

Received 1 September 2020; revised 15 February 2021; accepted 23 February 2021; final version received 7 April 2021. Corresponding Editor: Hunter S. Lenihan.

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INTRODUCTION

Diel patterns of movement are common in fishes, with vertical movements garnering particular emphasis. Mere meters of diving or ascending can expose an individual to large differences in trophic and physical environments (Neilson and Perry 1990, Fox and Bellwood 2011, Secor 2015). Pacific herring *Clupea pallasii* track zooplankton concentrations ascending at night and avoid predators in deeper daytime schools (Hay 1985). Bigeye tuna *Thunnus obesus* forage in deep cold waters and ascend to warm surface waters conducive to high assimilation rates and thermal recovery (Holland et al. 1992). Basking sharks *Cetorhinus maximus* range over a 1000 m deep pelagic seascape, prospecting for zooplankton (Sims et al. 2003). Under the lexicon of diel vertical migration behaviors, long-known for pelagic crustaceans (Cushing 1951), an active literature has engaged whether: (1) such behaviors in fishes are endogenous circadian rhythms; (2) they represent rhythmic movements that are masked or altered by changing conditions; or (3) they are circadian behaviors at all, but rather a subset of diel activity patterns dependent on ecological circumstance (Neilson and Perry 1990, Reebs 2002, Hobson et al. 2009, Nichol et al. 2013, Secor 2015). Circadian rhythms in fish activity are well-documented in laboratory studies, including manipulation of diel environmental cues (free-running and zeitgeber studies, e.g., Godin 1981, Sanchez-Vazquez et al. 1995, Bolliet et al. 2001). In the field, such manipulations are not possible and, in their place, circumstantial evidence is advanced on the adaptive consequences of diel movements including prey tracking, predator avoidance, station-keeping, navigation, courtship and spawning, sleeping, and energetic refuge (Neilson and Perry 1990, Reebs 2002, Arostegui et al. 2017). Long-duration biotelemetry and archival tagging studies increasingly point to behaviors that are facultative rather than rigid: those which, for weeks and months, can be remarkably persistent, but, when ecological circumstances change, are suddenly disrupted and altered (Nichol and Somerton 2002, Fox and Bellwood 2011, Nichol et al. 2013, Sigler and Echave 2019).

In studying noise effects on reef-associated black sea bass (Serranidae *Centropristis striata*), we observed an unexpected degree of vertical movement behavior (Fig. 1). Their vulnerability to bottom-fishing gear together with diver observations indicated that black sea bass should be a bottom-oriented, refuge-seeking, smaller-bodied Serranidae, with spawning presumed to occur near the seabed (Drohan et al. 2007). Yet, black sea bass implanted with depth-transponding tags often frequented pelagic waters, ascending >10 m above the seabed (Fig. 1). Still, this discovery was in keeping with Neilson and Perry's (1990) prediction that understudied demersal fishes might show an unexpected degree of diel vertical behaviors.

Black sea bass are among the most abundant and ubiquitous reef fish, distributed from the Gulf of Mexico to the Gulf of Maine. During winter and in regions north of Cape Hatteras (Fig. 2), they seasonally migrate from shallow shelf and coastal waters to deep shelf habitats (Miller et al. 2016). In comparison with some serranids, which spawn away from territorial reefs in large transient aggregations, black sea bass remain resident and spawn near natural and artificial reefs and wrecks, in temperatures of 10°–21°C (Farmer et al. 2017). Black sea bass are protogynous hermaphrodites: with early maturation of females (11–15 cm total length), and transitioning to secondary males at sizes >30 cm; small first-maturing (primary) males add complexity to the mating system (McGovern et al. 2002, Provost et al. 2017). Foraging likely occurs in adjacent soft bottom habitats as diets are dominated by decapod crustaceans, with fish, squid, and polychaetes also occurring (Frazer and Lindberg 1994, Hood et al. 1994, Drohan et al. 2007).

As a ubiquitous reef fish subject to important commercial and recreational fisheries, black sea bass have become a model species for understanding the impacts of offshore wind development. The U.S. Atlantic is undergoing rapid development of offshore wind farms with over 30 lease areas under development from the South Atlantic Bight to Gulf of Maine. Current industrial projects in the pipeline will result in thousands of turbines producing >28,000 MW, with new leased areas announced each year (NREL 2020). Black sea bass are a strong candidate study species for evaluating construction and maintenance impacts, and colonization to new turbine foundation structures (the reef effect) owing to their limited home range, site attachment, and adaptation to laboratory conditions (Stanley et al. 2020, Wiernicki et al. 2020).

Here, we systematically analyzed two sets of biotelemetry data collected in 2019 from black sea bass in the U.S. Mid-Atlantic Bight to address the following questions: (1) Are pelagic behaviors diurnal? (2) Are they persistent, indicative of an endogenously driven cycle? And (3) what environmental features—storms, vessel noise, and dolphin presence—can modify and disrupt diel movement behaviors? Deploying a predictive model, we confirmed strong diel rhythmicity throughout a 4-month period and related this to possible adaptive significance and relevance in efforts to develop black sea bass as a model species in offshore wind farm impact studies.

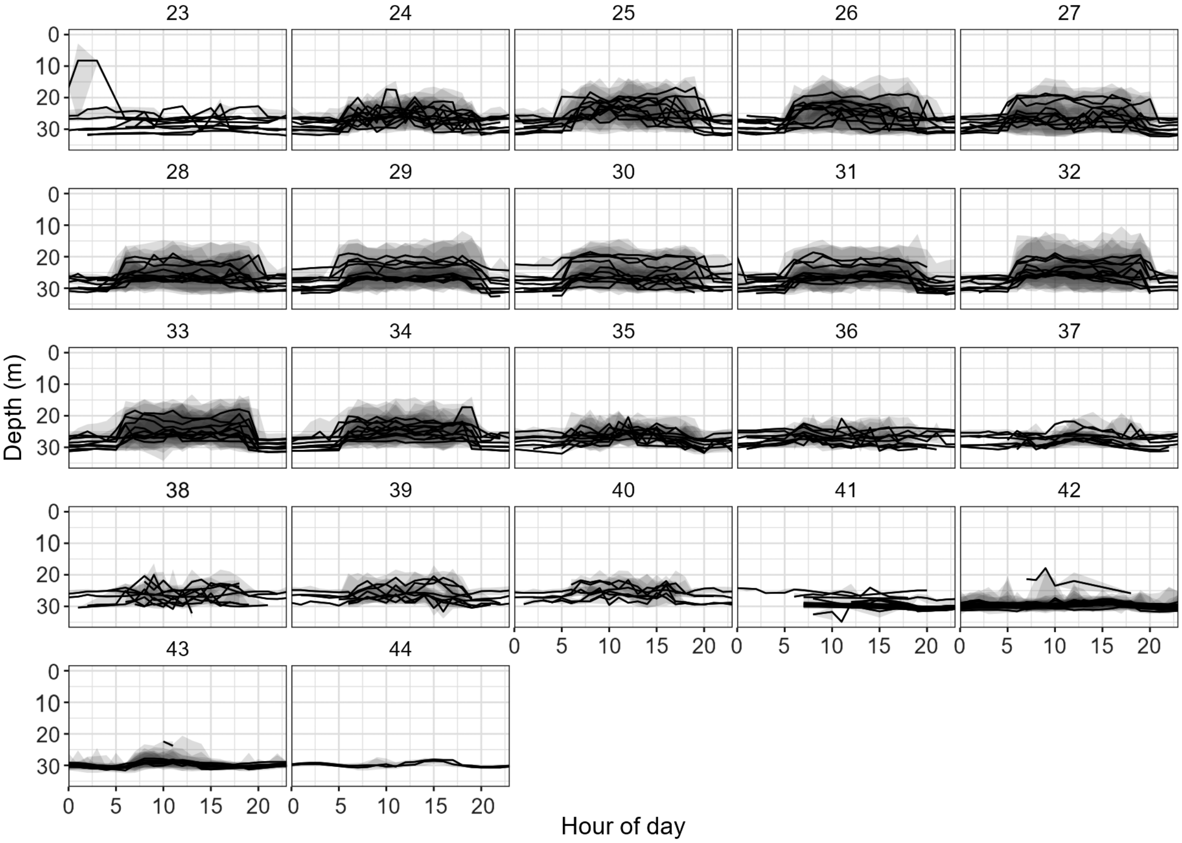

Fig. 1. Diel vertical behaviors of individual black sea bass *Centropristis striata* (black lines) and their distribution (gray band) by calendar week (7 June–29 October 2019). Releases of black sea bass implanted with acoustic transmitters occurred during weeks 23 and 42. Note period of vertical inactivity during night time hours throughout the series.

Materials and Methods

Study site

The two biotelemetry study sites (Fig. 2) were within the central portion of the species' range: the Mid-Atlantic Bight (MAB), a region of the U.S. continental shelf extending from the southern flank of Georges Bank (east of Cape Cod) to Cape Hatteras. Both sites attract recreational fishers and occur in U.S. federal waters (Loftus and Stone 2007, Wiernicki et al. 2020). Site 1 (mean depth = 30 m) was centered on a sunken freighter, the *USS Saetia* (1918), a 98 m vessel of mostly <2 m hull relief but with the mast and a bow section occurring at 3–4 m. Site 2 (mean depth = 26 m) occurred over the Great Eastern Reef, a deposition area of opportunistic materials (primarily concrete units and cable mounds) with <2 m relief. At site depths >20 m, this shelf region is characterized by seasonally-persistent thermal stratification. The Cold Pool is a denser layer of bottom water formed from the vernal heating of surface waters, and subsequent trapping of colder, saltier winter water below (Chen et al. 2018). The result is a highly stratified temperature gradient, which in early fall is rapidly destratified during storms through wind-driven mixing and cross-shelf advection (Lentz 2017). Wrecks at both sites (depths 22–32 m) support abundant aggregations of black sea bass, which have been the subject of focused telemetry studies (Secor et al. 2019, Wiernicki et al. 2020).

Biotelemetry

Telemetry array systems for two separate studies were combined to evaluate vertical

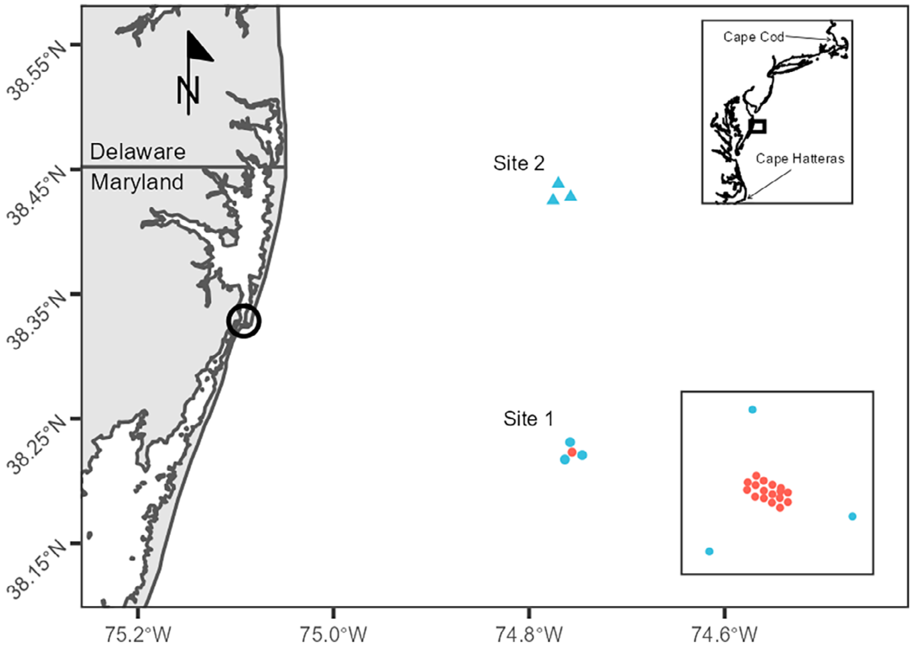

Fig. 2. Study sites for telemetered black sea bass *Centropristis striata* within the southern U.S. Mid-Atlantic Bight extending from Cape Hatteras (southern extent of inset) to Cape Cod (northern extent of inset). Receiver locations are shown by points. June array included sites 1 (blue circles) and 2 (blue triangles), and the October array was centered within Site 1 (lower inset, red circles). NOAA station 8570283 is demarcated by an open circle.

movements. The June array (Sites 1 and 2; Fig. 2) was composed of sets of three VEMCO (Innovasea Systems, Nova Scotia, Canada) VR2AR 69 kHz acoustic-release receivers deployed 7 June 2019 centered on two artificial reef sites where tagged fish had been released earlier that day (Fig. 2). Three receivers were positioned 800 m away from the release location at 0°, 120°, and 240° directions; the 800 m distance corresponded with 50% detectability within this region (O'Brien and Secor 2021). The October array included only Site 1 and was composed of a larger set of VEMCO VR2AR 69 kHz (n = 15) and VEMCO HR2 180 kHz receivers (n = 3), which were deployed 8 October 2019 (see inset; Fig. 2). Receivers were set up in a 3-rowed array centered on the *Saetia* wreck at 100-m distances. All receivers were moored onto the seabed with an upward-facing hydrophone with two 20.4 kg weight plates and suspended 1–2 m from the bottom with a buoy and were retrieved October 29.

Animal collection, surgical, and release procedures were approved by the University of Maryland Center for Environmental Science (UMCES) Institutional Animal Care and Use Committee (IACUC-F-CBL-160-10 and F-CBL-1907), and the US Department of Army Animal Care and Use Review Office (ACURO-DARPA-5534.03). On 7 June 2019, two sets of 15 black sea bass implanted with transmitters were introduced at each June array site; eight of these were VEMCO V9-2L transmitters, and seven were V9P-2L depth-transponding transmitters. Note that June tagging preceded receiver deployments and fish were captured and released on the same wreck or reef structure. On 7 October 2019, 27 depth-transponding tags were introduced into Site 1, of which 13 were V9P-2H 180 kHz transmitters. The 69 kHz transmitters emitted a coded signal at nominal 120-s intervals (range 60–180 s) for the June release and nominal 60-s intervals (range 30–90 s) for the October release. The 180 kHz transmitters emitted a signal at nominal 30-s intervals (range 20–40 s). Black sea bass were captured at reef sites (24–32 m depth) using rod-and-reel on a chartered recreational fishing boat (squid-baited 3/0 J hooks) and immediately placed in a 57-L tank containing ambient seawater until surgery.

Individuals below the legal recreational size (≤32 cm total length TL) were targeted for tagging in an effort to reduce transmitter loss from fishing mortality, although larger individuals were included, particularly in the October release to meet intended samples sizes (June Site 1 23.3–32.0 cm TL, mean = 27.8 ± 2.3 cm SD; June Site 2 24.0–33.1 cm TL, mean = 29.0 ± 2.5 cm SD; October Site 1 21.2–41.0 cm TL, mean = 33.4 ± 4.7 cm SD). Fish selected for surgery were transferred from the holding tank to a surgery tank containing a mixture of seawater and Aqui-S 20E (Lower Hutt, New Zealand; 10% eugenol) anesthetic (20 mg/L). Fish were deemed sufficiently anesthetized when pectoral fin and operculum movement slowed and equilibrium was no longer maintained. Individuals were then transferred to a sling in a surgery tank that allowed gills to remain immersed. Transmitters were inserted through a 1 cm incision made cranial to the vent and just lateral to the midline. Incisions were closed with one or two single surgical-knot sutures. Post-surgery fish were transferred back to the holding tank to monitor for recovery, which was identified when regular operculum movement and equilibrium resumed. Elapsed times between deck capture and release for the June releases, were 17.3 ± 7.0 min and 20.3 ± 5.4 min, respectively, for Sites 1 and 2. October sea state conditions in the wake of TS Melissa (Table 1) precluded data records on surgery times. Tagging and release conditions may have contributed to higher loss rates than for the June release (see *Results*). To promote recovery and reduce the risk of surface depredation by birds and large fishes, recovered fish were descended to half depth (~15 m) using a pressure-release device (Seaqualizer, Florida, USA) at the site of their capture.

Environmental data

Telemetry receivers logged bottom temperature every hour; hourly bottom temperatures were averaged across receivers for each site. The R package suncalc (Thieurmel and Elmarhraoui 2019) was used to calculate sun altitude above the horizon in radians, where 0 rad corresponds to the horizon, π/2 rad corresponds to the zenith, and negative values are below the horizon. Hourly tide level, measured as mean lower low water, was obtained from U.S. National Oceanic and Atmospheric Administration (NOAA) Station 8570283 (38°19.7′ N, 75°5.5′ W) at Ocean City Inlet, Maryland, USA. Time series data on observed wind speed were taken from US National Data Buoy Center Station 44009 (38°27.24′ N, 74°42.6′ W) and averaged to hourly speeds (m/s).

Table 1. Mid-Atlantic Bight storm events during 2019.

Name	Maximum wind speed date	Duration (h)	Maximum wind speed (m/s)
Tropical Storm Erin	Aug 26 21:00	45	9.8
Tropical Storm Dorian	Sep 7 00:00	46	14.8
Unnamed Wind Event	Sep 13 03:00	32	13.3
Tropical Storm Humberto	Sep 18 21:00	44	11.6
Tropical Storm Melissa	Oct 11 01:00	103	14.5

Notes: A storm was considered present in the area when wind speeds consistently increased over 5 m/s (3 or greater on the Beaufort Wind Scale). Wind speeds refer to average hourly velocity (m/s) recorded at US National Data Buoy Center Station 44009.

Acoustic recorders attached to telemetry receiver moorings were deployed at Site 1 (SoundTrap ST300, Ocean Instruments, New Zealand) and Site 2 (LS1, Loggerhead Instruments, Florida, USA) on 7 June 2019 with a sampling rate of 48 kHz, duty-cycled to record two minutes on and eight minutes off. The SoundTrap recorder was set to the low setting (sensitivity −185.4 dB re 1 V μPa^{-1}), and the LS1 recorder (sensitivity −180.0 dB re 1 V μPa^{-1}) was deployed with a gain of 2.05 dB re 1 μPa. Ambient sound pressure levels (root-mean-square) were calculated for each site using a custom script in MATLAB (version 2020a) within the expected hearing range of black sea bass (Stanley et al. 2020; frequency range 100 Hz–1 kHz) and the full broadband frequency range (10 Hz–24 kHz). The acoustic recorders were recovered on 30 October 2019, but owing to battery limitations, records were only available until 6 September 2019 at Site 1 and until 13 August 2019 at Site 2.

Movement data

Vertical movement data were averaged to yield mean hourly depths for the period 7

June–27 October 2019. Note that seabed depths were aliased by maximum hourly transmitter depths. Thus, referenced ascent behaviors is in relative depth or depth intervals (e.g., 10 m from the seabed). Still, three expelled transponders during October (Site 1) recorded depths that were similar to seabed depths measured over the same period by vessel sonar (Appendix S1). These same three transponders exhibited clear tidal oscillations and were used as a local measure of tide (Appendix S1) to reduce the influence of tide in depth records. Depths recorded by these transmitters during 22–27 October were regressed over the NOAA station tide levels, which were preliminarily orthogonally transformed to avoid collinearity of polynomial terms in the model. Let Tide_t^* be the transformed tide level at hour t, then

$$\text{Depth}_{tj} = \sum_{i=0}^{3} \beta_i (\text{Tide}_t^*)^i + \alpha_j + \varepsilon_{tj}$$

where β_i is the polynomial regression coefficients ($i = 0,\ldots,3$), $\alpha_j \sim N(0, \delta^2)$ is random intercept per jth transmitter ($j = 1,\ldots,3$), and $\epsilon_{tj} \sim N(0, \sigma^2)$ are the regression errors. The estimated coefficients $\hat{\beta}_i$ and transformed tide levels for the whole study period were used to remove tidal influence from all transmitter depth records (Appendix S1). To avoid using data from the expelled transmitters in further analysis, all records after 21 October were removed. The tide-adjusted depths were then divided by maximal tide-adjusted depths for each location to obtain relative depths in the interval [0,1], where 0 corresponds to surface and 1 corresponds to the bottom.

Modeling framework

Environmental drivers of depth behavior were tested using generalized additive models for location, scale, and shape (GAMLSS; Rigby and Stasinopoulos 2005). GAMLSS (see Appendix S2) allowed us to model the location (or the mean) of the underlying distribution while simultaneously modeling the scale (variance) and shape parameters. Usually, two shape parameters are used, characterized as skewness and kurtosis, but GAMLSS are extendable to more than four distribution parameters. We used non-linear semi-parametric form of GAMLSS

$$g_k(\theta_k) = f_{1k}(x_1) + f_{2k}(x_2) + \cdots + \boldsymbol{X}_k^* \beta_k^*$$

where the k-th distribution parameter, θ_k ($k = 1,\ldots, K$), was modeled using link function $g_k(\cdot)$ and a combination of

1. additive smooth terms obtained using penalized splines $f(\cdot)$ for most explanatory variables x (the non-parametric part of the model), and
2. parametric regression formulation $\boldsymbol{X}_k^* \beta_k^*$, where the design matrix $\boldsymbol{X}_k^*$ contains remaining (categorical) explanatory variables and β_k^* is the vector of regression coefficients.

The underlying distribution of the response variable was selected based on the characteristics of the data and minimal Akaike information criterion (AIC). For relative depth (continuous values in the range [0, 1]), a four-parameter beta-inflated distribution was used ($K = 4$), which is a beta distribution with appropriate standardizations that allow the response variable to include endpoints of the range [0, 1] (Stasinopoulos et al. 2008). Further model specification was done using a stepwise variable selection procedure in R based on generalized Akaike information criterion (Strategy A in Stasinopoulos and Rigby 2020). The smooth terms were restricted to use a maximum 7 degrees of freedom to control smoothness, and the smoothing parameters were estimated using local generalized cross-validation. Smooth terms were considered for sun altitude, day of the year, and bottom water temperature, while the categorical variable representing individual fish (transmitters) was not smoothed. Model for the location parameter (θ_1) also considered the response lagged by one hour (i.e., the relative depth one hour ago) as an additional explanatory variable that helped capture autoregressive dependencies in the data.

The (randomized) quantile residuals of the fitted models were checked using the standard diagnostic plots for homoskedasticity, uncorrelatedness, and normality. Statistical significance of the estimated model coefficients was assessed using individual t-tests, with significance level $\alpha = 0.05$. The shape of relationships captured by the model, particularly with the smooth terms, was studied by plotting the regression terms against their predictors.

Residuals, calculated as the difference between observed and fitted relative depths, were extracted to investigate whether noise disturbances owing to vessel or dolphin occurrences depressed daytime vertical behaviors. To reduce the confounding behavior of storms and destratification, the period 8 June–26 August was surveyed for excursions defined by extreme (>98.5th percentile) residuals of depressed activity, which corresponded to 50 h of concurrent sound records. These sound records were manually audited to identify the presence of three classes of noise disturbances using Raven Pro (Bioacoustics Research Program 2014); classes included all vessels, large vessels, and dolphin. Vessel presence was defined as any rotor noise generated while transiting or maneuvering in the area; a vessel was classified as large if the frequency content was concentrated below 1 kHz, indicative of larger shipping and cargo vessels (Hildebrand 2009); and whistles, echolocation clicks, or buzzes indicated the presence of dolphins. An equal number of control daytime hours (50 h) were randomly selected during the same period and audited as above to quantify typical presence of each noise disturbance class. Any selected hour that matched those already identified to include an excursion was rejected, and a new option was generated in its place until all 50 h were identified. The relative frequency of noise class presence was compared across excursion and control hours using a two-sided Fisher's exact test.

RESULTS

Site retention

There was strong retention by black sea bass at the two wreck sites, indicated by low loss rates following the early June releases (Fig. 3). After the immediate loss of several individuals, 15 and 11 individuals were detected through the third week of August; thereafter, increased loss rates were associated with storm events and ocean destratification (Fig. 3; Table 1). Still, without a larger receiver array, loss rates cannot be ascribed to departures, fishing or depredation with absolute confidence. High loss rates were observed for the second release of transmitters on 7 October 2019 into the October array; only four of the 27 released fish were detected 20 d later. Here, fish were released during the wake of a large storm (Table 1), which may have contributed to the high rates of loss.

Vertical movements

Vertical movements were apparent throughout summer months, but were suppressed in amplitude following late summer and early fall storms

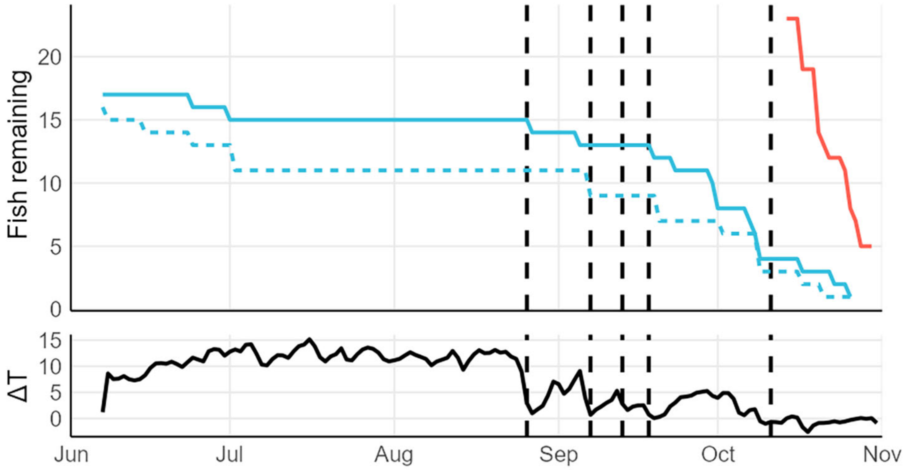

Fig. 3. Tagged fish loss rate (top) and destratification (bottom) at Sites 1 (blue solid line) and 2 (blue dotted line) for June and October (red line) releases. Loss levels are indicated by stepped drops in the number of fish detected at each site. Destratification is shown as the difference between surface and bottom temperature (ΔT), which approaches nil with the series of storms beginning in late August (indicated by vertical dotted lines; see also Table 1).

(Fig. 1). During summer, ascents occurred up to 15 m off the seafloor. Diel vertical behaviors—daytime ascents followed by nighttime bottom attachment—were apparent during the period of stable stratification: weeks 28–34. This behavior was subsequently disrupted by a series of storms during weeks 35–38 (Table 1). During week 42 (October), a second release of 27 black sea bass occurred and exhibited much smaller-amplitude vertical movements than the earlier-released fish.

Tide-adjusted vertical behaviors across individuals strongly coincided with sun altitude (Fig. 4). The covariance between sun altitude and vertical behaviors was remarkable in daily recurrence throughout the >4-month series. Vertical behaviors occurred as phases of nighttime bottom habitat use, rapid ascent during dawn, midwater daytime incidence, and then a rapid descent during dusk. The amplitude in vertical movements was diminished following the 26 August storm with subsequent gaps in the record owing to storm noise (Table 1), which masked the acoustic transmitters (Secor et al. 2019). Interestingly, high-amplitude vertical behaviors resumed following the 18 September storm, continuing until a large loss of tagged fish from the site associated with the 11 October storm (Fig. 3).

Model of diel movements

The GAMLSS model for relative depth included equations for the location and scale parameters (θ_1 and θ_2), while shape parameters were estimated without modeling their dependence on the covariates. The final model passed visual diagnostics of the residuals, and coefficients for all terms were statistically significant based on the *t*-tests. Results for the location parameter (θ_1, i.e., the mean) are presented below; other results are available in Appendix S2.

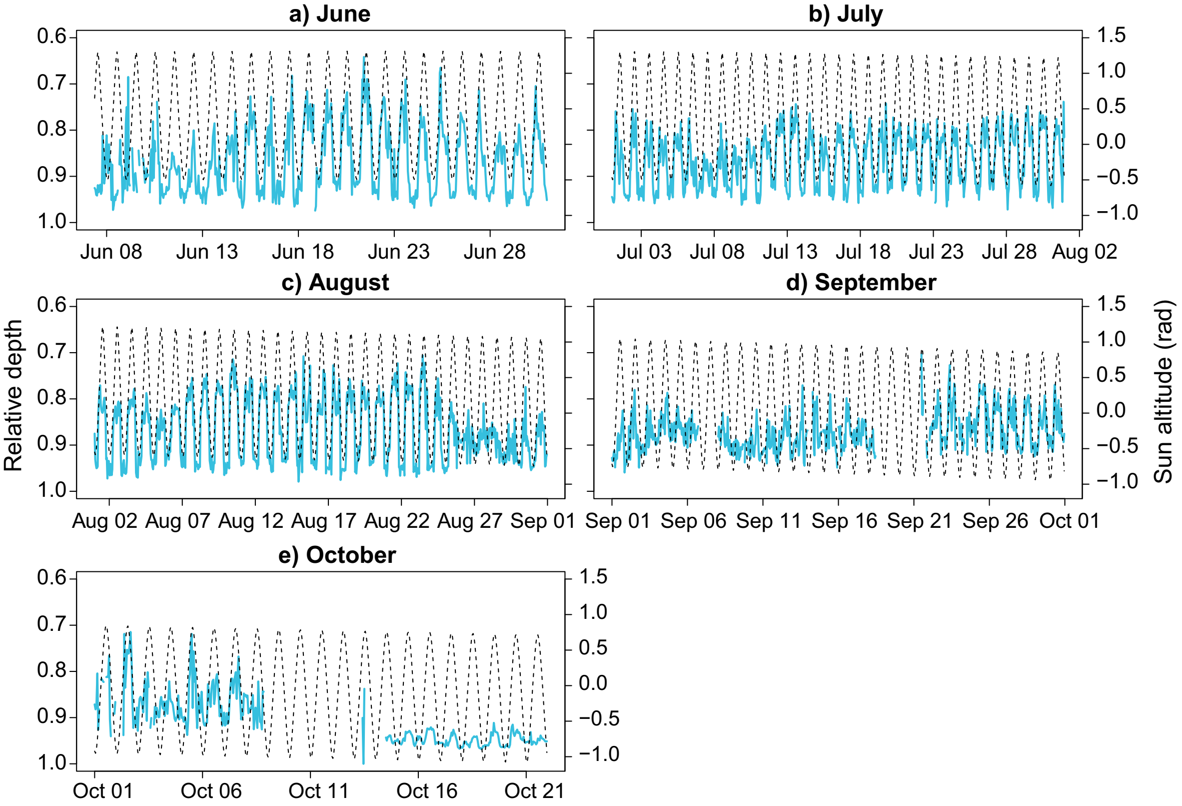

Fig. 4. Diel patterns in hourly vertical depth position (solid line) and sun altitude (dashed line) for tagged black sea bass *Centropristis striata*, by month. Note that positions are adjusted for tide, expressed relative to site maximum depth, and averaged for all tagged fish.

Partial effects plots revealed mean depth behaviors that were responsive to sun altitude, bottom temperature, and season (Fig. 5). Individual variation (transmitter effect) was high and exhibited modes of behaviors associated with each release. Those released into the June array exhibited negative additive effects (higher in water column), than those released into the October array. As expected, depth behaviors were strongly autocorrelated across hourly intervals. Depth deviated with sun altitude, where positive values (daytime) were associated with decreased depths. The influence of destratification is seen in the partial effect of bottom water temperature: fish depths rapidly increase as temperatures rise, associated with rapid water column mixing during storm-forced destratification (Fig. 3). The seasonal plot exhibited a full oscillation: the latter part of this trend is consistent with high-amplitude vertical behaviors observed following the 18 September storm event (day 262; Fig. 5), but the early part of the trend is inconsistent with reduced amplitude vertical behaviors between 26 August (day 238) and 18 September (day 262).

Excursions from diel vertical behaviors

For the period 7 June–26 August, ambient sound pressure levels (root-mean-square) were predominately between 104 and 108 dB re: 1 μPa at both sites (see Appendix S3). The incidence of bottom-oriented depth excursions was significantly higher in the presence of all vessels ($P = 0.04$) and in the presence of the subset of classified large vessels ($P < 0.001$; Table 2). Behavioral excursions were not associated with the presence of dolphin vocalizations ($P = 0.30$).

DISCUSSION

Persistent diel vertical behaviors

Diurnal rhythms in vertical movements were persistent for the entire four-month study period, a remarkable record in its consistency and duration despite frequent and strong environmental perturbations and likely seasonal changes in reproductive state and trophic conditions. Active movements during the daytime followed by their cessation at night, observed at both the individual and group scale (Figs. 1, 4), are strongly suggestive of an endogenous cycle, substantially less plastic than observed for other demersal (Humphries et al. 2017, Sigler and Echave 2019) or pelagic species (Schaefer and Fuller 2010, Andrzejaczek et al. 2019). Although a field trial cannot establish circadian free-running cycles, the strong correspondence between movement and sun altitude points to the likelihood of a cycle entrained to light, a common zeitgeber in endogenous activity rhythms (Godin 1981, Neilson and Perry 1990). Further, the rhythms occurred in a fairly homogenous thermal environment, indicating a non-supporting role for temperature (Neilson and Perry 1990). The persistence of the diurnal cycle, the rapid recovery of this cycle following large destratification events, and its resilience to frequent vessel and predator traffic all support a behavior that is more obligatory than facultative, an unexpected outcome of this study. In the literature, diel vertical movement persistence is typically on the order of days to weeks without interruption, although a similar duration (4 months) rhythm was documented for two open ocean porbeagle sharks *Lamna nasus* based on archival tag returns (Francis et al. 2015).

As black sea bass are reef-associated visual specialists, we propose that diel activity patterns are controlled by the nocturnal rhythm of resting within the reef structure. Rest and sleep within predation refuges allow for energy conservation during nighttime periods when foraging and mating would otherwise be less efficient and convey predation risk (Reebs 2002). The epitome example of cycles driven by sleep are parrotfishes (family Scaridae), which overnight in self-built cocoons (Ogden and Buckman 1973, Bruggemann et al. 1994), yet many reef fishes have diel cycles of inactivity associated with refuge behavior (Morrison and Carbines 2006). Even in the absence of shelter, rest may drive diurnal cycles, as in demersal skates and rays (Humphries et al. 2017). Resting and/or sleeping phases in black sea bass were directly observed in a rearing study (DHS, *personal observation*) where individuals aggregated and became completely quiescent in provided structure. Daytime activity relates to multiple functions including mating, foraging, and predator evasion, which change seasonally. Through all these functions, the nighttime period of inactivity is constant and we speculate that this resting period drives the cycle. Energetic gains owing to lower activity

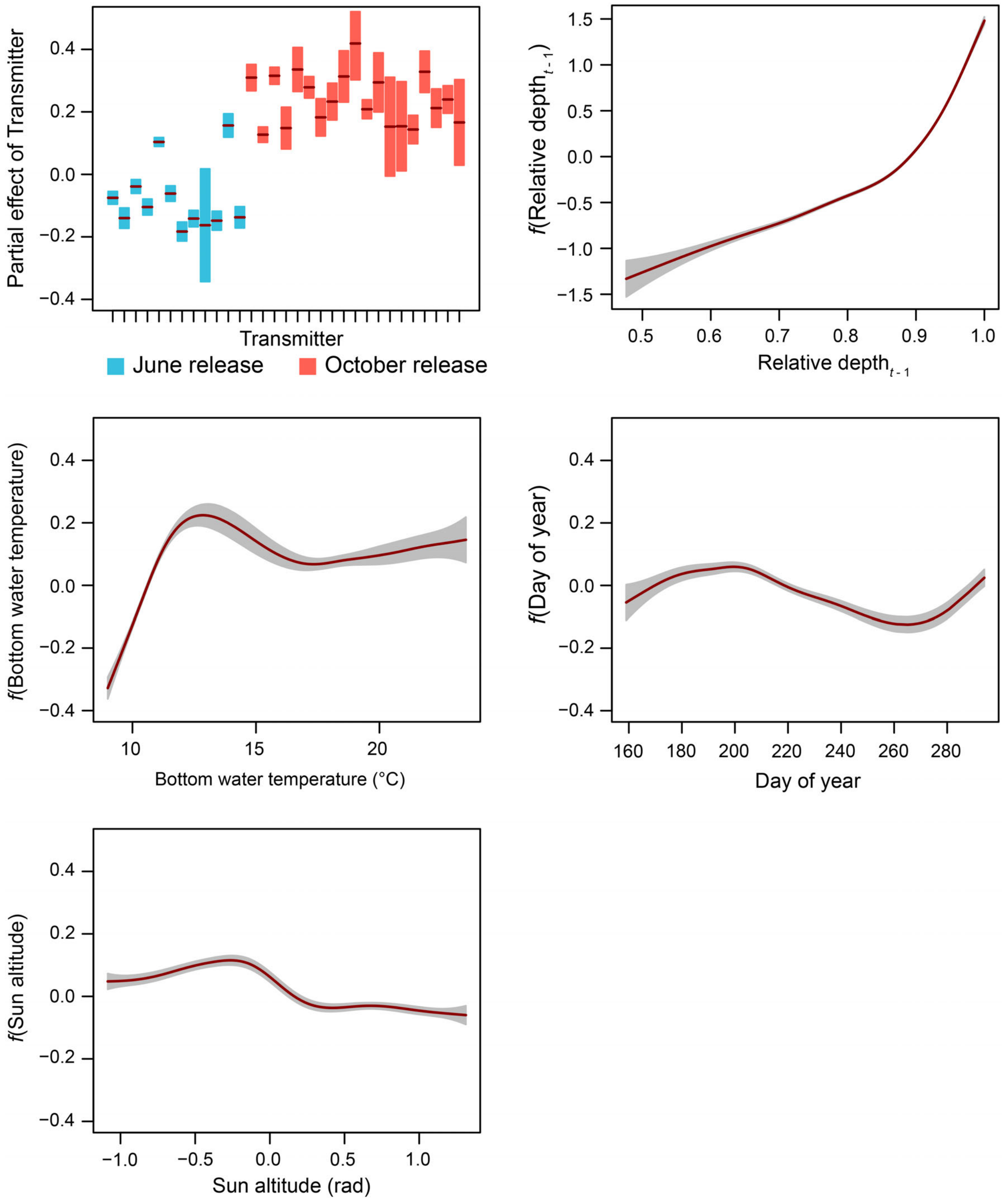

Fig. 5. The additive terms plot for the mean model for relative depths for tagged black sea bass *Centropristis striata*. Transmitters are coded by whether they were released into the June (blue) or October (red) arrays.

include increased assimilation and conversion efficiency, increased gamete provisioning, and memory capacity (associated with sleep; Reebs 2002).

The time series of diel movement cycles was recovered from two studies not specifically designed for the purpose of examining activity cycles. Two sets of fish released during June and

Table 2. Categorical analysis of behavioral excursions (i.e., movement toward the seabed) of black sea bass *Centropristis striata* associated with dolphin and vessel noise events for the top 1.5% of behavioral excursions and an equal number of control hours during which vessel noise and dolphin vocalizations were absent.

	Total positive hours		
Event type	Excursion	Control	Significance
Dolphin	16	22	NS
Vessel	42	32	*
Large vessel (<1 kHz)	40	18	***

* $P < 0.05$; *** $P < 0.001$.

October into two different arrays were employed to increase the sample size and duration of examined telemetry records. Both arrays were designed to evaluate different sources of anthropogenic noise (June array, pile driving; October array, vessel noise) on evacuation and movement activity (Secor et al. 2019, Wiernicki et al. 2020). Movement activity, indexed as serial detections between unique receivers (Fabrizio et al. 2014), was thought to represent horizontal movements and was depressed in the wake of storms. We initially sought to use this same index in the current study, but uncovered a bias indicating that this presumed horizontal movement index was influenced by diel changes in detection rates, whereby daytime (pelagic) detections were fourfold higher than nighttime detection rates (Fig. 6). This was further confirmation of higher diurnal activity, but also suggested that past inferences on how storms depressed movements (Secor et al. 2019, Wiernicki et al. 2020) were likely pertinent to vertical rather than horizontal behaviors.

Vertical position data included the combination of June and October releases. The October releases exhibited a different mode of vertical behavior, but this behavior was similarly influenced by sun altitude, bottom temperature (destratification), and season as were the June-released fish. A second interesting bias is that the long-term movements by June-tagged fish may have been a subset of behaviors associated with residency, not reflective of those individuals that were lost to the array. A large evacuation event in response to a September 2016 storm (40% of remaining individuals across three sites) allowed comparison of behaviors of resident v. evacuating individuals prior to the event, with no significant differences in movement activity (Secor et al. 2019). Still, movement activity index is a coarse index of activity, and modalities in exploratory and sedentary behaviors likely exist in black sea bass as they do in other fishes (Cote et al. 2010, Nakayama et al. 2012, Secor 2015). A fine-scale positioning analysis could uncover such behaviors. Regrettably, owing to data sharing restrictions and the brevity of deployment, we did not include the position analysis that the October array might have otherwise supported. An improved design would entail the long-term deployment of such a telemetry positioning system, which would simultaneously capture fine-scale vertical and horizontal movements, allowing three-dimensional analysis of diel activity space (McKinzie et al. 2014).

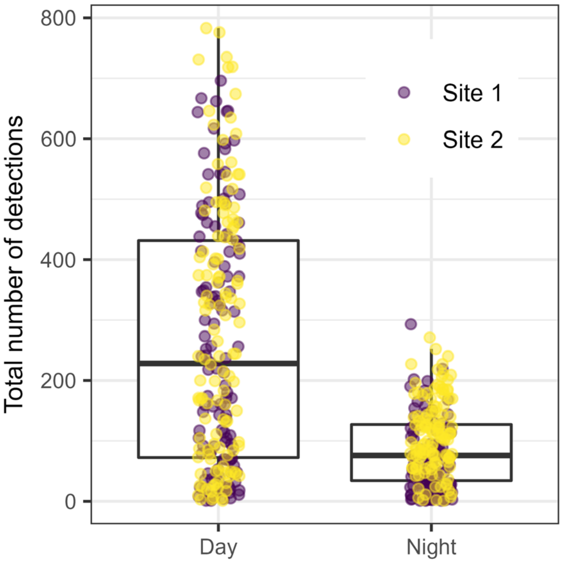

Fig. 6. Total number of daily detections for June-released black sea bass for daytime and nighttime periods. Box whisker plots are shown along with the total number of detections for each day at Site 1 and Site 2. Day was defined as periods in which the sun's altitude was greater than 0 radians.

Consequences of a daytime lifestyle

Diurnal activity cycles persisted through seasonal phases of reef recruitment, mating and reproduction, changed food web dependencies, and reef evacuation. In southern parts of their range, black sea bass are year-round residents in shallow shelf reef habitats, but in regions north of Cape Hatteras, spring and autumn migrations occur between offshore winter and nearshore summer habitats (Musick and Mercer 1977, Miller et al. 2016). In the MAB, springtime recruitment to nearshore reefs occurs over a several month period from April through July, and autumn emigration occurs from September to November (Fabrizio et al. 2014, Secor et al. 2019). Vertical movements were dampened owing to fall storms, but then resumed, sometimes at high amplitude during late September and early October. In avian ecology, such pulses of high activity are recognized as a restlessness syndrome, a precursor to seasonal migration (Berthold 1999). Speculating, fall emigrants could comprise two components: individuals evacuating owing to storms and others cued to leave owing to a seasonal endogenous trigger.

In contrast to a previous view that black sea bass deposit eggs near the seabed (Drohan et al. 2007), evidence presented is strongly indicative of pelagic spawning for this species: ascent behaviors consistent with courtship and spawning behaviors of other Serranidae (Bruggemann et al. 1994, Donaldson 1995, Martinez-Diaz et al. 2001). Diurnal vertical behaviors persisted during summer months when spawning in the MAB is expected (May–September; Provost et al. 2017). Black sea bass show sexual dimorphism in color and presence of a male nuchal hump, visual displays that would be consistent with daytime courtship and spawning. Spawning ascents are thought to give young advantage by placing them in warmer waters conducive to rapid development and growth, and by increasing advection and transport of larvae to inshore nursery habitats (Sancho et al. 2000, McKinzie et al. 2014). As a relatively small serranid species, black sea bass spawn on resident reefs, and do so frequently; spawning intervals for females in the field have been estimated to range from 2.7 to 4.6 d (McGovern et al. 2002). In captivity, the similarly sized Serraninae, spotted sand bass *Paralabrax maculatofasciatus*, was capable of daily spawning (Martinez-Diaz et al. 2001). In October, black sea bass reproduction ceases. Black sea bass were sampled for relative gonad weight in 2018 in this same region: in June and July, the mean gonadosomatic ratio was 5 ± 2.8% ($n = 75$; mean ± SD), and in October, it was 0.3 ± 0.2% ($n = 41$; Wiernicki 2019). Considering that diurnal vertical behaviors persisted thereafter, reproduction was unlikely the proximate driver of diurnal movement.

As visual and maneuvering specialists, black sea bass likely forage during daytime and evade predation through association with structure at night. Crustaceans are often dominant in the diets of adult black sea bass but squid and fish also frequently occur (Hood et al. 1994, Drohan et al. 2007). The relatively long assimilation times of crustaceans may positively bias their representation in stomach contents (Jackson et al. 1987, Lankford and Targett 1997). Conversely, pelagic fish and squid representation may have been biased low in past diet studies. Seasonality in diets are noted, and although not yet well-described, likely occur in temperate shelf ecosystems. Key predators in the MAB are sharks and dolphins. Dolphins are most common in this area during the summer months and have been primarily detected echolocating to search for prey at night (Bailey et al. 2018). Putative shark predators include sand tiger *Carcharias taurus*, dusky *Carcharhinus obscurus*, bull *Carcharhinus leucas*, and blacktip *Carcharhinus limbatus* sharks and are known from telemetry records to occupy the southern MAB June–October (Secor et al. 2020). Thus, as with reproduction, diurnal behaviors can be viewed as adaptive to foraging and predator evasion.

Whether black sea bass sleep as do other reef fishes (Reebs 2002) and some sharks (Kelly et al. 2020) is unknown. We have noted in the laboratory that when provided structure black sea bass can become completely quiescent for extended periods of time (DHS, *personal observation*). Diurnal snappers and other species are also described as sleeping as they remain inert for extended periods of time (Robertson and Sheldon 1979, Morrison and Carbines 2006). Inactivity and withdrawal at night likely have an important role in predation evasion, but by becoming sedentary black sea bass can allocate increased metabolism to growth and reproductive provisioning (Reebs 2002). The latter may be particularly important as black sea bass spawn frequently. Diel changes in metabolic allocations have been observed in other fishes, particularly for diurnal and nocturnal specialists (Liu et al. 1997, Fischer 2000, Lim et al. 2020).

Disruptions to daily routines

Wind and storm events that caused destratification in 2019 resulted in a bottom temperature increase of 10°–12°C in the span of six hours (Fig. 3). Prior to that period, experienced temperatures were fairly uniform as movements were restricted to sub-thermocline waters. The acute thermal changes brought about by water column mixing would result in accelerated respiration and homeostatic stress, causing problems in oxygen binding, protein synthesis, and even gene expression (Paajanen and Vornanen 2004, Gollock et al. 2006, Logan and Somero 2011). For an increase from 12° to 24°C, black sea bass would be expected to show twofold increased basal respiration rates and a 33% decline in aerobic scope (Slesinger et al. 2019). As a result, activity rates are expected to diminish as was observed in 2016–2018 telemetry studies at the same sites (Wiernicki et al. 2020). Indeed, we had expected black sea bass to become inactive following destruction of the Cold Pool, yet diurnal activity cycles persisted following several-day disruptions.

Refuge-seeking behaviors during daytime might also disrupt diurnal movement cycles. In tests of vessel and predator (dolphin) presence, we detected a small but significant daytime bottom-seeking behavior associated with vessel noise (particularly for large vessels), but not for dolphins. An increased sample size may have revealed a dolphin effect, but, in general, these excursions were likely quite brief given the persistence of diel cycles through the series. The study site experiences frequent vessel traffic from recreational and commercial fishing vessels and larger maritime vessels, the latter particularly during night, and black sea bass may have adapted to some extent to this noisy soundscape (Fouda et al. 2018).

Black sea bass have been proposed as a model species for wind energy impact studies because the species is ubiquitous and abundant in the MAB (Stanley et al. 2020, Wiernicki et al. 2020), which is currently where the offshore wind energy industry is centered within the USA (NREL 2020). As fish with small home ranges, their exposure can be manipulated and tested for construction and post-construction impacts. Pile-driving, vessel, and reef effect impacts have been prioritized (Boehlert and Gill 2010, Methratta and Dardick 2019), but an impact that has received little attention is artificial light, which could disrupt diurnal behaviors entrained to light:dark cycles. Our findings suggest that wind energy impacts may be best-understood as deviations from expected diurnal movement behaviors.

ACKNOWLEDGMENTS

We gratefully acknowledge support from the Maryland Department of Natural Resources and the Maryland Energy Administration (Grant Administrator Ms. Catherine McCall; Grant ID Number 14-18-2415 MEA). Some of this work was also sponsored by the Defense Advanced Research Projects Agency ("Persistent Aquatic Living Sensors Program"). The content of information does not necessarily reflect the position or policy of the U.S. Government, and no official endorsement should be inferred. Cpt. Dan Stauffer and the crew of the *F/V Fin Chaser* assisted in catching and tagging black sea bass, and deploying and retrieving acoustic receivers.

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