Mesoscale eddies release pelagic sharks from thermal constraints to foraging in the ocean twilight zone

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Mesoscale eddies are critical components of the ocean's "internal weather" system. Mixing and stirring by eddies exerts significant control on biogeochemical fluxes in the open ocean, and eddies may trap distinctive plankton communities that remain coherent for months and can be transported hundreds to thousands of kilometers. Debate regarding how and why predators use fronts and eddies, for example as a migratory cue, enhanced forage opportunities, or preferred thermal habitat, has been ongoing since the 1950s. The influence of eddies on the behavior of large pelagic fishes, however, remains largely unexplored. Here, we reconstruct movements of a pelagic predator, the blue shark (*Prionace glauca*), in the Gulf Stream region using electronic tags, earth-observing satellites, and data-assimilating ocean forecasting models. Based on >2,000 tracking days and nearly 500,000 high-resolution time series measurements collected by 15 instrumented individuals, we show that blue sharks seek out the interiors of anticyclonic eddies where they dive deep while foraging. Our observations counter the existing paradigm that anticyclonic eddies are unproductive ocean "deserts" and suggest anomalously warm temperatures in these features connect surface-oriented predators to the most abundant fish community on the planet in the mesopelagic. These results also shed light on the ecosystem services provided by mesopelagic prey. Careful consideration will be needed before biomass extraction from the ocean twilight zone to avoid interrupting a key link between planktonic production and top predators. Moreover, robust associations between targeted fish species and oceanographic features increase the prospects for effective dynamic ocean management.

remote sensing | oceanographic model | satellite telemetry | marine predator | mesopelagic

The pelagic ocean represents the largest habitat on Earth (99% of the biosphere) (1) and yields >80% of the fish consumed by humans (1, 2). While typically featureless to the human eye, open ocean ecosystems are highly dynamic in time and space when viewed from satellites (3). Mesoscale eddies are energetic entities that structure open ocean ecosystems on time scales of weeks to months and spatial scales of tens to hundreds of kilometers (4). Eddy processes at these scales provide controls on biogeochemical fluxes (4, 5) and affect biological communities, including lower trophic levels (6–8), marine mammals (9–12), birds (13), turtles (14, 15), and fishes (16). Coupling of biology and ocean physics at the mesoscale has, in some cases, identified specific features as "hotspots" of biological activity, spanning trophic levels from primary producers (17–20) to zooplankton and small fish (21), up to large pelagic fish (22, 23).

The Gulf Stream region off the northeast coast of the United States contains some of the most highly energetic eddies on Earth (3), which have significant impacts on ecosystem dynamics (23–26). In this region, large cyclonic eddies (CEs) are generated by southward meanders of the Gulf Stream. These CEs typically trap cold, productive water from the New England shelf during formation (27) and are thus often referred to as "cold-core rings." On the other hand, large anticyclonic eddies (ACEs) formed by northward Gulf Stream meanders (known as warm-core rings) transport anomalously warm, low productivity Sargasso Sea water north of the Gulf Stream (28). As a result of the trapping of oligotrophic waters, Gulf Stream ACEs have been characterized as warm, ocean "deserts" with low productivity (26, 29) (except see refs. 28 and 30). Eddies generated in the open ocean also propagate into the Gulf Stream region and can have remarkably different characteristics and vertical structure (26) from those that are formed in the area.

Significance

New dynamic approaches to managing marine fisheries promise more effective management in a changing climate. However, they require detailed knowledge of the links between oceanographic features and marine megafauna. Here, we demonstrate that satellite tracking of animal movements, combined with ocean remote sensing and numerical models, can provide this critical information for the most exploited pelagic shark in the Atlantic Ocean. We find that this predator dives deep in warm, swirling water masses called eddies that have traditionally been considered ocean "deserts." Sharks use these warm features as a conduit to forage in the ocean twilight zone, a region of the deep ocean that contains the largest fish biomass on Earth, highlighting the importance of these deep ocean prey resources.

Much of the existing research on these physical–biological interactions in eddies has been bolstered by recent advances in satellite oceanography that have facilitated the automatic identification and tracking of mesoscale eddies globally (3). These advances in our ability to observe and track mesoscale features have revealed rich regional variability in how eddies influence near-surface chlorophyll distributions (26) and how these features might influence pelagic predators (e.g., ref. 23). Debate regarding how and why predators use oceanographic features is ongoing (31), and quantitative links between eddies and large

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pelagic fishes have proved difficult to establish. Movements of fish in the open ocean often cannot be determined with sufficient accuracy to correlate their position with specific mesoscale oceanographic features (32, 33). However, if fishes are able to sense favorable conditions associated with mesoscale eddies, as has been suggested for turtles (14), seabirds (34), marine mammals (11), and indeed large white sharks (23), eddies are likely to have profound impacts on the ecology of a number of commercially and ecologically important fish species.

Here, we use electronic tags, Earth-observing satellites, and data-assimilating ocean forecasting models to quantify eddy use by the most heavily exploited pelagic shark in the Atlantic Ocean, the blue shark. We estimated shark behavior using a hierarchical, switching state-space model framework and reconstructed 3D movements of tagged sharks by combining accurate, satellite-based positions with a high-resolution time series of depth and temperature. Observed and simulated random-walk movements were collocated to the interior of mesoscale eddies tracked in maps of remotely sensed sea surface height. We then used a data-assimilating and eddy-resolving oceanographic model to contextualize shark movements, compare observed behavior to the marine environment, and develop eddy composites to determine vertical eddy structure. This unique combination of tools and analyses allowed us to quantify specific shark–eddy interactions and explore the influence of these dominant oceanographic features on a model marine predator.

Results

We deployed 2 types of satellite-transmitting tags on 15 blue sharks in the Gulf Stream eddy field to provide high-resolution, 3D movements of each individual shark. We recorded >2,000 tracking days and nearly 500,000 high-resolution depth-temperature time series measurements from tagged blue sharks. Fifty-eight percent (∼1,200 tracking days) of the standardized locations from the state-space model occurred in the Gulf Stream study area (Fig. 1*A*), and 78% of these Gulf Stream positions were recorded between October and February. Twenty-five percent of the recorded depth-temperature time series data could be matched to these concurrent locations in the Gulf Stream, effectively facilitating reconstruction of 3D movements. These data for each tagged individual were subsequently collocated to mesoscale eddies tracked in maps of sea level anomaly in the Gulf Stream study region.

Area-normalized histograms of shark positions ($n = 4{,}791$ Gulf Stream locations), as a function of distance from eddy centers, revealed that blue sharks were significantly more likely to be associated with the inner cores (see *SI Appendix* for definitions of eddy areas) of ACEs than of CEs (Fig. 1). Depth-temperature time series data indicated 30% of all Gulf Stream depth measurements were made within eddies and comprised 452 and 181 cumulative hours within anticyclonic and cyclonic eddy cores, respectively. The preference for ACEs was even stronger when considering only movements while in the foraging behavior mode (Fig. 1*D*). Among all standardized locations that were classified as foraging across the Northwest Atlantic (including inside and outside of the Gulf Stream region), 59% occurred in the Gulf Stream study region and 40% were within eddies. Within Gulf Stream eddies, 39% of depth time series data in ACEs was classified as foraging compared with 24% in CEs, and among the 15,024 depth time series data points in the Gulf Stream that were associated with the foraging behavior mode, 33% were in ACEs and 11% in CEs.

Distribution of time at depth in eddies suggested blue sharks foraged on diel vertically migrating, mesopelagic prey during dives. Tagged individuals spent 15% of their time in Gulf Stream ACEs, compared with 1.5% in CEs, at depths below 300 m during daytime hours. At night, sharks spent <1% of their time in the mesopelagic in eddies of either polarity (Fig. 2 *E* and *F*). While diving, sharks encountered anomalously warm temperatures at depth in ACEs (Fig. 2 *A* and *C*), often exceeding 10 °C above climatological values in the strata between 250 m and 350 m (*SI Appendix*, Figs. S1 and S2). Tagged sharks experienced negative temperature anomalies at depth in most CEs (Fig. 2 *B* and *D* and *SI Appendix*, Figs. S1 and S2), yet paradoxically the deepest dives were also in cyclonic eddies. We found that the CEs frequented by the tagged blue sharks were, in fact, anomalously warm compared with eddy vertical composites constructed from climatological observations (Fig. 2*B*). Tracking the warm CEs back to their formation indicated that they were of Sargasso Sea origin (not Gulf Stream cold-core rings) and had moved into the southern portion of the Gulf Stream study area. After accounting for the CEs originating in the Sargasso Sea, we found that tagged sharks rarely occupied cold-core Gulf Stream CEs and favored warm Sargasso-derived CEs instead (Fig. 3 *E* and *F*).

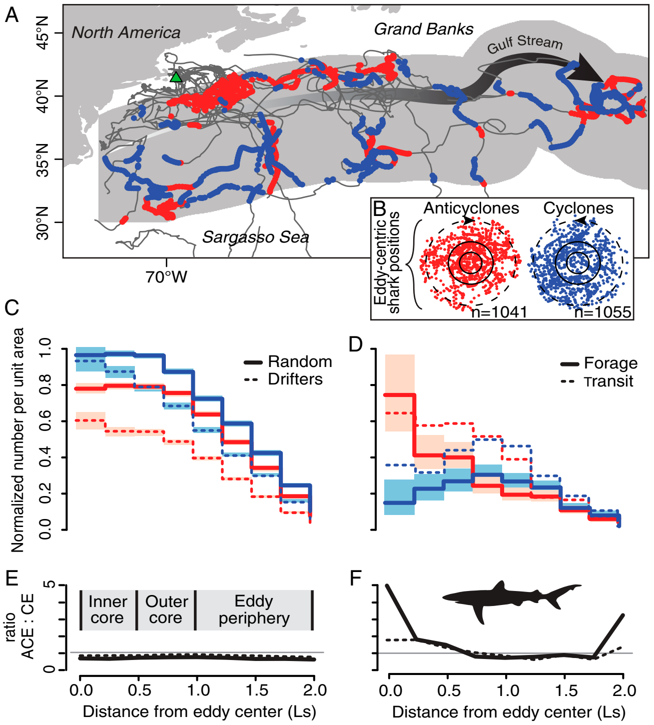

Fig. 1. Use of Gulf Stream eddies by satellite-tagged blue sharks. (*A* and *B*) Blue sharks tagged in New England (green triangle) frequented the Gulf Stream eddy field (*A*) and occupied anticyclonic eddies (ACEs) (red) and cyclonic eddies (CEs) (blue) at approximately the same frequency (*B*). (*C*) Eddy-centric histograms of random-walk simulations (solid line) and passive drifters (dashed line) exhibited higher frequency in CEs after controlling for eddy area. (*D*) Eddy-centric histograms of shark locations show they use eddy peripheries approximately equally between CEs and ACEs, but more positions classified as "foraging" (solid line) were collocated around the eddy interior compared with "transiting" locations (dashed line). Sharks showed a marked preference for the cores of ACEs relative to CEs, particularly while foraging (*D*). The ratios of ACE to CE positions across different regions of the eddies are shown in *E* for random-walk simulations (solid line) and drifters (dashed line) and in *F* for shark movement classified as foraging (solid line) and transiting (dashed line). Note confidence intervals have been removed from the transit mode in *D* to aid visualization.

The observed differences in temperature at depth among ACEs, Gulf Stream CEs, and Sargasso-derived CEs suggest that eddy effects on subsurface temperature modulate shark diving behavior (Fig. 3). Tagged sharks rarely ventured below the 12 °C isotherm (Fig. 3 *E* and *F*), which led us to develop a metric (D'; Eq. **1**) to quantify the relationship between shark maximum dive depth relative to the climatological mean depth of the 12 °C

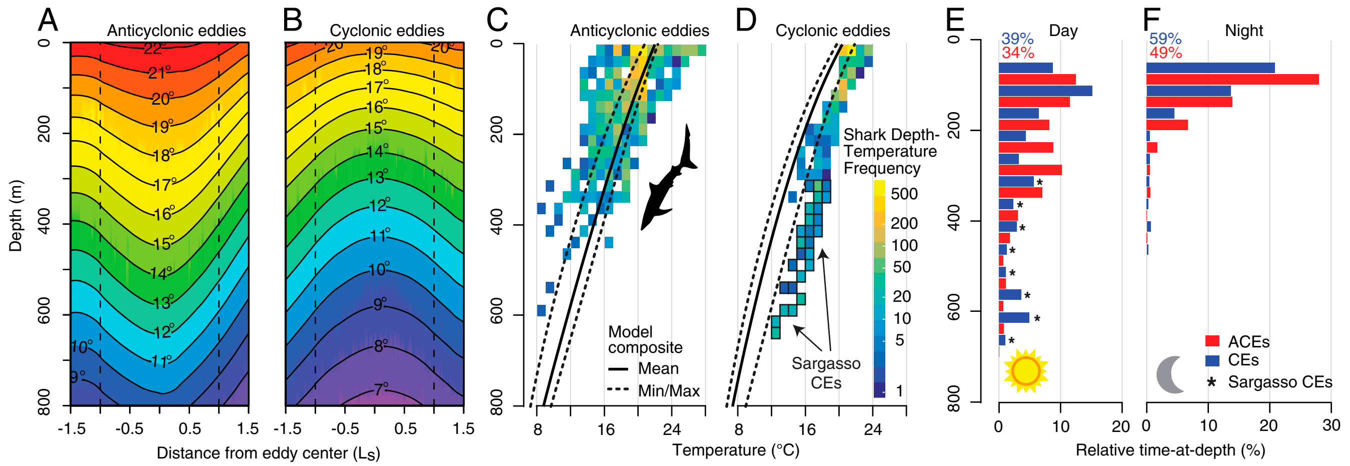

Fig. 2. Modeled eddy structure and aggregate blue shark dive behavior. (*A* and *B*) Modeled depth-temperature profile composites for 27 anticyclonic (*A*) and 28 cyclonic (*B*) eddies encountered by blue sharks. (*C* and *D*) Histograms of blue shark depth-temperature data while diving in cores of anticyclonic eddies (*C*) (n = 7,271) and cyclonic eddies (*D*) (n = 2,521) compared with model composite depth-temperature profiles. (*E* and *F*) Summary of blue shark time at depth during day (*E*) and night (*F*) occupation of anticyclonic (red) and cyclonic (blue) eddies. The 0- to 50-m depth bin has been removed to aid visualization. The highlighted depth-temperature cells (black outline, *D*) and time-at-depth bins (black asterisks, *E*) correspond to diving in Sargasso-derived cyclonic eddies.

isotherm. Values of $D' > 0$ are indicative of anomalously deep diving relative to the climatological mean isotherm depth. Dive profiles in ACEs were primarily characterized by positive D' while CEs more often exhibited $D' < 0$ (Fig. 3*E*), suggesting eddy modulation of water column structure controlled shark behavior in these features. We confirmed this observation by comparing climatological mean depth of the 12 °C isotherm to modeled in situ depth in eddies that showed ACEs consistently exhibited deepening of the 12 °C isotherm relative to climatological data (Fig. 3*F*).

Discussion

Mesoscale eddies are thought to structure pelagic ecosystems (4, 35). Recent work has shown the efficacy of incorporating these important, but ephemeral, oceanographic features into dynamic approaches to fisheries management (36, 37). However, these tools require detailed knowledge of the links between oceanography and fisheries targets or species of conservation concern. Our results demonstrate an approach that provides these data for the most heavily exploited pelagic shark in the Atlantic Ocean.

The Gulf Stream is one of the most dynamic regions of the world ocean and contains some of the most highly energetic eddies on Earth (3). Conventional wisdom suggests that cyclonic anticlockwise-rotating eddies are hotspots of biological activity while clockwise-rotating anticyclonic eddies are ocean deserts characterized by anomalously warm water void of significant fish biomass (29). However, our results suggest that blue sharks use the cores of anticyclonic ocean eddies as conduits to forage at depths that they would otherwise be unable to reach due to thermal constraints on their physiology. Our results are strikingly similar to conclusions drawn from earlier work on blue sharks that suggested thermal hysteresis facilitates maintenance of body temperatures significantly above ambient in the mesopelagic followed by abrupt termination of deep dives when muscle cools to 15 °C (38). We also observed similar oscillatory diving into the mesopelagic during daytime in both types of Gulf Stream eddies that was apparently constrained by temperature at depth. This behavior is consistent with the behavioral thermoregulation observed by earlier researchers (38) and is suggestive of foraging on vertically migrating mesopelagic prey.

Blue sharks are known to make extensive movements throughout the pelagic North Atlantic (39), and previous work has suggested the Gulf Stream may be an important overwintering habitat (40, 41). Previous studies tracking blue sharks in the Gulf Stream reported a high frequency of taxa that exhibit diel vertical migration, such as octopods (38) and mesopelagic fish (42), in their stomachs. In addition, mesopelagic dives by blue sharks were nearly always during daytime when the bulk of the mesopelagic community is at depth (43), and shark dive profiles were characterized by rapid descents with slower ascents, a pattern interpreted as prey searching behavior in sharks and tunas (38). Taken together, blue sharks are likely foraging for cephalopods and mesopelagic fishes, some of the blue sharks' primary prey items (42). These prey taxa are known to concentrate at depth in the Gulf Stream (44) and have been collected in high densities in ACEs (21, 45). Thus, our results suggest that Gulf Stream eddies may present important foraging opportunities, particularly during the overwintering period that comprised the majority of our study period, and, despite their low chlorophyll surface expression, ACEs may therefore provide more profitable foraging opportunities compared with CEs. The combination of warmer temperatures at depth and higher prey density would provide a powerful motivation for blue sharks to occupy the cores of ACEs compared with CEs. Endothermic white sharks apparently foraged deep in cold CEs in the same general area as the blue sharks we tagged (23). However, white shark dives were shorter in CEs than in ACEs, indicating that thermal physiology also constrains vertical movements of sharks capable of maintaining body temperatures significantly above ambient. These results further corroborate the role of physiology in regulating physical–biological interactions and suggest that more data are needed before concluding that either eddy type provides a better foraging environment.

Mesopelagic habitats in the open ocean contain the highest fish biomass on Earth (46). However, the deep ocean presents significant physiological challenges for epipelagic predators attempting to forage there. Our data suggest that ACEs may provide a conduit from the surface to the deep ocean due to anomalously warm temperatures at depth. This may enable blue sharks to overcome thermal constraints that would otherwise prevent them from accessing these resources. Our finding

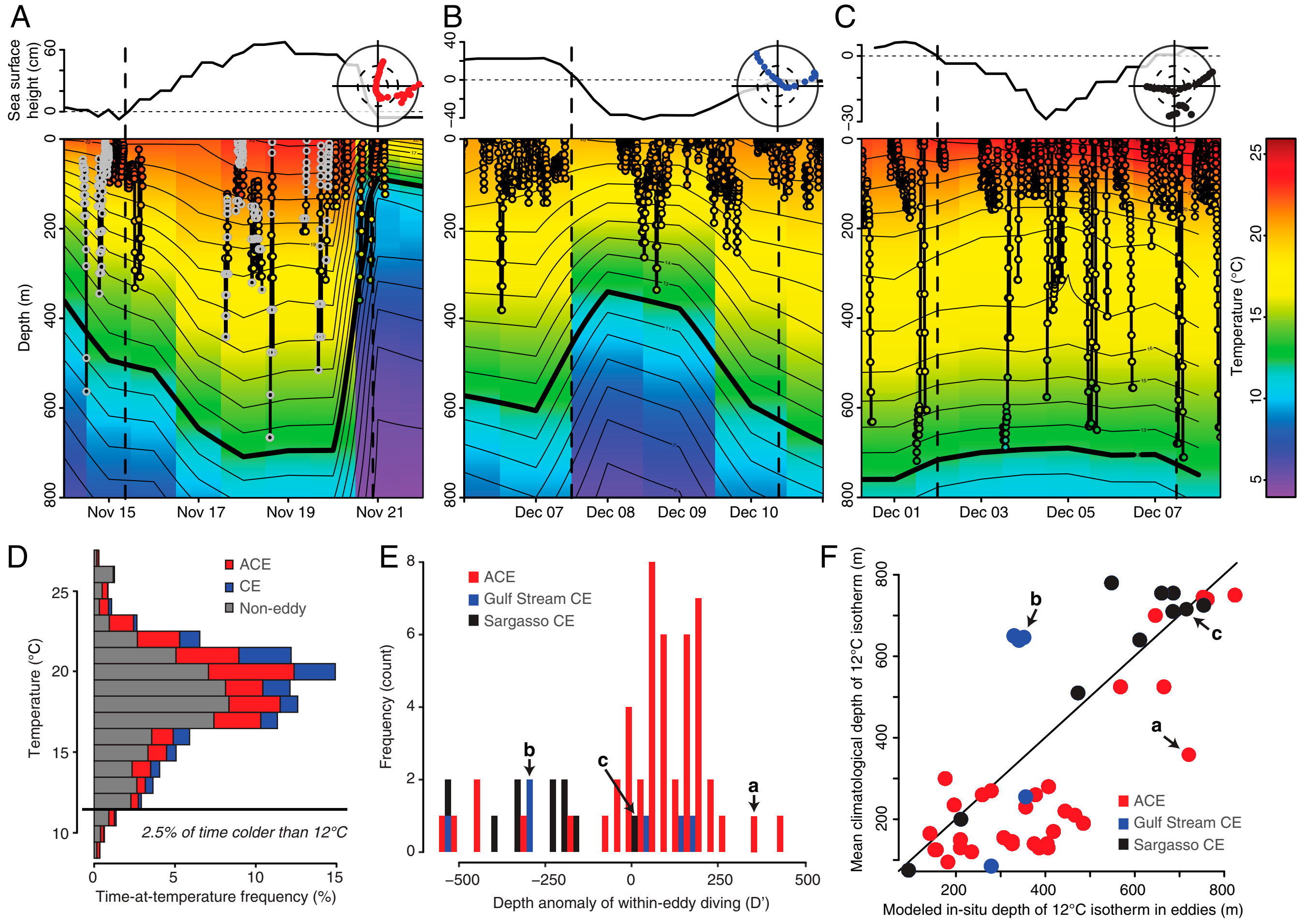

Fig. 3. Vertical eddy structure influences dive behavior. (*A*–*C*) Example dive profiles from blue sharks in anticyclonic (*A*) and cyclonic (*B*) Gulf Stream eddies and a cyclonic eddy of Sargasso Sea origin (*C*). *Upper* line plots indicate measured sea surface height from Aviso (*SI Appendix*, Eq. **S1**). *Upper Right* circular plots show geographic movements of the shark in eddy-centric coordinates (as in Fig. 1*B*). Water column structure in the eddies (color map, *A*–*C*) is modeled depth-temperature data from the HYbrid Coordinate Ocean Model (HYCOM). Colored points connected by solid vertical lines represent shark diving behavior (gray circles indicate no temperature data were transmitted by the tag for a given depth point in the time series). Dashed vertical lines indicate entry and exit of eddies based on sea surface height. Thin, labeled horizontal lines indicate isotherms at 1 °C intervals and the 12 °C isotherm is shown in bold. (*D* and *E*) Frequency histograms of the time-at-temperature distribution for all shark dive data in the Gulf Stream (*D*) and for the depth anomaly of within-eddy diving (*E*; Eq. **1**). (*F*) Positive D' indicates sharks dove below the climatological 12 °C isotherm, suggesting vertical downward displacement of isotherms by the eddy as shown by comparing climatological mean isotherm depth to in situ modeled isotherm depth within eddies.

that dynamic mesoscale eddies modulate connections between the surface ocean and biomass in the mesopelagic has significant management and policy implications. For instance, current management approaches ignore dynamic ocean processes in favor of static and space-based management approaches (47). While models to facilitate dynamic ocean management have recently been proposed (48), these approaches to managing pelagic fisheries require an improved understanding of the dominant physical–biological mechanisms structuring pelagic ecosystems. Similarly, efforts to calculate ecosystem services provided by mesopelagic animals remain remarkably imprecise, at least in part because they ignore the effect of mesoscale oceanographic features when scaling up from limited empirical data to global biomass estimates (49). Finally, we provide further evidence of the potential value of mesopelagic communities to large pelagic fishes that are a vital component of pelagic fisheries catches throughout the global ocean. Removal of mesopelagic biomass by industrial-scale fishing operations is therefore likely to have significant impacts on stocks of tuna, swordfish, and pelagic sharks. These impacts need to be quantified before informed policy can be developed for the sustainable and equitable use of resources in the ocean twilight zone.

Materials and Methods

Satellite Tagging and Track Analysis. Each blue shark (n = 15) was tagged with 2 electronic tags that provided accurate (<10 km error) satellite-based positions (fin-mounted Wildlife Computers SPOT tag) and a time series of depth and temperature every 2.5 min (tethered Wildlife Computers miniPAT; *SI Appendix*). Two additional blue sharks were tagged with SPOT tags only. Locations were speed filtered to remove spurious positions and were then fitted in a hierarchical fashion with a 2-state switching state-space model (SSM) (50) to estimate locations from the Argos data, infer behavioral state, and standardize the location time series (6-h resolution). Resulting positions were used to collocate depth and temperature data for reconstruction of 3D movements.

The SSM combined a process model that estimated movement parameters and an observation model that accounted for spatial uncertainty using Markov chain Monte Carlo chains. The model inferred a behavior state based on fitted movement parameters (correlation, γ; and turn angle, θ). Resident behavior (often referred to as area-restricted search or foraging) was characterized by θ near 180° and γ near 0 (short steps with large turn angles), while traveling (or transit) behavior produces movements in which θ is near 0° and γ near 1 (long, relatively straight tracks) between consecutive steps in the individual trajectories. The SSMs were fitted in JAGS (51) using the beam package (50) for R (52) (see *SI Appendix* for additional model details and assessment criteria). The raw tracking data are published in the Data One repository (53).

Eddies. Eddies identified and tracked in daily maps of sea surface height were acquired from the Mesoscale Eddy Trajectory Atlas distributed by Aviso that describes daily tracks of coherent mesoscale structures (eddies) based on maps of surface altimetry (3). Eddies with lifetimes greater than 4 wk are tracked based on their signatures in sea-level anomaly (SLA) fields. A custom meander filter was used to distinguish Gulf Stream meanders from the eddies of interest. Eddy subregions were defined according to the radial distance from the eddy center following ref. 14. Null eddy use was quantified by 2 independent methods: 100 correlated random-walk simulations per shark that sampled from observed turn angles and step lengths and 5 y of surface drifter data within the study region. Eddy vertical composites were constructed for shark-occupied eddies using HYCOM-modeled depth-temperature profiles and anomalies used climatological mean temperature from the World Ocean Atlas. Finally, we developed a metric (D') to quantify when eddies modulate shark dive depth by shifting the climatological 12 °C isotherm

$$D'(x, y, t) = D(x, y, t) - D_{12}(x, y, t), \tag{1}$$

where D' is the depth anomaly of each dive, D is the maximum depth of each dive, and D_{12} is the climatological mean depth of the 12 °C isotherm from the World Ocean Atlas. This metric indicates when eddies modulate shark dive depth by facilitating dives shallower ($D' < 0$) or deeper ($D' > 0$) than the climatological 12 °C isotherm. Eddy modulation of isotherm depth was further analyzed by comparing HYCOM-modeled in situ depth of the 12 °C isotherm within eddies with the climatological mean.

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