



Foraging behavior of a mesopelagic predator, the northern elephant seal, in northeastern Pacific eddies

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ABSTRACT

The role of mesoscale features in structuring trophic transfer in the mesopelagic zone is poorly understood. Deploying sensors on marine animals, or “biologging,” is a powerful tool to infer the organism’s behavior and simultaneously collect high-resolution oceanographic data to describe physical-biological interactions. We investigated whether mesoscale eddies are used by a mesopelagic predator, the northern elephant seal (*Mirounga angustirostris*), and if so, what mechanisms might create beneficial foraging conditions in association with eddies. We hypothesized seals would increase their foraging behavior in both cyclonic and anticyclonic eddies due to nutrient enhancement and physical aggregation of prey and that seals would dive deeper in anticyclonic eddies in response to a deeper prey field. We used tracking data and continuous *in situ* temperature measurements from 221 adult female northern elephant seals collected between 2004 and 2019. These predators primarily targeted myctophid fishes and squid throughout the northeast Pacific mesopelagic zone, foraging between approximately 400–800 m. Eddy encounters were identified using remotely sensed sea level anomaly data and confirmed visually with collocated sea level anomaly, *in situ* temperature, and *in situ* temperature anomaly. Over more than 30,000 days of data and >3 million temperature casts collected by seals, we found 129 high confidence encounters with anticyclonic eddies and 83 with cyclonic eddies. Overall, seals traveled more slowly and in a less directed manner while associated with eddies, particularly anticyclonic eddies, suggesting increased foraging behavior, especially in the California Current. Elephant seals spent more time at the edges of cyclonic eddies than their center. In contrast, they utilized both the interior and edge of anticyclonic eddies. This suggests that the aggregation of prey at the frontal region of an eddy is an important mechanism, whereas nutrient upwelling associated with an eddy play a more minor role in enhancing the seals’ prey field. Seal foraging behavior was not influenced by eddy age, size, amplitude, or rotational speed. The large sample size in this study showed considerable variation between individual behavioral responses, suggesting caution when extrapolating individual behavior to a population level. Our data show that both cyclonic and anticyclonic eddies can affect the seals’ prey field as demonstrated by enhanced foraging behavior. Still, the variation in behavioral responses resulting from individual foraging strategies, eddy histories, and possible spatiotemporal mismatches between eddy physics and biological responses relevant to mesopelagic predators merit further investigation.

1. Introduction

Understanding the biological significance of mesoscale oceanographic features is ecologically valuable, benefitting both marine spatial management and prediction of climate change effects on marine

ecosystems (e.g. Palacios et al., 2006; Woodson and Litvin 2015). Growing evidence suggests that marine predators use eddies, mesoscale features which can maintain physically distinct conditions from their surroundings altering phytoplankton (Gaubert et al., 2013) and zooplankton assemblages (Atwood et al., 2010; Bakun, 2006; Mackas

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et al., 2005). However, the influence of eddies on higher-trophic level organisms in the mesopelagic zone (200–1000 m below the surface) is challenging to document and only beginning to be understood. Deploying sensors on marine animals, or “biologging,” is a powerful tool used to collect oceanographic observations and simultaneously assess the relationship between an organism’s behavior and its dynamic oceanographic environment below the surface (Harcourt et al., 2019). Using this methodology, inferences about mesopelagic biota through the perspective of a diving predator offer new insights into the influence of eddies on deep-water organisms.

Eddy energetics can significantly enhance upper ocean mixing, renewing nutrients in surface waters and stimulating primary production (Flierl and McGillicuddy, 2002; Martin and Richards, 2001; Petersen et al., 2005). Entrainment of coastal water within eddies and subsequent movement offshore can transport nutrients and less mobile organisms (Flierl and McGillicuddy, 2002; Johnson et al., 2005). In addition, the edges of eddies can act as fronts and aggregate small organisms (Bakun, 2006; Legal et al., 2007; Schmid et al., 2020; Zhang et al., 2015). Higher trophic levels can be influenced by eddies including micronekton (Boyd et al., 1986; Della Penna et al., 2021; Della Penna and Gaube, 2020; Godø et al., 2012) and larger predators such as loggerhead sea turtles (Chambault et al., 2019; Polovina et al., 2006), leatherback sea turtles (Lambardi et al., 2008), albacore tuna (Zainuddin et al., 2008), king penguins (Cotté et al., 2007), northern fur seals (Pelland et al., 2014; Ream et al., 2005), and Steller sea lions (Lander et al., 2020). Some studies have observed eddy influences on mesopelagic micronekton community through acoustics (Della Penna et al., 2021; Della Penna and Gaube, 2020) but it remains a major challenge to document mid-trophic level mesopelagic organisms’ association with eddies at larger spatiotemporal scales. About a quarter of eddies worldwide extend to depths of 1000 m or more (Petersen et al., 2013), suggesting that they can directly impact the mesopelagic zone, and mesopelagic predators such as blue and white sharks (Braun et al., 2019; Gaube et al., 2018), melon-headed whales (Woodworth et al., 2012), and southern elephant seals (Bailleul et al., 2010; Campagna et al., 2006; Massie et al., 2016) associate with eddies. A closely related species, the northern elephant seal (*Mirounga angustirostris*), pursues mesopelagic prey in the northeast Pacific, where such mesopelagic predator studies relating foraging to eddies have not yet been conducted.

Adult female northern elephant seals range throughout the northeast Pacific, primarily targeting myctophid fish and squid (Goetsch et al., 2018; Naito et al., 2013, 2017; Yoshino et al., 2020). Elephant seals forage nearly non-stop during biannual offshore foraging trips (Adachi et al., 2021), the first lasting approximately 10 weeks after breeding in the winter and the second 8 months after molting in the spring (Robinson et al., 2012). Northern elephant seals are the only mesopelagic predator in the northeast Pacific for which a large dataset of tracking data exist, and previous work relating their foraging behavior to mesoscale oceanography has relied on remotely sensed data (Abrahms et al., 2018; Simmons et al., 2007). The northeast Pacific within the elephant seals’ range contains fewer large eddies than the western basin (Cheng et al., 2014; Roden, 1991), but the Gulf of Alaska and California Current are nonetheless significant eddy hotspots, with fewer eddies occurring in the North Pacific Transition Zone (Cheng et al., 2014). Eddies in these regions are on average 160 km across and persist for approximately 125 days, though they can persist for up to 3 years (Cheng et al., 2014; Crawford et al., 2000; Stegmann and Schwing, 2007). This study system therefore offers a valuable opportunity to investigate the relationship between eddy characteristics and the foraging behavior of a predator in the mesopelagic zone.

Subsurface oceanographic data derived from biologging instruments can improve our understanding of physical-biological interactions at fine scales (e.g. Bograd et al., 2010; Costa et al., 2012; Hussey et al., 2015). Many time-depth recorders designed primarily to study animal behavior also continuously sample temperature, providing high

horizontal resolution of temperature by collecting profiles during every dive an animal makes. Northern elephant seals appear to derive foraging benefits from mesoscale activity (Abrahms et al., 2018) and these continuous *in situ* temperature measurements can provide the first description of potentially relevant mesoscale features and the seals’ behavioral changes at fine scales. These observations can increase our understanding of mesopelagic dynamics in the northeast Pacific where observations are limited.

We evaluated the importance of mesoscale eddies for a population of northern elephant seals using a 15-year data set of 221 records of behavioral and *in situ* temperature data. Both cyclonic eddies and anti-cyclonic eddies were expected to enhance foraging opportunities due to nutrient upwelling and advection of productive coastal waters, respectively. We expected seals to make deeper dives within anticyclonic eddies due to mesopelagic prey being physically driven deeper within these downwelling, warm-core eddies (Godø et al., 2012; Samuelsen et al., 2012). In contrast, we expected shallower dives within cyclonic eddies due to colder water and increased productivity at shallower depths. Finally, we expected that prey would be more abundant within older eddies as they would have had more time to accumulate biomass.

2. Methods

2.1. Elephant seal tracking

221 adult female northern elephant seals carried satellite tags (Mk10, $n = 55$, or SPOT, $n = 147$, – Wildlife Computers, Redmond, WA; or CTD-SRDs – Sea Mammal Research Unit, St. Andrews, Scotland, $n = 19$) and time-depth-temperature recorders (Mk9, $n = 166$, or integrated into Mk10, $n = 55$, Wildlife Computers) between 2004 and 2019. Seals were instrumented at Año Nuevo State Park, California, USA (37.11°N , -122.33°W , $n = 201$) and Islas San Benito, Mexico (28.30°N , -115.37°W ; $n = 20$). Northern elephant seals from both colonies exhibit comparable behavior at sea (Kienle, 2019; Robinson et al., 2012). For instrument deployment and recovery, seals were chemically immobilized following established protocols (Robinson et al., 2012). Satellite transmitting tags were attached to the head and time-depth recorders, if separate, to the dorsal side between the axilla and sternum. All animal handling protocols were authorized by the University of California Santa Cruz Institutional Animal Care and Use Committee and conducted under National Marine Fisheries Service permit numbers 786–1463, 87–143, 14636, 17952, and 19108, and under Dirección General de Vida Silvestre permit numbers NÚMS/SGPA/DGVS/05734-2004 and NÚMS/SGPA/DGVS/05321-2005.

Pressure and temperature data were collected by the Mk9 or Mk10 instruments, which measure pressure with an accuracy of $\pm 1\%$ of reading from which depth can be estimated at 0.5 m resolution and temperature at a resolution of 0.05°C and accuracy $\pm 0.1^{\circ}\text{C}$. Depth and temperature readings were collected at least every 8 s throughout deployment, a sampling interval previously demonstrated to be sufficient to resolve thermal features using these instruments (Simmons et al., 2009). While the smaller number of CTD-SRDs ($n = 15$) deployed also collected temperature data, they are programmed to do so only approximately 4 times per day, providing far lower horizontal resolution than the continuously-recording Mk9 or Mk10s. As such, we did not use the CTD-SRD temperature data to identify eddy encounters at the fine scales required for this study. Depth data were zero offset corrected using a custom-written toolbox in MATLAB (Robinson et al., 2012). Previous evaluations of the temperature data collected by these instruments showed stability over time (Simmons et al., 2009), but out of caution, deep-water temperature measurements (>800 m) over time were visually inspected for signs of drift. Temperature measurements from the down- and up-casts from an individual dive were combined and interpolated to 1 m intervals using a Piecewise Cubic Hermite Interpolating Polynomial from the Gibbs Sea Water Oceanographic Toolbox in MATLAB (McDougall and Barker, 2011).

All seals were tracked using the Argos system (<https://www.argos-system.org/>); a subset of seals were additionally tracked with Fastloc® GPS. Where available, Argos error ellipse data were retained for the highest quality uncertainty estimates; these data were not available for older Argos data predating the implementation of a Kalman filter by the data provider. Erroneous locations on land were first filtered out by cross-referencing seal locations to bathymetry data (see Section 2.4). GPS and Argos location estimates were then further refined using the foieGras R package (version 0.7–7.9276, <https://github.com/ianjensen/foieGras>), which uses a continuous time state-space model incorporating location error estimates to filter the tracking data (Jonsen et al., 2020). We used a correlated random walk model and imposed a speed filter of 3 m/s. All analyses in R were carried out in version 4.1.1 (R Core Team, 2022). Locations were interpolated to 1-h intervals and assigned to each temperature cast based on time. Any interpolated locations with a standard error ≥ 30 km were omitted. These hourly interpolated locations were used to identify proximity to eddies (see Section 2.3); for statistical models, 12-h mean locations were used.

2.2. Behavioral metrics

The northern elephant seal dataset offers both lateral movement and vertical diving data. We used transit rate (horizontal velocity), which performs well as a simple proxy for northern elephant seal foraging behavior (Robinson et al., 2010). Lower transit rate is related to presumed higher foraging activity and higher transit rate to presumed lower foraging activity. Average transit rate as displacement over time was derived from the interpolated tracks over 12-h intervals. As an additional indication of behavioral state, movement persistence was derived from the foieGras state-space model for each 12-h window. This metric describes autocorrelation in direction and speed, ranging continuously between 0, indicating low persistence and frequent changes in direction and/or speed, likely foraging, to 1, indicating high persistence and infrequent changes in direction and/or speed, likely traveling (Jonsen et al., 2019).

Elephant seals exhibit drift dives that can be used as a metric of changes in body composition (fatter seals more buoyant and leaner seals less buoyant) and thus foraging success on the order of a few days to a week (Biuw et al., 2003; Crocker et al., 1997; Robinson et al., 2010; Webb et al., 1998). For all seal tracks in this study, daily average drift rate was calculated across all drift dives identified each day, then the change in drift rate was calculated over four-day intervals. Maximum dive depth, bottom time (the time that vertical velocity remains below 20% of ascent and descent rates), and number of “wiggles” (small vertical inflections likely associated with prey pursuit (Robinson et al., 2010)) were determined for each individual dive using a custom-written toolbox in MATLAB (Robinson et al., 2012). For diving behavioral analyses relative to eddies, we removed dives shallower than 100 m and all drift dives, as seals are unlikely to be foraging during these dives. We retained the temperature data from all dives regardless of likely behavior for eddy identification in section 2.3. As most elephant seals exhibit diel differences in dive depth, likely reflecting vertical migration of the prey field (Robinson et al., 2012), dive depth, bottom time, and number of wiggles were analyzed separately for daytime and nighttime dives. Daytime dives were distinguished from nighttime dives by calculating a solar elevation angle for the dives’ location and date using the SolarAzEl function in MATLAB (Koblick, 2021). Daytime was designated as solar elevation >0 .

2.3. Eddy identification

Each day of the trip, eddies within 50 km of a seal’s location were first identified as potential eddy encounters using the Mesoscale Eddy Trajectory Atlas (META2.0), produced by SSALTO/DUACS and distributed by AVISO (Chelton et al., 2011). Eddy encounters were confirmed visually using several metrics: (1) *in situ* temperature, (2) *in situ*

temperature anomaly, (3) sea level anomaly (SLA), and (4) comparison of *in situ* observations to eddy characteristics derived from the META. Temperature anomalies throughout the water column were calculated by subtracting climatological data (World Ocean Atlas 2018 monthly climatology 1955–2017, $\frac{1}{4}^\circ$ resolution) from the *in situ* temperature data collected by the seal tags. SLA data were obtained from Copernicus ($1/4^\circ$ resolution, dataset ID DATASET-DUACS-REP-GLOBAL-MERGED-ALLSAT-PHY-L4). Eddy encounters were only retained if all data sources agreed: the SLA data showed an elevation/depression consistent with the eddy polarity (cyclonic or anticyclonic) and approximate eddy amplitude determined from the META and the seal-derived data showed an appropriate warm/cold anomaly and/or deepening/shoaling of the mixed layer (Fig. 1). For each retained eddy association, the time at which the seal entered and exited the eddy was visually determined from the *in situ* temperature and temperature anomaly data (seals collected on average 104 temperature profiles per day, enabling high horizontal resolution for this determination). Eddy characteristics for the retained eddy encounters were derived from the META: eddy radius, eddy age, eddy rotational speed, eddy amplitude, and eddy polarity. For each eddy a seal encountered, we referenced the META to find the first day that particular eddy was identified and calculated the age of the eddy at the time of the seal encounter as the time difference between the first detection of the eddy and the day the seal encountered it. To normalize eddy age across eddies to assess the influence of eddy intensification and decay phases on seal behavior, we additionally represented eddy age at the time of a seal’s encounter as a percentage of the eddy’s observed lifespan (0%: first day eddy was identified in the META, 100%: last day eddy was documented in the META). Across all eddies in the study area, eddy rotational speed and amplitude tended to increase to a maximum during the first quartile if the eddy’s lifespan and decrease again during the third quartile (Fig. S2). We calculated and mapped the kernel density of eddies and hourly seal locations per square kilometer using the kernel density tool in ArcMap 10.7.1 using a geodesic method for distance calculations.

To compare diving behavior within an eddy to the outside of an eddy, we considered the dive parameters of interest (i.e., maximum dive depth, bottom time, and the number of wiggles). We pulled those parameters from dives made while the seal was within the eddy as well as dives covering an equal cumulative amount of time divided evenly between pre- and post-eddy encounter, with buffers in time (2 days pre-/post-encounter) and space (at least 0.1° from the eddy center) to ensure the animal was no longer associating with the eddy. The temporal buffer was expanded if the dives made before or after the eddy encounter in question were within 1 day of a potential encounter with another eddy (i.e., an eddy within 50 km of the seal, whether or not we could verify that the seal actually traversed the eddy) while keeping the time window of outside-of-eddy seal behavior unchanged. Differences in diving behavior within an eddy compared to behavior before and after the eddy encounter were determined using two-sample t-tests for each individual eddy encounter.

2.4. Additional oceanographic parameters

In situ sea surface temperature (SST) was calculated for each individual dive as the mean of *in situ* temperature collected in the upper 5 m of the water column. Mixed layer depth (MLD) was determined by applying the temperature-based algorithm presented in Holte and Talley (2009) to the *in situ* temperature data. Remotely-sensed observational gridded $1/25^\circ$ finite-sized Lyapunov exponents (FSLE) were extracted from AVISO (d’Ovidio et al., 2004) and the mean, maximum, and standard deviation of FSLE extracted within a 5 pixel radius (approximately 25 km) ± 2 days per day of seal data. FSLEs characterize the confluence of fluid parcels and are often used to identify Lagrangian structures; the FLSE will have higher values on fronts on the edges of eddies, with lower values in the center of eddies and more quiescent parts of the ocean with low dispersion (e.g. d’Ovidio et al., 2004).

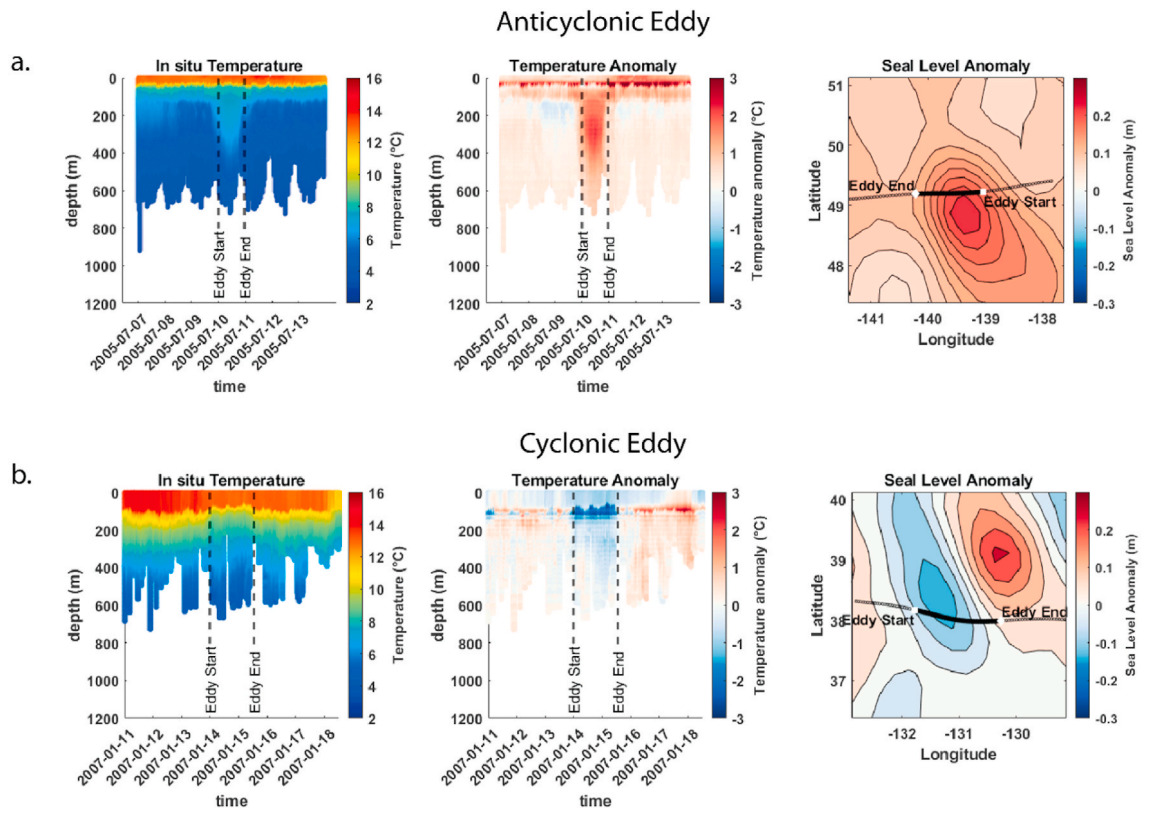


Fig. 1. Elephant seals profiling eddies, showing *in situ* temperature measurements on the left, temperature anomaly in the center, and remotely sensed sea level anomaly with seal's track overlaid on the right, for (A) an anticyclonic eddy in Gulf of Alaska and (B) a cyclonic eddy in the California Current.

Seafloor topography data at 1/60° resolution based on satellite altimetry and ship depth soundings were downloaded from the NOAA CoastWatch ERDDAP server (dataset ID usgsCeSS111, [Smith and Sandwell, 1997](#)) and a bathymetric depth was assigned to seal dives by calculating the mean of bathymetric depth over a 2 km square to account for the error associated with Argos-derived locations. Dives made in areas where water depth was shallower than 500 m were excluded from further analyses to focus on mid-water foraging on pelagic prey.

Given the seals' large and oceanographically variable range, data were divided into three subregions: the Gulf of Alaska, California Current, and North Pacific Transition Zone ([Fig. 2](#)). The California Current region was designated as south of 48°N, below variable positions of the North Pacific Current's southern bifurcation ([Cummins and Freeland,](#)

[2007; Sydeman et al., 2011](#)). In the absence of a well-defined division between the California Current and the interior of the subtropical gyre circulation ([Cummins and Freeland, 2007](#)), we used a western cut-off at -135°W, following the edge of an abundance of cyclonic eddies typical of eddies formed in the California Current ([Stegmann and Schwing, 2007](#)). The North Pacific Transition Zone was then designated as west of -135°W and between 28°N and 48°N between the subarctic frontal zone and subtropical frontal zone, taking into consideration interannual variability of the North Pacific Current ([Cummins and Lagerloef, 2004; Roden, 1991; Sydeman et al., 2011; Yuan and Talley, 1996](#)). Finally, observations were assigned to the Gulf of Alaska if they were north of the North Pacific Current, approximated at 48°N ([Cummins and Freeland, 2007](#)). These subregional designations incorporated the major hotspots

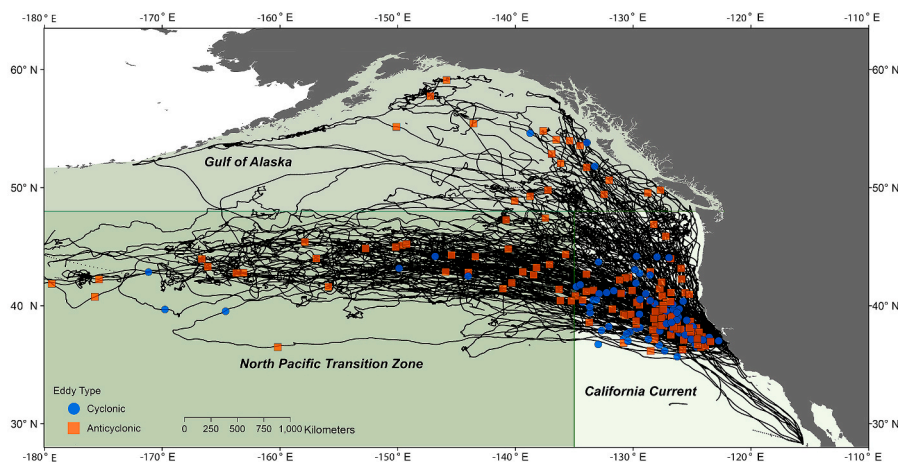


Fig. 2. Map showing elephant seal tracks (lines) and the locations of eddy encounters (blue circles and orange squares).

of eddy and seal activity (Fig. S1).

To evaluate the relationship between the mixed layer depth and the depth of the ferricline, we extracted iron profiles from a biogeochemical model (https://resources.marine.copernicus.eu/product-detail/GL_OBAL_MULTIYEAR_BGC_001_029029) at monthly resolution within 2° latitude and longitude of every eddy encounter. As this model is not data assimilating, it does not resolve specific eddies matching those the seals encounter in space in time. Instead, we used these data to determine the vertical iron distribution typical for the location and time without the perturbation of an eddy. For each iron profile, we first calculated the scaled first derivative of the iron concentration by depth, then found the depths containing the 75th percentile of the derivative to identify the depth region of most rapid change. As this depth zone of rapid iron increase typically spanned sections of 100–250 m, we assigned a ferricline “upper boundary” by identifying the 10th percentile of the depths associated with the iron change and a ferricline “lower boundary” as the 90th percentile of the depths associated with rapid concentration change. We additionally determined a “middle” using the 50th percentile. Profiles with iron concentrations ≥ 0.6 nmol/kg near the surface were assigned as having no ferricline as that concentration approximates the deep water iron concentration in the North Pacific (<https://www.mbari.org/science/upper-ocean-systems/chemical-sensor-group/periodic-table-of-elements-in-the-ocean/>). We then compared the median of the modeled ferricline upper boundary, middle, and upper boundary for each eddy encounter to the MLD calculated from the *in situ* temperature data both inside the eddies.

2.5. Statistical analysis

We tested the influence of eddy encounters on five behavioral variables: transit rate (horizontal speed) and movement persistence (a continuous variable between 0, suggesting convoluted movement likely associated with foraging, and 1 suggesting directed movement which is likely travel) from the entire trip, and dive depth, dive bottom time, and number of wiggles averaged over an eddy encounter (see Section 2.2 for detailed descriptions of behavioral metrics). We did this using generalized additive mixed models (GAMMs) in the “mgcv” package version 1.8–36 in R (Wood, 2017). While at sea, elephant seals must gain sufficient energy to recover energy stores lost during their fasting period on land and prepare for the next fasting period (Costa et al., 1986). Consequently, elephant seal at-sea behavior is strongly driven by internal factors. To account for this, we tested the influence of season (which of the two annual foraging trips a seal was undergoing), days since leaving the colony (representing their internal schedule of maximizing energy intake and the need to return to land to breed or molt), and drift rate (to represent past foraging success) on movement and diving behavior. We retained the intrinsic variables that explained the greatest amount of behavioral variance and were not colinear with one another (all retained variables had Pearson correlation coefficients ≤ 0.15). Subsequent addition of oceanographic variables to the intrinsic model tested further behavioral modulation by the local environment: eddies, mixed layer depth, sea surface temperature, FSLE, bathymetric depth, and distance from shore. For MLD and SST from *in situ* data, we calculated the mean and standard deviation within 12-h periods to match the timescale of the response variable. We also included latitude and longitude in the model due to the large geographic range covered and to account for spatial autocorrelation.

Using this full model, the effect of eddies on seal behavior was assessed using the difference in explanatory power (R^2 deviance) between a model containing eddy category (Table 1) and a model without this factor. When models resulted in a negative R^2 , we reported these as $R^2 = 0$ to indicate no explanatory power. Models built to assess the influence of eddies also contained oceanographic parameters representing water column mixing, temperature, and mesoscale activity metrics that can be associated with eddies but which seals will also encounter elsewhere (Table 1). This was designed to test whether seal behavior was

Table 1

Covariates included in mixed effects models testing the response variables transit rate, movement persistence, and diving behavior (12-h averaged).

Covariate Name	Covariate Description	Units
Season	Levels: Post-breeding foraging trip, Post-molt foraging trip	Categorical
DayinTrip	Days since seal left shore	Days
EddyCategory	Levels: Not in an eddy, In a cyclonic eddy, In an anticyclonic eddy	Categorical
FSLE_max	Maximum Finite-sized Lyapunov Exponent within ~25 km radius, 2 days	Days ⁻¹
SST_sd	Standard deviation of <i>in situ</i> SST across 12 h period	Degrees Celsius
MLD_mean	Mean <i>in situ</i> mixed layer depth across 12 h period	Meters
Lat,Lon	Latitude and longitude of seal's location	Decimal degrees
TOPPID	Unique ID for seal track	Categorical
EddyAge ^a	Days since eddy first detected in META	Days
EddyAmplitude ^a	Height difference between maximum sea level of eddy and the sea level of eddy perimeter	Centimeters
EddyRadius ^a	Radius of circle enclosing contour of maximum rotational speed	Kilometers
EddySpeed ^a	Average speed at radius defined above	Centimeters/Second

^a See Mesoscale Eddy Trajectory Atlas Product Handbook for detailed information. https://www.aviso.altimetry.fr/fileadmin/documents/data/tools/hd_bk_eddytrajectory_META2.0_DT.pdf Note that dataset releases may differ in reported units.

influenced specifically by mesoscale eddies or by oceanographic phenomena that, while characteristic of an eddy, could also represent other features such as fronts or jets.

GAMMs testing movement persistence were fit with a Gamma distribution while the diving behavior (dive depth, bottom time, and number of wiggles) and transit rate models were run with a Gaussian distribution. Individual seal was included as a random effect. The resulting models were evaluated for homogeneity (residuals vs. fitted), independence (residuals vs. covariates), and normality of residuals. They were additionally tested for spatial autocorrelation by calculating Moran's I using the package “ape” version 5.5 in R (Paradis and Schliep, 2019) (Table S4). Model outputs were visualized using the package “mgcViz” version 0.1.9 in R (Fasiolo et al., 2020).

To assess the amount of time seals spent in relative positions within the eddies, we used histograms of hourly seal locations relative to distance from eddy center represented as a percentage of the eddy radius, i. e., 100% represented the eddy edge, below 100% was inside the eddy, and above 100% was outside of the eddy. These data omitted locations with standard errors greater than 15 km to increase confidence in satellite-based locations and omitted transit rates faster than 6 km/h to remove data unlikely associated with foraging behavior.

3. Results

3.1. Eddy encounters

Of 221 seals tracked between 2004 and 2019, 119 individuals encountered eddies: 129 encounters with anticyclonic eddies and 83 encounters with cyclonic eddies (Figs. 2 and 3), compared to a nearly equal availability of eddies of either polarity in the total eddy field (50.6% cyclonic, 49.4% anticyclonic). The tracks of these seals were retained for further analyses. Seals spent 3.1 ± 7.4 (mean \pm sd) days within an eddy with no difference between cyclonic and anticyclonic eddies (3.1 ± 6.9 days in anticyclonic eddies, 3.1 ± 8.2 days in cyclonic eddies, *t*-test $p = 0.96$). All 221 tracked seals collectively collected 3.2 million temperature casts during 30,786 days at sea of which 733 were classified as within eddies, accounting for 2.4% of the seals' time. They spent a cumulative 478 days (65.2% of in-eddy time) in anticyclonic

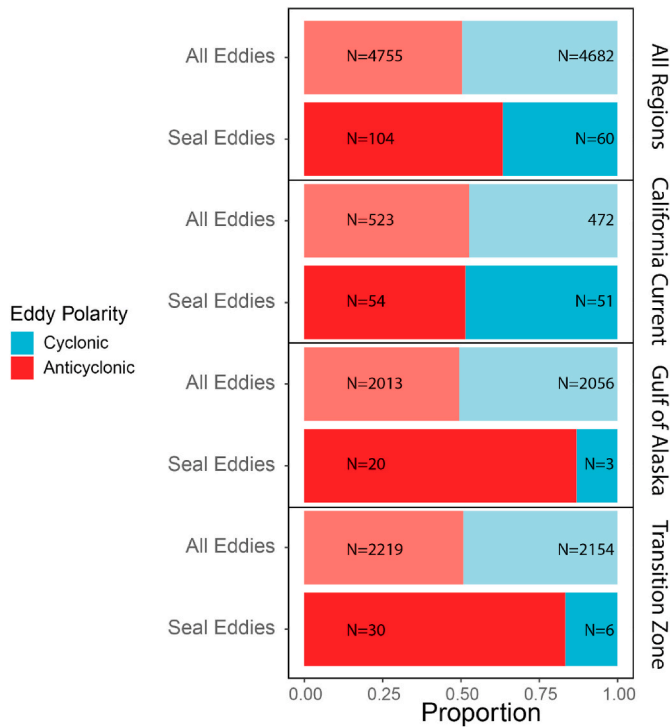


Fig. 3. Proportion of cyclonic and anticyclonic eddies by region for total eddies in study area and eddies encountered by seals. Numbers refer to number of individual eddies.

eddies and 255 days (34.8% of in-eddy time) in cyclonic eddies (Table S1). Just under half of the eddy-encountering seals (48.7%) encountered more than one eddy; no seal was observed to visit the same eddy a second time.

The area of highest kernel density of seal locations was in the California Current radiating out from the colonies, which overlaps with one eddy hotspot (Fig. S1). The other eddy hotspot, the coastal Gulf of Alaska, had a very low density of seals. Compared to all eddies identified in the META in the region during this time, eddies encountered by seals were on average significantly older (157 ± 132 days vs. 73 ± 79 days for all eddies), larger (in both radius, 70.4 ± 13.7 km vs. 67.1 ± 16.3 km for all eddies), and amplitude, 6.07 ± 4.03 cm vs. 3.94 ± 2.99 cm for all eddies), and had rotational speed (14.4 ± 6.8 cm/s vs. 9.8 ± 5.8 cm/s for all eddies) (*t*-test, $p < 0.001$, Fig. 4).

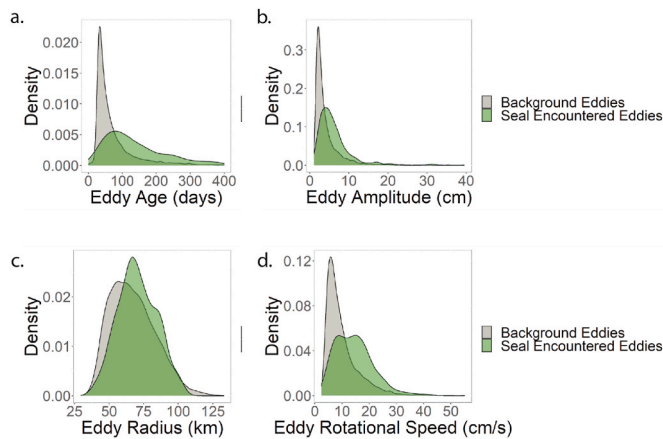


Fig. 4. Density of eddy properties of all mesoscale eddies in study area and those encountered by seals indicates seal-encountered eddies were on average older (a), larger (b, c), and faster (d).

None of the eddies had MLDs deep enough to reach the lower boundary of the modeled ferricline; only one eddy’s MLD reached the vertical center of the ferricline. About one quarter (25.1%) of the observed eddy MLDs reached the upper boundary of the modeled ferricline, about 2/3 cyclonic eddies and 1/3 anticyclonic eddies.

3.2. Horizontal movement behavior

After retaining the intrinsic variables explaining the greatest amount of behavioral variance, we came up with a null model for seal behavior (transit rate, movement persistence, and diving) including the season of the foraging trip (post-breeding or post-molt) and the timing within the foraging trip (days since leaving the colony). The addition of eddy category to the horizontal movement behavior models increased explanatory power (R^2) of the null model. It also increased explanatory power when the model included oceanographic variables characteristic of but not exclusively related to eddies that could induce a behavioral effect, such as a change in MLD (Table 1). Overall, elephant seals exhibited reduced transit rate (mean reduction by 38.4%) within eddies compared to outside of eddies, suggesting enhanced foraging behavior (Fig. 5). Similar trends were observed for movement persistence (Fig. S4). Visualizations of full model outputs can be found in the Supplementary Material (Fig. S3 and Fig. S4).

The strongest influence of eddies on transit rate occurred in the California Current, where the addition of eddy category to the models resulted in the highest increase to explanatory power (Table 2 and S2). In the California Current, both transit rate (Fig. 5 C, mean reduction 27.1%) as lower within eddies, with a particularly strong decrease in association with anticyclonic eddies (transit rate on average 29.4% lower in anticyclonic eddies than cyclonic eddies). This was the only subregion to contain a large sample size of both eddy types and eddy polarity did not appreciably improve explanatory power of models describing transit rate. Being in an eddy did not increase explanatory power for transit rate in the North Pacific Transition Zone (Table 2, Fig. 5 B). In the Gulf of Alaska, though eddy encounters had a mean reduction of 65.8% in transit rate, eddy encounters only increased the explanatory power of the transit rate models by a very small amount (Table 2 and S2). The same relative trends were observed in movement persistence reductions across regions (Fig. S4, Table S3). Change in drift rate was not well explained by eddy encounters.

Eddy characteristics (age, life stage, radius, amplitude, or rotational speed) did very little to further explain transit rate or movement persistence in association with either cyclonic or anticyclonic eddies within any region. The number of days since the start of the trip (normalized to trip length) explained the largest amount of variability in both transit rate and movement persistence in the models (Tables S2–S3). There was a weak linear effect of normalized eddy age in anticyclonic eddies in the Gulf of Alaska and the California Current, in which transit rate was slower in association with older eddies (Table S7). Absolute eddy age did not increase the explanatory power of the behavioral models (Table S7).

When encountering cyclonic eddies, the number of hourly seal locations peaked around the edges of the eddies (Fig. 6 top). When encountering anticyclonic eddies, locations were spread through the interior and across the edges of the eddies, a pattern especially pronounced in the Gulf of Alaska and the California Current (Fig. 6 bottom).

Season (post-breeding or post-molt) increased the explanatory power of the transit rate models (R^2 deviance 0.031). Models testing the influence of eddies for each season separately showed a stronger behavioral response to eddies during the post-molt trip than the post-breeding trip (R^2 deviance post-breeding 0, R^2 deviance post-molt 0.009).

3.3. Diving behavior

Diving behavior (maximum dive depth, bottom time, and the number of wiggles) was poorly explained by intrinsic models, in contrast to

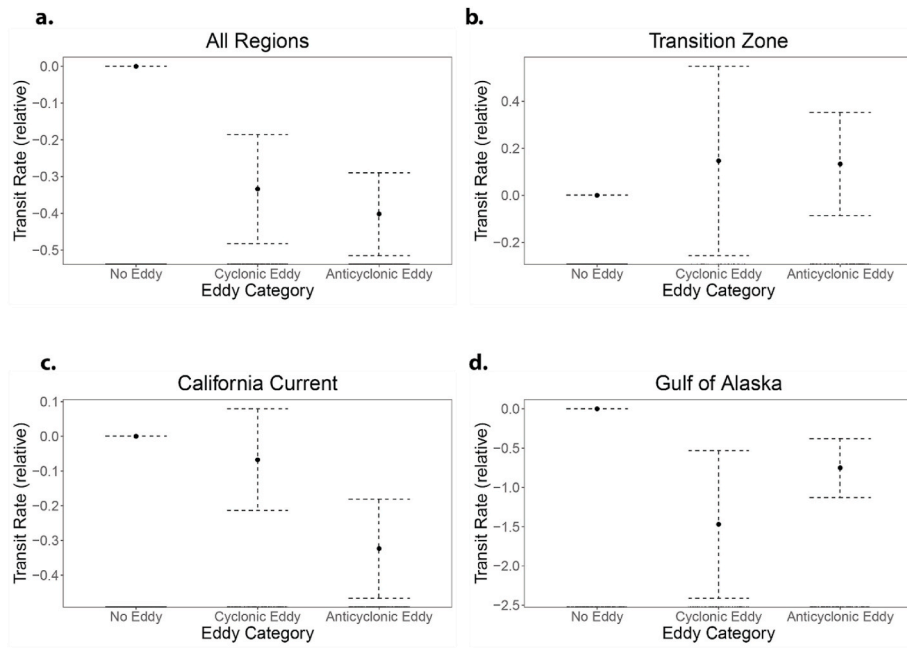


Fig. 5. Boxplots of GAMM output illustrating the effect of eddy encounters on horizontal transit rate. Vertical axes show transit rate relative to outside of eddies (i.e. transit rate outside of eddies are shown as 0 on the y axis such that increases in transit rate are positive and decreases are negative values). Error bars represent the 95% confidence interval. See Table S1 for sample sizes of eddies in each subregion.

Table 2

Summary of GAMMs testing the influence of eddies on elephant seal transit rate. Models were run for the whole dataset and for subregions individually. R^2 values for the full model are reported, R^2 for a model containing only the categorical factor “Eddy Category”, the reduced R^2 for the full model rerun with Eddy Category removed, and the R^2 deviance calculated as the difference between the full model and the reduced model without Eddy Category.

Response Variable	Full Model	R^2 full model	R^2 Eddy Category	R^2 reduced	R^2 deviance
Transit Rate All Regions	Season + s(DayinTrip)+EddyCategory + s(FSLE_max)+ s(SST_sd)+s(MLD_mean)+te(Lat,Lon)	0.343	0.066	0.323	0.019
Transit Rate California Current	Season + s(DayinTrip)+EddyCategory + s(FSLE_max)+ s(SST_sd)+s(MLD_mean)+te(Lat,Lon)	0.370	0.015	0.347	0.023
Transit Rate Transition Zone	Season + s(DayinTrip)+EddyCategory + s(FSLE_max)+ s(SST_sd)+s(MLD_mean)+te(Lat,Lon)	0.158	0.005	0.162	-0.004
Transit Rate Gulf of Alaska	Season + s(DayinTrip)+EddyCategory + s(FSLE_max)+ s(SST_sd)+s(MLD_mean)+te(Lat,Lon)	0.382	0.371	0.456	-0.074

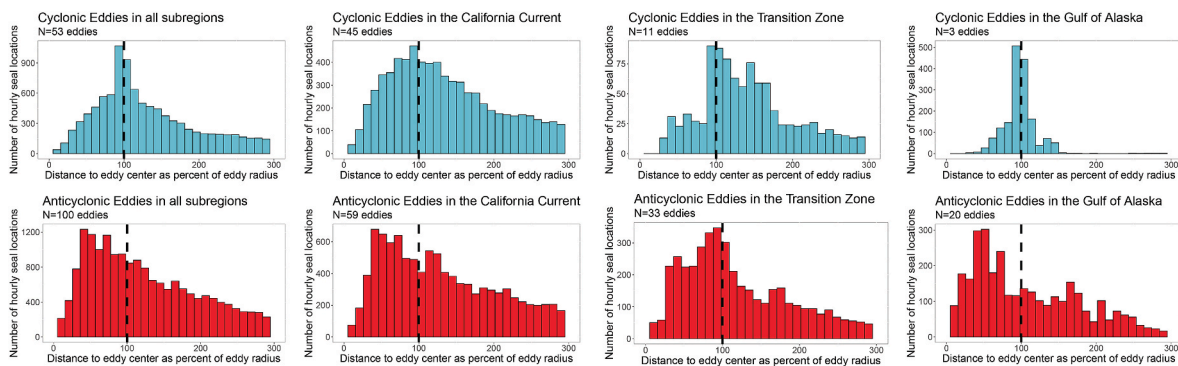


Fig. 6. Histograms of hourly seal locations by distance from eddy center split by eddy polarity and subregions. Vertical dashed line indicates eddy edge (100% of eddy radius) such that locations to the left of the line are inside the eddy and locations to the right are outside of the eddy. Note some individual eddies had moved into different subregions during separate seal encounters, resulting in sample size discrepancies between the subregions and all combined.

the two-dimensional behavioral metrics. Being in an eddy did not increase the explanatory power of intrinsic models for any dive behavior (Tables S8–S9). Once within an eddy, average nighttime dive depths were not different between eddy polarities; average daytime dive depth

was slightly deeper in anticyclonic eddies (580 ± 97 m) than cyclonic eddies (557 ± 137 m), which is unlikely biologically meaningful (Table S5, Fig. S5). Bottom time and the number of wiggles were not different between eddy polarities (Table S5, Fig. S5).

Just over half the eddy encounters elicited a significant change (two-sample *t*-test, $p < 0.05$) in average dive depth with approximately equal proportions of behavioral responses in opposite directions (increase and decrease) (Table S6). Just under half showed a difference in bottom time, also with comparable proportions of opposite behavioral responses. Fewer than 40% of eddy encounters showed a significant difference in the average number of wiggles. These proportions changed by $4.6 \pm 2.5\%$ (mean \pm sd) using the different temporal buffers around eddy associations considered (1 day, 2 days, and 5 days), showing low sensitivity to buffer choice.

4. Discussion

Our findings indicate that mesoscale eddies affect northern elephant seal foraging behavior, though with a high degree of individual variability. Seals decreased their transit rate and movement persistence when encountering eddies, behavioral responses associated with foraging (Jonsen et al., 2019; Robinson et al., 2010), suggesting that eddies may increase the density or abundance of mid trophic-level organisms in the mesopelagic zone. Across the study area, seals transited more slowly and showed lower movement persistence through anticyclonic eddies than through cyclonic eddies. While these two-dimensional movement patterns of seals suggest increased searching behavior, they cannot confirm increased prey capture. Foraging success can be estimated from changes in drift rate, but its temporal resolution did not match the resolution needed to identify energy gain while in an eddy. Encounters with mesoscale eddies lasted on average ~ 3 days (with some exceptions of long eddy associations), while changes in drift rate are detectable over a few days to a week (Biuw et al., 2003).

The northern elephant seals tracked in this study spent only a small fraction of their time at sea associated with mesoscale eddies. Previous work on southern elephant seals (*Mirounga leonina*), a closely related mesopelagic predator, found similar patterns, with mesoscale eddies also not a major habitat feature to most southern elephant seal populations. These studies observed behavioral responses to both cyclonic and anticyclonic eddies, though similarly with a high degree of individual variability (Bailleul et al., 2010; Bost et al., 2009; Campagna et al., 2006; D'Ovidio et al., 2013; Dragon et al., 2010). Northern elephant seals in this study encountered eddies that were on average larger, older, and of higher energy than the background eddy field. This may indicate that those eddies were more important to seals or reflect the eddies we were able to identify from the *in situ* temperature data. The eddy encounters we identified are likely a subset of the actual number of eddy encounters by seals, as we only retained high confidence encounters visible in both remotely sensed SLA and *in situ* temperature data. Seals encountered more anticyclonic eddies than cyclonic eddies, while the background eddy field contained approximately equal numbers of each, though this could be an artifact of our eddy detection method if anticyclonic eddies were more readily identified from the *in situ* temperature data. Seals usually did not spend an extended amount of time associated with eddies and we did not observe repeated visits to the same eddy. We found only one example of a seal that could be considered an eddy specialist, having spent approximately 30% of her time associated with eddies. However, when seals did encounter eddies, they usually changed their behavior.

Eddies had the greatest influence on seal behavior in the Gulf of Alaska and the California Current. The Gulf of Alaska is a major eddy hotspot in the Northeast Pacific with many long-lived anticyclonic eddies (Cheng et al., 2014). However, while visited by about half of the seals (153 of 221), only 7.6% of the total days at sea for all seals were spent within in the Gulf of Alaska. Therefore, a small fraction of the adult female northern elephant seal population is likely to encounter Gulf of Alaska eddies. In contrast, all seals pass through the California Current at the very least upon leaving and returning to the colony. This boundary current forms another Northeast Pacific eddy hotspot (Cheng et al.,

2014) and is therefore the most likely subregion where elephant seals would encounter eddies.

Both cyclonic and anticyclonic eddies triggered behavioral responses in seals. The only subregion with a near-equal number of encounters with both eddy types to best enable a comparison in seal behavior between eddy polarities was the California Current. Seal transit rate and movement persistence were not significantly different between cyclonic and anticyclonic eddies in the California Current, offering little evidence that these eddies of opposite polarity within the same subregion differ in the biological relevance to seals. The small number of encounters with cyclonic eddies in the North Pacific Transition Zone and the Gulf of Alaska precluded comparing behavioral responses to either polarity in those subregions. As there were differences in transit rate and movement persistence between cyclonic and anticyclonic eddies in the full dataset, these effects are therefore likely attributable to eddies differing across regions due to a variety of factors beyond their rotational direction. The additional eddy properties we considered (eddy age, radius, amplitude, and rotational speed) did little to further explain seal behavior. Biological factors that we were not able to test such as ecosystem state at the eddies' origin or trophic processes occurring throughout the eddy's lifespans may be relevant to foraging elephant seals.

In the absence of direct observations of the mesopelagic prey field, the trends in elephant seal behavior allow us to infer some possible mechanisms. Elephant seals may forage in eddies due to an increase in prey availability because of nutrient upwelling, altered mixing, advection of nutrient- and organism-enriched water, and/or aggregating prey items physically or behaviorally. Much of the offshore northeast Pacific is characterized as a high-nutrient low-chlorophyll (HNLC) region, where phytoplankton growth is limited by iron (Boyd et al., 2004; Martin et al., 1989). Eddies that inject nutrients from deep water or horizontally advect nutrients can increase local primary production. Enhancement of the base of the food web can then translate up trophic levels. Interestingly, elephant seals showed little interest in the center of cyclonic eddies where notable nutrient upwelling occurs. They also exhibited stronger foraging behavior in relation to anticyclonic eddies that generally downwell in their center (Gaube et al., 2014; McGillicuddy and Robinson, 1997; Palacios et al., 2006), using both the center and edges of these eddies. These behavioral patterns suggest that nutrient enhancement alone does not increase mesopelagic prey abundance or availability via trophic transfer. It is possible that vertical nutrient supply may not be occurring very frequently in this HNLC region, as few eddies in this study had MLDs deep enough to penetrate the ferricline and resupply iron to the surface. Alternatively, if eddy-induced nutrient upwelling does occur, it may not be operating at the spatio-temporal scales relevant to elephant seals.

In addition to vertical processes, a large component of the biological importance of large-scale anticyclonic eddies in the northeast Pacific, especially in the Gulf of Alaska, is in the horizontal direction: the stimulation of primary production by transporting nutrients offshore can result in elevated chlorophyll concentrations that persist across multiple seasons (Crawford et al., 2005; Johnson et al., 2005). As a result, it is not uncommon to find enhanced chlorophyll concentrations within these anticyclonic eddies (Crawford et al., 2007; Gaube et al., 2013, 2014). In fact, in the Gulf of Alaska, over half of surface chlorophyll may be found within anticyclonic eddies that cover only 10% of the area (Crawford et al., 2007). The optical complexity commonly associated with anticyclonic eddies in this region for this reason makes it more likely that prey shifting deeper as hypothesized would be due to thermal and/or nutrient availability factors rather than visual predator avoidance. On the other hand, anticyclonic eddies in the California Current tend to subduct coastal nutrients advected offshore and limit primary production (Gruber, 2011), and at least some eddies in the Transition Zone in this study did not form near the coast and therefore could not have advected coastal nutrients, making horizontal nutrient movement a less likely mechanism in these regions. In oligotrophic waters, such as are found through much of the North Pacific Transition Zone, anticyclonic

eddies' reduced stratification could increase convective mixing in their center and stimulate primary production as a deep chlorophyll maximum (Dufois et al., 2016). As an alternative or complementary mechanism to nutrient input, the entrainment of coastal water within eddies can advect planktonic organisms with limited mobility (Flierl and McGillicuddy, 2002), facilitating energy transfer through trophic levels and creating a pelagic community distinct from the eddy's surroundings. Greater prey availability within an eddy can then in turn attract more mobile species (Godø et al., 2012). It is likely some prey advection occurs inside these anticyclonic eddies as seals utilized the center and edges of these eddies. While we cannot rule out nutrient input as an influential mechanism in anticyclonic eddies, elephant seals more frequently targeting the edges of cyclonic eddies, likely taking advantage of aggregation at the eddy edges, rather than the center, which are usually nutrient-enriched, we hypothesize that nutrient input is a minor component of prey enhancement of interest to this mesopelagic predator at eddies.

Small scale currents at mesoscale features such as eddies may also physically entrain predators in a "quasi-planktonic" way (Della Penna et al., 2016). This effect may also be occurring here, but identifying seal trajectories and speeds relative to circulation at such small scales was not possible given the location errors inherent with Argos-based tracking. If the horizontal advection of plankton or the upwelling of nutrients were important mechanisms, we would expect older eddies to be more relevant to foraging seals as it would take time to develop an enhanced higher trophic level biomass in response. Seals on average showed stronger behavioral response to anticyclonic eddies, which tend to be longer-lived and have greater propagation distances than cyclonic eddies (Chelton et al., 2011), potentially allowing more time for the development of biological communities distinct from the eddy's immediate surroundings. However, anticyclonic eddies encountered by seals were not significantly older than the encountered cyclonic eddies nor were they further from their origin sites. We observed only a weak negative relationship between seal transit rate and normalized eddy age, and no relationship to absolute eddy age, in anticyclonic eddies. Eddies continually exchange water with their surroundings, which can reduce anomalous conditions within them with time (D'Ovidio et al., 2013; Gaube et al., 2014; Olson, 1986). Despite this, our observations agree more strongly with observations of the maintenance of altered biological conditions throughout the eddy's lifespan, such as Schmid et al. (2020) who observed sustained enhanced plankton concentrations within an eddy relative to its surroundings and Mackas et al. (2005) who saw a continuing development of the zooplankton community as the eddy was colonized by organisms from its surroundings. There remains a dearth of data on mid-to high trophic levels throughout the lifespan of eddies. Elephant seals showed foraging behavior throughout the eddies' lifespans, including young eddies.

Elephant seals not showing a preference for the upwelling-dominant interiors of cyclonic eddies and the limited likelihood of iron recirculation in the eddies we observed suggest a deemphasis on bottom-up processes in favor of alternative physical and/or biological mechanisms that enhance prey availability. Fronts develop on the edges of eddies, physically aggregating organisms or inducing frontal upwelling (Bakun, 2006; Legal et al., 2007; Schmid et al., 2020; Zhang et al., 2015), which can leave a biomass minimum in eddy centers (Godø et al., 2012). Modeling indicates that biomass increases at eddy edges are likely due in greater part to biological rather than physical mechanisms (Samuelson et al., 2012), highlighting the importance of considering multiple possible drivers beyond physics. Seals heavily used the edges of cyclonic eddies and, to a lesser extent, the edges of anticyclonic eddies, suggesting that frontal dynamics may be important in enhancing their prey field.

These potential ecological pathways leading to enhanced foraging opportunities for predators within eddies are difficult to disentangle and expectations of biology within eddies based on eddy polarity are often generalizations. For example, while anticyclonic eddies are traditionally

associated with low primary productivity, nutrient injection can still occur in anticyclones. The decay of an anticyclonic eddy can reverse the dominant direction of vertical water exchange (Flierl and McGillicuddy, 2002; Franks et al., 1986), and some foraging animals may benefit from this productivity increase fueled by this upwelling (Chambault et al., 2019). Vertical nutrient input can also occur as a result of reduced stratification or eddy-induced Ekman pumping in high-wind conditions, in which the dominant up- and downwelling patterns in cyclonic and anticyclonic eddies, respectively, are counteracted due to wind stress curl opposite of the eddy polarity (Dufois et al., 2016; Flierl and McGillicuddy, 2002; Franks et al., 1986). Certain eddies in the Gulf of Alaska have been documented to have an upwelled iron flux comparable in magnitude to dust deposition, the primary mechanism by which iron is delivered to the offshore North Pacific (Xiu et al., 2011).

Observations of biological responses to eddies are mixed. For instance, in contrast to the biomass minimum observation in the center of an anticyclonic eddy in Godø et al. (2012), a recent study acoustically sampled eddies in the North Atlantic and found the most intense mesopelagic acoustic backscatter in the interior of anticyclonic eddies, which strongly decreased towards their edges (Della Penna and Gaube, 2020). In our study, the variability in seal behavior suggests that some but not all eddies encountered by contained enhanced mesopelagic prey fields. There may also be a spatiotemporal mismatch between some physical processes within eddies and the occurrence of higher trophic level prey items (e.g. Abrahms et al., 2019; Bailleul et al., 2010; Barlow et al., 2021; Cotté et al., 2015; Guinet et al., 2001; Visser et al., 2011).

We observed a high degree of individual variability in behavioral responses to eddies, highlighting that small sample sizes cannot necessarily be extrapolated to population-level trends. When encountering eddies, the diving behavior of individual seals was quite variable. This suggests that the prey field did not shift vertically or that prey abundance increased in a predictable way in cyclonic or anticyclonic eddies. In addition to reflecting eddy variability, the range in behavioral responses can result from individual differences between seals' diving behavior and responsiveness to environmental cues are modulated by numerous confounding factors, such as predator avoidance, experience, and specialized foraging strategies (Abrahms et al., 2017; Beltran et al., 2021; Bradshaw et al., 2004). When the same seal encountered different eddies of the same polarity, the best test for individual specialization available in this dataset, behavioral responses were often inconsistent, suggesting further proximate internal or external factors influence behavioral decisions. Northern elephant seals forage over a vast region and can have variable diets (Goetsch et al., 2018). As such, individuals may show a wide range of foraging behaviors (Le Boeuf et al., 2000; Maxwell et al., 2012; Robinson et al., 2012) and respond differently to ocean dynamics. Such behavioral plasticity can buffer them from environmental changes (Abrahms et al., 2017; Goetsch et al., 2018; Holser, 2020), in contrast to other pinnipeds such as California sea lion (*Zalophus californianus*) (McHuron et al., 2018). Foraging within eddies is one of many foraging strategies employed by this species and most likely a result of opportunistic encounters. Only one seal in this study spent more than 20% of her foraging trip associated with eddies, so extended associations with these mesoscale features appear to be a viable but uncommon foraging strategy for northern elephant seals.

Eddies result in anomalous temperatures in their interiors relative to their immediate surroundings. As endothermic animals that maintain a large temperature gradient between their core and the ambient water, the temperature differences due to eddies are unlikely to have a direct effect on the seals the way they may on sharks (Braun et al., 2019; Gaube et al., 2018). The temperature anomalies within eddies (-0.55°C – 0.90°C) were an order of magnitude smaller than the vertical temperature gradients encountered during a typical deep dive (often 10°C or more). Thermal effects on the seals' prey are not well understood. Alewijnse et al. (2021) found very little effect of temperature on the metabolic rate of myctophids in the Southern Ocean. While we cannot assume myctophids in the North Pacific are physiologically

equivalent, this result suggests that extremely cold temperatures are unlikely to disadvantage myctophids. On the other end of the spectrum, the warm cores of anticyclonic eddies may increase growth and reproduction of mesopelagic organisms by increasing metabolic rates (Della Penna and Gaube, 2020; Proud et al., 2017), potentially increasing prey biomass. Determining whether the timescale of anticyclonic eddies' interaction with mesopelagic biota is sufficient for this positive thermal effect to influence a predator would likely require more direct sampling of mesopelagic organisms than is possible with predator tracking alone.

In agreement with a preference of southern elephant seals for (sub) mesoscale features during the post-molt trip but not the post-breeding trip documented in (Cotté et al., 2015), we observed a stronger reduction in transit rate and movement persistence during the post-molt trip than during the post-breeding trip. The northern elephant seals in this study did encounter eddies during the post-breeding trip so this does not seem to be an availability difference (127 eddy encounters during post-breeding, 88 post-molt). It is challenging to determine whether this seasonal difference in behavior is due to an internal or external influence. We have no way to directly test whether the wintertime eddies encountered during the post-breeding trip were of poorer foraging quality, but there was no significant difference in age or size of eddies between seasons. As internal factors such as trip timing explained more variability in behavior in our models than environmental factors, we hypothesize that this is the case here as well. The more muted behavioral response to the eddies encountered during the post-breeding trip may be due to the shorter nature of that trip, during which seals show faster transit rate and higher movement persistence. Perhaps the precise timing required discourages the seals from associating with mesoscale features. If so, this illustrates a confounding factor of behavior in attempting to assess oceanographic effects on a prey field through the eyes of a predator.

Seal behavior suggests that physical-biological mechanisms such as frontal aggregation and behavioral attraction are likely required to increase seals' foraging potential within eddies; trophic transfer originating with nutrient enhancement is likely insufficient. Both cyclonic and anticyclonic eddies can contain distinct populations of mesopelagic fish larva which are physically retained by eddies (Atwood et al., 2010; Contreras-Catala et al., 2012; Daudén-Bengoia et al., 2020; Muhling et al., 2007; Nishimoto and Washburn, 2002). This study contributes to a growing body of evidence suggesting an enhancement of adult mesopelagic fish populations (Della Penna and Gaube, 2020; Devine et al., 2021; Fennell and Rose, 2015), helping connect the dots from eddies to higher trophic levels in the mesopelagic. Previous studies of mesopelagic predator foraging behavior in relation to eddies have been limited to small sample sizes of animals and eddies (sample sizes 1 to ~ 40) (Bailleul et al., 2010; Campagna et al., 2006; Dragon et al., 2010; Massie et al., 2016). We show here that mesoscale eddies are one type of oceanographic feature that may enhance foraging opportunities for northern elephant seals at sea when encountered.

Biological resources in the open ocean are patchily distributed (Benoit-Bird et al., 2013; Haury et al., 1978; Mackas et al., 1985; Steele, 1978) with implications for predator ecology as well as resource management (e.g. Santora et al., 2012; Scales et al., 2014, 2018). The non-uniform distribution of prey items can be influenced by mesoscale features such as eddies. Our long-term northern elephant seal tracking suggests that Northeast Pacific eddies' biological relevance can extend to the mesopelagic zone and to a higher trophic level predator. While other predators in the Northeast Pacific such as northern fur seals (*Callorhinus ursinus*) (Pelland et al., 2014; Ream et al., 2005) and Steller sea lions (*Eumetopias jubatus*) (Lander et al., 2020) also use eddies, elephant seals are the first to demonstrate the relevance of eddies to the mesopelagic prey field in this region. Life in the mesopelagic zone is extremely abundant but poorly understood and vulnerable to anthropogenic pressures such as climate change and resource extraction (Caiger et al., 2021; Gjørseter and Kawaguchi, 1980; Irigoien et al., 2014; Lam and Pauly, 2005; Martin et al., 2020). Investigating

physical-biological mechanisms across trophic levels at these depths is therefore a research priority.

5. Conclusion

Our data show evidence of eddies affecting the seals' prey field, presumably through prey aggregation processes as seals used the edges of eddies more heavily than the interiors, with bottom-up processes playing a smaller role. Anticyclonic eddies triggered the strongest behavioral responses. The variability in behavioral responses suggests there is likely complexity in eddies' biological characteristics not well captured by their physical characteristics and some spatiotemporal mismatch between eddy physics and elephant seal prey species. These physical-biological mechanisms require further investigation and are especially relevant as the ocean undergoes unprecedented rapid change and its effects on deep sea biology and pelagic predators remain challenging to predict.

Author contributions

T.R. Keates: Conceptualization, Investigation, Data curation, Methodology, Formal analysis, Visualization, Writing – original draft; E.L. Hazen: Methodology, Formal analysis, Writing – review and editing; J. Fiechter: Methodology, Writing – review and editing; S.J. Bograd: Methodology, Writing – review and editing; R.R. Holsler: Investigation, Data curation, Writing – review and editing; P.W. Robinson: Investigation, Data curation; J.P. Gallo-Reynoso: Investigation, Funding acquisition, Project administration, Writing - review and editing; D.P. Costa: Conceptualization, Supervision, Project administration, Funding acquisition, Resources, Writing – review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The temperature data used in this study can be found in the MEOP database (<https://www.meop.net/>) and the seal tracking and diving data in a Dryad repository, DOI 10.7291/D18D7W.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2022.103866>.

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